The concept of digestible amino acids in diet formulation for pigs

R. Mosenthin\textsuperscript{a,}\textsuperscript*b, W.C. Sauer\textsuperscript{b}, R. Blank\textsuperscript{c}, J. Huisman\textsuperscript{d}, M.Z. Fan\textsuperscript{e}

\textsuperscript{a}Hohenheim University, Institute of Animal Nutrition, D-70593 Stuttgart, Germany
\textsuperscript{b}University of Alberta, Department of Agricultural, Food and Nutritional Science, Edmonton, Alberta, Canada T6G 2P5
\textsuperscript{c}University of Kiel, Institute of Animal Nutrition, Physiology and Metabolism, D-24098 Kiel, Germany
\textsuperscript{d}TNO–Nutrition and Food Research Institute, P.O. Box 15, NL-6700 AA Wageningen, The Netherlands
\textsuperscript{e}University of Guelph, Department of Animal and Poultry Science, Guelph, Ontario, Canada N1G 2W1

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Abstract

There is sufficient evidence that ileal rather than fecal amino acid digestibility values provide a more reliable estimate of protein digestion and amino acid absorption. In addition to differences in ileal amino acid digestibility values between feedstuffs there are large differences in ileal amino acid digestibility values within the same feedstuff. Furthermore, in addition to different processing conditions and inherent differences among samples of the same feedstuff, a large proportion of this variation can be attributed to different methodological approaches. In order to reduce the within variation associated with different methods for determination, methods specifically suitable for different feedstuffs are recommended. Differences in dietary amino acid levels are likely to be the largest single contributor to the variation in ileal amino acid digestibility values. Therefore, it is suggested to determine their plateau values, also referred to as dietary threshold levels, after which apparent digestibility values become independent of the dietary amino acid levels. The correction for non-specific endogenous protein and amino acid recoveries in ileal digesta allow for the transformation of apparent digestibility to standardised ileal digestibility values. The non-specific recoveries are related to the dry matter intake but independent of the type of feedstuff. In principle, standardised digestibility values should be the preferred approach in protein evaluation because these values reflect a fundamental property of the feedstuffs being independent of experimental conditions. However, estimates of endogenous recoveries are still confounded by the method used for determination, and further research is warranted in this area. © 2000 Elsevier Science B.V. All rights reserved.

Keywords: Pigs; Amino acids; Endogenous protein; Standardised ileal digestibility

1. Introduction

The concept of digestible amino acids for pigs has received a lot of attention and research effort. The nutritive value of protein for monogastrics is not only determined by the amino acid composition but
also by the digestibility of amino acids, in particular
the amino acids likely to be limiting. Pigs require a
diet with a balanced pattern of different indispens-
able amino acids for optimum performance in which
the protein supplements usually represent 20% of the
diet but make up approximately up to 35% of the
cost of the diet. One means to lower the cost of
protein is to reduce the concentration of amino acids
in the diets or to reduce the quantity of amino acids
possibly provided in excess of the actual require-
ment, i.e. to reduce the margin of safety. However,
this cannot be done efficiently without affecting
optimum performance unless the quantity of avail-
able amino acids in the diet and the quantity required
by the pig are known.

At this point it is important to distinguish between
the concepts of digestible and available amino acids. By
definition, apparent amino acid digestibility is
calculated as the percentage of amino acid intake that
does not appear in digesta or feces. Using the term
“apparent” implies that no correction for endogen-
ous amino acid losses has been made. On the other
hand, availability is defined as the proportion of the
amino acid in the diet that is absorbed in a form
suitable for utilisation (Sauer et al., 1989). Batterham
et al. (1979) introduced the slope-ratio technique for
measuring the availability of amino acids for tissue
synthesis. This animal growth assay provides a
combined estimation of digestibility and post-absorp-
tive utilisation of amino acids at the tissue level.
Batterham (1992) concluded from the results of
different studies that there is likely to be a dis-
crepancy between digestibility and availability values
when heat-treated or heat-damaged meals such as
cottonseed meal and meat and bone meal were
assayed. The differences were significant for lysine,
methionine, threonine and tryptophan but not for the
branched-chained amino acids. The aforementioned
amino acids are susceptible to the effect of heat, they
may be partly damaged and, if modified by the
Maillard-reaction, absorbed in a form which renders
these unavailable for protein synthesis (Hurrell and
Finot, 1985). Batterham (1992) concluded that par-
ticularly for cereals ileal digestibility values were the
most appropriate as these account for losses in
digestibility. In addition, assessing amino acid avail-
ability is expensive and time-consuming because it
provides an estimate of the availability of only one
amino acid per assay (Austic, 1983; Sibbald, 1987).
Furthermore, the results obtained may be confounded
by the influence of ingredients other than the test
amino acid such as starch, fibre, energy and protein
(Austic, 1983). Since this assay is obviously not
practical and applicable for all amino acids in all
feedstuffs, assessing amino acid digestibility may be
a more reasonable alternative from a practical point
of view. According to Williams (1995), the use of
apparent ileal amino acid digestibilities will still
improve the accuracy of diet formulation, and offers
a compromise between total amino acid values in
feedstuffs and amino acid availability.

The objective of this review is to evaluate the ileal
amino acid digestibility concept and to identify its
strengths and weaknesses. This evaluation will in-
clude physiological aspects by comparing apparent
fecal and ileal amino acid digestibilities values.
Furthermore, methodological sources of variation in
apparent ileal amino acid digestibility values includ-
ing the effects of methods for determination and
dietary amino acid level will be addressed. Finally,
the transformation of apparent ileal digestibility
values into standardised ileal digestibility values by
correction for non-specific endogenous amino acid
recoveries will be discussed.

