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## LOCAL ADAPTATION IN TWO SUBSPECIES OF AN ANNUAL PLANT: IMPLICATIONS FOR MIGRATION AND GENE FLOW

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**Abstract.**—Plant populations often adapt to local environmental conditions. Here we demonstrate local adaptation in two subspecies of the California native annual *Gilia capitata* using standard reciprocal transplant techniques in two sites (coastal and inland) over three consecutive years. Subspecies performance in each site was measured in four ways: probability of seedling emergence, early vegetative size (length of longest leaf), probability of flowering, and total number of inflorescences produced per plant. Analysis of three of the four variables demonstrated local adaptation through site-by-subspecies interactions in which natives outperformed immigrants. The disparity between natives and immigrants in their probability of emergence and probability of flowering was greater at the coastal site than at the inland site. Treated in isolation, these two fitness components suggest that migration from the coast to the inland site may be less restricted by selection than migration in the opposite direction. Two measurements of individual size (leaf length and number of inflorescences), suggest (though not strongly) that immigrants may be subject to *weaker* selection at the coastal site than at the inland site. A standard cohort life table is used to compare replacement rates ( $R_0$ ) for each subspecies at each site. Comparisons of  $R_0$ s suggest that immigrants are under a severe demographic disadvantage at the coastal site, but only a small disadvantage at the inland site. The results point out the importance of integrating over several fitness components when documenting the magnitude of local adaptation.

**Key words.**—Cohort life table, demography, density dependent, frequency dependent, gene flow, *Gilia*, local adaptation, migration, reciprocal transplant.

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Plant ecotypes have evolved in response to small-scale environmental variation as well as broad geographical gradients (Clausen et al. 1948; Jain and Bradshaw 1966; Antonovics and Bradshaw 1970; Waser and Price 1985; Nevo et al. 1986; Ehleringer and Clark 1988; Levin 1988; Schmitt and Gamble 1990; Galen et al. 1991; Waser and Price 1991, 1994; Sork et al. 1993; Kindell et al. 1996). Because plants are sessile, dispersal distances are typically low (Levin 1984; Fenster 1991), and local genetic differentiation is common (Epling and Dobzhansky 1942; Endler 1977; Harper 1977; Willson 1983; Levin 1984, 1988; Tilman 1986; Mayer et al. 1994). Locally adapted ecotypes may arise if different genetically controlled character states are selected for in different populations. To determine whether selection is responsible for genetic divergence among populations, individuals from each population must be reciprocally transplanted. If natives consistently outperform nonnatives in such an experiment, it is evidence for local adaptation through natural selection.

The strength of selection responsible for local adaptation may determine the success of seed or pollen migration and establishment among populations. The evolutionary importance of gene exchange between locally adapted plant populations has been recognized for a long time (Baker 1951; Stebbins and Daly 1961; Stebbins 1969; Grant 1981; Stace 1987; Hewitt 1988; Rieseberg and Wendel 1993; Waser and Price 1994); and seed and pollen migration can result in the transmission of genes (gene flow) among disjunct plant populations (Levin 1981, 1983, 1988, 1995; Clegg and Brown 1983; Ellstrand and Marshall 1985; Potts and Reid 1988; Campbell and Waser 1989; DePamphilis and Wyatt 1989;

Lumaret and Barrientos 1990; Ellstrand 1992; Godt and Hamrick 1993; Broyles et al. 1994; Ennos 1994). If selection is strong, immigrant genes may not establish, and populations may remain genetically distinct even if migration occurs among them.

Although there is a large body of empirical work on the prevalence of local adaptation in plants (see above), attention is only now being paid to the complex ecological, reproductive, and evolutionary dynamics of gene migration among differentiated plant populations. And while hybridization between plant taxa has clearly played a role in plant evolution in the past, increasing human activity and global environmental change are likely to increase rates of plant migration and produce novel environmental conditions appropriate for hybrid populations (Anderson 1949; Clegg and Brown 1983; Ellstrand 1992).

Here we address the demographic consequences of migration between differentiated plant populations and make predictions about the evolutionary outcome of migration. We used reciprocal transplant experiments with two subspecies of *Gilia capitata* in three years to test for local adaptation and model the dynamics of immigrant establishment. The two subspecies differ in morphology, life history, reproductive biology, habitat, and biogeography. Although crossing between the subspecies is restricted and strongly unidirectional, hybrids are vigorous and fertile (Grant 1950; Nagy 1995; Nagy 1997), making introgression a possible consequences of migration. However, the two populations studied are widely separated and almost certainly do not exchange seed or pollen naturally. Other populations are much closer, and have been observed to hybridize (Grant 1950). In one of the three years (1991) plant density and subspecies frequency were examined for their effects on native and immigrant survivorship and growth. We address four questions: (1) Are the

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subspecies locally adapted to their respective habitats? (2) Does population density or immigrant frequency affect subspecies performance? (3) Is local adaptation detectable in separate measures of performance across the life history of the organism? (4) What are the demographic and likely evolutionary consequences of seed migration between the subspecies?

## 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 display significant morphological differentiation (Grant 1950; Steele 1986; Day in Hickman 1993). Two subspecies, *G. capitata* ssp. *capitata* and *G. capitata* ssp. *chamissonis*, were chosen for this study because of their immediate common ancestry, yet strong morphological and ecological differences, and for their reported ease of cross-fertilization (Grant 1950). Populations of both subspecies are commonly small, discrete, and widely separated. Plants germinate in the fall, grow as rosettes during the winter, and bolt before flowering in the late spring and summer. The subspecies are insect-pollinated and are serviced by a variety of bees (Grant and Grant 1965; Nagy 1995). Dense capitata inflorescences present purple-colored flowers and offer rewards of nectar and pollen. Using classical genetic and taxonomic methods, Grant (1950, 1956) concludes that hybridization among divergent subspecies within the species complex is responsible for the evolution of several of the eight currently recognized subspecies. And while human land development appears to have destroyed many hybrid populations and neighboring populations of the two subspecies since Grant conducted his work forty years ago (Nagy, pers. obs.), this system is biologically and ecologically appropriate for exploring the evolutionary dynamics of migration and introgression.

*Gilia c. capitata* is common on the dry rocky slopes of central and northern California's Coast Range. It is a spindly plant (0.2–1.0 m) with self-incompatible, pale violet flowers (diam. 6–8 mm; Hickman 1993), each with three to six ovules/ovary and small amounts of pollen (relative to the other ssp.) or nectar (0–0.32  $\mu$ L; Nagy, unpubl. data). *Gilia c. chamissonis* (E. Greene) V. Grant is more limited in distribution and is found only on the coastal sand dunes of central California. Individuals of this subspecies are short (0.1–0.2 m) and compact, have self-compatible, dark purple flowers (diam. 9–10 mm; Hickman 1993), with 10–24 ovules/ovary, and about twice the pollen (Nagy 1997) and more nectar (0.16–0.78  $\mu$ L; Nagy, unpubl. data) than *G. c. capitata*. The two subspecies are similar in the number of flowers comprising each inflorescence (10–100) and in the number of inflorescences per plant (1–14) (Nagy, unpubl. data). Seeds of both subspecies are small (1–2 mm) and hard when dry, but possess a sticky mucilaginous coat that expands when wet, and likely serves to anchor seeds to the coarse, sandy substrate. Seeds may also adhere to a mobile substrate, and thereby disperse. Despite their divergence in ecological and reproductive characters, Grant (1950) reported 40–70% re-

productive compatibility between the subspecies. We have found crossing ability between the study populations of the two subspecies to be more restrictive (on the order of 10%) and unidirectional. *Gilia c. capitata* pollen can fertilize *G. c. chamissonis* ovules, but the reciprocal cross is rarely successful (< 1%; Nagy 1997).

The study was conducted at two sites separated by approximately 70 km, each home to a natural population of one of the two *Gilia* subspecies. The "inland site," where *G. c. capitata* grows, is located on the banks of Pope Creek in Pope Valley, Napa County, California, U.S.A. The region is characterized by a typical Mediterranean climate and chaparral plant community. Precipitation occurs exclusively during the winter months. Temperatures drop below 0°C during the winter rainy season, and can reach 45°C during the dry summers (J. Callizo, pers. comm. 1994; Nagy pers. obs.). *Gilia c. capitata* grows on a steep, south-facing, highly disturbed talus stream cut that is subject to erosion from flooding. The immediate plant community is sparse and includes perennial and annual grasses and a few other winter and spring annual forbs. *Gilia c. capitata* germinates in December, flowers in June, and matures seed in July.

