Influence of Photoperiod and Temperature on the Reproductive Diapause of Two Different Geographic Populations of the Mexican Bean Beetle (Coleoptera: Coccinellidae) and Their Cross Progeny[1]

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ABSTRACT The influence of temperature and photoperiod on the reproductive diapause of two Mexican bean beetle, *Epilachna varivestis* Mulsant, populations and their cross progeny was determined in laboratory tests. The fertility level of the El Salvador population exceeded that of the Maryland population under both diapause and non-diapause conditions. Changes in photoperiod had a greater impact on diapause in the El Salvador population, while the Maryland strain was more responsive to changes in temperature. Progeny of reciprocal crosses were more fertile than progeny of purebred crosses, suggesting hybrid vigor. Results indicated that in the Mexican bean beetle reproductive diapause is genetically inherited, has some degree of dominance, and that population differences due to temperature and photoperiod are probably adaptations to the specific population environments.

KEY WORDS *Epilachna varivestis,* genetics, adaptation, dormancy, Mexican bean beetle, photoperiod, diapause.

Auclair (1959) suggested that the Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, undergoes an adult reproductive diapause. Laboratory studies have since documented diapause in adult MBB and the interactions of temperature, photoperiod, precipitation, and host (Mellors *et al.* 1984 and references therein). Taylor and Schrader (1984), working with a MBB population from New Mexico, showed that the degree of diapause varies as a function of day length and suggested that differences in sexual maturation due to graded responses to photoperiod may be of ecological and evolutionary importance. All reported cases of seasonal adaptation by colonizing insect species have involved modification of diapause that already existed in the original population (Tauber *et al.* 1986). Introduced and native insect species that have expanded their geographic ranges should offer new and interesting information on the evolution of seasonal adaptations.

Although the biology of the MBB in the U.S. has been extensively researched, little is known about its biology in its supposed area of origin, the high plateau region of Central America (Landis and Plummer 1935). This area is characterized by daily rains and moderate temperatures during the growing season. This is presumably the climate to which this insect adapted in its evolutionary past. As the MBB spread throughout the U.S., field observations confirmed the negative

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effects of high temperatures and low humidities on its development and survival (Sweetman 1929). The effects of temperature, relative humidity, and host plant on development, survival, and fecundity of the MBB in the southeastern U.S. have been well documented (Mellors and Bassow 1983; Wilson *et al.*, 1982; Lockwood *et al.* 1979; Kitayama *et al.* 1979; and Bernhardt and Shepard 1978, 1979).

The objective of this study was to compare the influences of photoperiod and temperature on the reproductive diapause of two different geographic populations of the MBB and their cross progeny to detect a possible genetic basis for population differences.

Materials and Methods

Insect Colonies. The Maryland (MD) population of MBB used in this study was established from adult beetles collected in the field from snap beans, *Phaseolus vulgaris* L., on Maryland's Eastern Shore. The El Salvador (ES) population was established from adult beetles obtained from a laboratory colony at the Ornamentals Laboratory, USDA, ARS, Beltsville, MD. These adults were from a parent colony collected in San Vincente, El Salvador. This population was also collected from *Phaseolus* spps. Third generation laboratory reared adults were used in all tests. Insects of both populations were reared on 'Henderson' bush lima beans, *Phaseolus lunatus* L., under controlled conditions in a walk-in rearing room maintained at 24°C, 50-90% RH, and a photoperiod of 15:9 (L:D) (Stevens *et al.* 1975).

For each test, bean leaves containing egg masses were collected from the rearing cages of each population, placed in 100 mm diameter glass Petri dishes containing a cotton wick moistened with distilled water and incubated at 27°C, 70% RH, and a photoperiod of 15:9 (L:D). Neonate larvae, still in clusters on the bean leaves, were transferred to new plants immediately after hatching and placed in a controlled environment based on the nature of that particular test.

