



Review article, Non-ruminant

Dietary fiber and protein fermentation in the intestine of swine and their interactive effects on gut health and on the environment: A review



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ARTICLE INFO

Article history:

Received 23 August 2015

Received in revised form

30 November 2015

Accepted 1 December 2015

Keywords:

Bacterial protein synthesis

Crude protein

Dietary fiber

Gut health

Nitrogen excretion

Pig

ABSTRACT

Fermentation of both dietary fiber (DF) and protein in the pig intestine is a matter of interest because of their potential beneficial or harmful effects on gut health and on the environment. This paper reviews some of the relevant information available on DF and protein fermentation and their interactive effects on the gut environment of pigs and its contribution to emission of nitrogenous gases and odor from pig manure and piggeries. The fermentation of protein and the associated production of metabolic compounds are discussed in relation to DF fermentation, their impact on gut health, bacterial protein synthesis and nitrogen (N) excretion. Some nutritional strategies to reduce protein fermentation in the gut such as the reduction of the amount of crude protein (CP) in the diet and/or the inclusion of fermentable DF are also presented. Also, to cope with the negative impact of intensive pig production on the environment, different nutritional approaches such as reducing N excretion by lowering CP intake, shifting the N excretion pathway from urine to feces and lowering the pH of manure by lowering the pH of urine and feces have been reviewed. Overall, inclusion of DF and reduction of CP in pig diets seems to be an effective nutritional strategy that may counteract the negative effects of protein fermentation in the pig gut by reducing ammonia concentration, shifting N excretion pathways in the gut and minimizing the negative impact of intensive pig production on the environment.

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Abbreviations: AA, amino acid; BCFA, branched chain fatty acids; CHO, carbohydrates; CP, crude protein; DF, dietary fiber; GIT, gastrointestinal tract; N, nitrogen; NSP, non-starch polysaccharides; PWD, post-weaning diarrhea; SBP, sugar beet pulp; SCFA, short chain fatty acid; RS, resistant starch; WBC, water binding capacity.

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<http://dx.doi.org/10.1016/j.anifeedsci.2015.12.002>

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1. Introduction

The modern pig production systems are criticized for their negative impact on the environment due to nitrogenous gases excretion and odor emission from barns. Nitrogenous gases emitted from piggeries are also found to have a negative impact on the health of barn workers as well as the pigs themselves. Even low levels of ammonia (25 ppm) in pig barns induce nasal irritation and depression of growth in pigs (Urbain et al., 1994), while air quality in the confinement of a pig facility can cause acute respiratory responses in humans (Zhang et al., 1998). Thus, measures to mitigate nitrogenous gases excretion and odor emission from pig facilities need attention. To deal with these challenges, several alternative approaches have been forwarded, including nutritional manipulation in the swine feeding program. The effectiveness of these nutritional strategies in reducing nitrogenous gases and odor emission from piggeries and improving gut health and bacterial protein synthesis are based on the effects of diet composition, especially dietary fiber (DF) and protein, on nutrient digestibility and metabolism, and on the fermentation rates in the large intestine.

Ammonia emission from pig manure originates mainly from urea in the urine. Nitrogen (N) in the feces comprises undigested dietary N and endogenous N, mainly as amino acids (AA), and microbial N, partly present in nucleic acids. One approach to reducing ammonia emission is through dietary manipulation. In this respect, DF plays an important role in reducing ammonia emission (Aarnink and Verstegen, 2007) and improving gut health (Williams et al., 2001; Montagne et al., 2003). Dietary fiber is fermented by gut bacteria, producing short chain fatty acids (SCFA, Jha et al., 2010; Jha and Leterme, 2012), which in turn, supports the growth of beneficial bacteria and suppress harmful bacteria in the gut (Pieper et al., 2008). The gut bacteria induce a shift of N excretion from urea in urine to feces (Zervas and Zijlstra, 2002; Bindelle et al., 2009). On the other hand, the urea concentration in manure is highly dependent on protein nutrition and can be altered by changing dietary protein content. A reduction in dietary crude protein (CP), while balancing for AA, decreases the urinary and total N excretion (Zervas and Zijlstra, 2002) without affecting the performance and carcass quality of growing pigs (Jha et al., 2013; Morales et al., 2015). Moreover, unpleasant odor from stored pig manure results largely from compounds like sulfurous compounds, indolic and phenolic compounds, volatile fatty acids, and ammonia and volatile amines, which are the products of incomplete anaerobic digestion of protein and carbohydrate (CHO). Odors are mainly produced by the microbial conversion of feed components in the large intestine of pigs and after excretion by microbial conversion of excreta under anaerobic conditions in manure. It is generally accepted that odorous compounds produced by protein fermentation in the gastrointestinal tract (GIT) and in manure have a higher offensive sensory response and a higher magnitude of odor sensation than straight-chain volatile fatty acids produced from fermentable CHO. Therefore, CP is the first dietary component that should be altered to minimize odor.

To address these concerns and give a better understanding of interactive effects of DF and protein fermentation and their effects on gut health and on the environment, this paper has reviewed different aspects of DF and CP in swine nutrition. More specifically, DF and protein fermentation, and their pathways and end metabolic products are first briefly reviewed. Also, the nutritional approaches to reduce protein fermentation, the relation between CHO [both fiber and resistant starch, (RS)] and protein fermentation and its effects on gut health, bacterial protein synthesis as well as odor emission from pig manure have been highlighted. Finally, the impact on nitrogenous gases emission from piggeries and the strategies to reduce N excretion and odor emission are also assessed.

2. Physiology and biochemistry of carbohydrates and protein in pigs

The processes in the GIT of pigs are of great importance in understanding the influence of nutrition on metabolism. Microorganisms come in contact with undigested material or endogenous substrate to a considerable degree mainly in the lower parts of GIT, from the terminal ileum to the rectum. The GIT of the pigs can be divided broadly into three different compartments: stomach, small intestine and large intestine. The digestion start in the stomach, which has a lower pH, and a limited amount of microbial activity, may occur in the small intestine when the pig ingests high amounts of feed. Most of the available nutrients (CHO, protein, fat, minerals and vitamins) are absorbed in the small intestine. In the large intestine, undigested feed components (mainly DF, lipids and insoluble protein) and endogenous secretions are fermented by microorganisms. In this part, only SCFA and some vitamins can be absorbed, which contribute to the nutrient supply of the pigs.

Digestion is the process of chemical breakdown that allows absorption of nutrients by enzymes secreted into the lumen of the GIT (Tso and Crissinger, 2000). The enzymes are secreted by glandular cells in the mouth, chief cells in the stomach, exocrine cells in the pancreas, and brush-border intestinal glands (Johnson, 2001). Mammalian enzymes may hydrolyze

a limited number of linkages such as $\alpha(1-4)$ in starch and maltooligosaccharides, $\alpha(1-6)$ in starch and dextrans, $\beta(1-2)$ in sucrose, and $\beta(1-4)$ in lactose. Other linkages (e.g., $\beta(1-4)$ in cellulose) are not hydrolyzed by endogenous mammalian enzymes and need to be hydrolyzed by bacterial enzymes in the process of fermentation (Tso and Crissinger, 2000).

