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The Roles of Dietary Organic Trace Minerals on Animal Antioxidative Status, Gut Health, and Environmental Sustainability: A Review

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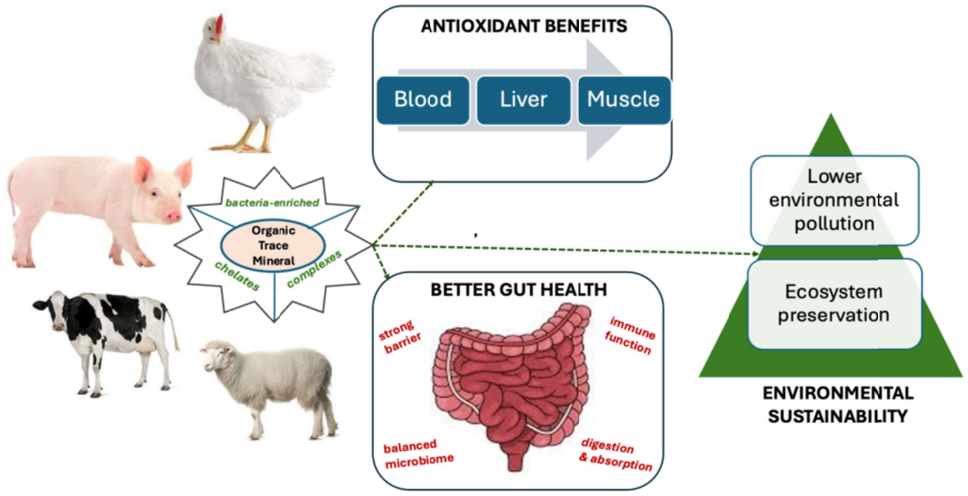
Abstract

The livestock industry is currently focused on improving production through sustainable nutrition practices. This has spurred scientists to investigate the potential of functional nutrients in providing health benefits beyond their nutritional value. The use of inorganic trace minerals (ITMs) has registered some successes but with some drawbacks arising from their low absorption rate, causing the excretion of copious amounts of trace minerals in manure, which pollutes the environment and becomes detrimental to soil physiology and crop health. Organic trace minerals (OTMs) are relatively more effective due to their stability and lower reactivity, although their functionality and pH depend on production processes. Here, we underscore the effects of OTM supplementation in animal diets to enhance the host's antioxidant capacity and gut health and promote environmental sustainability, as presented in the graphical abstract. Through adequate dietary OTM supplementation, animals can develop powerful resistance against the negative effects of physiological stressors or diseases by reinforcing the host's systemic antioxidant defenses and alleviating compromises on the gut's structure and functions, the gut being the primary site of nutrient digestion and absorption. The high cost of OTMs and the inconsistent outcomes of some across different animal species present significant limitations. Therefore, further research is needed to determine species-specific OTM requirements to optimize health and performance without over-supplementation. Also, researchers should further investigate the impact of OTMs, alone or in combination with other functional nutrients on animals' immunological responses during oxidative or pathological conditions.

Keywords: animal, antioxidant, gut, environmental sustainability, organic trace minerals

Graphical Abstract



1. Introduction

Trace minerals (TM) are essential nutrients that promote livestock health, performance, and productivity (Pajarillo et al., 2021). These nutrients are present in low levels in feedstuff utilized in the formulation of diets. Therefore, TMs are sourced exogenously and supplemented in animal feeds to bridge this nutrient gap for optimum performance (Nys et al., 2018). Inorganic trace minerals (ITMs) potentially bind with other ingredients or anti-nutritional factors such as fiber, tannins, and phytates in the gastrointestinal tract, yielding poor mineral bioavailability and utilization (Xiong et al., 2023). Due to the low bioavailability and cheap sources of ITMs, producers tend to supplement excess amounts in animals' diets, especially poultry, to meet their nutrient requirements (Bao & Choct, 2009). Although this works to meet the mineral nutrient requirement, over-supplementation leads to environmental pollution and soil health issues, altering chemical, biological, and physical properties and directly or indirectly affecting plant growth (Wan et al., 2020a).

Organic trace minerals (OTMs) or chelated minerals have more stability and less reactivity in the gastrointestinal tract, due to the binding of the central atom with ligands such as amino acids, lipids, or carbohydrates (Gayathri & Panda, 2018; Zamany et al., 2023a). Because of their higher bioavailability relative to ITMs, OTMs can be supplemented in animal feeds at much lower amounts than ITMs, making them more effective in animal production practices. In the literature, the use of lower levels of OTMs comparing ITMs has been reported to have no negative impact on the productivity of layers (Qiu et al., 2020a), broilers (Vishwanath et al., 2020), piglets (Zhang et al., 2021), and ruminants (Byrne & Murphy, 2022), and was found to reduce environmental pollution through lowered fecal mineral secretion (Qiu et al., 2020b).

Dietary OTMs can provide animal health and performance benefits (Byrne et al., 2023; Xiong et al., 2023). However, their utilization in animal husbandry practices is largely untapped. Therefore, this review aims to summarize the current knowledge on the roles of OTMs in enhancing animal antioxidant defense, gut health, and environmental sustainability. Additionally, it provides a foundation for future scientific study in this area, ultimately contributing to sustainable animal production.

2. Bioavailability and Utilization (OTM *vs.* ITM)

Organic trace minerals provide a more bioavailable, less antagonistic option with lower inclusion rates than inorganic sources (da Silva et al., 2022; Goff, 2018). They are stable chelated mineral complexes with a mineral ion (*e.g.*, magnesium (Mg), manganese (Mn), zinc (Zn), iron (Fe)) chemically or enzymatically bonded to a chelating agent or ligand, such as proteins, carbohydrates, lipids, organic acids, or amino acids (Byrne & Murphy, 2022; Holen et al., 2020; Schroeder, 2004; Swinkels et al., 1994). The chelation process reduces molecular size and maintains complex stability during metabolism and absorption in the gut, resulting in higher bioavailability of organic mineral forms (Brooks et al., 2013).

