11 Fiber in Swine Nutrition

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Introduction

Fiber can be defined as carbohydrates or lignin in plant materials that are indigestible by endogenous animal enzymes and have physiological effects on animals and humans. Cellulose is the most abundant carbohydrate in the nature, and it is important to find ways to utilize cellulose and other fibrous components or non-starch polysaccharides (NSP) in the diet for successful and sustainable future pig production.

Because of the increased usage of starch and oil in the biofuel industry in recent years, many co-products or by-products are available as a feed ingredient for swine production. Unfortunately, such alternative feed ingredients are rather high in fiber content. Pigs can obtain energy from fiber but only after microbial fermentation of the fiber in the gastrointestinal tract and subsequent absorption of volatile fatty acids (VFA), which may contribute to the energy status of pigs.

Although soluble fiber is easily fermented, fiber is, in general, not well utilized by pigs, especially insoluble fiber. The greater the concentration of fiber, the lower the overall digestibility of energy in the diet. Furthermore, fiber may reduce the digestibility of amino acids, lipids, and some minerals. Therefore, the fundamental and applied information on fiber or its utilization or both would have considerable impacts on the issue of not just utilizing fibrous components per se but also on the efficient utilization of alternative feedstuffs for swine production. The objective of this chapter is to briefly review fiber and its utilization by pigs, which may contribute to successful and sustainable swine production.

Definition of Dietary Fiber

There are numerous definitions of dietary fiber, but most of them either define dietary fiber as a group of compounds that are identified in analytical methods or as a group of compounds that have specific physiological functions (IOM, 2001). In the nineteenth century, the Weende procedure defined crude fiber as the organic residue that is insoluble in acid and alkaline treatments (Mertens, 2003). This portion of the diet was considered the de facto definition of dietary fiber and without real value to the animal (AACC, 2001).

Later, two researchers in separate ways proposed that this indigestible residue might improve human health (Kritchevsky, 1988). Denis Burkitt reported that bowel cancer is rare in humans

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who consume a "high residue diet," and Hugh Trowell suggested that high intakes of undigested residue help protect people in developing countries from ischemic heart disease (Burkitt et al., 1972; Kritchevsky, 1988; Carpenter, 2003). These conclusions triggered interest in dietary fiber, but it became clear that dietary fiber is a heterogeneous group of chemical components with multiple physiological functions and is therefore difficult to define (Carpenter, 2003).

It is now accepted that an accurate definition of dietary fiber must include the physiological effects of fiber (IOM, 2006). Therefore, an important aspect of the definition is that dietary fiber consists of carbohydrates that are indigestible by endogenous animal enzymes (AACC, 2001; IOM, 2006). The inclusion of this term in the definition is important, but difficult to measure (Englyst et al., 2007). The current definition of dietary fiber (AACC, 2001) includes the following aspects: (1) it is an indigestible portion of the diet, (2) it originates from carbohydrates or lignin, (3) it is a part of a plant, and (4) it has physiological effects in humans that improve laxation or attenuate blood cholesterol or glucose or both.

The definition of dietary fiber by the IOM separates the definition into three parts (i.e., dietary fiber, functional fiber, and total fiber). Dietary fiber consists of non-digestible carbohydrates and lignin that are intrinsic and intact in plants. Functional fiber consists of isolated, non-digestible carbohydrates that have beneficial physiological effects in humans, and total fiber is the sum of dietary fiber and functional fiber (IOM, 2006).

The term NSP is related to dietary fiber but does not cover all components that can be classified as dietary fiber (Elia and Cummings, 2007). For example, NSP does not include oligosaccharides and lignin, which were included in the definitions of dietary fiber by AACC (2001) and by IOM (2006). Therefore, use of the term NSP may not be an accurate description of fiber in feed ingredients because dietary fiber is not limited to NSP or plant cell walls (Cho et al., 1997).

The correct definition of dietary fiber is important for labeling the concentration of dietary fiber in human food products. In swine diets, it is important to clearly describe the components of dietary fiber that have nutritional and physiological effects in the animals and to define the components that contribute to the energy value of the feed ingredient. It is also important that analytical procedures are available to accurately determine the concentration of dietary fiber in animal feed and feed ingredients.

Analysis of Fiber in Animal Feed Ingredients

There are many methods to determine the concentration of dietary fiber in human food, animal feed, and feed ingredients. All methods include two basic steps: digestion of carbohydrates and other nonfiber components of the diet (i.e., protein and fat) and quantification of the undigested residue. The digestion procedure can use chemicals (e.g., acid, alkali, and detergent) or enzymes (e.g., amylase, amyloglucosidase, and protease). Measurement of the indigestible residue can be accomplished by weighing the residue (gravimetric) or by measuring chemical compounds in the residue using gas-liquid chromatography, or high-performance liquid chromatography. There are newer methods to study the composition and structure of non-starch polysaccharides in cell walls of plants and their relationship with degradation in the gut (Guillon et al., 2006). These methods include Raman Microspectroscopy, Fourier Transform Infrared Spectroscopy (FT-IR), immunolabeling, fluorescence, and mass spectroscopy, among others (Guillon et al., 2006).

Crude Fiber

This is a chemical–gravimetric method that is part of the proximate analysis of feed ingredients developed in the Agricultural Experimental Station in Weende, Germany (Grieshop et al., 2001).

The method separates carbohydrates into two portions, nitrogen free extract and crude fiber. Crude fiber is the residue that is left after digestion of a sample with 1.25% sulfuric acid and 1.25% sodium hydroxide (Cho et al., 1997; Furda, 2001). At the time of the procedure's development, it was known only that digestion included acid and alkaline processes, but the crucial enzymes were unknown (Mertens, 2003). The crude-fiber procedure is very robust and repeatable, but there is no relationship between crude fiber and the definitions of dietary fiber by AACC and IOM (Mertens, 2003) because the recovery of cellulose (40–100%), hemicelluloses (15–20%), and lignin (5–90%) is not complete (Grieshop et al., 2001; Mertens, 2003). However, the procedure is still used to regulate maximum crude-fiber guarantee level in swine feed (AAFCO, 2008).

Detergent Fiber Procedures

The detergent procedure is a chemical–gravimetric procedure that empirically relates the value from the analysis to the physiological properties of dietary fiber (Van Soest et al., 1991). The procedure was developed by Van Soest (1963) and it divides dietary fiber into neutron detergent fiber (NDF), acid detergent fiber (ADF), and acid detergent lignin (Robertson and Horvath, 2001). This procedure was an improvement over the crude-fiber procedure; however, it does not recover soluble dietary fiber such as pectins, mucilages, gums, and β-glucans (Grieshop et al., 2001). The lack of recovery of soluble dietary fiber components is less concerning in cereal grains such as corn and dried distillers grains with solubles (DDGS) that have high concentrations of insoluble fiber (Johnston et al., 2003) than feed ingredients such as soybean hulls and sugar beet pulp that also contain soluble dietary fiber. Other problems with the detergent procedure include the possible contamination of the residue with starch and protein, which reduces robustness and repeatability (Mertens, 2003).

