2404

Development of the Gypsy Moth (Lepidoptera: Lymantriidae) on Garry Oak and Red Alder in Western North America

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Environ. Entomol. 20(4): 1097–1101 (1991)

ABSTRACT The suitability of Garry oak (*Quercus garryana*) and red alder (*Alnus rubra*) as hosts for the gypsy moth, *Lymantria dispar* (L.), was assessed under laboratory conditions by observing larval survival, larval weights, foliage consumption, developmental period, pupal weight, and ova production. Survival was not significantly different between larvae fed Garry oak (98.7%) or red alder (97.4%). The mean maximum live larval weights were significantly different between sexes but not between diets. Females weighed 2,498 mg when fed Garry oak and 2,210 mg when fed red alder. Males weighed 894 mg when fed Garry oak and 737 mg when fed red alder. The mean amount of foliage consumed was significantly different between sexes but not diet. Female larvae consumed an average of 705 cm^2 of Garry oak and 678 cm^2 of red alder foliage. Male larvae consumed 247 cm^2 of Garry oak and 253 cm^2 of red alder foliage. The mean time from egg hatch to pupation was significantly different between sexes and diets. Female larvae pupated in 39.5 d on Garry oak and 48.1 d on red alder. Male larvae pupated in 33.4 d on Garry oak and 40.6 d on red alder. Pupal weights were not significantly different between sexes or diets. Male pupae weighed 554 mg from a larval diet of Garry oak and 572 mg from red alder. Female pupae weighed 1,846 mg from Garry oak and 1,711 mg from red alder. An average of 863 ova (Garry oak) versus 758 ova (red alder) was present in the reproductive tract of 2-d-old females, an insignificant difference. Pupal weights, frass production, and ova production were highly correlated. Nutritional indices indicated that Garry oak foliage was converted into biomass slightly more efficiently than that of red alder. These data indicated that foliage of either Garry oak or red alder provided a very suitable diet for the gypsy moth.

KEY WORDS Insecta, host suitability, *Lymantria dispar*, hardwoods

UPON INTRODUCTION INTO NORTH AMERICA, the gypsy moth, *Lymantria dispar* (L.), a polyphagous, univoltine herbivore, was able to colonize thousands and eventually millions of hectares rapidly in an environment with suitable host plants. Uncolonized regions may have the potential of supporting high-density populations because of the availability of plant species suitable for larval development. Larvae of the gypsy moth are best known for their ability to feed on and complete development on hundreds of plant species, mostly angiosperms, with a strong propensity for high fitness traits on foliage of oaks and other hardwood trees (Elkinton & Liebhold 1990).

In the late 1970s and early 1980s, the gypsy moth was present in a number of isolated populations in the Pacific Northwest and California. In 1983, the largest recovery of males (>19,000) at pheromone-baited traps throughout the Pacific Northwest occurred in Lane County, Oreg. (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. Two of the most abundant tree species in this forest type are Garry oak (*Quercus garryana* Dougl.) and red alder (*Alnus rubra* Bong.) (Franklin & Dyrness 1988). Gypsy moth larvae, pupae, and egg masses were very abundant on the Garry oak trees at the epicenter of the Lane County infestation (personal observation).

Identification of dominant plant species that are suitable for gypsy moth development can provide an indication of the ecological effect in major plant communities should establishment occur (Barbosa et al. 1983, Lechowicz & Jobin 1983, Lechowicz & Mauffette 1986). For instance, foliage of oak is known to be highly suitable as larval food and is typically infested as a preferred host in the field (Barbosa & Capinera 1977, Hough & Pimentel 1978, Rossiter 1987). Thus, plant communities in which oaks are the dominant species will likely be strongly affected by gypsy moth feeding. 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, Barbosa et al. 1983, Hough & Pimentel 1978, Miller et al. 1987, Miller & Hanson 1989a). In this study, the development of gypsy moth larvae fed foliage from Garry oak or red alder was monitored under experimental conditions in the laboratory to assess the suitability of these plants as hosts for the gypsy moth.

