

拮抗酵母菌对果蔬采后病害生防增效途径及机理研究进展

周雅涵¹, 罗 杨¹, 曾凯芳^{1,2,*}

(1.西南大学食品科学学院, 重庆 400715; 2.重庆市特色食品工程技术研究中心, 重庆 400715)

摘 要: 本文在总结拮抗酵母菌特点的基础上, 针对限制其商业化应用的主要原因, 重点阐述增强拮抗酵母菌对果蔬采后病害生防效力的途径及机理, 最后进一步提出拮抗酵母菌增效技术未来的研究方向。以此, 为拮抗酵母菌的商业化推广和应用及生物防治技术在控制采后果蔬病害中的应用提供指导。

关键词: 拮抗酵母菌; 生物防治; 果蔬; 采后病害; 增效

Recent Advances in Research on Approaches and Mechanisms of Improving Biocontrol Efficacy of Antagonistical Yeasts against Postharvest Diseases of Fruits and Vegetables

ZHOU Ya-han¹, LUO Yang¹, ZENG Kai-fang^{1,2,*}

(1. College of Food Science, Southwest University, Chongqing 400715, China;

2. Chongqing Special Food Programme and Technology Research Center, Chongqing 400715, China)

Abstract: Based on the characteristics of antagonistical yeasts and the major reasons for the limitation in commercial application, the current approaches and mechanisms of improving biocontrol efficacy of antagonistical yeasts against postharvest diseases of fruits and vegetables are discussed. Prospective directions for research on technologies for improving the biocontrol efficacy of antagonistical yeasts are also put forward. This paper will provide some guidance for the commercialization of antagonistical yeasts and the application of biological technology in postharvest disease control of fruits and vegetables.

Key words: antagonistical yeasts; biological control; fruits and vegetables; postharvest disease; synergism

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新鲜果蔬在采后贮运保鲜过程中, 由于病原物侵染、生理失调、机械损伤及成熟衰老等原因极易导致腐烂变质, 引起巨大损失, 其中侵染性病害是引起新鲜果蔬腐烂变质的主要原因^[1]。控制果蔬采后病害最常用的方法是使用化学杀菌剂, 但随着人们环保意识的增强和对食品安全的持续关注, 利用拮抗微生物替代传统化学杀菌剂控制果蔬采后病害已成为研究热点^[2]。拮抗酵母菌具有遗传稳定, 抑菌谱广; 营养要求低, 生长快的特点; 一般不产生对人和寄主有害的代谢产物; 对多种胁迫条件和逆境具有较强的耐受力, 对多数化学杀菌剂不敏感, 能与多种化学物质及物理方法结合使用, 因而作为采后生物防治的重要研究对象被广泛关注^[3]。然而与传统的化学杀菌剂比较, 拮抗酵母菌具有成本较

高, 使用不方便, 不能有效控制采前已潜伏在果蔬表面的病原菌, 并且受病原物浓度、果实生理状态和环境因素等方面的影响, 防治效果往往达不到要求或不稳定, 这些都限制了拮抗酵母菌的商业化应用^[4]。因此如何利用有效的方法提高拮抗酵母菌的生防效力是影响其商业化推广应用的关键性问题。

多年来的研究表明, 不同种属的拮抗酵母菌能和各种物理、化学或生物方法有效组合, 通过对病原菌、酵母菌、寄主三者发挥不同的作用来强化对病害的抑制, 产生附加甚至协同增效的作用效果。

1 酵母菌与有效抑菌方法的结合

1.1 与直接杀菌的方法结合

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作者简介: 周雅涵(1988—), 女, 硕士研究生, 研究方向为果蔬采后生物技术。E-mail: zhouyahan@126.com

