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Review: Nutrient and energy supply in monogastric food producing animals with reduced environmental and climatic footprint and improved gut health

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ABSTRACT

With more efficient utilisation of dietary nutrients and energy, diversified production systems, modifications of diet composition with respect to feedstuffs included and the use of free amino acids, the negative impact of animal food production on the environment and climate can be reduced. Accurate requirements for nutrients and energy for animals with differing physiological needs, and the use of robust and accurate feed evaluation systems are key for more efficient feed utilisation. Data on CP and amino acid requirements in pigs and poultry indicate that it should be possible to implement indispensable amino acid-balanced diets with low- or reduced-protein content without any reduction in animal performance. Potential feed resources, not competing with human food security, can be derived from the traditional food- and agroindustry, such as various waste streams and co-products of different origins. In addition, novel feedstuffs emerging from aquaculture, biotechnology and innovative new technologies may have potential to provide the lack of indispensable amino acids in organic animal food production. High fibre content is a nutritional limitation of using waste streams and co-products as feed for monogastric animals as it is associated with decreased nutrient digestibility and reduced dietary energy values. However, minimum levels of dietary fibre are needed to maintain the normal physiological function of the gastro-intestinal tract. Moreover, there may be positive effects of fibre in the diet such as improved gut health, increased satiety, and an overall improvement of behaviour and well-being.

Implications

The negative impact of monogastric animal food production on the environment and climate can be reduced if recently published data on ways to increase the efficiency of utilising dietary nutrients and energy are adopted. Furthermore, there are possibilities to diversify production systems, modify diet composition with respect to feedstuffs included and for more extensive use of free amino acids in feed formulation.

Introduction

To reach the UN Sustainable Development Goals (UN, 2015), the agri-food industry and the supply chain should focus on minimising the negative impact of animal food production on the environment and climate. With increasing knowledge, there are opportunities for more efficient utilisation of dietary nutrients and energy, diversified production systems and modifications of diet composition with respect to feedstuffs included and the use of free amino acids (**AAs**).

The key for more efficient feed utilisation is to have accurate requirements for nutrients and energy for animals with differing physiological needs (e.g. maintenance, growth, reproduction and lactation), and to use robust and accurate feed evaluation systems. These systems should predict the animal performance independent of the feed nutrient composition (i.e. the dietary proportions of carbohydrates, fat and protein). In this context, the hierarchy between feedstuffs is very important for feed formulation and the production economy, and it is highly dependent on the feed evaluation system used (Noblet et al., 1994; Stein et al., 2007; Wu et al., 2019; Ravindran, 2021).

Recent data on CP and AA requirements in pigs and poultry together with an increasing availability of free indispensable AA (**IAA**) indicate a possibility to implement IAA balanced diets with low- or reduced-protein content without any reduction in performance (Wang et al., 2018; Kidd et al., 2021). Lowering dietary CP content reduces the deamination of excess AA as well as N excretion (Le Bellego et al., 2001; Liu et al., 2021) which would reduce

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the environmental pollution of N and be beneficial for the climate (UN, 2015).

In most countries around the globe, there are potential feed resources, not competing with human food security that can be derived from the traditional food- and agroindustry. These comprise various waste streams and co-products of different origins. In addition, there are novel feedstuffs emerging from aquaculture, biotechnology and innovative new technologies (Bratosin et al., 2021; van der Heide et al., 2021). However, to fully utilise the nutritional potential of both novel and of various underutilised feed resources, and thereby allow an optimisation of diet composition, there is a need to characterise their chemical, physical and nutritional properties. A common nutritional limitation of using waste streams and co-products as feed for monogastric animals is the dietary fibre content. High dietary fibre content is an issue of major concern due to decreased nutrient utilisation and low net energy (**NE**) values (Noblet and Le Goff, 2001). However, to maintain the normal physiological function of the gut, minimum levels of dietary fibre must be included in the diet (Wenk, 2001). It has become evident that the fibre properties will determine the negative impact of dietary fibre on nutrient utilisation and NE value (Noblet and Le Goff, 2001) and that the impact may differ considerably between fibre sources and with age of the animal (Jørgensen et al., 2007). Moreover, there may be positive effects of dietary fibre such as improved gut health, increased satiety, as well as an overall improved behaviour and well-being (Wenk, 2001; Montagne et al., 2003; de Leeuw et al., 2008; de Lange et al., 2010; Bach Knudsen et al., 2012). Interestingly, despite the obvious need for dietary fibre in monogastric animals, there are not yet any specific requirements proposed for different categories of animals.

The aim of this review was to highlight some recent advances related to the energy and protein metabolism and nutrition in monogastric livestock with focus on feed evaluation, nutrient requirements, feed resource utilisation and gut health. Preliminary results have been published in an abstract form (Lindberg, 2022) at the 7th EAAP International Symposium on Energy and Protein Metabolism and Nutrition (ISEP 2022).

