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目 次

亚热带典型树种对模拟酸雨胁迫的高光谱响应.....	时启龙, 江 洪, 陈 健, 等 (5621)
珠江三角洲地面风场的特征及其城市群风道的构建.....	孙 武, 王义明, 王越雷, 等 (5630)
粤北山地常绿阔叶林自然干扰后冠层结构与林下光照动态.....	区余端, 苏志尧 (5637)
四种猎物对南方小花蝽生长发育和繁殖的影响.....	张昌容, 鄧军锐, 莫利锋 (5646)
普洱季风常绿阔叶林次生演替中木本植物幼苗更新特征.....	李帅锋, 刘万德, 苏建荣, 等 (5653)
喀斯特常绿落叶阔叶混交林物种多度与丰富度空间分布的尺度效应.....	张忠华, 胡 刚, 祝介东, 等 (5663)
格氏栲天然林土壤养分空间异质性.....	苏松锦, 刘金福, 何中声, 等 (5673)
种植香根草对铜尾矿废弃地基质化学和生物学性质的影响.....	徐德聪, 詹 婧, 陈 政, 等 (5683)
灌溉对三种荒漠植物蒸腾耗水特性的影响.....	单立山, 李 毅, 张希明, 等 (5692)
真盐生植物盐角草对不同氮形态的响应.....	聂玲玲, 冯娟娟, 吕素莲, 等 (5703)
鹿泉沟自然保护区寒温性针叶林演替优势种格局动态分析.....	张钦弟, 毕润成, 张金屯, 等 (5713)
不同水肥条件下 AM 真菌对丹参幼苗生长和营养成分的影响.....	贺学礼, 马 丽, 孟静静, 等 (5721)
垄沟覆膜栽培冬小麦田的土壤呼吸.....	上官宇先, 师日鹏, 韩 坤, 等 (5729)
不同方式处理牛粪对大豆生长和品质的影响.....	郭立月, 刘雪梅, 战丽杰, 等 (5738)
基于大气沉降与径流的乌鲁木齐河源区氮素收支模拟.....	王圣杰, 张明军, 王飞腾, 等 (5747)
基于能值理论的循环复合农业生态系统发展评价——以福建省福清星源循环农业产业示范基地为例.....	钟珍梅, 翁伯琦, 黄勤楼, 等 (5755)
低温暴露和恢复对棘胸蛙雌性亚成体生存力及能量物质消耗的影响.....	凌 云, 邵 晨, 颜志刚, 等 (5763)
暗期干扰对棉铃虫两个不同地理种群滞育抑制作用的比较.....	陈元生, 涂小云, 陈 超, 等 (5770)
水土流失治理措施对小流域土壤有机碳和全氮的影响.....	张彦军, 郭胜利, 南雅芳, 等 (5777)
不同管理主体对泸沽湖流域生态系统影响的比较分析.....	董仁才, 苟亚青, 李思远, 等 (5786)
连江鱼类群落多样性及其与环境因子的关系.....	李 捷, 李新辉, 贾晓平, 等 (5795)
溶氧水平对鲫鱼代谢模式的影响.....	张 伟, 曹振东, 付世建 (5806)
象山港人工鱼礁区的网采浮游植物群落组成及其与环境因子的关系.....	江志兵, 陈全震, 寿 鹿, 等 (5813)
填海造地导致海湾生态系统服务损失的能值评估——以套子湾为例.....	李睿倩, 孟范平 (5825)
城市滨水景观的视觉环境质量评价——以合肥市为例.....	姚玉敏, 朱晓东, 徐迎碧, 等 (5836)
专论与综述	
生态基因组学研究进展.....	施永彬, 李钧敏, 金则新 (5846)
海洋酸化生态学研究进展.....	汪思茹, 殷克东, 蔡卫君, 等 (5859)
纺锤水蚤摄食生态学研究进展.....	胡思敏, 刘 胜, 李 涛, 等 (5870)
河口生态系统氨氧化菌生态学研究进展.....	张秋芳, 徐继荣, 苏建强, 等 (5878)
嗜中性微好氧铁氧化菌研究进展.....	林超峰, 龚 骏 (5889)
典型低纬度海区(南海、孟加拉湾)初级生产力比较.....	刘华雪, 宋星宇, 黄洪辉, 等 (5900)
植物叶片最大羧化速率及其对环境因子响应的研究进展.....	张彦敏, 周广胜 (5907)
中国大陆鸟类栖息地选择研究十年.....	蒋爱伍, 周 放, 覃 玥, 等 (5918)
研究简报	
孵化温度对赤链蛇胚胎代谢和幼体行为的影响.....	孙文佳, 俞 霄, 曹梦洁, 等 (5924)
不同培肥茶园土壤微生物量碳氮及相关参数的变化与敏感性分析.....	王利民, 邱珊莲, 林新坚, 等 (5930)
施肥对两种莧菜吸收积累镉的影响.....	李凝玉, 李志安, 庄 萍, 等 (5937)

