Gen. Tech. Rep. PSW-100. Berkeley, CA. Pacific Southwest Forest and Range Experiment Station, Forest Service, U.S. Department of Agriculture; 1987.

Environmental Factors Influencing California Oakworm Feeding on California Live Oak[1]

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Abstract: Foliage consumption, frass production, assimilation efficiency and developmental rate are influenced by ambient temperature, sex, larval population density and the quality of host leaves. The larval feeding threshold lies between 1.7 and 4.4°C. The temperature optimum for larval development is approximately 20°C. Males have shorter larval and longer pupal periods and emerge shortly before females. Both high larval population density and leaf maturation tend to depress consumption and assimilation values and result in the production of smaller adults associated with diminished fecundity.

Throughout its recorded range, which extends in California along the coastal mountains from San Diego County north to Humboldt County (Harville, 1955) and into Oregon (Wickman and Kline, 1985) the California oakworm (Phryganidia californica (Pack.), feeds primarily on Quercus, Lithocarpus and Castanopsis.

The oakworm characteristically occurs at low population densities which periodically increase to outbreak levels resulting in severe defoliation to host trees (Furniss and Carolin, 1977).

In the San Francisco Bay Area, there are usually 2 generations per year. Oviposition customarily occurs in June and July and again in October and November. First and early second instar larvae overwinter on the lower leaf surface of California live oak (Quercus agrifolia Née). During the winter months there is usually little feeding and, if the temperature remains low for an extended period, populations may suffer high mortality. As the season progresses the developmental rate gradually rises in response to an increase in temperature. Because the distribution of host species (Harville, 1955; Griffin and Critchfield, 1972) clearly extends beyond the limits of the occurrence of sustained oakworm populations, it is probable that temperature and relative humidity are the major abiotic limiting factors. Within areas where temperature extremes allow the continued presence of oakworm populations, older instars may be found feeding at the margins of leaves of all age classes during the spring, summer and fall months.

Although it is associated with a large complement of natural enemies few quantitative assessments of their impact have been reported. Harville (1955) working with oakworm populations at Alum Rock Park in San Jose and Jasper Ridge at Palo Alto attributed approximately 20 percent of the observed mortality to the combined action of the predatory bug Podisus and the tachnid Actia and 50-75 percent to the parasitic wasps Brachymeria and Itoplectis. Later work by Horn (1974) reaffirmed the importance of these pupal parasites and related the parasitization percentage to pupal population density. Recently, Young (1980) showed that Itoplectis operates in a density dependent manner over host densities ranging from 6 to 13 pupae per m^2 while above this density the parasitization rate declines. The effectiveness of these primary pupal parasites may be reduced by as much as 63 percent through the action of secondary parasites (Horn, 1974).

The major pathogens, excluding the microbial control agent Bacillus thuringiensis; are protozoan and viral. Infection levels of 33-35 percent for Nosema and approximately 2 percent for Leidyana have been reported for an Orcutt population sampled between 1958 and 1960 (Lipa and Martignoni 1960, 1984). While the field incidence of viral infections has not been quantified, Harville (1955) regarded viral disease to be a primary mortality factor exceeded in importance only by mass starvation. Martignoni and Schmid (1961) by means of laboratory bioassays have demonstrated significant differences in viral resistance between oakworm population at Albany and Orcutt and suggested that tolerance, population density and the presence of the virus and its inductors may account for the recurrence of virus epizootics. Because susceptibility to infectious organisms is determined in part by body weight and pathogen dosage, feeding rates may be a major factor influencing mortality in natural populations.

The nutritive quality of host foliage has been reported to decline with leaf aging (Mattson, 1980) and in response to herbivore feeding (Shultz and Baldwin, 1982).

The effect of food quality and larval

[1]Presented at the Symposium on Multiple-Use Management of California's Hardwood Resources, November 12-14, 1986, Cal Poly, San Luis Obispo, Calif.

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population density on oakworm foliage consumption has been previously reported (Volney et al., 1983). The current study, an extension of that work covering both spring and summer generations, uses herbivore dry weights in computing nutritional indices and considers the influence of gender in oakworm herbivory.

