

反刍家畜胃肠道甲烷排放与减排策略

张秀敏, 王荣, 马志远, 王敏, 谭支良

引用本文:

张秀敏, 王荣, 马志远, 等. 反刍家畜胃肠道甲烷排放与减排策略[J]. 农业环境科学学报, 2020, 39(4): 732-742.

在线阅读 View online: <https://doi.org/10.11654/jaes.2020-0105>

您可能感兴趣的其他文章

Articles you may be interested in

pH调控对瘤胃液接种稻秸厌氧消化中水解菌及产甲烷菌的影响

邓玉营, 阮文权, 郁莉, 黄一波

农业环境科学学报. 2018, 37(4): 813-819 <https://doi.org/10.11654/jaes.2017-1599>

不同灌溉模式和施氮量条件下稻田甲烷排放及其与有机碳组分关系

王楷, 李伏生, 方泽涛, 董艳芳, 刘靖雯, 黄忠华, 罗维钢

农业环境科学学报. 2017, 36(5): 1012-1020 <https://doi.org/10.11654/jaes.2016-1581>

水分和秸秆管理减排稻田温室气体研究与展望

周胜, 张鲜鲜, 王从, 孙会峰, 张继宁

农业环境科学学报. 2020, 39(4): 852-862 <https://doi.org/10.11654/jaes.2020-0060>

我国农田土壤温室气体减排和有机碳固定的研究进展及展望

夏龙龙, 颜晓元, 蔡祖聪

农业环境科学学报. 2020, 39(4): 834-841 <https://doi.org/10.11654/jaes.2020-0108>

水旱轮作系统中土壤CH₄和N₂O排放研究进展

熊丽萍, 吴家梅, 纪雄辉, 彭华, 李尝君

农业环境科学学报. 2020, 39(4): 863-871 <https://doi.org/10.11654/jaes.2020-0101>



关注微信公众号, 获得更多资讯信息

张秀敏, 王 荣, 马志远, 等. 反刍家畜胃肠道甲烷排放与减排策略[J]. 农业环境科学学报, 2020, 39(4): 732–742.

ZHANG Xiu-min, WANG Rong, MA Zhi-yuan, et al. Enteric methane emissions and mitigation strategies in ruminants[J]. *Journal of Agro-Environment Science*, 2020, 39(4): 732–742.



开放科学 OSID

反刍家畜胃肠道甲烷排放与减排策略

张秀敏, 王 荣, 马志远, 王 敏*, 谭支良

(中国科学院亚热带农业生态研究所, 亚热带农业生态过程重点实验室, 长沙 410125)

摘 要:反刍家畜胃肠道甲烷排放是重要的温室气体排放源,减少反刍家畜胃肠道甲烷排放有助于缓解全球温室效应和提高家畜饲养效率。本论文从中国反刍家畜胃肠道甲烷排放现状、瘤胃甲烷生成机制、甲烷生成的日粮营养影响因子和甲烷减排策略与潜力4个方面系统综述反刍家畜胃肠道甲烷排放的研究进展。目前,中国反刍家畜甲烷总排放量超过10 Tg,占全球胃肠道甲烷排放的比例超过15%。反刍家畜胃肠道甲烷排放主要来自瘤胃和后肠道,其中瘤胃甲烷占胃肠道甲烷生成总量的80%以上。二氧化碳还原路径利用瘤胃内的氢和二氧化碳合成甲烷,是瘤胃内生成甲烷的主要路径。瘤胃内的氢还可被相关微生物利用,合成挥发性脂肪酸和微生物蛋白等代谢产物,进而被机体利用。减少反刍家畜胃肠道甲烷排放的关键在于促进瘤胃内氢的利用,以及阻断瘤胃内的氢被甲烷菌利用合成甲烷。甲烷减排的日粮营养调控策略包括优化日粮组成、改善饲料品质、提高瘤胃流通速率、添加氢池和甲烷抑制剂等。大多数营养调控策略的甲烷减排效果小于40%,最新研制的3-NOP抑制剂的甲烷减排效果最高可达80%。但是,一些减排策略的产业化应用还受添加剂残留、抗生素禁用、食品安全、产品价格和消费者喜好等因素影响。牧场管理和遗传选育也是降低甲烷排放量的重要手段,过去100年来已实现每千克标准乳的甲烷排放量减排效果为57%。未来反刍家畜胃肠道甲烷研究将主要集中在低排放品种的遗传选育、不同营养调控策略间的组合效果、甲烷减排的经济效益和可持续性、家畜生长性能与健康、食品安全、消费者喜好等方面。

关键词:胃肠道甲烷排放;瘤胃发酵模式;氢;营养调控;甲烷菌

中图分类号:X511 文献标志码:A 文章编号:1672-2043(2020)04-0732-11 doi:10.11654/jaes.2020-0105

Enteric methane emissions and mitigation strategies in ruminants

ZHANG Xiu-min, WANG Rong, MA Zhi-yuan, WANG Min*, TAN Zhi-liang

(Key Laboratory for Agro-Ecological Processes in Subtropical Region, Institute of Subtropical Agriculture, Chinese Academy of Science, Changsha 410125, China)

Abstract: Enteric methane emissions from ruminants is an important source of greenhouse gas production. Reducing enteric methane emissions from ruminants helps to alleviate global greenhouse effect and improve livestock feed efficiency. This study will review the latest researches of enteric methane emissions, and includes enteric methane emissions in China, mechanism of ruminal methanogenesis, the nutritional factors that affect methanogenesis, and strategies for methane inhibition. At present, enteric methane emissions exceed 10 Tg in China, which accounting for more than 15% of global enteric methane emissions. The enteric methane is mainly produced in the rumen and hindgut, and the methane from rumen accounts for more than 80% of enteric methane production. The carbon dioxide reduction is the major pathway of ruminal methanogenesis, which uses abundant hydrogen and carbon dioxide to produce methane. Hydrogen can also be used to

收稿日期:2020-01-30 录用日期:2020-04-01

作者简介:张秀敏(1989—),男,湖南湘西人,博士,主要从事反刍家畜能量代谢和胃肠道甲烷排放研究。E-mail: xmzhang@isa.ac.cn

*通信作者:王 敏 E-mail: mwang@isa.ac.cn

基金项目:国家自然科学基金项目(31922080,31561143009)

Project supported: The National Natural Science Foundation of China(31922080,31561143009)

produce volatile fatty acids and microbial proteins which can be utilized by the livestock. The key to reducing methane emissions is to promote the hydrogen utilization in the rumen and prevent hydrogen utilization from methanogenesis. Nutritional mitigation strategies include optimizing diet composition, improving feed quality, increasing rumen passage rate, adding hydrogen sinks and methane inhibitors. Most nutritional strategies have less than 40% reduction of enteric methane emissions, except the newly developed inhibitor, 3-NOP, which can reduce methane emissions by up to 80%. However, the industrial application of some strategies is also affected by other factors, such as additive residues, antibiotics prohibition, food safety, production prices, and consumer preferences. Farm management and genetic selection are also important strategies to reduce the methane emissions, and can reduce the methane emissions by 57% in terms of $\text{g} \cdot \text{kg}^{-1}$ milk during the recent 100 years. Further studies can be focused on genetic selection of low-emission breeds, the combined effects of different nutritional strategies, the economic benefits and sustainability of methane emissions reduction, livestock growth performance and health, food safety, and customer preferences and other aspects.

