

THE EVOLUTION OF RESISTANCE TO HERBIVORY IN *IPOMOEA PURPUREA*. I. ATTEMPTS TO DETECT SELECTION

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Abstract.—In this study, we looked for evidence of directional or stabilizing/disruptive selection on plant size and on the level of damage (resistance) caused by four types of herbivores in the annual morning glory *Ipomoea purpurea*. Selection was estimated by standard phenotypic regression analysis and by regression on breeding values. The phenotypic regression analysis revealed directional selection for all five characters (i.e., plant size and resistance to four types of herbivores) and indicated that plant size and resistance to corn-earworm damage were subject to stabilizing selection. By contrast, the analysis using breeding values revealed directional selection only for plant size and resistance to corn earworms, while none of the characters examined indicated stabilizing or disruptive selection. These results suggest that intermediate levels of damage in *I. purpurea* are, in general, not maintained by stabilizing selection. Rather, they may reflect either 1) a transient state that exists while directional selection pushes the population toward complete resistance (or, in one case, total absence of resistance) or 2) the evolution of susceptibility to damage by genetic drift.

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Several recent studies on natural plant populations have documented genetic variation in resistance to feeding by herbivores, particularly insects (Jones et al., 1978; Moran, 1981; Dirzo and Harper, 1982; Kinsman, 1982; Berenbaum et al., 1986; Fritz et al., 1986; Simms and Rausher, 1987, 1989). Such variation indicates that selection could either increase or decrease the mean amount of damage experienced by a plant. These observations are puzzling, because it is generally believed that damage by herbivores reduces plant fitness (Ehrlich and Raven, 1964; Mattson and Addy, 1975; Harper, 1977; Morrow and LaMarche, 1978; Janzen, 1979; Rausher and Feeny, 1980; Berenbaum, 1983; Futuyma, 1983; Crawley, 1983; but see Paige and Whitham [1987]). It might be expected, therefore, that natural selection would tend to decrease the mean level of damage (increase mean level of resistance) until all plants become completely resistant (no damage) or until additive genetic variation for resistance is depleted. This apparent paradox may be explained by any of the following hypotheses.

i) Genetic variation for damage is not sub-

ject to selection.—Several recent studies indicate that some plants may tolerate at least moderate amounts of feeding damage (Crawley, 1983; Paige and Whitham, 1987) without experiencing reductions in fitness. Under such circumstances, genotypes that reduce damage will not increase plant fitness. If there is also no cost associated with resistance, genetic variation for resistance (and hence for amount of damage) may be selectively neutral. If so, genetic variation for damage may persist for long periods, especially in large populations, and hence mean levels of damage may remain intermediate between those characteristic of complete resistance and those characteristic of total absence of resistance.

ii) An intermediate level of damage is maintained by stabilizing selection.—Stabilizing selection on the level of damage could occur if the factors underlying resistance are costly for plants to produce. Several workers have suggested that intermediate levels of resistance may often be maintained in plant populations by genetic trade-offs between the benefits (damage reduction) and costs (diversion of resources away from other characters that enhance fitness) associated with increasing allocation of resources to some resistance factor (Janzen, 1973a, 1973b; McKey, 1974; Feeny, 1976; Rhoades, 1979, 1983; Krischik and Denno, 1983; Coley et al., 1985). Simms

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and Rausher (1987) formalized these arguments and showed that stabilizing selection on the underlying resistance factor will occur when a) benefit levels off as allocation to resistance increases, b) cost is a linear or concave upward function of allocation to resistance, and c) fitness is higher for slightly resistant genotypes than for genotypes lacking resistance completely. The leveling off of benefit should occur, because at some allocation to resistance all herbivores are deterred, and further allocation to resistance will not reduce damage. If benefit increases linearly with allocation to resistance until leveling off occurs, the optimal genotype will correspond to complete resistance, and stabilizing selection will not favor an intermediate (nonzero) level of damage. However, if benefit increases at a decreasing rate, the optimal genotype will correspond to incomplete resistance, and stabilizing selection will favor an intermediate level of damage. Such declining marginal benefit may be expected when there is variation in the herbivore population for the level of allocation that is repellent or toxic.

iii) An intermediate level of damage is a transient state that occurs while directional selection moves the population toward complete resistance (or toward absence of resistance).—Such a nonequilibrium situation might arise, for example, if a species of herbivore has recently colonized an originally primarily nonresistant plant population that has some genetic variation for resistance. It might also be observed if genetic variation for resistance has recently arisen in a population with an established herbivore population.

