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黑茶微生物发酵的抗氧化物质特征与作用机制

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摘要 黑茶作为中国特有的后发酵茶类, 其品质与抗氧化功能依赖微生物介导的渥堆发酵对活性成分的转化, 且受发酵工艺与原料协同调控。本文系统梳理黑茶发酵过程中核心微生物菌种的功能及作用机制, 解析发酵衍生的抗氧化物质的结构特征, 深入阐述其在信号通路调控中的抗氧化机制, 并展望了未来研究方向与应用前景。旨在为黑茶发酵工艺精准优化与抗氧化功能产品产业化提供参考。

关键词 黑茶; 发酵菌种; 抗氧化机制; 茶褐素; 信号通路

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现代科学研究表明, 茶叶中富含的多种活性成分在抗氧化、抗炎及代谢调节等诸多方面展现出显著功效^[1]。当前, 氧化应激相关慢性疾病(如心血管疾病、神经退行性疾病)高发, 天然抗氧化剂的研发成为健康科学领域的核心方向^[2-3]。相较于未发酵的绿茶和半发酵的乌龙茶, 黑茶的后发酵过程使活性成分结构更稳定、生物利用度更高。黑茶的独特品质主要源于微生物介导的固态发酵体系。以乳酸菌为例, 它对绿茶进行发酵处理后, 发酵后茶叶的DPPH自由基清除率提高, 显著提升了黑茶的品质和抗氧化能力^[4]。在湿热环境与微生物共生的复杂条件下, 酶促转化与菌群代谢相互协同, 促使儿茶素类物质经氧化聚合生成茶褐素(theabrownins, TBs)、没食子酸(gallic acid, GA)等大分子活性成分^[5-6]。然而, 黑茶发酵过程中, 微生物菌群对活性物质转化的调控路径尚不明确, 黑茶特异性抗氧化物质的分子作用机制缺乏系统解析。对此, 本文系统综述了黑茶发酵菌种功能、抗氧化物质特性及作用机制, 旨在为黑茶发酵工艺精准优化与抗氧化功能产品产业化提供参考。

1 黑茶发酵微生物

普洱茶、茯砖茶、青砖茶等黑茶的发酵过程依赖复杂的微生物群落协同作用, 其主要抗氧化功能如

表1所示。发酵前期通常以霉菌为主, 霉菌负责分泌多种水解酶, 分解茶叶细胞壁及大分子物质。中后期酵母菌和细菌逐渐成为优势菌群, 负责风味物质生成、pH调节及深度转化^[7-8]。

在发酵初期(0~7 d), 霉菌占据主导, 黑曲霉(*Aspergillus niger*)通过分泌柠檬酸下调体系pH, 抑制杂菌生长的同时激活自身酶系。青霉产生青霉素进一步净化菌群环境, 此阶段茶多酚降解率达30%~35%, 初步生成茶红素^[9]。在发酵中期(8~21 d), 酵母菌与细菌(乳酸菌、芽孢杆菌)成为优势菌群。乳酸菌产酸维持酸性环境, 促进茶多糖降解。芽孢杆菌代谢产热使堆温升至40~45℃, 加速黑曲霉分泌多酚氧化酶, 茶褐素含量日均提升1.2%~1.5%^[9]。酿酒酵母则通过醇解反应增强茶褐素的脂溶性, 提升其在生物膜中的抗氧化效率。在发酵后期(22~30 d), 冠突散囊菌(*Eurotium cristatum*)在茯砖茶中大量增殖, 其代谢产生的胞外酶可进一步修饰茶褐素结构, 增加酚羟基数量, 显著增强自由基清除能力^[10]。此时菌群代谢趋于稳定, 活性物质(TBs、低聚糖)含量达到峰值, 抗氧化活性基本定型。

1.1 霉菌及其功能

霉菌主要包括黑曲霉、根霉(*Rhizopus* spp.)和冠

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突散囊菌等。黑曲霉作为一种曲霉属真菌,是普洱茶、茯砖茶等多种黑茶的核心发酵菌种,它主导纤维素酶、果胶酶等水解酶的分泌,有效降解茶叶细胞壁,释放茶多酚、蛋白质等内含物质。此外,黑曲霉还能促进表没食子儿茶素没食子酸酯(epigallocatechin gallate, EGCG)转化为表儿茶素没食子酸酯(epicatechin gallate, ECG)和没食子酸(GA),这一生物转化过程有助于提高活性成分的生物利用度^[11]。

