# 温度对甜菜夜蛾核型多角体病毒流行的影响

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摘要:在恒温条件下,研究了甜菜夜蛾 3 龄初幼虫感染核型多角体病毒后的病死速率、病死时间分布与温度关系。结果表明,在 29 C 以下,随温度的升高,病死率增加,幼虫病死速率加快,病死持续时间缩短;该病毒的热抑制温度在 27 C 左右。改进的 Schoolfield 模型、Stinner 模型可很好地描述幼虫病死速率与温度关系。甜菜夜蛾种群饲毒后的每日病死率可用时间-剂量-死亡率模型较好地拟合,模型模拟值与实测值有较好的吻合(Hosmer-Lemoshow 统计量检验不显著),方程中各项系数经 t 检验达极显著水平;不同温度下的幼虫累计病死时间分布可用 Weibull 模型、Gompertz 模型及 Logistic 模型拟合,模型经 F 检验显著,模型中各系数经 t 检验均达到或接近显著水平。用剩余平方和 Q 比较各模型的拟合程度,以 Logistic 模型拟合最好,Gompertz 模型次之,Weibull 模型拟合效果稍差。上述模型可以用来模拟分析不同温度下的幼虫病死时间分布和幼虫病死速率。

关键词:甜菜夜蛾,核型多角体病毒,疾病流行学,病死时间分布,时间-剂量-死亡率模型,非线性模型,温度

# Influence of incubation and inoculation temperatures on the epizootic of Spodoptera exigua nuclear polyhedrosis virus

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Abstract: Spodoptera exigua is one of the most important pests of vegetable plants grown in China, feeding mainly on the foliage and damaging the fruits. It was reported that the parasitoids and a nuclear polyhedrosis virus had a notable impact on the larvae of Spodoptera exigua—the virus is the most effective mortality factor. Epizootics in natural populations usually occurred and the temperature was one of the most important environmental factors affecting epizootics. In this paper, based on the systematic observation of temperature impacted on the early 3rd-instar host larvae in laboratory, the relationship between the virus epizootics and the temperature was studied, and several mathematical models were conducted. These results can be favorable to epizootology and field application of the virus.

In our experiments, S. exigua nuclear polyhedrosis virus was obtained from Shanghai, China, and the isolation was proved to be specific for beet armworm (BA). The larvae of BA used in the experiments were collected in Shanghai greenhouse and isolated in our laboratory. The standard procedures were used as precaution against contaminating microorganisms during the experiments. The seven constant temperatures (18, 20, 23, 26, 29, 32, 35 °C) were designed, the host larvae reared at a relative humidity of 85% and light of L: D 12: 12. The experiments were repeated for 4 times, and 30~40 larvae of BA were treated each time.

The results showed that (1) the virus-infected larvae started death mostly on  $2\sim3d$  after pests inoculation, and reached

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peak on  $4\sim5$ d when the early 3rd-instar larvae were treated with the virus concentration of  $1.32\times10^6$  PIBs/mL and incubated at the constant temperature from 20 °C to 35 °C. Between the temperature range of  $20\sim29$  °C, it was found that mortality and death velocity of virus-infected host larvae increased, the disease death duration of host larvae obviously shorten, and the time at that point larval mortality and diseased prevalence started and peaked was correspondingly advanced accompanied with the increased incubation and inoculation temperature. The virus caused a mortality rate of 43.3% of the host larvae at 18 °C, 90.6% at 29 °C, but 56.2% at 32 °C, which indicated the virus had a restricted thermal temperature. Based on the model ( $Y=-322.7362T+31.4028-0.5968T^2$ , R=0.9146, df=2, F=10.23, P=0.0267), the relationship between the infected larvae mortality and temperature. the restricted thermal temperature was estimated to be 26.3 °C. (2) The model describing the relationship between the mean lethal rate V(T) of nuclear polyhedrosis virus to the S. exigua larvae and inoculation. Incubation temperature (T) was drawn as follows:

$$V(T) = \frac{\rho(25\,\mathrm{C}\,)T/298*\exp[\Delta H_A^\#/R(T/298-1/T)]}{1+\exp[\Delta H_H/R(1/T_{1/2H}-1/T)]}$$

