茶叶微生物发酵过程中没食子酸代谢研究进展

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摘要 没食子酸是茶叶中的主要酚酸类化合物，在渥堆发酵、厌氧发酵和仓储陈化过程中均呈增加趋势，并与酯型儿茶素水解存在密切相关。黑曲霉、冠突散囊菌、烟曲霉、溜曲霉、*Aspergillus pallidofulvus* 促进茶叶微生物发酵过程中没食子酸的生物合成，这与其分泌的单宁酶等胞外酶有关。在液态发酵中，枯草芽孢杆菌、植物乳杆菌同样能分泌单宁酶，提高没食子酸含量。本文概述目前国内外关于茶叶微生物发酵过程中没食子酸代谢研究进展，阐述没食子酸的生物合成机制和保健功效，以期为微生物作用下没食子酸代谢调控机理的研究提供参考。

关键词 黑茶； 儿茶素； 渥堆发酵； 丝状真菌； 单宁酶
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茶叶是最受欢迎的风味、功能性植物饮料，消费人群占世界总人口的三分之二。按照发酵程度和加工工艺，传统上将茶叶分为绿茶、白茶、黄茶、红茶、乌龙茶(青茶)和黑茶六大基本类型。茶多酚是茶叶中主要呈味物质和功效成分，其含量占茶树鲜叶干物质重的 18%~36%，主要包括儿茶素类(Catechins)、黄酮醇类及其糖苷 (Flavonols and their glycosides)、黄酮类 (Flavones)、花青素类(Anthocyanins)和酚酸类(Phenolic acids)等，具有降低癌症和糖尿病发病几率，以及降血脂、抗肥胖、抗氧化、抗炎等多种生物学活性[1]。其中，儿茶素为茶多酚的主体成分，占茶多酚总量的 60%~80%[2]。在茶叶中共检出(+)-儿茶素(Catechin，C)、(+)-没食子儿茶素(Gallocatechin，GC)、(-)-表儿茶素 (Epicatechin，EC)、(-)-表没食子儿茶素(Epigallocatechin，EGC)等非酯型儿茶素及(-)-儿茶素没食子酸酯(Catechin gallate，CG)、(-)-表儿茶素没食子酸酯 (Epigallocatechin gallate，ECG)、(-)-没食子儿茶素没食子酸酯(Gallocatechin gallate，GCG)和(-)-表没食子儿茶素没食子酸酯(Epigallocatechin gallate，EGCG)等酯型儿茶素以及甲基化儿茶素、儿茶素糖苷和二聚儿茶素类等，如表没食子儿茶素-3′-*O* (3′-*O*-甲基) 没食子酸酯、表儿茶素-3′-*O*-葡萄糖苷、原花青素 B1 等[3]。

没食子酸(3，4，5-三羟基苯甲酸，Gallic acid)是茶叶中的主要酚酸类化合物，占茶树鲜叶干物质的 0.3~15.4 mg/g，受茶树品种、栽培时间、收获季节、鲜叶等级等因素的影响。如云南古茶树中，没食子酸、原儿茶酸 (3，4-二羟基苯甲酸，Protocatechuic acid)等酚酸含量较低[4-5]。在茶树中没食子酸的生物合成主要来自于莽草酸途径 (见图 1)，即：1)3-脱氢莽草酸脱氢酶催化 3-脱氢莽草酸(3-Dehydroshikimic acid)氧化和烯醇化形成没食子酸；2) 羟基化酶催化 3，4-二羟基苯甲酸(3，4-Dihydroxybenzoic acid) 苯环 C5 位羟基化形成没食子酸。同时，没食子酸通过没食子酰基-1-*O*-*β*-*D*-葡萄糖转移酶(UGGT)催化的尿苷二磷酸葡萄糖(Uridine diphosphate glucose，UDPG)依赖的酰基活化，为酯型儿茶素的生物合成提供酰基供体[6-7]。另外，没食子酸中羧基酯化为没食子酸甲酯(Methyl gallate)，提高了对山茶炭疽病原菌(*Colletotrichum camelliae*)、茶轮斑病病原菌(*Pseudopestalotiopsis camelliae-sinensis*) 的抗真菌活性[8]。在茶树生理、茶叶加工与仓储陈化过程中，没食子酸与儿茶素等黄烷醇代谢存在紧密联系。近年来，在没食子酸的保健功效、茶叶加工与仓储陈化的没食子酸代谢途径、微生物及其分泌的胞外酶对没食子酸代谢的影响等方面的研究取得新进