The fermentation is an energy-conservation process, in which electrons from a few reactions such as redox, hydrolysis, phosphorylation or lyses are transferred to part of the substrate. From this process, energy is derived, leading to the production of ATP, which is used for bacterial basal and growth metabolism. During fermentation of DF in the pig intestine, the microbes start breaking down polysaccharides into smaller polysaccharides or the constituent monosaccharides; but in these processes, the substrate is only partially oxidized and only a small amount of energy is extracted for microbial growth. The monomers are absorbed into the microbial cell and channeled into the pathways of central metabolism. The majority of anaerobic microorganisms of the large intestine, except *bifidobacteria*, use the glycogenesis pathway to degrade glucose to pyruvate via glucose-6-phosphate, which is later oxidized to acetate, propionate or butyrate. Pentose and pectin are first metabolized by the pentose phosphate pathway (Macfarlane and Macfarlane, 2003) starting from the pentose to fructose-6-phosphate and glyceraldehyde-3-phosphate via xylulose-5-phosphate. As a result, SCFA (acetate, propionate and butyrate) and gases (CO_2 , H_2 and CH_4) are the main end products of intestinal DF fermentation. Other metabolites such as lactate, ethanol and succinate are also formed by different types of bacteria (Drochner et al., 2004). With the possible exceptions of ethanol, these products do not accumulate in a healthy gut, because they serve as substrate and electron donors for cross-feeding bacteria and are further converted into SCFA (Macfarlane and Gibson, 1995). Further details on fiber fermentation and its effect on the pig intestinal physiology and health can be found in recent review papers (Aumiller et al., 2015; Jha and Berrocoso, 2015).

Proteins available to bacteria for fermentation are dietary proteins that escape digestion in the small intestine, along with some proteins of endogenous origin (Macfarlane et al., 1992). The end products of protein fermentation are also different from those of DF fermentation. The proteolytic fermentation results in the production of SCFA, especially branched chain fatty acids (BCFA, mainly iso-butyrate, valerate and iso-valerate). These BCFAs are formed by the metabolism of branched chain AA such as valine, leucine and isoleucine. Among the fermented proteins, about 30% are converted to SCFA, of which BCFA constitute between 16 and 23%, depending on the substrate type (Macfarlane et al., 1992; Cone et al., 2005). In addition, some potentially toxic metabolites like ammonia and amines (Cone et al., 2005) as well as malodorous compounds such as skatole and indole (Jensen et al., 1995) are also produced. The indolic, phenolic and sulfurous compounds in manure are produced from protein and come from three main pathways (Le et al., 2008). First, protein is partly fermented in the large intestine and the bacterial proteolysis induces the production of BCFA (mainly iso-butyrate, valerate, and iso-valerate), malodorous compounds, amines and ammonia originating from the deamination of AA and indolic and phenolic and sulfurous compounds. These compounds are then transferred to the liver, where these are detoxified to glucuronides and then excreted via urine. Second, unfermented protein in the feces can be fermented in the manure, and indolic, phenolic and sulfurous compounds are produced. Third, a small proportion of indolic, phenolic and sulfurous compounds are excreted directly via feces. In addition, sulfurous compounds in the manure can be produced from sulfates excreted via urine, which mainly originate from excreta of excess sulfur containing AA absorbed in the small intestine of the pig.

3. Effects of modulating the protein level in diets

Lowering the amount of CP in the diet (Htoo et al., 2007) is found to be effective in reducing protein fermentation in the gut. The fermentation of undigested dietary protein and proteins of endogenous origin entering the large intestine yields putatively toxic metabolites that can impair epithelial integrity and promote enteric disorder such as the incidence of post-weaning diarrhea (PWD). Most of the published work on piglets (Nollet et al., 1999; Htoo et al., 2007; Wellock et al., 2008) shows that feeding a low-protein diet after weaning decreased intestinal flow of N and protein fermentation indices in the GIT and that this is linked to a reduction in the incidence of PWD. In this respect, Heo et al. (2010) compared a high-protein diet that contained 240 g/kg CP with a low protein diet with 190 g/kg of CP and reported an increased N flow at the terminal ileum which caused a higher amount of N to be available for bacterial fermentation in the distal gut of the piglets at 35 d of age. Also, increases in microbial protein in the colon should be expected when a sufficient amount of fermentable CHO are present. Also, Htoo et al. (2007) reported that the protein content of pig starter diets can be reduced safely by about 200 g/kg while balancing with limiting AA according to ideal protein ratios, which will also reduce the production of potentially harmful microbial metabolites in the caecum.

3.1. Changes in the gut microbiota and fermentation end products that alter the gut health

Dietary and endogenous proteins are utilized in the GIT through microbial fermentation. Bacterial AA metabolism occurs via oxidative and reductive reactions including deamination and decarboxylation. A large variety of bacterial species such as *Escherichia coli*, *Klebsiella* spp., *Campylobacter* spp., *Streptococcus* spp., *Clostridium perfringens*, *Clostridium difficile* and *Bacteroides fragilis* have been reported as dominant protein fermenters. Bacterial AA utilization also contributes to the formation of SCFA in the GIT. Protein fermentation products such as ammonia can interfere with the oxidative metabolism of SCFA in colonocytes, likely inducing energy deficiency in the cell (Blachier et al., 2007). Decarboxylation of AA yields several biogenic amines such as histamine that can induce chloride secretion and diarrhea in the colon of pigs (Kröger et al., 2013).

Among the several factors responsible for diarrhea in pigs, enterotoxigenic strains of *E. coli* are major ones (Williams et al., 2001). The *E. coli* colonize the small intestine under multifactorial conditions and a high level of dietary protein predisposes to the condition. Heo et al. (2009) found that pigs challenged with *E. coli* had lower growth rate and decreased gain-to-feed ratio compared with non-challenged pigs from 28 to 70 d of age. However, there was a marked reduction in the incidence of diarrhea after infection with β -hemolytic *E. coli* and feeding a low-protein diet for 7 or 14 d after weaning. It suggests that protein fermentation selectively affects the microbiota in the gut and can influence the pig's health condition.

Increase in protein fermentation leads to increased ammonia and amine concentration in the colon (Macfarlane et al., 1992), whereas these compounds are found only in small amounts in a healthy colon. The increased ammonia concentration in the gut can negatively affect the development of the intestinal mucosa and villus height (Nousiainen, 1991; Davila et al., 2013), which in turn adversely affect the digestion and absorption processes in the intestine. Ammonia generated in the colon readily passes across the gut wall; thereby gaining access to other tissues of the body, which can be detrimental for the host's health (Cone et al., 2005; Bikker et al., 2006).