2. The ileal versus the fecal analysis method

After being consumed, dietary protein becomes
mixed with endogenous protein, and the combination
is subjected to digestion and absorption in the small
intestine. Free amino acids and small peptides which
are released by the digestive enzymes are usually
absorbed before entering the large intestine. How-
ever, there will be a certain amount of protein which
has not been digested and peptides and free amino
acids that have not been absorbed in the small
intestine. These along with other undigested dietary
components will pass into the large intestine and the
total is subjected to fermentation by the microflora.
The disappearance of amino acids from the large
intestine would not be necessarily a problem if the
disappearance represented absorption of amino acids
from the large intestine. However, several studies
clearly showed that protein digestion in the large
intestine makes little or no contribution to the protein
status of the pig (Zebrowska, 1973; Wünsche et al., 1982; Mosenthin et al., 1992). This can be attributed to the fact that the microflora in the large intestine have the capacity to deaminate amino acids and to use the carbon skeletons for energy. The amino nitrogen can be absorbed from the large intestine, mainly in the form of ammonia, which will be transported to the liver, converted to urea and excreted in the urine. Thus, the amino acids have disappeared from feces and are assumed to have been digested by the pig. In this case, apparent amino acid digestibilities obtained by the fecal analysis method are higher than those determined by the ileal analysis method. Cystine, threonine and tryptophan usually disappear to a large extent in the large intestine (Zebrowska et al., 1978; Sauer et al., 1982; Mosenthin et al., 1994). On the other hand, microbial net synthesis for methionine and sometimes for lysine has been reported in some studies resulting in lower fecal than ileal digestibility values (Sauer et al., 1982; Tanksley and Knabe, 1982; Sauer et al., 1991). An indication of the significance of the anabolic capacities of the intestinal microflora is that, depending on diet composition, between 50 to 90% of the total nitrogen in feces is of bacterial origin (Poppe et al., 1983; Kreuzer et al., 1989; Sauer et al., 1991).

In conclusion, due to microbial metabolism of nitrogenous material in the large intestine, only a relatively small proportion of the amino acid excretion in feces is directly related to the amino acids recovered at the distal ileum. Thus, depending on the amino acid and on the feedstuff, digestibility values obtained by the fecal analysis method overestimate (which is usually the case) or underestimate those obtained by the ileal analysis method. Therefore, it is now recognised that the ileal analysis method should be considered as an improvement over the fecal analysis method which was originally developed by Kuiken and Lyman (1948) for rats and which thereafter has been used extensively in studies with pigs (Dammers, 1964; Eggum, 1973).

A comparison of apparent fecal and ileal amino acid digestibilities in raw and heated soy flakes illustrates the inadequacy of the fecal analysis method for measuring amino acid digestibility values (Table 1). The difference between fecal and ileal digestibility values of amino acids in raw soy flakes averaged 30% whereas the corresponding difference in heated soy flakes was approximately 7%. Although fecal digestibilities indicated that heated soy flakes were a better nutrient source than raw soy flakes the magnitude of this difference was substantially underestimated (Vandergrift et al., 1983).

It is obvious that apparent ileal amino acid digestibilities are a more sensitive approach to describe the nutritive value of feedstuffs than fecal digestibilities. The poorer the protein quality of feed, the more important ileal digestibility values are compared to fecal digestibility values. Convincing evidence that ileal rather than fecal digestibility values should be used in practical diet formulation for growing pigs was provided by Dierick et al. (1988). In this study the performance of pigs was related to digestibility measurements. There was a higher correlation between average daily gain and ileal rather than fecal protein digestibility ($r = 0.76$ vs. $r = 0.34$). In the same order, for feed efficiency (kg feed/kg carcass gain) the correlation coefficients were $-0.87$ and $-0.65$, respectively. In agreement with these findings, apparent ileal lysine digestibility coefficients were found to accurately indicate the amount of dietary lysine available for growth (Moughan and Smith, 1985; Rademacher et al., 1995). These results provide sufficient evidence that nitrogen absorbed in the large intestine does not contribute significantly to protein synthesis in growing pigs.

### Table 1

<table>
<thead>
<tr>
<th>Amino Acid</th>
<th>Fecal Raw</th>
<th>Fecal Heated</th>
<th>Ileal Raw</th>
<th>Ileal Heated</th>
<th>Difference, %&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Raw</th>
<th>Heated</th>
</tr>
</thead>
<tbody>
<tr>
<td>Histidine</td>
<td>80</td>
<td>90</td>
<td>48</td>
<td>82</td>
<td>32</td>
<td>8</td>
<td></td>
</tr>
<tr>
<td>Isoleucine</td>
<td>68</td>
<td>84</td>
<td>43</td>
<td>78</td>
<td>25</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Leucine</td>
<td>68</td>
<td>87</td>
<td>37</td>
<td>80</td>
<td>31</td>
<td>7</td>
<td></td>
</tr>
<tr>
<td>Lysine</td>
<td>72</td>
<td>87</td>
<td>44</td>
<td>85</td>
<td>28</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Methionine</td>
<td>61</td>
<td>83</td>
<td>47</td>
<td>82</td>
<td>14</td>
<td>1</td>
<td></td>
</tr>
<tr>
<td>Threonine</td>
<td>65</td>
<td>83</td>
<td>32</td>
<td>72</td>
<td>33</td>
<td>11</td>
<td></td>
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<tr>
<td>Tryptophan</td>
<td>75</td>
<td>87</td>
<td>25</td>
<td>72</td>
<td>50</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Valine</td>
<td>64</td>
<td>85</td>
<td>35</td>
<td>78</td>
<td>29</td>
<td>7</td>
<td></td>
</tr>
</tbody>
</table>

<sup>a</sup> Vandergrift et al. (1983).

<sup>b</sup> Difference between fecal and ileal digestibility values.
3. Variation in apparent ileal protein and amino acid digestibilities

The apparent ileal digestibilities of protein and amino acids have been determined in a large number of samples from the most common feedstuffs used in pig nutrition. It is obvious that there are large differences in ileal protein and amino acid digestibility values between feedstuffs. The main factors responsible for these differences including methods for digesta collection, processing conditions and inherent dietary factors were previously discussed (Sauer and Ozimek, 1986; Knabe et al., 1989; Knabe, 1991; Mosenthin and Sauer, 1992; Mosenthin et al., 1997). In addition, there are also large differences in ileal amino acid digestibilities among different samples of the same feedstuff (Sauer et al., 1990). The extent of this variation depends on the type of feedstuff (Sauer and Ozimek, 1986; Mosenthin et al., 1997). The apparent ileal protein and amino acid digestibilities of various cereal grains, protein supplements of plant and animal origin and of legume seeds were compiled from a literature review by Mosenthin et al. (1997) and are summarised in Table 2.

