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Soy Oligosaccharides and Soluble Non-starch Polysaccharides: A Review of Digestion, Nutritive and Anti-nutritive Effects in Pigs and Poultry

M. Choct, Y. Dersjant-Li[1,] *, J. McLeish[2] and M. Peisker[1]
School of Environmental and Rural Science, University of New England, Armidale, NSW 2351, Australia

ABSTRACT : Soybean contains a high concentration of carbohydrates that consist mainly of non-starch polysaccharides (NSP) and oligosaccharides. The NSP can be divided into insoluble NSP (mainly cellulose) and soluble NSP (composed mainly of pectic polymers, which are partially soluble in water). Monogastric animals do not have the enzymes to hydrolyze these carbohydrates, and thus their digestion occurs by means of bacterial fermentation. The fermentation of soybean carbohydrates produces short chain fatty acids that can be used as an energy source by animals. The utilization efficiency of the carbohydrates is related to the chemical structure, the level of inclusion in the diet, species and age of the animal. In poultry, soluble NSP can increase digesta viscosity, reduce the digestibility of nutrients and depress growth performance. In growing pigs, these effects, in particular the effect on gut viscosity, are often not so obvious. However, in weaning piglets, it is reported that soy oligosaccharides and soluble NSP can cause detrimental effects on intestinal health. 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 or detriments of intestinal fermentation products to the host. This mirrors the needs for i) increasing efficiency of utilization of fibrous materials in monogastrics, and ii) the maintenance and improvement of animal health in antibiotic-free production systems, on the other hand. For example, ethanol/water extraction removes the low molecular weight carbohydrate fractions, such as the oligosaccharides and part of the soluble pectins, leaving behind the insoluble fraction of the NSP, which is devoid of anti-nutritive activities. The resultant product is a high quality soy protein concentrate. This paper presents the composition and chemical structures of carbohydrates present in soybeans and discusses their nutritive and anti-nutritive effects on digestion and absorption of nutrients in pigs and poultry. (**Key Words :** Soybean Carbohydrates, Non-starch Polysaccharides, Oligosaccharides, Ethanol/water Extraction, Soy Protein Concentrate)

INTRODUCTION

Soybean is the most widely used vegetable protein source for monogastric animals and is the most prevalent legume/oil seed crop in the world (FAO, 2008). However, soybeans contain nearly as much carbohydrates as protein yet the nutritional and/or anti-nutritional activities of these carbohydrates in animal feed are quite often ignored.

Poor growth performance has been observed when broilers were fed diets containing soybean meal (SBM) as the sole dietary protein source (Irish and Balnave, 1993). It was observed that the poor growth of broilers fed SBM as the sole protein source was more pronounced with meals processed in Australia compared with the meals processed in USA. This response was assumed to be related to the higher fiber content of Australian processed meals (Irish and Balnave, 1993). The poor growth performance could not be explained by the digestibility or the amount of essential amino acids, or the process of heat treatment of the SBM tested. A significant relationship was observed between the water-soluble xylose content of the soybean meals and the improvement in weight gain obtained when sunflower meal replaced some of the soybean meal. Measurement of free sugars in the supernatant of the digesta in the ileum indicated that the stachyose derived from the oligosaccharides of SBM appeared to exert an anti-nutritive effect when SBM was present at high concentrations as the sole protein source in broiler diets (Irish and Balnave, 1993).

Growing pigs can utilize SBM efficiently but weaning

* Corresponding Author: Y. Dersjant-Li. Tel: +31-75-6464212, Fax: +31-75-6464165, E-mail: Yueming.Derajant-Li@adm.com
[1] ADM Specialty Ingredients (Europe) B.V. Stationsstraat 76, 1541 LJ Koog aan de Zaan, The Netherlands.
[2] ADM Australia Pty. Ltd., Suite 1003 I Newland Street Bondi Jun ction NSW 2022 Australia.
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piglets respond to dietary SBM with reduced growth performance (Li et al., 1991; Friesen et al., 1993; Rooke et al., 1998). The anti-nutritive effects of soy oligosaccharides and soluble NSP have been observed in weaning piglets (Veldman, 1993; Pluske et al., 1998). It was reported that the removal of soluble NSP and oligosaccharide by ethanol/water extraction improved intestinal health and growth performance in weaning piglets (Hancock et al., 1990).

The chemical and nutritional properties of soybean carbohydrates have been extensively reviewed by Karr-Lilienthal et al. (2005). However, there is a scarcity of literature reviews on the anti-nutritional effects of soluble NSP and soy oligosaccharides on digestibility, intestinal health and growth performance in pigs and poultry.

The objectives of this paper are to review digestibility, nutritional values and anti-nutritional effects of soybean carbohydrates, with focus on the soluble non starch polysaccharides and oligosaccharides; and to evaluate the impact of ethanol/water extraction on soy carbohydrates composition.

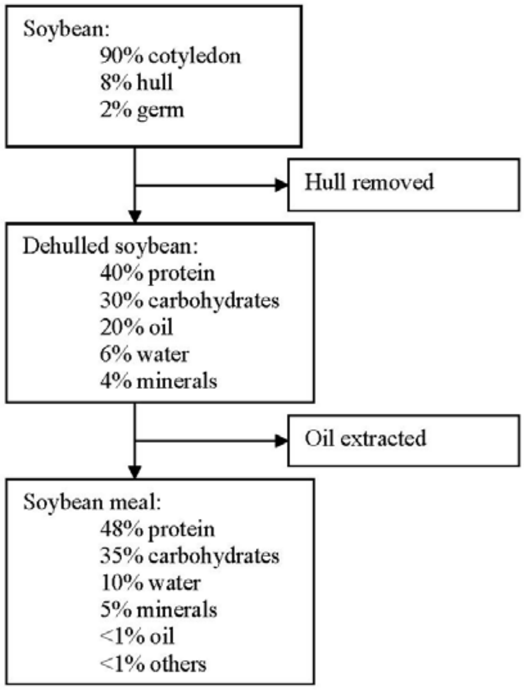


Figure 1. Nutrient composition of soybean and soybean meal.

CARBOHYDRATES IN SOYBEAN

The chemical composition of soybean and soybean meal

Soybeans have about 8% seed coat or hull, 90% cotyledons and 2% germ (USDA, 2009). Soybeans are not only a great source of high quality oil, but also are rich in protein and carbohydrates. Thus, dehulled soybeans contain 20% oil, 40% protein, 35% carbohydrates and 5% minerals on a DM basis (USDA, 2009). When the oil is extracted, the remainder, usually called the meal, has around 48% protein, 35-40% carbohydrates, 7-10% water, 5-6% minerals and less than 1% fat (3-4% of acid hydrolyzed fat) (USDA, 2009). The carbohydrates are the least understood constituent in soybean. Figure 1 summarizes this process.

Carbohydrates in soybean

The carbohydrates in soybean meal consist predominantly of non-starch polysaccharides (NSP) and free sugars, such as, mono-, di- and oligosaccharides (Choct, 1997). Starch is present at less than 1% (Choct, 1997). NSP are classified into three main groups, as shown in Figure 2, namely cellulose, non-cellulosic polymers and pectic polysaccharides.