3.2. Changes in the N emission in feces or urine and gases

The main nutrients of environmental concern are N, phosphorus and heavy metals, while the main gaseous losses are ammonia and methane (Aarnink and Verstegen, 2007; Beccacia et al., 2015). Most of the ammonia in pig manure originates from the breakdown of urea while a small amount comes from the breakdown of protein in feces (Aarnink et al., 1993). The activity of urease determines the rate at which urea is converted into ammonia. Urease is present only in feces, not in urine. Thus, the conversion of urea to ammonia only starts when urine mixes with feces or comes in contact with soiled floors (Aarnink et al., 1997). At the manure storage pit, protein breakdown from manure is a slow process, which might take weeks or even longer. Is it assumed that almost half of the N excreted by urine and feces can emit during storage of the manure inside the pigs' house and during surface application of the manure. On the other hand, the degradation of urea to ammonia and carbon dioxide can occur only in few hours, but the process is affected by several factors like ammonia concentration, pH, temperature, air velocity and emitting surface area (Aarnink and Verstegen, 2007).

To deal with the negative impact of intensive pig production on the environment, nutritional approaches have been suggested, such as reducing N excretion by lowering CP intake, shifting N excretion from urea in urine to protein in feces, and lowering the pH of manure by lowering the pH of urine and feces (Aarnink and Verstegen, 2007). The concentration of urea in urine and the pH of feces and urine are important characteristics of excreta to determine ammonia emission from a pig facility. The urea concentration of urine highly depends on the protein level of the diet (Jongbloed, 2008). Manipulating the protein content can thus change it. In practice, dietary protein levels generally exceed the pig's requirements and are thus not totally utilized by the pigs. Several studies have shown that the protein content of diet can be reduced by 3–4% without any negative effect on growing pig performance (Canh et al., 1998b; Ball and Möhn, 2003; Jha et al., 2013). Some portions of proteins, for example ~25% of protein in a typical corn-soybean meal based diet, cannot be utilized, due to unbalanced AA. These overabundant or unbalanced proteins/AA are broken down to N and excreted as urea in urine. Thus, supplying balanced protein/AA contents and matching the closest possible amount to the requirement of the pig can contribute to reduce N excretion.

Using a mathematical model, Aarnink et al. (1993) estimated that the reduction of CP by 10 g/kg in a diet can reduce ammonium N in manure by 9%, which is almost double that of the first documented report on the role of reduced CP level on reducing N excretion (Lenis, 1989). Confirming the model estimate, Mohn and Susenbeth (1995) found that a reduction of 200 g/kg in dietary protein can reduce N excretion by up to 35%, if the low-protein diets offer adequate AA concentration. Thereafter, several attempts were made to explore the in-depth relationship of CP content in diet and N excretion. Canh et al. (1998b), in comparing three levels of protein content (165, 145 and 125 g/kg), found that every 10 g/kg reduction in CP in diet reduced ammonia content of the manure by 10% and ammonia emission by 10–12%. The effect of CP and the ammonia reduction ratio was a little higher in this study than in studies reported by other researchers, which might be explained by the fact that the pH of the manure had been lowered. Similarly, Sutton et al. (1999) reported a 28% reduction of ammonium and total N concentration in manure when CP was reduced by 30 g/kg (from 130 to 100 g/kg) in corn-soybean meal-based diets supplemented with lysine, tryptophan, threonine and methionine in growing pigs. Such reduction in N can be expected from sows as well (Ball and Möhn, 2003). Reviewing several studies, Kerr (1995) noted that there is wide variation in the effect of reducing the CP content with AA supplementation on N excretion, ranging from 3.2 to 62% (average around 8.4%), which depends on the size of the pig, level of dietary CP reduction, and initial CP level in the control diet.

3.3. Changes in odorous compounds

The reduction of dietary CP in pig's diets and supplemental synthetic AA decreases manure concentrations of odorous compounds and maintains animal performance. In this respect, Hobbs et al. (1996) compared a control diet with 200 g/kg CP with a diet that contained with 140 g/kg CP and reported that reducing dietary CP but providing essential AA in an ideal protein ratio decreased the N excreted by the pig and the odorants produced in the resultant slurries. Similarly, Leek et al. (2007) reported a quadratic effect between odor emission rate and the level of dietary CP (130, 160, 190 and 210 g/kg). The authors observed that the reduction in odor rate between diets with 210 and 160 g/kg of CP decreased odorous products arising from the fermentation of protein. However, the odor rate increased as the concentration of dietary CP was reduced

below 160 g/kg but remained lower than the odor rate of diets containing 190 or 210 g/kg of CP. These results suggest that factors other than the CP level of the diet, such as protein and starch fermentation, as well as DF sources used, might modify the production of odorants. In this respect, [Miller and Varel \(2003\)](#) reported that fermentation of starch in manure also contributes to the production of odorous compounds and conclude that achieving an optimum dietary balance between CP and starch may minimize odor emissions.

4. Effects of modulating levels and sources of dietary fiber as a strategy to interact with protein synthesis and fermentation

Dietary fiber is associated with impaired nutrient utilization and reduced net energy values. However, a minimum of DF has to be included in the diet to maintain normal physiological functions in the GIT ([Wenk, 2001](#)). In addition, the inclusion of DF in swine diets could improve gut health by different mechanisms as a result of its fermentation activity and responses. Moreover, the negative impacts of DF are determined by the fiber properties and may differ considerably between fiber sources. In fact, the physiological properties of NSP and their fermentability are poorly predictable from the monomeric composition and are more related to their physico-chemical characteristics like solubility, viscosity, physical structure and water binding capacity (WBC; [Asp, 1996](#)).

The physico-chemical characteristics of DF, mainly solubility and WBC, and the level of neutral detergent fiber in the diet have greater influence on the fermentation of DF. Soluble fiber sources are fermented at a faster rate, mainly at the proximal colon, whereas insoluble fiber sources have a higher WBC and greater degree of swelling ([Oakenfull, 2001](#)) and are fermented at the distal colon ([Cho et al., 1997](#)). However, [Gutierrez et al. \(2013\)](#) reported that ileal fermentation of DF was not affected by the level of insoluble fraction of the fiber or the amount of substrate present. In contrast, [Graham et al. \(1986\)](#) reported that the amount of soluble DF affect the degree of fermentation before the end of the ileum, and the fermentation of DF in the small intestine is directly related to the proportion of soluble DF. Soluble DF sources are quickly fermented in the proximal colon, and microbial biomass can itself be fermented in the distal colon, places where the microorganisms present become available as fermentable protein. Therefore, a strategy to prolong fermentation of CHO to distal colon would be important. Insoluble DF sources are slowly fermented and maintain the fermentation throughout the large intestine, reducing the occurrence of proteolytic fermentation in the large intestine ([Shim et al., 2007](#)). In this respect, [Shim et al. \(2007\)](#) reported that a mixture of slowly fermentable (high-polymer inulin) and rapidly fermentable (low-polymer inulin) sources produces more total gas production and also may to prolong the fermentation of CHO to distal colon. Although the fibers are primarily fermented in the large intestine, a significant amount of DF, mainly the soluble fraction, is fermented in the small intestine as well ([Jørgensen et al., 1996](#); [Jha et al., 2010](#); [Jha and Leterme, 2012](#)). In this respect, [Böhmer et al. \(2005\)](#) found that more than 55% of dietary inulin, a highly fermentable and soluble fructan, was digested in the small intestine. The population of active bacteria becomes significant in the distal small intestine. As a consequence, the bacterial biomass accumulation occurring before the intestinal content reaches the large intestine contributes to a small but significant extent to the amino acid requirements of pigs ([Torrallardona et al., 2003](#)).