A recent review explored commercially available forms of OTMs and the potential reasons for their higher bioavailability in animals (Byrne & Murphy, 2022). In essence, the mineral-ligand interaction's strength and complexity enable higher solubility of mineral water and lipids in the gut lumen, reducing antagonism reactions (Byrne & Murphy, 2022; Zamany et al., 2023). The limited interaction between other probable chelators may be justified by this explanation, promoting its availability for tissue absorption and retention. Consequently, lower levels of OTMs compared to higher proportions of their inorganic forms in the diet may be equivalent in absorption and utilization efficiency (Zhang et al., 2024). Notably, proteinate chelates have shown the most significant benefits in poultry (Abdallah et al., 2009). Dietary OTM supplementation is becoming increasingly important because of its potency, even at a reduced concentration, minimizing the accumulation of residual components in the animal's body and fecal or urine excretion in the litter without compromising nutrient intake (Singh et al., 2015; Zhang et al., 2024). For environmental safety, the mineral-ligand bond, depending on the type, size, and stability (Singh et al., 2015), promotes the absorption of mineral elements through the cell membrane in alternative pathways (Leeson, 2003), reducing its excretion through feces and urine (Ammerman et al., 1998; Leeson, 2003). Although OTMs are often more bioavailable than their inorganic counterparts, they have negative consequences when oversupplied in the diet. For example, supplementing up to 200mg/kg copper-methionine (Cu-Met) chelate in broilers indicated an accumulation of Cu in the liver, causing toxicity and higher fecal excretion of Cu (Chowdhury et al., 2004). High dosage of selenium (Se)-yeast had the greatest negative effect on weight gain as well as higher concentrations of Se in the liver, breast, and feather of broiler chickens (Kim & Kil, 2020). High organic Cu supplementation in animals like pigs, poultry, and horses is safe (Clarkson et al., 2020). However, it can cause liver damage in ruminants, particularly sheep (Trouillard et al., 2021). Furthermore, selenium (Se) toxicity was confirmed in grazing buffaloes with weight loss, skin cracks, and hoof and joint problems (Ghoshi et al., 1993). Overall, the relatively higher bioavailability and digestibility of

OTMs make them a better source of minerals for farm animals with lower risks relating to intestinal absorption and environmental pollution, however, over or under-supplementation can still lead to significant problems in animal production.

3. Antioxidant Capacity

Physiological stressors generated from different production processes can compromise or jeopardize animal health, productivity, and economic gain (Puppel et al., 2015) due to the extreme production of free radicals in animal cells or tissues. To alleviate this oxidative condition, antioxidant nutrients can be supplemented in animal feeds to increase animals' endogenous antioxidant capacity to regulate these free radicals within a homeostatic range (Li et al., 2021). Though recognized for their nutritional value, OTMs have been found to possess antioxidant and anti-inflammatory properties, improving overall animals' immunological functions (Echeverry et al., 2016; Zhang et al., 2021). Organic trace minerals improve animal antioxidant capacity and immunological functions by serving as cofactors for antioxidant enzymes such as SOD and GPx, which neutralize harmful free radicals during oxidative stress, protect cells, support immune system function, and improve absorption and bioavailability (Leung, 1998; Palomares, 2022) Nevertheless, adequate or balanced supply, not excess, is necessary to ensure maximum antioxidant benefits while potential pro-oxidant effects are minimized (Staneviciene et al., 2023). Figure 1 demonstrates how trace minerals are co-factors for antioxidant enzymes and their impact on animal health and well-being. Minerals like Cu, Zn, Mn, and Se are co-factors of SOD, catalase, and GPX, which play an important role in lipid peroxidation and the antioxidant system (Ghasemi et al., 2020).

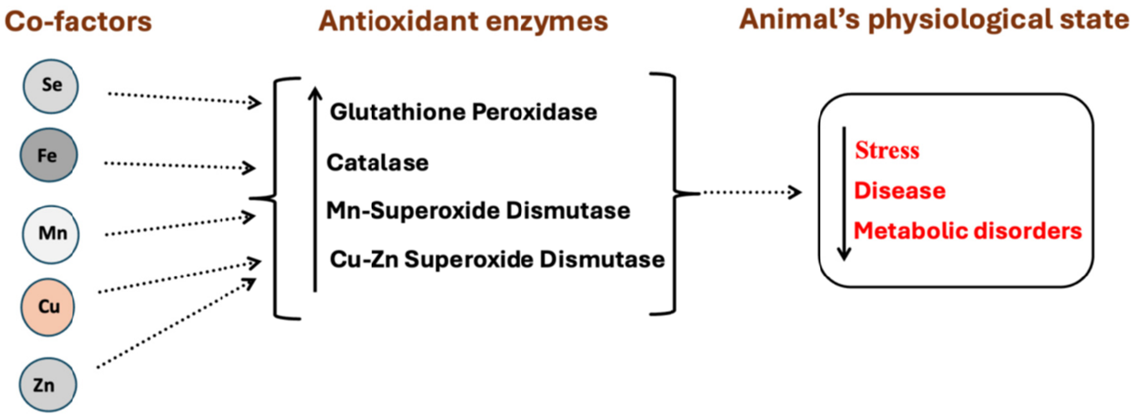


Figure 1. A schematic diagram showing how trace minerals act as co-factors for antioxidant enzymes and their impact on animal health

