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蚯蚓对土壤温室气体排放的影响及机制研究进展*

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摘要 土壤是温室气体的重要源和汇。蚯蚓是土壤物质循环的重要参与者, 能够直接或间接影响土壤CO₂、N₂O和CH₄等温室气体的产生和释放。蚯蚓呼吸产生的CO₂, 是土壤呼吸的重要组成部分; 蚯蚓自身肠道、分泌液、消化物和排泄物等微环境促进反硝化过程释放N₂O。蚯蚓还通过取食、掘穴、排泄等活动, 改变土壤理化性质、微生物组成和活性及其他土壤动物的组成, 影响地上植物生长, 调节土壤分解、矿化、硝化、反硝化和甲烷生成及氧化等生态过程, 间接影响土壤温室气体的排放。蚯蚓对土壤温室气体排放的影响逐渐受到重视, 但目前研究仍以室内培养和单因子环境条件的模拟为主, 缺少野外原位实验和多环境因子的交互实验研究。长期监测和同位素示踪技术, 是深入探讨蚯蚓影响温室气体排放机制的重要手段。温室气体类型上, CO₂和N₂O是研究热点, CH₄研究比较罕见。未来研究, 应重视不同生态类群蚯蚓与土壤理化特征、微生物组成、其他类群土壤动物和地上植物间的交互作用, 加强机制研究, 并关注土壤污染环境蚯蚓功能性状的变化; 综合评价蚯蚓对土壤温室气体排放和土壤碳氮固定的影响, 科学评估蚯蚓活动对土壤碳氮释放的促进或减缓作用。

关键词 土壤动物; 生态系统工程师; N₂O; CH₄; 土壤过程

中图分类号 S154 **文献标识码** A

温室气体浓度升高是全球变暖的主要原因。土壤是温室气体(CO₂、CH₄和N₂O)的重要排放源或汇^[1]。全球变化背景下温室气体排放驱动机制的深入研究表明, 土壤动物, 尤其是大型土壤动物(蚯蚓、白蚁和蚂蚁等)对温室气体排放具有重要的直接或间接调控作用^[2-3]。土壤动物作为生物地球化学循环(生物小循环)的驱动者, 通过直接产生微量气体、与微生物的取食关系和促进“地-气”间气体传输等方式影响微量气体代谢^[4-5]。目前, 全球变暖和人类活动强烈干扰背景下, 土壤动物对温室气体排放的影响逐渐受到重视, 报道日益增多^[6-8]。但土壤动物在土壤碳氮等元素循环中的作用、强度和机制, 依旧是土壤物质循环过程和模型研究的瓶颈^[9], 而这是阐明土壤温室气体排放

机制的关键之一。因此, 大型土壤动物对温室气体的调控功能受到特别关注, 并将构建融合土壤动物作用的C、N生物地球化学循环模型作为研究目标^[10-11]。

蚯蚓是广泛分布于各大陆地生态系统中的最典型的大型土壤动物之一, 目前已发现的陆栖蚯蚓约4 000种, 生物量巨大^[12]。而且, 蚯蚓能够通过取食、排泄、分泌黏液、挖掘洞穴等活动显著改善土壤结构, 提高土壤通气透水能力和肥力, 影响土壤物质循环和能量流动, 被称为“生态系统工程师”^[13-14]。蚯蚓通过自身呼吸、排泄和分泌, 直接产生温室气体; 也能够通过取食和掘穴等活动, 改变土壤结构、碳氮组成和土壤微生物及其他土壤动物的组成^[12, 15-16], 间接影响影响土壤温室气体

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的产生和释放。由于蚯蚓分布的广泛性和其生态功能的重要性,近年来国内外关于蚯蚓对土壤温室气体作用的研究不断增多^[12-16]。但目前研究仍较分散,还缺少专门针对蚯蚓对温室气体排放影响及其机理的系统梳理和总结。基于以上,本文对目前相关研究进行综述,旨在系统总结蚯蚓对土壤温室气体排放的影响特征和主要影响机制;并结合目前研究动态,对未来研究提出展望,为今后研究提供参考。

1 蚯蚓对土壤温室气体排放的影响

目前,蚯蚓对土壤温室气体的影响研究主要集中在CO₂、N₂O和CH₄;生态系统类型上,涵盖了森林、草地和农田生态系统;蚯蚓生态类群也包含了表栖、内栖和深栖等3类群的多个物种(表1)。

1.1 对土壤CO₂和CH₄排放的影响

土壤中CO₂主要来源于土壤无脊椎动物、植物根系呼吸和土壤微生物分解有机碳等生态过程^[9, 17]。尽管微生物活动释放CO₂占主导地位,但蚯蚓等高生物量的大型土壤动物作用,尤其是环境变化引起蚯蚓密度增加或外来蚯蚓大量入侵时,不容忽视^[18-21]。但目前专门针对蚯蚓体自身呼吸对土壤CO₂的直接贡献和蚯蚓活动对CO₂排放间接影响的研究并不多见,多数研究是作为评价微生物活性的指标出现。

蚯蚓体及其活动产生的土壤CO₂,是土壤呼吸的重要组成部分。Lubbers等^[3]综合评价以往研究得出,蚯蚓活动能够使土壤CO₂排放量平均提高33%。深栖蚯蚓*Lumbricus terrestris*和内栖蚯蚓*Aporrectodea caliginosa*对土壤总CO₂排放量贡献率为7%~58%^[22],表栖蚯蚓*Eisenia foetida*对土壤总CO₂排放量的贡献率达40%^[23]。但也有研究表明,蚯蚓活动对土壤CO₂排放的影响,主要集中在初始阶段^[24],随着培养时间的延长,作用效果逐渐减弱^[25],甚至相反^[26]。因此,蚯蚓对温室气体排放的影响具有一定的时效性。

不同生态类群的蚯蚓,对土壤CO₂释放的影响存在显著差异,这主要是由蚯蚓物种本身差别和土壤性质差异导致的。Crumsey等^[27]研究表明,深栖型蚯蚓*L. terrestris*对北美温带森林土壤CO₂排放量不产生影响,而内栖蚯蚓*Aporrectodea trapezoides*和表栖蚯蚓*E. foetida*同时接种能够使

