14 Bioavailability of Amino Acids, Lipids, and Carbohydrates in Feedstuffs

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Introduction

To formulate efficient swine diets, fundamental knowledge on energy and nutrient requirements, energy and nutrient contents of feedstuffs, and bioavailability of energy and nutrients in feedstuffs is required. Because not all of the energy and nutrients in feedstuffs are available to pigs, expressing the requirements and formulating diets based on the available or digestible energy and nutrients, rather than total concentrations of energy and nutrients, is more effective in precisely satisfying the pig's needs. However, it is questionable whether there is sufficient information on the nutritive value of individual feed ingredients to achieve this objective, and there is no agreement on how to address the bioavailability issue in practice.

Part of the difficulty is that the availability of the energy-containing nutrients (i.e., proteins, lipids, and carbohydrates) in feedstuffs is rather difficult and expensive to measure. For practical purposes, therefore, values for the digestibility of energy and nutrients are usually measured and used as an indicator of the bioavailability, even though it is recognized that digestibility may not always be equal to availability. Nevertheless, formulation of diets based on digestible energy and nutrients is an improvement over formulation on the basis of total energy and nutrients because pigs can utilize only the energy and nutrients that are available to them. It is also likely that formulation of diets based on digestible energy and nutrients will contribute greatly to the development of environmentally friendly, optimum feeding strategies for successful and sustainable pig production. In this chapter, the bioavailability of amino acids (AA), lipids, and carbohydrates will be reviewed briefly, and the bioavailability of minerals and vitamins will be discussed in Chapter 15.

Amino Acid Bioavailability

Amino acids (AA) are needed for synthesis of body proteins that are used for maintenance or production of meat or milk. Most feed ingredients contain some AA, but in most commercial diets fed to swine, the majority of the AA are supplied by soybean meal or another oilseed meal. Often, synthetic sources of Lys, Met, and Thr are also used to balance AA needs of the animals. However, not all AA in the diets are absorbed and can be utilized, and differences among feed ingredients exist in their ability to supply digestible AA. It is, therefore, important to assess the availability of AA in feed ingredients used in diets fed to swine.

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Relative Amino Acid Bioavailability

Only AA that can be incorporated into tissue proteins are bioavailable. Bioavailability is defined as the proportion of dietary AA that is absorbed in a chemical form that is suitable for protein synthesis (Batterham, 1992; Lewis, 1992). Bioavailability of AA may be measured using slope ratio techniques, in which the response of an animal to the intake of graded levels of an AA is measured (Batterham, 1992). The response variables are most often whole-body protein deposition (Batterham, 1992) or AA oxidation (Moehn et al., 2005). The response to the addition of AA from a test-feed ingredient is compared with the response to feeding a standard source of AA, and results are expressed as the relative bioavailability of AA.

Diets used for this procedure need to be deficient in only the AA in question and all levels of this AA need to be fed below the requirement of the animal. It is assumed that the response to the increased intake of the AA is linear. The slope ratio procedure is tedious and costly, and the determined values for AA availability are unique only to the experimental procedures used and may not be additive in a mixed diet (Gabert et al., 2001). For practical feed formulation, AA availability values measured by the slope ratio technique are, therefore, not used. Instead, the digestibility of AA is measured and used as an indication of the quantities of dietary AA that are available to the animal (Stein and Nyachoti, 2003).

Amino Acid Digestibility

The term "AA digestibility" does not refer to the digestion of AA; it refers only to the digestion of the peptide bonds connecting AA in a dietary protein (Fuller, 2003). Because the AA of undigested dietary proteins entering the large intestine may be fermented or metabolized by hindgut microbes before they are excreted from the animal in the fecal material, values for total tract digestibility of AA are not accurately predicting AA absorption by the animal (Sauer and Ozimek, 1986). To avoid the manipulation by hindgut microbes, the digestibility of AA by nonruminant animals is most correctly measured at the end of the small intestine and is referred to as ileal digestibility values (Sauer and de Lange, 1992). This creates a need for using techniques that allow for collection of ileal fluids at the end of the small intestine. Several techniques have been proposed for this, and comprehensive reviews of these techniques have been published (Gabert et al., 2001; Moughan, 2003). In North America, the installment of a T-cannula in the distal ileum of pigs (10–15 cm prior to the ileo-cecal valve) is the procedure of choice. This procedure has proven to be accurate and has a minimal trial-to-trial variation. Because the T-cannula, like most other procedures that are used for ileal fluid collections, does not allow for the total collection of the ileal output from the animal, an indigestible marker needs to be included to calculate changes in AA concentrations. Chromic oxide is often used for this purpose, but other markers exist. Ileal digestibility values are calculated using Equation 14.1 (Stein et al., 2007):

$$\text{AID}\ (\%) = (1 - [(\text{Aad}/\text{AAf}) \times (\text{Mf}/\text{Md})]) \times 100 \qquad (14.1)$$

where AID is the apparent ileal digestibility of an AA, AAd is the AA concentration in the ileal digesta DM (g/kg DM), AAf is the AA concentration in the feed DM (g/kg DM), Mf is the marker concentration in the feed DM (g/kg DM), and Md is the marker concentration in the ileal digesta DM (g/kg DM).

Amino acid digestibility values calculated using this procedure are called "apparent ileal digestibility values" to reflect the fact that these values are calculated simply by subtracting the ileal AA output from the intake of AA (Nyachoti et al., 1997; Mosenthin et al., 2000; Stein et al., 2007). The ileal output of AA that is used to calculate values for the AID of AA contain undigested dietary AA along with AA of endogenous origin. Endogenous AA are AA that were absorbed from the small intestine and then secreted into the intestinal tract in the form of endogenous proteins. Because of the presence of endogenous protein in the ileal output of AA, values for AID do not accurately represent the digestibility of the dietary proteins.

