

# Effects of Variably Resistant Soybean and Lima Bean Cultivars on *Pediobius foveolatus* (Hymenoptera: Eulophidae), A Parasitoid of the Mexican Bean Beetle, *Epilachna varivestis* (Coleoptera: Coccinellidae)

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**ABSTRACT** Laboratory studies were conducted to determine host-mediated effects of plant cultivars on *Pediobius foveolatus* Crawford. 'Henderson Bush' lima bean and 'Bonus', 'Williams', and 'Cutler 71' soybean were studied. Immature survival and longevity, and adult longevity and fecundity data were used to construct life tables for *P. foveolatus* parasitizing Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant, larvae on each cultivar. Fewer viable mummies and parasitoid progeny per host were produced on 'Cutler 71', but cultivar did not significantly affect fecundity. Consequently, relative to 'Cutler 71', the intrinsic rates of increase of *P. foveolatus* on the other cultivars were ca. 1.3-fold higher. Relative to intrinsic rates of increase of the MBB on the same cultivars, these results indicated that population growth potentials of *P. foveolatus* were less affected. Additionally, MBB mortality caused by unsuccessful parasitoid ovipositions was higher on the more resistant cultivars. Therefore, the higher the resistance exhibited by a cultivar to MBB, the greater the relative impact of the parasitoid population, assuming that cultivars do not affect parasitoid searching.

THE CONCURRENT USE of plant resistance and biological control to suppress insect pest populations has frequently been proposed, but rarely have the consequences of these plant-pest-natural enemy interactions been investigated. In principle, plant resistance and biological control are compatible strategies since both rely on suppression, not elimination, of the pest's population (Wilson and Huffaker 1976), function as density-independent and density-dependent mortality factors, respectively (Bergman and Tingey 1979), and are selective against the target pest population (Knipling 1979). Furthermore, such interacting suppression tactics may reduce the level of plant resistance required for economic pest suppression, and thus result in more temporally stable resistance by reducing selection pressures on the pest population (Beck and Maxwell 1976).

However, the compatibility of plant resistance and biological control is based on the assumptions that the plant resistance mechanism does not adversely affect the behavior of the biological control agent (e.g., Campbell and Duffey 1981), that the host's physiology is not altered to the extent that its suitability to the natural enemy is reduced, or that the host's developmental durations are not affected to such an extent that the host and natural enemy life cycles become unsynchronized. In reality, these assumptions may not be valid. It has been shown that the effectiveness of natural ene-

mies may be significantly affected by the plant species (Flanders 1953, Rabb and Bradley 1968) and cultivar (Wyatt 1970, Starks et al. 1972) upon which the host develops. Painter (1951) identified three potentially deleterious effects of plant resistance on natural enemies: 1) reduced searching efficiencies of natural enemies due to reduced host densities; 2) reduced size, sex ratio, or fecundity of natural enemy progeny due to decreases in the sizes of hosts; and 3) reduced natural enemy survival due to altered host physiologies. Conversely, plant resistance may enhance natural enemy efficiency or host-natural enemy synchrony when host exposure to attack is prolonged through altered behavior or slower development of the susceptible host stages (Adkisson and Dyck 1980). Therefore, an understanding of the modality of resistance is essential in appraising the compatibility of these two pest control strategies (Knipling 1979).

In 1966, the gregarious larval endoparasitoid *Pediobius foveolatus* Crawford was imported into the United States as a biological control agent of the Mexican bean beetle (MBB), *Epilachna varivestis* Mulsant (Angalet et al. 1968). Due to its inability to overwinter, annual inoculative releases were investigated in Maryland from 1972-1974 (Stevens et al. 1975a,b). The results of these studies suggested that *P. foveolatus* was capable of effectively suppressing MBB populations on soybean. However, subsequent periodic releases in the eastern Midwest have resulted in unexplained fluctuations in effectiveness. Field observations have suggested that some of these fluctuations possibly were

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due to variable plant-pest-natural enemy interactions on different cultivars of soybean (R.V.F., unpublished data).

Fluctuations in the effectiveness of periodic releases of *P. foveolatus* may be a result of plant-resistance mechanisms affecting the relatively new plant-herbivore-natural enemy associations. The parasitoid was collected in India from an epilachnine herbivore of solanaceous plants (Lall and Singh 1960); in the United States, the parasitoid is expected to affect the population densities of a new epilachnine host on leguminous plants. Additionally, plants of the genus *Phaseolus* appear to be the evolutionary hosts of MBB, and its association with soybean (*Glycine max* Merrill) is relatively recent (Kogan 1972). Furthermore, existing soybean cultivars exhibit variable resistance to the MBB (Kauffman et al. 1985).

