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番茄连作土壤中微生物群落的变化特征 及其重塑研究进展

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摘要 土壤微生物群落结构失衡是番茄连作障碍发生的重要因素之一。为探明番茄连作障碍发生机制,推动番茄产业的可持续发展,本文对番茄连作障碍土壤微生物群落的变化特征及其重塑技术研究进展进行了综述。番茄连作土壤中微生物多样性下降,土壤微生物群落结构由“细菌型”转变为“真菌型”,是番茄连作障碍发生的主要原因;轮作与间套作、嫁接、土壤消毒和施用有机肥均可重塑连作番茄土壤的微生物群落结构,有助于减轻连作障碍危害,尤其轮作与间套作豆科作物更有利于减轻番茄连作障碍危害。迄今,研究发现节杆菌属(*Arthrobacter*)、芽孢杆菌属(*Bacillus*)、假单胞菌属(*Pseudomonas*)、土壤红色杆形菌属(*Solirubrobacter*)细菌以及木霉菌属(*Trichoderma* spp.)真菌等微生物是有助于克服番茄连作障碍的功能微生物。开发与有机肥结合的生物有机肥,用于重塑农田土壤微生物群落的方法是一项极具开发前景的生物防控连作障碍发生的技术措施,但如何保障生物有机肥应用于不同环境中,功能微生物的定殖、存活与大量繁殖,是该项技术亟待解决的重要瓶颈问题。

关键词 番茄;连作障碍;功能微生物;菌群重塑;微生物群落结构

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番茄(*Solanum lycopersicum* L.)是茄科茄属的1年生草本植物,含有多种维生素,营养价值丰富,受到人们的广泛喜爱。联合国粮农组织统计数据显示,2021年番茄全球总产量达1.89亿t,在蔬菜作物中位居第一,我国番茄产量达6700万t,位居世界首位。近年来我国番茄市场需求量还在不断攀升,但由于耕作面积有限,番茄连作障碍问题日益凸显,严重制约了番茄产业的可持续发展^[1]。连作障碍是指在良好的田间管理下,作物仍出现生长发育放缓^[2]、产量和品质下降^[3]及发病率增加^[4]等现象。已有的研究发现,连作导致土壤出现理化性质劣化^[5]、涉及土壤碳、氮、磷循环的相关酶活性降低^[6]、自毒物质累积以及微生物多样性下降^[7]等现象。其中,土壤微生物对维护土壤生态系统稳定与健康尤为重要,因为它们不仅主导着土壤有机质的分解和土壤肥力的维持,而且稳定的微生物群落结构以及丰富的微生物多样性亦有助于维护土壤健康^[8]。

本文针对番茄连作障碍中的微生物作用机制以及防控研究进展进行综述,旨在基于微生物角度为防控番茄连作障碍提供理论支持,推动番茄产业的可持续发展。

1 番茄连作土壤中微生物群落结构的变化特征

土壤微生物群落结构是影响植物生长、发育和健康的主要因素,而根际土壤微生物与作物对土壤养分吸收和转化密切相关。已有的研究表明,连作导致作物根际微生物多样性下降,病原微生物丰度提高^[9-10],进而发生连作障碍^[11]。

土壤细菌种群是番茄连作土壤的敏感生物学指标^[12]。Su等^[13]使用3种不同类型的土壤进行番茄连作试验,发现番茄植株根际土壤细菌群落组成演替方向一致。即:番茄连作导致噬几丁质菌属(*Chitinophaga*)和马赛菌属(*Massilia*)等部分优势细菌属缺

