THE QUANTITATIVE GENETICS OF POLYPHAGY IN AN INSECT HERBIVORE. I. GENOTYPE-ENVIRONMENT INTERACTION IN LARVAL PERFORMANCE ON DIFFERENT HOST PLANT SPECIES

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Agriculturalists have long been aware that a cultivar or variety which is superior in yield or performance in one location may not retain its relative advantage in other environments (Dickerson, 1962; Comstock and Moll, 1963; Finlay and Wilkinson, 1963; Allard and Bradshaw, 1964). Variation among genotypes in phenotypic sensitivity to the environment, known as genotype-environment interaction (henceforth g-e), presents a practical problem for breeders because it may mean that no genotype is uniformly superior in all environments, necessitating the development of locally adapted varieties (Falconer, 1952; Falconer and Latyszewski, 1952; Dickerson, 1962).

In the study of natural populations, genotype-environment interaction estimates how much genetic variation exists for the exploitation of different environments or habitats. The presence or absence of g-e in fitness components thus provides a statistical test to distinguish the case in which genotypes are "specialized" and have higher performance in certain environments from that in which they are "generalized" and have equivalent relative performance across environments. If no one genotype has highest fitness in all situations, then genotype-environment interaction suggests the potential for the genetic differentiation of populations under prolonged selection in different environments.

Despite the utility of genotype-environment interaction as a statistical criterion for environmentally related genetic variation, few experimental studies have estimated the magnitude of g-e for quantitative (polygenic) characters in non-crop situations (Breece, 1969; Orozoco, 1976; Zuberi and Gale, 1976; Antonovics and Primack, 1982; Gupta and Lewontin, 1982; Marks, 1982; Jaenike and Grimaldi, 1983; Futuyma et al., 1984). The dearth of formal estimates of genotype-environment interaction is especially surprising in plant-herbivore systems, where it has long been thought that specialization on particular host plants may involve some "tradeoffs" for specialist herbivores (Dethier, 1954). To date, most experimental approaches to specialization in herbivores have employed comparisons among closely related species (e.g., Bush, 1974; Scriber and Feeny, 1979; Futuyma and Wasserman, 1981) rather than the examination of intraspecific host-related variation (but see Edmunds and Alstad, 1978; Mitter et al., 1979; Tabashnik et al., 1981; Tavormina, 1982; Alstad and Edmunds, 1983; Singer, 1983). The use of explicit genetic techniques to test hypotheses about host plant-related specialization has just begun (Tabashnik et al., 1981; Service and Lenski, 1982; Jaenike and Grimaldi, 1983; Rausher, 1983; Futuyma et al., 1984).

This paper presents a quantitative genetic analysis of the relative performance on two host plants of individuals within and among closely adjacent populations of the polyphagous herbivore Liriomyza sativae (Diptera: Agromyzidae). Because polyphagous species use a number of different host plants, they are commonly

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called "generalists." This study tests whether individuals within such species are also generalists, that is, whether they exhibit the same relative capabilities on different hosts. Alternatively, individuals could vary genetically in performance across the species' host plant range, and thus be relative "specialists" (Van Valen, 1965; Roughgarden, 1972). Polyphagous species need not all have the same make-up: estimation of the relative magnitudes of genetic variation within and among populations on different host plants provides an experimental assessment of how extant levels of host plant specialization at the population or species level are produced from the capabilities of individuals. Furthermore, the magnitude of genetic variation for performance across plants indicates the potential for evolution in patterns of host plant use. However, it should be noted that intraspecific genetic variation for performance on different resources is just one measure of the potential for evolutionary change in host plant use; variation in host preference behavior and resource availability are other important factors (see Singer, 1983).

Variation in two larval components of fitness, pupal weight and development time, was partitioned here into genetic, environmental and g-e interaction components using a half-sib mating design. Genotype-environment interaction was used as a statistical criterion for the existence of genetic variation in larval performance across host plants both within and among adjacent populations. Genetic correlations of larval characters within and among host plants were also estimated (Via, 1984b).

