

堆肥调控作物根际微生物组抑制植物病害的研究进展

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摘要: 我国有机废弃物总量大、养分储量高,是提高农田生态系统服务功能的重要资源。好氧发酵能够较容易地实现有机废弃物处理与资源化转化,发酵产物堆肥常对多种植物病害具有抑制作用。回顾了近年来堆肥抑病方面的研究进展,重点关注堆肥对根际微生物组结构和功能的调控作用及潜在调控途径,探讨了堆肥微生物组与土壤和根际微生物组的差异,堆肥对土壤物理生物化学特性的影响及生物非生物环境因子对根际微生物组的影响,旨在“堆肥-土壤-植物根际微生物组”互作系统提供初步认识。

关键词: 堆肥; 植物病害; 抑病; 土壤/根际微生物组

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Advances in Compost Regulation of Rhizospheric Microbiome to Suppress Plant Diseases

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Abstract: In China, huge amount of organic wastes is produced annually and it contains large quantity of nutrients and might serve as an important resource to enhance ecological services in agroecosystem. Aerobic fermentation is a widely used method for the treatment of organic waste and resource transformation, and composting may inhibit many plant diseases. In this review, we summarized recent progress in the mechanism of the disease suppressive of composts, focusing on its regulatory effects on the structures and functions of rhizosphere microbiome as well as potential regulatory pathways. We discussed the differences between composting microbiome and soil rhizosphere microbiome, effects of composting on soil biological and physicochemical properties, and biological and abiotic environmental factors on rhizosphere microbiome. This relevant summary might provide some primary understanding of the interaction system among compost, soil and plant rhizosphere microbiome.

Key words: compost; plant diseases; disease suppressing; soil/rhizosphere microbiome

据预测,到2050年,世界人口将增加至91亿^[1],全球对食品和纤维的需求量将比2017年增加70%^[2]。耕地是粮食生产的重要基础,但随着全球人口数量的激增和工业的快速发展,可耕土壤面积正在逐步减少。据调查数据显示,全球可利用农业

土壤面积仅剩约3%,且现有耕地面临着土壤肥力下降、化学肥料与农药污染、土壤酸化退化与水土流失等挑战^[3-4]。同时,作物土传病害也严重威胁着农业生产。例如,由病原真菌(*Fusarium oxysporum*, *Rhizoctonia solani*, *Verticillium dahliae*)、细菌(*Ralstonia*

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solanacearum, *Agrobacterium radiobacter*)、卵菌 (*Phytophthora capsici*, *Pythium ultimum*) 等导致的病害造成了严重的作物减产^[5-8]。而杀菌剂等化学农药的使用带来了抗生素抗性^[9]、水体与土壤的污染^[10]等一系列负面环境效应,加剧了农业生产与环境保护之间的矛盾。因此,探寻强化农田土壤生态服务功能等绿色安全的生产措施对促进农业的可持续发展具有重要意义。

另一方面,我国的有机废弃物产量大,已成为全世界最大的农业废弃物产生国,预计未来仍将以每年 10% 的速度递增。仅养殖场禽畜粪污达 38 亿 t (鲜重)^[11],其中的氮磷钾养分储量高达 7 000 万 t^[11],超过我国全年化肥养分总量约 1 000 万 t。目前有机废弃物处理与资源化率低(不足 40%)^[12],造成严重的养分损失和环境污染问题^[13]。第二次全国污染源普查结果表明,农业污染源总氮、总磷的排放量分别为 141.49 万 t 和 21.20 万 t。因此,有机废弃物无害化处理和资源化利用对生态环境保护和农业绿色发展具有重要的意义。好氧发酵是利用微生物降解转化有机废弃物形成堆肥,适合不同有机废弃物处理与资源化转化的需求,是国内外农业废弃物资源化利用的最重要的途径之一。

好氧堆肥在植物病害防治方面的作用很早就被认识到^[14]。大量的研究证实了堆肥能够抑制多种作物的真菌(枯萎病、黄萎病、腐霉病和丝核病等)和细菌(青枯病、斑疹病和叶枯病)病害^[15]。在一些实验中,堆肥甚至能够取得与化学药剂类似的防治效果^[16]。与化学农药不同,堆肥被认为是通过提升土壤生态系统服务功能来维持农田生态系统健康,是一种绿色的农业技术。本文综述堆肥通过调控土壤/根际微生物组抵抗作物病害方面的重要研究进展。

1 堆肥抑病的重要影响因素

前期的研究显示拮抗微生物和化学物质是堆肥抑制植物病害的关键因素。其中支持堆肥能够通过拮抗微生物抗病的证据链主要有两条:一是堆肥中存在大量对植物病原物有拮抗作用的微生物,如 *Pseudomonas*、*Bacillus*、*Enterobacte*、*Trichoderma*、*Gliocladium* 和 *Penicillium*^[17],添加这些拮抗微生