4.1. Changes in the gut microbiota and fermentation end products that alter the gut health

Beneficial effects of DF on intestinal functions and on the bacterial profile and fermentation are related to changes in the physicochemical characteristics of the digesta, including transit time, solubility, fermentability, viscosity or water retention capacity of the digesta. Differences between soluble and insoluble NSP have been shown to influence the digestive and fermentative processes in the growing pig. The fermentation of fiber sources by the GIT microbiota results in the generation of SCFA, and therefore, microbial fermentation in the hindgut has important implications for the gut health of the pig. [Molist et al. \(2009\)](#) reported an increase in the concentration of SCFA in the cecum of pigs fed diets containing 40–80 g wheat bran or 30–60 g SBP/kg of diet as compared with pigs fed a control diet without any fiber supplementation on 10–15 d post weaning. The authors concluded that the increases in the SCFA concentration with the NSP-rich diets could be associated with a higher water retention capacity of the digesta, which has been used as a predictor of the degradability of the DF ([Drochner et al., 2004](#)).

The inclusion of DF in the diet influences the composition and activity of microbiota in the GIT ([Williams et al., 2001](#)). This, in turn, may provide some protection against intestinal disorders. High or moderate amounts of DF increase the number of Lactobacilli and tend to decrease the number of some coliforms and reduce ammonia concentration in the small intestine ([Kreuzer et al., 1998](#)). [Berrocoso et al. \(2015\)](#) reported a decrease in *E. coli* and an increase of *lactobacillus* counts in the cecum of pigs at 43 d of age with the inclusion of SBP (50 g/kg) in diet as compared with control diet without any fiber supplementation. The authors attributed the beneficial effects of SBP inclusion to the fermentation of pectin present in SBP. Also, [Molist et al. \(2009\)](#) reported that diets with a higher amount of insoluble NSP (80 g/kg) or a combination of insoluble and soluble NSP (40 g/kg and 30 g/kg, respectively) promote a beneficial shift in the microbial colonization, with a higher butyric acid production in the large intestine and lower *enterobacteria* counts in the digesta. Similarly, [Gerritsen et al. \(2012\)](#) reported that the inclusion of insoluble NSP in the diet increases the stomach weight and the amylase activity in the intestinal brush border together with lower *E. coli* counts in the ileum and colon digesta. Diets low in soluble NSP, oligosaccharides or RS were found to reduce clinical dysentery in pigs experimentally infected with *Serpulina hydysentriae* ([Pluske et al., 1996](#); [Siba et al., 1996](#)), which was confirmed later by [Pluske et al. \(1998\)](#). In a companion study, [Pluske et al. \(1998\)](#) also found

that pigs fed a diet based on cooked white rice were fully protected against swine dysentery. [Mateos et al. \(2006\)](#) reported that the inclusion of up to 4.0% oat hulls into a low-fiber diet (5.5% NDF and 2.2% crude fiber) reduced PWD in weaning pigs from 21 to 41 d after weaning. Similarly, adding oat hulls to weaned pig diets based on extruded rice decreases protein fermentation, tends to decrease total biogenic amine concentrations, and decreases the incidence of PWD ([Kim et al., 2008](#)). This suggests that insoluble fiber sources like oat hulls could also reduce PWD, depending on the place where the protein is fermented in connection with fermentation of CHO and when there is an imbalance in the CHO:protein ratio entering the pig's large intestine.

4.2. Changes in the N emission in feces or urine and gases

Dietary fiber inclusion in pig diets also has been used extensively to reduce ammonia emission. The addition of NSP from soybean hulls and/or sugar beet pulp (SBP) in pig diets reduces the urinary N excretion ratio and, thereby, ammonia emission ([Mroz et al., 2000](#); [Beccacia et al., 2015](#)). In this respect, [Beccacia et al. \(2015\)](#) compared a control diet with a diet supplemented with 150 g/kg of orange pulp as a soluble fiber source and reported that the inclusion of soluble fiber led to a decrease of urinary N excretion ratio from 2.0 to 1.3. The authors noted that this reduction in the ratio could be due to an increase in the amount of N used for microbial protein synthesis in the hindgut, which is excreted in feces (organic N) instead of urine (urea N). However, other researchers reported discrepancies with respect to its effect on urinary N excretion ratio when more insoluble fiber sources were used. For example, [Zervas and Zijlstra \(2002\)](#) and [Bindelle et al. \(2009\)](#) reported that the inclusion of oat hulls in the diet did not reduce this ratio. Similar results were found in a study by [Canh et al. \(1997\)](#), where the increase in NSP content from 140 to 310 g/kg in the diet decreased the urinary N excretion ratio from 3.8 to 1.2 and the apparent N digestibility from 85 to 75%. Also, [Kreuzer and Machmüller \(1993\)](#) found that the addition of 100–220 g/kg NSP in pig diets reduce urinary N excretion by 20–28%. [Jongbloed \(2001\)](#) was able to show a clear relation between NSP content of the diet and the urinary N excretion ratio ([Fig. 1](#)).

Feeds with high contents of pectin and hemicellulose, like citrus pulp and SBP, are more effective DF sources to reduce N loss in manure as compared to cellulose from rye bran and RS from cassava ([Kreuzer et al., 1998](#)). This can be ascribed to their fermentative capacity, which affects the N utilization pattern in the intestines. [Sutton et al. \(1999\)](#) reported that the manure of pigs fed a grain-based diet lost 2.4% of the initial N in the form of ammonia, as compared to 1.4% with SBP-based diets during a 7-d storage period. Supplementing enzymes in cereal-based diets also affects ammonia emission. [Garry et al. \(2007\)](#) studied the effect of diets based on barley or wheat, supplemented or not with exogenous enzymes (endo-1,3(4)- β -glucanase and endo-1,4- β -xylanase) on ammonia emission in growing-finishing pigs. They found that the addition of an enzyme to the wheat-based diet decreased the rate of ammonia emission while the enzyme's addition to the barley-based diet increased both odor and ammonia emissions. Ammonia production from manure during 10 d was higher with maize- and wheat-based diets (11.3 and 12.1% of the N intake, respectively) than with barley-based diets (6.6%). This confirms the role of the NSP in the reduction of ammonia emission.

