Biology and Development of the Wild and Golden Sport of *Grapholita prunivora* (Lepidoptera: Tortricidae)

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ABSTRACT The development of the lesser appleworm, *Grapholita prunivora* (Walsh), was studied using immature apples as the food source. Degree-hour developmental rates for all life stages were calculated. Developmental rates in degree-hours at 25°C for the eggs, four instars, pupae, and adults were 1,503 (4 d), first larval ecdysis 1,109 (3 d posthatch), second larval ecdysis 1,941 (5 d posthatch), third larval ecdysis 3,186 (8 d posthatch), pupation 5,196 (13 d posthatch), and adult 8,925 (22 d posthatch), respectively. It was determined that 8.5°C was the lower thermal threshold for development of lesser appleworm eggs. Comparisons of growth, survival, and reproduction were made between two different laboratory populations, the wild type and a golden color sport (strain).

KEY WORDS Tortricidae, *Grapholita prunivora,* lesser apple worm

LESSER APPLEWORM, *Grapholita prunivora* (Walsh), is an obscure pest of pome fruits in the Pacific Northwest and is not considered to be of economic importance in commercial growing areas (Beers et al. 1993). However, it became a concern in the Pacific Northwest in the early 1990s as a quarantine issue on apples destined for export, particularly those to be shipped to Japan (Moffitt 1988). Lesser appleworm was first described as the plum moth by B. D. Walsh (Walsh 1868), which provided a detailed description of the adult and a brief description of the larva. Fletcher (1898) reported that the plum moth or lesser appleworm had been found infesting apples and hawthorn in British Columbia and Quebec, Canada. The name lesser appleworm was adopted in 1908 by Quaintance in preference to plum moth due to its tendency to cause injury to apples rather than plums. Quaintance (1908) published a comprehensive report on lesser appleworm, describing the life stages including the larva, cocoon, and pupa, noting that the egg had not been observed. His report included figures depicting larval injury to the apple. The larva of the lesser appleworm was initially described by Mackay (1959); this is considered to be the standard reference to larval stages. Brown (1953) studied the life cycle of the lesser appleworm in northeastern Oregon under field conditions. His work included a description of the larvae and moth, host plants, life history, and chemical and cultural control measures.

Surveys by the Washington State Department of Agriculture and the United States Department of Agriculture in the early 1990s indicated that the lesser appleworm is distributed throughout the fruit-producing areas of Washington and Oregon (Hathaway et al. 1994). As a result of quarantine concerns, lesser appleworm larvae were collected in 1992 from rose hips near Wapato, WA. A laboratory colony was established and tests were conducted to determine whether the accepted quarantine treatments for controlling codling moth, *Cydia pomonella* (L.) (Moffitt 1998, Hansen et al. 2000), would also be effective in controlling lesser appleworm. During the course of laboratory rearing, a golden color sport (strain) was discovered in the F_5 generation. This color sport is similar to the golden sport reported by Hutt and White (1975) that occurs in some codling moth populations. Results of laboratory and field studies on the golden sport of codling moth indicated that the golden sport population was comparable with the wild type in life history parameters, but it was not as active in the field as the wild population.

This study was conducted to characterize the different stages of the lesser appleworm, to quantify the developmental rates of these stages, and to compare the wild type and golden sport in regard to all rearing parameters.

Materials and Methods

Adults. Adult lesser appleworm moths, both wild type and golden sports, were obtained from laboratory colonies and reared on thinning apples, in the manner described by Mantey et al. (2000). Pupae were separated into 5-ml glass vials and were allowed to emerge in the vials to produce virgin stock. The moths were collected daily, and the sex of each adult was determined. The body length and the wing span of the adult moths were measured using a micrometer attached to a dissecting microscope, and body weights were obtained using a Cahn C-13 microbalance (Cahn Inc.,

