

Animal effects on ileal amino acid digestibility

Hans H Stein* and Martin Nyachoti[†]

* South Dakota State University,
Department of Animal and Range Sciences
Box 2170 Brookings SD 57007 USA.

[†]University of Manitoba,
Department of Animal Sciences
Winnipeg MB Canada R3T 2N2

Summary

Several animal factors may influence the degree to which pigs will digest dietary proteins prior to the distal ileum. The age of the animal clearly is important for protein digestibility in early life, but in pigs heavier than 60 kg, there is no evidence that body weight or age influences the digestibility of dietary proteins and the absorption of amino acids. Likewise, the amounts of non-specific endogenous amino acids lost at the distal ileum per kg dry matter intake may change in early life, but provided that feed intake is constant, these losses are not influenced by body weight in pigs heavier than 60 kg. The physiological status of the pig does not influence the endogenous losses either. There is, however, clear evidence that the calculated digestibility coefficients of amino acids are influenced by the feed intake of the animals. Because the non-specific endogenous amino acid losses per kg of dry matter intake decreases as feed intake is increased, apparent ileal digestibility coefficients increases as feed intake is increased from very low levels to a level that is close to two times the maintenance energy requirement. Further increases in feed intake are not associated with any measurable change in the apparent ileal digestibility coefficients. On the other hand, standardized ileal digestibility coefficients are linearly reduced as feed intake is increased reflecting the fact that pigs do reduce the efficiency of digesting dietary proteins as feed intake increases. Because the non-specific endogenous losses of amino acids influences the calculated apparent ileal digestibility coefficients, the factors that causes changes in endogenous losses are also important for determining digestibility coefficients

1. Introduction

The ultimate goal of swine production is the conversion of dietary proteins into tissue proteins that eventually can serve as a nutritious source of food for humans. To reduce dietary costs and to reduce the amount of non-utilized protein excreted from the animals, there is an economical as well as an environmental interest in increasing the efficiency of this conversion. For a dietary amino acid to be retained in tissue protein in the animal, it needs to be absorbed from the intestinal tract. While the absorption of amino acids – and other nutrients – is a concept that can easily be defined, it is difficult to measure. Instead, the digestibility of amino acids prior to the distal ileum is measured by quantifying the amino acids appearing at the end of the small intestine and subtracting these quantities from the amino acids ingested by the animal. Thus, it is assumed that dietary amino acids not appearing at the end of the small intestine were absorbed by the animal. It is also assumed that the animal can utilize amino acids that are absorbed from the intestinal tract for protein synthesis. It is recognized that there are exceptions to both of these assumptions (van Barneveld and Batterham, 1994; Ball et al., 2002). However, under practical circumstances the digestibility of amino acids prior to the distal ileum is considered a reasonably accurate measure of the quantities of amino acids available for protein synthesis in an animal (Williams, 1995; Mosenthin et al., 2000).

The ileal digestibility of amino acids can be expressed as apparent ileal digestible amino acids or as standardized ileal digestible amino acids (Mosenthin et al., 2000; Stein et al., 2001; Jansman et al., 2002). As a consequence, both apparent and standardized ileal digestibility coefficients of amino acids in a wide range of feed ingredients have been measured (c.f. NRC, 1998; Rademacker et al., 1999). The difference between these two expressions is whether or not the digestibility coefficients are corrected for the influence of the non-specific endogenous losses of amino acids. Therefore, both the quantities of endogenous amino acids lost at the distal ileum and the hydrolysis of dietary proteins in the small intestine are influencing the digestibility coefficients. The objective of the current paper is to review how the animal may influence these two factors.

2. Animal factors influencing endogenous gut amino acid losses

The classical definition of endogenous gut protein and amino acid losses is those found in digesta or in faeces of animals fed nitrogen-free diets (Mitchell et al., 1924). They are derived from digestive enzymes, mucoproteins, desquamated cells, serum albumin, peptides, amides and amines and include free amino acids (Moughan et al., 1992). These losses may also contain bacteria and swallowed body hair, although strictly speaking these two are not of endogenous sources. The contribution of the latter two sources is often neglected although there is evidence suggesting that ileal flora degrade substantial amounts of amino acids to form ammonia and amines and that 25-

50% of the total nitrogen in the ileum is bacterial bound. Therefore, microbial fermentation in the upper gut interferes with measurement of endogenous gut amino acid losses and may affect amino acid requirements of the pig (Dierick et al., 1986a,b; Schulze et al., 1994; Torrallardona et al., 1994).

