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EVOLUTIONARY ECOLOGY OF *DATURA STRAMONIUM* L. IN CENTRAL MEXICO: NATURAL SELECTION FOR RESISTANCE TO HERBIVOROUS INSECTS

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Abstract.—It has been assumed that herbivores constitute a selective agent for the evolution of plant resistance. However, few studies have tested this hypothesis. In this study, we look at the annual weed *Datura stramonium* for evidence of current natural selection for resistance to herbivorous insects. Paternal half-sib families obtained through controlled crosses were exposed to herbivores under natural conditions. The plants were damaged by two folivorous insects: the tobacco flea beetle *Epitrix parvula* and the grasshopper *Sphenarium purpurascens*. Selection was estimated using a multiple-regression analysis of plant size and of damage by the two herbivores on plant fitness measured as fruit production for both individual phenotypes and family breeding values (genetic analysis). Directional phenotypic selection was detected for both larger plant size and lower resistance to the flea beetles, whereas stabilizing phenotypic selection was revealed for resistance to *S. purpurascens*. However, performing the same analyses on the breeding values of the characters revealed directional and stabilizing selection only for plant size. Thus, no agreement existed between the results of the two types of analyses, nor was there any detectable potential for genetic change in the studied population because of selection on herbivore resistance. The narrow-sense heritability of every trait studied was small (all <0.1) and not different from zero. The potential for evolutionary response to natural selection for higher resistance to herbivores in the studied population of *D. stramonium* is probably limited by lack of genetic variation. Natural selection acts on phenotypes, and the detection of phenotypic selection on resistance to herbivores confirms their ecological importance in determining plant fitness. However, evolutionary inferences based solely on phenotypic selection analyses must be interpreted with caution.

Key words.—*Datura stramonium, Epitrix parvula,* heritability, Mexico, natural selection, plant resistance to herbivores, quantitative genetics, *Sphenarium purpurascens.*

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Many plant characters that confer resistance to herbivory probably evolved because of reciprocal antagonistic interactions between plants and herbivores (see Marquis 1992). Both coevolutionary theory of plants and herbivores (Ehrlich and Raven 1964) and plant defense theory (Feeny 1976; Rhoades and Cates 1976) assume that the defensive plant characteristics, both chemical and physical, have evolved to reduce or eliminate the damage of herbivores. Furthermore, associations between different plant species (Atsatt and O'Dowd 1976), and between plants and protective animals (Janzen 1966, 1969; Becerra and Venable 1989) may also have evolved to enhance the plant's resistance to herbivores. Numerous studies have shown that herbivores have detrimental effects on plant fitness components (see references below), and some have used such evidence to invoke an adaptive value for (putative) defenses and to conclude that Ehrlich and Raven's coevolutionary theory holds (e.g., Rockwood 1973). Yet few of these studies were specifically designed to assess the defensive role of a given trait (but see Dirzo and Harper 1982).

Generally, ecologists have assessed the ecological impact of herbivores on plants through the herbivores' effects on components of plant fitness (i.e., growth, survival and fecundity). Detrimental effects of herbivore damage have been detected for many plant species and on many plant characters (Jameson 1963; Kulman 1971; Rockwood 1973; Morrow and LaMarche 1978; Rausher and Feeny 1980; Crawley 1983, 1985; Louda 1983; Marquis 1984, 1990; Núñez-Farfán and Dirzo 1991; for a review, see also Marquis 1992). This implies, at least in part, that the potential for natural selection to anti-herbivore resistance exists in plants. However, few studies have been designed to both (1) quantify genetic variation in natural plant populations for resistance to herbivores (see Marquis 1991, 1992) or traits related to it (see Dirzo and Harper 1982) and (2) estimate natural selection (Gould 1983; Rausher 1988; Marquis 1991).

For cultivated plants, many studies have shown genetic variation for resistance to herbivores (Gould 1983; Smith 1989; Núñez-Farfán 1991). Although similar evidence from natural populations is available (Berenbaum et al. 1986; Simms and Rausher 1987; Marquis 1991, 1992), most of the evidence showing genetic variability for plant resistance to herbivores has been obtained through the use of clones (Moran 1981; Marquis 1984, 1990; Weis and Abrahamson 1986; Maddox and Root 1987; McCrea and Abrahamson 1987; Fritz and Price 1988; Sacchi et al. 1988; Anderson et al. 1989; Fritz 1990; Strauss 1990). Estimates of genetic variance for traits associated with resistance to herbivores as revealed through clonal studies may be biased by variance because of dominance, epistasis, and maternal effects. Inferences from such studies regarding the evolutionary consequences of selection (i.e., response) on plant resistance to herbivores could be misleading. Indeed, few careful studies of the role of natural selection on herbivore resistance have been conducted (Berenbaum et al. 1986; Rausher and Simms 1989; Simms and Rausher 1989; Simms and Fritz 1990; Marquis 1991). Such investigations require both a survey of genetic variation in plant resistance to herbivores and assessments of the actual selection on this phenotypic variation (see Simms and Rausher 1987, 1989; Rausher and Simms 1989).

In this study, we surveyed the within-population variation in resistance to herbivorous insects in *Datura stramonium* found in the Valley of Mexico (south Mexico City) and measured natural selection on this variation. We define plant resistance as directly related to plant damage caused by herbivores. Using a quantitative genetics methodology (see Simms and Rausher 1992), our goal was to assess, in this population of *D. stramonium,* the genetic variation for resistance to herbivores and simultaneously to measure current natural selection (cf. Lande and Arnold 1983) on characters related to plant resistance. A few recent studies, combining ecological and genetic approaches, have successfully measured natural selection on plant resistance to herbivores (see Berenbaum et al. 1986; Rausher and Simms 1989; Simms and Rausher 1989). However, more studies like these are needed to attain a more thorough picture of the role of natural selection and other evolutionary processes (e.g., genetic drift) on the evolution of plant resistance to herbivores.

