

连作根系分泌物加剧土传病害的机制和缓解措施研究进展*

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摘 要: 基于植物-土壤反馈理论, 连作体系中的根系分泌物必然在加剧土传病害发生中起重要作用, 但相关研究证据尚缺少系统总结。本文梳理了连作导致土传病害加剧的现象以及连作对典型根系分泌物组分的累积。从有利于土传病原菌由土体向根际迁移、增殖和致病(“利病”)、破坏根际有益微生物群落防线(“压益”)和毒害根系免疫系统(“自毒”)等三个方面, 揭示连作根系分泌物中某些物质促进土传病原菌入侵的机制。从根系分泌物角度阐述轮作、间作、套作、伴生和嫁接等多样性种植方式缓解连作土传病害的机制。提出鉴定“利病”、“压益”和“自毒”物质以及构建对应的消减技术途径, 可为土传病害绿色高效综合防控提供理论和技术支撑。

关键词: 连作障碍; 土传病原菌; 根系分泌物; 自毒物质; 根际微生物

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Research Advances on Mechanisms and Preventions of Soil-borne Diseases Exacerbated by Root Exudates in Continuous Cropping Systems

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Abstract: The rhizosphere microbial communities play a crucial role in assisting plants in dealing with soil-borne pathogens. When plants encounter specific soil pathogen invasions, they adapt the composition and quantity of root exudates to recruit beneficial microorganisms that can utilize these substances to resist soil pathogen infections. However, recent studies have revealed that certain root exudates can promote the occurrence of soil-borne diseases. This paper aims to provide a comprehensive review and summary of existing evidence regarding the role of root exudates in continuous cropping systems, which contribute to the occurrence and outbreaks of soil-borne diseases. The paper begins by presenting observations of soil-borne diseases exacerbated by continuous cropping and the accumulation of key root exudates. Subsequently, it summarizes the potential mechanisms through which some root exudates in continuous cropping promote the invasion of soil-borne pathogens. Considering the process of soil-borne pathogens causing plant diseases in continuous cropping involves introduction (soil to the rhizosphere), colonization (rhizosphere to root surface), and infection (root surface to root interior), the substances exacerbating soil-borne pathogen invasion in each stage are categorized into the following three groups based on their functions: 1) substances that facilitate the migration, proliferation, and pathogenicity of soil-borne pathogens from soil to the rhizosphere ("enriching pathogens"); 2) substances that disrupt the defense line of beneficial microbial communities in the rhizosphere ("suppressing beneficial microbes"); and 3) substances

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that hinder the root immune system ("self-toxic"). Subsequently, the paper explores the mechanisms of diversified cropping systems such as rotation, grafting, row intercropping, relay intercropping, and companion planting in alleviating soil-borne diseases from the perspective of root exudates. These mechanisms include: 1) enhancing the diversity of root exudates; 2) reducing the secretion of self-toxic substances by main crops; 3) secreting root exudates that suppress pathogens; 4) promoting the formation of a protective rhizosphere microbial community to enhance plant disease resistance and 5) regulating the synthesis pathways of metabolites to reduce the production of self-toxic substances. Finally, the paper outlines several green, efficient, safe, and comprehensive control strategies for soil-borne diseases. These strategies include: 1) identification of "enriching pathogens", "suppressing beneficial microbes" and "self-toxic" root exudates; 2) application of diversified planting, rootstock grafting, biochar, and organic fertilizer to regulate root exudates, improve soil microbial community structure, enhance plant growth, and reduce diseases; and 3) establishment of biodegradation technologies for identifying, isolating, and culturing bacterial and fungal strains capable of decomposing the "enriching pathogens", "suppressing beneficial microbes" and "self-toxic" plant root exudates.