The "coastal site," where *G. c. chamissonis* grows, is located on the stable vegetated back dunes of Bodega Head, in Bodega Bay, Sonoma County, California, U.S.A. Conditions here are more moderate, with winter temperatures approximately 10°C warmer and summer temperatures 10°C cooler than at the inland site. Precipitation here is also greater and extends longer into the spring (University of California Bodega Marine Laboratory records 1994; Nagy, pers. obs.). The community is a low coastal scrub composed of a mixture of perennials and annuals. The sandy substrate is subject to erosion by wind and rain. *Gilia c. chamissonis* germinates in December, flowers in July, and matures seed in August.

### *Experimental Design*

Reciprocal transplant experiments were used to test for local adaptation in the two *G. capitata* subspecies. Experiments were conducted in the home habitats of each subspecies in 1991, 1992, and 1993. The design was modified each year after obtaining the previous year's results, and in 1992 due to logistical constraints.

*1991 Experiment.*—Bulk seed of both subspecies was collected from mature fruits in the field at each site in summer 1990. Seeds were collected throughout the season from approximately one hundred haphazardly selected plants of varying size and seeds were stored in paper bags at room temperature until used for planting. Seeds require a one- to two-month after-ripening period to achieve maximum germination, and demonstrate no reduction in viability following storage for several years (Nagy, pers. obs.). In late December 1990, seeds of both subspecies were planted into four blocks at each site. Seeds of the two subspecies were identified with wooden toothpicks of different colors. Two seeds were stuck to each toothpick by first briefly wetting them, which caused the mucilage sheath to expand, placing them on the end of a toothpick, and allowing the mucilage to dry and cement the seeds to the wood. A total of 113 experimental toothpicks holding 226 inland seeds and 119 toothpicks holding 238

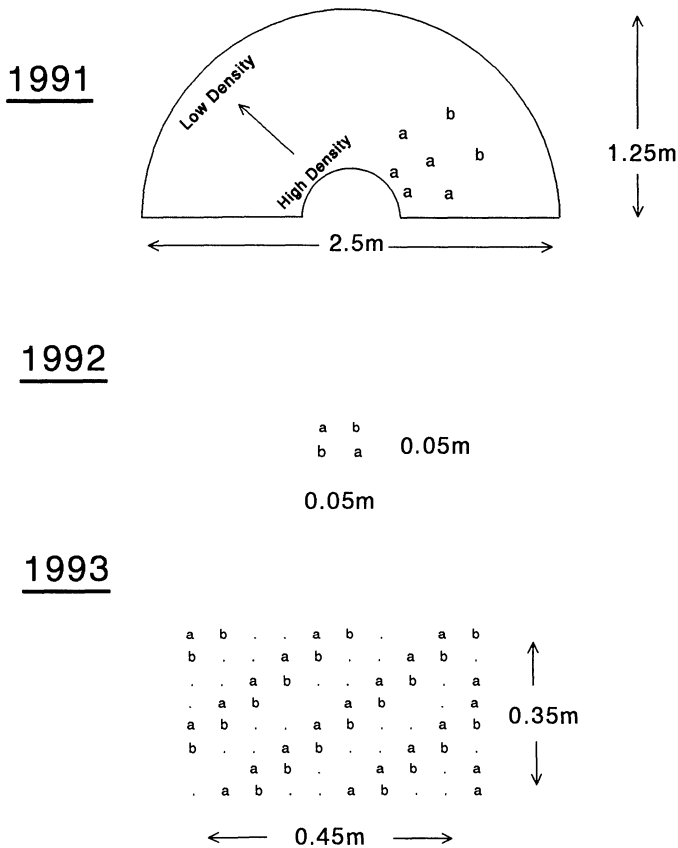


FIG. 1. Diagrams of three block structures used in three years (not to scale); *a* and *b* indicate the two subspecies. Hexagonal fan array consists of staggered concentric rows planted such that each individual has six nearest neighbors. Density decreases from the center of the arc outwards. Subspecies are arranged in the array so that all possible numbers of neighbors of each subspecies occur (frequency levels 0–6, 6 = all six nearest neighbors are same ssp. as subject, 0 = no nearest neighbors of same ssp.). The four plants in the 1992 array are arranged in a square 2 × 2 grid, 50 mm on a side. The 80 plants in the 1993 experimental blocks are separated by 50 mm and constitute a rectangular grid 450 mm × 400 mm. Dots in the 1993 block indicate positions of hybrid seed used in another experiment (Nagy, in press).

coastal seeds were planted in each block by sticking the toothpicks 1 cm into the loose soil. If two plants emerged from a location, a haphazardly chosen individual was thinned shortly after emergence. If no plant emerged, replacement seeds or seedlings were planted.

In 1991, plant density and subspecies frequency were included in the factorial design. Blocks were laid out in a hexagonal fan design (per Antonovics and Fowler 1985, Fig. 1). Plant density varied continuously from the base of the fan (8734/m<sup>2</sup>) to the margins (23/m<sup>2</sup>). For analysis, densities were divided evenly into three classes: high, medium, and low. Seven frequency levels (0, 0.17, 0.33, 0.50, 0.67, 0.83, 1) were defined as the frequency of plants belonging to the same subspecies as the subject plant, of six possible nearest neighbors. For example, if an individual of subspecies *a* was surrounded by four individuals of subspecies *a* and two of subspecies *b*, its frequency level was defined as 0.67. Frequency levels were distributed throughout the fan as evenly

as possible given geometric constraints (see Antonovics and Fowler [1985] for planting design). Individuals located on the edges of the blocks were not included in the analysis, since they did not have a full complement of neighbors to define their density or frequency levels.

**1992 Experiment.**—Due to a delay in planting the 1992 experiment, seedlings were planted into the field instead of seeds. Half of the seedlings of each subspecies were collected from the field immediately prior to planting, and half were raised in the greenhouse from bulk seed collected in 1991. Analysis indicated that seedling source (greenhouse or field) did not significantly affect later plant size ( $F_{1,218} = 3.14, P = 0.08$ ). In addition, when seedling source was included in two of the analyses (see below) the results were unaffected. Seedlings from the two sources were therefore pooled in all analyses. Seedlings of each subspecies with not more than two whorls of true leaves were transplanted into 40 blocks at each site in mid-January 1992. Sixty-eight percent of seedlings survived transplantation. Those that did not survive were replaced within seven days. Analysis of the 1991 experiment showed that site effects overwhelmed effects of local density and frequency, so the experiment was simplified to maximize detection of site and seed origin effects. Each of the 40 blocks per site was a square grid containing two seedlings of each subspecies, each separated by 50 mm (Fig. 1). Root crown diameter (correlated with above ground biomass,  $R^2 = 0.71$ ) was measured at the time of planting for use as a covariate in analyses.

**1993 Experiment.**—Seeds were planted as in 1991, but in a different block structure. Toothpicks holding seeds were positioned uniformly into 20 rectangular blocks per site (Fig. 1). Twenty toothpicks (40 seeds) of each type were planted into each block. Toothpicks were positioned in an 8 × 10 grid with 50 mm between each toothpick. Again, if two plants emerged from a location, a haphazardly chosen individual was thinned shortly after emergence.

In 1992 and 1993, blocks were protected from deer and rabbit herbivory with chicken-wire fencing and were covered with a fine light-transmitting mesh just before flowering to prevent pollen export to the native population. A small number of plants were lost to herbivory in 1991. Damaged plants were excluded from the analysis when appropriate. Insect netting was required in 1993, since plants were also being used in a controlled crossing experiment. In all three years, 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 *Gilia* was removed from the blocks. Due to high water in the creek bed in 1991, all experimental blocks at the inland site were washed away early in the season. Six of 20 blocks were also lost to winter floods in 1993. In 1992 and 1993, individuals were harvested immediately following senescence (mid to late June in 1992, and mid-July through mid-August in 1993). In 1991 plants were harvested before natural plant senescence.

