浓香型白酒发酵体系中己酸菌的研究进展

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摘 要：浓香型白酒发酵体系中己酸生成菌（以下简称“己酸菌”）的己酸合成代谢对提高浓香型白酒的发酵质量非常重要。因此，有必要深入全面了解浓香型白酒发酵体系中己酸菌的种类及其己酸合成代谢特征。本综述介绍了目前浓香型白酒发酵体系中已经分离的己酸菌株的种类多样性、系统进化关系、生理代谢特征、己酸合成代谢机制以及其与己酸菌、非己酸菌之间的协同代谢关系。本文可为理解己酸菌群在浓香型白酒发酵体系中的原位己酸合成代谢规律提供参考，为将来靶向提高己酸菌群在浓香型白酒发酵和生物质转化高附加值己酸工艺中进行己酸合成培养工程的应用提供理论依据。

关键词：浓香型白酒发酵体系；己酸菌株；代谢特征；己酸合成机制；己酸菌群；协同代谢

Research Progress on Caproic Acid-Producing Bacteria in Chinese Strong-Flavor Baijiu Fermentation Ecosystem

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Abstract: In the Chinese strong-flavor Baijiu (CSFB) fermentation ecosystem, the caproic acid-anabolism of caproic acid-producing bacteria (CPBs) is very important for improving the fermentation quality of CSFB. Therefore, it is necessary to thoroughly understand the types of CPBs and their caproic acid-anabolism characteristics. This minireview introduces readers to the diversity, phylogenetic relationship, physiological and metabolic characteristics, and caproic acid synthesis mechanism of CPBs isolated from the CSFB fermentation ecosystem as well as their synergistic metabolic relationships with other CPBs or non-CPBs. This paper provides a reference for understanding the *in-situ* caproic acid-anabolism pattern of CPBs from the CSFB fermentation ecosystem, and further provides a theoretical basis for the future targeted application of CPBs in CSFB fermentation and for CPBs culture engineering for the synthesis of high value-added caproic acid.

Keywords: Chinese strong-flavor Baijiu fermentation ecosystem; caproic acid-producing bacteria; metabolic characteristics; caproic acid anabolism; caproic acid-producing bacteria community; synergistic metabolism

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浓香型白酒是我国十二大香型白酒（浓香、酱香、清香、米香、芝麻香、馥郁香、老白干、豉香、药香、特香、兼香、凤香）之一，其产量和销量占白酒总量的70%以上[1]，因此，提高其发酵质量非常重要。占白酒含量约2%的风味物质中，四大酯（乳酸乙酯、乙酸乙酯、己酸乙酯和丁酸乙酯）对白酒品质影响最大[2]。在浓香型白酒中，就相对含量来说，己酸乙酯的相对含量（62.28%）最多，乳酸乙酯的相对含量（12.51%）最少；就评估酯类香气贡献的主要参数气味活性值（odorant activity value，OAV）和风味稀释因子（flavor dilution factor，FD）来说，己酸乙酯的OAV（26 890～137 558）和FD（4 096～59 049）远大于其余三者，而乳酸乙酯的OAV（5～8）和FD（1～32）最小[3]。在GB/T 10781.1—2021《白酒质量要求第1部分：浓香型白酒》中，己酸乙酯被定义为主要特征风味物质。己酸乙酯对浓香型白酒兼具菠萝香与辛辣味的独特酒香风味贡献最大[2-3]。质量较好的“优级”浓香型白酒中己酸乙酯的含量是普通一级浓香型白酒的175%～200%。因此，增加浓香型白酒中己酸乙酯的含量，降低乳酸乙酯的含量，即“增己降乳”是提高浓香型白酒发酵质量的有效途径[2-5]。己酸乙酯和乳酸乙酯分别由己酸和乳酸与乙醇通过酯化反应生成，因此，在发酵过程中，增加己酸产量同时降低乳酸产量有助于提高酿酒品质。

