

根结线虫对斜纹夜蛾幼虫生长及营养利用随龄期变化的研究^{*}

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摘 要 【目的】为明确南方根结线虫 *Meloidogyne incognita* 侵染对斜纹夜蛾 *Spodoptera litura* 幼虫的影响是否因幼虫的龄期而异。【方法】采用被南方根结线虫侵染和未被侵染的乌桕叶片饲喂斜纹夜蛾幼虫, 并测定不同龄期幼虫的生长(幼虫体重、发育历期、相对生长率)和营养利用(取食量、近似消化率、食物转化率)情况。【结果】随着幼虫龄期的增加, 斜纹夜蛾幼虫的取食量及发育历期呈上升趋势, 幼虫体重、相对生长率和食物转化率先上升后下降, 而近似消化率则先下降后上升。与饲喂未侵染南方根结线虫的乌桕叶片相比, 取食线虫侵染的乌桕叶片的斜纹夜蛾 2 龄幼虫近似消化率(0.78 ± 0.07)%显著增加了约 30%, 但斜纹夜蛾的 4 龄幼虫体重(0.12 ± 0.04)g、相对生长率(0.20 ± 0.06)g·g⁻¹·d⁻¹和食物转化率(0.54 ± 0.18)%分别降低了 61%、36%和 73%。线虫侵染处理与龄期互作对斜纹夜蛾的发育历期和取食量无显著影响。【结论】根结线虫侵染对斜纹夜蛾幼虫生长及其营养利用的影响因龄期而异, 线虫侵染处理虽显著增加了斜纹夜蛾 2 龄幼虫的近似消化率, 但却抑制了其 4 龄幼虫的生长及其营养利用。

关键词 地上-地下互作; 发育; 龄期; 斜纹夜蛾; 乌桕

Effects of the root-knot nematode, *Meloidogyne incognita*, on the growth and nutrient utilization of different instars of *Spodoptera litura* larvae

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Abstract 【Objectives】To examine whether the effects of the root-knot nematode, *Meloidogyne incognita*, infestation on *Spodoptera litura* larvae vary among different *S. litura* instars. 【Methods】*S. litura* larvae were randomly assigned to one of two treatment groups; one that was fed leaves of the Chinese tallow tree, *Triadica sebifera*, that were infested with *M. incognita*, and one that was fed nematode-free leaves, and differences in the growth (larval weight, development period, relative growth rate) and digestive ability (food intake, approximate digestibility, and food conversion rate) of these groups were measured and compared. 【Results】In general, food consumption and developmental period of *S. litura* gradually increased with larval development. Relative growth rate, larval weight, and food conversion rate first increased then decreased with larval development, whereas approximate digestibility first decreased, then increased, as larvae developed. The approximate digestibility of 2nd-instar larvae fed nematode infested leaves (0.78 ± 0.07)% was significantly higher (30%) than that of those fed nematode-free leaves. However, the larval weight (0.12 ± 0.04)g, relative growth rate (0.20 ± 0.06)g·g⁻¹·d⁻¹, and food conversion rate (0.54 ± 0.18)% of 4th-instar larvae fed nematode infested leaves was significantly lower

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(61%, 36% and 73%, respectively), compared to larvae fed nematode-free leaves. There was no significant interaction effect between nematode infestation and instar on developmental duration or food consumption. **[Conclusion]** Effects of root-knot nematode infestation on the growth and digestive ability of *S. litura* larvae varied with larval instar. Although nematode infestation significantly increased the approximate digestibility of 2nd-instar larvae, it greatly inhibited the growth and the digestive ability of 4th-instar larvae.

Key words above-and belowground interactions; development; instar; *Spodoptera litura*; *Triadica sebifera*