2.1 Sources of endogenous gut amino acid losses

Secretions entering the gastrointestinal tract from various sources contribute to the total endogenous amino acids in digesta. Of all these sources, the small intestine makes the largest contribution to the total amount of endogenous amino acids entering the gut lumen and, therefore, the total amount lost, followed by the pancreas and salivary glands (Low and Zebrowska, 1989; Souffrant, 1991, Krawielitzki et al., 1994). The contributions of various parts of the gastrointestinal tract to the endogenous nitrogen secretion into the gut lumen are shown in Table 1 (Low, 1985). These estimates, however, vary widely and the total amount of endogenous nitrogen entering the gut lumen has been estimated to range between 16 and 33 g per day in the growing pig (Souffrant, 1991). The contributions of bile, pancreatic secretions, and other gut tissues to endogenous nitrogen have been estimated to be 1.7, 1.9 and 7.1 g per day, respectively (Souffrant et al., 1993).

Include table 1 here

2.2 Efficiency of re-absorption of endogenous N in the gut

Nitrogen compounds of endogenous origin are digested just like dietary nitrogen and part of their products reabsorbed before reaching the distal ileum (Fuller, 1991). Free and peptide-bound amino acid components of endogenous nitrogen are readily reabsorbed and therefore make up only a small part of endogenous nitrogen at the terminal ileum (Moughan and Schuttert, 1991). It has been estimated that 70 - 80 % of endogenous protein secreted into the upper gut is hydrolyzed and reabsorbed before reaching the terminal ileum (Souffrant et al., 1986, 1993; Krawielitzki et al., 1994). This indicates that only about 20-30 % of the total endogenous nitrogen secretions into the upper gut are of concern when determining true ileal amino acid digestibilities. The bulk of endogenous nitrogen recovered at the distal ileum originate from deconjugated bile salts, desquamated cells and mucin protein because these are resistant to enzymatic hydrolysis (Taverner et al., 1981; Moughan and Schuttert, 1991). Consequently, proline and glycine, the main amino acids in mucin proteins, are the main contributors to endogenous nitrogen recovered at the distal ileum (Lien et al., 1997).

Endogenous amino acids that are secreted into the large intestine are often ignored even though they represent losses to the pig and contribute to the pig's dietary amino acid requirements. Similar to dietary protein, endogenous protein that enters the large intestine may be degraded by the microflora while fermentation products do not contribute towards the pig's amino acid supply. Based on the values presented in Table 1, endogenous protein secretions into

large intestine (13.4 g d^{-1}) exceed the ileal endogenous protein losses (10.1 g d^{-1} ; 25% of secretions into the upper gut). The impact of stimulating endogenous amino acid metabolism in the large intestine was recently demonstrated by Zhu et al. (2003) who observed a reduction in body protein retention when stimulating microbial fermentation in the hindgut of pigs fed threonine-limiting diets.

2.3 Basal versus specific endogenous ileal gut amino acid losses

Endogenous gut protein losses can be divided into two components namely, diet-independent (basal) losses and diet-specific (additional) losses. Basal endogenous amino acid losses are obligatory losses closely associated with the metabolic functions of the animal and are independent of diet type. Therefore, basal endogenous losses represent the minimum amount of losses that can be expected under any feeding situation (Nyachoti et al., 1997). Specific endogenous amino acid losses are dependent on the composition of the diet fed. They are higher in diets that contain factors that induce additional endogenous secretions. Such factors, which are discussed in detail elsewhere, include anti-nutritional factors like fibre, trypsin inhibitors, etc. (de Lange et al., 1989a; Schulze et al., 1995; Grala et al., 1998).