浓香型白酒的发酵是在传统泥窖中经固态发酵、固态蒸馏、陈酿、勾调而成，不直接或者间接添加非自身发酵产生的风味物质。因此，己酸的合成代谢对浓香型白酒的发酵质量具有重要影响[6]。以乳酸为底物的己酸合成代谢有利于提高浓香型白酒的发酵质量。浓香型白酒发酵体系中的己酸生成菌（以下简称“己酸菌”）主要聚居于窖泥[7]。己酸菌在老窖池窖泥中的丰度比新窖池窖泥中的丰度高约2 个数量级[8]。在发酵过程中，以高粱为主的粮食与大曲混合物被封存在窖泥中进行厌氧分批发酵（图1B）。每批次的浓香型白酒发酵阶段可以被分为发酵前期（0～25 d）和发酵后期[9]。在以合成乙醇为主的兼性发酵前期，微生物代谢形成包括水、醇、酸、酯等各种成分的液态混溶物“黄水”。在发酵后期，包括己酸菌在内的厌氧菌从窖泥迁移到酒醅-黄水固液混合物中，进行厌氧代谢[9]。在每批次发酵过程中，黄水中己酸菌的丰度随发酵后期的延长而逐渐增加[10]；而且，黄水中己酸菌的丰度随着发酵批次的增加而增加[11]。发酵结束后，一个窖池中最好的浓香型白酒往往来自与黄水共存的底层酒醅。具有较高丰度己酸菌的窖池倾向用于生产较高质量的浓香型白酒，正所谓“千年老窖万年糟，好酒全凭窖池老”。因此，有些浓香型白酒生产企业通过在生产批次中间向窖泥喷洒己酸菌液的方式（图1），或者制作高质量人工窖泥的方式提高包括己酸菌在内的窖泥菌群丰度，从而提高酿酒质量[12-13]。此外，己酸作为一种能源物质，以乙醇、乳酸等为底物合成己酸的己酸菌对酿酒废弃物的转化利用也具有重要作用[14-17]。

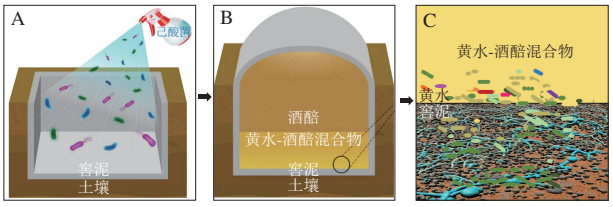


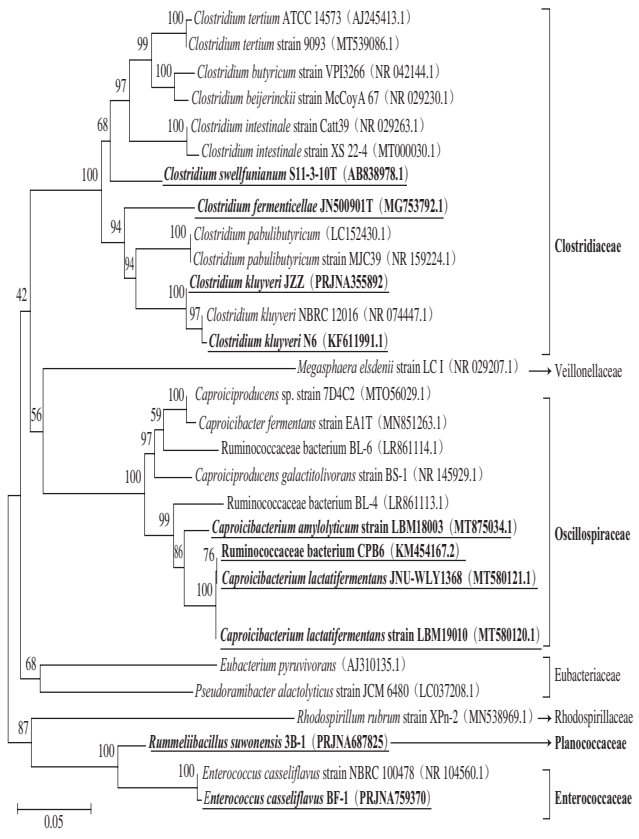
图 1 提高浓香型白酒发酵质量的喷洒己酸菌液方法（A）和浓香型发酵过程（B）中己酸菌群协同代谢（C）

Fig. 1 CPBs spraying method to improve the fermentation quality of CSFB (A), schematic of CSFB fermentation (B), and schematic of CPBs co-metabolism (C) during CSFB fermentation

基于己酸菌对浓香型白酒发酵的重要性，本文深入分析浓香型白酒发酵体系中己酸菌的种类多样性、系统进化关系、生理代谢特征、合成代谢己酸机制及其在浓香型白酒发酵体系的复杂代谢环境中与己酸菌、非己酸菌之间的协同代谢关系，探究己酸菌群在浓香型白酒发酵体系中的生长代谢规律，旨在为人工干预调控己酸菌的生长代谢以提升浓香型白酒发酵质量提供理论依据。