METHODS

Organism and Study Site

Liriomyza sativae is a serious pest of many vegetable crops (Solanaceae: tomato, eggplant and bell pepper; Cucurbitaceae: watermelon and cucumber; Leguminosae: snap bean, lima bean and cowpea) (Oatman, 1959; Oatman and Michelbarger, 1959; Musgrave et al., 1975; Parella, 1983). The generation time of L. sativae is from 15–18 days at summer field temperatures. Because the crops on which these flies feed generally last for several months, from three to seven generations can pass in a given field during a single season. Little is known about migration rates among fields during the season, but it is possible that many eclosing adults simply stay in the same field and feed on the plants available there. Thus, selection could potentially operate within fields during a season to improve performance on particular crop plants. However, crop rotation precludes the possibility of any long term association between selected genotypes and particular crop species: each year, the location of suitable host plants changes. Because populations on different crops are essentially mixed at yearly intervals, the long term evolution of Liriomyza in Sampson Co. may depend upon genetic variation over a variety of different crops.

For these experiments, I chose two crop species which differ on chemotaxonomic grounds (Gibbs, 1974), tomato (Lyco-persicon esculentum, var. "UC82B," Petoseed Inc., Saticoy, CA) and cowpea (Vigna unguiculata, var. "Dixie Lee," Wyatt-Quarles Seed Co., Raleigh, NC). All field-collected flies were taken from these varieties, and test plants were grown in the greenhouse from single seed lots.

Field collections of larvae for the parental generation were made from two pairs of adjacent cowpea and tomato fields at sites 1.2 km apart near the town of Newton Grove, NC. This is an area of family farms in which vegetable crops are grown in small plots (5–5 hectares) among larger fields of corn, soybeans and tobacco. The collections were intentionally made within a small geographical area in order to study variation within and among subpopulations on a local scale. In this case, the estimates of genetic variation and correlation over all subpopulations combined can reasonably be in-
The experimental design (Fig. 1) involved the growth of sibling larvae on each of the two crops. The larvae collected for the parental generation were allowed to complete development in the leaves in which they were collected and were then isolated as pupae to produce virgin adults. Single-pair matings were performed within groups collected from the same field (henceforth, "populations") in a nested half-sib mating design: several females were mated to a single male to generate both full- and half-sib families (Comstock and Robinson, 1948; Falconer, 1981). Male half-sib families were used to derive estimates of the additive genetic components of variance, while the variance among progenies of females within males consists of a combination of dominance variance, epistatic variance, and maternal effects (Falconer, 1981 p. 143). Female half-sib families could not be produced because the details of sperm storage are not known for this species. Thus, maternal effects could not be estimated here.

Mated females were offered the plant species for feeding and oviposition in a no-choice situation, first one species, then the other in the next trial. The first species offered was determined at random. Each 24-hour trial occurred in a different individual cage in which a female was exposed to two individual greenhouse-grown plants in 7.6 cm pots. Cowpea plants were in the cotyledon stage, tomatoes were in the 2-3 leaf stage. Any larvae in excess of four per plant were destroyed so that the measurements of pupal weight and development time would not be confounded by the density-dependent competition which can occur with crowding in the leaves (Parella, 1983). Each female experienced two trials on each plant species, or four individual plants per species, to produce a max-
mum of 16 progeny per plant species. In practice, the family size per plant species ranged from 6–16 individuals and 2 or 4 plants, causing the dataset to be unbalanced.

During larval development, the plants were incubated at 28 °C under “Daylight” fluorescent lights. Larvae drop from the leaves to pupate on the ground, so leaves containing experimental larvae were excised and placed in separate petri dishes shortly before pupation. Pupal weight on the fourth day after pupation was measured on a Cahn Model 28 electrobalance to the nearest .1 μg. Development time was estimated as the number of hours between oviposition (arbitrarily set at six hours after introduction of the female to the oviposition cage) and eclosion, which was checked hourly during the period in which nearly all eclosion occurs (0800 to 1800). Survival was not analyzed because it was uniformly high on both plant species.

Statistical Analyses

Analysis of Variance.—Data were analyzed as a partially hierarchical two-way unbalanced analysis of variance (Brownlee, 1960). The interactions are of most interest in the study of host plant specialization. For example, while the main effect of sire encodes differences among families in the “average” environment, the “Sire×Host” interaction term tests variation in the relative performance of half-sib families on the different hosts.

