Development Rates for the Seed Maggots *Delia platura* and *D. florilega* (Diptera: Anthomyiidae)

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Environ. Entomol. 15: 1022–1027 (1986)

ABSTRACT Duration of immature stages of seedcorn maggots (SCM), *Delia platura* (Meigen), and bean seed maggots (BSM), *D. florilega* (Zetterstedt), was determined at eight constant temperatures from 5 to 40°C. No SCM or BSM survived to second instar at either 5 or 40°C. No BSM survived to the adult stage at 35°C. Duration of immature stages varied from 240 days at 10°C to 17 days at 35°C. A computer model developed using the SCM development rate data closely simulated SCM development in the field during the growing season.

KEY WORDS *Delia platura, Delia florilega,* development rates

SEEDCORN MAGGOTS (SCM), *Delia platura* (Meigen), are cosmopolitan pests of many crops (Throne 1980). Data in the literature describing the effects of temperature on rate of development of immature stages of SCM are conflicting and incomplete (Harukawa et al. 1934, Reid 1940, Yathom 1970, Sanborn et al. 1982). Reported duration of immature stages varied between the studies, none of which included measures of dispersion associated with the reported mean (i.e., SEM or variance). Some measure of dispersion is essential for interpreting means and can be used in simulation models to simulate variation in development rate (Shaffer 1983, Wagner et al. 1984a).

SCM and closely related bean seed maggots (BSM), *D. florilega* (Zetterstedt), usually occur together in New York. They are difficult to differentiate, and in North America, the two species collectively are referred to as the "seed maggot complex." Kim (1983) determined duration of development of immature stages of BSM over a wide range of temperatures; however, he did not report the variance associated with the mean duration of each stage.

The objective of this study was to determine duration of each immature stage of SCM and BSM at constant temperatures in the laboratory. Equations describing the SCM development data were incorporated into a computer model and used to simulate SCM development in the field.

Materials and Methods

Seed maggots used in the study were taken from laboratory colonies maintained using rearing methods of Webb & Eckenrode (1978). Colonies were started with feral adults collected at the Robbins Research Farm, near Geneva, N.Y., during 1981 using techniques described by Kim & Eckenrode (1983).

Number of days required for SCM and BSM to complete development of each immature stage was determined at eight constant temperatures, 5, 10, 15, 20, 25, 30, 35, and 40°C, and artificial 16:8 (L:D) photoperiod. This range of temperatures was assumed to exceed that in which development of the two species would occur.

In the first test, 100 eggs (8–18 h old) of each species were placed individually in plastic diet cups (30 ml) (Bio-Serv, Frenchtown, N.J.) filled to a depth of ca. 1 cm with hardened plaster. The plaster was kept moist from water transported via a length (5 mm) of dental wick (Mohawk Dental Supply, East Syracuse, N.Y.) extending through a hole in the bottom of the container. The individual containers were randomly placed in uncovered transparent plastic boxes (27.5 by 33.5 by 10.5 cm), the bottoms of which were covered with six layers of paper towels laid over a piece of plastic net (6-mm mesh by 4 mm thick). Tap water was added to each box to a depth of <1 cm and absorbed by the plaster in each container via a dental wick. This method ensured constant high humidity in the containers. A hole (diam, 15 mm) in the plastic cover secured with nylon net allowed for air exchange. Each egg was surrounded by a ring of diet consisting of 1:1 lima bean meal/meat and bone meal. Food was added to the containers as required. SCM eggs were laid by second-generation laboratory females, and BSM eggs were laid by second- and third-generation laboratory females. Approximately 40% of eggs did not hatch at 10–30°C in the first test. Therefore, in a second test, 200 eggs (5–29 h old) of each species laid by third-generation laboratory females were placed at each

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Table 1. Duration (days) of immature stages of SCM and BSM at constant temperatures ($\bar{x}$ ± SEM)

