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Impact of functional lipids on intestinal health in swine and poultry

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Abstract

Intestinal health challenges – including dysbiosis, inflammatory disorders, and pathogen susceptibility – impose severe economic losses and welfare concerns in intensive livestock production. Functional lipids, defined as bioactive lipid molecules with physiological benefits beyond basic nutrition, offer promising solutions to these issues. This review establishes a comprehensive definition of functional lipids and elucidates their metabolic process. Using short- and medium-chain fatty acid glycerides as a prime example, we examine their significant roles in energy homeostasis, gut microbiota composition and diversity, immune modulation, and antibacterial and antiviral activities. Additionally, we critically evaluate their current applications and future industrial potential in livestock production, providing evidence-based recommendations for their optimal implementation in animal nutrition strategies.

Introduction

In the rapidly developing modern livestock industry, pigs and poultry are primary sources of meat, and their production efficiency and health status directly relate to food safety, public health, and economic benefits. However, with the widespread adoption of intensive farming models and the implementation of bans and reduction strategies on feed antibiotics, intestinal health issues in pigs and poultry have become increasingly prominent. These issues include impaired intestinal barrier function, imbalanced gut microbiota, low digestive efficiency, and the emergence of various intestinal diseases as a consequence (Ducatelle et al. 2023; Tang et al. 2022). These problems not only reduce animal production performance but also increase farming costs and disease risks. Therefore, exploring effective strategies for maintaining intestinal health is crucial for promoting the sustainable development of the livestock industry.

Lipids are generally recognized as a crucial form of energy storage, supplying the energy required by cells. Additionally, they are key components of cell membranes, forming a barrier and protecting the internal structures of cells. However, with ongoing scientific research, the diversity and complexity of lipids have become increasingly apparent, revealing that their functions in living organisms far exceed initial understandings (Florance and Ramasubbu 2022). Functional lipids are those lipid components with specific physiological functions, showing great potential in improving animal intestinal health (Dima et al. 2021). This paper reviews the applications and research advances of functional lipids in the intestinal health of pigs and poultry, discussing their mechanisms of action, effects, and potential applications, with the aim of providing scientific evidence and references for the rational application of functional lipids in livestock production, optimizing feed formulations, and improving animal production performance.

Types of fats and definition of functional lipids

Fats are triglycerides (TAGs) composed of glycerol and fatty acids, serving as important components and energy reserves in living organisms. Based on the saturation of fatty acids, fats can be classified into saturated and unsaturated fats, with unsaturated fats further divided into monounsaturated and polyunsaturated fats. According to the carbon chain length of fatty acids, fats can also be categorized as short-chain fatty acid glycerides, medium-chain fatty acid glycerides, and long-chain fatty acid glycerides. TAGs containing long-chain fatty acids (LCTs, >12 carbon atoms) can be broken down by various enzymes to provide the energy required for life activities. Medium-chain TAGs (MCTs, containing 6–12 carbon atoms) serve as excellent solvents for lipophilic bioactive substances and can act as carriers for nutrients and bioactive compounds (Dima et al. 2021). Compared to long-chain TAG, MCT can rapidly supply energy to the body and improve the digestibility and absorption of food, offering unique advantages.

Structurally simplifying from TAGs, monoglycerides (MAGs) represent glycerol molecules esterified with only a single fatty acid, which can range from short- to long chain. Depending on the position of the ester bond with glycerol, MAGs can be divided into two categories: 1-MAGs (α-MAGs) and 2-MAGs (β-MAGs). Common MAGs include glycerol monobutyrate (C4:0), glycerol monocaprylin (C8:0), glycerol monodecanoate (C10:0), glycerol monolaurate (C12:0), and others. α-MAG supplements serve as an alternative energy source, reducing the body's reliance on other energy nutrients like proteins, thereby indirectly promoting protein synthesis. Additionally, MAGs can be directly utilized by intestinal cells, helping to maintain intestinal integrity in poultry and promoting nutrient absorption and utilization (Aar et al. 2017). Notably, MAGs exhibit strong antibacterial, anticoccidial, and antiviral properties, and when used in combination with organic acids, essential oils, or probiotics, they can exert significant synergistic effects, positively impacting animal health, production performance, and feed digestibility (Baltić et al. 2017).

Distinct from these glycerol-based esters, branched fatty acid esters of hydroxy fatty acids (FAHFAs) constitute a novel class of bioactive lipid molecules (Zhu et al. 2021). Most endogenous FAHFAs share a common chemical structure characterized by an ester bond connecting a hydroxy fatty acid backbone and a fatty acid. Based on the position of the ester bond, FAHFAs can be divided into two main superfamilies: (1) branched FAHFAs, which are involved in regulating metabolism and immune responses, and (2) linear (ω-hydroxylated) FAHFAs, primarily used as biosurfactants and skin barrier matrices (Riecan et al. 2022). FAHFAs may become potential therapeutic targets for treating various metabolic disorders, such as type II diabetes, hepatic steatosis, cardiovascular diseases, and various cancers, generating significant interest in the field of human health (Benlebna et al. 2021).

Collectively, these diverse lipids – including MCTs, LCTs, MAGs, and FAHFAs – exemplify functional lipids, defined as lipid components with specific physiological functions and health benefits. They typically exhibit physiological activities such as anti-inflammatory, antioxidant, and regulation of gut microbiota and the immune system, positively impacting health. Structured lipids, phospholipids, and fatty acids, including the critically important polyunsaturated fatty acids, also fall under this broad category. Their significant impact on intestinal health has been extensively reviewed elsewhere (Durkin et al. 2021; Lee et al. 2022; Wei and Wang 2024). Here, we will specifically focus on the impact of short- and medium-chain fatty acid glycerides on intestinal health in pigs and poultry, providing valuable references for their rational application in the livestock industry.