There are substantial differences in apparent ileal protein and amino acid digestibility values among samples of the same cereal grain as reflected by large standard deviations. For protein and the indispensable amino acids the differences were largest in barley, ranging from 45–80%, 38–79%, 67–88% and 44–76% for protein, lysine, methionine and threonine, respectively. Some of the differences in apparent ileal protein and amino acid digestibilities may be attributed to differences in processing conditions and such factors as variety of grain, fertiliser application and environmental conditions which were discussed in detail by Sauer and Ozimek (1986) and Mosenthin et al. (1997). However, as shown in Table 2, there were relatively small differences in the average apparent ileal protein and amino acid digestibility values between different cereal grains compared with differences within the same cereal grain. The digestibility coefficients for wheat, barley,

<table>
<thead>
<tr>
<th>Ingredients</th>
<th>n^b</th>
<th>Crude protein</th>
<th>Lysine</th>
<th>Methionine</th>
<th>Threonine</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>DC</td>
<td>Range</td>
<td>SD</td>
<td>DC</td>
</tr>
<tr>
<td>Cereal grains</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Wheat</td>
<td>22</td>
<td>81</td>
<td>71–86</td>
<td>4.2</td>
<td>73</td>
</tr>
<tr>
<td>Barley</td>
<td>20</td>
<td>70</td>
<td>45–80</td>
<td>8.2</td>
<td>66</td>
</tr>
<tr>
<td>Corn</td>
<td>8</td>
<td>70</td>
<td>49–82</td>
<td>11.7</td>
<td>68</td>
</tr>
<tr>
<td>Triticale</td>
<td>6</td>
<td>78</td>
<td>76–82</td>
<td>3.0</td>
<td>72</td>
</tr>
<tr>
<td>Protein supplements</td>
<td></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Soybean meal</td>
<td>30</td>
<td>80</td>
<td>72–89</td>
<td>3.7</td>
<td>84</td>
</tr>
<tr>
<td>Canola meal</td>
<td>14</td>
<td>60</td>
<td>64–73</td>
<td>2.5</td>
<td>73</td>
</tr>
<tr>
<td>Cottonseed meal</td>
<td>12</td>
<td>75</td>
<td>67–86</td>
<td>5.7</td>
<td>66</td>
</tr>
<tr>
<td>Meat and bone meal</td>
<td>16</td>
<td>67</td>
<td>57–82</td>
<td>6.8</td>
<td>70</td>
</tr>
<tr>
<td>Fishmeal</td>
<td>7</td>
<td>76</td>
<td>72–82</td>
<td>3.9</td>
<td>83</td>
</tr>
<tr>
<td>Legume seeds</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Peas</td>
<td>9</td>
<td>73</td>
<td>69–76</td>
<td>2.7</td>
<td>81</td>
</tr>
<tr>
<td>Faba beans</td>
<td>6</td>
<td>74</td>
<td>69–77</td>
<td>2.8</td>
<td>80</td>
</tr>
</tbody>
</table>

^a Compiled from Mosenthin et al. (1997).
^b Number of observations.
^c Digestibility coefficient, mean values and range of values.
^d Standard deviation.
^e Values in parentheses following protein and methionine digestibility values indicate the number of samples in which the protein and methionine digestibility was determined.
corn and triticale ranged from 70 to 81%, 66 to 73%, 78 to 85% and 62 to 72% for protein, lysine, methionine and threonine, respectively. The large within rather than between variation in cereal grains indicates that methodological rather than other factors may be responsible for a large proportion of this variation.

A similar conclusion can be drawn for protein supplements and legume seeds. Once again, there were large differences in apparent ileal protein and amino acid digestibility values among samples of the same feedstuff, with relatively larger variations in cottonseed meal, meat and bone meal, fishmeal and faba beans and smaller in soybean meal, canola meal and peas (Table 2). With respect to the protein supplements and legume seeds, there seems to be less variation as compared to the cereal grains, with the exception of methionine which may be related to the analytical procedure (Sauer and Ozimek, 1986). However, similar to cereal grains, there were in most cases relatively small differences in the average apparent ileal protein and amino acid digestibility values between different protein supplements and legume seeds compared with differences within the same feedstuff.

In addition to different processing conditions and inherent factors among samples of the same feedstuff (e.g. fibre levels, anti-nutritional factors, variety of grain, fertiliser application, environmental conditions), a large proportion of this variation can be attributed to different methodological approaches. The major responsible methodological factors, those including methods of determination and dietary protein and amino acid levels, will be addressed.

4. Evaluation of methodological sources of variation in apparent ileal protein and amino acid digestibilities

4.1. The effect of methods for determination

There are three methods for measurements of nutrient digestibility in assay diets and assay feed ingredients. These methods are the direct, the difference and the regression method. The principles of these methods were previously described by Giger and Sauvant (1983) for ruminants and recently by Fan and Sauer (1995a,b) for pigs.

4.1.1. Direct method

Using this method the assay diet is formulated in such a manner that the assay ingredient provides the sole dietary nutrient in question. Therefore, the nutrient digestibility in the assay feed ingredient is equal to the corresponding value in the assay diet.

4.1.2. Difference method

This method involves the formulation of both a basal and an assay diet. In this approach the basal diet contains the basal feed ingredient which provides the sole assay nutrient in the diet, whereas the assay diet consists of a mixture of the basal and assay feed ingredient. Provided that there is no interaction in nutrient digestibility between the basal feed ingredients and the assay feed ingredient, the digestibility of the nutrient in question of the assay diet can be calculated by difference.

4.1.3. Regression method

In this method the basal and the assay feed ingredient are evaluated simultaneously. Under the condition that the basal and the assay feed ingredient provide the sole assay nutrient in the assay diets, and provided that there is no interaction between the two feed ingredients, the ingredients can be mixed at various graded levels. As a result more than two assay diets are formulated for digestibility measurements. The relationship between the nutrient digestibility in the assay diets and the contribution levels of the nutrient from the basal and assay feed ingredient to the assay diets can be expressed according to the following equation:

$$D_{Di} = D_B \times C_{Bi} + D_A \times C_{Ai}$$

where $D_{Di}$ = apparent digestibility of a nutrient in the assay diet (%); $D_B$ = apparent digestibility of a nutrient in the assay feed ingredient (%); $D_A$ = apparent digestibility of a nutrient in the basal feed ingredient (%); $C_{Ai}$ = contribution level (%) of a nutrient from the assay feed ingredient to the assay diet; $C_{Bi}$ = contribution level (%) of a nutrient from the basal feed ingredient to the assay diet.
The direct method has been applied especially to many of the cereal grains, in part, because most cereals are very palatable. However, as will be discussed in Section 4.2, the ileal digestibility values of amino acids in cereal grains determined with the direct method are influenced by their amino acid content in the assay diet. In addition to cereal grains the direct method may apply to the formulation of a semi-purified diet, usually based on corn starch, in which the assay ingredient provides the sole dietary amino acids. With respect to protein supplements and legume seeds, most measurements of apparent ileal digestibilities were carried out with the direct method. However, in case of some protein supplements or legume seeds, some of which are of poor palatability (e.g. blood meal) and/or have a high content of anti-nutritional factors (e.g. faba beans), the difference method was chosen for the determination of apparent ileal amino acid digestibility values. According to previous studies no effect of level of inclusion of soybean meal in the diet on apparent ileal amino acid digestibilities was obtained (Van Leeuwen et al., 1987). Similarly, studies by Imbeah et al. (1988) showed with the exception of lysine and phenylalanine no differences \((P > 0.05)\) between apparent ileal amino acid digestibilities in soybean meal and canola meal determined with the direct and difference method, respectively. It should be mentioned, however, that the studies by Imbeah et al. (1988) indicate the presence of associative effects, albeit of small magnitude, for some amino acids from barley and canola meal.

Recently, comprehensive studies were carried out by Fan and Sauer (1995a,b) in which the effect of the direct, the difference and the regression method on apparent ileal protein and amino acid digestibility values was determined. In these studies feed ingredients with a low, medium and high protein content such as barley, peas and canola meal, respectively, were tested as representative feed ingredients for cereal grains, legume seeds and protein supplements. Fan and Sauer (1995a) formulated 5 diets which were fed to 5 barrows with an initial body weight of 35 kg according to a 5×5 Latin square design. Diet 1 contained 90% barley providing the sole source of amino acids whereas diet 5 contained 42.6% canola meal as the sole source of amino acids in the diet. In diets 2, 3, and 4 barley and canola meal were the only amino acid sources and included at three levels, 67.5%, 45.0% and 22.5%, respectively for barley and 24.4%, 30.5% and 36.5% respectively for canola meal. Except for diet 1 all diets were formulated to contain 16% crude protein. The digestibility values for protein and amino acids in barley are compared in Table 3. For some of these amino acids ileal digestibility coefficients could not be estimated by the regression method. This was due to the fact that the differences in ileal digestibility values for these amino acids between the assay and the basal feed ingredient were not large enough to create linear responses.

Ileal digestibility coefficients in barley estimated by the regression method were not different \((P > 0.05)\) from values determined by the difference method when barley was included in the diet at a level of 67.5% (diet 2). However, at lower inclusion levels (22.5% and 45.0%) the ileal digestibility values of protein and amino acids in barley were underestimated (results not shown). This indicates that the difference method is only reliable at relatively high inclusion levels of the assay amino acids from the test feedstuff in the diets. In addition, the ileal digestibility values of protein and amino acids determined by the direct method were usually lower \((P < 0.05\) or 0.10) than those determined by the difference or regression method. Fan and Sauer (1995a) concluded that the direct method is not a valid approach for the determination of protein and amino acid digestibilities in feedstuffs with a low protein content.

On the other hand, for some low-protein feedstuffs of poor palatability such as rye, wheat bran and forage plants, the difference rather than the direct method has been used. For example, Kreienbring et al. (1988) reported that the apparent ileal digestibility values of amino acids in forage plants determined by the difference method varied considerably, indicated by large standard deviations. Since the amino acid contents in these forage plants were low and due to a poor palatability the inclusion levels in the assay diets were also low, the large variation likely resulted from the magnifying effect induced by the calculation process of the difference method. In conclusion, the difference method may not be suitable for these low-protein feedstuffs and the regres-
Table 3
Comparison of the apparent ileal crude protein and amino acid digestibility values (%) in barley with the direct, the difference and the regression methods\textsuperscript{1,2,3}

<table>
<thead>
<tr>
<th>Items</th>
<th>Methods of determination</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Direct method</td>
</tr>
<tr>
<td>Number of observations</td>
<td>5</td>
</tr>
<tr>
<td>Crude protein</td>
<td>56.6±1.88</td>
</tr>
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</table>

Amino acids

Indispensable

<table>
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<tr>
<th>Amino acid</th>
<th>Direct method</th>
<th>Difference method\textsuperscript{4}</th>
<th>Regression method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arginine\textsuperscript{d}</td>
<td>64.7±1.93</td>
<td>69.8±3.15</td>
<td>68.4±2.39</td>
</tr>
<tr>
<td>Histidine</td>
<td>69.5±2.68</td>
<td>71.9±3.56</td>
<td>70.5±2.27</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>61.1±3.29</td>
<td>66.9±4.80</td>
<td>–</td>
</tr>
<tr>
<td>Leucine</td>
<td>66.6±2.80</td>
<td>70.3±3.79</td>
<td>–</td>
</tr>
<tr>
<td>Lysine\textsuperscript{d}</td>
<td>54.1±4.18</td>
<td>61.3±4.93</td>
<td>59.3±4.65</td>
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<td>Phenylalanine</td>
<td>69.6±3.41</td>
<td>72.1±4.28</td>
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<tr>
<td>Threonine</td>
<td>53.3±3.12\textsuperscript{b}</td>
<td>62.4±3.90\textsuperscript{a}</td>
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<tr>
<td>Valine</td>
<td>62.6±2.96</td>
<td>67.2±3.94</td>
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Dispensable

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<tr>
<th>Amino acid</th>
<th>Direct method</th>
<th>Difference method\textsuperscript{4}</th>
<th>Regression method</th>
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<tbody>
<tr>
<td>Alanine\textsuperscript{d}</td>
<td>48.8±2.96\textsuperscript{b}</td>
<td>57.3±3.39\textsuperscript{a}</td>
<td>53.9±2.81\textsuperscript{b}</td>
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<td>Aspartic acid</td>
<td>50.5±3.83\textsuperscript{a}</td>
<td>62.1±4.68\textsuperscript{a}</td>
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<td>Glutamic acid</td>
<td>75.1±2.52</td>
<td>73.9±2.10</td>
<td>72.2±2.89</td>
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<td>Glycine</td>
<td>31.7±3.41\textsuperscript{a}</td>
<td>48.1±5.64\textsuperscript{b}</td>
<td>34.5±5.08\textsuperscript{b}</td>
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<tr>
<td>Serine</td>
<td>58.4±3.19\textsuperscript{a}</td>
<td>64.8±2.67\textsuperscript{b}</td>
<td>–</td>
</tr>
<tr>
<td>Tyrosine\textsuperscript{d}</td>
<td>51.5±3.88</td>
<td>61.2±5.62</td>
<td>58.2±3.43</td>
</tr>
</tbody>
</table>