Key words: Continuous cropping obstacle; Soil-borne pathogens; Root exudates; Autotoxins; Rhizosphere microorganisms

随着农业集约化程度和复种指数的增加,土传病虫害爆发、连作障碍现象日趋严重^[1-3]。研究表明,根际微生物在帮助植物抵御土传病原物入侵过程中发挥重要作用^[4-5]。当遭遇特定的土壤病原物入侵时,植物会采用呼救系统(Cry for help)特异性地调整根系分泌物组分和数量,招募能利用这些特殊物质的有益微生物,以抵御土壤病原菌侵染^[6-7]。然而,既然植物具备通过根系分泌物调控自身环境适应性的能力,为什么在连作体系下作物发生土传病害的概率仍然较高?基于植物-土壤反馈理论,连作系统中特定根系分泌物的持续输入可能会起到负面的调节作用。

根系分泌物在调控根际微生物结构和功能中发挥重要作用^[8],目前研究者多关注于优化根际微生物组或具有抑病功能的根系分泌物组分,但忽略了加剧土传病害发生的物质类型及其可能机制。按照物质类型分类,根系分泌物包括糖类、氨基酸类、有机酸类、酚酸类等^[9]。但这些根系分泌物的作用方式、促进土传病害发生的潜在机制尚缺少系统梳理和总结。考虑到连作体系中土传病原菌的致病过程主要包括引入(土体至根际)、定殖(根际至根表)、侵染(根表至根内)三个阶段,连作体系中的根系分泌物可能在土传病原菌入侵植物的各阶段均发挥作用。笔者认为每个阶段加剧土传病原菌入侵的根系分泌物按功能可分为以下三类:(1)利病,有利于土传病原菌在土壤的存活及其由土体向根际的迁移和增殖;(2)压益,破坏根际有益微生物群落;(3)自毒,毒害根系防御系统。为此,本文首先从“利病”、“压益”和“自毒”等三个方面,揭示连作根系分泌物加剧土壤生物障碍的机制以及建立消减“利病”、“压益”和“自毒”物质的技术途径,可为建立绿色、高效、安全的土传病害综合防控理论和技术提供支撑。

1 根系分泌物中的“利病”、“压益”和“自毒”物质

本文将对病原菌有趋化作用、促进病原菌快速增殖和根际定殖的根系分泌物组分统称为“利病”物质。常报道的根系分泌物中“利病”物质主要有可溶性糖(如葡萄糖、果糖和蔗糖)、有机酸(如苹果酸、柠檬酸、阿魏酸和肉桂酸)、游离氨基酸(如丙氨酸)和类黄酮^[10-12]等。例如烟草根系分泌物肉桂酸、肉豆蔻酸和富马酸能够吸引青枯菌并诱导其形成生物膜,增强了青枯菌的趋化性和运动性^[13-14]。根际酚酸类物质还可促进土传病原菌青枯菌的生长和烟草枯萎病的发生,且具有“低促高抑”效应^[15]。

根系分泌物中的“压益”物质指扰乱根际微生物群落,抑制有益微生物类群丰度或功能的物质。酚酸类物质是典型的“压益”物质,在连作体系中逐年积累^[16]。研究表明这类物质对根际土著微生物的生长有抑制作用,抑制土壤微生物胞外酶的活性(如脲酶、蔗糖酶等)^[17]。例如, ρ -羟基苯甲酸/邻苯二甲酸和香草醛的分泌使得根际有益细菌芽孢杆菌属、链霉菌属和溶杆菌属的数量降低,根际微生物群落结构失衡^[18-20]。

连作根系分泌物的积累不仅影响根际病原菌和土著微生物的生长与功能,也会直接影响植物的生长和抗性,该类物质称为“自毒”物质。在生长过程中,植物个体通过根系释放的化学代谢产物(根系分泌物),影响其自身和同种植物的生长发育,这种现象被称为“自毒作用”^[21]。“自毒”物质可损伤植物根细胞结构和功能,减弱植物根系活力,降低植物抗性^[22-24]。这类物质主要是脂肪酸、有机酸类,且其作用效果具有浓度效应。目前根系分泌物中发现的“自毒”物质有烟草中的邻苯二甲酸酯、黄瓜的 2,4-二氯苯甲酸和肉桂酸、芋头的苯甲酸以及大豆的苯甲酸、己二酸和对羟基苯乙酸^[25-29]。