Of which, R is 8.314J/(K·mol), and  $\rho(25\text{ C})$ ,  $\Delta H_A^{\#}$ ,  $\Delta H_B$  are unknown parameters. The model can well fit to describe the relationship between mean lethal rate to SeNPV of its host larvae and the temperature. Otherwise, some observed data were also well simulated by Stinner model. (3) The Time-dosage-mortality model  $(q_{ij}=1-\exp[-\exp(\gamma_j+\beta\log_{10}(d_i))]$ , of which,  $q_{ij}$  is the conditional mortality on the i day,  $\gamma_j$ ,  $\beta$  is unknown parameters,  $d_i$  is the functionary intensity of temperature under the virus-infected larvae on the i day ) can well fit to simulate the daily distribution of disease death time of host larvae from 1 to 8d after inoculation at the temperature of  $20\sim30$  C. Hosmer-Lemoshow test showed that the theoretic values well fitted to the observed data, and t-test indicated that the parameters of the model reached a significant level. Based on the TDM model and under the constant temperature of 20, 23, 26, 29 C, the LT<sub>50</sub> was estimated to be 5.725, 4.394, 3.746 and 3.286d, respectively. And the LT<sub>50</sub> to be 4.999, 3.762d at 26, 29 C, respectively. (4) The cumulative diseased death time distribution could be described by S-type models (Gompertz, Logistic, Weibull). And the stimulated result of Logistic model was better than those of Gompertz and Weibull models in terms of the nonlinear remainder sum of squares (Q values). All these models can be applied to virus epizootics forecast.

**Key words**: Spodoptera exigua; nuclear polydedrosis virus; disease epizootic; distribution of disease time; time-dosages-mortality model; nonlinear model; Temperature

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核型多角体病毒是甜菜夜蛾自然种群密度的重要调节因子,常在宿主种群中造成自然流行,是颇具应用前景的生物防治物<sup>[1~3]</sup>。温度是影响病毒病流行的重要环境因子,主要影响病死速率和病死率,温度高幼虫发病死亡的潜伏期缩短,而温度偏低时幼虫病死时间则明显延长。在大多数昆虫病毒中,如茶尺蠖(*Ectropis obliqua hypulina*)<sup>[4]</sup>、棉铃虫(*Heliothis zea*)<sup>[5]</sup>、黎豆夜蛾(*Anticarsia gemmatalis*)<sup>[6]</sup>等宿主的 NPV,高于 30°C时,作为衡量疾病流行程度的重要指标之一的幼虫病死率明显下降。寻求昆虫与温度之间相互关系的定量表达历来是昆虫生态学最为活跃的领域之一,其中以昆虫发育速率的数学模型研究最为深入。在病毒-昆虫宿主系统中,有关昆虫病死速率、病死时间分布与温度关系的数学模型研究较少<sup>[5,6]</sup>,在甜菜夜蛾病毒方面则未见报道。鉴于昆虫发育与病毒增殖、感染宿主过程中都存在多种酶促反应,且均由某些酶加以调控的共性,故引用描述昆虫发育速率的数学模型拟合幼虫病死速率与温度关系,同时引用时间-剂量-死亡率模型(Time-dose-mortality,简称 TDM)和 S 型生长模型描述温度对幼虫病死时间分布的影响,旨在为昆虫病毒流行学建模、田间应用,以及提高该病毒的工厂化生产技术提供资料。

### 1 材料与方法

# 1.1 材料

虫源为室内续代饲养1代的甜菜夜蛾3龄初幼虫。菜叶采自近期未施农药的青菜和甘蓝地。试验所用甜菜夜蛾核型多角体病毒由上海市华漕地区提供。在室内用甜菜夜蛾幼虫增殖一次后,将病死虫尸匀浆,经差速离心后的粗提液作试验用。按试验要求,用蒸馏水将粗提液稀释至所需浓度,用血细胞计数法计数多角体。

#### 1.2 试验设计

应用人工气候培养箱(ZRX-300D,杭州钱江仪器设备有限公司制造)控制温度,试验误差为 $\pm 1$  C ,利用箱内的日光灯控光,光照时间 L **万** 方 数据<sup>2</sup>,相对湿度控制在 85 % 左右。试验设 18、20、23、26、29、32、35 C 7 个饲毒、饲育温度。试验时用浓度为  $1.32\times10^6$  PIBs/ml 的病毒悬液渍洁净的青菜叶,在各处理温度下饲喂 3 龄初幼虫  $30\sim40$  头。24 h 后,双头饲养于放有无毒洁