CO₂初期排放量增加30%。深栖蚯蚓*Aporrectodea longa*与表栖蚯蚓*Lumbricus rubellus*混合接种均能增加土壤CO₂排放量,其中*L. rubellus*的作用更为重要^[28];而内栖蚯蚓*A. caliginosa*和表栖蚯蚓*L. rubellus*交互作用对土壤CO₂排放影响不明显^[5]。

农田生态系统中,蚯蚓活动的作用常与作物秸秆相关联。在农田土壤中接种蚯蚓和施加秸秆可导致CO₂排放量分别增加60%和1.35倍,而在施加秸秆的基础上接种蚯蚓能使土壤CO₂排放量再增加41%^[29-31]。表栖蚯蚓*L. rubellus*在秸秆表施土壤中能使CO₂累积排放量显著增加,而在秸秆混施土壤中作用不显著^[5]。深栖蚯蚓*A. longa*与表栖蚯蚓*L. rubellus*均能增加土壤CO₂排放量,但与秸秆(尤其是秸秆混施)的作用相比,蚯蚓对土壤CO₂排放量的增加十分微弱,甚至可忽略不计^[28]。

土壤CH₄的排放受到越来越多的关注,主要是因为CH₄增温潜力是CO₂的20倍^[1],且全球约1/3的CH₄源自土壤^[32]。部分研究表明,蚯蚓活动及其排泄物能够显著增加^[25, 33]或减少^[34]土壤CH₄排放。Kerneck等^[35]研究表明,内栖蚯蚓*Aporrectodea turgida*通过调节CH₄气体的产量和氧化率,能够有效降低洪泛期河滨土壤CH₄的净产量。使用覆盖层是减缓垃圾填埋场CH₄排放的有效措施,在稻田土覆盖层中添加蚓粪能使垃圾填埋场CH₄氧化速率增加0.97倍~4.1倍,从而减少CH₄排放,而作用的效果受加入蚓粪的比例、温度和湿度的影响^[36-37]。而山地草甸土壤中蚯蚓活动能促进CH₄的产生^[33],蚯蚓和蚓粪产生CH₄使得土壤CH₄总排放量增加^[25],蚯蚓活动还使热带人工林土壤从CH₄“汇”向“源”转变^[38]。

1.2 对土壤N₂O排放的影响

土壤是N₂O的主要来源,且N₂O增暖潜力分别是CO₂和CH₄的190倍~270倍和4.0倍~21倍^[1]。而且,相对于CO₂而言,蚯蚓影响N₂O产生和排放的过程更加复杂。土壤N₂O排放速率和累积排放量的变化,是目前蚯蚓对温室气体排放影响研究的主体和重点。蚯蚓能够增加土壤N₂O排放的30%~56%^[3, 5, 28, 39-40],被认为是移动的土壤N₂O排放“热点”。但也有少数研究发现*E. foetida*能够显著降低土壤N₂O的排放^[41]。依据蚯蚓功能类群、土壤性质和作用时间不同,蚯蚓对N₂O影响表现出增加或降低,加速或减缓,甚至无显著影响。

不同生态类群蚯蚓的作用差异显著,这可能

表 1 蚯蚓对土壤温室气体排放量的影响

生态系统 Ecosystem concerned	年份 Year	地区 Study area	研究方法 (培养时间) Method (Incubation time)	蚯蚓种名 Earthworm species	生态类群 Ecological group	蚯蚓对土壤温室气体排放的影响 Effect of earthworm on emission of greenhouse gases			参考文献 References
						CO ₂	CH ₄	N ₂ O	
农田	2005	意大利, 地中海沿岸	培养实验 (53 d)	赤子爱胜蚓 <i>Eisenia foetida</i>	表栖	贡献率40%			[23]
	2007	荷兰, 瓦赫宁根	培养实验 (50 d, 90 d)	红正蚓 <i>Lumbricus rubellus</i> 长流蚓 <i>Aporrectodea longa</i>	表栖 深栖	+	+1317% +308%		[28]
	2008	中国, 南京	培养实验 (21 d)	赤子爱胜蚓 <i>Eisenia foetida</i>	表栖	+60%			[29, 31]
	2013	中国, 南京	野外实验	威廉腔环蚓 <i>Metaphire guillelmi</i>	深栖		+		[43, 44]
	2008	加拿大, 魁北克	培养实验 (25 d)	正正蚓 <i>Lumbricus terrestris</i> L. 暗色流蚓 <i>Aporrectodea caliginosa</i>	深栖 内栖	二者共存时最高	0		[22]
	2010	马达加斯加	培养实验 (35 d)	黄颈透钙蚓 <i>Pontoscolex corethrurus</i>	内栖	+			[4]
	2010	荷兰, 瓦赫宁根	培养实验 (35 d), ¹⁵ N标记法	红正蚓 <i>Lumbricus rubellus</i> 暗色流蚓 <i>Aporrectodea caliginosa</i>	表栖 内栖	+			[5]
	2011	荷兰, 瓦赫宁根	培养实验 (35 d), ¹⁵ N标记法	红正蚓 <i>Lumbricus rubellus</i> 暗色流蚓 <i>Aporrectodea caliginosa</i>	表栖 内栖		+76%	先增加后降低	[91]
	2014	加拿大, 魁北克	培养实验 (69 d)	膨胀流蚓 <i>Aporrectodea turgida</i> 正正蚓 <i>Lumbricus terrestris</i> L.	内栖 深栖			高含水量时 (97%WFPS) 降低 34%, 低含水量时 (33%WFPS) 增加 50%	[47]

