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FREQUENCY-DEPENDENT SEED PRODUCTION AND HYBRIDIZATION RATES: IMPLICATIONS FOR GENE FLOW BETWEEN LOCALLY ADAPTED PLANT POPULATIONS

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Abstract.—Gene flow between genetically distinct plant populations can have significant evolutionary consequences. It can increase genetic diversity, create novel gene combinations, and transfer adaptations from one population to another. This study addresses the roles of frequency-dependent selection and mating system in gene exchange between two subspecies of *Gilia capitata* (Polemoniaceae). Long-distance migrants are likely to be rare in new habitats, and the importance of immigrant frequency to fitness, gene exchange, and ultimately introgression, has not been explored. To test for the importance of frequency in migration, a field experiment was conducted in which artificial populations (arrays) composed of different mixtures of the two subspecies were placed in the home habitats of both. Female function (seed production) and a portion of male function (hybridization rate) were compared for the two subspecies to assess the potential for gene exchange and introgression between them. Individual fitness (through both hybridization and seed production) for the inland subspecies varied with its frequency as an immigrant at the coastal site. Rare immigrants produced fewer seeds and fathered fewer hybrid offspring. In contrast, both forms of reproductive function were frequency independent for the coastal subspecies when it was an immigrant at the inland site. Seed production was high and insensitive to frequency, and immigrants from the coast never successfully fertilized the inland subspecies' seeds. To control for the effects of frequency-dependent pollinator behavior in the field, hand crosses were performed in the greenhouse using a range of pollen mixtures. The greenhouse experiment demonstrated that cross-fertilization is possible in only one direction, that cross-pollination in the other direction is only partially successful, and that pollen from the coastal subspecies has a strong negative effect on seed production by the inland subspecies. Experimental pollen supplementation in the field verified both the unilateral incompatibility and the negative effect of coastal pollen on inland plant seed production observed in the greenhouse. Contrasts between field array and greenhouse results suggest that pollinator behavior and other ecological factors act to exaggerate reproductive barriers between the two subspecies. In this system, immigrant frequency interacts with reproductive biology and pollinator ecology to enhance gene flow between the populations in one direction, while restricting gene establishment and introgression in the other direction.

Key words.—Floral neighborhood, frequency dependent, gene flow, *Gilia*, hybridization, introgression, pollen mixture.

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Because many plant species are capable of hybridizing, plant evolution is thought to be highly reticulate (Stebbins 1969). Since Anderson (1949) initiated the discussion of hybridization and introgression, there has been much debate over the actual importance of hybridization to plant evolution. Stebbins and Daly (1961) suggested that "hybridization between populations having markedly different adaptive properties . . . is one of the strongest factors bringing about evolutionary change." Others have argued that hybridization and introgression are strictly local and ephemeral occurrences that rarely have significant evolutionary consequences (Heiser 1973; and see Rieseberg and Wendel 1993 for review). Much of this controversy centers around the importance of gene flow through hybrid zones that may separate parapatric populations. There is, however, general agreement that hybridization, especially when followed by geographic or reproductive isolation, represents enormous evolutionary potential (Hewitt 1988) and is likely responsible for the evolution of a large number of plant species (Baker 1951; Stebbins 1969; Grant 1981; Rieseberg and Wendel 1993).

A number of ecological and genetic factors will determine how easily seeds or pollen can migrate from one population to another, and whether hybridization and genetic introgression

between the populations may occur. In this study I address the reproductive dynamics that may limit gene flow between divergent plant populations following successful seed or pollen migration and establishment. Of course, restricted seed or pollen movement (Harper 1977; Levin 1981, 1983, 1984, 1995; Ellstrand and Marshall 1985; Campbell and Waser 1989; Fenster 1991), local adaptation (Clausen et al. 1948; Jain and Bradshaw 1966; Antonovics and Bradshaw 1970; Ehleringer and Clark 1988; Levin 1988; Schmitt and Gamble 1990; Galen et al. 1991; Waser and Price 1991, 1994; Sork et al. 1993; Nagy 1995), and natural selection on hybrids (Charlesworth and Charlesworth 1979; Briggs and Walters 1984; Jordan 1991; Cruzan and Arnold 1993; Nagy 1995) are also important regulators of gene exchange among plant populations, but are not discussed here.