1 浓香型白酒发酵体系中己酸菌群组成分析

己酸菌作为一种产生高附加值中链脂肪酸的能源菌已有近百年研究历史。目前从自然环境分离的己酸菌属[18]有梭菌属（*Clostridium*）、*Megasphaera*、*Caproiciproducens*[19]、*Eubacterium*、*Rhodospirillum*、*Pseudoramibacter*、*Caproicibacterium*[20]、*Rummeliibacillus*[21]和*Enterococcus*[22]。在浓香型白酒发酵体系中，窖泥作为己酸菌的主要分离源，其表层的己酸菌丰富[8]。目前，从浓香型白酒发酵体系中分离纯化并鉴定的己酸菌株主要属于*Clostridium*、*Caproicibacterium*、*Enterococcus*和*Rummeliibacillus*。此外，通过现代高通量测序技术证实其中广泛存在*Caproiciproducens*[1,8-9,23-26]及未鉴定的*Clostridium*[27]。己酸菌株Ruminococcaceae bacterium CPB6最初分离时没有确定菌属[28]，后经过基因组学分析将其归为*Caproicibacterium*[29]。本研究查询了典型己酸菌株的16S rRNA基因序列，利用MEGA软件构建其与非浓香型白酒发酵体系来源己酸菌株的16S rRNA基因序列的系统发育树，以分析己酸菌株之间的进化关系，如图2所示。



加粗和下划线序列为表1中的代表己酸菌株；其余菌株为非浓香型白酒发酵体系来源己酸菌株；括号中为GenBank编号。

图2 通过代表己酸菌株16S rRNA基因序列构建的系统发育树

Fig. 2 Phylogenetic tree of representative CPBs based on 16S rRNA gene sequences

总结来说，目前从浓香型白酒发酵体系分离的己酸菌株主要集中在梭菌科（Clostridiaceae）和颤螺菌科（Oscillospiraceae）[30]，与通过高通量测序技术检测到的数据基本一致[8,29,31]。其中，从浓香型白酒发酵体系分离的Oscillospiraceae己酸菌株主要是新近分离的*Caproicibacterium*菌株，与从非浓香型白酒发酵体系分离的己酸菌株有一定遗传距离，亲缘性较远。Clostridiaceae的己酸菌株主要为*Clostridium*；浓香型白酒发酵体系来源的Clostridiaceae与非浓香型白酒发酵体系来源的Clostridiaceae亲缘关系更近。已经报道的从浓香型白酒发酵体系中分离的*Clostridium*有*Clostridium* sp. EFAS6[32]、*Clostridium beijerinckii*[33]、*Clostridium butyricum* JKY6D1[34]、*Clostridium tertium*、*Clostridium pabulibutyricum*和*Clostridium intestinale*[31]，其与非浓香型白酒发酵体系来源的*Clostridium*组成类似，这进一步证实浓香型白酒和非浓香型白酒发酵体系来源的*Clostridium*己酸菌的亲缘性更高。此外，从浓香型白酒发酵体系中还分离了两株分别来自动球菌科（Planococcaceae）和肠球菌科（Enterococcaceae）的己酸菌株。Zhang Huimin等[8]通过现代高通量测序分析窖泥菌群结构发现，尚未分离的3 个科（Eubacteriaceae、Veillonellaceae和Rhodospirillaceae）存在于窖泥菌群中。其中Eubacteriaceae的相对丰度稍高（1.75%～4.41%），Veillonellaceae和Rhodospirillaceae的相对丰度甚微。从浓香型白酒发酵体系中分离的己酸菌株代谢特征有所差异，Oscillospiraceae菌株普遍适宜弱酸性pH值（可低至4.5），以乳酸、淀粉和葡萄糖为代谢底物[20,28,35]，Clostridiaceae、Planococcaceae与Enterococcaceae菌株适宜弱酸性或中性pH值，以乙醇和葡萄糖为底物[21,31,36-37]。窖泥的多维理化环境为适宜不同理化条件的己酸菌提供了生长环境[8]。同时，适宜在不同理化条件下生存的己酸菌群为高效转化浓香型白酒发酵体系中丰富多样的底物（如乳酸、淀粉和葡萄糖等）创造了生理生化条件。而且随着窖池窖龄的增加，己酸菌丰度逐渐增加[38-39]，其合成己酸的能力越来越增强。增加浓香型白酒发酵体系中可以将乳酸转化成己酸的己酸菌相对丰度对提高浓香型白酒的发酵质量尤其重要[2-5]。最近通过16S rDNA高通量测序分析表明，浓香型白酒发酵体系中主要以乳酸为电子供体的己酸菌（如*Caproicibacterium*、*Caproiciproducens*）的相对丰度大于以乙醇为电子供体的己酸菌（如*Clostridium*）[29]。

