

亚致死浓度烯啶虫胺对水稻抗性物质 及褐飞虱生殖参数的影响

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摘要: 为明确烯啶虫胺对褐飞虱 *Nilaparvata lugens* 的防控效果, 采用稻茎浸渍法测定亚致死浓度烯啶虫胺对水稻生理生化指标以及褐飞虱雌成虫繁殖力的影响。结果表明, 亚致死浓度烯啶虫胺处理后, 水稻中草酸含量在第2天时无明显变化, 在第4天时升高了20.5%; 类黄酮含量分别升高了9.6%和40.6%; 游离氨基酸含量分别下降了20.1%和42.4%; 蔗糖含量在第2天时与对照间无显著差异, 在第4天时升高了38.5%。亚致死浓度烯啶虫胺对褐飞虱生殖存在显著影响, 雌成虫羽化2 d和4 d时, 卵巢中可溶性蛋白含量分别下降了31.2%和40.9%; 脂肪体中可溶性蛋白含量分别下降了19.0%和38.8%。亚致死浓度烯啶虫胺处理抑制了雌成虫卵巢发育, 褐飞虱卵黄原蛋白(*Nilaparvata lugens* vitellogenin, NIVg)基因表达量在第2天时与对照间无显著差异, 在第4天下降了57.5%; 同时显著影响了褐飞虱生殖力, 雌成虫产卵量减少了58.1%, 产卵历期缩短了36.7%, 寿命缩短了28.0%, 但对雌成虫产卵前期无显著影响。表明亚致死浓度烯啶虫胺处理后可能通过诱导水稻次生代谢产物含量上升来提高水稻对褐飞虱的抗性, 而且对褐飞虱繁殖力也有显著影响。

关键词: 烯啶虫胺; 褐飞虱; 水稻; 抗性物质; 生殖参数

Effects of sublethal concentrations of nitenpyram on resistance substances in rice and reproductive parameters of the brown planthopper *Nilaparvata lugens*

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Abstract: To elucidate the control efficacy of sulfoxaflor against the brown planthopper, *Nilaparvata lugens*, the rice stem impregnation method was employed to determine the effects of sublethal concentrations of nitenpyram on physiological and biochemical indices of rice, as well as on the reproductive capacity of female brown planthoppers. The results showed that the oxalic acid content of rice treated with sublethal concentrations of nitenpyram for two and four days showed no significant difference at two days and increased by 20.5% at four days. Flavonoids levels increased by 9.6% and 40.6%, respectively. The content of free amino acids decreased by 20.1% at two days and 42.4% at four days, respectively. The sucrose content showed no significant difference at two days but increased by 38.5% at four days after treatment with sublethal concentrations of nitenpyram. The sublethal concentration of nitenpyram significantly affected the reproduction of the brown planthopper. Soluble protein content in the ovaries of female adults decreased by 31.2% and 40.9% on days two and four post-emergence, respectively, and

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by 19.0% and 38.8% in the fat body. Nitenpyram inhibited ovarian development in female adults, with *Nilaparvata lugens* vitellogenin (*NIVg*) gene expression showing no significant difference at two days after emergence and a 57.5% decrease at four days after emergence. Additionally, it significantly affected the reproductive capacity of the brown planthopper, with the number of eggs laid by females decreasing by 58.1%, the oviposition period shortening by 36.7%, and lifespan decreasing by 28.0%, although there was no significant impact on the pre-oviposition period. This indicates that sublethal concentrations of nitenpyram induce an increase in secondary metabolites in rice to enhance resistance against the brown planthopper and significantly impact the reproductive capacity of the pest.

Key words: nitenpyram; *Nilaparvata lugens*; rice; resistance substances; reproductive parameter

褐飞虱 *Nilaparvata lugens* 属半翅目飞虱科,是我国为害水稻最严重的害虫之一(程家安等,2008;何帅洁等,2021;Zhu et al.,2023)。该害虫是一种以水稻韧皮部汁液为食的单食性害虫,主要通过刺吸水稻茎基部造成植株枯萎、倒伏等症状(张合红等,2022;Wu et al.,2020;Shi et al.,2023),而且可以传播水稻草矮病毒(rice grassy stunt virus,RGSV)和水稻齿叶矮缩病毒(rice ragged stunt virus,RRSV)等(Wang et al.,2022);其具有迁飞习性,对水稻生产造成巨大的经济损失,对生态安全构成严重威胁(陆明红等,2020;Jeevanandham et al.,2023;陆宴辉等,2023)。

目前,化学防治仍是防控褐飞虱的主要手段(Garrood et al.,2016;吴进才,2017;Wu et al.,2020)。但由于施用剂量和田间残留降解等原因,化学杀虫剂在环境中的毒力会随着时间的推移逐渐递减至亚致死浓度从而对存活个体产生亚致死效应(Dai et al.,2023)。药剂亚致死效应一方面能够缩短害虫寿命,降低其繁殖力,抑制害虫的种群数量(Huang et al.,2016;Zhang et al.,2021),另一方面却会导致害虫在亚致死浓度的选择压力下提高其对药剂的耐受性,并刺激害虫的生殖,导致害虫再猖獗(Rix et al.,2016;Wu et al.,2020)。药剂还可以诱导植物体内生理生化物质发生变化,如Wu et al.(2021)研究发现三氟苯嘧啶拌种处理提高了水稻体内草酸、类黄酮、总酚、胍胍质等物质含量及蔗糖/游离氨基酸比值,增强了水稻对褐飞虱的抗性。此外,也有研究表明,溴氰菊酯、三唑磷等杀虫剂在亚致死浓度下可以通过介导雌性褐飞虱生理响应和基因表达水平的变化,从而影响褐飞虱种群的增长与繁殖(Ge et al.,2010;Gong et al.,2023)。