*通信作者: 曾凯芳(1972—), 女, 教授, 博士, 研究方向为食品贮藏工程。E-mail: zengkaifang@163.com

臭氧处理、紫外线照射、化学杀菌剂等单独使用都对侵染果蔬的病原菌有直接杀灭作用,拮抗酵母菌与这些具有直接杀菌作用的物理化学方法联合运用能显著提高酵母的生防效力^[5-7]。有研究表明,臭氧处理能显著增强罗伦隐球酵母(*Cryptococcus laurentii*)对草莓灰霉病的控制效果^[5]。Stevens等^[6]发现用低剂量紫外线(254nm, UV-C)与Hansen隐球酵母(*Debaryomyces hansenii*)联合处理黄桃果实的效果与应用化学杀菌剂苯菌灵处理的效果相当。Lima等^[7]将对杀菌剂有抗性的生防酵母(*Rhodospiridium Kratochvilovae* LS11和*Cryptococcus laurentii* LS28)复合低剂量的杀菌剂Boscalid和Cyprodinil处理苹果果实,不但能有效控制扩展青霉(*Penicillium expansum*)对果实的侵染,减少果实表面杀菌剂的残留量,而且降低了展青霉毒素对果实的污染,二者在病害控制上展现出协同作用。

1.2 与抑制病原菌孢子萌发和芽管增长的方法结合

多数体外实验表明,不同浓度的乳链球菌素、丙酸钙、碳酸氢钠、壳聚糖等物质,能够抑制多种病原菌孢子的萌发和芽管的生长。在复合物浓度对拮抗酵母菌生长无明显抑制作用的前提下,酵母菌与这些物质复合使用能显著提高其生防效力。如将复合乳链球菌素的嗜油假丝酵母(*Candida oleophila*)细胞悬浮液先于病原菌*Botrytis cinerea*和*Penicillium expansum*接种于苹果伤口,果实发病率仅为4.7%,显著低于对照组和单独处理组的发病率^[8]。有研究证实罗伦隐球酵母(*C. laurentii*)与碳酸氢钠复合使用对番茄采后灰霉病和绵腐病有良好的控制效果^[9],碳酸氢钠不但能抑制病原菌孢子的萌发和芽管的延长,还可改变果实伤口的pH值,病原菌比拮抗菌对这些改变更敏感,因此进一步减弱了病原菌的生存能力。钼酸铵和酵母菌复合使用能提高酵母菌对金冠苹果和葡萄采后腐烂的控制水平^[10-11],钼酸铵能够强烈抑制磷酸酪氨酸磷酸酶(PTPase)的活性,从而影响对细胞代谢调节起重要作用的磷酸化和去磷酸化过程。壳聚糖作为一种可生物降解的天然物质单独使用能直接抑制扩展青霉在苹果伤口处的侵染,与罗伦隐球酵母(*C. laurentii*)复合使用在病害控制上表现出协同作用^[12]。此外,微波短时加热处理也能通过相同的作用机制来提高罗伦隐球酵母(*C. laurentii*)对梨青霉病的控制水平^[13]。

1.3 与病原菌分泌的水解酶活性的抑制方法结合

采后病原菌的致病机理复杂而众多,它们可以通过分泌不同的细胞壁水解酶直接突破果蔬表皮的防御机制。病原菌分泌降解寄主细胞壁水解酶的顺序为:果胶酶→半纤维素酶→纤维素酶,不同降解酶作用于不同细胞壁组分,协同降解果蔬细胞壁成分^[14]。研究表明,钙离子、气调贮藏(controlled atmosphere storage, CA)能抑制病原菌分泌的果胶溶解酶,如多聚半乳糖醛酸酶

(polygalacturonase PG)的活性^[15-16]。它们与罗伦隐球酵母(*C. laurentii*)及梅奇酵母(*Metschnikowia pulcherrima*)结合使用,能显著提高酵母对梨果实采后灰霉病,苹果果实采后青霉病的控制水平^[17-19]。

2 酵母菌与激发自身活性的方法结合

2.1 增强酵母菌在逆境中的生存能力

现有研究表明,酵母菌可以通过逆境和诱导培养,或复合脱脂乳、蛋白胨等保护性物质,来增强自身对各种胁迫的适应性,提高其拮抗效力。如清酒假丝酵母(*Candida sake*)在低水分活度的液体培养基培养后,细胞内会累积较高的海藻糖和糖醇,其在逆境中的存活能力和对苹果青霉病的控制效力都明显增强^[20-21]。酵母细胞内海藻糖的累积对细胞质膜和胞内敏感蛋白具有保护作用,能增强细胞对多种胁迫的适应性;而内源性糖醇的累积能够在降低细胞质水分活度的同时,不破坏酶的结构和功能,使细胞代谢活动能够在水分胁迫的条件下正常进行^[22-23]。Li等^[24]发现海藻糖作为内源或外源保护因子对拮抗酵母菌*C. laurentii*和*R. glutinis*在速冻,慢冻和冷冻干燥胁迫下都显示出保护作用,并且内外源海藻糖产生了协同作用。

