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Peter J. Martinat *Abbot Labratories*

Douglas C. Allen State University of New York

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1989

THE GREAT LAKES ENTOMOLOGIST

57

RESPONSE OF SADDLED PROMINENT (LEPIDOPTERA: NOTODONTIDAE) PUPAE TO DESICCATION, COLD TREATMENT, AND POST-COLD TREATMENT INCUBATION TEMPERATURE¹

Peter J. Martinat² and Douglas C. Allen³

ABSTRACT

Saddled prominent, *Heterocampa guttivitta*, pupae were placed at 1.5°C for 50 to 200 days, then incubated at one of four post-cold temperatures ranging from 10° to 26.7°C. Adults emerged from pupae exposed to all cold treatment periods. A few adults also emerged from pupae that were not exposed to cold. The time required for adult emergence following cold treatment declined with longer periods of cold treatment and higher post-cold incubation temperature. The interaction between these two main effects was also significant. Adult morphogenesis begins immediately after pupation, and continues until interrupted by cold temperature. When pupae were subjected to desiccating conditions prior to cold treatment, weight loss due to desiccation was accompanied by increased mortality. Desiccation occurred faster at 15.6° than at 18.0°C. Our results identify a physical factor which might contribute to pupal overwintering mortality: prolonged excessive drought conditions between time of pupation and the onset of cold.

In an investigation of abiotic factors important to the population dynamics of saddled prominent, Martinat and Allen studied laboratory responses of eggs and larvae to temperature and humidity (1987a), the relationship between outbreaks and drought (1987b), outbreak history and behavior (1988a), and caterpillar behavior in the forest (1988b). We report here additional studies on adult emergence and survivorship of overwintering pupae in the laboratory as influenced by duration of cold treatment and

The saddled prominent, *Heterocampa guttivatta* (Walker), (Lepidoptera: Notodontidae) is a periodic defoliator of northern hardwood forests where American beech, *Fagus grandifolia*, sugar maple, *Acer saccharum*, and yellow birch, *Betula alleghaniensis* are principle constituents. Outbreaks have occurred in northeastern United States and southeastern Canada every eight to twelve years since 1907. The species is indigenous and occurs throughout eastern United States and southeastern Canada where it overwinters as a diapausing pupa and emerges from late May to late June. Eggs are laid singly on the foliage of preferred hosts, and eclose in 9–10 days. There are five larval instars, and peak defoliation occurs from late July through mid-August. Mature caterpillars drop from the foliage, burrow into litter below the host tree, and form a loose pupal cell of silk and litter particles. Pupation occurs following a two to three day prepupal period. Other aspects of saddled prominent biology are reviewed in Patch (1908), Allen and Grimble (1970), and Allen (1973).

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²Chemical and Agricultural Products Division, Abbott Laboratories, North Chicago, IL, 60064.

³Department of Environmental and Forest Biology, College of Environmental Science and Forestry, State University of New York, Syracuse, NY, 13210.

58

THE GREAT LAKES ENTOMOLOGIST

Vol. 22, No. 2

Cold Treatment (Days)	Temperature Following Cold Treatment (°C.)	Number of Adults Successfully Emerged	Days to Adult Emergence Following Cold Treatment $(X \pm SE)$
50	10.0	4	76.5 ± 5.6
50	15.6	13	51.4 ± 3.7
50	21.1	15	24.3 ± 3.0
50	26.7	7	12.1 ± 1.8
100	10.0	8	63.8 ± 8.7
100	15.6	15	34.4 ± 3.0
100	21.1	24	16.3 ± 0.9
100	26.7	25	8.4 ± 0.5
150	10.0	5	47.4 ± 0.3
150	15.6	10	18.9 ± 0.6
150	21.1	10	11.1 ± 0.8
150	26.7	10	6.9 ± 0.5
200	10.0	8	51.4 ± 2.8
200	15.6	16	27.0 ± 1.3
200	21.1	11	9.4 ± 0.6
200	26.7	13	$8.2~\pm~0.9$

Table 1.—Effect of duration of cold treatment and incubation temperature following cold treatment on saddled prominent adult emergence time (n = 36 individuals per treatment).

incubation temperature following cold treatment. We also dissected pupae at regular intervals to determine the timing of adult morphogenesis.

When collecting pupae from natural populations for our laboratory studies, we noted numerous dead and apparently desiccated pupae in the forest litter. This suggested the hypothesis that pupae are sensitive to the moisture content of the litter. Therefore, we also studied the extent to which pupae can tolerate desiccating conditions and still complete development.

MATERIALS AND METHODS

This laboratory study was conducted during 1980 and 1981 using fall and spring collected pupae from areas of high population densities in Vermont and New York. Following collection, pupae were sorted into groups of equal size. Pupae from each collection location, host tree (if known), and sex, were distributed equally among all groups, to avoid confounding these factors. Pupae were then stored in moist vermiculite in an incubator at 16.7°C and a 12-hour photoperiod until used in experiments.