Materials and Methods

The Plant Species and Its Herbivores

Datura stramonium L. (Solanaceae) is a hermaphroditic annual plant, self-compatible, and with a mixed-mating system. The average estimated outcrossing rate is low (**t** = 1.3%), but variation in **t** has been observed (range: 0–18%) (Motten and Antonovics 1992). Pollen is moved by sphingid moths, honeybees, and bumblebees (Sharma 1972; Grant and Grant 1983; Motten and Antonovics 1992; A. Búrquez pers. comm. 1991; J. N.-F. pers. obs.).

This species is considered a weed in some countries (Weaver and Warwick 1984), but in Mexico it is a colonizing (ruderal) plant, most commonly encountered in disturbed habitats (J. N.-F. pers. obs.). Known as jimsonweed (The United States and Canada) or toloache (in Mexico), *D. stramonium* is noxious to cattle, and in some parts of Mexico it is used for medicinal purposes (Schultes and Hoffman 1979). The secondary chemical compounds found in it are mainly alkaloids, the more prevalent being hyosciamine, atropine, and scopolamine (Orville and Fischer 1946; Leete 1959; Sharova et al. 1976; Evans 1979). Several species of insects feed on it, some of which are monophagous specialists. The three-lined potato beetle, *Lema trilineata* (Coleoptera: Chrysomelidae), is a species closely associated with toloache and is present throughout most of the plant's geographic range (Kogan and Goeden 1970a,b; Kirkpatrick and Bazzaz 1979; Peterson and Dively 1981; J. N.-F. pers. obs.). All but the pupal stages of *L. trilineata*'s life cycle occur on toloache. This is the main herbivorous (folivorous) insect of *D. stramonium* in central Mexico. It may remove up to 100% of the leaf area of individual plants (J. N.-F. pers. obs.). The tobacco flea beetle *Epitrix parvula* (Coleoptera: Chrysomelidae) is another folivore that consumes foliage of solanaceous plants (Essig 1958), including *D. stramonium,* mainly during the plant's early life. This insect has been observed on young toloache at many places in central Mexico (J. N.-F. pers. obs.). The damage this insect produces consists of small holes on the leaf blade and, although damage may be severe on occasion, whole leaves are seldom completely consumed. A third folivorous insect is the grasshopper *Sphenarium purpurascens* (Orthoptera: Acrididae), known locally as "chapulín." This species is very abundant in the Valley of Mexico (particularly in the Pedregal de San Angel

where the study site is located) in late summer and fall (Márquez-Mayaudón 1968). Some studies (S. Careaga unpubl. data) indicate that this is a generalist herbivore. The chapulín eats many plant species, including toloache, which it damages extensively. The caterpillars of an unidentified moth (Lepidoptera: Noctuidae) also consume leaves of *D. stramonium* at the Pedregal de San Angel, but they are very scarce, and no caterpillars were observed on the plants studied during 1989.

The Study Site

From 1987 to 1989, a natural population (composed of several different isolated patches) of *D. stramonium* in the Pedregal de San Angel Ecological Preserve (19°20′02″N and 99°08′26″W), located within the campus of the National Autonomous University of Mexico (UNAM) in southern Mexico City, was studied to document its population dynamics (Cabrales Vargas 1991), insect herbivores, and population genetics (Núñez-Farfán 1991). The site is seasonal with summer rains averaging 800 mm per year, and a mean yearly temperature of 15.5°C. *D. stramonium* occupies newly disturbed habitats where the native vegetation has been removed.

Experimental Design

At the end of the 1987 growing season (November), seeds were collected from each of 450 individual plants that grew within a 50-ha area within the preserve. A subsample of 90 individuals were chosen randomly, and in the summer of 1988, their seeds were sown in a greenhouse to carry out controlled crosses. Because the plant is hermaphroditic, for the purpose of controlled crosses, several individuals ($N = 30$) were assigned to function as "male" plants, and others ($N = 60$) as "female" plants. We followed a North Carolina I design for the crosses (see Lawrence 1984). This is a nested design in which several female plants (dams) are mated with one male plant (sire) and is considered to produce unbiased estimates of additive genetic variance (see Mitchell-Olds 1986) and to provide estimates of potential underlying genetic variability in the population. This design allows estimation of the additive genetic variance through the sire component of the total phenotypic variance, free from maternal effects and dominance effects (Falconer 1981). The sire component of variance contains the fraction $[(1 + F_{is})/4]$ of the additive genetic variance (Dickerson 1960; Mitchell-Olds 1986) where F_{is} is the inbreeding coefficient; thus, occurrence of inbreeding in the population may "inflate" the estimated heritability of a trait. *D. stramonium* has a mixed mating system and thus produces seeds by outcrossing and selfing (this latter together with crosses between relatives contributes to inbreeding). We attempted to measure F_{is} using electrophoretic data to correct for overestimation on heritabilities, however we did not find any polymorphic loci out of 16 in the analyzed population (Núñez-Farfán 1991). In the present study, we mated two female plants to each 1 of 30 male plants, but in no one case was a given female plant mated with more than 1 male plant. To perform the crosses, flowers on female plants were emasculated 2 or 3 d before anthers dehisced and then covered with a fine-mesh bag; when a flower opened and the stigma was receptive, pollen from a male plant was deposited directly on the stigma. After this, the flower was marked (with a color wire) and bagged to avoid contamination with pollen from other plants (the crosses were carried out in a glasshouse and the pollen of *D. stramonium* was not moved by wind). The seeds resulting from the controlled crosses were stored at 5°C to simulate winter temperatures, and then were germinated in May 1989 in petri dishes within a controlled environment chamber (Conviron 630, Winnipeg, Manitoba, Canada), with a 12-h photoperiod and 25°C (day) and 15°C (night) temperatures. The number of germinated seeds for every paternal half-sib family was compared using a *G*-test of independence (Sokal and Rohlf 1981).