Feed formulation and feed utilisation

Predictions of digestibility

Accurate predictions of the digestibility of nutrients and energy in feed ingredients are key to the correct assessment of energy and protein values. However, despite the long history of research in feed evaluation, there is an ongoing debate regarding the accuracy of published (e.g. animal models and protocols) and of derived (e.g. *in vitro* and NIRS) or tabulated feedstuff values. This applies both to pigs and poultry and relates to the methodology used in bioassays for the evaluation of feedstuff nutrient content (Noblet et al., 1994; Wu et al., 2020; Chassé et al., 2021). In addition, there is a need for increased knowledge of the impact on digestibility of energy and nutrients of feed chemical characteristics, technological treatment, bioprocessing and animal-related factors, as well as possible interactions. Accurate predictions of feed energy values are built on flawless feedstuff data on energy digestibility, and the accuracy can be improved if the animal models and protocols used were standardised (Wu et al., 2020; Chassé et al., 2021). Major flaws in the bioassays used for energy digestibility determinations in poultry are applicable to monogastric animals in general. This is related to the use of a nutritionally imbalanced diet as the result of replacing part of a balanced diet with the test feedstuff; variable energy values of tabulated standard ingredients; inability of *in vitro* assays to accurately mimic the true metabolism occurring in live animals; and wrong computations or mathematic models used in the assays (Wu et al., 2020). Thus, for more accurate bioassays in feedstuff metabolisable energy (**ME**) evaluation for poultry, and to standardise the prediction of feedstuff ME values for poultry, Wu et al. (2020) proposed the use of two protocols: multiple linear regression and basal diet substitution methods.

The digestibility of CP and AA should preferably be determined at the ileal level and not at the faecal level (Stein et al., 2007; Ravindran, 2021) and can be expressed as apparent (**AID**), standardised (**SID**) or true (**TID**) ileal digestibility depending on how ileal endogenous AA (**IEAA**) losses are accounted for. The IEAAs represent AAs that are present in endogenously synthesised proteins secreted into the intestinal lumen. These proteins originate predominantly from various digestive secretions (bile, pancreatic enzymes, and gastric and intestinal secretions), mucoproteins and desquamated intestinal epithelial cells (Stein et al., 2007; Ravindran, 2021). In addition, there is a significant contribution to the N found in the ileal digesta from the gut microbial mass which is not accounted for (Ravindran, 2021). Interestingly, the AA profiles of the basal IEAA of chicken and pigs are similar as well as between the class of chicken (broiler, layers and roosters; Ravindran, 2021).

The AID of AA is defined as the net disappearance of ingested dietary AA from the digestive tract proximal to the distal ileum. The lack of additivity of AID in mixtures of feed ingredients is a concern with the use of AID in feed formulation and in the interpretation of experimental data. This is related to the effect of diet AA level on AID values and the relative contribution of IEAA to total AA in ileal outflow (Stein et al., 2007; Ravindran, 2021). In contrast, the TID reflects the proportion of the dietary AA that disappears from the digestive tract proximal to the distal ileum and only the undigested dietary AAs and not the IEAA in the ileal AA outflow are related to AA intake. However, insufficient available information on total (basic and specific) IEAA for pig and poultry feed ingredients used in practice is a major limitation to the use of TID for feed formulation. It was therefore recommended that SID, which is based on subtracting only the basal IEAA from the ileal outflow of AA, should be considered as an alternative to TID (Stein et al., 2007; Ravindran, 2021). As only the basal IEAAs are subtracted from the total ileal AA outflow, values for SID are intermediate between values for AID and TID and independent of dietary AA level. Moreover, it is recommended that basal IEAA losses of AA should be measured in digestibility experiments using a defined protein-free diet and that these losses are reported with observed AID and SID values (Stein et al., 2007; Ravindran, 2021).

Energy evaluation

A key for feed formulation and feed efficiency is a correct prediction of dietary energy available to the animal (Noblet et al., 1994; Wu et al., 2020). Feed formulation based on digestible energy or ME does not differentiate between the energy required for maintenance and production, and heat produced during digestion, metabolism and excretion (Noblet et al., 1994). In addition, energy expressed on a digestible energy basis will overestimate the contribution of energy from feedstuffs rich in protein and fibre, while energy contribution from feedstuffs rich in fat and starch will be underestimated. This will be less of a problem when the energy value is expressed on a ME basis, as energy losses related to protein and carbohydrate metabolism are accounted for. However, to also be able to account for the loss of energy as heat for digestion, metabolism and excretion NE was proposed as a replacement for ME (Schiemann et al., 1972). The hierarchy between feedstuffs obtained with the NE feed evaluation system is at present considered to be the most accurate system (Noblet et al.,1994; Wu et al., 2019). In practice, feedstuff evaluation and feed formulation based on NE have been implemented in horses (Vermorel and Martin-Rosset, 1997) and pigs (Noblet et al., 1994; NRC, 2012), but not yet in poultry (Wu et al., 2019).