在非连作情况下,植物也会分泌上述“利病”、“压益”和“自毒”物质,但这类物质随着连作年限的增加而累积,可能会加剧土传病害的发生。连作体系中积累的根系分泌物不仅包括前茬作物根系残体和分泌的物质在土壤中残留,当茬作物根系分泌的物质也会随着根系生长和土壤水分扩散在根际、根表等界面发挥作用,因此,以上三类物质之间存在功能重叠(表 1)。例如,阿魏酸和肉桂酸作为植物典型的自毒物质,同时也能够作为“利病”物质:刺激病原尖孢镰刀菌的孢子萌发,并增加根际镰刀菌的丰度和枯萎病的发病率^[30-31]。

表 1 代表性“利病”、“压益”和“自毒”物质的来源和功能

Table 1 Sources and functions of representative root exudates that facilitate pathogen, suppress PGPRs and toxic to plant

物质名称 Substance names	植物来源 Plant species	物质类型 Substance types	物质分类 Substance classification	功能 Functions
棕榈酸和邻苯二甲酸二丁酯 ^①	马铃薯	脂肪酸	利病	对立枯丝核菌具有显著的促进作 ^[32]
邻苯二甲酸和丙二酸 ^②	大豆	酚酸类、有机酸	利病	低浓度下对尖孢镰菌的生长有化感 ^[33]
肉桂酸和香兰素 ^③	茄子	有机酸、酚酸	利病、自毒	引起茄子自毒的同时促进黄萎病菌 ^[13]
富马酸、肉桂酸和肉豆蔻酸 ^④	烟草	有机酸	利病	吸引青枯菌并诱导其形成生物膜、诱导青枯菌的趋化性 ^[14]
异黄酮和柠檬酸 ^⑤	大豆	黄酮类和有机酸	利病	促进了大豆疫霉孢子的迁移和定殖 ^[34]
根皮苷 ^⑥	苹果	黄酮类	利病	吸引病原菌,引起苹果再植病 ^[12]
L-阿拉伯糖醇和棉子糖 ^⑦	黄瓜	糖类	利病	促进了尖孢镰刀菌的根系定殖 ^[35]
阿魏酸、水杨酸 ^⑧	西瓜	有机酸	利病	刺激尖孢镰刀菌的孢子萌发和孢子形成,促进真菌毒素产生 ^[36]
异黄酮 ^⑨	太子参	黄酮类	利病、压益	典型病原体的种群规模增大,有益细菌种群减少 ^[37]
对羟基苯甲酸 ^⑩	葡萄	酚酸类	利病、压益	直接造成有益细菌(如链霉菌和芽孢杆菌)的丰度降低,潜在病原真菌(如镰刀菌)丰度增高 ^[18]
邻苯二甲酸 ^⑪	百合	酚酸类	利病、压益、自毒	导致了土壤中真菌病原菌(如尖孢镰刀菌)的增加,并减少了植物有益细菌的数量 ^[19]
香草酸 ^⑫	黄瓜	有机酸、酚酸	压益	抑制了芽孢杆菌和假单胞菌的相对丰度 ^[20]
苯甲酸、水杨酸和丙二酸 ^⑬	豌豆、菜豆 和蚕豆	酚酸类、有机酸	压益	低浓度下显著降低了假单胞菌的生长 ^[29]
阿魏酸 ^⑭	黄瓜	有机酸	利病、自毒	抑制黄瓜幼苗生长,降低细菌多样