烯啶虫胺是由日本武田公司与先正达公司共同研发的第2代新型烟碱类杀虫剂,主要作用于昆虫神经系统的乙酰胆碱受体,对害虫的突触受体具有

神经阻断作用,使害虫神经系统遭到破坏,从而达到杀虫效果(Yoshida et al.,2013;闫虹江等,2021)。烯啶虫胺具有较强的内吸和渗透作用,其用量少、毒性低、持效期长,且对作物安全无药害,是防治刺吸式口器害虫的主要杀虫剂之一,目前广泛用于水稻、果树、蔬菜和茶叶等农业和园艺上稻飞虱、蚜虫、烟粉虱 *Bemisia tabaci*、白粉虱 *Trialeurodes vaporariorum*、叶蝉和蓟马等多种害虫的防治(Elbert et al.,2008;Wang et al.,2017;Khoa et al.,2018)。前期研究结果显示,烯啶虫胺对褐飞虱具有较好的防治效果,亚致死浓度 LC_{15} 烯啶虫胺对褐飞虱生长发育和繁殖存在不利影响(程世阳等,2020;刘章扬等,2023),但未有关于该药剂对褐飞虱生理、生殖以及水稻化学物质影响的研究报道。本研究通过测定亚致死浓度烯啶虫胺对水稻生理生化物质和褐飞虱生殖相关参数的变化来探究其对褐飞虱种群的防控效果及相关机制,以期为田间合理施用烯啶虫胺防控褐飞虱提供参考。

1 材料与方法

1.1 材料

供试水稻:水稻品种为扬稻6号(籼稻),由江苏里下河地区农业科学研究所提供。将种子浸泡发芽后,播种于高60 cm×宽100 cm×长200 cm的室外标准水泥池中,长至6叶期移栽至直径16 cm的塑料桶中种植,每桶3穴,每穴4株,至水稻分蘖期备用。试验全程采用0.18 mm防虫网覆盖,以防其他害虫侵入。

供试虫源:褐飞虱种群来自中国水稻研究所,在实验室内连续饲养多年且未接触任何药剂,取3龄若虫供试。饲养温度为 $(26\pm 2)^{\circ}\text{C}$,相对湿度为65%~75%,光周期为L 16 h:D 8 h。

药剂及试剂:96%烯啶虫胺(nitenpyram)原药,上海麦克林生物科技有限公司。Triton X-100,国药

集团化学试剂有限公司;水合茚三酮、蒽酮、三氯化钛,上海麦克林生物科技有限公司;FastPure Cell/Tissue Total RNA Isolation Kit、HiScript QRT Super-Mix 和 ChamQ SYBR qPCR Master Mix,南京诺唯赞生物技术有限公司;其他试剂均为国产分析纯。

仪器:Spark 20M 多功能酶标仪,瑞士 Tecan 公司;T100 PCR 扩增仪、CFX96 Touch 实时定量 PCR 仪,美国 Bio-Rad 公司;SZX16 立体式显微镜,日本 Olympus 公司;DS-Fi2 数码摄像头,日本 Nikon 公司;FA1004 电子天平,上海舜宇恒平科学仪器有限公司;GXZ-160D 人工气候箱,宁波江南仪器厂。

1.2 方法

1.2.1 亚致死浓度烯啶虫胺处理

采用稻苗浸渍法测定烯啶虫胺对褐飞虱亚致死效应。根据程世阳等(2020)研究结果,烯啶虫胺亚致死浓度 LC_{15} 为 0.009 mg/L。利用电子天平精准称取烯啶虫胺原药 90 mg,添加少量丙酮溶解配制成 9 mg/L 浓度的母液后加入含 0.1% Triton X-100 的蒸馏水稀释至 0.009 mg/L。选取长势一致的分蘖期水稻植株,洗净,剪成高约 10 cm 的连根水稻茎秆,晾干后浸入上述药液中 30 s,取出晾干后用湿润脱脂棉包裹根部,置于直径 21 cm、高 16 cm 的育苗杯中培育。烯啶虫胺处理后 2 d 和 4 d 取水稻茎秆测定水稻体内抗性和营养物质含量。以含 0.1% Triton X-100 蒸馏水培育的水稻为对照。1 个育苗杯为 1 个重复,每个育苗杯至少 10 株水稻,3 个生物学重复。

1.2.2 水稻草酸、类黄酮含量的测定

采用三氯化钛显色法测定水稻中草酸含量(程耀等,2011)。分别剪取处理 2 d 和 4 d 后长势一致的分蘖期水稻植株茎秆 1 g,将其剪碎后充分研磨,用超纯水 10 mL 冲洗至 50 mL 锥形瓶中,加入约 1/3 体积的活性炭,摇匀后静置脱色 30 min,脱色后于 4 ℃ 下以 3 000 r/min 离心 15 min 分离活性炭,一次脱色不完全时可多次脱色,直至溶液呈无色或略呈乳白色。取上清液 3 mL,加入 3% 三氯化钛(10% 稀盐酸配制)240 μ L,然后用多功能酶标仪在波长 400 nm 处测定吸光值。用草酸(分析纯)建立标准曲线,计算各样品中草酸含量。3 个生物学重复。

水稻中类黄酮含量测定参照宋元清等(2005)方法并加以改进。分别剪取处理 2 d 和 4 d 后长势一致的分蘖期水稻植株茎秆,擦拭干净后烘干,剪碎加入液氮在研钵中充分研磨,称取干粉 1 g 放入离心

