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Adult Host Preference and Larval Performance of *Liriomyza huidobrensis* (Diptera: Agromyzidae) on Selected Hosts

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ABSTRACT Adult feeding and oviposition preferences and larval performance of the pea leafminer, *Liriomyza huidobrensis* (Blanchard), were examined on pea, potato, lettuce, gai lan, celery, cucumber, and onion in the laboratory and field. Host preference for feeding and oviposition varied among pea leafminer subpopulations when density measures were used but not with proportional measures. Proportion of oviposition punctures may be a more appropriate measure of oviposition preference than egg density for leafmining flies, because it is not impacted by factors affecting stippling density. No correlations were found between preference and performance parameters in this highly polyphagous fly.

KEY WORDS oviposition preference, feeding preference, larval performance, pea leafminer, *Liriomyza huidobrensis*

THE PEA LEAFMINER, *Liriomyza huidobrensis* (Blanchard), is a highly polyphagous, cosmopolitan pest that has remained geographically isolated within the Holland Marsh since it was first found in southern Ontario in 1998 (McDonald et al. 2000). Pea leafminer can cause direct damage to the photosynthetic tissue of host plants because of larval leaf mining and esthetic damage because of oviposition and feeding punctures (stipples) produced by adult females (Spencer 1973). Although the pea leafminer has known hosts in at least 14 families of plants (Spencer 1990), little is known about adult host preferences and host suitability for development of larval stages in this leafminer species. The objectives of this study were to determine adult oviposition and feeding preferences of an Ontario population of pea leafminer for vegetable hosts potentially at risk in Ontario; to evaluate the performance of pea leafminers developing on those hosts; and to make preliminary examinations of preference-performance relationships in this highly polyphagous leafminer. Examination of the advantages and limitations of different measures of oviposition preference became an additional objective during this research.

Each oviposition event may be preceded by a series of visual, chemical, and tactile encounters that act in sequence and that may result in the acceptance of a host by one characteristic but rejection because of another (Singer 1986). This sequential progression toward host acceptance is particularly likely in agromyzid leafminers, where host tissue is punctured by the ovipositor causing a stipple from which females feed before, or immediately after, each oviposition

event (Parrella 1987, Reitz and Trumble 2002). The importance of stippling in assessing the suitability of hosts for oviposition is unknown, but agromyzid leafminer eggs must be laid in stipples. Oviposition preference in leafminers is often quantified using numbers of oviposition punctures, numbers of first-instar mines, or egg density measures (Mayhew 1998, Hawthorne 1999, Reitz and Trumble 2002). For leafminers, egg density may reflect, at least in part, the suitability of the host for feeding and not for oviposition per se, because some female leafminers are unable to detect deterrents and stimulants with their ovipositor and are only repelled from a host on feeding (Bethke and Parrella 1985). Consequently, an additional measure of oviposition preference, "proportion of oviposition punctures" on a host (i.e., proportion of stipples containing an egg), was examined to reflect the decision by a female to lay an egg once a stipple was created. The proportion of oviposition punctures should reflect oviposition preference in response to plant cues after feeding, but not plant or other factors restricting both oviposition and stippling damage on a leaf. Comparisons of oviposition measures were undertaken to determine which measure is most suitable for assessing oviposition preference in these leafmining flies.

Materials and Methods

Insect Collection and Maintenance

Adult pea leafminers were collected from celery (*Apium graveolens* L.) cultivar Florida 683 at the University of Guelph Muck Crops Research Station (MCRS), Kettleby, Canada, using a mouth aspirator

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and established in colonies at the University of Guelph in August 2001. Colonies were maintained in eight 90 by 60 by 60-cm Plexiglas cages with side ventilation and front access closures at $25 \pm 2^\circ\text{C}$ with a 16-h photoperiod. Colony host plants consisted of pea (*Pisum sativum* L.) cultivar Bolero, cucumber (*Cucumis sativus* L.) cultivar Calypso, and lettuce (*Lactuca sativa* L.) cultivar Ithaca M.I. grown under sodium lights in 10-cm pots. Sufficient plant matter to sustain ≈ 300 adults per cage was provided three times weekly, and all cages were supplemented with a sugar-water solution. Plants containing third-instar larvae were placed horizontally over collection trays lined with wax paper and a thin layer of sand. When all larvae had emerged from plants, the sand was sifted, and all pupae were placed into a ventilated cage (30 by 30 by 40 cm). On adult emergence, the flies were evenly distributed among the eight colony cages and maintained as described above.