The importance of intestinal health in pigs and poultry

A healthy gut is crucial for the overall metabolism, physiology, disease defense, and growth performance of pigs and poultry. However, there is currently a lack of precise and unified standards for defining "gut health." Based on the research by Kogut and Arsenault, a healthy gut is defined as "the ability of an animal to perform its physiological functions normally, resisting both exogenous and endogenous stressors through the prevention or avoidance of disease" (Kogut and Arsenault 2016). Celi *et al.* emphasized the importance of effective digestion and absorption of feed, maintaining the effective structure and function of the intestinal barrier, good interaction between the host and gut microbiota, and an effective immune status in gut health (Celi et al. 2017). Pluske *et al.* proposed that gut health should be viewed as a state of homeostasis within the gastrointestinal tract. They suggested that general criteria for assessing gut health in weaned pigs encompass efficient digestion and absorption of nutrients, effective waste excretion, functional and protective intestinal barriers, stable and balanced microbial communities, functional and protective intestinal immune systems, minimal stress/neuro-pathway activation, and a disease-free state (Pluske et al. 2018). In summary, a healthy gut should enhance the host's ability to cope with and adapt to infections/stress, helping animals achieve or maintain optimal growth, production, or performance levels.

In practical pig and poultry farming, gut health issues frequently arise, particularly in neonatal and weaned piglet populations. These animals have not fully developed their gut functions due to their age and physiological state, making them more susceptible to external factors (Tang et al. 2022). For high-yield poultry breeds, the high feed intake undoubtedly places a heavy burden on their digestive systems. This burden may lead to maldigestion and inadequate absorption of nutrients, further disrupting the balance of gut microbiota, thus triggering a series of gut health issues (Ducatelle et al. 2023). In recent years, the interactions between the digestive system and other organ systems have garnered increasing attention. For example, when the intestinal barrier is compromised, potentially harmful compounds and microorganisms can leak from the gut lumen into the portal circulation, directly entering the liver, which may disrupt liver cell metabolism and even lead to liver diseases. The gut–brain axis also indicates that gut health can influence neurotransmitter release and nerve signal transmission, subsequently affecting the animal's behavior and physiological state. Scientists have found that even minor gut health issues can significantly affect overall animal health and production performance (Bindari and Gerber 2022). Therefore, the gut health of pigs and poultry is closely linked to the overall health of the animals, making it an indispensable key factor in ensuring their production performance.

Metabolism of functional lipids in the intestine

After oral intake, functional lipids that orally intake are broken down into free fatty acids and other compounds under the action of lipase. These breakdown products then mix with phospholipids, cholesterol, and bile acids to form micelles. When lipid micelles enter the brush border membrane of intestinal epithelial cells, fatty acid-binding proteins (FABPs) bind to free fatty acids and transport them into the cytoplasm. FABP1 in the intestine tends to guide fatty acids toward oxidation to provide energy for cells, while FABP2 is more inclined to direct fatty acids toward re-synthesis of TAGs with MAGs under the action of diacylglycerol acyltransferase (DGAT) in the endoplasmic reticulum (Ko et al. 2020). MCTs and short-chain TAGs bypass the MAG pathway and are directly absorbed into the portal circulation, then transported to the liver for rapid oxidation or re-routing to form very low-density lipoprotein with the help of albumin. Newly synthesized TAGs primarily take two fates: one forms chylomicrons, while the other forms cytoplasmic lipid droplets (CLDs). TAGs produced by DGAT2 mainly contribute to the formation of chylomicrons and CLDs, while TAGs produced by DGAT1 primarily form endoplasmic reticulum lipid droplets and may help increase the size of chylomicron precursors, although the growth of CLDs in intestinal epithelial cells may be limited (Hung et al. 2017). Chylomicrons and CLDs share similar structural characteristics: both contain neutral lipids such as TAGs and cholesterol esters at their core, surrounded by a complex of phospholipid monolayers, free cholesterol, and various proteins (Ko et al. 2020). Chylomicrons are synthesized in the form of chylomicron precursors, a process primarily completed with the help of microsomal triglyceride transfer protein and apolipoprotein B48 (apoB48). The synthesized chylomicron precursors are transported from the endoplasmic reticulum to the Golgi apparatus through pre-CM transport vesicles, where they are further processed into mature chylomicrons. Chylomicrons are the main carriers of lipid transport, working in conjunction with lipoproteins to transport lipids to the basolateral membrane of intestinal epithelial cells and release them into the lymphatic system, effectively delivering lipids into the systemic circulation. As neutral lipid droplets continue to accumulate, newly formed lipid droplets separate from the endoplasmic reticulum membrane in a "budding" manner, subsequently becoming mature CLDs. Lipid droplets can either re-synthesize chylomicrons or serve as temporary storage sites for lipids. When lipid content is excessive, droplets can also be reconverted into fatty acids under the action of adipose triglyceride lipase or lysosomal acid lipase. CLDs are known to play important roles within cells, including energy storage, regulation of lipid metabolism, assembly and maintenance of cell membranes, signaling regulation, and modulation of inflammatory responses. Abnormal metabolism and regulatory disturbances of chylomicrons and CLDs may lead to gut damage through mechanisms such as lipid deposition, oxidative stress, inflammatory responses, impaired intestinal barrier function, and dysregulation of hydroelectrolytic balance (Demignot et al. 2014).

Impact of functional lipids on intestinal health in pigs and poultry

Impact of functional lipids on intestinal energy metabolism

Based on the metabolic pathways described earlier, we conclude that one primary metabolic fate of dietary functional lipids is to provide energy for the intestinal cells, which is primarily generated through fatty acid oxidation (FAO) (Ko et al. 2020). Compared to glucose metabolism, FAO is essential for the self-renewal of intestinal stem cells, which in turn maintains the integrity of the intestinal barrier and supports overall gut function (Chen et al. 2020; Mihaylova et al. 2018; Schell et al. 2017). Moreover, the increase of FAO activity and expression of genes related to FAO, such as Cpt1A and HADHA, in the intestine could further promote lipid uptake and transport. This adaptive response may help reduce elevated circulating lipid levels caused by a high-fat diet (Uchida et al. 2011). The enhancement of FAO is closely related to the activation of the nuclear receptor transcription factor PPARα. In the small intestine, PPARα upregulates the expression of genes associated with lipid catabolism, such as acyl-CoA oxidase (ACO) (Azari et al. 2013; Berger and Wagner 2002). Azari *et al.* found that intestinal-specific PPARα activation could reduce the content of CLDs by promoting FAO (Azari et al. 2013). Notably, many functional lipids – particularly MCTs – potentiate PPARα activation, thereby modulating energy metabolism pathways (Chamma et al. 2017; Pike et al. 2023; Zhang et al. 2016).

