Nutrient and Energy Utilization by Swine

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ABSTRACT: The digestibility of the energy containing nutrients (i. e., proteins, lipids, and carbohydrates) in feedstuffs included in diets fed to swine needs to be determined to obtain an accurate value for the energy contribution from these nutrients. 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, fatty acids, and monosaccharides in the small intestine. The ileal digestibility of these nutrients, therefore, needs to be determined. However, some carbohydrates escape enzymatic digestion in the small intestine and are fermented in the large intestine with a subsequent absorption of volatile fatty acids. These carbohydrates are called dietary fiber and they may significantly contribute to the energy status of the animal. It is, therefore, common to measure the total tract digestibility of dietary fiber. Phosphorus in feed ingredients is not an energy containing nutrient, but P plays a crucial role in energy metabolism in the body because it is an important part of high energy bonds such as AMP, ADP, and ATP. An accurate estimate of the digestibility of P in feed ingredients is, therefore also needed and recent research has indicated that the standardized total tract digestibility of P is the most accurate way to estimate P-digestibility.

Key words: amino acids, carbohydrates, digestibility, lipids, phosphorus

AMINO ACIDS

Most feed ingredients contain some AA that are used for synthesis of body proteins. In most commercial diets fed to swine, the majority of the AA are furnished by soybean meal or another oilseed meal, but crystalline sources of Lys, Met, and Thr are also often used. 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. However, it is time-consuming and very costly to measure the availability of AA in feed ingredients and for practical purposes the digestibility rather than the availability of AA is measured in feed ingredients. These values are subsequently used in feed formulation.

Amino Acid Digestibility

Because of the synthesis and catabolism of AA by the hindgut microbes, AA digestibility is most correctly measured as ileal AA digestibility (Sauer and Ozimek, 1986). It is necessary to collect ileal fluids at the end of the small intestine. Several techniques have been proposed for this and in North America, the installment of a T-cannula in the distal ileum of pigs (10 to 15 cm prior to the ileo-cecal valve) is the procedure of choice (Stein et al., 1998). This procedure has proven to be accurate and has a minimal trial to trial variation. An indigestible marker needs to be added to the diet because the T-cannula does not allow for the total collection of the ileal output from the animal. Chromic oxide is often used for this purpose, but other markers are available. Values for the apparent ileal digestibility (AID) of AA are calculated by subtracting the ileal output of AA from the dietary input (Stein et al., 2007). Because values for AID of AA contain the entire ileal output, AA of dietary origin as well as AA of endogenous origin are included in this calculation. These values are dependent on the concentration of AA in the diets (Fan et al., 1994) and values for AID are not additive in mixed diets (Stein et al., 2005). It is, therefore, necessary to correct AID values for the endogenous output of AA. Several different procedures exist for measuring endogenous losses of AA, but for practical feed formulation, basal endogenous losses need to be determined. Basal endogenous losses may be measured by measuring the ileal output of AA after feeding a protein-free diet (Stein et al., 1999) and it is believed that values for endogenous losses of all indispensable AA and most dispensable AA are accurately predicted using this procedure (Stein et al., 2007). By subtracting values for the basal endogenous losses from the ileal output of AA, values for the standardized ileal digestibility (SID) of AA are calculated. 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).

Utilization of AA

While SID values for AA in most feed ingredients are available and used in the feed industry, it is also recognized that not all digested AA are used to the same degree by all groups of pigs. Young pigs are highly efficient in digesting milk proteins (Mavromichalis et al., 2001), but the SID of AA in soybean protein and other AA is low in young pigs. However, as the pigs mature they increase the SID of AA from vegetable feed ingredients and SID values for AA by finishing pigs are not different from those in sows (Stein et al., 2001) if the level of feed intake is the same. However, the level of feed intake affects the SID of AA and SID values are linearly decreased as feed intake is increased (Moter and Stein, 2004). It is, therefore, important that the level of feed intake is taken into account when SID values are determined.

The concentration of dietary fiber may reduce AA digestibility and utilization of AA (Mosenthin 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. In contrast, dietary fat may increase the SID of AA (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; Schultze et al., 1995; Yu et al., 1996) because anti-nutritional factors increase the endogenous losses of AA. As a consequence, feed ingredients containing anti-nutritional factors usually have low SID values of AA. Heat treatment of feed ingredients may also reduce the digestibility of AA, and both the concentration and the digestibility of Lys is reduced if feed ingredients containing reducing sugars are heat treated (Pahm et al., 2008).

LIPIDS

Lipids serve 4 essential functions in swine diets: 1) lipids are important parts of the cell membranes in the body; 2) lipids are carriers of fat soluble vitamins; 3) dietary lipids are the sources of the 2 indispensable fatty acids for swine (i.e., linoleic acid and linolenic acid); and 4) lipids increase the energy concentration of the diet. Although the body contains a large number of different fatty acids, pigs are able to synthesize all fatty acids if they have sufficient supply of glucose and the 2 indispensable fatty acids in the diet.