Total Dietary Fiber

The procedure of Prosky is known as the total dietary fiber procedure (TDF; Method 985.29; AOAC, 2006) and has been modified to determine soluble and insoluble dietary fiber (Method 991.43; AOAC, 2006). The TDF procedure uses enzymes (e.g., amylase, glucoamylase, and protease) to mimic digestion in the small intestine, and then the residue is weighed (Prosky et al., 1984). The residue also is analyzed for undigested proteins and ash. The TDF procedure is more time-consuming and less reproducible than the crude-fiber and detergent methods, but values obtained by the TDF procedure are more representative of the concept of dietary fiber (Mertens, 2003). More work is needed to improve the TDF procedure to include low-molecular-weight indigestible carbohydrates and correct for contaminants of the indigestible residue (Gordon et al., 2007).

Enzymatic Chemical Methods

There are two commonly used methods that combine the initial steps of enzymatic digestion with chemical determination of sugars in the undigested residue (Theander and Åman, 1979; Englyst et al., 1982). The Uppsala method calculates dietary fiber as the sum of amylase-resistant polysaccharides, uronic acids, and Klason lignin (AOAC, 2006). The digestion step in the AOAC Method (994.13) uses a heat-stable α-amylase and amyloglucosidase (AOAC, 2006). The residue is divided into soluble and insoluble fractions by 80% ethanol. The neutral sugars released are quantified as alditol acetate derivatives by gas liquid chromatography and uronic acids chromatographically (Theander

and Åman, 1979). The NSP method developed by Englyst et al. (1982) is similar to the Uppsala method, but it excludes lignin and resistant starch from the final value (Grieshop et al., 2001).

Estimation of Dietary Fiber by Difference

For practical purposes, the concentration of indigestible nutrients in feed ingredients may be calculated as the sum of organic residues (OR) in a feed ingredient using the following equation:

$$\text{OR} = \text{dry matter (DM)} - (\text{ash} + \text{starch} + \text{sugars} + \text{crude protein} + \text{crude fat}).$$

This equation assumes that all starch and sugars are digested and absorbed in the small intestine and that carbohydrates other than starch and sugars are undigested by mammalian enzymes and, therefore, belong to dietary fiber (Noblet et al., 1994; de Lange, 2008).

Comparison of Methods to Measure Dietary Fiber

There is no single method of analysis of dietary fiber that precisely measures all carbohydrates that are covered by the definition of dietary fiber (NRC, 2007). The TDF procedure is the method that captures the most carbohydrates that are considered dietary fiber. However, some of the oligosaccharides, including fructooligosaccharides and some fructan polysaccharides, may not always be included in the values for TDF (NRC, 2007).

Physiological Properties of Dietary Fiber

The unique properties that differentiate dietary fiber from digestible polysaccharides are influenced by the chemical composition and the physical structure of the fiber. The physicochemical properties that are relevant to human and animal nutrition include solubility, water-holding and water-binding capacity, viscosity, and fermentability. These physicochemical properties of dietary fiber are responsible for physiological effects that may improve human well-being but they can also reduce animal production efficiency.

Solubility

Dietary fiber may be classified as soluble and insoluble fiber (Cho et al., 1997). Solubility of dietary fiber not only refers to the ability of the dietary fiber to dissolve in water (Oakenfull, 2001), but it can also be defined as its ability to dissolve in dilute acid, dilute base, or a buffer or enzyme solution that mimics the enzyme solution existing in the gastrointestinal tract (Cho et al., 1997). Soluble fiber may be separated from total dietary fiber by precipitation in ethanol after enzyme digestion (Cho et al., 1997).

Solubility of a dietary fiber is greatly influenced by the linkages between and among monosaccharide units that make up dietary fiber (Oakenfull, 2001). The linkages provide the physical structure that dictates the hydration property of dietary fiber. The β-(1–4) linkage among glucose units in cellulose allows for an ordered crystalline structure preventing the entrance of water molecules in the structure, thus making cellulose insoluble (Oakenfull, 2001). However, the presence of β-(1–3)

branching in β-glucan does not allow for the formation of an ordered crystalline structure similar to that of cellulose, thus, making β-glucan a soluble fiber (Oakenfull, 2001).

The solubility of dietary fiber does not provide information about the carbohydrate composition, physical structure, and degree of polymerization, but it is important because soluble and insoluble fiber differ in their physiological effects and overall contributions to human health and animal production. Soluble fiber results in increased digesta viscosity, which is responsible for reducing postprandial insulin and blood-glucose increases in humans and dogs (Dikeman and Fahey, 2006), whereas insoluble dietary fiber results in increased rate of digesta passage in the gastrointestinal tract and increased fecal mass (Chesson, 2006).

Water-Holding and Water-Binding Capacity

The physiological property of fiber is affected by the interaction between fiber and water. Fiber binds water through different mechanisms such as ionic interactions, hydrogen bonding, and enclosure of water involving capillary action (Chaplin, 2003). Because of these different binding mechanisms, soluble and insoluble fibers are capable of binding water (Oakenfull, 2001). The intensity of binding and the amount of water bound is largely dictated by the morphological structure and composition of fiber. The binding strength and the amount of water bound, therefore, vary among fiber sources (Cadden, 1987; Chaplin, 2003).

The ability of dietary fiber to hold water may be expressed in different ways. The expression "water-holding capacity" (WHC) describes the quantity of water that can be bound in fiber without the application of any external force, whereas "water-binding capacity" (WBC), or the preferred term "water-retention capacity," describes the quantity of water retained in a hydrated fiber after the application of an external force (Robertson et al., 2000). In the literature, however, these terms are used interchangeably (Ang, 1991; Leterme et al., 1998; Chaplin, 2003).

Several methods can be used to measure the capability of fiber to hold water. Water-holding capacity is measured by filtration (Chaplin, 2003) or by a Baumann apparatus (Auffret et al., 1994). Water-binding capacity can be measured by centrifugation, suction pressure, or the use of a dialysis tubing immersed in simulated gut contents (Stephen and Cummings, 1979; Cadden, 1987; Chaplin, 2003). These different methods evaluate different mechanisms of water binding. Measured values for WBC of fiber, therefore, depend on the method that was used to measure WBC. A European collaborative study has recommended standardized methods to evaluate WBC and other hydration properties of fiber (Robertson et al., 2000). This method is based on centrifugation, but modifications in terms of sample weight or centrifugal speed, are needed to minimize sample loss, which could affect the results (Robertson et al., 2000).