Impact of functional lipids on the gut microbiota

Increasing evidence suggests that functional lipids are closely related to the regulation of gut microbiota (Fig. 1). For instance, a study found that tributyrin increased the relative abundance of several bacterial genera, such as *Oscillospira, Oscillibacter, Mucispirillum*, and *Butyrivibrio*, which positively correlated with average daily gain and/or body weight in weaned piglets. Conversely, the abundance of *Mogibacterium, Peptococcus, Atopobium*, and *Collinsella* significantly decreased, correlating negatively with average daily gain and body weight. Furthermore, the reduction of *Collinsella* may be associated with improved intestinal barrier function and decreased gut permeability (Miragoli et al. 2021) (Table 1). Feeding a mixture of tributyrin and fennel to weaned piglets increased beneficial bacteria like *Lactobacillus reuteri, Lactobacillus amylovorus*, and *Clostridium butyricum*, while reducing pathogenic bacteria *Prevotella copri* (Dang et al. 2023). However, some studies found that tributyrin did not affect the numbers of *Escherichia coli* and *Enterobacteriaceae* in piglet feces, while *Lactobacillus* and *Bifidobacterium* counts significantly decreased (Sotira et al. 2020). This discrepancy may arise because the microbial results were based on specific strains detected via polymerase chain reaction, thus not representing the entire populations of these bacteria. Moreover, it was noted that *Butyrivibrio* could only be detected in pigs with higher feed efficiency, suggesting its potential role in enhancing feed utilization (Wu et al. 2018, 2020).

In broilers, adding tributyrin can increase the counts of *Bacillus* and *Lactobacillus* in the ileum and cecum while reducing pathogenic *E. coli* (Hu et al. 2021). Additionally, Gong *et al.* observed that after adding tributyrin, the increase of *Eisenbergiella* in the cecum might negatively affect feed conversion rates (Gong et al. 2021). Yang *et al.* found that butyric acid glycerides (a mix of 30% mono-butyrin, 50% di-butyrin, and 20% tri-butyrin) supplementation effectively reduced harmful bacteria such as *Mollicutes* and *Holdemania* in the cecum while significantly enhancing the diversity and abundance of *Bifidobacterium* (Yang et al. 2018). Furthermore, serum metabolites associated with *Bifidobacterium*, such as choline, dimethylamine, and succinate, were also significantly elevated, indicating that butyric acid glycerides can influence lipid and energy metabolism by modulating gut microbial metabolites. Numerous studies have investigated the effects of MAGs on intestinal microbiota in poultry. Research has demonstrated that dietary supplementation with a mixture of monocaprin and monooctanoin can reduce the abundance of *Proteobacteria* in the cecum of laying hens by approximately 5.86%. Notably, conditional pathogens within *Proteobacteria*, such as *Escherichia* and *Shigella*, have been shown to exert significant negative impacts on intestinal health (Liu et al. 2020). When broilers were fed with a combination of monocaprin and monolaurin, their intestinal microbiota exhibited age-dependent changes. At 3 and 7 weeks of feeding, the populations of *Firmicutes, Rikenellaceae* RC9 group, *Barnesiellaceae*, and *Collinsella* were significantly reduced, while the abundance of *Bacteroides* and *Lachnospiraceae* NK4A136 group was increased. The microbial community transitioned to a stable phase between weeks 7 and 10, and these microbial changes were potentially correlated with growth performance and feed conversion ratio in chickens (Liu et al. 2023). Overall, functional lipids contribute to optimizing the composition of gut microbiota, improving intestinal health in pigs and poultry, and promoting animal growth.

Regulatory effect of functional lipids on the immune response

Functional lipids significantly regulate the immune system in animals, exerting anti-inflammatory, antimicrobial, and immune-boosting effects. Recent studies have shown that the addition of

