DEVELOPMENTAL RATES OF *BAGOUS AFFINIS* (COLEOPTERA: CURCULIONIDAE) AT CONSTANT TEMPERATURES

K.E. Godfrey, and L.W.J. Anderson
USDA Aquatic Weed Control Research Laboratory
Vegetable Crops, 124 Robbins Hall
University of California
Davis, CA 95616

Bagous affinis Hustache (Coleoptera: Curculionidae) is a biological control agent of *Hydrilla verticillata* (L.f.) Royle (Hydrocharitaceae; hydrilla), a weed in ponds, lakes, and waterways. Adults feed on hydrilla stems and leaves that are left exposed as waters recede during the dry season or following a drawdown (Baloch et al. 1980). The adults oviposit in moist organic matter found in and among the exposed hydrilla stems (Bennett & Buckingham 1991). The larvae burrow in the soil beneath the exposed stems and feed on subterranean vegetative propagules called tubers (Baloch et al. 1980). The basic life history and host range of *B. affinis* has been studied (Buckingham 1988, Bennett & Buckingham 1991). However, other aspects of the life history of *B. affinis* need to be determined to assess its potential and optimize its use as a biological control agent. For example, information on the rate of development of each life stage can be used to predict the best time for release (i.e., when air and soil temperatures are above developmental thresholds). In addition, the time of egg hatch or completion of the larval or pupal stage in the field after release and the number of generations possible at a site in a given period of time can be estimated. Therefore, in this study we measured the rate of development of the egg, larval, and pupal stages at six constant temperatures and constructed simple linear thermal unit models. The range of temperatures used represent those typical of northern California from late spring through fall, the dry season when aquatic systems undergo natural drawdowns (NOAA 1985).

The rates of development of the egg, larval, and pupal stages were estimated at 18, 21, 25, 28, 30, and 32°C (± 1°C) constant temperature regimes. The weevils used in these experiments were maintained in laboratory culture for 8 to 14 generations and were from the same colony as that described by Godfrey et al. (1994).

B. affinis were reared individually in small, plastic containers (5.5 x 5.5 x 6.5 cm) to measure development at each temperature. Each container was filled with moist soil (a fine sandy loam), and five dioecious hydrilla tubers were buried 3 cm beneath the soil surface. Eggs were dissected from water-soaked wood (an oviposition substrate) that had been placed in colony cages for less than 24 hours. Each egg was placed on a piece of moist filter paper on the soil surface. The container was covered with aluminum foil to maintain humidity. The rearing containers were placed in a growth chamber (Model CEC 36-10HLE, Rheem Sherer, Weaverville, NC) at the appropriate temperature regime, and checked once daily for egg hatch. The time of day that the eggs were checked and the condition of the eggs (i.e., hatched or not hatched) were recorded.

The following number of eggs were placed at each temperature regime: 180 at 18°C; 145 at 21°C; 181 at 25°C; 135 at 28°C; 130 at 30°C; and 293 at 32°C. Differing numbers of eggs were used because the survivorship of *B. affinis* from egg to adult varied with temperature. In addition, measurement of developmental rate was attempted at 15°C (n=20) and 35°C (n=60), but no *B. affinis* survived to the adult stage.

Upon egg hatch, the containers were not disturbed until most *B. affinis* were third instars, except to mist the soil surface with tap water to maintain soil moisture. This period of no disturbance reduced the mortality imposed on first and second instars by handling. The length of time from egg hatch through most of the larval stage (i.e., period of no disturbance) was determined by trial and error. For the 18°C regime, the period of no disturbance was 25 d; for 21°C, 15 d; for 25°C, 12 d; for 28°C, 7 d; for 30°C, 5 d; and for 32°C, 3 d. After the period of no disturbance, the contents were sorted by hand to recover all *B. affinis* and tubers. Many of the *B. affinis* were inside the tubers, and most were third instar larvae, although a low percentage were pupae. For those individuals that were pupae, development was measured from egg to adult only. All larvae and pupae found were placed individually in small petri dishes (5.5 cm diam) with tubers and some soil. The larvae and pupae were checked daily, and the life stage and time of day were recorded.