Stage	Temp (°C)							
	5	10	15	20	25	30	35	40
SCM								
Egg	19.7 ± 5.7[a]	7.5 ± 1.7	3.5 ± 0.9	2.2 ± 0.2	1.6 ± 0.2	1.2 ± 0.3	1.4 ± 0.2	1.7 ± 0.4[a]
Larva	—	54.9 ± 9.5	26.9 ± 4.3	13.7 ± 2.9	10.6 ± 2.1	8.3 ± 1.9	7.6 ± 1.8	—
Pupa[b]								
Nondiapause	—	—	28.9 ± 1.4	15.4 ± 1.2	11.7 ± 0.7	8.9 ± 0.7	8.0 ± 0.6	—
Diapause	—	177.6 ± 43.5	181.8 ± 32.1	—	—	—	—	—
n[c]	0	11	54	82	83	71	10	0
BSM								
Egg	19.6 ± 3.0[a]	5.3 ± 0.7	3.3 ± 0.7	2.2 ± 0.4	1.6 ± 0.3	1.2 ± 0.3	1.3 ± 0.4[a]	1.7 ± 0.4[a]
Larva	—	47.8 ± 5.5	28.5 ± 4.6	13.3 ± 2.4	10.4 ± 1.6	8.4 ± 1.4	8.8 ± 0.3[a]	—
Pupa[b]								
Nondiapause	—	—	26.3 ± 2.2	14.3 ± 0.6	11.2 ± 0.7	9.4 ± 0.7	—	—
Diapause	—	176.8 ± 46.5	283.6 ± 73.3	—	—	—	—	—
n[c]	0	6	34	63	65	49	0	0

[a] Mean durations of the egg stage for SCM at 5 (n = 33) and 40°C (n = 26) and BSM at 5 (n = 23), 35 (n = 131), and 40°C (n = 41) were calculated from data for all eggs that hatched at these temperatures. Mean duration of the larval stage for BSM at 35°C (n = 3) was calculated from data for larvae that survived to the pupal stage at that temperature.

[b] At 15°C, 12 of 54 SCM and 20 of 34 BSM apparently diapaused.

[c] Number of insects surviving to the adult stage.

temperature. In a third test, 200 eggs (7–31 h old) of each species laid by third- and fourth-generation laboratory females were placed at each temperature.

Stage of development and sex of emerged adults were recorded every 0.5–7 days, depending on stage of development and temperature. The prepupal stage was included in the pupal stage.

For temperatures at which some individuals survived to the adult stage, only data from these individuals were analyzed because duration of larval stages was often lengthened in individuals that eventually died before reaching the adult stage and because sex of individuals could be determined only in adults. For temperatures at which no individuals survived to the adult stage, all data were used to determine duration of the egg and larval stages. Data from the three replications were pooled. An analysis of variance was used for all statistical comparisons ($\alpha = 0.05$).

Mean rate of development (mean of reciprocals of duration of stage) was calculated for each stage of each species at each temperature. Equations that describe the relationship between mean rate of development and temperature were developed using the mean rate of development at each temperature in the three replications (Wagner et al. 1984b). Data for pupae that diapaused at 15°C were not used to calculate parameters for the equations.

The general form of the equation presented by Wagner et al. (1984b) is

$$r(T) = \frac{\mathrm{RH025}\dfrac{T}{298.15}\exp\left[\dfrac{\mathrm{HA}}{1.987}\left(\dfrac{1}{298.15}-\dfrac{1}{T}\right)\right]}{1+\exp\left[\dfrac{\mathrm{HL}}{1.987}\left(\dfrac{1}{\mathrm{TL}}-\dfrac{1}{T}\right)\right]+\exp\left[\dfrac{\mathrm{HH}}{1.987}\left(\dfrac{1}{\mathrm{TH}}-\dfrac{1}{T}\right)\right]},$$

where $r(T)$ = mean rate of development at temperature T (°K). Wagner et al. (1984b) presented the theoretical basis for this equation and a computer program that can be used to estimate values for each of the six parameters in the equation.

Equations relating mean rate of development to temperature were incorporated into a computer model for simulating SCM development. Insects were moved through development stages and variation in development rate was simulated using a time-varying distributed delay (Manetsch 1976, as modified by A. J. Sawyer, Cornell University). Daily temperatures were assumed to vary sinusoidally, with the minimum and maximum occurring 12 h apart.

Simulation results were compared with SCM emergence in the field during 1981 (Throne & Eckenrode 1985). In the field study, feral SCM were allowed to oviposit in bean plots for 7 days, and the plots were covered with emergence traps. Time of emergence of the resulting progeny was recorded. This process was repeated each week from May through August 1981, and once each in September and October 1981. The computer simulations were initiated with 100 eggs on the dates that beans were planted in the emergence trap studies. Daily minimum and maximum soil temperatures at 5-cm depth from a weather station ca. 2 km from the emergence trap site were input to the model.

Direct comparison with the results of previous studies by Harukawa et al. (1934), Reid (1940), Yathom (1970), and Sanborn et al. (1982) was made possible by using the technique of Wagner et al. (1984b) to develop equations describing the relationship between mean rate of development and constant temperature for each of these studies.