2.4 Methods for estimating endogenous ileal N losses

There is a range of methods that have been used to estimate endogenous gut amino acid losses in pigs, including 1) feeding a protein-free diet, 2) feeding protein with an assumed 100% digestibility, 3) mathematical regression technique, 4) isotope dilution, 5) homoarginine and 6) peptide alimentation ultrafiltration (also known as enzymatically-hydrolyzed casein) techniques. These methods provide different estimates of endogenous gut amino acid losses and the magnitude of the differences vary between methods. Generally, feeding a protein-free diet or using the mathematical regression method provides similar estimates (Taverner et al., 1981; Furuya and Kaji, 1989; Donkoh et al., 1995). These estimates are also close to the estimates obtained using the peptide alimentation method, but they are significantly lower than estimates obtained with the isotope dilution technique and the homoarginine method in pigs fed protein-containing diets. For a detailed discussion on these methods and their use in estimating endogenous gut amino acid losses, please see reviews by Boisen and Moughan (1996), Nyachoti et al. (1997), Hodgkinson and Moughan (2000) and Jansman et al. (2002).

When the protein-free, peptide alimentation, or the regression techniques are used to estimate endogenous amino acid losses in pigs, basal losses are obtained. Correcting apparent ileal amino acid and N digestibility coefficients for the basal endogenous losses provides standardized ileal amino acid digestibilities, which are sometimes, incorrectly, referred to as true ileal amino acid digestibilities. Standardized ileal amino acids are no longer related to the amino acid or N level in the test diet and are likely to be more additive between feed ingredients than apparent ileal amino acid digestibilities (Mariscal-Landín, 1992; Fan et al., 1995). However, when the objective is to understand how

different feed ingredients or dietary components influence amino acid utilization in pigs, then specific endogenous losses associated with that component or diet composition need to be determined. For such estimates, techniques such as the isotope dilution or the homoarginine method should be used, even though each of these techniques has some limitations (Boisen and Moughan, 1996; Nyachoti et al., 1997).

It is likely that utilizing surgical techniques (e.g., ileal rectal anastomosis) that impacts the physiological status of the pig, might have important effects on basal endogenous amino acid losses (Hess and Sève, 1999). Significant increases in endogenous losses as the time after surgery was increased have been reported (Hess and Seve, 1999). This observation that could be, at least in part, attributed to the negative effects that ileal rectal anastomosis has on the physiology of the pig (Fuller, 1991). It is unlikely that this observation applies to pigs with T-cannulas as this procedure has little if any long-term effects on the physiology of the pig (Moughan and Smith, 1987).

2.5 Animal causes of basal ileal endogenous amino acid losses

Endogenous gut amino acid losses in pigs are influenced by many factors, including those related to the animal and diet. The effect of dietary factors is covered elsewhere in these proceedings and, therefore, only effects of animal related factors are discussed here.

2.5.1 Body protein status

When pigs are fed protein-free diets, the balance of body protein per se may influence endogenous gut amino acids losses. In two studies, the intravenous administration of amino acids reduced significantly the recovery of proline in ileal digesta of pigs fed protein-free diets, while the recovery of indispensable amino acids in ileal digesta was not influenced (de Lange et al., 1989b; Leterme et al., 1996). De Lange et al. (1989b) suggested that glutamine, which is released from muscles in pigs fed protein-free diets, may be converted to proline in intestinal tissue, while feeding protein-free diets per se does not influence the endogenous ileal losses of indispensable amino acids.

2.5.2 Body weight and feed intake

Body weight and feed intake are often confounded in digestibility studies making it difficult to establish independent effects of body weight and feed intake on endogenous gut nitrogen losses (Table 2).

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When endogenous amino acid losses were expressed as gram per day, body weight was found to have no effect on basal ileal endogenous losses (Hess and Seve, 1999) and only minor effects were noted by Furuya and Kaji (1992). However, the effect of body weight was significant in the studies by Sauer et al. (1977), Hess and Sève (1999), and Mariscal-Landín et al. (1995) when data were expressed in gram per kg dry matter intake. This was,

however, not the case in a study with both growing pigs and sows (Stein et al., 1999b), thus highlighting the inconsistencies among studies to establish the effect of body weight on ileal endogenous amino acid losses.

