1 General Introduction: A review of interactions between dietary fiber and the gastrointestinal microbiota and their consequences on intestinal phosphorus metabolism in growing pigs

1.1 Abstract

Dietary fiber is an inevitable component in pig diets. In non-ruminants, it may influence many physiological processes in the gastrointestinal tract (GIT) such as transit time as well as nutrient digestion and absorption. Moreover, dietary fiber is also the main substrate of intestinal bacteria. The bacterial community structure is largely susceptible to changes in the fiber content of pig's diet. Indeed, bacterial composition in the lower GIT will adapt to the supply of high levels of dietary fiber by increased growth of bacteria with cellulolytic, pectinolytic and hemicellulolytic activities such as *Ruminococcus* spp., *Bacteroides* spp. and *Clostridium* spp. Furthermore, there is growing evidence for growth promotion of beneficial bacteria, such as lactobacilli and bifidobacteria, by certain types of dietary fiber in the small intestine of pigs. Studies in rats have shown that both phosphorus (P) and calcium (Ca) play an important role in the fermentative activity and growth of the intestinal microbiota. This can be attributed to the significance of P for the bacterial cell metabolism and to the buffering functions of Ca-phosphate in intestinal digesta. Moreover, under P deficient conditions, ruminal NDF degradation as well as VFA and bacterial ATP production are reduced. Similar studies in pigs are scarce but there is some evidence that dietary fiber may influence the ileal and fecal P digestibility as well as P disappearance in the large intestine (LI), probably due to microbial P requirement for fermentation. On the other hand, fermentation of dietary fiber may improve the availability of minerals such as P and Ca which can be subsequently absorbed and/or utilized by the microbiota of the pig's LI.

(Key Words: Dietary Fiber, Bacteria, Fermentation, Phosphorus, Pigs)

1.2 Introduction

Dietary fiber is an inevitable component in diets of pigs as it is present in a variety of feedstuffs of plant origin including cereal grains and their by-products, grain legumes but also protein supplements produced from various oilseeds. In recent years, there is growing interest to increase the utilization of by-products originating from the production of bioethanol, such as distiller's dried grains, wheat-millrun and soy hulls, in the nutrition of ruminants and non-ruminants as well. Both, dry milling and distilling processes, remove most of the starch fraction from cereal grains, accumulating dietary fiber but also protein and minerals in the residuals (e.g. Spiehs et al., 2002; Huang et al., 2003; Slominski et al., 2004).

The dietary fiber fraction of these by-products has received growing attention as some fibrous compounds have shown characteristics of prebiotics (Shi et al., 2001; Konstantinov et al., 2004; Yin et al., 2004; Shim et al., 2007), while others were rather associated with the growth of potential pathogenic bacteria (McDonald et al., 2001). Recently, potential interactions between fibrous feedstuffs and the microbial ecology of the host animal have been described (Konstantinov et al., 2004; Hill et al., 2005; Owusu-Asiedu et al., 2006). It is well accepted that dietary fiber may affect digestive functions in the small intestine with consequences on digestion and absorption of nutrients (e.g. Bach Knudsen, 2001; Grieshop et al., 2001; Wenk, 2001; Montagne et al., 2003), however, there is little information on the consequences of microbial fermentation in the gastrointestinal tract (GIT) of pigs on mineral absorption and metabolism as it has been previously described for rodents (Demigné et al., 1989, Levrat et al., 1991).

In pigs, dietary fiber is the main substrate for bacteria in the GIT, and inclusion of dietary fiber has shown to promote bacterial growth, resulting in a higher fecal excretion of amino acids, lipids and minerals such as phosphorus (P) and calcium (Ca) of bacterial origin (e.g. Mosenthin et al., 1994; Bovee-Oudenhoven et al., 1997b; Wang et al., 2006). During microbial breakdown of complex structures of dietary fiber several nutrients such as amino acids and P may be released from bindings with fiber components (Larsen and Sandström, 1993). These nutrients may be absorbed and/or utilized by the microbiota of the pig's large intestine (LI). Thus, fermentation of dietary fiber may affect the intestinal availability of P and other minerals in pigs. On the other hand, studies in ruminants revealed that bacterial fermentation intensity in the rumen is dependent on the P supply of dietary or salivary origin. In fact, according to in *vitro* studies, bacterial degradation of cellulose and pectin is largely reduced under P deficient conditions (Wider, 2005).

In this review, the main focus will be on potential interactions between dietary fiber and the gastrointestinal microbiota and their effects on the intestinal P metabolism in growing pigs. Where applicable, data from other species are included to complete the discussion.