Keywords: methane emission; rumen fermentation; hydrogen; nutritional regulation; methanogen

甲烷(CH_4)是仅次于二氧化碳(CO_2)的全球第二大温室气体,占温室气体排放总量的16%^[1]。2018年,世界气象组织(WMO)的研究数据显示,大气中的二氧化碳和甲烷浓度分别为 $407.8 \mu\text{L} \cdot \text{L}^{-1}$ 和 $1869 \text{nL} \cdot \text{L}^{-1}$ ^[2]。尽管大气中的甲烷含量低于二氧化碳,但甲烷的增温潜能值是二氧化碳的28倍^[3],其对全球温室效应的贡献率为15%~20%^[1]。自然生态系统和人类活动是大气甲烷排放的两个重要来源。人类活动的甲烷排放来自畜牧业、固体废弃物、废水、稻田、生物质燃烧、煤炭开采和油气系统逃逸等,对全球甲烷排放的贡献率约为60%^[4],其中畜牧业甲烷排放约占人类活动的33%^[5]。畜牧业甲烷排放约占整个畜牧业温室气体排放的44%,来自于家畜胃肠道和粪便发酵,其中胃肠道排放占家畜甲烷排放总量的90%以上,是人类农业活动甲烷排放的最大来源^[6]。

自1980年至2018年,大气甲烷浓度呈逐步上升的趋势,由 $1650 \text{nL} \cdot \text{L}^{-1}$ 增加到 $1869 \text{nL} \cdot \text{L}^{-1}$ ^[7-8]。与此同时,全球牛肉、羊肉和牛奶消费量分别增长了12.6、5.4倍和9.3倍^[9],推动了反刍家畜养殖业的发展,同时也提高了胃肠道甲烷排放量。FAO统计结果显示:1980年全球肉牛、羊和奶牛胃肠道甲烷排放分别为45.7、2.32 Tg和17.7 Tg,2017年分别增加到53.6、5.17 Tg和18.8 Tg^[10]。另外,随着人类生活水平和物质需求的进一步提高,牛肉、羊肉和牛奶的消费量在未来仍然会继续保持增长势头^[11]。Bai等^[9]预测指出,2050年全球牛肉、羊肉和牛奶的消费量将比2010年分别增加57.1%、72.4%和80.6%。

胃肠道甲烷排放也是反刍家畜饲养过程中的重要能量损失,占日粮消化能的2%~12%^[12],占日粮代谢能的6.5%~18.7%^[13]。美国奶业协会统计数据显

示:胃肠道甲烷排放与奶牛饲养效率呈强负相关关系,若每千克标准乳的甲烷排放量减少2.5 g,每千克饲料将多生产300 mL标准乳^[14]。因此,反刍家畜胃肠道甲烷减排对于缓解全球温室效应和提高饲养效率具有重要意义,受到各国政府和科研人员的广泛关注。本论文将从中国反刍家畜胃肠道甲烷排放现状、瘤胃甲烷生成机制、甲烷生成的日粮营养影响因子和甲烷减排策略与潜力4个方面系统综述反刍家畜胃肠道甲烷排放的研究进展,并在此基础上总结各项措施的甲烷减排潜力。

1 中国反刍家畜胃肠道甲烷排放现状

目前,中国家畜饲养量已经超过美国和欧洲,为世界最大的畜牧业生产国^[9]。Zhou等^[15]首次估算了中国反刍家畜胃肠道甲烷排放总量,发现2003年胃肠道甲烷排放量约为10.1 Tg。王荣等^[16]根据IPCC缺省值估算,2010年中国反刍家畜胃肠道甲烷排放总量为6.6 Tg。黄满堂等^[17]报道,2015年中国反刍家畜甲烷总排放量为10.2 Tg。Zhuang等^[18]报道,中国家畜胃肠道甲烷排放量为14.3 Tg,占全球家畜胃肠道甲烷排放的18.7%。因此,中国家畜胃肠道甲烷排放在全球家畜胃肠道甲烷排放中占据重要地位,相关研究受到国际同行的广泛关注。

中国主要反刍家畜类型有肉牛、山羊、绵羊和奶牛。肉牛养殖数量最大,对我国胃肠道甲烷排放贡献最多。有研究显示:1995年中国肉牛胃肠道甲烷排放量占总量的78.6%;其次为山羊和绵羊,分别占9.8%和8.3%;奶牛胃肠道甲烷排放量最低,仅占3.3%^[16]。近年来,我国人民生活水平改善,反刍家畜饲养种群发生重大改变,奶牛饲养量有明显提高。根

据中国统计年鉴资料,2000年奶牛存栏量450万头,至2017年增加到1080万头^[19]。自2010年起,奶牛胃肠道甲烷排放量贡献率提升至13.1%,超过山羊和绵羊胃肠道甲烷排放总量,成为中国反刍家畜胃肠道甲烷排放的第二大来源^[16]。

反刍家畜胃肠道甲烷生成效率同日粮结构密切相关。纤维降解生成甲烷的效率高于非纤维碳水化合物^[14],其中纤维素和半纤维素发酵产生甲烷的效率是非纤维碳水化合物的2~5倍^[20]。我国优质粗饲料资源数量不足,反刍家畜养殖过程中对农作物秸秆(如玉米秸、稻草、麦秸)等低质粗饲料消耗较多,这些低质粗饲料中纤维含量较高,导致反刍家畜甲烷排放量较高,日粮能量利用效率低下^[21]。因此,我国反刍家畜胃肠道甲烷减排压力面临巨大挑战。

2 胃肠道甲烷生成机制

2.1 产甲烷菌和甲烷生成过程

反刍家畜胃肠道甲烷产生的部位为瘤胃和后肠道,其中瘤胃约占胃肠道甲烷生成量的80%以上^[22]。甲烷菌是反刍家畜胃肠道合成甲烷的微生物^[23],在分类学上属于古菌域、广古菌门。瘤胃甲烷菌主要来自甲烷杆菌目(Methanobacteriales)、甲烷微菌目(Methanomicrobiales)和甲烷马赛球菌目(Methanomassilicoccaceae),分别占甲烷菌总量的66%、15%和15%^[24-25]。

瘤胃内生成甲烷的前体物有二氧化碳、氢分子(H_2)、甲酸、甲基化合物和乙酸盐等^[24]。根据甲烷合成的前体物不同,可以将甲烷合成路径分二氧化碳还原、甲基营养型和乙酸异化3种路径。(1)二氧化碳还原路径:该路径以二氧化碳作为碳源,以氢分子作为电子供体^[26],因此也称为氢营养型路径。利用该路径合成甲烷的甲烷菌有甲烷短杆菌和甲烷微菌,约占甲烷菌总量的80%(表1)^[27]。二氧化碳先后分别被还

原为甲酰基、亚甲基和甲基,甲基随后转移至辅酶M形成甲基辅酶M,最后经过甲基辅酶M还原酶(MCR)生成甲烷^[24]。(2)甲基营养型路径:该路径以甲醇、甲基胺(甲胺、二甲胺、三甲胺、四甲胺)和甲基硫化物(甲硫醇、二甲基硫醚)为底物。在瘤胃内,甲烷马赛球菌目是主要的甲基营养型甲烷菌,约占甲烷菌总量的16%,主要利用甲胺和甲醇合成甲烷^[28]。在这一甲烷生成过程中,甲基化合物的甲基基团先转移至同源钴蛋白,然后转移至辅酶M生成甲基辅酶M,随后经MCR作用还原为甲烷^[25]。(3)乙酸异化路径:该路径以乙酸为底物,甲烷八叠球菌属(*Methanosarcina*)和产甲烷丝状菌属(*Methanosaeta*)是主要的乙酸营养型甲烷菌。这两类甲烷菌利用乙酸的分解反应生成甲基和羧基,其中甲基还原生成甲烷,羧基则氧化为二氧化碳^[24]。在这3条路径中,二氧化碳还原路径(反应式: $CO_2+4H_2\rightarrow CH_4+2H_2O$)是瘤胃内甲烷生成的主要路径。

2.2 瘤胃内氢代谢过程

瘤胃内氢以电子载体(如NADH、FADH、NADPH等)和氢分子两种形态存在。糖酵解是瘤胃内已糖代谢的最普遍方式,产生丙酮酸和NADH。其中,NADH需要被再氧化为NAD⁺来维持正常糖酵解过程和以丙酮酸为底物进行的一系列微生物代谢^[29]。在瘤胃内,大部分NADH的氧化过程生成氢,同时伴随ATP的产生($NADH+H^++ADP+P_i\rightarrow NAD^++ATP+H_2$),为微生物提供能量来源。从热力学角度来看,瘤胃内氢分压升高,将抑制NADH的氧化,进而阻断ATP产生^[30]。瘤胃内甲烷菌的重要功能在于利用CO₂将氢氧化为CH₄,以维持瘤胃内较低氢分压,使NADH的氧化过程顺利进行,确保ATP的正常生成,以维持瘤胃微生物的正常发酵功能^[30]。

