•研究报告•

施氮水平影响蚯蚓介导的番茄生长及抗虫性

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摘要: 过量施用氮肥不仅导致严重的生态环境问题, 还会限制土壤生物驱动的生态系统服务功能。蚯蚓的取食和掘穴等活动可以促进土壤肥力和植物生长, 进而影响植物与病虫害的关系。了解氮肥与害虫作用下蚯蚓对植物抗虫性的影响, 有助于揭示土壤动物的生态功能调控机制。采用蚯蚓(威廉腔环蚓*Metaphire guillelmi*)、西花蓟马(*Frankliniella occidentalis*)和氮肥用量的三因子完全交互设计, 利用番茄(*Lycopersicon esculentum*)盆栽实验探索了不同氮水平下蚯蚓对番茄生长及对植食者抗性的影响。结果表明, 在低氮条件下蚯蚓显著降低了番茄茎叶干生物量、根系干生物量及茎叶可溶性糖含量, 而茎叶的茉莉酸和水杨酸含量分别是无蚯蚓对照的 6 倍和 3 倍, 且伴随着西花蓟马数量下降了 58%。在高氮水平时, 蚯蚓未影响番茄茎叶茉莉酸、茎叶水杨酸含量及西花蓟马数量。蚯蚓介导的番茄营养物质(茎叶可溶性糖和茎叶全氮)和防御信号物质(茎叶茉莉酸和茎叶水杨酸)含量分别与西花蓟马数量呈显著的正相关和负相关。总之, 氮肥施用改变的土壤氮有效性通过改变植物资源和防御物质含量转变了蚯蚓介导的植物抗虫性响应; 全面了解土壤生物对植物生长的影响需要综合考虑土壤管理–土壤动物–植物病原物三者之间的关系。

关键词: 土壤动物; 植物化学组成; 害虫; 地上和地下部; 生态系统服务

Nitrogen levels modify earthworm-mediated tomato growth and resistance to pests

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Abstract: Excessive chemical nitrogen (N) fertilizer application causes serious environmental problems and affects the ecosystem services that depend on soil biota. Earthworms improve soil fertility and plant productivity via activities such as feeding, burrowing and casting, and alter the relationships between crop plants and pests by modifying plant primary and secondary productivity. In order to mechanistically understand the functional roles of soil fauna in ecosystem services, a pot experiment using tomatoes (*Lycopersicon esculentum*) was conducted in a greenhouse. The study used a complete factorial design that manipulated earthworm (*Metaphire guillelmi*) abundance, western flower thrips (*Frankliniella occidentalis*) and N input. Results showed that under low N-input conditions, earthworms significantly reduced shoot and root biomass and shoot soluble sugar content, and increased shoot jasmonic acid content (by 6 times) and shoot salicylic acid content (by 3 times), compared to treatments without earthworms. This was accompanied by the decrease of thrips abundance by 58%, indicating a remarkable suppression of aboveground pests by earthworms. However, under high N-input conditions, earthworm presence did not affect the contents of shoot jasmonic acid or shoot salicylic acid or thrips abundance by the end of the experimental period (45 days). The earthworm-mediated responses of plant nutrition (shoot soluble sugar and shoot total nitrogen)

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was significantly positively correlated with thrips abundance, whereas defense (shoot jasmonic and salicylic acid) was significantly negatively correlated. Changes to soil N availability due to N fertilizer input can shift the direction of earthworm-mediated plant resistance against herbivores by altering plant resource acquisition and secondary defense. Effects of earthworms on plant growth and resistance depend on soil management practices such as N fertilizer application. A comprehensive understanding of the roles of soil biota in mediating plant growth requires knowledge of the multifaceted relationships among soil management, soil fauna, and plant pathogens.