The effect of body weight on endogenous gut protein losses may be more important in younger pigs. Evidence exists that body weight has a significant influence on endogenous gut protein losses in younger pigs (Leibholz and Mollah, 1988; Stein, 1998). This might be related to the fact that younger pigs are known to have faster growth of the intestinal mucosa than older pigs (Low and Zebrowski, 1989). The body weight below which endogenous gut amino acid losses are dependent on body weight has not been determined. For instance, endogenous gut protein losses were significantly higher in 48-kg pigs consuming about 60 g dry matter per kg metabolic body weight ($\text{kg}^{0.75}$) as compared to 39-kg pigs consuming approximately 70 g dry matter per kg metabolic body weight ($\text{kg}^{0.75}$) (Mariscal-Landin et al., 1995). Subsequent studies from the same laboratory, however, failed to confirm these observations. Endogenous gut nitrogen losses were significantly higher in 45-kg pigs fed 50 g dry matter per kg metabolic body weight ($\text{kg}^{0.75}$) than when fed 70 or 90 g dry matter. However, at 77 kg body weight, dry matter intake had no effect on basal endogenous nitrogen and amino acid losses (Hess and Sève (1999). Clearly, there is a need for more information to determine whether expressing endogenous gut protein losses on the basis of other variables (e.g., intake of indigestible materials, water holding capacity etc) other than the intake of feed better explains variation in the recovery of endogenous gut protein losses at the distal ileum in pigs.

2.6 Amino acid composition of endogenous protein

The amino acid composition of basal ileal endogenous protein losses appears not to be influenced by the body weight of the pig. This profile was remarkably similar in pigs at 45 or 77 kg body weight when fed a protein-free diet at 50, 70, or 90 grams dry matter per kg metabolic body weight ($\text{kg}^{0.75}$) (Hess and Sève, 1999, Table 2). Similarly, in a study with growing pigs at 112 kg body weight and lactating and gestating sows fed to appetite a protein-free diet, the profile of basal endogenous amino acids were unaffected (Stein et al., 1999b) and closely paralleled those observed by Hess and Sève (1999) and Green et al. (1987).

It is less clear whether an interaction exist between body weight and dry matter intake. The results of Hess and Sève (1999) suggest no interaction between body weight and dry matter intake as the profile of basal endogenous amino acids was unchanged in pigs of 45 and 77 kg body weight regardless of dry matter intake. However, when restricting dry matter intake in gestating sows to 36 g DM per kg metabolic body weight ($\text{BW}^{0.75}$), the profile of basal endogenous amino acids was significantly altered compared to the profile of those sows allowed free access to feed (Stein et al., 1999b). The reason for this apparent discrepancy may be that there is a level of dry matter intake above which, there is no influence on amino acid composition of endogenous

protein, - but at lower levels of dry matter intake, there is an effect. However, this hypothesis needs to be experimentally tested.

Include Table 3 here

Finally, it appears that there are intrinsic factors specifically related to the individual pig that could lead to differences in basal endogenous amino acid losses among pigs. This is evidenced by the observation of Sève et al. (2000) in which differences in endogenous losses were observed in studies conducted in three different locations although identical diets and similar experimental protocols were used. Earlier, Hess and Sève (1999) observed that the individual pig had a significant effect on the variability of the amino acid composition of basal ileal endogenous losses and concluded that determination of basal endogenous amino acid losses should be included in any digestibility experiment to allow calculation of reliable true digestibility values. The actual aspect(s) of the pig that is responsible for these effects has not been clearly established.

3. Animal factors influencing apparent and standardized amino acid digestibility

Most amino acid digestibility coefficients have been measured using growing barrows in the weight range from 30 to 100 kg. In most studies, feed intake has been restricted to ensure that the animals would consume a set amount of feed every day. Routinely, the feed intake has been restricted to somewhere between 1 and 3 times the maintenance energy requirement of the animals. The digestibility coefficients obtained using this approach are subsequently being applied to all groups of animals. However, several animal factors may influence ileal digestibility coefficients.