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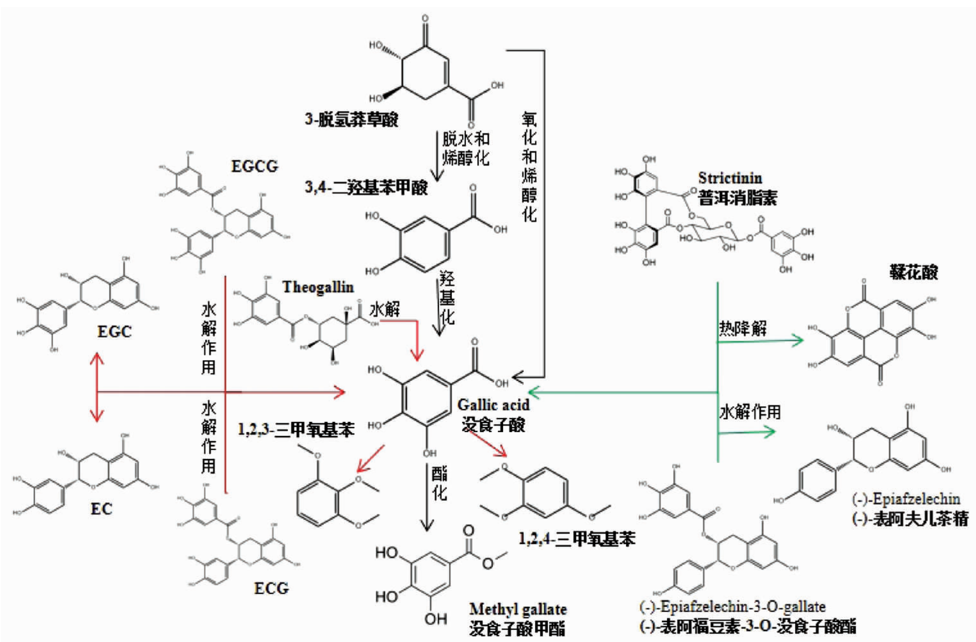
展。基于此,本文综述茶叶微生物发酵过程中没食子酸代谢研究现状，为其调控机理研究提供理论参考。

1　没食子酸的保健功效

1.1　抗氧化活性

现代医学表明活性氧自由基和多种神经退行性疾病、炎症、病毒感染、自身免疫病和消化系统疾病有关。没食子酸能提高抗氧化酶的活性,如超氧化物歧化酶(Superoxide dismutase,SOD)、谷胱甘肽过氧化酶(Glutathione peroxidase,GPx)和谷胱甘肽 *S*–转移酶 (Glutathione *S*–transferase,GST)，同时降低淋巴细胞内的活性氧自由基,以减少肝脏、淋巴细胞、结肠和肺内的 DNA 氧化损伤。没食子酸能保护肝细胞免受过氧化氢、四氯化碳和扑热息痛产生的氧化应激破坏；通过调节抗氧化酶活性,抑制脂质过氧化,降低丙二醛活性,发挥其对肝脏的保护作用，并减少四氯化碳引起的肝脏病变发生率。茶叶的抗氧化能力与儿茶素和没食子酸含量存在显著($P<0.05$)正相关[9]。