Adult Emergence Following Cold Dormancy. During winter, forest litter temperature in New England changes very little and usually remains between $0-5^{\circ}$ C., due to the insulating properties of snow cover (Leonard 1972, Surgeoner 1976, Salonius et al. 1977). Therefore, to simulate winter dormancy conditions in the forest litter, pupae receiving cold treatment were kept in moist vermiculite in 8 hour photophase, 16 hour scotophase at 1.5°C.

In mid-October 1981, 16 groups (18 males, 18 females per group) were placed in cold treatment. At 50 days four groups were removed from cold storage and one group was placed in each of four incubation chambers at 10.0° , 15.6° , 21.1° , and 26.7° C, and 12-hour photoperiod. Additional pupae were removed from cold storage at 100, 150, and 200 days and treated similarly, creating a 4 × 4 factorial design with duration of cold treatment and incubation temperature following cold treatment as main effects. Four

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THE GREAT LAKES ENTOMOLOGIST

59

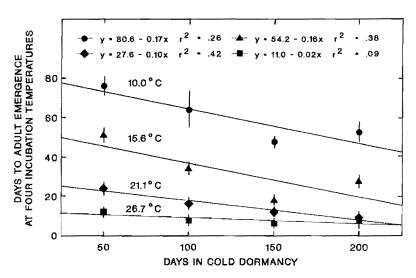


Figure 1. Regression of saddled prominent adult moth emergence time on cold treatment at four post-cold treatment incubation temperatures. Vertical bars indicate \pm standard error.

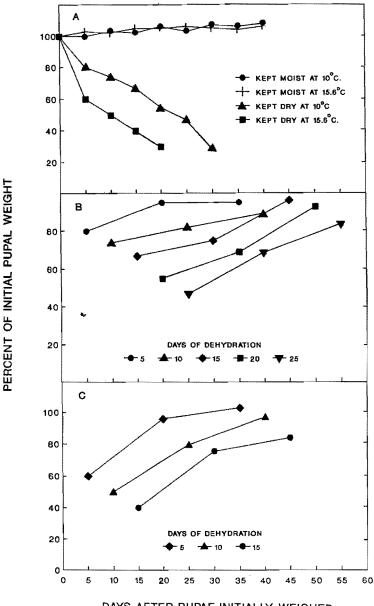
additional groups received no cold treatment, but were placed in incubation chambers at 10.0° , 15.6° , 21.1° , and 26.7° C, and 12-hour photoperiod. Survivorship to adult emergence was difficult to assess due to confounding effects of parasitoid attack, which averaged about 10% (Martinat 1984 lists pupal parasitoid species). Therefore, we assessed pupal survivorship following the termination of cold treatment. Stiff or distended pupae, or those which had lost more than 40% of their weight, were considered dead. Subsequent dissections revealed that pupae classified as dead were filled with white fungal hyphae or were putrefied. Living pupae usually responded to warming or touch by squirming or wiggling the abdomen. Adult emergence dates and days to emergence were recorded for unparasitized pupae.

Adult Morphogenesis. Pupae stored in moist vermiculite in an outdoor insectary were used to study the natural progression of adult morphogenesis. At two-week intervals, 10 pupae were removed and dissected to observe the development of adult morphological features.

Pupal Desiccation. Two weeks following field collection (mid-October), 16 groups of pupae (18 males, 18 females in each group) were removed from storage, and assigned to treatments. Main effects were length of time in dry verniculite (0, 5, 10, 15, 20, 25, 30, 35, 40 days), and temperature during these periods (10.0°, 15.6°C), giving a 9×2 factorial design. Following exposure to dehydrating conditions, pupae were returned to moist vermiculite and placed in cold storage at 1.5°C and 8 hour photophase, 16 hour scotophase. All pupae were weighed at the initiation of the experiment, and weighed again when returned to have died due to desiccation were excluded from determinations of mean weight. This gave estimates of weight change both during desiccation (at 5-day intervals) and during rehydration (at 15-day intervals) for surviving pupae. Pupal mortality was assessed in the manner described above. The two control groups (at 10.0° and 15.6° C.) that received no dehydration treatment were weighed at 5-day intervals for 40 days following initiation of the experiment, then placed in cold storage.

Statistical Analysis. Temperature and time period main effects and interactions were





DAYS AFTER PUPAE INITIALLY WEIGHED

Figure 2. Relationship between mean change in saddled prominent pupal weights and desiccation: (A) Weight change in control and dehydrating conditions. (B) Rehydration of surviving pupae that were dehydrated at 10.0° C. (C) Rehydration of surviving pupae that were dehydrated at 15.6° C.