*Characters Measured*

Demographic and growth data were collected on each experimental plant throughout the growing season. Four dif-

ferent measures of "performance" were selected to span the life history of the organism and were carefully defined so as not be confounded with one another. *Emergence* was calculated as the proportion of all seeds to emerge in a block (survival of seeds to the seedling stage). This variable was available for only the 1991 and 1993 experiments. *Leaf length* (length of longest leaf, mm) was measured on all individuals on a given date as a measure of plant size during the rosette stage. *Flowering* was calculated as the proportion of emergent plants to flower in a block (survival of seedlings to the flowering stage). Flowering was not defined relative to the seed stage (the standard  $l_x$  definition) to avoid confounding this variable with emergence. *Inflorescence number* (total number of inflorescences on a plant) was counted on all individuals at senescence in the 1992 and 1993 experiments. Seed production, a standard estimate of fitness, was not available in this study, since the insects that this species depends on for pollination were excluded. For emergence and flowering, block was the experimental unit, so sample size was at most (depending on the year and test) the number of blocks. For leaf length and inflorescence number, individual plants composed the experimental units. Number of plants per block varied depending on design (year) and within-block mortality.

#### Statistical Analysis

Where possible, parametric analyses of variance (ANOVA) were conducted on plant performance variables with year (three levels), site (two levels), and subspecies (two levels) as fixed effects (GLM procedure, SAS Institute 1988). Due to differences in design among the experiments, years were often analyzed separately. Density and frequency factors were added as categorical fixed effects when the 1991 data were analyzed alone. In analyses of leaf length and inflorescence number, block was treated as a random effect nested within site. Since emergence and flowering rate were calculated on a per-block basis, block represented the level of replication and was not included as a factor in the analysis. Sample sizes are given above bars in figures. Due to unequal sample sizes, type III sums of squares were used exclusively (SAS Institute 1988).

In this study, data are collected over three years and from four characters. All data are used to test for the presence of local adaptation (site-by-subspecies interaction). To minimize the chance of committing a Type I error (significant result,  $P < 0.05$ , by chance alone) all statistical results could be adjusted for multiple comparisons (Bonferroni adjustment for 12 comparisons; Rice 1989). This would require a critical  $P$ -value of 0.0042 for significance. It was decided not to impose such a strict criterion on each test. Instead, in all of the following discussion it is understood that no single result is enough to conclusively demonstrate local adaptation. We prefer to explore each result independently; laying out each as supporting evidence, instead of conclusive proof. If the reader is more comfortable with the more conservative level of significance, the  $P$ -value of 0.0042 can be applied to all of the tests. However, for none of the site-by-subspecies interaction tests does it change the result.

*Emergence*.—The proportion of plants to emerge per block

were analyzed in a fully factorial, three-way, fixed-effects ANOVA with year (1991 and 1993), site, and subspecies as main effects. Data required no transformation to satisfy assumptions of the analysis.

*Leaf Length*.—Length of longest leaf, a measure of vegetative performance correlated with plant biomass ( $R^2 = 0.82$ , Nagy 1995), was measured in all three years. Analyses were as described above except that block (nested within site) was included in the model, permitting the partitioning of microenvironmental effects. Separate analyses were conducted for each year due to differences in sampling dates among years. In 1991 a four-way ANOVA was conducted with subspecies, density (three levels), frequency (seven levels), and block as factors. Because of the loss of inland site blocks to flooding, only data from the coastal site were available. In 1991 leaf length at 81 d after planting was transformed as  $\ln(x + 1)$ . Since seedlings were used in 1992 instead of seeds, root crown diameter (mm) measured at planting was used as a covariate. The covariate did not significantly interact with any other factor (analysis not shown). In addition, the 1992 analysis was rerun with "seedling source" (greenhouse or field) as a factor to see whether it interacted with any of the other factors or changed the results; it did neither. For simplicity, and because seedling source was not of interest in the study, the analysis presented does not include the seedling source factor. Leaf length at 41 d after planting required no transformation in 1992. In 1993, leaf length at 83 d after planting was  $\ln$  transformed.

*Flowering*.—Data on the proportion of seedlings surviving to flower were available for all three years, but due to the loss of all experimental plants in 1991 at the inland site, and the limited opportunity to estimate this variable in 1992 (one value per site, see below), analyses were conducted separately by year. Effects of density and frequency were not tested in 1991 at the coast due to insufficient sample size. In 1991, flowering proportions were arcsine-square-root transformed to meet the assumptions of parametric analysis. A one-way, fixed-effects ANOVA was conducted to detect differences between subspecies at the coastal site (no inland data were available). Due to small block size in 1992, sitewide flowering was analyzed in a  $2 \times 2$  table of site and subspecies using a  $G$ -test (Zar 1984). Separate  $G$ -tests were performed to compare subspecies within each site. Given that seedling source did not affect the analyses of leaf length or inflorescence number (1992, see above and below) we decided not to include it in what would have been a more complicated set of contingency table analyses. In 1993, flowering proportions in each block were square-root transformed to best meet the assumptions of parametric analysis and data were analyzed with a two-way, fixed-effects ANOVA.

*Inflorescence Number*.—Number of inflorescences at harvest was available for the 1992 and 1993 experiments. Data were  $\ln$  transformed. In 1992, a three-way, mixed-model ANCOVA was conducted with site and subspecies as fixed effects and block within site as a random effect. Initial root-crown diameter was used as the covariate and did not interact with any of the other factors (analysis not shown). As above, the 1992 analysis was rerun with seedling source in the model to test for interactions and changes in the results; again, none were found. Seedling source is therefore not included in the

TABLE 1. Two-way, fixed-effects ANOVA on 1991 emergence. No data transformation was necessary.

Source	df	MS	F	P
Site	1	0.25	91.59	< 0.0001
Subspecies	1	0.008	0.31	0.59
Site × subspecies	1	0.0001	0.05	0.83
Error	12	0.003		

analysis presented here. Analyses of the 1993 data were identical to 1992 analyses, except that no covariate was used and the seedling source test was unnecessary.

*Subspecies Life Tables*

Standard cohort life tables (Crow and Kimura 1970; Futuyma 1986) were constructed for both subspecies at both sites using data from 1993 in which most variables were available. Values for  $F_x$  (total offspring produced at stage  $x$ , where  $x$  is one of three life-history stages) and  $m_x$  (offspring per individual surviving to stage  $x$ ,  $m_x = F_x/a_x$ ) were calculated in part from estimates for “fruits per inflorescence” (30 and 35 for *ssp. capitata* and *chamissonis*, respectively) and “seeds per fruit” (2 and 13, respectively) taken from unpublished data (Nagy). These estimated values are from flowering potted plants raised at the two sites and surrounded by 18 other flowering plants (potential mates). While it is likely that the absolute values of these estimates are biased by the plants’ growing conditions, relative comparisons between the subspecies is reasonable. The basic reproductive rate (or replacement rate),  $R_0$  ( $\sum l_x m_x$ ), is a prediction of the number of offspring (seeds) that will be produced by each original individual (seed) after a single, discrete, nonoverlapping generation. Since *G. capitata* is a hermaphrodite, the number of maternal individuals (“females,”  $a_x$ ) equals the total population size of each subspecies;  $l_x$  is the proportion of original individuals to survive to stage  $x$  ( $a_x/a_0$ ). The purpose of these tables is to summarize the effects of local adaptation as manifested in different performance measures and to make a prediction of overall relative performance by the two subspecies in the two sites.

RESULTS

*Emergence.*—In 1993, where subspecies differences in emergence were seen, the site-by-subspecies interaction indicates local adaptation. The full ANOVA on emergence rate found a significant three-way (year, site, subspecies) interaction ( $F_{1,88} = 5.44, P < 0.02$ ) indicating that seedling emergence varied with all three factors jointly. Results of this type are difficult to interpret. Therefore analyses were conducted separately by year (Tables 1, 2) with the recognition that years show dissimilar patterns. In 1991 the inland and coastal sites differed significantly with respect to emergence, but no difference was detected between subspecies (Table 1). Germination rates were approximately 10% at the inland site and 35% at the coast (Fig. 2). In 1993, subspecies germination differed between the two sites as indicated by the significant site-by-subspecies interaction (Table 2A). Analyses were therefore conducted separately for the two sites. At both sites subspecies had significantly different germination rates (Ta-

TABLE 2. (A) Two-way, fixed-effects ANOVA on 1993 emergence. (B and C). Separate analyses conducted for each site. No data transformation was necessary.