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封面图说: 冬天低空飞翔的丹顶鹤——丹顶鹤是鹤类中的一种, 因头顶有“红肉冠”而得名。是东亚地区特有的鸟种, 因体态优雅、颜色分明, 在这一地区的文化中具有吉祥、忠贞、长寿的象征, 是传说中的仙鹤, 国家一级保护动物。丹顶鹤具备鹤类的特征, 即三长——嘴长、颈长、腿长。成鸟除颈部和飞羽后端为黑色外, 全身洁白, 头顶皮肤裸露, 呈鲜红色。丹顶鹤每年要在繁殖地和越冬地之间进行迁徙, 只有在日本北海道等地是留鸟, 不进行迁徙, 这可能与冬季当地人有组织地投喂食物, 食物来源充足有关。

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陈元生, 涂小云, 陈超, 匡先钜, 薛芳森. 暗期干扰对棉铃虫两个不同地理种群滞育抑制作用的比较. 生态学报, 2012, 32(18): 5770-5776.

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暗期干扰对棉铃虫两个不同地理种群 滞育抑制作用的比较

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摘要: 至今, 所测试昆虫的光周期反应均表明, 光周期反应对暗期干扰高度敏感, 短暂的光脉冲都可在不同程度上逆转长夜效应, 抑制滞育的发生。在研究了棉铃虫 *Helicoverpa armigera* 泰安种群 (36. 15°N, 116. 59°E) 和喀佐种群 (41. 34°N, 120. 27°E) 光周期反应的基础上, 在滞育诱导的短光周期下 (L12:D12 和 L9:D15), 分别测试了暗期不同时段 1h 光脉冲对这两个不同地理种群滞育抑制的影响。25 和 22℃ 下的光周期反应显示了泰安种群在长暗期 11—14 h 的滞育率均显著低于喀佐种群; 泰安种群的临界暗长分别为 11. 7 h 和 11. 5 h, 喀佐种群分别为 10. 5 h 和 10. 3 h, 泰安种群均比喀佐种群长 1. 2 h。在所测试的暗期干扰实验中, 除了极少数光脉冲干扰点外, 泰安种群蛹滞育率显著低于喀佐种群, 但两者的滞育反应曲线基本相似。在短光周期 L9:D15 下, 泰安种群和喀佐种群均显示了光脉冲落入暗期的第 9—11 小时最有效地抑制了滞育的发生。在短光周期 L12:D12 下, 泰安种群和喀佐种群在 25℃ 时均显示了光脉冲落入暗期的第 3—4 小时和第 10 小时导致了最低的滞育发生; 但在 22℃ 时, 喀佐种群只在暗期的第 3—4 小时显示了最高的滞育抑制。这些结果揭示了偏南的泰安种群对暗期干扰的敏感性强于偏北的喀佐种群, 但这两个地理种群的最高光敏感位点基本相同。

关键词: 棉铃虫; 滞育; 光周期; 温度; 暗期干扰; 地理种群

A comparison of night-interruption on diapause-averting among two populations of the cotton bollworm, *Helicoverpa armigera*

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Abstract: Photoperiodic time measurement in insects can be affected by interrupting the dark phase of the light dark cycle with short supplementary light pulses. All the photoperiodic responses tested are highly sensitive to night interruption, and the long night effect is reversed by a light break. Most past studies revealed two points of apparent light sensitivity (the so-called A and B peaks), but the response pattern varied considerably among different species. Some species had only one peak (or trough), either A or B. Even the same species may have different patterns of response depending on the experimental conditions. However, it is still not clear whether differences exist in the effect of night-interruption on diapause-averting among different geographic populations. The cotton bollworm, *Helicoverpa armigera* (Hübner) is one of the most serious crop pests in Asia, Australia, Africa and Europe. The species is distributed across much of China and

