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恒温和变温对小菜蛾发育速率的影响

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摘要：研究了小菜蛾的发育速率在恒温和自然变温下的变化规律。恒温下小菜蛾在 8～32℃内能完成整个幼期的发育，在 30～32℃下发育最快。幼虫能完成发育的温度范围宽于卵和蛹。在模拟恒温下发育速率和温度关系时，王-兰-丁模型效果较好，而 Logistic 模型能较好地模拟适温区和低温区的发育速率，直线模型只能用于适温区内发育速率的模拟。恒温下的存活率和温度符合二次曲线关系。不同恒温下发育历期的分布符合“同形性质”。变温下，小菜蛾能够发育的温度范围比恒温下的广。在适温区，Logistic 模型、直线模型和王-兰-丁模型均能较好地模拟变温下小菜蛾的羽化进度，但在低温区，Logistic 模型和王-兰-丁模型模拟的效果优于直线模型。

关键词：小菜蛾；温度；存活；发育速率；模拟

Development rate of *Plutella xylostella* L. (Lepidoptera: Plutellidae) under constant and variable temperatures

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Abstract: The diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae) is a major pest of cruciferous crops worldwide. In the past, many studies have been conducted to provide valuable information on the temperature-dependant development of *P. xylostella*. However, scrutiny of the relevant literature indicated that more detailed knowledge of development and survival of *P. xylostella* in relation to temperature seemed desirable, especially at low and high temperatures. Such detailed information will be useful particularly for monitoring and population studies of *P. xylostella* in temperate and cool temperate regions, where this insect has become a more important pest in recent years. The purpose of this study was to examine the development rate and survival of *P. xylostella* at controlled temperatures over a wide temperature range, and to derive mathematic functions that can be tested for simulating the development of *P. xylostella* populations at natural temperature conditions.

Survival and development time from egg to adult emergence of *P. xylostella* were determined at 19 constant temperatures from 4～40℃, and were also measured at four natural temperature regimes including temperatures from −1.8 to 31.4℃. *Plutella xylostella* could complete its development from egg to adult emergence within the range from 8 to 32℃. The survival rates of the entire immature stage at constant temperatures were above 60% between 12～28℃, but decreased rapidly both above and below this temperature range, dropping to zero at 6 and 34℃. The temperature range for complete development varied between stages and also between larval instars, with larvae having the widest tolerance range,

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followed by pupae and eggs. When test insects were reared at a favorable temperature to a given stage and then moved to a low or high temperature to observe the development and survival of individual stages or instars at these unfavorable conditions, the low and upper temperature limits for complete development were <4 and 40℃ for third and fourth instars, <4 and 38℃ for second instar, <4 and 36℃ for first instar, 8 and 36℃ for pupa, and 8 and 34℃ for egg, respectively. The relationship between the survival rate of the pre-imaginal stage and temperature was described well by a quadratic equation.

The mean duration of development from egg to adult emergence decreased with an increase of temperature, varying from 119.0 days at 8℃ to 11.2 days at 32℃, with the shortest development times at 30℃ and 32℃. Three mathematical models, i.e., the linear (degree-day) model, the Logistic equation and the Wang-Lan-Ding model, were used to describe the relationships between development rate and temperature at constant conditions. A BASIC program, based on the Marquardt techniques, was used to fit the models to various data sets. The results showed that the Wang-Lan-Ding model offered the best description; the Logistic equation gave good description at mid and low temperatures, while the linear model gave good description only at mid temperatures.

In order to simulate population development at natural temperatures, the inherent variability of development rate between individuals must be considered. The distributions of development times of *P. xylostella* at constant temperatures were found to follow the "same shape property" and were simulated well by a Weibull function.

The linear, the Logistic and the Wang-Lan-Ding models were then each coupled with the Weibull function to simulate the process of adult emergence of each cohort at a given natural temperature regimes. Temperature data were used as inputs to each of the rate models to calculate the amount of development at each time interval, which was then accumulated by the method of rate summation to estimate the proportion of mean development at a given point of time. The proportion of mean development was then used as input to the Weibull function to estimate the proportion of adult emergence. To compare the differences between observed and simulated events of adult emergence, the observed number of days from birth to 15%, 50% and 85% of adult emergence in each trial were compared with those predicted by each of the three models. The comparisons showed that the Logistic model and the Wang-Lan-Ding model simulated the population development well at all four natural temperature regimes, the maximum deviations being within the range of −1.7 to +1.1 days. However, the linear model gave accurate simulations only at mid temperature range, but produced falsely longer durations of development when the amount of temperatures below 10℃ became substantial. These results showed that development rate models derived from constant temperature data, once appropriately chosen, could be used effectively to predict population development of *P. xylostella* in the field. This study has provided the development rate models as well as models of development time distribution that may be used to predict the population development of *P. xylostella* at a wide range of natural temperature conditions.