Cerritas, CA). One virgin male and one virgin female were paired in a single-pair mating cage (Neven et al. 2000). The cage consisted of two 473.2-ml clear plastic cups, one inverted on the other. The cup used as the upper half of the cage had the bottom removed and a piece of organdy glued in its place to allow for ventilation. A 26-ml plastic cup with a clear plastic lid was glued in the bottom of the lower half cup. A hole punch was used to penetrate the lid of the plastic cup. The 26-ml plastic cup was filled with water and the stem from a pear cutting was placed through the hole in the lid of the 26-ml plastic cup. The pear foliage served as the oviposition substrate. It was determined from previous tests that pear foliage was preferred over apple foliage as an oviposition site (Mantey et al. 2000). Five thinning apples were placed in the bottom of the cage to serve as a food source for the larvae as the eggs hatched. Each cage was examined daily and adult mortality counts were made. After the female died, she was dissected to determine mating status. The criteria used for mating status were the presence or absence of a spermatophore in the bursa copulatrix.

Nine days after the adult moths died, the foliage and apples were removed from the cage and examined. The number of eggs laid and the number hatched were determined by examination under a dissecting microscope. The foliage was discarded. The fruit was transferred to a clean, clear, plastic cup (473.2 ml) with an organdy lid for ventilation. These cups were held at 25°C, 50% RH, and a photoperiod of 16:8 (L:D) h until the F_1 generation emerged. The F_1 moths were counted and their sex determined.

To determine the time of day that oviposition took place, three cages of lesser appleworm adults were assembled. The standard mating and oviposition cage was used. Three different age ranges of wild type moths were studied: 0–24, 24–48, and 48–72 h. One cage of 0–72-h-old golden moths was included in the study. Pear foliage was present in each cage to provide oviposition sites. The foliage was replaced every hour for a 24-h period. At the end of each hour, the foliage was examined under the microscope, and the number of eggs deposited during the previous hour was recorded for each age. The length and width of 100 eggs were recorded from both the wild and golden strains.

To determine the optimum age for egg deposition, single-pair matings were conducted using both the wild type and golden sport. The standard single-pair mating cage was used as described previously. Pear foliage was placed in the mating cage to serve as the oviposition site. New pear foliage was placed in each cage daily. The removed foliage was examined, and the number of eggs deposited during the previous day was recorded.

Eggs. Single lesser appleworm eggs were collected by replacing the oviposition substrates in the mating and oviposition cages with thinning apples. The apples were suspended by wiring the stems of the apples to pear shoots with the leaves removed. The moths were allowed to oviposit for 1 h. The apples were removed and examined. If eggs were found, they were immediately taken to a microscope with a videocamera attached. A video cassette recorder (Sanyo VM4512A TV with Rainbow TV Zoom lens S6X11-II, Sanyo Electric Inc., Compton, CA) was activated, and the development of the egg was monitored until it hatched. The eggs were held at 25°C, 50% RH with a constant light for videocamera operation. The temperature in the room was monitored, so that degree-hour calculations for developmental rates could be determined. This was repeated four times.

Larvae and Pupae. Pear foliage on which lesser appleworm eggs had been deposited was removed from the mating and oviposition cages of the mass rearing project. Newly hatched, first instars were transferred by brush to thinning apples, one larva per apple. The apple with the larva was placed in a 29.6-ml jelly cup, which was covered with a lid. The insects were held at 25°C, a photoperiod of 16:8 (L:D) h, and 50–70% RH. The apples with the larvae were evaluated by destructive sampling at 24-h intervals starting at day 1 and ending with day 30. The cups with the infested apples were examined at the end of the first 24-h period, and the apples that did not have obvious larval entries were discarded. For the wild type, three replicates of 10 observations were completed and for the golden sport one replicate of five observations was completed. The evaluation consisted of the following criteria: natural mortality, weight, head capsule measurement (larval stage), determination of color with the aid of the Munsell Book of Color (see below), and determination of the number of degree-hours for development. Head capsule measurements were obtained using a dissecting microscope with an attached micrometer.