综上所述，随着培养组学的发展，包括己酸菌在内越来越多的菌株从窖泥中纯化出来[40-41]。值得注意的是，通过对比宏基因组数据与分离纯化菌株信息，仍然有大量潜在己酸菌未能实现分离纯化。分析其原因，一方面有可能与有些己酸菌的低丰度和难培养性有关；另一方面，与现有的传统分离纯化菌株需要培养基制作、倾倒平板、稀释涂布、菌落挑取、生化/测序鉴定等大量基础性重复操作流程所固有的耗时、耗力、耗钱且通量极低的特点有关。因此，浓香型白酒发酵体系中更多潜在新己酸菌的分离筛选需要借助厌氧微生物分离培养新技术的发展[32,42]，如集高通量分离、培养、鉴定于一体的新型菌群培养组学技术与装备[42]。

经过分子生物学鉴定的典型己酸菌株汇总如表1所示。

表 1 一些从浓香型白酒发酵体系中分离的己酸菌株详情

Table 1 Details of caproic acid-producing bacteria isolated from CSFB fermentation ecosystem

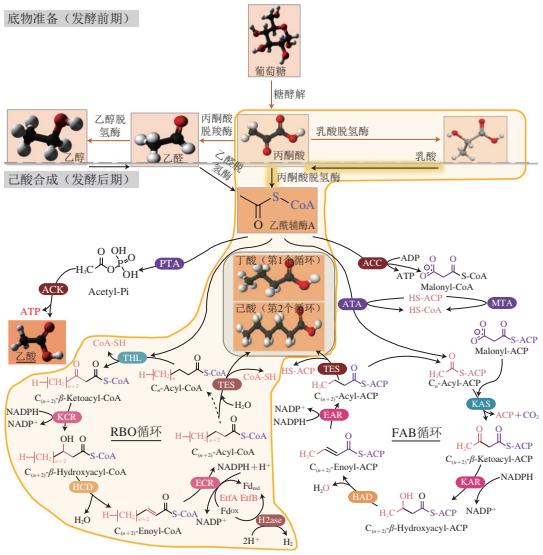
排序	菌株	科	形态特征	16S rRNA GenBank编号	主要底物	主要产物	主要理化条件	参考文献
1	Ruminococcaceae bacterium CPB6	Oscillospiraceae	厌氧、短棒状、产芽孢、革兰氏阳性	KM454167	葡萄糖、淀粉、乳酸等	乙酸、丁酸和己酸	pH 5.0～6.5；30～40 ℃	[28,43-44]
2	*Caproicibacterium amylolyticum* LBM18003^T	Oscillospiraceae	厌氧、棒状、可移动、产芽孢、革兰氏阳性	MT875034	葡萄糖、乳酸、淀粉等	丁酸和己酸	pH 6.5～7.0；30～37 ℃	[45]
3	*C. lactatifermentans* LBM19010^T	Oscillospiraceae	严格厌氧或厌氧、短棒状、革兰氏阳性、可移动	MT580120.1	己糖、淀粉和乳酸等	丁酸和己酸	pH 5.0～5.5；适宜温度35 ℃	[20,29]
4	*C. lactatifermentans* JNU-WLY1368	Oscillospiraceae	严格厌氧或厌氧、短棒状、革兰氏阳性、不可移动	MT580121.1	己糖、淀粉和乳酸等	丁酸和己酸	pH 5.0～5.5；适宜温度35 ℃	[20,29]
5	*Clostridium fermenticellae* JN500901^T	Clostridiaceae	严格厌氧、棒状、革兰氏阳性、不可移动、产芽孢	MG753792	乙醇等	己酸	适宜pH 5.0；适宜温度37 ℃	[37]
6	*Clostridium swellfunianum* S11-3-10^T	Clostridiaceae	严格厌氧、棒状、革兰氏阳性、可移动、产芽孢、呈单独或短链状	AB838978	葡萄糖、甘露糖和海藻糖等	乙醇、乙酸和氢气	适宜pH 7.3；适宜温度37 ℃	[36]
7	*Clostridium kluyveri* N6	Clostridiaceae	严格厌氧、棒状、产芽孢、有鞭毛	KF611991	乙醇、淀粉、葡萄糖等	丁酸、己酸和辛酸	适宜pH 7；适宜温度37 ℃	[46-47]
8	*Clostridium kluyveri* JZZ	Clostridiaceae	厌氧、杆状、革兰氏阳性、产芽孢	PRJNA355892	乙醇等	己酸	适宜pH 6.5；适宜温度37 ℃	[48-49]
9	*Enterococcus casseliflavus* BF-1	Enterococcaceae	厌氧、球状、革兰氏阳性、不产芽孢、	PRJNA759370	乙醇、葡萄糖等	己酸	适宜pH 7；适宜温度35 ℃	[22]
10	*Rummeliibacillus suwonensis* 3B-1	Planococcaceae	兼性厌氧、杆状、革兰氏阳性、产芽孢	PRJNA687825	乙醇、葡萄糖等	丙酸、丁酸、己酸	适宜pH 7；适宜温度33～37 ℃	[21]