Oviposition and Adult Feeding Preference

Laboratory Trial. A choice experiment was conducted in August 2002 with three pea leafminer subpopulations (colony, field, and greenhouse) originating from different sources within the Holland Marsh, Ontario, Canada, to examine adult oviposition and feeding preferences. Colony insects had been reared from pea, cucumber, and lettuce for 8–12 generations as described above; greenhouse insects were reared from snapdragon (*Antirrhinum majus* L.) leaves collected from an ornamental flower greenhouse located ≈ 1.8 km southwest of MCRS; and field insects were reared from spinach (*Spinacia oleracea* L.) leaves collected from field plots at MCRS. The latter two subpopulations were included to account for any induced preference that may have developed in the colony subpopulation because test plants included those used to rear this subpopulation. Pupae were collected from source plants as described above and placed individually into 02 gel caps (Parke-Davis Co., Brockville, Canada) using a camel hair brush and monitored for adult emergence.

Unmated males and females (25 each), ≈ 24 h old, were placed into a cage (30 by 30 by 40 cm) with a host from a different family than the test plants for 24 h to allow mating. The temporary mating host was removed, and six test plants, consisting of one each of Asian broccoli (*Brassica alboglabra* L.) cultivar gai lan, celery, pea, lettuce, cucumber, and potato (*Solanum tuberosum* L.) cultivar Shepody, were randomly placed in a 2 by 3 matrix in the center of the cage. Test plant age could not be synchronized because of varying development times; therefore, plants were selected for equivalent size and plant height. Pea plants were staked so that effective plant height was the same as that of the other hosts. Test plants were exposed to pea leafminers for 48 h, after which plants were assessed for stippling and oviposition. Five to seven replications were conducted for each subpopulation.

Because our preliminary data indicated that pre-hatch egg mortality occurs on some plant species,

oviposition was directly measured using a destructive egg staining technique and tissue samples from three plant strata representative of the whole plant. One new, one intermediate, and one old leaf were removed from each plant and placed into individual containers. A lactophenol and acid fuchsin solution was heated to 95°C , poured into each container to cover the leaf tissue, and left to cool overnight (procedure modified from Simonet and Pienkowski 1977). Eggs on both the top and bottom leaf surfaces were counted using a dissecting microscope ($\times 25$). Stipples (oviposition and/or feeding punctures) were counted in either five randomly selected fields of view ($0.8\text{ cm}^2/\text{view}$) or the entire leaf. Leaf area of all sampled leaves was determined using a leaf area meter (LI-3100; Licor, Lincoln, NE), and counts were converted to eggs per centimeter squared and stipples per centimeter squared.

Field Trial. Celery, gai lan, lettuce, pea, potato, and onion (*Allium cepa* L.) cultivar Fortress were included in a field experiment at MCRS (August to September 2002) with a randomized complete block design and four replications. Each block contained six beds (5 m long by 0.9 m wide), with one host plant grown per bed according to recommended between- and within-row spacings (Ontario Ministry of Agriculture and Food 2002). Shortly after seeding or transplanting in the field, the same host plants were planted in 12.5-cm pots in the greenhouse at the University of Guelph. One plant from the greenhouse was placed into each of the corresponding host plots in the field on 27 August, 10 September, and 24 September for 48 h. Potted plants were returned to Guelph where one leaf each of new, intermediate, and old tissue was removed and stained using the method previously described. Both upper and lower leaf surfaces were examined for eggs.

Data Analyses. Data for laboratory and field preference trials were analyzed by analysis of variance (ANOVA) using PROC GLM (SAS Institute 1999) after the appropriate log-transformation for density data or arcsine square-root transformation for proportional data. Two basic assumptions of ANOVA, i.e., (1) independent treatment and model effects and (2) random, independent, and normally distributed errors, were verified before analysis. Models included main effects and all interaction terms; where interactions were found, one-way ANOVAs were conducted separately for each subpopulation or exposure period. After ANOVA, means separations were performed using Tukey's honestly significant difference (HSD) test, with $\alpha = 0.05$ unless otherwise indicated. Regression analyses using PROC REG (SAS Institute 1999) were also conducted for each host individually to examine the relationship between egg and stippling densities in both the laboratory and field trials. In all cases, actual, rather than transformed, data are presented.