METHODS

In the initial experiments extending from February through August, 1981, third instar larvae were fed in 600 ml. waxed paper cups. The larvae had free access to weighed leaves which were changed 3 times per week. Leaf moisture was maintained by means of a cotton-plugged water-filled vial in which the excised leaf was inserted. Undamaged mature current flush (new) leaves and those from the previous (old) flush were selected from each of 2 trees differing in their oakworm infestation levels (sparse = less than 0.05 larvae per shoot; high = ca. 1.0 larvae per shoot). Initial population densities were 1, 2 and 4 larvae per feeding arena. Laboratory temperature and relative humidity was monitored by means of a hygrothermograph. Mean temperature ranged from 18.4°C to 24.5°C. Mean relative humidity ranged from 35.1 percent to 45.6 percent.

In later experiments (1986) utilizing foliage taken from 2 sparsely infested trees, growth rates were compared on newly flushed (immature) leaves and the preceeding generation's mature leaves. First instar larvae were reared singly at 20°C and 58 percent relative humidity in 13 dram plastic vials. The leaves fed to the larvae were changed 3 times per week. No attempt was made to maintain leaf moisture in these experiments. When adults emerged, clean vials were used as mating arenas. Leaves were changed 3 times per week to provide an ovipositional stimulus.

Consumption rates and utilization efficiencies were determined by means of the methods previously reported (Volney et al., 1983). All leaves were weighed prior to feeding (fresh weight) and the dry weights of leaf remnants and frass were obtained after a 24 hour ovenization at 105°C. Foliage consumption (I) was determined by subtracting the weight of the leaf remnant from the dry weight of the original leaf estimated from the regression relationship: (oven dry weight = 13.425 + 0.517 fresh weight; r^2 = 0.92; P = 0.0001).

The dry weight gain (G) was computed by subtracting the initial estimated dry weight of the larvae (larval dry weight = 0.356 + 0.151 larval wet weight; r^2 = 0.92; P = 0.001) from the estimated dry weight of the pupae (pupal dry weight = -3.6 + 0.273 pupal wet weight; r^2 = 0.95; P = 0.001).

The population density (D) in the feeding arena was determined by dividing the sum of the products of the number of live larvae (N) in each feeding period and its duration (t) by the total duration (T). (D = NT/T).

The mean weight (W) was obtained by dividing the sum of the products of the initial weight (w) of the larvae entering the feeding period (t) by T. (W = wt/T).

The following consumption and utilization rates were derived:

CR (consumption rate) = I/D.T (Mean dry weight of food consumed per larva per day)

FR (frass rate) = F/D.T (Mean dry weight of frass produced per larva per day)

CI (consumption index) = I/W.T (Mean dry weight of food consumed per mg. larval weight per day)

GR (growth rate) = G/W.T (Mean dry weight gained per mg. larval weight per day)

AD (approximate digestibility) = (I-F)/I (Proportion of ingested food assimilated)

ECI (efficiency of conversion of ingested food) = G/I (Proportion of ingested food converted to body substance)

ECD (efficiency of conversion of digested food) = G/(I-F) (Proportion of digested food converted to body substance)

RESULTS

Within the range of temperatures that allow survival (table 1) the population dynamics of the California oakworm is affected by many natural enemies (table 2).

Leaf age; the impact of herbivory (reflected in host infestation level), larval population density and sex are among many factors reported to influence consumption and utilization rates (Scriber and Slansky, 1981; Schowalter et al., 1986).

The results of feeding trials with immature leaves from the current flush, mature leaves from the current flush, and mature leaves from an earlier flush are presented in tables 3-5. The assimilation values fall within the ranges reported for lepidopterous larvae feeding on tree foliage (Slansky and Scriber, 1982).

Leaf Age

A diet of immature leaves is associated with more rapid developmental rates, larger insects and enhanced egg productivity (table 5). Larvae feeding on older mature leaves have lower CR and AD values.

No significant differences in developmental rate or insect size can be attributed to leaf age differences in mature leaves.

Infestation Level

As in the case with mature leaves, infestation level differences are not reflected in significant differences in consumption rate, nutritional efficiency, development or size.

Sex

Female larvae have appreciably higher CR, FR, GR, ECI and ECD values. These along with a longer larval period result in larger pupae and adults. Male larvae have higher AD values and a more rapid developmental rate.

Larval Population Density

At the highest population density, all of the consumption and assimilation values with the exception of ECD are drastically depressed resulting in the production of smaller pupae and adults.