Endogenous AA

Endogenous AA mainly consist of AA from digestive enzymes, mucoproteins, desquamated cells, serum albumin, peptides, free AA, amines, and urea (Moughan and Schuttert, 1991). The main sources of endogenous protein are saliva, gastric secretions, pancreatic juice, bile acids, and intestinal secretions (Low and Zebrowska, 1989; Tamminga et al., 1995). The intestinal secretions account for more than 60% of total endogenous secretions (Low and Zebrowska, 1989) and consist mainly of desquamated epithelium cells and mucin secreted by the goblet cells, as well as other glycoconjugates secreted by the enterocytes (Lien et al., 1997). Saliva and gastric, pancreatic, and bile secretions each contribute 8–10% of total endogenous output. It has been estimated that 70–80% of the endogenous AA that are secreted into the gastrointestinal (GI) of an animal are hydrolyzed and re-absorbed before reaching the distal ileum (Souffrant et al., 1993; Krawielitzki et al., 1994; Fan and Sauer, 2002). The remaining endogenous AA are mainly from deconjugated bile salts and mucin glucoprotein because these components are largely resistant to proteolysis and, therefore, escape re-absorption (Taverner et al., 1981; Moughan and Schuttert, 1991; Lien et al. 1997). Glycine accounts for more than 90% of the total AA content of bile acid, and mucin glycoprotein is rich in Pro, Glu, Asp, Ser, and Thr. There is also evidence that Pro, Gly, Thr, Ser, Asp, and Glu are absorbed more slowly from the intestinal lumen than are most other AA (Taverner et al., 1981). These AA are mainly absorbed as constituents of small peptides and are subsequently hydrolyzed in the enterocyte. However, this process is slow and, therefore, the net absorption rates of these AA is less than those of other AA (Holmes et al., 1974). It also has been suggested that the activity of pyrroline-5-carboxylate reductase (the enzyme that catalyzes Pro synthesis) is greater than that of the Pro degrading enzyme, Pro oxidase (Mariscal-Landin et al., 1995). Therefore, Pro, along with Gly, will accumulate in the enterocytes and diffuse into the lumen (Gardner, 1975). Because of these mechanisms, endogenous protein usually has a relatively high content of Pro, Gly, Thr, Ser, Asp, and Glu. Several estimates of the AA composition of endogenous protein have been published (Wünsche et al., 1987; Boisen and Moughan, 1996; Stein et al., 1999b).

The endogenous AA that are secreted into the intestinal tract may be divided into basal endogenous secretions and diet-specific endogenous secretions (Jansman et al., 2002; Stein et al., 2007). The basal endogenous AA consist of AA that are secreted into the gastrointestinal tract of fasted animals in addition to AA that are secreted in response to the DMI of the animals. These losses are usually measured as grams per kilogram dry matter intake (DMI). Recent evidence suggests that the quantity of endogenous losses (measured in g/kg DMI) depends on the DMI of the animal and declines as DMI increases. The reason for this decrease is that the fasting endogenous loss contributes a decreasing quantity of AA per kg DMI as DMI increases (Moter and Stein, 2004). As a consequence, only values for endogenous losses that are measured in animals given free access to feed are applicable for growing pigs and lactating sows, whereas values for endogenous losses of

AA by gestating sows should be measured in restricted fed animals to reflect commercial conditions (Stein et al., 1999b).

Basal endogenous losses may be measured by measuring the ileal output of AA after feeding a protein-free diet (Stein et al., 1999b). Although this procedure has been criticized for creating an un-physiological state in the animal, it is believed that values for endogenous losses of most AA are accurately predicted using this procedure (Stein et al., 2007). It is, however, recognized that the protein-free procedure sometimes yields unrealistic values for the endogenous losses of Gly and Pro. Alternative procedures to estimate basal endogenous losses of AA include the peptide alimentation procedure and the regression procedure (Stein et al., 2007). In North America, the protein-free diet is, however, the most commonly used procedure and basal endogenous losses of AA are calculated according to Equation 14.2 (Stein et al., 2007):

$$IAA_{end} = [AAd \times (Mf/Md)] \quad (14.2)$$

where IAA_{end} is the basal endogenous loss of an AA at the distal ileum (mg per kg DMI), AAd is the concentration of that AA in the digesta DM, Mf is the marker concentration in the feed DM, and Md is the marker concentration in the ileal digesta DM.

In addition to the basal endogenous losses, most feed ingredients also introduce diet-specific endogenous losses, which are mainly caused by fiber and anti-nutritional factors in the ingredient (Seve et al., 1994; Boisen and Moughan, 1996; Jansmann et al., 2002). The diet-specific losses may vary from almost none (in purified ingredients such as casein) to values that exceed the basal endogenous losses (as in ingredients that are high in fiber and anti-nutritional factors, such as canola meal or wheat middlings). Comprehensive reviews of endogenous losses and factors influencing endogenous losses have been published (Taminga et al., 1995; Boisen and Moughan, 1996; Nyachoti et al., 1997; Jansman et al., 2002). The variation in the total quantities of endogenous proteins that have been reported in the literature also has been published (Jansman et al., 2002).

The diet-specific endogenous losses of AA cannot be directly measured. However, it is possible to estimate the total endogenous losses (i.e., basal and diet-specific losses) of some AA using the so-called homoarginine technique, or the N^{15} isotope dilution technique. It is possible to estimate the losses of a few AA only if these procedures are used, and the losses of all other AA are subsequently calculated from these few AA by assuming that the AA composition of endogenous protein is always constant. It is, however, recognized that the AA composition of endogenous losses is not always constant (Stein et al., 1999b) and this may result in erroneous results for endogenous losses of AA predicted by the homoarginine or the N^{15} isotope procedure. The homoarginine and the N^{15} isotope dilution techniques are also tedious and expensive to use and are, therefore, not commonly used in practical feed-ingredient evaluation (Stein et al., 2007).

Standardized Ileal Digestibility of AA

Secretion of endogenous AA into the GI tract of pigs introduces several challenges when accurately estimating AA absorption, because these secretions are included in the ileal AA output that is used to calculate AID values. The endogenous AA comprise a relatively larger portion of the total AA output from pigs fed low-protein feed ingredients (i.e., cereal grains) compared with pigs fed ingredients with a greater protein concentration such as soybean meal. Therefore, values for AID that are measured for low-protein feed ingredients are usually underestimated (Donkoh and Moughan, 1994; Fan et al., 1994; Stein et al., 2005). Because of this underestimation, values for AID that are

measured in individual feed ingredients usually do not add up in a mixed diet that contains both low-protein feed ingredients and high-protein ingredients (Stein et al., 2005). However, if the values for ileal digestibility are corrected for the basal endogenous losses of AA, then this underestimation may be avoided. By doing that, the standardized ileal digestibility (SID) values are calculated according to the equation put forth by Stein et al. (2007):

$$SID = [AID + (IAA_{end}/AAf)] \quad (14.3)$$

where SID is the standardized ileal digestibility of an AA (%), AID and IAA_{end} are calculated according to Equations 14.1 and 14.2, respectively, and AAf is the AA concentration in the feed DM (g/kg DM). It was recently demonstrated that values for SID are additive in mixed diets, even if low-protein feed ingredients are incorporated in the diets (Stein et al., 2005). Thus, by using SID values, the problems associated with using AID values are eliminated, and for practical feed formulation, it is recommended that values for SID are used rather than values for AID. Discussions of the principles behind calculations of standardized ileal digestibility values have been published (Mosenthin et al., 2000; Jansman et al., 2002; Stein et al., 2007).

Methods Used to Determine Digestibility Values

The simplest and easiest method to use for calculating digestibility values is the so-called direct method. Using this approach, the assay feedstuff provides all the nitrogen and AA in the assay diet, and the AID of all AA is measured directly in the diet. In experiments in which the AID of cereal grains are determined (e.g., Lin et al., 1987; Green et al., 1987; Stein et al., 1999a; Pedersen et al., 2007), the feed ingredient under investigation usually provides approximately 90% of the assay diet, with the remaining part of the diet being provided by non-protein additives such as vitamins and minerals, oil, and possibly sucrose. Where AID are to be determined in protein concentrates (e.g., Green and Kiener, 1989; Fan et al., 1996; Stein et al., 1999a), the test feed ingredient usually provides only 20–50% of the total diet, and starch, oil, and sucrose are used as non-protein energy sources in these diets. The direct method has been widely used in digestibility experiments for a wide variety of feed ingredients, and the majority of the AID provided in the literature are obtained using this method.