Larval Performance

Individual plants of pea, cucumber, celery, lettuce, gai lan, and potato were exposed to pea leafminer

adults for 3 h in a colony cage with exposure for host species occurring on different days. Plants were monitored three times daily (1100, 1600, and 2000 hours) for egg hatch and pupation. Larvae were removed from within the leaf tissue using a pin if their hatching period was unknown, to prevent development of multiple larvae from different hatching periods on one leaf and to prevent intraspecific crowding. Although intraspecific interactions within a leaf were prevented, indirect interaction between larvae developing in different leaves of the same plant because of induced systemic effects cannot be ruled out for all hosts; thus, plants were considered as replications, and there were five to nine replications per host. As larvae reached maturity, each leaf was enclosed in a mesh bag to capture individuals that emerged. Each pupa was placed into a gel cap and larval development time was recorded. Because of difficulties in observing first-instar mines in some hosts (notably lettuce), larval development was measured in days from oviposition to pupation. Approximately 2 d after pupation, the pupae were weighed using a balance (AT250; Mettler, Greifensee, Switzerland) and monitored for adult emergence.

Data Analyses. Larval developmental time and pupal weight were analyzed by ANOVA using PROC GLM. As plants were considered as replicates, mean developmental times and pupal weights for each plant were used in ANOVA analyses. The basic assumptions of ANOVA were verified before analysis as described above. After ANOVA means, separations were performed using Tukey's HSD test, with $\alpha = 0.05$. Data for the proportion of larvae per plant to emerge as adults were analyzed by ANOVA after arcsine square-root transformation. In addition, correlation analyses were conducted to examine the relationships between larval development time and pupal weight, larval development time and proportion adult emergence, and pupal weight and proportion adult emergence per plant using data pooled for all hosts and for each host individually.

Preference and Performance Relationships

Adult preference and larval performance data obtained in the above laboratory trials for the colony subpopulation were used to examine preference-performance relationships in this subpopulation of pea leafminer. Data from these separate experiments were used as oviposition preference and larval performance could not be measured simultaneously because of the use of destructive egg staining techniques. Spearman's rank correlation analyses between preference (egg density, stippling density, proportion of oviposition punctures) and performance (larval developmental time, pupal weight, proportion adult emergence) parameters were conducted using mean values for each host.

Results

Adult Feeding and Oviposition Preference

Laboratory Trial. Analysis of stippling density (model, $F = 9.61$; $df = 29,256$; $P < 0.0001$) revealed statistically significant differences for the main effects of subpopulation ($F = 11.28$; $df = 2$; $P < 0.0001$), host ($F = 26.54$; $df = 5$; $P < 0.0001$), and leaf strata ($F = 8.12$; $df = 2$; $P = 0.0005$). Statistically significant host by subpopulation ($F = 7.08$; $df = 10$; $P < 0.0001$) and host by leaf strata ($F = 2.27$; $df = 2$; $P < 0.05$) interactions were also found. Intraplant variation in stippling was observed for some hosts; in celery, older leaves had lower stippling densities than intermediate or new leaves ($F = 11.48$; $df = 2$; $P < 0.0001$), and in cucumber, old and intermediate leaves had significantly lower stippling densities than new leaves ($F = 13.47$; $df = 2$; $P < 0.0001$). The significant host by subpopulation interaction was largely caused by differences in the prevalence of stippling on peas ($F = 8.31$; $df = 2,43$; $P < 0.001$) between the field and greenhouse subpopulations, and to a lesser extent, to differences in stippling on lettuce ($F = 4.67$; $df = 2,45$; $P < 0.05$; Fig. 1a). In all three subpopulations, stippling density was lower on gai lan than on most other hosts (colony: $F = 10.54$; $df = 5,118$; $P < 0.0001$; field: $F = 19.70$; $df = 5,84$; $P < 0.0001$; greenhouse: $F = 9.83$; $df = 5,66$; $P < 0.0001$).

