

Ovipositional Responses of Seedcorn Maggot, *Delia platura* (Diptera: Anthomyiidae), to Developmental Stages of Lima Bean

PAUL A. WESTON¹ AND J. R. MILLER²

Department of Entomology and Pesticide Research Center,
Michigan State University, East Lansing, Michigan 48824

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ABSTRACT Seedcorn maggot, *Delia platura* (Meigen), given a choice of several lima bean developmental stages, laid most eggs on germinating beans and emerging seedlings. Above-ground plant structures had no effect on ovipositional stimulation, but presence of breaks in the substrate surface and chemostimuli from germinating beans increased oviposition appreciably. Dry weights of female offspring were highest on freshly planted and germinating beans and lowest on emerging and upright seedlings; thus there was a poor match between host acceptance by adult females and suitability to larvae of plant growth stages. Use of this apparent suboptimal resource may result from an inability of females to detect seeds at early stages of germination.

KEY WORDS Insecta, oviposition, host preference, suitability

THE SEEDCORN MAGGOT, *Delia platura* (Meigen), is a widely distributed anthomyiid whose larvae feed on plants of many families (Ristich 1950) and on decaying organic matter (Miller & McClanahan 1969). Females lay eggs near these larval food resources (Barlow 1965, Miller & McClanahan 1969, Yu et al. 1975) and appear to be stimulated to oviposit primarily by olfactory cues (Barlow 1965) produced by microbes (Eckenrode et al. 1975).

Ibrahim & Hower (1979) found that emerging seedlings are the most acceptable developmental stage of soybean in ovipositional choice tests and that lima bean seedlings (*Phaseolus lunatis* L.) stimulate much more oviposition than even the most stimulatory developmental stage of soybean. Because lima beans are much more acceptable than soybean, it would be informative to determine if their acceptability changes with the plant developmental stage in a manner like that of soybean seedlings.

An aqueous extract of ground, germinating lima bean seeds did not stimulate appreciable *D. platura* oviposition, although lima beans that had germinated for 2-3 d elicited more oviposition than several other large-seeded crops (Yu et al. 1975). The ovipositional stimuli appear to be associated with the rhizosphere of germinating seeds rather than with the seed tissue itself. This is consistent with the finding of Eckenrode et al. (1975) that microbes produce ovipositional stimuli for the seedcorn maggot.

Here we evaluate the acceptability of several developmental stages of lima bean plants as ovi-

positional sites for the seedcorn maggot. We then attempt to pinpoint those characteristics of the most stimulatory developmental stages that elicit oviposition. In addition, we quantify the suitability of developmental stages of these seedlings for seedcorn maggot growth.

Materials and Methods

Choice Tests. The flies were from a population originally collected in Michigan and in culture for 1-2 yr. Cultures were maintained and choice tests were conducted in environmental chambers at $21 \pm 2^\circ\text{C}$ and $35 \pm 5\%$ RH with a 16:8 (L:D) photoperiod. Oviposition choice tests were conducted in cylindrical cages (50 cm diameter) with floors that rotated at 4 rph (Weston & Miller 1985). Oviposition treatments were presented in 80-ml styrofoam cups containing 40 ml of fine vermiculite topped with 20 ml of white silica sand. Treatments were evenly spaced around the circumference of cages housing about 100 flies of each sex and were removed after 24 h. Eggs were counted after the sand was carefully scooped from oviposition cups and mixed with water to float the eggs. All experiments used a randomized complete block design, and data were analyzed with ANOVA.

Acceptability of different stages of growth was determined by presenting flies simultaneously with plants in various developmental stages generated by planting lima beans (cv. Fordhook 242) daily in vermiculite in 80-ml styrofoam cups over several weeks. Plants were raised in a greenhouse and watered daily. The developmental stages chosen for bioassay were freshly planted seed, 48-h-old germinating seed, emerging seedling, and upright seedling (cotyledons fully exposed). A layer of silica

¹ Current address: Department of Horticulture and Landscape Architecture, N-318 Agr. Sci. Bldg. North, University of Kentucky, Lexington, Ky. 40546.

² To whom reprint requests should be addressed.

sand was placed over the vermiculite when plants reached the appropriate developmental stage. A fifth treatment, consisting of a cup of vermiculite and sand, was included as a negative control. This choice test was replicated 14 times.