An alternative procedure is the so-called difference method. Using this approach, a basal diet and an assay diet are formulated. The basal diet contains a basal protein-containing feedstuff, and the assay diet consists of a mixture of the basal diet and the assay feedstuff (Fan and Sauer, 1995a,b). The mixture is formulated to ensure that the CP concentration in the assay diet is at least 14–16%. The digestibility value of the assay feedstuff is calculated by difference, assuming there is no interaction between the digestibility values in the basal and the assay feed ingredients. However, the reliability of the digestibility values obtained with the difference method depends on the level of contribution of each AA from the assay feed ingredient; the greater the contribution of each AA, the more reliable are the results (Fan and Sauer, 1995a). The difference procedure is mainly used to measure the digestibility of AA in ingredients that have low palatability, such as yeast products or blood products (Mateo and Stein, 2007). Such ingredients cannot always be used at levels that will produce diets containing more than 10% CP, and, therefore, it is preferred to mix these ingredients with other ingredients that have better palatability and then use the difference procedure to calculate the digestibility values.

In Vitro Procedures to Estimate AA Digestibility

It has been suggested that AA digestibility in feed ingredients may be estimated using in vitro procedures rather than in vivo procedures. The most common in vitro procedure is the enzymatic procedure that consists of two steps that are supposed to simulate the conditions in the stomach and small intestine, respectively. In the first step, a small sample of the feed ingredient is incubated with pepsin at 39°C at pH 2 for approximately two hours. The pH is then raised to 6.8, and the sample is subsequently incubated with pancreatin (a mixture of pancreatic proteolytic enzymes) for six to eight hours. Samples are then filtrated and washed in ethanol and acetone and dehydrated. The filtrate is analyzed for CP and AA, and the concentration of CP and AA in the filtrate is believed to correspond to the undigested AA from the ingredients. This procedure was initially developed for predicting AA digestibility in mixed diets (Boisen and Fernandez, 1995). Alternatives to the procedure including longer incubation times were later introduced to predict AA digestibility in meat-and-bone meal (Qiao et al., 2004). One of the limitations of the procedure is that incubation of samples of only 0.5 g are often used. That leaves very small amounts of undigested samples in the filtrate and it may not be possible to accurately determine AA concentration in these samples. It is, therefore, necessary to use greater sample sizes and sometimes also to combine the filtrate from several samples to be able to analyze AA in the filtrate. The in vitro procedure is not commonly used to estimate AA digestibility in feed ingredients, but current work to improve this technique may result in a wider acceptance in the future.

Factors Affecting Digestibility of AA

Effect of Age and Physiological State of Animals

Young pigs are highly efficient in digesting milk proteins (Mavromichalis et al., 2001). However, the AID of AA in soybean protein is low in young pigs, but increases with the age of the animal (Wilson and Leibholz, 1981; Caine et al., 1997). The reason for the low digestibility of proteins of vegetable origin in young pigs is that the activity of some of the protein-digesting enzymes is low in early life (Moughan, 1993). It has been demonstrated that finishing pigs have digestibility values for feed ingredients that are similar to that of sows (Stein et al., 2001), provided that the level of feed intake is the same, but it is not clear when the digestive capacity of the pig reaches a plateau. It does appear, however, that the physiological state of the animal does not influence the digestibility of AA.

Effect of Level of Feed Intake

The AID of protein and AA will increase as feed intake increases from a level that is close to the maintenance requirement for energy to an amount that is approximately twice that level (Motor and Stein, 2004). However, further increases in feed intake do not change the AID (Sauer et al., 1982; Haydon et al., 1984; Albin et al., 2001b; Moter and Stein, 2004). The reason for the reduced AID by animals fed at a low level of feed intake is that the basal endogenous losses of AA at the end of the small intestine are elevated in animals on a low level of feed intake (Butts et al., 1993; Stein et al., 1999b; Moter and Stein, 2004). Because SID values are calculated by correcting AID for the basal endogenous losses, SID values are linearly decreased as feed intake is increased (Moter and Stein, 2004). Thus, because of the impact of endogenous AA losses, the influence of the level of feed intake on SID values is opposite the influence of feed intake on the AID values. The implication of these differences is that growing pigs and lactating sows that are used to measure AA digestibility values should be allowed ad libitum access to their diets because this is usually the way they are fed under commercial conditions. When AA digestibility values are measured for gestating sows, the animals should be restricted in their feed intake to reflect the feed intake of gestating sows kept under commercial conditions.

Effects of Chemical Composition of the Feed Ingredient

The concentration of CP and AA in the diets used to measure AA digestibility influences the measured values for AID as previously discussed. The level of dietary fiber may decrease the AID of AA because of the influence of fiber on the endogenous losses of AA (Mosenthin et al., 1994; Schulze et al., 1994; Lenis et al., 1996). This is particularly true if soluble dietary fiber is used, whereas insoluble dietary fiber may not always influence AA digestibility.

Dietary fat may increase the AID and SID of AA (Imbeah and Sauer, 1991; Li and Sauer, 1994; Cervantes-Pahm and Stein, 2008) because dietary fat may reduce digesta passage rate and thus provide more time for the proteolytic enzymes to hydrolyze dietary proteins. There is, however, no effect of the dietary level of fat on the endogenous losses of AA (de Lange et al., 1989).

Dietary anti-nutritional factors such as trypsin inhibitors, lectins, and tannins reduce ileal AA digestibility (Jansman et al., 1994; le Guen et al., 1995; Schulze et al., 1995; Yu et al., 1996). The main reason for these observations is that anti-nutritional factors increase the diet-specific endogenous losses of AA. As a consequence, both AID and SID values are reduced in diets or feed ingredients containing anti-nutritional factors.

Bioavailability of Lipids

Lipids are essential components for a variety of body functions in animals. Lipids also contain greater amounts of energy available to animals than carbohydrates and proteins, and, therefore, dietary lipids have been of special importance as a means to increase energy concentrations of swine diets.

