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Importance of feed efficiency for sustainable intensification of chicken meat production: implications and role for amino acids, feed enzymes and organic trace minerals

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Summary

Broiler chicken production is expected to increase significantly in the next decades to satisfy the poultry meat demand of a growing world population. In this scenario, one of the most important challenges for the poultry industry is to enhance bird productivity while remaining economically and environmentally sustainable. Feeding represents the major cost in raising of broiler chickens and has important implications for environmental impact, either directly or indirectly. Therefore, improving broiler capacity in converting ingested feed into body growth, which is generally referred to as feed efficiency (often expressed through the feed conversion ratio), is fundamental to promoting a sustainable intensification of poultry production. In this review, we highlight the importance of feed efficiency improvements in terms of overall sustainability for the broiler chicken production chain. Furthermore, the potential of feed additive-based nutritional strategies, such as the dietary administration of crystalline amino acids, proteases, phytases and organic minerals, is critically discussed in the light of their role in supporting the sustainable intensification of this crucial livestock sector.

KEYWORDS

Feed; feeding; nutrition; amino acids; minerals; enzymes; environment; feedstuffs

Introduction

Global food demand, especially of protein, is expected to increase sharply in the next decades driven by the growth of the world population (estimated to reach approximately 10 billion in 2050), socioeconomic changes such as greater urbanisation and higher incomes in developing countries, as well as a greater appreciation of the importance of high-quality protein for a healthy life (FAO 2009; Mottet and Tempio 2017). Of the main types of meat produced worldwide, poultry has recorded the highest absolute and relative growth rate during the last 50 years (Windhorst 2017). It is projected that poultry meat will continue to be the primary growth area of total meat production in the light of expanding global demand (Figure 1). This trend has been driven mainly by the greater affordability of chicken meat compared to red meats, the convenience and possible health benefits of the former, and religious and cultural issues (Baldi, Soglia, and Petracchi

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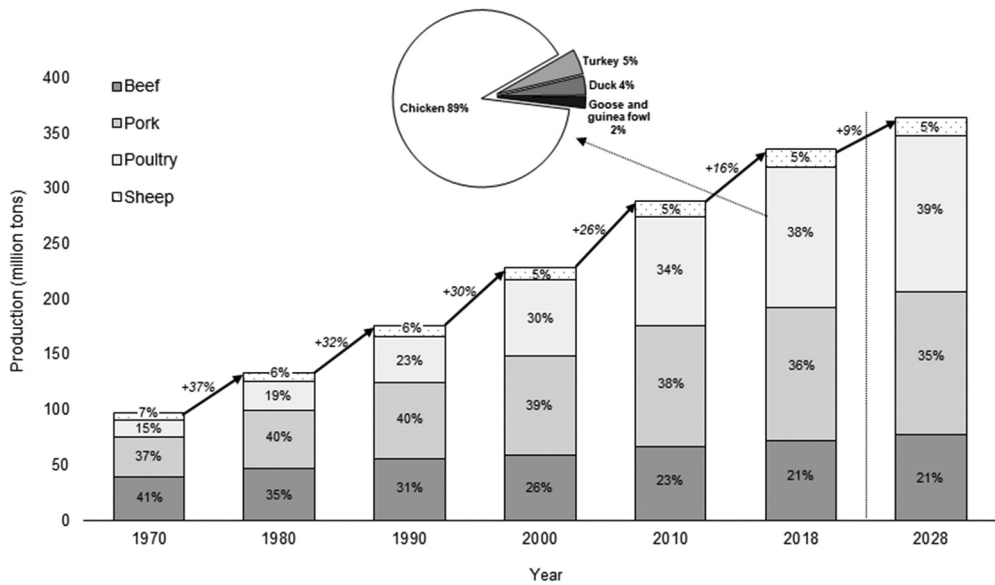


Figure 1. Evolution from 1961 to 2018 and projections from 2019 to 2028 of the global production of the four main types of meat produced worldwide (beef, pork, poultry and sheep). Own design, data source: FAO (2020)

2020a). Therefore, the poultry sector will play a significant role in ensuring food security for a growing world population (Mottet and Tempio 2017). This represents, on the one hand, an extraordinary opportunity, but on the other hand, an important challenge to be addressed. Indeed, the increasing public concerns regarding pressure and competition for limited natural resources, loss of animal and vegetable biodiversity, spread of antimicrobial resistance as well as environmental burden of livestock production, have reinforced the concepts of ‘sustainable intensification’ and ‘producing more by using less’ as refined strategies for feeding future generations (Tixier-Boichard 2020).