\textsuperscript{1} Fan and Sauer (1995a).
\textsuperscript{2} Mean and standard error of the mean.
\textsuperscript{3} Digestibility values calculated from diet 2 (67.5\% inclusion level of barley).
\textsuperscript{4} Means in the same row show a trend to increase (\(P<0.10\), by one-tailed Student’s t-test).
\textsuperscript{5} Means in the same row with different superscript letters differ (\(P<0.05\)).

The apparent ileal protein and amino acid digestibility values in canola meal determined by the direct, the difference and the regression methods are presented in Table 4. Similar to barley (Table 3), for some amino acids ileal digestibility values could not be calculated by the regression method since the differences in digestibilities for these amino acids between the assay (canola meal) and the basal feed ingredient (barley) were not large enough to create linear responses.

As shown in Table 4, the apparent ileal digestibilities of crude protein and amino acids in canola meal estimated by the regression method were not different (\(P>0.05\)) from those determined by the direct method, and were very close (\(P>0.05\)) to the values determined by the difference method at the higher inclusion levels of canola meal in the diet (30.5 and 36.5\%). However, these values were usually lower than those determined by the difference method when the assay ingredient (canola meal) was included at a relatively low level (24.4\%) in the diet (results not shown). With respect to the difference method, the apparent ileal digestibility values of amino acids in high-protein feedstuffs such as canola meal were overestimated (\(P<0.05\) or 0.10) when a low-protein feedstuff such as barley was the basal feed ingredient and when the inclusion level of the assay feed ingredient (canola meal) was relatively low in the assay diet. Therefore, it was recommended by Fan and Sauer (1995a) that a protein supplement rather than a low-protein feedstuff (e.g. cereal grains) should be the basal feed ingredient when the difference method is used.

On the other hand, for protein supplements of poor palatability such as blood meal the apparent ileal digestibility values of amino acids should be de-
Table 4
Comparison of the apparent ileal crude protein and amino acid digestibility values (%) in canola meal with the direct, the difference and the regressions methods

<table>
<thead>
<tr>
<th>Items</th>
<th>Direct method</th>
<th>Difference method</th>
<th>Regression method</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of observations</td>
<td>5</td>
<td>5</td>
<td>20</td>
</tr>
<tr>
<td>Crude protein</td>
<td>66.0±0.85</td>
<td>62.5±1.44</td>
<td>64.3±1.46</td>
</tr>
<tr>
<td>Amino acids</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Indispensable</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arginine</td>
<td>80.8±1.19</td>
<td>79.4±1.14</td>
<td>79.5±0.95</td>
</tr>
<tr>
<td>Histidine</td>
<td>80.0±0.78</td>
<td>77.4±1.19</td>
<td>78.7±1.09</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>69.3±0.77</td>
<td>65.3±1.58</td>
<td>–</td>
</tr>
<tr>
<td>Leucine</td>
<td>70.8±1.15</td>
<td>67.7±1.68</td>
<td>–</td>
</tr>
<tr>
<td>Lysine</td>
<td>73.7±0.79</td>
<td>70.7±1.10</td>
<td>71.8±1.38</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>70.8±1.18</td>
<td>67.9±1.90</td>
<td>–</td>
</tr>
<tr>
<td>Threonine</td>
<td>63.1±0.88</td>
<td>60.7±1.64</td>
<td>–</td>
</tr>
<tr>
<td>Valine</td>
<td>67.5±0.84</td>
<td>63.8±1.72</td>
<td>–</td>
</tr>
<tr>
<td>Dispensable</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Alanine</td>
<td>68.9±0.60</td>
<td>65.2±1.95</td>
<td>66.6±1.55</td>
</tr>
<tr>
<td>Aspartic acid</td>
<td>64.1±1.04</td>
<td>61.2±1.65</td>
<td>–</td>
</tr>
<tr>
<td>Glutamic acid</td>
<td>80.3±1.17</td>
<td>75.8±1.42</td>
<td>79.6±1.19</td>
</tr>
<tr>
<td>Glycine</td>
<td>63.4±1.95</td>
<td>63.7±1.28</td>
<td>62.0±1.89</td>
</tr>
<tr>
<td>Serine</td>
<td>65.0±0.64</td>
<td>62.0±1.65</td>
<td>–</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>66.0±0.81</td>
<td>64.5±1.53</td>
<td>64.5±1.49</td>
</tr>
</tbody>
</table>

\[ \text{a} \] Fan and Sauer (1995a).
\[ \text{b} \] Mean and standard error of the mean.
\[ \text{c} \] Digestibility values calculated from diet 4 (36.6% inclusion level of canola meal).

terminated by the regression rather than the difference method. This can be attributed to the fact that due to the low level of inclusion of these protein supplements in the assay diet, the ileal digestibility coefficients may not be reliable. For example, Knabe et al. (1989) reported that the ileal digestibility values of isoleucine calculated by the difference method for three samples of blood meal were 60, 70 and 80%, respectively. However, as was pointed out by the authors, these values do not represent the variation in apparent ileal digestibility values of isoleucine but are a reflection of experimental error since blood meal provided only 15% of the isoleucine content in the assay diet.

Fan and Sauer (1995a) concluded that the regression method is, in principle the most accurate approach for determining ileal digestibility values in protein supplements, in particular for protein supplements with a low level of inclusion in the assay diet due to poor palatability. In order to apply the regression method successfully for all amino acids, the basal and the assay feed ingredient should be paired in such a way that differences in apparent ileal digestibility values of amino acids between the two feed ingredients are large enough to create linear responses. With respect to the difference method, it is recommended that a protein supplement rather than a low-protein feedstuff (e.g. cereal grains) is the basal feed ingredient and that, in addition, the inclusion level of the test protein supplement is relatively high in the assay diet.