Henderson bean plants, 2-3 wk old, were used as host material in all tests. Paired adults were confined in wooden oviposition cages (26 × 26 × 29 cm high) with Saran screen (32 × 32 mesh) on top and all sides. Two plants in each oviposition cage were changed two or three times weekly (Mondays, Wednesdays, or Fridays) depending on the amount of foliar feeding in a particular test. At each change of plants, the number of egg masses and eggs per egg mass were recorded, sex of dead adults was determined, and foliar feeding noted.

Controlled Environments. Three environmental chambers were required to obtain the desired temperatures and photoperiods used in this study. Long-day or diapause averting conditions were represented by a photoperiod of 15:9 (L:D) (Stevens *et al.* 1975). Short-day or diapause inducing conditions were represented by a photoperiod of 10:14 (L:D) (Taylor 1984). Two constant (16 and 24°C) and one alternating (24:16°C) temperature regimes were used with a combination of photoperiods. The cryophase (low thermoperiod) in the alternating temperature regime coincided with the scotophase (dark photoperiod). Temperatures were maintained within ± 2°C and relative humidities fluctuated between 50 - 90%. All experiments were continuously monitored with Belfort (Model 5-594) hygrothermographs.

The three environmental chambers used in this study consisted of two walk-in and one reach-in chambers. Chamber A was the same room in which stock colonies of both populations were reared and maintained. Temperature was maintained at a constant 24°C and photoperiods of 15:9 and 10:14 (L:D) were provided through the use of black cloth and time clocks. Fluorescent lighting provided an illuminance of *ca.* 7.5 klx during the photophase (light photoperiod). Chamber B, the other walk-in box, was maintained at a constant 16 or 24°C or an alternating temperature of 24:16°C depending upon the test in progress. Photoperiods of 15:9 and 10:14 (L:D) were also available through the use of black cloth and time clocks. Fluorescent lighting provided an illuminance of *ca.* 4.2 klx. Chamber C, the reach-in box, was maintained at an alternating temperature of 24:16°C with a photophase of 10 h during the thermophase (high thermoperiod). A combination of fluorescent and incandescent lighting gave an illuminance of *ca.* 11.8 klx.

Test 1. This experiment was conducted to determine the effects of photoperiod on adult reproductive diapause of the two MBB populations and their reciprocal crosses. Two groups each of neonate larvae from laboratory reared MD and ES eggs were reared in Chamber B at a temperature of 24°C and photoperiods of 15:9 and 10:14 (L:D). After approximately 25 days, newly emerged adults were sexed and isolated according to population and photoperiod. At 2 days of age, five adults of each sex from the same and alternate populations that had been reared under identical photoperiods were paired and maintained under the same conditions as those used for their larval development. Four oviposition cages (replications) containing 5 males and 5 females were set up for each of the eight treatments made up of 2 photoperiods and 4 population cross combinations. Nineteen data sets (two observations per week) were recorded from ages 8 to 51 days by which time all adults of the MD purebred cross in the long-day 15:9 (L:D) photophase had died.

Test 2. This experiment was designed to determine the effects of photoperiod and temperature on adult reproductive diapause of the two MBB populations. Two groups each of neonate larvae from laboratory reared MD and ES eggs were reared in Chamber B at the alternating temperature regime of 24:16°C and photoperiods of 15:9 and 10:14 (L:D). Larval development of both MBB populations took 4-6 days longer at the short-day photoperiod. After approximately 40 days, newly emerged adults were sexed and isolated according to population and photoperiod. At 2 days of age, 5 males were paired in oviposition cages with 5 females from the same population and photoperiod. Two cages of each population were maintained in Chamber B at the alternating temperature of 24:16°C and photoperiods of 15:9 and 10:14 (L:D); similar conditions used for larval development. Two cages of each population were also maintained in Chamber A at a constant temperature of 24°C and photoperiods of 15:9 and 10:14 (L:D) for a total of eight treatments made up of 2 populations, 2 temperatures, and 2 photoperiods. Nine data sets (two observations per week) were recorded for each treatment from ages 10 to 38 days.

