Effects of Temperature, Humidity, and Soybean Maturity on Longevity and Fecundity of the Adult Mexican Bean Beetle, *Epilachna varivestis*[1,2,3]

K. KITAYAMA, R. E. STINNER, AND R. L. RABB

Department of Entomology, North Carolina State University, Raleigh 27650

ABSTRACT

Environ. Entomol. 8: 458–464 (1979)

The effects of temperature, humidity, and plant stage independently, as well as their interactions, on longevity and fecundity of adult Mexican bean beetles were studied.

Longevity was not affected by plant stage, but was affected by temperature and humidity, independently, as well as by their interaction. Longevity increased with increasing humidity and decreasing temperature.

Fecundity, as measured by 4 parameters (total egg masses, total eggs, egg masses per female per day, eggs per female per day), was affected by temperature, humidity and plant stage. Eggs per mass was affected by plant stage and humidity, but not by temperature (independently).

In general, fecundity was highest for beetles reared under intermediate temperatures, high humidity and feeding on mature soybean plants. No eggs were laid at 32°C, regardless of soybean plant stage and humidity.

In less than a century the Mexican bean beetle, *Epilachna varivestis* Mulsant (MBB), has spread from the southwestern U.S. to the southeast and thence to the entire east coast as far as Canada (Auclair 1959). Although this insect has not been considered a major pest of soybean *Glycine max* (Thomas), it causes sporadic defoliation in this crop and is now considered secondary only to *Heliothis zea* (Boddie) as an insect pest of soybean in North Carolina (Deitz et al. 1976).

Much information on the distribution of this and closely related species is available (Auclair 1959), as are data on the effects of various physical factors such as temperature, moisture and sunlight (Douglass 1928, Graf 1925, Howard 1921, 1931, Kogan 1971, 1972a, 1972b, Miller 1930, Pallister 1949, Sweetman 1932, Thomas 1924). Most of this information, however, deals with MBB on various *Phaseolus* spp., and does not provide an adequate basis for comparing beetle performance on various host species and phenological stages, which may produce nutritional effects.

The objectives of this study were to determine and quantify the relationships, if any, of soybean maturity to fecundity and longevity of adult MBB, and to examine these relationships. The quantification of these relationships is a necessary prerequisite to the development of a simulation model for the MBB.

The literature contains conflicting information with regard to the sensitivity of the MBB to temperature and humidity. Graf (1925) stated: "Since the Mexican bean beetle has shown an ability to be a serious and consistent pest in areas which show a wide variation in temperature and rainfall, this insect does not belong to the group which is readily influenced by different climatic conditions." The bulk of scientific evidence, however, supports the opposite view.

Howard and English (1924) reported that survival of MBB eggs was less than 0.2% when exposed continuously to temperatures reaching 26.7°–38.9°C for 3–5 days. Similar results for larvae and pupae have been reported by Howard (1921), Thomas (1924), and Marcovitch and Stanley (1930).

Marcovitch (1926), however, considered drought more limiting to the MBB than cold. Eddy and McAlister (1927) reported that the combination of high temperature and low humidity killed all stages. Their findings were substantiated by Sweetman (1929), who studied MBB in both irrigated and non-irrigated regions. He concluded: "The fact that drought periods in the east are nearly as disastrous to the bean beetle as normal precipitation in the dry-farm areas in the west is suggestive of a high moisture requirement on the part of the insect. This is apparently true of all stages of the insect and during the entire year."

Howard (1931) reported that MBB are very susceptible to climatic conditions and infestations may decrease due to dry, hot summer weather. Sweetman (1932) and Pyenson and Sweetman (1932) drew similar conclusions in separate studies.

Kogan (1972b) stated that the MBB has had only a short association with soybean and its relationships with this host are still rapidly evolving. Many reports exist which demonstrate that soybean is, as yet, a poor host for this species when compared to *Phaseolus* spp. (e.g., Friend and Turner 1931, White 1940).

Insects feeding on different phenological stages of a single host plant species also exhibit different survival and reproductive characteristics. In an initial study of MBB, Lockwood et al. (1979) demonstrated a dramatic increase in fecundity of beetles fed lima beans over those fed on post-blooming soybeans. In addition, there was a significant increase for adults fed on post-bloom as compared to pre-bloom soybean. Their study, however, did not consider in detail the whole spectrum of plant maturity and its possible interactions with temperature and humidity.