Source	df	MS	F	P
(A) Both sites:				
Site	1	0.002	0.19	0.67
Subspecies	1	0.04	4.07	< 0.05
Site × subspecies	1	0.29	26.74	< 0.0001
Error	76	0.01		
(B) Inland site:				
Subspecies	1	0.05	4.45	< 0.05
Error	38	0.01		
(C) Coastal site:				
Subspecies	1	0.28	29.29	< 0.0001
Error	38	0.01		

ble 2B, C), with natives being more likely to emerge than immigrants (Fig. 2).

*Leaf Length.*—Analyses of leaf length, a measure of size, lend weak support to the hypothesis that the subspecies are locally adapted. Only block was significant in the 1991 four-way ANOVA of leaf length at the coastal site (Table 3). The three-way ANCOVA conducted on leaf length in 1992 revealed significant site and subspecies main effects, but no interaction (Table 4). Size at planting, used as a covariate, also had a significant effect on leaf length (Table 4). In 1992,

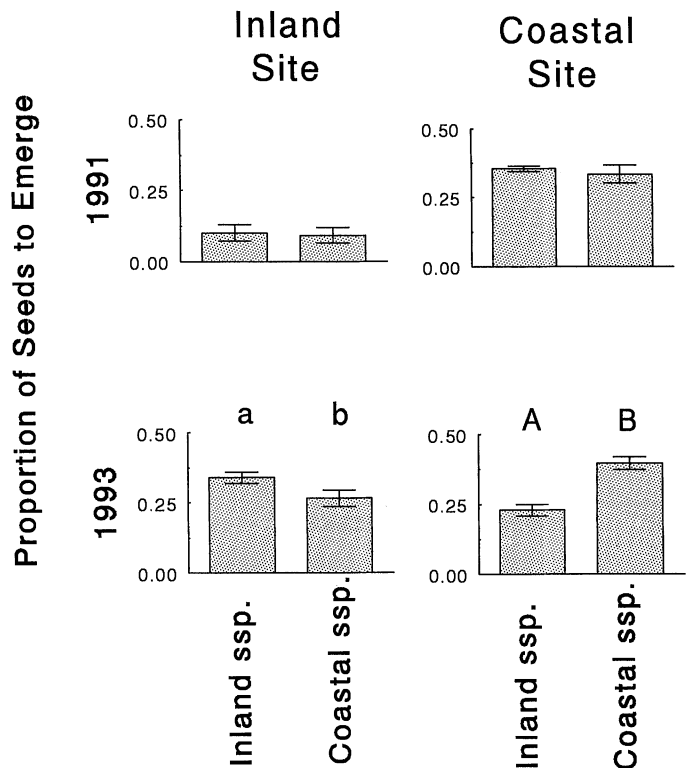


FIG. 2. Mean emergence ( $\pm$  SE) for years, sites, and subspecies (for 1991,  $N = 4$  blocks, and for 1993,  $N = 20$  blocks). Shared letters indicate nonsignificant differences between subspecies within a site and year as determined by separate analyses conducted for each site.

TABLE 3. Four-way, mixed-model ANOVA on 1991 leaf length at the coastal site; block is a random effect. Data were  $\ln(x + 1)$  transformed.

Source	df	MS	F	P
Subspecies	1	0.15	0.31	0.58
Density	2	0.13	0.23	0.79
Frequency	6	0.47	0.84	0.54
Subsp. × density	2	0.39	0.83	0.43
Subsp. × frequency	6	0.65	1.38	0.22
Density × frequency	12	0.32	0.57	0.87
Subsp. × dens. × freq.	12	0.38	0.81	0.64
Block	3	4.79	8.52	< 0.0001
Error	212	0.56		

plants of both subspecies were larger at the inland site, and the leaves of the inland subspecies were consistently longer than those of the coastal subspecies at both sites (Fig. 3). The three-way ANOVA for leaf length in 1993 uncovered a significant site-by-subspecies interaction (Table 5A), suggesting local adaptation. When the analyses were conducted separately by site, the inland site analysis showed a significant subspecies effect, but the coastal site analysis did not (Table 5B, C). In 1993, then, there is some evidence for local adaptation. Although there was no significant difference between subspecies at the coastal site, coastal plants were significantly smaller than natives at the inland site that year (Fig. 3). Therefore, leaf length varied between sites and subspecies in 1993, but gave no clear indication for reciprocal local adaptation. In all the analyses, there were significant block effects, indicating that microenvironmental variation also influences plant size.

**Flowering.**—The proportion of seedlings that survived to flowering, like emergence, gave a clear indication of local adaptation of these subspecies. The probability of flowering in 1991 differed significantly between the subspecies at the coastal site ( $F_{1,6} = 11.70, P < 0.01$ , Fig. 4). The 1992 analysis revealed a significant site-by-subspecies interaction as indicated by a significant  $G$ -test for the  $2 \times 2$  contingency table ( $G_3 = 29.66, P < 0.001$ ). Analyses by site indicated that natives flowered significantly more frequently at both sites (inland site  $G_1 = 6.92, P < 0.05$ , coastal site  $G_1 = 9.77, P < 0.005$ ; Fig. 4). The 1993 two-way ANOVA of flowering rate also indicated a significant site-by-subspecies interaction (Table 6A). Analysis by site showed significant subspecies effects at both sites (Table 6B, C). Natives outperformed immigrants, and both subspecies flowered more at home than away (Fig. 4).

TABLE 4. Two-way, mixed-model ANOVA on 1992 leaf length; block (nested within site) is a random effect. No data transformation was necessary.

Source	df	MS	F	P
Covariate	1	372.31	8.40	< 0.01
Site <sup>a</sup>	1	1487.18	22.12	< 0.0001
Subspecies	1	809.03	18.26	< 0.0001
Site × subsp.	1	17.78	0.40	0.53
Block (site)	71	72.24	1.63	< 0.01
Error	145	45.30		

<sup>a</sup> Site effect tested over  $MS = (0.8206 * MS[Block(Site)] + 0.1791 * MS[Error]) = 67.23$ , with  $df = 90.48$ .

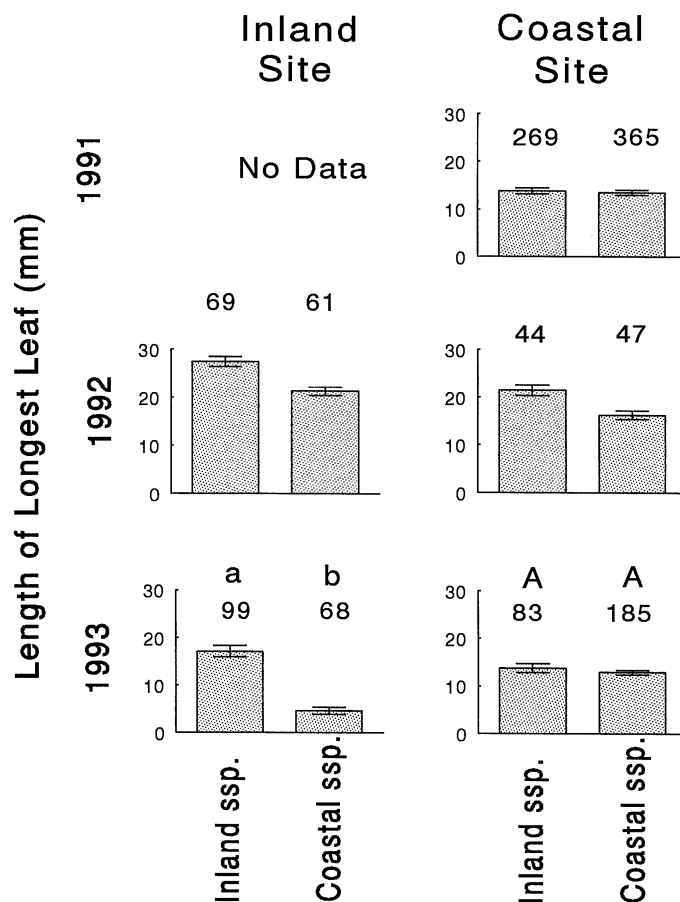


FIG. 3. Mean leaf lengths (mm, ± SE) for years, sites, and subspecies (number of plants,  $N$ , given above bar). Shared letters indicate nonsignificant differences between subspecies within a site and year as determined by separate analyses conducted for each site.