In this design, the genotype-environment interaction within populations was partitioned into components representing both additive gene-environment effects (from the “Sire×Host” term) and non-additive gene-environment effects (from the “Dam×Host” term). The “Sire×Host,” or additive, component expresses the extent to which alleles vary in their relative effects in two environments when averaged over all possible gene combinations. In the absence of maternal effects, the non-additive interaction estimated from the “Dam×Host” term expresses the extent to which different allelic combinations within loci (the dominance component) or between loci (the epistatic component) vary in their relative effects on the phenotype across host plants. Both additive and non-additive g-e interaction in fitness components can thus be interpreted as expressing genetic variation for the use of different hosts.

Females that did not have surviving progeny on both plant species were eliminated from the analysis. This improved the balance of the design, but made the resulting estimate of the interaction somewhat conservative. To guard against the estimation of scale-dependent genotype-environment interaction (Bulmer, 1981 Ch. 4; Falconer, 1981 p. 267), independence of the variance and the mean for both characters was verified via regression using full-sib family groups as observations: no transformation was required (Wright, 1968 Ch. 10). All analyses were performed using Type IV sums of squares from the General Linear Models procedure in SAS; these are appropriate for an unbalanced design in which the factors are correlated because each sum of squares is calculated for a model which includes all the other effects (Freund and Littel, 1981). Type IV expected mean squares, which take the unequal cell sizes into account, were also generated by SAS. These were used to identify appropriate error terms for each factor. “Population,” “Sire” and “Dam” were taken as random effects. Host plant species was a fixed effect. Populations from the different crops were not distinguished; differences among them were left to simultaneous testing procedures. F tests are all approximate. Synthesis of mean squares via the Satterthwaite approximation had a negligible effect on the F ratios when Type IV sums of squares were used (less than a 2% change). In no case did the Satterthwaite method affect the significance level of the results, so the more straightforward approximate tests are presented.

Variance Component Estimation.—
Because of strong dependence on the degrees of freedom of each factor, the significance tests on the observed components of variance in the ANOVA do not fully reveal the relative contributions of the underlying causal components to the phenotypic variance. Thus, to augment the ANOVA, the components of variance were estimated by a modification of Henderson’s Method I (Searle, 1971), in which estimates of the observed components of variance were obtained by solving the system of simultaneous equations prescribed by the mean squares (Type IV) and their expectations. Then, the causal components of variance were estimated from the usual theoretical relationships between genetic variance and the observed variance among half- and full-sib families ( Falconer, 1981 Ch. 9):

\[
V_S = \frac{1}{4} V_A + \frac{1}{16} V_{AA} \tag{1}
\]

\[
V_{DS} - 2V_S = \frac{1}{4} V_D + \frac{1}{8} V_{AA}
+ \frac{1}{8} V_{AD} + \frac{1}{16} V_{DD}
+ V_M \tag{2}
\]

where \( V_S \) = observed variation among sires, \( V_{DS} \) = observed variation among dams, \( V_A \) = additive genetic variance, \( V_D \) = dominance genetic variance, \( V_{AA} \) = additive-additive epistatic variance, \( V_{AD} \) = additive-dominance epistatic variance, \( V_{DD} \) = dominance-dominance epistatic variance and \( V_M \) = the maternal effect. Although epistatic variation is included in all sib analyses, it is usually assumed to be negligible (Falconer, 1981). Because \( \frac{1}{2} \) of the additive and \( \frac{3}{4} \) of the dominance components of genetic variation are included in the error (\( 3V_{DS} - 4V_S \)) was subtracted from the observed error mean square to obtain an estimate of \( V_E \). The total phenotypic variance was estimated as the sum of the causal components.

Occasionally the analysis of variance method results in the estimation of negative variance components (Searle, 1971; Kennedy, 1981). Here, the components are presented both with negative components treated as zero and with the negative components added into the estimate of phenotypic variance. Estimates of the variance components are only unbiased if the negative components are retained (Searle, 1971).

Unfortunately, the standard errors for the variance components and functions of the components like the heritability and the genetic correlation are unknown for complicated designs when data are unbalanced (Sokal and Rohlf, 1981 p. 215; S. R. Searle, pers. comm.). The usual formulae (e.g., Kempthorne, 1957 p. 246) rely on independence of the estimated mean squares, which occurs only with balanced data (Searle, 1971). With the correlations among mean squares which are characteristic of unbalanced data, the estimated sampling variance is biased in unknown directions by an unpredictable amount. Rather than present incorrect standard errors, the components and heritabilities are presented here with no errors attached, and therefore must be interpreted as providing only a qualitative picture. In principle, it is possible to use a resampling technique like the “jackknife” (Arveson and Schmitz, 1970; Miller, 1974) or the “bootstrap” (Efron, 1979, 1982) to estimate standard errors for variance components in unbalanced designs. However, because these resampling techniques require repeated executions of the analysis, they were impractical in this large a design.