As seedlings emerged, they were placed in 6-cm diameter jiffy pots (Jiffypots Products, Shippegan, Canada) and 2 wk later (by early July) were transplanted to an outdoor experimental plot (600 m^2). Twenty-five families of paternal half-sibs (some families failed to produce seeds and others seeds failed to germinate) were introduced to the field in a randomized block design (Cochran and Cox 1957) in two replicates. For each replicate, four to seven plants from each paternal family were planted. However, mortality left some families with one or zero individuals per replicate, and thus for the analyses, individuals of the two replicates were pooled. Twenty-two paternal half-sib families were used in the final analysis ($N = 355$; mean offspring number per paternal family = 16.13; range: 7–25).

The experimental plot was established within the area of the Pedregal de San Angel Preserve

in which the plants were exposed to their natural insect herbivores and experienced environmental conditions similar to sites where toloache plants grow naturally. To minimize the effects of soil variation (e.g., different levels of nutrients), a hole (30 cm in diameter and 30–35 cm in depth) was dug for each plant prior to transplantation and filled with a homogenized gardening soil. Plants were spaced 80 cm apart in a regular grid. Periodically, the plot was weeded to minimize interference from other plants, including toloaches that emerged naturally.

One month after transplant, plants were scored for number of leaves per plant and for damage by the flea beetles, *Epitrix parvula.* Proportional damage by flea beetles was taken as the number of leaves heavily damaged (i.e., a leaf with one or few small holes counted as undamaged) divided by the total number of leaves on a given plant. The chapulín, *Sphenarium purpurascens,* attacked the plants in their prereproductive and reproductive stages. Their damage to plants was high and was estimated at the reproductive stage by collecting all the leaves of each plant and measuring them in a leaf-area meter (Delta-T-Devices, Ltd., Cambridge, England). For a given plant, its relative damage was obtained by dividing its damaged leaf area by its total leaf area [which was obtained estimating the original area of each leaf based on its length, using the regression model: leaf area = $0.329 \cdot (\text{leaf length})^2$; $N = 120$, $r^2 = 0.987$, $P < 0.001$]. Final plant size was measured (as total height) for each plant at reproduction.

Resistance of a given plant to each herbivore was defined as 1 − relative damage (thus, resistance + relative damage = 1), following previous studies (Beck 1965; Jones et al. 1979; Berenbaum et al. 1986; Fritz and Price 1988; Rausher and Simms 1989; Smith 1989). For statistical analyses, relative damage was arcsine-transformed (Sokal and Rohlf 1981).

Relative individual plant fitness (w_i) was estimated by counting the total number of initiated fruits (i.e., fruits maturing seeds), divided by the population absolute mean ($\bar{W}$) for this character. Thus, $\bar{w} = 1$ (Lande and Arnold 1983). This estimation of fitness could be inaccurate if the number of initiated fruits is not positively correlated with fruit or seed set. However, for toloache, positive and high correlations between these reproductive characters have been found under natural conditions when the herbivores were abundant ($r = 0.77$, $N = 82$, $P = 0.05$, for correlation between initiated fruits and fruits producing seeds; data 1987 in Núñez-Farfán 1991) and when herbivores were scarce ($r \geq 0.81$, $N > 120$, $P < 0.05$; data from 1989; Cabrales Vargas 1991). This plant fitness estimate ignores the contribution of male function to total fitness, thus we treated this component as constant among families of *D. stramonium.*

Measurement of Natural Selection

Natural selection on the two measures of resistance to herbivores and plant size was estimated as suggested by Lande and Arnold (1983). By using multiple regression analysis of estimated relative fitness against three independent variables (damage produced by the two herbivores that attacked the plants and plant size), the directional selection gradients were estimated with

$$w_i = \beta_o + \sum_{i=1}^{n} \beta_i x_i + \epsilon, \qquad (1)$$

whereas the stabilizing/disruptive selection gradients were obtained with

$$w_i = \beta_o + \sum_{i=1}^{n} \beta'_i x_i + \sum_{i=1}^{n} \frac{1}{2} \gamma_{ii} x_i^2 + \sum_{i=1}^{n} \sum_{i<1}^{n} \gamma_{ij} x_i x_j + \epsilon, \qquad (2)$$

where x_i are the independent variables, w_i is the relative individual fitness, and β_i are partial regression coefficients (eq. 1); γ_{ii} and γ_{ii} are the quadratic coefficients (eq. 2). The linear coefficients, β_i in equation 1, are interpretable as directional selection gradients, and their signs indicate the direction of change expected from selection acting directly on the character i. The quadratic coefficients γ_{ii} indicate if a curvature in the relation between fitness and x_i is significantly concave downwards or upwards (see Mitchell-Olds and Shaw 1987; Phillips and Arnold 1989) and may suggest the operation of stabilizing (negative gamma) or disruptive selection (positive gamma), respectively (see Lande and Arnold 1983). The γ_{ij} coefficients suggest correlational selection on two given traits.