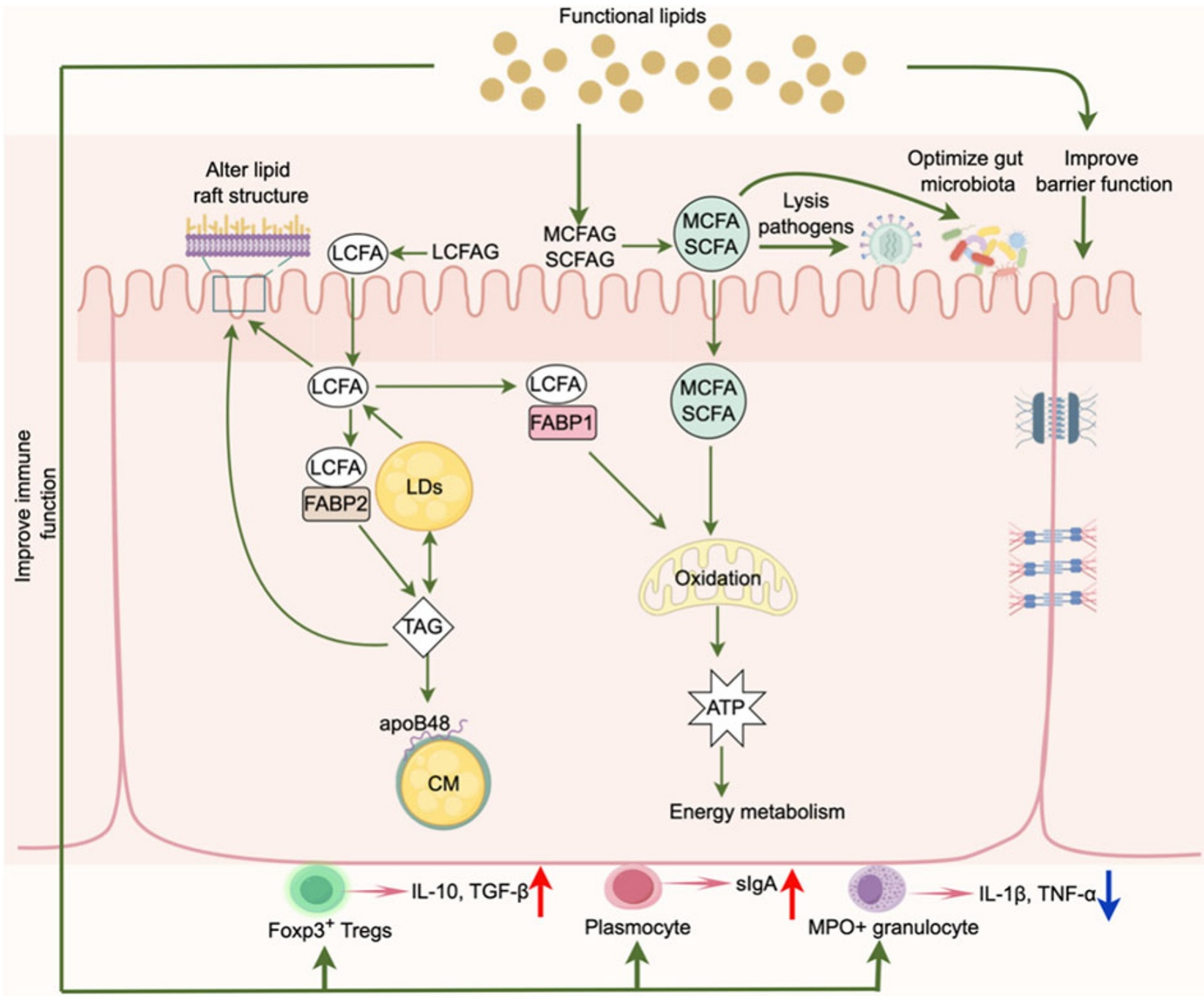

Figure 1. Mechanisms by which functional lipids improve intestinal health in pigs and poultry. Note: LCFAG, long-chain fatty acid glycerides; LCFA, long-chain fatty acids; MCFAG, medium-chain fatty acid glycerides; MCFA, medium-chain fatty acids; SCFAG, short-chain fatty acid glycerides; SCFA, short-chain fatty acids; Tregs, regulatory T cells; FABP, fatty acid-binding protein; TAG, triglycerides; LDs, lipid droplets; CM, chylomicrons; apoB48, apolipoprotein B48.

Table 1. Key findings on the use of functional lipids as feed additives

Additives	Dose	Animal age and experimental duration	Key findings	References
Tributyrin	0.2%	120 weaned piglets (28 ± 2 days), experimental period: 40 days	-Increased *Oscillospira, Oscillibacter, Mucispirillum*, and *Butyrivibrio* levels; decreased *Mogibacterium, Collinsella, Peptococcus, and Atopobium* levels	Miragoli *et al*. (2021)
Tributyrin	0.2%	120 weaned piglets (28 ± 2 days), experimental period: 40 days	-Improved ADG, reduced FCR -No significant effects on the populations of *E. coli* and *Enterobacteriaceae*; significantly reduced *Lactobacillus* spp. and *bifidobacteria* -Increased serum albumin, albumin/globulin (A/G) ratio, glucose, and HDL; decreased urea blood concentration; increased serum insulin concentration	Sotira *et al*. (2020)

(*Continued*)

Table 1. (*Continued.*)

Additives	Dose	Animal age and experimental duration	Key findings	References
Tributyrin and anise mixture	0.075% and 0.150%	150 twenty-one-day-old weaned pigs, experimental period: 42 days	-Linearly improved body weight, body weight gain, average daily feed intake, and feed efficiency -Increased *Lactobacillus reuteri, Lactobacillus amylovorus*, and *Clostridium butyricum* levels; decreased *Prevotella copri* level -Reduce fecal ammonia emission	Dang *et al*. (2023)
Trihexanoin	0.5%	20 weaned piglets (21 ± 2 days), experimental period: 20 days	-Reduced diarrhea rate; improved intestinal morphologic structure -Increased the concentrations of LDL, HDL, and total protein in plasma; decreased cholesterol concentrations and glutamyl transpeptidase activity in plasma -Decreased *Enterobacteriaceae* levels in the ileum, colon, and cecum	Wu *et al.* (2018)
Trilactic glyceride	0.5%	16 weaned piglets, experimental period: 20 days	-Decreased diarrhea rate and increased plasma D-xylose concentration -Reduced plasma LDL and cholesterol concentration, increased HDL levels, altered the expression of lipid metabolism-related genes -Increased *Bifidobacterium* genus level and decreased *Enterobacteriaceae* family level in the ileum, colon, and cecum	Wu *et al.* (2020)
Tributyrin	0.23, 0.46, 0.92, and 1.84 g/kg	540 one-day-old broiler, experimental period: 42 days	-Increased the ADG, gain/feed ratio, and European broiler index and improved the intestinal morphology -Increased *Bacillus* and *Lactobacillus* counts in ileal and cecal, decreased *Coliform* counts in cecal -Increased content of certain short-chain fatty acids	Hu *et al.* (2021)
Tributyrin	250 mg/kg	360 one-day-old broilers, experimental period: 63 days	-Increased final weight and decreased FCR -Increased creatine concentration in plasma -Increased *Bacteroidetes* phylum and *Eisenbergiella*, and decreased *Firmicutes* in cecal contents; *Eisenbergiella* was negatively correlated with FCR	Gong *et al*. (2021)
Mixture of glycerol monolaurate and glycerol monocaprylin	300 mg/kg	252 forty-week-old laying hens, experimental period: 24 weeks	-Increased the laying rate and decreased FCR -Increased the eggshell strength and thickness	Liu *et al.* (2020)

(*Continued*)

Table 1. (*Continued.*)