Different ingredients contain not only different amounts of soluble and insoluble NSP and oligosaccharides but also the structure and physiochemical characteristics of the NSP differ widely. Soybean NSP are composed mainly of a mixture of pectic polysaccharides such as rhamnogalacturonans (types I and II), arabinogalactan I and xylogalacturonan (Fransen, 1999). The carbohydrates in soybean consist of approximately 10% free sugars (5% sucrose, 4% stachyose and 1% raffinose) (Macrae et al., 1993) and between 20-30% NSP, in which approximately 8% are cellulose and the remaining are pectic

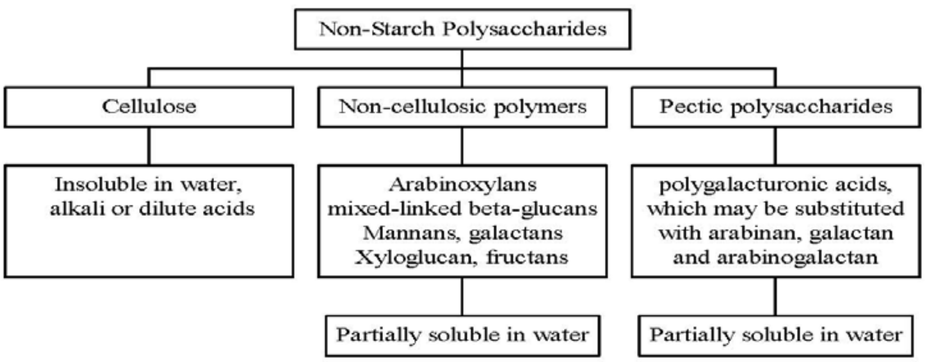


Figure 2. Classification of Non-Starch Polysaccharides (NSP).

polysaccharides (Choct, 1997). It is also worth mentioning that the carbohydrate composition of soybeans varies according to the geographical locations where the soybean was grown, harvest conditions and post-harvest processing (Karr-Lilienthal et al., 2005). Thus, it is not surprising to find that the level of sucrose ranges between 3-8%, raffinose between 0.1-1.5% and stachyose between 1 to 6%. Figure 3 shows the carbohydrate composition of soybean meal.

Besides the variation due to genotype and origin of soybean, the content of NSP may also be related to the method of analysis. Literature reports a large range of values for soy NSP and oligosaccharides as summarized in Table 1.

Dust et al. (2004) observed that extrusion conditions affected chemical composition of soy flour with the total dietary fiber, insoluble dietary fiber and soluble dietary fiber, respectively, being 28.9, 18.1 and 10.8% in mild extruded soy flour, and 26.6, 18.6 and 8.0%, respectively, in moderately extruded soy flour.

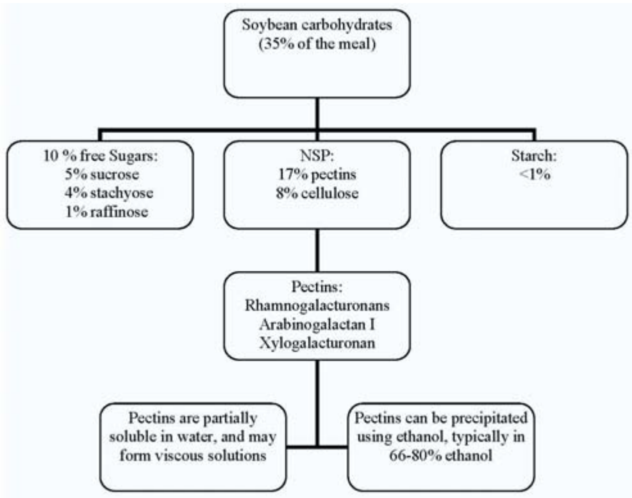


Figure 3. The types and amounts of various carbohydrates present in soybean meal.

Table 1. Carbohydrates in soybean meal (g/kg dry matter); mean values and SD

References	Bach Knudsen (1997)		Irish and Balnave (1993)[1]		Grieshop et al. (2003)[2]		Smits and Annison (1996)[3]
No of samples	6		10		10		
	Mean	SD	Mean	SD	Mean	SD	
Sucrose	70	11			65.8	11.3	
Raffinose	10	1			11.8	1.6	
Stachyose	47	4			49.8	5.2	
Verbascose	3	2			2.2	0.3	
Total sugar	137	16			166	14	
Total NSP	217	27	191.8	18.6	198*	9	303
S-NSP	63	10	27.3	4.9			139
Rhamnose	1	1	0.6	0.5			
Fucose			0.4	0.1			
Arabinose	9	2	5.3	1.1			
Xylose	2	1	1.1	1.0			
Mannose	5	1	2.1	0.6			
Galactose	16	3	5.7	1.9			
Glucose	6	3	3.1	1.3			
Uronic acids	25	4	10.7	2.6			
I-NSP	92	9	164.5	18.5			164
Rhamnose	2	0	2.3	0.5			
Arabinose	17	2	3.1	0.2			
Fucose			23.9	2.5			
Xylose	17	3	17.1	5.5			
Mannose	8	2	6.8	1.4			
Galactose	25	3	39.4	2.6			
Glucose	1	2	3.1	1.6			
Uronic acids	23	3	25.4	2.0			
Cellulose	62	18	44.2	10.6			
Klason Lignin	16	4					
Dietary fiber	233	26					
CHO and lignin							
Analyzed	400	15					
Calculated	416	17					

[1] SBM from different origins, soluble NSP was calculated by total NSP-insoluble NSP. [2] SBM collected at 10 US soybean processing plants.
[3] Adapted from Carre (1992) cited by Smits and Annison (1996), from data not corrected for residual proteins.
* Total non-structural carbohydrate.

Grieshop et al. (2003) reported that the total sugar content ranged from 13.6 to 17.9% of DM in SBM collected at 10 US soybean processing plants. Greater and Fehr (2000) reported that the mean total sugar content of 23 soybean cultivars grown at 8 Iowa locations in 1998 ranged from 19 to 21.4% on DM basis. The average total sugar contents were 10.6, 7.5 and 5.9%, respectively, in the seeds of *G. max*, *G. gracilis* and *G. soja* (Hymowitz and Collins, 1974). The seeds of *G. max* had a higher total sugar content, with the highest value being 16.6%.

Sugars content in soybean seeds were negatively correlated with protein content (Hartwig et al., 1997). The content of oligosaccharides (stachyose+raffinose+sucrose) was 96.7 and 103.3 g/kg DM respectively in year 1991 and 1992 in high oil soybean seeds; while it was 88.9 and 86.2 g/kg dm respectively in year 1991 and 1992 in high protein soybean seeds.

Chemical structures of the soy carbohydrates

The chemical structures of soy carbohydrates are highly complex and the exact formulae and amounts of some of the molecules are not known. However, it is well established that the main pectic polymers in soybean are rhamnogalacturonans with cellulose as the second most abundant carbohydrate in soybean meal (Choct, 1997). Oligosaccharides are characterised by α-galactosidic bonds between saccharose and galactose, and thus they are also known as α-galactosides. Figure 4 shows the molecular structures of cellulose, pectic polymers and oligosaccharides.