DISCUSSION

Leaf aging is associated with a decline in Nitrogen and water concentrations (Scriber and Slansky, 1981). Young, actively growing tissues contain the highest levels of Nitrogen (Puttick, 1986) and, as the growth rate begins to diminish the Nitrogen concentration drops sharply, decreasing gradually thereafter until just prior to senescence. Both ECI values and relative growth rates have been shown to be correlated with leaf Nitrogen and water content (Mattson, 1980; Scriber, 1978, 1984). These correlations serve to explain our observations relating leaf age and herbivore response throughout the growing season where the greatest differences occur between oakworm larvae feeding on young foliage and those feeding on mature leaves.

In contrast, Puttick has reported higher GR, ECI and ECD values for oakworm larvae feeding on mature leaves of Q. agrifolia. Since neither gender differences nor the influence of leaf age on growth rate and fecundity were considered it is difficult to compare her findings with those presented here.

While it is known that herbivory can result in the mobilization of facultative defenses in host trees (Schowalter et al., 1986) our data, derived from the feeding of mature leaves, gives only slight indication of this. The phenomenon may be more readily descernable in actively growing leaves sampled from trees exhibiting higher levels of infestation.

Disparities in weight between male and female larvae, pupae and adults have been attributed to differences in the length of the developmental period, a faster relative consumption rate and a higher ECI (Scriber and Slansky, 1981). Our data support these findings. While the CI values are essentially equal for the sexes, female larvae consume foliage at a faster rate over a longer period of time.

The slower developmental rate of female larvae suggests that the application of microbial insecticide during the last instar, while not affording current foliage protection, should serve to greatly reduce the population base of the succeeding generation.

Our data indicate that at high population densities increased intraspecific competition for food results in the production of smaller adults with lessened fecundity. This is supported by data (Milstead, unpublished) collected during two oakworm outbreaks in 1982 and 1986 where severe defoliation was associated with diminished oakworm size and fecundity.

It is clear from these results that foliage quality and population density can have profound consequences on the population dynamics of the oakworm.

Table 1—Influence of Temperature on Survival, Developmental Rate and Pupal Size of California Oakworm

Year, Season	Temperature C°	N	Survival Pct.	N	Larval Period (Days) $\bar{x} \pm SE$	Pupal Weight (Mg.) $\bar{x}$ ♀	$\bar{x}$ ♂	$\bar{x} \pm SE$ ♀ + ♂
1945[1]	1.7	20	0		-			
	4.4	20	0		-			
	10.0	20	30.0	6	178.0	113.0	99.3	106.2
	15.6	17	82.4	14	54.3	208.5	125.5	167.0
	18.3	20	68.4	14	43.8	191.8	127.1	159.5
	21.1	20	60.0	12	38.8	155.0	120.7	137.9
	27.2	21	20.0	4	47.0	123.0	104.0	113.5
	29.4	37	3.0					
	35.0	40	0					
1983, Spring	14.0	8	0	1	224PP			
	16.0	8	62.5	5	113.6 ± 5.7			81.8 ± 8.7
	18.0	8	62.5	5	84.8 ± 7.9			89.1 ± 9.0
	20.0	9	77.8	7	52.1 ± 1.5			145.2 ± 7.1
	26.0	10	70.0	3	64.7 ± 3.5			105.3 ± 9.9
1983, Summer	14.0	16	0		-			
	16.0	16	0		-			
	18.0	15	18.7	3	91.0 ± 5.8			109.4 ± 12.4
	20.0	16	25.0	5	59.5 ± 0.8			121.7 ± 6.7
	26.0	16	43.7	7	57.6 ± 1.0			87.0 ± 1.4

[1]from Sibray 1947

PPprepupa

Table 2--Natural Enemies of the California Oakworm

Host Stage	Pathogen (O)/Predator (P) Primary Parasite (PP)	Secondary Parasite (SP)	Primary Parasite Hosts
Egg	Podisus maculiventris (P)		
	Tetrastichus sp (PP)		
Larva	Entomophthora sp (O)		
	Borrelinavirus (O)		
	Nosema phryganidae (O)		
	Leidyana phryganidiae (O)		
	L. berkeleyi (O)		
	Mermithid nematode (PP)		
	Podisus (P)		
Pupa	Actia sp (PP)		
	Zenillia virilus (PP)	Mesochorus sp (SP)	Zenillia
	Beauveria bassiana (O)		
	Podisus (P)		
	Ephialtes ontario (PP)	Gelis tenellus (SP)	Ephialtes, Brachymeria, Itoplectis
		Dibrachys cavus (SP)	Ephialtes, Brachymeria, Itoplectis
	Brachymeria ovata (PP)		
	Itoplectis behrensii (PP)	Mastus acidulatus (SP)	Itoplectis
		Bathythrix sp	Itoplectis
	Leptocoris rubrolineatus (P)		
Adult	Podisus (P)		

