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Development of the Gypsy Moth (Lepidoptera: Lymantriidae) on Douglas-fir Foliage

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ABSTRACT Survival of larvae, developmental time, consumption, live weights, frass production, pupal weights, and adult female ova production of the gypsy moth, *Lymantria dispar* (L.), were monitored in the laboratory for a comparison of performance between a standard synthetic diet and Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco. Gypsy moth survival (96%), larval development (40 and 34 d at 22°C for females and males, respectively), and pupal weight (1,845 mg and 560 mg for females and males, respectively) on the standard synthetic diet were very similar to data found in the literature regarding highly suitable diets. However, performance of the gypsy moth on Douglas-fir was indicative of a suboptimal host. Survival of first instars on Douglas-fir ranged from 0 to 84%, depending upon temperature and foliage age. Development from first instar eclosion to pupation averaged 44.0 d (males) and 58.3 d (females) at 22°C. Male and female larvae consumed an average of 2,040.6 mg and 6,136.1 mg dry weight of foliage, respectively. Frass production averaged 1,277.9 mg (males) and 3,526.7 mg (females) dry weight. Values were low for nutritional indices of efficiency of conversion of ingested food (4.5–4.9%) and efficiency of conversion of digested food (11.4–12.1%). Live pupal weights averaged 424.2 mg (male) and 1,249.8 mg (female). Females produced an average of 615.7 ova. The highest correlations among the developmental parameters were between pupal weight : frass production and pupal weight : ova production.

KEY WORDS Insecta, Douglas-fir, gypsy moth, host suitability

THE GYPSY MOTH, *Lymantria dispar* (L.), is best known for its ability to feed on and complete its life cycle on hundreds of plant species, mostly angiosperms, with a strong propensity for high fitness traits on foliage of oaks and a few other hardwood trees (Elkinton & Liebhold 1990). Larval survival, larval development, pupal weights, and egg production are typically used to compare the effects of diet on gypsy moth fitness (Barbosa & Capinera 1977, Hough & Pimentel 1978, Barbosa et al. 1983, Miller et al. 1987, Miller & Hanson 1989a). Available data on gypsy moth larvae in the field suggest that they do not prefer or exhibit high fitness traits on foliage of conifers (Jobin 1981, Barbosa et al. 1983, Lechowicz & Maufette 1986). However, laboratory feeding tests indicate that certain species of pines, cedars, and firs are suitable for complete development of the gypsy moth (Daterman et al. 1986, Rossiter 1987, Miller & Hanson 1989b, Joseph 1990).

In the late 1970s and early 1980s, the gypsy moth was repeatedly introduced into the Pacific Northwest and California. In 1983, the largest recovery of males in the Pacific states (over 19,000) at pheromone-baited traps occurred in Lane County, Oregon (Johnson et al. 1989). A major portion of the plant community in this region of the Pacific Northwest consists of a mixed conifer–hardwood forest. One of the most abundant tree species in this forest type is Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco (Hitchcock & Cronquist 1973). Gypsy moth larvae, pupae, and egg masses were very abundant on the oak trees at the epicenter of this infestation. However, some Douglas-fir trees were partially defoliated, although to a much lesser extent than were oaks (J.C.M. pers. obs.; Daterman et al. 1986). During the event of range expansion into other regions of North America beyond the northeastern United States and Canadian provinces, the gypsy moth will encounter numerous species of conifers. The objective of this study was to document the development of gypsy moth larvae on Douglas-fir foliage.

Materials and Methods

The study was conducted in the laboratory because of Federal and State quarantine regulations in effect in Oregon. The experiments were conducted in 1984 and 1985 using larvae that eclosed from egg masses field-collected from oak trees in Oregon.

Development of the gypsy moth was assessed by observing time for larval growth to pupation, larval consumption of diet, larval weight, larval survival, frass production, pupal developmental period, pupal weight, and ova production in adult females.

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These developmental parameters were monitored using clipped twigs of Douglas-fir in water tubes at 22.0 ± 1.5°C.

Larval survival and development on Douglas-fir were compared between first instars reared individually (n = 25) on new foliage (about 3 wk after bud break) or old foliage (one-yr-old needles) at constant temperatures of 12, 17, 22, 27, and 33°C. The survival data from these trials were based on an overall total for each treatment. Also, 5 first instars were placed on foliage of 8 potted trees (n = 40) enclosed in screens located in a greenhouse at 23.0 ± 3.0°C. A standard synthetic diet (Bioserv 963L1, gypsy moth; Frenchtown, N.J.) was used to provide a highly suitable food source for comparison of survival and development for each temperature. The second instars used in the survival tests were fed artificial diet as first instars. All results with the exception of survival data involved first instars.