The main reasons for the delay in implementing the NE system in poultry are related to difficulties to measure NE and that published studies show no or variable correlations of NE with the composition of diet in poultry (Wu et al., 2020). The latter was claimed to be due to the lack of accuracy in ME measurements. Energy values used for feed formulation in poultry have mainly been the apparent ME (**AME**) without or with correction for N balance, while the true ME values without or with correction for N balance have been used to a lesser extent (Wu et al., 2019). The actual energy levels of feed ingredients for growing birds align more closely with AME than with AME corrected for N balance and should therefore preferably be used for poultry feed formulations (Wu et al., 2020). In contrast, it was proposed that a correction to 50% N retention as standard AME may be more representative of the metabolic situation in growing broilers (Cozannet et al., 2010).

Carré et al. (2014) reported that the efficiency of AME utilisation for NE (NE/AME) in growing chickens was 0.79 for carbohydrates, 0.85 for fat and 0.68 for CP. This was recently confirmed by Wu et al. (2019) in studies with growing broiler chickens. Overall, this is in good agreement with previously reported NE/ME values in growing pigs (Noblet et al., 1994), although with lower values for growing chickens. Thus, feed formulations on an NE basis may more accurately meet the energy requirement of the bird and may further enhance feed utilisation efficiency as it accounts for the energy lost as heat (Wu et al., 2019). Recently, Wu et al. (2019) performed linear regression analysis to generate prediction equations for dietary energy content and AME efficiency in broiler chickens. They showed that the NE content was positively related to AME and ether extract, but negatively related to CP. The equations generated in the study could accurately predict NE, and NE/AME using the AME value and chemical composition of feeds. Moreover, the NE prediction equations were validated on a separate set of diets with high correlation (r = 0.99) and accuracy.

Protein value

The basis for evaluation of the protein value of feed ingredients is an accurate assessment of the bioavailability of each of the dietary IAA and for estimating AA requirements (Wang et al., 2018; Ravindran, 2021). A major challenge is to choose methods and protocols for estimating AA bioavailability that are accurate, robust and easy to use in practice and that yield values that are additive in feed formulation (Stein et al., 2007; Ravindran, 2021).

The definition of bioavailability of dietary AA is the proportion of ingested dietary AA that is absorbed in a chemical form that make these AAs potentially suitable for metabolism or protein synthesis. This includes the impact of gut fermentation of AA and the impact of dietary factors on AA utilisation. In contrast, AA digestibility comprise enzymatic hydrolysis and microbial fermentation of ingested proteins and peptides and absorption of AA and peptides from the gut. Thus, there is a clear distinction between AA bioavailability and AA digestibility. However, due to the lack of methods for direct measure of AA bioavailability, measures of *in vivo* digestibility have been used to estimate AA bioavailability (Stein et al., 2007).

Advances in establishing the AA requirements for pigs together with an increasing availability of free AA will allow the reduction of the feed CP content while maintaining the supply of IAA (Wang et al., 2018; Kidd et al., 2021). However, to get reliable predictions of the dietary protein value for performance and tissue gain, the energy feed formulation should be performed on an NE basis instead of on a digestible energy or ME basis (Noblet et al., 1987). It has been shown that piglets and growing-finishing pigs fed low-protein diets with the same NE content and adequate AA supplementation will maintain growth performance, body composition, protein deposition and energy utilisation (Noblet et al., 1987; Le Bellego et al., 2001; Wang et al., 2018).

With increasing availability of free IAA, in addition to lysine, threonine, methionine and tryptophan, it will be possible to formulate diets with a lower proportion of protein-bound AA and higher proportion of individual free AA, but with the same CP content. However, there are reports indicating a negative impact on the animal performance of feeding diets with low- or reduced CP content supplemented with adequate free IAA (Chrystal et al., 2020; Peng et al., 2016; Wang et al., 2018). This raises questions whether the capacity to synthesise certain dispensable AA is sufficient when low-protein diets are used (Gloaguen et al., 2014; Chrystal et al., 2020). This includes glycine, which is used for uric acid synthesis, but may also include serine and 1-carbon units (van Milgen, 2021). It has been proposed that glycine equivalents (one glycine equivalent (g/kg) equals the sum of glycine + 0.7143 × serine) are the first-limiting dispensable AA in poultry diets and that inclusions of glycine and/or serine will permit more robust reductions in dietary CP content (Siegert and Rodehutscord, 2019). However, the negative impact on animal performance of diets with low- or reduced CP content supplemented with adequate IAA (Gloaguen et al., 2014; Chrystal et al., 2020) also lead to questions if N itself could be or become a limiting factor for the synthesis of dispensable AA (van Milgen, 2021).

