Effect of constant temperature on development and survival of *Lymantria albescens* Hori and Umeno and *Lymantria xyliana* Swinhoe (Lepidoptera: Lymantriinae) from Okinawa, Japan

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Abstract

We investigated the effect of temperature on the developmental and survival rates in the life stages of the Okinawan gypsy moth, *Lymantria albescens*, and the casuarina tussock moth *L. xyliana*, from Okinawa, Japan. Under laboratory conditions at constant temperatures of 17.5, 20.0, 22.5, 25.0, 27.5 and 30.0°C, the thermal threshold and thermal constant from larva to adult for *L. albescens* and *L. xyliana* were 9.1–9.9 and 8.4–11.0°C and 780.8–872.2 and 731.8–1,053.8 degree-days, respectively. Last-instar larvae of males of both species were mostly 6th instars, whereas a large number of female last-instar larvae were 6th and 7th instars. Survival rates of *L. albescens* and *L. xyliana* were very low at 30.0°C, indicating that these species in Okinawa are not resistant to temperatures higher than 30°C. Our results provide information for predicting the appearance of field populations of *L. albescens* and *L. xyliana* in Okinawa.

Key words: Okinawan gypsy moth; casuarinas tussock moth; degree-days; developmental zero; mortality

INTRODUCTION

The Okinawan gypsy moth, *Lymantria albescens* Hori and Umeno (Lepidoptera: Lymantriinae), is distributed in the Ryukyu Islands of Japan, including Ishigaki and Okinawa (Inoue, 1982; Pogue and Schaefer, 2007). *Lymantria albescens* was recorded as a pest of *Eucalyptus camaldulensis*, *Macaranga tanarius*, *Castanopsis seiboldii*, and *Elaeocarpus sylvestris* (Nasu et al., 2004; Tominaga, 2004; Pogue and Schaefer, 2007).

The Casuarina tussock moth, *L. xyliana* Swinhoe (Lepidoptera: Lymantriinae), is distributed in southern Japan, Taiwan, and China (Fujian, Guangdong) (Inoue, 1982; Pogue and Schaefer, 2007). In Japan, it is distributed in Shikoku, Kyushu and Okinawa (Inoue, 1982), and also in Yamaguchi prefecture in Honshu, Japan (Jinbo, 2001). The Casuarina tussock moth is a forest tree defoliator in Taiwan (Chang, 1991), especially in casuarina (*Casuarina equisetifolia*) and acacia (*Acacia confusa*)

forests, and fruit tree orchards (Chao et al., 1996). Sixty-three species of plants belonging to 29 families were recorded as the host plants of *L. xyliana* in Taiwan (Chao et al., 1996). The host plants of *L. xyliana* in Japan are not yet well known but likely consist of a wide range of species in many families.

It is important to predict life history events in these species for forest and fruit tree management; however, there have been no studies on the thermal constant and thermal threshold for these Okinawan species. Therefore, this paper presents the effect of temperature on the development and survival of *L. albescens* and *L. xyliana* collected in Naha, Okinawa, and reared under laboratory conditions at six constant temperatures. We also provide information on the numbers of larval instars.

MATERIALS AND METHODS

Insects. Egg masses of *L. albescens* and *L.*

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xylina were collected in Naha city, Okinawa, Japan (26°22'N, 127°71'E) in late February, 2006 and 2007. Nearly all egg masses of *L. albescens* and *L. xyлина* were collected on aerial roots of *Ficus microcarpa* in Okinawa. The collected egg masses were placed in Petri dishes, and kept at 20°C in incubators (SANYO, Osaka: MIR-253). We began rearing experiments using hatched larvae less than 24 h old.

Rearing methods for development and survival at different temperatures. We conducted rearing experiments of larval and pupal stages in incubators set at 17.5, 20.0, 22.5, 25.0, 27.5 and 30.0°C with a long-day photoperiod (16L8D). Humidity levels of 80% were maintained by placing two containers of water at the bottom of each incubator. We used the artificial diet of Bio-Serv (Frenchtown, NJ, USA: product #F9642B) for larval rearing. We dispensed about 80 ml of the diet into plastic containers (Sweetheart, Chicago, IL, US: ME6RX, 6 oz) with paper lids, and reared seven larvae in each container upside-down with the diet uppermost before 4th instar. After the 3rd instar, the larvae were placed individually in paper containers (Dixie Japan, Tokyo: GHCM06WN, 6 oz) with plastic lids in which 15 small holes provided ventilation. We filled plastic cups (FP CHUPA, Tokyo: CP070004, 1/2 oz) with the diet, and placed two cups in each paper container. The diet was replaced at regular intervals (2 d at 27.5 and 30.0°C, 3 d at 22.5 and 25.0°C, and 4 d at 20 and 17.5°C). We checked the survival, larval molt, pupation and adult emergence daily. Failures in larval and pupal molting, and dead larvae and pupae were not included in calculations of the thermal threshold and thermal constant in this study.