These recommendations for the determination of apparent ileal protein and amino acid digestibilities in high-protein feedstuffs were confirmed in further studies with peas (Fan and Sauer, 1995b). Peas represent feed ingredients with a medium protein content compared to protein supplements (e.g. oilseed products) with a relatively high and cereal grains with a relatively low protein content. Provided that the consumption of the assay diets is not limited due to poor palatability of the test feedstuff, the direct method may be also suitable to determine...
apparent ileal protein and amino acid digestibility values in legume seeds.

4.2. The effect of dietary protein and amino acid levels

With increasing levels of dietary protein from soybean meal the apparent fecal protein digestibility increased curvilinearly as was originally shown by Eggum (1973) in studies with rats. A similar relationship was established by Furuya and Kaji (1989) in pigs who reported differences in apparent ileal digestibility values of protein and amino acids in relation to their dietary contents. Therefore, values for apparent ileal amino acid digestibility are only valid under standardised conditions with respect to the protein and/or amino acid content of the assay diet. However, an examination of the literature reveals that in most cases the determination of apparent ileal amino acid digestibility values was carried out at different dietary amino acid levels as indicated by differences in dietary protein content. For example, the crude protein contents in corn starch-based soybean meal diets were 21, 14 and 12%, in studies by Holmes et al. (1974), Jørgensen et al. (1984) and Knabe et al. (1989), respectively. From a literature review Sauer and Ozimek (1986) and more recently Mosenthin et al. (1997) concluded that differences in protein and amino acid content in the assay diets may explain, in part, the variation in apparent ileal digestibility values of protein and amino acids among different samples of the same feedstuff.

As there is a scarcity of information about the effect of dietary protein and amino acid content on the corresponding apparent ileal digestibility values, Fan et al. (1994) initiated a comprehensive study in which 6 corn starch-based diets with graded levels of crude protein from soybean meal (4, 8, 12, 16, 20 and 24%) were fed to growing pigs according to a 6x6 Latin square design. As expected, there were large increases ($P<0.01$) in apparent ileal digestibility coefficients for protein and all amino acids with increasing levels of dietary protein. These increases were greatest at the lower protein levels; they became negligible at the higher levels as endogenous protein accounts for a smaller proportion of total protein in ileal digesta. The analysis of the digestibility values according to a segmented quadratic with plateau model resulted in quadratic relationships between the apparent ileal amino acid digestibility values and the amino acid content in the assay diet. These relationships are illustrated in Fig. 1 for leucine, lysine, methionine and threonine; a similar pattern was observed for the other amino acids. At lower dietary levels the apparent ileal amino acid digestibility values increased sharply; thereafter the increases became smaller and reached their individual plateau values after which there were no further increases which means that the digestibility coefficients became independent of the dietary amino acid levels. In this model the lower endpoints of 95% confidence intervals of the plateau digestibility values are defined to be the initial plateau digestibility values. By definition, the dietary protein and amino acid contents, corresponding to the initial plateau digestibility values, are referred to as the dietary threshold levels.

It should be emphasised, however, that the apparent ileal protein and amino acid digestibility values do not reach their initial plateau values simultaneously at the same dietary crude protein content (Fig. 2). The studies by Fan et al. (1994) clearly show that the dietary amino acid contents affect apparent ileal amino acid digestibility values, irrespective of the level of protein in the diet. The authors suggested that the level of inclusion of a feedstuff in the assay diet should be such that the amino acid contents in the assay diet are equal to or exceed the expected threshold levels in order to obtain the plateau values. Despite the fact that dietary factors such as fibre and anti-nutritional compounds may alter the ratio of exogenous to endogenous amino acids, thereby affecting the dietary threshold levels of protein and amino acids, these values are valuable for reference.

Fan et al. (1994) concluded from the literature that the total contents of crude protein and most amino acids in cereal grains are usually far below the threshold levels that were established in their study. As a result, small differences in dietary contents of crude protein and amino acids below the corresponding threshold levels will result in relatively large variations in the digestibility coefficients of amino acids, as dietary amino acid levels quadratically affect ileal amino acid digestibilities. Especially those amino acids present at low levels in cereal
grains (lysine, threonine and tryptophan) and/or amino acids of which the ileal endogenous recovery is relatively high (e.g., threonine) will be affected. In general, this applies also to protein supplements and legume seeds, especially for the limiting amino acids. The relatively large variation in the apparent ileal digestibility of methionine within samples of soybean meal and in methionine, cystine and tryptophan within samples of peas, can be attributed to the relatively low levels of these amino acids in the assay diets (Fan et al., 1994). In addition to the previously discussed effect of methods for determination, differences in dietary protein and amino acids contents are likely to be the most important single factor for the variation in ileal amino acid digestibility values within samples of the same feedstuff.

5. Standardised ileal amino acid digestibility values

If one accepts that the determination of amino acid digestibility values should be based on the ileal analysis method, one should recognise that ileal digesta contains variable amounts of endogenous protein originating mainly from digestive secretions, sloughed-off epithelial cells and mucins.

Adjustments for endogenous protein and amino acid recoveries, which may be extra stimulated by the presence of anti-nutritional factors such as lectins, trypsin inhibitors and tannins in the diet, allow for the determination of true ileal protein and amino acid digestibility values. In principle, true amino acid digestibility values should be the preferred approach.
because it reflects a fundamental property of the feedstuff being independent of experimental and dietary conditions.

Endogenous protein and amino acid recoveries in ileal digesta can be divided in a non-specific and a specific fraction. The non-specific recovery — also referred to as basal recovery — is related to the dry matter intake but independent of the type of feedstuff or diet. In contrast, the specific recovery — also referred to as extra recovery — is related to the composition of the feedstuff or diet (e.g. presence of inherent factors such as lectins, trypsin inhibitors and tannins).

Due to the non-specific recovery, values of apparent digestibility are influenced by the protein and amino acid levels in the assay diet. For a given amino acid, the apparent digestibility values increase exponentially with higher levels of intake because endogenous recoveries, as a percent of total recovery, decrease proportionally. By contrast, true amino acid digestibility values are not affected by the level of intake or amino acid content of the assay diet as illustrated in Fig. 3. True digestibility values

---

**Fig. 2.** The quadratic with plateau relationships between the apparent ileal crude protein and amino acid digestibility values and the dietary crude protein content (as-fed basis) (Fan et al., 1994).