**Results**

**Pupal Weight.**—The analysis of variance for pupal weight (Table 1) illustrates that most of the variance in this character is found in the main effects, not in the interactions. First, a strong sexual dimorphism in pupal size exists in this species (“Sex,” \( P < .0001 \)). In addition, progeny derived from different populations varied in average pupal weight over the plant species (“Population,” \( P < .034 \), as did the full-sib progenies of different female parents (“Dam,” \( P < .039 \)). No significant additive genetic variance could be detected in pupal weight (“Sire,” \( P = .339 \)). The significant effect of host
 TABLE 1. Analysis of variance for pupal weight. Sex = sex of the larva in each observation; Sire = male parent; Dam = female parent; Population = field from which parents were collected; Host = host plant species on which larvae were tested; Repl(Dam·Host) = replicate plant within dam and host plant combination; Within Repl = different larvae on the same plant. Sire, Dam, Repl and Within Repl are all nested within Population. *: SS/10^4.

<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>Type IV SS</th>
<th>M#</th>
<th>F ratio</th>
<th>F</th>
<th>P &gt; F</th>
<th>R²</th>
</tr>
</thead>
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<td>26,927</td>
<td>M1/M11</td>
<td>5.71</td>
<td>.0001</td>
<td>.72</td>
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<tr>
<td>Sex</td>
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<td>12,575</td>
<td>M2/M21</td>
<td>621.00</td>
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<td>.0342</td>
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<td>.3390</td>
<td></td>
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<td>21</td>
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<td>2.31</td>
<td>.0388</td>
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<td>Host</td>
<td>1</td>
<td>196</td>
<td>M6/M61</td>
<td>162.00</td>
<td>.0012</td>
<td></td>
<td></td>
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<tr>
<td>Population·Host</td>
<td>3</td>
<td>3</td>
<td>M7/M71</td>
<td>.07</td>
<td>.6596</td>
<td></td>
<td></td>
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<tr>
<td>Sire·Host</td>
<td>23</td>
<td>320</td>
<td>M8/M81</td>
<td>.54</td>
<td>.9180</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Dam·Host</td>
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<td>548</td>
<td>M9/M91</td>
<td>1.35</td>
<td>.1666</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Repl(Dam·Host)</td>
<td>140</td>
<td>3,182</td>
<td>M10/M11</td>
<td>1.12</td>
<td>.1948</td>
<td></td>
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</tr>
<tr>
<td>Within Repl</td>
<td>495</td>
<td>10,024</td>
<td>M11</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
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<td>36,951</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

Plant species (“Host,” P < .001) demonstrates that the two crop species chosen for these experiments are indeed experienced as different environments by the average leafminer. For pupal weight, none of the interactions are significant.

Examination of the variance components (Table 2) shows that roughly \( \frac{1}{2} \) of the main-effect (or overall) genetic variance is due to maternal or non-additive genetic effects \( (V_{NA+M}) \), with the remaining \( \frac{1}{2} \) of the overall variance additive genetic \( (V_A) \). Maternal effects are somewhat more likely to be manifest in the main effects than in the interaction, and so some of the variance among full-sib families may be due to phenotypic differences among the mothers rather than to genetic variation. The variance components also indicate that the additive and non-additive interactions together comprise 37.9% of the total phenotypic variance.

TABLE 2. Components of variance for pupal weight. Observed components are the components calculated directly from the ANOVA. \( V_{error} \) includes both variation among larvae within replicate plant and variation among replicate plants. \( V_{pop} \) = site of collection; \( V_{sire} \) = male parent; \( V_{dam}/sire \) = female parent; \( V_{host} \) = host plant species. Causal components were estimated using the techniques outlined in the Methods. \( V_A \) = additive genetic variance; \( V_{(NA+M)} \) = nonadditive genetic variance plus maternal effect; \( V_{(A)} \) = additive genetic component of genotype-environment interaction; \( V_{(NA+M)} \) = nonadditive component of genotype-environment interaction; \( V_p \) = total phenotypic variance.