冠突散囊菌是一种散囊菌纲真菌,俗称“金花菌”,它会分泌多种酶,催化茶叶中的多糖分解为低聚糖及单糖,促进茶多糖的益生功能^[12]。同时,冠突散囊菌所产生的胞外酶可催化茶叶中的多酚类物质发生氧化,在多酚氧化酶的协同作用下,多酚类物质经微生物酶促氧化形成茶黄素、茶红素和茶褐素^[13]。冠突散囊菌代谢产物可显著提升茶液中短链脂肪酸(如乙酸、丙酸)水平,促进脂肪代谢,从而改善肠道菌群平衡^[14]。例如茯砖茶在“发花”过程中,冠突散囊菌分泌水解酶将酯型儿茶素分解成GA和非酯型儿茶素后,这些物质继续被大量微生物释放的胞外

酶所氧化分解成简单的酚类^[15]。根霉是一种毛霉目真菌,它通过分解茶叶中的纤维素、果胶等多糖类物质,促进茶叶细胞壁的崩解,释放内含物质(如茶多酚、蛋白质等),同时生成具有胶质感可溶性物质,增强茶汤的稠厚度和顺滑度^[16]。

1.2 细菌、酵母菌及其功能

芽孢杆菌(*Bacillus* spp.)能产生蛋白酶、脂肪酶等多种酶类物质来分解茶叶中的纤维素等大分子物质,将其转化为更易被人体吸收的小分子物质,从而提升茶叶的口感和香气,其代谢产热也有助于维持堆温,促进其他微生物的酶促反应。乳酸菌(*Lactobacillus*)通过代谢产生的有机酸使发酵体系pH值下降,激活谷氨酸脱羧酶系统,促使茶氨酸向 γ -氨基丁酸(GABA)转化,使其含量提升,形成鲜醇滋味的化学基础^[17]。酸性环境同时抑制多酚氧化酶过度活化,避免茶多酚损失过多^[18]。酿酒酵母通过醇解反应产生醇类等风味物质,并可能促进茶红素等中间产物向分子质量更大、结构更稳定的茶褐素(TBs)转化,同时增强TBs的脂溶性,提升其在生物膜内的抗氧化效率^[19]。

表1 代表性黑茶发酵微生物及其抗氧化功能

Table 1 Representative dark tea fermentation microorganisms and their functions

菌种 Microorganism	代表茶类 Representative tea type	功能 Function	参考文献 Reference
黑曲霉 <i>Aspergillus niger</i>	普洱茶、茯砖茶、青砖茶 Puer tea, Fuzhuan brick tea, Qingzhuang brick tea	分泌纤维素酶、多酚氧化酶,催化儿茶素氧化聚合为茶褐素	[20]
乳酸菌 <i>Lactobacillus</i>	六堡茶,茯砖茶 Liupao tea, Fuzhuan brick tea	抑制多酚氧化酶过度活化,减少茶多酚损失	[21]
酿酒酵母 <i>Saccharomyces cerevisiae</i>	茯砖茶,六堡茶,普洱茶 Fuzhuan brick tea, Liupao tea, Puer tea	发酵后期产醇类物质,促进茶红素向茶褐素转化	[22]
根霉属 <i>Rhizopus</i>	茯砖茶,六堡茶 Fuzhuan brick tea, Liupao tea	分解果胶和淀粉,增加茶汤粘稠度	[23]
芽孢杆菌属 <i>Bacillus</i>	茯砖茶、六堡茶、青砖茶 Fuzhuan brick tea, Liupao tea, Qingzhuang brick tea	分泌蛋白酶降解蛋白质为氨基酸,与茶多酚形成复合物	[24]
冠突散囊菌 <i>Eurotium cristatum</i>	茯砖茶 Fuzhuan brick tea	分泌淀粉酶、水解酶,将茶多糖降解为低聚糖	[25]

2 黑茶主要抗氧化物质

2.1 茶色素

黑茶发酵中产生茶黄素、茶红素和茶褐素(TBs),均具有抗氧化功能,但茶褐素是黑茶发酵的标志性产物,也是其最重要的抗氧化成分之一。TBs是由茶黄素、茶红素进一步聚合形成,分子结构中含大量酚羟基、羧基及苯并吡喃酮基团。TBs具有强