				性，增加真菌多样性 ^[31]
2, 4-二氯苯甲酸 ^⑥	黄瓜	酚酸类	自毒	黄瓜植株的生长和果实产量显著下降 ^[25]
邻苯二甲酸酯 ^⑥	烟草	脂肪酸	自毒	抑制烟草种子萌发和幼苗生长 ^[26]
肉桂酸 ^⑦	黄瓜	有机酸	自毒	诱导了活性氧的光抑制和过度积累，从而抑制了黄瓜的生长 ^[27]
苯甲酸 ^⑧	芋头、人参	酚酸类	自毒	抑制芋头、人参幼苗的生长 ^[28,38]
苯甲酸、己二酸和对羟基苯乙酸 ^⑨	蚕豆	酚酸类	自毒	抑制蚕豆根长，嫩枝鲜重和干重 ^[29]
棕榈酸甲酯、棕榈烯酸甲酯、油酸甲酯 ^⑩	番茄	脂肪酸	自毒	抑制番茄下胚轴和根系生长 ^[39]

①Palmitic acid and dibutyl phthalate, ②Phthalic acid and malonic acid, ③Cinnamic acid and vanillin, ④Fumaric acid,trans-Cinnamic acid and Myristic acid, ⑤Isoflavone and Citric acid, ⑥Phlorizin, ⑦L-Arabinitol and Raffinose, ⑧Ferulic Acid and Salicylic acid, ⑨Isoflavone, ⑩4-Hydroxybenzoic acid, ⑪Phthalic acid, ⑫Vanillic acid, ⑬Benzoic acid, Salicylic acid and Malonic acid, ⑭Ferulic Acid, ⑮2,4-Dichlorobenzoic acid, ⑯Phthalates, ⑰Trans-Cinnamic acid, ⑱Benzoic acid, ⑲Benzoic acid, Adipic acid and 4-Hydroxyphenylacetic acid, ⑳Methyl palmitate, Palmitoleic acid methyl ester, Methyl oleate.

2 连作根系分泌物促进土传病害发生机制

2.1 “利病”：利于土传病原菌根际定殖和致病物质的积累

土传病原菌感染作物的前提是能够在土壤存活并在根际定殖，这依赖于土壤和根际中一些能够促进病原菌生长的小分子物质。单一作物连作多年后，某些根系分泌物在土体中逐年积累，对土著微生物具有一定的抑制作用^[40-41]，但可被土传病原菌高效利用，保障病原菌在休耕土壤中的存活，并在当季促进病原菌的趋化作用和产生物膜能力，病原菌受到这些信号物质（趋化性物质）的刺激后，从土体向寄主植物根际迁移，在根际定殖形成生物膜^[42-43]，并发挥其致病能力^[13]（图1，假说1）。

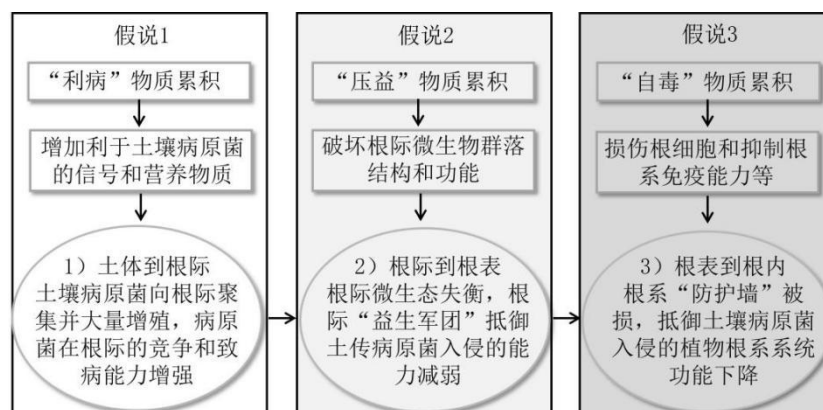


图1 根系分泌物加剧土传病害发生的假说

Fig. 1 Potential roles of root exudates in exacerbating soil-borne diseases development

该作用发生的机理主要表现为“利病”物质能够刺激病原菌的孢子萌发和菌丝生长、增强其趋化性、为病原菌提供碳源和增强其毒力相关基因表达^[14]。研究发现烟草根系化学信号物质富马酸可吸引土传病原青枯菌并诱导其形成生物膜，两种酚酸（苯甲酸和3-苯丙酸）均能够促进青枯菌的生长，而肉桂酸和肉豆蔻酸可通过诱导青枯菌的趋化性和运动相关基因的表达对其群集运动和趋化性起重要作用^[14,20]。而土传病原真菌的根系定殖与根分泌物中的糖、脂肪酸和糖醇相