1.3 Dietary fiber

1.3.1 Definition, classification and microbial fermentability

Dietary fiber is usually defined as the sum of plant polysaccharides and lignin that are not hydrolyzed by endogenous enzymes of the mammalian digestive system (Theander et al., 1994). According to this nutritional concept, the term dietary fiber refers to those polysaccharides that escape enzymatic digestion of the host animal including resistant starch, soluble and insoluble fiber as well as lignin. Dietary fiber represents the main constituent of the plant cell wall which contains a heterogeneous group of polysaccharides, such as cellulose, pectins, β-glucans, β-fructans, pentosans and xylans, differing considerably in terms of type, number and order of monosaccharides, the linkage between monosaccharides and the presence of side chains (Fan and Squires, 2003). These non-starch polysaccharides (NSP) can be hydrolyzed by microorganisms only, with subsequent production of volatile fatty acids (VFA) and various gases, i.e. CO_2, NH_3, CH_4, and H_2O (Jørgensen et al., 1996). There is general agreement that the cecum and proximal colon are the main sites of microbial fermentation in the pig. However, there is already substantial microbial activity in the distal part of the small intestine (Leser et al., 2002), so that fermentation of fibrous feed ingredients is assumed to be not restricted to the LI only.

The type and origin of dietary fiber greatly influences the site and degree to which it can be degraded (Table 1), mainly depending on the degree of lignification, solubility and structure of the NSP (Bach Knudsen, 2001). In general, both soluble and insoluble dietary fiber can be degraded by intestinal bacteria, but soluble fiber is more easily, rapidly and completely fermented than insoluble (Bach Knudsen and Hansen, 1991). The higher fermentability of soluble fiber (e.g. pectins, gums, β-glucans) can be attributed to its higher water-holding capacity allowing bacteria to easily penetrate the matrix and start degradation. Thus, with diets containing high soluble fiber levels, the microbial activity is generally increased (Bach Knudsen et al., 1991). By contrast, insoluble fiber (e.g. cellulose) cannot be penetrated easily by bacteria which limits its microbial breakdown in comparison to the soluble fraction (Schneeman, 1987). Hence, degradation of insoluble dietary fiber takes longer, occurring along the full length of the LI. Lignin is neither digestible for enzymes in the small intestine nor fermentable for intestinal bacteria (Graham et al., 1986), but it influences the fermentability of other fibrous components of the diet. As cellulose and lignin are closely associated within plant cell walls, cellulose becomes less accessible for microbial attack which depresses the rate and degree of fermentation in the LI.

Table 1. Characterization of fiber components based on fermentability (adapted from Tungland and Meyer, 2002).

Characteristic	Fibre component	Main source
Partial or low fermented	Cellulose	Plants (e.g. sugar beet, various brans, vegetables)
	Hemicellulose	Cereal grains
	Lignin	Woody plants
	Resistant starches	Corn, potatoes, grains, bananas, legumes
Well fermented	β-Glucans	Grains (oat, barley, rye)
	Pectins	Fruits, vegetables, legumes, sugar beet, potatoes
	Gums	Leguminous seed plants (guar, locust bean), seaweed extracts (carrageenan, alginates), plant extracts (gum acacia, gum karaya, gum tragacanth)
	Inulin	Chicory, Jerusalem artichoke, wheat
	Oligosaccharides	Fructooligosaccharides, galactooligosaccharides, lactulose

1.3.2 Physiological aspects of dietary fiber

The nutritional significance of dietary fiber and its role in digestive physiology of pigs has been described in detail in previous reviews (e.g. Dierick et al., 1989, Bach Knudsen, 2001; Grieshop et al., 2001; Wenk, 2001; Montagne et al., 2003). Diets high in fiber usually contain a lower energy density than low-fiber diets; thus decreasing growth rate and feed conversion ratio in growing pigs. Particularly, the soluble fiber fraction may interfere with the digestion of fibrous and non-fibrous feed components in the small intestine (Graham et al., 1986). Soluble fiber increases the volume and bulk of the small intestinal contents which is related to the water-holding capacity and viscosity of soluble fiber. However, increased viscosity of digesta results in lower transit time in the small intestine due to reduced intestinal contractions (Cherbut et al., 1990). This leads to a reduced mixing of dietary components with endogenous digestive enzymes, resulting eventually in lower nutrient digestibilities. Additional effects of soluble fiber in the GIT include increased total tract transit time, delay of gastric emptying, delay of glucose absorption, increase in salivary, pancreatic and bile secretion (Dierick et al., 1989), whereas insoluble fiber decreases the transit time in the total tract, supports water holding capacity and stimulates fecal bulking in non-ruminant animals (Montagne et al., 2003).