The WBC of fiber is an appropriate measure of bulk (Kyriazakis and Emmans, 1995) because the swelling property of fiber is positively correlated with WBC (Auffret et al., 1993). Soluble fiber usually has greater WBC than insoluble fiber (Auffret et al., 1994; Robertson et al., 2000). Cellulose and lignin are generally associated with low WHC and hemicelluloses are generally associated with high WHC (Shelton and Lee, 2000). Monosaccharide components of hemicelluloses that are positively correlated with WHC include arabinose and xylose (Holloway and Greig, 1984).

Viscosity

Viscosity refers to the ability of dietary fiber, particularly soluble dietary fiber, to thicken or form gels in solution (Dikeman and Fahey, 2006). Insoluble fiber is usually not associated with viscosity

although insoluble fiber may influence viscosity through its ability to absorb water (Takahashi et al., 2009).

The viscosity induced by dietary fiber is usually affected by the inclusion rate of dietary fiber, but the effect is not linear (Dikeman and Fahey, 2006). At a low concentration of soluble dietary fiber, the molecules in a solution are separated and are free to flow, but at a critical concentration, molecular movement becomes limited and physical entanglement of the dietary fiber molecules occur (Oakenfull, 2001). Thus, the viscosity of a solution with soluble dietary fiber increases rapidly with increasing concentration of pectin (Buraczewska et al., 2007). Measurement of viscosity involving dietary fiber in solution depends on the shear rate or the stirring rate of the liquid (Oakenfull, 2001). Greater shear rates result in low viscosity measurements (Dikeman and Fahey, 2006). In most studies, viscosity is measured using only one shear rate, but because different shear rates provide different viscosity values, comparison of viscosity values, whether in solution or in digesta, is not possible (Dikeman and Fahey, 2006). To overcome this limitation, measurement of viscosity using different shear rates is recommended to generate viscosity profiles for different dietary fibers (Dikeman and Fahey, 2006).

The viscosity of dietary fiber in solution or in digesta is also affected by molecular weight and particle size. At equal inclusion rates, high-molecular-weight guar gums produce more viscous solutions than low-molecular-weight guar gums (Dikeman and Fahey, 2006) and larger particle size also contributes to greater apparent viscosity in pig cecal contents than does small particle size (Takahashi and Sakata, 2002).

Cation-Binding Capacity

Dietary fiber also can bind minerals and organic molecules (Oakenfull, 2001). Free carboxyl groups and uronic acids (ionizable groups) are attached to metal ions. This attachment between fiber and minerals may prevent the absorption of minerals such as Ca^{+2}, Mg^{+2}, and Zn^{+2} (Cho et al., 1997). Part of the compounds in dietary fiber that bind minerals are phytates, but lignin and other co-passengers may also have effects on mineral absorption (Kritchevsky, 1988; Adlercreutz et al., 2006). Dietary fiber may also bind to organic molecules such as bile acids (Scheneeman, 1998) and lignin is among the strongest binding substances in dietary fiber (Kritchevsky, 1988).

Fermentation

The susceptibility of dietary fiber to microbial fermentation varies depending on the accessibility of dietary fiber to the microbial population in the hindgut (Oakenfull, 2001). The solubility and the WBC greatly influence the fermentation rate of dietary fiber. After absorption of water, dietary fiber swells, which increases the surface area of the polysaccharide for microbial action (Canibe and Bach Knudsen, 2001). Because soluble fiber has a higher WBC, and, therefore, a greater degree of swelling than insoluble fiber, soluble fiber is fermented at a faster rate than insoluble fiber (Auffret et al., 1993; Auffret et al., 1994; Oakenfull, 2001). Fermentation of soluble dietary fiber is mainly at the proximal colon, whereas fermentation of insoluble fiber is sustained until the distal colon (Cho, 1997).

Increase in fecal weight is mainly a function of fermentability of the fiber (Stephen and Cummings, 1979). Fermentable carbohydrates support microbial growth, which may contribute to an increase in fecal output by increasing fecal microbial mass (Cho et al., 1997). Undegraded residues from

poorly fermented dietary fiber also contribute to an increase in fecal output (Stephen and Cummings, 1979). Therefore, for dietary fiber that is composed of both soluble and insoluble fiber, the increase in fecal output is attributable to increases both in microbial fecal mass and in undegraded fiber residues (Cho et al., 1997). For purposes of laxation, official guidelines recommend dietary fiber that is coarsely ground (Jenkins et al., 1999). However, fecal output was similar between coarsely ground and finely ground wheat bran, but coarsely ground wheat bran resulted in higher frequency of bowel movement than finely ground wheat bran (Jenkins et al., 1999). Finely ground wheat bran, however, was fermented to a greater extent than coarsely ground wheat bran and the concentration of butyrate in the intestinal contents was greater if finely ground wheat bran was fed (Jenkins et al., 1999). These observations indicate that particle size may affect fermentability and the laxative effect of dietary fiber.

The major products of fiber fermentation are acetate, propionate, carbon dioxide, methane, and hydrogen (Lunn and Buttriss, 2007). The concentrations of each of these VFA vary depending on the chemical and physical structure of the dietary fiber (Lunn and Buttriss, 2007). However, acetate is the most abundant VFA, comprising about 60% of the total short chain fatty acid produced in the hindgut, whereas propionate and butyrate are produced in smaller quantities (Lunn and Buttriss, 2007).

Qualitative Aspects of Dietary Fiber Digestibility

Digestion

Digestion is the process of chemical breakdown that allows absorption of nutrients by enzymes secreted into the lumen of the gastrointestinal tract (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 dextrins, $\beta(1–2)$ 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). Digestion and absorption of nutrients occur in the small intestine, whereas fermentation occurs partially at the end of the small intestine and mainly in the large intestine.

Formation of VFA

The environment in the intestine requires that microbes live without oxygen. There are three types of microorganisms that can live without oxygen: anaerobic phototrophs, anaerobic respires (sulfate reducers, methanogens, and acetogens), and fermentative microorganisms (White, 2000; Müller, 2008). Fermentation is an energy-conservation process, in which electrons from redox reactions are transferred to part of the substrate, from which energy is derived. In this process, the substrate is only partially oxidized and only a small amount of energy is extracted for microbial growth (Müller, 2008).