<table>
<thead>
<tr>
<th>Observed components</th>
<th>Component</th>
<th>Negative components = 0 (%</th>
<th>Negative components added (%</th>
</tr>
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<tbody>
<tr>
<td>( V_{pop} )</td>
<td>( V_{pop} )</td>
<td>4.7</td>
<td>5.7</td>
</tr>
<tr>
<td>( V_{sire} )</td>
<td>( V_A )</td>
<td>14.4</td>
<td>17.4</td>
</tr>
<tr>
<td>( V_{dam}/sire )</td>
<td>( V_{NA+M} )</td>
<td>13.7</td>
<td>16.7</td>
</tr>
<tr>
<td>( V_{host} )</td>
<td>( V_{host} )</td>
<td>3.0</td>
<td>3.6</td>
</tr>
<tr>
<td>( V_{pop-host} )</td>
<td>( V_{pop-host} )</td>
<td>0</td>
<td>-1.0</td>
</tr>
<tr>
<td>( V_{sire-host} )</td>
<td>( V_{(A)} )</td>
<td>0</td>
<td>-20.4</td>
</tr>
<tr>
<td>( V_{dam/sire-host})</td>
<td>( V_{(NA+M)} )</td>
<td>48.0</td>
<td>58.3</td>
</tr>
<tr>
<td>( V_{error} )</td>
<td>( V_{error} )</td>
<td>16.8</td>
<td>19.5</td>
</tr>
<tr>
<td></td>
<td>( V_p )</td>
<td>344,945</td>
<td>284,128</td>
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Table 3. Analysis of variance for development time. See legend for Table 1.

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<tr>
<th>Source</th>
<th>d.f.</th>
<th>Type IV SS</th>
<th>M#</th>
<th>$F$ ratio</th>
<th>$F$</th>
<th>$P &gt; F$</th>
<th>$R^2$</th>
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<td>Model</td>
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<td>231,879</td>
<td>M1</td>
<td>M1/M11</td>
<td>3.81</td>
<td>.0001</td>
<td>.64</td>
</tr>
<tr>
<td>Sex</td>
<td>1</td>
<td>239</td>
<td>M2</td>
<td>M2/M11</td>
<td>.92</td>
<td>.3379</td>
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<tr>
<td>Population</td>
<td>3</td>
<td>837</td>
<td>M3</td>
<td>M3/M4</td>
<td>11</td>
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<tr>
<td>Sire</td>
<td>22</td>
<td>58,058</td>
<td>M4</td>
<td>M4/M5</td>
<td>3.04</td>
<td>.0084</td>
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<tr>
<td>Dam</td>
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<td>M5/M9</td>
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<td>Host</td>
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<td>M6/M7</td>
<td>13.34</td>
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<tr>
<td>Population•Host</td>
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<td>3,301</td>
<td>M7</td>
<td>M7/M8</td>
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<td>Sire•Host</td>
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<td>25,301</td>
<td>M8</td>
<td>M8/M9</td>
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<td>Dam•Host</td>
<td>18</td>
<td>14,496</td>
<td>M9</td>
<td>M9/M10</td>
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<td>Repl(Dam•Host)</td>
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<td>65,538</td>
<td>M10</td>
<td>M10/M11</td>
<td>1.79</td>
<td>.0001</td>
<td></td>
</tr>
<tr>
<td>Within Repl</td>
<td>495</td>
<td>129,193</td>
<td>M11</td>
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<tr>
<td>Total</td>
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<td>361,073</td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

variation even though neither interaction was estimated to be significant by the ANOVA. Finally, although the variation among populations and the effect of host plant species were significant in the analysis of variance, the variance component analysis illustrates that they contribute in only minor ways to the total phenotypic variation in pupal weight ($V_{pop} = 4.7\%$, $V_{host} = 3.0\%$).