续表

Ecosystem concerned	年份 Year	地区 Study area	研究方法 (培养时间) Method (Incubation time)	蚯蚓种名 Earthworm species	生态类群 Ecological group	蚯蚓对土壤温室气体排放的影响 Effect of earthworm on emission of greenhouse gases			参考文献 References
						CO ₂	CH ₄	N ₂ O	
草地	2007	荷兰, 瓦赫宁根	培养实验 (62 d)	长流蚓 <i>Aporrectodea longa</i>	深栖		前期 (3 ~ 12 d) 增加 30%, 后期 (44 ~ 62 d) 降低 50%	[39]	
施肥草地	2011	荷兰, 瓦赫宁根	培养实验 (72 d)	红正蚓 <i>Lumbricus rubellus</i> 暗色流蚓 <i>Aporrectodea caliginosa</i>	表栖 内栖		施肥后增加 50.8%	[40]	
撂荒草地	2012	爱尔兰	培养实验 (36 d)	<i>Aporrectodea icterica</i>	内栖		有机质含量高时增加 780%, 含量低时增加 1260%	[45]	
人工草场	2013	荷兰, 瓦赫宁根	野外实验	红正蚓 <i>Lumbricus rubellus</i>	表栖		+286% ~ 394%	[24]	
人工草场	2009	德国, 吉森	野外实验				+27% ~ 100%	[33]	
森林	2000	德国, 哥廷根	野外实验 (120 d)	正正蚓 <i>Lumbricus terrestris</i> L.	深栖		先增加 16% ~ 28% 后 CH ₄ 氧化速率降低 53%	[25]	
温带森林	2013	美国, 希博伊根	培养实验 (320 d)	赤子爱胜蚓 <i>Eisenia foetida</i> 梯形流蚓 <i>Aporrectodea trapezoides</i>	表栖 内栖		0	[27]	
亚热带人工林	2010	中国, 广东	野外实验 (15 d)	正正蚓 <i>Lumbricus terrestris</i> L. 西土寒突蚓 <i>Ocnerodrilus occidentalis</i>	深栖 内栖		增加 30%	[38]	
其他	2008	韩国	培养实验	(蚓粪)			-97%	[36]	
河岸缓冲带	2010	韩国	培养实验	(蚓粪)			-410%	[37]	
河岸缓冲带	2011	加拿大, 魁北克	野外调查				含水量越高, C、N 供给越充足, 增量越大	[46]	
河滨湿地	2015	加拿大, 魁北克	培养实验 (1 d)	膨胀流蚓 <i>Aporrectodea turgida</i>	内栖		-	[35]	
河岸潮土	2008	中国, 南京	培养实验 (20 d)	赤子爱胜蚓 <i>Eisenia foetida</i>	表栖		+153.7 ~ 186.3 mg kg ⁻¹	[30]	
试验田	2012	荷兰, 瓦赫宁根	培养试验 (320 d), ¹³ C 标记法	正正蚓 <i>Lumbricus terrestris</i> L. 红正蚓 <i>Lumbricus rubellus</i>	深栖 表栖		随秸秆深度增加而降低	[114]	

注: + 表示增加, - 表示降低 Note: + represents increase, - represents decrease

与有机质的取食难度和 N_2O 的传输距离有关。表栖蚯蚓更易取食有机物促进 N_2O 的产生，而深栖蚯蚓活动所产生的 N_2O 在向地表的长距离传输过程中逐渐被分解为 N_2 ，因此，表栖类群更能促进土壤 N_2O 释放量的增加^[28, 42]。而且，土壤表层有无植物残体、土壤有机质含量、营养状况及其在土壤剖面中的分布格局，均直接影响不同生态类群蚯蚓对 N_2O 增加的影响强度。表栖蚯蚓*L. rubellus*能显著增加秸秆表施土壤 N_2O 的排放速率和累积排放量^[5]；而内栖蚯蚓*A. caliginosa*和*A. longa*则使得土壤 N_2O 排放量先短暂的增加而后又显著降低^[39]。Giannopoulos等^[5]研究表明，内栖蚯蚓*A. caliginosa*可将植物残体混施土壤中 N_2O 累积排放量从 N_2O-N 1 350 mg kg⁻¹增加至2 223 mg kg⁻¹，内栖蚯蚓*Metaphire guillelmi*活动也能使秸秆表施土壤中 N_2O 释放量显著增加^[43, 44]。施肥草地系统中*L. rubellus*能够增加 50.8% 的 N_2O 排放^[40]，而没有氮输入的土壤中蚯蚓活动对 N_2O 释放作用不明显^[22]。内栖蚯蚓*Aporrectodea icterica*在低有机质含量和高有机质含量土壤中能分别使 N_2O 排放增加12.6倍和7.8倍^[45]，能使亚热带人工林土壤 N_2O 排放量增加66.3%^[41]，在具有充足N、C供给的河滨地带，蚯蚓对土壤 N_2O 的产生和释放有促进作用^[46]。

土壤湿度影响深栖蚯蚓的活动能力和生态功能的发挥，而且作用强度具有时间尺度差异。如，在33%土壤空隙含水率（Water-Filled Pore Space, WFPS）时，深栖蚯蚓*L. terrestris*和内栖蚯蚓*A. turgida*共同作用能够增加土壤 N_2O 排放的50%，而在97%WFPS条件下，则降低34%；同时，内栖和深栖蚯蚓混合接种能够显著降低干-湿交替土壤的 N_2O 的排放速率，减少 N_2O 累积排放量的82%^[47]。Bertora等^[39]发现，蚯蚓*A. longa*在高湿度土壤中，实验初期（3~12 d）增加 N_2O 排放约30%；而从44 d起，使 N_2O 排放量降低了50%。曾有蚯蚓活动的土壤经过冻融交替也能提高土壤 N_2O 排放量^[28]。

蚯蚓在自然野外条件下对 N_2O 排放的影响，除蚯蚓自身的功能特性外，还依赖于土壤理化性质和季节性的气象条件变化。如，秋季蚯蚓增加土壤 N_2O 排放，而春季蚯蚓作用不显著^[3]。

2 作用机制

蚯蚓活动可以通过直接或间接作用影响土壤温室气体（ CO_2 、 N_2O 、 CH_4 等）的排放。直接作用主要表现为蚯蚓自身的呼吸、取食、分泌、排泄等活动释放出温室气体，进入土壤成为土壤温室气体的一部分；间接作用主要通过与其生境中的土壤、微生物、植物等相互作用或参与土壤C、N循环过程而改变土壤温室气体的产生和释放（图1）。

2.1 蚯蚓直接生成温室气体

蚯蚓自身呼吸，是蚯蚓活动增加土壤 CO_2 排放量的一部分^[4]。 N_2O 的产生主要涉及：1）硝化过程（好氧环境），2）反硝化过程（厌氧、湿润环境），3）硝化细菌反硝化过程^[48]。蚯蚓肠道的厌氧环境、适宜的pH和湿度、充足的有机物质和硝酸盐、亚硝酸盐供应等，均有效促进肠道内反硝化细菌的生长和反硝化过程的进行^[49]，加速和增加蚯蚓肠道 N_2 和 N_2O 的排放^[50-52]。另外，蚯蚓体内外分泌的黏液（mucus）以及蚓粪（cast）也形成有利于反硝化作用进行的土壤环境，使得新鲜的蚓粪和蚯蚓洞穴成为释放 N_2O 的“热点”^[53]。