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0046-225X/91/1097–1101$02.00/0

Materials and Methods

Garry oak is the only native oak species in the Pacific Northwest west of the Cascade mountains and north of the Willamette Valley. This species of oak ranges from central California to southern British Columbia, primarily west of the Sierra Nevada and Cascade mountain ranges; maximum stand development is in the Willamette Valley of Oregon. Garry oak occurs on a variety of soils and is often found on poor forest sites such as southwest slopes and shallow rocky soils. Growth is slow, with longevity of up to 500 yr. Average yearly rainfall in areas where Garry oak is abundant ranges from 63 to 102 cm (Franklin & Dyrness 1988). Leaf buds begin opening in mid-April, later than most other indigenous trees and shrubs in the Pacific Northwest but synchronous with egg hatch of the gypsy moth in the Willamette Valley, Oregon (personal observation).

Red alder is one of the more prevalent hardwood species within the Douglas-fir dominated coniferous forest (Trappe et al. 1968, Franklin & Dyrness 1988). This species of alder occurs from southeastern Alaska to central California and generally within 163 km of the coast. Red alder typically occurs from sea level to 1,000 m where soils remain moist. Disturbed sites are readily colonized by red alder and growth is rapid. Leaf buds generally begin to open in late March and early April.

The study was conducted in the laboratory because of Federal and State quarantine regulations in effect in Oregon. The experiments were conducted in 1984 using larvae that eclosed from egg masses field-collected during November from oak trees in Lane County. All egg masses ($n = 500$) were collected from the trunks of five mature Garry oak trees within a 0.25-ha site where a population of the gypsy moth had occurred for at least one generation and was initially trapped in large numbers during the late summer of 1983.

Development of the gypsy moth was assessed by feeding larvae clipped twigs placed in water tubes and reared at $22.0 \pm 1.5°C$. Foliage was replaced every other day. Foliage used for feeding the larvae was obtained from the same tree on a given date over a selection of eight trees. We did this to reduce effects of wound responses in the physiology of the tree (see Schultz & Baldwin 1982) and to avoid single-tree bias (see Gross et al. 1990). All experiments were conducted from May through June when gypsy moth larvae would be feeding in the field in western Oregon.

The following developmental parameters were monitored: larval growth, larval consumption of diet, larval weight, larval survival, frass production, pupal weight, and ova production in adult females. Individual larvae were placed in 300-ml cups and monitored daily for survival and molting. Survival was assessed during three replicates per diet ($n = 25$ larvae per replicate, $n = 75$ larvae per diet). All other variables were assessed using 25 larvae. Cumulative consumption of foliage, larval weights before the ultimate instar, and cumulative frass production were measured every 2–4 d until pupation. The maximum larval weight of each individual was obtained by monitoring larvae on a daily basis during the ultimate instar because larvae initially gain weight and then lose weight just before pupation.

The quantity of foliage consumed by individual larvae was measured in the laboratory by placing a known leaf area into a 300-ml container holding a single larva. Measurements on the consumption of foliage were obtained by developing a dry weight–leaf area relationship for each sample date. The surface area of all fresh foliage was measured with a Li-Cor area meter, then placed into respective containers. An equal number of fresh leaves were measured for area, then dried and weighed to obtain the relationship between leaf area and dry weight for each feeding. At the time of foliage replacement, the remaining leaf matter was measured for the area, then dried and weighed to obtain a leaf area equivalency using the relationship derived for that sample of foliage. This process was repeated until each larva pupated. Larvae were always provided more foliage than they could consume.

The data on consumption, larval weight, and frass production 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 had ceased and weight loss occurred when larvae progressed 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 each diet. Also, an ECI was determined using pupal weights.

