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## SELECTION FOR NATIVE CHARACTERS IN HYBRIDS BETWEEN TWO LOCALLY ADAPTED PLANT SUBSPECIES

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**Abstract.**—Gene exchange between locally adapted plant populations can have significant evolutionary consequences, including changes in genetic diversity, introduction of adaptive or maladaptive traits, disruptive of coadaptive gene complexes, and the creation of new ecotypes or even species. The potential for introgression between divergent populations will depend on the strength of selection against nonnative characters. Morphologically variable  $F_2$  hybrids of two *Gilia capitata* subspecies were used to evaluate the strength of phenotypic selection and the response to selection in the home habitats of each subspecies. At both sites, traits diagnostic of the subspecies were subject to significant phenotypic selection, probably mediated by direct selection on unmeasured correlated characters. Phenotypic selection favored native morphologies in all but a single case; leaf shape of one subspecies was favored in both habitats. The strength of selection varied between sites, with one site selecting more strongly against nonnative characters. Offspring of the  $F_2$  hybrids showed a significant evolutionary response to selection when grown in a common environment. Evolution was in the direction of similarity with the subspecies native to the site where selection was imposed. This result reveals that native character states are adaptive and suggests that selection will maintain native morphologies even after a substantial influx of genes from an ecologically and morphologically distinct, and locally adapted subspecies.

**Key words.**—Evolution, geographic divergence, *Gilia*, hybridization, local adaptation, natural selection, phenotypic selection, reciprocal transplant, response.

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Because plants are sessile organisms and populations are often disjunct, adaptation of plant populations to local conditions is common. Reciprocal transplant experiments have demonstrated that in many cases native individuals have greater fitness than nonnatives (Clausen et al. 1948; Clausen and Hiesey 1958; Jain and Bradshaw 1966; Antonovics and Bradshaw 1970; Bradshaw 1984; Ehleringer and Clark 1988; Levin 1988; Schmitt and Gamble 1990; Galen et al. 1991; Waser and Price 1991, 1994; Nagy 1995; Nagy and Rice 1997). The characters responsible for this local adaptation are, however, largely unknown (but see Antonovics and Bradshaw 1970; Schat et al. 1996), in part because the mechanisms of selection are difficult to characterize, and because simultaneous divergence of many characters often accompanies local adaptation. Hence, it is rarely clear how many or which traits are important for fitness differences among locally adapted populations (Lande and Arnold 1983).

The present study explores the process of selection and subsequent evolution in artificial populations of hybrids between morphologically divergent, locally adapted subspecies of an annual plant. While the traits targeted by selection are not identified, characters diagnostic of both parental subspecies, and apparently correlated with adaptively important traits, are used to measure selection and the response to selection when hybrids are raised in the home habitats of both the parental subspecies.

By identifying the strength and direction of selective forces that act on traits characteristic of the subspecies, we can better understand and predict the dynamics of introgression and reticulate evolution. Both processes are common among plants, and are widely recognized for their importance in plant

evolution (Baker 1951; Stebbins and Daly 1961; Stebbins 1969; Grant 1981; Stace 1987; Hewitt 1988; Rieseberg and Wendel 1993; Arnold 1994; Rieseberg 1995). Migration by seed or pollen are prerequisites for gene exchange between divergent populations, but they may not be sufficient for the effective transmission of genes between locally adapted populations (Levin 1981, 1983, 1984, 1995; Clegg and Brown 1983; Ellstrand and Marshall 1985; Potts and Reid 1988; Campbell and Waser 1989; DePamphilis and Wyatt 1989; Ellstrand 1992; Ennos 1994). Immigrants must successfully hybridize with natives to introduce genes into the local population. Although introgressive populations and hybrid zones resulting from secondary contact may have high genetic diversity and new evolutionary potential, hybridization can reduce fitness by disrupting coadapted gene complexes or by introducing maladapted genes (e.g., “outbreeding depression,” Waser and Price 1994). As a result, it is difficult to predict whether migration between divergent populations will result in the coalescence of their gene pools. Despite the importance of these issues to biodiversity, there are very few studies on the fitness consequences of natural gene exchange among divergent populations or related taxa (Rieseberg and Wendel 1993; Arnold and Hodges 1995; but see Jordan 1991, 1992).

In this study I explore the evolutionary consequences of hybridization between locally adapted subspecies of the annual plant *Gilia capitata*. The subspecies differ genetically for a variety of morphological, phenological, and reproductive characters. Reciprocal transplant experiments have demonstrated that natives have higher fitness than immigrants in both habitats (i.e., are locally adapted; Nagy and Rice 1997). And although crossing between the subspecies is restricted and strongly unidirectional, hybrids are vigorous and fertile (Grant 1950; Nagy 1997; present study), making both establishment and introgression possible consequences of seed or pollen exchange between the subspecies.

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Gene exchange between populations was simulated by planting experimental, second generation hybrids ( $F_2$ ) into the home habitats of each subspecies. The use of hybrids in selection experiments can be useful for two reasons. First, hybrids express a broader range of phenotypes than either parent, making selection easier to detect. Second, the technique presents the opportunity for studying selection in habitats where contrasting selection on traits is expected. The multivariate phenotypic variation that distinguishes the two subspecies was summarized using a few diagnostic characters. Selection on these characters was used as a surrogate for selection on the parental phenotype as a whole. I do not argue that the characters examined are themselves under direct selection (although some may be), but instead that they serve as indicators for, and are likely correlated or linked with, unmeasured characters that are under direct selection. The characters were chosen for their power to distinguish the subspecies, not for their functional importance. Offspring of the hybrids raised in the selective environments were grown in a common greenhouse environment to test for a response to selection. Using this experimental approach, I addressed four questions: (1) Is there phenotypic selection on characters that differ between the subspecies? (2) Does selection favor native characters over those of nonnatives? (3) Does one generation of selection on experimental hybrid "populations" in the field result in an evolutionary divergence between those populations (a response to selection)? (4) If so, are native character assemblages re-created by selection?

## MATERIALS AND METHODS

### *Study System*

*Gilia capitata* Sims. (Polemoniaceae) is an herbaceous annual, native to the west coast of North America. The species is a complex of eight subspecies that occupy distinct ecological niches and are morphologically differentiated (Grant 1950; Steele 1986; Hickman 1993). Two subspecies, *G. capitata* ssp. *capitata* and *G. capitata* ssp. *chamissonis*, were chosen for this study for their close evolutionary relationship (the latter is purported to be recently derived from the former), their strong morphological and ecological differentiation, and for their reported ease of cross-fertilization (Grant 1950). Other features of the two subspecies' distribution and biology and the structure of the populations used in this study are described elsewhere (Grant and Grant 1965; Nagy 1995; Nagy and Rice 1997). Although most populations of the species are apparently isolated today, several subspecies within the complex are thought to be of hybrid origin—one, from the hybridization of the subspecies studied here (Grant 1950, 1956). This system is therefore highly appropriate for exploring the evolutionary dynamics of hybridization, natural selection, and local adaptation.