These three hypotheses may be distinguished by determining the type of selection acting on the level of damage (or resistance). (In keeping with common usage, [Painter, 1958; Beck, 1965; Carter, 1973; Horber, 1980], we define resistance operationally as the inverse of the proportion of foliage or pods damaged by herbivores.) Detection of stabilizing selection on damage would indicate that hypothesis ii is correct. By contrast, the occurrence of directional selection but not stabilizing selection would support hypothesis iii, while absence of both types of selection is consistent with hypothesis i.

The annual morning glory *Ipomoea pur-*

purea exhibits additive genetic variation for the percentage of leaf damage caused by four species of herbivorous insects and for number of seeds produced (fitness) (Simms and Rausher, 1987, 1989). The population we have studied is thus presumably capable of evolving a lower mean level of damage (increased resistance). The purpose of this study was to determine, at least in part, why this has not occurred. In particular, we attempted to distinguish among the three hypotheses presented above by determining the type and magnitude of selection operating on amount of damage.

MATERIALS AND METHODS

Organisms and Study Site

The plant-herbivore system we examined consisted of the annual morning glory *Ipomoea purpurea* and its main insect herbivores. These include specialists on the foliage of several genera in the Convolvulaceae: adults of the sweet-potato flea beetle *Chaetocnema confinis* (Chrysomelidae) (Jones et al., 1979; Rosenthal, 1985) and adults and larvae of the tortoise beetles *Deloyala guttata* and *Metriona bicolor* (Chrysomelidae). Generalist herbivores include larvae of the corn earworm, *Heliothis zea* Boddie (Lepidoptera: Noctuidae), which feed on the flowers and developing fruit of *I. purpurea*, and miscellaneous foliage-feeding generalists, primarily orthopterans.

The study site was an old agricultural field in Durham County, NC that had last been planted in soybeans in 1983 but has since only been disked every spring. A haphazard sample of seeds from this field was grown in the greenhouse and used in the experimental crosses described below.

Experimental Design

The plants used were a subset (control treatment) of those analyzed by Simms and Rausher (1989). Seeds were obtained from a replicated partial diallel cross, with each diallel involving a different set of ten parental plants. Within a diallel, each plant was used as a seed parent in crosses with five other plants and as a pollen parent in crosses with five other plants. This design yielded one reciprocal cross involving each plant and one other plant in the same diallel

(see Simms and Rausher, 1987). Because two plants failed to produce seed in time for the experiment, there were ultimately 2,840 experimental seeds from 140 full-sib families (which in turn were distributed among 30 male half-sib and 28 female half-sib families).

Seeds were germinated in Roottrainers® filled with potting mix. In late July 1985, when the seedlings had reached the two-leaf stage (about one week after germination), they were transplanted into the field, with seedlings from each full-sib family allocated randomly to four spatial blocks. Native vegetation in the field was not weeded during the experiment. Approximately two-fifths of the plants were destructively sampled for chemical analysis and, therefore, were not censused. Offspring of all families were represented in approximately equal numbers.

In late August we estimated damage as the proportion of the total leaf area missing due to feeding by folivores. For this estimation, a clear plastic grid with 0.59 cm² squares was placed over each leaf. The numbers of squares, to the nearest quarter, that covered damaged and undamaged portions of a leaf provided estimates of the area of each leaf prior to attack and the extent of folivore damage to each leaf. Because leaf margins were seldom damaged, the estimates of predamage areas were accurate. Since flea beetles and tortoise beetles each cause distinctive leaf damage, we were able to measure damage separately for each of three categories of folivores: 1) flea beetles, 2) tortoise beetles, and 3) other (generalist) insects. Damaged and predamage areas were summed over all leaves on a plant to yield total damage in each category and plant size (total leaf area), respectively. The proportion damage was then determined by dividing total area damaged by total leaf area. Because the damage census was conducted before any leaves senesced, we did not need to correct this measure for senescence. The proportion damage to pods was determined in similar fashion from a census of damaged and undamaged pods in late September. All proportions were arcsine(square root)-transformed prior to analysis (Sokal and Rohlf, 1969 pp. 386–387).