Key words: soil fauna; plant chemistry; pests; aboveground–belowground; ecosystem service

随着人口增长引起的农产品需求增加, 高强度集约化管理正成为促进农业生产的重要手段(Bommarco et al, 2013; 徐炜等, 2016)。然而, 高强度土地利用方式会导致土壤生物多样性丧失和生态系统服务功能受损(Tsiafouli et al, 2015; 潘开文等, 2016)。此外, 过量施用化肥也是降低作物抗病虫能力及导致病虫害暴发的主要因素(Larbat et al, 2012); 化学肥料施用引发的农药依赖性增强的反馈作用会进一步破坏生态平衡, 使人类的生产活动及人类健康与生态环境走向恶性循环(Aurélien et al, 2013; Bender et al, 2016)。在保护生态环境和农业可持续发展的要求下, 挖掘土壤生物的有益功能, 加强对植物–土壤生物之间互作关系的认识, 以减少对化肥农药的依赖, 指导病虫害综合管理和促进生态农业发展。因此, 系统了解关键土壤生物的生态功能及其对植物生长和抗虫性的影响机制, 显得尤为迫切且重要。

自然界的植物在生长过程中往往遭受植食者的取食压力, 在与植食者协同进化的过程中, 植物会进化出各种策略以提高自身的防御能力(Kempel et al, 2011)。土壤施肥措施特别是氮肥施用引起的土壤养分变化又调控着植物对植食者的抵抗能力(Bogaert et al, 2017)。氮素直接参与植物体内的生理生化过程并改变植物体内的组织液成分, 影响植物的营养组成(氨基酸和糖类等), 最终影响植食者的取食和植物的防御响应, 如土壤的高氮水平会使得植物体含氮量高、提高植物对害虫的适口性(Staley et al, 2010); 而氮素匮乏会导致植物因缺乏营养而不能正常生长甚至降低自身抗性引发害虫取食(Shokoofa & Emam, 2008)。越来越多的研究表明, 土壤生物对地上部系统从个体到群落及功能水平上均起着调控作用(傅声雷, 2007; 王邵军和阮宏华, 2008; Korres et al, 2016)。土壤生物能够直接或间接调控根系这一枢纽进而对植物地上部性状产生影

响(吴纪华等, 2007; Bardgett & van der Putten, 2014; Schädler & Ballhorn, 2017)。例如, 研究发现菌根真菌、根际促生菌等能促进植物的生长并调控植物抵御病虫害的能力(Aurélien et al, 2013; Tao et al, 2016)。已有的蚯蚓方面的研究表明, 蚯蚓可以促进植物对养分的吸收(Zhang et al, 2010), 其对植物促生效应的大小与方向还取决于土壤氮素水平(van Groenigen et al, 2014)。虽然蚯蚓对植物抗虫性的影响也取决于氮素水平, 但是却缺乏足够的实验证据。

一般认为提高土壤氮素有效性是蚯蚓促进植物生长或生产力的最主要机制(Bertrand et al, 2015)。荟萃分析归纳出蚯蚓影响植物生长的效果在土壤氮素贫瘠时更明显(van Groenigen et al, 2014)。值得注意的是, 蚯蚓提高植物氮含量的同时也导致以其为宿主的病虫害的发展(Wurst et al, 2010a)。氮素水平还能够改变植物用于防御的次生代谢物质的合成(Wurst et al, 2004), 间接影响植食者的取食及行为(Poveda et al, 2005; Loranger-Merciris et al, 2012)。植物次生代谢物质总酚、信号分子茉莉酸和水杨酸可以诱导一系列抗逆信号传导和防御反应, 可以抵御虫害(Caarl's et al, 2015)。研究者发现, 蚯蚓可提高植物生物量及养分含量, 增加植物耐受植食者的取食胁迫(Blouin et al, 2005)。最近的荟萃分析也表明了蚯蚓介导的植物抗性的资源分配模式受到植食者类型及土壤养分等因素的影响(Xiao et al, 2018)。迄今, 有关蚯蚓对植食者影响的研究多集中在刺吸者蚜虫上, 蚯蚓可以刺激抗性防御物质的产生, 从而降低蚜虫的数量(Lohmann et al, 2009)。有关蚯蚓对其他类型害虫影响的研究仍缺乏, 限制了对蚯蚓–植物关系调控作用的全面认识。蚯蚓影响植物生长和防御抗性的效应大小和方向会因各种生物和环境条件而变(Wurst, 2013)。依据生长–抗性权衡假说, 我们推测蚯蚓介导的植物生长与抗性之