Methods and Materials

Three experiments were conducted. The production

[1] Coleoptera: Coccinellidae.

[2] This study supported in part by funds provided by EMBRAPA and by NSF/EPA IPM project.

[3] Paper No. 5641 of the Journal Series of the North Carolina Agricultural Experiment Station, Raleigh, NC 27650. Received for publication Oct. 11, 1978.

0046-225X/79/0304-5807$00.75/0

of plant material was the same for all three. Bragg variety soybeans were planted, 10 seeds/25-cm pot, in a sandy loam: peat moss mixture (2:1) in the greenhouse. Plants were thinned to 2–3/pot, 3 wk after germination. Twenty pots were planted weekly, with a 14L:10D photoperiod (ten 500-W quartz lamps) and temperature range of 20°–40°C. Control of photoperiod was necessary because the rate of maturation and flowering of soybeans is influenced by daylength, and experimental plans entailed the simultaneous use of specific vegetative and flowering stages. The greenhouse was fumigated weekly with sulfa-TEPP to prevent build-ups of mites, aphids, and whiteflies.

Experiment 1 was to determine how soybean maturity affects the longevity and fecundity of adult MBB under greenhouse conditions. From plantings on May 31 through Sept. 9 (1976), 8 maturity stages were chosen as follows: vegetative stages V2, V4, V5, and reproductive stages R5-9 (after the classification of Hanway and Thompson 1971).

Each pot with the chosen soybean stage was placed in a screen cage 120×45×45 cm. Each treatment (maturity stage) was replicated 5 times. The cages were placed in a randomized block design in a greenhouse where the temperature was kept between 20° and 40°C, and plants watered daily.

Three pairs of beetles were released in each cage, for a total of 120 pairs. In order to have beetles of known age, pupae were collected from soybeans in Pasquotank Co., brought to the laboratory, and allowed to emerge at room temperature. One-day-old beetles were used. The experiment started Sept. 15 and ended Nov. 11, 1976.

Cages were checked every other day, and dead or missing males were replaced. Dead or missing females were not replaced. Eggs were collected and counted every other day. Egg viability was not determined. In order to avoid complete defoliation which could affect the fecundity, as well as the longevity of the beetles, plants were replaced when ca. 80% of the leaves had been fed upon.

Experiment 2 was designed to determine what effect, if any, leaf age (as indicated by position on plant) would have on adult longevity and fecundity. Leaf age varies from bottom to top and center to periphery of plants and age distribution changes as the plant matures. Since experimentation was planned (Experiment 3) to use excised trifoliates, this experiment was considered necessary in order to have a basis for avoiding sampling bias in selecting trifoliates for feeding the adults.

The experiment was conducted at 27°C and photoperiod of 14L:10D. Four soybean stages were used; R6, R7, R8, and R9. Leaf age was defined by its spatial position on the main stem of the plant. Three ages were used: lower leaves (senescing), middle leaves (mature), and upper leaves, as well as new secondary trifoliates which emerged from the leaf axils of older petioles (young). Each combination of leaf age and plant maturity was replicated 5 times. Each replicate consisted of 1 trifoliate and 2 pairs of beetles (1–2 days old) in a 14-cm petri dish lined with 15-cm filter paper dampened to keep moisture high.

[4] Aquapic® Inc., Kokomo, Ind.

Trifoliates were picked randomly from plants, and the same plants were used throughout the experiment such that beetles were allowed to feed on plants which changed maturity stages through time, similar to field conditions. In order to avoid possible effects of spatial position of the replicates, the petri dishes with beetles were stacked randomly. Leaves were changed every other day, and the filter paper every other week. Petri dishes were changed every 2 wk. Dead or missing males were replaced, but dead or missing females were not. Egg masses and number were collected and counted every other day.

The experiment was started Sept. 16. At termination (Oct. 21, 1976) 18 of 120 pairs of beetles were dead as follows: 8 pairs from lower leaves, 8 pairs from middle leaves, and 2 pairs from upper leaves.

Experiment 3 was designed to study the effects of plant stage, temperature and humidity, as well as their interactions, on adult longevity and fecundity. The experimental procedures were similar to those used in Experiment 2, in that trifoliates from plants of specified maturity were used in lieu of whole plants.

