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封面图说: 山坡岩羊图——岩羊属国家二级保护动物,因喜攀登岩峰而得名,又名石羊。贺兰山岩羊主要分布于海拔 1500—2300m 的山势陡峭地带,羊群多以 2—10 只小群为主。生境适宜区主要为贺兰山东坡(宁夏贺兰山国家级自然保护区)的西南部,而贺兰山西坡(内蒙古贺兰山国家级自然保护区)也有少量分布。贺兰山建立国家级自然保护区以来,随着保护区环境的不断改善,这里岩羊的数量也开始急剧增长,每平方公里的分布数量现居世界之首,岩羊的活动范围也相应扩大到低山 900 米处的河谷。贺兰山岩羊生境选择的主要影响因子为海拔、坡度及植被。

彩图及图说提供:陈建伟教授 北京林业大学 E-mail: cites.chenjw@163.com

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鲁艺芳, 严俊鑫, 李霜雯, 严善春. 不同光照强度下兴安落叶松对舞毒蛾幼虫生长发育及防御酶的影响. 生态学报, 2013, 33(22): 7125-7131.

Lu Y F, Yan J X, Li S W, Yan S C. Effects of the *Larix gmelinii* grown under different light intensities on the development and defensive enzyme activities of *Lymantria dispar* larvae. Acta Ecologica Sinica, 2013, 33(22): 7125-7131.

不同光照强度下兴安落叶松对舞毒蛾幼虫 生长发育及防御酶的影响

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摘要:为了探讨舞毒蛾对光照环境变化引起的落叶松抗性的变化是如何响应的,分析了不同光照强度处理的兴安落叶松对舞毒蛾幼虫生长发育状况和生理指标变化的影响。研究发现,取食 50% 和 25% 光照强度下生长的落叶松后,舞毒蛾幼虫平均体重、蛹重、化蛹率和羽化率与对照组相比均显著下降($P<0.05$)。幼虫体内保护酶 SOD、POD、CAT 和解毒酶 ACP、AKP、CarE、GSTs、MFO 活性与对照组(100% 光照)相比均显著降低($P<0.05$)且除 CAT 外在 50% 光照强度下降低最为显著($P<0.05$);4 龄和 5 龄幼虫取食同一光强处理的落叶松后,SOD、POD、CarE、GSTs 和 MFO 活性 5 龄显著低于 4 龄($P<0.05$),ACP 和 AKP 活性 5 龄却显著高于 4 龄($P<0.05$),表明昆虫在不同的发育阶段启用不同的排毒酶系。已有研究表明光照差异对取食人工饲料的舞毒蛾生长发育没有显著影响,对部分解毒酶活性有影响,表明光照增加了植物的抗性,同时降低了昆虫自身解毒酶。研究结果表明,采取适当的营林措施调节林分内的光照条件,可以提高落叶松的自主抗虫性,增强其抵御害虫危害的能力,有效控制害虫危害,减少化学农药的施用量。

关键词:光照强度; 落叶松; 舞毒蛾; 生长发育; 防御酶; 组成抗性

Effects of the *Larix gmelinii* grown under different light intensities on the development and defensive enzyme activities of *Lymantria dispar* larvae

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Abstract: *Larix gmelinii* is among the most ecologically and economically important timber species in northeastern China due to its cold hardiness, drought resistance and rapid growth. *Lymantria dispar* L. is a defoliating insect pest which seriously harms larch during outbreaks. Plants, including trees, employ an array of physical and chemical constitutive defense mechanisms that play an important role in protection from insect herbivory. Constitutive defenses are always present, and because they are maintained even in undamaged plants, they are affected by environmental factors to some degree. In many organisms light is a crucial environmental signal influencing natural physiological and developmental processes. Different light intensities could induce changes in plant defense systems. However, pest insects can detoxify ingested plant secondary metabolites with their biotransformation system. We studied the developmental and physiological responses of *Lymantria dispar* larvae to changes in the constitutive defenses of *Larix gmelinii* under three sunlight intensities (100%, 50% and 25% of natural sunlight intensity) mimicking the light conditions of forest edges, forest gaps and understories. The results showed that the detoxification enzyme activities of both fourth and fifth instar *L. dispar* larvae were significantly affected by their host *L. gmelinii* trees grown under the three different sunlight intensities. Compared with the control (100%