间的关系会依赖于土壤氮素水平, 氮素水平高低导致的植物能量储备差异使植物生长和抗性关系发生变化(Züst & Agrawal, 2017)。例如, 当土壤氮素匮乏时, 蚯蚓可促进矿化过程来缓解植物养分限制, 相应地, 植物储备能量的增加也提高了合成抗性物质的能力; 当氮素充足时, 植物生长速率较快, 相应合成的抗性物质含量较低, 在此条件下高植食压力发挥主导作用, 而高氮施用带来的蚯蚓摄取食物的元素不均衡及土壤结构和性质的改变, 可能会造成蚯蚓生理胁迫, 使蚯蚓对植物生长和抗性的影响均较弱(Brown et al, 2004; Mundim et al, 2017; Zheng et al, 2018)。

西花蓟马(*Frankliniella occidentalis*)是全球最重要的检疫性害虫之一, 严重危害蔬菜作物, 它以锉吸式口器取食植物的茎叶及花果, 严重时导致植物枯萎死亡(吕要斌等, 2011), 其对植物的破坏作用并不亚于在蚯蚓研究中普遍关注的蚜虫。特别是考虑到植食者与植物的相互关系在不同取食类型的植食者间存在明显差异(Xiao et al, 2018), 因此有必要了解更多植食者种类下蚯蚓的作用机制和影响因素。基于比较施氮量对蚯蚓介导的番茄生长及其对西花蓟马抗性的影响, 探究蚯蚓介导的植物生长及防御作用的影响, 旨在系统地了解蚯蚓的生态服务功能及植物抗虫性调控机制, 指导农业的绿色发展。

1 材料与方法

1.1 土壤的采集

土壤采自江苏省如东县农业生态功能调控研究基地的多年蔬菜地(120°42' E, 32°12' N), 属亚热带季风气候, 年平均气温15°C, 年均降水量1,042 mm。供试土壤为粘壤土, 取样深度为0–20 cm。鲜土采集后过5 mm 筛, 剔除大型土壤动物及根茬等残体。土壤质地为6.48%黏粒, 63.55%粉粒, 29.97%砂粒, 土壤pH值(水土比2.5: 1)为7.75, 土壤硝态氮含量为22.32 mg/kg, 铵态氮含量为0.96 mg/kg, 总有机碳和全氮含量分别为10.73 g/kg和0.52 g/kg。

1.2 实验设计和布置

采用3因子, 即蚯蚓、西花蓟马(western flower thrips, WFT)和氮肥用量的交互实验设计, 设置不施氮(0 kg N/ha) vs. 施高氮(240 kg N/ha), 获得土壤低氮(Low N)和高氮(High N)两个水平, 施高氮处理的施肥量为240 kg N/ha 的尿素, 地上部植食者

(–WFT = 无西花蓟马, +WFT = 接种西花蓟马)、蚯蚓(E0 = 无蚯蚓, E1 = 接入威廉腔环蚓(*Metaphire guillelmi*)) 3个因子, 重复6次, 总共 $2 \times 2 \times 2 \times 6 = 48$ 盆。

供试植物为番茄(*Lycopersicon esculentum*), 品种为“世纪红冠”, 具有抗病性及耐热性好、高抗番茄花叶病毒叶霉病、枯萎病和灰霉病等特性。挑选饱满番茄种子, 用10%的H₂O₂浸泡30 min进行表面灭菌并清洗, 在无菌水中浸泡12 h, 然后将番茄种子置于湿纱布中25°C下培养3 d发芽, 长至幼苗待用。供试西花蓟马由山东省农业科学院植物保护研究所提供。