Table 3--Influence of Mature Leaf Age, Host Tree Infestation Level, Sex and Larval Population Density on Mean Daily Consumption, Elimination, Growth Rate, and Assimilation Efficiency[1,2]

Factor	N	CR (Mg. dry wt./larva) $\bar{x} \pm$ SE	N	FR (Mg. dry wt./larva) $\bar{x} \pm$ SE	N	CI $\bar{x} \pm$ SE	N	GR $\bar{x} \pm$ SE	N	AD (PCT.) $\bar{x} \pm$ SE	N	ECI (PCT.) $\bar{x} \pm$ SE	N	ECD (PCT.) $\bar{x} \pm$ SE
Leaf Age														
NEW	30	16.61 ± 1.1	30	13.52 ± 0.7	30	1.99 ± 0.12	30	0.082 ± 0.005	30	17.1 ± 1.4	30	4.2 ± 0.2	30	31.8 ± 3.7
OLD	33	15.55 ± 0.6	33	13.26 ± 0.4	33	2.02 ± 0.08	33	0.085 ± 0.006	33	14.0 ± 1.6	33	4.3 ± 0.2	28	35.8 ± 4.5
Host tree Infestation Level														
SPARSE	33	16.36 ± 1.03	33	13.54 ± 0.67	33	1.99 ± 0.12	33	0.088 ± 0.006	33	15.4 ± 1.4	33	4.4 ± 0.2	32	35.4 ± 4.3
HIGH	30	15.72 ± 0.55	30	13.22 ± 0.5	30	2.02 ± 0.08	30	0.079 ± 0.005	30	15.6 ± 1.6	30	3.9 ± 0.2	27	28.6 ± 3.5
Sex														
♀	12	19.82 ± 1.1	12	16.18 ± 0.8	12	2.2 ± 0.14	12	0.109 ± 0.008	12	17.8 ± 2.7	12	5.0 ± 0.3	12	37.6 ± 6.4
♂	6	16.02 ± 1.8	6	12.30 ± 1.2	6	2.1 ± 0.12	6	0.090 ± 0.009	6	21.8 ± 4.3	6	4.3 ± 0.4	6	26.2 ± 7.1
Larval Density														
1 larva	18	18.55 ± 1.03**	18	14.89 ± 0.8**	18	2.16 ± 0.1**	18	0.102 ± 0.006**	18	19.1 ± 2.2**	18	4.8 ± 0.3*	18	33.8 ± 4.9
4 larvae	24	13.86 ± 0.55	24	12.25 ± 0.5	24	1.74 ± 0.1	24	0.070 ± 0.007	24	11.7 ± 1.4	24	4.0 ± 0.2	21	38.4 ± 5.5

[1]Values within a group followed by * and ** are significant at the 0.05 and 0.01 level respectively.

[2] Larval instars 1 and 2 excluded.

Table 4--Influence of Mature Leaf Age, Host Tree Infestation Level, Sex and Larval Population Density on Pupal Weight, Adult Weight and Duration of Developmental Period[1,2]