Feed resource utilisation

Feed protein content

A reduction of the feed CP content in monogastric animals has been made possible with the introduction of free AA, such as lysine, methionine, threonine, tryptophan, and valine. As a result, N excretion and the risk of gut disorders are reduced while maintaining the performance of pigs (Wang et al., 2018) and poultry (Kidd et al., 2021). In addition, using free AA supplementation makes it possible to use a broader range of protein feedstuffs in the diet and lower the dependency on soybean meal and fish meal, of which the production can have negative effects on the environment and climate (UN, 2015). Reducing the CP content in a standard cereal/soybean meal diet will lower the soybean meal proportion while increasing the proportion of cereals. Therefore, the diet will contain less intact protein-bound AA, higher inclusion of free AA and increased starch content.

A reduction of the feed CP content with free AA will reduce N excretion and the deamination of excess AA as well as the consecutive synthesis and excretion of urea (mammals) and uric acid (birds) in urine, water consumption and urine excretion.

This implies a reduction of energy loss in the urine from urea and uric acid, and energy expenditure for the synthesis of the excretion products (van Milgen, 2021). In addition, body protein turnover is lower and heat production is reduced which will increase the energy available for tissue deposition (Wang et al., 2018; Wu et al., 2019), particularly as fat in growing-finishing pigs (Noblet et al., 1987) and in broiler chickens (Chrystal et al., 2020).

Gloaguen et al. (2014) showed that soybean meal can be totally replaced in diets (wheat, barley, corn and soybean meal; 1.0–1.15% SID lysine) for piglets (10–20 kg) using cereals and free AA (methionine, threonine, tryptophan, valine, leucine, isoleucine, histidine and phenylalanine). In addition, the feed CP content could be reduced from 19.7 to 13.5% without any reduction in performance and with a decrease in N excretion of approximately 40%. However, a diet formulated without soybean meal with 13.0% CP content resulted in reduced feed efficiency, while the addition of glutamine to increase the CP content from 13.0 to 14.0% restored performance. In accordance, Peng et al. (2016) reported that reducing the dietary CP level from 20.0 to 15.3% (1.23 % SID lysine on an as-fed basis) in diets (corn, soybean meal, rapeseed meal and cottonseed meal) for piglets (13–35 kg) supplemented with free IAA did not impair growth performance and immunological parameters. In contrast, reducing the dietary CP level to 13.9% (1.23 % SID lysine on an as-fed basis) resulted in poor growth performance and organ development, and was associated with modifications of intestinal morphology and immune function.

In a recent study by Presto Åkerfeldt et al. (2019), growing-finishing pigs (32–117 kg) were fed restrictedly using two different feeding plans, single-phase and 2-phase. Within each feeding plan, three levels of CP (13.5, 14.5 and 15.5 g SID CP/g SID lysine) and two levels of lysine (single-phase, 0.76 or 0.85 g SID lysine/MJ NE, respectively; 2-phase, 0.89 and 0.71 or 0.98 and 0.79 g SID lysine/MJ NE, respectively) were studied. Two-phase-fed pigs had higher daily weight gain and better feed conversion in phase 1 than single-phase-fed pigs irrespective of dietary CP and lysine content. Single-phase-fed pigs fully compensated in phase 2, so that overall daily weight gain and feed conversion did not differ between single-phase-fed and 2-phase-fed pigs (1014 vs 1013 g/d; 24.5 vs 24.5 MJ NE/kg daily weight gain). Thus, the capacity for compensatory growth was shown by the single-phase-fed growing-finishing pigs resulting in similar performance and carcass traits as the 2-phase-fed growing-finishing pigs. A reduction in dietary CP from 15.5 to 13.8 g SID CP/g SID lysine and a reduction in lysine from 0.86 to 0.76 g SID lysine/MJ NE only slightly affected growth performance and carcass traits in single-phase-fed growing-finishing pigs. As a consequence, soybean meal inclusion could partly be reduced and replaced by cereals and locally produced protein feedstuffs with a 20% reduction in the N losses to the environment.

Broiler grower diet formulation (corn, soybean meal, meat and bone meal and distiller's grains) with use of free AA (methionine, lysine, threonine, valine, isoleucine and arginine) can reduce the inclusion of soybean meal with over 50% and reduce the CP content with more than 20% (Kidd et al., 2021). In broiler chickens, diet CP content could be reduced by 30 g/kg (from 210 to 180 g/kg) without negatively influencing performance (Chrystal et al., 2020). However, a further reduction in diet CP content (from 180 to 165 g/kg) with maintained IAA content reduced the feed conversion efficiency and increased the relative fat-pad weight.