DIGESTIBILITY AND NUTRITIVE VALUE OF SOY NSP

Digestibility

Digestion here refers to 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 NSP and some oligosaccharides, the digestibility of these carbohydrates is achieved by chemical (acid in the stomach in pigs and crop in chickens) and microbial

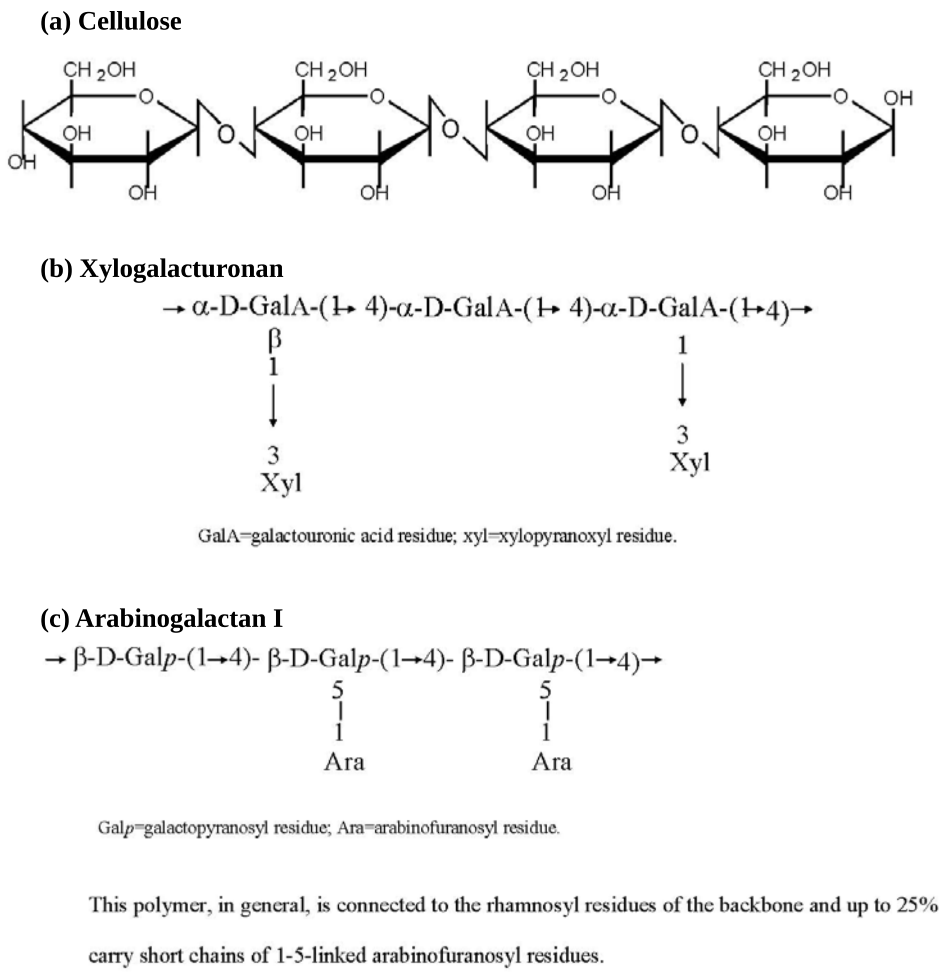
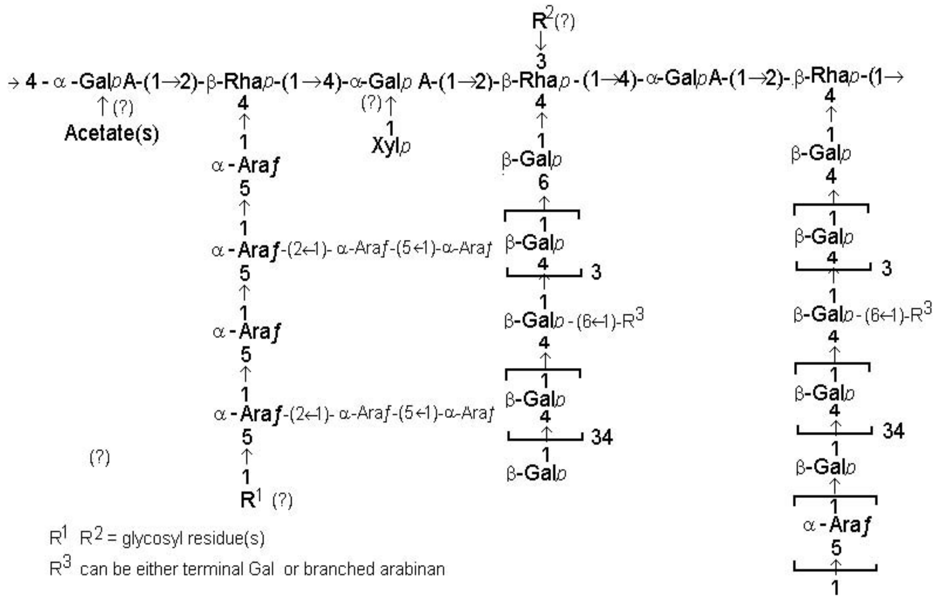
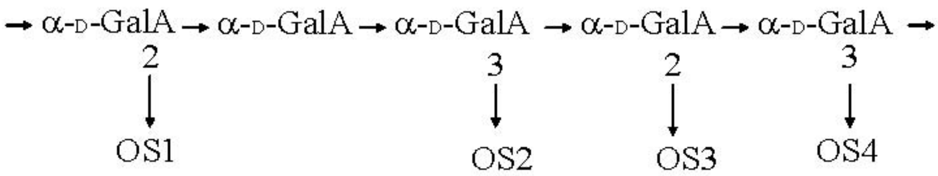


Figure 4. i) The chemical structures of soy carbohydrates.

(d) Rhamnogalacturonan I



(e) Rhamnogalacturonan II



GalA=galacturonic acid; OS1-4: 4 types of oligoglycosyl side chains attached to the O2 or O3 position of the backbone. The sidechains are highly complex residues containing rhamnose, apiose, 3-O-methyl-L-fucoese, 2-O-methyl-D-xylose, 3-C-carboxy-5-deoxy-L-xylose, 3-deoxy-D-manno-octulosonic acid, and 3-deoxy-D-lyxoheptolusaric acid).

(f) α-galactosides (soy oligosaccharides)

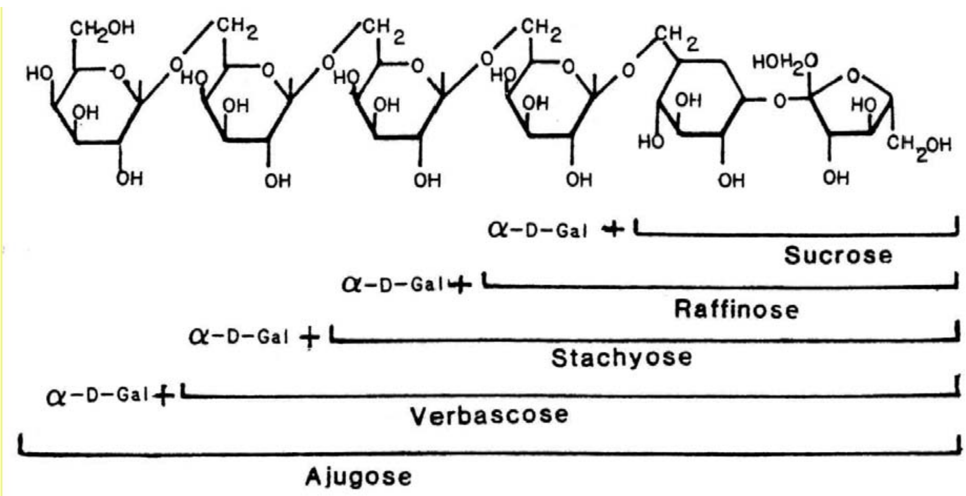


Figure 4. ii) The chemical structures of soy carbohydrates.

degradation. Indeed a large portion of NSP is digested by the large intestinal microflora in pigs. The digestibility of NSP is affected by a multitude of factors which include animal species, age of animals, solubility, chemical structure, and their quantity in the diet.