大的 Fe^{2+} 、 Cu^{2+} 螯合能力,能有效阻断Fenton反应,从源头上抑制羟基自由基的产生^[26]。TBs中含有丰富的酚羟基、羧基等活性官能团,能直接有效地清除DPPH·、ABTS⁺·、·OH等多种自由基。此外, TBs还能通过调节肠道菌群结构,促进短链脂肪酸生成,间接改善宿主抗氧化状态^[27]。Chen等^[28]发现,茯砖茶TBs可促进肠道益生菌(双歧杆菌、乳酸菌)增殖,同时抑制大肠杆菌生长,通过调节肠道微

生态间接增强机体抗氧化能力,而绿茶茶多酚无此调控作用。

2.2 茶多糖

茶多糖能有效缓解氧化应激,主要涉及直接清除自由基、增强抗氧化酶活性以及螯合铁离子等方面^[29-30]。纯化的茯砖茶茶多糖可通过重塑肠道菌群、促进SCFAs生成、抑制NF- κ B炎症通路,从而缓解结肠炎相关的氧化应激。Wang等^[31]发现,高分子质量茶多糖的DPPH·清除活性和脂质过氧化抑制能力均显著优于粗多糖,表明其高己糖醛酸含量和大分子结构协同增强抗氧化效果。雅安藏茶中的茶多糖对⁶⁰Co- γ 射线辐照损伤小鼠的抗氧化功能和造血系统有较强的保护作用,进一步证明了茶多糖的抗氧化作用^[32]。此外,绿茶多糖已被证实可降低血浆中的脂质过氧化物的含量,并增强血浆与脂蛋白抗氧化功能的作用^[33-34]。

2.3 茶多酚

茶多酚是茶叶中富含的多羟基酚类化合物的总称,主要包含儿茶素类、黄酮类、花青素和酚酸四大类活性成分^[35],其独特的邻苯二酚结构和多个活性羟基,赋予了该类化合物显著的生物活性。一方面,茶多酚的邻苯二酚结构具有独特的电子共轭体系,其邻位羟基中的氢原子可通过氢转移反应有效清除活性氧(reactive oxygen species, ROS)。另一方面,多个羟基形成的立体空间结构可螯合金属离子,阻断Fenton反应,从而抑制·OH的产生,使其具备优异的抗氧化能力^[36]。

茶多酚可通过调控蛋白激酶B(protein kinase B, PKB/Akt)、核因子 κ B(nuclear factor kappa B, NF- κ B)、表皮生长因子受体(epidermal growth factor receptor, EGFR)以及腺苷酸活化蛋白激酶(adenosine monophosphate-activated protein kinase, AMPK)等重要信号通路,发挥抗氧化、抗肿瘤、调节肠道菌群、抗炎及抗菌等多重生理功能^[37]。例如,茶多酚能够有效防止植物油和动物油脂的酸败,可被用于构建纳米载体应用于肿瘤治疗^[38-39]。对不同年份的普洱茶多酚体外抗氧化研究表明,茶多酚对小鼠酒精性胃损伤具有保护作用^[40]。体外模拟消化实验则显示,雅安藏茶中的茶多酚及茶多糖复合物能较好地调节肠道微生物^[41]。

2.4 酚酸化合物和茶氨酸

发酵过程中,酯型儿茶素(如EGCG)经冠突散囊菌、黑曲霉的酯酶水解生成GA,成为新增的抗氧

化成分^[42]。GA通过酚羟基直接清除自由基,以GA为主的酚酸类化合物在黑茶发酵过程中会新生成或含量增加^[43]。茶氨酸是赋予茶汤鲜爽滋味和愉悦焦糖香的关键物质,并能有效中和或掩盖由茶多酚等成分带来的苦涩感,从而塑造茶叶整体感官品质^[44]。茶氨酸通过多种机制发挥抗氧化作用,一方面,它能够显著缓解自由基对乙醇诱导的肝脏损伤,并通过提升超氧化物歧化酶(SOD)的活性增强整体抗氧化能力^[45]。另一方面,研究发现L-茶氨酸可通过抑制p38 MAPK信号通路的激活,有效减轻H₂O₂诱导的氧化损伤及炎症反应,预防细胞凋亡,并对肠道上皮屏障损伤起到保护作用^[46]。然而,在黑茶剧烈的渥堆发酵过程中,茶氨酸易被微生物降解转化,其残留量极低。因此,尽管体外研究表明茶氨酸具有抗氧化潜力,但在黑茶成品及其生理效应中,由茶氨酸直接发挥的抗氧化作用可能有限。