地上与地下植食性天敌常通过共同寄主植物而发生复杂的相互作用,然而互作类型可能因天敌的龄期而异(申思等,2021)。入侵植物是研究植物介导的地上-地下植食性生物相互作用的理想材料(Keane and Crawley, 2002)。天敌逃逸假说(The enemy release hypothesis)认为外来植物在被引入到一个新的区域后,由于逃逸了专食性天敌的取食危害,使得入侵植物在与其它植物的竞争中占据优势(Maron and Vil, 2001; Keane and Crawley, 2002)。然而,那些来自入侵地的广食性地上、地下天敌则会逐渐集聚到入侵植物上,并对入侵植物产生不同的影响(Wardle *et al.*, 2004; Johnson *et al.*, 2012)。生物阻抗假说(The biotic resistance hypothesis)认为入侵地的许多生物过程及生物因子(如广食性天敌)也可能抵御外来植物的入侵(Derivera *et al.*, 2005)。研究广食性天敌与植物间的互作能更好地理解入侵植物的生态和进化(Huang and Ding, 2016),然而这方面的研究在很大程度上被忽视(Inderjit, 2012; Prior *et al.*, 2015)。

乌柏 *Triadica sebifera* 是种大戟科 Euphorbiaceae 乌柏属 *Triadica* 的乔木,原产于亚洲,后作为油料和观赏树种于 18 世纪末引入美国,目前已成为美国很多地区入侵最为严重的木本植物之一(Bruce *et al.*, 1997; 刘佳, 2019)。在中国,有大量食叶害虫以乌柏为寄主植物,其中斜纹夜蛾 *Spodoptera litura* 就是危害最为严重的害虫之一(张家亮等, 2015),其隶属鳞翅目 Lepidoptera 夜蛾科 Noctidae, 别名莲纹夜蛾,是一种食性杂、分布广、具有较强的隐蔽性、暴发性的食叶害虫(陈亚青等, 2017)。近几年来,由于受气候及种植业结构调整(种植面积、设施栽培面积以及反季节蔬菜的种植等)等因素的影

响,使其已由原间歇性发生害虫上升为常发性的主要害虫,对经济作物造成重大损失(高春先, 2004; 吴琦, 2018)。南方根结线虫 *Meloidogyne incognita* 是乌柏地下病害之一(项瑶等, 2019),它作为一类广食性的植物寄生线虫,能严重抑制植物生长,每年对全球农林业造成约达 780 亿美元以上的巨大经济损失(Chen *et al.*, 2004; McCarter, 2008)。入侵植物与植食性天敌间的互作及入侵植物介导的多种天敌间的互作机制一直是生态学研究的热点之一(Blackburn *et al.*, 2011),但目前大多数的研究主要集中在对单一空间或单一类型天敌的研究,仅少量研究关注了地上-地下植食性天敌间的互作(Li *et al.*, 2020)。鉴于此,本研究以南方根结线虫侵染和未侵染的乌柏叶片饲喂斜纹夜蛾幼虫,比较不同龄期幼虫的生长发育和营养利用的差异,以进一步丰富入侵植物介导的地上-地下植食性生物互作理论,并能为乌柏的生物防治提供理论依据。

1 材料与方法

1.1 试验材料的准备

从野外采集斜纹夜蛾成虫,在实验室中饲养、配对(不存在回交),多代繁殖后,取 2 龄幼虫供试。实验所用南方根结线虫在番茄苗上进行扩繁。

从野外采集的乌柏种子去除蜡质外壳后,将种子埋在潮湿的沙子里,于 4 °C 下储存以打破种子的休眠。然后在温室内以 1:1 (草炭灰:壤土)的表土中播种种子。生长 1 个月后,将大小相近的幼苗单独移栽至花盆中(高=16 cm,直径=25 cm)。定期浇水以保持土壤湿润,并用 100 目尼龙网罩住乌柏幼苗,以隔绝其它昆虫为害(Li *et al.*, 2016)。

1.2 根结线虫接种

参考刘维志(2000)的方法配制 10 000 头/mL 的根结线虫的悬浮液。参照刘亚珍(2018)的方法进行南方根结线虫接种。选用种植 45 d 后的乌桕幼苗,用于接种南方根结线虫。在乌桕根部钻取 3 个深度约为 3 mm 小孔,用加样器注入 2 mL 根结线虫悬浮液,对照组注入 2 mL 无菌水,注入完成后用土壤将小孔覆盖。接种 1 个月后,检查南方根结线虫的侵染情况,选取有明显根结的乌桕幼苗进行实验。