关,如黄瓜、大豆、马铃薯连作后的根分泌物中的 L-阿拉伯糖醇、棉子糖、异黄酮、氨基酸以及柠檬酸、棕榈酸、邻苯二甲酸二丁酯、邻苯二甲酸和丙二酸等有机酸含量逐年增高,上述分泌物能够显著促进尖孢镰刀菌、疫霉菌和立枯丝核菌的孢子趋化、萌发和根际定殖^[32-35](表 1)。土传病原菌(如土传青枯菌)可代谢酚类自毒物质,而该能力对病原菌的致病过程是必不可少的^[44-45]。病原菌对自毒物质的降解与利用可能是病原菌在与土著微生物竞争中获得优势、进而致病的关键^[46-47]。因此,连作体系下作物根系分泌物中利病菌物质的累积,会促进病原菌向植物根际聚集并大量增殖,使其在植物根际存活的能力增强,更具竞争力。

2.2 “压益”:破坏根际微生物组的物质积累

土壤微生物群落是帮助植物根际抵御病原菌入侵的重要防线^[4-5]。这些微生物保护寄主的主要机制是通过与病原菌竞争营养物质和生态位点,产生拮抗性物质,诱导寄主抗性^[48]。通常认为土著有益微生物类群生物量降低、群落结构失衡是连作系统土传病害爆发的重要原因。相比轮作等其他种植方式,连作土壤中芽孢杆菌、酸杆菌、链霉菌、黄杆菌和黄单胞菌等有益微生物丰度降低,群落内部互作关系减弱,而乳酸菌、伯克霍尔德菌、腐生真菌、镰刀菌和曲霉菌等病原真菌的丰度增高^[49-52]。

连作积累的根系分泌物可通过抑制根际有益微生物丰度,使群落产抑菌次生代谢物的能力减弱,同时根际有益微生物的丰度降低,释放出大量生态位,增加土传病原菌的入侵概率^[37,46-47,53]

(图 1,假说 2)。Zhao 等^[37]发现太子参根系分泌物中异黄酮含量随着连作年限增加而不断上升,显著改变了根际土壤微生物群落的多样性和结构,使得病原菌与有益细菌的比例增加,从而导致太子参根际的微生态失衡和连作障碍的发生。更多的研究发现,外源添加“压益”物质阿魏酸和对羟基苯甲酸等酚类物质可改变黄瓜根际微生物群落结构、降低细菌群落多样性,选择性地抑制了黄瓜根际有益菌群^[53];土壤中添加人参自毒皂苷物质会富集潜在的致病真菌类群,如链格孢属、赤霉属和镰刀菌属,并降低了有益真菌类群的丰度,如支顶孢属和毛霉属^[47]。“压益”代谢物醋酸生育酚、瓜氨酸、半乳糖醇、十八烷基甘油和山萘酸等驱动的感病土壤中,一些具备降解自毒物质能力的细菌(如慢生根瘤菌属、链霉菌属、贪噬菌属)丰度下降,但招募了一些代谢小分子糖和酸的细菌(厌氧菌属、蛭弧菌属和黄杆菌属)^[54]。此外,根系分泌物“压益”的作用也会进一步影响下茬作物的生长。外源添加香豆酸减低了根际有益微生物的多样性,富集了可利用酚酸的真菌类群,加剧了病害的发生,同时阻碍了下茬植株幼苗对有益菌的招募,影响幼苗生长^[55]。