The microbiota in the large intestine synthesizes nitrogenous cell components and secretions from simpler molecules such as ammonia, AA and peptides, using CHO as the principle energy source. With an increased supply of CHO as an energy

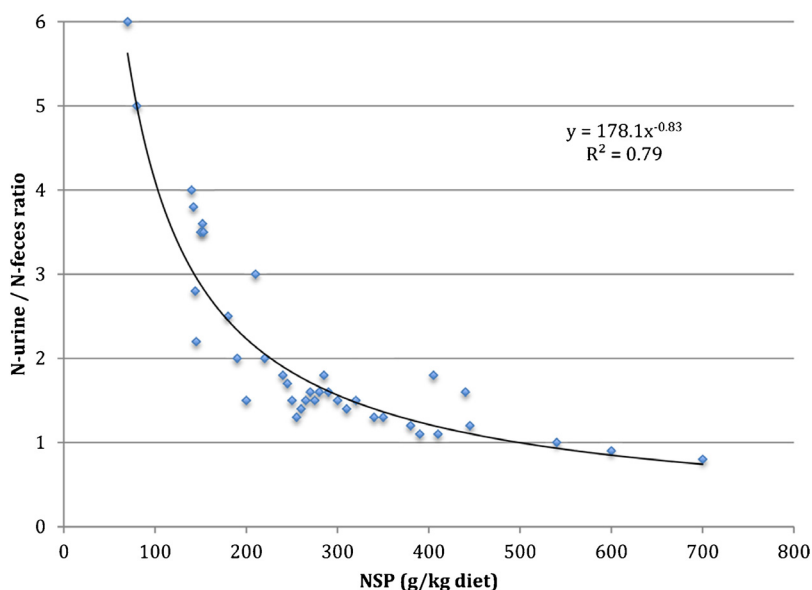


Fig. 1. Relation between non-starch polysaccharides (NSP) content of the diet and the urine N excretion ratio ([Jongbloed, 2001](#)).

source, any excess of indigestible protein is more likely to be incorporated into bacterial proteins than to be fermented and used as a source of energy (Houdijk et al., 1998). It is reported that 60–90% of fecal N is of bacterial origin (Rubio, 2003). Similarly, Cummings (1984) mentioned that most of the N excreted through the feces in humans and animals fed DF is considered to come from bacterial fermentation in the large intestine. The undigested protein available in the large intestine (which is of both dietary and endogenous origin) is utilized by resident bacteria as a source of N, resulting in increased bacterial proteins. The bacterial degradation of proteins starts in the stomach, as indicated by an increased formation of ammonia and, to a lesser extent, amines, phenol and p-cresol. Moreover, blood urea is the key supply of N for bacterial proliferation in the colon. In the presence of highly ureolytic bacteria in the cecum, the urea concentration gradient favors a net transfer of urea into the cecal lumen (Younes et al., 1995); thus bacteria enhance the urea transfer from blood to the large intestine (Morales et al., 2015). The ammonia generated by bacterial urease is used by bacteria for protein synthesis, which increases the amount of N present in the feces and decreases N excretion in urine, in the form of urea (Kirchgessner et al., 1994; Younes et al., 1995). The synthesis of microbial protein causes less ammonia to be reabsorbed from the colon.

Lowering the pH of feces and manure is also an efficient means of reducing ammonia emission since ammonia is soluble under its protonated form (NH_4^+). Microbial fiber fermentation in the large intestine results in the acidification of the digesta due to SCFA production, resulting in the reduction of the pH of feces and manure, while the opposite is found when protein is fermented, due to ammonia production. In a series of experiments, Canh et al. (1997, 1998a, 1998c) reported reduced pH of feces and manure when pigs were fed diets containing fermentable fiber sources, apart from the shift in N excretion pathway. For each increase of 100 g of non-starch polysaccharides (NSP) in pig diets, the pH of the slurry decreased by 0.12 units and ammonia emission was reduced by 5.4%. The decrease in pH was partly attributed to the decrease in the $\text{NH}_4\text{-N}$ content of the slurry as well as to increased SCFA concentration of the slurry following CHO fermentation (Canh et al., 1998a). Similarly, lowering the pH of urine can lower the pH of manure, thus reducing ammonia release from the storage. The urine pH can be altered by changing the electrolyte balance of the diet (Patience et al., 1987).

4.3. Changes in odorous compounds

Changes in DF content are also purported to affect odor emissions from manure, although the effect is more complicated than is the case for protein reduction. The presence of NSP influences the bacterial dynamics in the hindgut and directly impacts the production of odorous compounds such as SCFA, amines, and sulfides. In this respect, Canh et al. (1997) reported that an increase of fermentable CHO in diets increases manure SCFA concentrations. This increase may impact manure odor concentration, because SCFA are important odorous compounds in manure storage. De Camp et al. (2001) compared a control diet with diets supplemented with 100 g/kg soybean hulls as fiber sources and reported a 32% increase of total SCFA concentration in 6-week-stored manure and an 11% reduction in odor concentration. However, Gralapp et al. (2002) reported no difference in odor concentration when 100 g/kg distillers dried grain was added to the diets of finishing pigs. Finally, the pattern of odor emissions could be due to a number of reasons; for instance, limiting protein fermentation and increasing CHO fermentation in the large intestine can reduce the production of some of the most offensive-smelling compounds emanating from pig production. In this respect, both protein and CHO fermentation contribute to the production of acetic acid; however, the BCFAs, i.e. iso-butyric and iso-valeric acid, are produced exclusively from protein fermentation and have a more offensive odor than the straight-chain SCFAs (Mackie et al., 1998).

5. Conclusion

The reduction in CP content in the diet (less than 190 g/kg), together with the inclusion of moderately fermentable fiber sources will reduce the production of harmful microbial metabolites in the large intestine as well as the incidence of intestinal disorders in pigs. There is high bacterial N uptake when pigs are fed with fermentable fiber sources, suggesting that, in presence of higher levels of fiber substrate for fermentation, the resident microbiota in the large intestine retain more N for their own growth. There is, thus, increased bacterial protein mass and also a shift in N excretion pathway from urine to feces. The inclusion of soluble fiber leads to a decrease of urinary N excretion. Finally, dietary CP and DF manipulation is an effective tool to reduce nitrogenous gases from piggeries. Nitrogen excretion, ammonia emission from pigs, and manure concentrations of odorous compounds can be reduced substantially by strategically decreasing dietary protein and increasing fermentable fiber in pig diets, although the effect of changes in content of DF is relatively less complex than is the case for protein reduction. Therefore, the inclusion of DF and reduction in dietary protein content can be used as a nutritional strategy to optimize intestinal health of early-weaned pigs.

Acknowledgement

Postdoctoral fellow Dr Julio F. D. Berrocoso was partly supported from the USDA, Agricultural Research Service, Collaborative Research Fund (Agreement no. 58-5320-3-022).