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失,同时亦发现根瘤菌属(*Rhizobium*)和黄杆菌属(*Flavobacterium*)等部分特异有益细菌属会逐渐富集,表明番茄连作过程中细菌群落的变化是一个复杂的过程,而不是有益细菌单方面的耗竭或富集。Li等^[14]发现连作番茄植株根际土壤中,细菌丰富度和多样性均低于轮作土壤。同时,番茄连作土壤中,变形菌门(Proteobacteria)及放线菌门(Actinobacteria)细菌相对丰度均低于相应的轮作土壤。研究证实,土壤抗病性与变形菌门细菌和放线菌门细菌的相对丰度呈正相关^[15];变形菌门细菌在碳、氮和硫循环中起重要作用^[16];放线菌门细菌是一类异养菌,能够产生几丁质酶、脲酶、过氧化氢酶等土壤酶,在土壤有机质分解中发挥着主要作用^[17-18],同时产生抗生素以抑制各种植物病害。另一方面,康亚龙^[19]发现,番茄连作土壤中,细菌磷脂脂肪酸含量显著降低,真菌磷脂脂肪酸含量显著上升;土壤微生物优势菌群由细菌主导的状态转变为真菌主导,土壤生态系统的稳定性逐渐下降。孙文庆等^[20]亦发现,番茄连作土壤中土著细菌群落随着连作时间的延长数量减少或消失,同时某些真菌类群大量富集,导致土壤细菌和真菌群落结构失衡,根际有益菌数量减少而病原菌大量滋生,从而降低了番茄抵御病害的能力。此外,番茄连作多年后根系分泌物诱导土壤真菌丰度占比随着连作次数的增多而增加^[21]。如Lyu等^[22]发现温室连作番茄基质中假囊霉属(*Pseudogymnoascus*)、赤霉菌属(*Gibberella*)、棘壳孢属(*Pyrenochaeta*)等真菌相对丰度占比显著提高。

综上所述,番茄连作土壤中,细菌群落多样性下降,真菌丰度占比显著增加,土壤优势微生物类型由“细菌型”转变为“真菌型”。

2 番茄连作土壤中微生物群落的重塑技术

土壤微生物多样性和丰富性对维护土壤健康和促进作物生长发挥着重要作用^[23]。首先,细菌是陆地生态系统中,几乎所有生物地球化学循环过程的主要驱动因素,参与维护耕地土壤健康及保障土壤的主要因素之一^[24],病原微生物难以在细菌多样性丰富的土壤中生长和繁殖^[25]。其次,部分真菌亦具有降解、寄生、生产抗生物质等广泛的生态功能,同样有助于维护土壤健康与肥力^[25]。

2.1 轮作

与单一作物连作栽培相比,作物轮作是一种用

于保持土壤质量和作物生产力的一项重要农艺措施^[26]。轮作可通过根系分泌物数量和组成的差异影响土壤理化性质,进而改善土壤生物环境和克服连作障碍,实现可持续农业的目标^[27-29]。此外,轮作亦有助于重塑土壤微生物群落结构,减少土传病害的发生^[30-31]。因此,可以通过设计更具体和多样化的作物轮作模式来减轻连作栽培的负面影响^[32]。如Li等^[14]研究了轮作对番茄根际土壤细菌多样性和群落结构的影响,发现轮作土壤细菌丰富度和多样性均高于相应的连作土壤,且轮作土壤中变形菌门细菌及放线菌门细菌相对丰度均高于相应的连作土壤。研究证实,变形菌门细菌在促进植物生长、改善土壤生态环境方面发挥着重要作用^[33];放线菌门细菌能有效抑制土传病原微生物繁殖^[34]。而轮作不同作物,其根系分泌出相异的有机质,进而提高了包括变形菌门细菌和放线菌门细菌等土壤细菌的多样性与丰度^[35]。杨尚东等^[36]发现番茄轮作土壤中,微生物生物量碳、氮以及涉及碳、氮、磷循环的相关酶活性和土壤细菌多样性与丰富度等生物学指标均显著高于相应的番茄连作土壤。Lyu等^[22]发现轮作降低了番茄连作土壤中真菌的丰富度和多样性,尤其显著降低了引发番茄根腐病等土传病害的赤霉菌属(*Gibberella*)和棘壳孢属(*Pyrenochaeta lycopersici*)真菌的相对丰度^[37];邓玉清^[38]发现,轮作不仅有助于提高土壤养分的有效性,而且显著增加了土壤中可培养细菌的数量,显著降低了可培养真菌的数量,有利于维护土壤微生物群落保持“细菌型”结构,阻碍土壤微生物群落向“真菌型”转变。

2.2 间作

间作是指在同一生长季节在同一块土地上同时种植2种或多种作物的耕作方式^[39]。这种耕作方式对于维持和提高土壤质量亦十分重要^[40]。研究证实,间作具有提高土壤肥力以及资源利用率^[41]、增加作物产量^[42-43]、减少植株病虫害和杂草密度^[44-45]、提高根际微生物群落结构多样性^[46]等功能。如Fu等^[47]发现,马铃薯、洋葱与番茄间作,可有效降低番茄黄萎病的发病率与危害程度,其作用机制是间作的番茄植株抗病相关基因的表达量均高于相应的单作番茄。同样地,Li等^[48]发现,马铃薯、洋葱与番茄间作,显著提高了番茄植株根际土壤细菌群落多样性与丰富度;尤其提高了节杆菌属(*Arthrobacter*)、芽孢杆菌属(*Bacillus*)、假单胞菌属(*Pseudomonas*)细菌等具有促进植物生长的有益细菌属,降低了枝孢菌