Surrogate emerging seedlings were fashioned from 3-cm lengths of glass tubing (5 mm diameter) bent into a U with the straight ends parallel and in contact. This surrogate bean was pushed into the sand of oviposition cups so that about 0.5 cm projected above the sand surface; thus, it resembled a transparent hook of an emerging lima bean seedling. A 2×2 factorial arrangement (six replicates) of surrogates and 48-h germinating beans (planted 1 cm beneath the surface of the sand) was used to determine the contributions of the physical and chemical attributes of emerging seedlings in eliciting oviposition. The four treatments compared were moist sand, germinating bean, surrogate seedling, and surrogate plus germinating bean. Data were analyzed by factorial ANOVA.

To measure the effect of substrate texture on ovipositional stimulation, holes 1 cm deep were poked in the sand with a disk (5 cm diameter) studded with 17 evenly spaced aluminum rivets (3 mm diameter). Again, a factorial arrangement of holes and germinating bean (eight replicates) was used to determine the contributions of these two factors to ovipositional stimulation.

Finally, the impact of seed-borne chemostimuli on oviposition was determined by soaking 110 lima beans for 48 h at 21°C in 2 liters distilled, deionized water. Eighteen ml of this extract (leachate), representing one seed equivalent, was pipetted onto the dry sand layer in an oviposition cup. This extract was tested (five replicates) for ovipositional stimulation in choice tests with germinating beans and a moist sand control.

Suitability Experiment. The four developmental stages of lima bean plants used in the choice test were tested for their ability to support larval development. Plants were raised in plastic boxes (60 by 40 by 120 cm) containing an 8-cm layer of vermiculite-sphagnum-perlite potting mix. Holes drilled 5 cm apart on the bottom of the box allowed passage of water. The plastic boxes were set inside a plastic-lined trough (120 by 120 by 20 cm) with drain holes 5 cm above the bottom. Water trickled continuously into the trough, so the plastic boxes were continuously watered from below. Gravel in the bottom of the plastic boxes prevented the potting mix from becoming saturated with water. Gravel was placed in the trough around the plastic boxes to reduce algal growth. By watering from below, we hoped to maintain identical moisture levels in each experimental block. We now believe that watering from above would have worked equally well.

Pyramids of aluminum screen (6 mesh per cm) were placed over the boxes to trap flies as they emerged. The base of each pyramid was attached snugly to the plastic box with a wooden frame, and

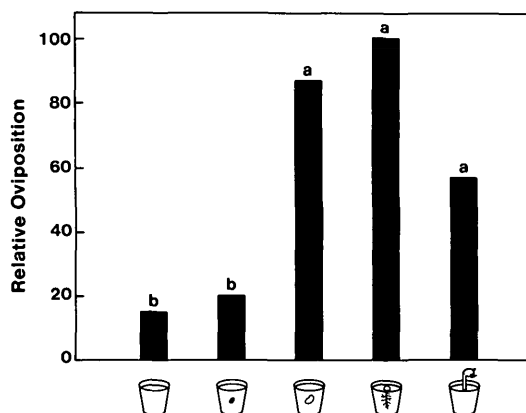


Fig. 1. Oviposition by *D. platura* on developmental stages of lima bean plants. From left to right, treatments are sand control, freshly planted seed, germinating seed, emerging seedling, and upright seedling. Bars accompanied by the same letter are not statistically different as determined by least significant difference test ($\alpha = 0.01$).

the top had a hole (3 cm diameter) opening into an acetate cone containing a 1-cm³ chunk of Raid insecticide strip (S. C. Johnson & Son, Racine, Wis.). The positively phototactic, emerging flies entered the cone traps and were killed within a few minutes. Dead flies fell onto a plaster-of-paris ledge inside the cone. Traps were inspected daily for flies, which were then sexed, dried in an oven at 80°C for 10 d, and weighed.

Planting of lima beans was staggered over time so that plants were in the desired developmental stage on a given day. Thirty plants were raised in each box. Newly eclosed larvae were transferred, one per plant, with a soft, small brush to the base of seedlings for stages having portions above the surface of the soil. For freshly planted seed, germinating seed, and soil control treatments, larvae were transferred to the side of a hole (3 mm diameter, 1 cm deep) poked in the soil above the seeds (imaginary in the case of soil control). Three replicates (blocks) were conducted over time. Only 10 larvae per treatment were available for the second replicate.

Voucher specimens have been deposited with the Entomology Museum, Michigan State University, East Lansing.