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60



THE GREAT LAKES ENTOMOLOGIST

61

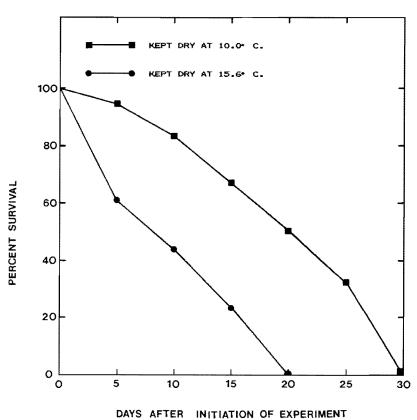


Figure 3. Effect of time in dehydration and temperature on survivorship of saddled prominent pupae.

tested by parametric (ANOVA) procedures. The general linear models procedure (PROC GLM, SAS Institute, 1985) with least-squares means and Type III sums of squares was applied to unbalanced (i.e., having unequal replication in the cells) designs.

RESULTS AND DISCUSSION

Adult Emergence. Required incubation time following cold treatment declined as the duration of cold treatment and incubation temperature increased (Table 1, Fig. 1). The interaction sum of squares was also highly significant (P<0.01). The magnitude of response to cold treatment period declined with higher post-cold incubation temperatures (i.e., slopes became flatter (Fig. 1). This is frequently observed in insects undergoing cold dormancy in a stage of their development; for example, eggs of gypsy moth, *Lymantria dispar* L. (Giese and Casagrande 1981), and pupae of fall webworm, *Hyphantria cunea* Drury (Morris and Fulton 1970). It is a poorly understood phenomenon confounded by the extent of diapause development and the control of diapause termination

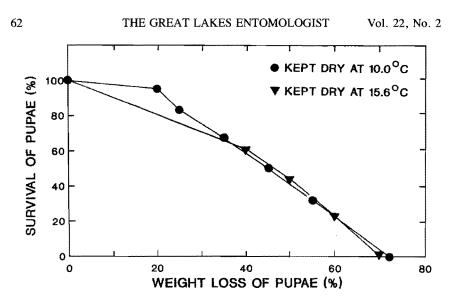


Figure 4. Relationship between survival and weight loss of desiccated saddled prominent pupae.

(Chapman 1971, Tauber and Tauber 1976). Our results gave a developmental threshold of 8.5° C and a heat requirement of approximately 200 degree-days (in Celsius) for adult emergence following cold treatment (using the method of Morris and Fulton, 1970). Pupal survival declined slightly with longer cold treatment (96% after 50 days, 90% after 100 days, 92% after 150 days, 88% after 200 days, n = 144 for each cold treatment period).

Adult Morphogenesis. By late October, adult features (head, wing pads, legs) were discernable in dissected pupae. By mid-November, most external features appeared nearly complete. Pupae dissected in January, February, and March showed no discernable further development. Pupae dissected in April showed progressive completion of adult features. Thirty-five percent of all pupae receiving no cold treatment produced adults, suggesting that a proportion of pupae do not enter diapause. We conclude that adult morphogenesis begins in the fall prior to overwintering and progresses until emergence, unless interrupted by cold-induced dormancy or diapause.

Pupal Dehydration. The mean weight of pupae kept in moist vermiculite remained unchanged or slightly increased at both incubation temperatures, but pupae transferred from wet to dry vermiculite lost weight immediately (Fig. 2a). Surviving pupae regained at least 80% of their original weights within 30 days following return to wet vermiculite (Figs. 2b, 2c). Fifty percent mortality occurred within seven days at 15.6° C, and within 20 days at 10.0° C (Fig. 3). Pupal survival declined linearly with weight loss (Fig. 4). Fifty percent mortality occurred within seven days at 15.6° C, and within 20 days at 10.0° C (Fig. 4). These results suggest that saddled prominent pupae are sensitive to the moisture content of the litter in which they overwinter. Their chances of survival may therefore be greatly diminished in drought conditions. The rate of desiccation increases with ambient temperature. In an outbreak situation, increased solar radiation due to the thinned canopy, as well as sparse new litter in the fall following defoliation, may increase the moisture deficit and deprive pupae of a suitable habitat. This, in turn, may be an important mortality factor that contributes to the collapse of the outbreak.

Saddled prominent caterpillars feed in midseason and thus escape excessively inclement and unpredictable weather (Martinat and Allen 1988b). Pupae, however, face extreme and unpredictable environmental conditions. Pupal densities in the fall are poorly correlated with defoliation the following season (Grimble and Newell, 1972). This may

https://scholar.valpo.edu/tgle/vol22/iss2/1 DOI: 10.22543/0090-0222.1667 1989

63

be due to unpredictable pupal mortality from a variety of causes, but our studies suggest at least one: excessive drying of the litter following pupation and prior to the onset of cold. Decreased snow cover and reduced litter may also deprive pupae of insulation, as has been observed with variable oakleaf caterpillar, *Heterocampa manteo* (Doubleday) (Surgeoner 1976).

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