盆栽实验在人工气候室中进行(温度25 ± 1°C, 光照时间16 h, 光照强度15,000 lux)。每盆装1.5 kg干重当量的土壤, 调节含水量为饱和持水量的60%, 并在25°C黑暗条件下培养1周。供试蚯蚓为从深层种向内层种的过渡类群, 现习惯称为内层种, 蚯蚓采集与盆栽土壤的采集地点相同。选择大小及生物量相近的蚯蚓清洗表面, 48 h排空肠道后洗净并称重(Dalby et al, 1996)。基于蚯蚓采集地田间密度(105条/m²), 蚯蚓的接种量为每盆3条总共10 ± 0.43 g, 各处理具体接种量见表1。当番茄幼苗有3片完全叶时移栽入盆, 所有盆钵每周随机换位3次以最小化位置效应, 每2 d浇50 mL蒸馏水。待番茄生长30 d时接入西花蓟马, 用软毛刷刷取成虫20头至2 mL离心管内待用, 雌雄比为1:1。每株番茄选择两片靠近顶端的叶片进行接种, 即每盆接种40头蓟马, 用250目纱网罩封住已接虫叶片, 防止西花蓟马逃逸。

1.3 采样和保存

西花蓟马接种15 d后进行破坏性采样。整个盆栽实验周期持续45 d, 采样时先将西花蓟马从接虫叶片上用吸虫管收集并计数。番茄植株地上部茎叶和地下部的根系及土壤等分别采集。采样时番茄根系几乎分布于整个土体。主要测定指标包括西花蓟马的数量、番茄营养物质、番茄防御物质及信号物质等。

1.4 分析方法

植株全氮采用 H₂SO₄-H₂O₂法消解, 凯氏定氮法测定(鲁如坤, 2000)。植株激素用高效液相色谱-串联质谱法(Hettenhausen et al, 2013)测定: 称取样品液氮研磨, 加入交联聚乙烯吡咯烷酮(PVPP)和乙酸乙酯冰浴超声后离心, 转移上清液到新离心管, 氮

表 1 不同处理下威廉腔环蚓的数量及生物量变化
Table 1 Changes in biomass and number of *Metaphire guillelmi* under different treatments

处理 Treatments		接种时 Inoculation time		采样时 Sampling time		蚯蚓失重率 Weight loss of the earthworm (%)
		数量 Number	生物量 Biomass (g)	数量 Number	生物量 Biomass (g)	
无西花蓟马 -WFT	低氮 Low N	3	10.49 ± 0.27	3	9.19 ± 0.34	12.39
	高氮 High N	3	10.35 ± 0.24	3	8.63 ± 0.47	16.62
接种西花蓟马 +WFT	低氮 Low N	3	10.19 ± 0.19	3	8.52 ± 0.22	16.39
	高氮 High N	3	10.27 ± 0.26	3	7.85 ± 0.66	23.56

Low N, 0 kg N/ha urea; High N, 240 kg N/ha urea.

吹浓缩, 加入70% 甲醇涡旋后离心, 将上清液过0.22 μm滤膜, 保存待测。植株酚类的测定采用福林酚比色方法(Ainsworth & Gillespie, 2007): 取20 mg 植株研磨成粉, 加95% 甲醇后黑暗浸提。离心后取上清液到新离心管, 添加斐林试剂和Na₂CO₃后室温黑暗反应2 h, 读取其在波长765 nm处的吸光值。

土壤全氮以半微量凯氏法测定。土壤微生物生物量碳(MBC)和土壤微生物生物量氮(MBN), 采用氯仿熏蒸法测定。土壤可溶性有机碳(DOC), 称取新鲜土壤于浸提瓶中加入超纯水振荡, 离心过滤膜稀释后用 TOC 仪(Elementar, Germany)测定。利用连续流动分析仪(SKALAR San++, Holland)测定土壤铵态氮和硝态氮含量。

1.5 数据分析

运用R 3.3.2软件进行数据分析与作图, 利用Kolmogorov-Smirnov和Levene方法检验数据的正态分布及方差异质性。采用多因素方差分析估计蚯蚓、氮素以及植食者因素对番茄生长和植物化学组成等指标的影响。通过Pearson’s相关性计算防御物质茎叶茉莉酸、茎叶水杨酸与西花蓟马数量之间的关系。