Organic trace minerals supplementation has been demonstrated to improve host systemic antioxidant status in healthy animals. For example, supplementation of turkeys and laying birds with a chelated complex of TM (Zn, Mn, Cu, Se, iodine (I), iron (Fe), and chromium (Cr)) increased serum total antioxidant capacity (TAC), superoxide dismutase (SOD), and catalase (CAT) activities (Ghasemi et al., 2023). In broiler breeders, a combination of proteinates of Zn, Fe, Mn, and Cu with Se-yeast supplementation enhanced blood total-SOD, Mn-SOD, and GPX activities while reducing malondialdehyde (MDA) content (Wang et al., 2019). In pigs, dietary inclusion of up to 20 ppm inorganic Zn ($ZnSO_4$) or Zn-Met in pigs showed similar serum glutathione peroxidase (GPX), CAT, and SOD activities (Uniyal et al., 2017). With HMSeBA supplementation, there was a surge in the spleen CAT and T-SOD activities in gilts (Li et al., 2021) and GPX activity in the seminal plasma of breeding boars (Horky et al., 2012). A recent study in dairy cows reported that the complete replacement of a composite mixture of ITMs by their organic forms in both pre-and postpartum diets had a similar effect on the FRAP, GPX, and SOD activities (Mion et al., 2023). In other ruminant studies, dietary Zn-amino acid supplementation enhanced blood TAC and SOD activities but reduced MDA levels in calves (Hou et al., 2023), while Se-enriched yeast likewise improved blood antioxidant status in gestating goats (Shi et al., 2018) and dairy cows (Gong et al., 2014).

As aforementioned, disease or oxidative conditions deplete the level of the body's endogenous antioxidants that act as the host's defense mechanism, compromising animal health and performance (Abdelnour et al., 2019; Das et al., 2016). Nevertheless, dietary OTM supplementation has been reported to exert a protective effect by increasing animal antioxidant status. For example, MHA-Zn chelate supplementation in coccidiosis-challenged birds resulted in higher blood Cu-Zn SOD and GPX activities, as well as a potential decline in MDA level (Trouillard et al., 2021), indicating a reduction in oxidative stress. Dietary organic SelenoSource (a.k.a. selenium yeast) has been reported to lower MDA content in multiparous sows (Zhang et al., 2020), increase the TAC and GPX activities in nursery pigs (Chao et al., 2019), and mitigate oxidative stress in diquat-challenged weaned piglets (Doan et al., 2020). High supplementation of amino acid complexes (Zn, Mn, Fe, Cu, I, Co, and Se) in Holstein bull calves alleviated heat stress effects by lowering plasma MDA and HSP70 while increasing SOD and GPX activities (Son et al., 2023). Additionally, dietary inclusion of 60mg/kg Zn-chelate of glycine hydrate elevated the duodenal SOD activity of lambs with nematode infection (Cobanova et al., 2020).

In animal nutrition practice, an oversupply of OTMs such as Se or Zn can become pro-oxidant, thereby affecting the antioxidant status of the animal (Hou et al., 2023; Son et al., 2023). This highlights the importance of providing animals with just the exact requirement per physiological state. The use of OTMs in the livestock industry is still emerging. Several organic mineral products have flooded the market, and some have shown positive outcomes on animal health. However, fewer studies have compared OTMs' antioxidant capacity within specific species, limiting knowledge for producers and nutritionists in the livestock industry. Additional antioxidant effects of OTMs in various farm animals are summarized in Appendix A.

4. Gut Health

The gastrointestinal tract, or gut (also referred to as the intestine), is known for nutrient digestion, metabolism, and absorption, possesses myriads of immune and epithelial cells, and acts as a barrier against the external environment (Kogut & Arsenault, 2016; Yu et al., 2012). The efficiency and effectiveness of the gut are a function of its structural and physiological state, affecting animal health and overall performance (Yang & Liao, 2019). Gut health is characterized by various structural and functional components such as morphology, integrity, immunity, microbiota, and bacteria metabolites (Bischoff, 2011; Kogut & Arsenault, 2016), collectively affecting nutrient digestibility and utilization within the gut. The structural and physiological components influencing gut health are presented in Figure 2. Appendix B shows an overview of the research on the effects of OTMs relative to their inorganic forms on animals' gut health and functions over the last two decades.

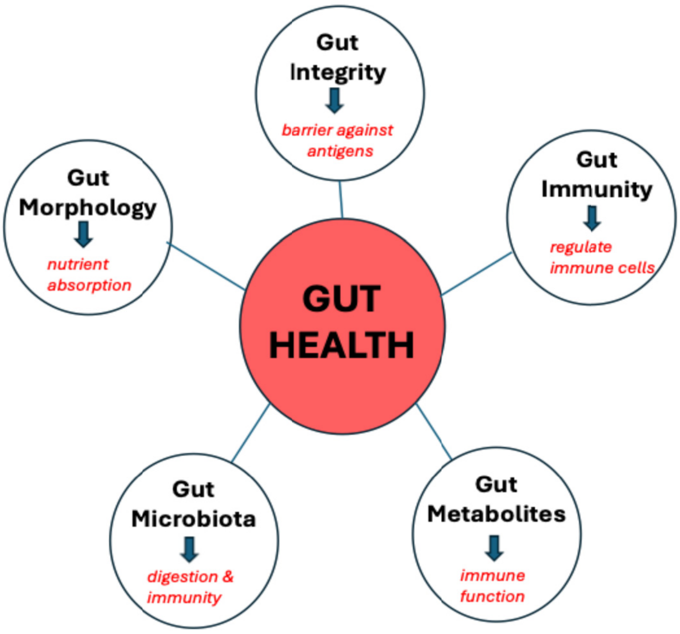


Figure 2. A schematic diagram showing the structural and physiological components influencing gut health

4.1 Gut Morphology

A well-developed and healthy intestinal epithelial morphology is crucial for optimal animal health, feed efficiency, and growth. The small intestine of most animals happens to be the site of nutrient digestion and adsorption, with its epithelium dispersed with finger-like cellular projections and invaginations commonly referred to as villus and crypt, respectively. Hampson (1986) reveals that longer villi and shorter crypts enhance the gut surface area, promoting better digestion and absorption (Ghasemi et al., 2023).

