Non-starch carbohydrates: Digestion and its secondary effects in monogastrics

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Summary

A large portion of non-starch carbohydrates (NSC) is digested by the microflora of the large intestine in pigs, but NSC digestibility in poultry is much lower. The fermentative breakdown of NSP can contribute up to 24% of the dietary energy in pigs, whereas it is estimated to contribute only 2-3% of the dietary energy in chickens. Although the chicken ferments oligosaccharides rapidly, its capacity to obtain energy from fermentation of non-starch polysacchardies (NSP) appears to be limited to an estimated amount of 42kJ per day. The NSC comprise a large number of diverse molecules, which when present in feed, can affect the gut microflora of mongastrics as well as may bring about changes to the endocrine systems, immune systems and the dynamic of the gut. These effects may be exacerbated during the process of digestion, in particular, in the presence of glycanase feed supplements. In addition, the digestibility of NSC is affected by animal species, the chemical structure, solubility and the absolute amount present in the diet. The current paper will focus on the non-starch carbohydrates rather than resistant starch and discuss the relationship between digestibility and chemical structure, solubility, and quantity of NSC in the diet for pigs and poultry.

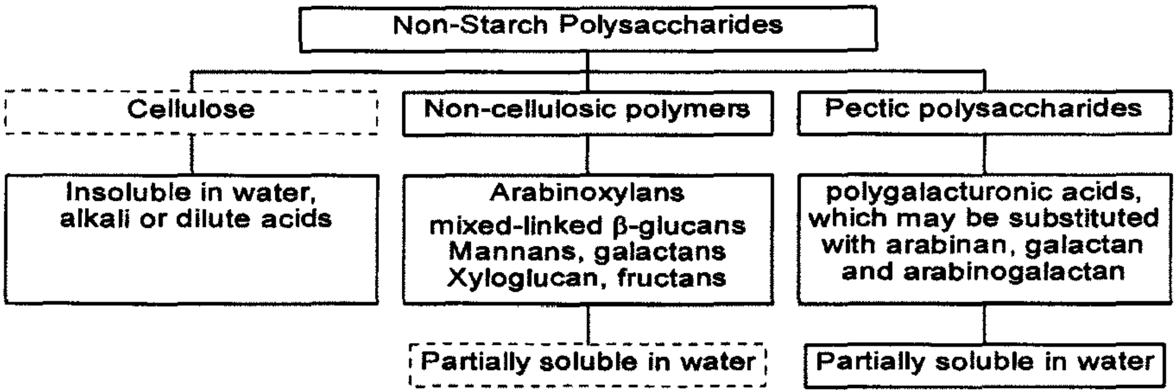
Introduction

The gut harbours a highly evolved and complex microbial ecosystem containing a vast number of diverse populations. For example, microbes make up approximately 600 g/kg of the wet weight of pig and poultry excreta. The proper feeding of monogastrics should therefore consider the provision of "correct" substrates for the microflora to keep it stable. Search for natural alternatives to antibiotics is a major research topic in the feed industry due to the ban of feed antibiotics in some countries. Carbohydrates reaching the large intestine of pigs and poultry determine largely the type and the activity of the gut microflora (Cummings 1981). This in turn is related to the dietary carbohydrates provided to the animal and their digestibility.

There has been an enormous interest in carbohydrates during recent years, which is driven by two very contrasting yet interrelated fields; one is human health work in dietary fibre and resistant starch, which has focused primarily on the effect of the fermentation products on gut health; the other is animal nutritional research, which has involved in establishing strategies to minimise the anti-nutritive activity of soluble non-starch polysaccharides (NSP) and to an extent to manipulate the fermentative characteristics of oligosaccharides for their prebiotic effects. Do all oligosaccharides modulate the gut microflora in a beneficial manner? What are the effects of the low molecular weight carbohydrates that form during the digestive process on the gut physiology and immune system? Answers to these questions are vague, but will at least provide food for thought.

Plant non-starch carbohydrates

Carbohydrates are the main components of plant ingredients, with starch as the major constituent. Starch is second only to cellulose in abundance in terms of polysaccharides synthesized by plants and represents the primary source of energy for many monogastric species, including humans. Starch is, however, not the scope of this paper. Other carbohydrate moieties present in plant ingredients include mono-, di-, oligo- and polysaccharides at various quantities and structures. In the literature, a number of different terms have been used to describe the polymeric carbohydrates other than starch, i.e. non-starch polysaccharides (NSP). 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).