Fitness was measured operationally by

collecting and counting all seeds produced by the experimental plants, including those that died before producing seeds. Seed production ended with the first killing frost on 7 December 1985. Seeds that were obviously dead were not counted. Germination assays indicated that more than 95% of seeds counted as living were alive. Because this fitness measure incorporates the effects of mortality over most of the growing season, it is probably a reasonable estimate of true fitness. However, we note that this measure does not include mortality that occurs during the first week after germination, nor does it explicitly include any effects of differences among plants in success as pollen donors.

Statistical Analysis

To determine the type and magnitude of selection acting on damage, we employed the partial-regression analysis described by Lande and Arnold (1983). In this analysis, selection gradients represent selection that acts directly on a particular character. We obtained the directional selection gradient, β_i , on character i from the partial-regression coefficients of a linear regression of the characters on relative fitness, w (i.e., absolute fitness divided by mean fitness), using the model

$$w = \sum_{i=1}^n \beta_i z_i + \text{error} \quad (1)$$

where z_i is the value of character i . We obtained stabilizing/disruptive selection gradients from the second-order coefficients, γ_{ij} , of a quadratic regression on relative fitness using the model

$$w = \sum_{i=1}^n \beta'_i z_i + \sum_{i=1}^n \sum_{j>i}^n \left(1 - \frac{1}{2} \delta\right) \gamma_{ij} z_i z_j + \text{error} \quad (2)$$

where $\delta = 1$ if $i = j$ and 0 otherwise. In general, if the distribution of \mathbf{z} departs from multivariate normal, $\beta_i \neq \beta'_i$. In this case, (1) provides the best estimates of the directional selection gradient, while (2) provides the best estimate of the surface of selective values, or "adaptive landscape." The significance of each parameter in (1) was de-

TABLE 1. Phenotypic and breeding-value correlations among total (predamage) leaf area and the proportion damaged by herbivores. Proportions were arcsine(square root)-transformed for analysis. Values above the diagonal are phenotypic correlations. Values below the diagonal are breeding-value correlations.

Trait	Trait				
	Leaf area	Herbivore damage			
		Corn earworm	Flea beetle	Tortoise beetle	Generalist insect
Leaf area	—	0.038	-0.118****	0.209****	0.151****
Herbivore damage:					
Corn earworm	-0.136	—	0.133****	0.048	0.034
Flea beetle	0.248	-0.088	—	-0.055*	-0.093****
Tortoise beetle	0.308	0.080	-0.041	—	0.077**
Generalist insect	0.053	0.294	-0.185	0.204	—

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; **** $P < 0.0001$.

terminated after the effects of all other parameters had been removed. For determining whether the quadratic terms in (2) contribute significantly, we first assessed whether the full model [Eq. (2)] provided a significantly better fit to the data than the reduced model [Eq. (1)], as suggested by Mitchell-Olds and Shaw (1987). If so, we then determined which quadratic parameters were significant, using the Bonferroni criterion (Timm, 1975 pp. 165–166) to correct for multiple comparisons.

This analysis was performed using individual plants as the units, in standard fashion. Because of the large number of individuals in our experiment, the sensitivity of this analysis to detect selection should be high. There are two potential problems with such a phenotypic analysis, however. First, environmental correlations (*sensu* Falconer, 1981 pp. 281–284) between characters and fitness may yield inaccurate estimates of selection (Price et al., 1988). A second, related problem pertains to measurement of stabilizing/disruptive selection on damage. In Simms and Rausher's (1987) model, stabilizing selection arises from a negative genetic correlation between resistance and some other (unknown) trait that is positively genetically correlated with fitness. Environmental correlations between resistance and that trait or between that trait and fitness may cause the corresponding phenotypic correlations to differ in sign from the genetic correlations. If this occurs, stabilizing selection on resistance may not be detected in a phenotypic analysis even

though it acts on the underlying genetic variation for resistance and vice versa.