Dietary lipids that are present in common feed ingredients contain different amounts of lipids and have varying fatty acid composition and most lipids are present in feed ingredients 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 and the apparent total tract digestibility of lipids in most feed ingredients fed to swine varies from 25 to 77% (Noblet et al., 1994). Because the microbes in the hindgut may synthesize lipids, lower values for the total tract digestibility of lipids compared with the ileal digestibility of lipids are often measured (Kil et al., 2010). This in particular is true if high fiber diets are fed because these diets provide a rich source of carbohydrates for the microbes in the hindgut. The endogenous losses of lipids are also increased in diets containing high fiber ingredients (Kil et al., 2010).

In general, unsaturated fatty acids are more digestible than saturated fatty acids because unsaturated fatty acids have a greater potential for micelle formation than 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 range 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 is 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 to 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 lenght (Cera et al., 1989; Straarup et al., 2006), even if the short chain fatty acids are predominantly saturated fatty acids. In experiments with weanling pigs it was observed that the apparent total tract digestibility of lipids from coconut oil is greater than the digestibility of lipids from corn oil or tallow (Cera et al., 1989) and apparent total tract digestibility values of short chain fatty acids of more than 90% was reported. For growing pigs, however, the effect of chain length of fatty acids on lipid digestibility is questionable (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 2 free fatty acids. A greater potential 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).

Lipid digestibility is also influenced by the form in which lipids are included in the diets because extracted lipids are more digestible than intact lipids (Kim et al., 2009; Kil et al., 2010). The reason for this difference in digestibility is believed to be that intact lipids are encased in the membrane of the lipid cells and therefore, more resistant to emulsification and enzymatic hydrolysis (Adams and Jensen, 1984; Li et al., 1990; Duran-Montgé et al., 2007). It is estimated that in commercial swine diets, approximately 60% of all the lipids are added as extracted lipids whereas 40% are intact lipids (Azain, 2001).

Utilization of Lipids

Absorbed lipids may either be used for essential functions in the body such as in the synthesis of cell membranes or used as precursors for the synthesis of other compounds. Lipids may also be oxidized to yield energy in the form of ATP and in animals that are in a negative energy balance, this will be the largest utilization of lipids. In lactating sows, dietary lipids may also be directly deposited in milk fat. However, if the dietary intake of lipids is greater than the needs for these functions, excess lipids will be stored in the body as body lipids, mainly in adipose tissue. Body lipids are stored in the form of triglycerides and function as an energy reserve for the animal. In growing animals, there is daily net deposition of body lipids that often exceeds the dietary intake of lipids and it is, therefore, believed that practically all dietary lipids will be directly deposited into adipose tissue in these animals and only a small part of the lipids are oxidized. There is, however, evidence that even in fast growing animals, a significant proportion of dietary lipids are oxidized immediately after the ingestion of a meal, but the extend of this oxidation is not known (Kil et al., 2011). It is believed that the efficiency of utilization of dietary lipids for synthesis of ATP is 66%, whereas the efficiency of directly depositing lipids into adipose tissue is 90% (Black, 1995). For the overall energetic efficiency it is, therefore, important to estimate the proportion of lipids that are oxidized vs. the proportion that are deposited in adipose tissue.

CARBOHYDRATES

In most swine diets, carbohydrates provide the majority of the energy. Carbohydrates are classified as monosaccharides, disaccharides, oligosaccharides, and polysaccharides with the polysaccharides being further divided into starch and nonstarch polysaccharides. The oligosaccharides and the non-starch polysaccharides are also often called dietary fiber. Monosaccharides, disaccharides, and starch are mostly digested in the small intestine using pancreatic and intestinal enzymes, which results in liberation of monosaccharides that are easily absorbed in the small intestine using active and passive transport mechanisms. Dietary fiber, in contrast, is mostly fermented in the hindgut by the microbes with a subsequent synthesis and absorption of volatile fatty acids that are easily utilized by the animal.

There is very limited secretion of carbohydrates into the intestinal tract of pigs and endogenous losses are, therefore, not observed. As a consequence, it is believed that the apparent digestibility of carbohydrates is an accurate measure of carbohydrate absorption and standardized or true digestibility is usually not reported.

Digestibility of monosaccharides and disaccharides is close to 100% in the small intestine, but with the exception of diets containing milk products, most diets fed to pigs contain very small amounts of mono- and disaccharides and these carbohydrates, therefore, usually contribute only a very small part of the total energy absorbed by pigs.

Small intestinal digestion of starch is also 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 in cereals (Canibe and Bach Knudsen, 1997) and values for ileal starch digestibility in field peas between 75 and 90% 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^{o}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). It has, however, 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 in the hindgut with a subsequent absorption of volatile fatty acids and the total tract digestibility of starch is, therefore, close to 100% for all feed ingredients (Wiseman, 2006; Stein and Bohlke, 2007). There is, however, a reduced energetic value of volatile fatty acids compared with glucose and from an energy efficiency stand point it is desirable to have as a high a small intestinal digestibility of starch as possible.