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attacks many host plants. The widely distributed *H. armigera* encounters a great diversity in climatic conditions in different places and shows different critical day lengths or night lengths (the day length that elicits 50% diapause response) among different geographic populations. In the present study, the photoperiodic response and effects of night-interruption on diapause-averting, in which the scotophases of L9:D15 (Light 9 h:Dark 15 h) and L12:D12 were interrupted by 1 h light pulse, were investigated at 22°C and 25°C in Taian (TA, 36.15°N, 116.59°E) and Kazuo (KZ, 41.34°N, 120.27°E) populations of the cotton bollworm *H. armigera*. The photoperiodic response curves showed that the incidences of diapause in the scotophases of 11—14 h were significantly lower in the Taian population than in the Kazuo population. The critical night length in the Taian population at 25°C and 22°C was 11 h 42 min and 11 h 30 min, respectively, and 1 h 20 min longer than that in Kazuo population (10 h 30 min and 10 h 18 min). In all night-interruption experiments, the incidences of diapause in almost all positions of light pulse in the Taian population were significantly lower than that in the Kazuo population. However, the diapause response curves were similar in the two populations. Under L9:D15, the incidence of diapause was inhibited most effectively in both the Taian population and the Kazuo populations when the light pulses were placed at 9—11 h in the darkness. Under L12:D12 the incidence of diapause was lowest at 25°C in both Taian population and Kazuo population when the light pulses were placed at 3—4 h and 10 h in the darkness. However, the Kazuo population only showed a peak of diapause-averting occurring in 3—4 h in the darkness at 22°C.

Our results reveal that effect of night-interruption on diapause-averting is different among different geographic population. The southern Taian population is more sensitive to night-interruption than the northern Kazuo populations, but the most highly photosensitive position is similar for both populations.

A light pulse plays two possible roles in photoperiodic time measurement. First it ‘initiates’ or ‘resets’ the clock; this has been called the ‘entraining agent’ or ‘priming agent’. Second it ‘measures’ a critical duration of day or night; this has been called the ‘inductive agent’ or ‘terminating agent’. The present study in *H. armigera* reveals that a light pulse can reset the process measuring night length, and thus influences the incidence of diapause.

Key Words: *Helicoverpa armigera*; diapause; photoperiod; temperature; night interruption; geographic population

暗期干扰试验是指在暗期不同时段采用单一的光照(亦称光脉冲)干扰昆虫的光周期反应。1949年 Dickson 首次将这种试验方案应用于昆虫梨小食心虫 *Grapholitha molesta* 幼虫滞育的研究,结果表明,在滞育诱导的短光周期(L12:D12)条件下,在暗期的中期给予 2 h 的光脉冲能够抑制滞育的发生^[1]。继后,它成为分析昆虫光周期时间测量特性的主要手段之一。通过这个试验可以探明是否光的启动或关闭重新启动了昆虫的时间测量,夜间的哪一时段对光最敏感^[2-3]。至今,所测试昆虫的光周期反应均显示了对暗期干扰高度敏感,短暂的光脉冲可在不同程度上逆转长夜效应,抑制滞育的发生^[4-15]。随着研究的不断深入,进一步揭示了不同的昆虫具有不同的光敏感位点^[16],即光脉冲对不同的昆虫具有不同的滞育抑制效果^[17-22]。有些种类分别在暗期初期和暗期后期显示对光脉冲最敏感,分别称为 A 峰和 B 峰或 A 槽和 B 槽^[23],有些种类仅显示 A 峰或 B 峰^[24-25];有些种类最高光敏感期出现在暗期的中期^[11, 13]。此外,由于实验条件的不同(如光脉冲长度、干扰的光周期背景、试验温度不同等),同种昆虫也可能出现不同的光敏感位点^[6, 11-15, 26-27]。那么,同种昆虫的不同地理种群之间是否也存在不同的光敏感位点、具有不同的滞育抑制效果?迄今尚未见报道。

棉铃虫 *Helicoverpa armigera* (Hübner) 是全球最重要的农业害虫之一,有关棉铃虫滞育诱导光周期反应的地理变异国内已有一些报道。研究表明,不同的地理种群对光周期的反应存在一定的差异,随着种群所处位置的南移,棉铃虫的临界光周缩短,对光周期反应的敏感性逐渐减弱^[28]。但有关棉铃虫暗期干扰的滞育反应,尚未见报道。为此,展了本项研究,旨在探明光脉冲对不同地理种群棉铃虫滞育抑制的作用效果,以期进一步了解该虫光周期时间测量的特点,为分析昆虫光周期控制滞育的进化提供基础资料。

1 材料与方法

1.1 供试虫源

供试棉铃虫分别于2010年7—8月采自山东泰安(以下简称为TA, 36.15°N, 116.59°E)、辽宁喀佐(以下简称为KZ, 41.34°N, 120.27°E),采集的均为高龄幼虫。幼虫在室内用人工饲料^[29]、在25℃、L16:D8的光周期条件下饲养,3龄前在24孔板内群养,3龄后在21孔冰格板内单养,成虫用复合维生素糖水饲喂^[30],成虫产卵后孵出的幼虫用于试验。