注:→. 显示茶树生理中没食子酸的主要代谢途径;→. 显示渥堆发酵中没食子酸的主要代谢途径;→. 显示普洱茶蒸压和茶叶厌氧发酵中没食子酸的来源。

图 1　茶树生理和茶叶加工中没食子酸的代谢途径

Fig.1　Metabolic pathway of gallic acid in physiology of tea plant (*Camellia sinensis* L.) and tea processing

1.2　抗癌作用

没食子酸通过调节参与细胞周期、转移、血管生成和凋亡等基因的表达,抑制癌细胞的增殖;并通过降低抗凋亡蛋白的活性，增加促凋亡蛋白的活性,诱导癌细胞凋亡。有研究表明没食子酸能诱导细胞产生高水平的拓扑 I 和拓扑 II 型 DNA 复合物，通过 DNA 链的永久性断裂引发癌细胞死亡。体外细胞试验表明,没食子酸能促进白血病、前列腺癌、乳腺癌、脑肿瘤、胃癌、宫颈癌、肺癌、结肠癌、骨肉瘤等不同癌症细胞的凋亡,IC_{50} 值从 0.1 mmol/L 到 24 mmol/L 不等[10–11]。

1.3　抗菌、抗病毒活性

没食子酸具有广谱的抗细菌、抗真菌和抗病毒活性。没食子酸通过调控 *pgaABCD* 基因表达、抑制活菌和大肠杆菌(*Escherichia coli*)生物膜的形成；通过调控 *mdoH* 基因表达和 OpgH 蛋白,有效抑制福氏志贺菌(*Shigella flexneri*)生物膜形成和生物活性;通过调节 ica 操纵子表达,对金黄色葡萄球菌(*Staphylococcus aureus*)具有特异性抗菌膜作用。另外，没食子酸能降低假单胞菌(*Pseu-*

domonas spp.)和肠杆菌(*Enterobacteriaceae spp.*)的细菌菌落丰度，并具有对皮肤真菌(*Trichophyton rubrum*，*Trichophyton mentagrophytes*，*Trichophyton violaceum*，*Microsporum canis*，*Trichophyton verrucosum*，*Trichophyton schoenleini*)和念珠菌(*Candida glabrata*，*Candida albicans*，*Candida tropicalis*)的抗真菌活性[12-13]。同时，没食子酸能抑制甲型流感病毒(H1N1)感染，并对乙肝病毒(Hepatitis B virus，HBV)、人鼻病毒(HRV-2和HRV-3)、丙型肝炎病毒(Hepatitis C virus，HCV)、人体免疫缺陷病毒(Human immunodeficiency virus-1，HIV-1)和单纯性疱疹病毒(Herpes simplex virus-1，HSV-1)等病毒传染具有一定抑制作用。没食子酸可通过协同作用，增强红霉素、庆大霉素、若氟沙星、环丙沙星、氨苄西林、青霉素和恶青霉素等其它抗生素的抗菌活性[14]。

1.4 没食子酸在心血管疾病治疗上的应用潜力

心肌缺血和心力衰竭是心血管病患的常见病、多发病。心肌缺血被定义为心肌供氧与需氧量不平衡所引起的状态，其中冠状动脉粥样硬化是主要原因。没食子酸通过提高SOD、过氧化氢酶(Catalase，CAT)、GST、GPx等抗氧化酶活性和谷胱甘肽、维生素C、维生素E等非酶抗氧化剂的抗氧化水平，抑制活性氧自由基对心肌细胞膜完整性和功能的有害影响，从而降低血清中心肌肌钙蛋白T(Cardiac troponin，cTnT)和肌酸激酶-MB(Creatine kinase，CK-MB)等与心肌梗塞相关的生物标志物。没食子酸可以显著降低血管紧张素II(Angiotensin II，Ang II)诱导心肌细胞大小的增加，减少横主动脉缩窄(Transverse aorta coarctation，TAC)刺激诱导的心肌肥厚、功能障碍和纤维化[15]。另外，没食子酸还能降低纤维化相关基因的表达，包括I型和III型胶原、纤连蛋白、结缔组织生长因子(Connective tissue growth factor，CTGF)和磷酸化Smad3，并抑制上皮-间质转化(Epithelial-mesenchymal transition，EMT)相关基因的表达，如*N*-钙黏蛋白、波形蛋白、*E*-钙黏蛋白、SNAI1和TWIST1，显示了没食子酸在慢性心力衰竭治疗中的应用潜力[16]。

