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•综述•

蚯蚓调控土壤微生态缓解连作障碍的作用机制

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摘要：连作障碍不仅严重影响作物产量，而且会导致土壤生物多样性下降、有益微生物减少及病原菌增加等一系列微生态失衡问题。土壤微生态失衡反作用于植物，导致植物发生更严重的病害、减产等。作为土壤生态系统工程师，蚯蚓的取食、掘洞和爬行等活动对土壤微生态具有重要的调控作用，既可以改善土壤环境，又可以强化土壤生物群落功能，有望为缓解作物的连作障碍问题提供一条新途径。本文总结了土壤微生态与土壤功能维持及蚯蚓调控土壤生物作用的研究进展，在此基础上，结合蚯蚓对化感物质降解作用的研究，分析了蚯蚓通过调控土壤微生态缓解作物连作障碍的微生物作用机制的三条途径：直接调控微生物群落、通过改变化感物质组成以及通过调控土壤动物区系调控微生物群落。蚯蚓对微生物群落的调控可改善失衡的土壤根际微生态，有效缓解作物连作障碍。

关键词：蚯蚓；连作障碍；土壤动物；化感物质；土壤微生物

Mechanisms of earthworms to alleviate continuous cropping obstacles through regulating soil microecology

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Abstract: Obstacles to continuous cropping seriously affect crop yield and also lead to a series of microecological imbalance problems, such as the decline of soil biodiversity, the decrease of beneficial microbes, and the increase of pathogens. The imbalanced soil microecology affects plants and can lead to more serious disease and even greater reduction of crop yield. As soil ecosystem engineers, earthworms have important regulating effects on soil microecology. Earthworms can improve the soil environment and strengthen the function of soil biological communities through their activities (e.g. feeding, burrowing and creeping), thus providing a potential way to alleviate microecological obstacles to continuous cropping. This paper reviews the progress made in research on soil microecology, soil function maintenance, and earthworm regulation of soil biological function. Three mechanisms that earthworms employ to alleviate obstacles to continuous cropping through soil microecology regulation were identified: direct regulation of soil microbial communities, regulation of microbial colonies by changing allelochemical composition, and regulation of soil fauna communities. Through earthworm regulation of microbial communities, an imbalanced soil microenvironment in the rhizosphere is corrected, thereby alleviating obstacles to continuous cropping.

Key words: earthworms; obstacles to continuous cropping; soil animal; allelochemicals; soil microbes

植物通过地上与地下部的物质交换持续影响其生存环境，环境的改变则反作用于植物，影响植物的生长和发育(Kulmatiski et al, 2008)。在自然生态系统中，土壤–植物的反馈作用是局域尺度保持植物多样性的重要驱动力量，土壤生物的综合作用不利于同种或者近缘种在相同的地点生长繁殖(Huang et al, 2013b; Teste et al, 2017)。然而，在农业生产中，随着耕地面积的减少、设施栽培的发展以

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及某些作物对特定气候和土壤的要求，在同一地块进行作物再植的现象普遍存在，导致连作障碍发生。连作障碍使作物生长发育不良、病害加重、品质下降，成为限制农业可持续发展的瓶颈。从土壤的角度讲，作物连作障碍导致土壤微生态系统紊乱，土壤生物多样性降低，生态系统稳定性下降。

生产上用来克服连作障碍的措施主要是土壤灭菌，该方法虽然在一定程度上缓解了连作障碍，但从长远看，对环境和土壤造成的危害是巨大且深远的。因此，人们也在探索一些环境友好的方法，希望通过调控土壤生态的方式缓解作物连作障碍。土壤生态的调控方式主要有两种：一种是调控环境，如施用某些土壤添加剂，改变土壤的理化性质，间接影响土壤生物；一种是调控生物，如接种某些具有拮抗功能的微生物，改变土壤微生物群落结构，间接影响土壤环境。相对于简单的土壤灭菌而言，调控土壤微生态的方式更符合整体、协调、循环、再生的原则，有利于农业的可持续发展。

蚯蚓是土壤生态系统中的大型无脊椎动物，由于其对土壤生态系统具有重要的调控作用，被誉为“土壤生态系统工程师” (Jones et al, 1994)。通常蚯蚓被认为能够促进植物的生长(Lee, 1985; Edwards & Bohlen, 1996)，而且其数量常被人们用作表征土壤健康的重要指标(Doran & Zeiss, 2000)。蚯蚓对土壤环境和土壤生物的调控作用已有大量报道，然而很少有研究关注蚯蚓对作物连作障碍的防控作用。本文通过分析连作障碍发生的生态学机理，总结了蚯蚓对土壤微生态的调控作用，以期为缓解作物连作障碍问题提供新的思路。