The experiment involved 4 temperatures (17°, 22°, 27°, and 32°C), 2 humidities, 5 plant stages (plus lima bean plants at the high humidity at 17° and 32°C, as a comparison against published work), and 15 trifoliates (1 pair of beetles/replicate). The cabinets measured 91×61×61 cm. Temperature was maintained ± 1°C using separate hot and cold air sources opened and closed by independent thermostatically controlled solenoids. The avg "low" and "high" RH conditions, respectively, for each temperature were as follows: 17°, 63 and 95%; 22°, 65 and 90%; 27°, 38 and 80%; 32°C, 33 and 70%.

Each cabinet contained boxes (27×46×53 cm) for humidity control. The boxes were constructed of 0.6-cm Plexiglas® with a removable front. Each box contained 3 removable screen shelves which held 15 cylindrical screen wire cages (10.5 cm high and 8.5 cm diam) with plastic petri dishes for each end. The bottom petri dish had a 1.5 cm diam hole which held a 10.3 cm long and 1.5 cm diam plastic water pik[4]. Relative humidities were obtained using a saturated aqueous solution of sodium hydroxide for the low humidity and water for the high humidity, placed in a plastic tray in the bottom of the humidity boxes.

The soybean plants used were Bragg variety and were planted and grown from late Dec. 1976 to mid-June 1977 in a greenhouse at a 16L:8D photoperiod. Five plant stages were chosen: V4, R5, R6, R8, and R9. One pair of newly emerged adults obtained from pupae collected on snap beans at the Central Crops Research Station, Clayton, N.C., was placed in each cage. Every other day, trifoliates were removed from the plants, the petioles placed under water, recut with a razor blade and inserted into water piks. This was necessary, as even momentary exposure of the cut petiole to air greatly reduced the vigor of the excised trifoliate. The water piks were then placed individually in the cylindrical screen cages. A total of 630 pairs of beetles was used. The beetles were checked every other day (½ of the experiment each day), and data recorded as described for Ex-

periment 2. All 15 replicates of a single plant stage were placed on a single shelf, the initial order determined by random number selection. In order to avoid possible humidity gradient effects, the shelves were rotated every other day.

Data Analyses

The following parameters were calculated for all experiments:

(1) Total female days were obtained by summing the length of life of each beetle expressed in days. This included the available data for lost and missing beetles. (This parameter was necessary to calculate egg masses per female per day and eggs per female per day.)

(2) Mean longevity was determined by first adding ½ day to the number of days each beetle was last observed to be alive. The individual longevities were then summed and the total divided by the number of beetles at the beginning of the experiment. Data from beetles which eventually escaped were not included.

(3) Total egg masses per treatment were determined by summing all egg masses laid in each replicate. (This parameter was used to determine number of egg masses per female per day.)

(4) Total eggs per treatment were obtained by summing all eggs laid in each replicate. (This parameter was used to determine the number of eggs laid per female per day.)

(5) Eggs per egg mass were calculated by dividing total number of eggs by total number of egg masses.

(6) Egg masses per female were computed by dividing the egg masses on each day by the number of females alive on that day, and summing the results over the length of the experiment.

(7) Eggs per female were calculated by dividing the number of eggs on each day by the number of females alive on that day, and summing the result over the length of the experiment.

(8) Egg masses per female per day were calculated by dividing the total egg masses by total female days.

(9) Eggs per female per day were computed by dividing total eggs by total female days.

All parameters were subjected to analysis of variance, and Duncan's multiple range test was calculated to determine where differences existed.

Results

Experiment 1

Analyses of variance were calculated for each of the parameters mentioned in Methods, with none of them exhibiting significant differences due to plant stages in spite of rather large absolute differences between observed maxima and minima (Table 1). The lack of significance may be attributable to 2 sources:

(1) The experiment was started at the end of summer, when teneral adults in the field were entering diapause. "Biological memory" from larval stages could have resulted in "signals" conflicting with photoperiod, food, etc. experienced by the adults;

(2) Although photoperiod was controlled in one adjoining greenhouse, the intensity of light, which varied among blocks, may have been below some critical level for some blocks. The analyses of variance presented were based on only 3 of the 5 blocks, since 2 of these blocks had beetles which produced no eggs (blocks IV and V).

At this time the role of photoperiod and light intensity has not been investigated.