管中,加入 60% 乙醇溶液 10 mL,混匀后将离心管置于 70 ℃ 条件下进行超声波处理,超声波功率保持 350 W,超声时间 30 min,然后以 3 000 r/min 离心 5 min 取上清液,同一样品按上述方法重复操作 3 次。将离心后的上清液转移至 25 mL 容量瓶中,用 60% 乙醇溶液定容至 25 mL。混匀后吸取定容的提取液 1 mL 于 25 mL 容量瓶中,加入 5% $NaNO_2$ 溶液 1 mL,混匀后静置 6 min,随后加入 10% $AlCl_3 \cdot 6H_2O$ 溶液 1 mL,混匀后静置 5 min。随后加入 4% NaOH 溶液 10 mL,再加入 30% 乙醇溶液定容,摇匀后静置 15 min。用多功能酶标仪在波长 415 nm 处测定吸光值。用芦丁标准品建立标准曲线,计算各样品中类黄酮含量。3 个生物学重复。

1.2.3 水稻蔗糖、游离氨基酸含量的测定

水稻蔗糖含量采用蒽酮比色法测定(李晓旭和李家政,2013)。分别取处理 2 d 和 4 d 后长势一致的分蘖期水稻植株茎秆,称取烘干的水稻茎秆 0.2 g,放入 50 mL 试管中,加入蒸馏水 10 mL,沸水浴 20 min 后取出冷却,用滤纸过滤至 25 mL 容量瓶中,再用蒸馏水冲洗几次残渣,最后定容至 25 mL。吸取 0.5 mL 定容的提取液于试管中,加入蒸馏水 1.5 mL,再加入蒽酮乙酸乙酯试剂(1 g 蒽酮溶于 50 mL 乙酸乙酯)0.5 mL 和浓硫酸 5 mL,充分振荡,立即沸水浴加热 5 min,然后冷却至室温,用多功能酶标仪在波长 620 nm 处测定吸光值。用蔗糖建立标准曲线,计算各样品中蔗糖含量。3 个生物学重复。蔗糖含量 = $(C_1 \times V_1 \times n_1) / (W_1 \times a_1 \times 1\ 000)$,式中, C_1 为标准曲线求得糖量, V_1 为提取液量, a_1 为吸取样品液体积, n_1 为稀释倍数, W_1 为组织质量。

采用茚三酮显色法测定水稻茎秆游离氨基酸含量(邵金良等,2008)。分别取处理 2 d 和 4 d 后长势一致的分蘖期水稻植株茎秆 1 g,加入 10% 乙酸溶液 5 mL,放入研钵中研磨至匀浆状态,将过滤液转移至 100 mL 容量瓶中,用 10% 乙酸溶液定容至 100 mL。吸取定容的提取液 1 mL 至 20 mL 试管中,加入蒸馏水 1 mL、抗坏血酸 0.1 mL 和水合茚三酮显色液 3 mL,摇匀后置于沸水浴中处理,显色 15 min,待冷却后加入 80% 乙醇溶液 10 mL,加蒸馏水定容至 25 mL。用多功能酶标仪在波长 570 nm 处测定吸光值。用氨基酸建立标准曲线,计算各样品中游离氨基酸含量。3 个生物学重复。游离氨基酸含量 = $(C_3 \times n_3) / (W_3 \times 1\ 000)$,式中, C_3 为标准曲线求得糖量, n_3 为总系数倍数, W_3 为组织质量。

1.2.4 褐飞虱卵巢和脂肪体可溶性蛋白含量测定

采用考马斯亮蓝法测定褐飞虱雌成虫卵巢及脂肪体可溶性蛋白含量(王琛柱和钦俊德,1996)。参照1.2.1将水稻植株经亚致死浓度烯啶虫胺处理后,选取褐飞虱3龄若虫接至水稻植株上,每杯育苗杯接入30头,置于温度为(26±2)℃、相对湿度75%~85%、光周期为L 16 h:D 8 h的人工气候箱中培养。待若虫羽化后,取羽化2 d和4 d后未交配的短翅雌成虫进行解剖,以正常羽化2 d和4 d未交配的雌成虫作对照,每组解剖10头,3个生物学重复。将解剖好的卵巢和脂肪体组织分别加入PBS溶液5 mL匀浆,取匀浆液以1 000 r/min离心20 min,取上清液用玻璃纤维过滤,保留滤液待分析。以牛血清蛋白绘制蛋白标准曲线。每试管内加入1 mL样品滤液和5 mL考马斯亮蓝G-250溶液混合摇匀,静置后在595 nm波长下测定吸光值。根据蛋白标准曲线计算可溶性蛋白含量。

1.2.5 褐飞虱卵黄原蛋白相关基因表达量的测定

参照1.2.4方法接入褐飞虱3龄若虫并待其羽化为雌成虫后,取羽化2 d和4 d后未交配短翅雌成虫测定褐飞虱卵黄原蛋白(*Nilaparvata lugens* vitellogenin, NIVg)和卵黄原蛋白受体(*Nilaparvata lugens* vitellogenin receptor, NIVgR)基因的表达水平。以正常羽化2 d和4 d未交配的褐飞虱雌成虫作对照。3个生物学重复,每个重复测定10头褐飞虱。利用FastPure Cell/Tissue Total RNA Isolation Kit试剂盒提取褐飞虱雌成虫的总RNA,用HiScript QRT Super Mix试剂盒去除基因组DNA,并反转录合成cDNA供试。