瘤胃内氢分子以溶解态和气体态两种形式存在^[31],仅溶解态氢能与瘤胃微生物接触,具有生物学

表1 瘤胃内主要甲烷生成路径及相关甲烷菌

Table 1 Major groups of methanogens and pathways of methanogenesis in the rumen

生成路径 Methanogenesis pathways	化学反应 Chemical reactions	甲烷菌 Methanogens
二氧化碳还原路径	$4H_2+CO_2\rightarrow CH_4+2H_2O$	甲烷短杆菌、甲烷微菌
	$4HCOOH\rightarrow CH_4+3CO_2+2H_2O$	甲烷短杆菌、甲烷微菌
	$CO_2+4C_3H_8O\rightarrow CH_4+4C_3H_6O+2H_2O$	部分氢营养型甲烷菌
	$4CO+2H_2O\rightarrow CH_4+3CO_2$	热杆菌、甲烷八叠球菌
甲基营养型路径	$CH_3OH+H_2\rightarrow CH_4+H_2O$	甲烷马赛球菌
	$4CH_3OH\rightarrow 3CH_4+CO_2+2H_2O$	甲烷八叠球菌、其他甲基营养型甲烷菌
	$4CH_3-NH_2+2H_2O\rightarrow 3CH_4+CO_2+4NH_3$	甲烷马赛球菌
乙酸异化路径	$CH_3COOH\rightarrow CH_4+CO_2$	甲烷八叠球菌、甲烷丝状菌

功能。大部分溶解态氢被甲烷菌利用生成甲烷,溶解态氢还可被其他耗氢微生物利用合成微生物蛋白和代谢产物,从而被动物机体利用^[32]。瘤胃内溶解态氢浓度变化范围一般是 $0.1\sim 50\ \mu\text{mol}\cdot\text{L}^{-1}$ ^[33],当甲烷生成受到抑制时,瘤胃内溶解态氢浓度可超过 $100\ \mu\text{mol}\cdot\text{L}^{-1}$ ^[34]。没有消耗的溶解态氢进入瘤胃顶端空间变成气体态氢,最后通过暖气的方式排放到大气中。

瘤胃内挥发性脂肪酸有乙酸、丙酸、丁酸、异丁酸、戊酸和异戊酸等,其中乙酸、丙酸和丁酸的含量占挥发性脂肪酸总量的90%以上。碳水化合物降解生成乙酸($\text{C}_6\text{H}_{12}\text{O}_6 + 2\text{H}_2\text{O} \rightarrow 2\text{C}_2\text{H}_4\text{O}_2 + 2\text{CO}_2 + 8\text{H}$)和丁酸($\text{C}_6\text{H}_{12}\text{O}_6 \rightarrow \text{C}_4\text{H}_8\text{O}_2 + 2\text{CO}_2 + 4\text{H}$)的过程释放氢,而碳水化合物降解生成丙酸($\text{C}_6\text{H}_{12}\text{O}_6 + 4\text{H} \rightarrow 2\text{C}_3\text{H}_6\text{O}_2 + 2\text{H}_2\text{O}$)的过程吸收氢^[33]。瘤胃内氢浓度同瘤胃发酵模式密切相关。当甲烷生成受到抑制时,瘤胃内氢浓度迅速提高,有助于抑制氢的生成和促进氢的利用,进而提高瘤胃内丙酸和丁酸的含量^[35-36]。另外,氢还可以被瘤胃微生物利用以合成瘤胃微生物蛋白,进而被机体利用^[37]。阻断瘤胃内氢代谢生成甲烷,促进氢利用合成代谢产物和微生物蛋白,有助于减少胃肠道甲烷排放和提高反刍家畜能量利用效率。

3 胃肠道甲烷排放的日粮影响因子

3.1 日粮组成和饲料品质

日粮的碳水化合物组成影响反刍家畜胃肠道甲烷排放。研究表明:日粮谷物类精饲料比例超过80%时,仅3%~4%的日粮总能将转化为甲烷能;当日粮全部为纤维类粗饲料时,超过10%的日粮总能将转化为甲烷能^[12]。日粮组成主要影响瘤胃挥发性脂肪酸组成^[38],改变瘤胃内氢的生成与消耗过程,调节甲烷菌合成甲烷所需氢的供给量,进而影响甲烷生成。高纤维类粗饲料日粮有利于瘤胃乙酸生成^[39],产生更多氢进而促进甲烷生成^[40]。谷物类精饲料日粮通常含大量的淀粉,这有利于瘤胃内丙酸的生成,抑制氢生成进而减少甲烷生成^[12]。与纤维相比,淀粉在瘤胃内的降解速率快,瘤胃内氢浓度迅速升高,这将抑制氢生成和促进氢利用,进而使更多氢用于合成代谢产物^[40]。另外,高谷物类精饲料日粮还会迅速降低瘤胃pH值,这将抑制甲烷菌活性,进而减少甲烷合成^[41]。适当增加日粮谷物类精饲料还可提高反刍家畜生产效率,进而减少单位动物产品的甲烷排放量^[42-43]。

饲料品质是影响反刍家畜胃肠道甲烷排放的另一重要因素。全球约75%的反刍家畜胃肠道甲烷来

源于饲喂低质量日粮的家畜^[44]。高品质饲料原料有助于家畜将更多的日粮能量用于生产,提高生产净能占食入总能的比例,进而降低生产每单位动物产品的甲烷排放量。提升饲料品质,尤其是粗饲料品质,对降低甲烷排放至关重要。高品质的粗饲料通常含有更高比例的非纤维碳水化合物,和较少木质化的中性洗涤纤维^[44-45]。利用玉米青贮和其他谷物青贮代替禾草青贮可提高日粮的整体品质,进而降低甲烷排放。与禾草青贮相比,谷物青贮的淀粉含量较高,这将促进丙酸生成,减少氢生成和甲烷排放^[40]。另外,高品质粗饲料还将增加家畜采食量,这将改善动物生产性能,减少饲料在瘤胃的滞留时间及瘤胃发酵程度,增强后肠道的营养消化,降低单位产品的甲烷排放量^[46]。

3.2 瘤胃流通速率

饲料的瘤胃流通速率通常与胃肠道甲烷排放呈现负相关关系^[47-48]。提高瘤胃流通速率将减少食糜在瘤胃中的滞留时间,降低食糜在瘤胃中的发酵程度,抑制氢的产生,增强后肠道对食糜的消化,降低单位消化物质的甲烷排放量。提高瘤胃流通速率还将减少瘤胃甲烷菌利用氢的效率,抑制甲烷排放量^[14]。另外,瘤胃流通速率也同瘤胃发酵模式密切关联,较高流通速率有助于丙酸生成,降低挥发性脂肪酸生氢效率,不利于甲烷生成^[33]。有研究表明,瘤胃流通速率对胃肠道甲烷排放量的影响效率约为28%^[49]。因此,瘤胃流通速率主要通过改变日粮的瘤胃消化率和发酵模式,影响微生物生长和增殖速率,减少甲烷菌与氢的接触时间,从而抑制胃肠道甲烷排放。

3.3 日粮氢池

氢池是指日粮中一些化合物,具有较强利用瘤胃内氢的能力,能够同甲烷菌竞争利用氢,抑制甲烷生成。这些化合物包括硝酸盐、硫酸盐^[50]、油脂和有机酸(富马酸、苹果酸、琥珀酸)^[48]等。硝酸盐和硫酸盐的作用效果显著,相关研究也较多。根据化学计量学计算结果($\text{NO}_3^- + \text{H}_2 \rightarrow \text{H}_2\text{O} + \text{NO}_2^-$, $\text{NO}_2^- + 3\text{H}_2 + 2\text{H}^+ \rightarrow 2\text{H}_2\text{O} + \text{NH}_4^+$; $4\text{H}_2 + \text{CO}_2 \rightarrow \text{CH}_4 + 2\text{H}_2\text{O}$),1 mol的 NO_3^- 在还原为 NH_4^+ 的过程中,可以消耗4 mol氢分子,从而使 CH_4 生成量减少1 mol。油脂中通常含有大量的不饱和脂肪酸,不饱和脂肪酸的生物氢化过程可同甲烷菌竞争氢^[51-52]。二羧酸(如富马酸、苹果酸)是瘤胃内丙酸生成的前体物,其转化成丙酸的过程与甲烷菌竞争氢,其中富马酸的甲烷抑制效果较好^[53]。另外,瘤胃微生物生长需利用氨态氮,氨态氮合成微生物蛋白的过程