Both soluble and insoluble fiber increase intestinal epithelial cell proliferation rate. For example, growing pigs fed with 10% wheat straw responded with 33 and 43% increase in jejunal and colonic cell proliferation rate, respectively. Moreover, there was an increase in cell death of jejunal and colonic cells by 65 and 59%, respectively, indicating that dietary fiber may stimulate intestinal cell turnover rate (Jin et al., 1994). As a result, nutrient digestion and absorption may be depressed. Recently, Hedemann et al. (2006) reported that villi and crypts of the small intestine were shorter in weaned pigs fed diets supplemented with pectin, while the villous height/crypt depth ratio was unaltered. Moreover, pectin significantly decreased the area of mucins in the crypts of the small intestine, indicating that pigs fed pectin may be more susceptible to pathogenic bacteria. In contrast, feeding of insoluble fiber diets improved gut morphology by increasing villi length and stimulating mucosal enzyme activity in comparison to piglets fed a diet supplemented with pectin as soluble source of fiber. In addition, it can be derived from the chemical composition of the mucin fraction that piglets fed diets high in insoluble fiber seem to be better protected against pathogenic bacteria than pigs fed diets high in soluble fiber (Hedemann et al. 2006).

Feeding of a high-fiber diet causes earlier satiety than a low-fiber diet due to gastric signals in response to the elongation of the stomach wall. This earlier satiety is of particular interest in pregnant sows. In fattening pigs, a diet low in fiber would be preferred to reach maximum intake of energy and nutrients (Wenk, 2001).

During microbial fermentation of fiber VFA, mainly acetate, propionate and butyrate, are produced to be subsequently absorbed and metabolized by the pig. One of the most important features of VFA is their trophic effect on the intestinal epithelium. Acetic, propionic and butyric acids are taken up by the colonic mucosa, though butyric acid appears to be the preferred energy source for the colonocytes (Roediger, 1980). After absorption into the portal blood system, VFA play an important role in the intermediary metabolism of the animal. Volatile fatty acids absorbed from the LI may provide up to 30% of the energy requirement for maintenance in growing pigs (Yen et al., 1991). Moreover, they are involved in the regulation of systemic effects, such as changes in glycemia, lipidemia, uremia and overall nitrogen balance (Tungland and Meyer, 2002). However, high production of VFA in the hindgut has been associated with an increased mucin secretion in the LI (Sakata and Setoyama, 1995). Moreover, in a recent study of Pié et al. (2007) a correlation between VFA and proinflamatory cytokines was reported, indicating that the regulation of cytokines may be linked with branched-chain fatty acids which originate from protein fermentation.

1.3.3 General description of interactions between dietary fiber and minerals

The reported effects of dietary fiber on digestion, absorption and utilization of minerals in pigs are not consistent. It has been generally accepted that the main absorption of minerals occurs in the small intestine. However, according to a study in rats, some highly fermentable dietary fibers, e.g. inulin, pectin and amylomaize starch, may shift the absorption of minerals, such as Ca and P, from the small intestine to the LI (Demigné et al., 1989). Lower pH in digesta of the LI as a result of increased VFA production due to fiber fermentation may improve the solubility of minerals, such as Ca-phosphate, thereby increasing their diffusive absorption via the paracellular route in the LI (Rémésy et al., 1993). In general, the binding of minerals by dietary fiber is related to its origin, and mediated through several mechanisms such as hydration, gelation, physical effects, ion binding capacity and bacterial activity (Van Soest, 1984). Components of dietary fiber and lignin that interact with minerals include the carboxyl group of uronic acids (i.e. hemicelluloses and pectin), carboxyl and hydroxyl groups of phenolic compounds (i.e. lignin), and the surface hydroxyl of cellulose (Kornegay and Moore, 1986). During microbial breakdown of these complex structures, several nutrients such as amino acids and P may be released from bindings with fiber components (Larsen and Sandström, 1993). These nutrients may be absorbed and/or utilized by the microflora of the pig's LI as it has been documented for bacterial nitrogen assimilation (Mosenthin et al., 1992).

1.4 Microbiota

1.4.1 Commensal microbiota in the GIT of pigs

The GIT of pigs harbors a large and diverse population of aerobic, facultative anaerobic and strictly anaerobic bacterial species. The number and composition of the bacteria in the different segments of the GIT vary considerably (Jensen and Jørgensen, 1994; Leser et al., 2002). Though the cecum and colon represent the main sites of bacterial activity in pigs, the proximal segments are also colonized by a complex indigenous microbiota (Savage, 1986; Jensen, 2001). The epithelium of the stomach is predominantly colonized by lactobacilli, but also by bifidobacteria, streptococci, clostridia