3.1 The effect of age and physiological status on amino acid digestibility

The ability of pigs to digest dietary proteins and subsequently absorb amino acids is to some degree dependent on the age of the animal. This is especially true in young pigs that are highly efficient in digesting the proteins present in milk (Mavromichalis et al., 2001). However, amino acid digestibility coefficients for soybean protein are low in young pigs, but increases with the age of the animals (Wilson and Leibholz, 1981). This difference in digestibility may be caused by a difference in enzyme secretions in young pigs as compared to older pigs. While 3 wk old pigs have similar activities of chymotrypsin as mature pigs, the activity of trypsin in 3 wk old pigs is only 10% of the activity in mature pigs (Moughan, 1993). Consistent with this observation, it has been reported that the apparent ileal digestibility of amino acids are higher in pigs that are 36 d old compared to pigs that are 27 d old (Caine et al., 1997). A similar observation was reported by Gabert et al. (1995). It also was indicated that the apparent ileal digestibility of amino acids in casein by 35 kg pigs is different

from that by 60 or 90 kg pigs (Stein, 1998). However, it is not clear when the digestive capacity of pigs reaches a plateau. Further experiments in this area are currently being conducted at South Dakota State University.

It has been reported that the apparent amino acid digestibility coefficients are similar in restricted-fed gestating sows and growing pigs given free access to feed (Stein et al., 1999a). However, the standardized ileal digestibility coefficients were higher in gestating sows than in growing pigs (Stein et al., 2001). The reason for this difference was that gestating sows had higher endogenous losses than did the growing pigs (Stein et al., 1999b) because of a lower feed intake. Therefore, it was concluded that the physiological status of the animal as such does not influence amino acid digestibility.

In conclusion, for pigs above 60 kg, amino acid digestibility coefficients are probably not influenced by age, BW, or physiological status of the animal to any significant extent. However, in pigs less than 60 kg, the amino acid digestibility coefficients change as the pigs mature.

3.2 Effect of level of feed intake on amino acid digestibility

The effect of the level of feed intake on apparent ileal digestibility coefficients has been reported in a few experiments (Sauer et al., 1982; Haydon et al., 1984; Albin et al., 2001). In these experiments, the level of feed intake did not influence apparent ileal amino acid digestibility coefficients. In a recent experiment, it was reported that apparent ileal digestibility coefficients for most amino acids increased as feed intake increased from a level similar to the maintenance energy requirement to a level that was twice that high (Rayadurg and Stein, 2003). However, by increasing the feed intake to three times the maintenance energy intake, no further increase in apparent ileal digestibility coefficients were observed. In the experiments reported previously (Sauer et al., 1982; Haydon et al., 1984; Albin et al., 2001), the lowest level of feed intake was around or above a level equal to two times the maintenance energy requirement. Thus, it may be concluded that the apparent ileal digestibility coefficients of feed proteins are not influenced by feed intake if the animals are fed more than two times the maintenance energy requirement, but reduced digestibility coefficients are observed if feed intake is lower than this level. The reason for the reduced apparent ileal digestibility coefficients by animals fed at a low level of feed intake is that the non-specific endogenous losses of amino acids at the end of the small intestine are elevated in animals on a low level of feed intake as was discussed above. By correcting the apparent ileal digestibility coefficients for the non-specific endogenous losses, the standardized ileal digestibility coefficients are calculated (Mosenthin et al. 2000; Stein et al., 2001; Jansman et al., 2002). Therefore, the standardized ileal digestibility coefficients are linearly decreased as feed intake is increased (Rayadurg and Stein, 2003). Thus, due to the impact of the endogenous amino acid losses, the influence of the level of feed intake on standardized ileal digestibility coefficients are opposite of the influence of feed intake on the apparent ileal digestibility coefficients. This is illustrated in Tables 4 and 5.

Include tables 4 and 5 here

3.3 Genetic variation in amino acid digestibility

It is generally assumed that different genotypes of pigs digest amino acids with the same efficiency although this assumption has not been experimentally documented. The total tract digestibility of nitrogen was reported not to differ between Dutch Landrace pigs and Meishan pigs (Kemp et al., 1991), but comparisons of amino acid digestibility coefficients at the end of the ileum between different genetic lines of pigs have not been reported. However, there are no indications that digestibility coefficients obtained by one genetic line cannot be extrapolated to other lines.