The length of time spent in each life stage was estimated because the exact time of molting was not known (the insects were checked only once per day). Therefore, we assumed that any change in life stage occurred at the midpoint between two consecutive daily checks. The length of time required for development from egg to adult was calculated by adding the times required to complete the egg, larval, and pupal stages. The mean time required to complete each life stage and from egg to adult was calculated for each temperature using the PROC MEANS (SAS Institute 1982). A simple linear thermal unit model was constructed by regressing the mean developmental rate of a life stage on temperature using simple linear regression (Steel & Torrie 1960; PROC REG, SAS Institute 1982). The mean developmental rate was defined as the reciprocal of the mean time required for completion of a life stage. The threshold temperature of each life stage was determined by extrapolation of the linear regression line to the *x*-axis. The thermal units required to complete development were calculated by first determining the number of thermal units required to complete development of a life stage at each temperature using:

$$DD = (T_1 - T_0)Dev$$

where DD is the thermal units in Celsius degree-days, T_1 is the experimental temperature (°C), T_0 is the threshold temperature (°C), and Dev is the mean number of days to complete a life stage (Arnold 1959, 1960). The mean thermal units required to complete development were then calculated for each life stage and for development from egg to adult.

Weevils successfully completed development at 18, 21, 25, 28, 30, and 32°C (Table 1). The percentage of eggs that survived to the adult stage was 5.6% at 18°C, 20.0% at 21°C, 16.0% at 25°C, 30.4% at 28°C, 18.5% at 30°C, and 8.2% at 32°C. At 15°C, 2 of 20 eggs hatched; however, neither larva survived to the adult stage. Eggs hatched at 35°C, but the individuals died early in the larval stage; little evidence of feeding was observed on the tubers.

The time for completion of all life stages of *B. affinis* was inversely related to temperature (Table 1). The mean time for egg hatch of *B. affinis* ranged from 3.0 d (32°C) to 11.3 d (18°C). For the larval stage, the mean development time ranged from 7.5 d (32°C) to 32.6 d (18°C), and for the pupal stage, from 3.3 d (32°C) to 11.9 d (18°C). The mean time for completion of development from egg to adult ranged from 13.7 d (32°C) to 55.6 d (18°C).

From the thermal unit models, completion of the egg stage was calculated to require 56.7 degree-days above 12.7°C (Table 2). Larvae required 127.2 degree-days above 14.5°C, and pupae, 60.1 degree-days above 13.4°C (Table 2). The combined life stages required 239.0 degree-days above 14.0°C (Table 2). The calculated threshold temperatures were slightly lower than the lowest temperature at which development

TABLE 1. MEAN NUMBER OF DAYS ± STD ERROR (N = NUMBER OF INDIVIDUALS) TO COMPLETE EGG, LARVAL, AND PUPAL STAGES AND FROM EGG TO ADULT FOR *B. AFFINIS* AT SIX CONSTANT TEMPERATURES.

	Temperature (°C)					
Stage	18	21	25	28	30	32
Egg	11.3	6.2	4.8	3.7	3.2	3.0
	± 0.17	± 0.09	± 0.08	± 0.08	± 0.05	± 0.05
	(n = 88)	(n = 69)	(n = 85)	(n = 83)	(n = 82)	(n = 85)
Larvae	32.6	20.7	13.5	8.2	8.4	7.5
	± 1.11	±0.48	± 0.29	± 0.13	± 0.23	± 0.19
	(n = 12)	(n = 27)	(n = 27)	(n = 33)	(n = 28)	(n = 27)
Pupae	11.9	8.0	5.6	4.2	3.5	3.3
	± 0.79	± 0.25	± 0.21	± 0.31	± 0.17	± 0.09
	(n = 9)	(n = 25)	(n = 25)	(n = 29)	(n = 24)	(n = 24)
Egg to Adult	55.7	35.0	23.7	15.7	14.7	13.7
	± 1.51	± 0.47	± 0.33	± 0.28	± 0.35	± 0.17
	(n = 10)[a]	(n = 29)[a]	(n = 29)[a]	(n = 41)[a]	(n = 24)	(n = 24)

[a]The n value for egg to adult is greater than that for pupae due to differences in larval developmental rates. Only total development time from egg to adult was measured for those individuals that had reached the pupal stage when the contents of the rearing containers were sorted.

would not occur in this study (15°C). The lower calculated threshold temperatures were probably due to the use of a linear equation to describe the non-linear relationship between temperature and rate of insect development (Wagner et al. 1984).