Experiment 2

Longevity.—Neither plant stage nor leaf age influenced the longevity of adult MBB during the 36 days of Experiment 2 (Table 2), but the interaction of these 2 variables had a significant effect. Beetles lived a significantly shorter time when fed on upper leaves than when fed on middle or lower leaves of plants at the R7 stage, and likewise for beetles fed on upper leaves of R7 compared to upper leaves of R8 and R9.

Fecundity.—Both total egg masses and total eggs were affected by plant stage, leaf age and their interaction. Eggs per female, eggs per female per day, egg masses per female, and egg masses per female per day were all affected by plant stage and leaf age, but not the interaction. Eggs per mass was affected by plant stage and its interaction with leaf age, but not by leaf age alone (Table 2). Although minor variations were apparent, all fecundity parameters with exception of eggs per mass tended to increase with increasing plant age and tended to be maximum for mature, but not senescent, leaves (middle leaves). Even though vegetative stages were not included, all fecundity parameters were affected by plant stage, with older plants more favorable for all of the factors studied.

With respect to leaf age, the middle leaves appeared to be most favorable, followed by lower and then upper leaves. This tendency was much less pronounced in the oldest (R9) plants. (It should be noted that the bottom leaves of the R9, R8, and R7 plants were similar since

Table 1.—Effects of soybean plant stage on MBB adult survival and fecundity under greenhouse conditions (Experiment 1; means of 3 replicates only, see text).

Initial plant stage	Longevity	Total egg masses	Total eggs	Egg masses/ female	Eggs/female	Egg masses/ female/day	Eggs/female/ day
V2	41.4	5.7	209.7	2.5	90.7	0.0253	1.7
V3	56.9	8.5	407.0	2.9	140.2	.0180	2.5
V4	52.4	4.3	150.7	2.0	65.1	.0170	1.1
R5	48.7	10.3	469.0	4.5	198.5	.0313	3.3
R6	50.8	12.0	501.0	4.3	181.8	.0287	3.3
R7	57.0	8.0	312.0	2.7	104.0	.0170	2.0
R8	36.8	8.3	415.7	4.2	215.5	.0333	3.3
R9	43.8	9.7	427.7	4.1	181.9	.0343	3.2

Table 2.—Effects of soybean plant stage and leaf age on MBB longevity and fecundity at 27°C (Experiment 2).

Initial plant stage	Leaf[a] position	Longevity[b]	Total[b] egg masses	Total[b] eggs	Egg[b] masses/ female	Eggs[b] female	Egg masses/ [b] female/day	Eggs/[b] female/day	Eggs/mass[b]
R6	L	35.2bc	5.4bcd	209bc	2.9bc	111bc	.08bc	3.0bc	37.1b
	M	30.2ab	5.0bc	232bc	3.1bc	142cd	.08c	3.8bc	46.1b
	U	32.5abc	1.7a	68a	0.7a	28a	.03a	1.1ab	48.6b
	Mean	32.6	4.0	170	2.2	94	.06	2.6	43.9
R7	L	30.7abc	4.8bc	212bc	3.3c	145cd	.10c	4.2c	43.1b
	M	34.6bc	8.2de	335cd	4.3cd	175cde	.12cd	4.8cd	40.1z
	U	27.9a	1.3a	29a	0.9a	21a	.02a	0.4a	25.1a
	Mean	31.1	4.8	192	2.8	114	.08	3.1	36.1
R8	L	36.0c	7.8cde	328cd	4.1cd	160cde	.11cd	4.6cd	43.4b
	M	30.9abc	6.4cde	309cd	4.5cd	208de	.11cd	5.2cd	46.9b
	U	34.5bc	2.6ab	93a	1.5ab	51ab	.04ab	1.3ab	38.6b
	Mean	33.8	5.6	243	3.4	140	.09	3.7	43.0
R9	L	33.1abc	6.5cde	294cd	4.0cd	183cde	.10c	4.5c	45.7b
	M	31.1abc	9.4e	430d	5.4d	236e	.15d	6.7d	45.0b
	U	36.0c	8.2de	368cd	4.1cd	190cde	.11cd	5.1cd	43.8b
	Mean	33.4	8.0	364	4.5	203	.12	5.4	44.8
Overall	L	33.7	6.1	261	3.6	150	.10	4.0	42.3
	M	31.7	7.3	327	4.3	190	.15	5.1	44.5
	U	32.7	3.5	140	1.8	73	.11	2.0	39.0
	Mean	32.7	5.6	242	3.2	137	.12	3.7	42.0

[a] L = lower, M = middle, U = upper.
[b] Values (not including means) in the same column followed by the same letter not significantly different.

once the leaves mature they remain fairly constant until senescence, when they rapidly abscise.)