Analysis of egg density (model, $F = 5.68$; $df = 29,256$; $P < 0.0001$) revealed statistically significant differences for the main effects of host ($F = 9.85$; $df = 5$; $P < 0.0001$) and leaf strata ($F = 9.40$; $df = 2$; $P < 0.0001$), but not subpopulation ($F = 1.55$; $df = 2$; $P > 0.05$). As well, significant host by subpopulation ($F = 5.82$; $df = 10$; $P < 0.0001$) and host by leaf strata ($F = 2.69$; $df = 10$; $P < 0.005$) interactions were found. The latter interaction indicated that, for celery and cucumber only, old leaves had lower egg densities than intermediate or new leaves ($F = 9.44$; $df = 2$; $P < 0.001$ and $F = 11.24$; $df = 2$; $P < 0.0001$, respectively). The host by subpopulation interaction was largely caused by differences in egg density on peas between the field and greenhouse subpopulations ($F = 7.13$; $df = 2,45$; $P < 0.005$) and to differences between the field subpopulation and the other two subpopulations in egg density on potato ($F = 8.31$; $df = 2,43$; $P < 0.001$; Fig. 1b). The colony subpopulation laid fewer eggs on gai lan than potato, cucumber, and lettuce and fewer eggs on celery than potato and cucumber ($F = 6.65$; $df = 5,118$; $P < 0.0001$). For the field subpopulation, fewer eggs were laid on gai lan than on pea, cucumber, and lettuce, and fewer eggs were laid on celery and potato than on pea and cucumber ($F = 8.72$; $df = 5,84$; $P < 0.0001$). In the greenhouse subpopulation, fewer eggs were laid on gai lan and pea than on potato ($F = 5.08$; $df = 5,66$; $P < 0.0005$).

Regression analyses with pooled subpopulations revealed significant relationships between oviposition and stippling densities for all hosts (in ascending order of r^2 : celery, $r^2 = 0.44$, $P < 0.0001$; potato, $r^2 = 0.45$, $P < 0.0001$; gai lan, $r^2 = 0.45$, $P < 0.001$; pea, $r^2 = 0.55$, $P < 0.0001$; lettuce, $r^2 = 0.74$, $P < 0.0001$; cucumber, $r^2 =$

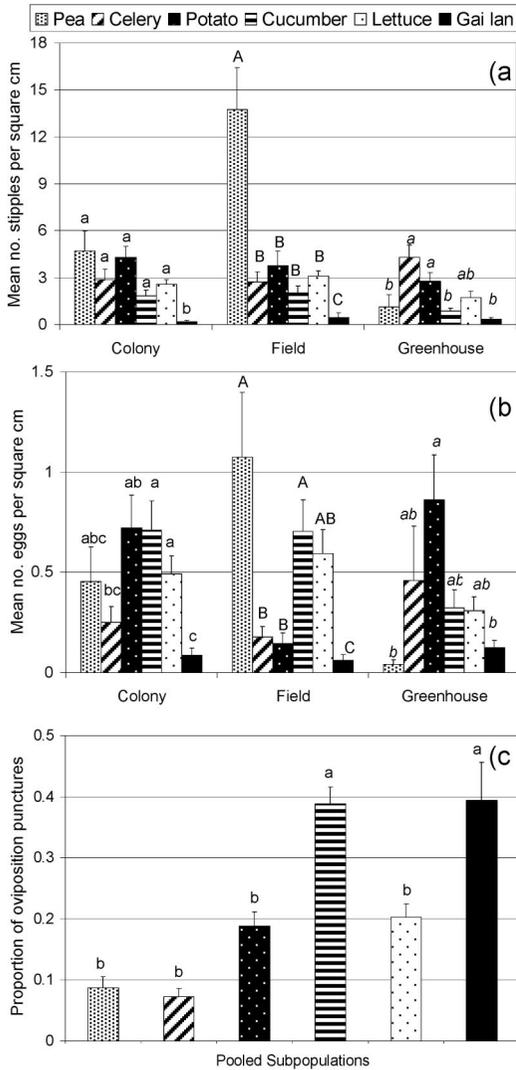


Fig. 1. Host preferences of three Ontario subpopulations of the pea leafminer, *L. huidobrensis* (Blanchard), in laboratory experiments, January to July 2002, University of Guelph, Guelph, ON: (a) stippling density, (b) egg density, and (c) proportion of oviposition punctures. Means \pm SE within a given subpopulation with the same letter are not significantly different (ANOVA and Tukey's HSD comparisons of means, $P > 0.05$).