根据本课题组已发表的数据(Ge et al., 2015)合成褐飞虱NIVg和NIVgR荧光定量引物,分别为NIVg-F(5'-GTGGCTCGTTCAAGGTTATGG-3')/NIVg-R(5'-GCAATCTCTGGGTGCTGTTG-3')和NIVgR-F(5'-AGGCAGCCACACAGATAACCGC-3')/NIVgR-R(5'-AGCCGCTCGCTCCAGAACATT-3'),以 β -actin为内参基因,引物为 β -actin-F(5'-TGCGTGACATCAAGGAGAAGC-3')/ β -actin-R(5'-CCATACC-CAAGAAGGAAGGCT-3'),引物委托生工生物工程(上海)股份有限公司合成。以cDNA为模板采用荧光定量PCR(real-time fluorescence quantitative PCR, RT-qPCR)技术进行基因表达量测定。20 μ L RT-qPCR反应体系:2×ChamQ SYBR qPCR Master Mix 10 μ L、10 pmol/L上下游引物各0.5 μ L、cDNA

2 μ L、ddH₂O 7 μ L。反应程序:95℃预变性3 min;95℃变性15 s,58℃退火30 s,72℃延伸20 s,循环39次。每个样品设置3个生物学重复,每个生物学重复设置3个技术重复。采用2^{- $\Delta\Delta C_t$} 法计算NIVg和NIVgR的相对表达量(Livak & Schmittgen, 2001)。

1.2.6 卵巢解剖观察

参照1.2.4方法接入褐飞虱3龄若虫并待其羽化为雌成虫后,取羽化2 d和4 d后未交配的短翅雌成虫进行解剖,以正常羽化2 d和4 d未交配的雌成虫作对照,每组解剖15头,3个生物学重复。在0.9%生理盐水中解剖雌成虫的内生殖系统,用镊子小心剥离黏附在内生殖器中的脂肪体和微气管,卵巢的完整形态通过立体式显微镜观察,并用数码摄像头拍照。

1.2.7 褐飞虱雌成虫繁殖参数的测定

参照Ge et al. (2015)方法测定亚致死浓度烯啶虫胺处理后褐飞虱雌成虫的繁殖参数。参照1.2.4方法接入褐飞虱3龄若虫并待其羽化为成虫后,取初羽化雌成虫与初羽化雄成虫按照1:1比例进行交配,放置于有1株分蘖期水稻苗的直径1.8 cm、高18 cm的玻璃试管中饲养。产卵前期每24 h更换新鲜水稻苗,在产卵历期每72 h更换新鲜的水稻苗,直至雌成虫死亡。以正常羽化的雌成虫与雄成虫交配处理作对照。记录雌成虫的产卵前期(从雌成虫羽化到开始产卵)、产卵历期、寿命和产卵量。3个生物学重复。

1.3 数据分析

试验数据采用DPS 7.05软件进行统计分析,应用独立样本 t 检验法对试验数据进行差异显著性检验。采用GraphPad Prism 7软件完成绘图。

2 结果与分析

2.1 亚致死浓度烯啶虫胺对水稻次生物质含量的影响

亚致死浓度烯啶虫胺处理对水稻中草酸、类黄酮含量产生显著影响。亚致死浓度烯啶虫胺处理水稻2 d后,与对照相比,水稻中草酸含量无显著差异($t=1.8$, $P=0.146$;图1-A),处理4 d后,水稻中草酸含量显著增加了20.5%($t=6.2$, $P=0.003$;图1-B)。处理2 d后,水稻中类黄酮含量显著增加了9.6%($t=5.9$, $P=0.004$;图1-C);而处理4 d后,水稻中类黄酮含量显著增加了40.6%($t=6.4$, $P=0.003$;图1-D)。

2.2 亚致死浓度烯啶虫胺对水稻营养物质含量的影响

亚致死浓度烯啶虫胺处理对水稻中蔗糖、游离氨基酸含量存在显著影响。处理水稻2 d后,与对照

相比,水稻中游离氨基酸含量显著下降了20.1%($t=8.4, P<0.001$;图2-A),处理4 d后,水稻中游离氨基酸含量显著下降了42.4%($t=6.5, P=0.003$;图2-B);

处理2 d后,水稻中蔗糖含量无显著变化($t=1.7, P=0.171$;图2-C),处理4 d后,水稻中蔗糖含量显著提高了38.5%($t=5.0, P=0.007$;图2-D)。