Unless migrants travel together in large numbers, the reproductive success of immigrant individuals in a nonnative population will depend on the effectiveness of pollen exchange between natives and immigrants. Insect pollinators often discriminate between floral types and may visit flowers nonrandomly (Brown and Clegg 1984; Epperson and Clegg 1987; Rausher et al. 1993; Nagy 1995). Any degree of preference or constancy by pollinators in mixed populations will reduce effective pollen exchange between immigrant and native individuals (Schmitt 1983; Real and Rathcke 1991). Pollinator preference and constancy can also be influenced by local population structure, especially the density and fre-

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quency of immigrants (Epperson and Clegg 1987; Christiansen 1988; Partridge 1988; Feinsinger et al. 1991; Arnold et al. 1993; Kunin 1993; Rauscher et al. 1993). For example, low immigrant frequency may result in strong pollinator discrimination against the immigrant phenotype (Epperson and Clegg 1987; Rauscher et al. 1993; Nagy 1995). Little work has been done on the reproductive impact of pollinator discrimination on fitness in polymorphic populations.

Reproductive compatibility is critical for successful genetic introgression between populations. Hybridization can occur as a result of pollen exchange between native and immigrant plants, or as a consequence of direct pollen immigration. While related taxa can often intercross, compatibility is not always complete. As a consequence, hybridization may be rare, even if pollen is exchanged. The direction of hybridization also may be biased such that crosses in one direction are more fertile than crosses in the other direction (Grant 1956; Grun and Radlow 1961; Ornduff 1969; Bohs 1991). Self-incompatibility systems may change the rate or direction of hybridization. For example, one might expect habitual selfers to mature less hybrid seed in the presence of immigrants than outcrossing taxa, simply because self pollen is well positioned to preempt and dilute incoming outcross pollen. Even in the absence of strict compatibility barriers, pollen and zygote competition could result in reduced gene exchange rates if local genotypes have an advantage in pollen tube growth, fertilization, viability, or development (Snow 1990; Marshall and Folsom 1991; Snow and Spira 1991; Waser and Price 1991; Arnold et al. 1993; Rigney et al. 1993; Carney et al. 1994).

Few empirical studies have explored the potential for reciprocal gene migration between divergent plant populations, and none has explored the effect of immigrant frequency on native and immigrant reproductive success and hybridization rates. While there is much exciting work on the genetics and reproductive biology of hybridization, and some recent studies of the distribution of hybrid individuals and populations with respect to potential selective agents (see Arnold and Bennett 1993 and others in the same volume; Cruzan and Arnold 1993, 1994; Rieseberg and Wendel 1993), no work has explicitly tested both the ecological and biological factors affecting the dynamics of gene exchange in one system. Studies of the evolutionary consequences of gene flow and hybridization are especially relevant today because increasing human transportation, development, and global environmental change are likely to increase rates of plant migration and thereby influence the evolution of previously isolated populations and higher taxa (Clegg and Brown 1983; Ellstrand 1992).