Microbes start breaking down polysaccharides into smaller polysaccharides or the constituent monosaccharides during fermentation of dietary fiber in the pig intestine (Müller, 2008). Depolymerization occurs with the combination of a few reactions (e.g., hydrolysis, redox, phosphorylation,

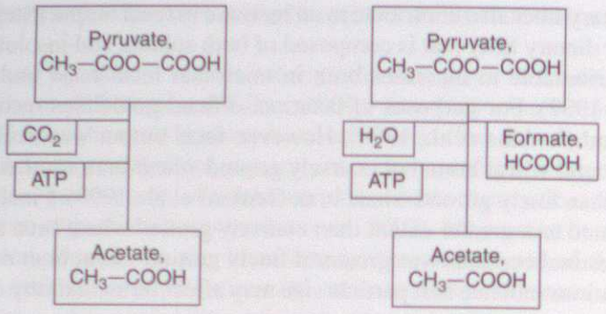


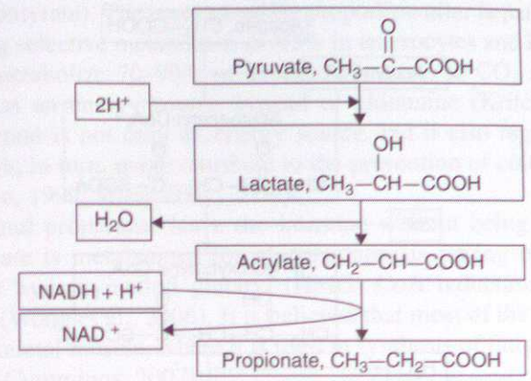
Figure 11.1 Synthesis of acetate from pyruvate during fermentation. Two different pathways may be used.

and lyases). The monomers are absorbed into the microbial cell and channeled into the pathways of central metabolism (White, 2000). Oxidation of hexoses (Embden-Meyerhof-Parnas or by Entner-Doudoroff) and pentoses (pentose phosphate) during fermentation converge at the formation of pyruvate, which is later oxidized to acetate, propionate, or butyrate (Figures 11.1, 11.2, and 11.3).

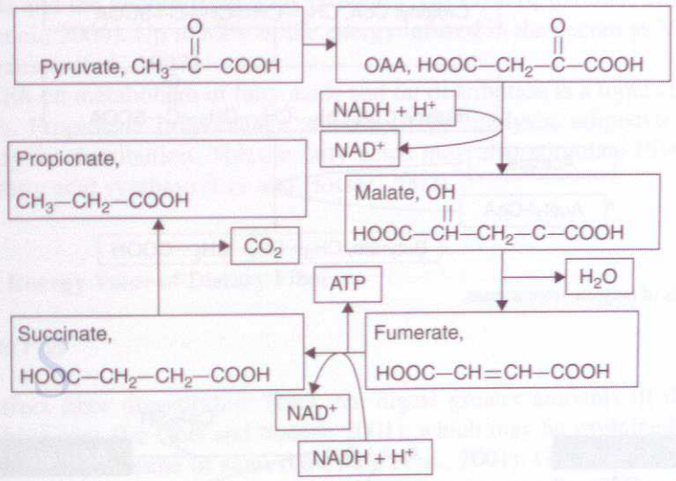
Absorption of VFA

The VFA that are produced by the microbes in the intestinal tract are excreted from the microbial cell into the intestinal lumen. Other microbes may use these products as a substrate and excrete a second product (anaerobic food chain). However, the pig absorbs some of the VFA and they all contribute to the energy status of the animal. Absorption of VFA in the pig's large intestine is a very efficient process (Barcroft et al., 1944). When VFA were infused in the cecum of growing pigs, less than 1% of those VFA were excreted in feces (Jørgensen et al., 1997). Absorption of VFA is proposed to occur by three mechanisms: (1) diffusion of protonated VFA, (2) anion exchange (Wong et al., 2006), and (3) transporter-mediated absorption (Kirat and Kato, 2006). Diffusion of protonated VFA is likely a minor form of absorption because at physiological pH, only 1% of all VFA in the intestinal lumen will be protonated (Cook and Sellin, 1998). If anion exchange is used, VFA are taken up into the enterocyte and HCO_3^- is released to the intestinal lumen (Cook and Sellin, 1998). More recent studies have documented the existence of active transportation of VFA. Active transporters of VFA belong to the monocarboxilate family, and MCT1 is the transporter present in the intestine of pigs (Welter and Claus, 2008). Another transporter expressed in human colonocytes is the sodium-coupled monocarboxylate transporter or SLC5A8 that may be implicated in absorption of VFA, especially butyrate (Thangaraju et al., 2008). The MCT1 transporter has been identified in pig intestinal cells, but it is not clear if the SLC5A8 is also present in pig colonocytes.

Absorption of VFA also facilitates absorption of other nutrients from the diet. Water and sodium are absorbed along with VFA (Yen, 2001). Plant lignans, diphenolic compounds similar to endogenous steroid hormones, are also co-transported by VFA (Bach Knudsen et al., 2006). Inulin improved the bioavailability of iron in corn and soybean meal diets in young anemic piglets (Yasuda et al., 2006). It is not clear if inulin increases absorption of Fe by increasing production of VFA, and thereby VFA increase absorption of Fe, or if VFA reduce luminal pH and increase solubility of Fe, or if VFA increase the expression of the Fe transporters (Tako et al., 2008).



(a)



(b)

Figure 11.2 **(a)** Synthesis of propionate from pyruvate using the acrylate pathway. **(b)** Synthesis of propionate from pyruvate using the randomizing pathway.

Metabolism of VFA

Volatile fatty acids are metabolized in three ways: (1) by colon cells that use them as a source of energy, (2) by the liver that uses propionate for gluconeogenesis, and (3) by adipose tissue and muscle (Wong et al., 2006). Oxidation of all VFA starts with their activation with coenzyme A (e.g., acetyl-CoA), and then they are channeled into pathways of central metabolism (Figure 11.4). Acetate is converted to acetyl-CoA, propionate becomes succinyl-CoA, and butyrate is turned into acetoacetyl-CoA (Nelson and Cox, 2008).

The concentration and molar proportions of VFA in portal blood is different from that in intestinal digesta, indicating that VFA are being metabolized in the intestinal cells (Argenzio and Southworth, 1974; Marsono et al., 1993). The typical VFA molar proportion in intestinal contents is 65:25:10

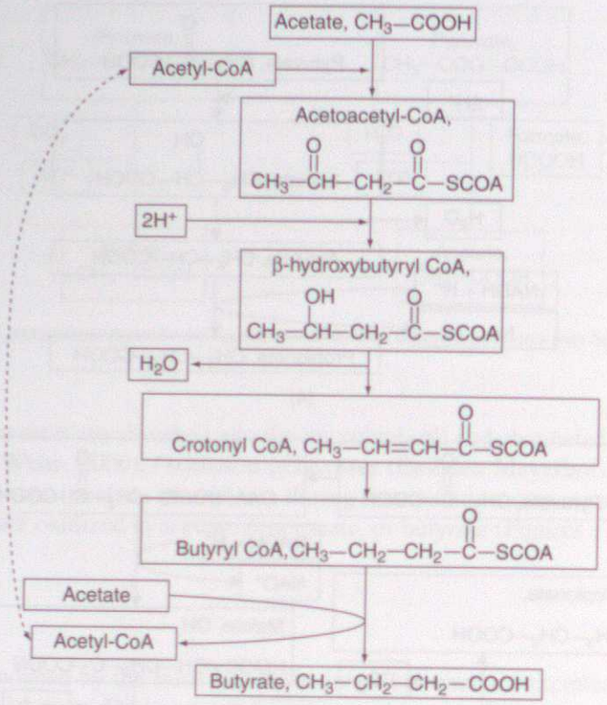


Figure 11.3 Synthesis of butyrate from acetate.

