

Feed Non-Starch Polysaccharides: Chemical Structures and Nutritional Significance

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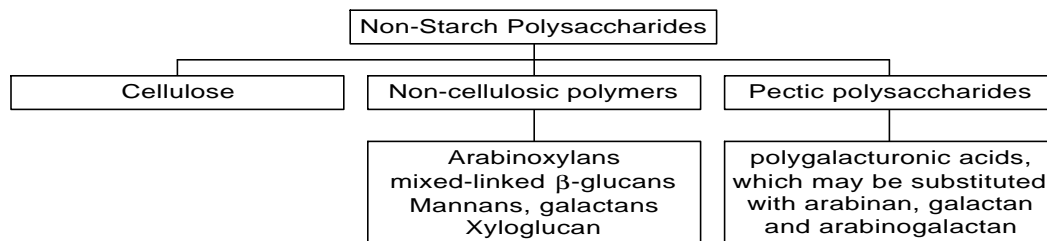
INTRODUCTION

Approximately two billion tonnes of cereal grains and 140 million tonnes of legumes and oil seeds are produced throughout the world each year, which yield an estimated 230 million tonnes of fibrous material as part of a variety of by-products. The fibre component of the grain consists primarily of non-starch polysaccharides (NSP) which in cereals form part of the cell wall structure. In legumes, NSP also play a role as an energy storage material. The role of fibre in monogastric diets has attracted much attention in recent years, due to the facts that (a) the soluble NSP elicit anti-nutritive effects, and (b) the utilisation of NSP as a feed material in monogastrics is very poor. These two factors are of significant concern because the world's population is on the increase whereas its food production is static. More efficient utilisation of potentially utilisable nutrients for food production is therefore of paramount importance to the sustainability of agriculture in the future. The current paper will describe the definition and classification of NSP, levels and chemical structures of various NSP found in different ingredients, and the nutritional significance of NSP in monogastric diets.

DEFINITION AND CLASSIFICATION OF NON-STARCH POLYSACCHARIDES

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, D-galactose, 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 term non-starch polysaccharides (NSP) covers a large variety of polysaccharide molecules excluding α -glucans (starch). The classification of NSP was based originally on the methodology used for extraction and isolation of polysaccharides. The residue remaining after a series of alkaline extractions of cell wall materials was called cellulose, and the fraction of this residue solubilised by alkali was called hemicellulose. The word hemicellulose was adopted because early researchers mistakenly regarded these polysaccharides as the precursors of cellulose. This is now known to be incorrect but the term is still commonly used. Some workers used the terms hemicelluloses and pentosans interchangeably because the pentose-containing polysaccharides make up the bulk of hemicelluloses (Neukom *et al.* 1967; Neukom 1976). Classification by differences in solubility lacks precision with respect to both chemical structures and biological functions. For example, 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 nutritional relevance of values obtained using these methods in monogastric nutrition therefore is questionable. The complexity in the structure and confusion in the nomenclature have made it almost impossible to draw a clear-cut classification of NSP, however, NSP fall into three main groups as shown below, namely cellulose, non-cellulosic polymers and pectic polysaccharides (Bailey 1973).

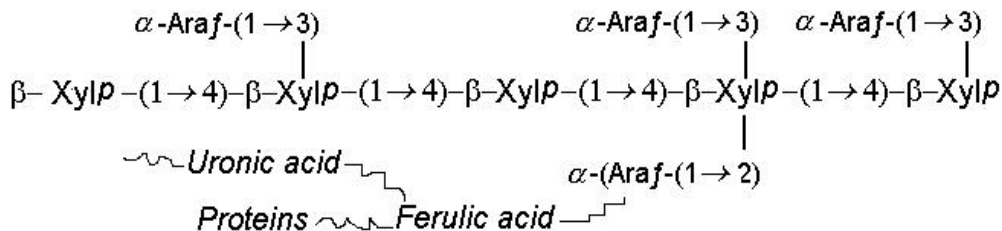


THE CHEMICAL STRUCTURE OF NSP FOUND IN FEED INGREDIENTS

Cellulose Cellulose is the most abundant organic compound in nature, comprising over 50% of all the carbon in vegetation. Cellulose is a linear homopolymer of (1→4)-β-glucose units. It is of high molecular weight and cellulose of up to 7,000-10,000 glucose units can be found in plant materials (Goring and Timell 1962). Individual cellulose chains lie side by side in bundles, held together by hydrogen bonds between the numerous neighbouring -OH groups, to form a "ribbonlike" twofold helix (Gardner and Blackwell 1974). Cellulose is believed to be identical in chemical composition regardless of the source, and it is insoluble in water and aqueous solutions of alkalis. Cellulose in cereal grain cell walls can be recovered from the insoluble residue left after vigorous extraction of cell wall material matrix components with alkalis (Mares and Stone 1973a). The simplified structure of cellulose is shown below:



Pentosans (arabinoxylans, xylans) The structures of cereal pentosans (arabinoxylans) are composed predominantly of two pentoses, arabinose and xylose, and their molecular structure consists of a linear (1→4)-β-xylan backbone to which substituents are attached through O2 and O3 atoms of the xylosyl residues (Perlin 1951). The major substituents are single arabinose residues although, in many instances, hexoses and hexuronic acids are present as minor constituents (Fincher 1975). Phenolics and proteins have also been reported to be present as side chains (Geissmann and Neukom 1973a; Neukom 1976). An important structural feature of most cereal arabinoxylans is that significant proportions of the substitutions occur at both the O2 and O3 atoms although the single arabinose residues are thought to be mostly linked to the O3 atoms (Mares and Stone 1973a). The molecular weights of arabinoxylans from cereal grains can be extremely high depending on the source and extraction method (Mares and Stone 1973b; Annison *et al.* 1992). Most of the arabinoxylans in cereal grains are insoluble in water because they are anchored in the cell walls by alkali-labile ester-like cross links rather than by a simple physical entrapment (Mares and Stone 1973b). But the arabinoxylans not bound to the cell walls can form highly viscous solutions and they can absorb about ten times their weight of water. In the presence of oxidative agents, such as H₂O₂/peroxidase, arabinoxylans can rapidly develop a gel network as a result of the re-establishment of cross-links (Geissmann and Neukom 1973a;b). The formation of gel coincides with the disappearance of feruloyl groups and fully cross-linked arabinoxylans hold up to 100g of water per g polymer (Izydorczyk *et al.* 1990). Not only can arabinoxylans establish covalent cross links, they may also form "junction zones" by intermolecular hydrogen bonding between unsubstituted regions of the xylan backbone (Fincher and Stone 1986). This non-covalent interaction of arabinoxylans may be of great importance in determining their conformational changes and solubility properties, and hence their anti-nutritional activities. A likely structure of the arabinoxylan is presented below:



Mixed-Linked- β -Glucans The β -glucan is found in most cereals, being particularly high in barley and oats. The ubiquitous structural feature of these polysaccharides is well established. It consists of a linear chain of glucose units joined by both β -(1 \rightarrow 3) and β -(1 \rightarrow 4) linkages (Bengtsson *et al.* 1990). In barley, the β -glucans contain approximately 70% (1 \rightarrow 4) linkages and 30% (1 \rightarrow 3) linkages, in which segments of two or three (1 \rightarrow 4) linkages are separated by single (1 \rightarrow 3) linkages (Parrish *et al.* 1960). Up to five contiguous (1 \rightarrow 3) linkages, however, have been reported to exist as minor structural features (Fleming *et al.* 1974). The molecular weight reported for the water-soluble β -glucans estimated by ultracentrifugation ranges from 200,000 to 300,000 (Igarashi and Sakurai 1965; Woodward *et al.* 1983), corresponding to degrees of polymerisation of 1,200-1,850 monomers. Although the mixed-linked β -glucans and cellulose are both comprised of β -linked glucose units there is little similarity in their physical properties. Incorporation of the β -(1 \rightarrow 3) linkages in the β -glucan molecules breaks the regular structure of β -(1 \rightarrow 4) chains, preventing close packing of the chains to give a more soluble polymer. Therefore, the β -glucans are often isolated by aqueous extraction followed by precipitation with ammonium sulphate (McCleary 1986). The properties are influenced by the extraction conditions. The viscosity of (1 \rightarrow 3),(1 \rightarrow 4)- β -glucans extracted at high temperatures is higher than those extracted at 40°C (Fleming and Kawakami 1977). A typical structure of β -glucans is shown below:



Pectic polysaccharides The term pectic polysaccharides refers to galacturonans or more commonly rhamnogalacturonans in which (1 \rightarrow 4)- α -D-galacturonan chains are interrupted at intervals by insertion of (1 \rightarrow 2)- α -L-rhamnose residues. Other constituent sugars attached as side chains include D-galactose, L-arabinose, D-xylose, and less frequently L-fucose and D-glucuronic acid. Most of these sugars occur in short side chains although D-galactose and L-arabinose are often found in multiple units. Extremely complicated side chains containing neutral pectic polymers such as galactans and arabinans, xyloglucans and galactomannans have been reported. The molecular weight of the pectins have been reported to range from 30,000 to 300,000 (Pilnik and Voragen 1970). In soybean, the L-rhamnose residues in the rhamnogalacturonan backbone have been shown to be joined consecutively and others to alternative with galacturonic acid residues (Aspinall *et al.* 1967). The carboxyl groups of the galacturonic acid residues of the pectic polymers can be highly methyl esterified (Aspinall and Jiang 1974), depending on their sources. The soluble pectins from mung beans, for instance, are highly methylated (Goldberg *et al.* 1994). Pectins with high degree of esterification are not susceptible to endo-polygalacturonase which requires at least two free carboxyl groups adjacent to each other (Jansen and MacDonnell 1945). Pectic polysaccharides are also found in cell walls of stems and leaves of cereals. No evidence has been documented for their occurrence in the maternal tissues of cereals, with the exception of rice (Shibuya and Nakane 1984). The structure of a pectic polymer from lupins by Cheethan *et al.* (1993) is shown below:

Cereal grains and their by-products The NSP in cereal grains are composed predominantly of arabinoxylans (pentosans), β -glucans and cellulose. Only small amounts of pectic polysaccharides are found in the stems and leaves of cereals. With the exception of rice (Shibuya and Nakane 1984), there is no evidence that they occur in the maternal tissues of cereals. Corn and sorghum contain very low levels of NSP, whereas wheat, rye and triticale contain substantial amounts of both soluble and insoluble NSP. The main soluble NSP in these grains are arabinoxylans, whereas barley and oats they are β -glucans.

Large amounts of cereal by-products are produced and these products contain high levels of cell wall components and are therefore usually rich in NSP and low in nutritive quality. For example, rice bran, a by-product of rice polishing, constitutes about 10% of paddy rice and consists of the seed coat, the major part of the germ and the outer layer of the kernel. The current world production of rice is approximately 530 million tonnes per annum (FAO 1994), of which 95% is produced in Asia. This means Asia alone produces some 50 million tonnes of rice bran a year. Rice bran contains approximately 20-25% NSP which consist of approximately equal amounts of arabinoxylans and cellulose (Saunders 1986). The types and levels of NSP cereals and their by-products are shown in Table 1.

Table 1. The types and levels of NSP present in some cereal grains and cereal by-products (% dry matter).

Cereal	Arabinoxylan	β -Glucan	Cellulose	Man	Gal	Uronic Acid	Total
Wheat ¹							
Soluble	1.8	0.4		t	0.2	t	2.4
Insoluble	6.3	0.4	2.0	t	0.1	0.2	9.0
Barley ¹							
Soluble	0.8	3.6		t	0.1	t	4.5
Insoluble	7.1	0.7	3.9	0.2	0.1	0.2	12.2
Rye ¹							
Soluble	3.4	0.9		0.1	0.1	0.1	4.6
Insoluble	5.5	1.1	1.5	0.2	0.2	0.1	8.6
Triticale ²							
Soluble	1.3	0.2		0.02	0.1	0.1	1.7
Insoluble	9.5	1.5	2.5	0.6	0.4	0.1	14.6
Sorghum ²							
Soluble	0.1	0.1		t	t	t	0.2
Insoluble	2.0	0.1	2.2	0.1	0.15	t	4.6
Corn ²							
Soluble	0.1	t		t	t	t	0.1
Insoluble	5.1		2.0	0.2	0.6	t	8.0
Rice (pearled) ²							
Soluble	t	0.1		t	0.1	0.1	0.3
Insoluble	0.2		0.3	t	t	t	0.5
Rice bran (defatted) ²							
Soluble	0.2	t		t	0.2	t	0.5
Insoluble	8.3		11.2	0.4	1.0	0.4	21.3
Wheat pollard ²							
Soluble	1.1	0.4		t	0.1	0.1	1.7
Insoluble	20.8		10.7	0.4	0.7	1.0	33.6

¹ Englyst (1989); ² Choct *et al.* Unpublished data.