Test 3. The purpose of this test was similar to test two. Additional treatments were included to determine the effects of reversing photoperiods for the larval and adult stages of development. Two groups each of neonate larvae from MD and ES eggs were reared in Chamber B at the alternating temperature regime of 24:16°C and photoperiods of 15:9 and 10:14 (L:D). Two additional larval groups from each population were reared in Chamber A at a constant temperature of 24°C and photoperiods of 15:9 and 10:14 (L:D). Larval developmental times were consistent with those of the previous tests. Larvae of both populations reared at 24°C, regardless of photoperiod, reached the adult stage in approximately 25 days. Larvae of both strains reared at 24:16°C took approximately 40 days to reach the adult stage at a photoperiod of 15:9 (L:D) and an additional 7 days at a photoperiod of 10:14 (L:D). Because of these differences in developmental times of first instars to the adult stage, the various treatments used in this experiment were set up on three dates at 7 day intervals. Within 2 days after emergence, adults were sexed and paired in oviposition cages. Five adults of each sex from the same population were used in each cage. Four oviposition cages (replications) from each of the eight larval treatments were maintained under the same enviromental conditions as those under which their respective larval populations were reared. An additional four oviposition cages from each of these same eight larval treatments were maintained under similar temperatures and opposite photoperiods as those used for larval development, thus doubling the number of treatments in this test to sixteen. A total of 64 cages representing 4 replications each of 2 populations, 2 temperatures, and 4 photoperiods were used in this test. Sixty-nine data sets (two observations per week) were recorded for each treatment from ages 7 to 245 days.

Test 4. This experiment was conducted to determine the effects of a short photophase and low temperature (cryophase) on adult reproductive diapause of cross progeny from the two MBB populations. One group each of neonate larvae from laboratory reared MD and ES eggs was reared in Chamber A under non-diapausing conditions of 24°C and a 15:9 (L:D) photoperiod. After approximately 25 days, newly emerged adults were sexed and isolated according to sex and population. At 6-10 days of age, forty females from each population were paired with forty males from each population in rearing cages under similar non-diapausing conditions as those used for larval development. One rearing cage containing forty females and forty males was set up for each of the four cross combinations. After 2 weeks, egg masses from individual cages were collected and incubated on three dates at 2 day intervals. One group each of neonate larvae, progeny from the above cross combinations, was reared in Chamber C at the alternating temperature regime of 24:16°C and a short-day photoperiod of 10:14 (L:D). Larval developmental times under these environmental conditions were similar to those found in tests 2 and 3, approximately 40-50 days. Within 3 days after emergence, adults from each cross combination were sexed and isolated. At 4-10 days of age, forty adults of each sex from the same cross were paired and maintained in rearing cages under the same diapause inducing conditions as those used for their larval development. A total of 8 cages representing 2 replications each of 4 cross combinations were used in this test. Thirty-eight data sets (two or three observations per week) were recorded for each treatment from ages 20 to 147 days.

Analyses. Because of differences in developmental times from egg hatch to adult emergence due to treatments applied to the larval stage, not all treatments in all adult oviposition tests began on the same date. Also, in some instances adults from one or more treatments within a specific test, which were set up on the same date, may differ in age from 1-4 days. To account for these differnces in age, treatments within each test were compared over the age of adults in each treatment, not the date data were recorded. Data recorded for each observation included the number of egg masses, total eggs, and the number of living males and females. Means for total eggs and eggs per female were based on the number of living females when data were recorded. No attempt was made to determine the percentage of ovipositing females. All tests were analyzed by analysis of variance in the GLM procedure of SAS (SAS Institute 1982). Means separations were performed using the least significant difference (LSD) test or the Duncan's multiple range test ($P < 0.05$).

Results

The approximate numbers of adults recovered from neonate larvae reared at 24°C and a 15 h photophase or 24:16°C and a 10 h photophase were similar for both MBB populations in all tests. These environmental parameters repesented both extreme diapause inducing and diapause averting conditions. At 24°C and a 10 h photophase or 24:16°C and a 15 h photophase significantly more ES larvae survived to the adult stage than did MD larvae. A shorter photophase or lower temperature, alone, had a greater negative effect on larval survival of the MD strain.