Carbohydrate and protein digestion dynamics

A balanced supply of energy-yielding nutrients and AA is required for optimal protein utilisation and deposition in pigs and poultry (Rerat et al., 1992; Weurding et al., 2003). However, digestibility values of nutrients (i.e. carbohydrates, protein and fat) at a given site (e.g. terminal ileum and total tract) used for feed formulation give no information on the availability of nutrients for protein deposition. Thus, the postabsorptive availability of AA is not always in synchrony with that of non-protein energy (i.e. mainly glucose).

Asynchrony between starch and protein digestion rates had a negative impact on feed utilisation and was reported to account for a major part (76%) of the variation in feed conversion ratio in broiler chickens (Liu and Selle, 2017). Complete separation of protein and carbohydrate intake within a day (two times feeding/day) in growing pigs decreased total tract apparent digestibility of organic matter and the protein retention (van den Borne et al., 2007). Moreover, the asynchronised feed allowance increased energy yield from AA degradation which was lost as heat. More prolonged periods of *de novo* fatty acid synthesis occurred during the day, which was followed by increased rates of fatty acid oxidation.

The digestive dynamics of dietary carbohydrates (i.e. starch and sugars) and protein involves the digestion process, the absorption and metabolism of sugars (mainly glucose), peptides and AA, and transport from the enterocytes to the portal blood. The extent, rate and sites of nutrient digestion along the small intestine are important for optimal utilisation of the diet. For efficient protein deposition and performance, glucose and AA should be bioavailable in balanced quantities at the sites of protein synthesis.

Starch is the main carbohydrate energy source in most pig diets and originates from plants of various botanic origins (e.g. cereals, tubers, roots and pulses). A major part of starch is digested in the upper part of the small intestine but due to different properties of starch between plants (Tan et al., 2021), the digestion rate in the gastro-intestinal tract will vary. As a consequence, this will impact glucose appearance kinetics in the portal circulation (van der Meulen et al., 1997; Martens et al., 2019).

Glucose and galactose are transported across the apical membrane of enterocytes by Na+/glucose co-transporter SGLT1, while fructose is transported down its concentration gradient by the Na + independent fructose transporter, GLUT5 (Shirazi-Beechey et al., 2011). However, SGLT1 is not expressed in any epithelial cells of the mammalian large intestine. Monosaccharides accumulated in the enterocyte exit the cell across the basolateral membrane into the portal blood by GLUT2, a Na+ independent monosaccharide transporter. GLUT2 is a bidirectional transporter that, depending on the glucose concentration gradient, can move glucose out or into the cell. The GLUT2 transporter is exclusively located on the basolateral membrane of enterocytes (Shirazi-Beechey et al., 2011). In addition to the basal capacity of the small intestine to absorb glucose by SGLT1, this capacity can be upregulated in the proximal and mid small intestine, but not in the distal small intestine, when gut content of monosaccharides increases (Moran et al., 2010). This is due to nutrient sensors expressed on the luminal membrane of endocrine cells that are activated by various dietary nutrients. It has been shown that response to sweet stimuli is absent in the chicken, and the domestic cat, as well as other obligate carnivorous members of the *Felidae* family (i.e. tiger and cheetah) which show no preference for and cannot taste sugars (Buddington et al., 1991; Shirazi-Beechey et al., 2011). Moreover, expression of SGLT1 in chicken small intestine was unresponsive to increased luminal glucose (Barfull et al., 2002).

Plasma glucose levels are elevated in diets with rapidly digestible starch. This may have consequences for protein and AA utilisation if it takes place when other nutrients are not yet absorbed. In contrast, diets with high amounts of resistant or slowly digestible starch will show more delayed plasma glucose levels (van der Meulen et al., 1997; Martens et al., 2019). Thus, differences in digestion kinetics in diets with similar amounts of digestible nutrients may result in different performances (Weurding et al., 2003).

In general, starch digestion is more rapid and complete than protein digestion (Liu and Selle, 2017). In addition, much of the gut energy expenditure is derived from the catabolism of certain AA (glutamate, glutamine and aspartate) rather than of glucose (Wu, 1998). Thus, in diets with low or reduced CP and increased cereal content, the small intestine will have an increased concentration of glucose from starch digestion which will compete with AA for absorption through their respective Na+ dependent pathways (Gilbert et al., 2008; Moss et al., 2018). In addition, the higher ileal digestibility of starch than that of CP and AA may have an impact on the dynamics of glucose and AA absorption and metabolism. Free AAs are absorbed into epithelial cells more rapidly than protein-bound AAs, while di- and tripeptides are absorbed more rapidly than free AA (Gilbert et al., 2008). Thus, due to the digestive dynamics of starch and protein, starch/protein ratios, and impact on the starch-glucose-insulin axis, maize was found superior to wheat as the basis of reduced CP broiler diets (Liu et al., 2021).