Grain legumes Grain legumes are used in monogastric diets mainly to supply protein. In addition to the protein, they also contain substantial amounts of NSP. Cellulose and xylans, which are the major NSP in cereal grains, are only found in the hulls or husks of most legumes. The NSP in the cotyledon of legumes are pectic polysaccharides. The carbohydrate composition of soybean, sunflower seeds and lupins is shown in Table 2. Compositional data on other legumes are scarce and therefore only soluble, insoluble and total NSP are described in Table 3 for selected legumes.

Other unusual ingredients The by-products of roots and tubers, vegetable oil sources such as coconut, and rubber processing are used in various countries as possible feed resources. One such product,

which has been of great interest in South East Asia recent years, is copra meal. Copra meal is the residue of coconut oil production. The world production of copra (the dried kernel of coconut palm) reached 5.5 million tonnes in 1994 (FAO 1994), which yielded some 1.8 to 2.3 million tonnes of copra meal. Its use in monogastric diets is limited due to a very high level of NSP (Purwadaria *et al.* 1995). It contains about 45-60% of NSP which consist predominantly of mannans (galactomannans and mannans), just over 10% cellulose and trace amounts of other polymers (arabinoxylolactans arabinomannogalactan and galactoglucomannans) (Saittagaroon *et al.* 1983; Zamora *et al.* 1989). Saittagaroon *et al.* (1983) reported that approximately 30% of the NSP is soluble in hot water, but their nutritional properties are yet to be defined.

THE ANTI-NUTRITIVE EFFECT OF SOLUBLE NSP

NSP include a range of compounds possessing different physicochemical properties. Their nutritional effects in monogastric animals are diverse and, in some cases, extreme. It is, however, generally conceded that the major detrimental effects of NSP are associated with the viscous nature of these polysaccharides, their physiological and morphological effects on the digestive tract and the interaction with the microflora of the gut. The mechanisms include altered intestinal transit time, modification of the intestinal mucosa, and changes in hormonal regulation due to a varied rate of nutrient absorption (Vahouny 1982).

Viscosity The viscosity of NSP depends on their solubility and molecular weights. Solubility of NSP, in turn, depends on the chemical structure of the NSP and their association with the rest of the cell wall components. Viscosity, however, is not specific to the sugar composition or linkage types present in the NSP. Furthermore, the physical effect of viscosity on nutrient digestion and absorption also appears to be similar regardless of the NSP sources. Generally, high gut viscosity decreases the rate of diffusion of substrates and digestive enzymes and hinders their effective interaction at the mucosal surface (Edwards *et al.* 1988; Ikegami *et al.* 1990). Soluble NSP interact with the glycocalyx of the intestinal brush border and thicken the rate-limiting unstirred water layer of the mucosa, which reduces the efficiency of nutrient absorption through the intestinal wall (Johnson and Gee 1981). The fact that the viscous property of NSP is a major factor in the anti-nutritive effect of NSP in monogastric diets is supported by the wide-spread use of enzymes in monogastric diets. The enzymes cleave the large molecules of NSP into smaller polymers, thereby reducing the thickness of the gut content and increasing the nutritive value of the feed (Bedford *et al.* 1991; Choct and Annison 1992).

Modification of gut physiology The soluble NSP can not only act as a physical barrier to nutrient digestion and absorption by increasing gut viscosity, but also change gut functions by modifying endogenous secretion of water, proteins, electrolytes and lipids (Johnson and Gee 1981; Angkanaporn *et al.* 1994). A prolonged consumption of soluble NSP is associated with significant adaptive changes in the digestive system in rats (Ikegami *et al.* 1990). The changes in the gut are characterised by enlargement of the digestive organs and increased secretion of digestive juices, accompanied by a decrease of nutrient digestion. The ability of certain NSP to bind bile salts, lipids and cholesterol is also well-documented (Vahouny *et al.* 1980; Vahouny *et al.* 1981). This property of NSP may influence lipid metabolism in the intestine. Furthermore, viscous NSP can enhance bile acid secretion and subsequently result in significant loss of these acids in the faeces (Ide *et al.* 1989; Ikegami *et al.* 1990). This, in turn, can result in increased hepatic synthesis of bile acids from cholesterol to re-establish the composite pool of these metabolites in the enterohepatic circulation. The continued "drain" of bile acids and lipids by sequestration, and increased elimination as faecal acidic and neutral sterols, may ultimately influence the absorption of lipids and cholesterol in the intestine. These effects could lead to major changes in the digestive and absorptive dynamics of the gut, with consequent poor overall efficiency in nutrient assimilation by the animal.