1 土壤微生态平衡

1.1 微生态平衡与健康土壤功能的维持

健康土壤是能够持续提供生物产品，保障空气质量和水源安全，对植物、动物和人类健康发挥重要作用的生命系统(Doran et al, 1996)。土壤微生物是维持土壤中各种生物化学过程动态平衡的核心，它在矿质养分循环、有机质更新、土壤结构及土壤肥力形成过程中发挥着重要作用(Brussaard et al, 2007; Lambers et al, 2009)。毋庸置疑，土壤微生物多样性是决定土壤健康与否的重要因素之一，并且是保持土壤抗病性的重要驱动力(Garbeva et al, 2004)。一般来说，土壤微生物多样性与土壤生物群落结构的复杂程度关系很大，一个微生物多样性较高的土壤生态系统，调节能力较强，稳定性就越高，土壤健康状况就越好(He et al, 2009; Nannipieri et al, 2010; Larkin, 2015)。决定土壤微生态平衡的关键在于土壤微生物与植物、土壤动物之间的相互作用(Garbeva et al, 2004; 陈小云等, 2007; Watkins et al, 2009)。在一个稳定的土壤生态系统中，土壤微生物与植物和土壤动物之间相互作用、各种生物类群之间的相互制约和相互依存关系使得整个土壤微生态系统处于稳定的状态，即土壤微生态平衡。

1.2 土壤生物间的相互关系

1.2.1 植物与土壤微生物的关系

土壤微生物的生存和繁殖依赖于从土壤中获得的碳源(Garbeva et al, 2004)，而土壤中的碳主要源于植物的光合产物(Bais et al, 2006)，因此，根际区土壤微生物的密度远远大于非根际区土壤(Berg et al, 2006)。根据对植物的作用，可以大体将植物根际微生物分为三类。第一类是根际促生菌，这类微生物能够通过自身分泌物促进植物根系的生长，或者通过诱导植物根系启动自身的免疫系统以抵御病原菌入侵，还能通过自身作用在相邻的植株之间进行信号传导(Song et al, 2010; Chung et al, 2015; Kim et al, 2015)。第二类是病原菌，它们可以分泌一些毒素抑制植物的生长，或者直接侵入植物体内，引发植物病害(Koike et al, 2009; Fang et al, 2012)。第三类是依赖植物资源但对植物没有直接反馈作用的微生物，这也是根际区种类和数量最多的一类微生物(Berendsen et al, 2012)。除了对植物的作用，这三类微生物之间也会相互促进或抑制(Toljander et al, 2007)，而植物除了为根际区微生物提供碳源以外，还会分泌一些次级代谢产物(或者植物残体腐解产生的物质)，这些物质进入土壤，对微生物有刺激或者抑制作用。植物对微生物、微生物对植物以及微生物之间都存在着相互作用(图1)。

1.2.2 植物与土壤动物的关系

植物作为生产者，是土壤生态系统中能量的主要来源。一方面，植物的根系为某些植食性线虫、昆虫提供了食物(Oka, 2010)；另一方面，植物地上部分凋落后进入土壤，为腐食性动物提供了生存和繁殖的能源(张雪萍等, 2001)。此外，植物还可以通过根系分泌物影响土壤动物，如草莓分泌的对羟基苯甲酸和对香豆酸可以使土壤中线虫总量和食细

菌线虫数量增加(李贺勤等, 2014), 而这些以植物或碎屑为食的小型动物会被体型更大的捕食性土壤动物如捕食性线虫、螨类、跳虫等取食(Moore et al, 1990), 从而使植物固定的能量流入动物。而动物的活动对植物的生长和抗病也有重要的作用(Schrader et al, 2013): 土壤动物可以通过直接取食作用来破碎植物地上部分的枯落物, 或者通过影响周围的理化环境、协同微生物的降解作用, 间接影响枯落物的分解, 从而促进土壤生态系统中物质循环, 为植物提供必要的营养元素(González & Seastedt, 2001; Zhang et al, 2018)。另外, 某些土壤动物还可以通过与植物地下部分作用, 诱导植物自身的抗虫、抗病的防御反应, 减少病虫害的发生(Blouin et al, 2005)。

1.2.3　土壤动物与微生物的关系

许多土壤中细菌和真菌是土壤动物食物的主要来源, 土壤中的食微动物(如某些线虫、螨类、原生动物、小型节肢动物等)通过取食细菌、真菌获得能量, 是外界能量输入土壤生态系统的重要途径(Sauvadet et al, 2016)。食细菌和食真菌的线虫可以通过取食作用调控微生物群落组成、结构和代谢活性, 并释放固持在微生物中的养分(吴纪华等, 2007)。原生动物可以进入到较小的土壤空隙中捕食细菌, 调节细菌群落结构(Corno & Jürgens, 2006)。