The transport of free AA across the brush-border membrane of intestinal epithelial cells is performed by a variety of different substrate-specific AA transporters. In addition, there is also transport of AA in the form of di- and tripeptides and peptide-like drugs by the broad specificity proton-coupled peptide transporter PepT1, of the solute carrier 15 family member 1 (Gilbert et al., 2008; Smith et al., 2013; Zwarycz and Wong, 2013). The same energy expenditure is required for the transport of single free AA as for the transport of peptides by PepT1 (Gilbert et al., 2008). In the intestine, PepT1 protein is abundantly expressed at the apical membrane of enterocytes in duodenum, jejunum and ileum, with little or no expression in normal colon (Smith et al., 2013). Other possible pathways for absorption of peptides from the intestinal lumen (i.e. through paracellular pathways, via tight junctions; passive diffusion through the enterocytes; or endocytosis) are quantitatively negligible and in most cases unlikely (Miner-Williams et al., 2014). Thus, it appears that the high-capacity, low-affinity intestinal transporter PepT1 is responsible for the absorption of peptides arising from dietary proteins and gastrointestinal tract secretions (Gilbert et al., 2008; Smith et al., 2013; Miner-Williams et al., 2014). The absorbed peptides are hydrolysed within the epithelial cells and released as free AA into the portal blood. However, there are data indicating that some intact peptides may escape hydrolysis and enter the portal blood intact via an unknown basolateral peptide transport system (Miner-Williams et al., 2014). Interestingly, Fernández-Fígares et al. (2019) reported that a major proportion of AA appearing in portal blood of growing Iberian pigs was in the form of peptide AA.

Feed conversion efficiency may be enhanced by rapidly digestible protein, and it has been suggested that free AA could be an alternative with the same properties (Liu and Selle, 2017). However, the digestive dynamics of free and protein-bound AA are inherently different in that free AA does not require digestion and is therefore directly available for absorption in the proximal small intestine and will thus appear in the portal circulation more rapidly than protein-bound AA (Wu, 2009). The absorption rate of AA (e.g. lysine, threonine, phenylalanine, tyrosine and arginine) in growing pigs was higher during the 1st hour after intra-duodenal infusion of a carbohydrate solution (maltose, dextrin) containing a protein hydrolysate (high content of peptides) than after infusion of the carbohydrate solution containing a mixture of free AA, but this difference quickly disappeared during the next couple of hours (Rerat et al., 1992). In addition, there was a large uptake of absorbed AA by gut epithelium. This uptake was higher after infusion of the free AA mixture than after infusion of the protein hydrolysate and was most pronounced for the branched-chain AA. Thus, as dietary AAs are the preferred fuel over glucose, the intestinal AA flux is affected by the presence of mucosal AA catabolism (Wu, 2009). In addition, intestinal mucosal cells use AA for protein synthesis, nucleosides, polyamides, and maintenance of the intestinal immune system (i.e. glutathione and mucin synthesis; Gilbert et al., 2008).

Gut health and welfare

The maintenance of gut health is determined by the interaction between the diet, the commensal microbiota and the mucosa, including the digestive epithelium and the mucus overlying the epithelium (Montagne et al., 2003; Bauer et al., 2006). The diet can support either beneficial or harmful input and is therefore key for a stable gut microbiota (Jha et al., 2019). The composition of the diet is critical for a balance between the gut, the microbiota and the gut environment and thereby prevents disturbances (i.e. dysbiosis) in the gut. Dietary carbohydrates and protein interact both with the mucosa and the microbiota and consequently have an important role in the control of gut health (Bach Knudsen et al., 2012; Gilbert et al., 2018). Development of a normal gut microbiota occurs gradually after birth and is affected by the maternal microbiota composition, the environment, the diet and the host genome (Patil et al., 2020). The diet has a direct influence on the establishment and development of a beneficial gut microbiome with the ability to resist invasion by exogenous microorganisms (i.e. colonisation resistance). In addition, the action of antimicrobial metabolites and maintenance of a low pH may reduce the impact of pathogenic bacteria (e.g. *Escherichia coli*, *Salmonella* and *Clostridia*). Furthermore, competition for adhesion sites and nutrients are important mechanisms to resist pathogen invasion (Patil et al., 2020).