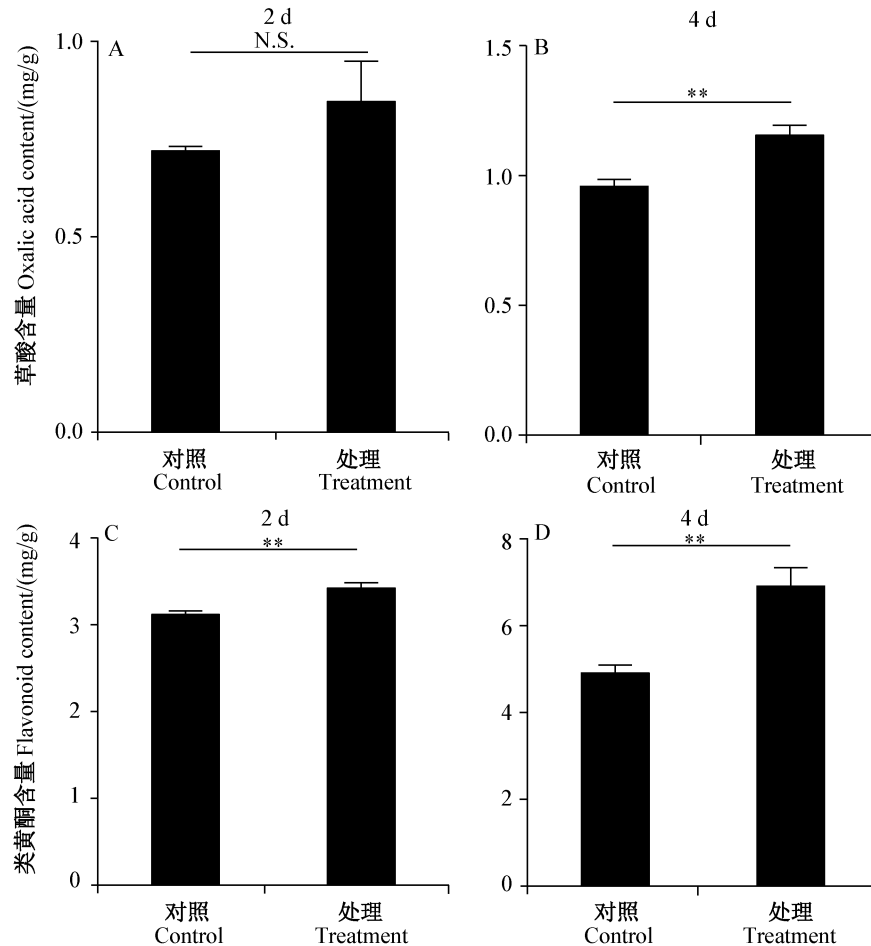


图1 亚致死浓度烯啶虫胺对水稻中草酸(A、B)和类黄酮含量(C、D)的影响

Fig. 1 Effect of sublethal concentration of nitenpyram on the content of oxalic acid (A, B) and flavonoids (C, D) in rice

图中数据为平均数±标准误。**表示处理与对照之间经独立样本 t 检验法检验差异显著($P<0.01$); N.S.表示无显著差异。Data are mean±SE. ** indicates significant difference between treatment and control groups by t test ($P<0.01$); N.S. indicates no significant difference.

2.3 亚致死浓度烯啶虫胺对雌成虫组织蛋白含量的影响

亚致死浓度烯啶虫胺对褐飞虱雌成虫卵巢及脂肪体可溶性蛋白含量存在显著影响。羽化2 d的褐飞虱雌成虫取食亚致死浓度烯啶虫胺处理的水稻后,卵巢中可溶性蛋白含量相比对照组显著下降了31.2%($t=12.1, P<0.001$;图3-A);羽化4 d显著下降了40.9%($t=17.8, P<0.001$;图3-B)。羽化2 d的褐飞虱雌成虫取食亚致死浓度烯啶虫胺处理的水稻后,脂肪体内可溶性蛋白含量相比对照组下降了19.0%($t=5.7, P=0.005$;图3-C);羽化4 d显著下降了38.8%($t=21.8, P<0.001$;图3-D)。

2.4 亚致死浓度对NIVg、NIVgR及卵巢发育的影响

亚致死浓度烯啶虫胺对羽化2 d褐飞虱雌成虫

体内NIVg表达量无显著影响($t=1.7, P=0.158$;图4-A),而羽化4 d后,褐飞虱雌成虫体内NIVg表达水平与对照组相比显著下降了57.5%($t=8.7, P<0.001$;图4-B)。而亚致死浓度烯啶虫胺处理对不同羽化时间的褐飞虱雌成虫的NIVgR的表达水平均无显著影响(羽化2 d: $t=0.6, P=0.575$;羽化4 d: $t=1.1, P=0.333$;图4-C~D)。

亚致死浓度烯啶虫胺处理同样对褐飞虱雌成虫卵巢发育均有不同程度的抑制。与对照相比(图5-A~B),取食亚致死浓度烯啶虫胺处理的水稻后,羽化2 d的雌成虫卵巢内没有观察到成熟的卵母细胞(图5-C),而羽化4 d的雌成虫体内只有少量成熟的卵母细胞(图5-D)。