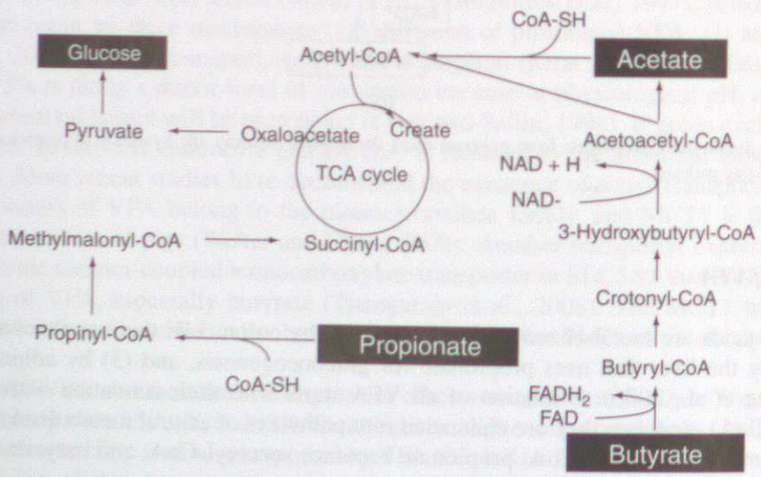


Figure 11.4 Oxidation of acetate, propionate, and butyrate.

(i.e., acetate:propionate:butyrate). The corresponding proportion after hepatic circulation, however, is 90:10:0, demonstrating selective metabolism of VFA in enterocytes and liver (Robertson, 2007).

Human colonocytes metabolize 70–90% of absorbed butyrate to CO_2 and ketone bodies and, therefore, use butyrate as an energy source instead of glutamine (Kritchevsky 1988; Elia and Cummings, 2007). Butyrate is not only an energy source, but it also regulates cell proliferation and differentiation, which, in turn, may contribute to the prevention of colorectal cancer and other diseases (Cook and Sellin, 1999; Wong et al., 2006).

Most of the acetate and propionate leave the intestine without being metabolized and reach the liver where propionate is metabolized for gluconeogenesis (Wong et al., 2006). Propionate metabolism may inhibit hydroxymethyl glutaryl (HMG) CoA reductase and, therefore, inhibit synthesis of cholesterol (Wong et al., 2006). It is believed that most of the acetate is transported to the adipose tissue and skeletal muscle, where it is used in synthesis of fatty acids or oxidization for ATP synthesis (Elia and Cummings, 2007).

Energy absorbed as VFA account for 67–74% of the total energy absorbed in the hindgut of pigs fed high-fiber diets and the energy from VFA provide 7.1–17.6% of the total available energy for the pig (Anguita et al., 2006). Up to 82% of the energy infused in the cecum as VFA is retained as body energy (Jørgensen et al., 1997).

The effect of VFA on metabolism of fatty acids and fat distribution is a topic of current research (Robertson, 2007). Propionate may change adipose tissue lipolysis, adipocyte size and differentiation, and body fat distribution. Volatile fatty acids may also stimulate PPARγ, acetyl-CoA carboxylase, and fatty acid synthase (Lee and Hosser, 2002).

Factors Affecting Energy Value of Dietary Fiber

Factors Inherent to Pigs

Age and breed affect fiber digestibility. Sows can digest greater amounts of dietary fiber than growing and finishing pigs (Le Goff and Noblet, 2001), which may be explained by a slower rate of digesta passage in the intestine of sows (Grieshop et al., 2001). Greater intrinsic ability of the microbial flora of sows to digest fiber may not be an important factor (Le Goff et al., 2003).

Meishan pigs have a greater ability to digest fiber than pigs from Western breeds (Fevriere et al., 1988; Kemp et al., 1991). Several other native breeds of pigs such as Mukota (Zimbabwe), Mong Cai (Vietnam), and Kunekune (New Zealand) have greater capacities for digestion of dietary fiber than pigs from commercial Western pig lines (Ndindana et al., 2002; Len et al., 2006; Morel et al., 2006). High-lean growing pigs also digest more energy than slow-growing pigs because of a greater concentration of cellulolytic bacteria in the large intestine of high-lean growing pigs (Varel et al., 1988). However, other experiments have not observed greater digestibility of dietary fiber in Meishan pigs than in pigs from Western breeds (Yen et al., 2004). There is no information about which portion of dietary fiber (insoluble versus soluble) native breeds digest better than Western breeds.

Factors Inherent to Diet

There are several processes that can be used to improve the microbial degradation of dietary fiber in fibrous feedstuffs, which may consequently increase the energy value of feed. These

processes include physical processes (e.g., grinding, heating, irradiation, and mechanical separation of plant parts) and chemical processes such as hydrolytic and oxidative agents. Sodium hydroxide may increase rumen digestibility of organic matter (OM) from 52% to 76% in barley straw and digestibility of DM by 22% in other crop residues (Fahey et al., 1993). The drawback of NaOH is that it can leak to soil where it is a pollutant. Anhydrous NH_3, NH_4OH, thermoammoniation, and urea have been used to treat fibrous materials, but the increase in digestibility is not as great as when using NaOH. In 32 experiments where crop residues were treated, digestibility of DM by ruminants increased by 15% (Fahey et al., 1993). Other chemicals such as $Ca(OH)_2$ and KOH have also been used to treat fibrous crop residues, but most of this work has been completed using ruminant animals and it is not known if similar results would be obtained with pigs.

Treatment of fiber with oxidative agents, such as ozone, increases in vitro DM digestibility from 44% to 67%. However, at ground level, ozone is also a pollutant, and, therefore, leaks to the environment and needs to be controlled (Fahey et al., 1993). Hydrogen peroxide may increase the apparent rumen digestibility of cellulose from 56.5% to 85.7% (Kerley et al., 1985) and sulfur dioxide can increase in vitro digestibility of DM by 80%. However, the extra sulfur in the treated feed may not be tolerable to animals (Fahey et al., 1993).