Dietary lipids that are present in common feed ingredients contain different amounts of lipids and have varying fatty acid compositions (Table 14.1), but lipids in all ingredients are predominantly present in the form of triglycerides (Stahly, 1984). Lipid digestion is different from the digestibility of other nutrients because lipids are poorly soluble in the aqueous environment of the gastrointestinal tract. Therefore, gastrointestinal lipid digestion requires specific sequential steps including emulsification, enzymatic hydrolysis, and micelle formation (Bauer et al., 2005). After digestion and absorption, most lipids are directly incorporated into body lipids or, to a lesser extent, oxidized to yield energy in the form of ATP in the body. It is assumed that all absorbed lipids are bioavailable, and availability is, therefore, most often determined based on digestibility, as is the case for most other nutrients. Although the digestibility of dietary lipids is dependent on the digestibility of individual fatty acids, the digestibility of fatty acids is usually not measured, and, in most cases, only the digestibility of the total quantity of dietary lipids is measured. Lipid digestibility may be affected by several factors. It is believed that the apparent total tract digestibility of lipids in most feed ingredients fed to swine varies from 25% to 77% (Noblet et al., 1994).

Physicochemical Properties of Lipids

Chemical Property of Fatty Acids

Degree of saturation and chain length of fatty acids in dietary lipids are important chemical properties that have a significant impact on micelle formation and lipid solubility in the gastrointestinal tract

Table 14.1 Crude fat and fatty acid composition in feed ingredients.

Ingredients	Crude fat, %	Fatty acid, % of total fatty acids					
		C16:0	C18:0	C18:1	C18:2	C18:3	U:S[1]
Corn[2]	3.7	11.1	1.8	26.9	56.5	1.0	6.52
Barley[2]	1.8	22.2	1.5	12.0	55.4	5.6	2.93
Sorghum[2]	2.9	13.5	2.3	33.3	33.8	2.6	4.56
Wheat bran[2]	3.4	17.8	0.8	15.2	56.4	5.9	4.24
Full fat soybean, extruded[2]	17.9	10.5	3.8	21.7	53.1	7.4	4.68
Soybean meal, 48% CP[2]	1.9	10.5	3.8	21.7	53.1	7.4	4.68
Soybean oil[3]	100	10.3	3.8	22.8	51.0	6.8	5.64
Sunflower oil[3]	100	5.4	3.5	45.3	39.8	0.2	8.47
Palm oil[3]	100	43.5	4.3	36.6	9.1	0.2	0.94
Beef tallow[3]	100	24.9	18.9	36.0	3.1	0.6	0.92
Choice white grease[3]	100	21.5	14.9	41.1	11.6	0.4	1.45
Lard[3]	100	23.8	13.5	41.2	10.2	1.0	1.44

[1] U:S is the ratio of unsaturated to saturated fatty acids.
[2] Adapted from Sauvant et al. (2002).
[3] Adapted from NRC (1998).

and, therefore, on lipid digestibility. In general, unsaturated fatty acids are more digestible than saturated fatty acids (Table 14.2) because unsaturated fatty acids have a greater potential for micelle formation than do saturated fatty acids (Freeman et al., 1968; Stahly, 1984). Unsaturated fatty acids may also aid in the digestion of saturated fatty acids by increasing micelle formation of saturated fatty acids, and the digestibility of saturated fatty acids is improved if unsaturated fatty acids are mixed with saturated fatty acids (Powles et al., 1993). Therefore, it has been suggested that the ratio of unsaturated to saturated fatty acids is an important determinant for lipid digestibility. Stahly (1984) concluded that apparent digestibility of lipids in swine diets ranges between 70% and 80% if the ratio of unsaturated to saturated fatty acids is above 1.5; however, apparent digestibility of lipids declined when the ratio was less than 1.3. Similar results were observed by Powles et al. (1995), who reported that an unsaturated-to-saturated ratio of less than 1.5 decreased the DE of dietary lipids fed to pigs of 12–90 kg BW.

Chain length of fatty acids also affects lipid digestibility. Fatty acids with a chain length of less than 14 carbons are more digestible than fatty acids with a longer chain length (Cera et al., 1989; Straarup et al., 2006), even if the short-chain fatty acids (SCFA) are predominantly saturated fatty acids. The reason is that SCFA are relatively more soluble in the aqueous environment of the intestinal tract than are long-chain fatty acids (LCFA), and, therefore, SCFA may be directly absorbed by epithelial cells without micelle formation (Ramírez et al., 2001). Short-chain fatty acids may also be more easily incorporated into and released from mixed micelles than LCFA (Bach and Babayan, 1982; Stahly, 1984). In experiments with weanling pigs it was observed that the apparent total tract digestibility of lipids from coconut oil was greater than the digestibility of lipids from corn oil or tallow (Cera et al., 1989), and apparent total tract digestibility values of SCFA of more than 90% was reported. For growing pigs, however, the effect of chain length of fatty acids on lipid digestibility is questionable (Table 14.2; Jørgensen et al., 2000).

The position and distribution of fatty acids on the triglyceride molecules may also affect lipid digestibility (Bracco, 1994). Pancreatic lipase specifically hydrolyzes the sn-1 and sn-3 ester-linkages of triglycerides, leading to a 2-monoglyceride and two free fatty acids. A greater potential

Table 14.2 Apparent total tract digestibility (ATTD) of lipids in the diets fed to pigs[1].

References	BW, kg	Basal diets	Supplemental lipids		
			Source	Inclusion, %	ATTD,%
Cera et al., 1989	6.1	Corn-SBM-whey	Tallow	8	81.8
			Corn oil	8	84.8
			Coconut oil	8	87.3
Li et al., 1990	5.6	Corn-SBM-whey-skim milk	—	0	40.8
			Soybean oil	10	80.1
			Coconut oil	10	88.0
			Blend (50%:50%)	10	85.6
Jones et al., 1992	5.3	Corn-SBM-whey-skim milk	Soybean oil	10	89.5
			Coconut oil	10	88.8
			Tallow	10	80.9
			Lard	10	84.8
Jin et al., 1998	5.8	Corn-SBM-whey	Coconut oil	10	83.4
			Corn oil	10	82.3
			Soybean oil	10	83.7
			Tallow	10	79.8
Jørgensen et al., 2000	35.0	Wheat bran-starch-sucrose	—	0	83.4
			Fish oil	15	92.8
			Rapeseed oil	15	93.4
			Coconut oil	15	88.4
Duran-Montgé et al., 2007	40–50	Barley	—	0	29.4
			Tallow	10	86.5
			HO sunflower oil[2]	10	84.7
			Sunflower oil	10	85.5
			Linseed oil	10	85.0
			Blend[3]	10	85.4
Kil, 2008	22	Corn-SBM	—	0	33.2
			Soybean oil	5	74.2
			Soybean oil	10	82.4
			Choice white grease	10	80.5
	84	Corn-SBM	—	0	49.1
			Soybean oil	5	73.1
			Soybean oil	10	82.1
			Choice white grease	10	81.9

[1] SBM = soybean meal.
[2] High-oleic sunflower oil.
[3] Lipid blend (5.5% tallow, 3.5% sunflower oil, and 1% linseed oil).

of 2-monoglycerides than free fatty acids for micellar incorporation, however, favors the digestion of fatty acids attached to the sn-2 position in triglycerides (Ramírez et al., 2001).