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sunlight intensity), the larval development (reflected by mean larval weight, pupation rate, mean pupal weight, adult emergence rate) of *L. dispar* was significantly inhibited after being fed on the needles of *L. gmelinii* grown under shaded conditions ($P<0.05$). The activities of the protective enzymes SOD, POD, CAT and detoxification enzymes ACP, AKP, CarE, GSTs, MFO in *L. dispar* larvae after fed on the needles of *L. gmelinii* grown under the shaded conditions (25% and 50% sunlight intensity) were significantly lower ($P<0.05$) than those in the larvae fed on the needles of *L. gmelinii* grown under the control (100% sunlight intensity) light condition. The activities of all the tested protective and detoxification enzymes excepting CAT were the most significantly inhibited after the larvae being fed on the needles of *L. gmelinii* grown under 50% sunlight intensity ($P<0.05$). These larval enzyme activities were significantly different ($P<0.05$) between fourth and fifth instar larvae while fed on the needles grown under the same light condition. The SOD, POD, CarE, GSTs and MFO activities in the fourth instar larvae were significantly higher than those of fifth instar larvae ($P<0.05$), while the ACP and AKP activities in the fifth instar larvae were significantly higher than those of fourth instar larvae ($P<0.05$). This result indicated that *L. dispar* might use different enzymes or enzyme complex for defense and/or detoxification during their larval development stages. However, light intensities did not show any significant direct effects on the growth development and defensive enzyme activities of *L. dispar* larvae on the artificial diets, indicating that the changes observed in *L. dispar* larval development and defensive enzyme activities were mainly caused by the larch resistance but not by the light intensity. Our results suggested that adjusting the light conditions rationally via silviculture approaches in the larch forests might not only increase the tree growth, but also increase the overall tree resistance to certain serious pest insects including *L. dispar*.

Key Words: light intensities; *Larix gmelinii*; *Lymantria dispar*; growth and development; defensive enzymes; constitutive resistances

植物与昆虫在长期的进化中,形成了相互适应的机制,各自发展出完备的防御体系。植物抗性是指植物抵御各种外来不良生存环境的能力,包括对不同病虫害、各种不良环境因子等的抵抗能力^[1-2]。林木对害虫的抗性,从来源可分为组成抗性和诱导抗性。组成抗性一直存在于植物中,即使未受危害的植物内也存在并始终发挥作用,被认为比诱导抗性更有价值,在抵御害虫危害中起着至关重要的作用^[3-4]。组成抗性存在许多不稳定因素,易随环境因子、植物营养甚至植物的成熟度等而变化,进而影响昆虫的行为、生长发育和繁殖等^[5]。与此同时,植食性昆虫为克服植物防御的作用,通常采用解毒、避毒、选择性贮毒等方式进行适应。昆虫利用解毒酶系和保护酶系进行解毒和排毒是其适应植物防御的重要方式^[6-7]。谷胱甘肽S-转移酶(glutathione S-transferase, GSTs)、酸性磷酸酯酶(acid phosphatase, ACP)、碱性磷酸酯酶(alkaline phosphatase, AKP)、羧酸酯酶(carboxylesterase, CarE)以及多功能氧化酶(multi-function oxidase, MFO)是昆虫体内重要的解毒酶系,参与各种外源毒物的代谢^[8]。超氧化物歧化酶(superoxide dismutase, SOD)、过氧化物酶(peroxidase, POD)和过氧化氢酶(catalase, CAT)是昆虫体内重要的保护酶^[9-10]。

兴安落叶松(*Larix gmelinii*)具有耐寒,耐旱,生长快等特性,是中国东北林区的主要造林树种,具有重要的生态及经济价值。舞毒蛾(*Lymantria dispar*)属鳞翅目毒蛾科,幼虫主要危害树木叶片,食量大、食性杂、严重时可在几周内将整株树木叶片全部吃光,是林业重要害虫^[11]。光因子在植物生长过程中起着至关重要的作用,光照的强弱能影响植物体内生物碱类、可溶性蛋白含量以及次生代谢防御物质等的变化,对植物的组成抗性有重要影响^[12-14]。光照强度的差异能够显著影响落叶松体内防御物质的变化^[15]。为探究在不同的光照条件下,害虫对兴安落叶松林危害的生态生理学机理,将兴安落叶松进行不同光照强度处理,研究舞毒蛾幼虫取食后的生长发育和生理生化响应,为采取适当的营林措施提高落叶松的自主抗虫性抵御害虫危害,减少化学药剂的用量提供理论依据。