伴随着氢的消耗,这也会同甲烷菌形成对氢的竞争利用^[54]。

3.4 甲烷菌抑制剂

甲烷菌抑制剂是指可以抑制甲烷菌增殖或活性的物质,以达到阻断甲烷菌利用氢合成甲烷的效果。这些抑制剂包括油脂、硝酸盐、3-硝基酯-1-丙醇(3-NOP)、莫能菌素、植物化合物和甲烷菌疫苗等。油脂对原虫具有毒性,进而减少附着在原虫上的甲烷菌数量,抑制甲烷生成。另外,游离脂肪酸和中链脂肪酸(C12和C14)也会对甲烷菌具有毒性,减少瘤胃内甲烷菌数量^[46-55]。硝酸盐在瘤胃中还原为氨的过程中产生中间代谢产物亚硝酸盐,而亚硝酸盐对甲烷菌具有毒性,可以直接抑制甲烷菌活性^[56]。3-NOP是一种化学结构与甲基辅酶M高度相似的小分子,可以与甲基辅酶M还原酶的活性位点结合,使甲基辅酶M还原酶失去活性,抑制甲烷生成。3-NOP是目前发现的甲烷减排效果最好的抑制剂,日粮中添加非常低浓度(如 $40\text{ mg}\cdot\text{kg}^{-1}$)的3-NOP,可以抑制瘤胃内甲烷生成,而且不影响家畜的机体健康^[57-58]。莫能菌素可以抑制原虫和革兰氏阳性菌的活性,减少用于合成甲烷的底物。另外,一些植物化合物(如单宁、皂素等)可以抑制生氢微生物活性,减少氢供给量,抑制甲烷生成。甲烷菌疫苗可以促使宿主的免疫系统产生甲烷菌抗体,以达到抑制甲烷菌活性的目的^[23]。

4 胃肠道甲烷排放的减排策略与潜力

4.1 营养措施

目前,减少甲烷排放的主要营养调控措施有:优化日粮组成,改善饲料品质;增加瘤胃流通速率;添加剂抑制甲烷合成。

4.1.1 优化日粮组成,改善饲料品质

优化日粮组成可通过改变日粮精粗比实现提高饲养效率和减少甲烷排放。利用玉米粒、豆粕和膨化大豆将泌乳奶牛日粮中非纤维碳水化合物的比例从32%提高至53%,每千克标准乳产生的甲烷降低约20%^[59]。奶牛日粮中非纤维碳水化合物比例每增加1%,每千克标准乳产生的甲烷将减少2%^[14]。相反地,奶牛日粮的中性洗涤纤维比例从31.5%提高至38%,其甲烷日排放量会增加23%^[60]。肉牛可消化中性洗涤纤维采食量增加147%,其甲烷日排放量提高127%^[61]。因此,提高日粮非碳水化合物含量、降低中性洗涤纤维含量是减少家畜甲烷排放的有效调节方

法。针对不同反刍家畜的研究发现,当增加日粮中精料的比例时,所有家畜的甲烷排放量都会降低。奶牛饲料精粗比从30:70提高至70:30,最高减排量达14%,绵羊饲料精粗比从20:80提升至50:50,最高减排量为6%,肉牛饲料精粗比从30:70提升至90:10,最高甲烷减排量达26%^[62]。因此,提高日粮中精料水平可以使甲烷排放量减少10%~30%(表2)。

改善粗饲料品质的方式包括在成熟度较低时进行收割或放牧、合适的储存方式(如青贮)等。成熟度高的植物在瘤胃发酵过程中会增加乙酸和氢的产量,从而增加每单位消化的粗饲料所产生的甲烷^[63]。也有研究发现,在苜蓿地放牧的肉牛比在禾草草地放牧的肉牛甲烷排放量高,是该研究中苜蓿的成熟度较高所致^[64]。青贮粗饲料比干粗饲料产生的甲烷要少,饲喂青贮玉米的奶牛甲烷排放量比饲喂干草的低20%^[65]。豆科牧草质量优于禾草,与饲喂禾本科饲草相比,饲喂豆科牧草时单位采食量的甲烷排放量要低。例如,用红豆草+梯牧草混合青贮饲喂绵羊时,甲烷排放量要比饲喂梯牧草青贮时低17%^[66]。用三叶草饲喂肉牛时甲烷排放量比用多年生黑麦草饲喂时的甲烷排放量低21%^[67]。在苜蓿地放牧的绵羊,与黑麦草草地放牧的绵羊相比,可以获得更高的体增质量,同时甲烷排放当量最多可以降低50%^[68]。因此,改善粗饲料品质可以有效降低甲烷排放量,其抑制效果变化范围较大,最高可达50%。

4.1.2 调控瘤胃流通速率

瘤胃流通速率越高,胃肠道甲烷排放量越低^[69-70]。当绵羊瘤胃流通速率增加35%时,甲烷排放量减少17%。当奶牛瘤胃流通速率增加37%时,甲烷排放量减少20%^[71]。日粮碳水化合物组成是影响瘤胃流通速率的重要因子,降低日粮中纤维含量将提高瘤胃流通速率^[33]。McCaughy等^[72]研究不同牧草类型对肉牛甲烷排放影响时发现:与单纯禾草相比,苜蓿-禾草混合饲草的纤维含量低,瘤胃流通速率高,甲烷排放量降低9%。另外,谷物饲料的纤维含量较低,有利于提高瘤胃流通速率,减少饲料在瘤胃中的消化降解。日粮谷物饲料添加量从11%增加至47%后,肉牛的甲烷排放量可以减少14%^[73]。饲料加工可以改变饲草特征,进而影响瘤胃流通速率。粗饲料的粉碎和制粒可增加瘤胃流通速率,明显减少甲烷排放,每单位采食量的甲烷减排效果约为20%~40%^[47]。因此,降低日粮纤维含量和适当的饲草加工将提高瘤胃流通速率,甲烷减排潜力可达9%~50%(表2)。

表2 主要甲烷减排措施
Table 2 Major strategies of methane mitigation

减排方案 Mitigation schemes	日粮措施 Dietary strategies	家畜类别 Animal types	减排效果 Reduction/%	参考文献 Reference
优化日粮组成	增加精料	奶牛	14	[62]
	增加精料	肉牛	26	[62]
	增加精料	绵羊	6	[62]
改善饲料品质	青贮替代干草	奶牛	20	[65]
	豆科牧草替代禾草	肉牛	21	[67]
	豆科牧草替代禾草	绵羊	50	[68]
提高瘤胃流通速率	苜蓿-禾草混合饲草代替禾草	肉牛	9	[72]
	增加谷物饲料	肉牛	14	[73]
	粗饲料粉碎、制粒	肉牛	20~40	[47]
甲烷抑制剂	油脂	肉牛、绵羊	10~25	[46]
	亚麻籽油	奶牛	64	[76]
	菜籽油	肉牛	18	[74]
	玉米油	奶牛	11	[75]
	玉米油	山羊	15	[52]
	硝酸盐	奶牛	16.5	[78]
	硝酸盐	奶牛	15	[32]
	硝酸盐	肉牛	18	[79]
	硝酸盐	绵羊	34	[80]
	硝酸盐	山羊	12	[81]
	硝酸盐	山羊	10	[82]
	3-NOP	奶牛	25~32	[57]
	3-NOP	奶牛	24	[83]
	3-NOP	肉牛	60	[84]
	3-NOP	肉牛	80	[85]
	3-NOP	绵羊	21~25	[86]
	莫能菌素	奶牛	7~9	[87]
	莫能菌素	肉牛	27	[88]
	莫能菌素	肉牛	27~30	[90]
	莫能菌素	山羊	28	[89]
	单宁	奶牛	26	[14]
	单宁	绵羊、山羊	12~46	[14]

4.1.3 添加剂调节瘤胃发酵

4.1.3.1 日粮添加油脂

向日粮中添加油脂是较为通行的甲烷减排方法。给肉牛提供占日采食量约5%的菜籽油,甲烷排放量可减少18%^[74]。奶牛日粮中添加1.38%的玉米油,甲烷排放量减少11%^[75],添加5.7%的亚麻籽油,甲烷排放量可减少64%^[76]。山羊试验也有类似发现,日粮中添加3%的玉米油可使甲烷排放量减少15%^[52]。日粮油脂含量每增加1%将降低甲烷排放量约5.6%,如日粮油脂添加量为1%~3%,可实现甲烷减排10%~25%,最高可达40%^[46]。另外,甲烷减排效果还会受油脂来源和脂肪酸组成等因素的影响。油脂通常分为瘤胃

惰性脂肪(脂肪酸钙盐或者硬脂酸)、油(植物油)、油料种子(完整、压碎或者压榨的)和饲料本身包含的内源性脂肪等。油脂来源不同会影响家畜的采食量,进而引起甲烷减排效果的差异。惰性和内源性脂肪对采食量通常没有影响;添加植物油的日粮中粗脂肪增加1%会使采食量降低(1.51±0.40)kg;添加油料种子(菜籽、大豆等)的日粮中粗脂肪增加1%会使采食量降低(0.90±0.52)kg^[14]。脂肪酸组成也会影响甲烷减排效果,例如中链脂肪酸(C12和C14)对瘤胃原虫有一定毒性,不饱和脂肪酸可以通过氢化过程与甲烷菌竞争氢。因此,不同脂肪酸组成的油脂具备的甲烷合成抑制能力存在差异,造成不同的减排效果^[77]。