The field portion of this study was conducted at two sites, each home to a natural population of one of the two *Gilia* subspecies. The "inland site" where *G. c. capitata* grows is on the south-facing, flood-disturbed, talus banks of Pope Creek, Napa County, California (38°36'N, 122°23'W). The region is characterized by a typical Mediterranean climate with a chaparral and blue oak-digger pine woodland community (Barbour and Major 1977). The "coastal site" where

*G. c. chamissonis* grows is on the stable, vegetated, back dunes of Bodega Head, Sonoma County, California (38°18'N, 123°03'W). The northern seashore community is composed of a mixture of perennials and annuals, dominated by *Baccharis* and *Lupinus* (Barbour et al. 1973; Barbour and Major 1977; Hickman 1993).

### *Experimental Design*

*F<sub>2</sub> Seed Production.*—In an  $F_2$  hybrid population, unlinked parental characters are highly dissociated. Reducing the correlation among parental characters makes it possible to detect selection on characters independently. Bulk seed of both subspecies was collected from mature fruits in the field at each site in the summer of 1990. Seeds were collected throughout the season from ca. 100 haphazardly selected plants at each site and were stored in paper bags at room temperature until used for planting. Seeds require a one- to two-month after-ripening period to achieve full germination, and demonstrate no reduction in viability following storage for several years (pers. obs.). During the spring of 1991 several hundred seeds were germinated and grown in the greenhouse on the University of California's Davis campus, in cylindrical 164-cm<sup>3</sup> pots, with a porous potting mixture, under 16-h days and temperatures of 10°C/25°C (min/max). Plants were watered daily and fertilized as needed. As plants flowered, crosses were made between the subspecies, using the coastal subspecies (*G. c. chamissonis*) as the pollen donor. Crosses were made in this direction to take advantage of *G. c. capitata*'s self-incompatibility, thus ensuring that the resulting progeny would be hybrid. The success rate of crosses of this kind is extremely low (< 1% of flowers produce fruit; pers. obs.), but by conducting large numbers of crosses, ample numbers of  $F_1$  seeds were produced. Seeds were collected from all fruits when mature. In April 1991,  $F_1$  seeds were stratified for one week in a moist peat-soil mixture at 6°C in the dark. Seeds and soil were then transferred to the greenhouse where 68  $F_1$  hybrid individuals from 20 *G. c. capitata* maternal families emerged. As  $F_1$  hybrids flowered, plants were self-fertilized by brushing adjacent inflorescences together. Self-fertilizations were made throughout the summer and fall of 1991, and  $F_2$  seeds from approximately 40  $F_1$  maternal families were collected as they matured and stored as above.

*Selection on  $F_2$ s Raised in the Field.*—To measure phenotypic selection in the field,  $F_2$  hybrids were raised at both sites. In late November 1992, seeds from both parental subspecies (bulk seed collected in the summer of 1992), and the greenhouse-produced  $F_2$  seeds, were planted into the field at both the inland and coastal sites.  $F_2$  seeds were chosen at random from the pool of greenhouse-generated seed. Seeds of the three types were identified with wooden toothpicks of different colors. Seeds were attached to toothpicks for planting by first briefly wetting them, causing a mucilage sheath to expand, and then placing them on the end of a toothpick. Drying cemented seeds to the wood. Two seeds were attached to each toothpick to ensure adequate sample sizes. Planting was accomplished by sticking the toothpicks into the loose soil. Twenty blocks were established at each site. Each block consisted of a 350-mm × 450-mm rectangular grid in which planting locations were separated by 50 mm (8 × 10 planting

positions). Toothpicks were placed in a regular and repeating grid-pattern in each block. Twenty toothpicks (40 seeds) of each seed type were planted into each block (as part of another study, a fourth seed type was planted in the blocks as well, completing the 80-position grid). If two seedlings emerged at a location, a haphazardly selected individual was discarded shortly after emergence.

The blocks were protected from deer and rabbit herbivory with chicken wire fencing, and from insect pollinators by a fine light-transmitting mesh, applied as plants flowered. Blocks were positioned along a meandering transect through the long, narrow populations at both the inland and coastal sites. The native community was left intact with the exception that all naturally occurring *G. capitata* were removed from within the blocks. At the inland site, six of the 20 blocks were lost to winter floods. Thirteen measures of performance, morphology, and life-history traits were collected throughout the growing season. Individuals were harvested as they senesced (mid-July through mid-August 1993). Fitness was estimated as the number of inflorescences per plant at harvest. This measure was selected over the other option (biomass) since inflorescence number does not vary systematically between the subspecies, while biomass does, making comparisons more cumbersome. Seed production (a standard estimate of fitness) was an inappropriate fitness estimate because all plants were hand pollinated (see below).

When plants flowered, hand crosses were made among all individuals of a type (two parental types and the  $F_2$ s). Each block, therefore, was a reproductively isolated population of haphazardly mating individuals of each genetic type. Since all available flowers were used during hand pollinations, paternal performance for each individual in a block should have been approximately proportional to its flower production. Crosses were made by moving a small, soft paint brush from plant to plant, making sure to contact both anthers and stigmas of as many flowers as possible. Repeated, and haphazard "visits" were made to each plant in a block during each pollination session. All open flowers were pollinated at least once per week during the flowering season. Although the pollinations were not conducted "blind," an effort was made to transfer large amounts of pollen among all individuals of a type. It is unlikely, therefore, that seed production was "pollinator-limited." As fruits matured, seeds were collected from each plant.

*Response to Selection by  $F_3$ s Raised in the Greenhouse.*—To measure the response to selection experienced in the field by  $F_2$  hybrids, the progeny of those hybrids were raised in a common greenhouse environment. In the spring of 1994, 49 randomly selected individuals of each subspecies, and 199  $F_3$  progeny of the  $F_2$  hybrids grown in the field, were raised from seed in the greenhouse. The number of  $F_3$  offspring raised from each  $F_2$  mother was proportional to the fitness of that mother in the field; that is, field-raised  $F_2$  plants with more inflorescences contributed more seed to the greenhouse  $F_3$  populations. All plants were germinated and grown in the greenhouse under conditions described above. A subset of the measurements taken in the field was recorded from these plants. Pure subspecies and  $F_3$  plants finished flowering in early July 1994.

*Character Reference Population.*—To identify morpholog-

ical characters for use in the phenotypic selection analysis, and the analysis of the response to selection, a separate group of 50 coastal, 50 inland, and 109  $F_2$  hybrid plants were raised from seed in pots outdoors adjacent to the greenhouse during the spring of 1992. These plants were not part of the selection experiment described above. Morphological characters were identified that were useful in distinguishing the two subspecies (see below). These  $F_2$  hybrid plants were considered "unselected," and were used as a baseline from which to measure the response to selection demonstrated by the  $F_3$  plants in the selection experiment.