2 浓香型白酒发酵体系中己酸菌代谢合成己酸机制

在发酵前期，浓香型白酒发酵体系中积累了葡萄糖、乳酸、乙醇、乙酸、丁酸等可以用于己酸合成代谢的底物。发酵前期是己酸合成代谢底物准备阶段。到发酵后期，己酸合成的底物随液态黄水聚集，为从窖泥迁移到黄水的己酸菌进行己酸合成代谢创造了理化环境[50-53]。

己酸菌合成己酸的主体代谢反应又被称为碳链延长反应。碳链延长反应包括最早在克氏梭菌（*Clostridium kluyveri*）体内发现的β-氧化逆反应（reverse β-oxidation，RBO）途径[54]和新近在禽波氏杆菌（*Bordetella avium*）、某种浮霉菌科（Planctomycetaceae）体内发现的脂肪酸合成反应（fatty acid biosynthesis，FAB）途径[55]。在浓香型白酒发酵体系的己酸菌体内普遍存在RBO途径[29,56-57]。目前尚无直接证据表明在浓香型白酒发酵过程中己酸菌群通过FAB途径合成己酸。然而，在通过以己酸菌属*Caproiciproducens*为主的己酸菌群进行以酿酒废水为底物的己酸合成代谢反应中，发现己酸菌群通过RBO和FAB两种代谢途径协同合成己酸[58]。

在浓香型白酒发酵体系中进行的主要己酸合成代谢反应途径如图3所示。RBO和FAB代谢途径均需要作为电子供体的底物提供电子，形成中间代谢物乙酰辅酶A。乙醇和乳酸是目前已知RBO途径中两种最常用的电子供体，其首先需要分别在乙醇脱氢酶和乳酸脱氢酶的作用下形成中间代谢物乙酰辅酶A，然后与作为电子受体的短链脂肪酸（如乙酸、丁酸）结合使其增加两个碳，完成一次RBO链延长反应（循环）。在FAB碳链延长反应中，乙酰辅酶A首先需要在羧化酶的作用下形成丙二酰辅酶A，它作为C2供体在转移酶的作用下连接到酰基转运蛋白（acyl carrier protein，ACP）上，进入循环的FAB碳链延长反应。相比于FAB途径，RBO途径更高效，因为FAB途径所需要的ACP会消耗更多ATP[55]。目前，RBO途径多被作为碳链延长反应的模式途径，因为以*Clostridium kluyveri*和Ruminococcaceae bacterium CPB6为代表的模式菌株体内具有进行RBO循环的全部酶，通过单菌株代谢即可进行碳链延长反应，生成目标产物己酸。可以参与FAB代谢的菌株普遍存在缺失FAB代谢酶系的情况，因此，FAB代谢途径存在于通过混合己酸菌群而非纯菌进行的己酸合成代谢体系中。RBO途径与FAB途径共同所需的中间代谢物乙酰辅酶A，主要是以代谢体系中的底物葡萄糖、己酸和乙醇等作为电子供体代谢形成丙酮酸，然后通过丙酮酸脱氢酶代谢形成乙酰辅酶A。梭菌属（*Clostridium*）的己酸菌株主要以乙醇为电子供体进行RBO碳链延长反应[32-34,36-37,46,48]；颤螺菌科（Oscillospiraceae）的己酸菌株主要进行以乳酸为底物和电子供体的RBO链延长反应[20,28-29,45]。很多菌具有转化淀粉、葡萄糖为己酸的代谢能力（表1）。肠球菌*Enterococcus casseliflavus* BF-1与鲁梅尔芽胞杆菌*Rummeliibacillus suwonensis* 3B-1可以以乙醇或葡萄糖为底物和电子供体进行RBO碳链延长反应[21-22]。在复杂的浓香型白酒发酵体系中，己酸菌群经过不断地分批发酵驯化，逐渐产生对外界环境的适应性[29,59]。