Pupal weight and adult female ova were measured in individuals 48 h after pupation or adult eclosion, respectively. The relationship between live (wet) and dry pupal weights was determined by measuring pupae from larvae reared on each diet ($n = 20$ per diet). The ovaries of adult females were dissected to count ova production. Only mature, full-sized ova were included in the count. We chose not to allow females to mate and deposit eggs (to measure fecundity) because we were working under quarantine conditions, and the presence of egg masses, fertile or not, was not desirable.

In addition to the aforementioned developmental parameters, the time for first instars to initiate feeding was observed. Four newly eclosed first instars were placed on fresh foliage in cups, replicated 10 times for each host species. The activity of the larvae was observed for up to 15 min every 4 h until all larvae were feeding.

Statistical analysis of all of the developmental variables was conducted by ANOVA and correlation after checking for normalcy in the distribution

Table 1. Development ($\bar{x} \pm$ SE) from eclosion of first instars to pupation, maximum larval weight, larval consumption, frass production, nutritional indices, pupal weight, and ova production of gypsy moths on foliage of Garry oak or red alder at 22.0 ± 1.5°C

Variable[a]	Garry oak		Red alder	
	♂	♀	♂	♀
Survival	98.7 ± 0.3a	98.7 ± 0.3a	97.4 ± 0.3a	97.4 ± 0.3a
Days to pupation	33.4 ± 0.3a	39.5 ± 0.4b	40.6 ± 0.4b	48.1 ± 0.5c
Maximum live larval wt, mg[b]	894 ± 14a	2,498 ± 126b	737 ± 30a	2,210 ± 86b
Maximum dry larval wt, mg[b]	156 ± 2.5a	435 ± 22b	128 ± 5.3a	385 ± 14b
Total consumption, cm²	247 ± 5.2a	705 ± 35b	253 ± 8.0a	678 ± 21b
Total consumption, mg (dry wt)	1,591 ± 135a	4,664 ± 206b	2,008 ± 64a	5,380 ± 170b
Total frass, mg (dry wt)	847 ± 28a	3,076 ± 154b	1,158 ± 46a	3,572 ± 129b
Nutritional indices, %[c]				
AD	47	34	42	34
ECI	10	9	6	7
ECD	21	7	15	21
Pupal live wt, mg[d]	554 ± 19a	1,846 ± 99b	572 ± 27a	1,711 ± 77b
Pupal dry weight, mg[d]	111 ± 3.7a	369 ± 20b	114 ± 5.3a	342 ± 15b
Pupal ECI, %	7	8	6	6
Ova production	X	863 ± 51a	X	758 ± 64a

Values within each variable followed by the same letter are not significantly different ($P < 0.05$, ANOVA).

[a] For survival data, $n = 25$ per replicate per diet, three replicates per diet. For the other developmental variables: Garry oak females, $n = 13$; red alder females, $n = 11$; Garry oak males, $n = 12$; red alder males, $n = 13$.

[b] Calculated from the equation $y = 0.174x$.

[c] AD, approximate digestibility; ECD, efficiency of conversion of digested food; ECI, efficiency of conversion of ingested food.

[d] Calculated from the equation $y = 0.200x$ where x is the live weight.

of the data and the spread of variance among mean values (Sokal & Rohlf 1981). Means ± SE are reported with an acceptance of significant differences at $P < 0.05$.

Results and Discussion

Larval Survival. Survival of first instars on Garry oak and red alder was not significantly different and was high (98.7 and 97.4%, respectively) (Table 1). Survival has been one of many criteria used to classify host suitability (Martinat & Barbosa 1987). High first-instar survival is indicative of a very suitable host plant and has been noted for gypsy moth on many broadleaf species of oaks, willows, and birches. In contrast, low first-instar survival suggests poor host quality and has been noted on many species of conifers, Asteraceae, and Oleaceae (Barbosa & Krischik 1987; Miller & Hanson 1989a,b).