1.5 抗肥胖作用

全球有超过19亿成年人超重，其中6亿人面临肥胖威胁。体内外研究表明，没食子酸通过抑制脂肪生成，改善胰岛素信号，减少促炎反应和氧化应激反应，发挥其抗肥胖作用[16]。没食子酸在9.2 μg/mL质量浓度下即可实现对胰脂肪酶活性的抑制，被认为是普洱茶中主要抗肥胖成分之一[17]。体外试验表明，没食子酸以及富含没食子酸的浸提液具有抑制*α*-葡萄糖苷酶、*α*-淀粉酶和脂肪酶活性的作用。动物实验表明，没食子酸具有减轻体重，改善脂肪肝，调节血糖，降低血液胆固醇、甘油三酯和低密度脂蛋白，减少脂肪组织中脂肪酸合成、脂朊脂酶和瘦素的mRNA表达。

1.6 其它药理活性

没食子酸能有效抑制胰岛素淀粉样蛋白原纤维的形成，对II型糖尿病、阿尔兹海默症、帕金森症、亨廷顿氏症等多种神经退行性疾病的发生有预防和神经保护作用[18]。没食子酸的促凋亡和抗炎活性促使其在变应性鼻炎和类风湿性关节炎治疗中有一定应用潜力。没食子酸通过减少胃酸的分泌，诱导内源性抗氧化剂和防御因子的释放，保护胃肠道黏膜层免受溃疡的侵袭[19]。另有研究证实，没食子酸能保护结缔组织免受物质毒害或辐射侵害。

2 茶叶加工与仓储陈化过程中没食子酸代谢

龙井43号茶树鲜叶加工的六大茶叶类型比较发现，黑茶中的没食子酸含量最高，红茶中次之，乌龙茶和白茶均显著($P<0.05$)高于绿茶和黄茶等不发酵茶叶[20]。Tang等[21]同样认为黑茶、红茶和乌龙茶等发酵茶叶中没食子酸含量较高，而绿茶、白茶和黄茶中含量较低。茶叶加工中没食子酸含量与发酵程度呈正比[22]。如普洱茶(熟茶)中没食子酸含量最高可达21.98 mg/g，而绿茶中没食子酸含量仅为1.67 mg/g。在红茶加工中，没食子酸形成与儿茶素减少存在一定正相关性[23]。由此可知，内源酶促发酵[24]和微生物发酵[25]均深刻影响儿茶素代谢，并促进茶叶中没食子酸等酚酸的积累。在普洱茶、茯砖茶[26]和六堡茶[27]等黑茶渥堆或后发酵中没食子酸均显著($P<0.05$)增加。