表 2 蚯蚓、氮素及植食者因素对土壤硝态氮、铵态氮、微生物生物量碳含量和微生物生物量氮含量影响的方差分析结果
Table 2 ANOVA results showing the effects of earthworm, nitrogen and herbivore on the contents of NO₃⁻-N, NH₄⁺-N, microbial biomass carbon and microbial biomass nitrogen in soils

变量 Variables	蚯蚓 Earthworm (E) (df = 1)	氮素 Nitrogen (N) (df = 1)	西花蓟马 Thrips (WFT) (df = 1)	E × N (df = 1)	E × WFT (df = 1)	N × WFT (df = 1)	E × N × WFT (df = 1)
硝态氮 NO ₃ ⁻ -N	18.49***	87.43***	8.21**	18.02***	3.51	6.67*	3.68
铵态氮 NH ₄ ⁺ -N	4.07	2.06	10.82**	1.91	27.26***	0.00	0.28
微生物生物量碳 Microbial biomass carbon	10.35**	1.00	60.26***	2.66	0.99	15.51***	2.00
微生物生物量氮 Microbial biomass nitrogen	11.94**	0.38	2.69	0.84	3.90	2.44	23.70***

* P < 0.05, ** P < 0.01, *** P < 0.001.

2 结果

2.1 土壤性质变化

蚯蚓对土壤矿质氮、微生物生物量的影响取决于氮素水平和西花蓟马(表2)。低氮时蚯蚓对土壤硝态氮含量无影响, 高氮时降低了硝态氮含量(图1)。在没有西花蓟马时, 蚯蚓增加了铵态氮含量, 接种西花蓟马后, 蚯蚓反而降低了铵态氮含量。接种蚯蚓增加了土壤微生物生物量氮, 但降低了微生物生物量碳含量(图1)。

2.2 番茄生长及营养物质变化

蚯蚓对番茄生物量及营养物质的影响与氮素水平和西花蓟马有关(P < 0.05, 表3)。蚯蚓和氮素的交互作用显著影响根系生物量和茎叶可溶性糖含量, 低氮时蚯蚓降低根系生物量和茎叶可溶性糖, 而高氮下无影响(表3, 图2)。蚯蚓作用增加了番茄茎叶全氮含量, 但降低了根系全氮含量(图2)。

2.3 番茄防御物质含量和西花蓟马数量的变化

蚯蚓对番茄茎叶茉莉酸、茎叶水杨酸及总酚的影响与氮素水平及西花蓟马有关(P < 0.05, 表3)。有西花蓟马时, 低氮下番茄的茎叶茉莉酸和水杨酸含

图 1 不同氮素条件下, 蚯蚓在西花蓟马(WFT)有无时对土壤硝态氮、铵态氮、微生物生物量碳和微生物生物量氮含量(平均值 $\pm$ 标准差, $n = 6$)的影响。-WFT和+WFT分别表示无西花蓟马和有西花蓟马。不同小写字母表示各处理间差异显著 (Fisher's LSD检验, $P < 0.05$)。

Fig. 1 Effects of earthworm *Metaphire guillelmi* on the contents of soil NO₃⁻-N, NH₄⁺-N, microbial biomass carbon and microbial biomass nitrogen in the absence or presence of western flower thrips (WFT) under low and high N inputs (mean $\pm$ SD, $n = 6$). In the figure, -WFT and +WFT indicate without and with western flower thrips, respectively. Means with different letters indicate significant difference among treatments (Fisher's LSD test, $P < 0.05$). Error bars are standard errors.

表 3 蚯蚓、氮素、植食者因素及其交互作用对番茄茎叶及根系营养和化学防御性状的影响

Table 3 Effects of earthworm, nitrogen, herbivore and their interactions on the nutrients and chemical traits of tomato shoots and roots