In turkey (Ghasemi et al., 2023) and young broilers (De Grande et al., 2020), replacing all ITM with its chelated complex led to better intestinal villus height (VH), crypt depth (CD) ratio, and surface area. Supplementing broilers with Zn-glycine increased intestinal VH and wall thickness (Ma et al., 2011), while organic Zn in low-protein diets also improved VH (Dong et al., 2023). Additionally, organic Se supplementation in laying hens increased VH but shortened CD in the duodenum and jejunum and elongated intestinal villi in reovirus-challenged broilers (Jessica et al., 2009).

High environmental temperatures can compromise or distort the intestinal anatomical structure due to the extreme production of ROS (Abuajamieh et al., 2020). However, supplementation of glycine complexed-Zn has been shown to have improved VH and intestinal epithelial surface area in poultry (Abuajamieh et al., 2020) and pigs (Pei et al., 2020) exposed to extreme temperatures. Furthermore, supplementing Zn-glycine or Zn-lactate in the diets of young pigs enhanced intestinal epithelial morphology by increasing the jejunal VH: CD while decreasing pro-apoptotic gene expression such as jejunal Bax (Diao et al., 2021). Also, gastric intubation of Zn-Met in LPS-challenged weanling pigs increased the count of jejunal goblet cells (Caine et al., 2009). Organic Cu complex supplementation in weanling pigs reduced CD and elongated VH, leading to a higher VH: CD in the duodenum and jejunum (Zhao et al., 2007). Ahmed et al. (Ahmed et al., 2016) observed that organic Se-yeast significantly impacted VH in goats' duodenum and jejunum. In ruminants, particularly sheep, Zn-Met supplementation significantly increased the VH and CD in the duodenum and jejunum (Jafarpour et al., 2015). To date, there is no adverse report on the effect of OTM supplementation on the intestinal structure of livestock.

4.2 Gut integrity, Permeability, and Immunity

The gut barrier, consisting of a mucus bilayer with immune cells interfacing with microbiota, plays a critical role in maintaining the integrity of the gut and protecting the body from harmful toxins and pathogens (Cundra et al., 2024) Controlling intestinal permeability, which is linked to chronic inflammatory diseases, requires regulation of the intestinal barrier (De Santis et al., 2015). The gut, the largest immune organ, can compromise its functions when subjected to stress or diseases (Chassaing et al., 2014). Stressors such as high ambient temperature, can damage pigs' intestinal health by increasing endotoxin permeability (Pearce et al., 2013). Besides, dietary nutrients have been reported to enhance intestinal barrier functions by alleviating inflammation and improving barrier integrity (Cundra et al., 2024; De Santis et al., 2015).

Supplementing chelated Zn-amino acid has been demonstrated to restore intestinal epithelial resistance, reduce endotoxins, and enhance the acute phase response (Pearce et al., 2015). Likewise, broilers fed amino acid-chelated trace minerals experienced reduced HSP70 expression and increased CLDN1 expression in the jejunum (Baxter et al., 2020). As a result, the amino acid-chelated mineral supplements enhanced the barrier functions of intestinal epithelial cells in these animals (Baxter et al., 2020; Nishii et al., 2019). Broiler chickens infected with coccidiosis showed a decline in the expression of OCLN and Muc-2 genes in the jejunum (Wickramasuriya et al., 2023). However, organic Se-yeast supplementation stimulated a remarkable upregulation in the expression of JAM-2 and OCLN genes, promoting intestinal barrier functions (Wickramasuriya et al., 2023; Z. Yang et al., 2020). In another study, dietary organic Zn (a partially hydrolyzed soy protein) inclusion mitigated inflammation and intestinal permeability by increasing the jejunal mRNA expression of IL-10 and IL-18 and upregulating IgA gene transcript and iNOS expression in the cecal tonsil of birds with necrotic enteritis (Bortoluzzi et al., 2019).

Pigs' intestinal integrity and immunity were found to have improved through dietary OTM supplementation (Richards et al., 2010). For instance, Zn-Met diets ameliorated gut inflammatory response through downregulating inflammatory cytokines, IFN-γ, TLR-2, and iNOS (Kidd et al., 1996). Likewise, in young pigs, this same diet stimulated the proliferation of goblet cells and upregulated mRNA expression of intestinal Muc-2 and OCLN genes (Diao et al., 2021). Over-supplementing Cu-proteinate, on the other hand, can hurt intestinal epithelial cells, which could cause inflammation, poor barrier function, and problems with normal cell turnover. (Li et al., 2019)

4.3 Gut Microbiota and Metabolites

The composition of gut microbiota is crucial for animal health, influencing the immune system and preventing harmful bacterial colonization (Guo et al., 2004; Muhammad et al., 2021). Research has demonstrated the significant benefits of organic Se on gut microbiota. For instance, organic Se increased beneficial bacteria and reduced pathogens such as *Escherichia coli* and *Salmonella* spp. in laying hens (Muhammad et al., 2021; Zainudin et al., 2023). Similarly, low levels of OTMs compared to higher levels of its inorganic forms in the diet of late-stage laying hens decreased harmful bacteria like *Barnesiellaceae* and *Clostridiales* in the cecum (Dong et al., 2022), further indicating the superiority of OTMs to ITMs in stimulating immunological response. As is known, the gut microbiota is influenced by micronutrient (*e.g.*, OTMs) supplementation, and the bioavailability of these mineral nutrients, in terms of absorption and host's utilization, affects their composition and functionality, either leading to beneficial or negative outcomes for gut health (Barone et al., 2022; Yang et al., 2020).