With the exception of one treatment combination (R7, upper leaves) in which an avg of only 25.1 eggs/mass was observed, there were no noticeable effects of either plant stage or leaf age on eggs per mass. This one low value may, in part, be due to a bias induced by the relatively short longevity (random error?) of the beetles in that treatment (27.9 days).

Experiment 3

Since Experiment 2 demonstrated that leaf age, as well as plant stage affected the MBB, and since observation did not indicate an obvious preference for leaves of a given age, all leaves, irrespective of type, were used in Experiment 3.

Longevity.—Temperature and temperature × plant stage interactions affected longevity. The other independent variables had no significant effect (Table 3). Longevity ranged from 38.8 days at 17°C to 7.0 days at 32°C. At the extreme temperatures (17° and 32°C), plant stage did not strongly affect longevity, but at the intermediate temperatures, longevity generally increased for the intermediate plant stages (R5, R6, R8) when compared to the younger (V4) or older (R9) plants.

Fecundity.—As in Experiment 2, total egg masses, total eggs, egg masses per female per day, and eggs per female per day were all affected similarly (Tables 4, 5).

Table 3.—Effects of temperature, RH, and soybean plant stage and their interactions on MBB adult longevity (Experiment 3).

Temp (°C)	RH	Initial plant stage[a] V4	R5	R6	R8	R9	Mean
	Low	38.3abcd	29.4bcdefgh	34.1abcdef	43.5ab	45.9a	38.2
17	High	43.6ab	33.8abcdefg	47.1a	29.5abcdefgh	42.2ab	39.2
	Mean	41.0	31.6	40.6	36.5	44.1	38.8
	Low	4.5k	26.1cdefghi	24.1defghij	7.7jk	17.5ghij	16.0
22	High	35.9abcde	24.2cdefghij	40.5abc	20.3efghijk	16.8hijk	27.5
	Mean	20.2	25.2	32.3	14.0	17.2	21.8
	Low	12.9ijk	9.0jk	21.8efghijk	12.7ijk	10.4ijk	13.4
27	High	11.2ijk	19.9fghijk	10.6ijk	16.2hijk	13.4hijk	14.3
	Mean	12.1	14.5	16.2	14.5	11.9	13.8
	Low	6.8k	5.4k	6.9k	12.1ijk	6.4k	7.5
32	High	6.0k	6.0k	4.0k	6.9k	9.7jk	6.5
	Mean	6.4	5.7	5.5	9.5	8.1	7.0
Overall means	Low	15.6	17.5	21.7	19.0	20.1	18.8
	High	24.2	21.0	25.6	18.2	20.5	21.9
	Mean	19.9	19.3	23.7	18.6	20.3	20.4

[a] Values (excluding means) followed by the same letter are not significantly different (5% level, Duncan's multiple range test).

Table 4.—Effects of temperature, RH, and soybean plant stage and their interactions on total eggs laid by MBB females (Experiment 3).

Temp[b] (°C)	RH	Initial plant stage[a] V4	R5	R6	R8	R9	Mean
17	Low	0.0h	0.0h	6.7efgh	0.0h	10.3defgh	3.4
	High	50.1bcde	24.6cdefgh	48.5bcdef	6.7efgh	60.4bc	38.1
	Mean	25.1	12.3	27.6	3.4	35.4	20.8
22	Low	39.6bcdefgh	36.1bcdefgh	73.8b	13.6cdefgh	8.3efgh	34.3
	High	47.3bcdef	46.2bcdefg	187.2a	56.1bcd	35.9bcdefgh	74.5
	Mean	43.5	41.2	130.5	34.9	22.1	54.4
27	Low	0.0h	0.0h	2.7	21.0cdefgh	1.0fgh	4.9
	High	1.3fgh	0.0h	0.0h	27.1cdefgh	2.4fgh	6.2
	Mean	0.7	0.0	1.4	24.1	1.7	5.6
Overall means	Low	9.9	9.0	20.8	8.7	4.9	10.7
	High	24.7	17.7	58.9	22.5	24.7	32.0
	Mean	17.3	13.4	39.9	15.6	14.8	21.4

[a] Values (excluding means) followed by the same letter are not significantly different (5% level, Duncan's multiple range test).
[b] At 32°C, no eggs were laid, regardless of plant stage or RH.