**Inflorescence Number.**—Although inflorescence number per plant varied widely across years and sites, there is some evidence for local adaptation with respect to this component of fitness. The three-way mixed model ANCOVA indicated

TABLE 5. (A) Two-way, mixed-model ANOVA on 1993 leaf length; block (nested within site) is a random effect. Data are  $\ln$  transformed. (B and C) Separate analyses conducted for each site.

Source	df	MS	F	P
<b>(A) Both sites:</b>				
Site	1	1.72	4.57	< 0.05
Subspecies	1	7.59	58.31	< 0.0001
Site × subspecies	1	4.80	36.84	< 0.0001
Block(site)	30	0.70	5.36	< 0.0001
Error	300	0.13		
<b>(B) Inland site:</b>				
Subspecies	1	8.08	53.25	< 0.0001
Block	11	1.19	7.84	< 0.0001
Error	85	0.15		
<b>(C) Coastal site:</b>				
Subspecies	1	0.33	2.69	0.10
Block	19	0.41	3.40	< 0.0001
Error	215	0.12		

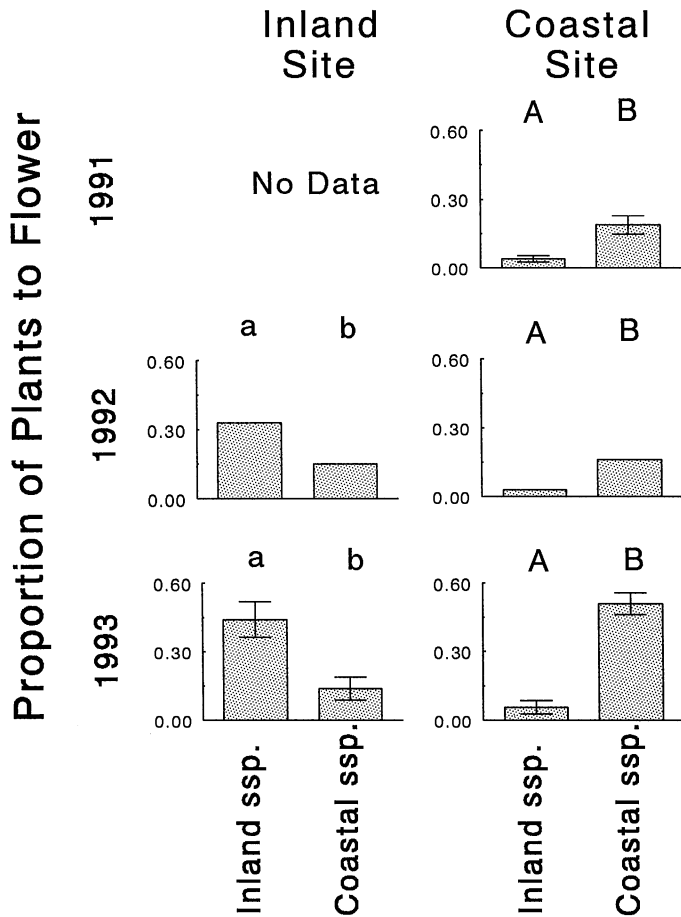


FIG. 4. Mean flowering ( $\pm$  SE) for years, sites, and subspecies (for 1991,  $N = 4$  blocks; in 1992 single estimates were made for each site; for 1993 inland site,  $N = 12$  blocks, for 1993 coastal site  $N = 20$  blocks). Shared letters indicate nonsignificant differences between subspecies within a site and year as determined by  $G$ -test in 1992, and separate ANOVAs conducted for each site in 1991 and 1993.

that both subspecies and sites differed with respect to inflorescence number in 1992 (Table 7). The coastal subspecies produced more inflorescences than the inland subspecies, and plants at the inland site producing more inflorescences than

TABLE 6. (A) Two-way, fixed-effects ANOVA on 1993 flowering. (B and C) Separate analyses conducted for each site. Data are square-root transformed.

Source	df	MS	F	P
(A) Both sites:				
Site	1	0.04	0.98	0.33
Subspecies	1	0.20	4.53	< 0.05
Site $\times$ subspecies	1	3.43	77.30	< 0.0001
Error	60	0.04		
(B) Inland site:				
Subspecies	1	0.79	13.92	< 0.001
Error	22	0.06		
(C) Coastal site:				
Subspecies	1	3.52	94.60	< 0.0001
Error	38	0.04		

TABLE 7. Three-way, mixed-model ANCOVA on 1992 inflorescence number; block (nested within site) is a random effect. Data are  $\ln$  transformed.

Source	df	MS	F	P
Covariate	1	0.12	1.35	0.256
Site	1	0.86	5.35	< 0.05
Subspecies	1	0.63	7.11	< 0.05
Site $\times$ subsp.	1	0.23	2.64	0.11
Block(site)	50	0.19	2.15	< 0.01
Error	38	0.09		

plants at the coastal site (Fig. 5). Inspection of the means suggests a slight advantage of natives at both sites, but the effect is not statistically detectable (Fig. 5, Tables 7). The 1993 analysis did reveal a strong site-by-subspecies interaction (Table 8A), and significant subspecies effects when the sites were analyzed separately (Table 8B, C). Natives produced significantly more inflorescences than immigrants, and both subspecies did better at home than away (Fig. 5). In all the analyses, there were significant block effects, indicating that microenvironmental variation influences inflorescence number.

*Subspecies Life Tables*

The cohort life tables provide a standard summary performance measure,  $R_0$ , for each subspecies at each site. While

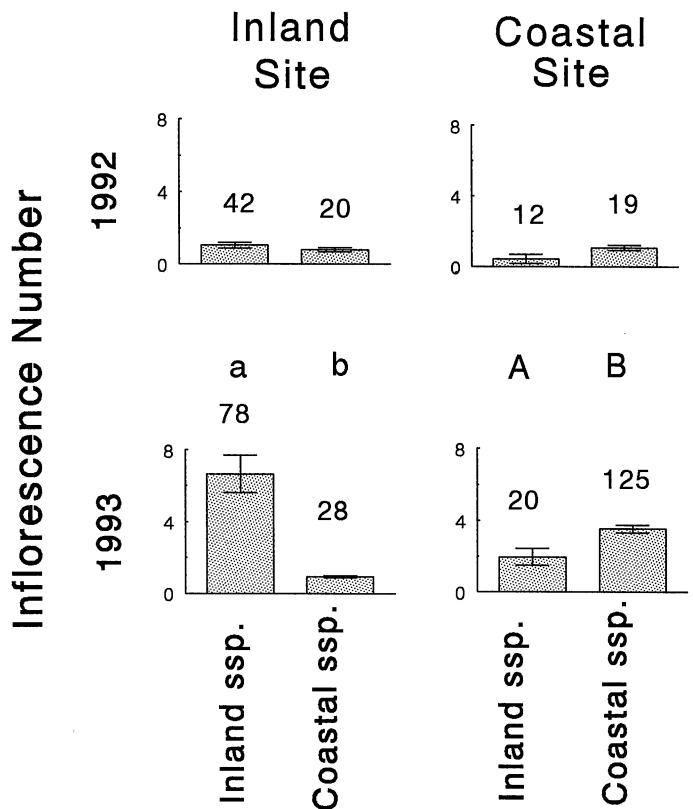


FIG. 5. Mean inflorescence number ( $\pm$  SE) for years, sites, and subspecies ( $N$  above bars). Shared letters indicate nonsignificant differences between subspecies within a site and year as determined by separate ANOVAs conducted for each site.