C_n和C_{n+2}.分别表示含有n 个和（n+2）个碳原子的碳链。PTA.磷酸转乙酰酶；ACK.乙酸激酶；THL.硫解酶；KCR.酮乙基辅酶A还原酶；HCD.羟酰辅酶A脱氢酶；ECR.烯脂酰辅酶A还原酶；TES.硫酯酶；ACC.乙酰辅酶A羧化酶；MTA.丙二酰转移酶；ATA.乙酰转酰酶；KAS.酮乙酰-ACP合成酶；KAR.酮乙酰-ACP还原酶；HAD.羟酰基ACP脱水酶；EAR.烯醇基ACP还原酶；H2ase.铁氧还蛋白氢化酶。

图 3 浓香型白酒发酵体系中主要己酸合成代谢的代谢通路[60]

Fig. 3 Major caproic acid synthesis pathways in CSFB fermentation ecosystem[60]

综上所述，浓香型白酒发酵体系中同时存在可以转化葡萄糖、乙醇和乳酸通过RBO碳链延长反应生成己酸的菌株。此外，具有不同代谢功能的复合己酸菌株还可以额外借助FAB代谢通路合成己酸。己酸菌群在浓香型白酒发酵体系中的己酸合成机制相对复杂，需要深入分析其协同代谢机制。

3 浓香型白酒发酵体系己酸菌群的协同代谢机制

目前对浓香型白酒发酵体系中己酸菌的研究主要集中在己酸菌株的分离、纯化、代谢特征分析以及其与协同菌株的协同代谢关系。理论上，目前所知浓香型白酒发酵体系中的己酸菌只可以通过RBO途径进行己酸合成代谢，混合菌群可以同时通过RBO和FAB途径进行协同己酸合成代谢。在实际浓香型白酒固液双相发酵体系中，与“黄水”共存的酒醅菌群与窖泥菌群被证实在己酸合成代谢中存在协同合作，前者用于乙酸、乳酸等底物准备，后者用于丁酸和己酸等产物生成[61]。Clostridiaceae的*Clostridium*被发现主要进行以乙醇为底物和电子供体的丁酸合成[62]，为己酸菌的己酸合成提供了电子受体丁酸；Oscillospiraceae的*Caproiciproducens*主要进行以乳酸为底物和电子供体的己酸合成[17]，己酸菌在己酸合成过程中存在协同代谢。己酸菌*Caproiciproducens*、*Clostridium*与非己酸菌*Lactobacillus*协同代谢过程中，*Lactobacillus*可提供*Caproiciproducens*用于己酸合成代谢的底物兼电子供体乳酸；同时*Caproiciproducens*转化乳酸形成乙酰辅酶A所释放的CO_2促进了乙醇向乙酰辅酶A的转化[17]。即浓香型白酒发酵体系中相对丰度最高的两个己酸菌群Clostridiaceae与Oscillospiraceae在己酸合成代谢过程中具有协同性。非己酸菌株*Novisyntrophococcus fermenticellae* JN500902被证实可通过与己酸菌株*Clostridium fermenticellae* JN500901共享代谢底物促进丁酸、己酸合成[63]。通过平板培养发现以乳酸为底物的己酸菌株*C. lactatifermentans* LBM19010、*C. lactatifermentans* JNU-WLY1368与Clostridiaceae的菌株具有生长协同性[29]。通过菌群之间的共发生网络分析证实，老窖池中丰度更高的己酸菌群受大曲菌群的影响与酒醅（黄水）菌群协同作用更强[64-65]。*Clostridium*与*Caproiciproducens*均与氢营养型的甲烷丝菌属*Methanosaeta*具有较强正相关，而且主要以乳酸为电子供体生成己酸的Oscillospiraceae整体与甲烷叶菌属*Methanolobus*、*Methanoplasma*、甲烷细菌属*Methanobacterium*均具有较强相关性[66]。以上结论与己酸菌和氢转移菌之间的协同代谢作用有利于己酸合成代谢的结论一致[65,67]。在非浓香型白酒的己酸生成代谢体系中己酸菌与酵母菌、甲烷菌、放线菌之间普遍存在共生关系[68]。窖泥菌群中普遍存在未分离的潜在己酸菌与非己酸菌之间具有共生或者代谢相关性的现象[69]。在浓香型白酒发酵体系中，己酸菌株*Clostridium kluyveri*与己酸菌[63,70-72]和产生乙酸的菌*Acetobacterium*[73]、产生丙酸的菌[74]、分解纤维素的菌[75]等非己酸菌之间也存在协同代谢关系。