According to Shao et al. (2014), dietary organic Zn supplementation in poultry raised the counts of *Lactobacillus* and total bacteria and lowered the counts of salmonella in the cecum. In another investigation, the supplementation of 90 mg/kg MHA-Zn in low protein broiler diets indicated more *Lactobacillus*, *Butyricoccus*, *Oscillospira*, *Ruminococcus*, and *Phascolarctobacterium* in the cecum (Dong et al., 2023). Similar effects were demonstrated in the pigs' cecum, where Zn-lactate supplementation boosted Lactobacillus species and decreased E. coli counts (Diao et al., 2021). Also, Zn-glycinate was found to stimulate *Clostridium* herbivorans populations in the cecum and colon of pigs, enhancing fiber digestibility more than inorganic zinc (Barszcz et al., 2021). Additionally, organic Se also increases beneficial intestinal bacteria in gilts (Li et al., 2021).

The amino acid (AA) complex (Zn, Mn, Fe, Cu, I, Co, and Se) supplementation in heat-stressed Holstein calves led to a higher population of *Christensenella,* which has been reported to affect rumen energy metabolism (Correia Sales et al., 2021; Son et al., 2023). OTMs can modify rumen microbiota composition in Holstein's calves, promoting fiber-degrading bacteria like *Treponema* and *Akkermansia* in fecal microbiota (Ji et al., 2023). In lambs, organic Zn supplementation reduced pathogenic bacterial enzyme activity in the colon (Bujňáková et al., 2023). Dietary inclusion of the Zn-AA complex in yearling rams reduced rumen bacterium diversity compared to those fed equivalent levels of inorganic Zn, implying the preponderance of beneficial rumen bacteria species as demonstrated by increased ADG and perhaps feed efficiency in rams fed Zn-AA complex diets (Ishaq et al., 2019). Dietary inclusion of 0.18g Se-yeast/Kg DM for sheep altered rumen microflora and increased total VFA and propionate concentration in the rumen fluid (Cui et al., 2021). Zinc-methionine supplementation in newborn Holstein calves decreased neonatal diarrhea by altering rectal bacterial diversity and increasing beneficial *Actinobacteria*, *Faecalibacterium*, and *Ruminococcus* (Chang et al., 2020).

Butyric acid promote nutrient digestibility and gut health by fostering villi growth and beneficial microbe proliferation (Correia et al., 2024; El-Saadony et al., 2022). Organic Se increased isobutyric and butyric acid in the cecal digesta of layer hens, with the high concentration of butyric acid reportedly associated with the inhibition of pathogenic bacteria through lethal intracellular accumulation and enzyme denaturation (Zainudin et al., 2023). Propionate, a gut microbial metabolite, is crucial in energy metabolism and supports gut health (Hosseini et al., 2011). HMSeBA supplementation altered rumen fermentation by increasing ruminal propionate concentration in dairy cows (Wei et al., 2019). Proliferation of beneficial microbes in the gut of animals is needed to prevent dysbiosis (Kogut, 2019). Since the gut is vulnerable to diseases, using OTMs to improve gut microbial activity can enhance immunity, thereby improving the health status of farm animals. Gut metabolites, generated by the host or the gut microbiota, are crucial for gut health and functions. They also provide an environment unsuitable (*i.e.*, lower pH) for the proliferation of harmful microbes. Thus, further research is needed to clearly understand and establish the roles of OTMs on the gut metabolic pool and the association with commensal gut microbes.

4.4 Nutrient Digestibility and Utilization

Dietary components significantly influence nutrient metabolism and utilization (Celi et al., 2017). For example, turkeys supplemented with OTMs enhanced nutrient utilization efficiency by increasing the digestibility of crude fat, energy, ash, and phosphorus (Ghasemi et al., 2023). Similarly, adding organic Zn (MHA-Zn) to low-protein diets improved the ileum apparent total tract digestibility (ATTD) of crude protein (CP) and nitrogen-free extract (NFE) in broilers (Dong et al., 2023), likely due to the upregulation of genes related to ileal absorption such as PepT1, SGLT1, MCT4, and MCT1 (Diao et al., 2021).

Dietary replacement of 100% commercial ITMs with lower levels (30-60%) of OTMs (amino acid- chelated) impact on nutritional digestibility and fecal mineral concentration was superior, according to a recent study in pigs (Xiong et al., 2023). Conversely, supplementing up to 20ppm inorganic Zn ($ZnSO_4$) or Zn-Met in pigs showed similar apparent digestibility of nutrients, including ADF, NDF, organic matter (OM), crude protein (CP), and ether extract (EE) (Uniyal et al., 2017). In another study comparing the effect of two organic Zn sources on nutrient digestibility in weaned pigs, 100mg/kg Zn-lactate indicated better ATTD than similar levels of Zn-glycine (Diao et al., 2021), suggesting potential variations in the digestibility of OTM sources. Zinc-methionine supplements helped buffalo calves digest nutrients better (Hassan et al., 2016), whereas Zn-complex of glycine hydrate and protein hydrolysate were absorbed and utilized similarly to inorganic

Zn-sulfate in lambs (Gresakova et al., 2021). Supplementing growing lambs with organic Zn and Se-yeast has enhanced the digestibility of OM, CP, and ADF (Alimohamady et al., 2013, 2019).