Dispersal by first-instar gypsy moths is affected by size, silking behavior, host suitability, and population quality (Leonard 1971, Capinera & Barbosa 1976, Lance & Barbosa 1981, McManus & Mason 1983). Differences in the time to initiate feeding on highly suitable hosts and poorly suited hosts may be related to the propensity to disperse. All larvae began feeding within 8–12 h ($\bar{x} = 10.2 \pm 0.1$, $n = 80$) from the time of eclosion on the foliage of Garry oak and red alder. The data were pooled because no significant differences were observed between diets. When offered an exclusive diet of Douglas-fir foliage, gypsy moth larvae did not initiate feeding for a period of 3.3 d (Miller et al. 1991). If gypsy moth larvae do not readily feed on a poorly suited host such as Douglas-fir, then dispersal may be more likely.

Larval Development. Larval development from eclosion of first instars to pupation was significantly slower on red alder than on Garry oak by 8.6 d (22%) for females and 7.2 d (22%) for males (Table 1). No supernumerary instars were observed during larval development on either diet. Gypsy moth larvae may complete development in 35–40 d on highly suitable diets (Hough & Pimentel 1978, Barbosa et al. 1983, Miller et al. 1987, Miller & Hanson 1989a). Given the two diets tested, the slower larval development on red alder could be detrimental to the gypsy moth in the field because of prolonged exposure to climate and natural enemies.

Larvae were significantly heavier on Garry oak (Table 1). Maximum larval weights on a diet of red alder were 82 and 89% of the larvae on a Garry oak diet. Also, larvae on Garry oak were heavier throughout development. For instance, a 48-h-old third instar weighed an average of 43.4 ± 2.8 mg (male) and 62.8 ± 5.3 mg (female) on Garry oak and 21.7 ± 1.8 mg (male) and 22.9 ± 1.4 mg (female) on red alder. Similarly, fourth instars on red alder weighed 35–45% of those on Garry oak.

Larval Consumption of Diet and Frass Production. Consumption of foliage was not significantly different for larvae of a given sex on either host plant (Table 1). Consumption of foliage by male larvae ranged between 35 and 38% of the amount of foliage consumed by females. The penultimate and ultimate instars of each sex accounted for 85–90% of the total biomass consumed over all instars. Total consumption averaged 17.9 (females) and 7.4 (males) cm²/d on Garry oak versus 14.1 (females) and 6.2 (males) cm^2/d on red alder. The ultimate instars consumed 40–50 cm^2/d. The leaf area of Garry oak and red alder foliage consumed compares to 856 cm^2 on a pyracantha and 1,100–1,800 cm^2 on a Japanese species of oak (Leonard 1974). Braham & Witter (1978) found sixth-instar females to consume a mean daily amount of 9.5 cm^2 of red oak.

Frass production was not significantly different between larvae of a given sex on either diet (Table 1). Males produced between 28 and 32% of the total frass produced by females. The amount of diet egested (dry weight) by either sex ranged between 53 and 67% of the dry weight ingested.

Nutritional Indices. Males and females exhibited dissimilar nutritional indices of AD and ECD, but the ECI was similar between the sexes (Table 1). When feeding on Garry oak or red alder, females had a lower index for AD. These data indicated that proportionately more frass was produced by females (67%) than males (53–58%) for each dry weight equivalent of foliage consumed. Also, when feeding on either Garry oak or red alder, females had a higher index for ECD. These data indicated that proportionately more of the food ingested was converted into biomass by females. The ECD for larvae of either sex on Garry oak was slightly higher than on red alder. Thus, proportionately more of the Garry oak foliage consumed was converted intc biomass. The ECI was similar between the sexes on each diet but dissimilar between diets. Larvae feeding on Garry oak were slightly more efficient in converting ingested food into biomass. Overall, the values for nutritional indices of gypsy moth larvae on Garry oak and red alder were similar to values obtained for gypsy moth larvae feeding on white oak (Barbosa & Greenblatt 1979) and higher than those reported from a diet of white pine (Sheppard and Friedman 1990) or Douglas-fir (Miller et al. 1991).