茶叶微生物发酵主要涉及糖基化、水解、羟基化、甲基化、缩合、氧化、乙酰化等一系列生化反

应[28-29]。其中,没食子酸的形成与酯型儿茶素水解存在紧密关联。在微生物及其分泌的胞外酶作用下,酯型儿茶素,如 EGCG 和 ECG 等首先水解为非酯型儿茶素(即:EGC 和 EC)和没食子酸(见图 1);随后,没食子酸经过环裂变、还原、水解、脱羧、脱甲基和脱羟化反应, 产生 2,5-二羟基苯甲酸(2,5-Dihydroxybenzoic acid)、间苯三酚(Phloroglucinol)、邻苯三酚(Pyrogallic acid)、没食子酸甲酯、水杨酸(Salicylic acid)、3,4-二羟基苯甲酸(3,4-Dihydroxybenzoic acid)、原儿茶酸和 2,3,4-三羟基苯甲酸(2,3, 4-Trihydroxybenzoic acid)等酚酸类化合物;再经进一步甲基化、脱羧反应等,转化为 1,2,3-三甲氧基苯(1,2,3-Trimethoxybenzene)和 1,2,4-三甲氧基苯(1,2,4-Trimethoxybenzene),构成普洱茶等黑茶陈香风味的物质基础[29-31]。因而,与普洱茶(生茶)相比,普洱茶(熟茶)中酯型和非酯型儿茶素含量较少,而没食子酸含量较高[32]。由于微生物群落结构和发酵程度差异,茯砖茶、千两茶、青砖茶、六堡茶等不同类型黑茶之间没食子酸和 6 种儿茶素含量均存在显著($P < 0.05$)差异[33]。另外,Ge 等[34]的研究发现,3-邻-没食子酰奎尼酸(Theogallin)的水解同样有助于没食子酸的生物合成(见图 1)。

湖北酸茶的厌氧发酵中,没食子酸大量累积,含量为 25.7 mg/g[35];经工艺优化后,没食子酸含量最高可达 54.4 mg/g,远超过其在五倍子中的含量。通过非靶向和靶向代谢组学分析,Zhang 等[36]揭示了酸茶厌氧发酵中不同于渥堆发酵中没食子酸生物合成的代谢途径, 确定 ECG、(-)-表阿夫儿茶精-3-没食子酸酯 ((-)-Epiafzelechin-3-*O*-gallate,EAF-G)和 7-没食子酰儿茶素(7-Galloylcatechin, 7-GC) 为没食子酸形成的主要前体物质,而 EGCG 含量保持稳定。如图 1 所示,在芽孢杆菌(*Bacillus*)、阿非彼菌 (*Afipia*)、拟杆菌(*Bacteroides*)、角质层杆菌(*Cutibacterium*)、代尔夫氏菌(*Delftia*)和希瓦氏菌(*Shewanella*)等细菌作用下,表阿夫儿茶精-3-没食子酸酯水解产生(-)-表阿夫儿茶精((-)-Epiafzelechin)和没食子酸。然而,由于加工工艺和原料差异,云南德昂族酸茶[37]在厌氧发酵中,没食子酸是否大量积累,其形成是否与酯型儿茶素水解有关值得进一步研究。热降解作用同样能促进普洱茶中普洱消脂素(又名木麻黄素,Strictinin,一种酚酸类化合物)分解为鞣花酸和没食子酸[38](见图 1),提高了普洱茶的抗病毒活性。

在白茶[39]、乌龙茶[40]和黑茶等茶叶的仓储陈化过程中,伴随着儿茶素、黄酮醇-*O*-糖苷和氨基酸的降低[41],没食子酸含量均呈增加趋势,这在一定程度上影响了茶叶的抗氧化能力[42]。Lee 等[43]发现,乌龙茶的周期性干燥促使 EGCG 降解,释放出大量的没食子酸, 并产生少量的杨梅素(Myricetin)、槲皮素 (Quercetin) 和山奈酚(Kaempferol)等黄酮醇。另外,没食子酸/5-没食子酰基奎尼酸(Gallic acid/5-galloylquinic acid)的比值随着乌龙茶仓储陈化周期的延长而提高[44],这主要源于乌龙茶仓储陈化中 EGCG 降解引起的没食子酸积累。普洱茶(生茶)仓储陈化过程中,没食子酸代谢受到仓储环境中温、湿度和微生物群落等因素的影响。湿热的仓储环境在一定程度上促进没食子酸的积累。Zhou 等[45]推断没食子酸主要来自于 EGCG、ECG、GCG 等酯型儿茶素的水解,这与普洱茶(熟茶)渥堆发酵中,没食子酸的代谢机理相似。另有证据显示,普洱茶(熟茶)仓储陈化中,*Aspergillus pallidofulvus*、*Aspergillus sesamicola* 等"金花菌"能显著($P<0.05$)提高没食子酸的含量[46]。