The solubility of NSP affects their digestibility in both pigs and poultry. In general, the soluble NSP are more digestible than the insoluble fraction. In pigs, the digestibility of the soluble NSP is near complete, but that of insoluble NSP, such as cellulose, ranges from 34-60% (Bach Knudsen and Hansen, 1991). NSP digestibility in poultry is lower. Carré et al. (1990) observed a NSP digestibility value of 13% in cockerels fed a diet containing 6.9% NSP, where the only source of NSP was from defatted, de-hulled soybean meal. In adult birds, Carré et al. (1995) suggested that the degradation of soluble NSP can be as high as 80-90%, whereas the insoluble polysaccharides remain un-degraded. Using an *in vitro* enzymatic digestion procedure, Honig and Rackies (1979) observed that the *in vitro* digestibility of total carbohydrates in whole soybeans, dehulled, defatted soy flour and soy hulls were 40.7, 58.4 and 2%, respectively. The apparent ileal and total tract digestibilities of NSP in the diet based on SBM, wheat and barley were 8.2 and 68% in piglets (Gdala et al., 1997). In early weaned piglets, the fecal apparent digestibility of soluble carbohydrates was more than 92% with a diet based on soybean meal (inclusion level of 42.2% in the diet), corn (inclusion level of 18% in the diet) and lactose (Turlington et al., 1989), indicating that soy soluble carbohydrates were extensively fermented by bacteria in the intestine. The total carbohydrate digestibilities in the ileum and colon were 67 and 89.7%, respectively. The authors suggested that structural carbohydrates from SBM are more soluble in acidic conditions than those from corn.

There is a large difference in NSP digestibility between pigs and poultry (Choct and Cadogan, 2001). In general, pigs can digest NSP better than chickens due to a better fermentative capacity in the large intestine and a longer digesta transit time (Choct and Cadogan, 2001). But difference in NSP digestibility also occurs within the same species. Carré et al. (1995) reported that for a corn-soy diet, NSP digestibility was significantly higher in adult cockerels than broilers. It is possible that as the bird ages, its gut microflora adapts to the NSP more efficiently by production of various glycanases. In pigs, the digestibility of NSP increases with the age of animals, since grower and finisher pigs can utilize dietary fiber better than young piglets. Gdala et al. (1997) reported that the digestibilities of xylose, arabinose, and uronic acids in a cereal and SBM based diet were 3.1, 6.8 and 2.7 (as % of intake), respectively, in the small intestine of 8-12 week old piglets. It was observed that enzyme supplementation in the diet did not affect ileal digestibility of NSP constituents in the SBM based diet.

The amount of NSP in the diet influences their digestibility (Choct and Annison, 1990). The effect of inclusion levels of NSP on their own digestibility is multifaceted. First, the anti-nutritive effect of NSP on nutrient digestion is 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.

Nutritional value of soy NSP

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 dietary energy.

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, 1981). After 12 h of *in vitro* fermentation of soy solubles that contained soy soluble NSP and oligosaccharides with swine fecal microflora, the production of short chain fatty acids were 2.4, 1.9, 0.7 and 5 mmol/g of OM for acetate, propionate, butyrate and total SCFA, respectively (Smiricky-Tjardes et al., 2003a). Acetate mainly enters the portal system to serve as an energy source for the periphery; propionate is metabolized 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 (Sakata, 1987). SCFA are believed to enhance sodium absorption, stimulate blood flow and regulate nutrient absorption (Sakata, 1987). 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, 1995). However, Jørgensen et al. (1996) reported that the total contribution of SCFA to the metabolisable energy available to the bird is approximately 42 kJ per day independent of the NSP source, which accounts for only 2-3% of the dietary ME. But the net efficiency of utilization of dietary energy via hind gut fermentation is estimated to be 65% and 50% of that of glucose absorbed in the intestine in adult cockerels and broiler chickens, respectively (Carré, 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 (Bach Knudsen and Hansen, 1991). This highlights the capacity of the pig to use a large amount of carbohydrates by hind gut fermentation. However, the net efficiency of utilization of energy via fermentation is still low in pigs (Yen et al., 1991).

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., 1981; Choct and Annison, 1990) and, to a lesser extent, in pigs (van Barneveld and Hughes, 1994). Soluble NSP increase the viscosity of the digesta, leading to changes in the physiology and the ecosystem of the gut (Angkanaporn et al., 1994). This is probably related to a slower digesta passage rate. 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 broilers by adding soluble NSP in the diet. 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, the net effect was decreased nutrient digestion accompanied by poor bird performance. Subsequent depolymerisation of the soluble NSP *in vivo* using glycanases overcame this problem. In growing pigs, these effects are often not so obvious, in particular the effect on gut viscosity. In weaning piglets, however, Pluske et al. (1998) showed that an elevated level of dietary soluble NSP was associated with increased pathogenesis of swine dysentery. Thus reducing the quantity of fermentable substrate entering the large intestine reduced the incidence of swine dysentery. The authors suggested that the presence of soluble NSP in weaner diets was detrimental for piglet growth and caused proliferation of *E. coli* in the small intestine.

The implication of increased dietary soluble NSP in the onset of other diseases, such as necrotic enteritis in poultry, has also been documented (Kaldhusdal and Hofshagen, 1992). It appears that if the NSP are completely hydrolyzed, 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 (Choct et al., 2006).

The depressive effect of dietary NSP on digestibility of nutrients depends on their inclusion levels, sources and composition (Murray et al., 1977; Freire et al., 2000). In general, it is accepted that increasing dietary NSP levels can have negative effects on the digestibility and rate of absorption of nutrients such as starch, protein and fat. In pigs, it was estimated that with each percentage increase of NDF (neutral detergent fiber), energy digestibility could be reduced by 0.4 to 1.8% for fiber from leguminous feeds and 0.9 to 1.0% for fiber from cereals (Fernandez and Jorgensen, 1986).

Murray et al. (1977) observed that the addition of gel-forming (soluble) polysaccharides (methyl cellulose and pectin) to a diet (6% as replacement of starch) caused a decrease in the apparent digestibility of nitrogen at the terminal ileum. The inclusion of an insoluble polysaccharide (10% of cellulose) as a replacement for starch had little effect on nitrogen digestibility. The authors suggested that gel-forming polysaccharides (such as soluble soy pectin) impaired the hydrolysis of protein rather than the absorption of the products of digestion. Freire et al. (2000) compared inclusion of 20% of wheat bran, sugar beet pulp, soybean hulls and alfalfa meal as respective fiber source to a low fiber basal diet in weaned piglets (7.9 kg BW). They found that soybean hulls (providing 49 and 73 g/kg hemicellulose and cellulose respectively) addition reduced the daily growth rate by 20% and increased the feed conversion by 17% compared with the other fiber sources. Replacement of wheat bran by soybean hulls decreased the total tract digestibility of DM and N by 4.5 and 21.5% respectively. With a constant nitrogen intake, soybean hulls reduced the daily nitrogen retention by 25% compared with the other fiber sources, while sugar beet pulp gave the best digestibility of nutrients. The authors suggested that soybean hulls seemed to be less appropriate to the low digestive capacity of the young pig. The above mentioned studies demonstrate that soy bean hull and soy soluble NSP (mainly pectin) can have negative effect on digestibility of nutrients and growth performance of young animals, *i.e.*, weaning piglets.

NSP can also bind nutrients and form complexes with digestive enzymes and some regulatory proteins in the gut. Angkanaporn et al. (1994) showed that soluble NSP markedly increased endogenous losses of amino acids in chickens. 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 feces in rats (Ide et al., 1989). In addition, certain NSP can bind bile salts, lipids and cholesterol (Vahouny et al., 1981) which could 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 fecal 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.