In diets with insufficient energy from carbohydrates, some bacteria may use protein as an energy source resulting in the formation of potentially toxic substances (Bauer et al., 2006; Gilbert et al., 2018). Carbohydrates and proteins that escape digestion in the small intestine will be digested and metabolised by commensal microbiota in the hindgut (Bach Knudsen et al., 2012; Gilbert et al., 2018). The non-digestible carbohydrates (e.g. non-starch polysaccharides; **NSPs**) will be degraded by microbial enzymes in the hindgut and the resulting degradation products are further metabolised through different pathways to short-chain fatty acids and gases (Bach Knudsen et al., 2012; Lindberg, 2014). However, it should be noted that there is substantial microbial activity along the entire gastrointestinal tract in pigs, starting already in the stomach (Patil et al., 2020). A diet (barley, oats, triticale, wheat and wheat bran) with a high NSP level (197–203 g/kg DM) and a high amount of insoluble NSP (162–173 g/kg DM) fed to weaned piglets (5–7 weeks of age) created a beneficial environment throughout the gastrointestinal tract (Högberg and Lindberg, 2004; 2006). This was manifested by promoting the production of lactic acid in the stomach and small intestine and butyric acid in the large intestine (Högberg and Lindberg, 2004; 2006). The high content of lactic acid in the stomach and small intestine can be explained by the metabolism of soluble NSP including mixed-linked β-glucans (Jonsson and Hemmingsson, 1991).

Protein fermentation metabolites (e.g. ammonia, biogenic amines, phenols and indoles) have been associated with gut health impairment (Gilbert et al., 2018). However, when sufficient fermentable carbohydrates are available, bacteria in the hindgut may utilise ammonia as an N source for its own growth. In poultry, high-protein diets play a role in the occurrence of wet litter which is a health-related problem. Dietary CP content and feed protein source are associated with water intake and excretion in poultry. The increase in water intake may be due to the need for water to excrete N (i.e. uric acid) from metabolism of excess AA. It has been demonstrated that an increase in diet CP content to broilers increases litter moisture content (Gilbert et al., 2018). Reduced-CP broiler diets improve litter quality (increased litter DM content and reduced litter N content) and reduce the incidence of foot-pad lesions and related conditions, which is beneficial for bird welfare (Liu et al., 2021).

In piglets, the change in diet and environment following weaning is associated with an increased prevalence of diarrhoea. This is linked to a drop in feed intake which leads to changes in gut epithelial morphology with decreased *villi* height and increased crypt depth. Consequently, brush-border enzyme activities and macronutrient digestion in the small intestine are reduced (Montagne et al., 2003). This may lead to more undigested carbohydrates and proteins reaching the hindgut, although the amount of undigested gut content reaching the hindgut depends on intake and diet composition. The incidence of postweaning diarrhoea is increased with high-protein diets and is commonly associated with rotavirus and enterotoxigenic *E. coli*, especially *E. coli* carrying the adhesin K88 (or F4) or F18, and with a high gut concentration of ammonia (Gilbert et al., 2018).

Lactic acid-producing bacteria (*Lactobacillus spp.* together with *Bifidobacterium* spp.) can be stimulated by prebiotic carbohydrates in the form of fructose-containing oligo- and polysaccharides. This may protect the animals from gut infection due to competitive exclusion. Moreover, fructose-containing oligo- and polysaccharides are readily fermentable and can potentially reduce the establishment and proliferation of pH-sensitive enteropathogenic bacterial strains (e.g. *E. coli*, *Salmonella* and *Shigella*).

Responses in gut environment and microbiota composition were correlated with functional bacterial groups and the dietary inclusion of chicory (*Cichorium intybus* L.) in weaned piglets (7 weeks old; Liu et al., 2012). In ileum, the inclusion of chicory roots (inulin-rich) was linked with lactic acid concentration in digesta and the relative abundance of lactic acid bacteria. In colon, the inclusion of chicory forage (pectin-rich) was associated with the relative abundance of butyrate-producing bacteria and colonic acetate concentration. Thus, diet type affected the fermentation products and pH in digesta and was correlated with shifts in the microbiota, demonstrating that chicory influences the intestinal microenvironment (Liu et al., 2012). Data suggest that diets rich in insoluble fibre may reduce the severity of postweaning diarrhoea, whereas diets high in soluble fibre was associated with increased susceptibility to develop postweaning diarrhoea (Bach Knudsen et al., 2012; Jha et al., 2019). Moreover, fibre-rich diets have also been associated with reduced occurrence of swine dysentery in growing-finishing pigs and of necrotic enteritis in poultry (Jha et al., 2019).