物常能抑制相应的植物病害;二是灭菌处理后,堆肥抑病作用会降低、甚至完全消除^[18-19]。例如, Antoniou 等^[20]通过灭菌和不灭菌堆肥的比较研究,发现灭菌后的堆肥对番茄生长的促进作用和对枯萎病 (*Fusarium oxysporum* f.sp) 和黄萎病 (*Verticillium dahliae*) 的抑制作用均下降。也有研究发现好氧堆肥能够提高作物的免疫力,例如诱导萝卜抵抗黑腐病菌引发的叶斑病^[21];诱导甜瓜的系统抗性,提高抵抗尖孢镰刀菌引发的枯萎病和灰葡萄孢引发的灰霉病的能力^[22]。这一作用或许也与堆肥中的有益微生物相关。从堆肥中分离出的微生物具有诱导植物病程相关蛋白如 β -1-3 葡聚糖酶、几丁质酶、过氧化物酶和多酚氧化酶等的表达能力,相关蛋白的表达能够帮助植物阻碍多种病原菌的入侵^[23-24]。

堆肥中含有多种与抑制病害相关化学物质(小分子酸、氨氮、腐殖质、酚类物质)、活性物质(PR 蛋白、大分子物质降解酶、抗氧化酶)和拮抗微生物等^[25-27]。堆肥的腐熟度、物料类型等也能够影响抑菌物质的数量、组成以及抑制病害的能力^[28],但是,不同研究之间的结果差异较大^[29]。

堆肥的抑病效果与土壤类型、耕作及其他农业措施、土传病害的类型等多种因素有关^[15, 28, 30]。如 Bernar 等^[31]发现堆肥虽然可以减少常规和有机农场中马铃薯丝核菌病的发病率,但在有机农场的抑病效果比常规农场高 15%。堆肥对不同病害如马铃薯丝核菌病和银腐病的抑病效果存在较大的差异^[31]。Larkin 等^[32]发现灌溉能够降低堆肥对马铃薯黑痣病和疮痂病的抑制作用。不同堆肥抑制病害的能力也存在较大的差异^[33],有一些甚至会出现促进病害(晚疫病、根腐病)的负面效果^[34]。但是目前尚未明确堆肥-环境-植物病害抑制之间的关键互作机制,相关理论基础的缺乏在一定程度上限制了堆肥在植物病害防治方面的大规模使用。

2 堆肥调控根际微生物组结构与潜在作用机理

根际微生物组是指定殖在根系周围狭窄区域(<10 mm)内的微生物,在作物健康的维系方面具有重要的作用^[35]。根际微生物的丰度上比土壤中高 1-2 个数量级,种群结构也存在较大的差异^[36-37]。

近年来根际微生物组在促进养分元素转化、病原物抑制等方面的重要作用逐渐被揭示^[38]。根际微生物能够矿化植物根分泌的或根附近土壤中的有机物,促进养分元素的循环与周转^[39];通过根际激发效应促进土壤中养分元素的释放^[40-41],影响不同植物之间竞争力^[42]。在植物病害防治方面,根际有益微生物可通过生态位竞争^[43]、产生抗生物质^[44]、产生细胞壁降解酶^[45]等途径直接作用于病原菌,从而降低其在土壤中的丰度至不可致病水平;也可通过产生植物生长激素、营养元素固定与分解、诱导系统抗性和群体感应等途径直接作用于植物本身,提高其抵抗力,从而降低植物感病风险^[46];在种群和群落层面上,根际的 *Proteobacteria*、*Firmicutes*、*Actinobacteria*、*Acidobacteria* 和 *Planctomycetes* 门等根际类群参与多种土传病害抑制^[47]。堆肥和生防微生物的使用常能改变根际微生物多样性,促进有益微生物如 *Sphingomonas*、*Paenibacillus*、*Sporothermodurans*、*Clostridium* 和 *Bacillus* 等的增殖,可使土壤向健康有利的方向发展,从而产生广谱抗病性^[48-51]。