Soybean meal contains about 30% of NSP, including 14 and 16% of soluble and insoluble NSP, respectively, on dry matter basis (Smits and Annison, 1996). Thus, inclusion of high levels of soybean meal will add high amount of soluble NSP in the diet and this will lead to an increased risk of intestinal disorder in weaning piglets.

SOY OLIGOSACCHARIDES

Digestibility of oligosaccharides

Lower molecular weight carbohydrates, such as oligosaccharides and fructans, are digested between 40-50% in the small intestine (De Schrijver, 2001) and are completely digested in the large intestine of the pig (Carré et al., 1990). Generally, the consequence of oligosaccharide digestion 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 (Spring et al., 2000). Coon et al. (1990) reported that ileal digestibility of raffinose and stachyose was very low in roosters (less than 1%), but the digestibility based on excreta collection was high (84 to 90%). Carré et al. (1990) estimated the apparent digestibility value for oligosaccharides to be 82% in cockerels fed a diet based on soybean meal and corn starch. In pigs, the apparent ileal digestibility of galactooligosaccharides was 77% in a diet containing soy solubles, while the apparent total tract digestibility for the same diet was 100% (Smiricky-Tjardes et al., 2003b).

Veldman et al. (1993) observed that the ileal digestibility coefficients of α-galactosides were 0.73 and 0.57, respectively, for a control diet containing corn starch and a test diet supplemented with soy velasses. The addition of soy velasses (ethanol/water extract from soy flakes, containing 15.2% stachyose and 2.8% raffinose) resulted in a 25% reduction in organic matter and crude protein digestibility in piglets (Figure 5). The authors suggested that the decrease in digestibility was the result of an increase in gut osmolarity and dilution of digestive enzyme activities and substrate concentrations. Similarly, Smiricky et al. (2002) observed that addition of soy solubles containing a high amount of raffinose and stachyose to a

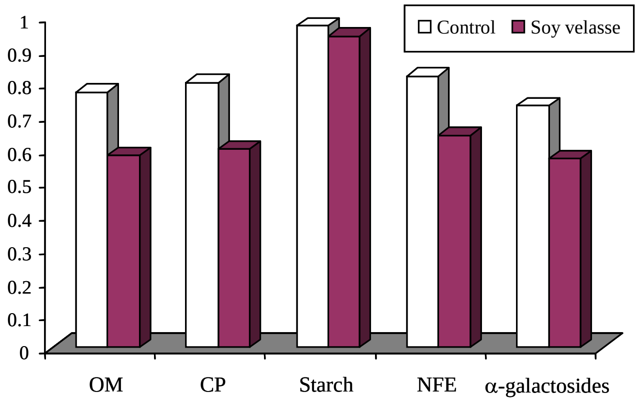


Figure 5. Ileal digestibility coefficients of organic matter (OM), crude protein (CP), starch, nitrogen free extract (NFE) and α-galactosides in experimental diets containing corn starch (control) or soy velasse respectively, in weaning piglets (Veldman et al., 1993).

SPC based diet reduced N and AA digestibility in growing pigs. The addition of α-galactosidase did not improve apparent or true ileal N and AA digestibility, except for the apparent and true digestibility for Val and Tyr.

Supplementation with a single enzyme (α-galactosidase, xylanase, β-glucanase, α-amylase, protease respectively) or with a mixture of enzymes (α-galactosidase+xylanase+ protease) to a cereal and SBM based diet did not improve ileal digestibility of low molecular weight sugars in piglets (Gdala et al., 1997).

Oligosaccharides and intestinal characteristics

It is proposed that a combination of non-digestible oligosaccharides that can be fermented throughout all sections of the gastrointestinal tract including the large intestine may result in prolonged prebiotic effects and prove useful as feed additives in the diets for pigs (Mosenthin and Bauer, 2000). In poultry, the role of dietary oligosaccharides is not clear. Those who look for the prebiotic effect of oligosaccharides often report change in the number and make up of the gut microflora indicative of a beneficial effect (Spring et al., 2000), 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 utilization of nutrients (Saini, 1989; Coon et al., 1990). Therefore, it is difficult to say whether oligosaccharides are "nutrients" or "anti-nutrients". The effect of oligosaccharides in intestinal microflora population is clearly related to the sources, type and concentrations.

Iji and Tivey (1998) reported that the effect of natural raffinose series oligosaccharides (Raffinose, stachyose, verbascose and ajugose) is different from the effects of synthetic (industrial) products on the productivity of broiler chickens. There is evidence of negative effects on animal health and productivity from the use of raffinose series oligosaccharides, but beneficial effects from the use of synthetic oligosaccharides. Due to the absence of α-galactosidase in the upper gastrointestinal tract of monogastric animals, the raffinose series oligosaccharides remain undigested as far as the lower gut, where they are fermented by intestinal bacteria and release gases which have been associated with flatulence in non-ruminant animals and humans. The digestion of raffinose series oligosaccharides may also alter the osmotic differences between the mucosa and plasma, and this may account for the diarrhea observed in animals on diets with high levels of legume seeds (Saini et al., 1989). The authors have suggested that the different response between synthetic and natural series raffinose may be attributed to the very low concentrations at which the synthetic raffinose are usually included in the diets.

In weaning piglets, Fledderus (2005) observed that the inclusion of soy oligosaccharides from soy solubles as a replacement for corn starch caused intestinal disturbance as indicated by more chyme production and higher microbial activity in the gut. The chyme production increased by 40%, total volatile fatty acid content by 60% and total biogenic amine content by 109% (Table 2). Soy oligosaccharides increased microbial activities as indicated by the increased ATP and VFA contents. Microbial activities increased the formation of harmful metabolites such as biogenic amines. Elevated biogenic amine production in the gut might lead to alteration of local and systemic animal physiological functions, such as enhanced enterocyte proliferation, increased gut motility and vaso-active effects, leading to lower nutrient utilization (Veldman et al., 1993).

Fledderus (2005) determined the effect of inclusion of soy oligosaccharides in the diet for weaning piglets on microflora composition in the ileal digesta. Addition of soy oligosaccharides had no significant effect on microflora composition, the number and type of bacteria per gram chyme. However, on a DM basis, more bacteria were produced in piglets fed the soy oligosaccharides supplemented feed as a result of the increased total chyme production. Due to the lack of a specific effect on beneficial bacterial populations, little potential is exhibited to exploit soy oligosaccharides as an integrated dietary pre-biotic.

In weaning piglets, the effect of natural soy oligosaccharides on microbiota composition may be different from synthetic oligosaccharides. It was observed that diet based on SBM providing 1% soy stachyose+raffinose did not significantly affect intestinal bacterial numbers in weaning piglets compared to the control diet (Zhang et al., 2003). Supplementation of 1% pure stachyose stimulated *Lactobacillus spp*., however addition of 2% pure stachyose significantly reduced intestinal lactobacteria and bifidobacteria. The different response between natural and synthetic stachyose may be explained by the difference in fermentation kinetics (Smiricky-Tjardes et al., 2003; Lan et al., 2005). Smiricky-Tjardes et al. (2003a,b) observed that synthetic raffinose and stachyose were more rapidly fermented *in vitro* than soy solubles that contributed the same amount of raffinose and stachyose. *In vitro* fermentation with swine fecal microflora showed a higher fermentation rate for soy solubles compared with other oligosaccharides (fructo-, manno- and xylo-oligosaccharides).