净甘蓝叶的培养皿中进行观察。同时,在每一温度处理中均设对照。每天观察记载幼虫发病和病死情况。试验重复 4 次。

#### 1.3 数据处理

采用 Schoolfield 模型<sup>[7]</sup>、Stinner 模型描述病死速率与温度的关系;用 TDM 模型<sup>[8]</sup>拟合不同温度处理下感病甜菜夜蛾幼虫每日条件病死率;用 S 型生长模型<sup>[9]</sup>如 Weibull 模型、Gompertz 模型及 Logistic 模型来拟合不同温度下甜菜夜蛾感染核型多角体病毒后的每日累计病死率。

1.3.1 Schoolfield 模型 Schoolfield [7] 等在 Sharpe 模型的基础上提出了如下模型:

$$V(T) = \frac{\rho(25\,\mathrm{C}\,)T/298 \times \exp\bigl[\Delta H_A^\#/R(T/298-1/T)\bigr]}{1+\exp\bigl[\Delta H_L/R(1/T_{1/2L}-1/T)\bigr] + \exp\bigl[\Delta H_H/R(1/T_{1/2H}-1/T)\bigr]}$$

式中, $\rho(25^{\circ}\mathrm{C})$ 是假定没有失活酶存在的情况下  $25^{\circ}\mathrm{C}$ 时变温动物的发育速率(本文指幼虫病死速率), $\Delta H_{L}^{*}$ 为活化焓, $\Delta H_{L}$ 与  $\Delta H_{L}$ 分别是与酶的高温或低温失活有关的焓的变化, $T_{1/2L}$ 是在控制酶处于 1/2 低温失活状况下的温度  $({}^{\circ}\mathrm{K})$ , $T_{1/2H}$ 是控制酶处于高温失活状况下的温度  $({}^{\circ}\mathrm{K})$ ,R 为气体常数,T 为绝对温度  $({}^{\circ}\mathrm{K})$ ,V(T)为温度 T 时的发育速率(本文指病死速率)。由于高温区对病毒增殖、毒力抑制显著,低温区的影响较小,且试验是在甜菜夜蛾存活温区的中、上部分进行,可不考虑低温影响,故将上式简化为:

$$V(T) = \frac{\rho(25\,\mathrm{C}\,)T/298 \times \exp[\Delta H_A^{\#}/R(T/298-1/T)]}{1+\exp[\Delta H_H/R(1/T_{1/2H}-1/T)]}$$

#### 1.3.2 S型生长模型

Stinner 模型 
$$V(T) = C/[1 + \exp(k_1 + k_2 T)]$$
  
Gompertz 模型  $Y = K \exp[-\exp(\beta - \gamma X)]$   
Logistic 模型  $Y = K/[1 + \exp(a - \lambda X)]$   
Weibull 模型  $Y = 1 - \exp[-(X/b)^c]$ 

**1.3.3** TDM 模型 甜菜夜蛾种群在病毒接种后天数  $t_j(j=1,2,3,\cdots,J)$ 内,被作用因子(饲毒、饲育温度)的强度  $d_i(i=1,2,3,\cdots,I)$  致死的条件病死率  $q_{ii}$ :

$$q_{ij} = 1 - \exp\left[-\exp(\gamma_i + \beta \log_{10}(d_i))\right]$$

式中, $\gamma_j$  为描述时间区间 $[t_{j-1},t_j]$ 的时间效应待估参数,其值反映了该时间区内的死亡率; $\beta$  为温度作用强度的待估参数。

1. 3. 4 模型的显著性检验 对 TDM 模型,分别采用 Pearson 卡方检验及 Hosmer-Lemoshow 统计量检验模型拟合值与实测值之间的差异;对 Schoolfield 模型和 S 型生长模型,用剩余平方和 Q 值来比较模型的拟合程度。模型拟合在计算机上用  $DPS^{[10]}$ 

软件进行。

#### 2 结果与分析

甜菜夜蛾 3 龄初幼虫感染核型多角体病毒后,随饲毒和饲育温度的升高,潜伏期缩短,病毒对宿主的致死速率加快,病死率增加(表 1),但温度高于 29  $\mathbb{C}$ 时,病死率反而下降,表明该病毒存在热抑制温度。根据表 1 数据求得幼虫病死率与温度关系: $Y = -322 \cdot 7362 + 31 \cdot 4028T - 0 \cdot 5968T^2$  ( $R = 0 \cdot 9146$ ; df = 2,  $F = 10 \cdot 23$ ,  $P = 0 \cdot 0267$ ),对函数求导,可求得函数的极大值为90. 3569,对应的温度为 26. 30932  $\mathbb{C}$  ,表明该病毒的抑制温度在 27  $\mathbb{C}$  以上。