1.3 斜纹夜蛾生长发育和营养利用测定

采集生长于相似部位的被线虫侵染的乌桕叶片及未被侵染的叶片,饲喂斜纹夜蛾并进行生长发育和营养测定。实验开始时,将斜纹夜蛾 2 龄幼虫 (M_0) 与乌桕叶片 (M_a) 称重,放入垫有湿润滤纸的培养皿(直径=10 cm)中,用封口膜密封,并将培养皿放在室温 28 °C、光周期为 L:D=12:12 的室内。在实验过程中,每 24 h 检查一次斜纹夜蛾幼虫的生长状况以及培养皿中水分情况和叶片的取食状况,并观察幼虫是否蜕皮,若蜕皮,当天称量幼虫体重 (M_1),直至实验结束。试验期间记录斜纹夜蛾每个龄期幼虫的发育历期 $N(d)$,并称取剩余叶片重量 (M_c)、幼虫重量 (M_1) 和粪便量 (M_e),以空白处理进行校正。每个处理 12 次重复。采用 Wheeler 等(2001)的方法计算各龄期幼虫生长指标和食物利用参数,具体如下:

$$\text{取食量 } M = M_a - M_c,$$

$$\text{相对生长率 (g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}) = \frac{2(M_1 - M_0)}{N(M_1 + M_0)},$$

$$\text{近似消化率 (\%)} = \frac{M - M_e}{M} \times 100,$$

$$\text{食物转化率 (\%)} = \frac{M_1 - M_0}{M - M_e} \times 100。$$

1.4 数据统计

采用重复测量方差分析比较根结线虫侵染乌桕对不同龄期斜纹夜蛾的生长指标(幼虫体重、发育历期、相对生长率)和营养利用状况(取食量、近似消化率、食物转化率)的影响,以龄

期为组内变量,线虫处理为组间变量,并考虑二者交互作用。多差异显著的方差分析结果采用 Duncan's 法进行多重比较分析,显著性水平为 $P < 0.05$ 。所有数据均采用 SPSS 24.0 软件进行统计与分析,用 SigmaPlot14.0 作图。

2 结果与分析

2.1 饲喂线虫侵染叶片处理对不同龄期斜纹夜蛾幼虫体重、相对生长率及发育历期的影响

龄期和线虫侵染处理对斜纹夜蛾的幼虫体重 ($F_{1,388, 18,045}=10.122, P < 0.05$) 和相对生长率 ($F_{2,095, 27,238}=47.686, P < 0.05$) 存在显著的交互影响。随着龄期增长,斜纹夜蛾末龄幼虫体重和相对生长率呈先上升后下降趋势。饲喂受线虫侵染的乌桕叶片使斜纹夜蛾 4 龄幼虫的体重 (0.31 ± 0.14) g 和相对生长率 (0.30 ± 0.08) $\text{g} \cdot \text{g}^{-1} \cdot \text{d}^{-1}$ 与饲喂未受侵染的乌桕叶片相比分别降低了 61% (图 1: A) 和 36% (图 1: B)。此外,线虫侵染处理与龄期对斜纹夜蛾幼虫发育历期无显著的交互影响 ($F_{1,819, 34,522}=50.874, P > 0.05$),但发育历期随龄长呈现上升趋势(图 1: C)。

2.2 饲喂线虫侵染叶片对不同龄期斜纹夜蛾取食量、近似消化率及食物转化率的影响

龄期和线虫侵染处理对斜纹夜蛾的近似消化率 ($F_{4,52}=3.985, P < 0.05$) 和食物转化率 ($F_{1,938, 25,192}=10.386, P < 0.05$) 存在显著的交互影响。饲喂受线虫侵染的乌桕叶片使斜纹夜蛾 2 龄幼虫的近似消化率 (0.78 ± 0.07) % 显著增加了约 30% (图 2: B), 但使斜纹夜蛾 4 龄幼虫的食物转化率 (0.49 ± 0.06) % 却降低了 73%。而斜纹夜蛾幼虫的取食量不受龄期和线虫侵染处理交互作用的影响 ($F_{1,298, 76}=0.301, P > 0.05$)。总体而言,随着龄期增加,其取食量呈上升趋势(图 2: A)。

3 讨论

植食性生物对植物的取食和利用是极其复杂的生理和行为过程,其生理过程及发育状态随生活史的变化表现出不同水平(张胜昔等, 2009)。食物品质是否能满足植食性生物不同龄期幼虫