2.3 “自毒”:破坏根系免疫能力的物质积累

正常情况下根系分泌物中的自毒物质对植物自身不会产生明显的负面作用,但自毒物质的持续积累同样会对自身造成伤害,影响植物生长和系统抗性。连作体系中酚酸类自毒物质,如羟基苯甲酸的含量随着连作年限的增加而不断累积,不仅抑制作物自身的生长,还加剧了病害的发生^[13,56]。花生结荚期根系分泌物中的苯乙酮能够促进花生青枯病菌的生长,同时对花生种子胚根的伸长、幼苗生长等有抑制作用,并且该促进和抑制作用均随根系分泌物添加浓度和连作年限的增加呈增强趋势^[57]。根系组织是植物抵御土传病原菌入侵的最后一道防线,自毒物质对植物根系造成的生理毒害,如损伤植物根系细胞膜通透性、根系活力和系统抗性等能力,使其抵御病原菌入侵的最后一道“防线”破损,难以阻碍病原菌的入侵,最终加剧土传病害的爆发(图 1,假说 3)。

常报道的根系分泌物自毒物质包括黄瓜的 2,4-二氯苯甲酸和肉桂酸^[25]、人参中的苯甲酸^[58]、三七中的人参皂苷^[59]。这些自毒物质对植物生长和抗性的影响机制主要有:(1)通过诱导过氧化氢和活性氧的过度积累、影响抗氧化防御系统酶活性、破坏细胞壁和改变细胞膜的渗透性,从而抑制根系生长和阻碍养分吸收^[60];(2)抑制有丝分裂和细胞周期相关基因的表达,造成细胞分裂和伸长减缓、胚根生长受到抑制,从而影响植物的生长发育^[61];(3)减少叶片蒸腾作用,降低胞间 CO₂ 浓度,降低参与光合电子传输链、光合磷酸化和卡尔文循环相关基因的表达,增强呼吸作用和减少光合作用,导致植物碳水化合物水平降低^[62-63]。

3 基于根系分泌物的连作障碍缓解策略

品种改良、多样性种植方式以及有机肥施加等措施已被证明可缓解连作土传病害的发生,但较少通过根系分泌物角度来探究其调控机制。因此本文针对“利病”、“压益”和“自毒”三大类根系分泌物,提出以下4种缓解连作障碍的策略(图2)。

3.1 栽培措施

间套作和轮作被证明是有效缓解土传病害的措施,主要通过间作、套作、轮作和填闲等方式增加种植体系中作物的种类,或者利用不同作物生长的时间差和空间差,种植一种或多种作物(图2,栽培措施);还包括在主栽作物种植密度不变的情况下,小规模种植能够帮助主作物降低病虫害、缓解连作障碍的伴生植物。研究表明,间套作和轮作主要通过以下三个方面缓解主栽作物土壤生物障碍。

3.1.1 提高根际分泌物多样性 白屈菜红碱对黄瓜枯萎病、黄瓜炭疽病、西瓜枯萎病和茄子枯萎病等均具有较好的防治作用^[64]。白屈菜与人参的轮作改变了根际土壤的代谢产物和微生物群落结构,有效降低了人参连作后根腐病的发生^[65]。

3.1.2 减少主栽作物分泌自毒物质 大蒜与番茄的间作可缓解番茄连作障碍,是由于大蒜根系分泌物中的二烯丙基二硫化物(DADS)不仅可降低番茄根系分泌物中自毒物质脂肪酸酯(例如棕榈酸甲酯、棕榈烯酸甲酯、油酸甲酯)的含量,还可提高番茄植株的根系活性和抗氧化酶含量^[39]。在番茄洋葱间作体系的番茄中与发病相关蛋白、木质素生物合成、激素代谢和信号转导相关的防御抗病基因的表达均高于番茄单作^[66]。

3.1.3 分泌“抑病”根系分泌物 罗勒作为伴生植物,不仅显著提高了主栽作物番茄的产量,其根系分泌物迷迭香酸能够降低土传病害的发生^[67-68]。万寿菊可通过其化感作用抑制番茄早疫病菌分生孢子萌发来降低番茄枯萎病的发生^[69]。芝麻、花生、番茄等作物与葱轮作可有效降低寄主作物青枯病发生程度,葱根系分泌物中的大蒜新素、大蒜辣素等多硫化合物对青枯菌具有较强的抑制能力^[70]。在分蘖洋葱的伴生系统中,分蘖洋葱根系分泌物花旗松素能够刺激番茄植株招募植物有益菌,如芽孢杆菌属的定殖,增强根际微生物组的抑病力,以防控土传病原大丽轮枝菌引起的黄萎病^[71]。