*Characters Measured.*—Thirteen morphological and phenological traits were considered in these analyses. Discriminant analysis and MANOVA were used to identify variables that differed significantly between the subspecies, and that accounted for most of the genetic variation between them in common garden conditions ("reference population plants," analyses not shown). From these analyses, four traits were selected for the measurement of phenotypic selection intensity and evolutionary response. The characters were chosen for their strength in distinguishing the subspecies and for their relatively low levels of correlation with each other. These traits were: (1) leaf shape, calculated as the number of leaf lobes on one side of the longest leaf divided by the length of the longest leaf, on the pinnately lobed rosette leaves 111 d after planting; (2) inflorescence diameter, measured on the primary inflorescence at flowering; (3) petal shape, calculated as petal lobe length divided by lobe width of a haphazardly selected flower on the primary inflorescence; and (4) flower color, quantified to the nearest 0.5 units on a scale of 0–5 (11 categories) by visually matching petal color to paint color samples on Pantone Color Formula Guide 26U (Pantone 1984). Petal color 1 was a very pale lavender, 5 was very dark purple. Petals with no perceptible color (white) were given a score of 0. Intermediate petal colors were assigned the appropriate 0.5 score. Flower color values 1–5 were assigned to matches with Pantone colors 263U through 267U, respectively. To the experimenter's eye, the Pantone color scale tracked flower color variation very closely. All size measurements were made in millimeters. The four characters were not highly correlated with each other in the  $F_2$  hybrids subjected to selection in the field (CORR procedure, SAS Institute 1988; Table 1), but it is likely that the measured characters are correlated with other unmeasured, and possibly adaptive, traits.

#### Statistical Analysis

*Phenotypic Selection in the Field.*—To measure phenotypic selection on the  $F_2$  hybrids in the field, I conducted a multiple regression analysis at each site using the four characters described above (Lande and Arnold 1983; Endler 1986). Partial regression coefficients of this analysis represent selection gradients ( $\beta$ ), and reflect the strength of selection acting independently on each trait in the model.

Relative fitness was regressed onto the standardized character values. Fitness was defined as the number of inflorescences per plant divided by the mean inflorescence number per plant for the site. The four independent variables were standardized to a mean of zero and variance of one for anal-

TABLE 1. Pearson correlation coefficients for 13 traits for F<sub>2</sub> hybrids grown in the field. Correlations above the diagonal are for the coastal site; correlations below the diagonal are for the inland site. Sample sizes for correlations range from 52 to 150. "Leaf shape," "inflorescence diameter," "petal shape," and "petal color" are defined in the text. Other character definitions: "leaf lobe" = (leaf lobe length)/(leaf length); "SLW" = specific leaf weight; "date flower" = days after planting to first flower; "size 139" = length of longest leaf at 139 d from planting; "crown diameter" = root crown diameter at first flower; "flower diameter" = diameter of gently flattened corolla; "date harvest" = lifespan in days from planting; "height harvest" = aboveground plant height at death; "dry weight" = aboveground dry weight at death.

	Leaf shape	Leaf lobe	SLW	Date flower	Size 139	Crown diam.	Inflorescence diam.	Flower diam.	Petal shape	Petal color	Date harvest	Height harvest	Dry weight
Coastal													
Inland													
Leaf shape	—	0.09	0.02	0.20	-0.55***	-0.48***	-0.41***	-0.18	-0.04	0.10	-0.05	-0.00	-0.28*
Leaf lobe	-0.16	—	-0.01	-0.07	0.10	-0.00	-0.00	0.03	0.12	0.19	-0.12	-0.03	0.04
SLW	-0.07	0.07	—	-0.33**	0.19	0.50***	0.38*	0.10	-0.04	-0.04	-0.14	-0.02	0.26*
Date fl.	-0.25	-0.29	-0.35*	—	-0.46***	-0.38***	-0.27*	-0.15	0.14	0.04	0.26*	0.24	-0.34**
Size 139	-0.57***	0.16	0.13	-0.16	—	0.80***	0.62***	0.34**	0.05	0.05	0.12	-0.11	0.70***
Crown diam.	-0.55***	0.24	0.17	-0.25	0.61***	—	0.74***	0.40***	-0.07	-0.01	-0.07	-0.31*	0.76***
Inf. diam.	-0.39*	0.19	0.11	-0.39	0.53***	0.71***	—	0.65***	-0.09	0.03	0.11	-0.23	0.56***
Flower diam.	-0.19	0.25	0.10	-0.40**	0.43**	0.51***	0.78***	—	-0.08	-0.13	0.24*	-0.12	0.30*
Petal shape	-0.25	-0.14	-0.12	-0.15	-0.03	0.19	0.14	0.21	—	-0.32**	0.07	0.05	-0.18
Petal color	0.05	-0.05	0.07	0.24	-0.06	-0.16	-0.06	-0.12	-0.22	—	0.02	0.09	0.17
Date harv.	-0.44***	0.04	0.10	-0.03	0.45***	0.49***	0.56***	0.59***	0.19	-0.20	—	-0.18	0.28*
Height harv.	-0.38***	-0.17	0.23	-0.12	-0.34**	-0.34*	-0.31*	-0.28	-0.16	0.02	-0.21	—	-0.21
Dry weight	-0.43***	0.16	0.22	-0.33*	0.33**	0.77***	0.60***	0.41**	0.42**	-0.31*	0.57***	-0.21	—

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ ;  $P$ -values not adjusted for multiple comparisons.

ysis so that selection gradient estimates would be comparable, and in the conventional units of standard deviations of the untransformed variable (Lande and Arnold 1983). One-way ANCOVA with block as a random categorical variable and the four traits as continuous variables (covariates) was used to emulate a multiple regression of fitness onto the four traits (GLM procedure, SOLUTION option, SAS Institute 1988).

Linear and quadratic regression models were analyzed for each site (see Lande and Arnold 1983). The two analyses were compared with an  $F$ -test to determine whether the addition of nonlinear terms significantly increased the predictive value of the model (Neter et al. 1985; Mitchell-Olds and Shaw 1987).

Transformation other than standardization of the independent variables makes interpretation of parameter estimates difficult (Lande and Arnold 1983). To confirm the parametric significance levels, confidence intervals surrounding the regression parameters were estimated by bootstrapping the regression 1000 times (Bruce 1991; Potvin and Roff 1993). Because bootstrapped significance tests confirmed those obtained from the parametric regression analysis, only the parametric analysis results are reported here. Linear and quadratic selection differentials ( $s$  and  $C$ ) were estimated as the covariances between the standardized variables and relative fitness (CORR procedure, SAS Institute 1988).