Development Time

In the main effects, the estimation of significant variation among sires for development time (Table 3, “Sire,” $P < .008$) indicates the presence of overall additive genetic variance in this character. This suggestion is upheld in the estimated variance components (Table 4), which reveal that 26.7–63.2% of the total phenotypic variance in development time is additive genetic. The significant main effect of host plant species, in contrast, comprises only 6.8–16.1% of the total variance. At present, the cause of the large negative component of variation among dams is unclear, although it is large enough to warrant some further examination. In contrast to pupal weight, no sexual dimorphism was estimated for development time (“Sex,” $P = .3379$, Table 4), and variation among populations contributed virtually nothing to the total phenotypic variance.

Genotype-environment interaction in development time was detected within populations in the analysis of variance (Table 3) at the level of dams (“Dam•Host,” $P < .041$). Examination of the variance components (Table 4)

Table 4. Components of variance for development time. See legend for Table 2.

<table>
<thead>
<tr>
<th>Observed components</th>
<th>Component</th>
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<th>Negative components added (%)</th>
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</thead>
<tbody>
<tr>
<td>$V_{pop}$</td>
<td>$V_{pop}$</td>
<td>-20.63</td>
<td>-20.63</td>
</tr>
<tr>
<td>$V_{sire}$</td>
<td>$V_A$</td>
<td>69.69</td>
<td>278.72</td>
</tr>
<tr>
<td>$V_{dam/sire}$</td>
<td>$V_{N+M}$</td>
<td>3.81</td>
<td>-542.28</td>
</tr>
<tr>
<td>$V_{host}$</td>
<td>$V_{host}$</td>
<td>71.20</td>
<td>71.20</td>
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<tr>
<td>$V_{pop•host}$</td>
<td>$V_{pop•host}$</td>
<td>1.20</td>
<td>1.91</td>
</tr>
<tr>
<td>$V_{sire•host}$</td>
<td>$V_{(A)}$</td>
<td>31.10</td>
<td>124.39</td>
</tr>
<tr>
<td>$V_{dam/sire•host}$</td>
<td>$V_{(N+M)}$</td>
<td>52.77</td>
<td>-37.72</td>
</tr>
<tr>
<td>$V_{error}$</td>
<td>$V_{error}$</td>
<td>333.35</td>
<td>566.77</td>
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<tr>
<td></td>
<td>$V_P$</td>
<td>1043.0</td>
<td>442.3</td>
</tr>
</tbody>
</table>
shows that from 11.9–28.1% of the phenotypic variance is additive genotype-environment interaction variance.

From an evolutionary perspective, a particularly important case of genotype-environment interaction involves a change in rank of genotypes in different environments. In such a case, if selection were to proceed separately in several environments, the selected populations would be expected to have different genetic constitutions. Such “crossing” interaction (sensu Haldane, 1946) is thus one way in which local genetic substructuring of populations within species can occur under selection in heterogeneous environments.

One way to check for changes in genotypic rank beyond the analysis of variance is to graphically construct the norms of reaction, that is, the mean phenotype for each family on the two hosts (Schmalhausen, 1949; Gupta and Lewontin, 1982). An analysis of the variance structure within host plants can then provide a test of whether families retain their relative positions in the alternate environment. The extent of the “additive” genotype-environment interaction (due to interaction at the level of sire) can be seen in the reaction norms plotted in Figure 2.

Although 11.9–28.1% of the phenotypic variance was attributed to additive genotype-environment interaction (Table 4), Figure 2 indicates that no significant changes in rank occur for the families which have variant slopes. In contrast, the overall additive genetic variance in development time is seen quite clearly here: the half-sib families with the shortest and longest development times retained their ranks in the two environments. In addition, the environmental main effect (“Host” in Table 4) can be seen as a shorter average development time on tomato.

A different picture emerges when the responses of full-sib families are plotted in this way (Fig. 3). Because of the large number of full sib families, they are plotted by population (field in which the parents were collected). Separate analyses of variance for full-sib families from each population revealed that interaction variance was only found in populations from Site I (Table 5). In panels A and B of Figure 3, several examples can be seen of families in these populations (indicated by arrows) which were average on one of the crops but which had significantly longer or shorter development times when they developed on the other crop. Panel C illustrates the overall genetic variation estimated in the pea population at the other location (Table 5, Site 2, “Family,” $P < .001$).

The Spearman rank correlations of full-sib family means for development time on the two plant species provide an additional estimate of the changes in family ranking, and are indicated on Figure 3. These non-parametric rank tests generally substantiate the results of the analyses of variance and the graphical analyses: when there is significant genotype-environment interaction and/or the lines cross, the genotypic rank in tomato can-
not be predicted by knowing the rank in pea (Fig. 3A, B, D).