In general, modern poultry production is relatively efficient and sustainable if compared to that of other livestock, with special regard to resources utilisation and environmental impact *per* unit of production output (Leinonen and Kyriazakis 2016; Tallentire, Leinonen, and Kyriazakis 2018). Indeed, for each kg of protein output, broilers require 27–28 kg of dry matter feed while emitting an average of 40 kg CO₂-eq, far less than ruminants (Mottet and Tempio 2017). However, the poultry sector still contributes to environmental impact mostly in terms of resources utilisation for the production of feedstuffs (*e.g.* land, water and nutrients), feed manufacturing and transport, as well as manure management and disposal (Leinonen and Kyriazakis 2016; Mottet and Tempio 2017). Poultry production is the livestock sub-sector contributing more to land utilisation for cereal production and accounts for an important share of global oilseeds production as has been highlighted in a recent report (Mottet and Tempio 2017). Among oilseeds, special attention should be reserved for soybean, whose cultivation, mostly occurring in South America, has been associated with several environmental impact issues (Leinonen and Kyriazakis 2016; Mottet et al. 2017; Mottet and Tempio 2017) and consumer concerns regarding sustainability and ecology of genetically modified organisms. Studies conducted

in different countries and productive scenarios, such as Italy (Bastianoni et al. 2010), United Kingdom (Leinonen et al. 2012), United States (Pelletier 2008), Finland (Katajajuuri, Grönroos, and Usva 2008), Portugal (González-García et al. 2014), Brazil and France (Da Silva et al. 2014), concluded that feeding and related activities are the most important factors affecting the environmental sustainability of the poultry industry. Furthermore, feeding also has a significant impact on the economic sustainability of the poultry industry representing up to 70% of the total production costs for raising meat-type chickens. In addition, of particular note from a sustainability standpoint is the observation that more than 60% of the raw materials used in poultry diets is in direct competition with human nutrition (e.g. corn, wheat, soybean, etc.; Mottet and Tempio 2017). Therefore, improving the ability of broiler chickens to convert ingested feed into body mass or edible products, which is generally recognised as the efficiency of feed utilisation or feed efficiency (FE), represents a cornerstone for the sustainable intensification of poultry production. According to these considerations, the next section of this review is devoted to the impact that FE improvements can have, either directly or indirectly, on sustainability aspects of broiler chicken production.

Feed efficiency and sustainable intensification: a key relationship

In poultry, FE is generally expressed as feed conversion ratio (FCR), which represents the ratio between feed intake and body weight gain for a specific period of growth. From another perspective, FE could also be considered as a homeostatic process representing the net result between 'energy intake', which is determined by the voluntary feed intake and the efficacy of digestive processes (i.e. nutrient digestion and absorption), and 'energy expenditure', which depends on the maintenance requirements, specific nutrients repartitioning mechanisms, and the rate of metabolic processes and intermediary metabolism in tissues and organs (for review, see Zampiga et al. 2018a). Consequently, broiler chickens presenting high FE typically have lower proportion of feed intake to body weight gain (Willems, Miller, and Wood 2013) possibly deriving from a greater digestive efficiency coupled with a more favourable nutrients repartitioning towards anabolic processes (Zampiga et al. 2018a).

From a practical perspective, higher FE indicates that a lower amount of feed is required *per* unit of production output (i.e. 1 kg of chicken meat) (Figure 2). As feeding represents the main production cost, any improvement in FE would positively affect the economic sustainability of the poultry chain, thereby enhancing human food security. With regard to the environmental impact, FE improvements can reduce the carbon footprint (i.e. global warming potential *per* production unit) by reducing greenhouse gas emissions, derived mainly from feed crop cultivation, transportation and processing of feed ingredients, and conversion of natural ecosystems, such as the Amazon rainforests, into cultivated land (Leinonen and Kyriazakis 2016; Mottet et al. 2017). Moreover, higher FE can reduce the eutrophication and acidification potentials of poultry production as efficient birds have a greater capacity of retaining dietary nitrogen and phosphorous, thereby limiting nitrate and phosphate excretion in manure and NH₃ emissions into the air (MacLeod et al. 2013; Leinonen and Kyriazakis 2016). Nevertheless, FE improvements can positively affect energy utilisation (e.g. fossil energy and electricity), conservation of animal and vegetable biodiversity, and 'feed-to-food'

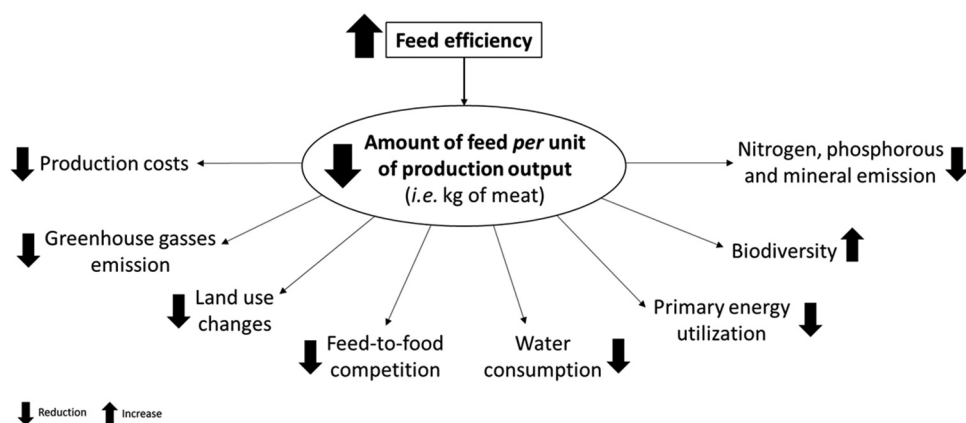


Figure 2. Potential sustainability benefits deriving from feed efficiency improvements in broiler chickens.

competition (Castellini, Petracci, and Sirri 2018). Finally, it is important to mention the impact of FE on the water footprint, which has gained relevance because of the concerns regarding climate change and drought conditions affecting many areas of the world. The poultry industry consumes remarkable quantities of water (4.3 m³ H₂O/ton of meat; Mekonnen and Hoekstra 2012), with feed ingredient production representing the most impacting phase (Mekonnen and Hoekstra 2010). Therefore, lowering the amount of feed required *per* unit of output can reduce the overall water utilisation by the poultry meat supply chain, whether considering crop cultivation, feed manufacturing, or drinking water intake. Indeed, birds consume 1.5 to 2.5 kg of water for each kg of feed ingested (National Research Council 1994).