Test 1. The effects of photoperiod on total eggs, eggs per female, eggs per egg mass, and adult survival are listed for all crosses (Table 1). Data for this and all other tests are presented as means over time which corresponds with adult age. All main effects except eggs per egg mass were significantly different. Total eggs were significantly greater in all crosses at the 15 h photophase. Within photoperiods the only significant difference in total eggs was a higher level in the ES × MD cross than in the MD × MD cross at the 15 h photophase. Eggs per female were significantly greater in the 15 h photophase than in the 10 h photophase for all crosses except the MD × MD cross which was greater but not significant. Within the 15:9 (L:D) photoperiod the crosses ES × ES and ES × MD had significantly greater eggs per female than the MD × MD cross. Within the 10:14 (L:D) photoperiod the MD × ES cross had significantly fewer eggs per female than the other crosses. The only significant difference in eggs per egg mass for crosses between or within photoperiods was a significantly higher rate in the MD × MD cross at the shorter 10 h photophase. Adult survival was significantly higher at the 10:14 (L:D) photoperiod for all crosses except the ES × ES cross which was similar at both photoperiods. Within photoperiods, adult survival of the MD × MD cross was significantly less than all other crosses in the 15 h photophase.

Test 2. Table 2 lists the effects of photoperiod and temperatue on total eggs, eggs per female, and eggs per egg mass of the two MBB populations. Total eggs and eggs per female of MD adults at 24°C constant and a 15 h photophase were significantly greater than all other treatments in either population. Differences between populations for the other treatments were not significantly different although egg production for the MD population was considerably greater than the ES population at 24°C constant and a photoperiod of 10:14 (L:D). No eggs were laid for either population at 24:16°C and a photoperiod of 10:14 (L:D) within the time frame this test was conducted (38 days). A reduction in temperature for both the MD and ES populations at both photoperiods caused a significant reduction in the total eggs and eggs per female. Within both populations, total eggs and eggs per female at 24°C and a 15 h photophase were significantly greater than the other treatments. MD adults laid significantly more eggs per egg mass than ES adults under both temperatures in the 15:9 (L:D) photoperiod. Within populations a significantly higher number of eggs per egg mass was recorded for MD females at

Table 1. Effects of photoperiod on the reproductive diapause of two populations of adult MBB and their reciprocal crosses reared on *Phaseolus* foliage at 24°C and photoperiods of 15:9 and 10:14 (L:D).

Photoperiod† and Cross	Means*			
	Total Eggs	Eggs/♀	Eggs/ Egg Mass	Adult‡ Survival %
15:9				
ES × ES	597.2 ab	42.6 ab	47.4 b	99.5 a
ES × MD	670.4 a	47.4 a	49.7 ab	79.9 b
MD × MD	489.7 b	31.3 cd	49.0 b	66.1 c
MD × ES	538.0 ab	37.4 bc	49.9 ab	84.1 b
10:14				
ES × ES	346.1 c	27.6 d	47.1 b	97.1 a
ES × MD	332.1 c	24.2 d	47.6 b	97.9 a
MD × MD	312.2 c	24.5 d	52.4 a	93.3 a
MD × ES	193.2 c	15.7 e	49.0 b	93.6 a

Means within a column followed by the same letter are not significantly different (P > 0.05; Duncan's multiple range test [SAS Institute 1982]).

* Means over time (nineteen data sets). Four replications, 5 males and 5 females each. Treatments terminated when adults were 51 days of age.

† Population: ES, El Salvador; MD, Maryland. First population in each cross is maternal parent.

‡ Adult survival during course of experiment.

Table 2. Effects of photoperiod and temperature on the reproductive diapause of two populations of MBB reared on *Phaseolus* foliage at 24:16°C and photoperiods of 15:9 and 10:14 (L:D).