The performance of this analysis requires the fulfillment of some statistical assumptions, among the most important of which is a multivariate normal distribution of variables before selection (Lande and Arnold 1983). If this assumption were not met, then the third and higher moments of

the multivariate normal distribution would not be zero, resulting in a correlation between the linear and quadratic coefficients (Lande and Arnold 1983; Phillips and Arnold 1989). This potential problem can be avoided by performing an orthogonal multivariate regression, or estimating the partial linear (directional) coefficients (β_i, in eq. 1) and the quadratic nonlinear (stabilizing/disruptive) ones (γ_{ii} and γ_{ij} in eq. 2), separately (Lande and Arnold 1983; Mitchell-Olds and Shaw 1987; Phillips and Arnold 1989). The β_i' coefficients from equation 2 are not interpretable as directional selection gradients here.

The regression analysis was first performed on individual (phenotypic) values. A second analysis was carried out on the breeding values of the variables. The breeding value of a given paternal plant is defined for a given character as 2 multiplied by the deviation of the mean value of its offspring with respect to the population mean for that character. The measurement of selection on breeding values avoids biases in the estimation caused by environmental correlations between fitness and the traits and measures selection directly on additive genetic variance (see Rausher 1992). The estimated coefficients, using breeding values (means), converge on the true parameters (as family-mean correlations) when the number of offspring on each paternal family is large (see Arnold 1981; Rausher and Simms 1989). In the present study, the number of plants per paternal family varied from 7 to 25.

To assess the shape of the fitness function in relation to damage by chapulines (see Results) we fitted a cubic spline (for details, see Schluter 1988). This flexible nonparametric technique uses generalized cross validation to minimize the sum of squared differences between predicted Y-values and the true regression (Schluter, program directions). Standard errors of predicted values were obtained from 1000 bootstrap regressions (this option is provided by the Schluter's program). Because multiple quadratic regression may reveal only a dip or a mode in the selective surface it can give misleading results (see Mitchell-Olds and Shaw 1987; Schluter 1988; Simms and Rausher 1992), and fails to reveal surfaces with multiple peaks.

Because natural selection for plant resistance to herbivores was evaluated for plants that survived until the reproductive stage, differences among families expressed in early life (germination and survival) may not be detected by the above analysis (Grafen 1988). Also, if there were less resistant genotypes that were killed by herbivores before reproduction, the above analysis may have failed to detect it (see Berenbaum et al. 1986). Therefore, germination (although this stage was not subject to herbivory) and plant survival among the different paternal half-sib families were analyzed (G-test of independence; Sokal and Rohlf 1981).

Heritability

Narrow-sense heritability (h^2) was obtained by means of two methods: (1) We estimated h^2 using the variance components (due to sires, dams, and error from the respective mean squares; see Falconer 1981) obtained through nested model II ANOVAs (least-squares estimation, Sokal and Rohlf 1981), and (2) through maximum-likelihood estimation (see Shaw 1987).

Because there are no exact tests of significance available for unbalanced designs, as was the case in the present study, we constructed a program to perform sample randomization tests (see Sokal and Rohlf 1981). This program performs the nested ANOVA to estimate the coefficients in the variance components and h^2 (true h^2); after this, the program repeatedly allocates, at random, maternal families within sires and estimates h^2 each time. We performed 2000 randomizations for each character analyzed and compared the true h^2 with the distribution of h^2 obtained (one tail, $\alpha = 0.05$). The null hypothesis states that there is no genetic variation (i.e., $h^2 = 0$) among sires and in that case, no difference is expected between the true h^2 and the population mean of h^2 obtained through randomly allocating maternal families within sires (for a similar analysis, see Mitchell-Olds 1986).

In addition, narrow-sense heritabilities for the analyzed traits were obtained as $h^2 = V_a/V_p$, where V_p is the total phenotypic variance of a trait ($V_p = V_a + V_d + V_e$) (Falconer 1981), after estimation of the additive genetic variance (V_a), nonadditive genetic variance (V_d), and environmental variance (V_e) using maximum-likelihood estimation (see Shaw 1987). This method of estimation can use groups of relatives with different degrees of relatedness and also can use unbalanced data sets; this method gives results similar to analysis of variance when the data are balanced. We used the unconstrained restricted maximum-likelihood (REML) option to estimate the variance components. Even though this option allows negative estimates of variance components (outside the expected range), these

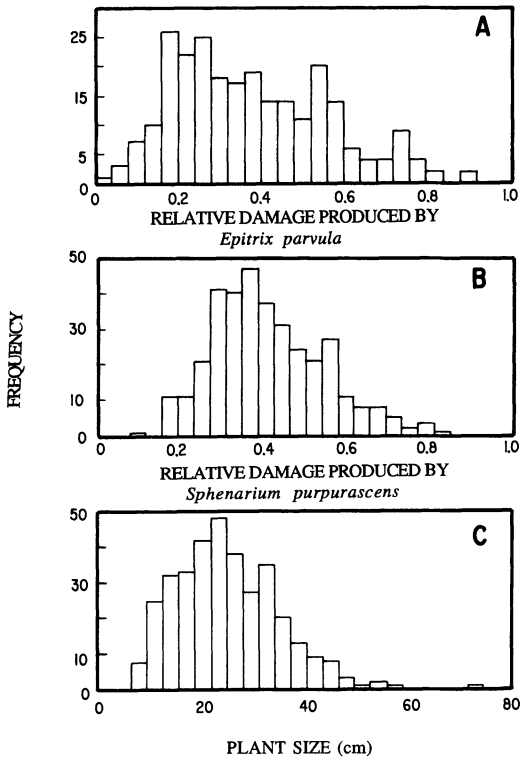

FIG. 1. Distribution of the relative damage produced by the insect herbivores *Epitrix parvula* (A), and *Sphenarium purpurascens* (B), and of plant size (C) in plants of *Datura stramonium* growing in the Pedregal de San Angel Preserve in 1989. $N = 333$ for the three distributions (see the text).

are unbiased (see Shaw 1987). The program gives the log-likelihood (L_{max}) of the estimated value; then to assess the significance of a given component, the program is run again setting one or more component(s) to zero (null hypothesis, for example $V_a = 0$), and the log-likelihood is obtained (L_o). The test of significance is based on the distribution of $-2(l)$, where $l = (L_o - L_{max})$. Under the null hypothesis $-2(l)$ has a central χ^2 distribution with r degrees of freedom (i.e., the number of parameters whose values where specified in the null hypothesis; for details, see Shaw 1987).