The developmental rates Y (measured as $1/(\text{developmental period in days})$) of various life stages (i.e., larva, pupa, and total development) were fitted to temperatures to obtain the relationship in terms of $Y=aT+b$, where T is temperature, and a and b are regression parameters. The thermal threshold ($T_0=-b/a$) and thermal constant ($K=1/a$) were obtained from the regression lines.

The developmental period and survival rate in each stage were compared among temperatures. Data on the developmental period was subjected to ANOVA followed by Tukey-Kramer's multiple comparison test. Data on the survival rates were subjected to the chi-square test.

RESULTS

L. albescens

The number of larval molts in *L. albescens* (Table 1) showed that the last larval instars were 5th, 6th and 7th instars in males, and 5th, 6th, 7th, and 8th instars in females. A large part of the last-instars were 6th instar (84.6%) in males, and 6th and 7th instars (62.9% and 34.8%, respectively) in females.

The survival rate at immature stages (1st-instar larvae to adults) of *L. albescens* (Table 2) was significantly different at different temperatures ($\chi^2=43.41$; $df=5$; $p<0.0001$), and was lowest at 30.0°C. In 6th instar larvae and pupae of *L. albescens*, survival was significantly different at different temperatures (6th instar: $\chi^2=31.38$; $df=5$; $p<0.0001$, pupa: $\chi^2=32.66$; $df=5$; $p<0.0001$), and was lowest at 30.0°C. Examination of survival rates at each developmental stage revealed that the higher mortality at 30.0°C was largely attributable to the death of 1st and 6th instar larvae and pupae, with survival dropping below 80% for these three developmental stages. Survival of other instar larvae was generally high.

The developmental periods of *L. albescens* at different temperatures (Table 3) decreased as temperatures increased from 17.5°C to 27.5°C.

Table 4 shows the regression equations for the developmental period against temperatures, values of thermal thresholds and thermal constants calculated for *L. albescens* using data from 17.5°C to 27.5°C (excluding data at 30°C). Although the last-

Table 1. Numbers of last-instar larvae of *Lymantria albescens* and *L. xyлина* from Okinawa in laboratory rearings

	Number of last-instar larva (%)			
	5th instar	6th instar	7th instar	8th instar
<i>L. albescens</i>				
Male	8 (6.8)	99 (84.6)	10 (8.5)	—
Female	1 (1.1)	56 (62.9)	31 (34.8)	1 (1.1)
<i>L. xyлина</i>				
Male	8 (11.4)	54 (77.1)	8 (11.4)	—
Female	1 (1.1)	36 (41.4)	46 (52.9)	4 (4.6)

Number of larva with each instar as the last-instar.

Numbers in parentheses indicate the percentage of larvae in each last-instar.

Table 2. Survival rates of larvae and pupae of *Lymantria albescens* and *L. xyliana* collected from Okinawa reared at different temperatures

Temperature (°C)	Survival (%)								
	1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar	7th instar	Pupa	Larva-adult
<i>L. albescens</i>									
17.5	31 (88.6)	31 (100)	31 (100)	31 (100)	31 (100)	30 (100)	11 (100)	30 (96.8)	30 (85.7)
20.0	35 (94.6)	34 (97.1)	33 (97.1)	33 (100)	32 (97.0)	32 (100)	9 (90.0)	29 (93.5)	29 (78.4)
22.5	64 (94.1)	64 (100)	63 (98.4)	61 (96.8)	59 (96.7)	55 (100)	9 (100)	59 (100)	59 (86.8)
25.0	58 (87.9)	58 (100)	57 (98.3)	55 (96.5)	54 (98.2)	51 (98.1)	13 (100)	52 (98.1)	52 (78.8)
27.5	38 (88.4)	38 (100)	37 (97.4)	36 (97.3)	34 (94.4)	30 (93.8)	4 (100)	30 (93.8)	30 (69.8)
30.0	19 (76.0)	19 (100)	19 (100)	17 (89.5)	15 (88.2)	11 (73.3)	6 (85.7)	6 (60.0)	6 (24.0)
<i>L. xyliana</i>									
17.5	36 (97.3)	36 (100)	35 (97.2)	34 (97.1)	34 (100)	34 (100)	13 (92.9)	30 (90.9)	30 (81.1)
20.0	35 (97.2)	34 (97.1)	33 (97.1)	33 (100)	32 (97.0)	32 (100)	23 (95.8)	28 (90.3)	28 (77.8)
22.5	54 (100)	52 (96.3)	50 (96.2)	49 (98.0)	49 (100)	45 (93.8)	19 (95.0)	41 (91.1)	41 (75.9)
25.0	61 (100)	57 (93.4)	57 (100)	54 (94.7)	54 (100)	46 (90.2)	23 (95.8)	38 (79.2)	38 (62.3)
27.5	20 (100)	20 (100)	20 (100)	20 (100)	20 (100)	15 (100)	1 (100)	19 (95.0)	19 (95.0)
30.0	17 (73.9)	17 (100)	15 (88.2)	15 (100)	14 (93.3)	9 (64.3)	8 (100)	1 (11.1)	1 (4.3)