Table 5.—Effects of temperature, RH, and soybean plant stage and their interactions on eggs/MBB female/day (Experiment 3).

Temp[b] (°C)	RH	Initial plant stage[a] V4	R5	R6	R8	R9	Mean
17	Low	0.00e	0.00e	0.11cde	0.00e	0.22cde	0.07
	High	0.78bcde	0.43bcde	0.82bcde	0.09de	0.94bcd	0.61
	Mean	0.39	0.22	0.47	0.05	0.58	0.34
22	Low	0.69bcde	0.71bcde	1.23b	0.31cde	0.31cde	0.65
	High	0.84bcde	1.00bc	3.95a	1.26b	1.33b	1.68
	Mean	0.77	0.86	2.59	0.79	0.82	1.16
27	Low	0.00e	0.00e	0.09de	0.83bcde	0.03de	0.19
	High	0.06de	0.00e	0.00e	0.89bcde	0.08de	0.21
	Mean	0.03	0.00	0.05	0.86	0.06	0.20
Overall means	Low	0.20	0.20	0.40	0.30	0.10	0.20
	High	0.40	0.40	0.20	0.60	0.60	0.60
	Mean	0.30	0.30	0.80	0.50	0.40	0.40

[a] Values (excluding means) followed by the same letter are not significantly different (5% level), Duncan's multiple range test).
[b] No eggs laid at 32°C, regardless of plant stage or RH.

Plant stage, humidity, and temperature as well as the temperature × humidity and temperature × plant stage interactions had a significant effect on all of these parameters. Overall, high humidity increased fecundity, with beetles laying almost twice as many egg masses (0.7 vs. 0.4) and three times as many total eggs (32.0 vs. 10.7).

As temperature increased from 17° to 22°C reproduction increased, then dropped dramatically at 27°C. At 32°C no eggs were laid, regardless of plant stage and humidity.

Fecundity also increased after plants changed from vegetative-early reproductive (V4, R5) to reproductive (R6), and then decreased as plants began to mature (R8, R9).

The effect of the plant stage × temperature interactions was apparent, with plant stage having its greatest effect at 22°C. Similar results were observed for the humidity × temperature and the plant stage × humidity × temperature interactions.

The avg number of eggs per mass was affected by plant stage and humidity (but not temperature) (Table 6). Eggs per mass were highest for the intermediate plant stages (R6, R8), regardless of temperature. In general, for eggs per mass under high humidity conditions, the differences were most noticeable for young (V4) and old (R9) plants.

Discussion

Longevity, as expected, was greatly affected by temperature, but not by plant stage or humidity (although humidity extremes were generally not obtained in this study. The major impact of the temperature × RH × plant stage effects appear to be with respect to fecundity.

If our ultimate objective is to develop the capability of predicting the numbers and timing of population out-

Table 6.—Effects of temperature, RH, and soybean plant stage and their interactions on MBB eggs/egg mass (Experiment 3).

Temp (°C)	RH	Initial plant stage[a] V4	R5	R6	R8	R9	Mean
	Low	—	—	43.5ab	—	29.0ab	36.3
17	High	39.2ab	40.5ab	42.5ab	50.0a	40.6ab	42.6
	Mean	39.2	40.5	43.0	50.0	34.8	39.5
	Low	25.4ab	31.1ab	47.4a	54.3a	36.0ab	38.8
22	High	41.1ab	37.2ab	46.9a	37.9ab	39.7ab	40.6
	Mean	33.3	34.2	47.2	46.1	37.9	39.7
	Low	—	—	19.0b	51.6a	14.0b	28.2
27	High	15.0b	—	—	41.3b	34.0ab	30.1
	Mean	15.0	—	19.0	46.5	24.0	29.2
	Low	—	—	—	—	—	—
32	High	—	—	—	—	—	—
	Mean	—	—	—	—	—	—
Overall means	Low	25.4	31.1	36.6	53.0	26.3	34.4
	High	31.8	38.9	44.7	43.1	38.1	37.8
	Mean	28.6	35.0	40.7	48.0	32.2	36.1

[a] Values (excluding means) followed by the same letter are not significantly different (5% level, Duncan's multiple range test).

breaks, then projecting the pattern, as well as the number, of eggs deposited is critical. The interaction of pattern and numbers can produce widely varying results. For example, a beetle population with a higher fecundity but a longer oviposition time may increase in density no faster than a population with lower fecundity and a shorter oviposition period.