0.93, $P < 0.0001$). A range of 44–93% of the variation in egg density was explained by variation in stippling density.

Analysis of the proportion of oviposition punctures (model, $F = 2.04$; $df = 53,217$; $P < 0.0002$) revealed a statistically significant difference only for the main effect of host ($F = 16.76$; $df = 5$; $P < 0.0001$), but not leaf strata ($F = 0.58$; $df = 2$; $P > 0.05$) or subpopulation ($F = 0.67$; $df = 2$; $P > 0.05$). A higher proportion of stipples on gai lan and cucumber contained eggs than all other hosts (Fig. 1c). The proportion of oviposition punctures was not correlated with stippling density

for any host (pea, $r = -0.03$, $P > 0.05$; cucumber, $r = -0.08$, $P > 0.05$; gai lan, $r = -0.15$, $P > 0.05$; lettuce, $r = -0.16$, $P > 0.05$; celery, $r = 0.19$, $P > 0.05$; potato, $r = -0.28$, $P > 0.05$).

Field Trial. Analysis of stippling density (model, $F = 13.67$; $df = 53,158$; $P < 0.0001$) revealed statistically significant differences for the main effects of exposure period ($F = 87.35$; $df = 2$; $P < 0.0001$) and host ($F = 89.21$; $df = 5$; $P < 0.0001$) but not for leaf strata ($F = 0.36$; $df = 2$; $P > 0.05$). A statistically significant host by exposure period ($F = 6.02$; $df = 10$; $P < 0.0001$) interaction was also found. Onion had higher stippling densities than gai lan in the first exposure period but not in subsequent exposures; lettuce had higher stippling densities than onion, celery, and gai lan in the second exposure period only; and potato had higher stippling densities than gai lan in the latter two exposure periods, but not in the first (Fig. 2a). Pea had consistently higher stippling densities than all other hosts in all exposure periods (first exposure period: $F = 26.08$; $df = 5,66$; $P < 0.0001$; second exposure period: $F = 38.24$; $df = 5,64$; $P < 0.0001$; third exposure period: $F = 29.43$; $df = 5,64$; $P < 0.0001$).

Analysis of egg density (model, $F = 7.98$; $df = 52,107$; $P < 0.0001$) revealed statistically significant differences for the main effects of host ($F = 25.64$; $df = 5$; $P < 0.0001$) and exposure period ($F = 46.88$; $df = 2$; $P > 0.0001$) and a significant host by exposure period interaction ($F = 7.63$; $df = 10$; $P < 0.0001$). Significant differences among hosts were observed in all three exposure periods (Fig. 2b). In the first exposure period, onion and pea had higher egg densities than gai lan, potato, and celery ($F = 10.08$; $df = 5,52$; $P < 0.0001$). In the second exposure period, pea had higher egg densities than all other hosts except lettuce; lettuce and potato had higher egg densities than gai lan, onion, and celery; and gai lan had higher egg densities than celery ($F = 34.93$; $df = 5,56$; $P < 0.0001$). In the third exposure period, pea had higher egg densities than gai lan and celery ($F = 5.08$; $df = 5,34$; $P < 0.005$).

Regression analyses by host, using pooled data for all exposure periods, revealed significant relationships between oviposition and stippling densities for all hosts (in ascending order of r^2 : celery, $r^2 = 0.47$, $P < 0.0001$; pea, $r^2 = 0.79$, $P < 0.0001$; potato, $r^2 = 0.82$, $P < 0.001$; gai lan, $r^2 = 0.93$, $P < 0.0001$; onion, $r^2 = 0.95$, $P < 0.0001$; lettuce, $r^2 = 0.97$, $P < 0.0001$). A range of 47–97% of the variation in egg density was explained by variation in stippling density.