变量 Variables	蚯蚓 Earthworm (E) (df = 1)	氮素 Nitrogen (N) (df = 1)	西花蓟马 Thrips (WFT) (df = 1)	E $\times$ N (df = 1)	E $\times$ WFT (df = 1)	N $\times$ WFT (df = 1)	E $\times$ N $\times$ WFT (df = 1)
茎叶干生物量 Shoot dry biomass	22.49***	117.88***	10.36**	2.39	1.64	5.86*	0.05
根系干生物量 Root dry biomass	13.77***	2.08	0.20	11.47**	0.00	0.22	1.68
茎叶可溶性糖 Shoot soluble sugar	25.21***	2.09	15.47***	17.79***	2.01	0.03	0.03
根系可溶性糖 Root soluble sugar	0.01	0.71	2.68	2.17	3.69	1.39	13.09***
茎叶全氮 Shoot total nitrogen	12.21**	182.83***	1.19	3.10	0.00	0.07	1.70
根系全氮 Root total nitrogen	20.37***	246.77***	15.21***	0.06	11.12**	2.79	2.11
茎叶游离氨基酸 Shoot amino acid	0.97	20.43***	7.57**	0.73	0.28	26.10***	8.31**
根系游离氨基酸 Root amino acid	46.10***	43.08***	7.38**	21.88***	14.80***	32.87***	0.96
茎叶酚 Shoot phenolics	2.36	36.23***	4.75*	1.50	2.26	0.31	29.01***
根系酚 Root phenolics	3.61	0.01	51.47***	9.75**	0.00	0.01	33.56***
茎叶水杨酸 Shoot salicylic acid	49.52***	0.08	0.11	72.61***	80.09***	18.73***	95.11***
茎叶茉莉酸 Shoot jasmonic acid	156.85***	3.54	26.94***	38.62***	83.52***	64.95***	116.73***

* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

图 2 不同氮素条件下, 蚯蚓在西花蓟马(WFT)有无时对番茄茎叶干生物量、根系干生物量、茎叶可溶性糖、根系可溶性糖、茎叶游离氨基酸、根系游离氨基酸、茎叶全氮和根系全氮(平均值 $\pm$ 标准差, $n = 6$)的影响。-WFT 和+WFT 分别表示无西花蓟马和接种西花蓟马。不同小写字母表示各处理间差异显著(Fisher's LSD 检验, $P < 0.05$)。

Fig. 2 Effects of earthworm *Metaphire guillelmi* on the contents of tomato shoot dry biomass, root dry biomass, shoot soluble sugar, root soluble sugar, shoot amino acid, root amino acid, shoot total nitrogen and root total nitrogen in the absence or presence of western flower thrips under low and high N inputs (mean $\pm$ SD, $n = 6$). In the figure, -WFT and +WFT indicate without and with western flower thrips, respectively. Means with different letters indicate significant difference among treatments (Fisher's LSD test, $P < 0.05$). Error bars are standard errors.

量在蚯蚓作用下是未接种蚯蚓处理的6倍和3倍;而高氮下蚯蚓降低总酚含量,对茎叶茉莉酸和水杨酸含量无影响(图3)。西花蓟马数量的变化与氮素水平和蚯蚓关系密切,在低氮时蚯蚓使西花蓟马的数量降低了58%,而高氮下无影响(图4)。在蚯蚓存在时,茎叶可溶性糖和茎叶全氮与西花蓟马数量显著正相关,茎叶茉莉酸和茎叶水杨酸含量与西花蓟马数量呈显著负相关,而无蚯蚓时上述关系不显著(图5)。

3 讨论

3.1 蚯蚓对番茄生长的影响

蚯蚓在低氮时降低了番茄茎叶干生物量、根系

干生物量和茎叶可溶性糖含量,而高氮时对番茄营养物质(可溶性糖、游离氨基酸和全氮)及生物量无影响;证实先前荟萃分析的结论,即蚯蚓介导的植物生长和养分分配受到土壤养分有效性的影响(van Groenigen et al, 2014)。蚯蚓活动影响着微生物活性、群落结构及多样性(伍玉鹏等, 2013; Bertrand et al, 2015; Gong et al, 2018),从而促进土壤有机氮矿化,扩大土壤活性氮库(张卫信等, 2007; Andriuzzi et al, 2016)。本研究中,蚯蚓活动增加了土壤微生物生物量氮,说明蚯蚓能够加速氮素周转,这与番茄茎叶全氮含量的增加相对应(Wurst, 2013; van Groenigen et al, 2014)。蚯蚓降低了番茄的生物量和茎叶可溶性糖,其原因可能与威廉腔环蚓属于内层