In growing pigs, Smiricky-Tjardes et al. (2003b) suggested that dietary galactooligosaccharides, including soy solubles, might be used as prebiotics as they increased fecal bifidobacteria and lactobacillus population, although addition of soy solubles to a basal diet reduced ileal and

Table 2. The effect of soy oligosaccharides on ileal chyme production, ATP, VFA and biogenic amines content expressed as g/kg dry matter chyme and g/kg dry matter feed respectively

	Control	+Soy oligosaccharides
Osmotic value (osmol/L)	0.364	0.403
Chyme production (g/d)	2,964	4,149
Chyme moisture secretion (g/d)	2,518	3,579
Chyme dry matter excretion (g/d)	446	570
ATP-content		
ng/g dry matter chyme	60.7	139.7
ng/g dry matter feed	19.2	71.6
Total VFA		
g/kg dry matter chyme	18.25	17.64
g/kg dry matter feed	5.58	8.91
Total biogenic amines		
g/kg dry matter chyme	248.6	289.2
g/kg dry matter feed	77.1	161.3

Table 3. The effect of SBM and stachyose on performance and incidence of diarrhea in weaning piglets (Zhang et al., 2003)

	Control	SBM	1% Stachyose	2% Stachyose
Weight gain (kg/d)[1]	0.25[a]	0.22[ab]	0.21[b]	0.17[c]
Feed intake (kg/d)	0.4	0.43	0.42	0.37
Feed conversion	1.61	1.95	2	2.17
Diarrhea[2]	2.05[a]	4.55[b]	2.35[a]	3.15[ab]

[1] Means with different superscripts differ at $p<0.05$.
[2] The incidence of diarrhea was expressed as the sum of days suffered from diarrhea for each pig during the first 14 days.

total tract DM, OM and N digestibility.

Oligosaccharides and performance

It is generally accepted that high levels of soy oligosaccharides, in particular stachyose and raffinose, can cause intestinal disorder in weaning piglets. Pigs do not have endogenous enzymes capable of digesting certain oligosaccharides, such as stachyose and raffinose (Veldman et al., 1993). The fermentation of oligosaccharides in the intestine can cause flatulence and diarrhea (Zhang et al., 2003).

Zhang et al. (2003) observed that supplementation of stachyose at an inclusion level of 1 and 2% reduced the growth rate of weanling piglets (Table 3). The recommended level of soybean galactooligosaccharides (stachyose+raffinose) in weaning piglets diet is not to exceed 1% when SBM is used as a main protein source. Furthermore, diarrhea incidences were highest in the SBM diet, lowest in the control diet and intermediate in the stachyose diets. Interestingly, the addition of 1% stachyose to the diet resulted in the similar performance as the SBM based diet. Soy stachyose may partially contribute to the post-weaning diarrhea problems, explaining the poorer performance of piglets when SBM is used as the sole protein source in weaning piglet diets.

Similar results were observed by Fledderus (2005), that is, a SBM based diet induced the highest incidence of diarrhea (6 days) compared with a positive control diet (3.6 days) and a SPC based diet (2.4 days) in weaning piglets. Total replacement of SBM with SPC as a protein source reduced diarrhea incidence and improved growth performance. This can be partially explained by the removal of indigestible oligosaccharides during the SPC processing.

In broilers, it was observed that the concentration of free sugars in the supernatant of the digesta from the distal small intestine demonstrated a number of significant negative correlations with performance (Irish and Balnave, 1993). Weight gain and feed intake were significantly correlated with the concentration of stachyose, raffinose and sucrose; feed conversion with the concentration of stachyose and raffinose. No such correlations with performance were found with the concentration of these sugars in the digesta from the proximal small intestine. The authors suggested that the oligosaccharides present in SBM may play some part in the poor performance of broilers fed SBM based diets. High concentration of oligosaccharides in the small intestine produce an osmotic effect, leading to fluid retention and an increased rate of passage that could adversely affect the absorption of nutrients.

Effect of carbohydrase

Kim et al. (2003) determined the effect of dietary inclusion of carbohydrases (containing mainly galactosidase, mannanase and mannosidase) to a corn-soybean meal based nursery piglets diet. The piglets were weaned at 21 days of age. Phase I, II and III diets contained 20, 25 and 32% soybean meal, respectively. They observed that the carbohydrases did not improve performance in phases I and II, but improved gain:feed ratio, and energy and AA digestibility in phase III. This study implies that the addition of galactosidase in phase I and II diets can not overcome the detrimental effect of soy oligosaccharides and soluble NSP in weaning piglets.

EFFECT OF ETHANOL EXTRACTION ON SOY CARBOHYDRATE COMPOSITION

Raw soybeans contain high amount of anti-nutritional factors (ANF) and need to be properly processed before their applications in animal feed. The nutritional value and quality of soy products differ due to differences in processing technology. The ANF in soybeans can be divided into heat labile and heat stable components. The most important heat labile anti-nutritional factor are trypsin inhibitors and lectins, which can reduce the digestibility and utilization of nutrients. The most important heat stable ANF are proteins exhibiting antigenic effects (soy antigens) and oligosaccharides. In the processing of soybean meal, only heat labile soy ANF is inactivated. Soybean meal therefore still contains high amount of heat stable ANF, *e.g.* soy antigens, oligosaccharides and soluble NSP. This limits the application of soybean meal in the feed for young animals, such as weaning piglets, as they are very sensitive to soy ANF.

Ethanol/water extraction of soybean flakes removes or inactivates heat stable soy ANF. Currently commercially available soy protein concentrates are produced by ethanol/water extraction of i) soy white flakes (produced by

Table 4. Typical carbohydrate composition (% as is) of soybean meal (SBM, derived from Table 1) and soy protein concentrate (SPC)

	Soybean meal	Soy protein concentrate*
Total NSP	17-27	16-18
Soluble NSP**	6-13	~2
Insoluble NSP	8-15	14-16
Total oligosaccharides	10-15	1-3
thereof Stachyose	4-4.5	~ 0.6
thereof Raffinose	0.9-1.1	~0.04

* Using Soycomil P as an example. Soycomil P is a feed grade soy protein concentrate produced by ADM Europoort B.V. The Netherlands
** Not including oligosaccharides.

removal of soy oil at low temperature) or ii), hipro-soybean meal. As it is out of the scope of this paper, the difference in these two production processes is not discussed. The classification and production processes of different soy protein products have been recently reviewed (Dersjant-Li and Peisker, 2008). The ethanol/water extract process allows the removal of soy oligosaccharides and soluble NSP. Ethanol extraction achieves a 90% reduction in the oligosaccharides present in soybean meal (Veldman et al., 1993). Simultaneously glycinin and β-conglycinin, the two most important storage proteins in soy, are denatured and eliminated their antigenic properties.

Removal of the ethanol-soluble components (mostly oligosaccharides) of soybean meals significantly elevated the true metabolizable energy of the diet and markedly improved chick performance (Leske et al., 1993). In weaning piglets, inclusion of soybean meal can cause intestinal disorder, increase the risk of diarrhea occurrences and reduce growth performance of the newly weaned piglets (Zhang et al., 2003). The negative effect of soybean meal in piglets is mainly caused by the heat stable ANF, *i.e.* soy antigens, oligosaccharides and soluble NSP.

Soy protein concentrate typically contains 65% crude protein on an as is basis and low indigestible soy carbohydrates (Peisker, 2001). The typical soy carbohydrates content in SBM and SPC is compared in Table 4. As shown in Table 4, the ethanol/water extraction process in SPC production removes most of the oligosaccharides and soluble NSP. This process improves soy protein quality and reduces soy ANF. Hancock et al. (1990) determined the effect of ethanol extraction of soybean flakes on performance of piglets, as well as the function and morphology of the pig intestine. It was observed that ethanol extraction improved nitrogen and amino acid digestibility, plasma lysine concentration, villus height, feed intake, growth rate and feed efficiency. Clearly, removal of indigestible carbohydrates, such as oligosaccharides and soluble NSP together with denaturation of soy antigens by ethanol/water extraction, can improve soy protein quality.