Key words: *Plutella xylostella* L.; temperature; survival; development rate; simulation

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小菜蛾(*Plutella xylostella* L.)**属鳞翅目菜蛾科，主要危害十字花科蔬菜。由于它分布广，适应力强，对杀虫剂的抗性发展快，危害大等特点，而使其成为蔬菜害虫防治的重点。在中国，其主要发生在长江流域及其以南地区。温度是影响小菜蛾发生的重要生态因子之一，进而影响到小菜蛾的危害程度。有关温度与小菜蛾发育速率关系的研究已有一些报道**[1~4]**，但都在温度范围的选取时有所局限，另外关于变温对小菜蛾发育进度的定量研究未见报道，因此本文在较大温度范围内研究了温度对小菜蛾发育速率的影响，并将其用于变温下发育进度的模拟，为预测其发生期提供理论依据。**

1 材料和方法

1.1 虫源 **小菜蛾于**1995**年**6**月采自杭州郊区甘蓝地，室内饲养在**25~30℃，50%~80% RH，**光照周期** L∶D=14h∶10h，**光照强度** 1000~1500lx **条件下进行。收集的蛹放于冰箱内**(4~6℃)**保存用于传代。**

1.2 寄主植物 甘蓝 *Brassica oleracea* var. *capitata*，品种为"京丰一号"。

1.3 实验设计 恒温试验在 4～42℃范围设置 19 个恒温，温度变幅±0.5℃，光照时间 L：D=12h：12h。温度控制设备为广东医疗器械厂生产的 LRH-150-G 型或 LRH-250-G 型光照培养箱。培养箱底部放置盛水托盘，保持相对湿度在 60%～90%之间。先将室内饲养的蛹放在 20℃下羽化，成虫交尾后，按李广宏等[5]的方法收集卵，产卵 2～3h 后，将卵先放入养虫笼[6]内，然后放入各恒温箱内，16℃及以上每温度下放置 30～80 头不等的虫量，16℃以下每温度下放置 90～200 头不等的虫量。30℃ 及以上温度下每天观察 3 次，16～28℃温度下每天观察 2 次，其余温度下每天观察 1 次，记录发育进度及死亡数。幼虫用新鲜菜叶直接饲喂，适时换叶。

变温试验在顶部覆盖，四周为纱窗的田间养虫室内进行，养虫室内自然光较弱，故另加 2 盏 40W 日光灯每天供光 12～14h，用英国产的电子记录仪 Tinytag 记录温度，具体试验条件见表 1。

表 1 自然变温下具体试验条件

Table 1 Natural temperature regimes during the experiment

编号 Trial	试验起止日期 Start and end dates	温度 Temperature(℃)				起始卵数 Number of eggs at start	羽化成虫数 Number of adults emerged
		平均温度 Mean	温度幅度 Range	平均日最低气温 Mean min.	平均日最高气温 Mean max.		
S1	1999-01-05～1999-04-11	9.6	-1.8～24.1	6.5	12.8	150	64
S2	1999-02-10～1999-04-23	12.0	6.9～24.1	8.9	15.2	300	231
S3	1999-05-11～1999-06-01	22.0	15.6～29.2	19.4	24.9	200	117
S4	1999-06-05～1999-06-25	21.9	18.1～31.4	19.9	24.1	185	130

1.4 数据分析 温度和发育速率的关系用直线模型、Logistic 模型和王-兰-丁模型模拟[7,8]。为了模拟不同恒温下发育历期的分布，依据发育历期分布的"同形性质"[9,10]，用各恒温下每一组个体的发育历期除以所在温度下所有个体的加权平均发育历期作为常态历期(x)，在常态历期 x 时完成发育的个体比例为 $F(x)$，用 Weibull 函数($F(x)=1-\exp\{-^{[(x-\gamma)/\eta]^\beta}\}$)模拟多个恒温下这两者间的关系，建立发育历期分布模型[11]。然后综合应用发育速率模型和发育历期分布模型，模拟自然变温下的发育进度[12,13]。具体方法是先将温度值输入发育速率模型，通过速率累积，算得常态历期 x，再将 x 值输入上述发育历期分布模型，算得 $F(x)$，即任一给定时刻完成发育的个体比例。模拟时取的时间间隔为 4h，用自编的 Basic 程序执行[12,13]。将模拟羽化进度为 15%、50%和 85%出现的日期与这 3 个羽化百分率实际出现的日期直接进行比较，确定其差异[14]。