Free (non-esterified) fatty acids in dietary lipids have a low digestibility because free fatty acids are less likely to enter the micellar phase than esterified fatty acids (Freeman, 1984) and they have a greater tendency to form insoluble mineral soaps in the intestinal tract (Ramírez et al., 2001). An increased concentration of free fatty acids may also inhibit micelle formation of other lipid metabolites by disturbing the balance between 2-monoglycerides and free fatty acids (Dierick and Decuypere, 2004). Therefore, increasing concentrations of free fatty acids in dietary lipids decreases lipid digestibility in weanling (Swiss and Bayley, 1976; Powles et al., 1994) and grower–finisher pigs

(Powles et al., 1993; Jørgensen and Fernández, 2000). However, DeRouchey et al. (2004) observed no difference in the digestibility of lipids and fatty acids for weanling pigs fed diets containing increasing amounts of free fatty acids from hydrolyzed choice white grease.

Physical Properties of Fatty Acids

Lipids in the diets are present as intact lipids in feed ingredients (e.g., corn and whole soybeans) or supplemental extracted lipids from animal or vegetable sources. For commercial corn-SMB diets fed to finishing pigs, approximately 40% of the lipids are intact lipids from corn and 60% are supplemental lipids (Azain, 2001). The fatty acids in intact lipids are less digestible than fatty acids in the supplemental lipids, because intact lipids are mostly encased in the membrane of lipid cells, and are therefore more resistant to emulsification and enzymatic hydrolysis than liquid lipids (Adams and Jensen, 1984; Li et al., 1990; Duran-Montgé et al., 2007; Kil, 2008). Therefore, physicochemical breakdown of lipid cell walls may improve the digestibility of intact lipids, and pelleting increases the digestibility of lipids by growing pigs fed diets containing corn, SBM, and no added lipids (Noblet and Champion, 2003). Likewise, the apparent digestibility of lipids by weanling pigs improved from 54.7% to 70.2% when the diet was pelleted (Xing et al., 2004). Both the apparent and the true digestibility of lipids in corn dried distillers grains with solubles is 19% greater than in corn, which indicates that the fermentation or other processing that takes place in an ethanol plant allows intact lipids to be more digestible (Kim et al., 2009).

Dietary Components that Influence Digestibility of Lipids

Dietary Fiber

Dietary fiber has a negative impact on lipid digestibility. Stahly (1984) noted that 1% additional increase in crude fiber concentration depresses the apparent digestibility of lipids by 1.3–1.5%. The negative effects of dietary fiber on lipid digestion have been attributed to increased passage rate of digesta and decreased solubility of lipids in the gastrointestinal tracts (Stahly, 1984). Dietary fiber can also promote the loss of endogenous lipids such as desquamated epithelial cells, bile acids, and microorganisms, leading to a reduction in the apparent digestibility of lipids (Bach Knudsen et al., 1991; de Lange, 2000). Although both the characteristics and the amount of dietary fiber affect lipid digestibility, it is likely that the characteristics of fiber are more important than the amount of fiber in the diet. Increasing amounts of purified cellulose has no impact on lipid digestibility, indicating that the simplified chemical structure of purified fiber may not interfere with lipid digestion (Kil et al., 2010). In contrast, soluble dietary fiber that increases digesta viscosity reduces lipid digestibility because increased viscosity disturbs enzymatic hydrolysis, micelle formation with bile acids, and the mucosal uptake of lipids (Smith and Annison, 1996).

Dietary Protein and Minerals

Dietary protein and minerals may interact with lipids in the gastrointestinal tracts and influence lipid digestibility. Increasing the amount of crude protein in the diet may increase the digestibility of lipids and fatty acids at the end of the ileum and over the entire intestinal tract (Just et al., 1980; Jørgensen et al., 1992). The specific effects of dietary protein on lipid digestibility may depend on protein quality (Frobish et al., 1970) and the concentration of lipids in the diet (Jørgensen et al., 1992). Although the mechanism by which dietary protein affects lipid digestion remains unclear, stabilization of micelle formation by undigested protein may contribute to the positive effect of protein on lipid digestibility (Meyer et al., 1976).

Lipid digestibility may also be affected by dietary minerals, because Ca and Mg have a tendency to form insoluble soaps with LCFA in the gastrointestinal tract, which may adversely affect lipid digestion (Stahly, 1984). High concentrations of Ca in the diets, therefore, decrease lipid digestibility by weanling and growing pigs (Jørgensen et al., 1992; Han and Thacker, 2006), but it is possible that the formation of soap mainly takes place in the large intestine and, therefore, does not influence absorption of lipids in the small intestine (Jørgensen et al., 1992).

Dietary Additives

Exogenous emulsifiers such as lecithin and lysolecithin have been expected to improve lipid digestion, because lipid digestion is greatly affected by the degree of emulsification and subsequent micelle formation. Jones et al. (1992) observed increased lipid digestibility of diets containing tallow in weanling pigs when either lecithin or lysolecithin was included. The extent of increased lipid digestibility of diets by lecithin or lysolecithin was 7.5% and 3.0%, respectively. Improved lipid digestibility when an emulsifier was included in the diet was reported in other experiments as well (Reis de Souza et al., 1995; Jin et al., 1998), but it has also been reported that emulsifiers had no positive effect on lipid digestibility (Soares and Lopex-Bote, 2002; Dierick and Decuypere, 2004; Xing et al., 2004). The inconsistent results that have been obtained regarding added emulsifiers may have been caused by variations in the sources and levels of dietary lipids that were used (Jones et al., 1992; Dierick and Decuypere, 2004) and the source of emulsifiers (Wieland et al., 1993; Dierick and Decuypere, 2004).

Exogenous lipase in the diets has been suggested to improve lipid digestibility, but it was not possible to confirm this hypothesis when lipase was added to a diet fed to growing pigs (Dierick and Decuypere, 2004). However, an antimicrobial agent (e.g., carbadox) has improved lipid digestibility in pigs by depressing microbial activity (Partanen et al., 2001; Wang et al., 2005). Lipid digestion is affected by the microorganism in the gastrointestinal tract, because increased microbial activity not only promotes irreversible bile catabolism, which leads to a reduction in active bile acids in the intestinal tracts (Smith and Annison, 1996), but it also increases microbial hydrogenation, which converts unsaturated fatty acids to less-digestible saturated fatty acids in the small intestine (Yen, 2001).

Effects of Animal Factors on Lipid Digestibility

Age of the Animal

Lipid digestibility is very low at weaning because newly weaned pigs are abruptly introduced to solid feed, which disturbs the lipid digestive and absorptive capacity of pigs because of a decline in pancreatic lipase activity (Lindemann et al., 1986). Weanling pigs, therefore, have a relatively low digestibility of dietary lipids, and the digestibility of lipids of dietary origin is less than that of lipids of vegetable origin (Cera et al., 1989; Jones et al., 1992; Jin et al., 1998). This indicates that weanling pigs have a lower digestibility of saturated fatty acids than that of unsaturated fatty acids. Lipid digestibility will, however, gradually increase during the postweaning period (Cera et al., 1989; Soares and Lopex-Bote, 2002; Straarup et al., 2006). The difference in digestibility between lipids of animal and vegetable origins seems to disappear as pigs become older. For example, in growing–finishing pigs, no difference between the two sources of lipids has been observed (Table 14.2; Agunbiade et al., 1992; Jørgensen and Fernández, 2000), and pigs may have complete digestive capacity for dietary lipids at approximately 40 kg (Wiseman and Cole, 1987; Agunbiade et al., 1992).