4.1.3.2 日粮添加化学抑制剂

硝酸盐可通过氢池和对甲烷菌的毒性来抑制甲烷生成,是较为常见且减排效果明显的甲烷抑制剂。Van Zijderveld 等^[78]在奶牛日粮中添加 NO_3^- ($21 \text{ g} \cdot \text{kg}^{-1} \text{ DM}$),甲烷排放量减少16.5%。Wang 等^[32]在奶牛日粮中添加 NO_3^- ($14.6 \text{ g} \cdot \text{kg}^{-1} \text{ DM}$),甲烷排放量减少15%。Lee 等^[79]在肉牛日粮中添加 NO_3^- ($25 \text{ g} \cdot \text{kg}^{-1} \text{ DM}$),甲烷排放量减少18%。Li 等^[80]在绵羊日粮中添加 NO_3^- ($8.8 \text{ g} \cdot \text{kg}^{-1} \text{ BW}$),甲烷排放量减少34%。Arif 等^[81]在山羊日粮中添加 NO_3^- ($22 \text{ g} \cdot \text{kg}^{-1} \text{ DM}$),甲烷排放量减少12%;Zhang 等^[82]发现用 NO_3^- ($4.7 \text{ g} \cdot \text{kg}^{-1}$)预处理的水稻秸秆饲喂山羊,甲烷排放量减少约10%。另外,因硝酸盐代谢过程中生成的亚硝酸盐具有毒性,过量添加和不当使用可能损害机体健康,进而限制其在生产实际中的广泛应用,目前硝酸盐降低反刍家畜甲烷排放潜力约为10%~35%(表2)。

3-NOP是帝斯曼公司研制的最新甲烷抑制制,近年来得到了科研和生产领域的广泛关注。Hristov 等^[57]在奶牛日粮中添加3-NOP(40 、 60 、 $80 \text{ mg} \cdot \text{kg}^{-1} \text{ DM}$),甲烷排放量减少25%~32%。Van Wesemael^[83]在奶牛日粮中添加3-NOP($1.6 \text{ g} \cdot \text{d}^{-1} \cdot \text{头}^{-1}$),甲烷排放量减少24%。Romero-Perez 等^[84]在肉牛日粮中添加3-NOP($2 \text{ g} \cdot \text{d}^{-1}$),甲烷排放量减少约60%。Vyas 等^[85]在育肥期肉牛日粮中添加3-NOP($200 \text{ mg} \cdot \text{kg}^{-1} \text{ DM}$),甲烷排放量减少达80%。Martinez-Fernandez 等^[86]在绵羊日粮中添加3-NOP($100 \text{ mg} \cdot \text{d}^{-1} \cdot \text{头}^{-1}$),甲烷排放量减少21%~25%。这些研究结果表明,3-NOP是一种非常有效的甲烷抑制剂,甲烷减排量高达20%~80%(表2),减排效果受到家畜种类、日粮组成、添加剂量等因素影响。3-NOP在动物产品中的残留还需要继续研究,其安全问题还没有得到充分确认,目前并没有被市场广泛应用。

4.1.3.3 莫能菌素

莫能菌素是一种抗生素,能显著抑制瘤胃甲烷生成,减少甲烷排放,在饲料中应用较为广泛。Odongo 等^[87]在奶牛日粮中添加莫能菌素($24 \text{ mg} \cdot \text{kg}^{-1} \text{ DM}$),发现甲烷排放量减少7%~9%。肉牛日粮中添加莫能菌素($33 \text{ mg} \cdot \text{kg}^{-1} \text{ DM}$)可以使甲烷排放量减少27%^[88]。Puchala 等^[89]在山羊日粮中添加莫能菌素($22 \text{ mg} \cdot \text{kg}^{-1} \text{ DM}$),发现甲烷排放量减少28%。但是,因瘤胃微生物存在对莫能菌素的适应性,其甲烷减排效果可能出现逐渐减弱的趋势。Guan 等^[90]在肉牛低精料和高精料里分别添加 $33 \text{ mg} \cdot \text{kg}^{-1} \text{ DM}$ 莫能菌素,发现饲喂低

精料日粮的肉牛在试验开始4周内的甲烷排放量减少27%,原虫数量减少77%,6周后甲烷减排效果消失,原虫数量恢复到初始水平。饲喂高精料日粮的肉牛在试验开始2周内的甲烷排放量减少30%,原虫数量减少83%,4周后甲烷减排效果消失,原虫数量恢复到初始水平。Grainger 等^[91]也发现长期补饲莫能菌素($471 \text{ mg} \cdot \text{d}^{-1}$)的奶牛甲烷排放量没有降低。因此,莫能菌素的甲烷减排效果为0%~30%,长期使用莫能菌素效果并不明显(表2)。近年来,随着政府对日粮抗生素应用的进一步监管,未来莫能菌素可能无法在畜牧业生产中应用。

4.1.3.4 其他化合物

植物次生代谢产物也能抑制甲烷生成,包括植物精油、单宁、皂素、类黄酮和有机硫化物等。植物精油主要是从大蒜、百里香、桉树、牛至、肉桂和大黄等植物中提取出来,体外模拟瘤胃发酵试验显示其甲烷抑制效果约10%~90%^[92],但其在体内长期抑制甲烷生成的效果还需要进一步研究^[93]。单宁是存在于很多植物中的一种多酚化合物,包括缩合单宁和水解单宁。Jayanegara 等^[94]分析了30项有关单宁的研究结果,发现单宁摄入量每增加 $1 \text{ g} \cdot \text{kg}^{-1} \text{ DMI}$,甲烷排放量将减少 $0.109 \text{ L} \cdot \text{kg}^{-1} \text{ DMI}$ 。Knapp 等^[14]发现,缩合单宁对绵羊和山羊的甲烷减排效果为12%~46%,对奶牛的甲烷减排效果为26%(表2)。海藻富含卤代化合物、三溴甲烷等化合物,具有抑制瘤胃甲烷生成的作用。Machado 等^[95]利用体外发酵试验初步研究20种热带海洋大型海藻,发现网地藻属(*Dictyota*)和海门冬属(*Asparagopsis*)能显著减少甲烷排放(92%和98%)。最近,Li 等^[96]在绵羊日粮中添加3%的*Asparagopsis taxiformis*,发现甲烷排放量最高可减少80%,对体增质量没有影响。

4.2 其他减排策略

改善牧场的管理方式也能降低牧场整体甲烷排放量。对放牧牧场而言,提高草地质量能显著减少甲烷排放。但是,如果放牧率增加,甲烷排放量会相应增加^[46]。集约化管理牧场能更加高效地利用饲草,提高饲料转化率,肉牛甲烷减排达到22%^[97]。反刍家畜遗传选育结合管理措施的改进也是减少甲烷排放的重要手段。以北美地区为例,过去一个世纪以来,牛奶产量增加400%,使生产每千克标准乳的甲烷排放量减少了57%^[98]。一个泌乳期内每增加100 kg产奶量,高产(>13 000 kg)和低产(<7000 kg)奶牛每千克标准乳甲烷排放量分别减少3.1%和7.3%。另外,反

刍家畜瘤胃微生物种群结构也受宿主遗传控制。对不同甲烷排放量的雄性后代牛进行瘤胃微生物分析,发现瘤胃甲烷菌种群结构和丰度具有显著差异^[99]。Shi 等^[100]针对高低甲烷排放的绵羊的研究结果显示,与低甲烷排放量的绵羊相比,高甲烷排放量的绵羊瘤胃内甲烷合成通路基因的转录水平高。此外,发现甲烷排放量高的肉牛瘤胃中琥珀酸弧菌科的相对丰度低,这可能是由于它生成的琥珀酸作为氢池可以与甲烷菌竞争氢^[101-102]。因此,改善牧场管理和利用遗传学方法结合瘤胃菌群结构对家畜进行选育,可以实现减少甲烷排放和提高家畜饲养效率。