References

- Aarnink, A.J.A., Hoeksma, P., Van Ouwerkerk, E.N.J., 1993. Factors affecting ammonium concentration in slurry from fattening pigs. In: Verstegen, M.W.A., den Hartog, L.A., van Kempen, G.J.M., Metz, J.H.M. (Eds.), *Nitrogen Flow in Pig Production and Environmental Consequences*, Pudoc-DLO. EAAP-Publication, Wageningen, The Netherlands, pp. 413–420.
- Aarnink, A.J.A., Swiestra, D., van den Berg, A.J., Speelman, L., 1997. Effect of type of slatted floor and degree of fouling of solid floor on ammonia emission rates from fattening piggeries. *J. Agr. Eng. Res.* 66, 93–102.
- Aarnink, A.J.A., Verstegen, M.W.A., 2007. Nutrition, key factor to reduce environmental load from pig production. *Livest. Sci.* 109, 194–203.
- Asp, N.G., 1996. *Dietary carbohydrates: classification by chemistry and physiology*. *Food Chem.* 57, 9–14.
- Aumiller, T., Mosenthin, R., Weiss, E., 2015. Potential of cereal grains and grain legumes in modulating pigs' intestinal microbiota – A review. *Livest. Sci.* 172, 16–32.
- Ball, R.O., Möhn, S., 2003. Feeding strategies to reduce greenhouse gas emissions from pigs. *Advances Pork Prod.* 14, 301–311.
- Beccacia, A., Calvet, S., Cerisuelo, A., Ferrer, P., García-Rebollar, P., De Blas, C., 2015. Effects of nutrition on digestion efficiency and gaseous emissions from slurry in growing-finishing pigs. I. Influence of the inclusion of two levels of orange pulp and carob meal in iso fibrous diets. *Anim. Feed Sci. Technol.* 208, 158–169.
- Berrocoso, J.D., Menoyo, D., Guzmán, P., Saldaña, B., Cámara, L., Mateos, G.G., 2015. Effects of fiber inclusion on growth performance and nutrient digestibility of piglets reared under optimal or poor hygienic conditions. *J. Anim. Sci.* 93, 3919–3931.
- Bikker, P., Dirkszager, A., Fledderus, J., Trevisi, P., Huerou-Luron, I.L., Lalles, J.P., Awati, A., 2006. The effect of dietary protein and fermentable carbohydrates levels on growth performance and intestinal characteristics in newly weaned piglets. *J. Anim. Sci.* 84, 3337–3345.
- Bindelle, J., Buldgen, A., Delacollette, M., Wavreille, J., Agneessens, R., Destain, J.P., Leterme, P., 2009. Influence of source and concentrations of dietary fiber on in vivo nitrogen excretion pathways in pigs reflected by in vitro fermentation and N incorporation by fecal bacteria. *J. Anim. Sci.* 87, 583–593.
- Blachier, F., Mariotti, F., Huneau, J.F., Tome, D., 2007. Effects of amino acid-derived luminal metabolites on the colonic epithelium and physiopathological consequences. *Amino Acids* 33, 547–562.
- Böhmer, B.M., Branner, G.R., Roth-Maier, D.A., 2005. Precaecal and faecal digestibility of inulin (DP 10–12) or an inulin/Enterococcus faecium mix and effects on nutrient digestibility and microbial gut flora. *J. Anim. Physiol. Anim. Nutr.* 89, 388–396.
- Canh, T.T., Verstegen, M.W.A., Aarnink, A.J.A., Schrama, J.W., 1997. Influence of dietary factors on nitrogen partitioning and composition of urine and feces of fattening pigs. *J. Anim. Sci.* 75, 700–706.
- Canh, T.T., Aarnink, A.J., Verstegen, M.W., Schrama, J.W., 1998a. Influence of dietary factors on the pH and ammonia emission of slurry from growing-finishing pigs. *J. Anim. Sci.* 76, 1123–1130.
- Canh, T.T., Aarnink, A.J.A., Schutte, J.B., Sutton, A., Langhout, D.J., Verstegen, M.W.A., 1998b. Dietary protein affects nitrogen excretion and ammonia emission from slurry of growing-finishing pigs. *Livest. Prod. Sci.* 56, 181–191.
- Canh, T.T., Sutton, A.L., Aarnink, A.J., Verstegen, M.W., Schrama, J.W., Bakker, G.C., 1998c. Dietary carbohydrates alter the fecal composition and pH and the ammonia emission from slurry of growing pigs. *J. Anim. Sci.* 76, 1887–1895.
- Cho, S., DeVries, J.W., Prosky, L., 1997. *Dietary Fiber Analysis and Applications*. AOAC Intl., Gaithersburg, MD, USA.
- Cone, J.W., Jongbloed, A.W., Gelder, A.H.V., Lange, L.D., 2005. Estimation of protein fermentation in the large intestine of pigs using a gas production technique. *Anim. Feed Sci. Technol.* 123–124, 463–472.
- Cummings, J.H., 1984. Microbial digestion of complex carbohydrates in man. *Proc. Nutr. Soc.* 43, 35–44.
- Davila, A.M., Blachier, F., Gotteland, M., Andriamihaja, M., Benetti, P.H., Sanz, Y., Tome, D., 2013. Intestinal luminal nitrogen metabolism: role of the gut microbiota and consequences for the host. *Pharm. Res.* 68, 95–107.
- De Camp, S.A., Hill, B.E., Hankins, S.L., Bundy, D.C., Powers, W.J., 2001. Effects of soybean hulls in commercial diet on pig performance, manure composition, and selected air quality parameters in swine facilities. *J. Anim. Sci.* 79 (Suppl. 1), S252.
- Drochner, W., Kerler, A., Zacharias, B., 2004. Pectin in pig nutrition, a comparative review. *J. Anim. Physiol. Anim. Nutr.* 88, 367–380.
- Garry, B.P., Fogarty, M., Curran, T.P., O'Connell, M.J., O'Doherty, J.V., 2007. The effect of cereal type and enzyme addition on pig performance, intestinal microflora, and ammonia and odour emissions. *Animal* 1, 751–757.
- Gerritsen, R., van der Aar, P., Molist, F., 2012. Insoluble nonstarch polysaccharides in diets for weaned piglets. *J. Anim. Sci.* 90, 318–320.
- Graham, H., Hesselman, K., Aman, P., 1986. The influence of wheat bran and sugar-beet pulp on the digestibility of dietary components in a cereal-based pig diet. *J. Nutr.* 116, 242–251.
- Gralapp, A.K., Powers, W.J., Faust, M.A., Bundy, D.S., 2002. Effects of dietary ingredients on manure characteristics and odorous emissions from swine. *J. Anim. Sci.* 80, 1512–1519.
- Gutierrez, N.A., Kerr, B.J., Patience, J.F., 2013. Effect of insoluble-low fermentable fiber from corn-ethanol distillation origin on energy, fiber, and amino acid digestibility, hindgut degradability of fiber, and growth performance of pigs. *J. Anim. Sci.* 91, 5314–5325.
- Heo, J.M., Kim, J.C., Hansen, C.F., Mullan, B.P., Hampson, D.J., Pluske, J.R., 2009. Feeding a diet with decreased protein content reduces indices of protein fermentation and the incidence of postweaning diarrhea in weaned pigs challenged with an enterotoxigenic strain of *Escherichia coli*. *J. Anim. Sci.* 87, 2833–2843.
- Heo, J.M., Kim, J.C., Hansen, C.F., Mullan, B.P., Hampson, D.J., Pluske, J.R., 2010. Feeding a diet with a decreased protein content reduces both nitrogen content in the gastrointestinal tract and post-weaning diarrhoea, but does not affect apparent nitrogen digestibility in weaner pigs challenged with an enterotoxigenic strain of *Escherichia coli*. *Anim. Feed Sci. Technol.* 160, 48–159.
- Hobbs, P.J., Pain, B.F., Kay, R.M., Lee, P.A., 1996. Reduction of odorous compounds in fresh pig slurry by dietary control of crude protein. *J. Sci. Food Agric.* 71, 508–514.
- Houdijk, J.G.M., Bosch, M.W., Verstegen, M.W.A., Berenpas, H.J., 1998. Effects of dietary oligosaccharides on the growth performance and faecal characteristics of young growing pigs. *Anim. Feed Sci. Technol.* 71, 35–48.
- Htoo, J.K., Araiza, B.A., Sauer, W.C., Rademacher, M., Zhang, Y., Cervantes, M., Zijlstra, R.T., 2007. Effect of dietary protein content on ileal amino acid digestibility, growth performance, and formation of microbial metabolites in ileal and cecal digesta of early-weaned pigs. *J. Anim. Sci.* 85, 3303–3312.
- Jha, R., Leterme, P., 2012. Feed ingredients differing in fermentable fibre and indigestible protein content affect fermentation metabolites and faecal nitrogen excretion in growing pigs. *Animal* 6, 603–611.
- Jha, R., Berrocoso, J.D., 2015. Review: Dietary fiber utilization and its effects on physiological functions and gut health of swine. *Animal* 9, 1441–1452.
- Jha, R., Rossnagel, B., Pieper, R., Van Kessel, A., Leterme, P., 2010. Barley and oat cultivars with diverse carbohydrate composition alter ileal and total tract nutrient digestibility and fermentation metabolites in weaned piglets. *Animal* 4, 724–731.
- Jha, R., Htoo, J.K., Young, M.G., Beltranena, E., Zijlstra, R.T., 2013. Effect of increasing co-product inclusion and reducing dietary protein on growth performance, carcass characteristics, and jowl fatty acid profile of grower-finisher pigs. *J. Anim. Sci.* 91, 2178–2219.
- Jensen, M.T., Cox, R.P., Jensen, B.B., 1995. 3-Methylindole (skatole) and indole production by mixed populations of pig fecal bacteria. *Appl. Environ. Microbiol.* 61, 3180–3184.
- Johnson, L.R., 2001. Digestion and absorption. In: Johnson, L.R. (Ed.), *Gastrointestinal Physiology*. Mosby, St. Louis, MO, USA, p. p120.
- Jongbloed, A.W., 2008. Environmental pollution control in pigs by using nutrition tools. *Rev. Bras. Zootec.* 37, 215–229.
- Jongbloed, A.W., 2001. Hebben voermaatregelen ter verlag van de ammoniakemissie een negatief effect op de vertering en benutting van nutriënten? (Do feeding measures for lowering ammonia emission have a negative effect on the digestibility and utilisation of nutrients?). In: Jongbloed, A.W., Blok, M.C. (Eds.), *Veevoeding en Ammoniakemissie uit Varkensstallen. Samenvattingen van de themamiddag*, 2174. Productschap Diervoeder, The Hague, The Netherlands, pp. 11–23.

