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CARBOHYDRATE AND FIBRE DIGESTION IN MONOGASTRIC ANIMALS

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SUMMARY

Non-starch carbohydrates (NSC) include non-starch polysaccharides (NSP) and oligosaccharides. A large portion of NSC is digested by the microflora of the large intestine in pigs, can contribute up to 50% of the dietary energy. But NSC digestibility is lower in the chicken because its capacity to obtain energy fermentation appears to be limited to an estimated amount of 24kJ per day. This is equivalent to only 2-3% of the dietary energy supply. The NSC comprise a large number of diverse molecules, which can affect the gut microflora of monogastric 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, particularly, 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 digestibility of NSP and discuss the relationship between digestibility and chemical structure, solubility, and quantity of NSP in pig and poultry diets. The digestibility of oligosaccharides and its effect on the gut microflora will be briefly discussed.

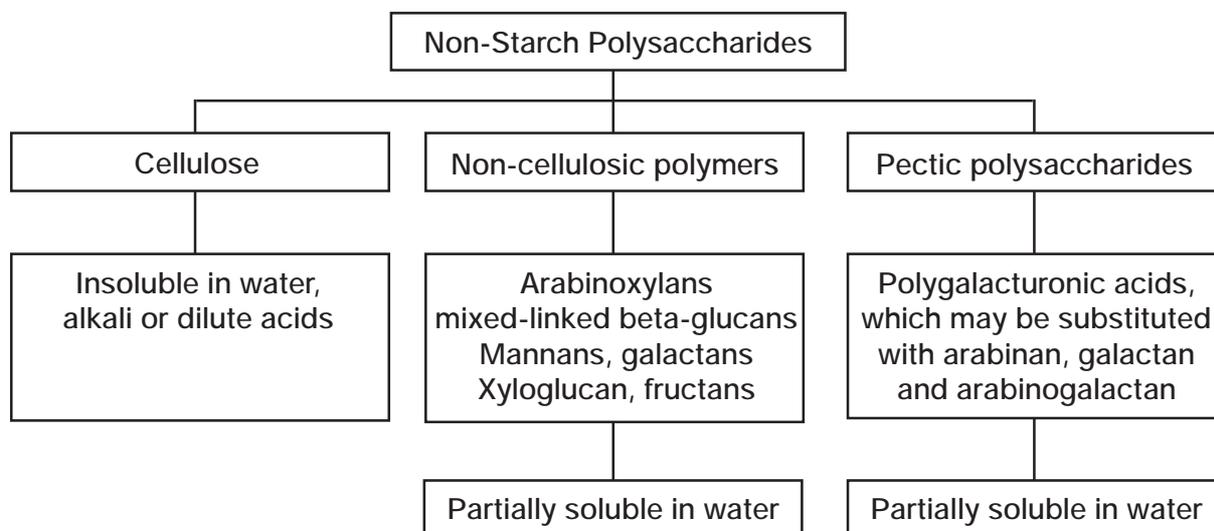
INTRODUCTION

Carbohydrates reaching the large intestine of pigs and poultry determine largely the type and the activity of the gut microflora (1). This, in turn, is related to the dietary carbohydrates provided to the animal and their digestibility. Traditionally, the interest in carbohydrates is

driven by two very contrasting yet interrelated fields; one is human nutrition and health work focusing primarily on the effect of dietary fibre on the maintenance of gut health and perhaps on lowering energy uptake; the other is animal nutritional research seeking to establish strategies to minimise the anti-nutritive activity of soluble NSP. Major research topics in animal nutrition have focused on the use of enzymes to improve the digestibility of NSP or on strategies to manipulate the fermentative characteristics of oligosaccharides for their prebiotic effects.

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 synthesised 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 feed include mono-, di-, oligo- and polysaccharides at various quantities and structures. Despite the general acceptance of the definition of dietary fibre (2) there are considerable discrepancies between different chemical analytical methods. In recent years, NSP are classified into three main groups as shown below, 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. What is important from an animal nutrition point of view is the understanding of the vastly different effects of soluble and insoluble NSP and oligosaccharides on nutrient digestion, and perhaps more importantly, on their fermentative characteristics and their secondary effects.