One solution to this problem is to eliminate the effects of environmental correlations by examining selection acting directly on breeding values (Crow and Nagylaki, 1976; Rausher, unpubl.). A multivariate regression of fitness on the traits, using breeding values, yields partial-regression coefficients analogous to those in the phenotypic analysis. These coefficients, however, indicate how fitness changes as the breeding value of each trait is altered. They thus represent selection acting on additive genetic variation for a trait, with the breeding values of other traits held constant.

We estimated breeding values for a trait as twice the deviation of the paternal half-sib family mean from the population mean (Falconer, 1981 p. 106). The resulting family-mean regression coefficients, like family-mean correlations, converge to the true regression coefficients for breeding values as the number of individuals per family increases (Arnold, 1981; Via, 1984). With half-sib family sizes of 50–60 individuals, our family-mean regression coefficients should be relatively unbiased (Arnold, 1981).

The estimates of selection gradients from the two analyses were compared using the model

$$w = \mathbf{x}^T \mathbf{B}_1 + (\mathbf{x} - \mathbf{z})^T \mathbf{B}_2 + \text{error},$$

where \mathbf{x} is the vector of estimated breeding values of the traits (or their squares and products when comparing stabilizing/disruptive/correlational selection gradients) for

TABLE 2. Directional (β) and stabilizing/disruptive selection gradients (γ) from phenotypic analysis. β' is the linear partial-regression coefficient of fitness on damage for character i in a multivariate quadratic regression. Values in parentheses are standard errors. The model and error sums of squares (and degrees of freedom) were 635.14 (5) and 860.25 (1,491), respectively, for the linear model, and these were 706.21 (20) and 789.19 (1,476) for the quadratic model. The significance levels noted below are the Bonferroni criteria for individual parameters for an overall significance level of $P < 0.05$.

Character	γ						
	β	β'	Herbivore damage				
			Leaf area	Corn earworm	Flea beetle	Tortoise beetle	Generalist insect
Leaf area	0.008 ^a (0.003)	0.010 ^b (0.0004)	-0.0000070 ^b (0.0000024)	-0.0025 ^b (0.0005)	0.001 (0.001)	-0.003 ^b (0.001)	-0.003 ^b (0.001)
Herbivore damage:							
Corn earworm	-0.119 ^a (0.026)	0.108 (0.046)	-0.0025 ^b (0.0005)	-0.3584 ^b (0.0546)	-0.013 (0.054)	0.002 (0.088)	0.107 (0.097)
Flea beetle	0.238 ^a (0.043)	0.249 ^b (0.044)	0.001 (0.001)	-0.013 (0.054)	0.077 (0.144)	0.345 (0.160)	0.061 (0.154)
Tortoise beetle	-0.169 ^a (0.070)	-0.079 (0.113)	-0.003 ^b (0.001)	0.002 (0.088)	0.345 (0.160)	-0.346 (0.285)	0.078 (0.273)
Generalist insect	-0.285 ^a (0.074)	-0.559 ^b (0.118)	-0.003 ^b (0.001)	0.107 (0.097)	0.061 (0.154)	0.078 (0.273)	0.994 (0.359)

^a $P < 0.01$; ^b $P < 0.0025$.

a plant's half-sib family, \mathbf{z} is the analogous vector of phenotypic values for an individual, and \mathbf{B}_1 and \mathbf{B}_2 are vectors of regression coefficients. The hypothesis $\mathbf{B}_1 = \mathbf{B}_2$, which was tested using standard contrasts for linear models (Searle, 1971 pp. 199–204), is equivalent to the hypothesis that the selection gradients estimated by the phenotypic and breeding-value analyses do not differ (D. Burdick, pers. comm.).