5 结论

畜牧业甲烷排放约占整个畜牧业温室气体排放的44%,是人类农业活动甲烷排放的最大源。中国反刍家畜胃肠道甲烷排放占全球胃肠道甲烷排放的18.7%,面临较大的胃肠道甲烷减排压力。反刍家畜瘤胃甲烷产量占胃肠道甲烷总量的80%以上,成为研究胃肠道甲烷排放的关键部位。减少反刍家畜胃肠道甲烷排放的关键在于促进瘤胃内氢的利用,以及阻断瘤胃内的氢被甲烷菌利用合成甲烷。目前,相关营养调控策略有优化日粮配置、提升饲料品质、增加瘤胃流通速率、添加氢池和抑制甲烷菌等。优化日粮配置和提升饲料品质可使甲烷减排量达6%~50%,增加瘤胃流通速率可使甲烷减排量最高达50%,添加氢池可使甲烷减排量最高达60%,抑制甲烷菌活性可使甲烷减排量最高达80%。但是,相关甲烷减排方法(如添加油脂和硝酸盐)还需要通过长期效应的检验。另外,牧场管理和遗传选育也是降低甲烷排放的重要手段。在生产实践中,还需要结合当前生产效率和甲烷减排潜力等方面的因素综合考虑,选择合理的甲烷减排方案。在今后的研究中,需加强对不同营养调控策略间的组合应用、甲烷减排效果的可持续性、低甲烷排放的家畜品种选育、家畜生产系统经济效益、食品安全和消费者喜好等方面的研究。另外,针对我国优质粗饲料缺乏、大量农作物秸秆用作粗饲料资源的现状,甲烷减排的策略目前应当主要集中于改善现有粗饲料品质,同时提高牧场管理水平,以实现减少甲烷排放和提高饲养效率的目的。

参考文献:

[1] De Visscher A, Van Cleemput O. Simulation model for gas diffusion and methane oxidation in landfill cover soils[J]. *Waste Management*,

2003, 23(7): 581-591.

- [2] WMO. Greenhouse gas bulletin[R]. Vienna: WMO, 2018.
- [3] Stocker T. Climate change 2013: The physical science basis: Working Group I contribution to the fifth assessment report of the Intergovernmental Panel on Climate Change[R]. Cambridge: Cambridge University Press, 2014.
- [4] Reay D S, Smith P, Christensen T R, et al. Methane and global environmental change[J]. *Annual Review of Environment and Resources*, 2018, 43:165-192.
- [5] Beauchemin K A, Kreuzer M, O'mara F, et al. Nutritional management for enteric methane abatement: A review[J]. *Australian Journal of Experimental Agriculture*, 2008, 48(1/2): 21-27.
- [6] Kumari S, Fagodiya R K, Hiloidhari M, et al. Methane production and estimation from livestock husbandry: A mechanistic understanding and emerging mitigation options[J]. *Science of the Total Environment*, 2020, 709:136135.
- [7] Kirschke S, Bousquet P, Ciais P, et al. Three decades of global methane sources and sinks[J]. *Nature Geoscience*, 2013, 6(10): 813-823.
- [8] Nisbet E G, Manning M R, Dlugokencky E J, et al. Very strong atmospheric methane growth in the 4 years 2014-2017: Implications for the Paris agreement[J]. *Global Biogeochemical Cycles*, 2019, 33(3): 318-342.
- [9] Bai Z, Ma W, Ma L, et al. China's livestock transition: Driving forces, impacts, and consequences[J]. *Science Advances*, 2018, 4(7): eaar8534.
- [10] FAO. Statistical database[R]. Roma: FAO, 2017.
- [11] Godfray H C, Beddington J R, Crute I R, et al. Food security: The challenge of feeding 9 billion people[J]. *Science*, 2010, 327(5967): 812-818.
- [12] Johnson K A, Johnson D E. Methane emissions from cattle[J]. *Journal of Animal Science*, 1995, 73:2483-2492.
- [13] Appuhamy J A, France J, Kebreab E. Models for predicting enteric methane emissions from dairy cows in North America, Europe, and Australia and New Zealand[J]. *Global Change Biology*, 2016, 22(9): 3039-3056.
- [14] Knapp J R, Laur G L, Vadas P A, et al. Invited review: Enteric methane in dairy cattle production: Quantifying the opportunities and impact of reducing emissions[J]. *Journal of Dairy Science*, 2014, 97(6): 3231-3261.
- [15] Zhou J B, Jiang M M, Chen G Q. Estimation of methane and nitrous oxide emission from livestock and poultry in China 1949-2003[J]. *Energy Policy*, 2007, 35(7): 3759-3767.
- [16] 王 荣, 邓近平, 王 敏, 等. 基于 IPCC Tier 1 层级的中国反刍家畜胃肠道甲烷排放格局变化分析[J]. *生态学报*, 2015, 35(21): 7244-7254.
WANG Rong, DENG Jin-ping, WANG Min, et al. Using intergovernmental panel on climate change Tier 1 to analyze the trends and distribution patterns of enteric methane emissions from ruminants in China during 1990-2010[J]. *Acta Ecologica Sinica*, 2015, 35(21): 7244-7254.
- [17] 黄满堂, 王体健, 赵雄飞, 等. 2015年中国地区大气甲烷排放估计及空间分布[J]. *环境科学学报*, 2019, 39(5): 1371-1380.

- HUANG Man-tang, WANG Ti-jian, ZHAO Xiong-fei, et al. Estimation of atmospheric methane emissions and its spatial distribution in China during 2015[J]. *Acta Scientiae Circumstantiae*, 2019, 39 (5): 1371-1380.
- [18] Zhuang M, Lu X, Caro D, et al. Emissions of non-CO₂ greenhouse gases from livestock in China during 2000-2015: Magnitude, trends and spatiotemporal patterns[J]. *Journal of Environmental Management*, 2019, 242: 40-45.
- [19] 国家统计局. 中国统计年鉴 2017[M]. 北京: 中国统计出版社, 2017. National Bureau of Statistics. China statistical yearbook (2017) [M]. Beijing: China Statistics Press, 2017.
- [20] Moe P W, Tyrrell H F. Methane production in dairy cows[J]. *Journal of Dairy Science*, 1979, 62(10): 1583-1586.
- [21] 朱伟云, 毛胜勇, 成艳芬. 反刍动物瘤胃甲烷产生机制及营养控制研究[M]//张宏福. 饲料营养研究进展. 北京: 中国农业科学技术出版社, 2010.
- ZHU Wei-yun, MAO Sheng-yong, CHENG Yan-fen. Study on the mechanism of methane production and nutritional control in the rumen of ruminantia[M]//ZHANG Hong-fu. Advanced research in feed nutrition. Beijing: China Agricultural Science and Technology Press, 2010.
- [22] Liebig M A, Gross J R, Kronberg S L, et al. Grazing management contributions to net global warming potential: A long-term evaluation in the Northern Great Plains[J]. *Journal of Environmental Quality*, 2010, 39(3): 799-809.
- [23] Hook S E, Wright A D, McBride B W. Methanogens: Methane producers of the rumen and mitigation strategies[J]. *Archaea*, 2010, 945785.
- [24] Liu Y, Whitman W B. Metabolic, phylogenetic, and ecological diversity of the methanogenic archaea[J]. *Annals of the New York Academy of Sciences*, 2008, 1125:171-189.
- [25] Poulsen M, Schwab C, Jensen B B, et al. Methylophilic methanogenic Thermoplasmata implicated in reduced methane emissions from bovine rumen[J]. *Nat Commun*, 2013, 4:1428.
- [26] Demirel B, Scherer P. The roles of acetotrophic and hydrogenotrophic methanogens during anaerobic conversion of biomass to methane: A review[J]. *Reviews in Environmental Science and Bio / Technology*, 2008, 7(2): 173-190.
- [27] Janssen P H, Kirs M. Structure of the archaeal community of the rumen[J]. *Applied and Environmental Microbiology*, 2008, 74 (12): 3619-3625.
- [28] Iino T, Tamaki H, Tamazawa S, et al. Candidatus Methanogranum caenicola: A novel methanogen from the anaerobic digested sludge, and proposal of Methanomassiliococcaceae fam. nov. and Methanomassiliococcales ord. nov., for a methanogenic lineage of the class Thermoplasmata[J]. *Microbes and Environments*, 2013, 28(2): 244-250.
- [29] Hegarty R S, Gerdes R. Hydrogen production and transfer in the rumen[J]. *Recent Advances in Animal Nutrition in Australia*, 1999, 12: 37-44.
- [30] Van Lingen H J, Plugge C M, Fadel J G, et al. Thermodynamic driving force of hydrogen on rumen microbial metabolism: A theoretical investigation[J]. *PLoS ONE*, 2016, 11(10): e0161362.
- [31] Wang M, Janssen P H, Sun X Z, et al. A mathematical model to describe in vitro kinetics of H₂ gas accumulation[J]. *Animal Feed Science and Technology*, 2013, 184(1/2/3/4): 1-16.
- [32] Wang R, Wang M, Ungerfeld E M, et al. Nitrate improves ammonia incorporation into rumen microbial protein in lactating dairy cows fed a low-protein diet[J]. *Journal of Dairy Science*, 2018, 101(11): 9789-9799.
- [33] Janssen P H. Influence of hydrogen on rumen methane formation and fermentation balances through microbial growth kinetics and fermentation thermodynamics[J]. *Animal Feed Science and Technology*, 2010, 160(1/2): 1-22.
- [34] Guyader J, Eugène M, Meunier B, et al. Additive methane-mitigating effect between linseed oil and nitrate fed to cattle[J]. *Journal of Animal Science*, 2015, 93:3564-3577.
- [35] Zhang X, Wang M, Wang R, et al. Urea plus nitrate pretreatment of rice and wheat straws enhances degradation and reduces methane production in in vitro ruminal culture[J]. *Journal of the Science of Food and Agriculture*, 2018, 98(14):5205-5211.
- [36] Wang M, Sun X Z, Janssen P H, et al. Responses of methane production and fermentation pathways to the increased dissolved hydrogen concentration generated by eight substrates in in vitro ruminal cultures[J]. *Animal Feed Science and Technology*, 2014, 194:1-11.
- [37] Ungerfeld E M. A theoretical comparison between two ruminal electron sinks[J]. *Front Microbiol*, 2013, 4: 319-333.
- [38] Bannink A, Kogut J, Dijkstra J, et al. Estimation of the stoichiometry of volatile fatty acid production in the rumen of lactating cows[J]. *Journal of Theoretical Biology*, 2006, 238(1): 36-51.
- [39] Moe P W, Tyrrell H F. Methane production in dairy cows[J]. *Journal of Dairy Science*, 1979, 62(10): 1583-1586.
- [40] Wang M, Wang R, Xie T Y, et al. Shifts in rumen fermentation and microbiota are associated with dissolved ruminal hydrogen concentrations in lactating dairy cows fed different types of carbohydrates[J]. *Journal of Nutrition*, 2016, 146(9): 1714-1721.
- [41] Reinart E, Yepes L, Sarmiento F, et al. Dietary effects on pH, temperature and ruminal methane emission by Holstein cows[J]. *Revista Facultad Nacional de Agronomía Medellín*, 2018, 71(1): 8437-8443.
- [42] Beauchemin K A, Henry Janzen H, Little S M, et al. Life cycle assessment of greenhouse gas emissions from beef production in western Canada: A case study[J]. *Agricultural Systems*, 2010, 103(6): 371-379.
- [43] Pelletier N, Pirog R, Rasmussen R. Comparative life cycle environmental impacts of three beef production strategies in the Upper Midwestern United States[J]. *Agricultural Systems*, 2010, 103(6): 380-389.
- [44] Castillo M. Forage quality: Concepts and practices[J]. *Better Crops with Plant Food*, 2017, 101(4): 29-31.
- [45] Boadi D, Benchaar C, Chiquette J, et al. Mitigation strategies to reduce enteric methane emissions from dairy cows: Update review[J]. *Canadian Journal of Animal Science*, 2004, 84(3): 319-335.
- [46] Beauchemin K A, Kreuzer M, O'mara F, et al. Nutritional management for enteric methane abatement: A review[J]. *Australian Journal*