2.1 堆肥微生物组中非主导种群的调控

从堆肥中分离出的 *Proteobacteria* 和 *Actinobacteria* 门的拮抗能够在番茄根际定殖,抑制青枯病^[52]。值得注意的是堆肥或其他有机肥中的微生物组与土壤和根际的微生物种群存在较大的差异。Zhao 等^[53]通过研究堆肥和土壤中的微生物群落发现,二者的细菌、真菌优势种存在明显差异,有机肥中的细菌优势种为 *Pedococcus*、*Bacillus* 和 *Klebsiella*, 真菌则为 *Pichia*, 而土壤中的细菌 *Planctomyces* 和 *Klebsiella* 相对丰度较大,真菌为 *Fusarium* 和 *Myrothecium*。Han 等^[54]研究也显示施用堆肥只能在短期内(<7 d)对土壤微生物组具有较大的影响。Shen 等^[55]也发现堆肥的抑病作用与其中的微生物丰度并无相关性。Wang 等^[56]分析了中国 16 省的 116 个堆肥样品,发现堆肥的核心微生物组主要由能够降解大分子有机物的微生物构成,但未包含已经报道能够抑制植物病害的微生物物种。事实上,堆肥微生物组结构常随堆肥过程而发生剧烈变化,而高温期(>55℃)常常会延续超过 5 d,较长的高温或能杀灭部分中温

菌,从而使其不能在堆肥腐熟期再增殖^[57]。另一方面,在好氧发酵后期有机物料被大量降解,物料含水率会较大地下降,不利于微生物的活动,因而堆肥中耐高温的厚壁菌门微生物常占主导地位^[56]。上述研究显示堆肥中的主要微生物在土壤或根际环境中的竞争力或较弱,或未直接参与植物病害的抑制,非主导种群或在植物病害抑制方面起关键作用。

添加外源拮抗菌能够强化堆肥的抑病作用^[58]。如,添加抑病的芽孢杆菌和木霉菌的堆肥可有效抑制尖孢镰刀菌引起的枯萎病^[59-60];添加地衣芽孢杆菌和甲基营养型芽孢杆菌能够强化堆肥对草莓枯萎病的防治效果,而病原微生物镰刀菌的数量降低了近 5 倍^[61];添加芽孢杆菌的堆肥可使西瓜枯萎病的发病率降低 41.9%^[62];添加解淀粉芽孢杆菌的生物肥料增加了香蕉根际细菌多样性,从而起到了抑制病原菌的效果^[63]。Huang 等^[64]制备的含 *Bacillus velezensis* H-6 的堆肥的施用同样对香蕉枯萎病有抑制作用。经拮抗微生物强化的堆肥对根际微生物的种群结构具有调控作用,增加有益微生物在根际的丰度。近期的一些研究显示能够帮助病原菌生长的其他根际微生物是影响病原菌侵入的关键^[65],因此降低此类微生物在堆肥中的丰度或能提高堆肥的抑病能力。

2.2 土壤微生物物理化学过程的间接作用

植物不仅从土壤中招募根际微生物,同时也在土壤中拓展根系、吸收水和营养元素,通过根系沉降作用输入碳源,与根系微生物形成一个动态的互作系统^[66]。因此,不难理解土壤的物理、化学和生物特性能够影响根际微生物组的结构和功能^[67]。好氧堆肥的农田应用不仅向土壤中注入了营养元素,同时也带入了大量的有机质、有益微生物、抑菌物质等,具有提高土壤有机质、肥力元素、土壤生物量、增加孔隙度等作用^[68]。长期使用堆肥能够全面提高农田生态系统的服务功能。例如,在中国农业大学曲周实验站开展的长期定位实验中发现堆肥能够增强作物的抗病能力^[69];改善土壤的品质,如土壤的有机质、NPK 等养分的含量,与常规体系相比提高了 1-1.4 倍^[70];降低了硝酸盐的淋失和 N_2O 的排放^[71-72];提高了土壤中不同形态的磷元素关

联性^[70]；提高了土壤中细菌的丰度（平均提高 1.8 倍），例如参与难降解碳代谢的微生物种群的相对丰度，如 *Ignavibacteria* 和 *Acidobacteria Gp6*；同时又降低了土壤中的氨氧化的细菌、古菌及厌氧氨氧化细菌的相对丰度，提高了含 *napA* 基因型的反硝化细菌的丰度^[70]。土壤生物物理化学特性的变化也能影响根际微生物组，如幼苗期茄子根际微生物组在施用和不施用堆肥处理组差异较大，但差异随作物的生长而逐渐减弱。在茄子盛果期根际强解磷细菌 *Enterobacteria* 的相对丰度显著提高，或与该生长期茄子对磷元素的需求较高相关^[73]。长期施用堆肥的土壤微生物组对辣椒疫病具有较好的抑制作用，发病率仅为常规土壤微生物组处理的 30%，同时拮抗芽孢杆菌（*Bacillus*）在辣椒根际的相对丰度显著提高，利用根系富集的拮抗芽孢杆菌合成抑病微生物组能显著提高辣椒对疫霉的抵抗^[74]，这证实了长期施用堆肥改造的土壤微生物组能够提高根际拮抗 *Bacillus* 的丰度抑制疫霉病。苗期富集根际拮抗菌如芽孢杆菌和假单胞菌等也能够影响作物之后的生长过程中对病原物的抵抗力^[75]。