RESULTS

Pairwise comparisons among degrees of damage caused by each type of herbivore and plant size (leaf area) indicate that these characters are phenotypically correlated (Table 1). Although the correlations are not strong (all are less than 0.21), five are highly significant ($P < 0.0001$). Consequently, multiple regressions of fitness on all traits are more appropriate than separate analyses of each trait for estimating selection gradients (Lande and Arnold, 1983).

The phenotypic analysis indicates that directional selection acted on all characters examined (β_i values in Table 2). Selection favored increased damage by flea beetles, decreased damage by all other folivores, and increased plant size. Addition of quadratic terms to the regression significantly im-

proved the fit of the regression model ($F_{[15, 1,476]} = 8.852$, $P < 0.001$), indicating that stabilizing, disruptive, or correlational selection acted on some of the traits. Stabilizing selection, indicated by negative values of γ_{ii} (Table 2), was significant only for plant size and damage caused by corn earworms. Analysis of damage due to other types of insects did not indicate stabilizing or disruptive selection.

Although the fitness surface represented by Equation (2) cannot be portrayed (it is a five-dimensional surface in six-dimensional space), it is possible to portray sections through that surface. Each curve in Figure 1 shows how fitness varies as damage caused by one herbivore type varies, with the remaining elements of \mathbf{z} held constant at their mean values. The range of variation shown is 0–100% defoliation (100% corresponds to a value of π for the transformed proportion damage), though it is doubtful that the mean amount of damage would ever closely approach 100%. The extreme right-hand portions of the curves thus probably represent irrelevant portions of the fitness surface.

The fitness curve for corn-earworm damage (Fig. 1A) exhibits a peak at an intermediate level of damage, which corresponds to the significant value of γ_{22} (Table

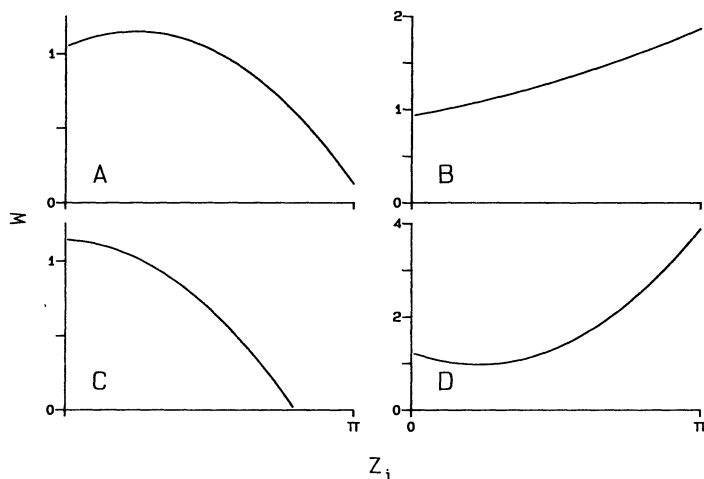


FIG. 1. Sections through the phenotypic fitness surface (adaptive landscape) estimated by multivariate quadratic regression of relative fitness, w , on z . Each section is parallel to an axis corresponding to damage by a particular type of herbivore and perpendicular to the other axes. All sections pass through the mean value of z_i . Sections represent the effect on fitness of variation in A) corn-earworm damage, B) flea-beetle damage, C) tortoise-beetle damage, and D) generalist insect damage.

2). By contrast, no such intermediate optimum occurs for damage caused by other types of herbivores (Fig. 1B–D), as indicated by the signs and magnitudes of the stabilizing/disruptive selection gradients.

All pairwise correlations among estimated breeding values are low and nonsignificant (Table 1), suggesting that the traits examined are genetically independent of each other. Although this result implies that the relationship between fitness and the breeding values of the traits could be analyzed separately for each trait, we report here the results of a multivariate analysis to allow direct comparison with the phenotypic analysis. Analysis of each trait separately produces qualitatively similar results and identical conclusions.

Linear regression using breeding values revealed significant directional selection to increase plant size (leaf area) and to decrease damage by corn earworms, while no significant selection on damage by other insects was detected (Table 3). Addition of quadratic terms to the regression did not significantly improve the fit ($F_{15, 91} = 2.67$, $P > 0.05$). Moreover, none of the individual quadratic terms was statistically significant when significance levels were adjusted for multiple comparisons. This analysis thus failed to reveal stabilizing selection on any of the characters examined.