The objectives of this study were 1) to determine the host-mediated effects of lima bean and soybean cultivars on the longevity, survival, and fecundity of *P. foveolatus* and 2) to evaluate, via life table statistics, the effects of these cultivars on the population growth of the parasitoid relative to that of the MBB.

#### Materials and Methods

*P. foveolatus* and MBB were cultured in the Department of Entomology at Purdue University. Rearing techniques were similar to those described by Stevens et al. (1975b) and Flanders (1984). Both cultures were maintained on 'Henderson Bush' lima bean.

'Henderson Bush' lima bean and 'Bonus', 'Williams', and 'Cutler 71' soybean were chosen for study because of their previously documented effects on MBB population growth (Kauffman et al. 1985). The plants were grown in a greenhouse at  $25 \pm 5^\circ\text{C}$  and at ca. 14:10 (L:D) photoperiod (existing light supplemented with timed fluorescent lights). Only plants that were in vegetative growth stages were used in the studies. In all studies, only late fourth-instar MBB larvae, the preferred stage for *P. foveolatus* oviposition and development (Stevens et al. 1975b), were used. All studies were conducted in environmental chambers at  $25 \pm 1^\circ\text{C}$ , 40-70% RH, and 14:10 (L:D) photoperiod.

Before the initiation of actual tests, parasitoids were first conditioned to each cultivar by rearing them through one generation on hosts that had developed from eggs to fourth instars on the respective cultivar. To eliminate potential variability in parasitoid performance due to superparasitism, a single oviposition per host was observationally verified. Following parasitoid oviposition, hosts were returned to the cultivar on which they had been reared to continue feeding. Adult parasitoids emerging from mummies (mummified remains of parasitized MBB larvae) on a cultivar were placed in a escapeproof plastic petri dish (15 by 100 mm). The top of the petri dish

was vented with a hole covered with cotton organdy. Honey and water were supplied. From 24-48 h after adult parasitoid emergence, fourth-instar MBB were placed in the petri dish for parasitoid oviposition to commence the studies of host-mediated cultivar effects on immature parasitoid survival and development. The hosts had been reared on the same cultivar as that on which the parasitoids had been reared. Single parasitoid ovipositions again were observationally verified. The number of hosts parasitized per cultivar ranged from 85-130, due to variations in their availability at the time of adult parasitoid emergence.

Following parasitoid oviposition, parasitized hosts were placed in ventilated petri dishes. Each petri dish was partially filled with moist sand, upon which an excised lima bean unifoliolate or soybean trifoliolate of the appropriate cultivar was placed. Sand and foliage were replaced daily until parasitized larvae either pupated, died, or mummified. Fourteen days after parasitoid oviposition, mummified hosts were removed from the petri dishes and individually placed in gelatin capsules. An incision was made in the dorsal abdominal sclerites of each mummy to ensure immediate escape of parasitoid adults. The mummies were monitored daily for adult parasitoid emergence. At emergence, the number of adults per mummy and their sex were recorded. Hosts that appeared to be parasitized (i.e., mummified) but from which no live adult parasitoids emerged were considered to be nonviable mummies if dead parasitoid pupae or adults were present in them. Hosts that died from undetermined causes were designated dead hosts.

Following an 8- to 16-h mating period, individual females from the previous experiment were placed in ventilated petri dishes with five fourth-instar MBB (previously determined to be a non-limiting daily supply for parasitoid oviposition) to determine cultivar effects on female longevity and fecundity. All submitted hosts were reared on 'Henderson Bush' lima bean, regardless of the cultivar on which the female parasitoids had developed, to standardize immature parasitoid mortality and developmental rates for determining parasitoid fecundity. 'Henderson Bush' lima bean was considered an optimal cultivar for MBB development (Flanders 1984, Kauffman et al. 1985). The five MBB larvae in each parasitoid oviposition unit were replaced every 24 h until the female died. Following the 24-h exposure period, the five MBB larvae from each parasitoid oviposition unit were placed in a petri dish containing moist sand and lima bean foliage to continue development. Subsequent treatment was the same as in the previous experiment.