2.3 根际/土壤微生物组的时空异质性及堆肥的改造作用

土壤微生物组是植物招募根际微生物组的库，多数研究显示长期施用堆肥或其他有机肥能够影响土壤微生物组的多样性，特别是 β 多样性。但在不同研究中，堆肥对微生物类群的作用往往存在差异^[70, 76]。堆肥的类型、施用量以及种植方式、作物的类型等多种因素或能共同决定最终形成的微生物组结构^[77]。有机农场常使用好氧堆肥补充土壤养分，前期我们在 30 个点开展了有机农业对土壤微生物组多样性影响的调研，发现有机农业通常能够显著改变土壤微生物的 β 多样性，但对 α 多样性无显著影响^[78]。多数微生物属对有机农业响应方式（正响应，负响应）与研究点相关^[78]。与定位实验基本一致的是有机农业倾向富集参与难降解碳代谢的微生物，抑制氨氧化细菌类群等^[78]。另一方面，土壤微生物组的结构往往也会随植物生长期而呈现动态变化。如豌豆、小麦和甜菜的根际微生物群落随着植物的生长期改变而产生动态变化^[79]；种植

3 个月和 6 个月甘薯的根际微生物群落存在显著差异^[80]；在拟南芥生长发育的 4 个不同生长期中，苗期的根际微生物群落与其他时期不同，同时链霉素合成相关的基因在抽薹期和开花期被显著诱导^[81]；我们对不同施肥体系下茄子和玉米根际解磷菌多样性研究发现，处于结果期的作物能够在根际富集大量解磷微生物^[73, 77]。这一结果显示不同生长期的植物对营养元素的内在需求或是其招募不同功能微生物的动力。因此，堆肥施用对土壤微生物组的影响或是动态的，即对微生物群落演替的影响。在曲周长期定位实验中，我们连续两年跟踪不同施肥处理下土壤微生物种群的演替，发现 *Flavobacterium* 和 *Pseudomonas* 等抗病微生物的影响存在较大的时间波动^[82]，但这种波动是否会对根际微生物组的结构和抗病功能产生影响尚需要进一步研究。但不可否认的是植物从不同土壤中招募根际微生物组的结构往往存在差异，如 Schreiter 等^[37]发现 3 种不同土壤中的生菜根际微生物组成存在显著差异；在以拟南芥为宿主的根际微生物组研究中，发现土壤类型是一个重要的影响因素^[83-84]。此外，土壤类型也能够影响葡萄和玉米的根际微生物结构组成^[85-86]。因此，解析堆肥施用对不同土壤、不同作物根际微生物组的结构和功能的影响，或能为利用堆肥调控根际微生物组，增强作物抑病性等绿色农业技术的研究提供一定的理论基础。

3 总结与展望

堆肥或通过改变土壤的物理化学和生物特性及向土壤中引入关键根际微生物等方式调控根际微生物组的结构、抑制植物病害，相关调控作用受环境因子如土壤类型，作物品种与发育、农业措施、外源添加拮抗微生物等多种因素的共同作用（图 1）。土壤的物理化学及生物特性的变化或能影响土壤微生物-病原菌、病原菌-作物、作物-根际微生物之间的互作，进而改变病原菌在土壤中的命运及其对寄主作物的趋化作用等，或影响作物系统获得抗性等。土壤和根际中的微生物的多样性、种群结构具有较大的可塑性、可变性和时空异质性的特点，具有普遍意义的作用机理的揭示依然面临巨大挑战。通过环境组学等前沿技术深入探讨“堆肥-土壤-

植物根际微生物组”互作系统,揭示关键作用机制及规律或能促进新型绿色抑病投入品的研发与应用,提高土壤肥力与农田生态服务功能,为“藏粮于地、藏粮于技”的国家战略贡献力量。

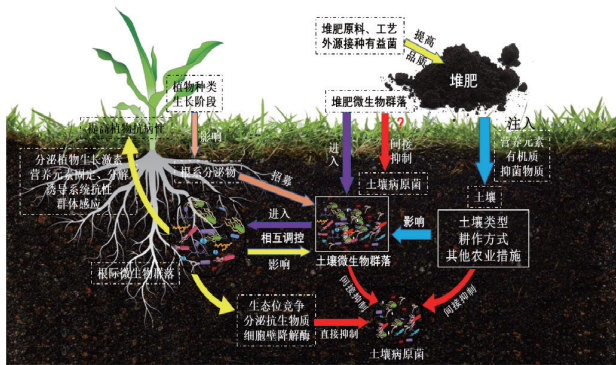


图1 堆肥抑制植物病害的机理模型

Fig. 1 Mechanism model of compost inhibiting plant diseases

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