Different ingredients contain not only different amounts of soluble and insoluble NSP but also the structure and physiochemical characteristics of the NSP differ widely. What is important from a nutritional point of view is the understanding of the vastly different effects of soluble and insoluble NSP on nutrient digestion and absorption in monogastric animals. The classic system of "fibre" analysis is not capable of providing vital information on the physiochemical characteristics of NSP and subsequent effects on digestion and absorption. For instance, the constituent sugars for the NSP in leguminous ingredients are similar to those found in cereal grains. But they are not necessarily linked in the same way as in cereals. Most legumes contain pectic polysaccharides as their main NSP, but these polymers also differ widely in terms of their molecular structures. For example, the major NSP in soybean and lupins are pectic polysaccharides, more precisely polyrhamnogalacturonans with various side chains (Perlin, 1962; Cheetham *et al.*, 1993), whereas in canola the occurrence of β-3,6)-linked galactose polymers, which are free of β-4)-linked galactose residues, as part of the pectic polymers has been reported (ref).

Digestibility of NSP and factors affecting it

The definition of "digestion" is the "disappearance of nutrients from the gut". However, digestion here refers to both the disappearance of nutrients from the entire gastrointestinal tract as well as from specific parts of the tract, e.g. ileal digestibility. Since pigs and poultry do not have endogenous enzymes capable of digesting oligosaccharides (excluding maltooligosaccharides) and NSP, the digestibility of these non-starch carbohydrates is achieved by chemical (acid in the stomach in pigs and crop in chickens) and microbial degradation. Indeed a large portion of NSP is digested by the pig, which occurs by the fermentation largely in the large intestine. NSP digestibility in pigs can be as high as 93% (Stanogias and Pearce, 1985). In poultry, the digestibility of NSP is lower. Longstaff and McNab (1986) reported that approximately 24% of wheat pentosans were digested by adult cockerels, whereas Choct *et al.* (1992) reported that the digestibility of NSP in 3-4 week old broilers fed a control diet was 21.7%.

It is, however, misleading to talk about NSP as one entity in terms of digestibility because digestibility of NSP is affected by a multitude of factors which include animal species, solubility, chemical structure, and their quantity in the diet.

Solubility of NSP

The solubility affects the digestibility of NSP in both pigs and poultry. Thus, in general the soluble NSP are more digestible than the insoluble fraction and the digestibility of the soluble NSP is almost complete in pigs (Bach Knudsen and Hansen, 1991) and 65% in poultry (Choct *et al.*, 1992). Much lower digestibility values for soluble NSP in poultry have been reported (Pettersson and Aman, 1989). Solubility of NSP not only influences that extent of their degradation in the gut, but also affects the digestibility of other nutrients. This will be discussed in a later section. But it appears that NSP of wheat have anti-nutritive effect on feed intake in weaner pigs because the use of a xylanase with affinity for both soluble and insoluble arabinoxylans can overcome the poor nutritive value of some wheats containing an elevated level of NSP (Cadogan, 1999). In pigs, the digestibility of insoluble NSP is also high. The digestibility of the total NSP in wheat and barley was approximately 65% (Fadel et al, 1988), whereas for a mixed cereal (wheat, barley and oats) diet, it was 48% (Graham *et al.*, 1986). In poultry, insoluble NSP are believed to have little or no effect on nutrient digestion. For instance, total recovery of crude fibre in the excreta of chickens has led to the proposal to use crude fibre as a marker in nutritional studies (Almquist and Halloran 1971). In contrast, the water-soluble fraction is assumed quickly digested (Carré, 1990). Pettersson and Aman (1989) reported that when broilers were given a diet containing equal proportions (30.5%) of rye and wheat, the digestibilities of soluble and insoluble pentosans, respectively were: 12.6% and 31.4% in the middle section of small intestine, 19.1% and 27.6% in the last section of small intestine, and 31.6% and 40.0% in the faeces. Similar overall digestibility of pentosans has been shown by other workers. Determining the pentosans as the alditol acetates of arabinose and xylose by gas chromatograph. Longstaff and McNab (1986) reported that approximately 24% of wheat pentosans were digested by adult cockerels. The large difference in the digestibility of cellulose and pentosans suggests that not only solubility of NSP, but also the chemical structure and sugar composition also affect digestibility.

