Interaction between Rumen Microorganisms and Dietary Fatty Acids (Post-print)

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Abstract

Fatty acids are important nutrients for ruminants. On one hand, fatty acids exert inhibitory effects on the growth of rumen microorganisms in ruminants, with unsaturated fatty acids showing more pronounced inhibition; on the other hand, rumen microbial communities can hydrogenate unsaturated fatty acids into saturated fatty acids through biohydrogenation. This paper reviews the interactions between dietary fatty acids and rumen microorganisms, covering research methods including in vitro culture methods and animal experimental studies, combined with molecular biology techniques, to provide new insights for regulating rumen microbial community or structure through dietary fat.

Full Text

Interaction between Ruminal Microbes and Dietary Fatty Acids

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Abstract: Fatty acids are crucial nutrients for ruminants. On one hand, fatty acids inhibit the growth of ruminal microorganisms, with unsaturated fatty acids exhibiting particularly pronounced inhibitory effects. On the other hand, ruminal microbial communities can hydrogenate unsaturated fatty acids into saturated fatty acids through biohydrogenation. This review synthesizes current research on the interactions between dietary fatty acids and ruminal microbes, covering methodologies including in vitro culture techniques, animal feeding studies, and molecular biological approaches, thereby providing new perspectives for manipulating ruminal microbial communities through dietary fat modulation.

Keywords: ruminal microbes; bacteria; protozoa; biohydrogenation; fatty acid

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Fat typically constitutes no more than 5% of the dry matter in ruminant diets, primarily composed of triglycerides, galactolipids, and phospholipids. Forages and most concentrate feeds provide fatty acids mainly as linoleic acid and -linolenic acid, while oilseeds such as flaxseed, sunflower seed, and rapeseed can supply oleic acid and other unsaturated fatty acids. Fat primarily serves as an energy source but also modulates the fatty acid composition of milk and meat. However, fat supplementation may affect feed intake and milk fat content. Recent research indicates that dietary fat can regulate ruminal microbial communities and reduce methane emissions. It is generally accepted that fatty acids inhibit ruminal microbial growth, while ruminal microbes hydrogenate fatty acids through a multi-step process influenced by fatty acid type and ruminal environment.

1.1 Effects on Rumen Bacteria

Oil supplementation broadly inhibits the growth of ruminal fiber-degrading and starch-digesting bacteria in vitro. Studies have shown that palmitic and stearic acids only reduce populations of certain strains of *Prevotella ruminicola* and *Butyrivibrio fibrisolvens*, whereas oleic acid exhibits stronger inhibition than these two fatty acids, suppressing most fiber-degrading bacteria while promoting the growth of *Selenomonas ruminantium* and *Prevotella ruminicola*. These findings align with Henderson's research, which demonstrated that propionate-producing bacteria are unaffected by oleic acid, whereas acetate- and butyrate-producing bacteria such as *Ruminococcus* and *Butyrivibrio fibrisolvens* are inhibited by oleic and saturated fatty acids. Low concentrations of linoleic or conjugated linoleic acid inhibit the growth of *Butyrivibrio fibrisolvens* A38, and 5 mg/L of linoleic acid also suppresses other *Butyrivibrio* species. Furthermore, long-chain polyunsaturated fatty acids like eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA) exhibit significantly stronger inhibition of *Butyrivibrio fibrisolvens* than linoleic acid, possibly due to extended bacterial adaptation periods. Similarly, -linolenic acid prolongs the adaptation period of *Propionibacterium acnes*. Conversely, genera such as *Prevotella*, *Megasphaera*, and *Selenomonas* are largely unaffected by linoleic and -linolenic acids.

Unlike in vitro studies that directly examine free fatty acids, in vivo trials investigate the effects of oil supplementation on ruminal microbes using techniques such as quantitative PCR and 16S rDNA sequencing. Most in vivo trials show weaker inhibitory effects than in vitro studies, likely because in vivo experiments cannot observe the impact of fatty acids on microbial adaptation phases. Fat supplementation inhibits the growth of *Fibrobacter* and *Ruminococcus*, but results for *Butyrivibrio* and *Prevotella* are inconsistent, possibly because these genera contain more species with diverse metabolic pathways and varying sen-

sitivities to linoleic acid. Additionally, dietary concentrate levels influence fat supplementation effects, with inconsistent results observed for *Acetitomaculum*, *Lachnospira*, and *Prevotella* across different concentrate levels.