Pupal Weights. Pupal weights were not significantly different for each sex on either diet (Table 1). However, males were only 30–33% of the female pupal weight. An ECI using pupal dry weights was very similar among the sexes and diets. As expected, these values were lower than the larval ECI because of weight loss during development from prepupa to pupa. Average live female pupal weights from larvae feeding on Garry oak or red alder foliage were similar to data reported for larvae that had fed on other highly suitable diets (Barbosa & Capinera 1977, Hough & Pimentel 1978, Barbosa et al. 1983, Miller et al. 1987, Miller & Hanson 1989a).

Ova Production. The production of ova by females from either diet was not significantly different. In general, the ova production in females from a diet of Garry oak or red alder was similar to the values reported for gypsy moths on highly suitable hosts (Hough & Pimentel 1978, Barbosa et al. 1983, Miller & Hanson 1989a). However, 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, whereas the other studies counted eggs after oviposition.

Correlations Among Developmental Variables. The relationships between developmental periods, body weights, frass, consumption, and ova production are relevant to assessing host plant suitability and for developing models of population effect in the field. For instance, the ability to predict consumption from frass measurements would be useful for determining defoliation potential. Also, the prediction of population change could in part involve the measurement of pupal weights for estimating female fecundity.

A correlation analysis of the developmental variables for first instars that developed into adult females on foliage of either Garry oak or red alder demonstrated that 4 of 10 relationships regarding both diets were correlated at a level of significance of $P < 0.05$, whereas two additional relationships were highly correlated on the Garry oak diet. Correlations were not significant for days of larval development to either pupal weight, number of ova, larval consumption, or frass production. Thus, developmental time did not provide a parameter capable of predicting other aspects of gypsy moth performance on the foliage tested.

Two of the highest correlations were for live pupal weight with ova production ($y = -295 + 1.6x$, $r^2 = 0.62$, $P = 0.001$) and larval frass with larval consumption (as dry weights) ($y = 32.0 + 0.44x$, $r^2 = 0.82$, $P = 0.0001$). The equations were derived by pooling data for development on Garry oak and red alder. Mean total frass production data (Table 1) were used in the equation for predicting consumption of both foliage types. Estimated consumption of Garry oak was 4,626 mg (actual observation was 4,664 mg). The estimated consumption of red alder was 5,420 mg (actual observation was 5,380 mg). Live pupal weight data (Table 1) were used in the equation for predicting ova production for both foliage types. The estimate for ova production on Garry oak was 844 (actual observation was 863). The ova production estimate on red alder was 785 (actual observation was 758). These relationships need to be tested with an independent data set.

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. On Douglas-fir, gypsy moth larvae consumed 1.6 (males) and 1.7 (females) times more foliage than frass produced (Miller & Hanson 1989b). In this study, female larvae consumed 1.5 times more dry weight foliage than they produced dry weight frass on Garry oak and red alder. Male larvae consumed 1.9 and 1.7 times more foliage than frass produced on Garry oak and red alder, respectively. The high degree of correlation between certain of these variables supports the practice of obtaining pupal weights and frass production from the field to predict fecundity and the amount of foliage consumed by the survivors in a given population of gypsy moths. Liebhold & Elkinton (1988) used frass traps to estimate larval density in the field.

In summary, the foliage of Garry oak and red alder provided a suitable diet for gypsy moth larvae. If the gypsy moth eventually becomes established in the Pacific Northwest, these two plants will be highly suitable hosts. As such, these species will serve as a resource important in the population dynamics of the gypsy moth.

Acknowledgment

The encouragement of G. E. Daterman and the assistance of K. West were very useful to our study. R. E. Berry, A. F. Moldenke, G. Joseph, and J. Wernz read previous drafts of the manuscript. Funding was provided by USFS grant agreement PNW-82-336, USDA-CRGO Pest Science grant 87-1-2478, and the Oregon State University Agricultural Research Foundation. This is Technical Paper 9473 of the Oregon Agricultural Experiment Station, Oregon State University.

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Received for publication 4 September 1990; accepted 5 March 1991.