Endogenous Losses of Lipids

The lipids in the ileal digesta or feces consist of undigested lipids from the diets and endogenous losses of lipids that originate from bile acids, desquamated cells, and microorganisms (Sambrook, 1979). The endogenous losses of lipids, therefore, make it challenging to interpret values for lipid digestibility. As is the case for amino acids, the apparent digestibility of lipids typically increases as the concentrations of dietary lipids increase, because the endogenous losses of lipids contribute a relatively greater amount of the total output of lipids if lipid intake is low, compared with greater levels of lipid intake (Jørgensen et al., 1993; Jørgensen and Fernández, 2000; Kil et al., 2010). Values for the true or standardized digestibility of lipids, however, are corrected for endogenous losses of lipids, and these values are, therefore, not affected by dietary lipid intake (Kil et al., 2010).

Methodology for Measuring Lipid Digestibility

Lipid Analysis

Lipids in diets, digesta, and feces have been analyzed using various extraction methods, but different methods may yield different values for the amount of lipids in those samples (Boisen and Verstegen, 2000), which may influence calculated values for lipid digestibility. Although different solvents may have an effect on lipid extraction, it has been suggested that acid hydrolysis prior to ether extraction is an important step for complete lipid extraction. Acid hydrolysis is more essential when lipid concentrations are analyzed in feces than in diets because the complex of minerals and fatty acid soaps that are formed in the intestinal tract of pigs is difficult to extract by solvents. However, acid hydrolysis allows fatty acids in these soaps to be extracted by solvents (Just, 1982). The apparent total tract digestibility of lipids in soybean oil is 7.3% greater when lipids in diets and feces are determined without acid hydrolysis, than if samples are acid hydrolyzed before ether extraction (Agunbiade et al., 1992). Therefore, acid hydrolysis prior to ether extraction is required to prevent overestimating lipid digestibility (Just, 1982).

Ileal Versus Total Tract Digestibility

Lipid digestibility has been measured either at the end of the ileum or over the entire intestinal tract. Ileal digestibility is often considered the better estimate for the bioavailability of lipids because lipids are mostly digested and absorbed before the end of the ileum (Nordgaard and Mortensen, 1995) and values for ileal digestibility are not affected by endogenous losses of lipids produced in the large intestine (Jørgensen et al., 2000). Especially, the digestibility of fatty acids should be measured at the end of the ileum rather than over the entire intestinal tract because of significant microbial hydrogenation of unsaturated fatty acids in the large intestine of pigs (Jørgensen et al., 1993; Duran-Montgé et al., 2007). The apparent digestibility of lipids is often greater at the end of the ileum than over the entire intestinal tract for pigs because of a net synthesis of endogenous lipids in the large intestine (Shi and Noblet, 1993; Reis de Souza et al., 1995). However, the difference seems to be negligible if the diets contain low amounts of fiber (Jørgensen et al., 2000; Kil et al., 2010), because of a low synthesis of microbial lipids in the large intestine of pigs fed low-fiber diets. However, in diets containing dietary fiber in amounts close to that observed in commercial diets, the total tract digestibility of dietary fiber is less than the ileal digestibility (Kil et al., 2010).

Total Collection Versus Index Method

Lipid digestibility is measured either by quantifying all lipids in the diets and excreta (total collection method) or by using spot collection and an indigestible marker (Adeola, 2001). Lipid digestibility measured by using chromic oxide as a marker may be less compared with that obtained by the total collection method (Reis de Souza et al., 1995). The reason for this may be that chromic oxide is likely to move separately from lipids in the gastrointestinal tract (Carlson and Bayley, 1972). It is, therefore, possible that a fat-soluble marker may be a better marker to use in lipid digestibility experiments.

Bioavailability of Carbohydrates

The main energy source for most humans and noncarnivorous animals are dietary carbohydrates of plant origin. The primary classification of carbohydrates is based on their chemical properties: degree of polymerization, type of linkages, and characteristics of the individual monomers (Cummings and Stephen, 2007). Using this classification approach, carbohydrates are grouped into sugars, oligosaccharides, and polysaccharides (FAO, 1998). The polysaccharides are usually divided into a group consisting of starch and glycogen and a second group consisting of dietary fiber. However, this classification does not provide information about the physiological attributes or nutritional contributions of these groups of carbohydrates when included in human or animal diets. To overcome this limitation, dietary carbohydrates may be classified based on digestibility by the small intestine (FAO, 2003; Cummings and Stephen, 2007; Englyst et al., 2007) or by ability to influence blood glucose level (glycemic or non-glycemic carbohydrates; Englyst and Englyst, 2005).

As is the case for most other nutrients, the bioavailability of carbohydrates is not often measured. Instead, the digestibility of different fractions of carbohydrates is measured and used as an indicator of availability. There is very limited secretion of endogenous carbohydrates into the intestinal tract and the endogenous contribution to the output of carbohydrates is usually ignored. Therefore, only apparent digestibility values are measured and unlike digestibility values for lipids and AA, no distinction among apparent, standardized, and true digestibility is made for carbohydrates. There is, however, a clear distinction between ileal digestibility and total tract digestibility, because there may be considerable degradation of carbohydrates in both the small intestine and the large intestine, and end-products that are absorbed in both sections of the intestinal tract may make significant contributions to the energy status of the animal.

Digestibility of Monosaccharides

Some monosaccharides, such as glucose, fructose, and galactose, are easily absorbed from the small intestine via energy-dependent transporters (Englyst and Hudson, 2000). Other monosaccharides, such as arabinose, xylose, and mannose, are passively absorbed in the small intestine, but the presence of these monosaccharides in food and feed is quantitatively small (Englyst and Hudson, 2000; IOM, 2001). Most monosaccarides are believed to be rapidly metabolized in the liver (Englyst and Englyst, 2005). Glucose, fructose, and galactose may be used in glycolysis, which will result in the synthesis of pyruvate and, subsequently, acetyl-CoA that may enter the citric acid cycle or be used for fatty acid synthesis.