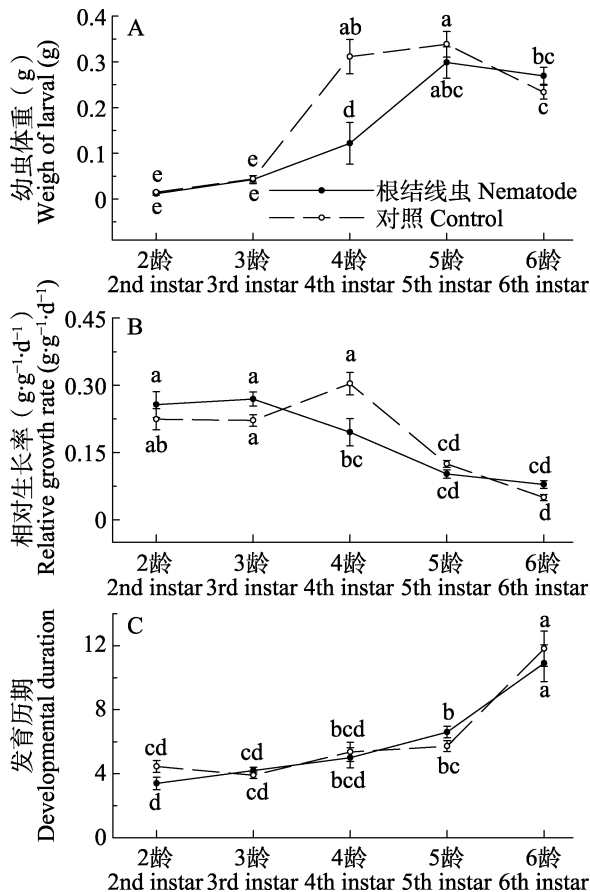


图1 根结线虫对不同龄期斜纹夜蛾幼虫体重、相对生长率和发育历期的影响

Fig. 1 Effects of the root-knot nematode on the larval weight, the relative growth rate and the developmental duration of different instars of *Spodoptera litura* larvae

不同小写字母表示数据间差异显著 ($P < 0.05$)。下图同。

Different lowercase letters indicated significant differences at the 0.05 level. The same below.

的营养需求是影响其生长发育的关键 (唐庆峰等, 2020), 通过比较不同龄期幼虫的生长和食物利用营养指标, 可以了解不同食物对植食性生物营养效益的差异, 从而明确食物对植食性生物生长发育的影响 (郭建国等, 2010)。本研究, 饲喂根结线虫侵染的乌桕叶片对斜纹夜蛾的幼虫体重、相对生长率、近似消化率及食物转化率的影响因龄期而异。这一结果可能是根结线虫侵染使乌桕叶片中的营养物质发生改变, 影响了斜纹夜蛾幼虫食物的品质。刘亚珍等 (2019) 研究表明根结线虫侵染显著降低乌桕的胞间 CO_2 摩尔分数、气孔导度和叶绿素含量, 改变乌桕叶片营养物质, 从而影响癭皮夜蛾 *Gadirtha inexacta*