CONCLUSION

Soybeans contain a high concentration of carbohydrates, consisting predominantly of NSP and free sugars, such as oligosaccharides. Oligosaccharides and about 45% of the NSP are soluble. These soluble components are one of the main factors responsible for the anti-nutritional effect of soybeans. Ethanol/water extraction process removes these soluble parts from soy efficiently and yields a high quality soy protein product.

REFERENCES

Angkanaporn, K., M. Choct, W. L. Bryden, E. F. Annison and G. Annison. 1994. Effects of wheat pentosans on endogenous amino acid losses in chickens. J. Sci. Food Agric. 66:399-404.

Antoniou, T., R. R. Marquardt and E. Cansfield. 1981. Isolation, partial characterization, and antinutritional activity of a factor (pentosans) in rye grain. J. Agric. Food Chem. 28:1240-1247.

Bach Knudsen, K. E. and I. Hansen. 1991. Gastrointestinal implications in pigs of wheat and oat fractions. Digestibility and bulking properties of polysaccharides and other major constituents. Br. J. Nutr. 65:217-232.

Bach Knudsen, K. E. 1997. Carbohydrate and lignin contents of plant materials used in animal feeding. Anim. Food Sci. Technol. 67:319-338.

Van Barneveld, R. J. and R. J. Hughes. 1994. The nutritive value of lupins for pigs and poultry. In: First Australian Lupin Technical Symposium (Ed. M. Dracup and J. Palta). Perth, Western Australia. pp. 49-57.

Carré, B., L. Derouet and B. Leclercq. 1990. The digestibility of cell-wall polysaccharides from wheat (bran or whole grain), soybean meal, and white lupin meal in cockerels, muscovy ducks, and rats. Poult. Sci. 69:623-33.

Carré, B., J. Gomez and A. M. Chagneau. 1995. Contribution of oligosaccharide and polysaccharide digestion, and excreta losses of lactic acid and short chain fatty acids, to dietary metabolisable energy values in broiler chickens and adult cockerels. Br. Poult. Sci. 36:611-629.

Choct, M. and G. Annison. 1990. Anti-nutritive activity of wheat pentosans in broiler diets. Br. Poult. Sci. 31:811-821.

Choct, M., R. J. Hughes, J. Wang, M. R. Bedford, A. J. Morgan and G. Annison. 1996. Increased small intestinal fermentation is partly responsible for the anti-nutritive activity of non-starch polysaccharides in chickens. Br. Poult. Sci. 37:609-621.

Choct, M. 1997. Feed non-starch polysaccharides: Chemical structures and nutritional significance. Feed Mill. Intern. June. pp. 13-26.

Choct, M. and D. J. Cadogan. 2001. How effective are supplemental enzymes in pig diets? In: Manipulating Pig Production VIII (Ed. P. D. Cranwell). Adelaide, South Australia. pp. 240-247.

Choct, M., M. Sinlae, R. A. M. Al-Jassim and D. Pettersson. 2006. Effects of xylanase supplementation on between-bird variation in energy metabolism and the number of Clostridium perfringens in broilers fed a wheat-based diet. Aust. J. Agric. Res. 57:1017-1021.

Coon, C. N., K. L. Leske, O. Akavanichan and T. K. Cheng. 1990. Effect of oligosaccharide-free soybean meal on true metabolizable energy and fiber digestion in adult roosters. Poult. Sci. 69:787-793.

Cummings, J. H. 1981. Short chain fatty acids in the human colon. J. Br. Soc. Gastroent 22:763-779.

Dersjant-Li, Y. and M. Peisker. 2008. Soy Protein Concentrates - a manifold product group - Classification, processing, nutritional value and feed application. Feed magazine/Kraftfutter 9-10: 16-22.

Dust, J. M., A. M. Gajda, E. A. Flickinger, T. M. Burkhalter, N. R. Merchen and G. C. Fahey Jr. 2004. Extrusion conditions affect chemical composition and *in vitro* digestion of select food ingredients. J. Agric. Food Chem. 52:2989-2996.

Fernandez, J. A. and J. N. Jorgensen. 1986. Digestibility and absorption of nutrients as affected by fiber content in the diet of the pig. Quantitative aspects. Livest. Prod. Sci. 15:53-71.

Fledderus, J. 2005. Possibilities of soy concentrate in piglet feeds without AGP's. Report No 728, Schothorst Feed Research, LELYSTAD, The Neterlands, pp. 1-22.

Food and Agriculture Organisation of the UN. 2008. Agricultural statistics. http://faostat.fao.org/

Fransen, C. T. M. 1999. Structural analysis of soy bean polysaccharides and transgalactosylation of products from lactose. PhD thesis. University of Utrecht, The Netherlands.

Freire, J. P. B., A. J. G. Guerreiro, L. F. Cunha and A. Aumaitre. 2000. Effect of dietary fibre source on total tract digestibility, caecum volatile fatty acids and digestive transit time in the weaned piglet. Anim. Feed Sci. Technol. 87:71-83.

Friesen K. G., R. D.Goodband, J. L. Nelssen, F. Blecha, D. N. Reddy, P. G. Reddy and L. J. Kats. 1993. The effect of pre- and postweaning exposure to soya bean meal on growth performance and on the immune response in the early-weaned pig. J. Anim. Sci. 71:2089-2098.

Gdala, J., H. N. Johansen, K. E. Bach Knudsen, I. H. Knap, P. Wagner and O. B. Jørgensen. 1997. The digestibility of carbohydrates, protein and fat in the small and large intestine of piglets fed non-supplemented and enzyme supplemented diets. Anim. Feed Sci. Technol. 65:15-33.

Geater, C. W. and W. R. Fehr. 2000. Association of total sugar content with other seed traits of diverse soybean cultivars. Crop Sci. 40:1552-1555.

Grieshop, C. M., C. T. Kadzere, G. M. Clapper, E. A. Flickinger, L. L. Bauer, R. L. Frazier and G. C. Fahey Jr. 2003. Chemical and nutritional characteristics of United States soybeans and soybean meals. J. Agric. Food Chem. 51:7684-7691.

Hancock, J. D., E. R. Peo Jr., A. J. Lewis and R. A. Moxley. 1990. Effects of ethanol extraction and heat treatment of soybean flakes on function and morphology of pig intestine. J. Anim. Sci. 68:3244-3251.

Hartwig, E. E., T. M. Kuo and M. M. Kenty. 1997. Seed protein and its relationship to soluble sugars in soybean. Crop Sci. 37:770-773.

Honig, D. H. and J. J. Rackies. 1979. Determination of the total pepsin-pancreatin indigestible content (dietary fiber) of soybean products, wheat bran, and corn bran. J. Agric. Food Chem. 26:1262-1266.

Hymowitz, T. and F. I. Collins. 1974. Variability of sugar content in seed of *Glycine max* (L.) *Merrill* and *G. soja Sieb* and Zucc. Agron. J. 66:239-240.

Ide, T., M. Horii, K. Kawashim and T. Yamamoto. 1989. Bile acid conjugation and hepatic taurine concentration in rats fed on pectin. Br. J. Nutr. 62:539-550.

Iji, P. A. and D. R. Tivey. 1998. Natural and synthetic oligosaccharides in broiler chick diets. World's Poult. Sci. J. 54:129-143.