The vectors of directional-selection gradients estimated by the phenotypic and breeding-value analyses differ significantly ($F_{[5, 1,486]} = 2.36$, $P < 0.05$). However, this difference is due entirely to a difference in the magnitude, but not direction, of selection on corn-earworm damage ($F_{[1, 1,486]} = 9.89$, $P < 0.002$), with the breeding-value analysis indicating stronger directional selection to reduce damage (greater magnitude of β). Directional-selection gradients do not differ for any of the other traits examined ($P > 0.20$ in all cases).

Finally, the vector of stabilizing/disruptive and correlational selection gradients estimated by the phenotypic analysis does not differ significantly from that estimated by the breeding-value analysis ($F_{[15, 1,456]} = 1.56$, $P > 0.05$). In addition, none of the individual γ_{ij} values differ significantly for the two analyses ($P > 0.012$ in all cases; for an overall significance level of $P = 0.05$ [the Bonferroni criterion for multiple comparisons requires $P < 0.0033$ for an individual γ_{ij} to be considered significant]).

DISCUSSION

Our results provide little support for the hypothesis that intermediate levels of damage by herbivores are maintained in *Ipomoea purpurea* by stabilizing selection (hypothesis ii in the Introduction). We did not

TABLE 3. Directional (β) and stabilizing/disruptive selection gradients (γ) from breeding-value analysis. β ' is the linear partial-regression coefficient of fitness on damage for character i in a multivariate quadratic regression. Values in parentheses are standard errors. The model and error sums of squares (and degrees of freedom) were 2.556 (5) and 1.280 (24), respectively, for the linear model and these were 3.601 (20) and 0.235 (9) for the quadratic model. The significance levels noted below are the Bonferroni criteria for individual parameters for an overall significance level of $P < 0.05$.

Character	β		γ				
			Leaf area	Herbivore damage			
				Corn earworm	Flea beetle	Tortoise beetle	Generalist insect
Leaf area	0.010 ^a (0.002)	0.008 (0.004)	-0.0008 (0.0004)	-0.020 (0.020)	0.033 (0.042)	-0.067 (0.060)	-0.042 (0.091)
Herbivore damage:							
Corn earworm	-0.706 ^a (0.188)	-1.022 ^b (0.046)	-0.020 (0.020)	1.220 (2.500)	-0.444 (2.939)	-4.026 (2.216)	-2.127 (0.097)
Flea beetle	0.405 (0.043)	-0.602 (0.044)	0.033 (0.042)	-0.444 (2.939)	9.872 (12.276)	-0.766 (7.995)	25.854 (10.923)
Tortoise beetle	0.212 (0.507)	-0.220 (0.767)	-0.067 (0.060)	-4.026 (2.216)	-0.766 (7.995)	-50.826 (19.845)	1.588 (10.912)
Generalist insect	0.723 (0.606)	1.153 (1.402)	-0.042 (0.091)	-2.127 (0.097)	25.854 (10.923)	1.588 (10.912)	15.990 (20.669)

^a $P < 0.01$; ^b $P < 0.0025$.

find evidence of significant stabilizing selection in either the phenotypic or the breeding-value analysis for damage by flea beetles, tortoise beetles, or generalist insect herbivores. Interpretation of the results is less clear for damage by corn earworms. For this insect species, the phenotypic analysis revealed significant stabilizing selection. By contrast, the breeding-value analysis revealed, if anything, disruptive selection, though this trend was not statistically significant. One interpretation of these results, which relies on the lack of significant difference between the stabilizing/disruptive selection gradient for corn-earworm damage in the two analyses, is that stabilizing selection does occur but is only revealed by the more sensitive phenotypic analysis. An alternate interpretation, however, is that the phenotypic analysis is biased by environmental correlations (see Materials and Methods) and indicates apparent stabilizing selection when none exists. Under this interpretation, the failure to detect differences between the analyses for the corn-earworm stabilizing-selection gradient is due to the low sensitivity of the statistical test employed. Thus, although our results are consistent with the existence of stabilizing selection on corn-earworm damage, they do not definitively demonstrate its operation.