Since the various independent variables may affect the different measures of fecundity differentially, these effects must be separated in order to realistically extrapolate the observed relationships to field situations.

Plant stage affected fecundity as expressed by all 7 parameters. Although results were somewhat different among the 3 experiments (e.g., the fecundity was highest for beetles fed on R9 plants in Experiment 2, and on R6 plants for Experiments 1 and 3) it is clear that young plants (particularly preblooming) are considerably less suitable for egg production. This same trend was observed by Lockwood et al. (1979) and here with respect to leaf age (Experiment 2).

Beetles fed on upper leaves (young) laid significantly fewer eggs than beetles fed on middle and lower leaves for most plant stages. When fed on upper leaves of older plants (R9), however, beetles did not lay fewer eggs compared to those fed on middle and lower leaves. (The upper leaves of R9 plants appear comparable in physiological age to middle and lower leaves of younger plants). These results are consistent with the hypothesis that physiologically young tissue is not as suitable for egg production as is mature plant tissue.

Although food quality as well as quantity affects fecundity, the specific nutritional elements and biochemical pathways involved are poorly understood. Henderson and Kampreth (1970) found that foliage nitrogen accumulation in soybean peaked at 110–120 days after planting. In Experiment 1 and 3, fecundity showed a strong tendency to increase when beetles started feeding on R6 plants, ca. 120 days after planting. Todd et al. (1972) reported a significant increase in MBB numbers on non-nodulated soybean plants which had heavy nitrogen fertilization. Furthermore, they found a strong correlation between leaf protein and MBB density on these non-nodulated soybeans (but not on nodulated soybeans).

The number of eggs per mass was not affected by plant stage, which would seem to indicate that a certain level of nutrients is required to produce an egg mass and that a mass will not be laid (or perhaps produced internally) unless that level is present.

Both humidity and temperature affected MBB fecundity. In Experiment 3, fecundity was higher at high than low RH. These results are in agreement with the reports of several authors (Eddy and McAlister 1927, Sweetman 1929, Howard 1931).

It is interesting to note that eggs per mass were affected by humidity, but not by temperature. Since water balance can be critical to any poikilothermous species at any temperature, and since egg deposition involves water loss to the eggs, it seems consistent with the previous observations that more eggs per mass were produced under high than low humidity. The effects of humidity were compounded by an interaction with plant stage, further evidence for the importance of nutritional stress.

As a metabolic process, egg production was strongly affected by temperature. All measures of fecundity peaked at 22°C and actually dropped to zero at 32°C for beetles fed on all soybean stages (beetles fed on limas producted an avg of 32.0 eggs/female at 32°C).

Although these data represent a baseline of information on the effects of temperature, humidity, soybean growth stage, and their interactions on the longevity and fecundity of the Mexican bean beetle, there are several areas of research which need to be explored in much greater depth before the quantitative relationships can be accurately elucidated. The physiological pathways and mechanisms of the interactions revealed in this ecologi-

cally oriented study remain a challenge to the physiologists and biochemists. Photoperiod and light intensity have not been investigated, yet may play important roles in egg production and adult reproductive dormancy.

With respect to nutrition, the soybeans grown in the greenhouse pose some problems. Although they were morphologically very similar to field grown plants (e.g., stem diameters, leaf size, total plant size and shape), no chemical analyses were performed to determine chemical similarity. Because of the importance of plant maturity (and resultant nutritional qualities) demonstrated in these studies, future work in this area should include such comparative chemical analyses.

REFERENCES CITED

Auclair, J. L. 1959. Life history, effects of temperature and relative humidity and distribution of the Mexican bean beetle *Epilachna varivestis* Mulsant (Coleoptera: Coccinellidae) in Quebec with a review of the pertinent literature in North America. Ann. Soc. Entomol. Que. 5: 18–43.