3.4 Microbial fermentation in the small intestine

The reason why amino acid digestibility coefficients are measured at the end of the small intestine rather than over the entire gastro intestinal tract is to avoid the manipulation of undigested feed proteins by large intestinal microflora (Sauer and Ozimek, 1986; Sauer and de Lange, 1992). It is assumed that the disappearance of dietary amino acids prior to the distal ileum is a result of enzymatic hydrolyzation of feed proteins and subsequent absorption of amino acids. While this assumption is probably valid for the majority of the feed proteins disappearing prior to the distal ileum it may not be entirely accurate. Although the majority of the gastro-intestinal microflora are located in the hind gut of monogastric animals, it is also recognized that there is a substantial microbial population inhabiting the small intestine. It has been estimated that between 25 and 50% of the nitrogen appearing at the distal ileum is of microbial origin (Wünche et al., 1991; le Guen et al., 1995). It also has been reported that approximately 20% of the DM found in digesta of ileostomised pigs is of bacterial origin, further indicating that a large microbial population inhabits the upper intestinal tract of pigs (Rowan et al., 1992). Recently, it was reported that so-called non-digestible oligosaccharides were close to 100% digested prior to the distal ileum of growing pigs (Smiricky et al., 2002). Because the digestion of these oligosaccharides requires enzymes not secreted by monogastric animals, this observation further indicates that an active microflora is present in the small intestine. The implication of these findings is that some of the amino acids that have disappeared prior to the distal ileum may have been deaminated by the bacteria rather than absorbed by the animal, which will lead to an overestimation of the digestibility coefficients for these amino acids. The bacteria may also transaminate amino acids, which can lead to a net synthesis of some amino acids and subsequently an underestimation of the digestibility coefficients for these amino acids. Thus, the microflora in the small intestine may manipulate the predicted digestibility coefficients of individual amino acids. Whether this manipulation leads to significant errors in the estimated absorption of amino acids is not known and the overall effect of the microflora in the upper

digestive tract on the prediction of amino acid digestibility coefficients still needs to be elucidated. In addition, it is likely that both the age of the animals and the type of diet fed to the animals influence the size and the activity of this microflora. Thus, the activity of the upper tract microflora and the effects this microflora has on the prediction of protein digestibility and absorption remains an area that requires further research.

4. Conclusion

Important progress has been achieved during recent years in our understanding of how proteins are digested and amino acids are absorbed in pigs. It is evident that pre-cecal amino acid digestibility coefficients that are corrected for the non-specific endogenous losses and measured in animals fed at or close to the voluntary feed intake most precisely predicts the amounts of amino acids being absorbed by a pig. The major inaccuracies in these digestibility coefficients related to the animals are caused by inaccuracies in the estimation of endogenous losses of amino acids, by low levels of feed intake for experimental animals, and by manipulations of intestinal amino acids by the upper tract microflora. Future research will be directed at finding ways to increase the predictability of the absorption of dietary amino acid by more accurately measuring digestibility coefficients.

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Table 1. The amounts (g d^{-1}) of endogenous protein (Nx6.25) entering the gut of a growing pig as estimated by Low (1985)^a

Source	Amount	% of Total
Saliva/gastric juice	3.1	5.8
Bile	2.5	4.7
Pancreas	2.5	4.7
Small intestine	32.1	59.9
Large intestine	13.4	25.0
Total	53.6	100

^a for a 40 kg pig consuming a barley-fishmeal or barley-soya diet at 1.7 kg d^{-1} .

Table 2. Basal ileal endogenous nitrogen losses in pigs at different body weights expressed as either as amounts per day or amounts per dry matter intake.

Reference	Animal class (BW, kg)	Feed intake (g BW ^{-0.75} d ⁻¹)	Ileal endogenous N losses	
			Daily (g d ⁻¹)	Relative to DMI (g kg ⁻¹)
Sauer et al. (1977)	Growing pigs (45 to 75)	51	-	2.69
		63	-	2.56
		72	-	2.05
Hess and Sève (1999)	Growing pigs (45)	50	1.64	2.12
		70	1.86	1.70
		90	2.13	1.51
	Growing pigs (77)	50	1.08	0.91
		70	1.74	1.08
		90	1.95	0.94
Stein et al. (1999b)	Growing pigs (112)	79	-	1.99
	Gestating sows, (215)	90	-	1.80
	Lactating sows (235)	73	-	1.50
Furuya and Kaji (1992)	Growing pigs (49)	43	3.13	4.58
	Growing pigs (92)	41	3.91	3.81

Table 3. Profile (% of total amino acids excluding proline) of basal endogenous amino acids in growing pigs, gestating sows and lactating sows fed a protein free diet¹.