Selection on phenotypes will not necessarily result in a shift in allele frequencies within a population, and predictions made by a phenotypic selection analysis are based on some assumptions not tested here (see Lande and Arnold 1983; Mitchell-Olds and Shaw 1987). Perhaps the most important of these assumptions is that the traits under selection have a significant additive genetic component. All four characters analyzed here were chosen for their ability to distinguish the parental subspecies in a common environment, and therefore have a genetic component. But to confirm that the subspecies differed significantly in trait expression in each of the selective environments, and thus that genetically based variation was exposed to selection, two-way, mixed-model MANOVAs were conducted separately for each site on the F<sub>2</sub> hybrids and the parental subspecies grown in the field (GLM procedure, Wilks'  $\lambda$ -tests, SAS Institute 1988). The four traits of interest were the dependent variables, and plant type (inland ssp., coastal ssp. or hybrid; fixed effect) and block (random effect) served as independent variables. Data were natural-log transformed prior to analysis. Tukey's Studentized Range Tests were used to test differences of factor levels when main effects were significant (Zar 1984).

*Response to Selection.*—Phenotypic selection analysis measures only the correlation of phenotypic trait expression with fitness. To test for a genetic response to selection, I raised the F<sub>3</sub> hybrids (produced by the F<sub>2</sub> plants grown in the field) in a common greenhouse environment and tested for differences in trait expression between the hybrid "populations" from the coastal and inland sites. To do this, I conducted a nested, mixed-model MANOVA on the F<sub>3</sub> populations from the two sites (selection treatments). The four traits served as dependent variables. Independent variables were site (inland or coastal selection history; fixed effect) and block (nested within site; random effect) (GLM procedure, Wilks'  $\lambda$  used to test overall site and block effects, SAS

Institute 1988). The four dependent variables were natural-log transformed to reduce heteroscedasticity among treatment cells. A significant effect of site would indicate that site-specific selection was responsible for genetic divergence between the offspring of the  $F_2$  hybrids subjected to selection at the two sites. Genetic drift and microsite variation in selection—other possible sources of divergence—act independently in each block. Their effects will therefore be accounted for in the block term of the analysis.

To test for the effect of growing environment on trait expression in the  $F_2$  plants in the field, I conducted a nested, mixed-model MANOVA (model same as above). An overall site effect would indicate that environmental factors affect trait expression significantly and would raise concern about the potential for maternal environmental effects to confound genetic effects in the  $F_3$  progeny raised in the greenhouse. If trait expression was not influenced by growing environment, then it is unlikely that trait expression in greenhouse-grown progeny would be affected by maternal environment.

To summarize the response to selection by the two experimental hybrid populations, I performed a multivariate cluster analysis using both  $F_3$  hybrid populations, and representatives of the two parental subspecies. Normalized root-mean-square distance phenograms were constructed based on means of the four morphological traits (CLUSTER procedure STD METHOD = AVERAGE, SAS Institute 1988). Separate phenograms were generated to compare hybrids from each of the two selection histories with the pure subspecies pools. Tighter clustering within the tree indicates greater genetic similarity between hybrid or subspecies groups.

A cluster analysis of identical design was conducted on  $F_2$  plants and members of the parental subspecies grown outdoors in 1992 (the reference population). The purpose of this analysis was to summarize similarities between hybrids and the two subspecies prior to habitat-specific selection (pre-selection). This cluster analysis is used as a baseline from which to compare phenograms generated from the “selected”  $F_3$  populations.

## RESULTS

### Trait Correlations

A number of the 13 variables measured on the  $F_2$  field plants were correlated with one another (Table 1). Of the 12 combinations (total for both sites) of the four variables chosen for selection analysis, three had correlations greater than 0.30. At both sites, leaf shape and inflorescence diameter were negatively correlated (Table 1), indicating that hybrid plants with more lobes per unit leaf length had smaller inflorescences. The correlation between leaf shape and inflorescence diameter was in the opposite direction from that observed in a comparison of the parental subspecies (Table 2), suggesting that hybridization successfully decoupled these characters and that selection may act on them independently. At the coastal site, petal color and shape were correlated such that long, thin petals tended to be lighter in color than shorter, rounder petals. The petal shape and color correlation is consistent with the correlation found when the two parental subspecies are compared (Table 2), suggesting that these traits are linked to some degree and were not de-

TABLE 2. Trait means (SE,  $n$  below) for four diagnostic traits measured on two *Gilia capitata* subspecies and their  $F_2$  hybrids at the coastal site (A) and at the inland site (B). Subspecies were significantly different in all four characters and at both sites (see text, analysis not shown). Shared letters within each row indicate means are not significantly different as indicated by MANOVA Tukey's test at  $P < 0.05$ .

(A) Coastal site:			
Character	Inland spp.	$F_2$	Coastal spp.
Leaf shape	0.20 (0.01) <sup>a</sup> 62	0.22 (0.01) <sup>b</sup> 150	0.23 (0.01) <sup>b</sup> 152
Inflorescence diam.	17.65 (1.01) <sup>a</sup> 10	19.23 (0.62) <sup>a</sup> 72	23.16 (0.59) <sup>b</sup> 122
Petal shape	4.16 (0.35) <sup>a</sup> 10	2.13 (0.05) <sup>b</sup> 71	1.57 (0.02) <sup>c</sup> 120
Petal color	0.90 (0.10) <sup>a</sup> 10	2.36 (0.06) <sup>b</sup> 71	3.24 (0.05) <sup>c</sup> 120
(B) Inland site:			
Character	Inland spp.	$F_2$	Coastal spp.
Leaf shape	0.18 (0.01) <sup>a</sup> 89	0.25 (0.01) <sup>b</sup> 76	0.32 (0.03) <sup>c</sup> 38
Inflorescence diam.	15.33 (1.58) <sup>a</sup> 66	13.69 (0.68) <sup>a</sup> 47	13.14 (1.23) <sup>a</sup> 19
Petal shape	3.94 (0.10) <sup>a</sup> 63	2.34 (0.07) <sup>b</sup> 47	1.58 (0.06) <sup>c</sup> 18
Petal color	0.82 (0.04) <sup>a</sup> 65	2.30 (0.09) <sup>b</sup> 47	3.42 (0.12) <sup>c</sup> 19

coupled completely by a generation of recombination. There were no other significant correlations between pairs of the four traits in the hybrid populations, and the correlations observed were not very large.

### Phenotypic Selection in the Field

The overall linear phenotypic selection analyses were significant at both sites (coastal site  $F_{20,45} = 1.97$ ,  $P < 0.03$ ,  $R^2 = 0.47$ ; inland site  $F_{14,25} = 4.30$ ,  $P < 0.0008$ ,  $R^2 = 0.71$ ). At the coastal site the predictive value of the model was not improved significantly by the addition of quadratic terms (comparison of linear and quadratic models  $F_{10,35} = 1.36$ , ns). At the inland site the quadratic model was significantly more powerful (comparison of models  $F_{10,15} = 5.25$ ,  $P < 0.005$ ) than the linear model, but none of the quadratic terms were significant. Therefore only the linear models for both sites are reported here (Table 3, Fig. 1). It should be emphasized that an indication of “direct selection” indicates only that selection is not a significant function of other variables in the model. “Direct selection” could really be indirect selection through unmeasured characters. Since the characters analyzed were not chosen for functional reasons, it is in fact assumed that direct, or indirect, selection on them is through unmeasured correlated characters. All references to direct or indirect selection in these results are within the context of the model only. This point is especially relevant with respect to the floral characters measured, since it is hard to imagine how selection would have acted directly on them in an experiment where selection during pollination was prevented.