2.5 微生物分泌物

发酵微生物在生长代谢过程中分泌的次级代谢产物和细胞成分(内生性分泌物)对黑茶的整体抗氧化活性可能发挥着独特的协同增强作用^[47]。其中,特征菌株冠突散囊菌所产生的“金花菌素”,主要指的是一系列蒽醌类、生物碱类等次级代谢产物,其本身已被证实具有直接清除自由基的能力,并可能通过调控Nrf2等细胞内信号通路间接发挥效应^[48-49]。此外,黑曲霉、乳酸菌等多种微生物在发酵过程中合成的胞外多糖,在结构上不同于茶叶本源多糖,它们不仅能够直接发挥抗氧化作用,更重要的是可作为益生元调节肠道菌群平衡,进而通过“菌群—肠道—机体”轴间接缓解系统性氧化应激^[50]。

3 抗氧化作用机制

黑茶的抗氧化活性源于发酵衍生的特异性物质,包括TBs、修饰茶多糖、残留茶多酚及GABA等。这些成分主要通过直接清除活性氧/自由基、螯合金属离子、调节肠道菌群以及激活内源性抗氧化信号通路等多种机制协同发挥作用。

3.1 直接清除自由基与金属离子螯合

黑茶抗氧化物质通过直接清除自由基与螯合金属离子,阻断氧化链式反应。黑茶中TBs、茶多酚的酚羟基可通过氢转移反应,直接清除·OH、O₂^{-·}、ABTS⁺·等自由基。杨高中等^[51]以DPPH·、ABTS⁺·及O₂^{-·}等清除率为指标,发现陈化六堡茶的茶多酚含量与其抗氧化活性呈显著正相关,证

实茶多酚是决定其氧化防御能力的关键效应分子。此外,茶多糖与茶黄素可通过邻位羟基与 Cu^{2+} 、 Fe^{3+} 形成稳定络合物,抑制Fenton反应衍生的 $\cdot\text{OH}$ 产生。Sharma等^[52]发现茶黄素的相关官能团能迅速与 Cu^{2+} 形成稳定的络合物,可使 Cu^{2+} 催化的脂质过氧化率降低。Wang等^[31]利用超滤分级将黑茶多糖拆分为TPs1~TPs3,证实高分子量组分TPs3在5 mg/mL时对 Fe^{2+} 的螯合率达78.12%,显著高于TPs1与TPs2,从而有效阻断 Fe^{2+} 介导的 $\cdot\text{OH}$ 生成,发挥靶向抗氧化作用。

3.2 调节肠道菌群

黑茶抗氧化物质可通过调节肠道菌群间接增强机体抗氧化能力。短链脂肪酸可通过GPR43受体激活肠道上皮细胞的Nrf2通路,增强肠道抗氧化屏障功能。安化黑茶茶多糖、茶褐素可提升肠道拟杆菌门/厚壁菌门比值,促进短链脂肪酸生成,其含量提升2~3倍^[53]。此外,荷叶黑茶提取物可改善内生湿热征患者的肠道菌群结构,使双歧杆菌丰度提升2.8倍,同时降低炎症因子IL-6含量,间接减轻氧化应激^[54]。

3.3 激活内源性抗氧化信号通路

茶多酚不仅能显著上调Nrf2及其下游关键效应分子血红素氧合酶-1(heme oxygenase-1,HO-1)的表达,还能同步下调其负调控因子Kelch样环氧丙烷相关蛋白1(kelch-like ECH-associated protein 1,Keap1)的表达水平^[55]。例如,在衰老的人真皮成纤