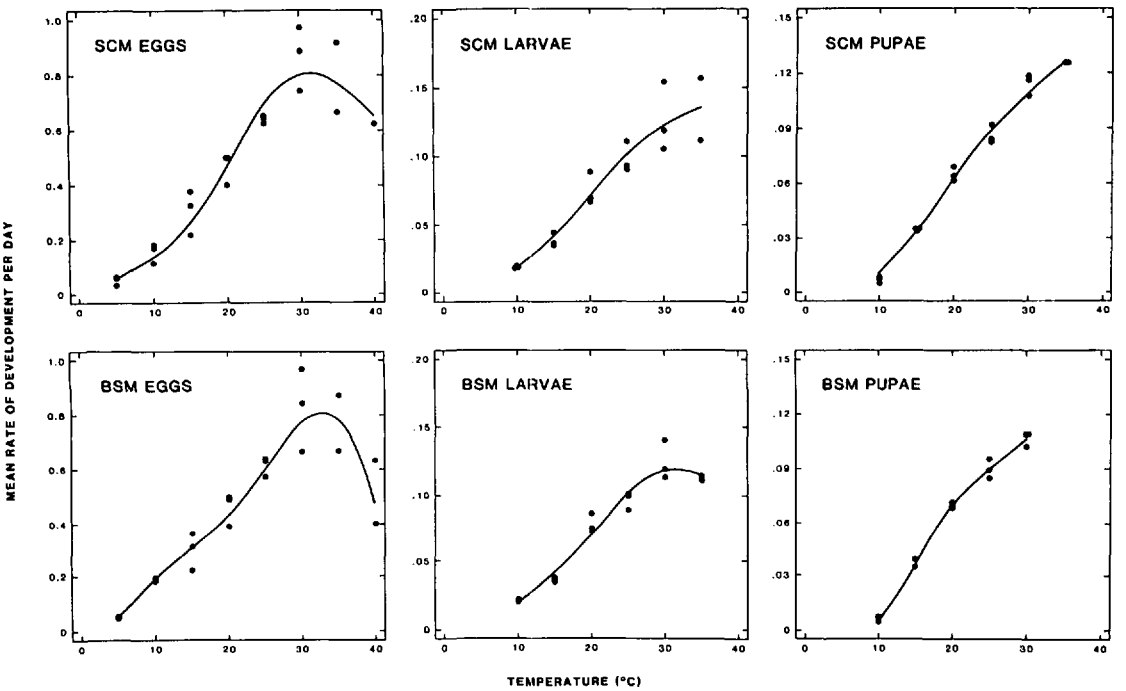

Fig. 1. Rates of development of immature stages of SCM and BSM. The line represents the model of Wagner et al. (1984b) fit to the data (●). The three points at each temperature represent the three replicates.

Results

Duration of immature stages of SCM and BSM generally decreased as temperature increased to the optimum temperature (Table 1; duration of each immature stage, including each of the three instars, for each sex of SCM and BSM is listed in Throne [1983]). Differences between the sexes, within each species, in the duration of the immature stages were not significant. No SCM or BSM survived to the second instar at 5 or 40°C. At 35°C, no BSM survived to the adult stage and half of the SCM adults were unable to emerge completely from the puparium. At 15°C, 22% of SCM and 50% of BSM surviving to the adult stage apparently diapaused, as evidenced by a bimodal emergence period, while at 10°C, all individuals surviving to the adult stage apparently diapaused. However, diapause was not physiologically confirmed. Differences between diapause and nondiapause individuals at 15°C in the duration of the egg and larval stages were not significant.

Parameters for equations describing the relationship between temperature and mean rate of development for immature stages of SCM and BSM are shown in Table 2. Observed rates of development and the fitted lines for the two species are shown in Fig. 1. The computer model closely simulated emergence in the emergence traps during most of 1981 (Table 3).

Table 2. Parameters for equations describing the relationship between temperature and rate of development of SCM and BSM using the method of Wagner et al. (1984b)

Stage	Parameter						R^2
	RH025	HA	HL	TL	HH	TH	
SCM							
Egg[a]	1.2018160	23,889.79	—	—	34,799.71	299.6956	0.94
Larva[a]	0.3754853	31,612.96	—	—	31,608.46	292.7199	0.91
Pupa[a]	0.9640887	47,931.53	—	—	43,849.61	289.2572	0.99
BSM							
Egg[b]	0.6124694	11,741.73	−90,734.1	279.0593	58,494.88	310.1995	0.91
Larva[a]	0.1885952	24,447.24	—	—	34,530.15	299.1018	0.95
Pupa[c]	0.0898957	5,717.71	−81,327.3	287.4518	—	—	0.99

[a] Four-parameter model with high-temperature inhibition.
[b] Six-parameter model.
[c] Four-parameter model with low-temperature inhibition.