表 1 不同温度饲毒、饲育下,甜菜夜蛾 3 龄初幼虫感染核型多角体病毒后的校正死亡率、潜伏期、平均致死时间
Table 1 Mortality, incubation period, and mean lethal time of *Spodoptera exigua* NPV to its host larvae inoculated with SeNPV suspension(1.32

 $imes 10^6\,\mathrm{PIBs/mL}$ ) and incubated at varied temperature

温度(℃)	潜伏期(d)	校正病死率(%)	平均致死时间±标准误(d)
Temperature	Incubation period	Revised mortality	Mean lethal time $\pm S$ e
18	8	43.33	11.0000±1.9200a
20	4	72.22	$5.6980 \pm 1.4910b$
23	3	86.67	$4.7710 \pm 0.9214 \mathrm{bc}$
26	3	90.00	$4.3704 \pm 0.9667c$
29	2	90.63	$3.2414 \pm 0.6356d$
32	2	56.25	$3.2196 \pm 0.8782 d$
35	2	53.13	$3.3521 \pm 0.9963d$

<sup>\*</sup> 表中同了**n** 美人相同字母的平均数间差异未达 0.05 显著水平 Means within a column followed by the same letter are not significantly different (P<0.05, Duncan's multiple range test)

# 表 2 幼虫病死速率与温度关系的数学模型及其统计检验

Table 2 Regression models for the relationship between diseased death rate and temperatures, and the statistic test for models

<b>模型</b> Models	模型系数 Model coefficients	<b>检验值</b> <i>t</i> values	显著水平 P values	<b>检验值</b> F values	显著水平 P values	剩余平方和 Residual sum of squares <i>Q</i>
Stinner 模型	C = 0.3161	12.1106	0.0003	29.8471	0.0039	0.0025
	$K_1 = 5.4011$	3.1874	0.0333			
	$K_2 = -0.2645$	3.0236	0.0390			
Schoolfild 模型	$\rho(25^{\circ}\text{C}) = 0.3488$	0.9323	0.4199	15.9195	0.0240	0.0024
	$\Delta H_A^{\neq} = 101381.4035$	1.1247	0.3425			
	$\Delta H_H = 154458.4288$	3.5446	0.0382			
	$T_{1/2H} = 301.8525$	20.1495	0.0003			

#### 2.1 对幼虫病死速率的影响及模拟

幼虫病死速率与温度关系的模拟模型参数及其统计检验结果列于表 2.2 个模型的检验均达到显著水平,模型中除  $\Delta H_A^{\#}$  和  $\rho(25\,\mathbb{C})$  外,其余系数均达到极显著水平,表明模型能很好地拟合试验数据(图 1)。

### 2.2 对幼虫每日病死率的影响

甜菜夜蛾幼虫在高温( $\geqslant$ 29  $\bigcirc$ )下饲毒和饲育,第 2 天开始病死,第  $4\sim$ 5 天达病死高蜂,低于此温度,病死始期和高蜂期分别在  $3\sim$ 4d 和  $5\sim$ 6d。

用 TDM 模型模拟饲毒后 8d 内幼虫在病毒繁殖的适温范围 内( $20\sim29^{\circ}$ C)的每日病死率,结果见表 3 和图 2。

从表 3 可见,不同时间下的参数  $\gamma_i$  值不同,表明了条件病死 to temperatures

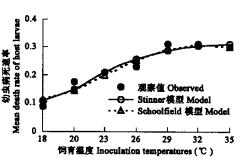


图 1 甜菜夜蛾幼虫病死速率与温度关系及模型模拟

Fig. 1  $\,$  The relation of mean lethal rate of SeNPV to its host larvae

率是时间相关函数,从而说明将作用因子和时间纳入同一模型中进行统一分析的重要性及可靠性。 $\gamma_j$ 值的大小反映了幼虫饲毒后,感病幼虫在某个时段内的死亡率高低。从表 3 可见,在饲毒后的 6 d 内,随饲毒后时间的增加, $\gamma_j$  值随之增大,但 7 d 后  $\gamma_j$  值减少,这与试验观察结果一致。TDM 模型经 Pearson 卡方检验显著,但 Hosmer-Lemoshow 统计量检验不显著,这样复杂的模型要通过 Pearson 卡方检验显得过于苛刻,因而只要能通过 Hosmer-Lemoshow 拟合度测试,表明模型仍能较好地拟合试验数据。模型各系数经 t 检验相关极显著。