维细胞模型中,普洱茶多糖可显著提高SOD和谷胱甘肽过氧化物酶(glutathione peroxidase,GPx)等关键抗氧化酶的基因表达量,从而在效应层面实现抗氧化保护^[56]。此外,在热应激环境下,茶氨酸干预能有效激活小鼠体内的内源性抗氧化酶系统,表现为SOD、GPx和过氧化氢酶(catalase,CAT)活性的显著增强^[57]。

藏茶茶褐素可与Keap1结合,使其构象改变,释放Nrf2并促进其入核,结合抗氧化反应元件(ARE),上调下游HO-1、GPx等抗氧化酶的基因表达。例如,藏茶TBs干预LPS诱导的炎症小鼠后,肝组织Nrf2磷酸化水平显著升高,HO-1蛋白表达受抑,血清与肝脏总抗氧化能力同步增强,骨髓ROS阳性细胞比例下降约40%,有效逆转氧化应激微环境^[58]。

AMPK/沉默信息调节因子2相关酶1(sirtuin 1,SIRT1)/过氧化物酶体增殖物激活受体 γ 辅助激活因子1 α (peroxisome proliferator-activated receptor γ coactivator-1 α ,PGC-1 α)通路是调控线粒体功能的核心。例如,茶多酚能显著提升p-AMPK/AMPK、SIRT1和PGC-1 α 等关键因子的表达水平,从而促进线粒体生物合成并增强线粒体自噬,改善衰老糖尿病大鼠的线粒体功能^[59]。类似地,茶黄素也可显著提升慢性间歇缺氧模型幼鼠肺组织中的p-AMPK、SIRT1和PGC-1 α 蛋白表达水平^[60]。EGCG被证明能增加棕色脂肪组织中的线粒体生物合成并调节相关基因表达^[61](图1)。

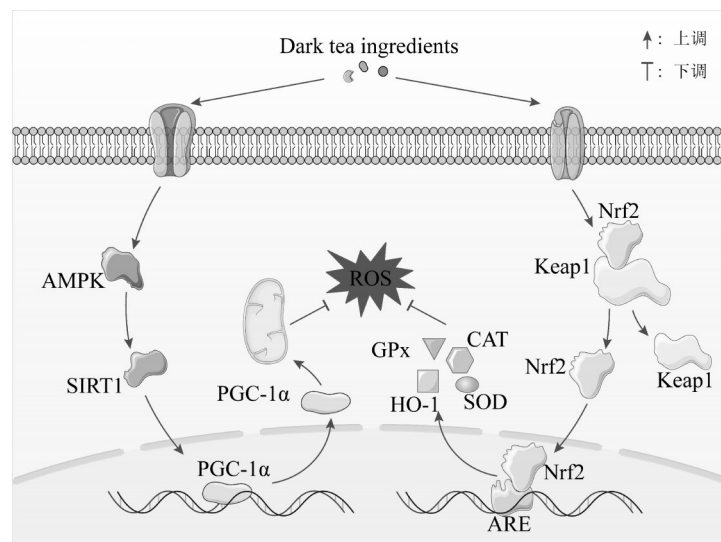


图1 黑茶抗氧化机制示意图

Fig.1 Antioxidant mechanism of dark tea

4 应用前景

4.1 食品领域

黑茶来源的抗氧化物质能通过调节食品体系的氧化还原环境抑制有害微生物的生长繁殖,从而有效延缓食品的氧化变质进程。例如,将黑茶抗氧化提取物添加至食用油中,可显著降低油脂的过氧化值与酸价,延长其货架期^[62-63]。当应用于肉制品(如香肠、腊肉)中,既能抑制肌红蛋白氧化导致的色泽劣变,又能减少脂肪氧化产物(如醛类、酮类)的生成,维持产品的风味与质地^[64]。

黑茶部分成分(如GA、茶褐素)还可与食品中的蛋白质、碳水化合物等基础营养素形成协同作用,在不破坏食品原有营养结构的前提下,为食品赋予额外的健康属性。例如,在乳制品(如酸奶、乳饮料)或谷物食品中添加适量黑茶抗氧化提取物,不仅能丰富食品的活性成分种类,还能通过其天然属性提升产品的市场竞争力^[65-67]。