Digestibility of Disaccharides

The disaccharides sucrose (glucose and fructose) and maltose (two glucose units) are present in varying amounts in many feed ingredients. These two disaccharides are digested by the enzymes sucrase and maltase, respectively, to their monosaccharide constituents before absorption (Englyst and Hudson, 2000). Sucrase and maltase are brush-border enzymes that specifically break α-(1-2)

and α-(1-4) glycosidic linkages, respectively. Lactose is a disaccharide that is present only in milk and contains a glucose and a galactose unit that is connected by a β-(1-4) glycosidic linkage. The brush-border enzyme lactase hydrolyzes this linkage, which results in release of galactose and glucose (Englyst and Hudson, 2000). Sucrose, maltose, and lactose are believed to be completely digested in the small intestine, and, therefore, the ileal digestibility is considered to be 100%. The absorbed glucose from these disaccharides is rapidly reflected in an increase in blood glucose concentration. Thus, dietary monosaccharides, as well as dietary disaccharides, are called glycemic carbohydrates because of the immediate increase in the blood glucose level after the consumption of these carbohydrates (Englyst and Englyst, 2005).

Digestibility of Oligosaccharides

The three main oligosaccharides that are naturally present in feed ingredients include raffinose, stachyose, and verbascose. These oligosaccharides are mainly found in beans, legumes, cotton seeds, and molasses. The majority of the oligosaccharides in practical diets fed to swine are those present in soybean meal that often contains between 4% and 7% oligosaccharides. Raffinose consists of one unit of glucose, one unit of fructose, and one unit of galactose. Stachyose and verbascose have a structure that is similar to raffinose with the exception that they contain two or three units of galactose, respectively. The glucose and fructose units in the oligosaccharides are connected by an α-(1-2) glycosidic linkage, whereas an α-(1-6) linkage connects glucose to galactose and also connects the galactose units in stachyose and verbascose. Raffinose, stachyose, and verbascose are commonly called α-galactosides. The glycosidic linkages in the α-galactosides may be hydrolyzed by the enzyme α-galactosidase. Pigs do not, however, synthesize this enzyme in the intestinal tract, and raffinose, stachyose, and verbascose are, therefore, considered indigestible by porcine enzymes (Canibe and Bach Knudsen, 1997). However, it has been demonstrated that the ileal digestibility of α-galactosides is between 50% and 80% (Bengala-Freire et al., 1991; Canibe and Bach Knudsen, 1997; Smiricky et al., 2002), which indicates that there is a considerable fermentation taking place in the small intestine of pigs. The total tract digestibility is considered to be 100% because any α-galactosides that are not fermented in the small intestine are rapidly fermented in the large intestine.

In addition to the three α-galactosides, several synthetic oligosaccharides may also be used in diets fed to swine because they are believed to have prebiotic effects. These oligosaccharides include fructooligosaccharides and transgalactooliogosaccharides and they may also be partly fermented in the small intestine (Smiricky-Tjardes et al., 2003). Other oligosaccharides include fructans, levans, and mannan-oligosaccharides that may also be present in diets fed to pigs. However, to the best of our knowledge, there is no information on the digestibility of these oligosaccharides. Nevertheless, it is evident that both natural and synthetic oligosaccharides are partly fermented in the small intestine and almost completely fermented in the large intestine. From an energetic perspective, it is not important where in the digestive tract the fermentation takes place because the end product in both cases is SCFA, which are easily absorbed throughout the intestinal tract. However, because oligosaccharides are fermented with a subsequent absorption of SCFA rather than glucose, they are considered non-glycemic carbohydrates (Englyst and Englyst, 2005).

Digestibility of Starch

Starch is the principle carbohydrate in most diets fed to pigs (Wiseman et al., 2006; Bach Knudsen et al., 2006). Starch is unique among carbohydrates because it occurs in nature as granules and is composed of amylose and amylopectin polymers (BeMiller, 2007). Most cereal starches contain

about 25% amylose and 75% amylopectin (BeMiller, 2007). Amylose is predominantly a linear chain of glucose residues linked by α-(1-4) glycosidic bonds, although a few α-(1-6) bonds may occur as side chains (BeMiller, 2007; Cummings and Stephen, 2007). Amylopectin is a large, highly branched polymer composed of both α-(1-4) and α-(1-6) glycosidic linkages (Cummings and Stephen, 2007). Starch that is composed predominantly of amylopectin is referred to as waxy starch (BeMiller, 2007).

Digestion of starch in pigs and humans starts when the food is mixed with salivary amylase secreted in the mouth (Englyst and Hudson, 2000). This digestion process is short because salivary amylase is deactivated by the low pH in the stomach as the food is swallowed (Englyst and Hudson, 2000). However, starch digestion occurs predominantly in the small intestine where starch is hydrolyzed to maltose, maltotriose, and isomaltose (also called α-dextrins) by pancreatic and intestinal α-amylase and isomaltase (Gray, 1992; Groff and Gropper, 2000). Maltase, which is an intestinal brush-border enzyme, hydrolyzes maltose and maltotriose to its glucose monomers whereas isomaltase (also called α-dextrinase) hydrolyzes the α-(1-6) glycosidic linkage of isomaltose to produce two glucose molecules (Groff and Gropper, 2000). Although enzymes can completely digest starch, the rate and extent of starch digestion varies depending on several factors including (1) the nature of crystallinity of the starch granule or the source of starch, (2) the amylose-to-amylopectin ratio, and (3) the type and extent of processing of the starch (Cummings et al., 1997; Englyst and Hudson, 2000; Svihus et al., 2005). Amylose seems to be more resistant to enzymatic digestion than amylopectin (Svihus et al., 2005). Because of the different factors that affect starch digestibility, starch can be further classified as rapidly available starch or slowly available starch, based on its rate of digestion and glucose appearance in the blood (Englyst et al., 2007).

Small intestinal digestion of starch is an efficient process, and, for most cereal grains, the ileal digestibility of starch is greater than 90% (Bach Knudsen et al., 2006; Sun et al., 2006; Wiseman, 2006). For peas, the ileal digestibility of starch is less than cereals (Canibe and Bach Knudsen, 1997) and values between 75% and 90% for ileal starch digestibility in field peas have been reported (Sun et al., 2006; Wiseman, 2006; Stein and Bohlke, 2007). Potato starch, however, has a much lower digestibility than that of all other feed ingredients, and the ileal digestibility of starch in raw potatoes is less than 40% (Sun et al., 2006).

For all feed ingredients, the ileal digestibility of starch can be improved by heat treatment. As an example, ileal starch digestibility in extruded field peas increased from 89.8% in raw field peas to 95.9% in field peas that were extruded at 155°C (Stein and Bohlke, 2007). The reason for the improved digestibility of extruded starch may be that extrusion results in increased gelatinization, which is believed to increase digestibility (Svihus et al., 2005). However, it has been demonstrated that starch digestibility is not influenced by diet pelleting (Svihus et al., 2005; Stein and Bohlke, 2007).

The starch that is not digested in the small intestine is called resistant starch and will enter the large intestine. Resistant starch is rapidly fermented with a subsequent absorption of SCFA, and, therefore, the total tract digestibility of starch is close to 100% for all feed ingredients (Wiseman, 2006; Stein and Bohlke, 2007). There is, however, a reduced energetic value of SCFA compared with glucose, and from an energy efficiency standpoint, it is desirable to have as a high a small-intestinal digestibility of starch as possible.