1 材料与方法

1.1 植物材料

5月,在黑龙江省哈尔滨市松北区森林生态工程学院实验苗圃内,选用4年生兴安落叶松苗移植于盆中,

恢复生长1个月。6月初,选用健康、长势一致的落叶松苗(株高相近,针叶健康无病虫害)随机分为3组,进行遮阴处理。对照组自然光照(不遮阴);另外2组分别罩1层和2层遮阴网,光照强度约为对照组的50%和25%。每个处理组内50株幼苗,对其进行持续遮阴处理。

1.2 供试昆虫处理与收集

舞毒蛾卵块采自黑龙江省哈尔滨市东北林业大学实验林场。卵块在室内光照培养箱中孵化,温度(25 ± 1)℃,相对湿度(70 ± 7)%,光周期(16L:8D)。幼虫以人工饲料(中国林业科学研究院森林生态环境与保护研究所提供)饲喂备用。7月初选择新蜕皮的、个体大小发育一致、健康的舞毒蛾2龄幼虫,饥饿24h后移置到不同遮阴处理的落叶松苗枝条上,每株4头舞毒蛾幼虫,每个处理组接200头幼虫。每日观察记录舞毒蛾幼虫生长发育状况,选取蜕皮不超过24h的4龄、5龄幼虫,饥饿24h后称量其体重,置于-80℃冰箱备用,以测定舞毒蛾幼虫体内代谢酶系的活性,直至所有幼虫化蛹或死亡。收集各植株上的蛹,统计总化蛹数,计算化蛹率,待化蛹4d后用电子天平称蛹重。羽化试验在养虫室中进行,温度(25 ± 1)℃、相对湿度(70 ± 7)%、光照(16L:8D),统计总羽化数并计算羽化率。取食对照组松苗的幼虫记为对照;取食罩1层和2层遮阴网松苗的幼虫分别记为T₁和T₂。

1.3 主要仪器与试剂

仪器:D-37520冷冻离心机(德国)、电热恒温水浴锅(上海森信实验仪器有限公司)、UV-240紫外分光光度计(Biochtm Ltd. Cambridge CB4 OF J. England)、TES-1335型数字照度计(台湾泰仕电子工业股份有限公司)、光照培养箱(宁波江南仪器厂RXZ-280C型)。

试剂:考马斯亮蓝G-250、牛血清蛋白(BSA)、甲硫氨酸(Met)、核黄素(VB₂)均为Amresco公司产品;还原型谷胱甘肽(GST)、1-氯-2,4-二硝基苯(CDNB)、乙二胺四乙酸二钠盐(EDTA)、二硫苏糖醇(DTT)、苯基硫脲(PTU)、苯甲基磺酰氟(PMSF)、对硝基苯甲醚(4-Nitroanisole)、毒扁豆碱(eserine)、固蓝B盐(Fast blue B salt)等均为Sigma公司产品;还原型辅酶Ⅱ四钠(NADPH-Na₄)为Rocha公司产品;α-萘酚(1-Naphthol)为天津市博迪化工有限公司产品;愈创木酚(O-Methoxyphenol)为天津市光复精细化工研究所产品;α-乙酸萘酯(α-NA)和过氧化氢(H₂O₂)为国药集团化学试剂有限公司(上海)产品。

1.4 测定方法

1.4.1 解毒酶活性测定

ACP、AKP、CarE、GSTs和MFO的酶源制备和活性测定分别参照鄢杰明^[8]、冯春富^[16]和李慧^[17]等人的方法,并略作修改。取舞毒蛾4龄幼虫,每3头为1个重复,5龄幼虫,每2头为1个重复,均重复3次(下同)。酶活性测定时酶液加入量分别为0.1、0.75、0.02、0.1mL和1mL。

1.4.2 保护酶活性测定

SOD、POD和CAT的酶源制备和活性测定参照廖月枝^[18]和鄢杰明^[9]的方法并略作修改。酶活性测定时SOD和POD酶液加入量分别为0.2mL和0.6mL。