Table 3. Differences in sampling dates between simulated and observed (simulated − observed) dates of 10, 50, and 90% SCM emergence in bean plots, Geneva, N.Y., 1981

Wk	Simulated − observed dates of emergences (differences in sampling dates)[a]		
	10%	50%	90%
1	−1	−2	−5
2	−3	−2	−2
3	−1	−2	−4
4	−2	−1	−3
5	−1	−2	−3
6	−1	0	0
7	−1	0	+1
8	+1	+1	+2
9	+1	+2	+1
10	+6	−2	−4
11	−3	−4	−7
12	−1	−1	−3
13	−1	−1	−1
14	+3	−2	−3
15	−2	−1	−1
16	+3	−2	−10
17	−7	−5	−5
18	−2	−2	−3

Simulated and observed dates are from Throne & Eckenrode (1985).

[a] Each sampling date represents a 2- to 3-day period.

Parameters for equations describing the relationship between rate of development and temperature for the data from the studies of Harukawa et al. (1934), Reid (1940), Yathom (1970), and Sanborn et al. (1982) are listed in Table 4. A comparison of the estimated duration of each stage of SCM from each of the four previous studies and the present study is shown in Table 5. Estimated duration of a stage is shown at 5°C intervals, but only for temperatures that were within the range of the original study. Duration of the egg stage was relatively consistent throughout the studies. At temperatures >15°C, duration of the larval stage was consistent among the studies; however, at 15°C, duration of the larval stage varied between 15.8 and 26.9 days. At 10°C, duration of the larval stage varied between 38.3 and 54.9 days. Duration of the pupal stage was fairly consistent throughout the studies except for the study of Sanborn et al. (1982). In that study, pupal development was much more rapid, especially at lower temperatures.

Discussion

This is the first time that variation in rate of development has been quantified for SCM or BSM. These data enable the development of more realistic simulation models for use in pest management programs by incorporating the intrinsic variation in rate of development in an SCM population. If a model is developed using only mean rates of development, then output from the model will be only mean time required to complete development. Such models can be used to simulate mean timing of events accurately, but usually are not useful for simulating population dynamics.

SCM development rate data from this study and previous studies (Table 5) differed in two ways. First, duration of the larval stage varied greatly among the studies at temperatures <20°C. Second, rate of pupal development was much more rapid at all temperatures in the study of Sanborn et al. (1982). The differences between the results of these

Table 4. Parameters for equations describing the relationship between temperature and rate of development of SCM reported in previous studies

Stage	Parameter						R^2
	RH025	HA	HL	TL	HH	TH	
Harukawa et al. (1934)							
Egg[a]	0.6337785	7,689.098	−43,404.9	283.8329	118,566.1	307.4899	0.88
Larva[a]	0.1466889	8,823.539	−57,483.5	285.0428	640,992.1	306.5116	0.95
Pupa[b]	0.1181051	4,110.852	−31,139.5	288.3951	—	—	0.98
Reid (1940)							
Egg[c]	0.8887484	17,132.71	—	—	27,798.64	301.9724	0.74
Larva[c]	0.1180381	16,292.88	—	—	57,561.32	307.6329	0.95
Pupa[d]	0.0941417	3,503.816	—	—	—	—	0.83
Yathom (1970)							
Egg[b]	0.7843385	15,185.06	−178,547	280.8312	—	—	0.99
Larva[d]	0.1117081	13,566.49	—	—	—	—	0.93
Pupa[d]	0.0884673	12,406.30	—	—	—	—	0.95
Sanborn et al. (1982)							
Egg[b]	0.6483525	7,744.56	−137,944	280.9307	—	—	0.99
Larva[d]	0.1037220	11,096.11	—	—	—	—	0.98
Pupa[c]	0.6402744	28,618.50	—	—	33,867.34	291.7163	0.99

Parameters were calculated using the method of Wagner et al. (1984b).

[a] Six-parameter model.

[b] Four-parameter model with low-temperature inhibition.

[c] Four-parameter model with high-temperature inhibition.