Chemical structure

The differential use of various carbohydrates by different bacteria is a common knowledge. Thus, it is not difficult to postulate that carbohydrates with different chemical structures could be digested differently. In pigs, Bach Knudsen and Hansen (1991) reported that between 64-75% of the β-glucans were digested by the time the digesta reaches the ileum, whereas cellulose, arabinoxylans and uronic acids were totally undigested. The whole tract digestibility of β-glucans was almost complete whereas, that of cellulose ranged from 34% in a diet containing whole wheat flour, pericarp and testa to 60% in a diet consisted of whole wheat flour only. Arabinoxylan digestibility followed a similar pattern as cellulose, but the values were slightly higher, whereas that of uronic acids were lower. Furthermore, the digestibility of these polysaccharides was similar regardless of whether they were from wheat or from oats. Another study (Goodlad and Mathers, 1991), however, demonstrated that NSP from peas were more digestible than those from wheat in pigs (65% vs. 85%). There are also large differences in the digestibility of the component sugars in pigs and poultry. At low levels of inclusion, the component sugars in pea NSP are almost completely digested by pigs, whereas digestibility values range between only 17% to 52% in chickens (Jørgensen *et al.*, 1996). Table 1 presents the digestibility values of different sugars in pea NSP by pigs and poultry.

Table 1. Digestibility coefficients of NSP in peas and their constituent sugars by chickens and pigs.

Carbohydrate	**Chickens**[1]	**Pigs**[2]
NSP	0.28	0.84
Non-cellulosic NSP	-	1.02
Cellulose	-	0.54
Arabinose	0.30	1.04
Xylose	0.17	1.03
Mannose	0.52	0.72
Galactose	0.36	1.02
Glucose	0.31	0.71
Uronic acids	0.39	0.94

[1] From Jørgensen *et al.*, 1996; [2] From Goodlad and Mathers, 1991.

It, however, must be stressed that generalising NSP digestibility values according to their sources and chemical structures may be misleading. For example, the digestibility of cellulose from whole wheat flour was 60%, whereas cellulose from wheat flour plus pericarp and testa was only 24% (Bach Knudsen and Hansen, 1991); the digestibility of soluble citric pectin was 67.2% (Carré *et al.*, 1995), whereas soluble pectic polysaccharides from lupins were only 7.9% in chickens (Carré *et al.*, 1990). This highlights the complexity of factors affecting NSP digestibility in monogastric animals. Not just the chemical structure per se, but the whole cell wall structure affects the digestibility of a particular component within it. For example, the degree of lignification of the cell wall, cross links between cell wall components, and perhaps the formation of "junction zones" could all have an effect on NSP digestibility in a given species (Fincher and Stone, 1986).

Species and age of the animal

There is a large difference in NSP digestibility between pigs and poultry. In general, pigs can digest NSP better than chickens (see Table 1) due to a better fermentative capacity in the large intestine and a longer digesta transit time. While the mechanism of polysaccharide degradation and the structural factors determining the extent of hydrolysis are independent of the host species and of the site within the gastro-intestinal tract, the microbial population directly or indirectly involved in polysaccharide fermentation can show considerable variation. Bolton (1955) showed pentosan digestibilities of 4% in 2-week old chickens, and of 19% in adult birds. This may suggest that an NSP degrading microflora develops as the birds become older. Carré *et al.* (1995) reported that for a corn-soy diet, NSP digestibility was significantly higher in adult cockerels than broilers. The inference that an age-related development of the gut microflora of the chicken has recently been demonstrated by Petersen *et al.* (1999) where the gut viscosity of birds fed barley or wheat based diets decreased with age. It is possible that as the bird ages, its gut microflora adapts to utilise the NSP more efficiently by production of various glycanases.

Level of NSP in the diet

The amount of NSP in the diet influences the digestibility of NSP. Table 3 shows the data of Jørgensen *et al.* (1996), who demonstrated a dose-response type depression in the NSP digestibility in poultry fed three different fibre sources (pea fibre, wheat bran and oat bran) at three levels. .

Table 3. Effect of dietary fibre source and level on digestibility (%) and metabolisability of feed by chickens (after Jørgensen *et al.*, 1996).

Fibre source	Control	Pea Fibre		Control	Wheat Bran		Control	Oat Bran	
Fibre level	4.5%	14.9%	25.1%	4.5%	13.2%	20.3%	4.5%	9.1%	12.7%
Ileal DM	85	76	60	85	72	60	86	80	67
Energy Meta	87	74	59	87	76	65	88	80	69
NSP	28	6	12	33	19	16	33	35	25

The effect of inclusion levels of NSP on their own digestibility is multifaceted. First, the anti-nutritive effect of NSP on nutrient digestion and absorption is negatively related to the dietary concentration of NSP (Choct and Annison, 1990); second, the capacity of the gut microflora of the chicken is simply limited in digesting large amounts of NSP within the short transit time of the digesta.