属(*Cladosporium*)等潜在的病原细菌属的相对丰度。另一方面,张海春等^[49]还发现生菜-番茄和芹菜-番茄间作不仅显著提高了番茄平均单果质量与产量,还显著提高了番茄植株根际土壤中细菌和放线菌数量,显著降低了真菌数量。

2.3 嫁接

嫁接是园艺作物生产中常用的一种提高作物抗逆性的繁殖方法。番茄嫁接不仅有助于提高植株抗土传病害的能力^[50-51],而且亦有利于提高其果实品质^[52]。刘娜等^[53]发现,番茄嫁接植株根际土壤中,不仅土壤微生物生物量碳、氮以及蔗糖酶、脲酶和磷酸酶活性显著高于自根番茄植株根际土壤,而且嫁接植株根际土壤中,可培养细菌数量显著高于相应的番茄自根植株,而真菌数量则显著低于自根植株。此外,庞师婵等^[54]还发现,与番茄自根植株相比,番茄嫁接植株根际土壤中,微生物生物量碳、氮以及可培养细菌数量显著高于自根植株,且拟杆菌门(*Bacteroidetes*)细菌相对丰度占比显著高于相应的番茄自根植株。研究证实,拟杆菌门细菌是指示土壤健康的重要指标之一^[55],具有潜在的生物防治能力^[56]。简言之,嫁接植株砧木和接穗相互作用,诱导根系分泌物组成发生变化,具有重塑根际土壤微生物群落结构的效果,从而提高了嫁接植株对土传病害的抗性^[57-59]。

2.4 土壤消毒

土壤消毒可消灭土壤中的病原微生物。现阶段常用的土壤消毒方法主要包括物理方法和化学方法。

Tan等^[60]利用强还原土壤灭菌法(reductive soil disinfestation, RSD)对番茄连作土壤进行处理,发现与未处理连作土壤相比,芽孢杆菌属、梭菌属(*Clostridium*)和粪球菌属(*Coprococcus*)等隶属厚壁菌门(*Firmicutes*)的细菌相对丰度显著上升;RSD处理后期,土壤中真菌的Alpha多样性降低,被孢霉门(*Mortierellomycota*)真菌相对丰度随着RSD处理时间的延长逐渐降低,同时曲霉菌属(*Aspergillus*)和镰刀菌属(*Fusarium*)真菌相对丰度均显著低于未处理连作土壤。伍朝荣^[61]对番茄土壤进行厌氧消毒(anaerobic soil disinfestation, ASD)处理,发现消毒后土壤pH值及土壤有机质、全氮、碱解氮和速效钾含量显著提高,土壤中青枯菌数量显著降低。秦绍龙^[62]发现利用氯氧消毒剂处理土壤,能够提高设施番茄土壤中细菌数量/真菌数量值(B/F),优化土壤微生物菌

群结构,抑制土壤微生物群落由“细菌型”向“真菌型”转化,同时降低番茄根结线虫发病率,减少番茄畸形果的出现,有效提高番茄产量。冯明祥等^[63]将石灰氮、棉隆及阿维菌素等农药混用进行番茄土壤消毒,亦发现番茄根结线虫的发病率显著降低,同时显著降低番茄枯萎病发生率,提高番茄产量。另一方面,由于物理方法和化学方法消毒土壤时存在有益有害微生物一并被杀灭以及化学方法存在农药残留等环境污染弊端,开发与利用无环境污染且可持续发展的生物技术减轻连作障碍危害,是将来农业规模化生产不可或缺的技术。

2.5 施用有机肥

木醋液是生物炭和木炭生产的二次产物,现阶段已广泛应用于土壤改良、促进作物养分吸收和植物病害控制^[64]。木醋液中含有各种功能物质,不仅有利于作物生长而且具有增强作物抗逆性的功效^[65]。此外,木醋液还能溶解土壤矿物质和碳酸盐,改良土壤理化性质,同时提高土壤微生物多样性,对土传病害有很好的抑制作用^[66]。肖健等^[67]发现,木醋液具有改善连作番茄根际土壤微生物群落结构,抑制病原菌生长,改良连作番茄植株根际微环境生态的功能。如木醋液提高了连作番茄植株根际土壤中,有益微生物节杆菌属及土壤红色杆形菌属(*Solirubrobacter*)细菌,以及显著降低了病原微生物油壶菌属(*Olpidium*)真菌的相对丰度占比。郭伊娟^[68]亦发现,部分植物(如蛇床子等)提取物亦有助于改良番茄连作土壤,提高连作土壤细菌多样性和丰富度指数,增加有益微生物的数量。