Analysis of the proportion of oviposition punctures (model, $F = 3.67$; $df = 53,140$; $P < 0.0001$) revealed statistically significant differences for the main effects of host ($F = 17.45$; $df = 5$; $P < 0.0001$) and exposure period ($F = 5.8$; $df = 2$; $P < 0.005$), but not for leaf strata ($F = 1.35$; $df = 2$; $P > 0.05$). A significant host by exposure period ($F = 3.45$; $df = 10$; $P < 0.0005$) interaction was also observed. In all three exposure periods, lettuce always had a higher proportion of oviposition punctures than did some other hosts (Fig. 2c), but the relationship among hosts varied with exposure period. In the first exposure period, the pro-

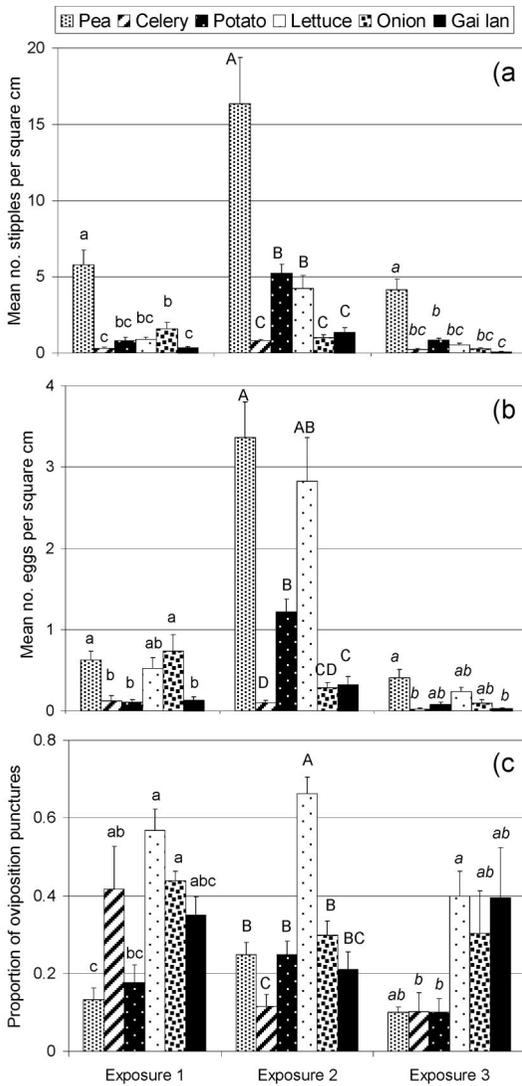


Fig. 2. Host preferences of the pea leafminer, *L. huidobrensis* (Blanchard), in field experiments conducted during three exposure periods (27–29 August, 10–12 September, and 24–26 September 2002), Muck Crops Research Station, Kettleby, ON: (a) stippling density, (b) egg density, and (c) proportion of oviposition punctures. Means \pm SE within a given exposure period with the same letter are not significantly different (ANOVA and Tukey's HSD comparisons of means, $P > 0.05$).

portion of oviposition punctures was higher on lettuce than onion and higher on celery than pea ($F = 7.62$; $df = 5,59$; $P < 0.0001$); in the second exposure period, the proportion of oviposition punctures was higher on lettuce than all other hosts and lower on celery than all hosts except gai lan ($F = 17.62$; $df = 5,64$; $P < 0.0001$); and in the third exposure period, the proportion of oviposition punctures was higher on lettuce than potato and celery ($F = 3.83$; $df = 5,53$; $P < 0.005$). The proportion of oviposition punctures was not correlated with stippling density for any host, except

Table 1. Effect of host plant on performance of the pea leafminer, *L. huidobrensis* (Blanchard), as indicated by larval development time (days from oviposition to pupation), pupal weight, and proportion of larvae emerging as adults

Host	Larval development time (d; mean \pm SE) ^a	Pupal weight (mg; mean \pm SE) ^b	Proportion of adult emergence ^c
Cucumber	10.64 \pm 0.26a	0.62 \pm 0.02c	0.75 \pm 0.05
Celery	10.08 \pm 0.10ab	0.95 \pm 0.03a	0.65 \pm 0.08
Gai lan	9.77 \pm 0.02ab	0.80 \pm 0.05ab	0.89 \pm 0.05
Lettuce	8.51 \pm 0.22bc	0.77 \pm 0.04bc	0.81 \pm 0.06
Potato	7.88 \pm 0.88c	0.79 \pm 0.05abc	0.79 \pm 0.10
Pea	7.68 \pm 0.09c	0.82 \pm 0.04ab	0.74 \pm 0.08

Means in the same column followed by the same letter are not significantly different, ANOVA and Tukey's HSD comparisons of means, $\alpha = 0.05$.