DIGESTIBILITY OF NSP AND FACTORS AFFECTING IT

The definition of “digestion” is the “disappearance of nutrients from the gut”. Digestion here refers to the disappearance of nutrients from the entire gastrointestinal tract as well as from specific parts of the tract, eg, ileal digestibility. Since pigs and poultry do not have endogenous enzymes capable of digesting NSP and certain oligosaccharides, the digestibility of these 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 large intestinal microflora in pigs, thus NSP digestibility in pigs can be as high as 93% (3). In poultry, however,

the digestibility of NSP is lower. Carré *et al.* (4) reported the digestibility values of NSP for adult birds range from 21.9% in a wheat based diet to 13% in a lupin based diet. 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 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% (5). NSP digestibility in poultry is lower. Pettersson and Åman (6) 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. In contrast, Carré *et al.* (7) suggested that in adult birds the degradation of soluble NSP

can be as high as 80-90%, whereas the insoluble polysaccharides remain undegraded. The total recovery of crude fibre (insoluble) in the excreta of chickens has led to the proposal to use crude fibre as a marker in nutritional studies (8). 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

Bacteria have preferences in their use of various carbohydrates. Thus, it is not difficult to postulate that carbohydrates with different chemical structures could be digested differently. Studies *in vitro* showed that the linkage types in sugars determines the extent of fermentation of different carbohydrates (9). In pigs, between 74-88% of the β -glucans were digested by the time the digesta reaches the ileum, whereas cellulose, arabinoxylans and uronic acids were totally undigested in the ileum (5). The whole tract digestibility of β -glucans was almost complete, whereas that of cellulose ranged from 34% in a diet containing whole wheat flour with the pericarp and testa to 60% in a diet consisted of whole wheat flour only. Pentosan digestibility followed a similar pattern as cellulose, but the values were slightly higher, whereas that of uronic acids was lower. Furthermore, the digestibility of these polysaccharides was similar regardless of whether they were from wheat or from oats. Another study (10), however, demonstrated that NSP from peas were more digestible than those from wheat in pigs (85% vs. 65%), with 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 0% to 18% only 17% to 52% in chickens (11). Table 1 compares the digestibility values of different sugars in

pea NSP by pigs and poultry.

The digestibility values of NSP, however, should not be generalised according to their sources and chemical structures. For example, the digestibility of cellulose from whole wheat flour was 60%, whereas cellulose from wheat flour plus pericarp and testa was only 24% (5); the digestibility of soluble citric pectin was 67.2% (7), whereas soluble pectic polysaccharides from lupins were only 7.9% in chickens (4). 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 (12).

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. But the difference in NSP digestibility also occurs within the same species. Thus, Bolton (13) showed pentosan digestibilities of 4% in two-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.* (7) 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.* (14) 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 their digestibility. Table 2 shows the data of Jørgensen *et al.* (11), 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. The effect of inclusion levels of NSP on their own digestibility is multifaceted. First, the anti-nutritive effect of NSP on nutrient digestion is negatively related to the dietary concentration of NSP (15); 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.

Table 2. Effect of dietary fibre source and level on digestibility (%) and metabolisability of feed by chickens (after Jørgensen *et al.*, 1996).

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 (16,15) and, to an extent, in pigs (17). Soluble NSP increase the viscosity of the digesta, leading to changes in the physiology and the ecosystem of the gut (18,19). 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 (20). Choct *et al.* (19) 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 pigs, these effects are often not so obvious, in particular the effect on gut viscosity. However, Pluske *et al.* (21) 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 (22). It appears 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 (23).

NSP can also bind nutrients and form complexes with digestive enzymes and some regulatory proteins in the gut. Angkanaporn

et al. (18) showed that soluble NSP markedly increased endogenous losses of amino acids in chickens. The gut secretes some 20 hormones or regulatory peptides (24), 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 in rats (25). In addition, certain NSP can bind bile salts, lipids and cholesterol (26) 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 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 (27) and are completely digested in the large intestine of the pig (4). Studies in poultry have shown ileal digestibility values of 52% and 62% for oligosaccharides present in canola meal and sunflower meal, respectively (28) and 86.7% and 99% in broilers and adult cockerels, respectively (7). Generally, the consequence of oligosaccharide digestion is an increase in the number of *Lactobacilli* and *Bifidobacterium*, and a decrease in *Clostridia* and *Enterobacteria* (29). Other oligomers, such as manan-oligosaccharides, are believed to physically bind to pathogens as well as

stimulate the immune system (30). 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.*, (31) 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 interferes with nutrient digestion or absorption. In poultry, the role of dietary oligosaccharides is not clear. 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 (30), 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 (32,33). 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 (1). However, Canibe *et al.* (34) were unable to detect any differences in the molar ratio of short chain fatty acids (SCFA) in different segments of the large intestine of pigs, despite the fact that individual sugars had vastly different rates of fermentation. 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 metabolised 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 (35). SCFA are believed to enhance sodium absorption, stimulate blood flow and regulate nutrient absorption (35). 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 (7). However, Jørgensen *et al.* (11) 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 (7). 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 (5). Feeding ungelatinised potato starch to pigs, Mason (36) 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 low in pigs (37).