Population† and Treatment		Means*		
		Total Eggs	Eggs/♀	Eggs/ Egg Mass
Photoperiod	**Temp**			
ES				
15:9	24	343.4 b	17.2 b	41.5 c
15:9	24:16	126.4 c	6.3 c	41.5 c
10:14	24	120.7 c	6.0 c	44.3 bc
10:14	24:16	0.0 d	0.0 d	0.0 d
MD				
15:9	24	480.2 a	24.0 a	47.6 b
15:9	24:16	108.7 cd	5.4 cd	51.7 a
10:14	24	224.8 c	11.2 c	45.4 bc
10:14	24:16	0.0 d	0.0 d	0.0 d

Means within a column followed by the same letter are not significantly different (P > 0.05; Duncan's multiple range test [SAS Institute 1982]).

* Means over time (nine data sets). Four replications, 5 males and 5 females each. Treatments terminated when adults were 38 days of age.

† Population: ES, El Salvador, MD, Maryland. Adults were reared and tested at a constant temperature of 24°C in addition to the alternating temperature regime of 24:16°C used in the larval stage.

24:16°C and a photoperiod of 15:9 (L:D). Little or no differences were observed in adult survival for population or treatment effects.

Test 3. Significant variation was observed among populations, temperatures, and photoperiods for total eggs, eggs per female, eggs per egg mass, and adult survival (Table 3). Total eggs and eggs per female were significantly greater in ES females, and at a constant temperature of 24°C. All four photoperiods were also significantly different from one another for these same variables. Female adults reared under the long-day photoperiod had greater egg production than those reared under the short-day photoperiod. Short-day conditions during larval development also caused a significant decline in egg production from larvae reared under long-day conditions. Significantly greater numbers of eggs per egg mass were observed for MD females, 24°C, and the short-day larval short-day adult photoperiod. Adult survival was significantly greater in ES population adults, the alternating temperature regime of 24:16°C, and the short-day photoperiod used for adult rearing.

Table 3. Effects of photoperiod and temperature on the reproductive diapause of two populations of MBB reared on *Phaseolus* foliage at 24 and 24:16°C and photoperiods of 15:9 and 10:14 (L:D).

	Means*			
Main Effects†	Total Eggs	Eggs/♀	Eggs/ Egg Mass	Adult‡ Survival %
Population				
ES	868.0 a	13.62 a	46.5 b	41.6 a
MD	353.3 b	8.31 b	49.2 a	33.9 b
Temperature				
24°C	801.4 a	24.27 a	47.8 a	22.7 b
24:16°C	419.9 b	5.39 b	46.7 b	52.9 a
Photoperiod				
15:9 - 15:9	540.7 a	22.69 a	46.9 b	31.3 b
10:14 - 15:9	359.2 b	16.75 b	47.1 b	31.2 b
15:9 - 10:14	221.6 c	8.04 c	46.4 b	42.9 a
10:14 - 10:14	99.8 d	3.53 d	49.7 a	45.6 a

Means within a column followed by the same letter are not significantly different (P > 0.05; Duncan's multiple range test [SAS Institute 1982]).

* Means over time (sixty-nine data sets). Four replications, 5 males and 5 females each. Treatments terminated when all females died or adults were 245 days of age.

† Populations: ES, El Salvador; MD, Maryland. Photoperiod in first column is that under which larvae were reared, second column represents photoperiod under which adults were reared and tested.

‡ Adult survival during course of experiment.