Factor	Sex	Pupal wt. (Mg.) N	Pupal wt. (Mg.) $\bar{x} \pm SE$	Adult wt. (Mg.) N	Adult wt. (Mg.) $\bar{x} \pm SE$	Larval Period (Days) N	Larval Period (Days) $\bar{x} \pm SE$	Pupal Period (Days) N	Pupal Period (Days) $\bar{x} \pm SE$	Total (Days) N	Total (Days) $\bar{x} \pm SE$
Leaf Age											
NEW	♀	34	112.0 ± 4.9	20	83.2 ± 0.5	32	33.7 ± 1.2	32	7.3 ± 0.3	32	40.9 ± 1.2
OLD		30	118.9 ± 6.5	18	83.1 ± 8.4	30	32.2 ± 1.2	30	7.4 ± 0.2	30	39.5 ± 1.2
NEW	♂	25	79.9 ± 3.2	15	36.3 ± 4.7	25	27.8 ± 0.9	25	9.6 ± 0.5	25	37.3 ± 1.0
OLD		31	77.3 ± 3.2	19	34.3 ± 3.4	31	28.0 ± 0.9	31	9.6 ± 0.4	31	37.6 ± 1.0
Tree Infestation Level											
SPARSE	♀	34	116.2 ± 5.5	22	83.2 ± 7.1	32	32.8 ± 1.4	32	7.5 ± 0.3	32	40.3 ± 1.3
HIGH		30	114.1 ± 5.9	16	83.0 ± 6.9	30	33.1 ± 1.0	30	7.2 ± 0.3	30	40.2 ± 1.1
SPARSE	♂	28	78.0 ± 3.1	19	37.3 ± 4.2	28	27.2 ± 1.0	28	9.6 ± 0.4	28	36.8 ± 1.1
HIGH		28	78.9 ± 3.4	15	32.5 ± 3.4	28	28.6 ± 0.8	28	9.6 ± 0.4	28	38.2 ± 0.9
Sex	♀	64	115.2 ± 4.0**	38	83.1 ± 4.9**	62	32.9 ± 0.9**	62	7.3 ± 0.2**	62	40.3 ± 0.9*
	♂	56	78.5 ± 2.3	34	35.2 ± 2.8	56	27.9 ± 0.6	56	9.6 ± 0.3	56	37.5 ± 0.7
Larval Density											
1 larva	♀	12	128.7 ± 9.0	8	93.6 ± 8.1	12	30.8 ± 1.8	12	7.7 ± 0.4	12	38.4 ± 1.9
4 larvae		36	111.8 ± 5.2	20	80.3 ± 6.7	35	33.8 ± 1.0	35	7.3 ± 0.3	35	41.1 ± 1.0
1 larva	♂	6	87.6 ± 4.8	3	44.9 ± 11.6	6	28.3 ± 2.8	6	10.5 ± 0.2	6	38.8 ± 2.8
4 larvae		33	77.2 ± 2.8	20	33.7 ± 3.4	33	27.6 ± 0.7	33	9.9 ± 0.3	33	37.5 ± 0.7

[1]Values within a group followed by * and ** are significant at the 0.05 and 0.01 level respectively.

[2]Larval-instars 1 and 2 excluded.

Table 5--Influence of Leaf Maturity on Weight, Duration of Developmental Period and Egg Production[1]

Host Plant	Sex	Larval Period (Days) $\bar{x} \pm SE$ N	Immature foliage	N	Mature foliage	Pupal Weight (Mg.) $\bar{x} \pm SE$ N	Immature foliage	N	Mature foliage	Adult Weight (Mg.) $\bar{x} \pm SE$ N	Immature foliage	N	Mature foliage	Total Eggs laid per ♀ $\bar{x} \pm SE$ N	Immature foliage	N	Mature foliage
1	♀	7	52.0±3.9	17	54.9±0.6	7	151.6±11.3**	17	97.6±4.6	7	121.4±9.2**	17	79.0±3.7	9	141.8±20.8**	12	77.3±8.1
	♂	4	37.5±1.9**	9	45.1±1.3	4	90.0±10.8**	9	58.0±2.6	4	53.6±7.9**	9	29.6±2.7				
2	♀	7	44.4±2.3	2	56.5±7.5	7	147.1±22.5	2	105.5±17.3	7	123.6±19.0	2	83.8±12.8	9	152.7±36.0	2	82.0±20.0
	♂	4	36.3±3.3**	11	45.6±1.0	4	93.4±13.7**	11	58.8±2.4	4	41.1±3.4	11	36.6±2.5				

[1]Values within a row followed by * and ** are significant at the 0.05 and 0.01 level respectively.

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Interest and concern about hardwoods in California has been increasing dramatically. This symposium addressed the State's hardwood resources and included sessions on silviculture, protection and damage factors, urban forestry-recreation, wildlife, wood products-utilization, inventory-measurements, range, and policy and regulation. Use and value of the hardwood resource will continue to grow as the population increases, the resource diminishes, and new uses for hardwoods develop.

Retrieval Terms: damage factors, inventory, measurements, policy, protection, range, recreation, regulation, silviculture, urban forestry, utilization, wildlife, wood products