在对生防酵母(*Cytophobasidicum infirmominiatum*)的研究中发现,甜菜碱诱导培养酵母细胞,不但能提高细胞自身抗氧化酶系统的活性,增强酵母对氧化胁迫的适应性,还促进了酵母细胞在苹果伤口处的快速生长^[25]。外源性保护剂如脱脂乳、蛋白胨、麦芽糖等,因富含蛋白质、维生素、糖等,添加在活细胞制品中不仅可以修复细胞质膜的损伤,而且能为细胞抵抗渗透应力的损伤提供保护。嗜油假丝酵母(*Candida oleophila*(strain O))与这些外源性保护剂结合使用,能显著增强酵母细胞在干燥或缺水的条件下对苹果青霉病的控制力^[26]。

2.2 激发酵母产生有拮抗作用的物质

通过在培养基中添加相应的物质诱导培养酵母细胞,能刺激酵母自身分泌有拮抗效力的物质。Calvente等^[27]发现,通过诱导培养粘红酵母(*Rhodotorula glutinis*),可使细胞内大量累积一种与铁高度亲和的低分子有机物——粘红酵母酸(rhodotorulic acid)。病原菌孢子的萌发需要大量吸纳铁离子,粘红酵母酸的存在能延缓病原菌孢子的萌发。Sansone等^[28]用粘红酵母结合粘红酵母酸使用,能显著提高酵母对扑海因抗性菌株*Botrytis cinerea*的控制效力。也有研究表明,几丁质诱导培养罗伦隐球酵母(*C. laurentii*),能刺激酵母细胞分泌几丁质酶的活性,显著提高酵母对梨青霉病的抑制效果^[29]。

3 酵母菌与对果蔬起防御作用的方法结合

3.1 与强化果蔬固有抗性的物质复合

细胞壁的结构组成在果蔬的天然抗性方面起到一定作用,通过复合相应的化学物质,能增强果蔬细胞壁和膜结构的完整性,强化果蔬固有的结构抗性。 Ca^{2+} 可以与细胞壁中的果胶相结合,在果胶酸之间或果胶酸与其他带羧基的多糖之间形成交叉链桥,增强寄主细胞壁的强度和膜结构的完整性,使病原菌分泌的果胶酶软化细胞壁的能力降低^[30]。研究表明,用季也蒙假丝酵母(*Candida guilliermondii*)和膜醭毕赤酵母(*Pichia membranifaciens*)复合氯化钙处理桃果实,能显著增强酵母对葡萄根霉菌(*Rhizopus stolonifer*)的生防效力^[31]。孙萍等^[32]在控制柑橘采后青霉病的研究中也发现粘红酵母(*R. glutinis*)复合 Ca^{2+} 使用对病害具有良好的控制效果。

3.2 与诱导果蔬抗病性的方法结合

作为生物性激发子,拮抗酵母菌单独使用对采后果蔬的抗病诱导能力有限,研究发现拮抗酵母菌与非生物性物理化学诱抗因子相互配合,如结合热处理或复合水杨酸(SA)、吲哚-3-乙酸(IAA)、赤霉素(GA_3)、茉莉酸甲酯(MeJA)等处理果蔬,通过调节果蔬组织活性氧代谢,刺激果蔬防御酶的活性,能显著增强酵母的抗病诱导能力。

