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盐池滩羊肉品质特性及其潜在调控机理探讨

杨攀平¹, 李惠侠^{1*}, 胡亚美^{2*}

(1. 南京农业大学动物科技学院, 江苏南京210095; 2. 宁夏大学动物科技学院, 宁夏银川750021)

摘要: 盐池滩羊是宁夏当地的优良特色畜种, 因其肉质鲜嫩、膻味轻、大理石纹明显而深受消费者青睐。但随着封山禁牧政策的实施和舍饲圈养的现代化畜牧业发展, 致使滩羊肉品质下降, 故提升滩羊肉品质风味, 改善肉品质性状成为研究者及生产者关注的重点, 而明确滩羊肉品质特征及其影响因素的作用机制对于提升羊肉品质具有重要意义。本研究从营养、遗传和环境阐述其对肌内脂肪沉积和肌纤维分化的影响及作用机理, 重点总结了瘤胃微生物对滩羊肉品质的代谢调控作用, 以期为提高滩羊肉品质奠定理论基础。

关键词: 盐池滩羊; 瘤胃微生物; 肌内脂肪; 肌肉纤维; 肉质

Exploration of meat quality characteristics of Yanchi Tan sheep and the potential regulatory mechanisms

YANG Pan-ping¹, LI Hui-xia^{1*}, HU Ya-mei^{2*}

1. College of Animal Science and Technology, Nanjing Agricultural University, Nanjing 210095, China; 2. College of Animal Science and Technology, Ningxia University, Yinchuan 750021, China

Abstract: The Yanchi Tan sheep is an excellent local breed in Ningxia, China. It is highly favored by consumers because of its tender meat, light mutton flavor, and distinct marbling. However, the implementation of mountain enclosures and grazing ban policies, coupled with the development of modern intensive animal husbandry, has led to a decline in the meat quality of Tan sheep. Improving the flavor and quality characteristics of Tan sheep meat has become a key focus for both researchers and producers. Elucidating the meat quality traits of Tan sheep and the underlying mechanisms of the influencing factors is of great significance for enhancing the overall quality of sheep meat. This study explores the effects and mechanisms of nutrition, genetics, and environment on the deposition of intramuscular fat and muscle fiber differentiation. In particular, we focus on how the metabolic regulation of rumen microbiota affects the meat quality of Tan sheep. The results of this study provide a theoretical knowledge base to guide efforts in improving the meat quality of this breed.

Key words: Yanchi Tan sheep; rumen microbiota; intramuscular fat; muscle fiber; meat quality

随着社会的进步和人民生活水平的提高, 优质、健康且高端的羊肉需求量逐年增加。羊肉是优质动物膳食蛋白的重要来源, 风味独特, 营养丰富, 深受消费者喜爱。盐池滩羊是国家级畜禽资源保护品种, 具有耐干旱、抗严

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作者简介: 杨攀平(1997—), 男, 甘肃庆阳人, 在读博士。E-mail: climbing123@163.com

* 通信作者 Corresponding author. E-mail: lihuixia@njau.edu.cn, huyamei@nxu.edu.cn

寒、耐盐碱和抗逆性强等特征^[1],其肉质细嫩、不膻不腻和鲜嫩多汁等特点被誉为羊肉界的“劳斯莱斯”^[2]。近年来,随着封山禁牧政策实施,长期圈养使得生活习性改变,以及畜禽肉市场的激烈竞争和过度追求速成肉致使滩羊肉品质下降^[3]。因此,亟须了解滩羊肉的品质特征,明晰肉质的影响因素及其分子调控机制,而目前关于滩羊肉品质影响因素及调控机制的研究报道较少。本研究总结了滩羊肉的营养和风味特征,分别从品种与宿主遗传、营养、饲养模式和瘤胃微生物等方面阐述其对肌内脂肪含量和肌纤维分化的影响及作用机理,分析了瘤胃微生物代谢对滩羊肉品质营养和风味的影响,并从“微生物—肠—脑轴”和“微生物—肠—肌肉轴”探讨滩羊胃肠道微生物对肉品质的潜在作用机理,以期提升滩羊肉品质提供理论依据。

1 滩羊肉质特征及营养属性

滩羊是肉裘毛兼用的地方特色畜种,长期的自然选择和人工培育形成了鲜嫩多汁、色泽红润、膻味轻且易消化,大理花纹明显且分布均匀的肉质特征^[3]。滩羊肉风味独特,营养丰富,被列为宁夏六大特色产业之一,图1总结了近年来滩羊相关报道中的肉质营养成分和属性。