2 结果和分析

2.1 恒温下发育历期

小菜蛾在 8～32℃范围内能完成全世代的发育，在 34℃下，虽然卵能孵化，但都在 1 龄幼虫期死亡。34℃及以上温度下各虫态的发育历期是将试虫在 28℃下饲养至其前一虫态末期时放入相应温度下观察所得，而低于 8℃的温度下各虫态的发育历期是将试虫在 20℃下饲养至其前一虫态末期时放入相应温度下观察所得。

由表 2 可知，卵在恒温下可完成发育的温度范围最窄，为 8～34℃，其次是蛹，为 8～36℃，再次是预蛹，而幼虫在恒温下可完成发育的温度较宽，4℃和 6℃下各龄幼虫皆可完成发育，在高温下随着龄期的增加，能完成发育的温度就越高，3 龄和 4 龄幼虫在 40℃下亦能完成发育。幼期各虫态发育历期随温度升高而缩短，发育最快的温度在 30℃或 32℃，其中卵、2 龄幼虫和雄蛹在 32℃下发育最快，而 1 龄、3 龄、4 龄幼虫和雌蛹发育最快出现在 30℃。雄蛹发育历期一般要比雌蛹的长，平均为雌蛹的 1.1 倍。

2.2 温度对存活率的影响

恒温下幼期各虫态和整个幼期的存活率见表 3。卵的存活率(即孵化率)除了在 34℃下较低外，其余均在 90%以上。在 12～32℃内，各虫态存活率大多在 80%以上；温度低于 12℃，存活率多下降，当温度低于 8℃和高于 32℃时，整个幼期的存活率为 0。整个幼期的存活率和温度的关系符合二次曲线，曲线方程为：S

$=-1.787T^2+28.22T-30.78$（S 为存活率，T 为温度，拟合度 $R=0.9381$）。在 12℃和 28℃之间，存活率较高，超出这个范围，存活率大为降低。

表 2　小菜蛾幼期各虫态在不同恒温下的发育历期（d）（平均±标准误）

Table 2　Development time (mean±SE) of *Plutella xylostella* at constant temperature

温度（℃）Temperature	卵 Egg	1 龄 1st instar	2 龄 2nd instar	3 龄 3rd instar	4 龄 4th instar	预蛹 Prepupa	蛹（雌）Pupa（♀）	蛹（雄）Pupa（♂）	总历期① Total
4		47.9±0.70	34.6±0.56	41.8±1.52	51.7±3.37	12.0±0.48			
6	ID②	29.3±0.37	31.8±0.36	24.8±0.27	30.0±1.27	9.8±0.43	ID	ID	
8	20.8±0.08	13.0±0.06	14.4±0.11	12.9±0.09	15.2±0.13	5.1±0.12	35.3±0.37	39.8±0.74	119.0 ±1.07
10	15.4±0.08	10.8±0.11	11.4±0.14	9.6±0.11	11.0±0.18	4.1±0.14	24.9±0.24	27.8±0.21	88.2 ± 0.82
12	12.8±0.03	8.2±0.04	7.9±0.13	6.7±0.11	8.0±0.12	3.2±0.06	18.0±0.14	20.9±0.10	66.3 ± 0.58
14	8.4±0.05	4.6±0.15	5.2±0.12	4.6±0.06	5.4±0.05	1.9±0.08	10.8±0.12	12.3±0.08	41.6 ± 0.30
16	6.4±0.04	4.3±0.07	4.1±0.05	3.3±0.06	4.4±0.05	1.5±0.04	9.1±0.09	10.7±0.09	33.8 ± 0.32
18	4.7±0.10	3.6±0.11	3.8±0.09	2.8±0.06	3.7±0.04	1.2±0.05	6.7±0.06	7.3±0.08	26.7 ±0.26
20	4.0±0.05	2.5±0.10	3.3±0.12	2.3±0.19	3.2±0.15	0.96±0.03	5.3±0.06	6.1±0.07	21.9 ±0.23
22	3.5±0.07	2.1±0.11	2.8±0.12	1.9±0.12	2.5±0.16	0.79±0.10	4.5±0.17	5.1±0.16	18.4 ± 0.21
24	3.0±0.09	2.0±0.05	2.2±0.08	1.5±0.04	2.0±0.04	0.68±0.16	3.8±0.23	4.3±0.33	15.3 ± 0.22
28	2.4±0.07	1.6±0.17	1.4±0.10	1.3±0.11	1.7±0.28	0.53±0.18	3.1±0.24	3.3±0.28	12.1 ± 0.21
30	2.3±0.05	1.5±0.03	1.3±0.04	1.1±0.04	1.5±0.04	0.62±0.02	2.6±0.13	3.0±0.03	11.1 ± 0.22
32	2.2±0.08	1.5±0.16	1.0±0.15	1.3±0.16	1.7±0.15	0.60±0.17	2.9±0.16	2.8±0.16	11.1 ± 0.20
34	2.5±0.06	1.6±0.02	1.2±0.02	1.6±0.07	1.8±0.01	0.57±0.09	2.9±0.01	3.2±0.01	
36	ID	1.6±0.17	1.4±0.04	1.3±0.13	2.2±0.04	0.51±0.10	4.0±0.00	4.2±0.17	
38		ID	1.2±0.09	2.0±0.06	2.9±0.10	ID	ID	ID	
40			ID	2.3±0.11	3.3±0.06				
42				ID	ID				