1.4.3 酶源蛋白质含量测定

采用考马斯亮蓝G-250染色法。每个重复测定3次。

1.5 数据统计分析

采用SPSS 18.0统计软件进行方差分析。采用one-way ANOVA进行单因素差异显著性分析,以LSD(最小显著法)在0.05水平下检验取食不同光照强度处理的兴安落叶松对舞毒蛾幼虫平均体重、蛹重以及防御酶活性影响的差异显著性。

2 结果与分析

2.1 取食不同光照强度处理的兴安落叶松对舞毒蛾生长发育的影响

从表1可以看出,取食遮阴处理的落叶松针叶后,4龄和5龄舞毒蛾幼虫的平均体重均显著低于对照组,且随光照强度的减弱体重显著下降;取食50%和25%光照强度条件下生长的落叶松针叶后,舞毒蛾蛹重显著

低于对照组幼虫,化蛹率和羽化率也随着光照强度减弱而降低。表明遮阴处理的落叶松显著抑制了舞毒蛾的生长发育。

表 1 不同光照强度条件下取食落叶松针叶对舞毒蛾生长发育的影响

Table 1 The development of *Lymantria dispar* feed on the needles of *Larix gmelinii* grown under different light intensities

处理 Treatment	幼虫平均体重/(g/头)		化蛹率/% Pupation rate	平均蛹重/(g/头) Mean weight of pupa	羽化率/% Emerged adult rate			
	Mean weight of larva							
	4 龄 Forth Instar	5 龄 Fifth Instar						
对照	0.0367±0.0017 a	0.1268±0.0026 a	35.50	0.4873±0.0526 a	78.87			
T1	0.0083±0.0008 b	0.0981±0.0020 b	25.50	0.2813±0.0168 b	54.90			
T2	0.0036±0.0012 c	0.0475±0.0046 c	17.00	0.0516±0.0010 c	38.24			

表中体重($n=50$)和蛹重($n=30$)数据均为平均值±标准误;化蛹率(%)=(蛹总数/试虫总数)×100%;羽化率(%)=(羽化成虫总数/化蛹总数)×100%;同列不同小写字母表示不同光照强度条件下,取食落叶松针叶后舞毒蛾幼虫平均体重及蛹重差异显著($P<0.05$)

2.2 不同光照强度条件下取食落叶松针叶对舞毒蛾幼虫体内保护酶活性的影响

与对照组幼虫相比,取食两种遮阴处理的落叶松针叶后,舞毒蛾4龄和5龄幼虫体内3种保护酶活性均显著降低(图1)。SOD和POD活性在取食50%光照强度条件下的落叶松后降低最显著;CAT活性在取食25%光照强度条件下的落叶松后降低最显著。舞毒蛾4龄和5龄幼虫取食同一光照强度处理的落叶松后,体内保护酶活性差异显著($P<0.05$)。SOD和POD活性5龄显著低于4龄($P<0.05$),CAT则反之(图1)。