Numbers in parentheses indicate the percentage of larvae that survived in each instar.

Survival of 8th instar larvae was 100%: one larva at 25°C in *L. albescens*, and three larvae at 22.5°C and one larva at 20°C in *L. xyliana*.

Table 3. Developmental periods of larvae and pupae of *Lymantria albescens* and *L. xyliana* collected from Okinawa at different temperature

Temperature (°C)	Developmental period in days (mean±SD)											
	Male				Female (6th instar)				Female (7th instar)			
	<i>n</i>	Larva	Pupa	Larva-adult	<i>n</i>	Larva	Pupa	Larva-adult	<i>n</i>	Larva	Pupa	Larva-adult
<i>L. albescens</i>												
17.5	14	79.3±4.4 a	30.9±1.2 a	110.2±5.0 a	5	82.4±2.9 a	29.2±0.8 a	111.6±2.2 a	9	91.8±3.6 a	28.4±1.1 a	120.2±3.1 a
20.0	13	53.2±5.2 b	20.0±1.4 b	73.2±4.8 b	9	57.4±3.1 b	18.1±1.5 b	75.5±5.4 b	6	61.6±2.7 b	17.5±0.7 b	79.2±2.2 b
22.5	28	44.7±2.9 c	16.2±1.0 c	60.9±2.6 c	18	45.6±3.1 c	14.3±1.5 c	59.9±2.6 c	7	56.4±6.5 c	14.1±1.1 c	70.5±6.7 c
25.0	27	39.3±3.1 d	13.7±0.7 d	53.0±3.0 d	11	40.7±2.8 d	11.8±0.6 d	52.5±2.7 d	7	47.1±7.4 d	11.8±1.1 d	58.9±2.6 d
27.5	14	33.0±3.5 e	11.4±1.0 e	44.5±4.1 e	12	36.1±2.8 e	9.8±0.7 e	46.0±2.8 e	1	39.0 d	9.0 d	48.0 d
30.0	3	31.0±0.0 e	10.0±0.0 e	41.0±0.0 e	1	32.5 de	10.5 de	43.0 de	1	39.0 d	9.5 d	46.5 d
<i>L. xyliana</i>												
17.5	15	86.3±5.5 a	29.4±1.7 a	115.7±5.6 a	5	84.8±3.5 a	27.2±0.8 a	112.0±3.4 a	10	95.9±4.0 a	25.4±0.8 a	121.3±3.9 a
20.0	6	60.6±3.2 b	18.1±1.0 b	78.7±3.6 b	2	58.3±3.9 b	15.5±0.7 b	73.8±3.2 b	17	71.6±3.5 b	16.6±1.1 b	88.2±3.6 b
22.5	16	45.8±3.7 c	15.6±0.9 c	61.4±3.7 c	9	49.2±5.6 c	13.7±0.8 bc	62.9±5.3 c	10	60.9±4.5 c	13.6±0.7 c	74.5±4.4 c
25.0	14	41.8±4.2 cd	12.7±0.8 d	54.5±3.9 d	8	37.9±3.1 d	12.1±2.0 cd	50.0±2.4 d	9	53.9±2.7 d	10.7±0.9 d	64.6±2.6 d
27.5	2	30.0±3.5 e	12.3±0.4 d	42.3±3.2 e	12	34.2±2.2 d	10.8±0.9 d	45.0±2.0 e	—	—	—	—
30.0	1	38.0 de	11.0 d	49.0 cde	—	—	—	—	—	—	—	—

Values followed by different letters in the same column are significantly different (Tukey-Kramer test, $p<0.05$).