There are four different species of olethreutid larvae that can be found in fruit of the apple: codling moth, *Cydia pomonella* (L.); oriental fruit moth, *Grapholita molesta* Busck; cherry fruitworm, *Grapholita packardi* Zeller; and lesser appleworm. These four species are easily confused in the field, but in the laboratory they can be differentiated by the absence or presence of an anal comb. Chapman and Lienk (1971) attempted to separate the larvae on the basis of color by boiling the larvae and preserving them in 70% ethyl alcohol. Lesser appleworm is the only larva to retain its pinkish color. In an attempt to characterize the larval coloration in a nondestructive sample, the color of the lesser appleworm larvae were characterized using the Standard Method of Specifying Color by the Munsell System (Munsell Book of Color 1905). A complete explanation of the Munsell System can be found at http://www.it.lut.fi/ip/research/color/database/munsell.html.

Determination of Degree-Hours for Development. To calculate the number of degree-hours needed for a specific biological event to occur, the threshold temperature for development had to be determined. Newly hatched first instar lesser appleworms were transferred to thinning apples, one larva per apple per 29.6-ml cup. The test subjects were held at 25°C and a photoperiod of 16:8 (L:D) h for 24 h. The larvae were then reared at 15, 20, or 25°C until the adults emerged. The mean number of hours from larval hatch until

Table 1. Longevity and fecundity of wild-type and golden sports of adult lesser appleworm

Status	Type	No. pairs	Sex	Longevity	SE	No. spermatophores[a]	No. eggs	Range	% Hatch	% Survival[b]
Mated, laid eggs	Wild	114	♀	11.1	0.31	1.02	42.0 ± 2.9	1–136	81.9 ± 1.8	44.3 ± 2.8
	Wild	114	♂	10.6	0.33					
	Gold	39	♀	13.5	0.77	1.00	35.6 ± 4.1	1–88	71.1 ± 3.6	22.8 ± 3.5
	Gold	39	♂	11.4	0.56					
Mated, no eggs	Wild	22	♀	9.6	2.05	1.00	0.0	0.0	0.0	0.0
	Wild	22	♂	9.9	2.11					
	Gold	11	♀	14.9	4.50	1.00	0.0	0.0	0.0	0.0
	Gold	11	♂	12.3	3.71					
Unmated	Wild	51	♀	11.2	1.57	0.00	0.0	0.0	0.0	0.0
	Wild	51	♂	9.3	1.30					
	Gold	31	♀	9.2	1.65	0.00	0.0	0.0	0.0	0.0
	Gold	31	♂	10.7	1.92					

[a] Number of spermatophores observed from female dissections.
[b] To adulthood.

adult emergence was calculated for each temperature. The temperature threshold was calculated using the procedure described by Pitcarin et al. (1991).

Field Study. A field study to determine the time of day that lesser appleworm males are most active was conducted in 1992 in a hawthorn thicket located near Walla Walla, WA. Pherocon 1-C traps baited with commercially available lesser appleworm pheromone, a mixture of (*Z*)- and (*E*)-8-dodecenyl acetates (Roelofs and Cardé 1974) were placed in the thickets. The traps were checked every 30 min from 1,300 to 2,100 hours and then left overnight. The trapping was conducted on 13 May, 21 May, 3 June, 15 July, and 26 August.

Statistics. Data were tabulated using Lotus 1-2-3 (Lotus [1993]. Lotus 1-2-3. V.I.O. IBM Software Group, Cambridge, MA) and QuattroPro (QuattroPro 2000. Word Perfect Office. V.9.0. Corel Corporation). Initial analyses (means, STD, SE, percentages, *t*-test, F-test, one-way analysis of variance [ANOVA]) were performed using QuattroPro, version 9.0. Final analyses were performed using SAS (SAS 2002. The SAS System for Windows. Release 8.02. SAS Institute Inc. Cary, NC). One-way and factorial ANOVAs (type × sex) with Tukey's were performed on weights of larvae, pupae and adults, single-pair mating data, head capsule lengths, wing span, and wing lengths.

Results

Adults. There was a significant difference in the mean longevity (days) of wild and golden sports (Table 1). The golden sport lived 11.32 d, whereas the wild type lived an average of 10.4 d ($F = 4.45$, df = 267, $P = 0.035$,). Also, mated individuals lived slightly longer than unmated individuals, with longevities of 11.69 and 10.10 d, respectively ($F = 14.89$, df = 187, $P < 0.0001$). Females and males lived approximately the same length of time with longevities of 11.27 and 10.51 d, respectively ($F = 3.68$, df = 267, $P = 0.665$). Means ranged from 9.2 d ± 1.65 d for unmated golden females to 14.9 d ± 4.5 d for mated golden females that did not lay eggs. The SEs varied widely from 0.31 d for the wild-type mated females that laid eggs to 4.5 d for golden mated females that laid no eggs.