图3 不同氮素条件下, 蚯蚓在西花蓟马(WFT)有无时对番茄茎叶酚、根系酚、茎叶水杨酸和茎叶茉莉酸(平均值 $\pm$ 标准差, $n = 6$)的影响。-WFT 和+WFT 分别表示无西花蓟马和接种西花蓟马。不同小写字母表示各处理间差异显著(Fisher's LSD 检验, $P < 0.05$)。

Fig. 3 Effects of earthworm *Metaphire guillelmi* on the contents of tomato shoot phenolics, root phenolics, shoot jasmonic acid and shoot salicylic acid in the absence or presence of western flower thrips (WFT) under low and high N inputs (mean $\pm$ SD, $n = 6$). In the figure, -WFT and +WFT indicate without and with western flower thrips, respectively. Means with different letters indicate significant difference among treatments (Fisher's LSD test, $P < 0.05$). Error bars are standard errors.

图4 蚯蚓和氮素水平对植食者西花蓟马(WFT)种群数量(平均值 $\pm$ 标准差, $n = 6$)的影响。不同小写字母表示各处理间差异显著(Fisher's LSD 检验, $P < 0.05$)。

Fig. 4 Effects of earthworm and nitrogen level on the abundance of western flower thrips (WFT) (mean $\pm$ SD, $n = 6$). Means with different letters indicate significant difference among treatments (Fisher's LSD test, $P < 0.05$). Error bars are standard errors.

种, 不仅对农田耕作和化肥施用等农事活动的抵抗力强, 其本身对土壤结构和根系的生物扰动能力也很强。尤其是在盆栽条件下, 根系生长范围和蚯蚓活动空间有限, 蚯蚓对根系的破坏作用与地下部植食者类似, 从而对番茄的生长产生负面影响(Kaplan et al, 2018)。西花蓟马侵袭番茄后, 可溶性糖从地上部茎叶向地下部根系转移, 茎叶游离氨基酸也因此增加, 表明番茄在应对生物胁迫条件下, 其养分资源发生转移与再分配(Kempel et al, 2011)。有文献也证明蚯蚓活动能够造成根系破损, 特别是未形成保护皮层的幼小细弱根及根尖, 更容易受到物理扰动的损害, 同时蚯蚓扰动也会破坏菌根菌丝网络和有益真菌对植物的促进作用(Brown et al, 2004)。相比低氮水平, 高氮引起蚯蚓生物量降低的程度更大, 尽管蚯蚓具有保持身体元素稳态的能力,

图5 蚯蚓介导的番茄营养物质(茎叶可溶性糖和茎叶全氮)及信号物质(茎叶茉莉酸和茎叶水杨酸)与西花蓟马数量(WFT)的关系

Fig. 5 Regressions between western flower thrips (WFT) abundance and contents of tomato shoot soluble sugar, shoot total nitrogen, shoot salicylic acid and shoot jasmonic acid.

但高氮条件下蚯蚓摄取食物的元素不均衡会抑制其生长(Zheng et al, 2018)。此外,除了高氮水平使得植物对蚯蚓介导的氮素矿化过程依赖性降低外,氮肥的施用伴随着 pH 的下降,也会影响栖居于土壤内的蚯蚓,因此蚯蚓在高氮条件下对植物生长的影响较弱甚至被掩盖(Brown et al, 2004)。先前的综述也发现,在67项研究中有9%的结果显示出蚯蚓降低了植物生物量(Scheu, 2003),除了蚯蚓取食和生物扰动破坏了植物根系外,有关蚯蚓影响根际微生物群落的间接作用现在还缺乏研究。蚯蚓对植物生长的影响可能取决于植物种类、土壤与植食者类型的综合作用(Kaplan et al, 2018),今后应该加强有关蚯蚓影响植物生长的机制研究。