Furthermore, the supplementation of Cu-proteinate (10-20mg/kg DM) in the lambs' diet enhanced the digestibility of OM, CP, NDF, and non-fibrous carbohydrates (NFC) (Dezfoulian et al., 2012). Additionally, HMSeBA supplementation increased the absorption of CP, NDF, ADF, and Se in dairy cows (Wei et al., 2019). Supplementation of Mn glycinate chelate in lambs' diets has also been associated with improved fiber digestibility and enhanced Mn utilization by rumen bacteria (Gresakova et al., 2018).

5. Environmental Sustainability

As aforementioned, inorganic forms of essential trace minerals such as Zn, Cu, Se, Mn, cobalt (Co), and chromium (Cr) are important feed additives in livestock nutrition (Akbar & Khorram Del, 2021). However, their low bioavailability requires that they be supplemented in higher quantities to meet animal nutritional needs. Consequently, over-supplementation causes high amounts of these trace minerals, such as Cu or Zn, to be excreted in manure, which may cause soil and water contamination, affecting soil health, crop performance, and aquatic ecosystem (Wan et al., 2020). The bioaccumulation of these minerals in soil and water bodies enters the food chain by consuming contaminated water, crops, or animal products that could predispose humans to pathological conditions such as anemia, liver toxicity, neurological defects, and gastrointestinal issues (Karim, 2018; Leitzmann et al., 2003). Hence, there is a need for superior forms of TMs, such as OTMs, that require relatively lower supplementation to enhance livestock production and support better public health outcomes (Byrne & Murphy, 2022; Zafar & Fatima, 2018).

OTMs in animal feed can reduce the accumulation of minerals in animal manure (Brugger & Windisch, 2015). For example, dietary supplementation of chelated Zn and Cu in pigs' diets significantly reduced fecal concentrations of these minerals by 50% without affecting the pigs' performance (Creech et al., 2004). When pigs excrete a lower proportion of these OTMs in their feces due to their higher digestibility (Xiong et al., 2023), there is less accumulation in the soil (Creech et al., 2004). Nollet et al. (Nollet et al., 2007) replaced ITMs with OTMs up to seven times lower for Mn, Fe, Zn, and Cu in broiler diets and found that broilers supplemented with lower levels of OTMs excreted lower mineral amounts than those fed ITMs. Reducing mineral loss through excretion can minimize environmental contamination and improve animal performance (Qiu et al., 2020; Świątkiewicz et al., 2014). Exploring the high bioavailability, digestibility, and absorption of OTMs can improve sustainable animal production and proffer beneficial effects on the environment by reducing the number of mineral footprints in animal excreta thereby fostering environmental sustainability.

6. Conclusions and Future Perspectives

Dietary OTM supplementation offers a sustainable nutritional strategy with substantial health benefits, including boosting host systemic antioxidant defenses, gut health, and immune functions, supporting environmental sustainability goals. The relatively high cost of OTMs and the lack of information on optimal supplementation dosage across different animal species pose significant limitations. Addressing these challenges necessitates further research into using precision OTM supplementation to match specific animal physiological requirements and production goals, in a balanced synergy with inorganic mineral forms, other dietary components, or additives. Alternatively, dietary OTM supplementation during critical phases, including pregnancy, parturition, weaning, and lactation, or when animals are sick or stressed could be cost-effective for production. Practices without over-supplementation of OTMs are crucial for animal performance, human food safety, and public health, as they prevent nutrient imbalances and toxicity. Given OTMs' positive effects on gut health and blood, liver, and muscle antioxidant status, more studies could explore their potential, singly or combined with other functional nutrients, in enhancing intestinal antioxidant status and mitigating stress, metabolic disorders, and disease challenges undermining the gut effectiveness and growth performance of food-producing animals.

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Abbreviations

CLDN: claudin, FRAP: ferric reducing antioxidant power, GPx: glutathione peroxide, HSP10: heat shock protein, HMSeBA: hydroxy-methyl seleno-butanoic acid, IFN-γ: interferon gamma, IgA: immunoglobulin A, IL: interleukin, iNOS: inducible nitric oxide synthase, JAM: junctional adhesion molecule, LPS: lipopolysaccharide, MCT1: monocarboxylate transporter, MDA: malondialdehyde, MHA: methionine hydroxyl analog, mRNA: messenger ribonucleic acid, Muc-2: mucin-2, OCLN: occludin, PEPT1: peptide transporter, SOD: superoxide dismutase, SGLT1: sodium-glucose cotransporter 1, TLR: toll-like receptor, VFA: volatile fatty acid.

Appendix A

Overview of the research during the past two decades concerning the effects of OTMs on animals' antioxidative status[a]