Treatment differences between populations for total eggs and eggs per female are presented in Fig. 1. Egg production of the ES population was at least approximately twice that of the MD population in all treatments and significantly different except in the two treatments having short-day photoperiods during both larval and adult development (SSH & SSL) and the long-day larval short-day adult, 24:16°C treatments (LSL). Eggs per female were significantly higher for ES females in the long-day larval and adult photoperiod at 24°C (LLH) and all four treatments containing the alternating temperature regime of 24:16°C (LLL, SLL, SSL, & LSL). Treatment effects within populations were quite variable for all parameters. Any changes or combinations of changes in photoperiod or temperature from the diapausing averting conditions of the long-day larval and adult rearing photoperiods at 24°C (LLH) caused a significant reduction in total eggs and eggs per female for both MBB populations. Within the ES population all treatments were significantly different from one another for eggs per female except in two cases. Non-significant differences were demonstrated between the two treatments with long-day adult photoperiods at 24:16°C (LLL & SLL) and between the two treatments with short-day adult photoperiods at 24:16°C (SSL & LSL). The only non-significant treatment differences for eggs per female in MD adults were between the short-day larval long-day adult photoperiod at 24:16°C (SLL), and the short-day larval short-day adult photoperiod at 24°C (SSH) and between the two treatments with short-day larval and adult photoperiods at 24:16°C (SSL & LSL). Short-day conditions during adult development at the alternating temperature regime of 24:16°C caused the greatest reduction in eggs per female for both MBB populations.

Test 4. The effects of rearing progeny from parental and reciprocal crosses of the two MBB populations under diapause inducing conditions on total eggs, eggs per female, eggs per egg mass, and adult survival are presented in Table 4. Egg production was greater in females from reciprocal cross progenies than in females from purebred cross progenies and significantly lower in females from the MD × MD cross. Eggs per female were also significantly greater in females from reciprocal cross progenies than in females from purebred cross progenies, with the highest rate demonstrated in females from the ES × MD cross. Female progeny from the ES × ES cross had a significantly greater number of eggs per egg mass than progeny from the MD × ES or MD × MD crosses. Adult survival was significantly different for progeny of all cross combination, with the progeny of the ES × ES cross the highest and progeny of the MD × MD cross the lowest.

Discussion

Diapause is a physiological state that has genetic and environmental components. In most insects it is the primary process that synchronizes the annual rhythm of an insect's life cycle with appropriate seasonal conditions (Tauber and Tauber 1979). It serves as an important adaptive mechanism for dormancy during periods of unfavorable environmental conditions such as low winter temperatures, extreme summer heat, periods of drought, and seasons in which appropriate food is not available (Beck 1980). While an insect's set of diapause responses is genetically based, environmental conditions cue the expression of diapause (Tauber *et al.* 1986).