Table 2. The types and levels of carbohydrate polymers and monomers in selected legumes (% dry matter)

Sample	Starch	Total NSP	Cellulose	Rhamnose	Fucose	Arabinose	Xylose	Mannose	Galactose	Glucose	U.Ac ¹
<i>Soybean</i> ²											
Soluble		2.7	-	0.1	t	0.5	0.1	0.2	0.6	0.2	1.1
Insoluble		16.5	4.4	0.2	0.3	2.4	1.7	0.7	3.9	0.3	2.5
Total	1.0	19.2	4.4	0.3	0.3	2.9	1.8	0.9	4.5	0.5	3.6
<i>Sunflower seeds</i> ²											
Soluble		4.5	-	0.2	0.1	0.6	t	0.1	0.3	t	3.2
Insoluble		23.1	8.7	0.3	0.1	3.0	5.3	1.1	0.9	0.4	3.4
Total	1.4	27.6	8.7	0.5	0.2	3.6	5.3	1.2	1.2	0.4	6.6
<i>Lupins</i> ³											
Soluble		4.6	-	0.3	t	t	t	t	3.3	0.1	0.8
Insoluble		32.0	1.2	0.5	t	3.9	0.7	0.1	22.9	0.2	2.5
Total	0.4	36.6	1.2	0.8	t	4.9	0.7	0.1	26.2	0.3	3.3

¹. Uronic acids; ². From Irish and Balnave (1993); ³. Choct et al. unpublished data.

Table 3. Soluble, insoluble and total NSP contents of some grain legumes (% dry matter)

Legume	Soluble NSP	Insoluble NSP	Total NSP	Reference
Chick peas	3.3	7.4	10.7	Englyst and Commings 1988
Peas	2.5	32.2	34.7	Graham and Aman 1987
Navy bean	5.7	1.7	17.4	Chang <i>et al.</i> 1989
Pinto bean	6.3	13.1	19.4	Chang <i>et al.</i> 1989
Rapeseed	11.3	34.8	46.1	Carré 1992

Interaction with gut microflora Dietary supplementation with antibiotics partially improves the nutritive value of rye (MacAuliffe and McGinnis 1971), suggesting that the anti-nutritive effect of NSP may be mediated by the gut microflora. The positive effect of antibiotics appears to be related to the elimination of fermentative microorganisms (mainly butyric acid producers) from the small intestine. Wagner and Thomas (1978) reported that the anaerobic counts were two to three logarithmic cycles higher in the ileum of birds fed rye or pectin-enriched diets compared with those fed a corn-soy diet, and they were reduced by five logarithmic cycles when penicillin was added to the diets. In a recent study, it was demonstrated that addition of soluble NSP in broiler chicken diets significantly elevated fermentation in the small intestine. Subsequent *in vivo* depolymerisation of the soluble NSP using glycanases almost totally overcame this problem. Under normal circumstances, facultative anaerobes dominate the small intestinal microflora and strict anaerobes make up nearly the entire caecal microflora of the chicken (Salanitro *et al.* 1978). Soluble NSP increase the residence time of digesta in the intestine (Goh and Gohl 1977; van der Klis and van Voorst 1993), which may decrease oxygen tension and favour the development of anaerobic microflora. It is unknown whether a sudden change of gut ecology is detrimental to the efficiency of nutrient utilisation. It is, however, clear that proliferation of some anaerobic organisms can lead to production of toxins and deconjugation of bile salts which are essential for the digestion of fat. Also, the efficiency of nutrient utilisation through microbial conversion of digestible carbohydrates, such as starch and glucose, to volatile fatty acids (Müller *et al.* 1989; Carré *et al.* 1995).