TABLE 8. (A) Three-way, mixed-model ANOVA on 1993 inflorescence number; block (nested within site) is a random effect. (B and C) Analysis broken down by site. Data are  $\ln$  transformed.

Source	df	MS	F	P
(A) Both sites:				
Site	1	0.39	0.45	0.51
Subspecies	1	1.49	4.16	< 0.05
Site $\times$ subspecies	1	20.52	57.28	< 0.0001
Block(site)	31	1.69	4.73	< 0.0001
Error	216	0.36		
(B) Inland site:				
Subspecies	1	19.29	39.24	< 0.0001
Block	12	3.28	6.67	< 0.0001
Error	92	0.49		
(C) Coastal site:				
Subspecies	1	4.79	18.47	< 0.0001
Block	19	0.69	2.67	< 0.0006
Error	124	0.26		

$R_0$  is not intended as an absolute replacement rate here, it does serve to compare the relative success of each subspecies in the two habitats. At both sites the native has a larger  $R_0$  than the nonnative (Table 9). This suggests that when survivorship and fecundity measures are combined using a standard demographic model, natives outperform migrants. This supports the hypothesis that the subspecies are locally adapted, although no statistical significance can be attached to this result. It should be noted that the fecundity estimates taken from other data (used to calculate  $m_x$ ) do not contribute to this pattern and therefore do not pose a potential bias in the interpretation. The only bias these estimates *do* contribute is a tendency for *G. c. chamissonis* to be more fecund than *G. c. capitata*, in both sites.

## DISCUSSION

### Local Adaptation

Some degree of local adaptation was detected in the analyses of emergence, flowering, and inflorescence number. For these three variables, natives performed better than immigrants when raised in replicated common gardens at both sites. Strength is added to the conclusion that the study populations are locally adapted by the fact that the three variables reflect fundamentally different performance measures taken at distinct phases in the life cycle. And while performance in these three measures may be correlated ("fit" plants may score high in many areas), they serve, we would argue, as distinct measures of performance. The tests that did not detect local adaptation should not, however, be discounted. They serve to remind us that the choice of variables to examine is very important and that other sources of variation aside from the factors of interest can dominate an analysis. Differences among years (Jordan 1992) and microsites (Stratton 1992), for example, may overwhelm other effects. A phenotypic selection analysis conducted on this system confirms that selection favored native character states in 1993 (Nagy, in press). It should be remembered that all of the significant site-by-subspecies interaction tests satisfy the conservative multiple comparisons level of significance ( $P < 0.0042$ ) in-

TABLE 9. Cohort life tables for two subspecies at two sites for 1993.

(A) Inland site					
Stage (x)	$a_x$	$l_x$	$F_x$	$m_x$	$l_x m_x$
Inland subspecies:					
Seed (0)	746	1.00	0	0	0
Emergence (1)	254	0.34	0	0	0
Flowering (2)	66	0.09	28,552	432.61	38.29
					$R_0 = 38.29$
Coastal subspecies:					
Seed (0)	754	1.00	0	0	0
Emergence (1)	204	0.27	0	0	0
Flowering (2)	19	0.03	8645	455.00	11.47
					$R_0 = 11.47$
(B) Coastal site					
Stage (x)	$a_x$	$l_x$	$F_x$	$m_x$	$l_x m_x$
Inland subspecies:					
Seed (0)	802	1.00	0	0	0
Emergence (1)	184	0.23	0	0	0
Flowering (2)	10	0.01	1800	180.00	2.25
					$R_0 = 2.25$
Coastal subspecies:					
Seed (0)	800	1.00	0	0	0
Emergence (1)	320	0.40	0	0	0
Flowering (2)	122	0.15	200,391	1642.55	250.49
					$R_0 = 250.49$

dicating the results are not likely a product of testing the same hypothesis multiple times. Differentiation between these two populations of *G. capitata* is therefore very likely due, at least in part, to evolutionary adaptation to local conditions.

Of concern in common-garden experiments is the impact of environmental maternal effects. The seed used in these experiments were collected directly from the field. Therefore, in addition to the seed differing genetically by subspecies, they also differ in the environment in which they matured. It is well known that environmental maternal effects can affect juvenile, growth, and even adult characters (Roach and Wulff 1987; Rossiter 1996). If the maternal environment contributes to performance as measured by any of the variables in this study, we would expect that effect to be expressed similarly in both sites. In only one case, leaf length, does one subspecies show an overall trend of outperforming the other. In all other cases, even where effects are not significant, neither subspecies dominates in both sites. Maternal effects would not be expected to contribute to the site-by-subspecies interactions observed. If maternal environmental effects did interact with site *in the same way* that genetic effects do, then it would be impossible for us to distinguish them in this study. Another effect the maternal environment can have is to increase variation among maternal families in the characters measured (Roach and Wulff 1987). It is therefore likely that strong maternal effects would tend to obscure the results found here, not contribute to them.

Evidence for local adaptation was detected in emergence rate, but not in both the years it was measured. In 1993, immigrant seeds at the inland site were 78% as likely to emerge as native seed, whereas at the coast, immigrants per-

formed only 58% as well as natives. This disparity in relative emergence rates between the sites not only suggests that immigrant seeds are at a disadvantage, but that the disadvantage may be greater at the coastal site.

Some of the strongest evidence for local adaptation came from the analysis of the proportion of plants to flower (flowering). These results are highly consistent among years. Immigrants at the inland site grew slowly and rarely bolted or initiated flower production (Nagy, pers. obs.); their survivorship to flowering was 30–45% that of natives. In contrast, immigrants at the coastal site did bolt and mature flower buds, but a great many of them developed a necrotic inflorescence and died prior to anthesis (Nagy, pers. obs.). At the coast, immigrants performed only 11–19% as well as natives. As for emergence, the flowering results suggest that selection against immigrants at the coastal site is stronger than at the inland site.

The inflorescence number results are not as consistent. Only in 1993 was evidence for local adaptation detected. At the inland site in 1993, immigrants produced only 14% as many inflorescences as natives; at the coast, immigrants produced 55% as many as natives. This is the reverse relationship observed for emergence or flowering; selection against immigrants appears strongest at the inland site based on inflorescence number. However, if differences in estimated seed production per inflorescence are considered, the reproductive disparity at the inland site disappears (see  $m_x$ , Table 9A), and the reproductive difference at the coastal site is increased, resulting in the same inland site-biased establishment rate predicted above.

One prediction that can be made from these results is the direction in which immigrant establishment is most likely to succeed. Based in the emergence and flowering results, and the adjusted reproductive rates, we would expect immigrant establishment at the *inland site* to be more successful than at the coastal site, simply because selection against immigrants is less strong at the inland site. However, based on *unadjusted* inflorescence number as a measure of performance, we might predict immigrants to be most successful at the *coastal site*. The leaf length data, while not conclusive on their own, are at least consistent with the latter prediction. The two variables that reflect *survival of individuals* (emergence and flowering), and therefore the strength of viability selection, suggest that immigrants may have a better chance of establishment at the inland site. The two variables that measure *individual size* (leaf length and inflorescence number) suggest that immigrants to the coast may have a better chance. And while the latter scenario is not our conclusion, it points out how different measures of performance can give contrasting predictions about the strength of natural selection, as well as its ecological and evolutionary consequences. Biases in the strength of different forms of selection could have strong implications for the transmission of genetic variation between populations. Immigrants that reproduce in small numbers (a population bottleneck) will deliver less genetic variation to a recipient population than immigrants that reproduce in high numbers (Leberg 1992). The potential for different forms of selection to result in different demographic and introgressive consequences is an area worth further study.

A few studies have reported an apparent immigrant ad-

vantage in reciprocal transplant experiments (Levin 1984; Schmidt and Levin 1985; Jordan 1992). In this study, leaf length illustrated a trend toward apparent immigrant advantage at one site, while all the other characters measured confirmed the much more common pattern of a native advantage. This surprising pattern could be caused by pleiotropic or correlational interactions with other traits (Jordan 1992), or by maternal effects as discussed above. No studies, to our knowledge, have discussed different forms of selection (e.g., viability and fecundity) in exploring migrant establishment between locally adapted populations. The results and trend observed here illustrate the importance of analyzing a variety of performance measures throughout the life cycle.