The general statement that modern poultry production is relatively sustainable and environment friendly is mostly based on the impressive FE potential of current commercial broiler chicken strains (Leinonen and Kyriazakis 2016; Castellini, Petracci, and Sirri 2018), which are approximately twice as efficient as swine and four times more efficient than cattle (Siegel 2014). However, Tallentire, Leinonen, and Kyriazakis (2018) have recently pointed out that the artificial selection for efficiency, which has represented the main strategy for improving this trait in broilers over the last 50 years (Zuidhof et al. 2014), will face biological limits and animal welfare concerns much earlier than predicted by the poultry industry, suggesting that the biological potential for further improvements *via* selection is limited compared to what has been achieved in the past. Consequently, these considerations have reinforced the importance of nutrition for further improving productive efficiency of broiler chickens. In this scenario, the dietary administration of feed additives can represent an important nutritional approach to promote greater FE, with potential positive implications on production costs and environmental impact.

Feed additive-based strategies and sustainable intensification

The feed additives field has grown at an unprecedented pace in recent years resulting in a wide range of products with different specificities, as classified in the EU Regulation

1831/2003. Therefore, providing a complete overview of all the potential feed additive strategies and related mechanisms is unrealistic in this review. According to the aim of this paper, the present section is dedicated to a critical discussion regarding the use of certain feed additives to address specific issues that may affect the sustainable intensification of broiler chicken production. In particular, our attention was focused on the potential of specific nutritional strategies in improving the utilisation of critical dietary nutrients, such as nitrogen, phosphorus and trace minerals, which currently represent major concerns for the poultry industry due to their direct impact on both productive efficiency and environmental sustainability.

Precision amino acid formulation

Dietary protein has always represented a hot topic in poultry nutrition due to its importance for bird performance and health, production costs, and environmental impact associated with nitrogen excretion (Beski, Swick, and Iji 2015). One of the most ambitious goals of the modern poultry industry is to reduce dietary crude protein concentrations with respect to the current standards without impairing bird growth performance, FE and health. Recent studies have proved that such reduction is possible, although to a different extent, as long as an adequate dietary amino acid profile that meets the bird's requirements is maintained (Belloir et al. 2017; De Cesare et al. 2019; Chrystal et al. 2020). Therefore, an accurate estimation of the amino acids requirement of modern broiler hybrids is paramount for identifying the optimal dietary amino acid profile that can maximise FE, while maintaining crude protein at a minimum concentration. However, the amino acids requirement is a dynamic and multifaceted concept, which is influenced by several factors including broiler strain, gender, age and physiological conditions (Kidd and Tillman 2016). In this scenario, the use of feed-grade crystalline amino acids can be useful to finely tune the concentration of dietary amino acids, allowing the birds' needs to be met more accurately while limiting nitrogen excesses, with positive implications for environmental impact, feeding costs and caecal microbiota composition, as undigested protein can serve as substrate for the development of undesirable bacteria (Kidd et al. 2013; Kidd and Tillman 2016).

Lysine is typically the second limiting amino acid in corn-soybean meal diets and its concentration is critical to set the minimum for the other essential amino acids when applying the ideal protein concept (Baker 2009). Thus, Kidd and Tillman (2016) highlighted the necessity for continuous assessment of lysine needs in modern broiler strains. As the importance of lysine in supporting muscle development and FE is widely recognised (Leclercq 1998), its dietary concentration has been gradually increased over the last 25 years to fulfil the requirement of broiler lines characterised by enhanced muscle mass and growth potential. Confirming such observations, Cerrate and Corzo (2019) calculated that the digestible lysine concentration has been rising by 0.009% *per* year from 2001 to 2017, resulting in current recommendations (Aviagen 2019) that are about 30% higher than the NRC values (expressed on a total basis; National Research Council 1994). Kidd and Tillman (2016) indicated that the digestible lysine concentration that can maximise FCR response generally ranges from 1.19% to 1.38% during 1–14 d, 0.99% to 1.21% during 14–28 d and 0.91% to 1.05% during 28–49 d. Recent estimations provided by Akbari Moghaddam Kakhki et al. (2019), as well as digestible lysine

concentrations suggested by breeding companies (Cobb-Vantress 2018; Aviagen 2019), broadly fall within the ranges delineated by Kidd and Tillman (2016). On the other hand, Sharma et al. (2018) stated that increasing digestible lysine concentrations beyond current industry standards (*i.e.* up to 1.15% from 14 to 34 d) could further improve performance and FE. However, excessively increasing the concentrations of digestible lysine can be a double-edge sword. Recent studies (Cruz et al. 2017; Meloche et al. 2018) demonstrated that digestible lysine concentrations can affect growth pattern but also the incidence of breast myopathies such as white striping and wooden breast (for review see Barbut (2019); Petracci et al. 2019), with elevated lysine densities associated with a greater occurrence of meat quality defects. Breast meat abnormalities represent a great concern for the overall sustainability of the poultry industry due to the huge economic losses experienced by processors (due to discarding and/or downgrading of meat, breast trimmings as well as the training of expert personnel designated for grading and sorting) and retailers (due to consumers' complaints and/or reduced willingness to buy) (Baldi, Soglia, and Petracci 2020b). Therefore, defining the optimal digestible lysine concentration to balance FE, breast meat yield and occurrence of meat quality defects in modern broiler hybrids is crucial for the sustainable intensification of poultry production.