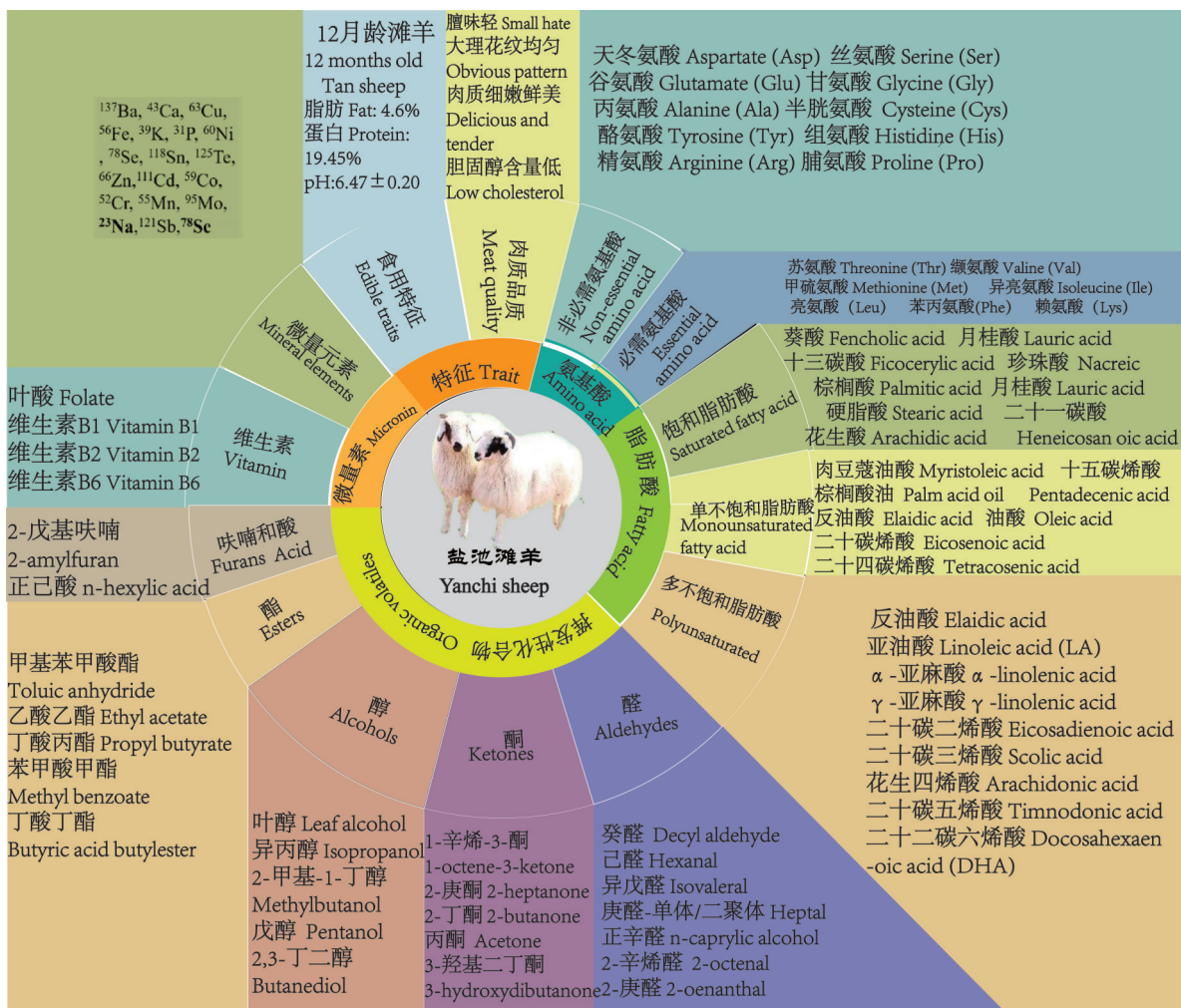


图1 滩羊肉营养组分及风味物质^[4-8]

Fig. 1 Nutrient components and flavor substances of Tan mutton

2 影响滩羊肉品质的主要因素

肉质性状是衡量畜禽品种经济特征的重要指标之一,其受宿主遗传、营养、环境、饲养管理模式等多因素综合影响。除了以上外在因素之外,肌肉本身的形态结构和化学组成直接决定肌肉品质,其中肌内脂肪

(intramuscular fat, IMF)被认为是改善羊肉品质性状的关键因子,其对肉质的嫩度、口感、多汁性和系水力等具有重要影响。另外,通过剖析肌肉组织结构发现肌纤维在运动收缩、结构支撑和能量转化中起核心作用,是另一个提高羊肉品质的重要因素。