The time of emergence, number, and sex of parasitoid progeny emerging from mummies were recorded. Adult longevity, number of effectively parasitized hosts (i.e., viable mummies), daily fecundity, and daily sex ratio of the progeny were calculated. Only data from mated females (i.e.,

**Table 1.** Effects of cultivar on immature *P. foveolatus* survival and duration of development at 25 ± 1°C, 40–70% RH, and a 14:10 (L:D) photoperiod

Cultivar	Hosts exposed	$\bar{x} \pm SE$				
		% Viable mummies	% Dead hosts	% Nonviable mummies	Progeny/host	Duration of immature development (days)
Lima Bean						
'Henderson Bush'	85	65.7 ± 6.0a	17.8 ± 4.4c	8.6 ± 3.4a	7.4 ± 0.7a	15.1 ± 0.2ab
Soybean						
'Bonus'	89	36.8 ± 8.3b	54.6 ± 8.4b	4.8 ± 3.9a	4.8 ± 1.1b	14.6 ± 0.3ab
'Williams'	118	54.4 ± 7.2ab	39.3 ± 7.7b	4.8 ± 2.7a	6.6 ± 0.9ab	14.2 ± 0.1b
'Cutler 71'	130	16.4 ± 4.2c	78.4 ± 4.4a	0.7 ± 0.7a	1.9 ± 0.5c	15.3 ± 0.6a

Percent and numerical data were transformed by arcsine and log transformations, respectively, prior to analyses. Means followed by the same letter are not significantly different ( $P \leq 0.05$ ; Duncan's [1955] multiple range test).

those that produced female progeny) were included in the analyses.

Life tables were constructed and statistics calculated for *P. foveolatus* parasitizing MBB on each of the cultivars by methods described by Andrewartha and Birch (1954), Krebs (1978), and Southwood (1978). Immature parasitoid mortality was calculated for each cultivar by the following formula:

$$\% \text{ immature mortality (IM)} = \left\{ \frac{[(NVM + DH)/(VM + NVM + DH)] \times 100 \right\} - IMV,$$

where VM was the number of viable mummies per cultivar, NVM was the number of nonviable mummies per cultivar, DH was the number of dead hosts in excess of nonparasitized fourth-instar MBB mortality on the cultivar (see Kauffman et al. 1985), and IMV was the percent immature mortality of parasitoid eggs, larvae, and pupae within viable mummies. In previous studies (R. V. Flanders and L. W. Bledsoe, unpublished data), immature mortality (i.e., through the egg, larval, and pupal stages) of *P. foveolatus* was found to be ca. 10% in viable mummies on 'Henderson Bush' lima bean. In this study, IMV was assumed to be 10% for all cultivars. Similarly, age-specific fecundity of the adult parasitoids was corrected to account for the 10% immature parasitoid mortality in hosts feeding on 'Henderson Bush' lima bean.

### Results and Discussion

The percentage of viable mummies and the number of parasitoid progeny produced per host were highest on 'Henderson Bush' lima bean and lowest on 'Cutler 71' soybean (Table 1;  $P \leq 0.05$ ; analysis of variance [ANOVA]). There was a significant negative correlation between percent viable mummies and dead hosts ( $r^2 = 0.98$ ,  $P \leq 0.05$ ; ANOVA), suggesting that cultivar affected the survival of parasitized hosts. Females comprised 85% of the parasitoid progeny for all cultivars. The duration of immature parasitoid development was longer ( $P \leq 0.05$ ; ANOVA) on 'Cutler 71' than on

'Williams', but the other cultivars were not significantly different from each other or these two cultivars.

Adult female parasitoid longevity was longest after developing in hosts reared on 'Henderson Bush', but was only significantly different ( $P \leq 0.05$ ; ANOVA) from that on 'Williams' (Table 2). Although the number and percent of viable mummies were lowest on 'Williams', there were no significant differences among the cultivars ( $P > 0.05$ ; ANOVA). Cultivar did not significantly affect the number of progeny per female, progeny per viable mummy, or sex ratio ( $P > 0.05$ ; ANOVA).

Net reproductive rates on 'Henderson Bush', 'Bonus', and 'Williams' were 2.5-, 2.6-, and 1.4-fold greater, respectively, than on 'Cutler 71' (Table 3). Generation time was nearly the same on 'Henderson Bush', 'Bonus', and 'Cutler 71', but was shortest on 'Williams'. Consequently, the intrinsic rates of increase were nearly the same on 'Henderson Bush' and 'Bonus'. The intrinsic rates of increase on 'Henderson Bush', 'Bonus', and 'Williams' were each ca. 1.3-fold greater than on 'Cutler 71'.