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

Fermentation in the large intestine of dietary fiber varies among feed ingredients and among different types of fiber (Bindelle et al., 2008) and is 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 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), but only limited information about the effectiveness of these procedures are available at this time.

Utilization of carbohydrates

End-products of carbohydrate digestion include monosaccharides (mainly glucose) and volatile fatty acids. Both of these end-products may be used for the synthesis of ATP or they may be used for fatty acid synthesis if the energy from ATP is not immediately needed by the animal. Monosaccharides may also be used as precursors in the synthesis of a number of other compounds including AA and lactose. One of the volatile fatty acids, propionic acid, may be converted to glucose via gluconeogenesis, but that is not the case for the other volatile fatty acids. The efficiency of utilization of energy from monosaccharides is close to 70%, whereas the overall efficiency of utilization of energy in fiber is less than 60% (Black, 1995). If more fiber is included in the diet, the efficiency of utilization of energy will, therefore, be reduced.

PHOSPHORUS

Historically, P-availability in feed ingredients has been measured using a slope ratio assay with the response to increased concentrations of P from a test ingredient being expressed relative to the response obtained to feeding increasing levels of a standard source of P (Cromwell, 1992). The availability of P in the test ingredient is, therefore, a relative availability value and the actual value of the availability of P in the test ingredient depends on the availability of P in the standard that is used. As a consequence, it is possible that a given feed ingredient may have different values for the relative availability of P if different standards were used. It is also believed that values for the relative bioavailability of P in feed ingredients are not additive in mixed diets and it is both labor intensive and expensive to determine values for the relative bio-avialbility of P because experimental animals have to be sacrificed.

To overcome some of these challenges, P digestibility rather than the relative availability of P may be measured. The total tract digestibility of P is usually measured, because there is no difference between ileal and total tract digestibility values (Bohlke et al., 2005; Dilger and Adeola, 2006; McGinnis et al., 2007). Most often, pigs are fed a diet in which the test ingredient provides all the P, and feces are collected quantitatively over a 5 to 7 day period after a 4 to 7 day adaptation period. The apparent total tract digestibility of P is then calculated for the diet and this value also represents the apparent total tract digestibility of P in the ingredient. At the same time, the basal endogenous losses of P is measured using a P-free diet, and values for the apparent total tract digestibility of P are then converted to values for the standardized total tract digestibility of P (Petersen and Stein, 2006; Almeida and Stein, 2010).

The main advantage of using values for standardized total tract digestibility of P is that these values are additive in mixed diets, they are relatively easy and inexpensive to determine, and values are repeatable among different studies. For practical feed formulation, it is, therefore, most accurate to utilize values for standardized total tract digestibility of P.

Most feed ingredients of plant origin have a relatively low digestibility of P because most P in these ingredients is bound in the phytate complex. In contrast, P in ingredients of animal origin is generally well digested and absorbed and values for the digestibility of P in these ingredients is often between 60 and 90% (Sauvant et al., 2004). The P in inorganic sources of P is also well digested and digestibility values between 80 and 98% may be obtained in these ingredients (Petersen and Stein, 2006). If plant ingredients are fermented, the digestibility of P is increased (Pedersen et al., 2007) and the same is the case if microbial phytase is added to the diet (Cromwell et al., 1995; Almeida and Stein, 2010). It is, therefore, possible to achieve a relatively high digestibility of P in diets fed to swine if fermented ingredients and phytase is used in the diets (Almeida and Stein, 2010)

Utilization of P

Almost 80% of all absorbed P is stored in the bones to give the animal structural stability (Cromwell, 1970). The remaining 20 to 25% of the absorbed P is utilized in soft tissue where it is incorporated into plasma membranes as part of phospholipids. Phosphorus also provides the backbone of RNA and DNA and it is used in almost all cells in the body via the energy molecules AMP, ADP, and ATP (Bauman, 2004; Anderson et al., 2006). Thus, P has a variety of functions in the body of pigs and is essential for sustainability of life. The requirement of P for maximum bone mineralization is greater than that for maximum growth and it is common to feed growing animals less P than required for maximum bone mineralization. However, animals intended for breeding are usually fed a greater level of P in the diet to maximize bone mineralization and increase longevity.

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Table 1. Crude fat and fatty acid composition in feed ingredients

Ingredients	Crude Fat (%)	Fatty acids (% of total fatty acids) C16:0	C18:0	C18:1	C18:2	C18:3	U:S ratio[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 ratio is the ratio of unsaturated to saturated fatty acids.

[2]Adapted from Sauvant et al. (2002)

[3]Adapted from NRC (1998).

Table 2. Apparent total tract digestibility (ATTD) of lipids in the diets fed to pigs.

References	BW, kg	Basal diets	Supplemental lipids		ATTD of lipids,[1] %
			Source	Inclusion level, %	
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]Apparent total tract digestibility of lipids in the diets.

[2]High-oleic sunflower oil.

[3]Lipid blend (5.5 % tallow, 3.5% sunflower oil, 1% linseed oil).