**Fig. 3.** Schematic illustration of apparent and true amino acid digestibilities as a function of dietary amino acid level.
allow accurate comparisons between different feedstuffs, even if these are fed in different quantities. Furthermore, true digestibility values are likely to be more additive between feed ingredients than apparent values (Mariscal–Landin, 1992).

It is therefore suggested that for use in feed evaluation values of apparent digestibility should be transformed into values of true digestibility (Sève, 1994; Boisen and Moughan, 1996a; Boisen, 1998). Therefore, the term “standardised ileal digestibility” was introduced by Mariscal–Landin (1992). It describes the transformation of apparent amino acid digestibility values into values of standardised digestibilities by correction for non-specific amino acid recoveries in ileal digesta according to the following equation:

\[
\text{SID} (%) = \frac{\text{AID} (%) \times \text{Non-specific endogenous amino acid recoveries (g/kg DMI)}}{\text{Dietary amino acid content (g/kg DM)}} \times 100
\]

where SID = standardised ileal digestibility values; AID = apparent ileal digestibility values; DMI = dry matter intake.

Standardised ileal digestibility values of protein and amino acids in feedstuffs for pigs were published by Jondreville et al. (1995), CVB (1998) and Degussa (1998). The calculation of standardised ileal protein and amino acid digestibilities requires an estimate of the amount of non-specific endogenous protein and amino acid recoveries in ileal digesta. Several methods have been developed and applied to quantify these recoveries. These include conventional methods such as feeding protein-free diets, the regression method and feeding diets containing protein sources (e.g. casein) with an assumed 100% digestibility. Other methods include the peptide alimentation ultrafiltration method, also referred to as the enzymatically hydrolysed casein (EHC) method, the homoarginine method, isotope dilution techniques and calculation methods based on the difference between the in vitro and in vivo digestibility of protein and amino acids. Comprehensive descriptions and evaluations of these methods were provided by Tamminga et al. (1995), Boisen and Moughan (1996b) and Nyachoti et al. (1997). According to Nyachoti et al. (1997) estimates of endogenous protein and amino acid recoveries in ileal digesta are not only affected by animal and dietary factors but also differ for various methods. For example, Boisen and Moughan (1996b) reported that the non-specific endogenous protein recoveries varied between 10 and 15 g/kg dry matter intake when protein-free diets were fed. However, under more physiologically normal conditions (i.e. when protein-containing diets were given), the non-specific recoveries accounted for about 20 g/kg dry matter intake. Nyachoti et al. (1997) concluded that estimates of endogenous protein and amino acid recoveries obtained with the regression method as well as with feeding protein-free-diets should be referred to as the minimum values that are not related to the protein and amino acid content of the diet.

For the calculation of standardised digestibility coefficients two different approaches were introduced in practice. Jondreville et al. (1995), in association with Eurolysine and the Technical Institute for Cereals and Forages (ITCF), based their calculations for the correction of non-specific endogenous ileal protein and amino acid recoveries on data that were obtained by feeding protein-free diets to growing pigs. On the other hand, Rademacher et al. (1999) transformed values of apparent ileal protein and amino acid digestibility to values of standardised digestibility by using existing literature data on endogenous recoveries of protein and amino acids in ileal digesta. These authors selected 33 experiments from the literature including experiments carried out at the TNO Nutrition and Food Research Institute, Department of Animal Nutrition and Physiology (ILOB) in Wageningen, The Netherlands. The determination of average values for the non-specific endogenous protein and amino acid recoveries in ileal digesta was based on different experimental approaches. These included conventional methods such as feeding protein-free diets without (n = 16) or with parenteral infusion of amino acids (n = 1) (e.g. De Lange et al., 1989a,b), the regression method (n = 3) (e.g. Fan et al., 1995c) and the feeding of highly digestible protein sources such as wheat gluten or casein (n = 11) (e.g. Chung and Baker, 1992). In addition, the corrections for non-specific protein and amino acid recoveries in ileal digesta were based on the EHC method (n = 2) (e.g. Butts et al., 1993). It should be mentioned that the diets in the experiments selected by Rademacher et al. (1999) contained no specific anti-nutritional factors.
and not more than 8% cellulose or purified neutral detergent fibre (NDF). The data of these experiments were pooled and mean values for non-specific losses of protein and amino acid recoveries were calculated.

The feeding of protein-free diets as described by Jondreville et al. (1995) gives lower estimates of non-specific endogenous and amino acid recoveries as compared to estimates by Rademacher et al. (1999) which were based on different experimental approaches as outlined in Table 5. These differences were highest for threonine which is present in relatively large concentrations in endogenous protein (Holmes et al., 1974; De Lange et al., 1989a; Sauer et al., 1991; Mosenthin et al., 1994).

Standardised ileal digestibility coefficients for crude protein and amino acids were compared by correcting the corresponding apparent digestibility values for non-specific crude protein and amino acid recoveries according to the approach by Jondreville et al. (1995) and Rademacher et al. (1999), respectively (Table 6). The effect of transforming apparent into standardised digestibility values is of small magnitude in high-protein feedstuffs such as soybean meal. Furthermore, the values are not affected by the experimental approach used for corrections. However, this effect is much more pronounced in low-protein feedstuffs such as barley and sugar-beet pulp because of the higher proportion of endogenous to exogenous (dietary) recoveries of protein and amino acids in ileal digesta. In addition, the standardised ileal protein and amino acid digestibilities differ considerably between the methods used for correction of non-specific endogenous recoveries. For example, the large differences in standardised ileal threonine digestibility values for barley and in particular for sugar-beet pulp are a reflection of the different values (0.25 vs. 0.61 g/kg DMI) for non-specific endogenous ileal recoveries of threonine obtained by Jondreville et al. (1995) and Rademacher et al. (1999), respectively.

As a result, these sources of variation decrease the sensitivity and liability of standardised ileal amino acid digestibility values between different feedstuffs. In addition, this variation may misrepresent the real variation among samples of the same feedstuff.