CONCLUSION

The digestibility of NSP in pigs and poultry is affected by many factors including the physical and chemical 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) increasing efficiency of utilisation of fibrous materials in monogastrics, and (b) the maintenance and improvement, of animal health in the future years of antibiotic-free production systems.

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

Carbohydrate	Chickens ¹	Pigs ¹
NSP	0.12	0.84
Non-cellulosic NSP	-	1.02
Cellulose	-	0.54
Arabinose	0.13	1.04
Xylose	0.14	1.03
Mannose	0.00	0.72
Galactose	0.15	1.02
Glucose	0.18	0.71
Uronic acids	0.02	0.94

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

Table 2. Effect of dietary fibre source and level on digestibility (%) and metabolisability of feed by chickens (after Jørgensen *et al.*, 1996).

Fibre source	Control	<u>Pea Fibre</u>		Control	<u>Wheat Bran</u>		Control	<u>Oat Bran</u>	
Inclusion level	4.5%	18.7%	37.5%	4.5%	18.7%	37.5%	4.5%	18.7%	37.5%
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

REFERENCES

- Cummings JH. Short chain fatty acids in the human colon. *J Br Soc Gastroent* 1981;22:763-779.
- Trowell H, Southgate DAT, Wolever TMS, Leeds AR, Gassull MA, Jenkins DJA. Dietary fibre redefined. *Lancet* 1976;967.
- Stanogias G, Pearce GR. The digestion of fibre by pigs. The effects of amount and type of fibre on apparent digestibility, nitrogen balance and rate of passage. *Br J Nutr* 1985;53:513-30.
- Carré B, Derouet L, Leclercq B. 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* 1990;69:623-33.

5. Bach Knudsen KE, Hansen I. Gastrointestinal implications in pigs of wheat and oat fractions. Digestibility and bulking properties of polysaccharides and other major constituents. *Br J Nutr* 1991;65:217-232.
6. Pettersson D, Åman P. Enzyme supplementation of a poultry diet containing rye and wheat. *Br J Nutr* 1989;62:139-49.
7. Carré B, Gomez J, Chagneau AM. 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 Sc* 1995; 36:611-629.
8. Almquist HJ, Halloran HR. Crude fiber as a tracer in poultry nutrition studies. *Poult Sci* 1971;50:1233-1235.
9. Salvador V, Cherbut C, Barry JL, Bertrand D, Bonnet C, Delortlaval J. Sugar composition of dietary fibre and short chain fatty acid production during in vitro fermentation by human bacteria. *Br J Nutr* 1993;70:189-197.
10. Goodlad JS, Mathers JC. Digestion by pigs of non-starch polysaccharides in wheat and raw peas (*Pisum sativum*) fed in mixed diets. *Br J Nutr* 1991;65:259-70.
11. Jørgensen H, Zhao X, Bach-Knudsen KE, Eggum BO. 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* 1996;75:379-395.
12. Fincher GB, Stone BA. Cell walls and their components in cereal grain technology. St Paul, Minnesota: American Association of cereal chemists 1986. pp.207-295.
13. Bolton W. The digestibility of the carbohydrate complex by birds of different ages. *Agric Sci* 1955; 46:420-425.
14. Petersen ST, Wiseman J, Bedford MR. Effects of age and diet on the viscosity of intestinal contents in broiler chicks. *Br Poult Sci* 1999;40:364-70.
15. Choct M, Annison G. Anti-nutritive activity of wheat pentosans in broiler diets. *Br Poult Sci* 1990;31:811-821.
16. Antoniou T, Marquardt RR, Cansfield E. Isolation, Partial characterization, and antinutritional activity of a factor (pentosans) in rye grain. *J Agric Fd Chem* 1981;28:1240-1247.
17. van Barneveld RJ, Hughes RJ. The nutritive value of lupins for pigs and poultry. In: First Australian Lupin Technical Symposium; 1994; Perth, Western Australia; 1994. Pp.49-57.
18. Angkanaporn K, Choct M, Bryden WL, Annison EF, Annison G. Effects of wheat pentosans on endogenous amino acid losses in chickens. *J Sci Fd Agric* 1994;66:399-404.
19. Choct M, Hughes RJ, Wang J, Bedford MR, Morgan AJ, Annison G. Increased small intestinal fermentation is partly responsible for the anti-nutritive activity of non-starch polysaccharides in chickens. *Br Poult Sci* 1996;37:609-21.