另一方面,徐金强等^[69]发现大蒜秸秆还田显著提高番茄连作土壤中的细菌数量,显著降低番茄根结线虫发病率和根结指数。徐赛等^[70]发现有机无机肥配施可改善番茄连作土壤中微生物群落组成;其中,芽孢杆菌属和土胞杆菌属(*Terrisporbacter*)等有益细菌相对丰度占比增加。赵政^[71]亦发现化肥与木霉菌肥配施,有助于提高连作番茄根际微生物多样性及土壤养分有效性;孙彩霞等^[72]发现腐殖酸调理剂具有提高土壤变形菌门和放线菌门细菌相对丰度、降低酸杆菌门(*Acidobacteria*)和芽单胞菌门(*Gemmatimonadetes*)细菌相对丰度的效果。康萍芝等^[73]发现哈茨木霉制剂可提高设施连作番茄植株根际土壤细菌数量,抑制尖孢镰刀菌(*Fusarium oxysporum*)等有害真菌的繁殖。Zheng等^[74]发现生物有机肥不仅可显著提高番茄连作土壤中有机碳、全氮、全

磷、全钾含量,而且显著提高连作番茄土壤细菌的丰富度和多样性,表明施用有机肥是一项具有重塑连作番茄土壤微生物群落功效的方法。

3 结 语

番茄连作障碍问题与土壤微生物群落的变化息息相关,其作用机制十分复杂。近年来,研究发现番茄连作土壤中微生物多样性下降,土壤微生物群落结构由“细菌型”土壤转变为“真菌型”土壤,是番茄发生连作障碍重要的原因之一。

重塑连作番茄土壤微生物群落结构是有效缓解、预防番茄连作障碍的关键。轮作、间套作、嫁接、土壤消毒以及施用有机肥等措施均能够有效重塑土壤微生物群落,提升土壤中的微生物多样性。其中,将有机肥与节杆菌属(*Arthrobacter*)、芽孢杆菌属(*Bacillus*)、假单胞菌属(*Pseudomonas*)、土壤红色杆菌属(*Solirubrobacter*)细菌以及木霉菌属(*Trichoderma* spp.)真菌等功能微生物结合施用,是一项极具开发前景的生物防控连作障碍发生的技术措施。但如何保障生物有机肥中有益功能微生物在不同环境中的定殖与存活,发挥出应有的功能与效果,是该项技术亟待解决的重要瓶颈问题。

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Progress on changing characteristics and reconstruction of microbial communities in soil under tomato continuous cropping

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Abstract The structural imbalance of microbial communities in soil is one of the important factors for the occurrence of obstacles for tomato continuous cropping. This article reviewed the changing characteristics of microbial communities in soil and the reconstruction techniques in tomato continuous cropping to study the mechanism of obstacles for tomato continuous cropping and promote the sustainable development of the tomato industry. The decrease in microbial diversity in soil under tomato continuous cropping and the structure shift of microbial communities in soil from "bacterial" soil to "fungal" soil are the main reasons for the occurrence of obstacles for tomato continuous cropping. Rotation and intercropping, grafting, soil disinfection, and application of organic fertilizer can reconstruct the structure of microbial communities in soil under tomato continuous cropping, helping to reduce the harm of obstacles for continuous cropping, especially rotation and intercropping of leguminous crops are more conducive to reducing the harm of obstacles for tomato continuous cropping. So far, studies have found that functional microorganisms including *Arthrobacter*, *Bacillus*, *Pseudomonas*, *Solirubrobacter*, and *Trichoderma* spp. are beneficial in overcoming obstacles for tomato continuous cropping. The development of bio-organic fertilizers combined with organic fertilizers for reconstructing the microbial communities in farmland soil is a highly promising technical measure for biological prevention and control of obstacles for continuous cropping. However, how to ensure the colonization, survival, and large-scale reproduction of functional microorganisms in the application of bio-organic fertilizers in different environments is an important bottleneck problem that urgently needs to be solved in this technology.

Keywords tomato (*Solanum lycopersicum* L.); obstacles for continuous cropping; functional microorganisms; reconstructing the microbial communities; microbial communities

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