①在计算总历期时，将雌蛹和雄蛹的平均历期作为蛹的历期 In the calculation of total development time, the mean time of both female and male pupae was used for that of the pupal stage；②不能完成发育 Incomplete development

表 3　小菜蛾不同虫态和龄期在不同恒温条件下的存活率（%）

Table 3　Percent survival of various stages and instars of *Plutella xylostella* at constant temperature

温度（℃）Temperature	卵 Egg	1 龄 1st instar	2 龄 2nd instar	3 龄 3rd instar	4 龄 4th instar	预蛹 Prepupa	蛹 Pupa	整个幼期 Egg to adult
6	0							0
8	98.9	73.5	92.3	76.7	71.7	69.7	78.3	20.1
10	96.9	77.0	82.5	90.0	75.0	68.5	67.6	19.2
12	95.8	79.8	96.7	93.2	96.3	96.2	98.7	63.0
14	100.0	93.3	97.6	97.6	100.0	100.0	90.0	80.0
16	100.0	80.0	98.3	94.9	100.0	100.0	94.6	70.7
18	100.0	100.0	91.5	98.2	88.7	97.9	91.3	71.2
20	98.6	97.1	98.5	100.0	100.0	98.5	81.8	76.1
22	93.9	93.6	100.0	93.1	92.6	100.0	92.0	69.7
24	88.1	97.3	100.0	94.4	100.0	100.0	94.1	76.2
28	97.4	94.6	100.0	97.1	91.2	100.0	90.3	73.7
30	94.3	76.0	100.0	86.8	100.0	90.9	90.0	50.9
32	93.0	88.7	91.5	95.4	90.2	100.0	73.0	47.4
34	57.6	0.0						0.0

2.3　恒温下发育速率和温度关系的模拟

依据表 2 的数据，用直线模型、Logistic 模型和王-兰-丁模型模拟发育速率和温度的关系。根据 3 个模型的特点，每一模型拟合数据的温度范围做了相应的取舍[12,14]，其中直线模型取 10～30℃，Logistic 模型取 4～32℃，王-兰-丁模型取 4～40℃。参数值和拟合度列于表 4，整个幼期发育速率和温度的模拟见图 1。其中 Logistic 模型和王-兰-丁模型的拟合度较高，但 Logistic 模型不能有效地模拟高温下的发育速率，而王-兰-丁模型对于among实验温度范围内的发育速率，均能给出很好的模拟。相比之下，直线模型只在中温区内模拟度较高。

表 4 不同模型模拟小菜蛾发育速率和温度关系的参数值和拟合度

Table 4 Parameter values of three models describing the relationships between temperature and development rate of *Plutella xylostella*