As previously mentioned, the dietary lysine concentration serves as a basis for expressing the minimum concentration of the other essential amino acids in the diet. Based on this assumption, if the dietary concentration of digestible lysine is subjected to variations, the concentration of the other essential amino acids should be modified accordingly to maintain the ideal amino acid profile. If this is not done, broiler chickens may experience marginal deficiencies of important amino acids which can limit growth and FE or impair health and welfare. This aspect is particularly relevant considering the remarkable increase of digestible lysine concentrations in commercial diets during the past decades. For instance, the optimal arginine:lysine ratio underwent a substantial reduction from the NRC value (calculated on a total amino acid basis) to current recommendations (determined on a digestible amino acid basis; Wu 2014; Cobb-Vantress 2018; Aviagen 2019). The results of our investigation (Zampiga et al. 2018b) showed that the arginine:lysine ratios currently adopted in commercial diets, at least when animal protein sources are not allowed in feed formulation (*i.e.* 105%, 105%, 106% and 107% in starter, grower I, grower II and finisher phase, respectively), are inadequate to achieve the maximum productive potential of modern fast-growing broilers. At the same time, increasing such ratios by 10% (*i.e.* 115%, 115%, 116% and 117%, respectively) generated positive effects on FE without showing any negative outcome on meat quality attributes, foot pad condition, and the incidence of breast myopathies. However, further step-wise increases of the arginine:lysine ratio (+20 and 30% compared to the above-mentioned baseline) yielded no significant improvements in growth performance and FE, while reducing the occurrence of some breast meat abnormalities (Zampiga et al. 2019). These results corroborate those previously reported by Corzo (2012), who indicated that the FCR response from 1 to 14 d can be optimised at an arginine:lysine ratio of 114%, and also by Jahanian and Khalifeh-Gholi (2018).

Likewise, the recommended ratios of threonine and valine to lysine have experienced remarkable reductions over time as well. Intriguingly, Kidd and Tillman (2016) suggested that more research is needed for these amino acids. The authors reported that several studies provided optimal threonine:lysine ratio above 70%, which is higher than that

generally considered adequate. Indeed, current primary breeders' recommendations for threonine identified ratios to lysine ranging from 65% to 68% depending on the bird's age (Cobb-Vantress 2018; Aviagen 2019), while those indicated by Wu (2014) are slightly higher (67–70%). Recently, Akbari Moghaddam Kakhki et al. (2019) estimated 7.89 and 12.1 g/kg as optimum digestible threonine and lysine concentration from 1 to 10 d of age, corresponding to a ratio of 65%. Conversely, Ahmed et al. (2020) showed that a 10% increase in digestible threonine compared to the NRC (1994) values (threonine:lysine = 0.74 and 0.77 in starter and grower phase, respectively) significantly improved FE and other important aspects including carcass traits, gut health and immunity-related parameters.

As for valine, which is the fourth limiting amino acid in vegetable-based diets, Kidd and Tillman (2016) reported that the optimal ratio to lysine should be from 68 to 79%, yet highlighting that such wide range might be problematic in practical conditions. Current primary breeders' recommendations fall within that interval (73–75% and 75–76%, Cobb-Vantress 2018; Aviagen 2019, respectively) while Wu (2014) suggested that 80% can be considered optimal from 21 to 56 d. Similarly, Schedle et al. (2019) reported an ideal valine:lysine ratio of 80% during the growing-finishing phase. In a recent paper, Agostini et al. (2019), evaluating the effects of valine:lysine ratios ranging from 63% to 93% on broilers growth performance, identified 80% (0–12 d), 75% (0–28 d), and 78% (0–35 or 0–42 d) as optimum ratios for enhancing FCR. In addition, the authors stated that carcass and breast meat yield were not significantly influenced by the different ratios. As for other amino acids, Franco et al. (2017) found no significant difference in FE assessing digestible phenylalanine+tyrosine:lysine and leucine:lysine ratios ranging from 94% to 118% and 93% to 121%, respectively, in Cobb-500 broilers from 8 to 17 d. Nevertheless, the authors suggested that for both, an optimal value could be fixed at 112%. Moreover, it has also been reported that a histidine:lysine ratio of 34% was able to maximise FE from 8 to 17 d (Franco et al. 2017). Finally, important advances have also been achieved for non-essential amino acid requirements, especially for glycine and serine (*i.e.* glycine equivalents) which represent the first-limiting non-essential amino acids in poultry diets (Corzo 2012; Ospina-Rojas et al. 2012; Siegert and Rodehutschord 2019; Hilliar et al. 2020).