In total, 187 single-pair crosses were attempted for the wild type and 81 for the golden sport. There were fewer golden sport mating attempts due to lack of availability of the golden moths. The golden sport was not as fecund as the wild type, where 73.7 and 61.7% of the wild type and golden sports, respectively, mated successfully. Three (2.2%) of the mated, wild-type females mated twice as indicated by two spermatophores present in the bursa copulatrix. None of the golden females mated more than once. (Note: In this study, it was observed that some wild-type female lesser appleworms mated up to five times in the laboratory.) Not all mated females laid eggs; 16 and 22% of the wild-type and golden females, respectively, did not oviposit. The number of eggs hatching was significantly lower ($F = 225.7$, df = 227, $P < 0.0001$) for the golden sport, from 81.9% for the wild type compared with 71.1% for the golden sport. The survival rate of the larvae to adult was also significantly lower ($F = 78.1$, df = 373, $P < 0.0001$) for the golden sport.

Table 2. Comparison of the adult weights and pupal weights (milligrams) of males and females of wild-type and golden sports

Type	Sex	Mean adult weight (mg)	Range	*n*	Mean pupal weight (mg)	Range	*n*
Wild	♀	4.61 ± 0.068a	2.8–6.8	100	6.6 ± 0.097a	3.0–8.1	114
Wild	♂	4.27 ± 0.055b	2.8–5.9	100	6.6 ± 0.059a	4.3–8.1	114
Gold	♀	4.52 ± 0.063b	2.8–5.8	99	6.7 ± 0.299a	4.6–9.0	30
Gold	♂	4.45 ± 0.071b	2.2–6.4	99	6.6 ± 0.211a	4.1–8.7	30

Means followed by the same letter are not statistically different from one another (Tukey's test).

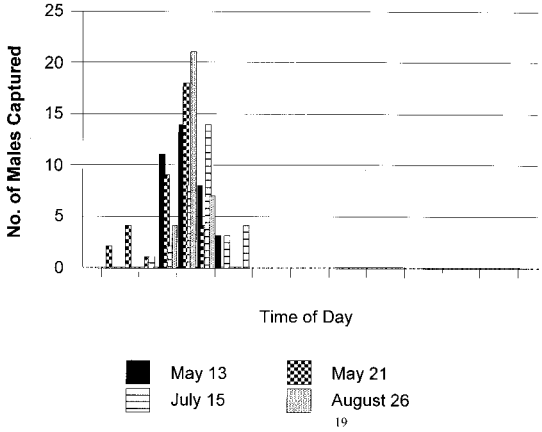

Fig. 1. Hourly catches of lesser appleworm males responding to pheromone-baited sticky traps near Walla Walla, WA, in 1992.

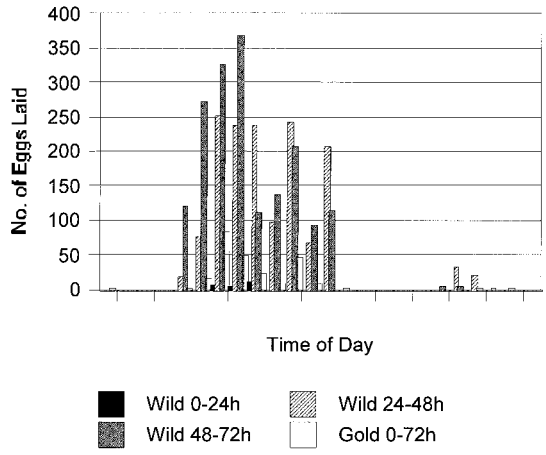

Fig. 2. Number of eggs laid per hour by wild-type and golden sport lesser appleworm females held in standard oviposition cages in a greenhouse environment. Each cage held 500 adults.