Additives	Dose	Animal age and experimental duration	Key findings	References
			-Increased levels of serum follicle-stimulating hormone, luteinizing hormone, estradiol, glucose, Ca, serum total cholesterol, triglycerides, and HDL-C -Increased abundance of some beneficial genera, such as *Lachnospiraceae_ NK4A136_group* and *Romboutsia*, and decreased the abundances of *Proteobacteria, Faecalibacterium*, and Alistipes in cecum	
Free tributyrin (fTB) and lipid microencapsulated tributyri (mTB)	1750 mg/kg	108 twenty-eight-day-old weaned pigs, experimental period: 21 days	-No differences in growth performance -Decreased number of goblet cells; reduced expression of occludin -fTB upregulated the expression of TNF-α and IFN-γ; mTB downregulated the expression of IFN-γ	Tugnoli *et al.* (2020)
Tributyrin and monolaurin blend	5 kg/t	Trial 1: 168 weaned pigs, experimental period: 4 weeks Trial 2: 244 weaned pigs, experimental period: 6 weeks	-No difference in growth performance compared to the high ZnO levels, reduced FCR -Thickening of intestinal mucosa -Increased number of Foxp3-positive regulatory T cells and decreased number of MPO-positive granulocytes	Papadopoulos *et al.* (2022)
Monolaurin	100 mg/kg	32 twenty-one-day-old piglets, experimental period: 11days	-Reduced diarrhea rate and improved small intestine morphology -Decreased PEDV levels -Reduced serum levels of IL-6 and IL-8	Zhang *et al.* (2022)
Monoglyceride blend containing butyric, caprylic, and capric acids	0.03% and 0.05%	210 one-day-old broiler chickens, experimental period: 42 days	-Weight increase at 21 days, no difference at 42 days -Increased intestinal goblet cell count -Dose-dependent downregulation of intestinal TNF-α -No significant change in cecal short-chain fatty acids	Sacakli *et al.* (2023)
Monolaurin	500 and 1000 mg/kg	480 one-day-old broilers, experimental period: 56 days	- Improved ADG -Volatile fatty acids increased at 28 days and decreased at 56 days -Serum levels of IgM and IgY increased	Lan *et al.* (2021)
Medium-chain glycerides	3%	528 twenty-four-day-old weaned piglets, experimental period: 14 days	-From days 3 to 7, the weight gain to feed ratio increased by 18.5%. After 14 days, the weight gain to feed ratio increased by 8.3% -Decreased the quantity of *coliform* bacteria in the contents of the colon and rectum	Yen *et al.* (2015)

free tributyrin to the diets of weaned piglets can trigger inflammatory responses in the small intestine, upregulating the expression levels of TNF-α and IFN-γ. In contrast, microencapsulated tributyrin can reduce IFN-γ expression in the distal colon (Tugnoli et al. 2020). This may be because short-chain fatty acids need to be fermented by gut microbiota in the hindgut for their production. While free tributyrin is broken down into butyrate by lipases in the small intestine, leading to abnormal accumulation and subsequently triggering an inflammatory response. Conversely, microencapsulated tributyrin avoids premature breakdown in the small intestine, allowing for slow butyrate release in the hindgut, thereby exerting its anti-inflammatory and antimicrobial activities. The combination of tributyrin and monolaurin in the diet increases the number of Foxp3-positive regulatory T cells with anti-inflammatory functions and decreases MPO-positive granulocytes, alleviating weaning-induced inflammatory responses (Papadopoulos et al. 2022). Monolaurin alone can also increase the number of eosinophils in the blood, modulating the immune system (Wang et al. 2024). A mixture of MAGs containing butyrate, caprylic acid, and capric acid can dose-dependently reduce IL-1β and TNF-α gene expression in the intestines of broilers, affecting intestinal metabolic function and integrity (Sacakli et al. 2023). In the presence of pathogen infection, glycerides exhibit significant anti-inflammatory effects. Studies have found that monolaurin can reduce IL-6 and IL-8 levels in the serum of piglets infected with porcine epidemic diarrhea virus (PEDV) (Zhang et al. 2022). Furthermore, glycerides can influence the acquired immune response. Research by Lan *et al.* shows that monolaurin can effectively increase immunoglobulin levels in the serum of broilers, which can recognize and bind to pathogens, activating innate immune effector cells to clear pathogens (Lan et al. 2021). Additionally, it has been found that increased circulating antibodies may be related to decreased pro-inflammatory cytokines at the gene or protein level (Appleton et al. 2024). In summary, functional lipids can not only regulate the innate immune response but also enhance the acquired immune response, contributing to improved animal performance and disease resistance.

Mechanisms of antibacterial and antiviral actions of functional lipids

Functional lipids, particularly MAGs, exhibit significant antibacterial and antiviral activities. Phillips *et al.* conducted an animal study in which piglets were fed a diet containing MAGs. The feed was contaminated with ice blocks containing viable PEDV to simulate natural infection. After 20 days of continuous infection, PEDV levels were detected in rectal swabs. Results indicated that 54.8% of piglets in the control group tested positive for PEDV, while all piglets in the group receiving 1.5 kg/t of the MAG mixture tested negative, demonstrating a 100% prevention of PEDV infection and transmission by the MAG mixture (Phillips et al. 2022). Monolaurin demonstrates strong inhibitory effects against various enveloped viruses, including PEDV, African swine fever virus, yellow fever virus, mumps virus, and Zika virus. Its antiviral activity is attributed to its ability to disrupt the viral envelope. However, the effectiveness of monolaurin can be influenced by the maturity state of the viruses (Ackman et al. 2020; Welch et al. 2020; Zhang et al. 2022). Similarly, MAGs can disrupt bacterial membranes, especially in Gram-positive bacteria. Mechanistically, MAGs interact with phospholipid membranes by forming micelles, compromising the membrane integrity and functionality. MAGs are more biologically active than free fatty acids due to their ability to form micelles at lower concentrations. Lipid rafts, which are specialized microdomains in cell membranes rich in cholesterol and specific lipids, provide a stable environment for viral proteins to cluster and interact with receptor proteins. Research has shown that medium-chain and long-chain TAG can remodel or disrupt lipid rafts, affecting their structure and function (Boisramé-Helms et al. 2014). Viruses like porcine reproductive and respiratory syndrome virus and PEDV utilize lipid raft-mediated endocytosis to enter cells, suggesting that functional lipids might prevent viral entry by altering raft structures (Wei et al. 2020; Yang et al. 2015). Additionally, the carbon chain length of fatty acids affects the inhibitory activity of glycerides. For instance, capric (C10) and lauric (C12) acids exhibited the highest potencies among fatty acids, while corresponding MAGs with equivalent chain lengths were typically even more potent (Ackman et al. 2020; Jackman et al. 2020; Valle-González et al. 2018). However, some studies, such as one by Namkung *et al.*, challenge this notion, showing that butyric acid exhibited the strongest inhibitory effect against *Salmonella typhimurium* and *Clostridium perfringens*, followed by monobutyrin, while tributyrin showed the weakest antibacterial activity in the absence of lipase (Namkung et al. 2011). Given that the release of butyric acid from butyrin glycerides depends on the assistance of lipase in the small intestine, Namkung *et al.* suggested that the influence of lipase activity should be carefully considered when applying butyrin glycerides for bacterial inhibition in vivo (Namkung et al. 2011).