1.2 Effects on Protozoa, Methanogens, and Fungi

Research indicates that flaxseed oil significantly reduces total ruminal protozoal abundance, with more pronounced inhibition under high-concentrate diets, primarily suppressing *Dasytricha*, *Entodinium*, and *Epidinium*. However, other studies report no effect of flaxseed oil on total protozoal abundance. Regarding specific fatty acids, lauric acid more effectively reduces protozoal numbers than myristic or stearic acids. Generally, higher fatty acid unsaturation correlates with stronger protozoal inhibition, though effects also depend on animal species and diet type, potentially explaining discrepancies across studies. Early research on methanogens showed that oleic and saturated fatty acids reduce *Methanobrevibacter ruminantium* abundance, the most predominant methanogen in the rumen. Recent studies demonstrate that fatty acids with 8–14 carbons (from linseed and coconut oil) and long-chain polyunsaturated fatty acids with 20–22 carbons (from fish oil) have no direct effect on methanogen abundance or community structure. Fewer studies have examined fungal effects, though *Neocallimastix frontalis* growth is inhibited by linoleic acid in vitro, and Boots et al. confirmed that linoleic acid suppresses *Neocallimastix* growth.

1.3 Mechanisms of Action on Rumen Microbes

Three mechanisms explain fatty acid effects on bacteria: (1) Lipids coating dietary particles impair microbial attachment, reducing fiber degradation and fibrolytic bacterial growth. Supplemental fiber can partially restore fiber digestibility and bacterial populations, though some studies show increased bacterial attachment to solid digesta with fat addition. (2) Fat forms salts with cations, limiting bacterial access to essential cations and affecting growth. Calcium supplementation can prevent reductions in fiber digestibility and bacterial abundance. However, this theory cannot fully explain all negative effects, as different fatty acids vary in salt stability—saturated fatty acid salts are more stable than unsaturated ones, so calcium addition may further inhibit bacterial growth by providing more calcium to saturated fatty acids. (3) Direct toxicity of fatty acids, potentially by adsorbing to bacterial cell walls and blocking nutrient uptake. While linoleic acid compromises cell integrity, sensitivity varies among genera: *Butyrivibrio fibrisolvens* is less sensitive than *Butyrivibrio hungatei* and *Butyrivibrio proteoclasticus*. This suggests differences in membrane fluidity and specific metabolic pathway effects. *B. fibrisolvens* produces butyrate via butyryl-CoA transferase, whereas *B. hungatei* and *B. proteoclasticus* use butyrate kinase, indicating unsaturated fatty acids may inhibit butyrate-producing bacteria by affecting butyrate synthesis pathways. Additionally, polyunsaturated fatty acids affect acyl-CoA and ATP, causing metabolic blockage. The mechanism of protozoal inhibition remains unclear but may involve incorpora-

tion of fatty acids or hydrogenation products into cell membranes, hindering nutrient metabolism, or altered chemotaxis and substrate acquisition.

2.1 Rumen Microbes and Fatty Acid Degradation

Biohydrogenation begins with microbial lipolysis of acylglycerols, releasing free fatty acids and glycerol. Free fatty acids remain adsorbed to dietary particles or are absorbed by bacteria attached to solid digesta. This step lipolyzes most unsaturated fatty acids. The three major unsaturated fatty acids follow distinct hydrogenation pathways. The first step involves isomerase conversion of one cis double bond to trans, forming different conjugated linoleic acid (CLA) isomers, with trans-11 CLA being the predominant isomer. This also includes conjugated linolenic acid (CLnA) isomers with double bonds at carbons 7–15, CLA isomers at carbons 7–14, and trans fatty acids at carbons 7–11, each formed through specific pathways. This reaction typically metabolizes over 70% of oleic acid, 80% of linoleic acid, and 90% of -linolenic acid. The second step is reduction, first of cis double bonds then trans double bonds. Since trans double bond reduction is slower, trans fatty acids accumulate in the rumen or flow to the small intestine at higher concentrations than CLA.