#### *Demographic Predictions Following Migration*

The replacement rate ( $R_0$ ) is a function of both the probability of survivorship and the reproductive performance of individuals in a population throughout their life cycle. Replacement rate predictions for both immigrant and native populations were moderate to large at both sites (Table 9). This standard demographic model, however, does not consider the seed dispersal phase, which is likely to result in the loss of many seeds before they find safe germination environments (Harper 1977), thereby lowering the effective  $R_0$ . In addition, the estimate for  $R_0$  excludes mortality due to the large-scale stochastic processes, such as floods, observed during the course of our experiments. In addition it is likely that years differ substantially, and only one year was sampled in the cohort analysis. For these reasons we focus here on the relative performance predictions for each subspecies within a site, rather than the absolute replacement rates calculated.

Based on the 1993 cohort analysis, natives at the coastal site have a greater than 100-fold advantage over immigrants. Since relative immigrant performance is so low, the successful transmission of immigrant genes to the coastal site for more than a generation will depend largely on the fertilization of native ovules by the original immigrants. Hybridization between immigrant pollen and native coastal ovules occurs about 1% of the time in artificial field populations of equal subspecies mixtures, and crosses in the other direction are never seen in the field (Nagy 1997). These observations indicate that while hybrids will form in mixed populations, and hybridization rates may increase with immigrant representation, the successful introduction of immigrant genes will be rare following a migration event.

The demographic model predicts that migration inland will be much more likely than migration to the coast. In 1993 natives outperformed immigrants by only a factor of about three. In addition, immigrants at the inland site mature hybrid seed at a comparatively high rate (10–20% in equal mixtures of the subspecies; Nagy 1997). Because immigrants will likely persist in relatively high numbers following migration, and because fertilization of immigrant ovules by native pollen is relatively common, migration to the inland site may be successful at introducing coastal genes into the inland gene pool. It is at the inland site that gene migration will be most successful and where the evolutionary consequences of genetic exchange will be most pronounced.

Interestingly, at the inland site, natives have evolved an

almost complete incompatibility with coastal pollen (Nagy 1997). The unilateral incompatibility observed in this system is consistent with models that describe the evolution of reproductive barriers as a consequence of maladapted gene immigration (Lewis and Crowe 1958; Grant 1966; Hogenboom 1972; Coyne and Orr 1989; Otte and Endler 1989). Selection for the maintenance of *G. c. capitata*'s self-incompatibility system could also result in a subspecies incompatibility system evolving (Grun and Radlow 1961; Grun and Aubertin 1966). Low rates of hybridization in this system are also due to pollinator-mediated assortative mating in mixed populations (Nagy 1995). The evolution of full reproductive isolation (speciation) may, in fact, be proceeding asymmetrically in this system, with the strongest selection for isolation occurring in the inland subspecies that experiences the highest potential rate of hybridization and introgression following a migration event.

In addition to serving as a model system, the dynamics described here may reflect the actual, historical process of introgressive evolution between *G. c. capitata* and *G. c. chamissonis*. The demographic model demonstrates that, were seed migration to occur between these two populations, its success would be heavily biased in the inland direction. Grant (1950) argues that a third subspecies, *G. c. tomentosa*, is a stabilized hybrid between *G. c. capitata* and *G. c. chamissonis*. This study uses present-day evidence for local adaptation and a demographic model to predict the probable pathway by which this third subspecies evolved. Grant (1950) documented numerous introgressive populations in western central California, and observed intermediate populations occurring near both habitat types. Our findings suggest that the initial hybridization events leading to the evolution of *G. c. tomentosa* were in all likelihood results of migration by *G. c. chamissonis* into *G. c. capitata* populations. This hypothesis could be further explored using chloroplast DNA analysis (McCauley 1995).

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#### LITERATURE CITED

- ANDERSON, E. 1949. Introgressive hybridization. Wiley, New York.
- ANTONOVICS, J., AND A. D. BRADSHAW. 1970. Evolution in closely adjacent plant populations. VIII. Clinal patterns at a mine boundary. *Heredity* 25:349-362.
- ANTONOVICS, J., AND N. L. FOWLER. 1985. Analysis of frequency and density effects on growth in mixtures of *Salvia splendens* and *Linum grandiflorum* using hexagonal fan designs. *J. Ecol.* 73:219-234.
- BAKER, H. G. 1951. Hybridization and natural gene-flow between higher plants. *Biol. Rev.* 26:302-337.
- BEGON, M., J. L. HARPER, AND C. R. TOWNSEND. 1986. Ecology: individuals, populations and communities. Blackwell Scientific Publications, Sunderland, MA.
- BROYLES, S. B., A. SCHNABEL, AND R. WYATT. 1994. Evidence for long-distance pollen dispersal in milkweeds (*Asclepias exaltata*). *Evolution* 48:1032-1040.
- CAMPBELL, D. R., AND N. M. WASER. 1989. Variation in pollen flow within and among populations of *Ipomopsis aggregata*. *Evolution* 43:1444-1455.
- CLAUSEN, J., D. D. KECK, AND W. M. HIESEY. 1948. Experimental studies on the nature of species. III. Environmental responses of climatic races of *Achillea*. Carnegie Inst. Washington Publ., No. 581.
- CLEGG, M. T., AND A. H. D. BROWN. 1983. The founding of plant populations. Pp. 216-228 in C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas, eds. Genetics and conservation. Benjamin/Cummings, Menlo Park, CA.
- COYNE, J. A., AND H. A. ORR. 1989. Patterns of speciation in *Drosophila*. *Evolution* 43:362-381.
- CROW, J. F., AND M. KIMURA. 1970. An introduction to population genetic theory. Harper and Row, New York.
- DEPAMPHILIS, C. W., AND R. WYATT. 1989. Hybridization and introgression in Buckeyes (*Aesculus*: Hippocastanaceae): a review of the evidence and a hypothesis to explain long-distance gene flow. *Syst. Bot.* 14:593-611.
- EHLERINGER, J. R., AND C. CLARK. 1988. Evolution and adaptation in *Encelia* (Asteraceae). Pp. 221-248 in L. D. Gottlieb and S. K. Jainm, ed. Plant evolutionary biology. Chapman and Hall Ltd., London.
- ELLSTRAND, N. C. 1992. Gene flow by pollen: implications for plant conservation genetics. *Oikos* 63:77-86.
- ELLSTRAND, N. C., AND D. L. MARSHALL. 1985. Interpopulation gene flow by pollen in wild radish, *Raphanus sativus*. *Am. Nat.* 126:606-616.
- ENDLER, J. A. 1977. Geographic variation, speciation and clines. Princeton Univ. Press, Princeton, NJ.
- ENOS, R. A. 1994. Estimating the relative rates of pollen and seed migration among plant populations. *Heredity* 72:250-259.
- EPLING, C., AND TH. DOBZHANSKY. 1942. Genetics of natural populations. VI. Microgeographic races in *Linanthus parryae*. *Genetics* 27:317-332.
- FENSTER, C. B. 1991. Gene flow in *Chamaecrista fasciculata* (Leguminosae) II. Gene establishment. *Evolution* 45:410-422.
- FUTUYMA, D. J. 1986. Evolutionary biology. 2d ed. Sinauer, Sunderland, MA.
- GALEN, C., J. S. SHORE, AND H. DEYOE. 1991. Ecotypic divergence in alpine *Polemonium viscosum*: genetic structure, quantitative variation, and local adaptation. *Evolution* 45:1218-1228.
- GODT, M. J. W., AND J. L. HAMRICK. 1993. Patterns and levels of pollen-mediated gene flow in *Lathyrus latifolia*. *Evolution* 47:98-110.
- GRANT, V. 1950. Genetic and taxonomic studies in *Gilia* I. *Gilia capitata*. *El Aliso* 2:239-316.
- . 1956. The influence of breeding habit on the outcome of natural hybridization in plants. *Am. Nat.* 90:319-322.
- . 1966. The selective origin of incompatibility barriers in the plant genus *Gilia*. *Am. Nat.* 100:99-118.
- . 1981. Plant speciation. Columbia Univ. Press, New York.
- GRANT, V., AND K. A. GRANT. 1965. Flower pollination in the phlox family. Columbia Univ. Press, New York.
- GRUN, P., AND M. AUBERTIN. 1966. The inheritance and expression of unilateral incompatibility in *Solanum*. *Heredity* 21:131-138.
- GRUN, P., AND A. RADLOW. 1961. Evolution of barriers to crossing of self-incompatible with self-compatible species of *Solanum*. *Heredity* 16:137-143.