除捕食作用以外, 土壤动物的活动还可以提高土壤养分的矿化率, 从而影响土壤微生物量和群落结构(朱永恒等, 2012)。土壤动物类群之间也会通过

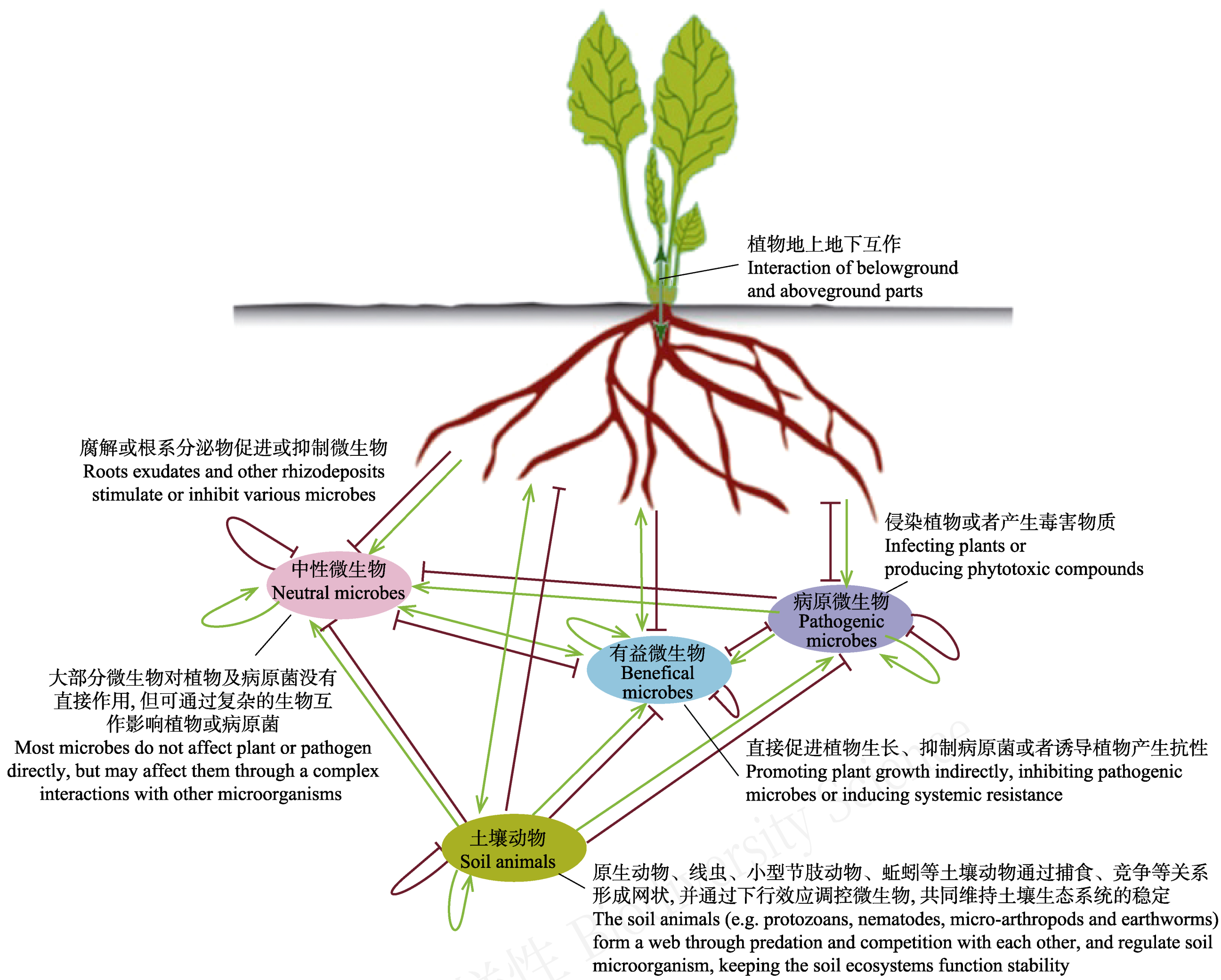

图1　基于各功能群相互作用的土壤微生态平衡(仿自Berendsen et al, 2012)。其中绿线加箭头表示促进作用, 红线加短线表示抑制作用。

Fig. 1　The balance of ecosystem (based on the interaction of functional groups) (modified from Berendsen et al, 2012). Green line indicates promoting effect and red line indicates inhibiting effect.

相互作用，依靠复杂的反馈和负反馈机制维持土壤动物群落组成的相对稳定(Geisen et al, 2016; 杜晓芳等, 2018)。

综上所述，土壤中植物根系、微生物、动物之间的作用主要是通过“物流”联系起来的：一种“物流”是通过取食与被食关系形成的食物链，主要体现在植物与动物、微生物与动物以及动物与动物之间的直接作用上；另一种是非食物链“物流”，即生物之间并不直接接触，而是通过分泌或者腐解产生的物质建立联系，主要体现在植物与微生物、微生物与微生物之间的间接作用上。生物之间的这些作用，既有促进，也有抑制，其方向和强度是通过系统内部信息传递控制的。完善的信息传递系统使得系统内部各组分保持相对稳定的状态。在健康土壤中，植物病原菌因受到土壤生态系统内部各种作用的制约，种群不会无限制扩大，就不会引起植物大规模病害的暴发(Janvier et al, 2007)。因此，在植物地下部所处的土壤中，各种生物通过食物链与非食物链物流相互作用，交织形成网状结构，生态系统完善的信息传递功能使这张网有条不紊地发挥作用(图1)。