Anaerovibrio lipolyticus is the primary triglyceride-degrading bacterium, comprising approximately 0.05% of ruminal abundance based on 16S rRNA sequencing, and possesses three lipase-encoding genes. These enzymes show strong activity against lauric and myristic acids, though dietary fatty acids mainly consist of palmitic and stearic acids. Some *Butyrivibrio fibrisolvens* strains can hydrolyze lipid esters and galactolipids, while other *Butyrivibrio* species degrade triglycerides. Additionally, *Clostridium*, *Propionibacterium*, *Staphylococcus*, and *Selenomonas* exhibit lipolytic activity. Unni et al. purified a lipase from *Pseudomonas aeruginosa*, and antibodies against purified *Pseudomonas* lipases also inhibit lipolytic activity in *A. lipolyticus*, *B. fibrisolvens*, *Propionibacterium avidum*, and *P. acnes*, suggesting similar genetic characteristics among ruminal bacterial lipases. Liu et al. established a dairy cow ruminal metagenomic library, identifying two fatty acid-binding proteins with affinities for 16- and 18-carbon fatty acids. Liu et al. and Privé et al. also isolated 14 novel lipases from bovine ruminal metagenomes, primarily acting on short- and medium-chain fatty acid esters, though the bacterial sources of these lipases remain unidentified. Protozoal lipolysis is poorly understood, as protozoa engulf lipolytic microbes, complicating assessment of their intrinsic lipolytic activity.

2.2.1 In Vitro Trials

Butyrivibrio plays a crucial role in biohydrogenation, with its 16S rRNA gene abundance averaging 3.4% of the ruminal community, including 0.25% *B. fibrisolvens*, which colonizes the rumen within two days after birth. *B. fibrisolvens* has an optimal pH of 7.0–7.2, with activity inhibited at low pH. This species reduces linoleic acid to oleic acid rather than stearic acid, while other *Butyrivibrio* species can produce stearic acid from linoleic acid. The cis-9, trans-11

CLA reductase of *B. fibrisolvens* requires iron, tocopherol hydroquinone, and NADH for catalytic activity. This enzyme recognizes conjugated double bonds, and 18-carbon unsaturated fatty acids enhance its transcriptional expression. Besides reducing cis-9, trans-11 CLA, this bacterium can reduce trans-10, cis-12 CLA and cis-9, trans-11, cis-15 CLnA, but cannot reduce trans-11, cis-15 linoleic acid. *B. fibrisolvens* cannot utilize polyunsaturated fatty acids EPA and DHA, whereas *B. proteoclasticus* can. Paillard et al. and Hussain et al. identified metabolic differences among dozens of *Butyrivibrio* isolates in linoleic acid metabolism, with most converting linoleic acid to vaccenic acid, though -linolenic acid metabolism pathways vary among strains, with *B. fibrisolvens* MDT-5, A38, and MDT-10 producing trans-11, cis-13 CLA, trans-11, cis-15 linoleic acid, or vaccenic acid.

Beyond *B. fibrisolvens*, other bacteria isolated from the rumen or digestive tract can isomerize linoleic acid to cis-9, trans-11 CLA, primarily belonging to *Clostridium*, *Pseudobutyrivibrio*, *Lactobacillus*, *Propionibacterium*, *Bifidobacterium*, *Eubacterium*, *Roseburia*, *Enterococcus*, and *Pediococcus*. *Lactobacillus* produces CLA through a hydration-dehydration process with hydroxy fatty acid intermediates. *Rumincoccus albus* F2/6 converts linoleic and -linolenic acids to oleic acid, though its ruminal activity remains unknown. Unlike *B. fibrisolvens* which produces trans-11 double bonds, *R. albus* F2/6 primarily generates trans-10 oleic acid. *Megasphaera elsdennii* YJ-4, isolated from dairy cows fed high-starch diets, produces trans-10, cis-12 CLA from linoleic acid, as does strain T81, though Maia et al. found purified *M. elsdennii* T81 cannot produce trans-10, cis-12 CLA, and its ruminal abundance is often below detection limits. *Propionibacterium acnes* isolated from sheep rumen can produce trans-10, cis-12 CLA but cannot further reduce CLA, and can isomerize -linolenic acid to various linolenic acids without further reduction to linoleic or oleic acids. The linoleic acid isomerase of purified *P. acnes* ATCC6919 requires flavin adenine dinucleotide (FAD) as a cofactor and is insensitive to excess substrate.