表 3 时间-温度-条件死亡率模型参数估计及统计检验

Table 3 Parameters estimated from the modeling of time-dosage-mortality of SeNPV

参数 Parameters	方程系数 Coefficients	标准误差 Standard error	t <b>值</b> t values	显著水平 ♭ values	
β	9.9972	2.1448	4.6610	0.0002	
$\gamma_1$	-17.6819	3. 1472	5.6183	0.0000	
$\gamma_2$	-15.3868	3.0622	5.0247	0.0000	
$\gamma_3$	-14.7556	3.0059	4.9089	0.0000	
${m \gamma}_4$	-14.1804	2.9670	4.7794	0.0001	
$\gamma_5$	-14.8883	2.9789	4.9979	0.0000	
${m \gamma}_6$	-15.3612	2.9743	5.1646	0.0000	
$\boldsymbol{\gamma}_7$	-16.6770	3. 1353	5.3192	0.0000	
erson <b>卡方检验值</b> Chi-square		44. 4322> $X_{0.05}^2$ =32. 6710			
Iowmer-Lemeshow 统计量 Statistic value		6. $6450 < X_{0.05}^2 = 15.507$			

#### 2.3 幼虫病死时间 $LT_{50}$ 和 $LT_{90}$ 的估计

表 4 列出了由  $\mathrm{TDM}$  模型估计的  $LT_{50}$ 和  $LT_{90}$ 值。在  $20\sim29$   $\mathrm{C}$  的适温范围内,随饲毒、饲育温度的升高,病毒对感病幼虫致死中时间和**万万物**据

#### 2.4 感病幼虫病死时间分布及模拟

幼虫病死时间分布的 Gompertz 模型、Logistic 模型和 Weibull 模型参数估计结果列于表 5。从各模型的剩余平方和 Q 大小可见,3 种模型均能很好地拟合试验数据。通过比较 Q 值大小,Logistic 模型拟合效果最好,Gompertz 模型次之,Weibull 模型稍差。3 种模型的 F 检验也有类似结果(表 6)。 Gompertz 和 Weibull 模型模拟结果见图 3。

从图 3 可见,3 龄初饲毒,在各饲育温度下幼虫病死持续时间随温度上升而缩短,反之延长。

#### 3 讨论

大多数昆虫病毒在低温下的复制速率较高温下慢,且高温对大多数昆虫病毒有一定的抑制作用,即大多数昆虫病毒有热抑制温度。本文研究结果表明,甜菜夜蛾感病幼虫在 $18\sim29$  C温度范围内饲育,死亡率随温度上升而增加,>29 C时,死亡率下降,根据感病幼虫死亡率与温度关系的回归模型推测出的热抑制温度在27 C,低于大多数昆虫病毒的热抑制温度,如家蚕( $Bombyx\ mori$ )[11] NPV的热抑制温度为35 C,茶尺蠖 NPV[4]、棉铃虫 NPV[5]分别为34 C和40 C,表明在不同的昆虫病毒—宿主系统中,病毒的热抑制温度是不同的。一些研究表明[4],温度对病毒的抑制作用,受宿主感染虫龄和高温持续时间的影响,本研究尚未考虑这些因素。

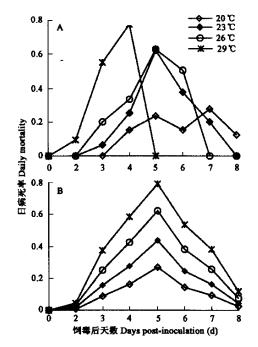


图 2 感染 SeNPV(A)和 TDM 模型模拟(B)的甜菜夜蛾种群随时间和温度变化的日病死率

Fig. 2 Conditional mortality probability of *S. exigua* infected by SeNPV (A) and estimated by TDM model (B) varying with temperature after inoculation.

表 4 不同温度作用下甜菜夜蛾核型多角体病毒对宿主幼虫的致死 时间

Table 4  $LT_{50}$  and  $LT_{90}$  values estimated by the TDM model at different constant incubation temperatures

致死时间		温度 Ter	mperature(°C	)
Lethal time (d)	20	23	26	29
$LT_{50}$	5.7253	4.3943	3.7458	3. 2856
$LT_{90}$			4.9985	3.7623

本研究结果表明,在 29 C以下,感病幼虫死亡率随饲毒后时间的延长而增加(C>1),高于此温度时,死亡率下降(C<1),但在高温下(>29 C),Weibull 模型拟合效果不理想,表明该模型可能更适用于模拟中低温下的病虫死亡时间分布。Logistic 模型符合甜菜夜蛾病死率在低温下随温度上升而增加,高温下随温度上升而降低的规律,但未能反映出高温下病死速率下降的特性。