1.2 试验方法

整个幼虫期在25℃和22℃下分两组试验,第一组在光周期L9:D15、L10:D14、L11:D13、L12:D12、L13:D11、L14:D10、L15:D9和L16:D8条件下观察棉铃虫泰安种群(TA)和喀佐种群(KZ)的光周期反应,确定其临界暗长(诱导50%个体进入滞育的光周期界限);第二组暗期干扰的光周期背景采用L9:D15和L12:D12(均为滞育诱导的光周期),暗期处理采用人工方法进行,在暗期每隔1h给予1h的光干扰(光照强度为500—700 lx),在整个幼虫期的每天的暗期均是如此。各处理设3次重复。以上实验均在新苗光照培养箱GZX-250BS-Ⅲ中进行,光照强度为500—700 lx,箱内的温度变化为±0.5℃。

棉铃虫滞育蛹的判断依据蛹的眼点移动情况判断,在上述各条件下幼虫化蛹后10 d眼点位置仍无变化的蛹判定为滞育个体^[31]。然后统计各处理的滞育率。

试验数据中各处理间滞育率的差异分析采用SPSS13.0软件中的Crosstabs(交叉表)法中的卡方检验法(Chi-square)。

2 结果

2.1 滞育诱导的光周期反应

不同地理种群棉铃虫滞育诱导的光周期反应结果见图1。从图1可知,在25℃下,TA种群在长暗期10—14 h的滞育率显著低于KZ种群,TA种群临界暗长(11 h 42 min左右)比KZ种群的临界暗长(10 h 30 min左右)延长了1 h 12 min。在22℃下,TA种群在长暗期10—15 h的滞育率也显著低于KZ种群,TA种群临界暗长(11 h 30 min左右)比KZ种群的临界暗长(10 h 18 min左右)也延长了1 h 12 min。结果表明,偏南的TA种群棉铃虫对滞育诱导的光周期的反应比KZ种群更弱些。

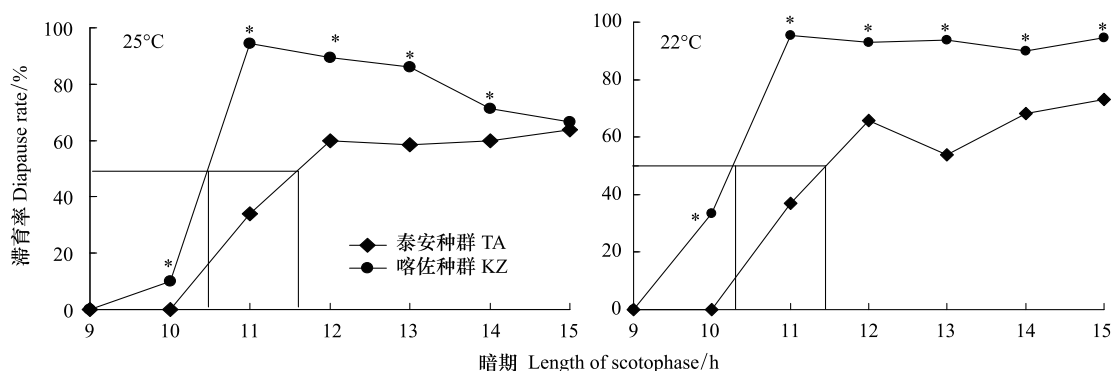


图1 不同地理种群棉铃虫滞育诱导的光周期反应

Fig. 1 Photoperiodic response curves for diapause induction in different geographic populations of *H. armigera*

图中“*”表示在相同暗期点两种群滞育率有显著性差异(Chi-Square 检验, $P < 0.05$),每观察点的样本数为45—107头

2.2 不同地理种群暗期干扰的滞育反应

棉铃虫TA种群和KZ种群在25和22℃、光周期L9:D15和L12:D12下,暗期不同时段采用1h光脉冲的滞育反应结果见表1和图2。从图2可见,在绝大多数光干扰位点,TA种群的滞育率均显著低于KZ种群(Chi-Square 检验, $P < 0.05$),但两种群呈现出相似的滞育反应曲线。