2.2.2 In Vivo Trials

In addition to in vitro studies, inoculating goats fed high-linoleic acid diets with *B. fibrisolvens* increased ruminal linolenic acid and total CLA concentrations, confirming its involvement in biohydrogenation. Long-chain polyunsaturated fatty acids from fish oil or algae reduce linolenic acid to stearic acid. Since *B. proteoclasticus* is the most studied stearic acid-producing bacterium, these supplements could affect its abundance. Although Abughazaleh et al. observed reduced *B. proteoclasticus* abundance with fish oil in continuous culture, fish oil supplementation in steers and lactating cows did not affect its abundance, suggesting this species plays only a minor role in stearic acid production. Similarly, algal inhibition of biohydrogenation is unrelated to any *Butyrivibrio* abundance changes. High-throughput sequencing studies also found no positive correlation between *B. proteoclasticus* or *Butyrivibrio* abundance and biohydrogenation, but identified correlations between biohydrogenation products and various bac-

teria including *Clostridiales*, *Ruminococcaceae*, *Veillonellaceae*, *Fibrobacter*, and *Acetobacter*. However, these studies remain inconclusive because: (1) biohydrogenation is a detoxification rather than nutritional process for bacteria, so biohydrogenating bacterial abundance may correlate more strongly with energy substrate concentration than with harmful polyunsaturated fatty acid levels; (2) sequencing methods have limitations, as most studies cannot fully identify all biohydrogenating bacteria or only measure DNA concentration without reflecting dietary effects at the RNA level; (3) active bacterial enzyme synthesis does not necessarily correlate with biohydrogenation efficiency, and factors like ruminal pH may also affect enzyme activity. Protozoal hydrogenation remains unclear—protozoa can engulf bacteria that continue hydrogenating within protozoal cells, yet linoleic acid is not metabolized in protozoa-only systems, and defaunation does not affect ruminal linoleic acid metabolism. Ruminal fungal contribution to linoleic acid biohydrogenation is also limited.

2.3 Additive Regulation of Biohydrogenation

Previous studies commonly regulated biohydrogenation by altering fat sources, but this approach offered limited and coarse control. Recent research focuses on direct manipulation of ruminal microbial communities based on the principle that most dietary fats are acylglycerols requiring lipolysis before biohydrogenation. Thus, slowing lipolysis can effectively inhibit biohydrogenation. Three main strategies exist: (1) Lipase inhibitors—In vitro studies show that the esterase inhibitor pyridostigmine bromide effectively inhibits lipase activity and prevents linoleic acid loss, while lipase antibodies inhibit lipolytic bacteria such as *A. lipolyticus* and *B. fibrisolvens*. (2) Isolating strains with specific enzyme activities—Fukuda et al. isolated *B. fibrisolvens* MDT-5 with high linoleic acid isomerase activity but minimal CLA reductase activity, proposing its use as a probiotic to control biohydrogenation products in animal products. Apás et al. found that supplementing certain *Lactobacillus*, *Bifidobacterium*, and *Enterococcus* species increased cis-9, trans-11 CLA content in goat milk. (3) Plant extracts—In vitro addition of essential oils decreases or increases *B. fibrisolvens* abundance, explaining ruminal biohydrogenation product profiles. Tannins reduce *B. proteoclasticus* while increasing *B. fibrisolvens* abundance, consistent with vaccenic acid accumulation observed by Vasta et al. Conversely, saponins strongly inhibit *B. fibrisolvens* growth but do not affect ruminal biohydrogenation.

3 Summary

The biochemical processes and bacterial species involved in biohydrogenation are extremely complex, with fiber-degrading bacteria—particularly *Butyrivibrio* —playing important roles. Dietary fat supplementation may modulate ruminal microbial community composition and function, thereby affecting ruminant performance. However, current research remains heavily focused on in vitro trials, and the interactive effects between ruminal microbes and fatty acids are not

fully understood. Future studies should emphasize in vivo research using refined omics-based approaches to identify specific regulatory microbes, elucidate relevant enzymatic mechanisms, and characterize microbe-host interactions to enable better ruminal microbial manipulation through dietary fat.

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Note: Figure translations are in progress. See original paper for figures.