Phenotypic correlations among traits were obtained by standard Pearson product-moment correlation coefficients (see Arnold 1981; Via 1984), whereas genetic correlations were obtained through Pearson product-moment correlations on breeding values of the characters (see Falconer 1981; Arnold 1981; Via 1984).

RESULTS

Great intrapopulation phenotypic variation was found for plant size and for damage by the two insect herbivores that attacked the plants of *Daturu stramonium* in the Pedregal de San Angel in 1989 (fig. 1). Plant size ($\bar{x} = 24.76$ cm, SD = 9.9 cm) and relative damage to plants by chapulines, *Sphenarium purpurascens* ($\bar{x} = 0.34$, SD = 0.18) were continuously normally distributed (Kolmogorov-Smirnov tests: $D = 0.065$, $P = 0.1$; $D = 0.066$, $P = 0.09$, respectively), whereas relative damage by flea beetles ($\bar{x} = 0.54$, SD = 0.3) departs significantly from a normal distribution (Kolmogorov-Smirnov test: $D = 0.101$, $P = 0.003$).

All correlations among the three traits, except one, were not significant either at the phenotypic or genetic level (table 1). Plant size was positively correlated at the phenotypic level with damage produced by chapulines ($r = 0.284$, $P < 0.001$; $N = 333$), but the genetic correlation, although similar in magnitude, was not significant ($r = 0.26$, $P > 0.1$; $N = 22$). The correlations, both genetic and phenotypic, between damage by flea

TABLE 1. Phenotypic (above diagonal) and genetic (below diagonal) correlations between plant size and damage produced by *Epitrix parvula* and *Sphenarium purpurascens* in *Datura stramonium*. Sample size for phenotypic correlations is 333 plants and for genetic correlations 22 families. Significance of correlations, in parenthesis, is provided.

Trait	Plant size	Damage by *Epitrix parvula*	Damage by *Sphenarium purpurascens*
Plant size	–	0.075 (> 0.1)	0.284 (< 0.001)
Damage by			
Epitrix parvula	−0.126 (> 0.2)	–	−0.059 (> 0.2)
Sphenarium purpurascens	0.266 (> 0.1)	−0.122 (> 0.2)	–

TABLE 2A. Analysis of phenotypic selection on plant size and relative damage by herbivores in *Datura stramonium*. β_i represents the directional selection gradients, γ_{ii} the stabilizing/disruptive selection gradients, and γ_{ij} the coefficients of correlational selection among traits, β'_i is the linear coefficient in the multivariate quadratic regression and is not used in the interpretation (see text). Standard errors of the coefficients are given in parenthesis.

Plant character	β_i	β'_i	γ_{ii}	γ_{ij} Damage by *Epitrix parvula*	γ_{ij} Damage by *Sphenarium purpurascens*
Plant size	0.026***	0.016**	0.0001 NS	0.004 NS	0.001 NS
	(0.001)	(0.007)	(0.0001)	(0.003)	(0.006)
Damage by					
Epitrix parvula	0.152***	−0.015 NS	0.042 NS		0.044 NS
	(0.026)	(0.124)	(0.048)		(0.148)
Sphenarium purpurascens	−0.091 NS	1.066***	−0.874***		
	(0.061)	(0.348)	(0.235)		

N, 333; ** $P \leq 0.01$; *** $P \leq 0.001$; NS, not significant.

beetles and damage by chapulines were small (≤ 0.13) and not significant ($P > 0.05$) (possibly the absence of correlation is caused by the fact that different insects attacked the plants at different stages, that is, young and reproductive plants, respectively). This result suggests a lack of trade-offs for resistance to different herbivores in this plant species. However, because our sample size for genetic correlations is small, the power of the tests (i.e., $1 - \beta$; see Toft and Shea 1983) is low, and we may not have been able to detect modest trade-offs. For instance, only correlations of 0.6 (or −0.6) would be detected as significant at α (two tailed) = 0.05, and $1 - \beta = 0.85$ (Cohen 1988) with the present design. Conversely, the observed genetic correlation between damage by chapulines with plant size would be significant if the number of families was close to 80 (see Cohen 1988).

Directional phenotypic selection was detected for plant size and for damage by flea beetles (table 2A). These two directional selection gradients (β_i) were positive, showing that higher relative fitness was attained by larger plants and by those plants experiencing higher levels of damage (i.e., less resistance) by *Epitrix parvula*. Alternatively, no directional selection was detected for damage by *S. purpurascens*. Adding the second-order terms, 63% of the variance was explained by the model (table 2B), and all quadratic, and correlational selection gradients but one were statistically nonsignificant (table 2A). Stabilizing selection was found only for damage by chapulines. Using the significant coefficients from the quadratic multivariate regression (for plant size and damage by chapulines), a response surface ("adaptive landscape") was constructed (fig. 2A). It shows that for a given plant size, relative fitness is higher for plants with intermediate levels of resistance to *S. purpurascens*, and as plant size increases, relative plant fitness increases steadily. In addition, nonparametric regression showed that the stabilizing mode of selection for resistance to chapulines holds (fig. 2B). Though the surface estimated with the cubic spline differs slightly from the curve estimated by quadratic regression, they have quite similar trajectories; both almost coincide in the "optimum phenotype" in resistance (i.e., that with higher fitness; cf. fig. 2A,B). The correlational selection coefficients for these two traits (table 2A) indicate that selection did not act on them simultaneously.