在25℃、L9:D15条件下,TA种群和KZ种群均显示了两个明显的滞育抑制槽,A槽均出现在暗期的第6

h,其间的1h光脉冲分别导致了73.04%和53.85%个体发育;TA种群B槽出现在暗期的第10—11h,KZ种群B槽出现在暗期的第9—11h,其间的1h光脉冲导致了83%以上的个体发育(图2A)。相似的结果也出现在22℃、L9:D15条件下,落入在暗期第6h和9—11h的光脉冲最有效地抑制了滞育的发生(图2C)。上述结果表明,TA种群最高光敏感位点落在暗期第10—11h,KZ种群最高光敏感位点落在暗期第9—10h。

在25℃、L12:D12条件下,TA种群和KZ种群也显示了两个明显的滞育抑制槽,A槽出现在暗期第3—4h,此时的光脉冲导致了100%个体发育;B槽出现在暗期的第10h,此时的光脉冲也导致了几乎100%个体发育(图2B)。在22℃、L12:D12条件下,TA种群分别在暗期的第3—5、7和10h显示了最高的滞育抑制,100%个体发育;而KZ种群仅在暗期的第3—4h显示了最高的滞育抑制,发育个体均超过了90%(图2D)。

表1 棉铃虫TA种群和KZ种群在暗期干扰下的滞育率

Table 1 The incidence of diapause between Taian and Kazuo populations of *H. armigera* under night interruption

处理 Treatment	25℃, L9:D15				25℃, L12:D12				22℃, L9:D15				22℃, L12:D12			
	滞育率%		样本数		滞育率%		样本数		滞育率%		样本数		滞育率%		样本数	
	TA	KZ	TA	KZ	TA	KZ	TA	KZ	TA	KZ	TA	KZ	TA	KZ	TA	KZ
1	63.89	66.67	58	48	56.14	82.46	57	57	73.33	94.59	60	74	62.07	100.0	58	39
2	60.94	73.33	87	60	9.62	25.00	52	48	44.44	73.68	54	57	47.36	72.00	57	50
3	57.69	76.92	74	65	0.00	0.00	53	52	50.00	96.77	64	62	0.00	4.17	57	48
4	62.50	71.19	72	59	0.00	0.00	48	49	64.71	88.24	68	51	2.86	6.67	70	45
5	47.95	50.00	73	60	13.04	25.00	46	56	73.08	84.62	52	39	5.26	45.45	57	44
6	26.56	46.15	64	78	40.47	69.23	42	52	0.00	27.78	54	54	65.38	78.18	52	55
7	50.00	77.08	68	48	34.18	61.91	79	42	31.25	84.21	64	57	39.29	89.80	56	49
8	30.65	25.00	62	56	17.46	56.00	63	50	4.55	90.00	44	60	71.70	70.59	53	68
9	16.98	0.00	53	62	9.52	35.48	42	62	0.00	9.09	42	44	65.45	88.00	55	50
10	0.00	3.33	79	60	4.35	0.00	46	44	0.00	2.63	44	38	26.67	69.57	45	46
11	1.28	6.25	78	64	3.45	30.43	58	46	0.00	4.55	42	42	34.88	84.21	43	57
12	34.78	42.86	69	42					64.28	87.50	56	48				
13	56.67	73.08	60	52					44.44	75.00	54	40				
14	42.11	63.64	76	44					73.68	85.71	38	42				

TA: 泰安种群 Taian population; KZ: 喀佐种群 Kazuo population

3 讨论

本研究结果显示,光脉冲对不同地理种群棉铃虫滞育的抑制效果存在明显差异,即棉铃虫对暗期干扰的滞育反应存在地理变异。本试验首次揭示了低纬度(36.15°N)的棉铃虫TA种群对暗期干扰的反应比高纬度(41.34°N)的KZ种群更敏感,即在相同的光周期和温度条件下,TA种群在绝大多数光脉冲干扰位点的滞育发生率均显著低于KZ种群,且TA种群滞育抑制槽更宽(图2)。这两个地理种群在暗期干扰试验中出现的差异主要是由这两个地理种群对光周期的敏感性不同所致,如图1所示,TA种群棉铃虫在绝大多数短光照条件下的滞育率均显著低于KZ种群,TA种群棉铃虫对光周期反应的敏感性比KZ种群更弱,即对暗期要求更高。结果还显示,虽然在绝大多数光干扰位点TA种群的滞育率显著低于KZ种群,但两种群呈现出相似的滞育反应曲线,最高光敏感也基本相似,这也反映了同种昆虫不同地理种群对光周期反应的相似性。