Trace mineral	Organic form	Dosage	Species	Experiment duration[b]	Stressor/ Disease	Parameter(s) investigated	Antioxidant status (comparing inorganic form)[c]	References
Zinc (Zn)	Bioplex-Zn	40 mg/kg	Broilers	Day 1 to Day 42		Blood	Lower plasma MDA	Aksu et al., 2010
	Zn-glycinate	60~80 mg/kg	Broiler breeders	39th to 47th week		Blood and liver	Higher liver and serum Cu-Zn SOD, higher serum T-SOD, and lower liver MDA	Zhang et al., 2017
	12% pure zinc (Zinpro company)	30 mg/kg	Leghorn layers	80 weeks		Blood and liver	Higher serum SOD	Niknia et al., 2022
	Zn-picolinate	60 mg/kg	Japa-nese quails	10 days	Heat stress	Blood and liver	Lower serum and liver MDA	Sahin et al., 2005
	Zn-glyphosate	100 mg/kg	Weaned piglets	35 days		Blood	Higher serum T-AOC and Cu/Zn SOD, higher liver GPX and T-AOC	Liu et al., 2020
	Zn-valine	65~80 mg/kg	Weaned piglets	35th to 63rd day		Blood and liver	Higher serum and liver SOD and GPX, and liver T-AOC	Zhang et al., 2024
	Zn-proteinate	120 mg/kg	Weaned piglets	4th to 8th week		Spleen	Higher spleen SOD and GPX and lower spleen MDA	She et al., 2017
	Zn-methionine	50 mg/kg	Lambs	20th to 26th week	Transportation Stress	Kidney	High serum TAC	Soumar et al., 2020
	Zn-proteinate	80 mg/day	Pre-weaned holstein calves	Day 1 to Day 51		Blood	Higher serum GPX and T-AOC, Lower serum MDA	Liu et al., 2023
Selen-nium (Se)	Selenomethionine and Se-yeast	0.15 mg/kg	Broiler breeder	Day 1 to Day 41		Breast muscle, liver, and kidney	Higher muscle TAC, liver and kidney CAT, possibly higher liver GPX, and lower kidney and muscle MDA	Li et al., 2018
	Sel-plex (Alltech Inc.)	0.3 mg/kg	Broiler	Day 1 to Day 42	Oxidative stress	Blood	Higher serum GSH and lower serum MDA	Boostani et al., 2015
	Selenohomolanthione and selenomethionine	0.57 mg/kg	Broiler	Day 1 to Day 42		Blood	Both had higher plasma GPX and SOD	Celi et al., 2013
	Se-enriched bacteria	0.3 mg/kg	Broiler	Day 1 to Day 42		Blood, liver, and kidney	Higher serum GPX, higher kidney GPX and CAT, higher liver CAT, lower serum MDA	Dalia et al., 2017
	Se-yeast	0.4 mg/kg	Broiler	Day 15 to Day 29	Corticosterone	Blood	Higher serum GPX, SOD, and T-AOC	Fan et al., 2009
	Selenomethionine	0.3 mg/kg	Local chinese subei chickens	50 to 90 days		Blood and breast muscle	Higher serum and muscle GPX, lower serum MDA	Li et al., 2018b
	Se-yeast	0.3~0.5 ppm	Layers	21 to 27 weeks		Blood	Higher serum GPX	Meng et al., 2019
	Selenomethionine	0.3 mg/kg	Finishing pigs	40 days		Liver and muscle	Higher liver and muscle GPX, lower liver and muscle MDA	Zhan et al., 2007
	Selenomethionine	0.3 mg/kg	Gestating through Lactating	60 days		Offspring kidney, liver, pancreas, muscle, and serum	Higher SOD and GPX, lower MDA in offspring organs	Zhan et al., 2011
	Selenomethionine	0.43 mg/kg	Gestating pig	1 month (pre farrowing to lactation)		Offspring Blood	Higher plasma GPX	Falk et al., 2020
	Se-yeast	0.3 mg/kg	Peripaturient Dairy cow	4 weeks pre-calving to parturition		Blood	Lower plasma MDA, higher GPX	Gong & Xiao, 2018
	Se-yeast and selenomethionine	0.1 mg/kg DM	Beef cattle	60 days		Longissimus dorsi	Lower MDA	Huang et al., 2023
	Se-yeast	0.4 mg/kg	Sheep	3 months		Liver and duodenal mucosa	Lower tissue MDA	Čobanová et al., 2017
	Sel-plex (Alltech Inc.)	0.3 mg/kg	Ewes and lambs	4 months		Blood	Higher GPX and SOD, lower MDA	Novoselec et al., 2022
	Jevsel-101	0.15 mg/kg	Lambs	90 days		Blood	Higher serum GPX, lower serum MDA	Kumar et al., 2009
	Hydroxyl-selenomethionine (HMSeBA)	0.3-0.5 mg/kg	Mid-lactation Holstein	8 weeks		Blood	Higher serum GPX and SOD, lower serum MDA	Sun et al., 2017

Others	Iron (Fe)-glycine	160 mg/kg	Broilers	Day 1 to Day 42		Liver	Higher liver Cu/Zn SOD	Ma et al., 2012
	Fe-glycine	160 mg/kg	Broilers	Day 1 to Day 21		Blood	Higher serum CAT, XOD, and SOD	Sun et al., 2015
	Copper (Cu)-methionate	20 mg/kg	Broilers	Day 1 to Day 42		Blood	Both had similar effect on serum GPX and SOD	Wu et al., 2020
	Fe-glycine	120 mg/kg	Layers	30 to 42 weeks		Blood	Higher serum SOD and GPX, lower MDA level	Sarlak et al., 2021
	Manganese (Mn)-bioplex	120 mg/kg	Layers	20 to 28 weeks		Blood	Higher plasma T-AOC	Piešová et al., 2019
	Mn-proteinate	120 mg/kg	Layers (broiler breeders)	18 to 32 weeks	Heat stress	Heart and breast muscle	Higher heart MnSOD and CuZnSOD, higher breast muscle SOD	Zhu et al., 2016
	Fe-glycine	90 mg/kg	Weanling pigs	Day 35 to Day 75		Liver	Higher liver SOD and SDH	Feng et al., 2009
	Chromium (Cr)-Methionine	3 mg/kg	Lambs	8 weeks	Heat stress	Blood	Lower serum MDA, higher erythrocytes GPX and SOD	Seifalinasab et al., 2022
	Cr-Methionine	1 mg/kg	Lambs	20th to 26th week	Transportation stress	Liver	Lower liver MDA, higher liver T-AOC, SOD, and GPX.	Soumar et al., 2020

Note. [a] This table provides a summary of the effects of certain OTMs compared to an inorganic form on antioxidant status measured in animals.