Amino acid	Body weight, kg				
	45	77	112	235 ²	215 ³
Indispensable amino acids					
Arginine	4.91	4.87	4.51	4.29	4.28
Histidine	2.54	2.29	1.95	2.17	2.19
Lysine	5.51	5.30	5.34	5.85	4.70
Phenylalanine	4.87	4.72	4.26	4.15	4.32
Leucine	8.52	8.01	7.38	7.05	7.18
Isoleucine	7.02	6.83	4.89	4.49	4.06
Valine	7.08	7.37	6.13	6.09	5.48
Methionine	1.47	1.88	1.54	1.49	1.29
Threonine	6.56	6.43	6.58	7.19	7.31
Tryptophan	1.12	1.64	1.89	1.77	2.09
Dispensable amino acids					
Aspartic acid	9.97	10.28	10.96	11.32	9.73
Glutamic acid	12.05	12.24	14.22	13.56	12.11
Serine	6.51	6.30	5.62	6.44	6.06
Glycine	7.76	7.66	10.80	11.01	16.43
Alanine	6.59	6.42	7.38	7.22	6.54
Cystine	2.83	3.30	2.95	2.66	2.80
Tyrosine	4.49	4.44	3.75	3.33	3.45

¹Derived from data by Hess and Sève (1999) and Stein et al. (1999b);

²Gestating sows and ³Lactating sows allowed ad libitum feed intake.

Table 4. Apparent ileal digestibility coefficients of crude protein and amino acids (%) in soybean meal by growing pigs as affected by level of feed intake ^{ab}

Feed Intake	Level 1 ^c	Level 2 ^c	Level 3 ^c	SEM ^d	P-Value	
					Linear	Quadratic
CP	66.2 ^y	70.8 ^x	69.9 ^x	0.83	0.0096	0.0038
Indispensable AA						
Arginine	85.9 ^y	87.7 ^x	88.6 ^x	0.48	0.0023	0.1038
Histidine	82.2 ^y	84.7 ^x	83.2 ^{xy}	0.57	0.1944	0.0056
Isoleucine	73.2 ^y	76.6 ^x	75.6 ^{xy}	0.87	0.0764	0.0209
Leucine	75.6 ^y	78.6 ^x	77.3 ^{xy}	0.69	0.0976	0.0084
Lysine	78.2 ^x	80.6 ^x	78.9 ^x	1.1	0.6692	0.0718
Methionine	78.8 ^x	78.8 ^x	77.2 ^x	0.86	0.2386	0.3842
Phenylalanine	77.4 ^y	79.9 ^x	79.0 ^x	0.81	0.1658	0.0419
Threonine	66.1 ^y	71.2 ^x	70.1 ^x	0.85	0.0069	0.0038
Tryptophan	70.0 ^y	75.8 ^x	75.0 ^x	1.30	0.0207	0.0421
Valine	75.4 ^x	78.2 ^x	77.4 ^x	1.2	0.2484	0.1348
Mean Indispensable AA	76.3 ^y	79.2 ^x	78.0 ^x	2.26	0.0237	0.0485
Dispensable AA						
Alanine	62.7 ^x	67.3 ^x	66.0 ^x	1.9	0.2334	0.1414
Aspartic acid	76.2 ^x	78.4 ^x	76.5 ^x	1.2	0.8682	0.0925
Cysteine	63.7 ^y	68.2 ^x	68.9 ^x	1.1	0.0084	0.0655
Glutamic acid	80.8 ^x	80.7 ^x	79.0 ^x	1.0	0.2397	0.2622
Glycine	49.4 ^y	59.0 ^x	59.8 ^x	3.0	0.0043	0.0436
Proline	52.7 ^x	51.8 ^x	59.4 ^x	4.7	0.3196	0.9988
Serine	73.2 ^y	77.3 ^x	76.1 ^x	0.66	0.0093	0.0016
Tyrosine	76.2 ^y	79.8 ^x	78.0 ^{xy}	1.03	0.2295	0.0179
Mean, Dispensable AA	66.9 ^y	70.3 ^x	71.6 ^x	2.39	0.0020	0.0369
Mean, all AA	72.7 ^y	75.3 ^x	75.7 ^x	2.07	0.0039	0.0270

^a From Rayadurg and Stein (2003)

^b n=6.