instar was 6th instar in almost all males (85%), 6th and 7th instars as the last-instar were 63% and 35% in females, respectively. Female values for 6th and 7th last-instars are shown separately. The thermal threshold (Table 4) for male larvae was estimated

to be 9.4°C, that for male pupae was 11.0°C, and for female larvae with 6th and 7th instars as the last-instar it was 8.1 and 9.1°C, respectively. For female pupae with 6th and 7th instars as the last-instar it was 11.7 and 12.2°C, respectively. The

Table 4. Regression equation of developmental period, thermal threshold and thermal constant for *Lymantria albescens* and *L. xyliana*

	Regression equation	r^2	Thermal threshold (°C)	Thermal constant (degree-days)
<i>L. albescens</i>				
Male				
Larva	$Y = -0.01581 + 0.00168T$	0.880	9.4	594.8
Pupa	$Y = -0.05891 + 0.00533T$	0.924	11.0	187.6
Larva-adult	$Y = -0.01267 + 0.00128T$	0.925	9.9	780.8
Female (6th instar)				
Larva	$Y = -0.01187 + 0.00147T$	0.869	8.1	681.9
Pupa	$Y = -0.07603 + 0.00648T$	0.899	11.7	154.2
Larva-adult	$Y = -0.01106 + 0.00121T$	0.928	9.1	826.5
Female (7th instar)				
Larva	$Y = -0.01232 + 0.00136T$	0.903	9.1	736.5
Pupa	$Y = -0.08313 + 0.00684T$	0.942	12.2	146.2
Larva-adult	$Y = -0.01134 + 0.00115T$	0.939	9.9	872.2
<i>L. xyliana</i>				
Male				
Larva	$Y = -0.02019 + 0.00183T$	0.882	11.0	546.2
Pupa	$Y = -0.06145 + 0.00558T$	0.937	11.0	179.3
Larva-adult	$Y = -0.01499 + 0.00137T$	0.936	11.0	731.8
Female (6th instar)				
Larva	$Y = -0.01886 + 0.00177T$	0.917	10.7	565.2
Pupa	$Y = -0.04939 + 0.00529T$	0.830	9.3	189.1
Larva-adult	$Y = -0.01371 + 0.00132T$	0.951	10.4	756.3
Female (7th instar)				
Larva	$Y = -0.00783 + 0.00107T$	0.906	7.3	932.4
Pupa	$Y = -0.08260 + 0.00706T$	0.932	11.7	141.7
Larva-adult	$Y = -0.00795 + 0.00095T$	0.942	8.4	1,053.8

Regression equations calculated based on the values obtained at temperatures from 17.5 to 27.5°C.

Y and T in regression equations show (1/developmental period in days) and temperatures (°C), respectively.

thermal constants (Table 4) were 594.8 degree-days for male larvae, and 187.6 degree-days for male pupae. Female larvae with 6th and 7th instars as the last-instar required 681.9 and 736.5 degree-days, respectively, while female pupae with 6th and 7th instars as the last-instar needed 154.2 and 146.2 degree-days, respectively.

L. xyliana

The number of larval molts in *L. xyliana* (Table 1) was 5th, 6th and 7th instars in males, and 5th, 6th, 7th, and 8th instars in females. Most of the last-instars were 6th instar (77.1%) in males, and 6th and 7th instars (41.4% and 52.9%, respectively) in females.

The survival rate of the immature stages (1st instar larvae to adults) of *L. xyliana* from Okinawa (Table 2) showed that the survival of 1st instar larvae to adults was significantly different at different

temperatures ($\chi^2=56.46$; $df=5$; $p<0.0001$), being lowest at 30.0°C. In 1st and 6th instar larvae and pupae, survival was significantly different at different temperatures (1st instar: $\chi^2=40.17$; $df=5$; $p<0.0001$; 6th instar: $\chi^2=25.47$; $df=5$; $p<0.0001$; pupa: $\chi^2=42.87$; $df=5$; $p<0.0001$), and was lowest at 30.0°C. The higher mortality at 30.0°C was largely attributable to the death of 1st and 6th instar larvae and pupae, with survival dropping below 75% for these three developmental stages. The survival of other instars was generally high (frequently about 90%).

Developmental periods of *L. xyliana* at different temperatures (Table 3) decreased as temperature increased from 17.5°C to 27.5°C.