The mean lengths of the forewing and wingspans of wild-type adult lesser appleworm were 3.5 ± 0.016 and 8.0 ± 0.040 mm, respectively, for the females, and 3.5 ± 0.016 and 8.0 ± 0.038 mm, respectively, for the males. The golden sport was slightly smaller with forewing and expanse lengths at 3.3 ± 0.023 and 7.5 ± 0.058 mm, respectively, for the females and 3.1 ± 0.032 and 7.2 ± 0.063 mm, respectively, for the males.

The weights of the wild-type and golden adults were not significantly different (Table 2). The weights of wild type females, 4.61 ± 0.068 g were significantly different from males, 4.27 ± 0.055 g ($F = 20.53$, df = 169, $P < 0.0001$). The weights of the females and males of the golden sport were not significantly different.

Several observations were made concerning the behavior of the adults. The activity level of the adult moths in the mating and oviposition cages increased at 1,100 hours and peaked from 1,600 to 2,000 hours. Female moths called in the late afternoon and early evening, resulting in the occurrence of mating pairs resting on the upper and lower sides of pear leaves. These observations in the laboratory correspond closely to what was observed in the 1992 field test (Fig. 1).

Eggs. The mean length and width of lesser appleworm eggs were 0.73 ± 0.006 mm × 0.56 ± 0.004 mm for the wild type. The mean length and width of golden sport eggs were slightly smaller at 0.070 ± 0.007 mm × 0.55 ± 0.005 mm, but did not differ significantly.

We determined from linear regression that 8.5°C was the lower thermal threshold for development of lesser appleworm eggs. The mean number of degree-hours for egg development to hatch was 1,503 degree-hours (±19.69) or ≈4 d at 25°C. Observations were made during the developmental period. Approximately 4 h after the egg was laid, a white ring started to form. A red ring formed ≈24 h after the egg was laid, and it was during the red ring stage that the eyes became prominent, ≈72 h after the egg was laid. The head capsule was not evident until the fourth day of development. Hatch occurred from 6 to 12 h after the head capsule started to darken.

Lesser appleworm females, both wild type and golden sports, laid most of their eggs between 1,500 and 2,300 hours. A few eggs were laid between 500 and 700 h (Fig. 2). The 0–24-h-old females did not produce any eggs. Observations revealed that the females spent this first 24-h period calling and mating. The highest mean percentage of eggs laid per day was day 3 for wild-type females and day 4 for golden females (Fig. 3). No eggs were laid on day one for either group. Oviposition occurred for up to 14 d in both groups.

Larvae. The lesser appleworm has four instars (Fig. 4) based on head capsule measurements of >400 larvae. The range for first instar head capsule measurements was from 0.0200 to 0.0225 mm, the range for second instar was from 0.0275 to 0.0325 mm, the range for third instar was from 0.0450 to 0.0550 mm, and the range for fourth instar was from 0.0675 to 0.0775 mm.

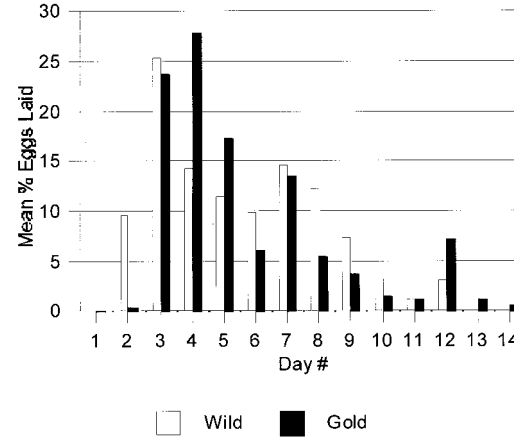

Fig. 3. Mean percentage of eggs laid per day for wild-type and golden sport lesser appleworms.