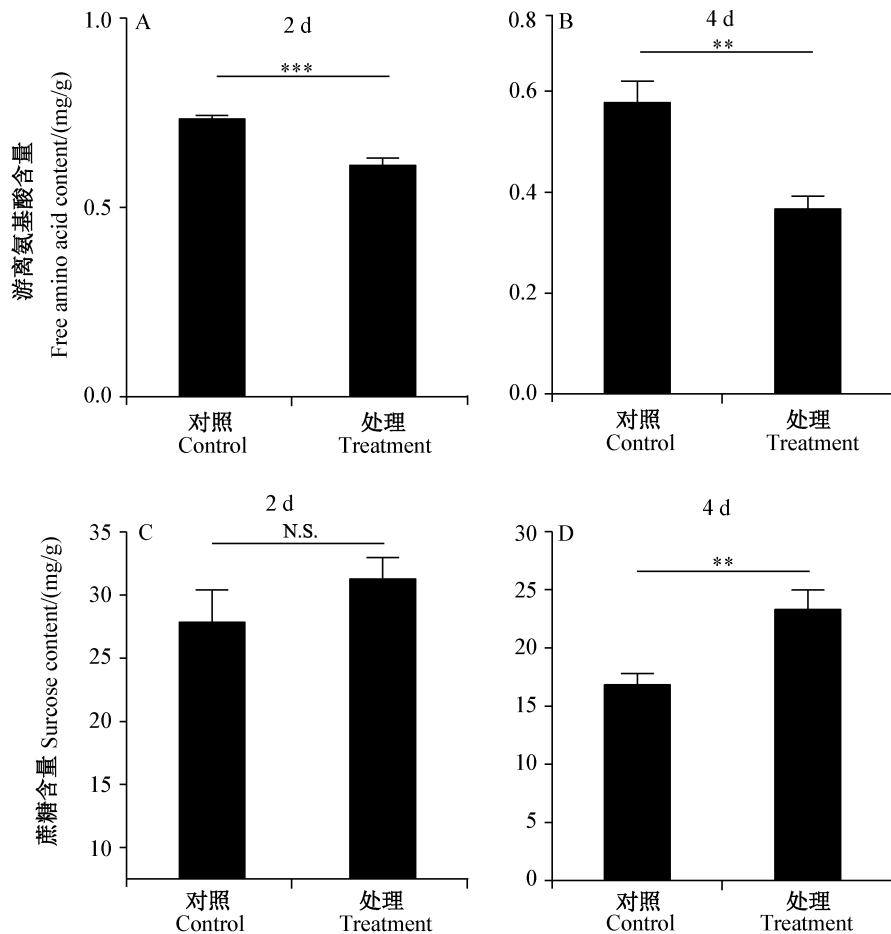


图2 亚致死浓度烯啶虫胺对水稻中蔗糖(A、B)和游离氨基酸(C、D)含量的影响

Fig. 2 Effect of sublethal concentrations of nitenpyram on the content of sucrose (A, B) and free amino acids (C, D) in rice

图中数据为平均数±标准误。**和***表示处理与对照之间经独立样本 *t* 检验法检验差异显著 ($P < 0.01$ 和 $P < 0.001$)；N.S. 表示无显著差异。Data are mean±SE. ** or *** indicates significant difference between treatment and control groups by *t* test ($P < 0.01$ or $P < 0.001$); N.S. indicates no significant difference.

2.5 亚致死浓度烯啶虫胺对雌成虫繁殖参数的影响

亚致死浓度烯啶虫胺还能够显著影响褐飞虱雌成虫主要的生殖参数。与对照组相比,亚致死浓度烯啶虫胺处理后,褐飞虱雌成虫产卵量显著减少了58.1% ($t=9.0$, $P < 0.001$),且雌成虫寿命($t=8.6$, $P < 0.001$)与雌成虫产卵历期($t=5.5$, $P=0.005$)分别显著缩短了28.0%和36.7%,但产卵前期与对照组相比无显著差异($t=5.5$, $P=0.067$;表1)。

3 讨论

已有研究表明,外源农药的喷施会引起水稻植株体内生理生化物质代谢发生改变,从而影响褐飞虱种群参数以及生殖参数(Wu et al., 2004; Xi et al., 2022)。本研究结果显示,亚致死浓度烯啶虫胺处理水稻4 d后,与对照相比,水稻体内草酸含量升高了20.5%,水稻机体草酸可能对褐飞虱生殖以及子代

种群数量起到抑制作用。草酸是植物组织中一种常见的二羧酸,可以保护寄主植物免受植食性害虫的侵害(Kang et al., 2023)。有研究表明,水稻中草酸含量与对褐飞虱的抗性显著正相关,抗性品系水稻中草酸含量显著高于正常品系(商科科, 2012; 李明阳等, 2020)。类黄酮是植物中一类分布最为广泛的次生代谢产物,可作为抗氧化剂减少植物组织中的活性氧(reactive oxygen species, ROS),同时抑制植食性害虫的取食和生长发育,在植物组成型防御中起到关键作用(Mierziak et al., 2014; Himanshi et al., 2023)。在本研究中,亚致死浓度烯啶虫胺处理水稻2 d和4 d后,与对照相比,类黄酮含量分别升高了9.6%和40.6%,类黄酮含量的升高可能对褐飞虱雌成虫的卵巢发育以及生殖力有一定抑制效果。这与其他研究结果一致,如凌冰等(2007)研究发现,在人工饲料中添加类黄酮外源也能够显著降低褐飞