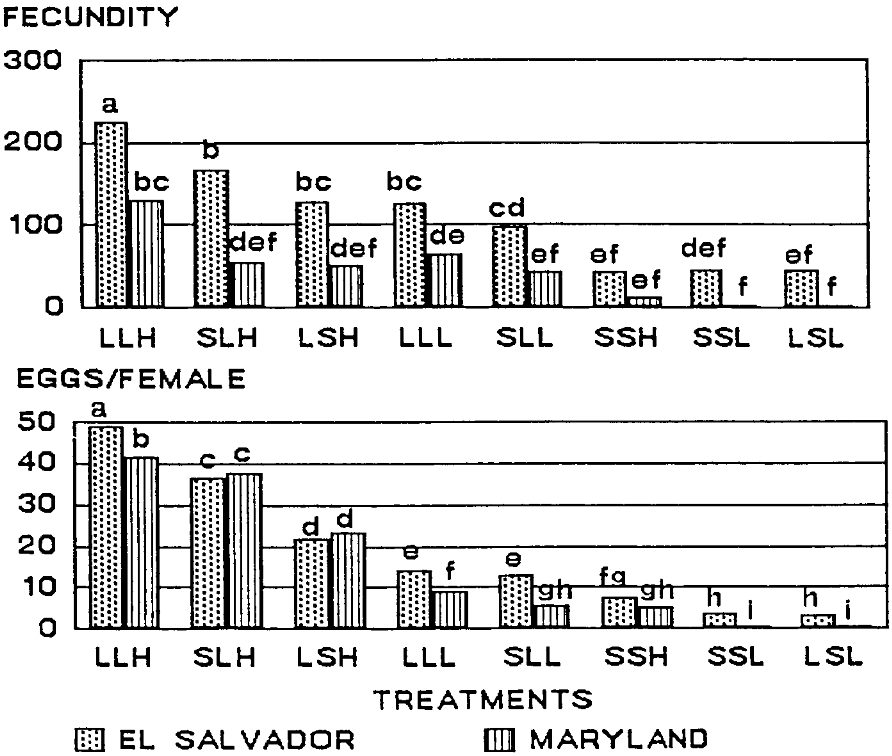

Fig. 1. Mean total eggs and eggs per female for two populations of MBB reared under eight different temperature-photoperiod combinations from 7 to 245 days of age. First letter in treatment indicates long-day (L) or short-day (S) larval photoperiod; middle letter indicates long-day (L) or short-day (S) adult photoperiod; and last letter indicates high (H) or low (L) temperature regime. Different letters (a, b, c, etc.) between columns indicate statistically significant differences ($P < 0.05$; DMRT) between populations and treatments.

Taylor (1984) showed that MBB males in diapause can contain mature sperm and will mate with both diapause and non-diapause females, whereas diapause females do not contain mature eggs but will mate. Diapause inducing and averting conditions in Taylor's (1984) study consisted of 12.5:11.5 and 15.5:8.5 (L:D), respectively. In our study we also fixed temperature and photoperiodic conditions to obtain the desired results. However, in nature, both temperature and day length are constantly changing over time and can lead to the development of various levels of diapause. Identifying an insect as being in diapause can be difficult since the only standard we have is to compare its physiological state with that of an arbitrary norm assumed to represent the non-diapause condition. Both sexes of diapausing MBB were shown to have greater dry weights, enlarged fat bodies, reduced inactive gonads, reduced respiration rates and lower water contents than

Table 4. Fecundity of progeny from two populations of MBB and their reciprocal crosses reared on *Phaseolus* foliage at 24:16°C and a 10:14 (L:D) photoperiod.

	Means*			
Cross†	Total Eggs	Eggs/♀	Eggs/ Egg Mass	Adult‡ Survival %
ES × ES	217.3 a	6.6 b	49.9 a	87.7 a
ES × MD	297.3 a	11.0 a	48.6 ab	83.1 b
MD × ES	273.3 a	9.5 a	47.1 b	76.7 c
MD × MD	108.9 b	6.2 b	46.6 b	60.7 d

Means within a column followed by the same letter are not significantly different ($P > 0.05$; Duncan's multiple range test [SAS Institute 1982]).

* Means over time (thirty-eight data sets). Two replications, 40 males and 40 females each. Treatments terminated when adults were 147 days of age.

† Population: ES, El Salvador; MD, Maryland. First population in each cross is maternal parent.

‡ Adult survival during course of experiment.

reproductively active beetles (Pfaender *et al.* 1981). While the present study concentrated on the effects of temperature and photoperiod, other factors are known to influence reproductive characteristics such as the host plant and the phenological stage of that host, moisture, light intensity, and population density.

Under the non-diapause conditions in test one, total eggs and eggs per female were much higher in the ES population. Reciprocal cross progeny were more fertile than purebred progeny with the same maternal parents. Under short-day conditions these differences no longer existed. In test two, larvae were reared at the lower temperature and under both long-day and short-day photoperiods. This was one of the few tests in which the MD population was more fertile than the ES population. This was also the shortest test in duration and may not have allowed the ES population to express its reproductive potential. Larvae and adults were reared under all combinations of temperature and photoperiod in test three. In practically all cases, those treatments containing the ES population had a higher rate of egg production than those with the MD population. The greatest differences in eggs per female between populations were demonstrated in those treatments with low temperatures, suggesting as in test two that temperature has a greater negative effect on fecundity in the MD population. Conversely, the greatest reductions in eggs per female for the ES population were the result of short-day photoperiods during adult development. In test four, the larval and adult stages of progeny from purebred and reciprocal crosses of the two MBB populations were reared under diapause inducing conditions of low temperature and short-day photoperiod. Fecundity and adult survival for all crosses containing the ES population as either the maternal or fraternal parent were significantly greater than those of the MD × MD purebred cross. Eggs per female were significantly greater in adults from the reciprocal cross progeny than from the purebred cross progeny. These data suggest that hybrid vigor is being expressed in the reciprocal cross progeny and that these diapause conditioning responses are genetically controlled.