The simple linear thermal unit models derived in this study will be useful in future *B. affinis* release programs. The models provide information on the appropriate time

TABLE 2. STATISTICS GENERATED FROM REGRESSION ANALYSES OF MEAN *B. AFFINIS* DEVELOPMENT RATE ON TEMPERATURE, AND THRESHOLD TEMPERATURES (T_0), AND MEAN DEGREE-DAYS (*DD*; STD ERROR) REQUIRED FOR DEVELOPMENT OF EACH *B. AFFINIS* LIFE STAGE.

	Y				T_0	DD
Stage	Intercept	Slope	r^2	Prob>F	(°C)	(°C-day)
Egg	-0.23	0.018	0.99	0.0001	12.7	56.7
	(0.023)	(0.0009)				(1.27)
Larvae	-0.116	0.008	0.96	0.0001	14.5	127.2
	(0.021)	(0.0008)				(5.03)
Pupae	-0.232	0.017	0.99	0.0001	13.4	60.1
	(0.031)	(0.0012)				(1.37)
Egg to Adult	-0.59	0.004	0.98	0.0001	14.0	239.0
	(0.008)	(0.0003)				(6.27)

for release, that is when the mean soil temperature is at least 14°C, the threshold for development of *B. affinis* from egg to adult. In addition, the models allow developmental events to be predicted under different temperature regimes. This forecasting method can be used to determine which *B. affinis* life stage may be most prevalent or how many generations may have occurred at specific time intervals after release.

We acknowledge Dr. K. Steward and Mr. P. Madeira for supplying some of the tubers used in this study, and Dr. D. Gee for technical assistance in the laboratory. We thank Drs. C. Barfield, R. O'Neil, and K. Yeargan for reviewing an earlier draft of this manuscript. This research was supported with a grant from the California Department of Food and Agriculture. This article reports results of research only. Mention of a proprietary product does not constitute an endorsement or a recommendation for its use by USDA.

SUMMARY

B. affinis successfully developed from egg to adult at 18, 21, 25, 28, 30, and 32°C, but could not complete development at 15 and 35°C. Simple linear thermal unit models were constructed from the data. Completion of the egg stage required a mean of 56.7 degree-days above 12.7°C; the larval stage, a mean of 127.2 degree-days above 14.5°C; the pupal stage, a mean of 60.1 degree-days above 13.4°C; and from egg to adult, a mean of 239 degree-days above 14°C.

REFERENCES CITED

ARNOLD, C.Y. 1959. The determination and significance of the base temperature in a linear heat unit system. Proc. American Soc. Hort. Sci. 74:430-445.

ARNOLD, C.Y. 1960. Maximum-minimum temperatures as a basis for computing heat units. Proc. American Soc. Hort. Sci. 76:682-692.

BALOCH, G.M., SANA-ULLAH, AND M.A. GHANI. 1980. Some promising insects for the biological control of *Hydrilla verticillata* in Pakistan. Trop. Pest Manage. 26: 194-200.

BENNETT, C.A., AND G.R. BUCKINGHAM. 1991. Laboratory biologies of *Bagous affinis* and *B. laevigatus* (Coleoptera: Curculionidae) attacking tubers of *Hydrilla verticillata* (Hydrocharitaceae). Ann. Entomol. Soc. America 84: 420-428.

BUCKINGHAM, G.R. 1988. Reunion in Florida - hydrilla, a weevil, and a fly. Aquatics 10: 19-25.

GODFREY, K.E., L.W. J. ANDERSON, S.D. PERRY, AND N. DECHORETZ. 1994. Overwintering and establishment potential of *Bagous affinis* (Coleoptera: Curculionidae) on *Hydrilla verticillata* (Hydrocharitaceae) in northern California. Florida Entomol. 77:221-230.

NOAA. 1985. Climatography of the United States No. 20, climate summaries for selected sites, 1951-1980, California. USCOMM-NOAA. Asheville, NC 7/84/200.

SAS INSTITUTE, INC. 1982. SAS user's guide: statistics, 1982, edition. Cary, NC.

STEEL, R.G.D., AND J.H. TORRIE. 1960. Principles and procedures of statistics. McGraw-Hill Book Company, Inc., New York, NY.

WAGNER, T.L., HSIN - I WU, P.J.H. SHARPE, R.M. SCHOOLFIELD, AND R.N. COULSON. 1984. Modeling insect development rates: a literature review and application of a biophysical model. Ann. Entomol. Soc. America 77:208-225.