Results

Choice Tests. The acceptability of lima bean plants increased with plant age to the emerging seedling stage (Fig. 1). This five-choice test was not precise enough (in the statistical sense) to reveal with high confidence whether the decline in the number of eggs received by upright seedlings was significant; therefore, a two-choice test was conducted with emerging and upright seedlings. This test showed that emerging seedlings stimulate more oviposition than upright seedlings; the former re-

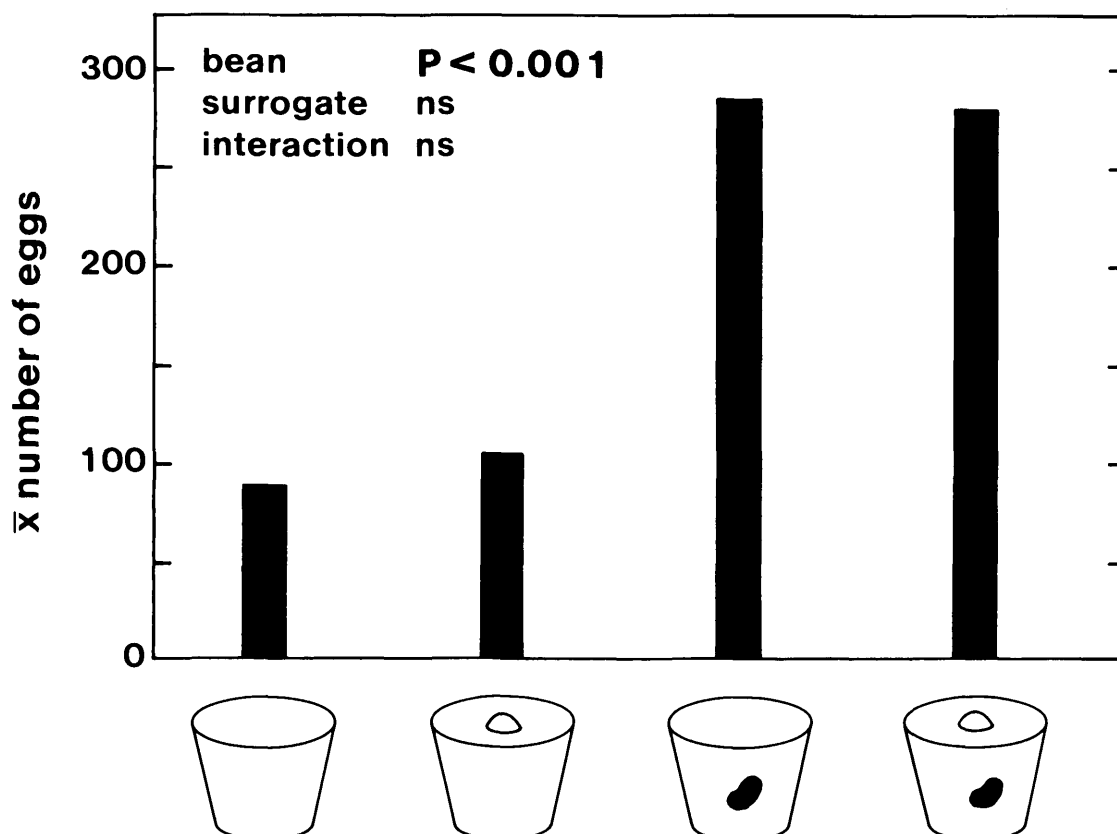


Fig. 2. Oviposition by *D. platyura* on factorial arrangement of surrogate seedlings and germinating beans. From left to right, treatments are sand control, surrogate bean, germinating seed, and surrogate plus germinating seed. Significance of factors is indicated in the box.

ceived more than twice as many eggs (362 versus 162; $P < 0.05$, t test). Therefore, the search for seedcorn maggot ovipositional stimuli focussed on germinating seeds and emerging seedlings.

Seedling surrogates had no effect on seedcorn maggot oviposition (Fig. 2). The two treatments containing germinating beans received considerably more eggs than the no-bean treatments, and both treatments in each pair received similar numbers of eggs. Thus, there was no interaction between the presence of surrogates and the presence of germinating beans.

Holes in the substrate enhanced oviposition (Fig. 3). Not surprisingly, the presence of germinating beans was more effective than holes at eliciting oviposition. Again, there was no interaction between the two factors.

In contrast to the results of Yu et al. (1975), aqueous extract of germinating lima beans strongly stimulated *D. platyura* oviposition (Table 1). Indeed, the extract appeared to be even more stimulatory than germinating beans in soil, although this difference was not statistically confirmed.