Selection analysis performed on breeding values of the three traits, revealed a quite different

TABLE 2B. The analysis of variance and adjusted multiple R^2 for each regression from table 2A.

	Multiple linear regression					Multivariate quadratic regression				
Source	SS	df	F	P	R^2	SS	df	F	P	R^2
Model	24.016	3	175.25	≤ 0.0001	0.597	24.815	9	62.58	≤ 0.0001	0.625
Residual	15.029	329				14.230	323			

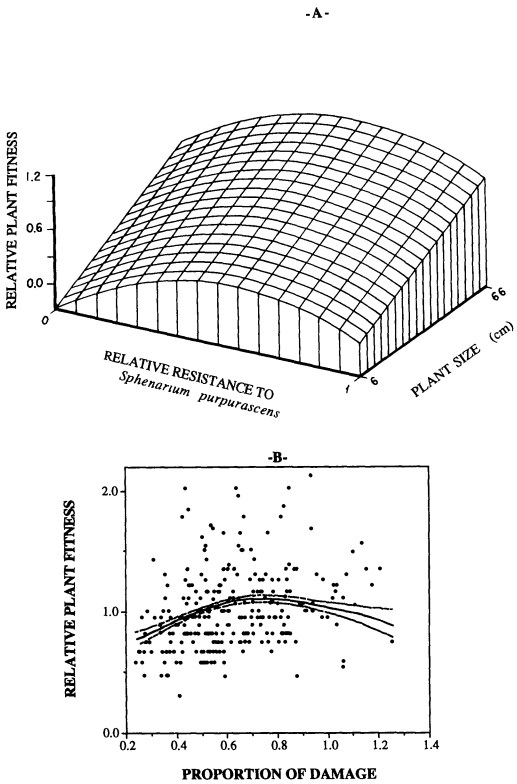

FIG. 2. A. Response surface of relative plant fitness with respect to plant size (height) and resistance (1-relative damage) to *Sphenarium purpurascens* in *Datura stramonium*. This "adaptive landscape" was constructed using the significant selection gradients obtained from the multivariate quadratic regression of plant fitness on plant size and damage by herbivores (cf. table 2A). B. Fitness surface of *D. stramonium* in relation to damage by *S. purpurascens* using a nonparametric regression (continuous line). Standard errors of predicted values (dashed lines) were obtained through bootstrap regression replicates (see text). Points indicate observed values. Damage values are in (square root) arcsine transformation (e.g., 0.2 = 0.04 and 1.4 = 0.97 of proportional damage).

picture of natural selection. Directional selection on plant size was detected (table 3A), and adding second-order terms the model improved the fit (R^2 = 0.71, table 3B) but only significantly for plant size (concave downwards). None of the selective gradients for plant resistance to herbivores or the correlational ones were statistically significant. We did not detect any effect of natural selection on the additive genetic variation of resistance to herbivores or on the correlations between resistance and plant size.

The mean percentage of germination and plant survival were relatively high in the population [$\bar{x}$ = 60.73 ± 4.31% (SE); $\bar{x}$ = 77.91 ± 2.97% (SE), respectively]. Neither the number of seeds germinated nor the number of plants that survived until reproduction varied among paternal half-sib families (G = 26.47, df = 24, P < 0.25; G = 12.6, df = 21, P < 0.9, respectively). This implies that selection estimates on breeding values at the reproductive stage were not affected by survival selection.

No genetic differences among paternal half-sib families were detected for the three traits (table 4). The narrow-sense heritabilities were very small for every character (the highest was 0.079 for damage produced by *S. purpurascens*). However, none of the estimated heritabilities were significantly different from zero using either REML (table 4) or least-squares estimation (randomization tests). Judging from the distribution of heritabilities generated by allocating maternal families randomly within sires (fig. 3), in every case, the estimated heritability (true h^2) was not significantly different from the population of heritabilities ($P \gg 0.05$). We found no evidence of additive genetic variance in the measured traits in the population of *D. stramonium* in central Mexico in 1989. This result agrees with the absence of selection on breeding values.

DISCUSSION

This study failed to detect natural selection for (sensu Sober 1984) resistance to herbivores in the annual plant *Datura stramonium*. Although large amounts of phenotypic variation in plant size and damage caused by the two herbivores were found in the population, and although there exists a clear phenotypic (ecologically relevant) relationship of damage by chapulines with plant fitness in this plant species (table 2A; see also Núñez-Farfán 1991), the lack of additive genetic variation for these plants' characters may limit their potential for further evolutionary response (sensu Endler 1986) to selection for higher resistance to herbivores.

Some other studies in which a few genes determine the production of defensive secondary compounds have detected selection acting on resistance to herbivores (Jones 1962; Dirzo and Harper 1982; see also Endler 1986). However, because it is thought that control of plant resistance to herbivores by one or few genes is rare (Gould 1983), models of quantitative genetics are required (Simms and Rausher 1987, 1992; Simms and Fritz 1990). Two previous studies that used the Lande and Arnold (1983) method

TABLE 3A. Directional (β_i), stabilizing/disruptive (γ_{ii}) and correlational (γ_{ij}) selection gradients obtained through the regressions of relative fitness on the breeding values (additive genotypes) of characters in *Datura stramonium*. Coefficients and symbols as in table 2.