### 6. Conclusions

The ileal rather than fecal analysis method should be used for determining amino acid digestibility. Values determined with this method reflect the digestive utilisation of amino acids in feed ingredients by pigs. Ileal amino acid digestibility values

### Table 5

Comparison of non-specific endogenous crude protein and amino acid recoveries in ileal digesta with different experimental techniques (g/kg DMI)

<table>
<thead>
<tr>
<th>Method Observations</th>
<th>Protein-free diet&lt;sup&gt;a&lt;/sup&gt; ( n = 20 )</th>
<th>Other methods&lt;sup&gt;b&lt;/sup&gt; ( n = 33 ) (including protein-free diet method)</th>
<th>Difference (%) Protein-free diet = 100</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein</td>
<td>7.15</td>
<td>11.82</td>
<td>165</td>
</tr>
<tr>
<td>Arginine</td>
<td>0.20</td>
<td>0.39</td>
<td>195</td>
</tr>
<tr>
<td>Cystine</td>
<td>0.10</td>
<td>0.21</td>
<td>210</td>
</tr>
<tr>
<td>Histidine</td>
<td>0.09</td>
<td>0.19</td>
<td>211</td>
</tr>
<tr>
<td>Isoleucine</td>
<td>0.19</td>
<td>0.38</td>
<td>200</td>
</tr>
<tr>
<td>Leucine</td>
<td>0.30</td>
<td>0.49</td>
<td>163</td>
</tr>
<tr>
<td>Lysine</td>
<td>0.27</td>
<td>0.40</td>
<td>148</td>
</tr>
<tr>
<td>Methionine</td>
<td>0.09</td>
<td>0.11</td>
<td>122</td>
</tr>
<tr>
<td>Phenylalanine</td>
<td>0.23</td>
<td>0.34</td>
<td>148</td>
</tr>
<tr>
<td>Threonine</td>
<td>0.25</td>
<td>0.61</td>
<td>244</td>
</tr>
<tr>
<td>Tryptophan</td>
<td>0.08</td>
<td>0.14</td>
<td>175</td>
</tr>
<tr>
<td>Valine</td>
<td>0.24</td>
<td>0.54</td>
<td>225</td>
</tr>
</tbody>
</table>

<sup>a</sup> Jondreville et al. (1995).

<sup>b</sup> Rademacher et al. (1999).

<sup>c</sup> Protein-free diet method \( n = 16 \); Protein-free diet method with parenteral infusion of amino acids \( n = 1 \); Regression method \( n = 3 \); Diets with casein or wheat gluten \( n = 11 \); Enzyme hydrolysed casein (EHC) method \( n = 2 \).
Table 6
Comparison of apparent and standardised ileal crude protein and amino acid digestibility values in soybean meal, barley and sugar-beet pulp

<table>
<thead>
<tr>
<th>Ingredients</th>
<th>Soybean meal</th>
<th>Barley</th>
<th>Sugar-beet pulp</th>
</tr>
</thead>
<tbody>
<tr>
<td>Crude protein g/kg DM</td>
<td>512</td>
<td>130</td>
<td>119</td>
</tr>
<tr>
<td>AID^a</td>
<td>85</td>
<td>78</td>
<td>48</td>
</tr>
<tr>
<td>SID^a</td>
<td>86</td>
<td>84</td>
<td>54</td>
</tr>
<tr>
<td>SID^a</td>
<td>87</td>
<td>87</td>
<td>58</td>
</tr>
<tr>
<td>Lysine g/kg DM</td>
<td>30.8</td>
<td>4.7</td>
<td>3.6</td>
</tr>
<tr>
<td>AID</td>
<td>89</td>
<td>72</td>
<td>44</td>
</tr>
<tr>
<td>SID</td>
<td>90</td>
<td>78</td>
<td>52</td>
</tr>
<tr>
<td>SID</td>
<td>90</td>
<td>81</td>
<td>55</td>
</tr>
<tr>
<td>Methionine g/kg DM</td>
<td>7.5</td>
<td>2.3</td>
<td>1.4</td>
</tr>
<tr>
<td>AID</td>
<td>90</td>
<td>84</td>
<td>57</td>
</tr>
<tr>
<td>SID</td>
<td>91</td>
<td>88</td>
<td>63</td>
</tr>
<tr>
<td>SID</td>
<td>91</td>
<td>89</td>
<td>65</td>
</tr>
<tr>
<td>Threonine g/kg DM</td>
<td>19.5</td>
<td>4.3</td>
<td>3.3</td>
</tr>
<tr>
<td>AID</td>
<td>84</td>
<td>73</td>
<td>22</td>
</tr>
<tr>
<td>SID</td>
<td>85</td>
<td>79</td>
<td>30</td>
</tr>
<tr>
<td>SID</td>
<td>87</td>
<td>87</td>
<td>40</td>
</tr>
</tbody>
</table>

^a,b Compiled from Jondreville et al. (1995).
^c Apparent ileal digestibility values.
^d Standardised ileal digestibility values according to Jondreville et al. (1995). (Refer to Table 5).
^e Standardised ileal digestibility values according to Rademacher et al. (1999). (Refer to Table 5).

provide an estimate of amino acid availability values and should be used in feed evaluation.

Apparent ileal amino acid digestibility values from the literature, determined with ileal analysis method, showed considerable variation among different samples of the same feedstuff. In addition to different processing conditions and inherent factors among samples of the same feedstuff, a large proportion of the differences can be attributed to approaches in methodology.

Differences in dietary amino acid levels are likely to be the largest single contributor to the variation of ileal amino acid digestibility values within the same feedstuff. Dietary amino acid levels quadratically affect ileal amino acid digestibility values. In order to remove the effect of dietary amino acid levels, the plateau apparent ileal amino acid digestibility values should be determined.

Finally, methods for determination can also result in differences in ileal amino acid digestibility values within the same feedstuff. In order to eliminate this variation, methods of determination specifically suited for different feedstuffs are recommended. For cereal grains, the regression and the difference method rather than the direct method should be used. In protein supplements, the direct, the difference and the regression method are all suited for the determination. However, for feedstuffs including some protein supplements and byproducts that can only be included at low levels in the assay diets, the regression rather than the direct or the difference method should be used.

Further research is warranted to identify, to quantify and finally to eliminate potential methodological sources of variation in the determination of non-specific endogenous ileal protein and amino acid recoveries in order to obtain reliable estimates for the transformation of apparent digestibility values into values of standardised digestibilities.

References


Nyachoti, C.M., de Lange, C.F.M., McBride, B.W., Schulze, H.,