在光周期时间测量中,光脉冲可能起着两种作用:(1)启动或调整光周期钟,作为“导入因子”^[32]或“启动因子”^[20];(2)测量临界暗长或日长,称为“诱导因子”^[32]或“中止因子”^[20],即光脉冲中断了暗长的测量过程,并重新调整光周期钟进行下一次测量,从而将光脉冲分隔的两个暗长分别作为两个不同的暗期看待,只要光脉冲分隔的前后两个暗期的长度短于临界暗长,滞育就被有效抑制^[13, 33]。光脉冲对棉铃虫滞育反应的影响,不存在上述第(2)种作用,即与分隔的暗期长度无关,光脉冲可能起“启动或调整光周期钟”作用。

据Furunishi等报道,在24h昼夜循环的长夜光周期中,1h光脉冲出现在比临界暗期少1h左右的位点

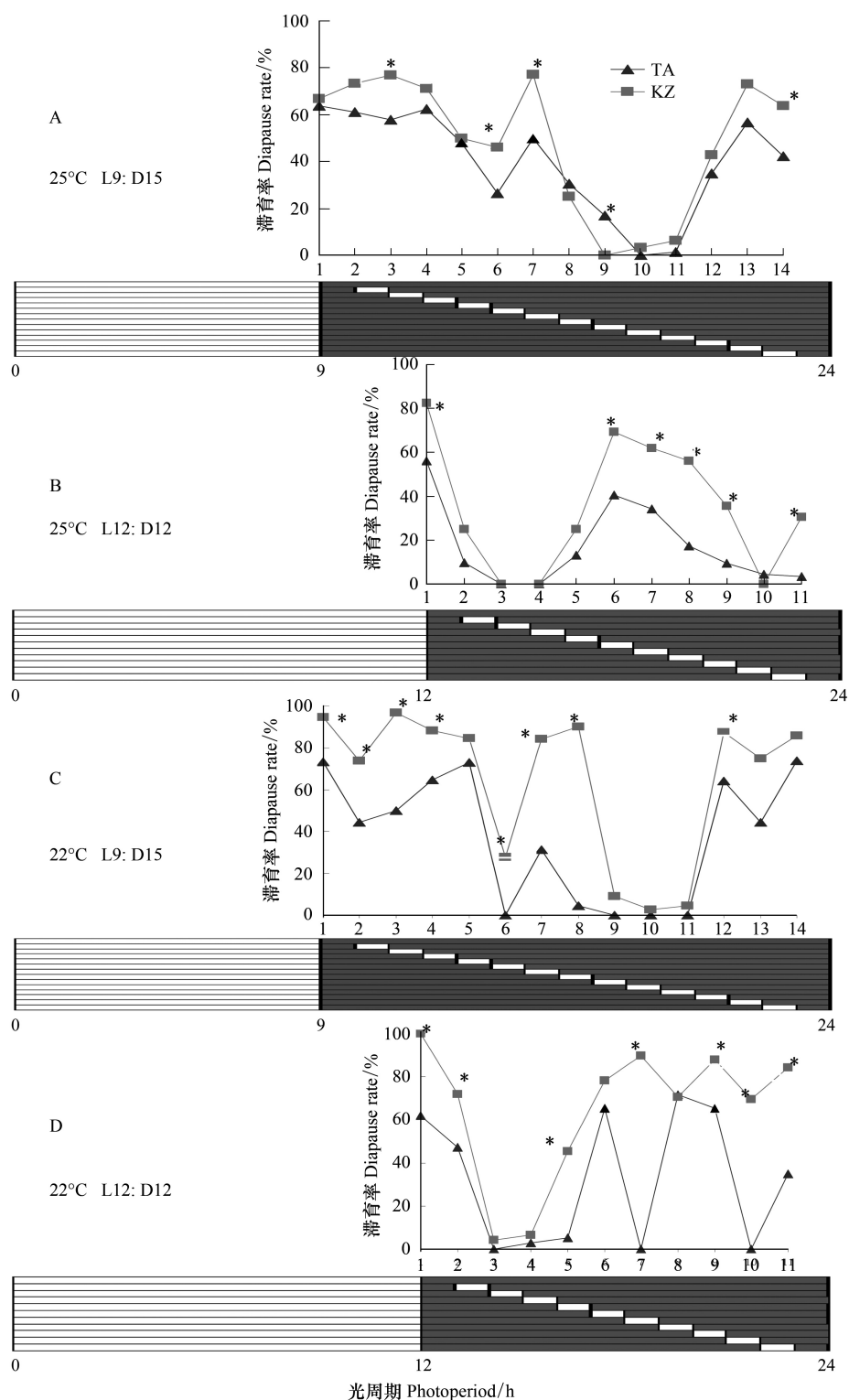


图2 棉铃虫 TA 种群和 KZ 种群在 25℃ 和 22℃、光周期 L9:D15 和 L12:D12 下, 暗期不同时段采用 1h 光脉冲的滞育反应

Fig. 2 The incidence of diapause between Taian and Kazuo populations of *H. armigera* under L9:D15 or L12:D12 at 25 °C or 22 °C when the scotophases were interrupted by the light pulse of 1h