*Leaf Shape.*—The number of lobes per unit leaf length is under negative directional selection at both sites (Table 3, Fig. 1). The selection differential,  $s$ , is significant at the coast,

TABLE 3. Linear directional phenotypic selection gradients ( $\beta \pm$  SE) and differentials (s) in units of standard deviations of the character mean, for selection on  $F_2$  hybrids at the coastal site (A) and at the inland site (B).

(A) Coastal site:		
Character	$\beta$ (SE)	s
Leaf shape	-0.46 (0.20)*	-0.29**
Inflorescence diam.	0.44 (0.18)*	0.44***
Petal shape	-0.06 (0.15)	-0.07
Petal color	0.07 (0.14)	0.13
(B) Inland site:		
Character	$\beta$ (SE)	s
Leaf shape	-0.30 (0.26)	-0.30*
Inflorescence diam.	0.54 (0.20)*	0.54**
Petal shape	0.50 (0.15)**	0.60***
Petal color	-0.43 (0.20)*	-0.38*

\*  $P < 0.05$ , \*\*  $P < 0.01$ , \*\*\*  $P < 0.001$ .

but smaller than  $\beta$  (the selection gradient), suggesting that correlations with other variables in the model mitigate selection on leaf shape slightly.  $\beta$  at the inland site is also negative, but is smaller than at the coastal site and is not significant. The selection differential for leaf shape at the inland site is of identical magnitude and direction as the selection gradient, indicating that there is no effect on selection on leaf shape though correlated characters at the inland site (within the scope of the model). Plants with leaves with fewer lobes are more fit at both sites. Therefore, selection at both sites favors the inland morphology (Table 2).

**Inflorescence Diameter.**—Inflorescence size is under strong and significantly positive directional selection at both sites (Table 3, Fig. 1). In addition, at both sites  $s = \beta$ , indicating that selection on this character is independent of selection on other variables included in the analysis, despite its significant correlation with leaf shape (Table 1). Plants with larger inflorescences are more fit at both sites.

**Petal Shape.**—Petal shape is under strong and significant positive directional selection at the inland site but not the coastal site (Table 3, Fig. 1). The large  $\beta$  at the inland site indicates that petal shape itself is under significant selection independent of the other three traits, but the slightly larger selection differential indicates that a long, thin petal shape is further favored by selection on correlated traits. Plants with narrow petals are favored at the inland site, whereas petal width, and traits correlated with petal width, are not correlated with fitness at the coast.

**Petal Color.**—Petal color is under similar selection as petal shape (Table 3, Fig. 1). Large and significant gradients and differentials are seen at the inland site but not at the coastal site.  $\beta$  and  $s$  are similar, indicating that much of the selection is direct but that some reduction in selection strength occurs through correlations with one or more of the other three variables. Plants with light-colored petals have significantly greater fitness than those with dark-colored petals at the inland site, but petal color is not associated with fitness at the coastal site.

At both sites, the parental subspecies and the  $F_2$  hybrids differed when all four characters were considered (MANOVA, coastal site:  $F_{8,332} = 57.01$ ,  $P < 0.0001$ ; inland site:

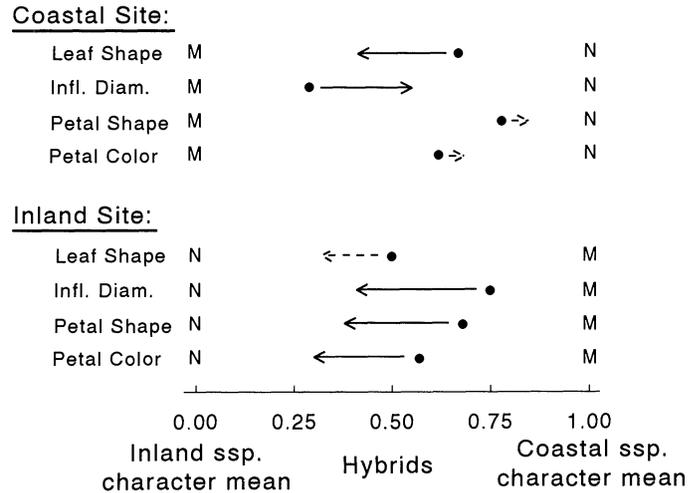


FIG. 1. Trait means expressed on a relative scale for the  $F_2$  hybrid populations grown in each of the two field sites. Inland and coastal subspecies values are measured in the field, transformed to zero and one, respectively, and indicated with "N" or "M," depending on status as native or migrant (= nonnative) at a site. Relative  $F_2$  hybrid means are indicated by dots. See Table 3 for absolute means. Solid arrows indicate direction and relative magnitude of significant directional selection gradients; dashed arrows indicate direction and magnitude of nonsignificant gradients.

$F_{8,192} = 54.15$ ,  $P < 0.0001$ ), and in most pairwise comparisons the four diagnostic traits differed among plant types (Table 2). These results confirm the existence of genetic variation between subspecies in the field, and suggest that phenotypic selection on these traits would be expected to cause evolutionary shifts.

#### Response to Selection

There are significant genetic differences between the offspring of  $F_2$  hybrids exposed to different selective regimes. Nested, mixed-model MANOVA detected a significant overall site effect on greenhouse-raised  $F_3$  plants when all four traits were considered together ( $F_{4,17} = 5.15$ ,  $P < 0.007$ , Tables 4, 5). In contrast, MANOVA found no significant overall effect of site on trait expression by  $F_2$  hybrids growing in the field ( $F_{4,24} = 2.06$ ,  $P = 0.12$ ), indicating that the environment does not significantly affect overall expression of these traits. It is reasonable to conclude, then, that differences between the  $F_3$  hybrid populations are due to divergent evolution resulting from a single generation of natural selection.

**Leaf Shape.**—Leaf shapes of  $F_3$  offspring of individuals selected at the coastal site differed significantly from those selected at the inland site, when grown in a common greenhouse environment (Table 4). The number of lobes per millimeter of leaf length for inland-selected hybrids was 28% less than the number of lobes on coast-selected hybrids (Table 5). In fact, the difference in leaf shape between  $F_3$  populations separated by only a single generation of selection was greater than the difference between either of the  $F_3$  populations and the subspecies native to the site of selection (Table 5, Fig. 2).