Suitability Experiment. Survivorship on the various developmental stages of lima bean ranged from 13 to 21% and was not significantly different (Table

2). No larvae survived on the soil control. Weights of males did not differ significantly among treatments, but the dry weight of females fed on freshly planted and germinating seeds was almost twice that of females reared on emerging or upright seedlings (Table 2). In addition, females feeding on freshly planted and germinating seeds took about 4 d less to complete development than females feeding on emerging seedlings.

Discussion

Like those of soybean plants, emerging lima bean seedlings are the most stimulatory developmental stage for seedcorn maggot oviposition, in the latter case at least because microorganisms associated with germinating beans are intimately involved in the production of ovipositional stimulants (Eckenrode et al. 1975). As seeds germinate, exudates and populations of microbes in the rhizosphere presumably increase up to the time that cotyledons emerge from the soil; these increases are probably accompanied by increased production and emanation of ovipositional stimulants. Once the cotyledons emerge from the soil, however, seed exudates and, thus, ovipositional stimulants, decline. Therefore,

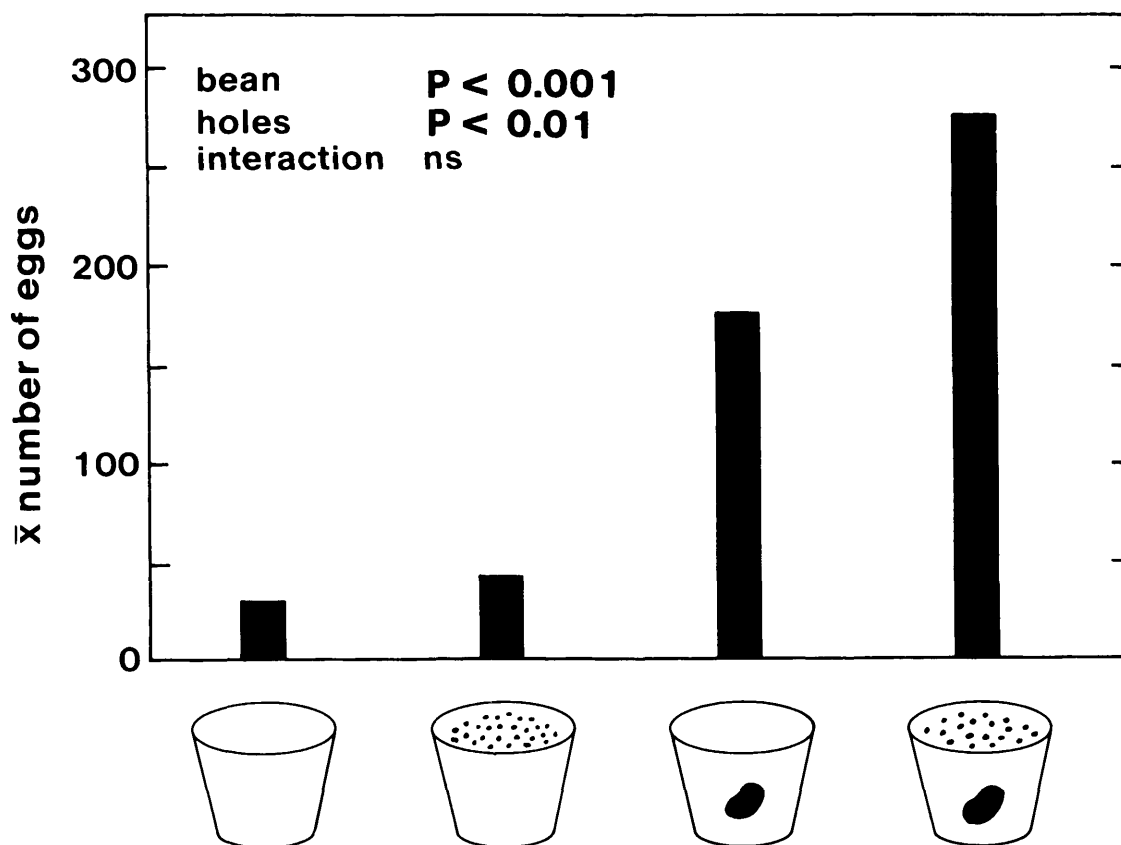


Fig. 3. Oviposition by *D. platura* on factorial arrangement of holes in substrate and germinating beans. From left to right, treatments are sand control, holes, germinating seed, and holes plus germinating seed. Significance of factors is indicated in the box.

it is probably not coincidental that lima bean and soybean seedlings are most stimulatory at emergence.