图中“*”表示在相同光脉冲点两种群滞育率有显著性差异 (Chi-Square 检验, $P < 0.05$)

上时, 滞育抑制效果最好^[34]。本研究在短光周期 L9:D15 条件下 1h 的暗期干扰试验也得到相似的结果, 25℃ 时, TA 种群 1 h 光脉冲出现在暗期第 10—11 小时位点 (临界暗长 11.7 h), KZ 种群 1 h 光脉冲出现在暗期第

9—10 小时位点(临界暗长 10.5 h),滞育抑制效果最好(几乎 100% 个体发育)(图 2A);22℃ 时,TA 种群在暗期第 9—11h 位点(临界暗长 11.5 h),KZ 种群在暗期第 10 h 位点(临界暗长 10.3 h),光脉冲敏感性最高(100% 个体发育)(图 2C)。然而,在短光周期 L12:D12 条件下,这两个种群的光脉冲最敏感期出现在暗期的第 3—4 h,其被光脉冲分隔后的暗期长度为 8—9 h(图 2B、D),没有接近临界暗长。这说明,光脉冲对滞育的抑制效果与干扰的光周期背景有关。

此外,光脉冲对滞育的抑制效果与试验温度也密切相关^[6, 13]。这点在本实验中也得到证实,在不同的光周期背景下,温度与抑制效果呈现出不同的关系。在光周期 L9:D15 条件下,两种群在 22℃ 比在 25℃ 光脉冲敏感位点更多(图 2A、C),相对应位点的光脉冲滞育抑制效果更强,特别是 TA 种群在 22℃ 下 1 h 光脉冲最敏感位点是暗期启动后的第 6—11 h,表现出现了很宽的滞育抑制槽,而 25℃ 下则为第 10—11 h;在 L12:D12 条件下,则出现相反的情况,两种群各自相同位点的 25℃ 下的光脉冲敏感性均比 22℃ 强,特别是在暗期的后期表现更明显(图 2B、D)。

棉铃虫暗期干扰实验也进一步提示了,即使在同种昆虫中,暗期干扰的反应模型及其对滞育的抑制效果也会随所干扰的地理种群的不同,干扰的光周期背景不同和实验温度的差异而发生变化。