As indicated in the Introduction, one

mechanism that could generate stabilizing selection on level of damage is the existence of a genetic trade-off between the costs and benefits associated with the resistance factor(s) responsible for genetic variation in damage. Although costs of resistance are frequently assumed to be common (see Simms and Rausher [1987] for references), Simms and Rausher (1987, 1989) found no evidence of such genetic costs for resistance to the four insects examined here. That result, which indicates that genetic trade-offs cannot generate stabilizing selection on damage in *I. purpurea*, is consistent with the general lack of evidence for stabilizing selection in this study. Moreover, if the apparent stabilizing selection on corn-earworm damage revealed in our phenotypic analysis is real (i.e., reflects a similar pattern of selection on genetic variation for resistance; see above), it must be generated by some mechanism other than by a trade-off between costs and benefits of resistance. One possible mechanism is that a low-to-moderate level of damage by corn earworms is beneficial to *I. purpurea*, as in some plants (e.g., Paige and Whitham, 1987), while heavy damage is detrimental. We emphasize, however, that this possibility remains speculative.

The existence of an intermediate mean level of corn-earworm damage, as well as

genetic variation for that trait, cannot be explained by selective neutrality of that variation (hypothesis i). Both the phenotypic and breeding-value analyses indicate that selection acted during our study to decrease damage (increase resistance). The evolutionary interaction between corn earworms and *I. purpurea* thus does not appear to be at equilibrium. This result is perhaps not surprising, since the numerically dominant hosts of the corn earworm in many parts of North Carolina are primarily agricultural crops. Recent changes in local agricultural practices may have led to migration of corn earworms from nearby agricultural fields into the *I. purpurea* population we examined. Hence, selection pressures generated by the corn earworm may be a relatively recent phenomenon. Unfortunately, we currently have no information addressing this possibility. Whether selection will eventually lead to the evolution of complete resistance, assuming that current conditions persist, depends on whether the apparent stabilizing selection on this trait is real (see above).

It is less clear whether directional selection acted on levels of damage caused by flea beetles, tortoise beetles, and generalist insect herbivores. For all three folivores, the phenotypic analysis indicated significant directional selection, while the breeding-value analysis revealed none. As with stabilizing selection on corn-earworm damage, this discrepancy can be interpreted in at least two ways: 1) selection occurred, but the breeding-value analysis was not sufficiently sensitive to detect it; or 2) the apparent selection revealed by the phenotypic analysis is due to environmental correlations between level of damage and fitness (Price et al., 1988). Our results thus do not allow us to differentiate between selective neutrality (hypothesis i) and transientness (hypothesis iii) as explanations for the observed intermediate mean levels of damage caused by these insect herbivores. As noted above, however, stabilizing selection (hypothesis ii) can be ruled out.

In a study of selection on furanocoumarins in wild parsnip, Berenbaum et al. (1986) demonstrated that several of these secondary compounds reduce damage to seeds caused by the parsnip webworm. They also

provided some evidence suggesting that a cost is associated with production of one of these resistance factors and concluded that this constraint prevents the evolution of greater resistance, even though additive genetic variation for resistance is present. Our general failure to find such constraints, as manifested by stabilizing selection on resistance, indicates that they do not universally explain intermediate levels of resistance in plant-insect interactions and raises the question of how frequently they lead to co-evolutionary "stalemates" (sensu Berenbaum et al., 1986) in nature.

Our inability to rule out the selective neutrality of variation in resistance to flea beetles, tortoise beetles, and generalist insects suggests that, in *I. purpurea* and perhaps in other plant species, the evolution of resistance to herbivores may be governed largely by genetic drift. This observation raises the additional question of how frequently apparent resistance traits have truly evolved as mechanisms to reduce feeding damage (e.g., Jermy, 1976, 1984; Janzen, 1980). Answers to these questions will be obtained only through additional attempts to determine the type and magnitude of selection pressures acting on resistance to herbivores in natural plant populations.

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