**Inflorescence Diameter.**—There was not a significant difference in inflorescence size between offspring of hybrids

TABLE 4. Nested mixed-model MANOVA on four traits measured on the F<sub>3</sub> hybrid generation grown in the greenhouse. Site is a fixed effect and block(site) is random. Data are natural-log transformed.

Character	Source	df		MS		F	P
		num., den.	num., den.	num., den.	num., den.		
Leaf shape	Site	1, 90.1	1.34, 0.11	12.72	< 0.0006		
	Block(site)	20, 173	0.12, 0.10	1.16	0.29		
Infl. diam.	Site	1, 47.9	0.10, 0.04	2.47	0.12		
	Block(site)	20, 173	0.07, 0.33	2.68	< 0.0003		
Petal shape	Site	1, 29.9	1.79, 0.07	24.18	< 0.0001		
	Block(site)	20, 173	0.15, 0.02	6.84	< 0.0001		
Petal color	Site	1, 40.8	2.86, 0.11	26.48	< 0.0001		
	Block(site)	20, 173	0.19, 0.05	3.48	< 0.0001		

subjected to selection in the two sites (Table 4). F<sub>3</sub> hybrid populations from both sites were intermediate with respect to the two parental subspecies (Table 5, Fig. 2).

*Petal Shape.*—Petal shape differed significantly between hybrid populations from the two selection regimes (Table 4). The length:width petal shape ratio for offspring of coast-selected hybrids was 30% less than that for the inland-selected hybrids (Table 5). The absolute amount of divergence between F<sub>3</sub> populations was greater than the difference between coastal natives and coast-selected hybrids, but less than the difference between inland natives and inland-selected hybrids (Table 5, Fig. 2).

*Petal Color.*—Petal color also exhibited a significant divergence between offspring of hybrids selected at different sites (Table 4). Petal color of the offspring of inland-selected hybrids was 25% lighter than that of hybrids selected at the coast (Table 5). As for petal shape, the difference between petal colors of the two hybrid populations was greater than the difference between coast-selected hybrids and coastal natives, but less than the difference between inland-selected hybrids and inland natives (Table 5, Fig. 2).

When the relative positions of the means of the preselection F<sub>2</sub> population and the postselection F<sub>3</sub> population are compared with parental population means, all four traits demonstrated a shift in the direction of increased similarity to natives of the site of selection (Fig. 2).

Phenograms constructed using cluster analysis confirm that the progeny from hybrids selected at each site were morphologically more similar to natives of that site than to natives of the other site (Fig. 3). Divergent F<sub>3</sub> hybrid populations grouped with the subspecies native to the site where F<sub>2</sub> plants experienced selection. In other words, the overall response to selection was in the direction of similarity with

natives at both sites. The cluster analysis conducted on parentals and the “preselected” F<sub>2</sub>s revealed that hybrids tended to resemble the coastal native (Fig. 3; unpubl. data). However, the clustering distances between the unselected F<sub>2</sub> population and the two subspecies is intermediate to distances between either selected F<sub>3</sub> population and either subspecies. Selection in each site has, therefore, increased the morphological similarity between hybrid populations and plants that are native to that site.

## DISCUSSION

In this study, experimental hybridization served to model the evolutionary consequences of gene exchange between divergent taxa. Phenotypic selection analysis on recombinant hybrids between two locally adapted subspecies of *G. capitata* demonstrated that native character states impart higher fitness than nonnative character states. In addition, natural selection acts to re-create native phenotypes at both sites. These results suggest that natural selection will tend to counter introgression between these populations, and that subspecies differentiation will be maintained. The findings also suggest that the evolution of hybrid populations will proceed at different rates at the two sites.

### *Phenotypic Selection and Evolutionary Response*

*Leaf Shape.*—Selection on leaf shape favored fewer lobes per unit leaf length at both sites. At the inland site, indirect selection favored hybrids that resembled natives, whereas at the coastal site direct selection (as defined within the analysis) favored the *nonnative* condition of fewer lobes. For this trait, estimated selection differentials were of sufficient strength to cause a 16% decrease in lobe number at the coastal

TABLE 5. Trait means (SE, *n* below) for the inland subspecies, F<sub>3</sub> hybrid populations selected at the two sites, and the coastal subspecies grown in the greenhouse. Shared letters within each row indicate means are not significantly different as indicated by MANOVA test at *P* < 0.05 (Table 4). See Table 2 for between-parental subspecies comparisons.

Character	Inland ssp.	Inland F <sub>3</sub> pop.	Coastal F <sub>3</sub> pop.	Coastal ssp.
Leaf shape	0.12 (0.01)	0.13 (0.01) <sup>a</sup>	0.18 (0.01) <sup>b</sup>	0.20 (0.01)
	49	52	147	49
Inflorescence diam.	18.89 (0.40)	21.78 (0.48) <sup>a</sup>	22.90 (0.31) <sup>a</sup>	25.36 (0.43)
	49	51	146	49
Petal shape	4.32 (0.10)	2.87 (0.09) <sup>a</sup>	2.01 (0.03) <sup>b</sup>	1.71 (0.02)
	49	51	146	49
Petal color	0.69 (0.04)	1.84 (0.08) <sup>a</sup>	2.46 (0.04) <sup>b</sup>	2.97 (0.05)
	49	50	146	49

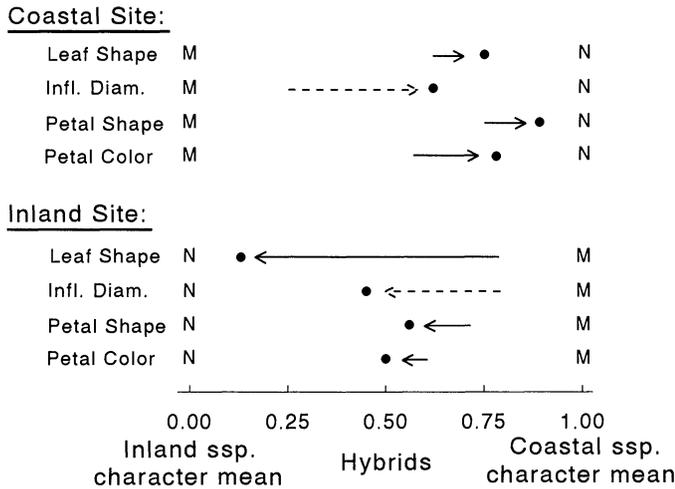
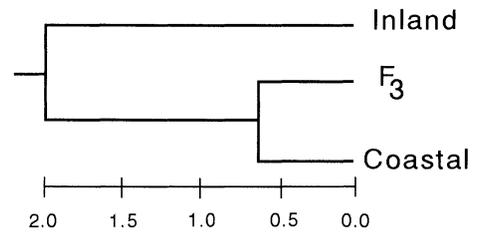


FIG. 2. Trait means expressed on a relative scale for the F<sub>3</sub> hybrid populations grown in the greenhouse. Inland and coastal subspecies values are those measured in the greenhouse, transformed to zero and one, respectively, and indicated with "N" or "M" depending on their status as native or migrant (= nonnative) at the site of hybrid selection. Relative F<sub>3</sub> hybrid means are indicated by dots. See Table 5 for absolute means. Arrows indicate direction and magnitude of difference in values relative to values measured on parental generation in the field. Solid arrows indicate significant divergence between hybrid populations as indicated in Table 4; dashed arrows indicate nonsignificant divergence. Magnitudes (arrow lengths) should be viewed with caution since they are based on preselection and postselection measurements taken in different environments.