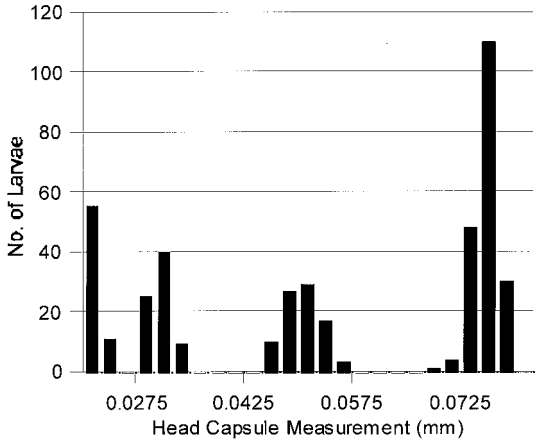

Fig. 4. Head capsule measurements (millimeters) of 419 lesser appleworm larvae.

First instar is the shortest larval stage, lasting 2 to 3 d (Table 3). On day 3 with the degree-hour total ≈1,100, one-half of the larvae had molted to the second instar. Beginning with day 5, there were considerable differences in individual developmental rates, resulting in overlapping of life stages. Second instar continues from day 3 through day 9, third instar continues from day 5 through day 12, and fourth instar continues from day 8 through day 20, all at 25°C.

Determination of larval color using the Munsell System showed that color is consistent within each instar. The first and second instars were 10YR/eight-sixths. The third instars were 10YR/nine-fourths with a color difference in the gut region of 7.5YR/7/12. This color difference is probably due to a more well-developed gut containing food in various stages of digestion. The color of the fourth instars was 10R/5/10.

Table 4. Weights and ranges of weights of the four instars of both the wild-type and golden sport of lesser appleworm

Color	Instar	*n*	Mean weight (± SE) (mg)	Range (mg)
Wild	1	59	0.059 ± 0.004a	0.012–0.182
	2	73	0.239 ± 0.019a	0.031–0.866
	3	83	1.478 ± 0.119b	0.834–7.771
	4	196	7.608 ± 0.167c	1.891–12.273
Gold	1	9	0.233 ± 0.117a	0.033–0.876
	2	19	0.447 ± 0.132a	0.051–1.606
	3	11	1.624 ± 0.212b	0.539–2.572
	4	35	5.701 ± 0.350c	2.073–9.195

Means within a color having the same letter are not statistically different from one another (Tukey's test).

First and second instar weights were not significantly different within the two populations (Table 4). However, the weights of the third instars of both populations were different from the other instars within those populations ($F = 581.4$, $P < 0.0001$ for wild type; $F = 69.2$, $P < 0.0001$ for golden), but not between the two populations (Table 4). The fourth instar of both populations was significantly different from the other instars within those populations ($F = 581.4$, $P < 0.0001$ for wild type; $F = 69.2$, $P < 0.0001$ for golden), and was also significantly different between the populations ($F = 8.10$, $P < 0.0001$).

Table 3. Degree-hours for development of the life stages of the wild-type lesser appleworm

Days Posthatch	Degree hour	% 1st Instar	% 2nd Instar	% 3rd Instar	% 4th Instar	% Pupa	% Adult
1	348	100.0					
2	714	100.0					
3	1,109	51.7	48.3				
4	1,520		100.0				
5	1,941	3.7	85.2	11.1			
6	2,372		25.9	74.1			
7	2,782		8.3	91.7			
8	3,186		3.7	63.0	33.3		
9	3,673		3.6	21.4	75.0		
10	4,053			16.7	83.3		
11	4,236			17.2	82.8		
12	4,835			3.7	96.3		
13	5,196				96.7	3.3	
14	5,683			7.4	81.5	11.1	
15	6,017		3.6		75.0	21.4	
16	6,539		3.6	7.1	28.6	60.7	
17	6,825			10.0	23.3	66.7	
18	7,181				17.9	82.1	
19	7,664				3.6	96.4	
20	8,071				3.3	96.7	
21	8,495					100.0	
22	8,925					93.3	6.7
23	9,288				3.7	74.1	22.2
24	9,613					51.7	48.3
25	9,779					23.3	76.7
26	10,477					7.1	92.9
27	10,824					6.7	93.3
28	11,149						100.0
29	11,624					11.1	88.9
30	11,904					10.3	89.7

Table 5. Percentage of survival from neonate larvae to adult for both wild and golden populations

Type	*n*	1st instar	2nd instar	3rd instar	4th instar	Pupa
Wild	900	96.6	94.6	94.6	94.1	93.9
Gold	150	92.7	90.0	90.0	89.3	89.3

Pupae. The pupal stage is the longest lasting immature stage of the lesser appleworm, lasting at least 9 d. The pupae were ≈4.8 mm in length. The mean pupal weights for the wild-type and golden sport males and females were not significantly different (Table 2). The mean weights for all pupae regardless of sex or color was ≈6.6 mg. The color of the pupae using the Munsell Book of Color was 7.5YR/6/10.

