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连作对土壤微生物菌群影响及修复研究进展

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摘 要 连作可短时间内带来经济效益，满足日益增长的粮食等农产品需求，但长期连作会加速土壤退化，导致作物减产和病害率增高，破坏土壤微生物结构平衡，不利于土壤生态系统的可持续发展。良好的土壤生态系统中有益微生物、有害微生物及植物间维持着相对平衡。微生物群落结构直接指示整个土壤生态系统的转化方向。通过总结前人在连作对土壤微生物菌群的影响及其修复连作土壤障碍方面的研究结果，探讨修复方式的利弊及其未来的研究方向，旨在为连作障碍土壤修复和植物生长发育创造良好条件，为保持土壤微生物群落结构平衡、保证土壤生态系统的可持续发展提供理论依据。

关键词 微生物群落失衡；有益微生物；有害微生物；土壤健康；修复技术叠加

土壤是生命孕育的重要基础，同时也对生命体间的交流起着重要作用，不但支撑着其内植物和微生物的生存，也将二者紧密联系起来。在健康的土壤生态系统中，植物分泌糖类等营养物质供土壤微生物利用，而微生物也通过改变土壤养分有效性等方式影响植物生长[1]。微生物群落结构在一定程度上决定着土壤内物质循环过程，以及该土壤生态系统的抵抗力和稳定性。例如，解磷细菌的存在有助于土壤内磷营养的释放[2]；根际有益微生物可降低病虫害对植物的侵染效果[3]，协助植物和土壤生态系统抵抗外来侵害[4]；硫杆菌（*Thiobacillus*）的存在可协助改善植物生长环境[5]，维持植物在盐渍土壤中的稳定生长[6]。此外，土壤内各种营养元素或重金属元素通过微生物自身代谢被有效性或固化，真菌与细菌的组成与比值也决定着土壤作物的发病率和产量。微生物菌群结构直接关系到土壤生态系统的发展[7]，且对农作物营养及产、质量有直接影响[8-9]。

目前普遍的耕作模式有连作、轮作、单作和间作等。此外，凿耕和旋耕等因地制宜的耕作技术也在逐渐发展。不同耕作方式对土壤理化性质及内部微生物群落结构均有重要影响，在一定程度上决定土壤的生物与非生物结构[10-12]。因连作可在短期内满足特种粮食需求，所以许多地区将其作为主要的耕作方式。但随着连作的普遍存在和年限加长，因此引起的各种负面问题也显现出来，包括土壤病虫害增多、抵抗力变弱、土壤出现板结、营养元素不均衡以及土壤性质退化导致作物质量下降等[13]。连作也会引起土壤内微生物群落发生改变[14]。研究表明，连作状态下草莓[15]和菠萝[16]土壤微生物群落发生改变，潜在病原菌增加，有益菌减少，有害病原菌增多[17]，土壤性质退化[18]。长此以往，土壤无法维持其原有的良性生态循环，土地健康及作物质量难以得到保证。

为保护土壤生态系统，目前已广泛推广轮作和间作模式，但研究[19]表明，连作对土壤造成的负面影响难以通过简单改变耕作模式来消除。因此，需要探索更加主动有效的修复手段。目前已有大量研究致力于修复连作土壤环境，其中包括添加有机物[20]、土壤熏蒸[21]和土壤微生物修复等[22]。本文总结了连作影响土壤微生物群落的途径及国内外针对土壤连作导致的土壤微生物群落失衡的修复经验，并在此基础上提出叠加技术的修复模式，讨论将不同修复技术合理结合，修复土壤微生物群落结构的可行性，希望能对有效修复连作土壤营养及结构、缓解植株连作障碍提供帮助。

1 连作对土壤微生物生存环境的影响

土壤的形成及利用与土壤内细菌群落密切相关[23]，而微生物群落结构也与土壤内 pH、磷含

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量、氮含量、酶活性和植株健康状态等指标显著相关[24-25]。