2 蚯蚓对土壤生物的调控作用

2.1 蚯蚓对土壤动物的调控作用

土壤动物对土壤生态系统功能的维持具有重要作用。根据体宽，土壤动物可以分为小型(microfauna，平均体宽小于0.1或0.2 mm)、中型(mesofauna，平均体宽在0.1或0.2–2 mm之间)、大型(macrofauna，平均体宽大于2 mm)及巨型土壤动物(megafauna，平均体宽大于2 cm) (Wurst et al, 2013)。蚯蚓作为土壤中的大型动物，可以通过下行效应调控其他中型和小型动物。

以威廉腔蚓(*Metaphire guillelmi*)为例，Tao等(2011)研究表明，蚯蚓可以取食线虫，导致线虫丰富度下降。Boyer等(2013)以南美暗蚓(*Pontoscolex corethrurus*)为材料，同样发现蚯蚓可以取食线虫，并能够降低土壤中线虫囊泡和卵的数量。Ilieva-Makulec和Makulec (2002)研究表明，接种粉正蚓(*Lumbricus rubellus*) 30天后，食细菌、食真菌以及植食性线虫丰富度均表现出降低的趋势。除了直接取食外，蚯蚓的掘洞等行为也会影响线虫的生活环境，改变它们在不同土层的分布情况(Tao et al, 2009; Andriuzzi et al, 2016)。

另外，也有相关研究报道了蚯蚓对螨类和原生动物等土壤动物的调控情况。Mclean和Parkinson (1998)利用中宇宙系统(mesocosm)模拟了表居型(epigeic)八毛枝蚓(*Dendrobaena octaedra*)对甲螨群落的影响，研究表明，接种蚯蚓3个月后甲螨类多样性升高，6个月后其丰富度也显著提高。本课题组前期研究表明，接种赤子爱胜蚓(*Eisenia fetida*) 6个月后土壤中螨类各亚目的丰富度显著提高(伍玉鹏等, 2013)。Bonkowski和Schaefer (1997)研究表明，流蚓属(*Aporrectodea*)的*A. caliginos*可以取食自由活动的原生动物，对原生动物的分布有重要的影响。

此外，蚯蚓与土壤跳虫关系密切，但是由于研究者所关注的蚯蚓和跳虫种的不同，得出的结论是多样的。Marinissen和Bok (1998)研究发现，蚯蚓的活动增加了土壤的孔隙度，从而使得跳虫数目和种类增加；Salmon和Ponge (2001)研究发现流蚓属的蚯蚓*Aporrectodea giardi*及绿色异唇蚓(*Allolobophora chlorotica*)的活动可以增加跳虫*Heteromurus nitidus*的数量，并分析原因是蚯蚓分泌的粘液以及排出的尿液可以强烈吸引这类跳虫；而Gao等(2017)研究却表明，远盲蚓属(*Amynthas*)的蚯蚓*A. agrestis*入侵后，造成曲毛裸长跳虫(*Sinella curviseta*)数量减少。

蚯蚓活动对主要土壤动物类群的调控作用影响了土壤食物网功能的发挥，进而会间接影响土壤微生物的群落。

2.2 蚯蚓对土壤微生物的调控作用

蚯蚓和微生物的关系是非常复杂的，微生物是蚯蚓营养的主要来源，同时蚯蚓通过与微生物共同作用降解有机物质的过程促进微生物活性的提高(Li et al, 2002)，并且蚯蚓可以通过自身活动协助微生物在土壤中传播(Edwards & Bohlen, 1996)。蚯蚓可以通过改善微生境(排粪、作穴、搅动)、提高有机物的表面积、直接取食、携带传播微生物等方式影响土壤微生物数量、活性、组成和功能，还可以通过改变土壤结构来加速土壤营养物质的循环，影响微生物的群落结构(Edwards & Fletcher, 1988; Natal- da-Luz et al, 2012; Akca et al, 2014)。

2.2.1 影响微生物量、活性和多样性

土壤微生物量是土壤重要的源和汇，对土壤养分循环和植物生长具有重要作用(Singh et al, 1989),

大量研究报道蚯蚓活动会影响土壤微生物量。Burtelow等(1998)在美国东北部森林中研究了夏威远盲蚓(*Amynthas hawayanus*)入侵对土壤微生物的影响, 发现蚯蚓入侵后会形成明显的斑块(patches), 斑块内部土壤微生物量碳、氮显著提高。Li等(2002)发现纽约中部阔叶林中蚯蚓的入侵能够显著提高土壤微生物量。姚影等(2015)利用微宇宙实验研究了蚯蚓对施入秸秆后土壤有机碳的影响, 结果表明赤子爱胜蚓能提高土壤微生物量。伍玉鹏等(2013)在探索蚯蚓改良盐碱地的作用时, 也发现接种赤子爱胜蚓能显著提高土壤微生物量。Bi等(2018)在研究蚯蚓对草莓枯病的抑制作用时, 同样发现赤子爱胜蚓和威廉腔蚓能提高土壤微生物量。