2.1 肌内脂肪含量

肌内脂肪是指沉积在肌肉内或肌纤维间的脂肪,其含量与肉质风味、嫩度和多汁性呈正相关^[9]。IMF 含量与肌肉组织内脂肪细胞数量相关,肌肉生长与代谢影响肌内脂肪沉积,如肌肉含量多或糖酵解活性高的组织 IMF 含量较少^[10],Zhang 等^[11]证明滩羊肌肉中的总纤维数与 IMF 含量呈负相关。IMF 是一种高度可遗传性状,受多个基因的复杂调控,滩羊 IMF 受到 *ADIPOQ*、*FABP4*、*PLIN1*、*PPARGC1A* 等的正向调控^[11]。近年发现,表观遗传因子 miRNA 对草食动物的肌内脂肪也有重要调节作用,如 miR-27a 通过靶向 CPT1B 抑制绵羊前脂肪细胞的增殖而负调控 IMF 合成^[12],miR-340-5p 和 miR124-3p 通过靶向 ATF7 调节支链氨基酸的分解代谢负调控脂肪合成^[13]。性别也会影响 IMF 含量,雌性滩羊的脂肪沉积性能优于雄性滩羊^[14]。另外,研究表明,哺乳动物脂肪沉积与厚壁菌门/拟杆菌门的高比例呈正相关,在其他反刍动物中也发现瘤胃微生物丰度在脂肪沉积中发挥重要作用,Xiong 等^[15]证明了牦牛瘤胃微生物在脂肪沉积中的相关性,瘤胃微生物通过代谢产生短链脂肪酸(short chain fatty acids, SCFAs)调节胰岛素水平促进脂肪沉积。Wang 等^[16]利用数量遗传学分析方法剖析宿主遗传和瘤胃微生物对湖羊体重增加的贡献,并通过微生物全基因组关联分析(microbial genome-wide association study, mGWAS)发现毛螺菌属(*Lachnospiraceae* ND3007 group)通过发酵产生挥发性脂肪酸直接或间接使湖羊体重增加。尽管肌内脂肪含量影响盐池滩羊肉质风味的报道较少,但基于其他畜禽的研究报道,本研究推测盐池滩羊肌内脂肪含量会影响肉质风味(表 1),且肌内脂肪沉积可能由宿主遗传和瘤胃微生物共同影响。

表 1 不同添加剂对滩羊肉品质的影响

Table 1 Effects of different additives on meat quality of Tan sheep

日粮添加剂 Dietary additive	滩羊肉品质差异 Difference of meat quality of Tan sheep	参考文献 References
甘草 <i>Glycyrrhiza uralensis</i>	提高肾脂和皮下脂肪的亚油酸含量,提高羊肉的风味。Increase the content of linoleic acid and subcutaneous fat, improve the flavor of mutton.	[17]
柠条 <i>Caragana microphylla</i>	脂肪组织中不饱和脂肪酸含量增加;提高肉质中粗蛋白、粗脂肪和氨基酸含量。The content of unsaturated fatty acids in adipose tissue increased. The contents of crude protein, crude fat and amino acid in meat were increased.	[18–19]
百里香 <i>Thymus mongolicus</i>	肌肉中脂肪酸含量增加(多不饱和脂肪酸)、提高羊肉的鲜味。The fatty acid content in the muscle is increased (polyunsaturated fatty acid), which improves the umami flavor of the lamb.	[20–21]
黄芪 <i>Astragalus membranaceus</i>	0.10% 黄芪添加促进肌纤维形成,提高熟肉率和嫩度,缓解 pH 下降,改善肉质。Adding 0.10% <i>A. membranaceus</i> promotes muscle fiber formation, improves cooked meat rate and tenderness, alleviates pH drop and improves meat quality.	[22]
地椒 <i>Thymus quinquecostatus</i>	提升肌肉的保水力,提高背最长肌中与风味相关氨基酸(蛋氨酸、天冬氨酸、谷氨酸及丙氨酸等)含量,胆固醇含量降低,增加肌肉中多不饱和脂肪酸(n-6 PUFA)水平。Improve muscle water retention, increase the content of flavor-related amino acids (methionine, aspartic acid, glutamic acid and alanine, etc.) in longissimus dorsi muscle, reduce cholesterol content, and increase the level of polyunsaturated fatty acids (n-6 PUFA) in muscle.	[23]
苦豆子 <i>Sophora alopecuroides</i>	改善滩羊肌肉中脂质分布,改善肌内脂肪含量提高肉品质。Improve the lipid distribution in the muscle of Tan sheep, improve the intramuscular fat content and improve the meat quality.	[24]

2.2 肌纤维分化和类型

骨骼肌由不同肌肉纤维组成,肌纤维类型的比重是影响肉品质最重要的因素之一。研究表明 I 型肌肉纤维比例增加能延缓 pH 降低的速度,提高羊肉的系水力、多汁性和风味^[25]。肌纤维数量在动物出生后已基本恒定,在动物生长发育过程中,基因和转录因子的时空特异性表达以及机体特定的兴奋及收缩运动,使得不同纤维类型在机体的不同部位之间相互转化并表现出不同的肉质特征^[26],Cui 等^[27]表征了滩羊背最长肌和肱二头肌的差异基