综上，浓香型白酒发酵体系中己酸菌群资源丰富，众多类似功能的己酸菌群具有多底物代谢功能冗余性[76]。浓香型白酒发酵体系中复合己酸菌群的多底物代谢功能冗余性使其在低pH值（3.15～3.77）、低还原糖、低水分活度的非适宜己酸菌代谢环境中[51-52]，可通过己酸菌群内以及与非己酸菌之间产生协同代谢效应，更容易实现单一菌株很难实现的多种底物高效降解，进而生长繁殖、合成己酸[60]。己酸菌群作为浓香型白酒发酵体系中具有己酸合成功能的一类菌群，需要与浓香型白酒发酵代谢协同一起参与己酸的合成代谢；己酸菌群亦可利用发酵副产物中糖类、乳酸和乙醇的转化合成己酸，通过合成微生物共培养物提高生物工艺是目前重要的研究方向[77]，其作为合成培养工程的一部分可以提供比单菌发酵更优越的生物过程工艺[60,78]。关于浓香型白酒发酵体系中己酸菌与己酸菌和非己酸菌之间的协同代谢机制，尚有大量空白有待进一步研究，比如己酸菌群从新窖泥非优势地位到老窖泥优势地位的更迭进化过程中，己酸菌群与己酸菌群、非己酸菌群协同代谢机制以及窖泥理化微环境的变化规律。对浓香型白酒发酵体系中己酸菌群协同合成己酸机制的解析有利于靶向提高浓香型白酒发酵品质，也能够为通过己酸菌群合成高附加值己酸提供理论基础。

4 结 语

己酸菌群作为浓香型白酒发酵菌群的重要组成部分，加强其己酸合成功能有助于提高己酸产量，从而提高己酸乙酯的产量，这对改善浓香型白酒的发酵品质非常重要。近年来，随着基因组学与培养组学技术的发展，浓香型白酒发酵体系作为一个天然的己酸菌群富集驯化库，其中己酸菌的分离纯化、己酸合成生理代谢特征、己酸合成机制和协同代谢多样性研究获得飞速发展。目前，从浓香型白酒发酵体系分离的己酸菌株主要属于Oscillospiraceae和Clostridiaceae。由于不同菌属的己酸代谢特征差异，适宜在不同的理化条件下进行己酸合成代谢，例如Oscillospiraceae的己酸菌比较适宜弱酸性环境，Clostridiaceae的己酸菌比较适宜中性环境。浓香型白酒发酵体系己酸菌均可通过RBO途径合成己酸，其中Oscillospiraceae倾向于以乳酸为电子供体生成乙酰辅酶A进入RBO途径合成己酸，而Clostridiaceae倾向于以乙醇为电子供体生成乙酰辅酶A进入RBO途径合成己酸。两

者均可代谢速效碳源葡萄糖。此外，己酸菌群具有协同通过FAB代谢途径合成己酸的潜力。在浓香型白酒发酵体系中，己酸菌与己酸菌、非己酸菌之间普遍存在协同代谢关系，这有助于综合利用代谢环境的各种碳源和差异化理化环境，且有助于提高己酸菌群的己酸合成功能。

相信随着培养组学的发展，借助集高通量分离、培养、鉴定于一体的新型菌群培养组学技术与装备，将从浓香型白酒发酵体系中分离鉴定出越来越多的己酸菌株。同时，更多己酸菌株的己酸合成代谢特征解析有助于了解浓香型白酒发酵体系中复杂的混合菌群协同代谢机制。

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