虱的存活率以及排蜜露量; Silva et al. (2016) 研究结果也显示食物中高浓度的类黄酮会引起草地贪

夜蛾 *Spodoptera frugiperda* 幼虫发育历期延长, 幼虫体重与蛹重以及生殖力均显著降低。

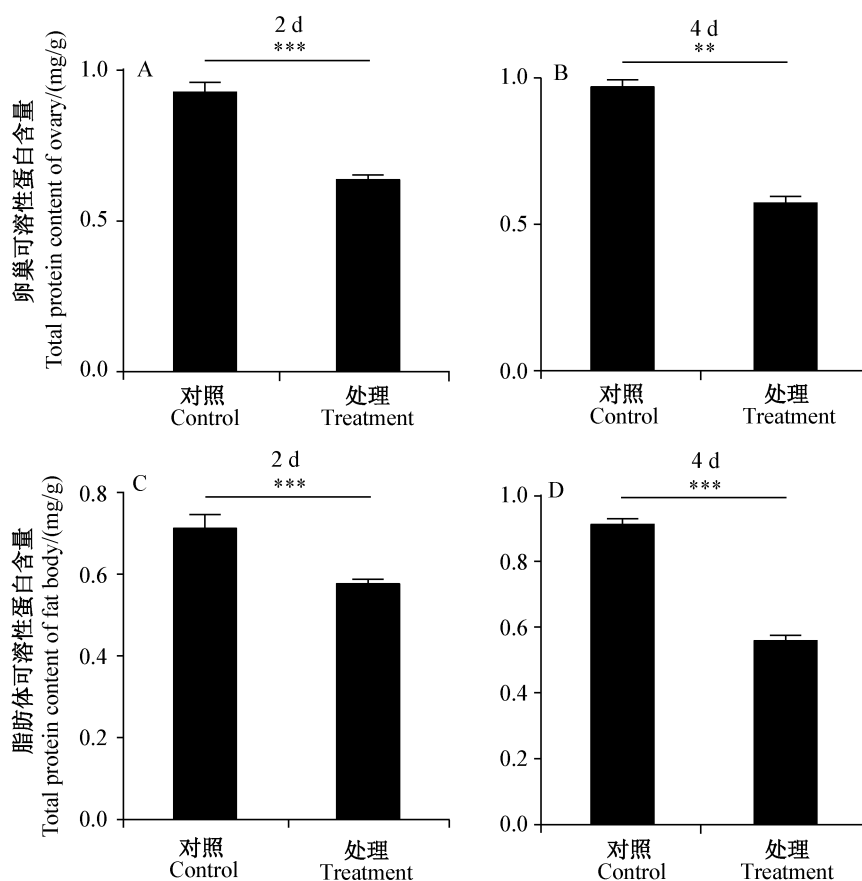


图3 亚致死浓度烯啶虫胺对褐飞虱雌成虫卵巢(A、B)以及脂肪体(C、D)中可溶性蛋白含量的影响

Fig. 3 Effects of sublethal concentrations of nitenpyram on soluble protein content in ovaries (A, B) and fat bodies (C, D) of female *Nilaparvata lugens*

图中数据为平均数±标准误。**和***表示处理与对照之间经独立样本 *t* 检验法检验差异显著 ($P < 0.01$, $P < 0.001$)。Data are mean±SE. ** or *** indicates significant difference between treatment and control groups by *t* test ($P < 0.01$ or $P < 0.001$).

寄主植物作为植食性昆虫的主要营养来源, 不仅可以影响植食性昆虫的生长发育表现, 也可以通过体内营养物质的含量影响植食性昆虫对杀虫剂的易感性 (Vogelweith et al., 2011; Wang et al., 2021; 宋程飞等, 2022)。糖以及氨基酸是植物生长发育、机体代谢所需的重要物质 (Hildebrandt et al., 2015; Li et al., 2020; 麦翠珊等, 2023)。已有研究表明, 植物机体内可溶性糖和氨基酸含量的变化会影响植物对害虫的抗性, 以及害虫对杀虫剂的敏感性 (韩永强等, 2017; Liu et al., 2020)。本研究发现亚致死浓度烯啶虫胺处理水稻 2 d 和 4 d 后, 与对照相比, 2 d 时蔗糖含量无显著差异, 4 d 时升高了 38.5%, 游离氨基酸含量分别下降了 20.1% 和 42.4%, 即水稻体内碳氮比相对增加, 而水稻中碳氮比的增加可能抑制

了褐飞虱卵巢发育以及繁殖。Wu et al. (2021) 也得到相似的结论, 即三氟苯嘧啶拌种处理水稻后蔗糖含量显著增加, 游离氨基酸含量显著减少, 碳氮比上升, 从而抑制褐飞虱的取食。在对草地贪夜蛾的研究中同样发现, 食物中碳氮比升高, 幼虫免疫力降低, 更易受病毒侵染 (Povey et al., 2014)。寄主植物碳氮比的变化会直接影响害虫的营养摄入 (Zhao et al., 2024)。碳氮比的升高意味着植物体内的氮含量相对减少, 而氮是蛋白质、核酸等生物大分子的基本组成元素, 对昆虫的生长发育和繁殖至关重要 (Awmack & Leather, 2002), 氮缺乏会导致昆虫体内蛋白质合成受阻, 进而影响其生长速率和生殖能力 (Rode et al., 2017)。