3 微生物及其分泌的单宁酶对茶叶中没食子酸代谢的影响

如上所述,在茶叶(深)加工中,普洱茶等黑茶的渥堆发酵和酸茶的厌氧发酵以及白茶、乌龙茶和红茶的酶促氧化发酵[47]均能促进没食子酸的积累。然而,有氧发酵和厌氧发酵中,没食子酸生物合成途径和前体物质存在一定差异。表 1 汇总了部分文献报道的茶叶中分离纯化的微生物及其分泌的单宁酶、漆酶等胞外酶对没食子酸代谢的影响。普洱茶、茯砖茶等黑茶中分离出的黑曲霉(*Aspergillus niger*)、冠突散囊菌(*Eurotium cristatum*)、焦曲霉 (*Aspergillus ustus*)、溜曲霉(*Aspergillus tamarii*)、*Aspergillus pallidofulvus*、*Aspergillus sesamicola* 和 *Penicillium manginii* 等优势茶源真菌, 均能在茶叶微生物发酵中促进没食

子酸的形成。在接种发酵中没食子酸急剧增加后大幅度降低[48-49],含量最高在18.8~23.8 mg/g之间。在茶叶微生物有氧发酵中,黑曲霉、冠突散囊菌、烟曲霉(*Aspergillus fumigatu*)、溜曲霉等真菌菌株分泌单宁酶催化EGCG、ECG和GCG等酯型儿茶素水解产生没食子酸,通过真菌漆酶、多酚氧化酶、过氧化物酶等胞外酶,促进没食子酸、儿茶素等进一步缩合、氧化、聚合形成茶褐素等水溶性茶色素[50]。

单宁酶(Tannase,EC 3.1.1.20)是催化酯型儿茶素水解产生没食子酸的主要酶类,EGCG、GCG和ECG对应的Km值分别为14.89,16.13,3.57 mmol/L[51]。黑曲霉分泌单宁酶的酶催试验表明[52]:单宁酶除催化酯型儿茶素形成没食子酸外,还产生食子酸乙酯(Ethyl gallate)、原花青素类(A2、B2和B3)、儿茶素聚合物等代谢物,这在一定程度上提高了茶叶的抗氧化能力。在厌氧发酵中,枯草芽孢杆菌(*Bacillus subtilis*)、植物乳杆菌(*Lactobacillus Plantarum*)分泌单宁酶催化单宁酸转化为没食子酸,产生少量双没食子酰基或三没食子酰基葡萄糖[53]。而泡盛曲霉(*Aspergillus awamori*)和酿酒酵母(*Saccharomyces cerevisiae*)同样能在厌氧发酵或液态发酵中促进单宁酸或酯型儿茶素向没食子酸的转化。单宁酶外源添加的酶促发酵亦可提高没食子酸含量,改善茶叶品质。真菌分泌的漆酶(Laccase,EC 1.10.3.2)虽然能催化EGCG氧化形成少量没食子酸,但主要用于茶褐素等茶色素的生产[54]。短乳杆菌(*Lactobacillus brevis*)和植物乳杆菌(*Lactobacillus plantarum*)等乳酸菌促进没食子酸脱羧形成邻苯三酚,再经*O*-甲基化后可形成1,2,3-三甲氧基苯等甲氧基苯。

表1 微生物菌株及其分泌的胞外酶对没食子酸代谢的影响

Table 1 Effects of microbial strains and their released extracellular enzymes on gallic acid metabolism