因谱,筛选到 Ca^{2+} 、FoxO 和 AMPK 信号通路以及 *FBXL5* 等 8 个参与肌纤维分化的关键基因,并证实了 *circ_0017336-miR-23a-FBXL5* 调控网络在肌纤维分化中的重要调控作用。Gao 等^[28]探究不同放牧时间对滩羊肉品质的影响,发现放牧时间越长,肉品质更优良,肌肉色泽稳定;日粮中添加 1.0%(干物质基础)能降低滩羊 II a 型肌纤维和 II b 型肌纤维比例,增加肌肉持水力^[29];饲料中添加黄芪多糖能增加滩羊粗纤维的生长,改善屠宰性能^[17]。低水平的甲状腺激素会导致 MHC 亚型由快速向缓慢转变:MHC IIB→MHC IIX→MHC IIA→MHC I^[26],但目前尚未有相关激素对滩羊肉品质影响的研究报道。另外,瘤胃微生物对肌纤维类型转化也可能具有重要影响,Liu 等^[30]开展的体内试验,在苏尼特羔羊饲料中添加益生菌(植物乳杆菌 HM-10 和干酪乳杆菌)调节瘤胃菌群丰度,发现 I 型肌纤维比例显著增加。

3 滩羊肉质调控机制研究进展

通过改变肌内脂肪沉积和肌肉纤维类型转化提高羊肉品质已成为肉品科学和畜牧业生产领域的研究热点,进一步探究骨骼肌生长发育机理为肉品质提升和遗传改良奠定理论依据。本部分从转录因子、基因参与重要信号通路的调控和瘤胃微生物代谢调控两方面探讨滩羊优良肉品质的可能发生机制。

3.1 分子调控机制

肌内脂肪和肌纤维类型组成都属于中等遗传性状。Ma 等^[31]使用 Illumina Ovine SNP 600 K BeadChip 对滩羊的拷贝数变异(copy number variation, CNV)进行全基因组检测,发现主要变异与脂质代谢相关,且主要富集于 AMPK 信号通路、Notch 信号通路和 VEGF 信号通路中,推测可能通过调控肌内前体脂肪细胞分化影响脂肪沉积。AMPK 被视为促进反刍动物(牛、羊)大理石纹生成的分子靶标^[32-33],AMPK 能调节 C/EBP β 、PPAR γ 、C/EBP α 的表达效应生成脂肪^[34],血管内皮生长因子(vascular endothelial growth factor, VEGF)是调控血管生成的重要因子,通过激活 Akt/mTOR 诱导角质形成细胞和血管平滑肌细胞等^[35-36]。 Ca^{2+} 、FoxO 和 AMPK 信号通路调控 ACACB、ATP6V0A1、ASAH1、EFHB、MYL3、SFSWAP 和 *FBXL5* 作用于滩羊肌纤维分化中^[27]。Wnt 信号通路在脂肪沉积和肌纤维转化过程中起重要作用,I 型纤维转化主要基于 Wnt/ Ca^{2+} 和 Wnt/PI3K 信号通路调节 T 细胞核受体(nuclear factor of activated T-cells, NFAT)促进/诱导慢型肌纤维转化^[37],调节肌肉生长抑制蛋白(myostatin, MSTN)、脂肪酸结合蛋白(heart-type fatty acid binding protein, H-FABP)和钙蛋白酶抑制蛋白(calpain small subunit, CAST)的活性^[38](图 2)。研究发现,MicroRNA 介导的转录后调控参与 IMF 生成具有重要作用。miR-27b 可靶向结合 PPAR γ 调控脂肪沉积,miR-30b 可促进脂肪前体细胞增殖分化^[27]。

3.2 瘤胃微生物作用机制

动物是由宿主和共栖微生物构成的“共同体”,瘤胃微生物代谢产生 SCFAs、胆汁酸等活性物质通过直接或间接调控宿主的免疫防御、营养吸收和生产性能发挥,维护宿主健康稳态。反刍动物的瘤胃中定殖着数以万计的