蚯蚓生命活动和代谢，呼出的 CO_2 量与蚯蚓体长、生物量和活性有关，但还缺少蚯蚓自身排放量与生物量等指标的定量关系。蚯蚓自身直接排放 N_2O 的速率约为 N_2O 2.5~25 ng h⁻¹ g⁻¹ 蚯蚓（鲜重），但与整个土壤系统 N_2O 的排放总量相比，数量很小^[39, 49]。同时，蚯蚓取食土壤的量和排泄量很少，亦不足以对整个土壤的 N_2O 释放产生显著影响^[4]。Borken等^[25]在短期的无土培养蚯蚓的实验中发现，蚯蚓体表和排泄物能释放 CH_4 ，使得 CH_4 排放量增加。

2.2 蚯蚓对温室气体排放的间接影响机制

2.2.1 对土壤结构的影响 蚯蚓活动能够改变其“蚓触圈”（drilosphere）的土壤结构^[54]，而改变土壤温室气体的形成环境和排放条件，主要体现在蚯蚓对土壤颗粒组成、土壤孔隙度、持水能力、有机质含量和土壤层次改变等方面^[39, 55]。

蚯蚓既能压实土壤，也能使土壤变得疏松，这通常与蚯蚓类群和土壤质地有关。“压实型”蚯蚓活动使土体密度增加5%~8%，土壤孔隙度降低3%^[56-57]，例如，*P. corethrurus*使土体密度由1.12

g cm^{-3} 增加至 1.13 g cm^{-3} , 土壤孔隙度由58%下降至53%^[58]。而有些个体较小的“疏松型”内栖蚯蚓能增强土壤孔性^[59]。此外, 蚯蚓排泄的蚓粪孔隙度较一般土壤高20%^[60]。蚯蚓活动能影响土壤团聚体的形成和组成。蚯蚓*Millsonia anomala*能够促进土壤大团聚体(粒径 $> 50 \text{ mm}$)的形成^[56]。Alegre等^[58]研究发现蚯蚓(*P. corethrurus*)活动, 使粒径 $> 10 \text{ mm}$ 的土壤团聚体所占比例增加7.6%, 粒径 $< 2 \text{ mm}$ 团聚体减少7.1%, 而对中等粒径(2~10 mm)团聚体没有影响。蚯蚓取食、消化和排泄等活动改变所取食土壤的颗粒组成和团聚体结构而形成新的微环境, 使原先暴露的有机质被新的团聚体包围起来, 提高了土壤碳的稳定性; 而原有团聚体中的有机质可能重新暴露而被分解^[61-62]。

蚯蚓活动还能提高土壤渗透率, 提高土壤湿度^[63]。蚯蚓的生存与活动对土壤水分十分敏感, 当土壤含水量很低时, 蚯蚓会分泌黏液制造一个微小的湿润空间以维持生存, 但其活动性会急剧降低甚至休眠以减少水分散失, 对土壤性质和过程的影响微弱; 而在适宜蚯蚓生活的湿润土壤中, 蚯蚓活动性增强, 对土壤温室气体排放的影响也相应增强^[39]。

2.2.2 对土壤微生物的影响 蚯蚓与体内微生物种群之间存在共生关系。蚯蚓肠道适宜的微环境有利于反硝化细菌的生长^[40, 51-52], 其中的反硝化细菌数量是土壤中的35倍~256倍^[64]。蚯蚓肠道消化和运送食物过程中分泌的黏液有利于微生物与有机物质接触, 促进有机质分解和微生物生长繁殖^[53, 65]。

蚯蚓取食、挖掘和排泄等活动, 能够改变“蚓触圈”内土壤微生物的组成和活性。蚯蚓活动能够激发土壤微生物活性, 提高土壤有机碳的有效性, 增加土壤基础呼吸量; 而且, 蚯蚓与有机质含量、微生物活性间的交互作用将进一步改变土壤碳氮原有的平衡关系^[66]。热带蚯蚓*P. corethrurus*能够显著增加土壤微生物量氮含量^[67]。Stromberger等^[68]运用磷脂脂肪酸法(PLFA)和 ^{13}C 、 ^{15}N 标记法研究表明, 深栖蚯蚓*L. terrestris*活动使“蚓触圈”土壤微生物量和C含量较周围土壤分别增加58%和23%, 并能促进凋落物中的C向土壤深层迁移, Groffman等^[69]发现蚯蚓活动分别降低和增加土壤有机质层和矿质土壤层的微生物量, 且二者相

比, 矿质土壤层增量较大。蚯蚓活动还会改变土壤微生物组成。Dempsey等^[70]野外实验研究发现, 夏秋季节蚯蚓活动使土壤中细菌/真菌比例增加2倍以上, Enami等^[71]也发现深栖蚯蚓*Pheretima hilgendorfi*活动不仅增加水稻秸秆混施土壤中总微生物量, 还增加细菌数量。*Allolobophora hrabei*排泄活动能降低土壤中细菌和真菌群落的丰富度而增加古生菌的丰富度, 其中对细菌群落的影响最显著^[72]。有蚯蚓活动的土壤中, 反硝化细菌数量较一般土壤多出35倍~256倍^[73]。

蚯蚓排泄物适宜土壤微生物种群的扩增^[53, 74]。蚯蚓排泄物中土壤微生物的多样性显著高于对照土壤^[75], 而且蚓粪中细菌和真菌生物量和活性都高于周围土壤, 促进 CO_2 和 CH_4 的产生并增强土壤环境异质性^[76]。在垃圾填埋场生物覆盖层中添加蚓粪, 能增加甲烷氧化菌的密度和多样性^[34], 进而加速甲烷氧化^[77]。淹水环境中, 蚯蚓掘穴和排泄活动能加速 O_2 在土壤中的流通, 使甲烷氧化菌种群增长高达100倍, 并增加其种群密度和多样性, 改变甲烷氧化菌群落组成^[35]。在好氧土壤环境中, 蚯蚓排泄物中含有丰富的可降解C, 使得微生物大量繁殖, 微生物呼吸为产甲烷菌创造了适宜的厌氧生境, 从而加速产甲烷菌的生长繁殖^[33]。