表 5 幼虫病死时间分布与温度关系的数学模型参数估计

Table 5 Parameters estimated from the modeling of Gompertz Logistic and Weibull for the relationship between the diseased death time distribution and temperatures

「何育温度 Gompertz 模型 Incubted temp. Gompertz model			Logistic 模型 Logistic Model				Weibull 模型 Weibull Model				
(°C)	K	β	γ	Q	K	a	λ	Q	b	с	Q
18	0.6009	3.7636	0.3534	0.0012	0.4800	8.0992	-0.7415	0.0014	16.7548	3.3040	0.0149
20	0.6582	3.6102	0.7984	0.0032	0.6322	6.2895	-1.2581	0.0065	8.0337	2.2340	0.0324
23	0.9182	5.9598	1.4727	0.0040	0.9000	9.0410	-2.0951	0.0004	4.8887	4.6972	0.0382
26	0.9228	3.8025	1.0905	0.0074	0.9090	6.5664	-1.6826	0.0039	4.5344	3.6279	0.0339
29	0.9150	4.5206	1.8155	0.0033	0.9063	27.2704	-13.9562	0.0000	3.1334	4.3572	0.0478
32	0.5696	3.0640	1.2951	0.0016	0.5653	5.2611	-1.9261	0.0008	8.2823	0.9495	0.0711
35 <b>7</b>	5方数据	2.4567	0.9920	0.0141	0.5402	4.7221	-1.5924	0.0102	9.2264	0.9653	0.0634

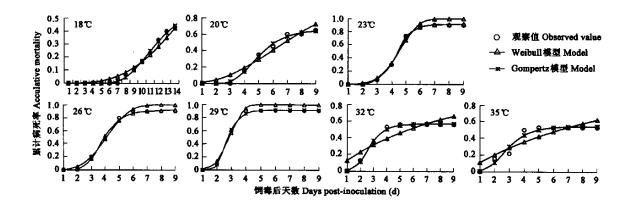


图 3 不同温度下甜菜夜蛾累计病死时间分布及模拟

Fig. 3 Distribution of cumulative diseased time of larvae of S. exigua infected by SeNPV at temperatures of 18~35 °C

#### 表 6 幼虫病死时间分布与温度关系数学模型的 F 检验

Table 6 F test for the model of the relationship between the diseased death time distribution and incubation temperatures

饲育温度	Gompertz 模型 Model		Logistic <b>†</b>	莫型 Model	Weibull 模型 Model	
Incubation temp.	F <b>值</b>	显著水平	F <b>值</b>	显著水平	F <b>值</b>	显著水平
( ,C )	F values	P values	F values	P values	F values	P values
18	1533. 991	0.0000	1324.709	0.0000	362.906	0.0000
20	582.882	0.0000	281.759	0.0000	126.555	0.0000
23	526.337	0.0000	11290.575	0.0000	248.176	0.0000
26	520.210	0.0000	973.864	0.0000	258.371	0.0000
29	1020.971	0.0000	6465.624	0.0000	157. 283	0.0000
32	713.224	0.0000	1349.981	0.0010	30.71	0.0000
35	71.813	0.0006	99.000	0.0021	31.444	0.0001

机率值分析方法是经典的处理农药生物测定数据方法,剂量效应和时间效应指标分别由相互独立的经验模型所确定,但时间效应和剂量效应的相互分离是该法的重大缺陷[8]。为解决这一问题,Robertson等[13]提出应用重对数模型(Complementary log-log model,也称时间-剂量-死亡率模型)分析生物测定数据,此后在国际上逐渐流行[13-14],正在取代已沿用半个世纪的机率值分析方法。由于 TDM 模型能将时间和剂量效应统一到一个模型中,模型的各个参数又有确切的生物学意义,因此已成为昆虫和植物保护工作者的有用工具[8]。本研究引进 TDM 模型用于分析温度对甜菜夜蛾病毒流行的影响,结果表明在该病毒繁殖的适温范围内,该模型可用于模拟感病幼虫 8d 内每天病死率,作者曾试图用 TDM 模型分析低温区和高温区在全世代内的整个病死动态过程,但结果不令人满意。该模型可以模拟 19~35 C范围内斜纹夜蛾感病种群在饲毒后 11d 内的每日病死时间分布(另文发表),表明 TDM 模型可能更适用于对温度适应广的 NPV,但是否普遍适用于其它 NPV-昆虫系统则有待验证。

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