All experiments used foliage (mixed new and old unless specified otherwise) that was seasonally appropriate for the presence of larvae in Oregon (May–June). Foliage was replaced every other day. Individual larvae were placed in 300-ml cups and monitored daily for survival and molting. Larval weights, consumption of foliage, and frass production were measured every 2–4 d until the final instar and daily during the final instar. Foliage consumption was quantified at each feeding by two measures: (1) counts of needles before foliage was placed in the cups and after larval feeding, and (2) dry weight equivalent of the foliage put into the cups before feeding and the dry weight after feeding. The number of needles was converted to a dry weight equivalent by subsampling needles from the foliage used at each feeding date, measuring the dry weight per 100 needles, and then calculating total foliage dry weight presented to the larvae based on the total needle count. The dry weight data were obtained for a comparison of ingestion and egestion on the basis of biomass. Larvae were always provided more foliage than they could consume.

The data on consumption, larval weights, and frass weights were used to calculate three nutritional indices (Waldbauer 1968): approximate digestibility [AD], efficiency of conversion of digested food [ECD], and efficiency of conversion of ingested food [ECI]. Maximum larval weights were used in the formulae because feeding ceases and weight loss occurs when larvae progress into a prepupal condition. The relationship between larval live weights and dry weights was determined from a cohort (n = 25 per diet) of larvae reared on synthetic diet and Douglas-fir foliage. A range of weights was obtained by sampling larvae from the third to fifth instars.

Live pupal weights and adult female ova production were measured in 48-h-old individuals. The relationship between live and dry pupal weights was determined by measuring pupae from larvae reared on synthetic diet and foliage of Douglas-fir (n = 20 per diet). The ovaries of adult females were dissected to count ova. Only mature, full-sized ova were included in the count. We chose not to allow females to mate and deposit eggs, which would then be used to measure fecundity, because we were working under quarantine conditions and the presence of egg masses (whether fertile or not) was not desirable.

Statistical analysis of all of the developmental parameters was conducted by ANOVA and correlation. The data on survival, expressed as the actual number surviving and dying, were analyzed with a Chi-square test of independence (Sokal & Rohlf 1981).

Table 1. Survival ($\bar{x}$ ± SE for pooled means) of first instar gypsy moths in the laboratory on foliage (mixed age, new, and 1-yr-old) of Douglas-fir [DF] and a synthetic diet

Diet Temperature	No. larvae	% Survival[a]
Synthetic diet[a]		
13, 17, 22, 27, 33°C	125	96 ± 5.7d
DF clipped, mixed age		
13°C	25	0a
17°C	25	24b
22°C	25	84cd
27°C	25	20b
33°C	25	0a
DF clipped, new only, 22°C	25	72c
DF clipped, old only, 22°C	25	24b
DF potted tree, 23°C	40	62 ± 13.1c

[a] No significant differences occurred among temperature treatments for synthetic diet so the data were pooled.

[b] Letters indicate significant differences in number of larvae surviving, Chi-square, $P < 0.05$. No significant differences were observed in the sex ratio of survivors.

Results and Discussion

Larval Survival. Survival of first instars on Douglas-fir ranged from 0–84%, depending upon temperature and foliage age (Table 1). On Douglas-fir, survival of first instars was significantly higher at 22°C than at 17°C, 27°C, 13°C, or 33°C (X^2 = 10.7, df = 1, $P < 0.005$). Survival of first instars on synthetic diet averaged 96% and did not differ significantly among temperature treatments. The survival data demonstrated that temperature extremes promoted higher mortality among larvae on Douglas-fir. Survival of larvae in the potted tree trial was not significantly different from the clipped foliage trial at approximately the same temperature.

Larval survival differed significantly between diets of new and old foliage (Table 1). First instar survival was 84% on foliage that was a mixture of new and old, 72% on new foliage but only 24% on old foliage (X^2 = 8.0, df = 1, $P < 0.005$). These data suggest that synchrony between egg hatch and bud break could affect larval survival on Douglas-fir. However, second instar survival ranged from

Table 2. Mean values ± SE and sample size (*n*) for development from eclosion of first instars to pupation, maximum larval weight, larval consumption, frass production, nutritional indices, pupal weight, and ova production of the gypsy moth on synthetic diet [SD] or foliage of Douglas-fir [DF] at 22.0 ± 1.5°C