蚯蚓对微生物量的影响作用可能与肠道厌氧环境有关, Drake和Horn (2007)发现蚯蚓肠道内可培养厌氧细菌数量最高能达到未被取食土壤的4,000倍。但是也有研究表明蚯蚓活动会降低土壤微生物量。Eisenhauer等(2011)研究了蚯蚓入侵北美北部阔叶林的过程, 发现蚯蚓可使土壤微生物量降低达42%。Gomez-Brandon等(2011)在研究安德爱胜蚓(*Eisenia andrei*)消化道的作用时, 发现安德爱胜蚓粪便中的土壤微生物量低于其食物中的量。Zhang等(2000)向土壤中接种赤子爱胜蚓和威廉腔蚓, 处理土壤24 h后发现, 两种蚯蚓均会显著降低土壤微生物量。

土壤微生物活性对植物生长有重要作用, 一般用土壤呼吸和土壤酶活性进行表征。多数研究表明蚯蚓具有提高土壤微生物活性的作用。在对纽约州一阔叶林蚯蚓入侵的研究中, Li等(2002)发现, 蚯蚓可使土壤基础呼吸提高5倍, 底物诱导呼吸提高6.7倍, 土壤微生物代谢熵提高3倍。Schaefer等(2005)研究了石油泄漏污染的土壤中接种陆正蚓(*Lumbricus terrestris*)、绿色异唇蚓及赤子爱胜蚓28天后, 土壤呼吸作用均显著增强, 而不接种蚯蚓的土壤呼吸则无显著变化; 同时研究者观察到, 赤子爱胜蚓与陆正蚓对土壤呼吸作用的影响大于绿色异唇蚓。Barbosa等(2017)发现蚯蚓提高了土壤呼吸和微生物量, 促进了菜豆(*Phaseolus vulgaris*)的生长。Cao等(2016)在研究土霉素污染的土壤中蚯蚓对养分循环的作用时发现, 接种赤子爱胜蚓的土壤脲酶活性显著提高。Zhang等(2016)研究表明, 在轻度盐碱胁迫(EC = 4.41 mS/cm)的土壤中接种赤子爱胜蚓, 土壤过氧化氢酶活性显著提高。本课题组研究了蚯蚓在连续100天对植物残体产生的酚类物质降解过程的影响, 发现蚯蚓的活动加速了酚类物质降解过程中微生物群落的演替, 而且接种蚯蚓的处理组中土壤脱氢酶活性高于同一时期取样的对照组(毕艳孟, 2016)。Huang等(2013a)发现, 在处理果蔬废弃物的过程中, 无论接种成熟的赤子爱胜蚓还是其幼蚓, 土壤脱氢酶活性均显著低于对照处理。李欢等(2016)研究蚯蚓菌根对土壤酶活和甘薯根系生长的作用时, 发现接种蚯蚓可以显著提高土壤脲酶和碱性磷酸酶活性, 从而促进甘薯的生长。

针对蚯蚓对土壤微生物多样性的作用也有大量研究。Lipiec等(2016)研究了蚯蚓打洞行为对微生物的影响, 发现蚯蚓洞穴土壤中平均颜色变化率(averagewell color development, 表征微生物对碳源利用的指标)显著高于周围土壤。郑宪清等(2015)利用定位实验, 研究了威廉腔蚓对土壤微生物多样性的影响, 发现投放蚯蚓后, 土壤微生物的Simpson和Shannon-Wiener多样性指数显著高于对照组。代金君等(2015)研究了蚯蚓肠道对重金属污染土壤微生物群落的影响, 发现经过蚯蚓过腹作用, 土壤微生物Shannon-Wiener多样性指数显著高于未经蚯蚓取食的土壤, 且赤子爱胜蚓和壮伟远盲蚓(*Amynthas robustu*)对微生物多样性的作用无显著性差异。Zhang等(2013)也研究了赤子爱胜蚓肠道对微生物群落的作用, 发现细菌在蚯蚓肠道中多样性先增加后减少, 最后保持稳定的状态。

蚯蚓对土壤微生物的作用是复杂和多样的, 不同的研究可能得出不同甚至相反的结论, 这可能与研究者选取土壤的性质、接种蚯蚓的密度以及选用蚯蚓的生活型及种属差异等因素有关。但是这些因素如何影响蚯蚓对微生物的调控作用及其作用机理等问题, 仍然需要系统深入的研究。

2.2.2　改变微生物群落结构

蚯蚓对微生物调控作用的研究除集中于对微生物总体生物量、活性、多样性的影响以外, 还有许多关注了蚯蚓对微生物群落结构的调控。

蚯蚓的取食偏好是改变微生物群落结构的重要因素。Shan等(2013)利用同位素标记研究了威廉腔蚓食物的主要来源, 证实相对细菌而言, 该蚯蚓更喜欢取食真菌。除了蚯蚓的取食偏好, 其肠道对微生物群落的塑造作用也能够改变不同微生物所