20. Wagner DD, Thomas OP. Influence of diets containing rye or pectin on the intestinal flora of chicks. *Poult Sci* 1978;57:971-975.
21. Pluske JR, Durmic Z, Pethick DW, Mullan BP, Hampson DJ. Confirmation of the role of rapidly fermentable carbohydrates in the expression of swine dysentery in pigs after experimental infection. *J Nutr* 1998;128:1737-44.
22. Kaldhusdal M, Hofshagen M. Barley inclusion and avoparcin supplementation in broiler diets. 2. Clinical, pathological, and bacteriological findings in a mild form of necrotic enteritis. *Poult Sci* 1992;71:1145-53.
23. Sinlae M, Choct M. Xylanase supplementation affects the caecal of broilers. *Proc Aust Poult Sci Symp* 2000; 12: 209.
24. Unväs-Moberg K. The endocrine system of the gut during growth and reproduction, role of afferent and efferent mechanisms. *Proc Nutr Soc Aust* 1992;17: 167-176.
25. Ide T, Horii M, Kawashim k, Yamamoto T. Bile acid conjugation and hepatic taurine concentration in rats fed on pectin. *Br J Nutr* 1989;62:539-550.
26. Vahouny GV, Tombes R, Cassidy MM, Kritchevsky D, Gallo LL. Dietary fibres. VI: Binding of fatty acids and monolein from mixed micelles containing bile salts and lecithin. *Proc Exp BiolMed* 1981;166:12-16.
27. De Schrijver R. Dietary oligosaccharide supplements: effects on digestion in pigs. *The Proceedings of the 8th Symposium on Digestive Physiology in Pigs*. In Press. June, 2000, Uppsala, Sweden.
28. Kocher A, Choct M, Broz, J. The Effects of Enzyme Addition to Broiler Diets Containing High Levels of Canola or Sunflower Meal. *Poult Sci* 2000 (in press).
29. Nemcova R, Bomba A, Gancarcikova S, Herich R, Guba P. Study of the effect of Lactobacillus paracasei and fructooligosaccharides on the faecal microflora in weanling piglets. *Berl Munch Tierarztl Wochenschr* 1999;112:225-8.
30. Spring P, Wenk C, Dawson KA, Newman KE. The effects of dietary mannaoligosaccharides on cecal parameters and the concentrations of enteric bacteria in the ceca of salmonella-challenged broiler chicks. *Poult Sci* 2000;79:205-211.
31. van Barneveld, RJ, Olsen, LE, Choct M. Lupin oligosaccharides depress the apparent ileal digestion of amino acids by growing pigs. In: *Manipulating Pig Production*. Cranwell, P.D. (ed). P.230.
32. Saini, H.S. Legume seed oligosaccharides. *Proc Rec Adv Res Antinutrive Fact Legume Seed*, Wageningen 1989; pp329-341.
33. Coon CN, Leske KL, Akavanichan O, Cheng TK. Effect of Oligosaccharide-free soybean meal on true metabolizable energy and fiber digestion in adult roosters. *Poult Sci* 1990;69:787-793.

34. Canibe N, Bach-Knudsen KE, Eggum BO. Apparent digestibility of non-starch polysaccharides and short chain fatty acids production in the large intestine of pigs fed dried or toasted peas. *Acta Agric Scand (Animal Science)* 1997;47:106-116.
35. Sakata T. 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* 1987;58:95-103.
36. Mason VC. Role of large intestine in the process of digestion and absorption in the pig. In: *Current concept of digestion and absorption in pigs*. Reading: Hannah Research Institute (Partridge IG, Low, AG eds); 1980. pp112-129.
37. Yen JT, Nienaber JA, Hill DA, Pond WG. Potential contribution of absorbed volatile fatty acids to whole-animal energy requirement in conscious swine. *J Anim Sci* 1991; 69:2001-2012.