In addition to directly damaging membrane structures, monolaurin can lower intestinal pH by increasing the abundance of acid-producing bacteria like *Lachnospiraceae* and *Christensenellaceae*, thus inhibiting the growth of harmful microorganisms. The supplementation of a mixture of tributyrin and monolaurin or MAG lactate in diets can thicken the mucosa of the jejunum and ileum in piglets, promoting intestinal mucosal growth and thereby enhancing the intestinal barrier function to prevent pathogen invasion (Hou et al. 2014; Li et al. 2023; Papadopoulos et al. 2022). More importantly, pathogens rarely develop resistance to these glycerides, making functional lipids a promising alternative to antibiotics with broad application prospects.

Research progress on functional lipid products: applications and industrialization of short- and medium-chain fatty acid glycerides

Given the numerous advantages of functional lipids, particularly short- and medium-chain fatty acid glycerides, they are increasingly recognized as key factors in promoting animal growth and improving production efficiency. Researchers have conducted extensive studies on their practical applications. For instance, Yen *et al.* found that adding 3% MCT to the diet of weaned piglets improved their weight gain-to-feed ratio by 18.5% from days 3 to 7, and by 8.3% after 14 days (Yen et al. 2015). Papadopoulos *et al.* conducted trials in two pig farms with the same genetic background but different management practices (weaning time, antibiotic use). They found that adding mixtures of tributyrin and monolaurin significantly enhanced piglet growth performance without significant differences compared to high zinc oxide groups while notably reducing feed conversion rates (Papadopoulos et al. 2022). Another study by Sotira *et al.* showed that feeding 0.2% tributyrin to 120 weaned piglets for 40 days significantly increased average daily weight gain and reduced feed conversion rates (Sotira et al. 2020). Dang *et al.* discovered that a mixture of tributyrin and fennel could dose-dependently improve weight gain, feed intake, and feed conversion ratio in weaned piglets, positively impacting the digestibility of dry matter, crude protein, and energy, and linearly reducing ammonia emissions in feces (Dang et al. 2023). These studies indicate that adding short- and medium-chain fatty acid glycerides positively affects pig growth. However, the growth-promoting effects of tributyrin in broilers remain controversial, with varying results across different studies (Gong et al. 2021; Li et al. 2015). Nevertheless, some researchers suggest that adding butyrate products to low-protein and/or metabolizable energy diets can improve weight gain and feed conversion in broilers (Hu et al. 2021). In terms of layer hens, Liu *et al.* reported that feeding 300 mg/kg of medium-chain alpha-MAGs (containing monolaurin and mono-caprylic acid) to 40-week-old hens maintained egg production rates above 90% at 56 weeks, compared to a decline to 84.42% in the control group. Additionally, eggshell hardness and thickness significantly increased (Liu et al. 2020). In summary, functional lipid products significantly benefit animal health and growth, holding substantial application value in formulating cost-saving and high-efficiency feed for livestock and poultry.

Conclusion

Functional lipids play a crucial role in gut health for swine and poultry. They not only provide energy and nutrients to support the normal functioning of intestinal mucosal cells but also exhibit antimicrobial activity, reduce intestinal inflammatory responses, and maintain gut immune balance. Additionally, functional lipids can regulate gut microbiota composition and balance, stabilizing gut microecology. Therefore, the rational use of functional lipids can effectively improve gut health in swine and poultry, promoting healthy growth.

Given the potential advantages of functional lipids, they will significantly advance the livestock industry through in-depth research and development, along with their scientific and reasonable application in livestock feed and production. Future explorations should focus on:

(1) Utilizing advanced omics technologies to systematically analyze and identify novel functional lipid compounds, and investigating the impacts of FAHFAs and unsaturated MAGs on gut health in swine and poultry.
(2) Optimizing application strategies, including optimal dosages, timing, and duration; improving the formulation and production processes of functional lipids to enhance stability, solubility, and bioavailability (e.g., using nanoemulsion technologies and carrier delivery systems); exploring synergistic effects of various functional lipids or functional lipids with other nutrients; and emphasizing fatty acid balance to maximize benefits for gut health.
(3) Conducting long-term observational studies to comprehensively evaluate the long-term effects and potential risks of functional lipids on gut health in swine and poultry, ensuring that their production and use align with sustainable development requirements.

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Conflicts of interest. The authors declare that they have no competing interests.

References

Aar PRJVD, Molist F and Klis JDVD (2017) The central role of intestinal health on the effect of feed additives on feed intake in swine and poultry. *Animal Feed Science and Technology* **233**, 64–75.

Ackman JA, Hakobyan A, Zakaryan H *et al*. (2020) Inhibition of African swine fever virus in liquid and feed by medium-chain fatty acids and glycerol monolaurate. *Journal of Animal Science and Biotechnology* **11**(1), 114.

Appleton SR, Ballou A and Watkins KL (2024) Use of monoglycerides and diglycerides to mitigate poultry production losses: A review. *Veterinary Sciences* **11**(3), 101.

Azari E, Leitner C, Jaggi T *et al*. (2013) Possible role of intestinal fatty acid oxidation in the eating-inhibitory effect of the PPAR-α agonist Wy-14643 in high-fat diet fed rats. *Public Library of Science ONE* **8**(9), e74869.