Process of NSP digestion and its effect on the host

The process of NSP digestion in pigs and poultry has the commonality of acid digestion in the upper part of the gut (stomach in pigs and crop in chickens) and microbial fermentation in the lower part of the small intestine and of the entire large intestine. In poultry, a small amount of physical digestion may occur as fibrous materials go through the gizzard where they are ground to fine particles. This section will attempt to cover the effect of NSP on nutrient digestion and absorption, on the gut microflora; the digestion of oligosaccharides and its fermentation products; the effect of the short chain fatty acids (SCFA) on the gut; and the contribution of SCFA to the dietary energy value.

The anti-nutritive effect of NSP

Elevated levels of NSP, in particular, the soluble fraction lead to decreased nutrient digestion and absorption in poultry (Antoniou *et al.*, 1983; Classen and Bedford, 1990; Choct and Annison, 1990) and to an extent in pigs (van Barneveld, 1998). Once NSP are solubilised in the lumen, the result is an increase in the viscosity of the digesta, which leads to changes in the physiology and the ecosystem of the gut (Angkanaporn *et al.*, 1994; Choct *et al.*, 1996). This is probably achieved by slowing down the rate of digesta passage (Gohl and Gohl, 1977; van der Klis and van Voorst, 1993). A slow moving digesta with low oxygen tension in the small intestine could provide a relatively stable environment where fermentative microflora can establish (Wagner and Thomas, 1978). Choct *et al.* (1996) demonstrated a large increase in fermentation in the small intestine of broiler chickens by adding soluble NSP in the diet. Although at first it could be thought that increased production of VFA would increase the energy content of the feed, but due to the drastic change in the gut ecosystem, i.e., fermentation in the small intestine, the net effect was decreased nutrient digestion accompanied by poor bird performance. Subsequent in vivo depolymerisation of the soluble NSP using glycanases largely overcame this problem. In pigs, these effects are often not so obvious, in particular the effect on gut viscosity. However, Pluske *et al.* (1999) showed that an elevated level of dietary soluble NSP was associated with increased the pathogenesis of swine dysentery in weaner pigs. The implication of increased dietary soluble NSP in the onset of other diseases, such as necrotic enteritis in poultry, has also been documented (Riddel and Kong, 1992; Kaldhusdal and Kofshagen, 1992). It should be borne in mind that if the NSP are completely hydrolysed, the anti-nutritive effect on nutrient digestion and absorption and its association of the pathogenesis of certain diseases could be eliminated. A large reduction in number of *Clostridium perfringens*, the causative bacterium for necrotic enteritis in poultry, by enzyme supplementation has recently been reported (Sinlae and Choct, 2000).

NSPs can also bind nutrients and form complexes with digestive enzymes and some regulatory proteins in the gut. Angkanaporn *et al.* (1994) showed that addition of soluble arabinoxylans to a broiler diet markedly increased endogenous losses of amino acids, leading to significant depression in the apparent digestibility of protein in the ileum. The gut secretes some 20 hormones or regulatory peptides (Unväs-Moberg 1992), some enhance nutrient absorption, and others depress it. Feed components that have effects on endogenous protein secretion ought to have an effect on hormonal secretions. 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). In addition to the modification of the gut physiology, certain NSP can also bind bile salts, lipids and cholesterol (Vahouny *et al.* 1980; Vahouny *et al.* 1981). The net effect may be an altered lipid metabolism in the intestine, resulting 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.

Oligosaccharides

Lower molecular weight carbohydrates, such as oligosaccharides and fructans, are digested between 40-50% in the small intestine (De Schrijver, 2000) and are completely digested in the large intestine of the pig (Back Knudsen and Hansen, 1991). A similar digestibility value has been reported in poultry, which shows ileal digestibility values of 52% and 62% for oligosaccharides present in canola meal and sunflower meal (Kocher *et al.*, 2000). Extensive degradation of oligosaccharides occurs in the caeca of the bird, especially in adult birds. Thus, Carré *et al.* (1995) demonstrated that digestibility of β-galactosides was 86.7% and 99% in broilers and adult cockerels, respectively.