- Jorgensen, H., Zhao, X.Q., Eggum, B.O., 1996. The influence of dietary fibre and environmental temperature on the development of the gastrointestinal tract, digestibility, degree of fermentation in the hind-gut and energy metabolism in pigs. *Br. J. Nutr.* 75, 365–378.
- Kerr, B.J., 1995. Nutritional strategies for waste reduction-management: nitrogen. In: Longenecker, J.B., Spears, J.W. (Eds.), *New Horizons in Animal Nutrition and Health*. The Inst. Nutr. Univ. North Carolina, Chapel Hill, Raleigh, NC, USA, pp. 47–68.
- Kim, J.C., Mullan, B.P., Hampson, D.J., Pluske, J.R., 2008. Addition of oat hulls to an extruded rice-based diet for weaner pigs ameliorates the incidence of diarrhoea and reduces indices of protein fermentation in the gastrointestinal tract. *Br. J. Nutr.* 99, 1217–1225.
- Kirchgessner, M., Kreuzer, M., Machmüller, A., Roth-Maier, D.A., 1994. Evidence for a high efficiency of bacterial protein synthesis in the digestive tract of adult sows fed supplements of fibrous feedstuffs. *Anim. Feed Sci. Technol.* 46, 293–306.
- Kreuzer, M., Machmüller, A., 1993. Reduction of gaseous nitrogen emission from pig manure by increasing the level of bacterially fermentable substrates in the ration. In: Verstegen, M.W.A., den Hartog, L.A., van Kempen, G.J.M., Metz, J.H.M. (Eds.), *Nitrogen Flow in Pig Production and Environmental Consequences*. EAAP-Publication, Pudoc-DLO, Wageningen, The Netherlands, pp. 151–156.
- Kreuzer, M., Machmüller, A., Gerdemann, M.M., Hanneken, H., Wittmann, M., 1998. Reduction of gaseous nitrogen loss from pig manure using feeds rich in easily-fermentable non-starch polysaccharides. *Anim. Feed Sci. Technol.* 73, 1–19.
- Kröger, S., Pieper, R., Schwelberger, H.G., Wang, J., Villodre Tudela, C., Aschenbach, J.R., Van Kessel, A.G., Zentek, J., 2013. Diets high in heat treated soybean meal reduce the histamine-induced epithelial response in the colon of weaned piglets and increase epithelial catabolism of histamine. *PLOS One* 8, e80612.
- Le, P.D., Aarnink, A.J.A., Jongbloed, A.W., Peet-Schwering, C.M.C., van, der., Ogink, N.W.M., Verstegen, M.W.A., 2008. Interactive effects of dietary crude protein and fermentable carbohydrate levels on odour from pig manure. *Livest. Sci.* 114, 48–61.
- Leek, A.B.G., Callan, J.J., Reilly, P., Beattie, V.E., O'Doherty, J.V., 2007. Apparent component digestibility and manure ammonia emission in finishing pigs fed diets based on barley, maize or wheat prepared without or with exogenous non-starch polysaccharide enzymes. *Anim. Feed Sci. Technol.* 135, 86–99.
- Lenis, N.P., 1989. Lower nitrogen excretion in pig husbandry by feeding: Current and future possibilities. *Neth. J. Agri. Sci.* 37, 61–70.
- Macfarlane, G.T., Gibson, G.D., 1995. Microbiological aspects of the production of short-chain fatty acids in the large bowel. In: Cumming, J.H., Rombeau, J.L., Sakota, T. (Eds.), *Physiological and Clinical Aspects of Short-Chain Fatty Acids*. Cambridge University Press, Cambridge, UK, pp. 87–105.
- Macfarlane, S., Macfarlane, G.T., 2003. Regulation of short-chain fatty acid production. *Proc. Nutr. Soc.* 62, 67–72.
- Macfarlane, G.T., Gibson, G.R., Beatty, E., Cummings, J.H., 1992. Estimation of short-chain fatty acid production from protein by human intestinal bacteria based on branched-chain fatty acid measurements. *FEMS Microbiol. Lett.* 101, 81–88.
- Mackie, R.L., Stroob, P.G., Varel, V.H., 1998. Biochemical identification and biological origin of key odor components in livestock waste. *J. Anim. Sci.* 76, 1331–1342.
- Mateos, G.G., Martin, F., Latorre, M.A., Vicente, B., Lazaro, R., 2006. Inclusion of oat hulls in diets for young pigs based on cooked maize or cooked rice. *Anim. Sci.* 82, 57–63.
- Miller, D.N., Varel, V.H., 2003. Swine manure composition affects the biochemical origins, composition, and accumulation of odorous compounds. *J. Anim. Sci.* 81, 2131–2138.
- Möhn, S., Susenbeth, A., 1995. Influence of dietary protein content on efficiency of energy utilisation in growing pigs. *Arch. Anim. Nutr.* 47, 361–372.
- Molist, F., Gómez de Segura, A., Gasà, J., Hermes, R.G., Manzanilla, E.G., Anguita, M., Pérez, J.F., 2009. Effects of the insoluble and soluble dietary fibre on the physicochemical properties of digesta and the microbial activity in early weaned piglets. *Anim. Feed Sci. Technol.* 149, 346–353.
- Montagne, L., Pluske, J.R., Hampson, D.J., 2003. A review of interactions between dietary fibre and the intestinal mucosa, and their consequences on digestive health in young non-ruminant animals. *Anim. Feed Sci. Technol.* 108, 95–117.