菌株	效益	备注
黑曲霉和烟曲霉[55]	发酵0~36 h,没食子酸呈增加趋势,含量达8 mg/g,随后大幅度降低	没食子酸主要来自酯型儿茶素中没食子酰基酯键的水解
冠突散囊菌[56]	37 ℃发酵7 d后,没食子酸含量达2.38%	没食子酸是发酵散茶中的主要抗氧化剂
冠突散囊菌PW-1	接种发酵4 d时,茯砖茶中没食子酸含量即可达到最大[57]	该菌株在西路边销茶的加工生产中有一定应用前景[58]
冠突散囊菌[59]	发花后,茶叶中没食子酸含量大幅度增加	发花中没食子酸主要来自于酯型儿茶素的水解,降低茶叶的苦涩味
黑曲霉、溜曲霉、烟曲霉[60]	分泌单宁酶催化酯型酚类化合物水解产生没食子酸;糖苷水解酶和糖基转移酶促进黄酮及其糖苷的水解和合成	酚类化合物被漆酶和香草醇氧化酶氧化或聚合,苯醌还原酶降解酚类化合物中的芳香环
A. pallidofulvus,*A. sesamicola*和*P. manginii*[61]	*A. pallidofulvus*等茶源真菌大幅度提高没食子酸含量,发酵后茶叶中含量可达(18.77 ± 1.26)mg/g[25]	*A. pallidofulvus*和*A. sesamicola*有助于茶叶微生物发酵中山奈酚、槲皮素和杨梅素等黄酮类化合物的生物合成
黑曲霉RAF106[62]	液态发酵中将酯型儿茶素降解为非酯型儿茶素和没食子酸	黑曲霉分泌的单宁酶为催化酯型儿茶素水解的胞外酶;氮源影响绿茶儿茶素的生物转化
黑曲霉JMU-T5528分泌的单宁酶[51]	单宁酶催化EGCG、GCG和ECG水解为EGC、GC和EC,并产生没食子酸;最适pH 3.0~7.0,温度40~60 ℃	对应EGCG、GCG和ECG等底物的酶Km浓度分别为14.89,16.13,3.57 mmol/L
黑曲霉分泌的单宁酶[52]	催化酯型儿茶素水解为非酯型儿茶素和没食子酸,并产生没食子酸乙酯、原花青素类和儿茶素聚合物	单宁酶水解或儿茶素聚合均能提高茶叶的抗氧化能力
黑曲霉FJ0118克隆的嗜热单宁酶[63]	催化EGCG、ECG酯型儿茶素水解为EGC、EC等非酯型儿茶素和没食子酸[63]	该酶的最佳反应温度为80 ℃;70 ℃单宁酶萃取40 min绿茶中茶多酚回收率提升2.1倍

(续表 1)

菌株	效益	备注
单宁酶[64]	单宁酶促进秋季绿茶和绿茶浸提液中的没食子酸酯儿茶素水解产生非酯型儿茶素和没食子酸,并与 pH 值呈显著相关性	没食子酸有助于绿茶的回甘和夏秋茶品质的提升;单宁酶能提高抗氧化能力,影响挥发性组分[65]
泡盛曲霉 (*Aspergillus awamori*)BTMFW032[66]	分泌嗜酸单宁酶,催化单宁酸的酯基转移作用形成没食子酸丙酯,并同时产生没食子酸	条件优化后，嗜酸单宁酶和没食子酸产量提高 1.5 倍以上,揭示其在液态发酵生产没食子酸的应用潜力
枯草芽孢杆菌 AM1、植物乳杆菌 CIR1	两株细菌的最大没食子酸产量分别为 24.16, 23.73 g/L；单宁酶产量达 1 400,1 239 U/L[53]	两株细菌均可用于单宁酶的生产，催化单宁酸转化为没食子酸
酿酒酵母 (*Saccharomyces cerevisiae*)71B[67]	在液态发酵中，促进 EGCG、ECG 水解产生没食子酸,分泌酯水解酶,促进绿原酸的酯键水解形成咖啡酸和奎尼酸	酿酒酵母增加芳樟醇、脱氢芳樟醇、2-苯乙醇、二氢猕猴桃内酯形成花果香味,而抗氧化能力保持稳定
曲霉属真菌分泌的漆酶 (EC 1.10.3.2)[50]	催化 EGCG 氧化,产生游离儿茶素、酯型儿茶素、没食子酸和茶色素	在真菌漆酶用量 10 μg,反应温度 70 ℃,自然 pH 值,反应时间 150 min 的条件下,EGCG 的氧化率达 69.72%
短乳杆菌 145 和植物乳杆菌 292 乳酸菌[68]	茶叶浸提物液态发酵中，促进山奈酚糖苷、槲皮素糖苷、杨梅酮糖苷水解形成相应的黄酮醇,没食子酸脱羧形成邻苯三酚	EGCG、ECG、EGC 等儿茶素在液态发酵中保持稳定；乳酸菌提高酚类生物利用度和保护细胞免受氧化应激