2.2.3 与其他土壤动物的互作 蚯蚓和其他土壤动物, 如线虫、甲虫、跳虫、螨类以及其他土壤节肢动物之间存在竞争、共生和捕食等相互关系。蚯蚓在短时间内能使土壤线虫数量显著减少, 而且蚯蚓密度越大, 对线虫(尤其是食菌线虫)数量的影响越显著; 随着时间延长和线虫的逐渐适应, 蚯蚓对线虫群落的影响逐渐减弱^[78-79]。Monroy等^[80]研究表明, 表栖蚯蚓*E. foetida*在凋落物分解初期会显著增加土壤节肢动物数量, 尤其是跳虫和螨类。外来蚯蚓(*Dendrobaena octaedra*, *L. terrestris*)入侵, 则会降低土壤中小型节肢动物多度, 改变甲螨类群落组成^[81]。捕食性甲虫能驱赶蚯蚓至深层土壤中, 增强蚯蚓对土壤物理性质、养分循环的影响^[82]。土壤动物群落组成和功能的变化, 会进一步改变其在土壤C、N的矿化中的作用, 影响土壤温室气体的排放^[83]。

2.2.4 与植物的互作 蚯蚓活动因加速有机质矿化、改善土壤理化性质而有利于植物生长^[84]。蚓粪营养物质丰富, 为植物生长提供N和P等养分来源^[85], 促进植物N吸收^[86], 提高植物生产

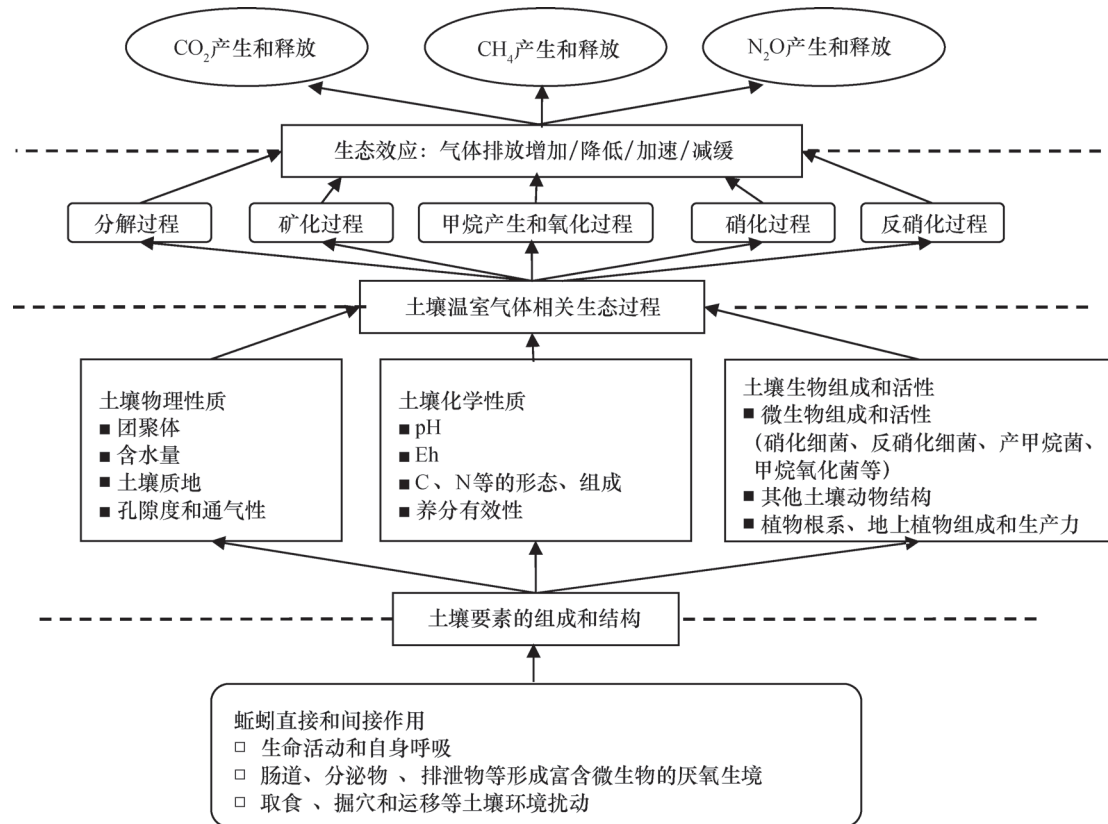


图1 蚯蚓对土壤温室气体排放的影响机制

Fig.1 Mechanism of earthworms affecting emission of greenhouse gases from soil

量^[87]，并能有效防止盐分胁迫的发生^[88]。热带内栖蚯蚓*P. corethrurus*活动促进热带果树的生长^[67]和作物产量增加^[89]。加拿大白杨林中蚯蚓*D. octaedra*入侵使草本植物地上生物量增加^[90]。植物生长状况和生物量的改变，将直接影响到植物根系的呼吸和植物根际环境，改变土壤温室气体排放的量和动态，但目前还缺少影响机制研究。

2.2.5 不同生态类群蚯蚓的互作 根据生活习性和功能的不同，蚯蚓通常被分为3个功能类群，即深栖类（Anecic）、内栖类（Endogeic）、表栖类（Epigeic）。表栖类，一般居住于土壤与凋落物交接的表层几厘米土层，以土表新鲜的有机植物残体为食并将地表凋落物混入土壤中，加速凋落物的分解^[91]；内栖类，常生活于较深的10~15 cm土层中，以土壤有机质为食物来源，挖掘水平洞穴能力强，常以非永久性水平洞穴为主；深栖类，常居于更深的土壤层中，以挖掘永久性垂直洞穴为主，取食土壤表层半分解植物残体并将凋落物与更深的土层混合^[92-94]。栖居特征和取食习性不同，使得不同生态类群的蚯蚓在土壤物质循环过程中扮