Starch can be classified as rapidly digestible, slowly digestible and resistant to enzymatic digestion (Bach Knudsen et al., 2012; Tan et al., 2021). Amylose is a type of resistant starch, which increase the amount of digesta reaching the distal gut for fermentation. This is due to increasing amylose proportion in starch and the subsequently decreased digestibility by pancreatic α-amylase in the small intestine. Resistant starch acts as prebiotic to modulate gut microbiota by changing the intestinal microbial composition and function. Increasing dietary amylose content in pigs immediately postweaning increased the fermentative activity in the hindgut with increased short-chain fatty acid concentration and lowered pH. Butyrate produced by resistant starch fermentation is the primary energy source for the colonocytes and is regarded as the modulator of intestinal barrier function and immunity (Tan et al., 2021). Furthermore, this was also associated with increased *Bifidobacterium spp*., which together with the acidification of the gastrointestinal tract may benefit gut health in young pigs (Fouhse et al., 2015). Thus, it appears reasonable to assume that the amount of starch that is available for fermentation in the distal part of the gastrointestinal tract is linked to changes in microbiota profile and to the selective increase of beneficial bacteria in the gut (Tan et al., 2021).

Choudhury et al. (2021) showed the beneficial impact of early feeding of solid food on microbiota development as well as pig health and performance during the weaning transition. In their study, early-fed piglets had access to a customised fibrous diet from two days after birth until weaning in addition to mother's milk. The early-fed piglets had a relatively stable postweaning microbiota compared with control piglets which suckled mother's milk only. Interestingly, the early-fed piglets showed an accelerated microbiota maturation which was characterised by increased microbial diversity, preweaning emergence of postweaning-associated microbes and a more rapid decline of typical preweaning microbes. Moreover, in the early-fed piglets, the individual eating behaviour scores quantitatively correlated with the accelerated development of their microbiome. They had a more even relative weight gain and tended to reach a higher relative weight gain. In addition, the early-fed piglets had reduced diarrhoea scores in the first-week postweaning.

To further improve our understanding of the underlying biology related to gut health problems, Gilbert et al. (2018) suggested that data from samples in healthy and sick animals should be integrated. This could include metabolomics, microbiomics and gut epithelium pathology data, and may generate important associations between metabolite concentrations, microbiota composition and gut health.

Organic monogastric animal food production

Rules for organic production in EU (EU, 2018; articles 5 & 6) promote sustainable agriculture which comprise efficient and restricted use of external inputs and non-renewable resources. After 2025, all feed for organically produced monogastric livestock should come from organic feed sources. Thus, the protein quality of feed ingredients is of utmost importance since animal requirements for IAA should be fulfilled without the addition of free AA (Eriksson et al., 2009; EU, 2018). However, there is limited availability of regional and organic protein-rich feed ingredients in the EU to fulfil the IAA requirements of monogastric livestock (van der Heide et al., 2021). There are different approaches to increase protein availability in a sustainable manner in feed for organic monogastric animals such as improving the protein quality of existing ingredients, make better use of underutilised feed resources and search for novel feed ingredients.

Microbial conversion of low-cost organic waste to feed products is an attractive approach to support sustainable use of available biomass and the circular bioeconomy and with the potential to reduce environmental pollution. The NSPs of natural organic waste originating from agriculture and forestry are attractive sources for single-cell protein production (Kihlberg, 1972; Bratosin et al., 2021). However, the waste must be pretreated chemically or enzymatically to transform NSP to fermentable sugars (Ritala et al., 2017; Pihlajaniemi, et al., 2020). High quantities of single-cell protein with high CP content (Ritala et al., 2017) and an adequate AA profile (Kihlberg, 1972; Bratosin et al., 2021) can be produced by microorganisms, such as algae, yeast, fungi and bacteria, due to their fast growth rate. In addition to proteins, single-cell protein contains carbohydrates, nucleic acids, lipids, minerals and vitamins. Single-cell protein has been used as an effective substitute for more expensive protein sources such as fish and soybean products (Ritala et al., 2017). However, a high content of nucleic acids can be a limitation for the use of single-cell protein (Kihlberg, 1972).

Van der Heide et al. (2021) presented extensive data showing the potential of some novel feed ingredients (i.e. starfish, mussel, insects and forage crop extracts) to fulfil the CP and AA requirements in organic monogastric production and thereby partly substitute fish meal or soybean meal in the diet. The use of forage crop extracts (grass and legumes) as a source of CP and IAA for pigs and poultry looks very promising. Furthermore, biotechnological production of single-cell protein from the lignocellulosic fraction of grass silage after extraction of the plant juice could provide a novel and synergistic alternative to the present use (e.g. biogas) of the residual fibre fraction (Pihlajaniemi et al., 2020).

Conclusions

Recent published data on ways to increase the efficiency of utilising dietary nutrients and energy, diversify production systems, modify diet composition with respect to feedstuffs included and more extensive use of free amino acids in feed formulation will together, if implemented, contribute to reduce the negative impact of animal food production on the environment and climate and improve gut health.

Ethics approval

Not applicable.

Data and model availability statement

The data were not deposited in an official repository. The data that support the study findings are available from the author upon request.

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Author contribution

JEL: Conceptualisation, methodology, investigation, writing, review and editing.

Declaration of interest

The author declares that no competing financial interests exist regarding this work.

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