[b] Duration with intervals refers to the animal's age at the beginning of the experiment to the animal's age at the end of the experiment. Without interval refers to the exact experiment duration.

[c] For each study, the effect of an ITM was compared to one or two OTM forms.

GPX = Glutathione peroxidase, SOD = Superoxide dismutase, CAT = Catalase, T-AOC = Total Antioxidant Capacity, MDA = Malondialdehyde.

Appendix B

Overview of the research during the past two decades concerning the effects of OTMs on animals' gut health and functions[a]

Trace mineral	Organic form	Dosage	Species	Experiment duration[b]	Stressor/ Disease	Parameter(s) Investigated	Gut health (comparing inorganic form)[c]	References
Zinc (Zn)	Zn-amino acid complex	60 ppm	Broilers	Day 1 to Day 36		Duodenum	Higher VH, decreased relative abundance of Proteobacteria	De Grande et al., 2020
	Zn-glycinate	30 mg/kg	Broilers	Day1 to Day 40		Jejunum	Better intestinal immunological response through expression of IL-17 and TGF-β4	Levkut et al., 2017
	Zn-glycinate	80 to 120 mg/kg	Broilers	Day 1 to Day 35		Cecum, jejunum	Higher cecal tonsil and jejunum gene expression of IL-Iβ and claudin-2, respectively	Ng et al., 2022
	Zn-glycinate	100 mg/kg	Broilers	Day 1 to Day 42		Jejunum and ileum (mixed)	Better intestinal immunological stimulation through IgA and IgG expression	Marek et al., 2017
	Zn-methionine	80 mg/kg	Broilers	Day 1 to Day 35		Ileum	Higher VH, VW, VH:CD, lower CD	Khan et al., 2024
	Zn-glycine	70 mg/kg	Cherry valley ducks	Day 1 to Day 35		Jejunum	Higher VH, higher expression of IgA and IgG, and Mucin-2 mRNA level	Chang et al., 2023
	Zn-glutamate	200 mg/kg	Weaned piglets		*Escherichia coli K88*	Small intestine	Both forms had similar effects on VH in the duodenum, jejunum, and ileum	Mazzoni et al., 2010
	Zn-amino acid complex	100 ppm	Pigs	32 days		Jejunum and ileum	Downregulated proinflammatory cytokine IL-18, Upregulated TLR2 gene expression in ileum	Medida et al., 2023
	Zn-amino acid complex	40 mg/kg	Holsten steer	4 months	Heat stress	Jejunum and ileum	Higher jejunum and ileum VH	Opgenorth et al., 2021
	Zn-methionine	80 mg/day	Dairy calves	14 days	Diarrhea	Rectum	Both forms played similar role in reducing the incidence of diarrhea	Chang et al., 2020
Selenium (Se)	Bacterial organic Se	0.3 mg/kg	Broilers	Day 1 to Day 42		Small intestine	Higher VH and better Se retention	Dalia et al., 2020
	Se-yeast	0.3 ppm	Broilers	Day 1 to Day 21	Avian reovirus challenge	Duodenum and ileum	Higher VH and VH:CD, lower VW, and CD	Read-Snyder et al., 2009
	Hydroxy analog of selenomethionine (HMSeBA)	0.3 mg/kg	Maternal sows	Gestation through weaning	LPS	Ileum	Lower inflammation level by suppressing nuclear factor-Kb (NF-kB) and ERK/Beclin-1 signaling	Mou et al., 2021
	HMSeBA	0.3 mg/kg	Gilts	Weaning to slaughter		Small intestine	Higher jejunum IgA, higher abundance of *Ruminococcaceae* and *Phascolarctobacterium* and reduced population of *Parabacteroides* and *Prevotellaceae*	Li et al., 2021
	Se-yeast	0.375 mg/kg	Wean piglets	4 weeks	*Salmonella typhimurium*	Feces	Higher digestibility of DM, CP, CF and reduced amount of *E. coli* in faeces	Lv et al., 2020
	HMSeBA	0.3 to 0.6 mg DM/kg (*in vitro*)	Holsten cows	48 hrs		Rumen	Higher invitro gas production associated with higher abundance of *Prevotella* and *Prevotellaceae-UCG-003*, but lower abundance of *Ruminicoccus-1*	Zheng et al., 2022
Manganese (Mn)	Mn-Bioplex or Mn-Glycinoplex (Alltech Inc.)	120 mg/kg	Layers	8 weeks		Jejunum	Both organic forms had similar effect with inorganic form in reducing the thickness of adherent jejunal mucus gel	Piešová et al., 2019
	Mn-chelate of lysine and glutamic acid	20 mg/kg	Wean dairy calves	4 weeks		Feces	Higher apparent nutrient digestibility, higher retention of Fe, P and Mn, higher population of Proteobacteria and Spirochaetota, genera-*Alloprevotella*, *Clostridia*, *Treponema*, etc.	Ji et al., 2023

Note. [a] This table provides an overview of the impact of certain OTMs compared to an inorganic form on the gut health of various animals.

[b] Duration with intervals refers to the animal's age at the beginning of the experiment to the animal's age at the end of the experiment. Without interval refers to the exact experiment duration.

[c] For each study, the effect of an ITM was compared to one or two OTM forms.

VH = Villus height, CD = Crypt depth, VW = Villus width, IL-17 = Interleukin, TGF = Transforming Growth Factor, Ig = Immunoglobulin, TLR = Toll-Like Receptor, ERK = Extra-cellular Signal Regulated Kinase, DM = Dry matter, CP = Crude protein, NDF = Neutral Detergent Fiber, ADF = Acid Detergent Fiber.

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