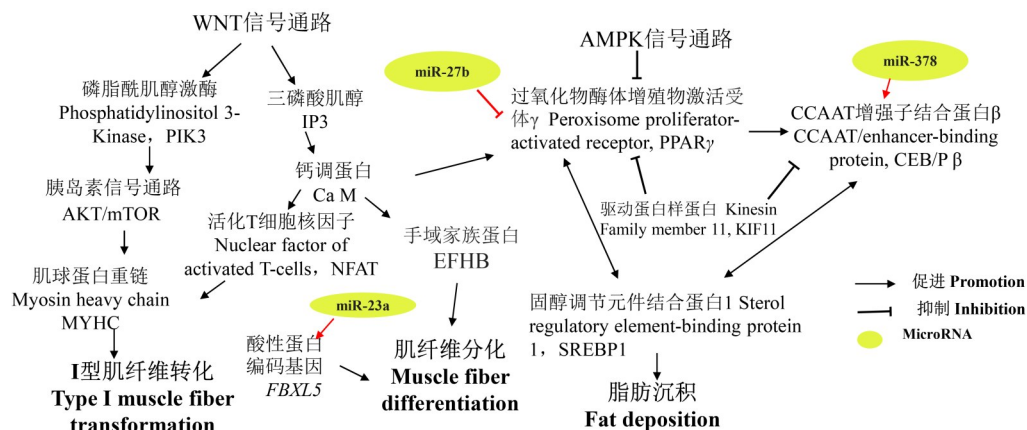


图 2 信号分子/转录因子的调控分子途径

Fig. 2 Regulatory molecular pathways of signaling molecules/transcription factors

微生物,包括原核生物(细菌和古菌)和真核生物(真菌和原虫),它们能将人类无法消化食用的植物源木质纤维素等非均质聚合物转化为高营养的肉、蛋和奶等供人类食用。研究表明,单胃动物肠道微生物与肉品质密切相关,本节结合盐池滩羊以及其他反刍动物的研究进展,阐述瘤胃微生物可能对肉质机理的影响。

3.2.1 饲料改善盐池滩羊肉质的作用机制 牧草是反刍动物获取营养物质的重要来源,是改善动物肉品质和风味的重要途径。盐池地处荒漠草原,属典型的大陆性季风气候,日照长且昼夜温差大的特点益于牧草中脂肪酸沉积^[39](牧草中的脂肪酸类型如图3所示)。日粮中营养组分影响肉中脂肪酸成分,滩羊采食富含多不饱和脂肪酸(polyunsaturated fatty acids, PUFAs)的植被利于其在肉中沉积。PUFAs 含有多种风味前体,食用后也能降低心血管类疾病、糖尿病、肿瘤的发病率^[40]。此外,牧草中富含单宁、白藜芦醇、黄酮等生物活性物质可通过调节瘤胃微生物多样性和生物发生途径改善肉品质重要营养和风味前体物质的合成。生物氢化作用是瘤胃微生物降低不饱和脂肪酸毒性的生物过程,通过加氢反应降低肉质中不饱和脂肪酸含量,劣化肉质风味。单宁通过降低丁酸弧菌属的菌群丰度抑制生物氢化反应,增加瘤胃液中活性物质 C18:1 t11(牛痘酸, vaccenic acid, VA)和 C18:2 c9-t11(瘤胃酸, rumen acid, RA)含量以及支链脂肪酸(branched-chain fatty acids, BCFA)浓度^[41]。白藜芦醇(*Resveratrol*)可激活去乙酰化酶 1(sirtuin 1, SIRT1),抑制 AMP 激酶信号通路(AMP-activated protein kinase, AMPK)促进脂肪沉积^[42]。日粮中添加沙棘(*Hippophae rhamnoides*)果渣通过促进转录因子 ZNF423、PPAR γ 和 C/EBP α 表达,提高 ACC 和 FAS 酶活性,促进甘油三酯合成,增加羊肉 IMF 沉积^[43]。上述研究结果表明,日粮通过调节瘤胃菌群丰度和生物发生过程,改善肉质脂肪酸谱,提高不饱和脂肪酸含量,另一方面,饲料中的生物活性物质可作用于脂质生物合成关键基因影响脂质生物合成过程。