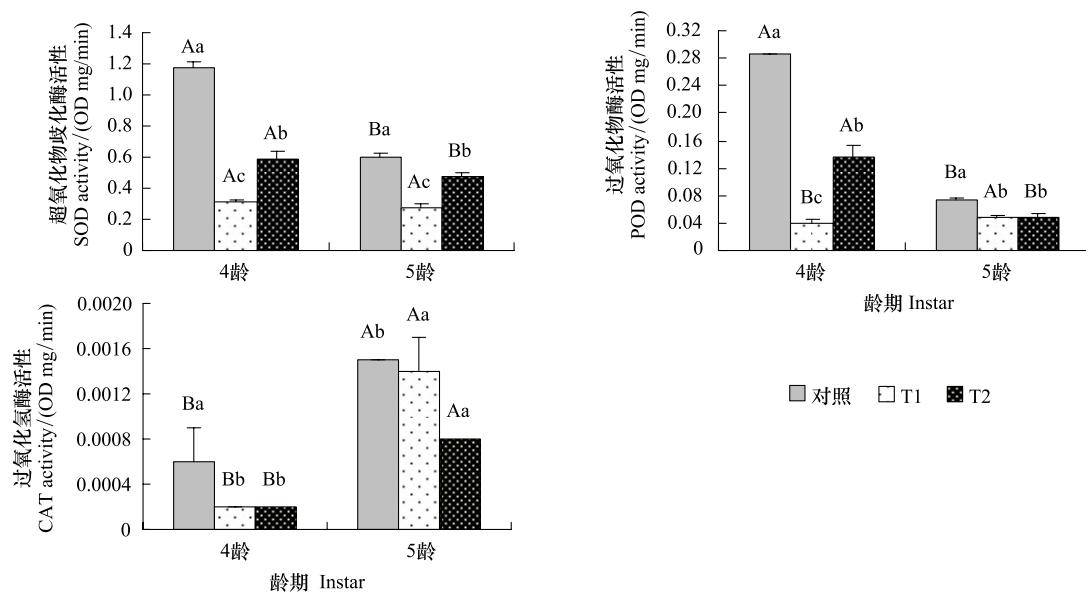


图 1 不同光照强度条件下取食落叶松针叶对舞毒蛾幼虫体内 3 种保护酶活性的影响

Fig.1 The protective enzymes activities of the *Lymantria dispar* larva feed on the needles of *Larix gmelinii* seedlings grown under different light intensities

图中数据标注均为平均值±标准误($n=3$);不同小写字母表示相同龄期的舞毒蛾幼虫取食不同光照强度条件下的落叶松针叶后,体内保护酶活性差异显著($P<0.05$),不同大写字母表示取食同一光照强度条件下的落叶松针叶后,4龄和5龄间保护酶活性差异显著($P<0.05$);相同表示差异不显著

2.3 取食不同光照强度处理的兴安落叶松对舞毒蛾幼虫体内解毒酶活性的影响

如图2所示,与对照组幼虫相比,取食两种遮阴处理的落叶松针叶后,舞毒蛾4龄和5龄幼虫体内5种解毒酶活性均显著降低($P<0.05$),在50%光照强度下降低最显著($P<0.05$)。舞毒蛾4龄和5龄幼虫在取食同一光照强度处理的落叶松后,GSTs、CarE和MFO活性5龄显著低于4龄($P<0.05$),而ACP和AKP活性5龄显著高于4龄($P<0.05$)。