Variable[a]	Sex	
	Male	Female
Days to pupation		
SD from instar I	34.1 ± 0.4 (12)	39.7 ± 0.8 (13)
DF from instar I	44.0 ± 1.6 (11)	58.3 ± 1.3 (14)
Maximum larval weight (mg)		
SD, live	763.5 ± 43.6 (12)	2,433.3 ± 173.2 (13)
SD, dry	137.6 ± 7.8 (12)	438.4 ± 30.5 (13)
DF, live	510.1 ± 33.2 (11)	1,653.3 ± 77.8 (14)
DF, dry	92.7 ± 6.0 (11)	298.7 ± 14.4 (14)
Consumption		
DF (no. needles)	389.8 ± 29.3 (11)	1,040.1 ± 89.8 (14)
DF (mg, dry)	2,040.6 ± 132 (11)	6,136.1 ± 543 (14)
Frass		
DF (mg, dry)	1,277.9 ± 84.7 (11)	3,526.7 ± 331 (14)
Larval nutritional indices, DF		
AD	37.4% (11)	42.5% (14)
ECI	4.5% (11)	4.9% (14)
ECD	12.1% (11)	11.4% (14)
Pupal weight (mg)		
SD—live	560.3 ± 39.0 (12)	1,845.1 ± 137.7 (13)
SD—dry	112.1 ± 7.8 (12)	369.5 ± 27.6 (13)
DF—live	424.2 ± 22.0 (11)	1,249.8 ± 62.0 (14)
DF—dry	85.3 ± 4.3 (11)	250.6 ± 12.7 (14)
Pupal ECI, DF	4.2% (11)	4.1% (14)
Ova production		
SD from instar I	—	845.2 ± 48.0 (13)
DF from instar I	—	615.7 ± 42.0 (14)
DF from instar II	—	555.2 ± 41.3 (12)

[a] Larval dry weight calculated from the equation $y = 0.18x$; pupal dry weight calculated from the equation $y = 0.20x$ where x is the live weight. Nutritional indices calculated for maximum larval weights on DF only. AD, approximate digestibility; ECD, efficiency of conversion of digested food; ECI, efficiency of conversion of ingested food.

94 to 100% and did not differ significantly among any of the treatments. These data suggest that dispersal onto Douglas-fir by second instars could result in larvae completing development without further dispersal.

Larval Development. Larval development from eclosion of first instars to pupation was slower in the treatment involving Douglas-fir (males: $F = 10.4$; df = 11,10; $P < 0.01$; females: $F = 15.6$; df = 12,13; $P < 0.01$) (Table 2). Larval development on the synthetic diet was 77% (males) and 68% (females) of the time required for development on Douglas-fir. The rate of gypsy moth development on Douglas-fir was slower than on highly suitable hosts as reported by Hough & Pimentel (1978) and would rank as a class 2 host in the developmental model described by Casagrande et al. (1987).

The occurrence of supernumerary instars and the duration of the first instar differed significantly between the diets of Douglas-fir and synthetic diet ($F = 12.3$; df = 1,24; $P < 0.01$). First instars on Douglas-fir wandered for 3.3 ± 0.4 ($\bar{X}$ ± SE) d ($n = 25$) before initiating feeding. First instars on synthetic diet would initiate feeding within 1.5 ± 0.2 d ($n = 25$). No larvae on the synthetic diet developed through an extra instar. However, 35% of the larvae developed through six (males normally five) or seven (females normally six) instars on Douglas-fir.

Slow larval development could be detrimental to the gypsy moth in the field because of prolonged exposure to climate and natural enemies. On more suitable diets (i.e., foliage of certain oaks, alders, rosaceous species, and willows) larvae completed development in 35–40 d (Hough & Pimentel 1978, Barbosa et al. 1983, Miller et al. 1987, Miller & Hanson 1989a). In addition to host-induced effects of reduced growth rates, the environment typical of much of the Douglas-fir forest in the Pacific Northwest is at higher elevations where lower average daily temperatures would reduce larval growth rates and survival.

Larvae were heavier on the synthetic diet. Typically, a 48-h-old third instar weighed an average of 53.0 ± 5.4 mg ($n = 25$) when fed synthetic diet but only 25.4 ± 2.2 mg ($n = 25$) when fed Douglas-fir. Maximum larval weights on a diet of Douglas-fir were 68% of the maximum weights obtained on synthetic diet (Table 2).

Larval Consumption of Diet. Consumption of foliage differed significantly between the sexes ($F = 7.3$; df = 10,13; $P < 0.01$) (Table 2). Male larvae consumed an average of 33% of the amount of diet that females consumed. The penultimate and ultimate instars consumed 90–95% of the total biomass consumed over all instars.

Frass Production. The production of frass while feeding on Douglas-fir was also significantly different between the sexes ($F = 6.5$; df = 10,13; $P < 0.01$) (Table 2). Males produced about 33% of the amount of frass produced by females. The larvae egested nearly 60% of the Douglas-fir foliage ingested.