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CONTENTS

Hyperspectral characteristics of typical subtropical trees at different levels of simulated acid rain	SHI Qilong, JIANG Hong, CHEN Jian, et al (5621)
Wind fields and the development of wind corridors in the urban metropolis of the Pearl River Delta	SUN Wu, WANG Yiming, WANG Yuelei, et al (5630)
Dynamics of canopy structure and understory light in montane evergreen broadleaved forest following a natural disturbance in North Guangdong	OU Yudian, SU Zhiyao (5637)
The influence of 4 species of preys on the development and fecundity of <i>Orius similis</i> Zheng	ZHANG Changrong, ZHI Junrui, MO Lifeng (5646)
Woody seedling regeneration in secondary succession of monsoon broad-leaved evergreen forest in Puer, Yunnan, Southwest China	LI Shuaifeng, LIU Wande, SU Jianrong, et al (5653)
Scale-dependent spatial variation of species abundance and richness in two mixed evergreen-deciduous broad-leaved karst forests, Southwest China	ZHANG Zhonghua, HU Gang, ZHU Jiedong, et al (5663)
The spatial heterogeneity of soil nutrients in a mid-subtropical <i>Castanopsis kawakamii</i> natural forest	SU Songjin, LIU Jinfu, HE Zhongsheng, et al (5673)
Effects of <i>Vetiveria zizanioides</i> L. growth on chemical and biological properties of copper mine tailing wastelands	XU Decong, ZHAN Jing, CHEN Zheng, et al (5683)
Effects of different irrigation regimes on characteristics of transpiring water-consumption of three desert species	SHAN Lishan, LI Yi, ZHANG Ximing, et al (5692)
The response of euhalophyte <i>Salicornia europaea</i> L. to different nitrogen forms	NIE Lingling, FENG Juanjuan, LÜ Sulian, et al (5703)
Dynamic analysis on spatial pattern of dominant tree species of cold-temperate coniferous forest in the succession process in the Pangquangou Nature Reserve	ZHANG Qindi, BI Runcheng, ZHANG Jintun, et al (5713)
Effects of AM fungi on the growth and nutrients of <i>Salvia miltiorrhiza</i> Bge. under different soil water and fertilizer conditions	HE Xueli, MA Li, MENG Jingjing, et al (5721)
The dynamics of soil respiration in a winter wheat field with plastic mulched-ridges and unmulched furrows	SHANGGUAN Yuxian, SHI Ripeng, HAN Kun, et al (5729)
Cattle dung composted by different methods had different effects on the growth and quality of soybean	GUO Liyue, LIU XueMei, ZHAN Lijie, et al (5738)
Nitrogen budget modelling at the headwaters of Urumqi River Based on the atmospheric deposition and runoff	WANG Shengjie, ZHANG Mingjun, WANG Feiteng, et al (5747)
Evaluating the ecosystem sustainability of circular agriculture based on the energy theory: a case study of the Xingyuan circular agriculture demonstration site in Fuqing City, Fujian	ZHONG Zhenmei, WENG Boqi, HUANG Qinlou, et al (5755)
Effects of cold exposure and recovery on viability and energy consumption in the sub-adult female giant spiny frogs (<i>Paa spinosa</i>)	LING Yun, SHAO Chen, XIE Zhigang, et al (5763)
A comparison of night-interruption on diapause-averting among two populations of the cotton bollworm, <i>Helicoverpa armigera</i>	CHEN Yuansheng, TU Xiaoyun, CHEN Chao, et al (5770)
Effects of soil erosion control measures on soil organic carbon and total nitrogen in a small watershed	ZHANG Yanjun, GUO Shengli, NAN Yafang, et al (5777)
Comparative analysis of Lugu Lake watershed ecosystem function under different management authorities	DONG Rencai, GOU Yaqing, LI Siyuan, et al (5786)
Relationship between fish community diversity and environmental factors in the Lianjiang River, Guangdong, China	LI Jie, LI Xinhui, JIA Xiaoping, et al (5795)
Effect of dissolved oxygen level on metabolic mode in juvenile crucian carp	ZHANG Wei, CAO Zhendong, FU Shijian (5806)
Community composition of net-phytoplankton and its relationship with the environmental factors at artificial reef area in Xiangshan Bay	JIANG Zhibing, CHEN Quanzhen, SHOU Lu, et al (5813)
Emergency appraisal on the loss of ecosystem service caused by marine reclamation: a case study in the Taozi Bay	LI Ruiqian, MENG Fanping (5825)
Assessing the visual quality of urban waterfront landscapes: the case of Hefei, China	YAO Yumin, ZHU Xiaodong, XU Yingbi, et al (5836)
Review and Monograph	
Advances in ecological genomics	SHI Yongbin, LI Junmin, JIN Zexin (5846)
Advances in studies of ecological effects of ocean acidification	WANG Siru, YIN Kedong, CAI Weijun, et al (5859)
Advances in feeding ecology of <i>Acartia</i>	HU Simin, LIU Sheng, LI Tao, et al (5870)
Research progress on ammonia-oxidizing microorganisms in estuarine ecosystem	ZHANG Qiufang, XU Jirong, SU Jianqiang, et al (5878)
Recent progress in research on neutrophilic, microaerophilic iron(II)-oxidizing bacteria	LIN Chaofeng, GONG Jun (5889)
A comparison study on primary production in typical low-latitude seas (South China Sea and Bay of Bengal)	LIU Huaxue, SONG Xingyu, HUANG Honghui, et al (5900)
Advances in leaf maximum carboxylation rate and its response to environmental factors	ZHANG Yanmin, ZHOU Guangsheng (5907)
10-years of bird habitat selection studies in mainland China: a review	JIANG Aiwu, ZHOU Fang, QIN Yue, et al (5918)
Scientific Note	
The effects of incubation temperature on embryonic metabolism and hatchling behavior in the Red-banded Snake, <i>Dinodon rufonotatum</i>	SUN Wenjia, YU Xiao, CAO Mengjie, et al (5924)
Sensitivity analysis and dynamics of soil microbial biomass carbon, nitrogen and related parameters in red-yellow soil of tea garden with different fertilization practices	WANG Limin, QIU Shanlian, LIN Xinxian, et al (5930)
Effect of fertilizers on Cd uptake of two edible amaranthus herbs	LI Ningyu, LI Zhian, ZHUANG Ping, et al (5937)

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