Taken together, important results have been obtained in the field of precision amino acid nutrition of broilers, allowing remarkable reductions of dietary crude protein concentrations without negative effects on bird performance. Future studies of sustainable intensification of broiler production should be focused on assessing the most suitable digestible lysine concentration that can optimise FE response as well as meat quality traits and yield. On the other hand, available information regarding the optimal amino acid ratios within the ideal protein is sparse, thus research is encouraged to provide greater insights in this topic.

Protease

The administration of exogenous proteases is a promising nutritional approach to enhance dietary nitrogen utilisation by supporting the activity of endogenous proteases (Walk et al. 2018). As reported by Lee, Bedford, and Walk (2018), exogenous proteases have been included for many years into enzyme cocktails with minimal evidence regarding the explicit value of this enzyme. On the other hand, the development of mono-

component proteases during the last decade has increased the research interest in this field. The potential benefits associated with protease include improvements in both growth performance and environmental impact indicators mainly because of increased dietary nitrogen retention (Cowieson et al. 2016; Lee, Bedford, and Walk 2018). Moreover, exogenous protease can also improve overall ingredient quality by reducing variability, thus promoting the utilisation of low-digestible protein sources that can replace soybean meal in broiler diets (Cowieson et al. 2016; Lee, Bedford, and Walk 2018).

However, the results available in the literature regarding the effects of the supplementation with exogenous proteases in broiler diets are controversial. Leinonen and Williams (2015) applied a Life Cycle Assessment modelling approach to investigate the environmental impact of feeding broilers with either standard soybean-based diets or reduced-protein diets supplemented with protease. The results highlighted that protease administration diminished the environmental impact of both feed manufacturing, mostly by decreasing CO₂ emissions from land use changes related to soybean production, and the broiler raising phase, in which the reduction of NH₃ emissions had a primary role. However, Leinonen and Kyriazakis (2016) also pointed out that the environmental benefits deriving from this feeding strategy can be compromised or completely lost in case of detrimental outcomes on productive performance or liveability. In this regard, Lee, Bedford, and Walk (2018) conducted a meta-analysis study on data deriving from more than 67 experimental trials, carried out on poultry and swine, in which a total of 44 different proteases have been tested. Overall, the relative mean response of poultry to protease was a reduction of FCR and an enhancement of amino acids digestibility in the order of 1% and 1.6%, respectively. However, the positive effects of protease supplementation appeared to be significantly influenced by the performance of the control group, with the protease yielding limited improvements when FE is inherently high and when other enzymes, such as phytase and non-starch polysaccharide degrading enzymes (NSPase), are included in the diet (Lee, Bedford, and Walk 2018). As stated by the authors, these results may indicate that it could be difficult to observe a significant protease response in high-performing broilers. In addition, as the benefits associated with the use of protease could be provided by other exogenous enzymes already present in the formula (*e.g.* phytase may indirectly increase amino acids digestibility), its inclusion in a multi-component enzyme strategy might not be strictly necessary (Lee, Bedford, and Walk 2018). The results reported by Walk and Poernama (2019), who found no significant improvement in growth performance when protease was added to a low nutrient-density diet containing both phytase and xylanase, seem to support this hypothesis. It is noteworthy to consider that the inclusion of phytase and NSPase in commercial broiler diets is a widespread practice worldwide, especially on wheat-based diets. Therefore, if the scenario described by Lee, Bedford, and Walk (2018) is confirmed, these aspects could represent an important limitation to large-scale use of exogenous proteases in broiler chicken diets. For such reason, studies have tried to shed a light on this aspect of protease application. Walk et al. (2018) investigated the effects of the administration of several proteases in protein-deficient diets that were also supplemented with phytase and xylanase. The authors observed, in two separate trials, no significant improvements in growth performance and, in some cases, even a deterioration of FE in 17- and 18-d-old chicks although apparent ileal amino acids digestibility was generally

enhanced. Furthermore, exogenous proteases failed to improve growth performance and FE even when supplemented in nutrient adequate diets containing neither phytase nor xylanase (Walk et al. 2019). Intriguingly, the authors also reported that the bird response to protease was significantly influenced by the dietary concentration of the enzyme, with the highest dosage associated with a significant reduction of weight gain and feed intake. On the contrary, Cowieson et al. (2018) showed that protease administration in a nutritionally-marginal negative control diet (wheat/soybean based, with phytase and xylanase) improved FCR, as well as apparent ileal digestibility of nitrogen and amino acids, in broiler chickens at 35 d. It has also been reported that a mono-component protease was able to significantly enhance body weight and FE when supplemented to either a standard or a reduced protein content diet both including xylanase and phytase (Cowieson et al. 2019). Additionally, the authors observed beneficial effects of protease supplementation on the digestibility of some amino acids and starch, as well as apparent metabolisable and net energy content of the diet (Cowieson et al. 2019). Therefore, it is not possible at this time to provide a definite conclusion regarding the efficacy of exogenous proteases on FE and growth performance of broiler chickens. Further investigations will hopefully clarify whether additional performance benefits can be obtained through this feeding strategy when broilers are fed diets with high digestibility and containing multiple enzymes. In addition, specific molecular insights regarding nutrients repartitioning and metabolic aspects may provide clues to explain the inconsistent results observed in productive performance although amino acids digestibility is generally improved.