1.1 连作下土壤理化性质对微生物生存环境的影响

连作可能通过影响土壤理化环境影响土壤微生物群落。微生物群落结构受 pH、碳氮比[26]、有机质[27]、土壤深度[28]和土壤利用类型[29]等因素的影响。连作可改变土壤含水量和营养成分有效性等营养环境，从而降低有益微生物丰富度[30]。连作可显著降低根际土壤内全氮和有效氮含量[31]，而根际土壤全氮含量显著影响细菌群落变化。此外，连作还可改变土壤渗水性和孔隙度等物理环境，从而影响微生物生存[32]。

1.2 连作下植株对微生物生存环境的影响

连作可能通过改变土壤理化性质影响植物生长，从而对土壤微生物群落结构进行二次作用。例如，连作下植株代谢途径改变[33]，导致植物生长偏离正常方向，根系分布及根系分泌物均发生变化，影响到根际土壤理化性质和酶活性等土壤微生物生存环境[26]。

1.3 土壤微生物生存环境的改善

土壤盐分和营养元素在土壤微生物群落生存环境维持中起着重要作用[34]。营养元素的补充可使连作土壤恢复原有营养环境，但直接施用化肥或试剂补充可能对土壤微生物结构起负面影响。例如，硫肥可促进黑麦草生长，但同时降低线虫和有益菌群的丰度，虽然短期内利大于弊，但并不利于土壤生态系统的长期健康维持[35]。目前主要通过有机肥、作物还田或堆肥的方式补充土壤营养元素。例如，通过添加磷泥或其他营养元素过剩的土壤补充相应元素[2]；通过堆肥可改善连作引起的土壤退化，提高可利用的氮、磷、钾和有机质含量，同时还可使部分有益微生物增加，抑制连作引起的病原菌活动[17]；有机肥的重复适当施用可以改善环境，促进微生物群落活动[36]。生物炭通过改良土壤微生物生存环境及影响细菌群落结构，从而促进作物在连作条件下的生长[37]。

2 连作对土壤有益与有害微生物比例的影响

土壤生态系统很大程度上依赖于其内各生物的相互作用，而有益微生物与有害微生物的比例则暗示着该土壤生态系统的演替发展。

2.1 连作下有益与有害微生物比例的变化

连作影响根系有益微生物的相对丰富度[38]及病害拮抗菌属的相对丰度[39]，使植物与土壤微生物群落间的相互作用失去原有平衡[40]，以及土壤线虫[41]和病原菌等微生物的含量和种类[42]发生变化。连作下根际土壤 pH 发生变化，土壤微生物群落内真菌与细菌比例遭受干扰[43]，植株病害相关微生物生存优势增加[44]。连作还导致土壤内氮硫循环相关细菌减少，病原菌富集[45]。总之，连作打破植物和土壤内微生物之间相互作用的平衡，使生态系统向不健康的方向发展，对植物根际土壤微生物起消极影响，从而降低植物营养，使植物病害率增加。

2.2 土壤有益与有害微生物比例的改善

添加有益真菌或细菌可在不过分改变土壤生态系统的状态下，改善土壤营养及质量[46]，也可通过互作效应影响土壤有害微生物的群落结构，防止植株感病[47]。其中菌根真菌能影响土壤结构、含盐量和持水能力等性状，常被利用于缓解土壤连作障碍[48]，例如丛枝菌根真菌（arbuscular mycorrhizal fungi，AMF）可作为生物肥料，增加根际土壤有益微生物和矿质元素，改善土壤环境，促进人参[22]和花生[49]等作物的生长，抑制根腐病。AMF 还可通过调节植物生长激素促进连作中番茄生长及根系发育相关有益基因的表达[50]。此外，很多其他有益微生物也可以缓解连作障碍，例如拟茎点霉属内生菌（*Phomopsis liquidambari*）的定植可改善根际微环境、养分吸收和病害发生率，促进连作花生生长[51]。根际促生菌（plant growth promoting rhizobacteria，PGPR）可缓解酸性连作土壤中的铝毒和生姜青枯病[52]。硫杆菌可通过降低土壤 pH 抑制某些病原菌，从而促进植物生长，同时其与硫离子结合有利于植株对酸的耐受性，硫杆菌还可通过促进交换性钠离子的还原改良盐渍土质[5-6]。有益微生物的添加可通过促进植株生长或微生物间互作效应改善土壤内微生物群落结构。