综述

占比例。Chapuis-Lardy等(2010)在研究蚯蚓对于土壤中CO_2和N_2O释放的作用时发现，被南美岸蚓(*Pontoscolex corethrurus*)取食并排泄后的土壤中真菌总量相对于未被取食的土壤显著下降。蚯蚓肠道对不同类型的土壤微生物有不同的影响，真菌大部分被杀死，而生长较快的细菌会迅速生长繁殖并进入有机质含量更高的蚯蚓粪中(Thakuria et al, 2010)。另外，蚯蚓对土壤环境的改变也是导致细菌/真菌比例变化的原因。Dempsey等(2011)通过仲夏和初秋时期对阔叶林土壤的调查发现，蚯蚓能够显著提高细菌真菌比例，并推测这与蚯蚓活动改变土壤有机质层有关。

许多研究表明，蚯蚓活动可以直接减少病原菌的数量。Wolfarth等(2011)利用流蚓属蚯蚓*Aporrectodea caliginosa*结合覆盖秸秆残渣，显著降低了镰刀菌属(*Fusarium*)的生物量和镰刀菌酸的浓度；类似地，Oldenburg等(2008)在利用陆正蚓降解小麦秸秆的过程中发现，该蚯蚓能够降低镰刀菌的生物量和镰刀菌酸的浓度。Elmer和Ferrandino (2009)通过挖掘沟壑的方式调控田间蚯蚓种群数量，发现蚯蚓种群的增大有利于减少茄子种植土壤中大丽轮枝菌(*Verticillium dahlia*)的数量。Bonkowski等(2000)通过对5种蚯蚓取食真菌偏好的研究发现，蚯蚓可以取食镰刀菌、丝核菌等植物病原菌。

也有研究表明，蚯蚓通过提高根际促生菌及病原拮抗菌的数量，间接促进植物的生长，抑制病害发生。Wu等(2012)研究了威廉环毛蚓(*Pheretima guillelmi*，即上文提到的威廉腔蚓)和根际促生菌的协同作用，发现该蚯蚓能够显著提高*Azotobacter chroococcum*、*Bacillus megaterium*和*B. mucilaginous*三种根际促生菌的丰度，进而强化了细菌加速养分循环的作用。Elmer (2009)系统研究了陆正蚓对芦笋、茄子和番茄病害的作用，发现蚯蚓的引入提高了土壤中荧光假单胞菌及丝状放线菌等有益菌群的密度，从而有效抑制了三种蔬菜病害的发生。除了关于蚯蚓增加土壤中有益微生物的报道，还有研究直接从蚯蚓粪中获得了病原拮抗菌。Gopalakrishnan等(2011)从以植物秸秆为原料的蚯蚓粪中分离获得5株对镰刀菌有拮抗作用的细菌，能够有效防控鹰嘴豆的枯萎病。本课题组从以牛粪为原料的蚯蚓粪中分离获得对植物病原菌具有显著抑制作用的球孢链霉菌(*Streptomyces globisporus*)和丁香苷链霉菌(*S. syringini*)，并将该蚯蚓粪施入黄瓜种植土壤，显著降低了黄瓜苗期的立枯病和枯萎病的病情指数(胡艳霞等, 2002)。

3 蚯蚓对缓解连作障碍的作用

3.1 连作导致微生态失衡

不同植物的根系分泌物或者残体腐解产生的物质是不同的，由此它们对土壤生物尤其是微生物群落有不同的选择作用(Zhang et al, 2014; Abbasi et al, 2015; Vaitauskiene et al, 2015)，使得土壤微生物群落及其作用的方式呈现出多样化。然而，在农田连作的环境中，作物种类单一使得植物根系分泌或者残体腐解产生的物质趋向于单一化，定向选择某些根际区的微生物，导致根际区微生物多样性降低，使系统信息传递功能以及系统内部生物之间的相互促进和制约关系，甚至整个土壤生态系统功能遭到破坏。主要表现为微生物的活性和多样性降低(Liu et al, 2014)、细菌/真菌比例下降(甄文超等, 2005; Li et al, 2014)、病原菌增加(Ye et al, 2004; Niu et al, 2011)。大多数土传病原菌既能营腐生生活，又能营寄生生活，一般会在根系区生长并繁殖到一定的数量再侵染宿主细胞，或者在宿主内扩繁到足够的数量才能有效地侵染宿主组织(Berendsen et al, 2012)。而根际区失衡的微生物群落环境恰好为这些病原菌的繁殖提供了条件，导致植物病害发生。根际微生物群落失衡，除了表现为病原菌增加外，还体现在有益微生物的减少上。许多微生物在土壤营养循环中发挥着重要作用(Gyaneshwar et al, 2003; Jing et al, 2017)，因此，功能紊乱的微生物群落可能影响土壤养分的循环，限制植物对营养的利用，造成作物生长不良、病害加剧。