Irish, G. G. and D. Balnave. 1993. Non-starch polysaccharides and broiler performance on diets containing soyabean meal as the sole protein concentrate. Aust. J. Agric. Res. 44:1483-1499.

Jørgensen, H., X. Zhao, K. E. Bach-Knudsen and B. O. Eggum. 1996. The influence of dietary fibre source and level on the development of the gastrointestinal tract, digestibility and energy metabolism in broiler chickens. Br. J. Nutr. 75:379-395.

Kaldhusdal, M. and M. Hofshagen. 1992. Barley inclusion and avoparcin supplementation in broiler diets. 2. Clinical, pathological, and bacteriological findings in a mild form of necrotic enteritis. Poult. Sci. 71:1145-1153.

Karr-Lilienthal, L. K., C. T. Kadzere, C. M. Grieshop and G. C. Fahey Jr. 2005. Chemical and nutritional properties of soybean carbohydrates as related to nonruminants: A review. Livest. Prod. Sci. 97:1-12.

Kim, S.W., D. A. Knabe, K. J. Hong and R. A. Easter. 2003. Use of carbohydrases in corn-soybean meal-based nursery diets. J. Anim. Sci. 81:2496-2504.

Lan, Y., B. A. Williams, S. Tamminga, B. Boer, A. Akkermans, G. Erdi and M. W. A. Verstegen. 2005. *In vitro* fermentation kinetics of some non-digestible carbohydrates by the caecal microbial community of broilers**.** Anim. Food Sci. Technol. 123-124:687-702

Leske, K. L., C. J. Jevne and C. N. Coon. 1993. Effect of oligosaccharide additions on nitrogen-corrected true metabolizable energy of soy protein concentrate. Poult. Sci. 72:664-668.

Li, D. F., J. L. Nelssen, P. G. Reddy, F. Blecha, R. D. Klemm, D. W. Giesting, J. D. Hancock, G. L. Allee and R. D. Goodband. 1991. Measuring suitability of soya bean products for early-weaned pigs with immunological criteria. J. Anim. Sci. 69:3299-3307.

Macrae, R., R. K. Robinson and M. J. Sadler. 1993. Soya beans. In: (Ed. R. Macrae, R. K. Robinson and, M. J. Sadler), Encyclopaedia of Food Science, Food Technology and Nutrition. Academic Press; London. 1993:4215-4218.

Mosenthin, R. and E. Bauer. 2000. The potential use of prebiotics in pig nutrition. Asian-Aust. J. Anim. Sci. 13:315-325.

Murray, A. G., M. F. Fuller and A. R. Pirie. 1977. The effect of fibre in the form of various polysaccharides on the apparent digestibility of protein in the pig. Anim. Prod. 24:139.

Nemcova, R., A. Bomba, S. Gancarcikova, R. Herich and P. Guba. 1999. Study of the effect of Lactobacillus paracasei and fructooligosaccharides on the faecal microflora in weanling piglets. Berl. Munch Tierarztl Wochenschr 112:225-228.

Peisker, M. 2001. Manufacturing of soya protein concentrate for animal nutrition. Cahiers Options Mediterraneennes. 54:103-107.

Pluske, J. R., Z. Durmic, D. W. Pethick, B. P. Mullan and D. J.

Hampson. 1998. Confirmation of the role of rapidly fermentable carbohydrates in the expression of swine dysentery in pigs after experimental infection. J. Nutr. 128: 1737-1744.

Rooke, J. A., M. Slessor, H. Fraser and J. R. Thomson. 1998. Growth performance and gut function of piglets weaned at four weeks of age and fed protease-treated soya-bean meal. Anim. Feed Sci. Technol. 70:175-190.

Saini, H. S. 1989. Legume seed oligosaccharides. Proc. Rec. Adv. Res. Antinutritive Fact Legume Seed, Wageningen, pp. 329-341.

Sakata, T. 1987. Stimulatory effect of short-chain fatty acids on epithelial cell proliferation in the rat intestine: A possible explanation for trophic effects of fermentable fibre, gut microbes and luminal trophic factors. Br. J. Nutr. 58:95-103.

De Schrijver, R. 2001. Dietary oligosaccharide supplements: effects on digestion in pigs. In: Digestive Physiology of Pigs (Ed. L. E. Lindberg and B. Ogle). CABI Publishing, UK. pp. 121-123.

Smiricky, M. R., C. M. Grieshop, D. M. Albin, J. E. Wubben, V. M. Gabert and G. C. Fahey Jr. 2002. The influence of soy oligosaccharides on apparent and true ileal amino acid digestibilities and fecal consistency in growing pigs. J. Anim. Sci. 80:2433-2441.

Smiricky-Tjardes, M. R., E. A. Flickinger, C. M. Grieshop, L. L. Bauer, M. R. Murphy and G. C. Fahey Jr. 2003a. *In vitro* fermentation characteritics of selected oligosaccharides by swine fecal microflora. J. Anim. Sci. 81:2505-2514.

Smiricky-Tjardes, M. R., C. M. Grieshop, E. A. Flickinger, L. L. Bauer and G. C. Fahey Jr. 2003b. Dietary galactooligosaccharides affect ileal and total-tract nutrient digestibility, ileal and fecal bacterial concentrations, and ileal fermentive characteristics of growing pigs. J. Anim. Sci. 81:2535-2545.

Smits, C. H. M. and G. Annison. 1996. Non-starch polysaccharides in broiler nutrition - Towards a physiologically valid approach to their determination. World's Poult. Sci. J. 52:203-221.

Spring, P., C. Wenk, K. A. Dawson and K. E. Newman. 2000. The effects of dietary mannaoligosaccharides on cecal parameters and the concentrations of enteric bacteria in the ceca of salmonella-challenged broiler chicks. Poult. Sci. 79:205-211.

Turlington, W. H., G. L. Allee and J. L. Nelssen. 1989. Effects of protein and carbohydrate sources on digestibility and digesta flow rate in weaned pigs fed a high-fat, dry diet. J. Anim. Sci. 67:2333-2340.

Unväs-Moberg, K. 1992. The endocrine system of the gut during growth and reproduction, role of afferent and efferent mechanisms. Proc. Nutr. Soc. Aust. 17:167-176.

United States Department of Agriculture. 2009. USDA National Nutrient Database for Standard Reference Release 18. http://www.nal.usda.gov/fnic/foodcomp/Data/SR18/sr18.html

Vahouny, G. V., R. Tombes, M. M. Cassidy, D. Kritchevsky and L. L. Gallo. 1981. Dietary fibres. VI: Binding of fatty acids and monolein from mixed micelles containing bile salts and lecithin. Proc. Exp. Biol. Med. 166:12-16.

Veldman, A., W. A. G. Veen, D. Barug and P. A. van Paridon. 1993. Effect of α-galactosides and α-galactosidase in feed on ileal piglet digestive physiology. J. Anim. Physiol. Anim. Nutr. 69:57-65.

Wagner, D. D. and O. P. Thomas. 1978. Influence of diets containing rye or pectin on the intestinal flora of chicks. Poult. Sci. 57:971-975.

Yen, J. T., J. A. Nienaber, D. A. Hill and W. G. Pond. 1991. Potential contribution of absorbed volatile fatty acids to whole-animal energy requirement in conscious swine. J. Anim. Sci. 69:2001-2012.

Zhang, L. Y., D. F. Li, S. Y. Qiao, J. T. Wang, L. Bai, Z. Y. Wang and I. K. Han. 2001. The effect of soybean galactooligosaccharides on nutrient and energy digestibility and digesta transit time in weaning piglets. Asian-Aust. J. Anim. Sci. 14:1598-1604.