3 连作对土壤微生物菌群结构的影响

连作除影响土壤内有益与有害微生物比例外，也影响土壤内整体的微生物群落结构。其影响的差异主要与连作年限和种植作物种类有关。

3.1 连作年限与作物对土壤微生物菌群结构的影响

连作作物和年限不同，土壤微生物群落结构的变化也存在显著差异，长期连作有利于寄主特异性病原菌发展[53]。土壤真菌群落在棉花连作后发生很大变化，病原菌也随连作年限急速增长，在

连作 10 年左右达到峰值[42]。但同时有研究者[54]发现，长期连作后大豆产量出现先减后增的趋势，推测大豆连作年限在某个节点后的增长可以刺激土壤抗病能力的提高。连作对草莓的影响可按时间变化分为 3 个阶段，依次是土壤理化性质变化、真菌等土壤生物因子发生显著变化和自毒物质产生抑制生长[13]；烟草种植土壤细菌群落结构在时间尺度上有明显的变化，其青枯病的发病率也与连作年限的积累显著相关[55]；苎麻连作后期有益微生物减少，且有害微生物积累严重，导致土壤脆弱，植株病害加重[56]。

3.2 土壤微生物菌群结构的改善

可通过物理措施或改善耕种管理模式修复连作对土壤微生物群落结构的损害。种植还原性作物可重建土壤微生物群落，并抑制土传病害[57]。高温下，碳酸氢铵或亚硫酸氢钠熏蒸有助于缓解西瓜连作病害，提升果实质量，平衡土壤微生物，改善土壤特性[21]。覆盖植物可改善土壤环境，促进本土有益菌 AMF 活动[30]，但要考虑到土壤的补水需求[58]。施用微生物修复基质也可改良土壤，修复土壤微生物群落，有利于植物健康[59]。土壤小动物（例如蚯蚓）的引入有助于农田生态系统维持良好的土壤微生物结构[60]。

随着耕作经验的积累，保护环境和可持续发展意识的增强，人们针对种植及耕作模式进行了许多改善，保护性耕作概念也逐渐发展起来。其中免耕和轮作因操作简单及可改良土壤而广泛应用，免耕和轮作有助于维持豆科植物根际根瘤菌种群结构和多样性[61]。轮作对土壤微生物群落影响显著，可平衡农业生态系统，防止特定土壤资源过度消耗[62]。同时，轮作有利于部分与菠萝产量积极相关菌属的活动，轮作下菠萝产量高于连作[16]。但需注意，不同轮作方式对作物生长及根际土壤微环境的影响也可能不同[63]。适当休耕能帮助土壤微生物恢复，耕作土壤中微生物生物量更低，免耕土壤中基因量更大且恢复更快[64]。不同土地利用类型以及作物生长阶段对土壤微生物的影响也需注意[26,65]。有研究尝试通过种植马铃薯修复豆科连作后的土壤微生物群落[66]；轮作苜蓿和葱可修复连作高粱的根际环境[67]；广藿香与姜黄、生姜间作可提高土壤优势菌群数量，改善细菌代谢及酶活性[68]。耕翻、深松和旋耕等耕作方式对有机碳积累[69]、氮素分布[12]及土壤微生物[68]的影响正成为研究热点。然而，保护性耕作模式在调节植物营养元素、土壤微生物结构等方面仍存在周期长、效果缓慢等不足。因此，仍需探索更为有效快速的修复手段。