Table 4 shows the regression equations for the developmental period against temperatures, values of thermal thresholds and thermal constants calculated for *L. xyliana* using data from 17.5°C to

27.5°C (excluding data for 30°C). The last-instar was 6th instar in more than 77% males, but in females, two types of last-instar were observed, 6th instar (41%) and 7th instar (53%). These values are shown for females for each type of last-instar. The thermal threshold for both larvae and male pupae was identical at 11.0°C. The thermal thresholds for female larvae with 6th and 7th instars as the last-instar were 10.7 and 7.3°C, respectively, and for female pupae were 9.3 and 11.7°C, respectively. The thermal constants required 546.2 degree-days for male larvae, and 179.3 degree-days for male pupae. Female larvae with 6th and 7th instars as the last-instar required 565.2 and 932.4 degree-days, respectively, and female pupae 189.1 and 141.7 degree-days, respectively.

DISCUSSION

Regression analysis for developmental rates during larval and adult stages predicted a temperature threshold of 9.1–9.9°C, and thermal constant of 780.8–872.2 degree-days for *L. albescens*. The corresponding values for *L. xyliana* were 8.4–11.0°C, and 731.8–1,053.8 degree-days. These values are similar for *L. albescens* and *L. xyliana* collected in Okinawa, and indicate that both Okinawan species show similar physiological responses to temperature.

Furuta (1973) concluded that the thermal threshold of the female larval stage of Sapporo (Hokkaido) *L. dispar* was between 6.5 and 9.5°C. Thermal thresholds of *L. albescens*, the most southern Lymantriinae in Japan, are within the range of those of larval stages in Hokkaido *L. dispar*, the most northern subspecies in Japan. *Lymantria (P.) albescens* hatches in early March (mean day temperature in March between 1999 and 2008 at Naha, Okinawa, Japan=18.9°C, calculated by using data on the web site of the Japan Meteorological Agency, <http://www.data.jma.go.jp/obd/stats/etrn/index.php>), and emerges in early June (mean in June=27.0°C). On the other hand, Hokkaido *L. dispar* hatches in early May (mean in May at Sapporo, Hokkaido, Japan=12.8°C), and emerges in early August (mean in August=22.5°C). Although there are great differences in latitude (Naha: 26°12'N, Sapporo: 43°3'N), there was little difference in mean temperatures during the developmental periods between species. These

differences in developmental periods indicate that both species have evolved so as to hatch and emerge at similar and optimal temperatures in different respective regions.

Kiritani (1997) reported that the thermal threshold from egg to adult for 83 Lepidopteran species was $10.4 \pm 2.4^\circ\text{C}$ (mean $\pm$ SD), and the thermal constant for 80 Lepidopteran species was 463.3 ± 153.5 degree-days. The thermal thresholds of *L. albescens* and *L. xyliana* of Okinawa estimated in the present study were within the range for the 83 Lepidopteran species, but our estimate of the thermal constants was higher than that for the 80 Lepidopteran species. The development of *L. albescens* and *L. xyliana* in Okinawa requires a greater period at the effective temperature, because both species are among the largest Lepidoptera reported by Kiritani (1997).

In larva-adult of *L. albescens* and *L. xyliana* of Okinawa, the thermal constant for males tended to be lower than for females, and the thermal threshold for males tended to be higher than for females (Table 4). Similar phenomena were reported for *Planococcus kraunhiae* (Arai, 1996), *Galerucella nipponensis* (Toda and Yano, 1986) and *Megacopta punctissimum* (Tayutivutikul and Yano, 1990). We think that the higher thermal constant for females than for males can be attributed to the difference in body size and to the cost of producing eggs.

The survival rates at 30.0°C tended to be lower than under other temperature conditions in *L. albescens* and *L. xyliana* (Table 2). High mortality occurred in 1st and 6th instar larvae and pupae. Survival rates from egg to adult in tropical-subtropical species of *Eurema* and *Catopsilia* remained high up to 28°C (Jones et al., 1987). These data suggest that subtropical lepidopteran species are not resistant to temperatures higher than 30°C.

Yeh et al. (2006) reported that the last-instar larvae of *L. xyliana* ($n=30$) were 5th instar in males and 5th and 6th instars in females in the Bagua Mountain area of central Taiwan. We obtained 5th to 7th instars in males and 5th to 8th instars in females of *L. xyliana* from Okinawa. Larval molts are different among the same sex in both regions, and are more diverse in Okinawan *L. xyliana*.

Ficus microcarpa was recorded as a host plant of *L. xyliana* in Taiwan (Chao, 1996), but not as a host plant of *L. albescens* (e.g. Schaefer et al., 1988) and *L. xyliana* in Japan. We collected egg masses of

L. albescens and *L. xyliana* from *F. microcarpa* in Okinawa; therefore, *F. microcarpa* is probably also an additional host plant of *L. albescens* and *L. xyliana* in Okinawa, but this remains to be confirmed.

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