- of *Experimental Agriculture*, 2008, 48(2): 21–27.
- [47] J B. Methane abatement strategies based on genetics and dietary manipulation of ruminants: A review[J]. *Archivos de Zootecnia*, 2018, 67(259): 448–458.
- [48] Pragna P, Chauhan S S, Sejian V, et al. Climate change and goat production: Enteric methane emission and its mitigation[J]. *Animals*, 2018, 8(12): 235.
- [49] Okine E K, Mathison G W, Hardin R T. Effects of changes in frequency of reticular contractions on fluid and particulate passage rates in cattle[J]. *Journal of Animal Science*, 1989, 67:3388–3396.
- [50] Van Zijderveld S M, Gerrits W J, Apajalahti J A, et al. Nitrate and sulfate: Effective alternative hydrogen sinks for mitigation of ruminal methane production in sheep[J]. *Journal of Dairy Science*, 2010, 93(12): 5856–5866.
- [51] Patra A K. The effect of dietary fats on methane emissions, and its other effects on digestibility, rumen fermentation and lactation performance in cattle: A meta-analysis[J]. *Livestock Science*, 2013, 155(2/3): 244–254.
- [52] Zhang X M, Medrano R F, Wang M, et al. Corn oil supplementation enhances hydrogen use for biohydrogenation, inhibits methanogenesis, and alters fermentation pathways and the microbial community in the rumen of goats[J]. *Journal of Animal Science*, 2019, 97(12): 4999–5008.
- [53] Mcallister T A, Newbold C J. Redirecting rumen fermentation to reduce methanogenesis[J]. *Australian Journal of Experimental Agriculture*, 2008, 48(2): 7.
- [54] Czerkawski J W. An introduction to rumen studies[M]. Oxford, UK: Pergamon Press, 1986.
- [55] Benchaar C, Hassanat F, Martineau R, et al. Linseed oil supplementation to dairy cows fed diets based on red clover silage or corn silage: Effects on methane production, rumen fermentation, nutrient digestibility, N balance, and milk production[J]. *Journal of Dairy Science*, 2015, 98(11): 7993–8008.
- [56] Lee C, Beauchemin K A. A review of feeding supplementary nitrate to ruminant animals: Nitrate toxicity, methane emissions, and production performance[J]. *Canadian Journal of Animal Science*, 2014, 94(4): 557–570.
- [57] Hristov A N, Oh J, Giallongo F, et al. An inhibitor persistently decreased enteric methane emission from dairy cows with no negative effect on milk production[J]. *Proceedings of the National Academy of Sciences*, 2015, 112(34): 10663–10668.
- [58] Jayanegara A, Sarwono K A, Kondo M, et al. Use of 3-nitrooxypropanol as feed additive for mitigating enteric methane emissions from ruminants: A meta analysis[J]. *Italian Journal of Animal Science*, 2018, 17(3): 650–656.
- [59] Aguerre M J, Wattiaux M A, Powell J M, et al. Effect of forage-to-concentrate ratio in dairy cow diets on emission of methane, carbon dioxide, and ammonia, lactation performance, and manure excretion[J]. *Journal of Dairy Science*, 2011, 94(6): 3081–3093.
- [60] Dong L, Li B, Diao Q. Effects of dietary forage proportion on feed intake, growth performance, nutrient digestibility, and enteric methane emissions of holstein heifers at various growth stages[J]. *Animals*, doi: 10.3390/ani9100725
- [61] Kennedy P M, Charmley E. Methane yields from Brahman cattle fed tropical grasses and legumes[J]. *Animal Production Science*, 2012, 52(4): 225.
- [62] Van Gastelen S, Dijkstra J, Bannink A. Are dietary strategies to mitigate enteric methane emission equally effective across dairy cattle, beef cattle, and sheep?[J]. *Journal of Dairy Science*, 2019, 102(7): 6109–6130.
- [63] Khan K, Khan S, Ullah S, et al. Nutritive value, fiber digestibility and methane production potential of tropical forages in rabbits: Effect of species and harvest maturity[J]. *The Journal of Animal and Plant Sciences*, 2017, 27(4): 1094–1100.
- [64] Chaves A V, Thompson L C, Iwaasa A D, et al. Effect of pasture type (alfalfa vs. grass) on methane and carbon dioxide production by yearling beef heifers[J]. *Canadian Journal of Animal Science*, 2006, 86(3): 409–418.
- [65] Martin C, Ferlay A, Mosoni P, et al. Increasing linseed supply in dairy cow diets based on hay or corn silage: Effect on enteric methane emission, rumen microbial fermentation, and digestion[J]. *Journal of Dairy Science*, 2016, 99(5): 3445–3456.
- [66] Niderkorn V, Copani G, Martin C, et al. Effects of including bioactive legumes in grass silage on digestion parameters, nitrogen balance and methane emissions in sheep[J]. *Grass and Forage Science*, 2019, 74(4): 626–635.
- [67] Beever D E, Thomson D J, Ulyatt M J, et al. The digestion of fresh perennial ryegrass (*Lolium perenne* L. cv. Melle) and white clover (*Trifolium repens* L. cv. Blanca) by growing cattle fed indoors[J]. *British Journal of Nutrition*, 1985, 54(3): 763–775.
- [68] Waghorn G C, Hegarty R S. Lowering ruminant methane emissions through improved feed conversion efficiency[J]. *Animal Feed Science and Technology*, 2011, 166/167: 291–301.
- [69] Goopy J P, Donaldson A, Hegarty R, et al. Low-methane yield sheep have smaller rumens and shorter rumen retention time[J]. *British Journal of Nutrition*, 2014, 111(4): 578–585.
- [70] Hammond K J, Pacheco D, Burke J L, et al. The effects of fresh forages and feed intake level on digesta kinetics and enteric methane emissions from sheep[J]. *Animal Feed Science and Technology*, 2014, 193: 32–43.
- [71] Huhtanen P, Ramin M, Cabezas-Garcia E H. Effects of ruminal digesta retention time on methane emissions: A modelling approach[J]. *Animal Production Science*, 2016, 56(3): 501.
- [72] Mccaughy W P, Wittenberg K, Corrigan D. Impact of pasture type on methane production by lactating beef cows[J]. *Canadian Journal of Animal Science*, 1999, 79(2): 221–226.
- [73] Mc Geough E J, O'kiely P, Hart K J, et al. Methane emissions, feed intake, performance, digestibility, and rumen fermentation of finishing beef cattle offered whole-crop wheat silages differing in grain content [J]. *Journal of Animal Science*, 2010, 88(8): 2703–2716.
- [74] Pinares-Patiño C S, Franco F E, Molano G, et al. Feed intake and methane emissions from cattle grazing pasture sprayed with canola oil [J]. *Livestock Science*, 2016, 184:7–12.
- [75] Judy J V, Bachman G C, Brown-Brandl T M, et al. Reducing methane