Deitz, L. L., J. W. Van Duyn, J. R. Bradley, Jr., R. L. Rabb, W. M. Brooks, and R. E. Stinner. 1976. A guide to the identification and biology of soybean arthropods in North Carolina. N.C. Agric. Exp. Stn. Tech. Bull. 238. 264 pp.

Douglass, J. R. 1928. Precipitation as a factor in the emergence of *Epilachna corrupta* Mulsant from hibernation. J. Econ. Entomol. 21: 203–13.

Eddy, C. O., and L. C. McAlister. 1927. The Mexican bean beetle. S.C. Agric. Exp. Stn. Bull. 236. 38 pp.

Friend, R. B., and N. Turner. 1931. The Mexican bean beetle in Connecticut. Conn. Agric. Exp. Stn. Bull. 332: 71–108.

Graf, J. E. 1925. Climate in relation to Mexican bean beetle distribution. J. Econ. Entomol. 18: 116–21.

Hanway, J. J., and H. E. Thompson. 1971. How a soybean plant develops. Iowa State Univ. Coop. Ext. Serv. Spec. Rept. 53. 17 pp.

Henderson, J. B., and E. J. Kampreth. 1970. Nutrient and dry matter accumulation by soybeans. N.C. Agric. Exp. Stn. Tech. Bull. 197. 27 pp.

Howard, N. F. 1921. The Mexican bean beetle and its bearing on Florida citrus growing. Florida St. Pl. Bd. Quart. Bull. 6: 15–24.

1931. The effect of 1930 drought upon insect populations: The effect on the Mexican bean beetle. J. Econ. Entomol. 24: 660–2.

Howard, N. F., and L. L. English. 1924. Studies on the Mexican bean beetle in the Southeast. USDA Bull. 1243. 50 pp.

Kogan, M. 1971. Feeding and nutrition of insects associated with soybean. 1. Growth and development of the Mexican bean beetle *Epilachna varivestis* on artificial media. Ann. Entomol. Soc. Am. 64: 1044–50.

1972a. Feeding and nutrition of insects associated with soybean. 2. Soybean resistance and host preferences of the Mexican bean beetle *Epilachna varivestis*. Ibid. 65: 675–83.

1972b. Intake and utilization of natural diets by the Mexican bean beetle, *Epilachna varivestis*. A multivariate analysis. P. 107–26. *In* Rodriguez, J. R., [ed.] Insect and Mite Nutrition. North-Holland Publishing Company, Amsterdam. 702 pp.

Lockwood, D. F., R. L. Rabb, R. E. Stinner, and R. K. Sprenkel. 1979. The effects of 2 host plant species and phenology on 3 population parameters of adult Mexican bean beetle in North Carolina. J. Ga. Entomol. Soc. (In press).

Marcovitch, S. 1926. Supplementary investigations of the fluosilicates as insecticides with observations on the effect of heat and drought on the Mexican bean beetle. Tenn. Agric. Exp. Stn. Bull. 134. 13 pp.

Marcovitch, S., and W. W. Stanley. 1930. The climatic limitations of the Mexican bean beetle. Ann. Entomol. Soc. Am. 23: 666–86.

Miller, D. F. 1930. The effect of temperature, relative humidity and exposure to sunlight upon Mexican bean beetle. J. Econ. Entomol. 23: 945–55.

Pallister, J. C. 1949. Mexican bean beetle. Natur. Hist. 58: 162–5.

Pyenson, L., and H. L. Sweetman. 1932. The effects of temperature and moisture on the eggs of *Epilachna corrupta*. Bull. Brooklyn Entomol. Soc. 26: 221–6.

Sweetman, H. L. 1929. Precipitation and irrigation as factors in the distribution of the Mexican bean beetle, *Epilachna corrupta* Muls. Ecology 10: 228–44.

1932. The effects of temperature and moisture on the distribution of the Mexican bean beetle, *Epilachna corrupta* Muls. Ann. Entomol. Soc. Am. 25: 224–40.

Thomas, F. L. 1924. Life history and control of the Mexican bean beetle. Ala. Agric. Exp. Stn. Bull. 221. 99 pp.

Todd, J. W., M. B. Parker, and T. P. Gaines. 1972. Populations of Mexican bean beetles in relation to leaf protein of nodulating and non-nodulating soybeans. J. Econ. Entomol. 65: 729–31.

White, W. H. 1940. The Mexican bean beetle. Smithson. Inst. Ann. Rept. 95: 343–56.