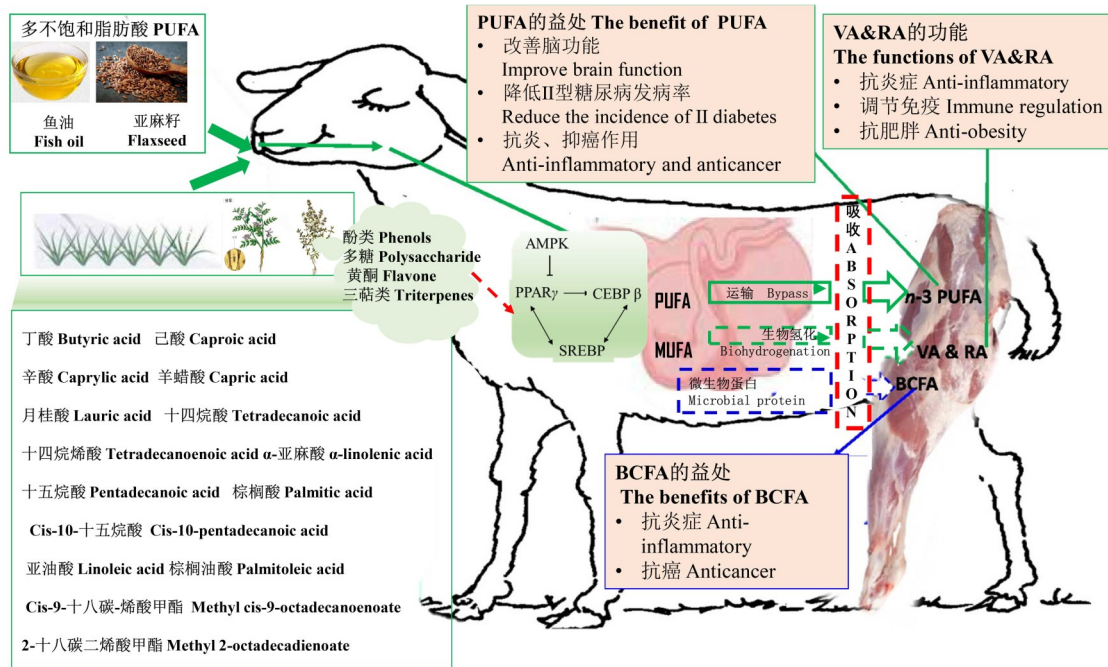


图3 饲料对滩羊肉质脂肪酸谱的可能影响途径

Fig. 3 Possible influence of diet on fatty acid profile of Tan sheep meat

3.2.2 饲养模式影响胃肠道功能及滩羊肉品质 饲养模式是影响动物肉品质的重要因素。Wang等^[44]发现放牧组滩羊的瘦肉率显著高于舍饲组,且肉质中甜味氨基酸(Gly、Ala、Ser和Thr)和鲜味氨基酸(Glu和Asp)含量以及 ω -3多不饱和脂肪酸(ω -3 PUFA)含量高于舍饲组。郭帅等^[45]研究表明,舍饲组滩羊的肌内脂肪含量、嫩度以及pH稳定性明显优于放牧组。Gao等^[28]研究发现长期放牧利于滩羊肉色的形成和稳定。饲喂模式引起的肉品质风味差异与瘤胃功能代谢相关。Zhang等^[46]研究表明不同饲喂方式的滩羊瘤胃微生物存在显著差异,放牧