演不同的角色，具有不同的生态功能。

不同类群蚯蚓各自对土壤的改造活动，能够改变其他类群蚯蚓的土壤生境条件和对土壤资源利用的有效性。不同类群间的交互作用对土壤 N_2O 产生和释放有显著影响^[5, 40]。不同类群的蚯蚓共存，会相互影响蚯蚓洞穴系统结构，如内栖蚯蚓能促进深栖蚯蚓掘穴活动的增加^[95]。不同类群的蚯蚓相互作用，可促进土壤C矿化和 CO_2 的释放^[22, 96]。Crumsey等^[27]培养实验表明，前45天，内栖蚯蚓*A. trapezoides*与表栖蚯蚓*E. foetida*共同作用能使土壤 CO_2 通量增加30%，而任一单一种类蚯蚓却没有影响。不同类群间的相互作用，还能影响地上植物对土壤N的吸收^[40]。内栖蚯蚓可以直接利用深栖蚯蚓洞穴内所存储的有机物质、促进 N_2O 产生，而内栖蚯蚓在利用表栖蚯蚓洞穴和其中的有机物质的同时，其排泄物会堵塞洞穴、影响表栖蚯蚓的活动，对 N_2O 产生和释放不利^[40]。

2.3 蚯蚓对产生温室气体的相关生态过程的调控

2.3.1 分解过程 蚯蚓活动促进土壤微生物生长繁殖，增强微生物活性，改变微生物群落组成，

调节有机质分解过程^[14]。某些种类的蚯蚓(如, *P. corethrurus*)可以通过取食和消化,直接促进有机质的分解^[97]。蚯蚓对有机质分解的作用与蚯蚓生态类群、有机质种类和地理位置有关^[14]。Haimi和Huhta^[98]对西欧亚寒带针叶林土壤中凋落物分解的研究表明蚯蚓显著促进了针叶树凋落物的分解。Liu和Zou^[97]发现外来入侵蚯蚓促进热带牧场和森林落叶的分解,而对根的分解没有影响。但Decaëns等^[99]在哥伦比亚野外实验研究表明本地蚯蚓*Martiodrilus carimaguensis*降低牧草凋落物的分解速率,Araujo等^[100]实施的97 d室内控制实验研究发现蚯蚓对热带森林凋落物的分解没有明显影响。

2.3.2 矿化过程 蚯蚓取食土壤有机质,经过消化、排泄使其分解为简单有机化合物或发生矿化释放矿质养分^[101]。蚯蚓还通过促进微生物对有机质的矿化,来增加土壤C、N的释放^[96, 102-105]。蚯蚓取食土壤微生物可加速微生物生物量氮(Microbial Biomass Nitrogen, MBN)的矿化,提高土壤矿质N含量^[98, 100]。当有外源N输入,提高土壤N供给时,蚯蚓活动会显著提高土壤N的矿化潜力^[106]。

然而,蚯蚓取食、掘穴等活动使有机质混入土壤并形成大的土壤团聚体,以及蚯蚓排泄物形成的微团聚体具有稳定的结构,对土壤有机质(Soil Organic Matter, SOM)形成物理保护,可以避免SOM的迅速矿化和C的释放^[107],从而提高土壤碳的稳定性^[62, 108-109]。但是在没有碳输入(如秸秆还田)的土壤中,蚯蚓活动会持续消耗有机质并在蚓粪中发生矿化,降低土壤C含量^[110]。秸秆还田有利于促进蚯蚓固碳作用的发挥^[111]。

2.3.3 硝化和反硝化过程 蚯蚓往往通过增强微生物活性来促进土壤硝化和反硝化作用,这一过程可以加速 N_2O 产生和释放,也可以促进 N_2O 分解和消耗,因而蚯蚓对土壤 N_2O 排放的影响为对二者的平衡结果。

蚯蚓体内的反硝化细菌,可使土壤 N_2O 排放量升高16%~33%^[9, 64]。蚯蚓取食和挖掘洞穴等活动,改变土壤结构和通气性能,创造有利于反硝化作用的环境条件,影响土壤 N_2O 的排放^[25, 112]。表栖蚯蚓的觅食过程使其周围的土壤被压实,形成有利于微生物活动的好氧或厌氧环境,促进硝化、反硝化或硝化细菌的反硝化作用进行,进而产生 N_2O ;相反,内栖蚯蚓洞穴较小,压实作用不

明显, N_2O 的产生和增加也不显著^[40]。蚯蚓活动也能加速土壤 N_2O 分解和消耗。蚯蚓的取食、掘穴等活动提高土壤孔隙度、促进土-气界面的气体交换,使土壤中 N_2O 分解作用进行得更为彻底,最终以 N_2 的形式释放到大气中,从而降低土壤 N_2O 排放^[113]。在含水量高的土壤中,蚯蚓活动性增强能显著提高反硝化细菌的活性,使 N_2O 被充分分解为 N_2 而降低 N_2O 排放^[47];深栖蚯蚓将凋落物搬运至深层土壤中,充分的有机物质供给促使深层 N_2O 完全转化,同时深层 N_2O 沿土壤剖面向上运移过程中也会逐渐转化为 N_2 ,进而降低土壤 N_2O 释放量^[114]。

2.3.4 CH_4 产生和氧化过程 在土壤淹水或水分过饱和等厌氧环境中,产甲烷菌厌氧消化有机质产生 CH_4 ,并经由维管束植物或土壤孔隙直接排出;而在好氧环境中,甲烷氧化菌消耗 CH_4 生成 CO_2 。土壤 CH_4 的产生和释放是这两个过程平衡的结果^[115]。内栖蚯蚓*A. turgida*在水分饱和土壤中,能促进甲烷氧化菌的生长而消耗产甲烷菌产生的 CH_4 气体,从而降低 CH_4 净排放量^[35]。在通气状况良好的土壤环境中,蚯蚓取食、消化和排泄促使产甲烷菌生长繁殖,提高其活性,从而促进 CH_4 的产生^[33]。在垃圾填埋场生物覆盖层中添加蚓粪能增加甲烷氧化菌的密度和多样性,促进 CH_4 氧化而降低排放^[4, 6-7, 116]。

3 研究展望

尽管目前已有较多的研究证明了蚯蚓及其活动对土壤温室气体排放的影响,但整体而言,研究仍主要集中在对“现象”揭示,还缺少对“机理”的深入探讨。建议今后应加强如下几方面的研究:

(1) 重视蚯蚓生物学特性研究

对蚯蚓繁殖特征和取食、挖掘和扩散等行为特性的生物学研究,是深入揭示蚯蚓生态功能的基础^[55]。例如,蚯蚓能改变土壤微生物群落组成和结构,但其对微生物的取食具有选择性^[23];同时蚯蚓的活动具有水分、时间限制性^[25, 39, 47]等。明确不同类群蚯蚓对土壤环境的需求和对环境胁迫的响应与适应,是合理评估不同类群蚯蚓对土壤温室气体排放影响的基础。深入研究不同生态类群蚯蚓与其“蚓触圈”土壤的孔隙度、营养分布格局、颗粒组成、温湿度、微生物和地上植物组成及根际环境的交互作用,将蚯蚓放在土壤生态系统的尺度

内, 研究蚯蚓类群-土壤理化环境-食物网关系, 合理揭示其对土壤温室气体排放的影响。加强同一土壤系统中, 不同类群蚯蚓的交互作用研究。特别加强和重视, 在地上植物和其他土壤动物共存环境下的模拟和控制实验。

(2) 加强蚯蚓对土壤 CH_4 排放的影响和对 CO_2 和 N_2O 排放影响的机制研究

尽管 CH_4 的增温潜力较高^[67], 但 CH_4 多在厌氧(如淹水)环境(如水稻田、沼泽和湿草甸)中产生, 常被认为不适合蚯蚓生存而很少有研究涉及^[3]。实际上季节性淹水的湿地(如季节性淹水的洪泛草甸)中也有一定数量蚯蚓定居, 且对环境具有更强的敏感性^[117-118]; 而且蚯蚓已经被广泛应用到人工湿地中^[119-120]。所以, 今后研究应关注蚯蚓对 CH_4 等其他温室气体排放的影响, 并从甲烷产生、氧化和排放等过程揭示其作用机理。

目前研究主要集中在蚯蚓影响土壤 CO_2 和 N_2O 排放速率和累积排放量的“现象”研究, 缺少对相关机理的深入揭示。今后, 需要关注蚯蚓影响土壤 CO_2 和 N_2O 排放的以下相关要点: 蚯蚓生态类群功能差异, 不同生态类群蚯蚓间的交互作用, 植物残体与蚯蚓的交互作用, 不同生态类群蚯蚓对土壤团聚体结构和颗粒组成等物理性质的影响, 蚯蚓“蚓触圈”土壤微生物结构特性, 蚯蚓对其他土壤动物(线虫, 跳虫, 螨类和线蚓等)的影响及其交互作用, 蚯蚓对地上植物根际环境的影响等内容。

(3) 加强系统研究, 综合评估蚯蚓对土壤温室气体源汇功能的净作用

蚯蚓对土壤温室气体排放的影响, 不仅是众多生态过程的综合结果, 也是蚯蚓众多生态功能的一个环节。蚯蚓活动促进土壤 CO_2 产生和释放的同时^[121], 也产生稳定的土壤微团聚体增强土壤C的稳定性, 综合评估两方面的影响, 才能合理阐释蚯蚓对土壤C的净固定量^[122]。相似的, 蚯蚓活动一方面能够激化微生物活性, 促进土壤硝化和反硝化作用, 加速 N_2O 产生和释放; 另一方面, 也能通过提高土壤通气性和氧气含量, 促进 N_2O 进一步分解和消耗。同理, 蚯蚓活动能够通过调节产甲烷菌和甲烷氧化菌的活性, 既能促进 CH_4 的产生, 又能加速 CH_4 的氧化。因而, 合理评估蚯蚓对土壤C和N贮量的影响, 需要综合考虑蚯蚓对温室气体“源”和“汇”作用的平衡。

(4) 室内模拟和田间原位实验相结合的长期

大尺度研究

由于室内培养实验条件易于控制, 目前关于蚯蚓生态功能的研究以室内模拟为主。而模拟条件与野外实际的环境差距较大; 模拟实验结果可能放大或缩小蚯蚓的作用, 阻碍了相关结论向野外条件的推算。因此, 要加强多因子的协同和交互作用实验, 提高室内培养实验的科学性; 同时, 加强室内模拟实验与田间原位实验相结合, 深入揭示蚯蚓的作用及其机制。

同时, 由于蚯蚓改变土壤环境需要一定的作用时间, 土壤系统对蚯蚓活动的适应和平衡也需要一个过程。例如, 短时间内, 蚯蚓活动常促进土壤有机质矿化和植物生长, 但随着时间延长, 则可能会增加土壤养分流失, 降低植物初级生产力^[123]。又如, 蚯蚓活动使土壤 CO_2 和 N_2O 排放量先显著增加, 之后又显著降低^[25, 39]。因此, 开展长期实验研究是系统揭示蚯蚓生态效应的重要手段。此外, 目前的研究是分散的、“点”状的研究(表1), 尚缺乏“带”状、“面”状的区域研究。例如, 在区域内确立沿温度带、干湿带、垂直带的研究网络, 系统探讨蚯蚓对土壤温室气体的作用。甚至根据蚯蚓的入侵(如, 蚯蚓欧洲种入侵到美洲), 开展跨大洲的大尺度的比较研究。

(5) 综合应用同位素和分子等研究手段

同位素技术已经被广泛运用到生态学各个领域, 尤其是食物网、生态系统物质循环的研究中, 并对野外实验尤为有利^[102]。目前, ^{13}C 和 ^{15}N 示踪, 在研究蚯蚓的取食策略和营养关系方面应用较为成熟^[124-117], 并逐渐被用于探讨蚯蚓与土壤C、N周转^[21, 128]和土壤温室气体排放的关系^[5, 91]。同位素方法, 已经成为定量区分土壤温室气体中碳、氮来源和揭示蚯蚓和非生物驱动因子的重要手段, 但整体研究仍处于起步阶段。同位素技术和分子技术的耦合应用, 例如磷脂脂肪酸(PLFA)-同位素技术(Stable Isotope Probing, SIP)、DNA-SIP和焦硫酸测序(Pyrosequencing)等方法, 可以有效确定蚯蚓穴中对有机质起降解作用的特定微生物和小型土壤动物类群^[68, 129], 为深入揭示蚯蚓对土壤微生物和其他类群土壤动物的调控作用提供技术支持。由于蚯蚓与土壤 N_2O 的产生和释放关系密切并受到广泛关注^[3], 运用分子手段尤其是高通量测序来研究硝化和反硝化过程中的功能菌种类组成、多样性和丰度, 对深入探索蚯蚓作用的内在