The results of the surrogate seedling experiment suggest that above-ground plant structures play little or no role in stimulating seedcorn maggot oviposition. The slight increase in oviposition observed in the five-choice experiment as plants progressed from germinating seeds to emerging seedlings is most probably because of increased production of microbial metabolites with time, or from increased release of microbial volatiles as the seedling breaks the soil surface. The color of the emerging seedling may influence oviposition, but its effect, if any, is trivial; emerging seedlings receive only slightly more eggs than germinating ones.

In the absence of host-plant cues, crevices can elicit oviposition by *D. platura* (Weston & Miller 1987). Thus, merely providing a ready place for an ovipositor to be inserted increases the ovipositional acceptability of a substrate (Fig. 3).

Chemicals had the greatest effect on seedcorn maggot oviposition. Even in the complete absence of germinating beans, aqueous extracts of seeds stimulated as much oviposition as did germinating beans. It is not possible to determine from our

experiments whether olfactory or gustatory cues are responsible for this stimulation. The data of Barlow (1965), however, strongly implicate olfaction as a major releaser of oviposition by *D. platura*.

The finding that chemicals alone in an appropriate soil substrate are largely responsible for stimulating seedcorn maggot oviposition contrasts with the picture for the onion fly, *Delia antiqua* (Meigen), a close (Harris et al. 1986) relative. *D. antiqua* specializes on a few *Allium* species, mainly onion, *Allium cepa* L. Although it was once thought that oviposition by *D. antiqua* required only moist soil and propyl-containing alkyl sulfides, it is now well established that normal oviposition results from the synergistic interaction of visual, physical, and

Table 1. Oviposition by *D. platura* on lima bean extract

Treatment	Mean no. eggs (\pm SD)
Moist sand	36 \pm 27b
Germinating seed	85 \pm 52a
Lima bean extract	188 \pm 146a

Means followed by the same letter are not statistically different as determined by least significant difference test ($\alpha = 0.05$) on data transformed to $\log(x + 1)$.

Table 2. Suitability of different developmental stages of lima bean for growth and survival of *D. platyura*

Developmental stage	Survivorship (%)	Larval + pupal duration (d) $\bar{x} \pm SD$	Female dry wt (mg) $\bar{x} \pm SD$
Soil (no seed)	0b	—	—
Freshly planted seed	13.0 \pm 9.0a	19.1 \pm 2.5b	2.08 \pm 0.39a
Germinating seed	18.9 \pm 1.9a	19.5 \pm 3.8b	2.07 \pm 0.50a
Emerging seedling	20.7 \pm 1.3a	23.4 \pm 3.9a	1.04 \pm 0.31b
Upright seedling	14.4 \pm 12.6a	21.6 \pm 3.3ab	1.18 \pm 0.48b

Means within columns followed by the same letter are not statistically different as determined by least significant difference test ($\alpha = 0.01$).

chemical cues (Miller & Harris 1985, Harris et al. 1987). Likewise, the cabbage fly, *Delia radicum* (L.), another close relative, apparently requires a complex of sensory cues for normal oviposition (Zohren 1968).

An explanation for the lack of ovipositional stimulation by above-ground bean seedling parts is that cues from post-emergent plants are correlated with reduced rather than higher larval fitness (Table 2). Survival on the various developmental stages of *P. lunatis* did not differ statistically in this test (where overall survival was low possibly because of excess moisture), yet developmental times were significantly longer on emergent plants, and females weighed significantly less than when reared on pre-emergent bean plants. Fecundity in Diptera is directly proportional to female body weight (Finch & Coaker 1969, Vogt et al. 1985). The more taxonomically specialized herbivores *D. antiqua* and *D. radicum* (responsive to cues from various sensory modalities) are not rewarded for oviposition on the earliest developmental stages of their host plants. Rather, these flies are thought to realize a greater reproductive advantage by ovipositing on emergent plants large enough to support development of several larvae.

The lack of congruence between ovipositional responsiveness of *D. platyura* and suitability of resources for larval development was most pronounced with freshly planted bean seeds. Although such beans are suitable for larval development (Table 2), they do not stimulate oviposition strongly. We believe this lack of responsiveness is because these seeds have not developed a full complement of ovipositional stimuli. This result underscores the importance of considering detectability in instances of poor congruence between animal responsiveness and resource suitability.

Because *D. platyura* appears to be under selective pressure to oviposit on unapparent, newly germinating seeds, we predict evolution will favor increased olfactory sensitivity of this fly compared with *D. antiqua* and *D. radicum*. Also, the use of a more ephemeral and widely distributed resource by *D. platyura* may warrant higher risk-taking and, hence, less ovipositional fastidiousness than is found in *D. antiqua* and *D. radicum*.

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