Contribution of Energy from Fermentation

Digestibility of Dietary Fiber

Fermentation of dietary fiber varies among feed ingredients and among different types of fiber (Bindelle et al., 2008). Data from 51 digestibility experiments show that the apparent ileal digestibility (AID) of dietary fiber in pigs fed high-fiber feed ingredients is between 10% and 62% (Back Knudsen and Jørgensen, 2001). The apparent total tract digestibility (ATTD) of cellulose varies between 23% and 65% in barley, 24% and 60% in wheat and wheat by products, 10% and 84% in rye and rye fractions, and 13% and 42% in bran and hulls of wheat, corn, and oats. The average ATTD of TDF in DDGS produced from corn is 47.5% and varies among sources from 29.3% to 57.0% (Urriola et al., 2009). The ATTD of soluble dietary fiber (92.0%) is greater than the ATTD of insoluble fiber (41.3%; Urriola et al., 2009).

Amount of VFA Produced Per Gram of Fermented Fiber

Each gram of fermented fiber may yield different amounts of VFA depending on the type of fiber that is fermented. Alpha galactosides such as raffinose and stachyose from soybeans yield more gases (CH_4 and H_2), cause flatulence, and produce less VFA during fermentation in the large intestine than fermentation of cellulose and hemicellulose (Liener, 1994). Acetate, propionate, and butyrate are the VFA produced in the largest concentration and, therefore, the only VFA reported in most experiments. The relative production of these VFA may vary slightly depending on the substrate that is fermented (Topping and Clifton, 2001), but for practical purposes the ratios between acetate, propionate, and butyrate may be assumed to be constant (de Lange, 2008). However, fermentation of branched chained amino acid (AA) yield branched chain VFA (isobutyrate, isovalerate, and valerate), so the concentration of the branched chained VFA depends on the degree to which branched chained AA were fermented. In most circumstances, the production of the three branched-chained VFA is less than 5% of the total VFA production.

Moles of ATP Produced Per Mole of VFA Absorbed and Metabolized

The moles of ATP produced from each mole of VFA that is oxidized by the animal are 10 ATP for acetate, 18 ATP for propionate, and 28 ATP for butyrate. The energy that is produced from each ATP is similar for all three VFA and average about 20 kcal/mole of ATP (Blaxter, 1989). This value is also similar to the energy obtained after utilization of ATP from other nutrients.

Negative Effects of Fiber on Energy and Nutrient Digestibility

Effects on Energy Digestibility

Increasing fiber concentration by increasing the inclusion of wheat bran in the diet (0–40%) progressively decreased total tract energy digestibility (Wilfart et al., 2007). The reduction in dietary energy digestibility was associated with a reduction in DM and OM digestibility (Wilfart et al., 2007). Adding a mixture of wheat bran, maize bran, soybean hulls, and sugar beet pulp to increase dietary fiber concentrations also reduced total tract energy digestibility in pigs with a corresponding reduction in carbohydrate digestibility (Le Gall et al., 2009). The degree of energy reduction was calculated to be 1% for each 1% increase in NDF concentration (Le Gall et al., 2009). The solubility of the fiber influences energy digestibility because total tract digestibility of beet pulp is greater than that of soybean hulls (Mroz et al., 2000). The presence of lignin in dietary fiber can also reduce energy digestibility (Wenk, 2001). The reduction in energy digestibility is a consequence of the substitution of digestible CP and carbohydrates, such as starch, with CP and carbohydrates bound to less-digestible cell wall components of fiber sources; the influence of the physiochemical characteristics of the fiber on the digestion and absorption processes of the dietary nutrients; and the physiological effects of fiber on the gastrointestinal tract (Le Gall et al., 2009).

Effects on Amino Acid Digestibility

Addition of 7.5% citrus pectin to a diet based on soybean meal and cornstarch reduced the AID of CP and AA by 8.2–28.7 percentage units, respectively (Mosenthin et al., 1994). A reduction in the standardized ileal digestibility (SID) of CP and AA was also observed when 4% or 8% apple pectin was added to a diet based on wheat, corn, and soybean meal (Buraczewska et al., 2007). A linear decrease in ileal N digestibility was observed in pigs when purified NDF that was processed from wheat bran was added at increasing levels to a diet based on soy isolate and cornstarch (Schulze et al., 1994). Adding 15% purified wheat NDF also reduced the AID of AA by 2–5.5 percentage units, except for the AID of Cys, Ala, and Gly, which were reduced by 18, 16, and 12 percentage units, respectively (Lenis et al., 1996). Increasing the concentration of NDF from 2.72% to 4.16% by adding graded levels of soy hulls (3–9%) to soybean meal (SBM)-cornstarch-based diets also induced a linear or quadratic reduction in AID and SID of most AA (Dilger et al., 2004). However, when 10% cellulose and barley straw was added to a SBM-cornstarch-based diet, the AID of AA, except Leu and Gly, was not reduced (Sauer et al., 1991). Such a reduction in AID of CP and AA was also not observed when graded levels of Solka floc (4.3–13.3%) were added to a SBM-cornstarch-based diet fed to young pigs (Li et al., 1994). In contrast, when carboxymethylcellulose was added to diets, SID of CP and AA increased (Larsen et al., 1994; Bartelt et al., 2002; Fledderus et al., 2007). Insoluble and poorly fermentable fibers, such as cellulose, impact CP digestibility through

their water-holding properties, whereas soluble fibers, such as carboxymethylcellulose and pectin, mediate their effects through their viscosity properties.

Dietary fiber can reduce the efficiency of CP and AA utilization by impairing the digestion process, decreasing CP absorption, or increasing endogenous CP and AA loss (Mosenthin et al., 1994). When 20% purified wheat bran NDF was fed to pigs, Schulze et al. (1995) observed an increase in ileal N flow with 59% of the N being endogenous. Addition of graded levels of pea inner fibers to protein-free diets resulted in an exponential increase in ileal N flow, which was correlated with increased WHC of the diet (Leterme et al., 1998). The ileal flow of epithelial cells also increased exponentially with a corresponding linear increase in crude mucin and bacteria (Leterme et al., 1998). When a viscous and nonfermentable fiber (carboxymethylcellulose) was added, mucin secretion and endogenous N loss also increased, but without a change in ileal bacterial population (Bartelt et al., 2002; Piel et al., 2004). However, an increase in some ileal populations of bacteria was observed by Owusu-Asieda et al. (2006) when viscous and fermentable fibers, such as guar gum, were fed to pigs. In contrast, adding cellulose, an insoluble and poorly fermentable fiber, at 3.31–16.5% to the diet did not induce an increase in endogenous CP and AA loss, which may be the reason for the absence of a reduction in the AID of CP and AA of the diets when cellulose was added (Li et al., 1994). The level and the source of dietary fibers are important factors that influence endogenous CP and AA losses (Sauer and Ozimek, 1986), and inclusion of cellulose may reduce the AID of AA only if a certain threshold level is exceeded (Li et al., 1994).