4 修复技术集成的管理模式

相比于不健康的土壤生态系统，健康土壤生态系统的土壤往往存在更丰富的营养条件，有益于植物生长的土壤微生物群落及在合理耕种条件下植株健康生长（图 1）。

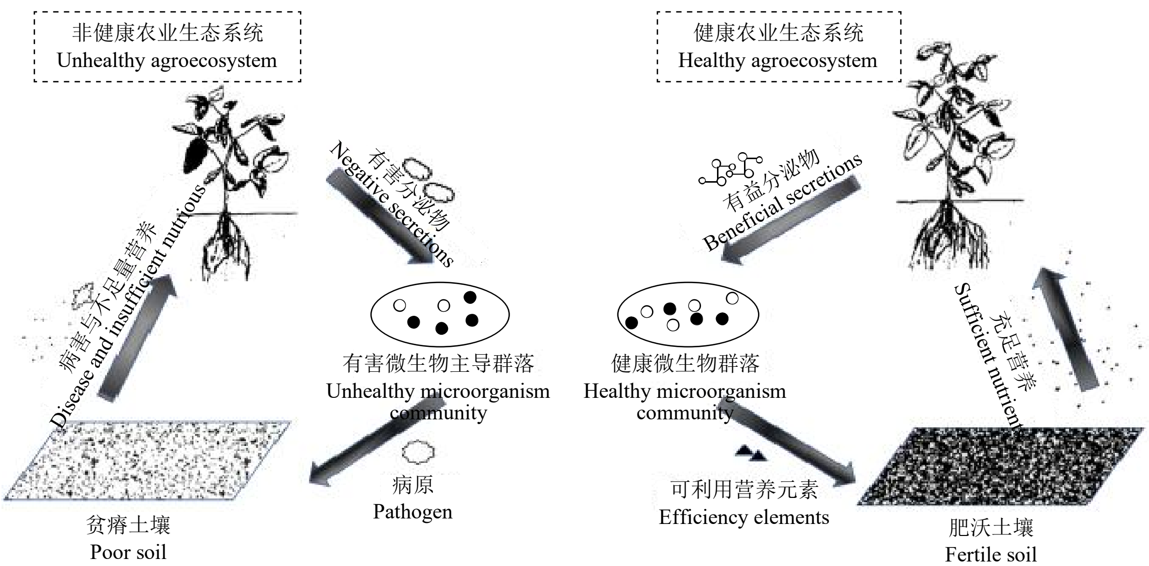

图 1 健康与非健康农业生态系统下植物、微生物与土壤之间的互作关系

Fig.1 Interactions among plants, microorganisms and soil in healthy and unhealthy agroecosystems

连作导致的微生物群落失衡及植物生长障碍来源于方方面面，包括但不限于改变土壤结构、微生物群落、酶活性、营养结构和营养物质含量。同时，修复技术也多种多样，间作可通过植物间互作降低自毒效应[70]，促进植物营养分配[71]；腐殖酸等有机物的施用可以提高植物营养及抗胁迫相关酶的活性[72]；轮作和覆盖植物更替可以改善土壤结构，促进微生物群落恢复[73]，微生物可抑制病原菌活动[74]或改善土壤性质[5]，等等。因此，可通过叠加补充土壤营养元素、改变微生物群落及调整耕作模式等措施修复土壤。

有研究证明各修复技术在连作土壤修复过程中的综合作用。例如硫杆菌与 AMF 联合接种在改善土壤结构的同时提高了根际环境中碳、氮、磷和硫等营养物质含量[75]；AMF 与外源钙联合使用可促进花生连作育苗[49]；配合植物特性，结合间作和轮作 2 种种植方式，对土壤进行复合改良，可抑制植株病害，改善其表型和营养价值[76]；无机肥与有机肥配合施用可提高土壤磷有效性[77]；种植体系变化加生物炭协助改善系统内碳封存[78]。玉米和大豆轮作结合施肥对土壤肥力和作物产量的提高有显著积极影响[79]，通过堆肥与接种功能菌株相结合可调节土壤性质，消除西瓜连作障碍[80]。因此，将连作、轮作、施肥和接菌等技术集成融合，作为土壤修复复合技术，在解决植物连作障碍、改善土壤微生物群落和维持土壤健康方面具有重大意义[81]。适当结合各修复手段，有助于构建健康的可持续发展农业土壤生态系统（图 2）。