- production with corn oil and calcium sulfate: Responses on whole-animal energy and nitrogen balance in dairy cattle[J]. *Journal of Dairy Science*, 2019, 102(3): 2054–2067.
- [76] Martin C, Rouel J, Jouany J P, et al. Methane output and diet digestibility in response to feeding dairy cows crude linseed, extruded linseed, or linseed oil[J]. *Journal of Animal Science*, 2008, 86(10): 2642–2650.
- [77] Beauchemin K A. Dietary mitigation of enteric methane from cattle[J]. *CAB Reviews: Perspectives in Agriculture, Veterinary Science, Nutrition and Natural Resources*, 2009, 4(35): 1–18.
- [78] Van Zijderveld S M, Gerrits W J, Dijkstra J, et al. Persistency of methane mitigation by dietary nitrate supplementation in dairy cows[J]. *Journal of Dairy Science*, 2011, 94(8): 4028–4038.
- [79] Lee C, Araujo R C, Koenig K M, et al. Effects of encapsulated nitrate on enteric methane production and nitrogen and energy utilization in beef heifers[J]. *Journal of Animal Science*, 2015, 93: 2391–2404.
- [80] Li L, Davis J, Nolan J, et al. An initial investigation on rumen fermentation pattern and methane emission of sheep offered diets containing urea or nitrate as the nitrogen source[J]. *Animal Production Science*, 2012, 52(7): 653.
- [81] Arif M, Sarwar M, Mehr-Un-Nisa, et al. Effect of supplementary sodium nitrate and sulphur on methane production and growth rates in sheep and goats fed forage based diet low in true protein[J]. *Journal of Animal and Plant Sciences*, 2016, 26(1): 69–78.
- [82] Zhang X, Medrano R F, Wang M, et al. Effects of urea plus nitrate pretreated rice straw and corn oil supplementation on fiber digestibility, nitrogen balance, rumen fermentation, microbiota and methane emissions in goats[J]. *Journal of Animal Science and Biotechnol*, 2019, 10: 6.
- [83] Van Wesemael D, Vandaele L, Ampe B, et al. Reducing enteric methane emissions from dairy cattle: Two ways to supplement 3-nitrooxypropanol[J]. *Journal of Dairy Science*, 2019, 102(2): 1780–1787.
- [84] Romero-Perez A, Okine E K, Mcginn S M, et al. Sustained reduction in methane production from long-term addition of 3-nitrooxypropanol to a beef cattle diet[J]. *Journal of Animal Science*, 2015, 93(4): 1780–1791.
- [85] Vyas D, Mcginn S M, Duval S M, et al. Effects of sustained reduction of enteric methane emissions with dietary supplementation of 3-nitrooxypropanol on growth performance of growing and finishing beef cattle[J]. *Journal of Animal Science*, 2016, 94(5): 2024–2034.
- [86] Martínez-Fernández G, Abecia L, Arco A, et al. Effects of ethyl-3-nitrooxy propionate and 3-nitrooxypropanol on ruminal fermentation, microbial abundance, and methane emissions in sheep[J]. *Journal of Dairy Science*, 2014, 97(6): 3790–3799.
- [87] Odongo N E, Bagg R, Vessie G, et al. Long-term effects of feeding monensin on methane production in lactating dairy cows[J]. *Journal of Dairy Science*, 2007, 90(4): 1781–1788.
- [88] Vyas D, Alemu A W, Mcginn S M, et al. The combined effects of supplementing monensin and 3-nitrooxypropanol on methane emissions, growth rate, and feed conversion efficiency in beef cattle fed high-forage and high-grain diets[J]. *Journal of Animal Science*, 2018, 96(7): 2923–2938.
- [89] Puchala R, Leshure S, Gipson T A, et al. Effects of different levels of lespeche and supplementation with monensin, coconut oil, or soybean oil on ruminal methane emission by mature Boer goat wethers after different lengths of feeding[J]. *Journal of Applied Animal Research*, 2018, 46(1): 1127–1136.
- [90] Guan H, Wittenberg K M, Ominski K H, et al. Efficacy of ionophores in cattle diets for mitigation of enteric methane[J]. *Journal of Animal Science*, 2006, 84(7): 1896–1906.
- [91] Grainger C, Williams R, Eckard R J, et al. A high dose of monensin does not reduce methane emissions of dairy cows offered pasture supplemented with grain[J]. *Journal of Dairy Science*, 2010, 93(11): 5300–5308.
- [92] Patra A K, Yu Z. Effects of essential oils on methane production and fermentation by, and abundance and diversity of, rumen microbial populations[J]. *Applied and Environmental Microbiology*, 2012, 78(12): 4271–4280.
- [93] Cobellis G, Trabalza-Marinucci M, Yu Z. Critical evaluation of essential oils as rumen modifiers in ruminant nutrition: A review[J]. *Science of the Total Environment*, 2016, 545–546: 556–568.
- [94] Jayanegara A, Leiber F, Kreuzer M. Meta-analysis of the relationship between dietary tannin level and methane formation in ruminants from in vivo and in vitro experiments[J]. *Journal of Animal Physiology and Animal Nutrition*, 2012, 96(3): 365–375.
- [95] Machado L, Magnusson M, Paul N A, et al. Effects of marine and freshwater macroalgae on in vitro total gas and methane production[J]. *PLoS One*, 2014, 9(1): e85289.
- [96] Li X, Norman H C, Kinley R D, et al. *Asparagopsis taxiformis* decreases enteric methane production from sheep[J]. *Animal Production Science*, 2018, 58(4): 681.
- [97] Deramus H A, Clement T C, Giampola D D, et al. Methane emissions of beef cattle on forages: Efficiency of grazing management systems[J]. *Journal of Environmental Quality*, 2003, 32(1): 269–277.
- [98] Capper J L, Castaneda-Gutierrez E, Cady R A, et al. The environmental impact of recombinant bovine somatotropin (rbST) use in dairy production[J]. *Proceedings of the National Academy of Sciences of the United States of America*, 2008, 105(28): 9668–9673.
- [99] Leeb T, Roehe R, Dewhurst R J, et al. Bovine Host genetic variation influences rumen microbial methane production with best selection criterion for low methane emitting and efficiently feed converting hosts based on metagenomic gene abundance[J]. *PLoS Genetics*, 2016, 12(2): e1005846.
- [100] Shi W, Moon C D, Leahy S C, et al. Methane yield phenotypes linked to differential gene expression in the sheep rumen microbiome[J]. *Genome Research*, 2014, 24(9): 1517–1525.
- [101] Danielsson R, Dicksved J, Sun L, et al. Methane production in dairy cows correlates with rumen methanogenic and bacterial community structure[J]. *Front Microbiol*, 2017, 8: 226.
- [102] Wallace R J, Rooke J A, Mckain N, et al. The rumen microbial metagenome associated with high methane production in cattle[J]. *BMC Genomics*, 2015, 16: 839.