3.2 蚯蚓对番茄抗虫性的影响

植物对植食者的抗性受植物营养物质及化学防御物质变化的影响(Kempel et al, 2009)。值得注意的是,本研究发现蚯蚓介导的生长和抗性之间并非此消彼长的关系,蚯蚓可以同时促进植物营养积累以及防御抗性。氮含量的增加会提高茎叶适口性,增加西花蓟马的种群数量。而茉莉酸和水杨酸通过细胞膜信号级联反应,调控着抗性相关酶的活性及抗性基因的表达,进而刺激植物防御植食者(Jana et al, 2010; Puga-Freitas & Blouin, 2015)。有研究证明蚯蚓会影响植物的信号途径(Lohmann et al, 2009)、刺激植物叶片和皮下组织的防御化合物产生(Wurst et al, 2010);如 Lohmann 等(2009)发现蚯蚓会促进叶片中次级防御化合物(如硫代葡萄糖苷)的形成来降低蚜虫数量。植物生长和抗性所依赖的初级和次级代谢途径是相互交织的,大多数理论都强调资源的最优分配及生长和防御之间存在此消彼长的权衡(Wurst et al, 2010; Kempel et al, 2011)。蚯蚓改善土壤环境和调节土壤生物群落,理论上可以影响植食作用下资源在植物生长和防御之间的分配(张宁等, 2012; Wurst, 2013)。与我们的推测相符,蚯蚓影响的方向和程度因土壤氮素水平而变化。在高氮条件下,蚯蚓对植物生长及抗性作用并不明显;低氮条件下,蚯蚓促进植物对氮素的吸收,同时也刺激了番茄抗性化合物(茎叶酚)和抗性信号分子(茎叶茉莉酸、茎叶水杨酸)的合成,可能由于在抵抗西花蓟马上植物消耗了大量的能量,反而使其生长因蚯蚓的存在而显示出被抑制的表象(Burghardt, 2016; Mundim et al, 2017)。碳氮平衡假说表明,土壤资源

有效性可以调节植物碳水化合物的储存,改变植物组织中碳基化感化合物的含量(Jarzomski et al, 2000)。已有的证据表明低氮条件下植物会产生更多代谢化合物,如蚯蚓在氮充足条件下降低了车前草(*Plantago lanceolata*)中环烯醚萜类化合物的浓度,抑制植食者(Wurst et al, 2004)。

随着蚯蚓-植物-植食者相互作用研究的不断深入,越来越多的研究结果表明,蚯蚓介导的化学防御物质的产生还受到植物基因型、土壤养分有效性、植食者类型等生境因子的影响(Morris et al, 2006; Puga-Freitas & Blouin, 2015)。因此,深入揭示蚯蚓对植物防御病原物的影响机制需要同时考虑来自土壤管理和病虫害暴发等多方面的因素。本研究仅涉及防御信号和总酚指标,未测定抗性相关酶活性及抗性基因等;茉莉酸和水杨酸发挥其功能作用并非简单的线性途径,不同途径构成复杂的信号转导网络,共同调控植物的防御抗性(Derksen et al, 2013)。蚯蚓对植物生长及抗性的影响机制极其复杂,其影响程度和方向仍难以得到一致的结论。蚯蚓介导的植物抵抗植食者的能力还可能取决于根际微生物组(Wurst & Forstreuter, 2010; Paudel et al, 2016),如土壤中的一些有益微生物能促进植物防御物质的合成(Eisenhauer et al, 2010; 李欢等, 2011; Pineda et al, 2015)。今后应更重视蚯蚓介导的上行效应(Bottom-up effects),有关研究将有助于发展土壤生态管理措施,促进土壤动物资源的调控和利用,发挥土壤生物在植物防御病虫害方面的作用。

4 结论

植物的抗虫性高低与植物体营养物质及防御物质含量有关。本研究发现蚯蚓介导的植物防御化合物以及抗逆信号可以加强其对地上部虫害的抗性。植物生长和抗性之间的关系受土壤养分水平的影响,蚯蚓仅在低氮时提高了植物的抗虫性。可见,养分富集条件下植物与土壤动物的互利关系受到破坏。今后应基于野外自然条件或较长时空尺度、结合土壤生物群落的系统分析及植物防御代谢组学研究,剖析蚯蚓介导的植物生长及抗性的关系及调控机制。

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