[d] Two-parameter model.

studies may be due to intrinsic or extrinsic factors. Development rates are known to differ between populations of a species from different geographic areas (e.g., Obrycki & Tauber 1982). The insects used in the studies on SCM development rate were from Japan (Harukawa et al. 1934), Israel (Yathom 1970), North Carolina (Reid 1940), and New York (Sanborn et al. 1982; present study). Intrinsic differences between the populations of SCM used in these studies may account for some or all of the differences in development rates between the studies.

Extrinsic factors would also be expected to have differed between the studies. Although all of these studies report constant temperature conditions, these conditions may vary due to improvements in environmental chambers over the 50-year time span of the studies and to inaccuracies in the environmental monitoring or calibration equipment. Light and humidity conditions often were not controlled or reported. Food source varied among the experiments. The length of time and the conditions under which insects are reared in the laboratory must certainly affect their response to environmental conditions (e.g., Chambers 1977). Before the work of Kim & Eckenrode (1983), establishment of SCM laboratory cultures was laborious and difficult. Therefore, SCM that had been reared in the laboratory for many years were often used in experiments.

The final criterion for determining the validity of development rate data is field validation. Higley & Pedigo (1984) reported that the data of Sanborn et al. (1982) agreed with SCM development in Iowa. In the present study, SCM development rate data, which differed from those of Sanborn et al. (1982), were found to simulate adequately SCM development in New York. The results of these simulation studies emphasize that simulation models must be validated in the geographic region in which they will be used.

Harris et al. (1966) suggested that at temperatures >24°C, all SCM and BSM pupae estivate, with resulting high mortality. For our samples of SCM and BSM, 25°C was quite favorable for development, as indicated by survival and development rate. Constant temperatures of 30°C were also favorable for development of both species; however, at 35°C, no BSM and only 10 SCM survived to the adult stage. Half of the surviving SCM were unable to completely emerge from the puparium. This suggested that adverse effects of high temperatures, rather than estivation, may be responsible for the high SCM mortality observed at 35°C. Although the initiation of estivation may be dependent upon both temperature and moisture (Masaki 1980), moisture conditions in each of these studies should have been quite high. This indicates that differences in high temperature thresholds for development between the studies are probably due to inherent differences between the populations of insects used. As Higley & Pedigo (1984) have already pointed out, additional studies are required to determine the factors responsible for initiation, maintenance, and termination of estivation in SCM throughout their range.

Table 5. Comparison of mean duration of immature stages of SCM from published studies

Temp (°C)	Present study	Sanborn et al. (1982)	Yathom (1970)	Reid (1940)	Harukawa et al. (1934)
Egg					
5	19.7	—	—	—	—
10	7.5	3.7	5.6	5.7	7.3
15	3.5	2.5	3.2	3.5	3.4
20	2.2	2.0	2.0	2.3	2.2
25	1.6	—	1.3	1.8	1.6
30	1.2	—	—	1.5	1.3
35	1.4	—	—	1.5	2.5
40	1.7	—	—	—	—
Larva					
10	54.9	—	—	38.3	—
15	26.9	19.1	20.5	22.8	15.8
20	13.7	13.5	13.5	13.9	9.5
25	10.6	9.6	9.0	8.9	6.9
30	8.3	—	—	6.6	5.3
35	7.6	—	—	7.3	—
Pupa					
10	—	24.9	—	—	—
15	28.9	12.8	24.2	—	22.8
20	15.4	8.4	16.4	—	13.7
25	11.7	7.1	11.3	10.6	9.9
30	8.9	—	—	9.5	8.0
35	8.0	—	—	—	—
Egg to adult[a]					
15	59.3	34.4	47.9	—	42.0
20	31.3	23.9	31.9	—	25.4
25	23.9	—	21.6	21.3	18.4
30	18.4	—	—	17.6	14.6
35	17.0	—	—	—	—

Duration of development was estimated by fitting equations to the original data. Data for pupae that diapaused were not included. Parameters for the equations are listed in Table 4.

[a] Sum of the mean duration of the egg, larval, and pupal stages.

Duration of immature stages of nondiapause, BSM was similar to that reported by Kim (1983). In the present study, biology of BSM in the laboratory differed from that of SCM in two ways. First, at 15°C, a greater percentage of BSM pupae diapaused. Second, the upper temperature threshold for BSM development was lower than that for SCM. Assuming that the diet was equally satisfactory for the two species, these results indicate that BSM develop in a narrower temperature range than SCM.

Acknowledgment

We thank Emmett Lampert, George Schaefers, and Ron Stinner for reviewing a previous version of the manuscript.

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Received for publication 25 October 1985; accepted 2 June 1986.