机理有重要价值。

(6) 关注污染土壤环境中蚯蚓对温室气体排放的作用

土壤污染是当前所面临的严重问题, 农药、化肥的施用以及养殖、农村生活污水等造成的农业面源污染、固体废弃物污染等, 是造成土壤污染的重要原因^[130-131]。有研究显示土壤污染对蚯蚓的生理生态特征具有重要影响。李志强等^[132]发现, 当土壤中 Cu^{2+} 浓度 $> 60 \text{ mg kg}^{-1}$ 时对蚯蚓的生长具有抑制作用, 超过 100 mg kg^{-1} 后铜污染浓度提高与污染接触时间延长均会加剧抑制程度, 严重时出现负增长; 宋玉芳等^[133]研究表明Cu、Zn、Pb、Cd单一及复合污染对蚯蚓具有急性致死及亚致死效应; 此外, 石油烃污染会导致蚯蚓产生回避行为或中毒死亡^[134], 苯并[a]芘、农药污染会使蚯蚓体腔细胞抗氧化酶活性下降^[135-136]。土壤污染对蚯蚓的毒性效应, 会直接影响其代谢速率、活动性、密度和群落结构, 进而使其生态功能发生变化, 间接影响土壤温室气体排放。因此, 污染土壤环境中蚯蚓对温室气体排放的作用在未来的研究中应加以关注。

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ADVANCEMENT IN STUDY ON EFFECT OF EARTHWORM ON GREENHOUSE GAS EMISSION IN SOIL AND ITS MECHANISM

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Abstract Soil is an important source and sink, as well, of greenhouse gases (GHGs). Earthworms are a major component of the soil fauna, and a soil animal the highest in biomass in the soil. Being termed as soil ecosystem engineers, they play an crucial role in formation of soil physical-chemical properties and structure and in recycling of soil matter and nutrients through their feeding, burrowing and casting activities, thus directly or indirectly affecting the generation and emission of GHGs (CO₂, N₂O and CH₄) in the soil. On one hand, the respiration of earthworm is an important part of soil respiration; in micro-environments, like guts, exudate, digesta and feces, anaerobic conditions, proper moisture content and rich C and N supply are favorable to growth and multiplication of denitrifying bacteria, thus greatly increasing biomass and activity of the bacteria, which in turn stimulates the emission of N₂O during the process of denitrification (N₂O 2.5 ~ 25 ng h⁻¹ g⁻¹ fresh earthworm), as is shown in recent studies. And N₂O emission is higher from earthworm feces than from the soil in its surroundings. On the other hand, through feeding, burrowing and excreting, earthworms also cause changes in soil properties, composition and activity of soil microbes and some other ecological processes (e.g. decomposition, nitrification and denitrification), thus

indirectly affecting GHGs emission. The activity of earthworms in the soil helps mix soil with plant residues and reshape soil pores and aggregates, thereby affecting soil moisture dynamics, aeration and content and availability of nutrients. Aerobic and anaerobic micro-environment within earthworm-made aggregates may also have some effect on decomposition and denitrification. Moreover, the macroaggregates formed by earthworms through their activities, in the long run, help C sequestration in microaggregates. Earthworms help blend plant residues with soil in their guts by feeding, thus expanding contact between microbes and organic matter, and alter composition and structure of the microbial community through their digestion and excretion processes. The interactions between earthworms and denitrifying and methanotrophic microbes cause formation of “drilosphere”, where N_2O emission increases and CH_4 emission decreases. These effects are usually affected by soil moisture content, organic matter content and earthworm species. Based on their feeding and burrowing behaviors, earthworms are typically divided into three ecological groups: epigeic, endogeic and anecic species. Because of the differences in food accessibility and in distance the gases have to go through from the soil to the atmosphere, the three groups of earthworms differ sharply in ecological function, and the interactions between the groups make the effects on soil GHGs more complex. Besides, earthworm activities may also affect other soil fauna, such as mites, collembola, nematodes, isopods, enchytraeids, etc. in biomass and activity in their habitats. By the above-described indirect means, earthworms alter composition, structure and functions of the soil ecosystem. However, little is known about the effects of earthworm-plant interactions on GHGs balance in the soil. Besides, further researches are needed to fully understand interactions between different ecological groups of earthworms. To sum up, earthworms affect CO_2 , CH_4 and N_2O emissions mainly by regulating the ecological processes of carbon and nitrogen, such as decomposition, mineralization, nitrification, denitrification, methanogenesis and methanotrophy. Effects of earthworms on emission of GHGs have attracted more and more attention. Although much research has been done on the impacts of earthworms on soil CO_2 and N_2O emissions, little has been reported on CH_4 efflux. In view of the serious soil pollution problems, it is essential to unfold studies on changes in effects and potential role of earthworms in polluted soils. As for research techniques, current studies are still mainly based on short-term indoor incubation and simulation of one-factor environment. As the in-lab manipulated and simplified environments are far from good enough to reflect accurately the real conditions of the nature, it is urgent to start long-term in-situ field experiments and multi-environmental factor interaction experiments, because the functions of earthworm in the soil vary with the seasons; In addition, molecular and isotope tracing techniques have become available as effective tools for studies to expose biological and ecological mechanisms of earthworms' effects on emissions of GHGs. It is essential, in future, to pay more attention to interactions of the different ecological groups of earthworms with soil properties, composition of soil microbes, other species of soil animals and plants growing on the surface of the soil, to intensify the study on mechanisms with stress on changes in earthworms' function in polluted soils; to review comprehensively the effects of earthworms on emission of GHGs from the soil and carbon sequestration in the soil; to scientifically evaluate the effects of earthworm activities promoting or mitigating emissions of C and N from the soil.

Key words Soil fauna; Ecosystem engineer; N_2O ; CH_4 ; Ecological process

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Cover Picture: Reclamation of a highly saline-sodic wasteland of takyric solonetz while cropping *Lycium barbarum* L. with drip irrigation (by Zhang Tibin)

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