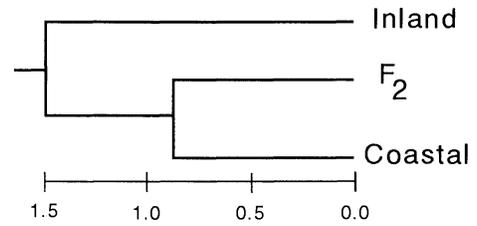
site, and an 11% decrease at the inland site, if leaf shape was entirely heritable. Analysis of the evolutionary response displayed by the offspring of these hybrids indicated a significant divergence due to the selection regimes at the two sites. Given the strength and direction of phenotypic selection measured in the field, this response was not expected. In particular, the apparent shift by both hybrid populations toward the native condition at each site was not predicted; phenotypic selection at the coastal site favored a leaf morphology similar to the nonnative condition. However, in light of the fact that, for the other three traits, selection was always in the direction of similarity to the native, correlations or interactions with unmeasured characters under selection are likely to have caused the observed pattern. Selection on unmeasured characters correlated with the trait of interest can cause unexpected selective responses, since the effect of selection on the correlated character may outweigh the effect of apparent direct selection on the subject trait (Lande and Arnold 1983). It is interesting to note that correlations between leaf shape and other measured, but unanalyzed, characters were strongest at the inland site, and it is here we see the strongest evolutionary response. This observation supports the idea that selection on this trait may be a function of selection on other adaptive characters.

**Inflorescence Diameter.**—Significant positive directional selection was detected on inflorescence diameter at both sites, yet no detectable divergence was observed between the hybrid populations when grown in the greenhouse. Because native subspecies always produced larger inflorescences in the field, selection for large inflorescence size was in the

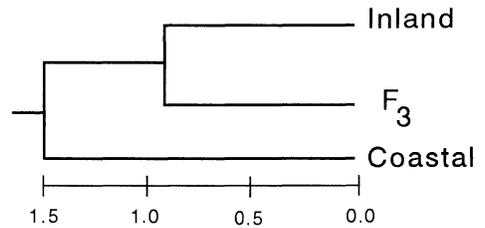
(A) Coastal Selection



(B) Pre-Selection



(C) Inland Selection



**Root Mean Distance**

FIG. 3. Phenograms based on four traits illustrating morphological similarity between greenhouse-raised members of both subspecies and (A) F<sub>3</sub> offspring of coast-selected hybrids, (B) the unselected F<sub>2</sub> population raised in 1992; and (C) F<sub>3</sub> offspring of inland-selected hybrids.

native direction at both sites. Although the absolute direction of selection is not site specific, the pattern of selection consistently favored the native phenotype. This was reflected in the evolutionary response by the F<sub>3</sub> progeny, where the trend was for hybrid inflorescence size to resemble native inflorescence size in the common greenhouse environment.

**Petal Shape.**—Selection for increased petal length relative to petal width was strong at the inland site only. The direction of selection is consistent with the hypothesis that native character states are adaptive at the inland site, but neutral at the coastal site. The strength of the estimated selection differential at the inland site would be sufficient to cause up to a 12% shift in petal shape in the direction of the native morphology, and there was a significant divergence in petal shape between the F<sub>3</sub> populations selected at the two sites. This is apparently in response to the strong selection at the inland site alone. Petal shape in both F<sub>3</sub> populations tended to resemble the coastal subspecies more closely than the inland

subspecies, but evolutionary divergence shifted the inland-selected hybrid population in the direction of the inland native. Thus, petal shape expressed by hybrids (or unmeasured characters correlated with petal shape) have adaptive consequences at the inland site, while petal shape is neutral at the coast. It is also possible, that because  $F_2$  phenotypes tend to resemble the coastal subspecies' phenotype more closely than that of the inland subspecies even before selection, selection on petal shape at the coastal site may simply not be detected as easily as it is at the inland site, where the hybrid phenotype differs dramatically from that of the native phenotype.

*Petal Color.*—The pattern of selection on petal color was similar to that observed for petal shape. Selection was strong at the inland site, absent at the coast, and acted primarily through “direct” effects on fitness (not via other characters in the model). There were some mitigating effects on the strength of selection by correlated characters as indicated by the slightly reduced selection differential, compared with the selection gradient. Selection on petal color at the inland site was strong enough to cause up to a 10% shift in color toward the native condition, and there was a significant divergence between the selected  $F_3$  populations in petal color. This, again, is in apparent response to the strong selection imposed at the inland site and lack of selection imposed at the coastal site. Petal color (more likely unmeasured characters linked or correlated with color) is adaptively important at the inland site but not at the coast. The disparity between the selection strengths at the two sites could again be due to the  $F_2$  hybrids' tendency to resemble the coastal subspecies. This trend could bias interpretation of the specific adaptive importance of petal color.

It seems likely that the petal shape and color characters, which are so diagnostic of the subspecies, are linked to other traits that are ultimately responsible for the coastal subspecies' poor performance at the inland site. Traits like flower size or color are important to plant fitness through their role in pollinator attraction. Selection on floral traits has been observed as a function of pollinator behavior and pollination success (Campbell et al. 1991; Johnston 1991). Because selection on floral characters was eliminated by using controlled pollination, it is extremely unlikely that floral traits themselves were under direct selection in this experiment.

*All Characters.*—The results from all four traits demonstrate that selection was strong, and caused significant genetic divergence between the two  $F_3$  hybrid populations. In all but a single case, phenotypic selection favored the native condition, and in all cases divergence between the hybrid populations was in the direction of similarity with the native. This supports the hypothesis that native character states (measured and unmeasured) are adaptive and are subject to natural selection.

It is possible that character combinations were under selection in addition to, or instead, of native characters individually. Epistatic interactions among native genes can play a role in local adaptation (see review by Fenster et al. 1997). However, the phenotypic selection analysis presented here does indicate that selection on some of the characters is independent from selection on others, suggesting that interactions among characters are not necessary for selective ad-

vantage. The results, therefore, illustrate more than just selection for certain character assemblages, or even for general “nativeness,” but imply at least some independent selection for distinct portions of the native genome.

Phenotypic selection and evolutionary response was strongest overall at the inland site. This is likely due in part to the tendency for  $F_2$ s to resemble the coastal subspecies. As a consequence, hybrids were morphologically more similar to natives at the coastal site than hybrids were to natives at the inland site. This pattern reflects a dominance component in gene expression following hybridization between these two subspecies, and while it does complicate our understanding of the relative adaptive values of traits in the two sites (inland genes may be partially masked in hybrids), it does not affect our predictions about the evolutionary dynamics of gene exchange in the system.