^c Level 1 = Kg body weight^{0.75} x 106 Kcal ME.

^c Level 2= Kg body weight^{0.75} x 106 Kcal ME x 2.

^c Level 3= Kg body weight^{0.75} x 106 Kcal ME x 3.

^d Standard error of the mean.

^{x, y} Means within a row lacking a common superscript differ ($P < 0.05$).

Table 5. Standardized ileal digestibility coefficients of crude protein and amino acids (%) in soybean meal by growing pigs as affected by level of feed intake ^{ab}

Feed					P -value	
	Level 1 ^c	Level 2 ^c	Level 3 ^c	SEM ^d	Linear	Quadratic
Intake						
CP	91.4 ^x	89.2 ^x	84.4 ^y	1.10	0.0012	0.4640
Indispensable AA						
Arginine	96.7 ^x	96.6 ^x	94.4 ^x	1.40	0.2350	0.5492
Histidine	92.4 ^x	91.8 ^x	88.8 ^x	1.10	0.0455	0.4313
Isoleucine	86.3 ^x	86.6 ^x	83.3 ^y	0.71	0.0124	0.0887
Leucine	87.1 ^x	87.3 ^x	84.0 ^y	0.60	0.0040	0.0658
Lysine	90.3 ^x	89.7 ^x	85.9 ^y	1.20	0.0249	0.3494
Methionine	91.7 ^x	88.6 ^x	84.5 ^y	1.10	0.0012	0.8901
Phenylalanine	87.6 ^x	87.8 ^x	84.9 ^y	0.69	0.0174	0.1251
Threonine	88.3 ^x	85.9 ^{xy}	81.0 ^y	1.9	0.0212	0.6845
Tryptophan	86.6 ^x	87.5 ^x	82.3 ^x	2.0	0.1366	0.3201
Valine	88.2 ^x	87.6 ^x	84.4 ^y	0.85	0.0088	0.3559
Mean Indispensable AA	89.5 ^x	88.7 ^x	85.4 ^y	0.24	0.0046	0.3250
Dispensable AA						
Alanine	86.1 ^x	84.6 ^x	79.5 ^y	1.50	0.0097	0.6443
Aspartic acid	87.9 ^x	87.4 ^x	84.0 ^x	1.90	0.1462	0.5319
Cysteine	86.8 ^x	84.5 ^{xy}	80.6 ^y	1.9	0.0404	0.9309
Glutamic acid	90.3 ^x	88.3 ^{xy}	85.5 ^y	1.20	0.0140	0.7835
Glycine	100.2 ^x	92.4 ^{xy}	84.7 ^y	3.30	0.0068	0.8790
Proline	158.7 ^x	131.9 ^x	128.2 ^x	14.70	0.1546	0.4748
Serine	91.0 ^x	88.9 ^{xy}	84.9 ^y	1.50	0.0143	0.6323
Tyrosine	88.9 ^{xy}	89.7 ^x	85.4 ^y	1.40	0.0827	0.1422
Mean dispensable AA	98.7 ^x	93.5 ^{xy}	89.1 ^y	7.03	0.0139	0.7545
Mean all AA	93.6 ^x	90.9 ^{xy}	87.0 ^y	4.05	0.0057	0.9212

^a From Rayadurg and Stein (2003)

^b n=6.

^c Level 1 = Kg body weight^{0.75} x 106 Kcal ME.

^c Level 2= Kg body weight^{0.75} x 106 Kcal ME x 2.

^c Level 3= Kg body weight^{0.75} x 106 Kcal ME x 3.

^d Standard error of the mean.

^{x, y} Means within a row lacking a common superscript differ ($P < 0.05$).