Digestibility of Dietary Fiber

Dietary fiber is defined as carbohydrates that are not digested or are poorly digested in the small intestine, but are completely or partially fermented in the large intestine (De Vries, 2004). The

concept of small-intestinal indigestibility is also shared by the terms "unavailable carbohydrates" and "non-glycemic carbohydrates" (Englyst et al., 2007). Non-starch polysaccharides, resistant starch, non-digestible oligosaccharides, and sugar alcohols belong to the group of carbohydrates that are classified as dietary fiber (Englyst and Englyst, 2005; Englyst et al., 2007). Most (80–90%) of the carbohydrates present in plant cell walls are non-starch polysaccharides (Cummings et al., 1997) and differ from monosaccarides, disaccharides, and starch (the available carbohydrates) in that they do not contain α-(1-4) glycosidic linkages, which are characteristic of available carbohydrates (Englyst et al., 2007). However, the current definition of dietary fiber recognizes that carbohydrates, other than those present in plant cell walls, provide similar physiological effects as plant cell-wall carbohydrates (De Vries, 2004). Thus, dietary fiber includes non-starch polysaccharides that are plant cell-wall components, as well as those that are not cell-wall components.

Cellulose and hemicelluloses are the most common non-starch polysaccharides in cell walls, but lignin is also considered part of the fiber component in feed ingredients. Cellulose comprises 10–30% of the non-starch polysaccharides in food and is a linear, unbranched chain of glucose units with β-(1-4) linkages (Cummings and Stephen, 2007; BeMiller, 2007). Because of the nature of the glycosidic linkages, cellulose is not digested by endogenous enzymes secreted by the animal (BeMiller, 2007). Hemicellulose differs from cellulose in that it is a branched-chain polysaccharide composed of different types of hexoses and pentoses (Cummings and Stephen, 2007). The most common hemicellulose in annual plants, including cereal grains, is xylan (BeMiller, 2007). Xylan consists of a xylose backbone that may be linear or highly branched (BeMiller, 2007). Side chains are present in the linear or branched core structure and are usually composed of arabinose, mannose, galactose, and glucose (Cummings and Stephen, 2007). Some hemicelluloses also contain uronic acids that are derived from glucose (glucuronic acid) or from galactose (galacturonic acid) and the presence of uronic acids gives hemicelluloses the ability to form salts with metal ions such as calcium and zinc (Southgate and Spiller, 2001; Cummings and Stephen, 2007). Because some of the hemicelluoses are soluble, hemicellulose has a greater fermentability in the large intestine of pigs than does cellulose.

Carbohydrates that are not components of the plant cell wall but are considered dietary fiber include pectins, gums, non-digestible oligosaccharides, and resistant starches. A key feature of pectins is that they are composed primarily of linear polymers of galacturonic acids that are linked together by α-(1-4) linkages (BeMiller, 2007). Pectins may also contain side chains of rhamnose, galactose, and arabinose (Cummings and Stephen, 2007). Gums are natural plant polysaccharides, but may also be produced by fermentation. Naturally occurring gums can be formed as exudates from plants or shrubs that are physically damaged, or they can be a part of the seed endosperm (BeMiller, 2007). An example of an exudate gum is gum arabic and an example of a gum from seed endosperm is guar gum. Xanthan gum and pullulan are examples of gums produced from fermentation.

Dietary fiber may also be classified according to solubility. Lignin, cellulose, and some of the hemicelluloses are considered insoluble dietary fiber, and the non–cell wall components, along with the remaining hemicelluloses, are considered soluble dietary fiber.

The ileal digestibility of dietary fiber is generally low and reflects the fact that prececal fermentation is limited in pigs. For most feed ingredients, therefore, ileal digestibility of total dietary fiber is less than 25% (Bach Knudsen and Jorgensen, 2001; Urriola et al., 2010). However, the ileal digestibility of soluble dietary fiber is much greater than for insoluble dietary fiber (Urriola, 2010; Urriola et al., 2010). Feed ingredients that contain mostly soluble dietary fiber have an ileal digestibility of total dietary fiber that may be greater than 50% (Urriola, 2010).

Fermentation of dietary fiber in the large intestine varies among feed ingredients and among different types of fiber (Bindelle et al., 2008). It is also greatly influenced by the concentration

of lignin and insoluble fiber in the ingredients. For total dietary fiber in co-products derived from maize, the apparent total tract digestibility is between 40% and 60% (Bach Knudsen and Jørgensen, 2001; Stein et al., 2009; Urriola et al., 2010). However, feed ingredients containing mostly soluble dietary fiber may have total tract digestibility of fiber that is above 80% (Le Goff et al., 2002; Urriola, 2010; Urriola et al., 2010). However, fermentability and total tract digestibility of dietary fiber may be influenced by pelleting and extrusion and possibly other processes (Beltranena et al., 2009). Only limited information about the effectiveness of these procedures is available at this time, however.

Summary

The bioavailability of the energy-containing nutrients (i.e., proteins, lipids, and carbohydrates) in feedstuffs included in diets fed to swine is difficult and expensive to measure. Therefore, for practical purposes, values for the digestibility of these nutrients are usually measured and used as an indicator of bioavailability, although it is recognized that, particularly for protein, digestibility may not always be equal to bioavailability. Proteins, lipids, and the enzymatically digestible fraction of the carbohydrates (i.e., disaccharides and starch) are digested prior to the cecum, with a subsequent absorption of AA, triglycerides, and monosaccharides in the small intestine. Protein and lipids that are not absorbed in the small intestine will enter the large intestine, and although no absorption takes place in the large intestine, microbes in this part of the intestinal tract may ferment these nutrients, which may result in a change of concentration. Therefore, values for total tract digestibility of AA and lipids may be inaccurate, and, instead, ileal digestibility values should be measured.

Carbohydrates that escape enzymatic digestion in the small intestine (i.e., dietary fiber) are also fermented in the large intestine with a subsequent synthesis and absorption of SCFA, which contribute to the energy status of the pig. As such, digestibility of carbohydrates is divided into a small intestinal digestible fraction that results in absorption of monosaccharides and a fermentable fraction that results in absorption of SCFA in the large intestine. For protein and lipids, there are substantial endogenous secretions into the intestinal tract, and apparent digestibility values do not always represent the digestibility of the nutrients in the feed ingredients. Therefore, estimates for the basal or the total endogenous losses are used to correct the apparent digestibility values, and values for standardized or true digestibility are calculated. In the case of carbohydrates, endogenous secretions into the intestinal tract are believed to be negligible and values for the apparent digestibility are thus representative of the digestibility of the carbohydrates in feed ingredients.

In conclusion, the bioavailability of proteins and lipids is estimated by calculating the standardized ileal digestibility of AA and the true ileal digestibility of lipids, respectively. For carbohydrates, bioavailability is estimated by determining the apparent ileal digestibility of disaccharides and starch and the apparent total tract digestibility of dietary fiber.

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