Plant character	β_i	β'_i	γ_{ii}	γ_{ij} Damage by *Epitrix parvula*	γ_{ij} Damage by *Sphenarium purpurascens*
Plant size	0.650***	0.585***	−0.032*	0.625 NS	0.501 NS
	(0.108)	(0.168)	(0.014)	(0.554)	(2.345)
Damage by					
Epitrix parvula	1.509 NS	4.258 NS	5.425 NS		13.109 NS
	(2.626)	(3.106)	(12.416)		(23.87)
Sphenarium purpurascens	−2.764 NS	−2.632***	−21.466		
	(4.886)	(7.364)	(56.66)		

N, 22; ** $P \leq 0.01$; *** $P \leq 0.001$; NS, not significant.

TABLE 3B. The analysis of variance and adjusted multiple R^2 for each regression from table 3.

	Multiple linear regression					Multivariate quadratic regression				
Source	SS	df	*F*	*P*	R^2	SS	df	*F*	*P*	R^2
Model	0.529	3	12.295	≤ 0.0001	0.587	0.739	9	6.772	≤ 0.0001	0.711
Residual	0.290	18				0.146	12			

found natural selection for resistance to herbivores. In both *Pastinaca sativa* (Berenbaum et al. 1986) and *Ipomoea purpurea* (Rausher and Simms 1989), directional selection for higher resistance to herbivores was detected. In *P. sativa*, the level (total amount or proportion) of chemical compounds in seeds and leaves, furanocoumarins, promoted resistance to the insect *Depressaria pastinacella*, and levels of these chemicals were heritable (Berenbaum et al. 1986; Zangerl and Berenbaum 1990). In *I. purpurea*, although the cause of resistance to the *Heliothis zea* caterpillars is unknown, additive genetic variation for overall resistance to herbivores was detected (Simms and Rausher 1987, 1989; Rausher and Simms 1989).

It seems plausible that the absence of additive genetic variation in resistance to herbivores in the studied population of *D. stramonium* could be the main cause of the absence of selection on breeding values we found: the estimates of narrow-sense heritabilities for plant size and damage produced by the two herbivores were not statistically distinguishable from zero. The heritability values found for resistance to *Epitrix parvula* and *Sphenarium purpurascens* (−0.23 and 0.079, respectively) in the present study are smaller than those found for resistance in two other wild plants. Heritabilities of 0.42 and 0.94 were measured for the two compounds in seeds of *P. sativa* that confer resistance to *D. pastinacella* (Berenbaum et al. 1986), and for resistance to *Chaetocnema confinis*, *I. purpurea* has a heritability of 0.099 (Simms and Rausher 1987). In addition, absence of additive genetic variation for other quantitative traits (in the same and in other populations of *D. stramonium*) and monomorphism at 16 enzymatic loci in 60 families indicate that overall little genetic variation is present in the study population (Núñez-Farfán 1991). However, other explanations are possible.

First, it is possible that genetic variation in resistance to herbivores exists in the studied population, but it was not expressed or was effectively neutral to the herbivores that attacked the plants in 1989. Genetic variation in resistance to other herbivores may be present (for instance, the specialist *Lema trilineata*), but the outcome of quantitative genetic analyses under hypothetical environmental conditions is not easily anticipated. Some evidence exists that plant resistance to herbivores varies with time (e.g., Marquis 1984, 1990; Karban 1992) and is especially dependent on the kind of herbivore (see Fritz and Price 1988; Rausher and Simms 1989; Marquis 1990; see also Simms and Fritz 1990). In a long-term study with the neotropical shrub *Piper arieianum*, Marquis (1990) showed that the resis-

TABLE 4. Narrow-sense heritability (h^2) for each trait in the studied population of *Datura stramonium* obtained through maximum-likelihood (REML) and least-squares (LS) estimation. The χ^2 value and probability (P) for the hypothesis that the additive genetic variance (V_a) is not different from zero is given for each trait (see the text for details) in the REML analysis. Total phenotypic variance (V_p) estimated by means of REML is also presented.

Character	REML				LS			
	V_a	V_p	h^2	χ^2	P	h^2	P	h^2*
Plant size	6.73	98.53	0.068	0.34	> 0.50	0.016	0.47	0.22
Damage by								
Epitrix parvula	−0.023	0.198	−0.148	2.27	> 0.25	−0.231	0.91	0.19
Sphaenarium purpurascens	0.0009	0.041	0.003	0.0004	> 0.90	0.079	0.27	0.18

* h^2 represents the value of heritability that would be significant at $P = 0.05$, following randomization tests; see figure 3.

tance ranking among plant genotypes changed through time and that a genotype resistant to one species of herbivore may not be resistant to another. However, in other species resistance to herbivores can be maintained through time. In the *Solidago-Eurosta* system, the ranking in resistance among plant genotypes was constant through time (see Weis and Abrahamson 1986; McCrea and Abrahamson 1987; Anderson et al. 1989; see also Maddox and Root 1987). It may be that in *D. stramonium* what seems like a population without genetic variation for resistance to a set of generalist herbivores, could be genetically variable in resistance to other species.

Other conditions may also preclude the detection of genetic variation in resistance to herbivores (Fritz 1990): (1) resistance may not be detected in certain environments, and (2) major genotype-environment interactions can obscure the detection of genetic variation (but see Fritz 1990; Strauss 1990). Insect herbivores' population sizes may vary through space and time making selective pressures not easily detectable over short time periods or small spatial scales. Furthermore, if insect herbivores possess genetic variation for resistance to plant defenses, matching resistant herbivores with resistant plants and nonresistant herbivores with susceptible plants may mask variation in resistance in the plant population (i.e., by showing all plants with equivalent levels of damage). Also, plant characteristics (e.g., plant size, tissue nutrient concentration, secondary chemistry) can vary with environmental conditions (see Marquis 1992), in ways that affect the damage received by herbivores and minimize the importance of genetic variation in resistance to them.