Survival Rates. The survival rate from first through fourth instars to adults was not significantly different between the wild type and golden sport (Table 5) (paired *t*-tests, $P > 0.06$). The survival rate from pupa to adult was identical for both groups. Once the fourth instar had successfully pupated, adult emergence followed with a >90% success rate (Table 3).

Discussion

The life cycle of the lesser appleworm at 25°C required 26 d to complete. The egg required 4 d to hatch, after which the neonate larvae entered the apple. There were four instars, and it took 12 d for the larvae to mature. The mature larvae left the apple and spun a cocoon. The pupal stage lasted at least 9 d. The adults emerged and the female spent the first day calling and mating, after which oviposition began. These results are consistent with those of Taylor (1909), in which eggs took ≈5 or 6 d to hatch under average orchard conditions in Missouri. Larvae spent an average of 17 d in the fruit, followed by a pupal period of 12–16 d. He reported that the entire life cycle from oviposition to adult emergence was 45–47 d.

Our results indicated high daily survival, ranging from 80 to 100% when a single larva was placed on an apple in a cup. This survival rate is in sharp contrast that of 44.3 and 22.8% for the wild type and golden sport, respectively, reported for the single-pair matings. This difference may be the result of the females in the single-pair mating ovipositing in proximity to sometimes as many as 50–60 eggs on a single apple. Such crowding may be a stress factor leading to competition among the larvae for survival. This oviposition in proximity has not been observed in the field and is probably a result of laboratory conditions. Significant amounts of mold were present in some of the rearing containers of the single-pair mating cages, possibly causing the increased mortality, however many of these highly contaminated containers contained viable larvae.

The life history data were used to identify the key factors causing increased mortality of the golden sport over the wild type. Successful matings were 12.0% less for golden than wild-type females. The golden female laid 15.0% fewer eggs than the wild-type female, and the percentage of eggs hatch was also less for the golden sport. It is interesting to note the differences in the measurements of wing span and lengths we found were considerably smaller than those reported by Chapman and Lienk (1971) for a wild type occurring in New York State. They reported that the mean length of the forewing and wingspan was 5.0 and 10.7 mm, respectively, for the female and 4.9 and 10.6 mm, respectively, for the male. However, there is no indication what the basis for these differences is at this time.

The measurements of egg length and width are within the ranges previously reported. Taylor (1909) reported average egg measurements of 0.68 × 0.53 mm, and Foster and Jones (1909) reported egg measurement ranges of 0.53 to 0.70 mm in length and 0.51 to 0.55 mm in width. We also found that the development of the embryo, from the opaque, red ring, and black head stages, was similar to the development of the codling moth embryo described by Richardson et al. (1982). Although the developmental stages of the eggs of these two species are similar, the differences in egg size should aid in avoiding confusion of the two species in the field.

Field mating behavior data we collected are similar to the data reported by Gentry et al. (1975) who showed that lesser appleworm males in Georgia responded to pheromone-baited traps from 1,700 to 2,000 hours. It is interesting that this response is similar for moths from such distant geographical regions. However, it seems that lesser appleworm from Washington is attracted over a longer time span than the population in Georgia. This may be a response to daylength differences between the two regions.

In the field, lesser appleworm and codling moth have similar life cycles. Historically, the chemical measures used to control codling moth, control lesser appleworm as well. With the trend toward the use of sex pheromone and other species specific means to control codling moth, the probability that lesser appleworm will become a pest of economic importance in commercial orchards is increasing. The biological and developmental data presented here provides the information needed to effectively construct a program for control of lesser appleworm should it become a pest of concern.

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