Although the anti-nutritive effect of soluble NSP has been discussed under three separate headings, it should be borne in mind that these mechanisms are all interrelated. They are all dependent on the polymeric nature of the NSP because once the polymers are cleaved into smaller fragments, their anti-nutritive activity is largely eliminated.

THE ROLE OF INSOLUBLE NSP IN MONOGASTRIC DIETS

The insoluble NSP make up the bulk of the total fibre in diets, but they have little or no effect on nutrient utilisation in monogastric animals (Carré 1990). Begin (1961) showed no detrimental effect, other than simple nutrient dilution, when up to 21% of cellulose is added to poultry diets. The insoluble NSP, however, are not inert and their roles in monogastric nutrition can not be neglected. One of the most important attributes of insoluble NSP is their ability to absorb large amounts of water and maintain normal motility of the gut (Stephen and Cummings 1979). This is essential for the consistency of the excreta in monogastric animals.

Elevated levels of insoluble fibre in the diet shorten the residence time of digesta (Kirwan *et al.* 1974) and some argue that this may lead to lower nutrient digestibilities. The rationale is that the longer the feed is exposed to the digestive processes in the gut, the more complete its digestion. This, however, may not be true under all circumstances. As discussed earlier, soluble NSP can increase gut viscosity and slow digesta transit time in chickens, which allows the proliferation of fermentative organisms in the small intestine, which is detrimental (Choct *et al.* 1996). Depolymerisation of the NSP with enzymes can greatly increase the digesta transit time (Choct *et al.* unpublished data). It is believed that when gut viscosity is decreased and nutrient digestion and absorption are enhanced, the indigestible feed materials pass through the gut quickly and insufficient time is available for anaerobic microflora to establish in the upper part of the gut.

In Australia, some wheats have very low apparent metabolisable energy values when fed to broiler chickens (Mollah *et al.* 1983). The poor ME values are due to increased levels of soluble NSP in the wheats (Annison 1991; Choct *et al.* 1995). Rogel *et al.* (1987) demonstrated that adding coarsely-ground oat hulls (more than 90% NSP, of which 99% is insoluble) to low-ME wheat diets largely ameliorated poor nutritive quality of the wheats. The effect of the oat hulls on digesta transit time was demonstrated where addition of 10% oat hulls increased the rate of digesta passage significantly (Rogel 1985). Fine-grinding of the oat hulls, however, rendered them ineffective. The water-holding capacity of fibre changes with particle size. In studies with humans, a coarse wheat bran preparation significantly shortened the digesta transit time and showed beneficial effects on colonic function, whereas a fine bran preparation was completely without effect (Kirwan *et al.* 1974). These authors demonstrated that the beneficial effect of bran was dependent on the water holding capacity, which is a function of particle size. Thus, milling the coarse bran to a particle size of 1 mm almost halved the water holding capacity from 6.15 g to 3.54 g of water per g of bran. It is possible that the effectiveness of the coarse fibre was due to its ability to hold

large amounts of water, thereby preventing increased solubilisation of NSP. The net effect was an increased rate of digesta passage, giving little time for fermentative organisms to establish in the gut, especially in the small intestine. This highlights the possibility that perhaps at an appropriate ratio between the soluble and insoluble fractions, the anti-nutritive effect of the soluble NSP may be minimised.

THE CURRENT UNDERSTANDINGS AND THE FUTURE OPTIONS FOR NSP IN MONOGASTRIC DIETS

The anti-nutritive activity of soluble NSP with well-defined chemical structures, e.g., arabinoxylans and β -glucans in cereal grains, is eliminated effectively by supplementation of the feed with xylanases and β -glucanases which cause a partial depolymerisation of the NSP to smaller polymers so that their ability to form highly viscous digesta is greatly reduced. Enzymes capable of effectively cleaving various pectic polysaccharides are, however, yet to be produced.

The fermentative capacity of the chicken is limited and therefore it absorbs most of its energy as monomeric sugars. The current enzymes are not designed to degrade NSP to monomeric sugars within the food transit time of the pigs and poultry. The future challenge for the feed industry is, therefore, to produce highly efficacious enzymes which will lead to the utilisation of both soluble and insoluble NSP as an energy source for monogastric animals.

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