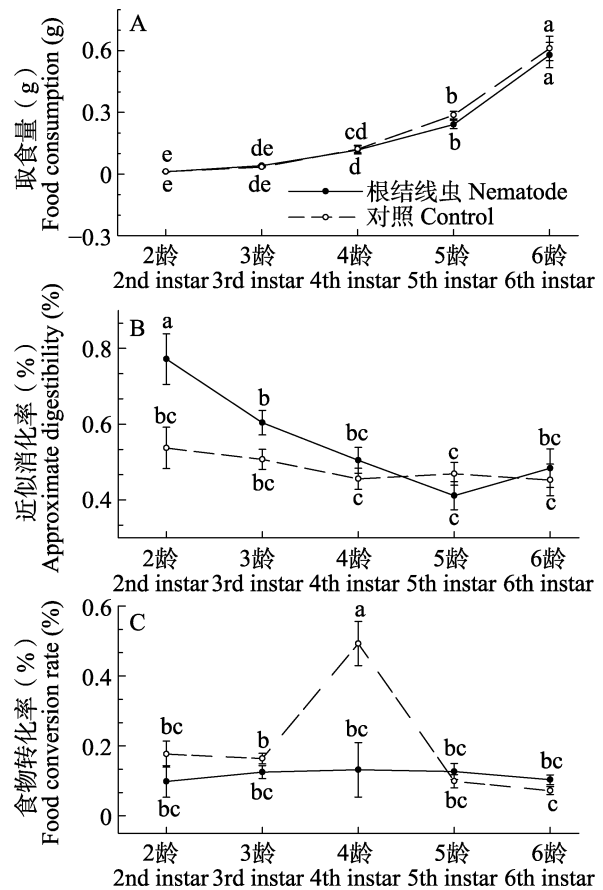


图2 根结线虫对不同龄期斜纹夜蛾取食量、近似消化率和食物转化率的影响

Fig. 2 Effects of the root-knot nematode on the food consumption, the approximate digestibility and the food conversion rate of different instars of *Spodoptera litura* larvae

的生长。León 和 Sánchez-Serrano (2001) 研究也发现根结线虫侵染能改变小麦叶片中的必需氨基酸含量, 从而影响寄主蚜虫的生长。植物在遭受天敌胁迫后, 能通过提高相应的次生代谢物以抵御外来的侵害 (Rani and Jyothsna, 2010), 而植物次生代谢物水平通常随着植物个体发育以及生物因子和非生物的变化而变化。

项瑶等 (2019) 研究表明根结线虫侵染乌桕叶片后能促进斜纹夜蛾幼虫的生长发育, 然而, 该研究只分析了斜纹夜蛾幼虫在短期内的生长发育, 未进行整个龄期研究。本研究发现, 取食被线虫侵染的乌桕叶片后, 斜纹夜蛾 2 龄幼虫对食物有较高的消化能力。这可能是根结线虫侵染后改变了乌桕叶片的营养物质成分, 因此, 幼龄斜纹夜蛾需要提高其食物消化率以保证其正常

生长发育(项瑶等, 2019)。卢毅等(2016)、李晓红(2016)及龙莹等(2020)对寄生生物的寄生时间研究发现, 寄生时间显著影响着寄主的生长发育。

本研究发现受根结线虫感染的乌桕叶片处理对斜纹夜蛾 4 龄幼虫具有明显的抑制作用。虫害诱导的次生化合物能直接影响幼虫发育, 还会破坏昆虫的消化吸收系统和植食性昆虫体内酶的活性, 以干扰昆虫对营养的吸收利用(Jansen and Groot, 2004; 李进步等, 2008)。研究表明当寄主植物遭受昆虫取食时, 一些次生物质的含量也会发生显著性变化(胡增辉等, 2009)。昆虫体内次生物质的累积可能会导致其体内某些激素异常, 对幼虫的存活产生负面影响(王晓丽等, 2014)。Yuan 等(2020)研究也发现随着龄期增加, 解毒酶在美国白蛾 *Hyphantria cunea* 体内的解毒作用越来越重要。斜纹夜蛾取食被根结线虫侵染的乌桕叶片后, 随着体内次生物质的含量及有毒物质的聚集, 自身的消化吸收系统和解毒酶的活性可能被降低, 导致其生长发育受到影响。此外, 斜纹夜蛾幼虫可能通过降低相对生长速率和近似消化率来减少过多食入植物次生代谢物和有毒物质, 以保证其正常的生长发育, 这与 Beninger 等(2004)对粉纹夜蛾 *Trichoplusia ni* 幼虫研究相似。

入侵植物-植食性天敌互作及入侵植物介导的多种天敌间互作是国内外生态学家广泛关注的重要研究内容(Ali and Agrawal, 2012; Wang et al., 2014), 来自入侵地的广食性地上-地下天敌及其互作可能间接影响其是否能成功入侵。本研究发现根结线虫侵染对斜纹夜蛾幼虫的影响因龄期而异。线虫侵染处理虽显著增加了斜纹夜蛾 2 龄幼虫的近似消化率, 但却抑制了其 4 龄幼虫的生长和营养利用, 因此, 这种消极影响可能间接降低斜纹夜蛾幼虫的最终羽化率, 从而减轻其对乌桕的危害程度。然而, 受环境因子的影响, 室内或田间控制实验结果与在自然生态系统中的实验结果可能不一致(石宁, 2016), 因此未来需要在自然生态系统中开展更多的实验以进一步验证室内实验结果。

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