The consequence of the digestion of oligosaccharides in general is an increase in the number of Lactobacilli and Bifidobacterium, and a decrease in Clostridia and Enterobacteria (Nemcova *et al.*, 1999). Other oligomers, such as manan-oligosaccharides, are believed to physically bind to pathogens as well as stimulate the immune system (Newman, 1994). The majority of the literature data suggest that rapidly fermentable oligosaccharides stimulate beneficial microflora in the gut, leading to improved health in pigs. However, van Barneveld *et al.* (1997) showed that removal of the galactosides from lupins improved the energy digestibility of the diet in weaner pigs, suggesting that an excessive amount of oligosaccharides in the small intestine modify gut physiology, which may lead to poor enzymatic digestion of nutrients. In poultry, the role of dietary oligosaccharides is very much unclear. Those who look for the prebiotic effect of oligosaccharides often report the change in the number and make up of the gut microflora indicative of a beneficial effect (ref), whereas those who investigate the performance related parameters argue that an elevated level of oligosaccharides in poultry diets increases fluid retention, hydrogen production and diarrhea, leading to impaired utilisation of nutrients (Saini, 1989; Coon *et al.*, 1990; Leske *et al.*, 1993). Therefore it is difficult to say whether oligosaccharides are "nutrients" or "anti-nutrients". Perhaps the complexity of the role of oligosaccharides in animal nutrition may be appreciated from the number of different carbohydrate oligomers that can potentially be available to the gut microflora. For example, if oligosaccharides are defined as carbohydrates with up to 10 sugar units, then a simple enzymatic degradation of the arabinoxylan in wheat, in theory, can produce over a hundred different oligomers depending on the number of sugars and the position (O2, O3 or both) of the arabinose on the xylose. The production of various xylo- and arabnoxylo-oligomers in the gut due to the use of exogenous feed enzymes is possible.

Fermentation products

There are some vague correlations between the type of carbohydrates and their fermentation products. For example, fermentation of soluble pectins produces approximately 80% acetate and only a small amount of butyrate, whereas guar gum produces less acetate and more butyrate (Cummings, 1991). The metabolism of acetate, propionate and butyrate is different. Acetate mainly enters the portal system to serve as an energy source for the periphery; propionate is metalised in part by the colonocytes, but primarily by the liver; butyrate is the most important fuel for the colonocytes in humans and pigs. A rapid entrance of fermentable substrates into the hind gut can lead to the production of lactic and succinic acids (Sakada, 2000). Short chain fatty acids (SCFA) are believed to enhance sodium absorption, stimulate blood flow and regulate nutrient absorption (Sakata, 1991). Numerous other roles are suggested for SCFA, but they are beyond the scope of this paper. What is of direct relevance to animal nutrition is the energy contribution from these acids. In poultry, most of the fermentative products are absorbed effectively (Carré *et al.*, 1995). However, Jørgensen *et al.* (1996) reported that the total contribution of SCFA to the metabolisable energy to the bird is approximately 42 kJ per day independent of the NSP source, which accounts for only 2-3% of the dietary ME. An equivalent of 2% of the dietary ME was lost as lactic acid and acetate in the excreta and a 0.2% as from hydrogen production. But the net efficiency of utilisation of dietary energy via hind gut fermentation is estimated to 65% and 50% of that of glucose absorbed intestine in adult cockerels and broiler chickens, respectively (Carré *et al.*, 1995). In pigs, the fermentative break down of NSP in the large intestine can provide between 10-24% of the dietary energy for maintenance with an additional 1-4% of energy coming from the flow of organic acids produced in the ileum, depending on the type and amount carbohydrates in the diet (Back Khudsen and

Hansen, 1991). Feeding ungelatinised potatoe starch to pigs, Mason (1980) found that between 33-44% of the ME for maintenance was derived from hind gut fermentation. This highlights the capacity of the pig to use a large amount of carbohydrates by hind gut fermentation. The net efficiency of utilisation of energy via fermentation, however, is still very low in pigs (50%).

Conclusion

The digestibility of NSP in pigs and poultry is affected by many factors including the characteristics of the polysaccharides, the cell wall structure of the plant from which they are derived, and the level of dietary NSP. To examine the digestibility of non-starch carbohydrates in monogastrics, consideration must be given to the anti-nutritive effect of the NSP on nutrient digestion and absorption on one hand, as well as the potential benefits of the fermentation products to the host. This mirrors the needs for (a) the efficient utilisation of fibrous materials for food production, and (b) the maintenance, and possibly, improvement, of animal health in the future years of antibiotic-free production systems.

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