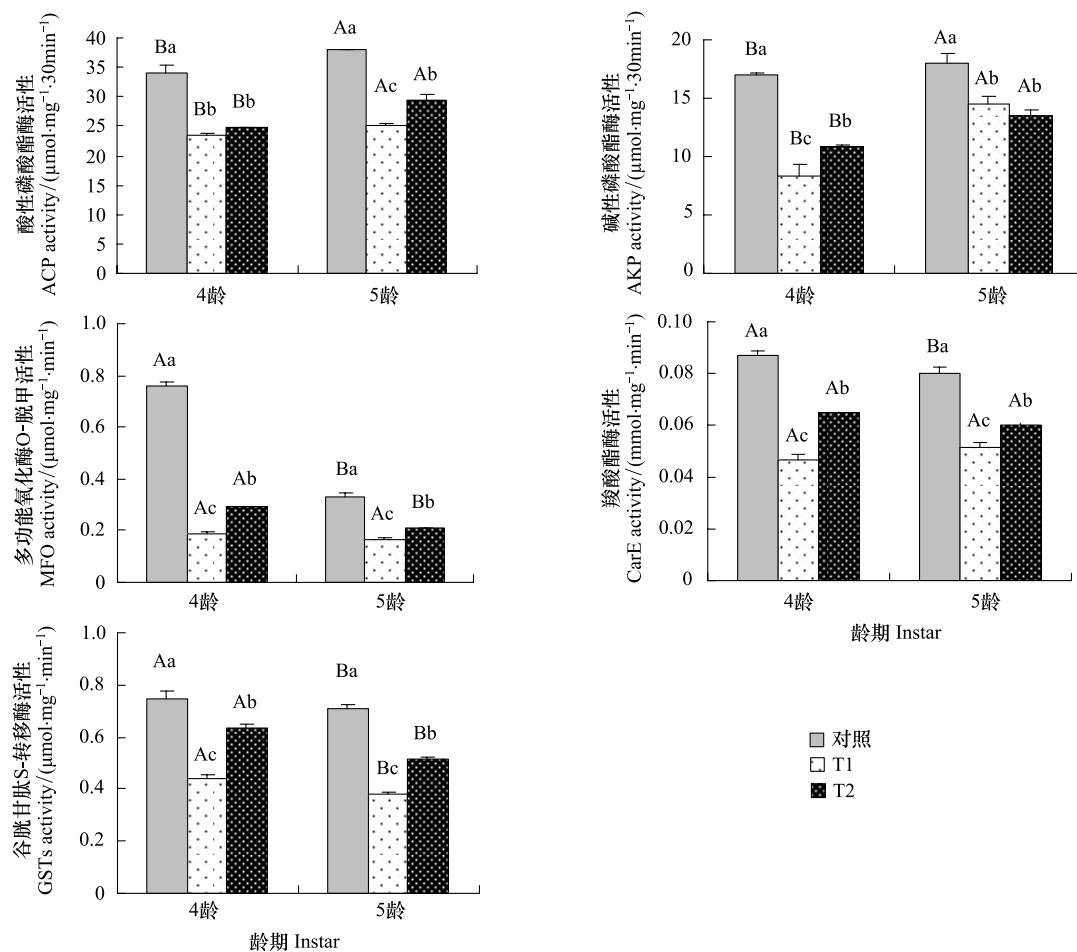


图2 不同光照强度条件下取食落叶松针叶对舞毒蛾幼虫体内5种解毒酶活性的影响

Fig.2 The detoxifying enzymes activities of the *Lymantria dispar* larva feed on the needles of *Larix gmelinii* seedlings grown under different light intensities

3 结论和讨论

自然生态系统中,植物为了避免植食性昆虫的危害而产生对昆虫有毒害作用的防御性化学物质,对取食的幼虫有较大的毒性作用,影响其消化和营养吸收^[19-23]。组成抗性是植物一种固有的特性,其抗性程度会因光照、水分、营养等环境条件的变化而发生改变^[24-25]。光照是影响植物生长的主要环境因子之一,不同的光照强度能够引起植物体内防御性物质的改变,引起植物化学防御体系的改变^[15,23,26-27]。昆虫可通过体内复杂的代谢酶系来抵御植物的防御。与对照组相比,取食遮阴处理的落叶松后,舞毒蛾4龄和5龄幼虫体内防御酶系活性显著降低($P<0.05$),且除CAT外在50%光照强度下降最为显著($P<0.05$);舞毒蛾幼虫平均体重、化蛹率、蛹重以及羽化率等生长发育指标均显著下降($P<0.05$)。在50%光照强度条件下,兴安落叶松具有较强的组成抗性^[15],说明舞毒蛾生长发育和防御酶活性显著降低的原因是遭遇了具有较强抗虫性的寄主。结合光照对落叶松组成抗性以及舞毒蛾生理生化的影响,从植物抗虫性的角度说明,害虫在光照充足的条件下容易暴发成灾,而在适当的遮阴条件下发生受抑制的根本原因。

同一光照强度处理的落叶松,对舞毒蛾生长发育过程的不同阶段有显著影响,SOD、POD、CarE、GSTs和MFO活性5龄显著低于4龄($P<0.05$),而ACP和AKP活性5龄却显著高于4龄幼虫($P<0.05$)。磷酸酯酶是昆虫体内重要的代谢酶系,在昆虫生长发育及对外源有毒物质的解毒代谢方面具有重要的作用,能够影响昆虫正常的生理作用^[28]。说明昆虫在不同的发育阶段启用不同的排毒酶系,幼虫进入5龄阶段,其体内磷酸酯酶活性被显著激发。廖月枝等关于不同杀虫剂对舞毒蛾幼虫代谢酶系影响的研究发现,幼虫体内保护酶活

性5龄低于3龄,而ACP和AKP活性5龄高于3龄^[29],与本研究结果相似。李慧、鄢杰明等在不同杀虫剂对舞毒蛾幼虫毒力测定的研究中发现,其龄期越大LC₅₀也越高,对药剂敏感性越差,抗药性越强^[30-31],其磷酸酯酶在5龄时也表现出较高的活性。

以往关于光照对昆虫影响的研究主要围绕农业害虫展开,并且主要研究对其行为和生长的影响^[32-33],本研究首次从植物抗性角度出发,分析了光照强度差异引起的植物抗性变化对昆虫生长发育和防御生理的影响。在林业生产中针对阳坡光照比较充足的林分,可以适当增加林分郁闭度,为林木营造光照较弱的生长环境,进而通过提高林木自身的抗性来抵御害虫危害;在需要利用化学农药进行防治时,应在舞毒蛾对药剂较敏感且重要解毒酶系尚未有效启动的幼龄时期,对其进行防治,将收到更有效的防治效果。

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