- HARPER, J. L. 1977. Population biology of plants. Academic Press, London.
- HEWITT, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. *Trends Ecol. Evol.* 3:158–167.
- HICKMAN, J. C. 1993. The Jepson manual: higher plants of California. Univ. of California Press, Berkeley.
- HOGENBOOM, N. G. 1972. Breaking breeding barriers in *Lycopersicon*. 5. The inheritance of the unilateral incompatibility between *L. peruvianum* (L.) Mill. and *L. esculentum* Mill. and the genetics of its breakdown. *Euphytica* 21:405–414.
- JAIN, S. K., AND A. D. BRADSHAW. 1966. Evolutionary divergence among adjacent plant populations. 1. The evidence and its theoretical analysis. *Heredity* 21:407–441.
- JORDAN, N. 1992. Path analysis of local adaptation in two ecotypes of the annual plant *Diodia teres* Walt. (Rubiaceae). *Am. Nat.* 140:149–165.
- KINDELL, C. E., A. A. WINN, AND T. E. MILLER. 1996. The effects of surrounding vegetation and transplant age on the detection of local adaptation in the perennial grass *Aristida stricta*. *J. Ecol.* 84:745–754.
- LEBERG, P. L. 1992. Effects of population bottlenecks on genetic diversity as measured by allozyme electrophoresis. *Evolution* 46:477–494.
- LEWIS, D., AND L. K. CROWE. 1958. Unilateral interspecific incompatibility in flowering plants. *Heredity* 12:233–256.
- LEVIN, D. A. 1981. Dispersal versus gene flow in plants. *Ann. Mo. Bot. Gard.* 68:233–253.
- . 1983. An immigration-hybridization episode in *Phlox*. *Evolution* 37:575–581.
- . 1984. Immigration in plants: an exercise in the subjunctive. Pp. 242–260 in R. Dirzo and J. Sarukhan, ed. *Perspectives on plant population ecology*. Sinauer, Sunderland, MA.
- . 1988. Consequences of stochastic elements in plant migration. *Am. Nat.* 132:643–651.
- . 1995. Plant outliers: an ecogenetic perspective. *Am. Nat.* 145:109–118.
- LUMERAT, R., AND E. BARRIENTOS. 1990. Phylogenetic relationships and gene flow between sympatric diploid and tetraploid plants of *Dactylis glomerata* (Gramineae). *Plant Syst. Evol.* 169:81–96.
- MAYER, M. S., P. S. SOLTIS, AND D. E. SOLTIS. 1994. The evolution of the *Streptanthus glandulosus* complex (Cruciferae): genetic divergence and gene flow in serpentine endemics. *Am. J. Bot.* 81:1288–1299.
- MCCAULEY, D. E. 1995. The use of chloroplast DNA polymorphism in studies of gene flow in plants. *Trends Ecol. Evol.* 10:198–202.
- NAGY, E. S. 1995. Ecological and evolutionary factors influencing gene migration between two subspecies in the *Gilia capitata* complex. Ph.D. diss. Univ. of California, Davis.
- NAGY, E. S. 1997. Frequency-dependent seed production and hybridization rates: implications for gene flow between locally adapted plant populations. *Evolution* 51:703–714.
- NAGY, E. S. In press. Selection for native characters in hybrids between two locally adapted plant subspecies. *Evolution*.
- NEVO, E., A. BEILES, D. KAPLAN, E. M. GOLDENBERG, L. OLSVIG-WHITTAKER, AND Z. NAVEH. 1986. Natural selection of allozyme polymorphisms: a microsite test revealing ecological genetic differentiation in wild barley. *Evolution* 40:13–20.
- OTTE, D., AND J. A. ENDLER. 1989. Speciation and its consequences. Sinauer, Sunderland, MA.
- POTTS, B. M., AND J. B. REID. 1988. Hybridization as a dispersal mechanism. *Evolution* 42:1245–1255.
- RICE, W. R. 1989. Analyzing tables of statistical tests. *Evolution* 43:223–225.
- RIESEBERG, L., AND J. F. WENDEL. 1993. Introgression and its consequences in plants. Pp. 70–109 in R. G. Harrison, ed. *Hybrid zones and the evolutionary process*. Oxford Univ. Press, New York.
- ROACH, D. A., AND R. D. WULFF. 1987. Maternal effects in plants. *Annu. Rev. Ecol. Syst.* 18:209–235.
- ROSSITER, M. 1996. Incidence and consequences of inherited environmental effects. *Annu. Rev. Ecol. Syst.* 27:451–476.
- SAS INSTITUTE, INC. 1988. SAS/STAT user's guide. Rel. 6.03 ed. SAS Institute Inc., Cary, NC.
- SCHMIDT, K. P., AND D. A. LEVIN. 1985. The comparative demography of reciprocally sown populations of *Phlox drummondii* Hood. I. Survivorship, fecundity, and finite rates of increase. *Evolution* 39:396–404.
- SCHMITT, J., AND S. E. GAMBLE. 1990. The effect of distance from the parental site on offspring performance and inbreeding depression in *Impatiens capensis*: a test of the local adaptation hypothesis. *Evolution* 44:2022–2030.
- SORK, V. L., K. A. STOWE, AND C. HOCHWENDER. 1993. Evidence for local adaptation in closely adjacent subpopulations of northern red oak (*Quercus rubra* L.) expressed as resistance to leaf herbivores. *Am. Nat.* 142:928–936.
- STACE, C. A. 1987. Hybridization and the plant species. Pp. 115–127 in K. M. Urbanska, ed. *Differentiation patterns in higher plants*. Academic Press, Orlando, FL.
- STEBBINS, G. L. 1969. The significance of hybridization for plant taxonomy and evolution. *Taxon* 18:26–35.
- STEBBINS, G. L., AND K. DALY. 1961. Changes in the variation patterns of a hybrid population of *Helianthus* over an eight-year period. *Evolution* 15:60–71.
- STEELE, K. P. 1986. Systematic investigation of the capitata *Gilias*. Ph.D. diss., Univ. of California, Santa Barbara.
- STRATTON, D. A. 1992. Life-cycle components of selection in *Eriogon annuus*. I. Phenotypic selection. *Evolution* 46:92–106.
- TILMAN, D. 1986. Evolution and differentiation in terrestrial plant communities: the importance of soil resource:light gradient. Pp. 359–380 in J. Diamond and T. J. Case, ed. *Community ecology*. Harper and Row, New York.
- WASER, N. M., AND M. V. PRICE. 1985. Reciprocal transplants with *Delphinium nelsonii* (Ranunculaceae): evidence for local adaptation. *Am. J. Bot.* 72:1726–1732.
- . 1991. Outcrossing distance effects in *Delphinium nelsonii*: pollen loads, pollen tubes, and seed set. *Ecology* 72:171–179.
- . 1994. Crossing-distance effects in *Delphinium nelsonii*: outbreeding and inbreeding depression in progeny fitness. *Evolution* 48:842–852.
- WILLSON, M. F. 1983. *Plant reproductive ecology*. Wiley, New York.
- ZAR, J. H. 1984. *Biostatistical analysis*. Prentice-Hall, Englewood Cliffs, NJ.

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## LINKED CITATIONS

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## LINKED CITATIONS

- Page 4 of 7 -



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*American Journal of Botany*, Vol. 81, No. 10. (Oct., 1994), pp. 1288-1299.

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*Evolution*, Vol. 43, No. 1. (Jan., 1989), pp. 223-225.

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## LINKED CITATIONS

- Page 5 of 7 -



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*Annual Review of Ecology and Systematics*, Vol. 18. (1987), pp. 209-235.

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## LINKED CITATIONS

- Page 6 of 7 -



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*Taxon*, Vol. 18, No. 1, Smithsonian Summer Institute in Systematics 1968, Part 1. (Feb., 1969), pp. 26-35.

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