- Morales, A., Buenabad, L., Castillo, G., Arce, N., Araiza, B.A., Htoo, J.K., Cervantes, M., 2015. Low-protein amino acid-supplemented diets for growing pigs: Effect on expression of amino acid transporters, serum concentration, performance, and carcass composition. *J. Anim. Sci.* 93, 2154–2164.
- Mroz, Z., Moeser, A.J., Vreman, K., van Diepen, J.T., van Kempen, T., Canh, T.T., Jongbloed, A.W., 2000. Effects of dietary carbohydrates and buffering capacity on nutrient digestibility and manure characteristics in finishing pigs. *J. Anim. Sci.* 78, 3096–3106.
- Nollet, H., Deprez, P., Van Driessche, E., Muylle, E., 1999. Protection of just weaned pigs against infection with F18+ *Escherichia coli* by non-immune plasma powder. *Vet. Microbiol.* 65, 37–45.
- Nousiainen, J.T., 1991. Comparative observations on selected probiotics and olaquinox as feed additives for piglets around weaning. 2. Effect on villus length and crypt depth in the jejunum, ileum, caecum and colon. *J. Anim. Physiol. Anim. Nutr.* 66, 224–230.
- Oakenfull, D., 2001. Dietary fiber in human nutrition. In: Spiller, G.A. (Ed.), *Physical Chemistry of Dietary Fiber*. CRC Press, Boca Raton, FL, USA, pp. 33–47.
- Patience, J.F., Austic, R.E., Boyd, R.D., 1987. Effect of dietary electrolyte balance on growth and acid-base status in swine. *J. Anim. Sci.* 64, 457–466.
- Pieper, R., Jha, R., Rossnagel, B., Van Kessel, A.G., Souffrant, W.B., Leterme, P., 2008. Effect of barley and oat cultivars with different carbohydrate compositions on the intestinal bacterial communities in weaned piglets. *FEMS Microbiol. Ecol.* 66, 556–566.
- Pluske, J.R., Siba, P.M., Pethick, D.W., Durmic, Z., Mullan, B.P., Hampson, D.J., 1996. The incidence of swine dysentery in pigs can be reduced by feeding diets that limit the amount of fermentable substrate entering the large intestine. *J. Nutr.* 126, 2920–2933.
- Pluske, J.R., Durmic, Z., Pethick, D.W., Mullan, B.P., Hampson, D.J., 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.
- Rubio, L.A., 2003. Carbohydrates digestibility and faecal nitrogen excretion in rats fed raw or germinated faba bean (*Vicia faba*)- and chickpea (*Cicer arietinum*)-based diets. *Br. J. Nutr.* 90, 301–309.
- Siba, P.M., Pethick, D.W., Hampson, D.J., 1996. Pigs experimentally infected with *Serpulina hyodysenteriae* can be protected from developing swine dysentery by feeding them a highly digestible diet. *Epidemiol. Infect.* 116, 207–216.
- Shim, S.B., Verdonk, J.M.A.J., Pellikaan, W.F., Verstegen, M.W.A., 2007. Differences in microbial activities of faeces from weaned and unweaned pigs in relation to *in vitro* fermentation of different sources of inulin-type oligofructose and pig feed ingredients. *Asian-Aust. J. Anim. Sci.* 20, 1444–1452.
- Sutton, A.L., Kephart, K.B., Verstegen, M.W.A., Canh, T.T., Hobbs, P.J., 1999. Potential for reduction of odorous compounds swine manure through diet modification. *J. Anim. Sci.* 77, 430–439.
- Torrallardona, D., Harris, C.I., Fuller, M.F., 2003. Pigs' gastrointestinal microflora provide them with essential amino acids. *J. Nutr.* 133, 1127–1131.
- Tso, P., Crissinger, K., 2000. Overview of digestion and absorption. In: Stipanuk, M.H., Caudill, M.A. (Eds.), *Biochemical and Physiological Aspects of Human Nutrition*. Saunders, PA, USA, pp. 75–106.
- Urbain, B., Gustin, P., Prouvost, J.F., Ansay, M., 1994. Quantitative assessment of aerial ammonia toxicity to the nasal mucosa by use of the nasal lavage method in pigs. *Am. J. Vet. Res.* 55, 1335–1340.
- Williams, B.A., Verstegen, M.W.A., Tamminga, S., 2001. Fermentation in the large intestine of single-stomached animals and its relationship to animal health. *Nutr. Res. Rev.* 14, 207–227.
- Wellcock, I.J., Fortomaris, P.D., Houdijk, J.G.M., Wiseman, J., Kyriazakis, I., 2008. The consequences of non-starch polysaccharide solubility and inclusion level on the health and performance of weaned pigs challenged with enterotoxigenic *Escherichia coli*. *Br. J. Nutr.* 99, 520–530.
- Wenk, C., 2001. The role of dietary fibre in the digestive physiology of the pig. *Anim. Feed Sci. Technol.* 90, 21–33.
- Younes, H., Garleb, K., Behr, S., Remesy, C., Demigne, C., 1995. Fermentable fibers or oligosaccharides reduce urinary nitrogen excretion by increasing urea disposal in the rat caecum. *J. Nutr.* 125, 1010–1016.
- Zervas, S., Zijlstra, R.T., 2002. Effects of dietary protein and fermentable fiber on nitrogen excretion patterns and plasma urea in grower pigs. *J. Anim. Sci.* 80, 3247–3256.
- Zhang, Y., Tanaka, A., Dosman, J.A., Senthilselvan, A., Barber, E.M., Kirychuk, S.P., Holfeld, L.E., Hurst, T.S., 1998. Acute respiratory responses of human subjects to air quality in a swine building. *J. Agr. Eng. Res.* 70, 367–373.