模型 Model	参数 Parameters	卵 Egg	1 龄 1st instar	2 龄 2nd instar	3 龄 3rd instar	4 龄 4th instar	蛹(雌) Pupa(♀)	蛹(雄) Pupa(♂)	总历期 Total
直线模型	t±SE	7.3±0.14	7.3±0.41	7.2±0.82	7.6±0.24	7.0±0.41	7.8±0.24	7.9±0.28	7.4±0.20
Degree-	k±SE	52.1±0.89	33.7±1.61	36.1±3.34	27.9±0.81	37.4±1.67	64.8±2.0	72.7±2.69	268.2±6.48
day	R^2	0.9778	0.9804	0.9506	0.9748	0.9802	0.9867	0.9823	0.9859
逻辑斯蒂模型	K	0.6082	0.4877	0.9159	1.0389	0.4096	0.4083	0.3959	0.1079
Logistic model	a	3.8161	4.2279	4.2865	4.1488	4.2616	4.2366	4.274	3.9548
	b	0.1685	0.2917	0.1975	0.1925	0.2966	0.2039	0.1971	0.1839
	R^2	0.9965	0.9915	0.9616	0.998	0.9966	0.9973	0.9965	0.9968
王-兰-丁模型	H	0.6104	0.9314	1.2382	1.2136	0.7856	0.3783	0.3802	0.1215
Wang-Lan-Ding	T_L	3.26	1.52	0.97	0.22	−0.12	4.25	4.22	2.58
model	T_H	34.78	37.94	38.78	41.6	42.21	36.42	36.5	35.49
	T_O	22.69	20.48	22.12	21.39	19.56	20.58	21.34	22.79
	r	0.1683	0.2113	0.216	0.1919	0.1998	0.205	0.1987	0.1742
	δ	0.55	1.83	1.29	3.78	4.82	0.4	0.46	1.62
	R^2	0.9943	0.9897	0.9844	0.9966	0.9966	0.9974	0.9965	0.9961

2.4 发育历期分布的模拟

考虑在极端温度下死亡率较高及在高温下相对观察间隔(相对于平均发育历期)较长,所观察的发育历期频次分布代表性差[7,11],故只选择了 8～22℃各恒温下整个幼期的发育历期频次分布的数据,将每一恒温下各个体的发育历期标准化,即求各组个体的常态历期,用 Weibull 函数模拟的结果如下:

$$F(x) = 1 - \exp(-[(x - 0.78)/0.23]^{5.76}) \qquad R = 0.9849$$

式中,x 为常态历期,$F(x)$为累积相对频率(图 2)。

2.5 变温下羽化进度的模拟

将发育历期分布函数与每一发育速率模型耦连,模拟变温下的羽化进度,并与实测值进行比较(图 3)。根据 3 个羽化比例的模拟值和实测值之间的差异可知,在 4 次变温实验中,Logistic 模型和王-兰-丁模型的预测值的差异均较小(−1.7～+1.1d)。但是,直线模型只在较高的温度下准确地模拟了羽化进度,在 S1 和 S2 试验中,3 个羽化百分率出现日期的模拟值和实测值相差 2.5～12.5d,而在 S3 和 S4 试验中,差异仅为−0.1～+1.1d。

3 讨论

在定量确定昆虫发育速率和温度的关系研究中,常用的方法是在实验室一系列恒温下测定发育历期,然后用适当的模型去模拟,有关模型的报道和比较已有很多[15～17]。本文选择了直线模型,Logistic 和王-兰-丁模型模拟小菜蛾发育速率和温度的关系,并对 3 个模型的结果进行比较。根据建立的发育速率和温度关系的模型,再用于田间变温条件下的发育进度的预测。虽然有人对恒温数据用于变温研究提出疑问[18],但依据恒温下发育速率所建立的模型可以准确地模拟变温下的发育进度[7,13,14,17]。

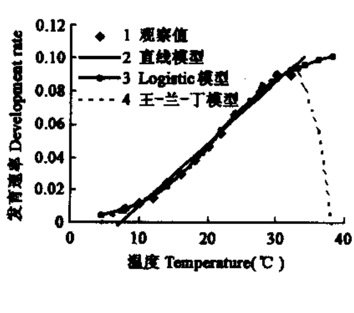

图 1 小菜蛾幼期(卵到羽化)发育速度和温度关系的模拟

Fig. 1 Relationships between temperature and development rate of *Plutella xylostella*