In contrast to the variation seen within populations, much less variation exists among the means of the different populations (Fig. 4). Comparison of Figures 3 and 4 illustrates that the genetic variation in performance across host plants which was seen within populations might well have been overlooked had the analyses focused instead on variation among the mean values of populations on the two plant species.

**DISCUSSION**

This study employed the formal techniques of quantitative genetics to ask a specific question: are individuals within a polyphagous species genetically generalized in performance on different host plants? In so doing, estimates of the magnitude of quantitative genetic variation in host plant related characters were produced. These parametric estimates supplement the qualitative evidence, chiefly from population crosses and selection experiments, that characters associated with host plant use in herbivores and pathogens are indeed genetically based (Smith, 1941; Gallun et al., 1961; Hatchett and Gallun, 1970; Knerer and Atwood, 1973; Day, 1974; Groth and Person, 1977; Gould, 1979; Wasserman and Futuyma, 1981; Pathak and Heinrichs, 1982; Jae-nike and Grimaldi, 1983; Futuyma et al., 1984). The study of genetic mechanisms of insect-host plant evolution requires quantitative estimates of several popu-
Table 5. Analysis of variance for development time by site and population. Sites are pairs of adjacent cowpea and tomato fields which are 1.2 km apart; Sex = sex of the larva in each observation; Family = full-sib family; Host = host plant species in which larva was tested; Repl = individual plant of a particular species; Within Repl = different larvae on a single plant. Repl is nested within Family × Host combination. \( * P < .05, \) \( ** P < .01, \) \( *** P < .001. \)

<table>
<thead>
<tr>
<th>Source</th>
<th>Pea Site 1</th>
<th>Tomato Site 1</th>
<th>Pea Site 2</th>
<th>Tomato Site 2</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>SS</td>
<td>F</td>
<td>R²</td>
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<tr>
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<td>46,657</td>
<td>4.07</td>
<td>.67</td>
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<tr>
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<td>1.33</td>
<td>.87</td>
</tr>
<tr>
<td>Family</td>
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<td>23,383</td>
<td>2.00</td>
<td>.87</td>
</tr>
<tr>
<td>Host</td>
<td>1</td>
<td>268</td>
<td>.28</td>
<td>.87</td>
</tr>
<tr>
<td>Family × Host</td>
<td>11</td>
<td>10,715</td>
<td>2.99*</td>
<td>.51</td>
</tr>
<tr>
<td>Repl</td>
<td>33</td>
<td>10,764</td>
<td>1.69†</td>
<td>.51</td>
</tr>
<tr>
<td>Within Repl</td>
<td>117</td>
<td>23,102</td>
<td>120</td>
<td>21,500</td>
</tr>
<tr>
<td>Total</td>
<td>175</td>
<td>76,960</td>
<td>166</td>
<td>78,106</td>
</tr>
</tbody>
</table>

This seems reasonable to consider genetic parameters with shorter development times.
on one host than another as “specialized.” The conclusion that the genetic specialization of *L. sativae* on different hosts has potential evolutionary consequences is valid even if the genetic variance in the “Dam-Host” term is primarily non-additive. First, the proportion of additive and dominance variance depends on gene frequency (Falconer, 1981 p. 118), and secondly, it is known that non-additive variance can be involved in differentiation of partially subdivided populations (Crow and Kimura, 1970 p. 244).

**Genotype-environment Interaction and “Host Races”**

Figures 3A and 3B illustrate that genotypes did change rank in development time on the two hosts: several genotypes which were average on one of the plant species were either slower or faster than others when reared on the alternate plant species. Thus, populations of this species could diverge in genetic composition under prolonged selection on different hosts even if the same value of the phenotype were favored in each environment; different genotypes would be expected in the selected group on each plant. However, no population-level specialization was observed here. Genetic variation was within populations on different crops, not between them (Table 3).