An explanation for the absence of genetic variation for resistance to herbivores in toloache and the consequent lack of further evolutionary response to selection could be that natural selection has eroded genetic variation in this trait over time, as described by the fundamental theorem of natural selection (Fisher 1958) (but see below). If some plant populations maintain genetic variation for resistance to herbivores (cf. Berenbaum et al. 1986), it would be expected that selection could improve resistance until it is "complete" (perfect resistance). However, it is not clear whether in *D. stramonium* natural selection has eroded genetic variation, or if it has been lost from the population because of other process (e.g., genetic drift and/or inbreeding; especially in this species because a fraction of the seeds are produced by selfing). Furthermore, although genetic differences may be present in this population, the variation could have been neutral to the herbivores present in 1989. Plants may tolerate damage by herbivores without loss of fitness (Berenbaum and Zangerl 1992), or even compensate for this damage: this could explain the positive selection gradients for damage produced by the flea beetle *E. parvula*. A similar result has been reported for the flea beetle *Chaetocnema confinis* (Rausher and Simms 1989).

The small amounts of genetic variability detected in *D. stramonium*, in metric traits (Núñez-Farfán 1991) and in enzymatic loci (Warwick 1990; Núñez-Farfán 1991) suggest that stochastic processes have probably influenced the erosion of genetic variation in this species. The reduced effective population sizes estimated by Núñez-Farfán (1991) and Cabrales Vargas (1991), coupled with the colonizing habit (see a discussion in Slatkin 1987) of *D. stramonium* give some support to this hypothesis.

Another possible explanation may be provided by phenotypic plasticity in the analyzed characters: the high phenotypic plasticity displayed by colonizing (weedy) plants (Baker 1974; Bazzaz

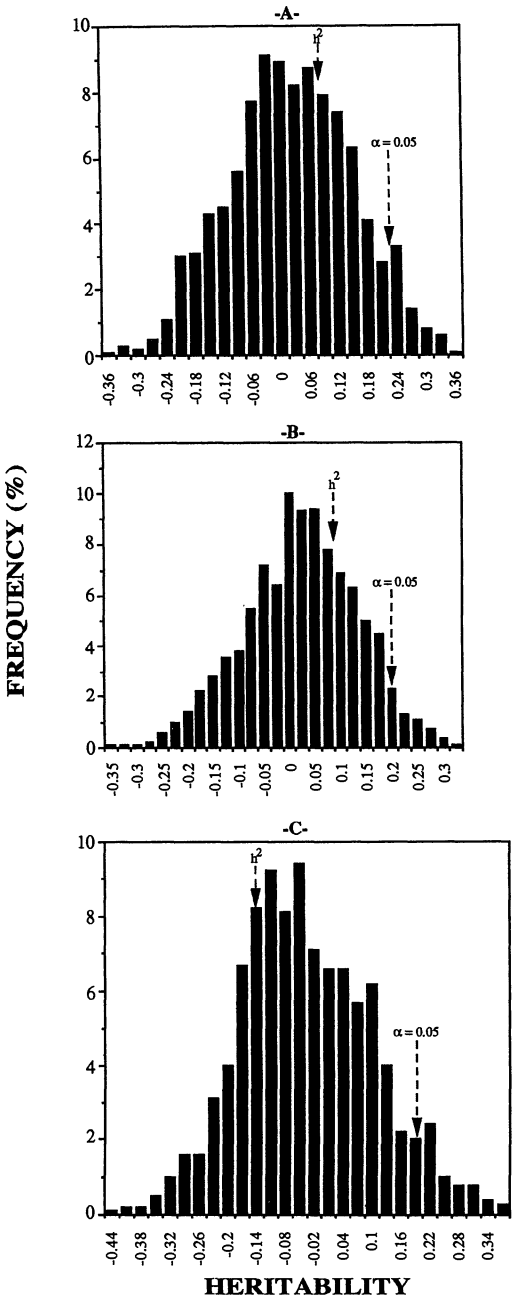

FIG. 3. Distribution of heritabilities obtained through sample randomization tests (see text). The highest value estimated of true-h^2 for every trait and the one-tailed 5% rejection region are indicated by arrows. (A) is plant size, (B) is damage produced by *Sphenarium purpurascens,* and (C) is damage by *Epitrix parvula.*

1986) may preclude consistent (progressive) selection for further resistance in some populations. Even in the presence of genetic variation, plasticity may minimize the significance of differences among genotypes in resistance and/or fitness in an environment heterogeneous at the small-scale level (see Bradshaw 1965; Bazzaz and Sultan 1987; Sultan 1987); mean values of resistance for different genotypes may be similar although their reaction norms differ. If so, selection on plasticity rather than on resistance mean value would be expected.

Using a breeding design, this study has attempted to detect both additive genetic variation for resistance to insect herbivores and natural selection on this resistance for *D. stramonium,* but in contrast with the results found in the only two similar studies available to date (Berenbaum et al. 1986; Simms and Rausher 1987, 1989; Rausher and Simms 1989), we found no evidence of additive genetic variation for resistance to two herbivorous insects. Hence, little support existed for a potential for evolutionary response to natural selection by herbivores. Because we detected phenotypic selection for the analyzed traits but no selection on their breeding values, we suggest that evolutionary inferences based solely on the phenotypic analysis of selection be taken with caution.

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