^a $F = 8.80$; $df = 5,36$; $P < 0.0001$.

^b $F = 6.37$; $df = 5,36$; $P < 0.0005$.

^c $F = 1.36$; $df = 5,36$; $P > 0.25$.

lettuce, where the correlation was weak (pea, $r = 0.04$, $P > 0.05$; celery, $r = -0.05$, $P > 0.05$; gai lan, $r = -0.13$, $P > 0.05$; potato, $r = 0.19$, $P > 0.05$; onion, $r = 0.25$, $P > 0.05$; lettuce, $r = 0.40$, $P < 0.05$).

Larval Performance

A significant host effect was observed for both larval development time and pupal weight. Larval developmental time was longest on cucumber, celery, and gai lan and shortest on pea and potato (Table 1). Pupal weights were significantly heavier on celery than on lettuce and cucumber; cucumber also had significantly lower pupal weights than gai lan and pea. There were no significant differences in pupal weights between pea, gai lan, lettuce, and potato. No significant difference in the proportion of adult emergence was detected among the six hosts tested in the laboratory.

No significant correlation was found between larval development time and pupal weight in analyses with all hosts pooled ($r = -0.18$, $n = 42$, $P > 0.20$) or when correlation analyses were conducted separately for each host. No significant correlations were found between proportion adult emergence and either larval development time ($r = -0.29$, $n = 42$, $P > 0.05$) or pupal weight ($r = 0.12$, $n = 42$, $P > 0.45$) in analyses with all hosts pooled or when analyses were conducted separately for each host.

Preference and Performance Relationships

In the colony subpopulation, no correlations were found between the preference measures and any of the performance measures (i.e., stippling density: larval development time, $r = -0.74$, $n = 6$, $P > 0.05$, pupal weight, $r = 0.25$, $n = 6$, $P > 0.50$, proportion adult emergence, $r = -0.51$, $n = 6$, $P > 0.25$; egg density: larval development time, $r = -0.26$, $n = 6$, $P > 0.60$, pupal weight, $r = -0.61$, $n = 6$, $P < 0.20$, proportion adult emergence, $r = -0.18$, $n = 6$, $P > 0.70$; proportion of oviposition punctures: larval development time, $r = 0.52$, $n = 6$, $P > 0.25$, pupal weight, $r = -0.69$,

$n = 6$, $P > 0.10$, proportion adult emergence, $r = 0.67$, $n = 6$, $P < 0.14$).

Discussion

Observed correlations between egg and stippling densities indicate that, regardless of how often a female chooses to lay an egg in a stipple, the response on a given host is relatively consistent and that either there is overlap in feeding and oviposition cues or feeding cues are used to determine host suitability for oviposition. For leafmining flies, the egg density measure does not represent host acceptability for oviposition alone, because this measure may confound density-dependent effects related to stippling that are unrelated to oviposition acceptability. Egg density is a more appropriate measure, however, than proportion of oviposition punctures for predicting the relative amounts of damage host plants will experience, and stippling damage can be used as an indicator of the presence of eggs. Where a consistent amount of oviposition occurs across a range of stippling densities, the proportion of oviposition punctures avoids stippling-dependent effects and is thus a more appropriate measure of oviposition preference than is egg density in these flies. Density measures are susceptible to bias related to the comparative size of the host leaf and of the sampling area. For example, gai lan had a very low acceptability according to the egg density measure, but when stippling occurred, gai lan was very acceptable for oviposition, as indicated by the high proportion of oviposition punctures on this host. Low stippling and oviposition densities on gai lan are explained by the pattern of stippling on this host: the majority of stipples occurred around the extreme perimeter of leaves, whereas the broad central leaf area was virtually untouched. This pattern is likely related to lower amounts of surface waxes on the leaf margins of brassicaceous plants (Bodnaryk 1992). A similar stippling pattern was observed on pea but was not reflected in the egg and stippling density measures in the same way as for gai lan because of differences in leaf size. A randomly placed 0.8-cm² sampling area on gai lan could fall near a leaf margin with high numbers of stipples or over a central portion of the leaf with no stipples; the same limitation of the density measures would have been apparent for pea, if a proportionately smaller sampling area had been used. Differential distribution of stipples and eggs among host plant species has been observed for *L. huidobrensis* on other hosts (Hammad and Nemer 2000). Where stippling patterns are not random on a leaf, the proportion of oviposition punctures is a better indicator of oviposition acceptability of a host than is egg density per leaf.