3.2 蚯蚓促进化感物质降解

作为土壤生态系统中的分解者，蚯蚓的活动能够促进土壤中许多物质降解，其中一些物质是对植物或土壤微生物有重要调节作用的化感物质。酚类物质就是一类重要的化感物质，其在连作土壤中的累积常被认为是造成作物连作障碍的原因之一(吴宗伟等, 2009; 李贺勤等, 2014)。Butenschoen等(2009)利用同位素标记的方法研究了土居型神女辛石蚓(*Octolasion tyrtaeum*)对儿茶酚的作用，结果表明，该蚯蚓能够通过提高微生物活性影响儿茶酚的矿化过程。Bi等(2016)研究表明，接种表居型赤子爱

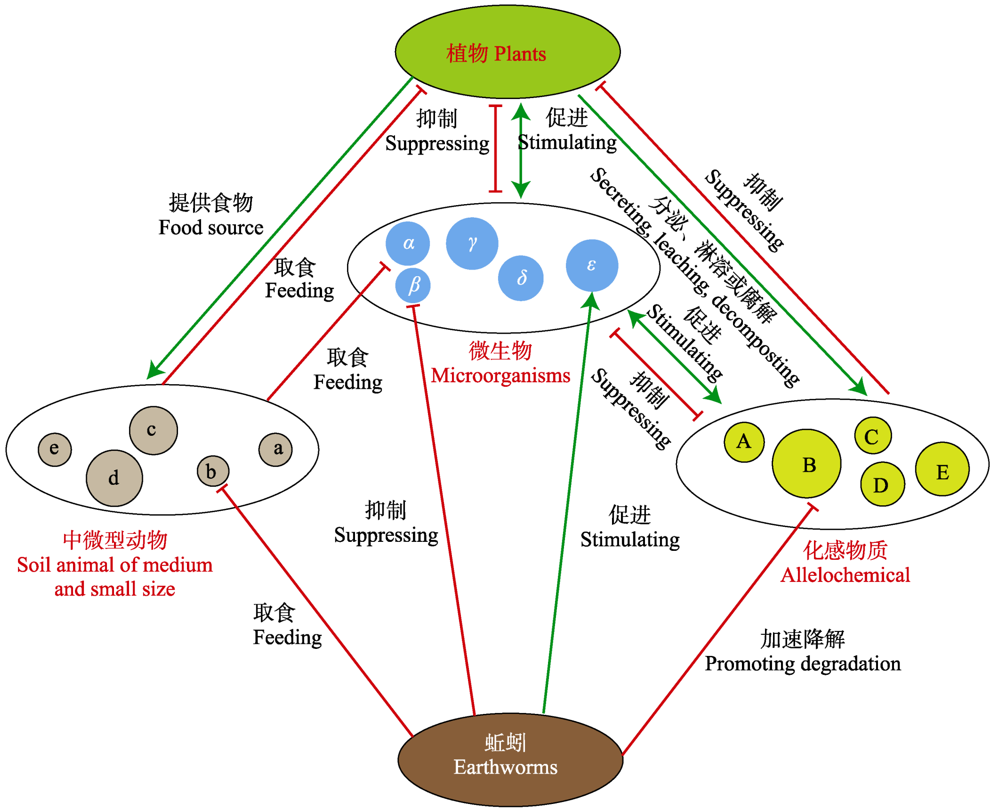

图2　蚯蚓调控连作障碍的土壤微生态机制
Fig. 2　The mechanism of earthworm regulating soil microecology

胜蚓和上食下居型威廉腔蚓均能加速酚类物质的降解, 且降解过程中需要微生物的参与。Yahaya等(2017)研究发现, 赤子爱胜蚓和枝蚓属(*Dendrobaena*)的*D. veneta*处理果园内枯枝落叶, 能加速木质素的降解, 使得酚类物质含量显著降低。Mohan等(2011)评价了3种蚯蚓(赤子爱胜蚓, *Eudrillus eugenia*和*Anantapur species*)对苯酚的耐受和降解能力, 发现赤子爱胜蚓耐受能力最强, 可以耐受100 ppm的苯酚, 并在72 h内对该浓度的苯酚降解率达100%。在研究蚯蚓对草莓枯萎病的防控效果时, Bi等(2018)发现威廉腔蚓可以加速酚酸的降解, 且对原儿茶酸和对香豆酸的降解效果优于其他酚酸, 并分析该作用可能会降低草莓枯萎病病情指数。本课题组在对西瓜连作的研究中还发现, 新鲜蚯蚓粪对香豆酸和丁香酸的降解能力较强, 由此可以改变土壤中不同种类酚酸的比例(许永利, 2006)[①]。除了酚类化感物质以外, 也有研究表明蚯蚓的活动可以改变土壤中不同脂肪酸类物质的比例(Sampedro & Whalen, 2007)。目前尚未见有关蚯蚓对其他类化感物质降解的报道。