Kauffman et al. (1985) found that the population growth of MBB under conditions similar to this study was greatest on 'Henderson Bush' lima bean and least on 'Cutler 71' soybean. In this study, 'Cutler 71' similarly, but indirectly, affected the population growth potential of *P. foveolatus*, primarily by affecting the viability of mummies and progeny per host. These effects apparently were due to altered host physiology and consequent lowered host suitability for the development of *P. foveolatus* immatures. Percentages of dead hosts were 1.6- to 2.2-fold greater than those reported by Kauffman et al. (1985) for unparasitized hosts on the same cultivars. By combining the number of viable mummies and dead hosts, host mortality caused by parasitoid oviposition was similar on all cultivars, regardless of the level of resistance of a particular cultivar to MBB population growth.

A comparison of the life table statistics of *P. foveolatus* with those previously reported for MBB (Kauffman et al. 1985) indicated that the potential

**Table 2.** Effects of cultivar on adult *P. foveolatus* longevity and fecundity at 25 ± 1°C, 40–70% RH, and a 14:10 (L:D) photoperiod

Cultivar	Total ♀♀	Fecund ♀♀	$\bar{x} \pm SE$			
			Longevity (days)	Viable mummies/♀	% Viable mummies/♀	Progeny/♀
Lima Bean						
'Henderson Bush'	8	6	9.6 ± 1.7a	5.2 ± 1.7	12.7 ± 5.4	58.0 ± 21.5
Soybean						
'Bonus'	11	10	7.5 ± 1.5ab	6.6 ± 1.5	18.7 ± 2.8	64.8 ± 13.9
'Williams'	7	5	4.5 ± 0.7b	1.4 ± 0.5	8.3 ± 2.9	16.1 ± 4.9
'Cutler 71'	7	3	6.1 ± 1.8ab	6.4 ± 3.0	12.8 ± 6.2	63.3 ± 30.4

Means followed by the same letter are not significantly different ( $P \leq 0.05$ ; Duncan's [1955] multiple range test).

of the parasitoid to suppress MBB populations is greatest on 'Cutler 71', the most resistant cultivar. Intrinsic rates of increase of *P. foveolatus* parasitizing MBB on 'Cutler 71', 'Bonus', 'Williams', and 'Henderson Bush' were 13.2-, 5.0-, 3.9-, and 2.1-fold greater than those of the MBB on the same cultivars. This was primarily due to the shorter generation time of *P. foveolatus*, which was from 34–42% shorter than that of the MBB. Additionally, increased developmental times of MBB on more resistant cultivars (Kauffman et al. 1985) suggest that susceptible host stages may be exposed longer to ovipositing female parasitoids than on less resistant cultivars. Field parasitism rates consequently may increase on resistant cultivars or remain the same as on susceptible cultivars depending on the degree of host density reduction caused by plant resistance (as discussed by Adkisson and Dyck 1980).

These results demonstrate compatibility of plant resistance and biological control by *P. foveolatus* under the defined conditions. The results however cannot be directly extrapolated to field situations, since the direct or indirect effects of the cultivars on parasitoid searching were not determined. Thus, the differential rates of population growth between the host and the parasitoid may be nullified or reversed by alterations in parasitoid searching on different cultivars. Alterations in levels of resistance or susceptibility of host plants at different phenological stages, or changes or variations in

certain climatic factors also may affect the plant-host-parasitoid relationship. However, the results do suggest that the potential of *P. foveolatus* to suppress MBB populations increases with the level of cultivar resistance and that the effects of soybean cultivars should be considered in field evaluations of *P. foveolatus*. Additionally, increases in MBB mortality caused by less successful parasitoid ovipositions (i.e., dead hosts) should be considered along with mortality caused by more successful ovipositions (i.e., viable and nonviable mummies) in field evaluations.

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**Table 3.** Life table statistics of *P. foveolatus* parasitizing fourth-instar MBB larvae on lima bean and soybean cultivars at 25 ± 1°C, 40–70% RH, and a 14:10 (L:D) photoperiod

Cultivar	Net reproductive rate (♀ progeny/♀ parent)	Generation time (days)	Intrinsic rate of increase (per ♀/day)
Lima Bean			
'Henderson Bush'	50.9	18.5	0.212
Soybean			
'Bonus'	52.5	18.5	0.214
'Williams'	29.1	16.5	0.205
'Cutler 71'	20.3	18.9	0.159

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