Differences in apparent host preference with these two oviposition measures support the occurrence of a sequential decision-making process in leafminers when determining oviposition acceptability of a host: i.e., a female first receives stippling cues from tarsal and/or ovipositor contact with the host plant and subsequently receives oviposition cues in the course

of stippling and/or feeding. The suggestion that stippling cues are obtained largely through contact chemoreception is supported by behavioral observations in which the presence of a surfactant on celery leaves decreased stippling by individual pea leafminer females (J. Levac and R. H. Hallett, unpublished data). Each successive stippling and oviposition event is apparently independent of the preceding stippling event and its outcome, as evidenced by the consistency seen for each host in the proportion of oviposition punctures among subpopulations.

The proportional measure of oviposition preference provided a more consistent assessment of preference in *L. huidobrensis* than did density measures. No consistent feeding or oviposition preferences were apparent from stippling and egg density measures, with the exception of a nonpreference for gai lan. Gai lan had lower stippling and egg densities than some or all other hosts in both the laboratory and the field. Mayhew (1998) observed similar results when *Sonchus arvensis* L. was consistently the least preferred host for oviposition by the chrysanthemum leafminer, *Chromatomyia syngenesiae* Hardy, whereas the most preferred host species differed in three separate tests. On the basis of the proportion of oviposition punctures, pea, celery, potato, and lettuce were consistently less preferred in the laboratory study than cucumber and gai lan, irrespective of subpopulation.

Relative oviposition preference for celery and potato was low, although both are major hosts of *Liriomyza* spp. on a global basis (Leibee 1984, Trumble 1985, Heinz and Chaney 1995, Weintraub and Horowitz 1998, Weintraub 2001), and rapid larval development on potato and high pupal weights suggest that both are suitable hosts. However, relative preference depends on the host complex being compared (Smyth et al. 2003); in a study of 47 host species, Wei et al. (2000) found that *Brassica* spp., *Lactuca* spp., *Allium* spp., pea, and celery all ranked within the top one-third of preferred plants for adult feeding. Alternatively, our results may be related to the cultivars employed, or the prevalence of pea leafminer in monocultures of these hosts may be caused by an absence of more highly preferred hosts and sufficient larval survival for population growth to occur.

Intraplant variation in stippling and egg densities was observed for some hosts but not others, indicating the importance of including multiple leaf strata in preference comparisons among hosts. For celery and cucumber, older leaves contained fewer stipples and eggs than intermediate and new leaves in the laboratory experiment. Pea leafminer preference for young celery leaves and plants may be related to higher nitrogen content (Minkenberg and Fredrix 1989, Bernays and Chapman 1994) or to lower furanocoumarin concentrations in young than old tissues (Diawara et al. 1995). Cucurbitacin concentrations in cucumber leaves are lower than in roots, fruits, and cotyledons (Metcalf et al. 1982), but relative concentrations among leaf tissues of different ages are undocu-

mented. The host plants examined here presented an array of chemical, nutritional, and morphological challenges to larvae, but pea leafminer larvae were able to survive and develop to pupation on a wide variety of hosts. Pea leafminer larvae may have broadly targeted detoxification systems that are capable of coping with various plant chemistries (Isman 1992), but differences in larval performance characteristics among hosts indicate that larvae are affected by the characteristics of the tissue in which they are developing.

The potential for population divergence in host preference has been shown for other *Liriomyza* species (Tavormina 1982, Via 1984, Via 1986), and a general principle proposed that insects that developed on a given host will show greater preference for that host than will conspecifics that developed on a different host (Tavormina 1982). After 8–12 generations of development on cucumber, lettuce, and pea, adults from the colony subpopulation did not exhibit any absolute preference for these hosts, nor was their preference for these hosts greater than that of the greenhouse and field subpopulations. A lack of preference–performance correlations, as observed in this study, may facilitate the maintenance of polyphagy and thus contribute to expansion of the geographic range of the pea leafminer.

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