3.3　蚯蚓调控连作障碍土壤微生态机制

在正常的土壤系统中, 由于地上部分植物是多样的, 其分泌、淋溶或腐解产生的化感物质与土壤微生物、土壤动物以及植物根系之间具有相互促进和抑制作用, 共同作用的结果使土壤生态系统处于平衡态, 土壤能够稳定地发挥功能。但是, 连作导致地上部分植物长期单一化, 使得土壤中化感物质不均衡累积, 多样性下降; 同时由于单一植物对土壤动物的选择, 使得土壤动物类群定向改变, 造成动物区系平衡被打破, 多样性下降, 功能紊乱; 植物的单一化还会导致土壤微生物群落的组成类群定向改变, 微生物区系平衡被打破。增加的化感物质以及功能紊乱的动物区系进一步加剧微生物区系的失衡, 造成生态系统稳定性下降, 系统原本具有的抑制病原菌的能力降低, 导致植物病原菌数量增加, 作物病害发生。

蚯蚓能够直接调控微生物, 影响微生物的总量、活性和多样性, 改变微生物的比例(Li et al, 2002;

①许永利 (2006) 蚯蚓粪解除西瓜连作障碍的效果及机理初探. 硕士学位论文, 中国农业大学, 北京.

Wu et al, 2012; 郑宪清等, 2015; Barbosa et al, 2017)。另外, 蚯蚓作为生态系统的分解者, 能够加速化感物质的降解, 而且可能改变土壤中化感物质的比例, 调整失衡的化感物质(Bi et al, 2018)。同时, 蚯蚓作为土壤生态系统的高级消费者, 能够取食某些中、小型土壤动物, 通过下行效应调控土壤动物区系, 提高土壤动物的多样性(Mclean & Parkinson, 1998; 伍玉鹏等, 2013)。化感物质多样性和动物多样性的恢复, 可进一步影响土壤微生物。根据上述总结和分析可知, 蚯蚓对微生物的调控作用主要有三条途径: 一是直接调控微生物群落; 二是通过改变化感物质比例调控微生物群落; 三是通过调控土壤动物区系调控微生物群落。三条途径的综合作用共同改善了土壤根际微生态, 从而缓解了作物连作障碍(图2)。

4 展望

蚯蚓在土壤生态系统中具有重要的作用, 包括促进有机质分解和养分循环、对土壤理化性质的改变, 以及与植物、微生物和其他动物的相互作用(张卫信等, 2007)。与蚯蚓相关的研究涵盖了环境、生物以及农业等诸多领域。在农业领域, 关于蚯蚓的研究主要集中在改良污染土壤(Natal-da-Luz et al, 2012; Cao et al, 2016)、影响土壤温室气体排放(Wu et al, 2015; Zhu et al, 2016)、促进土壤养分循环(Cao et al, 2016; Angst et al, 2017)及防控植物病虫害(Loranger-Merciris et al, 2012; Hume et al, 2015)等方面, 而通过蚯蚓调控土壤系统改良连作土壤的研究相对较少。结合植物连作障碍发生的过程和现有关于蚯蚓作用的研究, 笔者认为蚯蚓具有缓解连作障碍的潜力。这一作用主要是通过调控微生物实现的。近年来, 分子生物学技术的发展为土壤中不可培养微生物的研究提供了新工具, 提升了人们对土壤微生物研究的深度和精度, 有关蚯蚓与微生物关系的研究逐渐增加。蚯蚓一方面可以通过取食、掘洞和爬行等行为直接影响微生物群落; 另一方面还可以通过改变动物区系和化感物质间接调控微生物群落。根据笔者对文献的总结, 目前关于蚯蚓对微生物直接作用的研究较多(Li et al, 2002; Dempsey et al, 2011; Wu et al, 2012; 曹佳等, 2015; Barbosa et al, 2017), 而通过改变动物区系和化感物质间接影响微生物的研究较少(Ilieva-Makulec & Makulec, 2002; Bi et al, 2018)。蚯蚓既是分解者又是消费者, 其对微生物的间接调控作用是不可忽视的。

植物连作造成化感物质多样性的下降, 不仅会导致土壤微生物群落失衡, 而且会直接影响到植物的生长。研究表明, 以酚酸为代表的化感物质在一定条件下不仅抑制植物的发芽和生长, 还会抑制植物的光合、呼吸等生理活动, 使植物抗病能力下降(Jilani et al, 2008)。因此, 研究蚯蚓与连作土壤中化感物质的关系, 以及蚯蚓加速某些化感物质降解的机理, 对调控连作土壤环境具有重要意义。

同样, 连作造成的土壤动物区系失衡, 尤其在植物根际区, 也会直接影响植物。例如某些作物连作后会造成根结线虫的增加(时立波等, 2010), 根结线虫不但可对根系造成直接破坏, 还能使根系更容易受到病原菌侵染, 加重植物的连作病害(Mota et al, 2013)。而目前关于蚯蚓与土壤动物区系关系的研究也相对较少。

必须指出, 作物连作障碍的问题是植物进化过程中产生的一种自然现象, 对植物自身而言, 有利于避免近亲繁殖, 提高自身的适合度(fitness); 对于生态系统而言, 有利于提高生物多样性。而在农业生态系统中, 人们为了获得特定的产品, 某些时候不得不进行重茬种植。因此, 充分发挥土壤生态系统的自修复作用以及利用土壤食物网的相互作用关系以减少连作障碍对作物和土壤的影响, 是农业可持续发展的有效途径。

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