Effects of fiber on pancreatic secretions and enzyme activity may also be modulated by the physicochemical properties of fiber. Barley-based or wheat-based diets increased bile and pancreatic juice secretions compared with cornstarch-, casein-, and cellulose-based diets without affecting enzyme output (Low, 1989). However, when 400 g of wheat bran were added to isonitrogenous and isocaloric diets, chymotrypsin and trypsin secretions were greater than when pigs were fed diets without wheat bran (Langlois et al., 1986). In contrast, addition of pectin to SBM-based diets did not increase pancreatic secretions and did not affect secretions and enzyme activities of trypsin and chymotrypsin (Mosenthin et al., 1994). However, dietary carboxymethylcellulose may reduce pepsin activity in the stomach without affecting trypsin and chymotrypsin activities (Larsen et al., 1993).

Effects on Mucin Production and Endogenous Losses of Energy

The goblet cells of the gastrointestinal tract secrete mucin, a high-molecular-weight glycoprotein that lubricates the epithelial surface and protects the gut from physical abrasions, chemical aggressions, and microbial pathogenic attachments that may compromise gut health (Forstner and Forstner, 1994; Tanabe et al., 2006). Mucin also plays an important role in digestion and absorption of nutrients, and changes in mucin secretions may change the dynamics of absorption of dietary nutrients and endogenous molecules in the gut (Tanabe et al., 2006).

Several studies have shown that dietary fiber increases mucin secretion. The intestinal concentration of amino sugars in mucin (glucosamine and galactosamine) increased linearly as graded levels of wheat straw, corncobs, and wood cellulose were added to protein-free diets fed to pigs (Mariscal-Landín et al., 1995). Feeding carboxymethylcellulose, a viscous but nonfermentable fiber, also increased crude mucin concentration and output at the end of the ileum and the number of total ileal goblet cells per villus in the small intestines of weaned pigs increased (Piel et al., 2005). Supplementation of 5% citrus fiber to a purified diet also produced a substantial increase in small-intestinal mucin secretion (Satchithanandam et al., 1990).

In the stomach, the bulk-forming property and the fermentability of fiber did not affect mucin secretion, but in the cecum, the fermentability of fructooligosaccharide and beet pulp increased mucin secretion (Tanabe et al., 2006). A similar observation was reported by Libao-Mercado et al. (2007), when the addition of pectin stimulated mucin and mucosal CP synthesis in the colon but not in the jejunem.

The mucin molecule is composed of a protein backbone with attached carbohydrate side chains. One of the two regions of the mucin molecule has a protein backbone composed of Pro, Ser, and Thr. This region is resistant to proteolytic digestion because 80% of the protein backbone is protected by oligosaccharides, of which, the carbohydrate components are fucose, galactose, N-acetyl galactosamine, N-acetyl glucosamine, and sialic acids (Montagne et al., 2004). Because of the proteolytically resistant region of mucin, it is poorly digested, and, therefore, contributes substantial amounts of endogenous CP and carbohydrates in the ileal digesta (Lee et al., 1988; Lien et al., 1997).

Endogenous CP and AA recovered from the ileal digesta are mostly from pancreatic enzymes, epithelial cells, bacterial cells, and mucin, whereas endogenous carbohydrates are mostly from mucin (Lien et al., 1997, Miner-Williams et al., 2009). Endogenous CP and AA that are not reabsorbed before the end of the ileum are utilized by microbes in the hindgut of pigs (Souffrant et al., 1993; Libao-Mercado et al., 2009). Very little mucin is recovered in the feces, which further indicates that mucin in the hindgut is fully fermented (Lien et al., 2001).

Effects on Utilization of Other Nutrients

Carbohydrates

Adding wheat bran to a barley-based diet did not affect starch digestibility (Högberg and Lindberg, 2004) and adding 20 and 40% wheat bran to a cereal-based diet did not affect starch digestibility (Wilfart et al., 2007). Ninety-nine percent of the starch was digested in the small intestine and no starch was detected in the feces (Högberg and Lindberg, 2004; Wilfart et al., 2007). In contrast, to increase dietary fiber from 12% to 38%, the addition of graded levels of wheat bran, maize bran, soybean hulls, or sugar beet pulp in similar proportions reduced the ATTD of carbohydrates (Le Gall et al., 2009). The addition of guar gum also reduced glucose absorption from the jejunum by 50% (Rainbird et al., 1984). Similar observations were reported by Nunes and Malmlof (1992) and Owusu-Asiedu et al. (2006), where guar gum, but not cellulose, reduced plasma glucose concentration in pigs. The digesta viscosity induced by guar gum may have reduced the diffusion rate of glucose from the lumen to the epithelial cells causing a reduction in the absorption of glucose (Rainbird et al., 1984; Kritchevsky, 1988).

Lipids

The addition of 20% or 40% wheat bran to a cereal-based diet reduced the ATTD of ether extract by 7–12% compared with the control diet (Wilfart et al., 2007). Addition of beet pulp to a basal diet also reduced the AID and ATTD of fat, whereas the addition of wheat bran did not (Graham et al., 1986). In contrast, adding a combination of triticale, wheat, and wheat bran as a source of fiber to cereal-based diets improved the AID and ATTD of fat compared with the control diet (Högberg and Lindberg, 2004). This observation indicates that the solubility of diets containing different sources of fiber influences fat digestibility because when a mixture of wheat bran, maize bran, soybean hulls, and sugar beet pulp was added at graded levels to a low-fiber diet, the ATTD of fat was not affected, despite increasing levels of total dietary fiber in the diet (Le Gall et al.,

2009). The level of dietary fiber inclusion also influences lipid digestibility, because decreasing fat digestibility was observed as coconut expeller, soybean hulls, or sugar beet pulp were added at graded levels to a low-fiber control diet (Canh et al., 1998).

Minerals

Dietary fiber is composed of polysaccharides that may bind minerals, but the results of studies on dietary fiber's effects on mineral digestibility have not been consistent. Addition of 6% cellulose depressed the apparent absorption of Ca, P, Mg, and K. Serum concentrations of Ca, P, Cu, and Zn per unit of mineral ingested were also lower in sows fed high-fiber diets containing a combination of corncobs and wheat bran or oats and oat hulls compared with corn-SBM diets (Girard et al., 1995). In contrast, the addition of oat hulls, soybean hulls, and alfalfa meal did not affect total tract digestibility of Ca, P, Zn, or Mn (Moore et al., 1988). Likewise, the AID and ATTD of Ca, P, Mg, and Zn was not affected by the addition of 6% inulin to diets fed to pigs (Vanhoof and De Schrijver, 1996). The AID of ash was also not affected by the addition of 20% and 40% wheat bran to a low-fiber diet, but the ATTD of ash was reduced if high levels of wheat bran were added to the diet (Wilfart et al., 2007).