Nutritional Indices. Males and females had similar nutritional indices when feeding on Douglas-fir (Table 2). Approximate digestibility was similar to values obtained by Barbosa & Greenblatt (1979) for gypsy moth larvae feeding on grey birch, white oak, and synthetic diet. Efficiency of conversion of digested food was 20–50% below values obtained with five broad-leaf species (Barbosa & Greenblatt 1979). Sheppard & Friedman (1990) reported ECI values for third instar gypsy moths that had fed on white pine that were similar to those we observed for larvae on Douglas-fir. Barbosa & Greenblatt (1979) reported values that were twice as high for gypsy moth larvae that had fed on white oak and

Table 3. Relationships of correlation among the developmental variables for first instars that developed into female gypsy moths on foliage of Douglas-fir in laboratory feeding tests (n = 15)

Variables	r^2	P	Equation
Development days : Pupal weight	0.3302	0.0250	$y = -26.910x + 2{,}820.9$
Development days : No. ova	0.1572	0.1434	$y = -12.507x + 1{,}345.8$
Development days : Larval consumption	0.2126	0.0837	$y = -122.019x + 13{,}206.8$
Development days : Larval frass	0.2959	0.0361	$y = -78.484x + 8{,}110.1$
Larval consumption : Larval frass	0,4695	0.0048	$y = 0.374x + 1{,}255.0$
Pupal weight : Larval consumption	0.4909	0.0036	$y = 0.124x + 495.5$
Larval consumption : No. ova	0.3391	0.0228	$y = 0.069x + 193.4$
Pupal weight : No. ova	0.7336	0.0001	$y = 0.577x - 105.3$
Pupal weight : Larval frass	0.7940	0.0001	$y = 2.745x + 96.8$
No. ova : Larval frass	0.4680	0.0049	$y = 3.130x + 1{,}600.7$

American beech; values for larvae on grey birch were five times higher. Our data indicated that gypsy moth larvae did not convert Douglas-fir biomass into animal biomass as efficiently as larvae on more suitable hosts. These data further suggest that Douglas-fir is nutritionally an inferior host for the gypsy moth. Low nitrogen content and the presence of terpenes may account for the lower quality of a Douglas-fir diet (Joseph 1990).

Pupal Weights. Pupal weights were significantly higher for each sex in the treatment involving synthetic diet (males: $F = 4.9$, df = 11, $P < 0.05$; females: $F = 6.8$, df = 12, $P < 0.01$) (Table 2). Average live female pupal weights were similar to weights reported for larvae that had fed on other suitable diets (Barbosa & Capinera 1977, Hough & Pimentel 1978, Barbosa et al. 1983, Miller et al. 1987, Miller & Hanson 1989a). The value for a modified ECI based on pupae (using larval ingestion data and pupal weight substituted for larval weight) was 4.2% (males) and 4.1% (females). As expected, these values were lower than the larval ECI because of weight loss during development from prepua into pupa.

Ova Production. Diet had a significant effect on the number of ova ($F = 4.2$; df = 12,13; $p < 0.05$) (Table 2). An insignificant difference in ova production was noted between larvae fed Douglas-fir from the first or second instar. These data suggest that if larvae dispersed from a broadleaf host onto Douglas-fir in the second instar, then reproductive potential would be similar to individuals that occurred on Douglas-fir from the first instar. In general, the ova production in females from a Douglas-fir diet was 50–60% of the values reported for gypsy moths on highly suitable hosts (Miller & Hanson 1989a). Our data on ova production cannot be compared directly with the results of Hough & Pimentel (1978) or Barbosa et al. (1983) because we dissected ova and the other studies counted eggs after oviposition.

Correlations among Developmental Variables. A correlation analysis of the developmental variables for first instars that developed into adult females on foliage of Douglas-fir demonstrated that eight of ten relationships were correlated at a level of significance of $P < 0.05$ (Table 3). Correlations were not significant for days of larval development: number of ova and days of larval development: larval consumption. The highest correlations were between pupal weight : frass production and pupal weight : ova production. These relationships were consistent with the correlations between pupal weights : larval consumption, and larval consumption : frass production. The high degree of correlation between these variables suggested that measurements of pupal weights from the field could accurately predict fecundity and the amount of foliage consumed by the survivors in a given population of gypsy moths. Also, a measurement of frass in the field could be used to predict consumption. Liebhold & Elkinton (1988) used frass traps to estimate larval density in the field. Mathavan & Pandian (1974) found that larvae of various species of moths consumed 1.5 times more dry weight foliage than they produced dry weight frass. Larvae of the gypsy moth on Douglas-fir consumed 1.59 (males) and 1.74 (females) times the amount of foliage relative to frass.

In summary, the gypsy moth was capable of completing development from first instar eclosion to adult eclosion on a strict diet of Douglas-fir foliage. However, Douglas-fir was not an optimal diet for larval development. Studies addressing the physiological and genetic basis for larval development, feeding behavior, and survival on Douglas-fir need to be conducted to further our understanding of the potential for gypsy moth to adapt to this novel host.

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