Although genotype-environment interaction provides the potential for population-level specialization, the degree to which herbivore populations on different host plants actually diverge to form so-called “host races” (e.g., Jaenike, 1981) must depend also on the migration rate among host plants. The flies for this study were sampled from an extremely diverse agricultural system of small plots in which the suitable vegetables change location every year, replaced by unsuitable crops like soybeans or tobacco. Crop rotation may result in massive “migration” due to yearly mixing of genotypes from different crops during spring colonization, and could preclude divergence among populations in different fields by setting the response to selection back at the beginning of each season. Thus, little progress might be made, even if selection within fields was largely unopposed by migration during a season. In contrast, in a more homogeneous cropping situation where large acreages of single varieties are grown in the same location for several years, one might expect migration from alternate crops to be lower and to find a larger amount of crop-related specialization than was seen here. Such long-term continuity between insect populations and host plants may partially explain why most current examples of host races involve tree-feeding species (e.g., Knerer and Atwood, 1972, 1973; Bush, 1974, 1975; Phillips and Barnes, 1975; Edmunds and Alstad, 1978).

A “host race” can be defined as a group of individuals which genetically differ in host plant related characters from individuals on other hosts, and which do not interbreed with individuals from other groups due to divergent host preferences (Jaenike, 1981). A “Population-Host” interaction in an experimental design in which populations are collected from different hosts provides a statistical test for the existence of specialization at the population level (c.f. Jaenike, 1981). If individuals within populations are also monitored, as they were here, much more information can be garnered: genotype-environment interaction, that is, specialization at the individual level, can be detected even if populations on the whole are not specialized.

**The Need for Multi-environment Genetic Studies**

In simplest outline, the detection of genotype-environment interaction means that the effects of genotype and environment are not independent. Therefore, because genotypes can vary in the magnitude and direction of phenotypic change which they experience across environments, the estimation of genetic variation in only a single environment may be inflated because genetic variation and genotype-environment interaction vari-
ance are pooled in the observed variance among families (Brownlee, 1960; Comstock and Moll, 1963; Gupta and Lewontin, 1982; Via, 1984a). Figure 3A illustrates this point. If the variance among families were estimated only in cowpeas, then the estimated "heritability" would predict the response to selection only if it occurred on peas in the absence of migration from populations selected on other crops: such migrants have high performance only in the environment in which they were selected, and are likely to reduce the population mean in other environments. Therefore, to get an interpretable estimate of genetic variation, one must either assume that genotype-environment interaction is not present, or explicitly estimate its magnitude by replicating genotypes (or family members) across environments. For organisms in heterogeneous environments, only studies which address the possibility of genotype-environment interaction will produce realistic estimates of the genetic parameters required for microevolutionary theory (e.g., Lande, 1979, 1982; Via and Lande, in prep.).

Lewontin (1974) and Gupta and Lewontin (1982) have argued that the genotype-environment interaction term in the analysis of variance is less useful than is the norm of reaction, that is, the graphical representation of the response of each genotype to a change in the environment. However, the reaction norms taken alone are not statistically testable. A joint approach seems necessary. For an evolutionary interpretation, the most useful way to view gene-environment interactions mathematically is in the context of genetic correlations between the expression of characters across environments. This subject is considered in a companion paper (Via, 1984b).

The actual intensity of selection on L. sativae in the field is unknown at present, as is the extent of migration among crops. Although the information currently available on characters involved with host plant use is simply too limited to predict the detailed evolutionary trajectory of L. sativae, this experiment demonstrates that genotypes within this species are non-uniform in their relative capabilities on different host plants. The variation among genotypes within this "generalist" species thus makes it a likely candidate for evolutionary change in its host plant relations at some future time.

SUMMARY
Within a polyphagous species, individuals may either be generalists or be genetically variable in their capabilities on different potential hosts. Using the pest species Liriomyza sativae (Diptera: Agromyzidae), the hypothesis that individuals are generalized was tested by estimating the extent of overall genetic variation and genotype-environment interaction in pupal weight and development time for siblings reared on two plant species. Parents of the test larvae were sampled from closely adjacent fields of the two crops. The existence of significant genotype-environment interaction for development time within populations suggests that directional or stabilizing selection on either crop separately could lead to differences in the genetic composition of populations, and thus, to the evolution of genetically based host plant specialization at the population level. However, populations originating from the two crops differed very little in average responses to the two plant species, indicating that population divergence has not occurred in this system. The absence of "host races" in this species may be due to frequent migration among crops, given the close spatial proximity of the test fields and yearly crop rotation.

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