Phytase

The environmental issues related to phosphorus utilisation and the antinutritional effect of phytic acid are well known (Selle and Ravindran 2007; Dersjant-Li et al., 2015; Li et al. 2016) and a detailed description of these topics is beyond the scope of this paper. Briefly, the antinutritional effect of phytic acid is mainly due to the electronegative charge carried by its phosphate groups when the environmental pH is close to neutrality. In this condition, that can be easily found along the gastrointestinal tract of the chicken, phytic acid can chelate remarkably large amounts of minerals (forming salts of phytic acid called phytates), proteins, and carbohydrates, leading to the establishment of insoluble complexes that escape the digestive processes and thus are subsequently excreted with negative consequences on animal performance and environmental pollution (Cowieson et al. 2016; Vieira et al. 2018). However, rapid hydrolysis of the esters bonds that sustain the phosphate groups by the enzymatic action of phosphatases, such as phytases, can limit the antinutritional effect of the phytic acid (Vieira et al. 2018).

Although the activity of endogenous phytases and phosphatases in the gastrointestinal tract of poultry has been demonstrated (Tamim, Angel, and Christman 2004), efficacy is limited by an increasing tendency for insoluble phytate formation as a consequence of the high calcium concentration in commercial diets (Cowieson et al. 2016; Vieira et al. 2018). Consequently, the use of exogenous phytases obtained from certain fungi or bacterial species has become a widespread practice in poultry nutrition worldwide, accounting for approximately 60% of total sales in the feed enzyme market (Markets and Markets 2015). In the proximal gastrointestinal tract, exogenous phytases are able to reduce most of the

phytic acid into lower esters with limited chelation capacity, thereby reducing the antinutritional effects described above while enhancing phosphorous availability (Cowieson et al. 2016). Indeed, Bougouin et al. (2014) were able to conclude from a meta-analysis that broilers receiving phytase supplementation at 1,039 FTU/kg of diet (mean calcium:total phosphorous ratio = 1.6) showed an 8.6% average increase in phosphorus retention compared to a 48.4% baseline achieved by control birds, with positive implications in terms of overall production sustainability.

Great attention has also been directed at the potential performance improvements that can be achieved by administering exogenous phytases at unconventionally high doses (*i. e.* 'phytase super-dosing': >2,500 FTU/kg of feed; Cowieson, Wilcock, and Bedford 2011). In particular, the role of the *myo*-inositol, the central core of the phytic acid molecule that can be released after the enzymatic action of the phytase, has generated increasing interest within the scientific community. Indeed, this compound is involved in a plethora of metabolic and regulatory processes including lipid signalling, osmolarity, and glucose and insulin metabolism (reviewed by Gonzalez-Uarquin, Rodehutsord, and Huber 2020). Therefore, it could be considered as one of the main potential factors contributing to the improved bird performance that result from phytase addition to poultry diets. Several studies have shown that phytase supplementation can increase *myo*-inositol concentration in both intestinal contents and blood (Schmeisser et al. 2017; Sommerfeld et al. 2018; Babatunde et al. 2019; Walk et al. 2019), thereby making this molecule available for the metabolism of peripheral tissues. Sommerfeld et al. (2018) reported that higher FE can be achieved in 22-d-old broilers by supplementing either phytase in nutrient-deficient diets or *myo*-inositol in adequately formulated diets, respectively. Based on their observations, the authors concluded that *myo*-inositol was likely to be the main factor involved in FE improvements and its release after complete dephosphorylation of phytates should be considered an important benefit derived from phytase administration. Consistently, higher *myo*-inositol plasma concentrations have been associated with improvements in FE and breast meat weight in broilers fed moderate phosphorus-deficient diets supplemented with phytase (Schmeisser et al. 2017). In addition, the transcriptomic analysis carried out in that study revealed important insights regarding the role of low molecular weight phytate esters and *myo*-inositol on breast muscle metabolism and development. Conversely, Farhadi et al. (2017) did not detect significant effects on broilers growth performance when either exogenous phytase or *myo*-inositol were added to a phosphorus-deficient diet. Despite this, the authors suggested that *myo*-inositol may have supported the performance of birds fed the phosphorus-deficient diet, resulting in comparable performance to those birds receiving a nutrient-adequate diet. Cowieson et al. (2016) concluded that the overall effects of phytase super-dosing on growth performance of broilers can be influenced by several aspects such as *myo*-inositol yield (which in turn is affected by phytate concentration and accessibility to phytase), bird's capacity of converting *myo*-inositol-mediated signals to lean gain, and the provision of diets with adequate nutrients concentrations (*e.g.* amino acids and energy) which might be necessary to support protein accretion, down-regulation of gluconeogenesis, and thus better FE. In particular, Moss et al. (2019) demonstrated that digestible lysine and calcium are the two major dietary factors affecting growth performance and FE response (in a positive and negative fashion, respectively) of

Table 1. Summary of recent studies evaluating the use of organic trace minerals in broiler nutrition.