安化黑茶中的茶多糖、茶多酚、茶褐素等活性成分与金花菌协同作用,可有效调节肠道菌群结构,进而发挥降脂、抗炎、免疫调节、改善糖代谢及保肝等多重生理功能。Guo等^[68]将茶多酚化学锚定于二氧化硅,制得了茶多酚-二氧化硅复合物(silica-s-TP),在丁苯橡胶中显著抑制了热氧老化,长期防护效果优于传统胺/酚类抗氧化剂,并兼具无喷霜和低迁移等实用优势。在功能性食品开发方面,黑茶多糖-钙复合物被证实可促进大鼠骨再生,骨密度提升率达18.6%,可用于开发功能性补钙食品^[69]。

然而,黑茶茶多酚、茶褐素等活性成分存在提取效率低、稳定性差等问题,限制了其在食品加工中的应用。为突破这一局限,Massounga等^[70]采用明胶-玉米醇溶蛋白作为复合壁材,通过电喷雾微胶囊技术对茶多酚进行包埋,可显著提升其稳定性。经180℃高温烘焙后,微胶囊化儿茶素的保留率由游离态的60%显著提升至85%,有效延缓了加工过程中的活性损失。针对黑茶茶多酚提取率低、能耗高的问题,工艺优化是重要突破口。Zeng等^[71]研究表明,在超声功率240 W、温度60℃、料液比1:40条件下,可显著提高茶多酚得率;进一步耦合AB-8大孔树脂纯化,产物纯度由约13%跃升至50.62%,该耦合工艺为破解茶多酚提取高能耗、低得率的难题提供了节能增效的新方案。

4.2 医药领域

黑茶抗氧化物质在代谢综合征、神经退行性疾

病的辅助治疗中具有潜力。Su等^[72]证实黑毛尖蛋白提取物可高效抑制 α -葡萄糖苷酶,活性优于阿卡波糖($IC_{50}=0.12$ mg/mL)。该提取物通过阻断糖吸收通路降低血糖,经脾脑轴信号可降低糖尿病小鼠的空腹血糖值。在神经保护方面,Raj等^[73]发现,茶氨酸可逆转曲马朵诱导的帕金森病运动障碍,使脑内SOD活性升高1倍以上,多巴胺水平恢复至接近正常。其作用机制涉及重启线粒体复合体I和IV的活性、抑制氧化应激及神经炎症等。

现有研究多局限于细胞与动物实验,人体临床试验数据缺乏。建议开展多中心、大样本临床试验,如针对2型糖尿病患者的黑茶提取物干预实验,监测血糖、氧化应激指标的变化,为其医药应用提供循证依据。未来研究可从三方面突破:一是利用宏基因组、代谢组学技术,解析黑茶发酵的微生物代谢网络,筛选高产抗氧化物质的功能菌株;二是通过X射线晶体衍射、分子对接等技术,阐明茶褐素、修饰茶多糖与靶点蛋白的结合机制,为靶向抗氧化剂设计提供理论基础;三是开发智能化发酵设备,实现渥堆温度、湿度的实时调控,推动黑茶抗氧化功能产品的产业化升级^[74]。

5 结论

黑茶独特的后发酵过程是在霉菌、酵母菌和细菌等微生物群落协同作用下完成的。这些微生物通过分泌多种酶类,有效地将茶叶原料中的儿茶素、多糖等大分子物质转化为TBs、低聚糖、没食子酸等特征性抗氧化物质。茶褐素和经微生物修饰的茶多糖是黑茶中最为重要的抗氧化物质。研究表明,黑茶的抗氧化功效是通过多机制协同实现的,主要包括直接清除自由基和螯合金属离子、通过调节肠道菌群平衡间接增强宿主抗氧化能力,以及激活Nrf2/ARE和AMPK/SIRT1/PGC-1 α 等内源性抗氧化信号通路。

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Characteristics and mechanisms of antioxidants in microbial fermentation of dark tea

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Abstract The quality and antioxidative function of dark tea as a unique post-fermented tea in China depend on the transformation of active components mediated by microbial-inducing piled fermentation, and are regulated by the technology of fermentation and raw materials in synergy. This article systematically reviewed the functions and mechanisms of core microbial species during the process of fermentation in dark tea, analyzed the structural characteristics of antioxidants derived from fermentation, and elaborated in depth on the mechanisms of antioxidation regulated by signaling pathway. The directions of studies and application in the future were prospected as well.

Keywords dark tea; strains for fermentation; antioxidation mechanism; theaflavin; signaling pathway

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