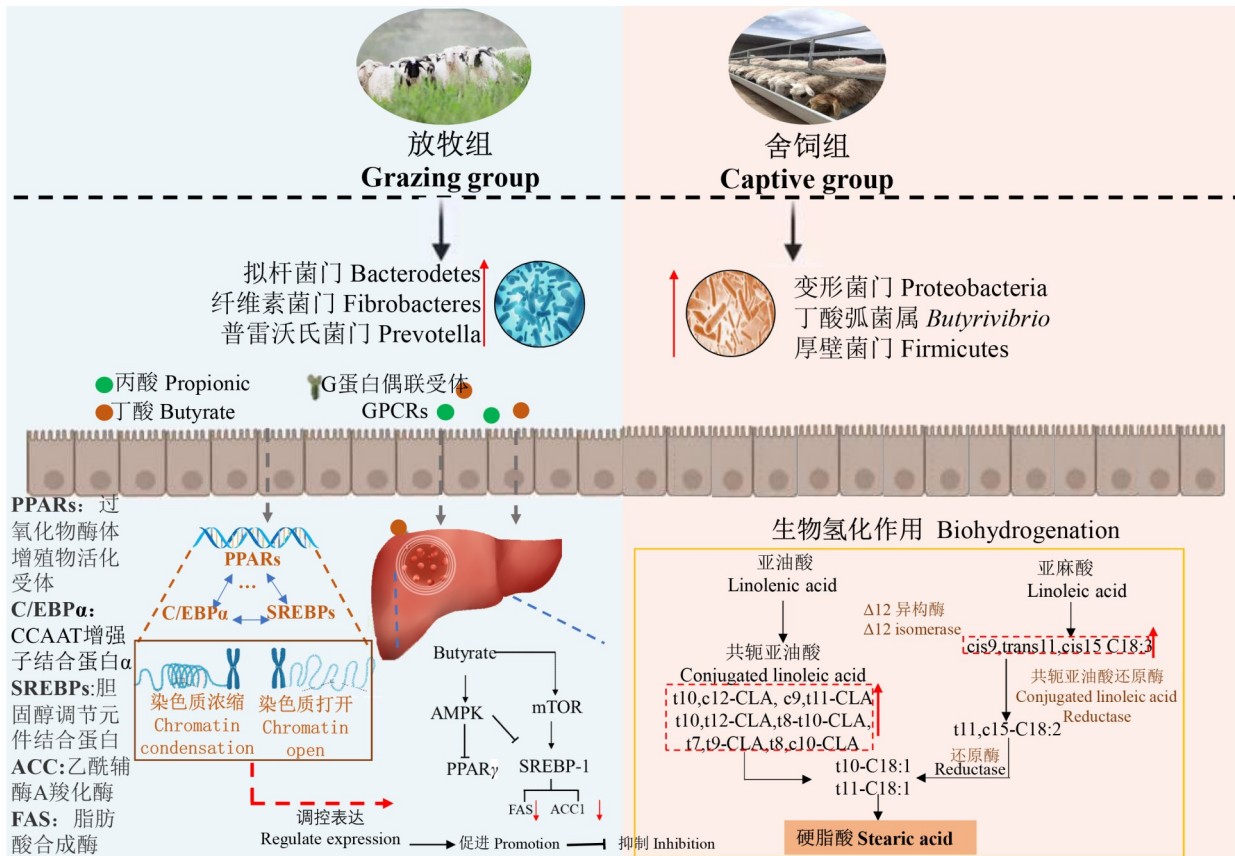


图4 不同饲喂模式对滩羊瘤胃代谢的影响

Fig. 4 Effects of different feeding patterns on meat quality of Tan sheep

组中拟杆菌门和普雷沃氏菌门的丰度低于舍饲组,其中拟杆菌能利用植物纤维发酵产生丙酸和丁酸,在小鼠中已被证实丁酸盐是一种 AMPK 激活剂,通过级联调控抑制肝脏 (ACC1 和 SREBP1) 和腹部脂肪 (FAS、PPAR γ 和 LPL) 中脂肪生成基因的表达,阻遏脂肪沉积^[47]。厚壁菌门是舍饲组的优势菌群,其与动物的脂肪沉积呈正相关^[48]。舍饲组富集着多种与生物氢化作用相关的细菌, *Butyrivibrio* 属和 *Pseudobutyrvibrio* 属能分泌 *cis*-9, *trans*-11 共轭亚油酸异构酶或还原酶参与亚油酸、亚麻酸等共轭脂肪酸的生物氢化,进而影响肉质中脂肪酸组成和肉质风味^[44-49](图 4)。故舍饲有利于脂肪沉积和生产性能发挥,而放牧更利于生产优质风味营养的肉质。另外,圈养饲喂可能会导致动物恐惧、焦虑等应激行为,影响胃肠道微生物结构与功能,可能通过“微生物-肠-脑轴”等远端调控途径影响机体代谢,影响肌内脂肪沉积与肌纤维分化调控羊肉性状,但仍需进一步研究证实。

3.2.3 瘤胃微生物代谢对滩羊肉品质的潜在作用机制 胃肠道是动物消化食物、吸收营养的场所,反刍动物瘤胃发酵产生的 SCFA 不仅是宿主代谢活动的能源物质,同时也是连接瘤胃与机体代谢互作的媒介,参与糖代谢、蛋白质合成和脂肪沉积等。目前,瘤胃微生物对肉品质的调控主要聚焦于“微生物-肠-脑轴”和“微生物-肠-肌肉轴”介导肌内脂肪沉积、肌纤维类型转化调控^[10, 30],可能的作用模式如图 5 所示。SCFAs 为主要效应信号分子,通过循环系统调节脂肪酸结合蛋白 (fatty acid binding protein, FABP)、肉碱棕榈酰转移酶 2 (carnitine palmitoyltransferase 2, CPT2)、脂肪酸合成酶 (fatty acid synthase, FASN)、硬脂酰辅酶 A 去饱和酶 (stearoyl-CoA desaturase, SCD) 和乙酰辅酶 A 羧化酶 (acetyl-CoA carboxylase, ACC) 等脂肪代谢相关蛋白的表达活性,促进脂肪酸从头合成^[50], SCFAs 经血液循环至肌肉组织中,激活过氧化物酶体增生物激活受体 γ (peroxisome proliferator-activated receptor, PPAR γ), 选择性诱导 FABP3 和 CPT1 表达调控脂肪酸摄取和 β 氧化^[51], 影响肌肉特征与脂肪沉积;瘤胃代谢产生短链脂肪酸或神经递质前体,如乙酰胆碱,可调节神经系统促进胰岛素分泌,通过高表达胆固醇调节元件结合蛋白 1 (sterol regulatory element-binding protein 1, SREBP1) 等间接促进肝脏中脂

肪酸合成和肌肉中脂肪沉积。另外,细菌分泌的内毒素也会对肌肉发育产生影响。研究发现LPS水平升高与骨骼肌收缩丧失相关,这可能是LPS激活了肌肉蛋白的泛素-蛋白酶体分解途径导致诱发萎缩^[52]。LPS通过TLR-NF- κ B和自分泌/旁分泌TNF- α 途径抑制成肌分化蛋白(myoblast determination protein, MyoD)和肌生成素表达,上调MSTN表达进而抑制C2C12细胞分化,且LPS对肌肉分化的抑制作用表现出浓度依赖性^[53]。因此,调控瘤胃菌群稳态对于反刍动物肉质风味提升和改善肌肉发育都具有重要作用。