3.2.1 调节果蔬组织活性氧代谢

果蔬组织受到病菌或诱导因子的诱导能短时间内产生大量的活性氧,此时必须通过活性氧清除系统来保持体内活性氧水平的动态平衡。研究发现果蔬组织在受到拮抗酵母菌和非生物诱抗因子的双重诱导时,其体内的活性氧代谢相关酶类,如过氧化物酶(POD)、超氧化物歧化酶(SOD)、过氧化氢酶(CAT)、多酚氧化酶(PPO)的活性会显著提高。这些酶能专一性的清除果蔬体内活性氧或阻止活性氧的形成,对果蔬组织起到保护作用^[33]。研究表明,IAA结合罗伦隐球酵母(*C. laurentii*)使用能不同程度刺激梨和苹果果实CAT、POD、PPO、SOD活性的增强,复合处理强化了对果实青霉病和灰霉病的抗病诱导能力^[34-35]。

3.2.2 刺激果蔬防御酶的活性

β -1,3-葡聚糖酶和几丁质酶作为果蔬体内典型的病程相关蛋白,在分解真菌细胞壁组分、保护寄主组织上有明显的协同作用^[36]。Cao等^[37-38]研究发现茉莉酸甲酯(MeJA)和氯化钙复合膜醭毕赤酵母(*P. membranifaciens*)使用,能诱导枇杷果实 β -1,3-葡聚糖酶和几丁质酶的活性显著提高,增强拮抗酵母菌对枇杷炭疽病的控制效果。热处理结合季也蒙假丝酵母(*C. guilliermondii*)和膜醭毕赤酵母(*P. membranifaciens*)联合运用也能显著诱导番茄果实中这两类防御酶活性的升高^[39]。

苯丙氨酸解氨酶(PAL)、PPO、POD作为重要的防御酶,参与果蔬体内酚类化合物、植保素、木质素等多种抗性物质的合成。研究表明拮抗酵母菌通过与其他激发子结合使用能显著刺激这些酶的活性,提高酵母的生防效力。在罗伦隐球酵母(*C. laurentii*)生防效力改良的

研究中发现,酵母与SA、 GA_3 、MeJA复合处理樱桃、苹果、梨、桃果实后,能不同程度地诱导果实POD、PPO、PAL活性的上升,复合处理在对果实病害的抗性诱导方面展现出良好的协同效应^[40-43]。

3.3 与延缓果蔬成熟衰老的方法结合

果蔬在采后成熟衰老过程中,其组成抗病性机制和可诱导的抗性反应能力都会不断弱化,从而导致果蔬组织对病原菌的敏感性不断提高^[44]。脂氧合酶(LOX)参与 $\text{O}_2\cdot$ 和单线态氧等自由基的形成和膜脂过氧化过程,能导致植物组织膜脂的损伤和乙烯的生成,因此与采后衰老关系密切。研究发现,将拮抗酵母菌与气调贮藏^[45]、热处理^[46]等物理因子整合或复合相应化学物质^[47-48]使用,能延缓果蔬组织成熟衰老,提高酵母菌对病害的控制力。在增强罗伦隐球酵母(*C. laurentii*)对扩展青霉(*P. expansum*)生防效力的研究中发现,酵母复合6-BA处理苹果果实或复合 GA_3 处理梨果实都能抑制果实LOX的活性和丙二醛(MDA)含量的上升,延缓细胞质过氧化^[47-48]。

4 结 语

控制果蔬采后腐烂是一个涉及采后生理、采后病理及贮藏技术等多方面的综合技术。拮抗酵母菌与相应的物理、化学、生物方法有效组合能很好的解决酵母单独应用时高效性和持久性欠缺的问题,为拮抗酵母菌的商业化应用和推广提供技术支持。

拮抗酵母菌生防效力的提高涉及多重机制的联合作用,然而,现在大多数研究仅停留在增效作用抗病效果的研究上,缺乏对相关机理的深入研究和探讨。因此,进一步开展生防酵母增效机理的研究,并以此为依据探索提高酵母菌拮抗效力的新途径、新技术、新方法;利用基因工程技术或蛋白质组学技术筛选与酵母拮抗效力有密切关系的关键基因和蛋白质,或在分子水平上定向改造酵母菌,提高其生防效力等都将为发展以酵母为核心的采后病害生物学控制技术提供坚实的理论基础和实践保障。

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