Reference	Tested minerals	Organic source	Main effects of organic minerals on sustainability-related traits
Echeverry et al. (2016)	Zn, Mn, Fe, Cu, Se	Proteinates	No significant effect on feed conversion ratio and body weight, lower feed intake. No available information on mineral excretion.
Kwieciń et al. (2016)	Zn	Chelate of glycine	No significant effect on feed conversion ratio and body weight at slaughter either compared to positive or negative control. No available information on mineral excretion.
Siri et al. (2016)	Zn, Cu, Mn	Chelates of methionine hydroxy-analogue	Improved body weight, daily weight gain and feed conversion ratio. No effect on breast myopathies occurrence. No available information on mineral excretion.
Bakhshalinejad, Akbari Moghaddam Kakhki, and Zoidis (2018)	Se	Chelate of methionine and yeast proteinate	Improved daily weight gain, feed conversion ratio, and European production efficiency factor. No available information on mineral excretion.
De Marco et al. (2017)	Zn, Cu, Mn, Fe	Chelates of glycine and amino acids	No significant effect on feed conversion ratio during the whole period of trial either compared to negative or positive control groups. Similar feed intake and body weight compared to positive control. Reduction of mineral excretion when organic TM sources were supplemented at 50% of control group dosage (100% inorganic). Total replacement of inorganic TM with organic ones led to similar or higher excretion levels.
Carvalho et al. (2018)	Cu, Fe, Mn, Zn	Proteinates	No significant changes in production traits. Excretion levels of trace minerals varied quadratically in relation to the dietary inclusion levels of organic minerals (diets with 50% and 75% of organic minerals reduced the excretion levels of all trace elements).
M'Sadeq et al. (2018)	Cu, Fe, I, Se, Mn, Zn, Cr	Yeast proteinates and hydroxychloride	Improved feed conversion ratio and weight gain. Higher apparent digestibility of Cu and Zn in broilers receiving yeast proteinate trace minerals compared to other sources.
Olukosi, van Kuijk, and Han (2018)	Zn, Cu	Hydroxychloride	Improved gain to feed at 35 d and in the overall period of trial. No significant effect on body weight gain and feed intake. Higher breast meat yield. No available information on mineral excretion.
Ao et al. (2019)	Fe, Mn, Cu, Zn, I, Se	Proteinates	Higher weight gain and feed intake, and improved feed to gain ratio. Reduced mortality. No available information on mineral excretion.
Bortoluzzi et al. (2019)	Zn	Proteinate	Beneficial effects on performance traits (improved feed conversion ratio, body weight gain, and mortality) of broilers challenged with coccidiosis plus <i>C. perfringens</i> . No available information on mineral excretion. Improved feed conversion ratio. No available information on mineral excretion.
Güz et al. (2019)	Cu, Mn, Zn, I, Se (+Ca and P)	Proteinates (Ca and P from bones)	Greater weight gain and feed intake (tendency), resulting in comparable feed to gain ratio. No effect on breast myopathies occurrence. No available information on mineral excretion.
Olukosi, van Kuijk, and Han (2019)	Zn, Cu	Hydroxychloride	Improved feed conversion ratio and liveability throughout the trial, as well as enhanced body weight at slaughter. No significant effect on mineral excretion, with the only exception of Mn at 48 d. Linear correlation between dietary mineral levels and the concentrations of Cu, Mn and Zn in the litter.
Veira et al. (2020)	Zn, Cu, Mn, Fe	Proteinates	

broilers fed phytase-supplemented diets, thereby further reinforcing the need for defining optimal concentrations of these nutrients in commercial diets.

Taken together, the dietary supplementation with exogenous phytases has consistently proved to be a valid nutritional strategy in view of a sustainable intensification of broiler production, with benefits that are definitely wider than merely increasing phosphorus digestibility and removing the nutritional impediments represented by phytates. As stated by Cowieson et al. (2016), 'phytate-free nutrition is complex and is more than just the removal of phytate from the diet and liberation of phosphate and inositol. Phytate-free nutrition is the creation of a diet landscape that can accommodate the beneficial effects of phytate removal, phosphate and inositol generation, and translate these to FCR and weight gain responses'. In this scenario, expanding knowledge of the effects of lower inositol phosphate esters and *myo*-inositol on physiological and metabolic aspects of broilers, as well as identifying potential strategies to limit insoluble phytate generation and enhance phytase activity, is crucial to further improving productive efficiency and sustainability.

Organic trace minerals

In addition to nitrogen and phosphorus, the use by the poultry industry of trace minerals (TM) such as copper (Cu), manganese (Mn) and zinc (Zn) has become a concern because of the implications for environmental pollution. Feedstuffs used in poultry feed formulation generally contain inadequate concentrations of TM, which are therefore added to broiler diets in the form of inorganic salts, such as carbonates, oxides, or sulphates (Nys et al. 2018). The limited knowledge of the TM requirements of modern broiler chickens, as well as the high availability and low cost of these additives, have contributed to the widespread nutritional strategy of adopting large safety margins for these nutrients to compensate for the low bioavailability of inorganic TM sources and to avoid any risk of deficiencies (Nys et al. 2018). However, such practice promotes greater mineral excretion and thus accumulation in manure which, when used as fertiliser, could have negative outcomes on the environment (e.g. soil quality, surface and ground water pollution) and crop productivity (Nollet et al. 2007; Wan et al. 2020). Consequently, the dietary concentrations of certain TM have been regulated in the European Union scenario, with maximum concentrations for chickens of Zn and Cu equal to 120 and 25 mg/kg of complete feed, respectively (European Commission 2016; European Food Safety Authority 2016).