Baltić B, Starčević M, Đorđević J *et al*. (2017) Importance of medium chain fatty acids in animal nutrition. IOP Conference Series: Earth and Environmental Science **85**, 012048.

Benlebna M, Balas L, Gailliet S *et al*. (2021) Potential physio-pathological effects of branched fatty acid esters of hydroxy fatty acids. *Biochimie* **182**, 13–22.

Berger J and Wagner JA (2002) Physiological and therapeutic roles of peroxisome proliferator-activated receptors. *Diabetes Technology & Therapeutics* **4**(2), 163–174.

Bindari YR and Gerber PF (2022) Centennial review: Factors affecting the chicken gastrointestinal microbial composition and their association with gut health and productive performance. *Journal of Poultry Science* **101**(1), 101612.

Boisramé-Helms J, Said A, Burban M *et al*. (2014) Medium-chain triglyceride supplementation exacerbates peritonitis-induced septic shock in rats: Role on cell membrane remodeling. *Shock* **42**(6), 548–553.

Celi P, Cowieson AJ, Fru-Nij F *et al.* (2017) Gastrointestinal functionality in animal nutrition and health: New opportunities for sustainable animal production. *Animal Feed Science and Technology* **234**, 88–100.

Chamma CM, Bargut TC, Mandarim-de-lacerda CA *et al.* (2017) A rich medium-chain triacylglycerol diet benefits adiposity but has adverse effects on the markers of hepatic lipogenesis and beta-oxidation. *Food & Function* **8**(2), 778–787.

Chen L, Vasoya RP, Toke NH *et al.* (2020) HNF4 regulates fatty acid oxidation and is required for renewal of intestinal stem cells in mice. *Gastroenterology* **158**(4), 985–999.e9.

Dang X, Lee H, Lee SJ *et al.* (2023) Tributyrin and anise mixture supplementation improves growth performance, nutrient digestibility, jejunal villus height, and fecal microbiota in weaned pigs. *Frontiers in Veterinary Science* **10**, 1107149.

Demignot S, Beilstein F and Morel E (2014) Triglyceride-rich lipoproteins and cytosolic lipid droplets in enterocytes: Key players in intestinal physiology and metabolic disorders. *Biochimie* **96**, 48–55.

Dima C, Assadpour E, Dima S *et al.* (2021) Nutraceutical nanodelivery; an insight into the bioaccessibility/bioavailability of different bioactive compounds loaded within nanocarriers. *Critical Reviews in Food Science and Nutrition* **61**(18), 3031–3065.

Ducatelle R, Goossens E, Eeckhaut V *et al.* (2023) Poultry gut health and beyond. *Animal Nutrition* **13**, 240–248.

Durkin LA, Childs CE and Calder PC (2021) Omega-3 polyunsaturated fatty acids and the intestinal epithelium-A Review. *Foods* **10**(1), 199.

Florance I and Ramasubbu S (2022) Current understanding on the role of lipids in macrophages and associated diseases. *International Journal of Molecular Sciences* **24**(1), 589.

Gong L, Xiao G, Zheng L *et al.* (2021) Effects of dietary tributyrin on growth performance, biochemical indices, and intestinal microbiota of yellow-feathered broilers. *Animals (Basel)* **11**(12), 3425.

Hou Y, Wang L, Yi D *et al.* (2014) Dietary supplementation with tributyrin alleviates intestinal injury in piglets challenged with intrarectal administration of acetic acid. *British Journal of Nutrition* **111**(10), 1748–1758.

Hu Q, Yin F, Li B *et al.* (2021) Dietary tributyrin administration improves intestinal morphology and selected bacterial and short-chain fatty acid profiles in broilers under an isocaloric feeding regime. *Frontiers in Microbiology* **12**, 715712.

Hung YH, Carreiro AL and Buhman KK (2017) Dgat1 and Dgat2 regulate enterocyte triacylglycerol distribution and alter proteins associated with cytoplasmic lipid droplets in response to dietary fat. *Biochimica Et Biophysica Acta-Molecular and Cell Biology of Lipids* **1862**(6), 600–614.

Jackman JA, Boyd RD and Elrod CC (2020) Medium-chain fatty acids and monoglycerides as feed additives for pig production: Towards gut health improvement and feed pathogen mitigation. *Journal of Animal Science and Biotechnology* **11**, 44.

Ko CW, Qu J, Black DD *et al.* (2020) Regulation of intestinal lipid metabolism: Current concepts and relevance to disease. *Nature Reviews Gastroenterology and Hepatology* **17**(3), 169–183.

Kogut MH and Arsenault RJ (2016) Editorial: Gut health: The new paradigm in food animal production. *Frontiers in Veterinary Science* **3**, 71.

Lan J, Chen G, Cao G *et al.* (2021) Effects of α-glyceryl monolaurate on growth, immune function, volatile fatty acids, and gut microbiota in broiler chickens. *Poultry Science* **100**(3), 100875.

Lee YY, Tang TK, Chan ES *et al.* (2022) Medium chain triglyceride and medium- and long chain triglyceride: Metabolism, production, health impacts and its applications - a review. *Critical Reviews in Food Science and Nutrition* **62**(15), 4169–4185.

Li H, Zhang Y, Xie J *et al.* (2023) Dietary supplementation with mono-lactate glyceride enhances intestinal function of weaned piglets. *Animals (Basel)* **13**(8), 1303.

Li J, Hou Y, Yi D *et al.* (2015) Effects of tributyrin on intestinal energy status, antioxidative capacity and immune response to lipopolysaccharide challenge in broilers. *Asian-Australasian Journal of Animal Sciences* **28**(12), 1784–1793.

Liu T, Ruan S, Mo Q *et al.* (2023) Evaluation of dynamic effects of dietary medium-chain monoglycerides on performance, intestinal development and gut microbiota of broilers in large-scale production. *Animal Nutrition* **14**, 269–280.

Liu T, Tang J and Feng F (2020) Medium-chain α-monoglycerides improves productive performance and egg quality in aged hens associated with gut microbiota modulation. *Journal of Poultry Science* **99**(12), 7122–7132.