Cluster analyses confirmed the existence of strong evolutionary responses to natural selection in the field, and point to the overall adaptive superiority of “native” phenotypes. When all four traits were combined into a single multivariate distance measurement, hybrid populations subjected to natural selection at each site resembled natives of that site more closely than they resembled the subspecies native to the other site. Based on a comparison with the 1992 cluster of “preselection”  $F_2$  individuals, the magnitude of the response to selection was strongest at the inland site. This can be seen by comparing the relative differences between the two phenograms for the selected hybrid populations with the phenogram for the preselection hybrids (Fig. 3). Selection at the inland site was more effective at removing nonnative genetic variation than it was at the coastal site. This result agrees with the predictions made based on the phenotypic selection analysis and the MANOVA on individual  $F_3$  traits, each of which indicated that selection at the inland site was stronger than at the coastal site.

#### *Environmental Effects*

Because phenotypic measurements were made on offspring grown in a common greenhouse, differences between the  $F_3$  populations cannot be attributed to variation in their growing environment. Effects carried over from the  $F_2$  maternal environments, however, may influence the expression of characters in their offspring (Roach and Wulff 1987).  $F_3$  trait expression, therefore, could be influenced by nongenetic, site-specific environmental effects experienced by their parents, or by the  $F_3$  individuals themselves as seeds. I attempted to control for this possibility by conducting pollinations on, and collecting seed from, both parental subspecies that grew alongside the  $F_2$  hybrids in every block in the field. By growing these offspring in the greenhouse, I could have tested directly for maternal (and paternal) environmental effects on all of the four traits. Unfortunately, because of low seed production by the nonnatives at each site, I was not able to conduct this test. However, the fact that there was not a significant overall site effect on the four traits measured on the  $F_2$  hybrids grown in the two sites suggests that environmental factors have little impact on expression of the four subject traits. Because there was no detectable effect of growing environment on the morphology of  $F_2$  parents in the field,

the significant effect of site on  $F_3$  trait expression detected in the greenhouse was likely a genetic effect, rather than a maternal environmental effect.

#### *Implications for Gene Exchange*

Gene flow between populations can potentially transfer adaptations between gene pools. Because the two subspecies I studied form fertile hybrids, there is the potential for gene transmission between these locally adapted populations. For example, morphological variation present at the inland site includes leaf shapes that impart high fitness at both sites; gene flow from the inland site to the coast would carry with it preadapted variation that could enhance hybrid fitness at the coast. The transfer of adaptations through hybridization between divergent populations has been documented in both plant and animal systems (e.g., Stebbins and Daly 1961; Caprio and Tabashnik 1992). The formation of fertile hybrids can also act as a stepping stone for gene migration, effectively increasing the potential range of gene movement (Potts and Reid 1988). However, the results from this study suggest that even though selection favored the nonnative leaf morphology, the evolutionary response was in the direction of the native (i.e., "less fit") condition. This apparent maladaptation might be accounted for by correlations with unmeasured characters that were themselves under selection. Character correlations could, therefore, inhibit the establishment of preadapted morphologies in this case. Theory predicts that selection against even a few genes following immigration may slow the introgression of other genes (Spirito 1990).

Another possible consequence of gene movement among locally adapted populations is the transfer of maladapted genes. Gene flow from the coast to the inland site would bring alleles for darker colored, more rounded petals than are normally found in populations of the inland subspecies. Morphologies of this kind would reduce hybrid fitness and would be at a selective disadvantage. Until these deleterious alleles were eliminated from the population, they would lower the population's mean fitness. Based on the large selection gradients I observed for petal shape and color, selection should be effective at rapidly removing much of the maladapted variation in these floral traits.

The conclusions drawn here are consistent with the results from a reciprocal transplant experiment in which it is demonstrated that *G. c. capitata* and *G. c. chamissonis* are locally adapted to their native habitats (Nagy and Rice 1997). The reciprocal transplant study also demonstrated a bias in the potential for establishment. Because of especially poor survivorship of immigrants at the coastal site, successful migration to the coast is expected to be low. Migration to the inland site was limited not by low survivorship rates, but by poor growth and fertility. In the present study, traits were under stronger selection at the inland site than the coastal site, suggesting that overall nonnative fitness is lower at the inland site. The discovery of relatively weak selection against nonnative character states in  $F_2$  hybrids at the coastal site is interesting in light of the results from the reciprocal transplant experiment that indicated very strong selection against the immigrant subspecies. Detection of only weak selection on hybrids at the coastal site may have resulted from the mor-

phological similarity between hybrids and coastal natives. However, it also may reflect the fact that most of the selection at the coast was in the form of differential mortality. Multivariate regression analyses exclude observations in which even a single variable is missing. Therefore, plants that did not survive to flowering (those for which the floral trait measurements are missing) were not included in the phenotypic selection analysis, and any selection that resulted in early plant death is not reflected in the selection gradients or differentials presented here. The phenotypic selection analysis on these characters is therefore insensitive to early viability selection (observed by Nagy and Rice at the coastal site), but not to variation in individual performance (more important at the inland site). The response phenograms, however, reflect the impact of both types of selection and reflect measurable evolutionary shifts, consistent with the strong selection indicated by the reciprocal transplant study at both sites.

In conclusion, few studies to date have attempted to measure selection on traits in hybrid populations. Most have addressed only associations between environmental conditions and hybrid character states (Benson et al. 1967; Arnold and Bennett 1993 and references therein). In one of the first studies of its kind, Jordan (1991) demonstrated the adaptive value of native traits using phenotypic selection analysis of experimental hybrid populations. However, phenotypic selection does not necessarily result in evolutionary response, and indeed as I have shown here, the response does not always mirror the direction or intensity of phenotypic selection. Therefore, to accurately predict evolution, it is necessary to quantify the response to selection. In doing so, I have made the observation that genetic divergence between hybrid populations exposed to different environments follows selection for native characters.

In this study, I have demonstrated that phenotypic selection on hybrid populations can result in evolutionary response. I have also shown that natural selection will maintain subspecies differentiation following gene exchange between the two study populations and that unmeasured adaptive traits can be "tracked" with morphologically markers. It is reasonable to assume, therefore, that selection in other habitats can also direct the independent evolution of resident populations. It should not be surprising then to see the wide array of local variation that occurs in this species complex (Grant 1950). Furthermore, the two sites studied here present different levels of "resistance" to introgression. Because selection against nonnative traits was stronger at the inland site than at the coastal site, introgression at the coast should be easier. It appears that introgressive hybridization has been important in the evolution of several *G. capitata* subspecies, and this study shows that natural selection will be very important in determining the potential for introgression, and direction in which it is likely to proceed.

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