In test one, we combined parents of the two populations. Under diapause averting conditions, fecundity was greater in those crosses with mixed parents.

When we submitted progeny from such crosses as we did in test four to diapause inducing conditions, we were able to measure phenotypic responses being transferred from parent to progeny in such a manner as to suggest the presence of one or more dominant genes controlling these responses. Our results differed from those of Danilevskii (1965) who demonstrated that the photoperiodic response of hybrids of selected lepidopterous species obtained by crossing geographic strains of the same species or of different species was intermediate between the response of the parents.

From the different tests in this study, it is obvious that both temperature and photoperiod regulate diapause in both the MD and ES populations of MBB used in this study. The fertility level of the ES population exceeded that of the MD population in three out of four tests under both diapause and non-diapause conditions. Although there were no significant treatment x population interactions in any of the tests, the ES population was influenced more by photoperiod while the MD population was influenced more by temperature. How do we explain these differences in reproductive potential and diapause characteristics? One way is to conduct studies which show that diapause is genetically determined and environmentally controlled as we have attempted to do.

In the central plateau region of Mexico where it is said to originate, the MBB has apparently adapted to the extremes of precipitation and temperature found in this area. Here it will remain quiescent through the dry, hot spring and emerge with summer rains. In Maryland, the MBB remains quiescent through a normally moist, warm spring and emerges with warmer summer rains. This relatively late emergence for both geographic locations is apparently an adaptive behavior to ensure an abundant supply of host plants when overwintered adults emerge from diapause. It is probable that, due to domestication of host-plants in the U. S., the MBB has evolved a seasonal cycle that coincides with that of its host.

The MBB has become an important defoliator of soybeans, *Glycine max* (L.) Merrill, in the Middle Atlantic region (Mellors and Bassow 1983). Formerly, it was only a pest of *Phaseolus,* which includes snap and lima beans. Landis and Plummer (1935) reported that the MBB is a widely distributed and destructive pest of beans (*Phaseolus*) in Mexico. In El Salvador, the MBB was observed to be a minor pest of beans and required no insecticidal treatments (Smiley 1974). If the MBB can be an economic pest of *Phaseolus* in the U. S. and Mexico, why, then, is it not a serious pest in El Salvador? Perhaps, there is an inadequate supply of suitable host plants or there is an ecological balance of parasites, predators, or entomophageous microorganisms which prevent economically damaging pest populations from developing. In the tropics, physical conditions may be suitable for growth and reproduction year round of both the MBB and its natural enemies which could lead to a constant, stable ecosystem. On the other hand, the MD population of MBB is subjected to extremes in temperature and photoperiod not experienced by the ES population. The MD population in order to survive has had to adapt to these extremes. Diapause is a factor which helps control population dynamics. A halt in reproductive activity and a gradual decline in metabolism in the fall ensures reproduction and survival of the individuals the following year.

Klassen *et al.* (1970) discussed the theoretical potential of introducing seasonal asynchrony into pest populations as a pest management tool. They presented calculations showing the possibility of suppressing insect populations by overflooding a native population with individuals bearing dominant conditional, lethal traits.

Inability to diapause would be considered such a trait. To be useful, such traits must be inherited and must have a degree of dominance so they may be expressed in hybrid individuals. Does such a trait exist? Our research shows that in the MBB, reproductive diapause is genetically inherited, has some degree of dominance, and at the same time is highly adaptive. In our situation, the introduced physiological deviate (the ES population) does not lack the ability to survive unfavorable environmental conditions but instead is as well adaptive as the local MD population. A comparison of the two MBB populations and their progeny under an artificial environment shows that genetic and physiological variability have allowed for adaption and range expansion.

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