4 结语与展望

没食子酸是普洱茶(熟茶)等黑茶中的主要特征品质成分之一。在黑茶的渥堆发酵、酸茶的厌氧发酵和茶叶的仓储陈化中，没食子酸均呈增加趋势,是连接儿茶素和酚酸的关键代谢物。本文概述了没食子酸的抗氧化、抗癌、抗肥胖、抗菌、抗病毒作用及其在心血管疾病治疗和预防的应用潜力。因而，富含没食子酸等特色茶叶的加工生产不仅能提高夏秋茶树资源的利用效率，同时也有望提升茶叶的保健功效。茶叶微生物发酵中,黑曲霉、溜曲霉、枯草芽孢杆菌和植物乳杆菌等分泌的单宁酶,能催化 EGCG、ECG 和 GCG 等酯型儿茶素、(-)-表阿夫儿茶精-3-没食子酸酯、3-邻-没食子酰奎尼酸和单宁酸中没食子酰基酯键的水解产生大量的没食子酸,并产生一定量的没食子酸乙酯、花青素和儿茶素聚合物等副产物。某些菌株能将茶叶微生物发酵中没食子酸含量提高到 20 mg/g 以上，为富含没食子酸茶叶的生产提供了菌种保障。单宁酶的外源添加同样能提升夏秋茶的没食子酸含量,改善茶叶品质。尽管目前已确定微生物主要通过分泌、释放单宁酶催化 EGCG 等前体物质中没食子酰基酯键的水解产生没食子酸。然而,茶叶微生物发酵中合成与降解代谢机理尚未清晰，尤其缺乏微生物-单宁酶-没食子酸代谢及其调控机理的系统研究。因此,在明晰了茶叶微生物发酵中单宁酶等胞外酶催化没食子酸形成的基础上，没食子酸调控机理的研究不仅为揭示茶叶微生物发酵中没食子酸的代谢途径及其分子调控机制，也将为富含没食子酸等特色茶叶的加工生产奠定理论基础。

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Research Advances on Gallic Acid Metabolism during Tea-leaves Microbial Fermentation

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Abstract As the main phenolic acid in tea-leaves, gallic acid all showed increasing trends during pile-fermentation, anaerobic fermentation and aging storage, and had closely connection with the hydrolyzation of ester catechins. Due to the secreted extracellular enzymes, such as tannase, *Aspergillus niger*, *Eurotium cristatum*, *Aspergillus fumigatu*, *Aspergillus tamarii* and *Aspergillus pallidofulvus* promoted the biosynthesis of gallic acid during the inoculated fermentation. Additionally, *Bacillus subtilis* and *Lactobacillus plantarum* both could secrete tannase to enhance gallic acid content in the submerged fermentation. This article reviewed the lasted literature at home and abroad to explore the impacts of microorganisms and released extra-cellular enzymes on gallic acid metabolism. This paper summarized the research progress about gallic acid metabolism during tea-leaves microbial fermentation, and elaborated the biosynthesis mechanism and health efficacy of gallic acid, which would contribute to the research about the regulation mechanism of gallic acid metabolism under effects of microorganisms.

Keywords dark tea; catechins; pile-fermentation; filamentous fungi; tannase