Effect of Dietary Fiber on Nitrogen Excretion and Manure Characteristics

A major impact of dietary fiber on nitrogen excretion in pigs is the shift of nitrogen excretion from the urine to the feces. The presence of fiber causes enhanced microbial fermentation in the hindgut, and, thus, the ammonia produced by the fermentation of dietary and endogenous protein is used for bacterial metabolism and growth (Zervas and Zijlstra, 2002). Therefore, there is an overall reduction in the concentration of ammonia available for absorption by the blood to be brought to the liver for urea synthesis (Mroz et al., 2000; Zervas and Zijlstra, 2002). As a consequence, urinary nitrogen excretion is reduced. The shift from urinary to fecal nitrogen excretion is dependent on the level of dietary fiber, because increasing the inclusion of sugar beet pulp linearly decreases the urinary-to-fecal nitrogen excretion ratio (Bindelle et al., 2009). The magnitude of response from the shift from urinary to fecal nitrogen excretion is also modified by the source of fiber, because the urinary-to-fecal nitrogen excretion ratio of barley-based diets is lower than maize- and wheat-based diets, and diets containing beet pulp have lower urinary-to-fecal nitrogen excretion ratios than diets with tapioca meal (Canh et al., 1997; Leek et al., 2007). Fermentable fiber, such as pectin and potato starch, has a stronger impact on shifting nitrogen excretion from urine to feces, compared with poorly fermentable fiber, such as cellulose (Pastuszewska et al., 2000). A gradual substitution of sugar beet pulp with oat hulls also increased the urinary-to-fecal nitrogen excretion ratio (Bindelle et al., 2009). This reduction in urinary nitrogen excretion is an advantage in the light of environmental concerns about ammonia emission in pig-production systems (Aarnink and Verstegen, 2007).

Increasing fiber in the diet linearly increases the amount of daily fecal-matter excretion in pigs (Moeser and van Kempen, 2002). However, there is a corresponding reduction in fecal DM with increasing fiber intake, indicating a substantial contribution of water to the fecal bulk from pigs fed high-fiber diets (Canh et al., 1998). Manure pH is also reduced with the addition of dietary fiber, and manure pH of pigs fed diets with soybean hulls and beet pulp was lower compared with pigs fed a control diet without soybean hulls and sugar beet pulp (Mroz et al., 2000). The manure from pigs fed diets containing 22% NDF from soybean hulls also had lower pH compared with the manure from pigs fed diets containing 6% and 12% NDF (Moeser and van Kempen, 2002). The reduction in the pH of the manure was attributed to the presence of high concentrations of volatile fatty acids in the feces (Canh et al., 1998). The concentration of VFA was dependent on the level and source of fiber (Canh et al., 1998).

Summary

Fiber comprises carbohydrates or lignin in plant materials that are indigestible by endogenous animal enzymes, and, as such, cause physiological effects in animals and humans. Fiber may be analyzed using different procedures, but the total dietary fiber analysis most accurately describes the fiber concentration in feed ingredients. This analysis may be expanded to include values for soluble and insoluble fiber.

Because of the increased usage of starch and oil in the biofuel industry, many feed ingredients that are now being fed to swine have high concentrations of fiber. However, fiber is not well utilized by pigs and the greater the concentration of fiber in the diet, the lower the digestibility of DM and OM. Animals and humans may obtain energy from fiber only after microbial fermentation of the fiber in the gastrointestinal tract and subsequent absorption of VFA. Acetate, propionate, and butyrate are the three VFA produced in greatest concentrations as fiber is fermented, and they all contribute to the energy status of pigs.

Soluble fiber is easily fermented, and total tract disappearance of soluble fiber may be greater than 90%. However, insoluble fiber is not easily fermented and the disappearance of insoluble fiber over the entire intestinal tract is often less than 50%. Therefore, increased concentrations of fiber in the diet will reduce overall energy digestibility of the diet. Fiber may also reduce the digestibility of AA due to increased endogenous AA losses in pigs fed high-fiber diets. Fiber induces increased production of mucin, which is one of the reasons for increased endogenous losses of AA. The total tract digestibility of lipids and minerals is also reduced in high-fiber diets, but dietary fiber may shift nitrogen excretions from urine to feces, which may contribute to a reduced synthesis of ammonia.

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12 Enzymes and Enzyme Supplementation of Swine Diets

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Introduction

Sustainable swine nutrition requires a sound understanding of enzyme supplementation in diets. The need to supply animals with nutritionally adequate diets contributes to the excretion of nutrients into the environment and the depletion of resources (for example, rock phosphate is used to meet P needs). The method currently used to meet animal needs is unsustainable because there is a finite supply of resources and a limit to which plants can use excreted nutrients effectively.

The use of exogenous enzymes can reduce dependence on non-renewable feed resources and nutrient excretion. This may ultimately reduce the costs of swine production because of expected faster growth (less nutrient intake per weight gain), less cost outlay for animal waste disposal (reduced nutrient excretion), and reduced use of mineral supplements (e.g., dicalcium phosphate).

To demonstrate how enzyme supplementation contributes to sustainable swine nutrition, this chapter first describes the inefficiencies associated with the digestive process in pigs, and then discusses the enzymes used in swine production and their effect on growth and nutrient utilization. The future of enzyme supplementation in swine nutrition is also discussed.

Brief Overview of the Digestive Process in the Pig

Digestion that starts in the mouth of the pig is insignificant because of the presence of a very small quantity of salivary α-amylase (Corring, 1980). The exocrine pancreas produces the most digestive enzymes in pigs. The enzymes produced by the pancreas are carbohydrases, proteases, lipases, and nucleases (Cranwell, 1995) and are used in the digestion of carbohydrates, protein, and fat. The products of pancreatic digestion are broken down to simple sugars (monomeric units) by brush-border enzymes or enzymes located at the brush-border membrane area.

Fermentation is aided by the length of time that digesta stays in the large intestine. The microflora in the large intestine produce enzymes that are capable of hydrolyzing ingested fiber (Yen, 2001). The most important products of the fermentation of carbohydrates and protein are the volatile fatty acids (VFA), which may account for up to 30% of the maintenance energy requirement of mature pigs (Rérat et al., 1987) and bacterial amino acids (AA).

Generally, carbohydrates, protein, and lipids are well digested by pigs because they have the complement of enzymes needed for hydrolyzing complex compounds into their building blocks.

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