综上,选择合适的轮作或间作作物可调控植物向地下生态系统输入根系分泌物的数量和构成,对修复土壤微生物群落结构、改善植物生长和降低病害发生至关重要。

3.2 品种改良

目前一些研究还发现采用抗病砧木嫁接作物、筛选低自毒和抗病基因型品种可调控根系分泌物,进而实现土传连作障碍的消减(图2,品种改良)。

3.2.1 嫁接 将高感青枯病的番茄品种嫁接至茄子砧木上可显著降低樱桃番茄青枯病的发病率,并且改善了嫁接植株根际微环境^[72]。同时,嫁接后番茄根系分泌物能够显著促进番茄幼苗的生长,并且抑制青枯菌的增殖^[73]。此外,嫁接通过根系分泌物的直接拮抗作用和形成保护性的根际微生物菌群间接增强植物抗病性。例如,嫁接西瓜根系分泌物中的有机酸(潜在的自毒素)显著减少,而植物防御相关代谢产物,如有机硫化合物和苯类化合物显著富集;嫁接后根际土壤中镰刀菌的丰度显著降低,同时潜在的有益细菌类群,如链霉菌和鞘氨醇单胞菌在嫁接西瓜根际显著富集^[74]。

3.2.2 低自毒和抗病品种 筛选低自毒和抗病基因型品种,可通过调控植物代谢物的合成途径来降低三类物质的合成,从而减轻作物连作障碍。王梓等^[38]研究表明,转录因子 *WRKY7* 在人参响应化感自毒物质苯甲酸胁迫的过程中表达量显著上调,表明该基因参与了人参响应苯甲酸胁迫的过程。Bu 等^[75]利用病毒诱导基因沉默(VIGS)系统成功地沉默了黄瓜中的甘油-3-磷酸酰基转移酶 6 基因(*GPAT6*),从而减轻根系分泌物肉桂酸对黄瓜的自毒作用。

3.3 有益菌筛选与应用

采用生物降解技术是克服植物“利病”、“压益”和“自毒”三大类物质的一种有效措施^[76]（图2，有益菌筛选与应用）。主要指从土壤中分离出一些具有分解植物“利病”、“压益”和“自毒”三类物质能力的细菌，从而缓解作物的连作障碍^[77]。球形节杆菌和恶臭假单胞菌等菌株能够显著降解阿魏酸、对羟基苯甲酸、丁香酸等对百合、西瓜、杨树、草莓和桃树幼苗生长有自毒作用根系分泌物^[78-79]。根际分离的伯克霍尔德菌株 B36 能够利用三七分泌的自毒物质人参皂苷，用于自身生长和生物膜的形成，增强对病原菌的拮抗能力和在根际土壤中的定殖能力^[80]。

3.4 功能性物质的施用

生物质炭、有机肥等功能性物质也能通过直接或间接调控根系分泌物来缓解作物连作障碍（图2，功能性物质的施用）。例如，生物质炭能吸附土壤中的有害物质，降低田间自毒物质的含量，减弱自毒物质对植物生长的影响，并增加有益菌的生物量、生长速率和产孢量^[81-82]。研究也表明，生物质炭通过增强番茄根系分泌物对有益微生物的趋化性和促进生物膜形成的能力，从而帮助番茄有效地招募抑病型根际微生物组来防控枯萎病^[83]。生物质炭联合植物根际促生菌（PGPBs）通过调控根系分泌物，促进土著有益微生物大量增殖，抑制土传病害发生，进而减缓太子参连作障碍^[84]。有机肥可促进根际假单胞菌、芽孢杆菌等有益微生物的定殖和相互作用，增强多菌种生物膜在根-微生物组界面的组装来保护植物免受病原菌感染^[85]。由芽孢杆菌等功能菌株制备的生物有机肥能够通过调节土壤理化性质、根际微生物群落和降低病原菌数量，消减西瓜和花生的连作障碍^[86-87]。此外，氨基酸肥料的施加能够通过激发土壤微生物活性，降低尖孢镰刀菌的丰度来缓解黄瓜连作障碍^[36]。磷石膏专用复混肥的施用不仅可显著提高红壤地区花生产量，还可有效缓解连作障碍^[88]。