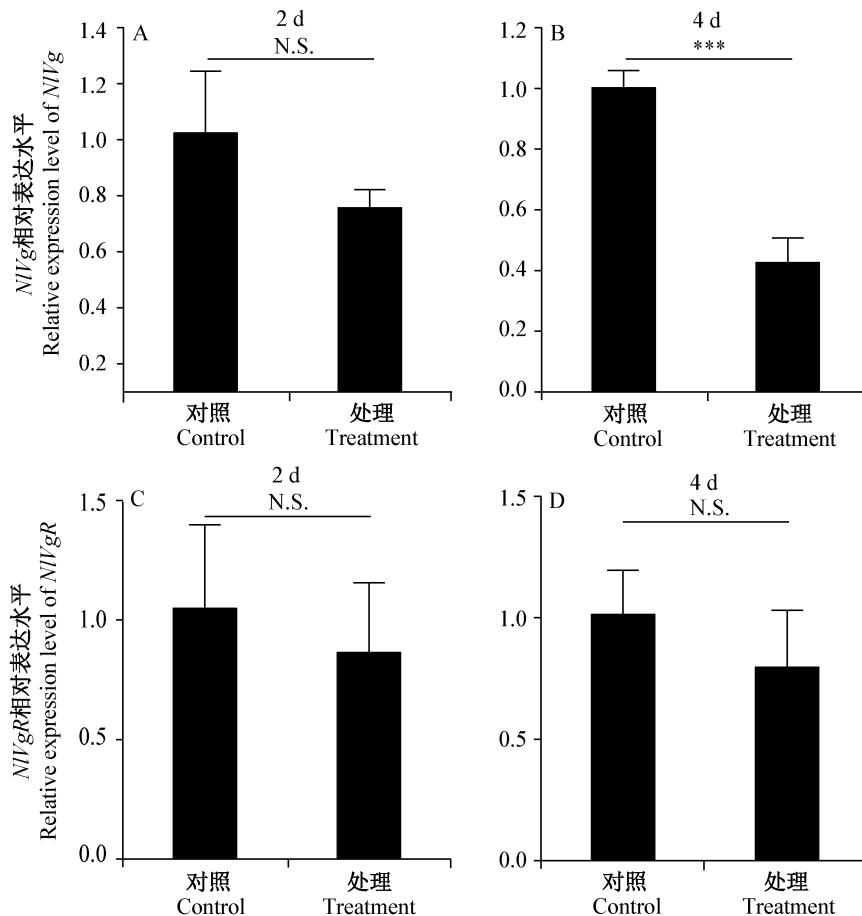


图4 亚致死浓度烯啶虫胺对褐飞虱雌成虫 *NIVg* (A、B) 和 *NIVgR* (C、D) 表达量的影响

Fig. 4 Effects of sublethal concentrations of nitenpyram on the expression level of *NIVg* (A, B) and *NIVgR* (C, D) in female adult *Nilaparvata lugens*

图中数据为平均数±标准误。***表示处理与对照之间经独立样本 *t* 检验法检验差异显著 ($P < 0.001$)；N.S. 表示无显著差异。Data are mean±SE. *** indicates significant difference between treatment and control groups by *t* test ($P < 0.001$); N.S. indicates no significant difference.

亚致死浓度烯啶虫胺除了能够引起水稻生理生化物质发生改变从而降低褐飞虱生殖力,也会直接作用于褐飞虱产生亚致死效应。本研究结果表明,3龄若虫取食烯啶虫胺处理的水稻后,褐飞虱雌成虫在羽化2 d和4 d时,卵巢中可溶性蛋白含量分别下降了31.2%和40.9%;脂肪体中可溶性蛋白含量分别下降了19.0%和38.8%;褐飞虱雌成虫 *NIVg* 表达水平在羽化4 d时下降了57.5%;并且雌成虫产卵量减少了58.1%、产卵历期下降了36.7%以及寿命缩短28.0%。*Vg*和*VgR*是调节昆虫繁殖力的重要蛋白质,*Vg*为胚胎发育提供了营养来源,在昆虫的脂肪体内合成,之后被分泌到血淋巴中,最终通过*VgR*介导的内吞作用进入卵母细胞(Tufail & Take-da, 2009; Shen et al., 2019; 赵静等, 2021)。已有研究表明,亚致死浓度杀虫剂会影响害虫生殖相关基因 *Vg* 和 *VgR* 的表达水平、卵巢发育以及生殖

力,如 LC_{10} 和 LC_{30} 甲胺基阿维菌素处理后,荔枝蛀蒂虫 *Conopomorpha sinensis* 雌成虫的 *CsVg* 和 *CsVgR* 的表达水平显著降低,卵巢发育和繁殖力受到抑制(Yao et al., 2018); LC_{10} 噻虫嗪显著降低了白背飞虱 F_1 代雌成虫产卵量(杨航等, 2017); LC_{10} 、 LC_{15} 和 LC_{20} 烯啶虫胺处理后中红侧沟茧蜂 *Microplitis mediator* 成蜂寿命、雌雄比例以及成蜂体质量均有所降低(闫虹江等, 2021)。当亚致死浓度烯啶虫胺作用到害虫时,可能会影响其能量代谢,导致能量短缺,从而将体内能量资源优先分配给生存所需能量,因此影响其生殖力(Shi et al., 2011; Gong et al., 2023)。

本研究分别从亚致死浓度烯啶虫胺对水稻体内生理生化指标的变化以及褐飞虱雌成虫生殖参数的影响2方面分析了亚致死浓度烯啶虫胺对褐飞虱的影响,有助于进一步评价烯啶虫胺对褐飞虱种群的

控制效果及控制机理,而烯啶虫胺如何引起水稻生理生化指标发生变化以及水稻响应烯啶虫胺而产生的“增强抗性”与“牺牲营养”之间的权衡还有待进一步研究。



A~B: 羽化2 d和4 d的健康褐飞虱雌成虫卵巢；C~D: 亚致死浓度烯啶虫胺处理后，羽化2 d和4 d的褐飞虱雌成虫卵巢。A~B: Ovaries of *Nilaparvata lugens* healthy females at two or four days after emergence; C~D: ovaries of *N. lugens* females treated with sublethal concentrations of nitenpyram at two or four days after emergence.

图5 亚致死浓度烯啶虫胺对褐飞虱雌成虫卵巢发育的影响

Fig. 5 Effects of sublethal concentrations of nitenpyram on ovarian development in *Nilaparvata lugens* females

表1 亚致死浓度烯啶虫胺对褐飞虱雌成虫生殖参数的影响

Table 1 Effect of sublethal concentrations of nitenpyram on reproductive parameters of *Nilaparvata lugens* females

生殖参数 Reproductive parameter	对照组 Control	处理组 Treatment
产卵量 No. of eggs laid per female	250.0±15.9 a	104.7±2.7 b
雌成虫寿命 Longevity of females	25.0±0.6 a	18.0±0.6 b
雌成虫产卵前期 Preoviposition period of females	3.3±0.3 a	5.0±0.6 a
雌成虫产卵历期 Oviposition period of females	20.0±0.6 a	12.7±1.2 b

表中数据为平均数±标准误。同行不同小写字母表示处理与对照之间经独立样本 *t* 检验法检验差异显著 ($P<0.01$)。Data are mean±SE. Different lowercase letters in the same row indicate significant difference between treatment and control groups by *t* test ($P<0.01$).

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