1. Observed; 2. Degree-day; 3. Logistic; 4. Wang-Lan-Ding

发育速率模型往往只考虑了种群的平均发育速率,由于种群存在个体差异,因此在模拟变温下的发育进度时,还要考虑个体间的差异。Sharpe 等[9]和 Curry 等[10]通过对变温动物发育速率控制机理的研究,发现

每一种昆虫发育速率的变异系数基本不随温度变化。由于发育历期只是发育速率的一种转换形式(倒数),故发育速率分布的内在一致性必然导致发育历期分布的内在一致性。因此,只要取一个常态化的相对历期消除温度的影响,如以各温度下每一组个体的发育历期除以所在温度下所有个体的加权平均发育历期作为常态历态期,同一种群在不同恒温下的发育历期分布必然趋于一致,这就是发育历期分布的"同形性质"。通过对多种昆虫在不同恒温下个体间发育历期变异的分析,已证明这种性质广泛存在[7,11,19]。将发育历期"同形性质"的特性与恒温下发育速率和温度的模型联合应

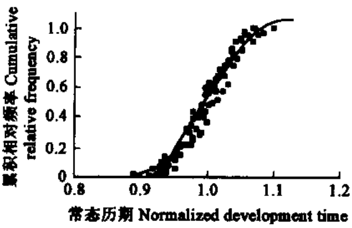

图 2　小菜蛾在 7 个恒温下的常态历期累计相对频率

Fig. 2　Cumulative relative frequency of normalized complete development of *Plutella xylostella*

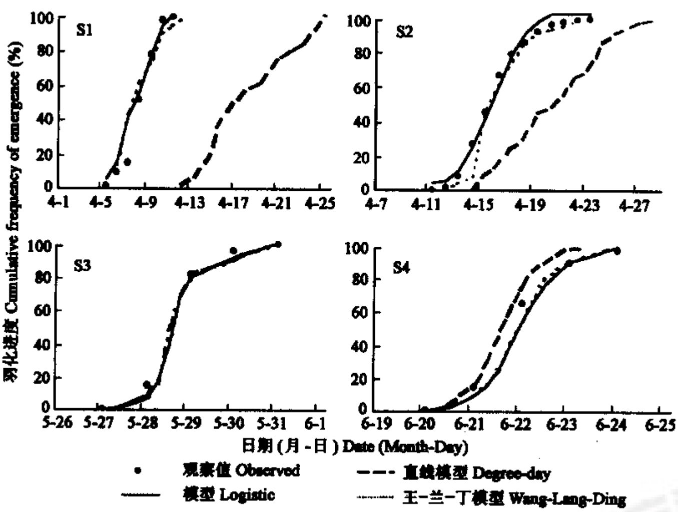

图 3　小菜蛾在 4 种自然变温条件下羽化进度和模型预测进度的比较

Fig. 3　Observed and simulated cumulative frequency of emergence in *Plutella xylostella* at four natural temperature regimes

用于变温下的发育进度的预测时,能达到较好的效果[12, 14, 17, 20]。

考虑种群间的个体差异,用 Weibull 函数模拟了小菜蛾发育历期的分布,结果符合"同形性质"(图 2)。在将其与所选模型联合预测小菜蛾在变温下的羽化进度时,Logistic 和王-兰-丁模型均能给出很好的模拟效果。刘树生和孟学多[7, 12 14]在用王-兰-丁模型模拟桃蚜和萝卜蚜在变温下的羽化进度时,发现在低温下有明显的偏离。王-兰-丁模型在模拟恒温低温下的发育速率时可出现偏差(图 1),比实测值要低,因此,如果低温强度较大或持续时间较长,就会影响王-兰-丁模型的模拟效果。但在此温度条件下,Logistic 模型仍能达到较好的模拟效果,因此,在低温强度较大的情况下,Logistic 模型的模拟效果可能要比王-兰-丁模型好[7]。

相比较而言,直线(日度)模型只能模拟中温区内小菜蛾的羽化进度,而在低温区的模拟则发生了明显的偏离(图 3),说明直线模型低估了低温下小菜蛾的发育。尽管如此,许多昆虫能通过生理或行为特性(如夏眠,迁飞等)来适应或逃避不利的生存环境,故可避免暴露在极端温度下[21, 22],因此在作变温下发育进度的预测时要考虑这种适应性。尽管温度的变化会导致一些模型在预测上的偏离,但只要模型选择恰当,根

据恒温试验结果所得的模型可以准确预测各种变温下的发育速度[13, 14, 20]。

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