The increasing concerns regarding mineral pollution have stimulated interest in nutritional strategies that reduce mineral excretion while not compromising productive performance and health status of broilers. Within this context, the use of organically complexed or chelated minerals as substitutes for their inorganic analogues has increased in the poultry industry. Organic TM complexes are compounds constituted by a central metal atom together with ligands such as amino acids, carbohydrates, or lipids (reviewed in Saripinar-Aksu, Aksu, and Önel 2012). Świątkiewicz, Arczewska-Włosek, and Jozefiak (2014) concluded that organic TM can be considered an effective source of microelements that has higher bioavailability and efficacy compared to inorganic sources. The results of more recent studies dealing with the use of organic TM in broiler nutrition have been summarised in Table 1. In keeping with the aim of this review, emphasis is on

outcomes that relate to sustainability traits, namely improvements in FE and reduction of mineral excretion. Considering productive performance, several studies consistently reported improvements in FE when organic TM were substituted for inorganic minerals, regardless of the dosage and the specific features of the tested organic minerals (Sirri et al. 2016; Bakhshalinejad, Akbari Moghaddam Kakhki, and Zoidis 2018; M'Sadeq et al. 2018; Olukosi, van Kuijk, and Han 2018; Ao et al. 2019; Güz et al. 2019; Vieira et al. 2020). Overall, these results agree with the previous considerations of Świątkiewicz, Arczewska-Włosek, and Jozefiak (2014). Furthermore, positive effects on performance traits (*i.e.* improved FE and body weight gain, and lower mortality) associated with the dietary use of organic TM have also been observed in broilers challenged with coccidiosis plus *Clostridium perfringens* (Bortoluzzi et al. 2019). Finally, the lack of significant improvements in performance traits or FE (as observed in some studies reported in Table 1) should not necessarily be viewed negatively as, in some cases, it has been demonstrated that similar growth performance and efficiency can be achieved by supplementing organic minerals at lower concentrations compared to inorganic sources (Echeverry et al. 2016; Kwiecień et al. 2016; De Marco et al. 2017; Carvalho et al. 2018; Olukosi, van Kuijk, and Han 2019), with potential economic and environmental benefits.

Furthermore, some papers provided evidence that feeding broilers diets enriched with organic TM can diminish mineral excretion (De Marco et al. 2017; Carvalho et al. 2018; M'Sadeq et al. 2018), which is fundamental for limiting the environmental impact of broiler production as previously discussed. On the other hand, Vieira et al. (2020) reported no significant effect of the TM source on mineral excretion (with the only exception of Mn at 48 d of broilers age), although they found that lower concentrations of TM in feed reduced Zn, Cu and Mn concentrations in the litter. Finally, an interesting aspect emerged in some studies (De Marco et al. 2017; Carvalho et al. 2018): mineral excretion was not significantly affected by the mineral source when organic TM were used at 100% of the recommended concentration for inorganic minerals. Indeed, De Marco et al. (2017) demonstrated that similar growth performance and lower mineral excretion can be achieved by using organic TM at 50% of the recommended dosage for inorganic ones, whereas the complete substitution (100%) of inorganic minerals with organic sources led to comparable or higher excretion. Similarly, Carvalho et al. (2018) observed a quadratic response on mineral excretion in relation to the dosage of organic minerals, with lowest values detected in birds fed diets with 50% and 75% of organic TM compared to those receiving diets with 100% organic or inorganic minerals. Together, these results indicate that there is a need for a better understanding of mineral nutrition in broiler chickens, with particular regard to the accurate determination of the TM requirements of modern broiler hybrids and the bioavailability of organic sources. Indeed, as the use of large safety margins can no longer be considered a sustainable approach in modern poultry production, such information will allow an accurate calibration of the dietary concentrations of TM that optimise animal productivity and environmental sustainability.

Conclusions and future perspectives

The current broiler production scenario, characterised by the shortage of available natural resources and increasing public concerns regarding environmental impact and

animal welfare, clearly indicates that the sustainable production intensification is the only approach that can be pursued by the modern poultry industry to fulfil the growing demand for poultry meat. In this scenario, improving FE in broiler chickens represents a primary goal because of the positive implications in terms of environmental and economic sustainability resulting from greater efficiency of diet utilisation. For this to be achieved, an accurate understanding of the nutritional requirements of modern broiler chickens along with a rational utilisation of feed additives can improve overall productive efficiency while addressing important environmental concerns by reducing the excretion of dietary nitrogen, phosphorus and trace minerals. Additional research on the above-mentioned topics is encouraged to further optimise resource utilisation, animal productivity and health, and production costs, while preserving the environment. However, it is important to consider that many other aspects are involved in poultry production sustainability. For instance, enhancing overall productivity of broiler chickens raised in alternative farming systems, such as free-range or organic which represent a growing share of market in the EU, or exposed to adverse environmental conditions (e.g. thermal stress) represent additional challenges for sustainability. Moreover, urgent measures should be taken to limit the impact of growth-related breast muscle abnormalities, which are seriously compromising the sustainability of the entire poultry meat chain and resulting in significant economic losses. Therefore, a multi-actor approach including breeding companies, researchers, as well as poultry nutritionists and producers, is fundamental to promote the sustainable intensification of poultry production and reach the noble goal of feeding future generations in an efficient and sustainable way.

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