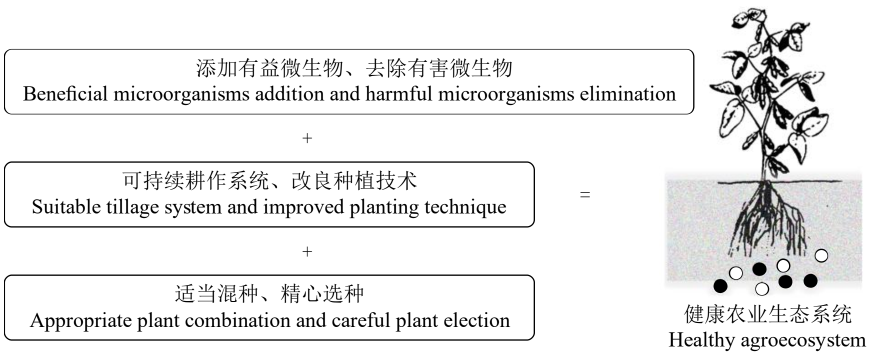

图 2 修复技术叠加的管理模式

Fig.2 Management mode with superposed restoration techniques

5 展望

连作弥补了耕地面积不足和粮食需求高等问题，同时也带来了土壤退化和温室气体排放过量等环境问题[82]。如何在获取利益的同时减少对环境资源的消耗，维持生态平衡，是农业生态所面临的重要问题。因此，如何进行连作障碍土壤的修复、构建健康土壤环境和维持较高的生产力水平是亟需解决的科学问题。

为此，提出 3 点建议：

第一，利用现代技术手段挖掘与解读土壤微生物群落数据及其代谢信息。基因组学和代谢组学等技术充分分析土壤微生物群落动态[83]，充分了解土壤生态系统有益微生物、病原微生物及其他微生物生理生化代谢状况，应用农业生态系统的平衡原理，为健康的耕作模式构建提供理论依据。

第二，持续关注微生物修复技术。生态系统中微生物群落与土壤功能之间存在着密切的相关性[84]，探究连作模式下有益微生物的群落功能及其结构变化，并研究施入有益微生物处理后土壤的功能变化，全面解析微生物修复技术缓解连作障碍的机制，形成作物连作条件下构建适宜的微生物群落结构技术。

第三，改良耕作模式，加强综合管理。通过研究不同作物在不同耕作模式下土壤理化性质的变化[85]，分析不同作物的生态需求，包括喜好营养元素、生长环境及生长节律等，探寻作物轮作和间套作的地域模式；并探究不同修复技术之间，以及不同耕作模式与不同修复技术之间的叠加集成效应，以期建立修复效益最大化的管理模式，构建可持续发展的农业生态系统。

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Research Advances on the Effects of Continuous Cropping on Soil Microbial Community and Restoration Techniques

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Abstract　Continuous cropping can bring economic benefits and meet the growing food demand in the short run, but it is not conducive to the sustainable development of soil ecosystem. Long term of continuous cropping can cause a lot of problems such as soil degradation, crop yield reduction, disease rate increase and destroy the balance of soil microbial structure. In a healthy soil ecosystem, beneficial microorganisms, harmful microorganisms and plants maintain a relatively balanced interaction. Microbial community structure often directly implies the development of the whole ecosystem. This article summarizes the effects of continuous cropping on soil microbial community and the previous experience of repairing continuous cropping soil obstacles, discuss the advantages and disadvantages of current remediation methods, in order to provide some suggestions for repairing continuous cropping obstacles and ensuring the sustainable development of soil ecosystem.

Key words　Unbalanced microbial community; Beneficial microorganisms; Harmful microorganisms; Soil health; Superposed restoration techniques