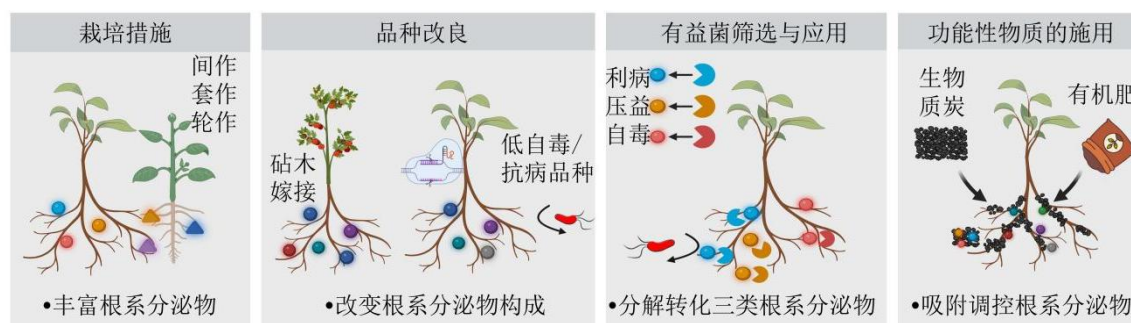


图2 基于根系分泌物的连作障碍缓解策略

Fig. 2 Strategies for redacting continuous cropping disorder by management of root exudation

4 展望

根系分泌物对植物的影响具有两面性，既可招募有益微生物促进生长，也累积有害物质阻碍植物根系发育和养分吸收并加剧病害发生。目前在利用有益微生物增强植物抗病能力或优化根际微生物群落等方面解决连作障碍的研究取得了较大的进展，进一步系统鉴定“利病”、“压益”和“自毒”物质，探究其在介导“植物-土壤-微生物”反馈互作中的作用机制，建立相应的根际靶向调控策略，对连作土传病害的综合解决具有重要意义。

4.1 连作体系中“利病”、“压益”和“自毒”物质的鉴定

鉴定并验证“利病”、“压益”和“自毒”物质及其对植物、病原菌和根际有益菌的作用机制；基于对不同作物及不同品种“利病”、“压益”和“自毒”根系分泌物组分的鉴定结果，针对性地选择种植作物品种，制定合理的种植模式。此外，三类物质鉴定过程中，尤其是“利病”物质鉴定，要注重相对性，尤其是对于病原菌相比其他土著微生物具有更强促进作用的碳源。

4.2 三大类物质消减措施下的“植物-土壤-微生物”反馈互作机制

研究多样性种植、嫁接、生物质炭和有机肥施用等措施下根系分泌物的浓度,从“植物-土壤”互作角度,建立“利病”、“压益”和“自毒”物质与植物激素、关键基因表达以及根际关键微生物的关系,阐明调控和消减三大类根系分泌物影响植物养分吸收、生长发育、系统抗性以及微生物组的机制。

4.3 “利病”、“压益”和“自毒”物质的根际靶向调控策略

构建靶向消减“利病”、“压益”和“自毒”物质的技术,可高效降低连作土传病害。例如,筛选定向利用或降解三大类物质的根际微生物,构建可同时降解“利病”和“自毒”物质的根际合成菌群。此外,基于对三大类物质种类合成代谢途径的解析,对作物进行基因靶向改造,定向培育产三大类物质较少、抗病物质较多的作物品种。

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