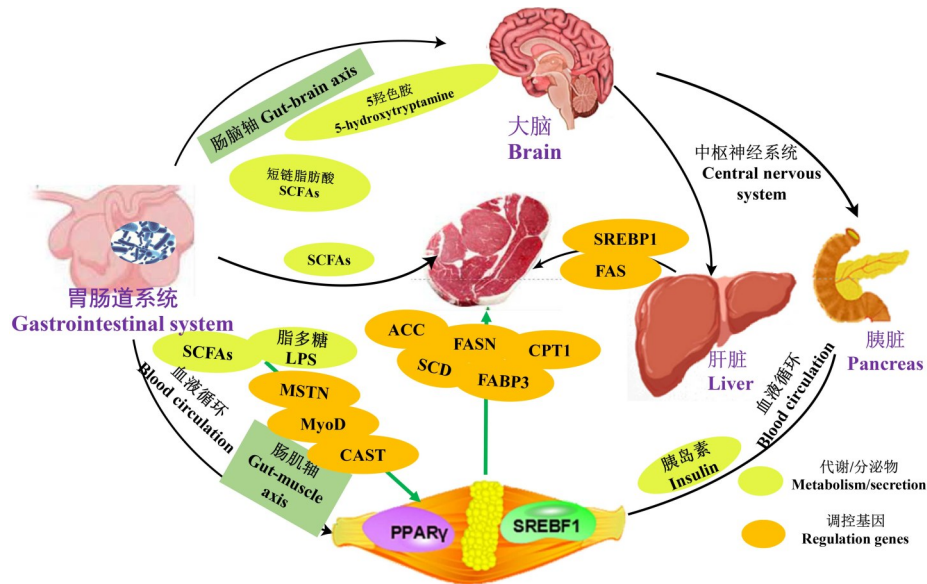


图5 胃肠道微生物对骨骼肌发育和肌内脂肪沉积影响模式

Fig. 5 Model of effects of gastrointestinal microorganisms on skeletal muscle development and intramuscular fat deposition

4 小结与展望

综上所述,盐池滩羊肉质鲜嫩,膻味轻且大理花纹明显等优良肉质性状是由宿主遗传、饮食和饲喂方式等共同作用于肌内脂肪沉积和肌纤维转化的结果,其中瘤胃微生物直接或间接调节肌肉脂肪酸谱和肌肉发育,影响肉质风味和营养价值。关于影响滩羊肌内脂肪沉积和肌纤维分化的转录因子和代谢通路已取得了一些研究进展,这些研究为进一步提升滩羊肉品质提供理论依据。然而,早期滩羊以优良裘皮生产著称,对于肉质的研究进展较慢。有关优良滩羊肉品质提升,以及饮食、环境、管理和宿主遗传之间的互作对于肉质性状改善存在一些需要进一步探究的关键科学问题和挑战,主要包括:1)精准育种技术的开发。基因组测序技术挖掘与性状密切相关的遗传变异是家畜育种与肉质性状改良的重要途径,应用选择信号法、全基因关联分析和全基因选择分析、筛选及定位肉质性状相关变异,构建完善育种模型以选育优良性状;2)多组学联合分析滩羊肉品质性状代谢分子机制。对于肉品质研究,肌纤维类型、脂肪酸和氨基酸组成以及肌内脂肪沉积相关代谢物等影响肉质风味和嫩度的因素都应纳入肉质评价指标中,并将风味组、代谢组、脂质组等多组学技术与基因组联合应用,筛选与滩羊肉品质和嫩度相关的候选基因和靶标代谢物,构建基因的调控网络,揭示营养物质的肉质调控机理和分子作用途径,从候选基因的转录前、转录后和表观遗传方面探究滩羊肉品质调控机制。3)精细化经营模式开发。饲料组分与饲养模式都是影响滩羊肉品质的重要因素,以滩羊生长阶段为时间轴,合理调整营养成分与饲养模式,构建高品质优质滩羊肉的管理模式。4)关注瘤胃微生物对肉品质、风味的贡献。瘤胃微生物对于饲料消化利用、能量物质转化、脂肪沉积和肉质风味都具有重要影响,关于瘤胃微生物对滩羊肉品质性状影响的研究较少,也尚未有详细报道有关瘤胃微生物的作用途径和机理。总之,从宿主遗传、营养和饲喂管理模式以及瘤胃微生物4方面开展滩羊肉品质研究,筛选影响肉品质的分子标记,深入探究候选基因的表达与功能,是未来滩羊肉品质改善的重要方向。

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