Mihaylova MM, Cheng CW, Cao AQ *et al.* (2018) Fasting activates fatty acid oxidation to enhance intestinal stem cell function during homeostasis and aging. *Cell Stem Cell.* **22**(5), 769–778.e4.

Miragoli F, Patrone V, Prandini A *et al.* (2021) Implications of tributyrin on gut microbiota shifts related to performances of weaning piglets. *Microorganisms* **9**(3), 584.

Namkung H, Yu H, Gong J *et al.* (2011) Antimicrobial activity of butyrate glycerides toward *Salmonella typhimurium* and *Clostridium perfringens*. *Journal of Poultry Science* **90**(10), 2217–2222.

Papadopoulos GA, Poutahidis T, Chalvatzi S *et al.* (2022) Effects of a tributyrin and monolaurin blend compared to high ZnO levels on growth performance, faecal microbial counts, intestinal histomorphometry and immunohistochemistry in weaned piglets: A field study in two pig herds. *Research in Veterinary Science* **144**, 54–65.

Phillips FC, Rubach JK, Poss MJ *et al.* (2022) Monoglyceride reduces viability of porcine epidemic diarrhoea virus in feed and prevents disease transmission to post-weaned piglets. *Transboundary and Emerging Diseases* **69**(1), 121–127.

Pike B, Zhao J, Hicks JA *et al.* (2023) Intestinal carnitine status and fatty acid oxidation in response to clofibrate and medium-chain triglyceride supplementation in newborn pigs. *International Journal of Molecular Sciences* **24**(7), 6066.

Pluske JR, Turpin DL and Kim J (2018) Gastrointestinal tract (gut) health in the young pig. *Animal Nutrition* **4**, 187–196.

Riecan M, Paluchova V, Lopes M *et al.* (2022) Branched and linear fatty acid esters of hydroxy fatty acids (FAHFA) relevant to human health. *Pharmacology and Therapeutics* **231**, 107972.

Sacakli P, Ö.ö Ç, Ceylan A *et al.* (2023) Performance and gut health status of broilers fed diets supplemented with two graded levels of a monoglyceride blend. *Journal of Poultry Science* **102**(2), 102359.

Schell JC, Wisidagama DR, Bensard C *et al.* (2017) Control of intestinal stem cell function and proliferation by mitochondrial pyruvate metabolism. *Nature Cell Biology* **19**(9), 1027–1036.

Sotira S, Dell'Anno M, Caprarulo V *et al.* (2020) Effects of tributyrin supplementation on growth performance, insulin, blood metabolites and gut microbiota in weaned piglets. *Animals (Basel)* **10**(4), 726.

Tang X, Xiong K, Fang R *et al.* (2022) Weaning stress and intestinal health of piglets: A review. *Frontiers in Immunology* **13**, 1042778.

Tugnoli B, Piva A, Sarli G *et al.* (2020) Tributyrin differentially regulates inflammatory markers and modulates goblet cells number along the intestinal tract segments of weaning pigs. *Livestock Science* **234**, 103996.

Uchida A, Slipchenko MN, Cheng JX *et al.* (2011) Fenofibrate, a peroxisome proliferator-activated receptor α agonist, alters triglyceride metabolism in enterocytes of mice. *Biochimica Et Biophysica Acta-Biomembranes* **1811**(3), 170–176.

Valle-González ER, Jackman JA and Yoon BK (2018) Characterizing how acidic pH conditions affect the membrane-disruptive activities of lauric acid and glycerol monolaurate. *Langmuir* **34**(45), 13745–13753.

Wang C, Zhang Q, Ji C *et al.* (2024) Effects of monolaurin on intestinal barrier, blood biochemical profile, immunity and antioxidant function in porcine epidemic diarrhoea virus-infected piglets. *British Journal of Nutrition* **131**(2), 185–192.

Wei W and Wang X (2024) Medium- and long-chain triacylglycerol: Preparation, health benefits, and food utilization. *Annual Reviews of Food Science and Technology* **15**(1), 381–408.

Wei X, She G, Wu T *et al.* (2020) PEDV enters cells through clathrin-, caveolae-, and lipid raft-mediated endocytosis and traffics via the endo-/lysosome pathway. *Veterinary Research* **51**(1), 10.

Welch JL, Xiang J and Okeoma CM (2020) An analogue to a factor secreted by lactobacillus, is virucidal against enveloped viruses, including HIV-1. *mBio* **11**(3), e00686–20.

Wu T, Li K, Lyu Y *et al.* (2020) Trilactic glyceride regulates lipid metabolism and improves gut function in piglets. *Frontiers in Bioscience-Landmark* **25**(7), 1324–1336.

Wu T, Li K, Yi D *et al.* (2018) Dietary supplementation with trihexanoin enhances intestinal function of weaned piglets. *Journal of Molecular Sciences* **19**(10), 3277.

Yang Q, Zhang Q, Tang J *et al.* (2015) Lipid rafts both in cellular membrane and viral envelope are critical for PRRSV efficient infection. *Virology* **484**, 170–180.

Yang X, Yin F, Yang Y *et al.* (2018) Dietary butyrate glycerides modulate intestinal microbiota composition and serum metabolites in broilers. *Scientific Reports* **8**(1), 4940.

Yen HC, Lai WK, Lin CS *et al.* (2015) Medium-chain triglyceride as an alternative of in-feed colistin sulfate to improve growth performance and intestinal microbial environment in newly weaned pigs. *Animal Science Journal* **86**(1), 99–104.

Zhang H, Li Y, Hou X *et al.* (2016) Medium-chain TAG improve energy metabolism and mitochondrial biogenesis in the liver of intra-uterine growth-retarded and normal-birth-weight weanling piglets. *The British Journal of Nutrition* **115**(9), 1521–1530.

Zhang Q, Yi D, Ji C *et al.* (2022) Monolaurin confers a protective effect against porcine epidemic diarrhea virus infection in piglets by regulating the interferon pathway. *Frontiers in Immunology* **12**, 797476.

Zhu Q, Hao J, Yan J *et al.* (2021) FAHFAs: Biological functions, analysis and synthesis. *Progress in Chemistry* **33**(7), 1115–1125.