Here I examine how reproductive compatibility, frequency-dependent seed production and hybridization, and interactions between these factors affect introgression in two subspecies of the *Gilia capitata* complex. I investigate the evolutionary consequences of long-distance migration of seed or pollen by exploring the reproductive dynamics that affect both immigrant and native fitness in mixed populations. In particular, I address the question: does rarity per se impart special disadvantages or advantages to the reproduction and ultimate success of an immigrant genotype? Three experiments were designed to simulate the ecological and repro-

ductive processes of migration. First, to simulate successful seed immigration, I conducted a field experiment in which native insects mediated all pollinations within experimental populations composed of different subspecies mixtures (frequencies) of flowering plants. I then conducted a greenhouse experiment in which crosses were made using controlled mixtures of pollen from the two subspecies. Last, I conducted a second field experiment in which pollen migration was simulated by supplementing naturally growing plants with experimental immigrant pollen. With these experiments I address the following questions: (1) Does the frequency of immigrant plants influence seed production or hybridization rate in experimental field populations? (2) Does the frequency of immigrant pollen alone affect seed production or hybridization rate in controlled greenhouse crosses? (3) How might pollinator behavior and plant reproductive biology interact in establishing the potential for, and direction of, introgression between populations of *G. capitata*?

MATERIALS AND METHODS

Study System

Gilia capitata Sims. (Polemoniaceae) is an herbaceous annual that is 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; Hickman 1993). Two subspecies, *G. capitata* ssp. *capitata* and *G. capitata* ssp. *chamissonis*, were chosen for this study because of their strong morphological and ecological differences and for their reported ease of cross-fertilization (Grant 1950). Populations of both subspecies are typically 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 serviced primarily by a variety of insects (Andrenidae, Halictidae, Megachilidae, and Apidae in the Hymenoptera; Bombyliidae in the Diptera, among others; Grant and Grant 1965; Powell and Hogue 1979; Nagy 1995). While many populations are apparently isolated today, hybridization within the complex is responsible for the evolution of several of the eight currently recognized subspecies (Grant 1950, 1956). This system is therefore highly appropriate for exploring the evolutionary dynamics of migration and introgression.

Gilia capitata capitata is common on the dry rocky slopes of central and northern California's Coast Range. It is a tall, spindly plant (0.2–1.0 m) with small, self-incompatible, pale violet flowers (diam. 6–8 mm; Hickman 1993), each with few ovules (3–6/ovary) and small amounts of nectar (0–0.32 μ L, unpubl. data) and pollen (Nagy 1995). *Gilia capitata chamissonis* (E. Greene) V. Grant has a more limited distribution than *G. c. capitata*; it is found only on the coastal sand dunes of central California. This subspecies is short (0.1–0.2 m) and compact. It has large, self-compatible, dark purple flowers (diam. 9–10 mm; Hickman 1993), with more ovules (10–24/ovary), twice the pollen (Nagy 1995), and more nectar (0.16–0.78 μ L, 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, unpubl. data). Seeds of both subspe-

cies are small (1–2 mm) and have no specialized dispersal mechanism. In fact, a sticky mucilaginous coat that expands when wet likely serves to anchor seeds to the coarse substrate. Despite their divergence in ecological and reproductive characters, Grant (1950) reported 40–70% reproductive compatibility between the subspecies. *Gila capitata capitata* and *G. c. chamissonis* germinate in December, flower in June and July, and mature seed in July and August, respectively.

The field portions of this study were 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. 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. 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).

The greenhouse portion of this study was conducted at the University of California’s Davis campus. Plants were grown in cone-shaped pots (21 cm deep, 164 cm³) with a porous potting mixture that allowed good drainage. They were watered daily and fertilized as needed to maintain plant sizes similar to those found in the field. The greenhouse was maintained under 16-h days and temperatures of 10°C/25°C (min/max) unless otherwise noted.

Field Array Experiment

Rationale.—The frequency of immigrants and natives in a population can affect pollinator foraging behavior and cause deviations from random mating among natives and immigrants. I used artificial arrays of flowering plants to measure the impact of immigrant frequency on seed production and hybridization rate for both natives and immigrants. The experiment was conducted in the home habitats of each subspecies for three consecutive years.

Design.—Approximately 400 individuals of each subspecies were raised each year in the greenhouse between March and July of 1991, 1992, and 1993. Plants were grown from bulk seed collected from each site the previous summer. The seeds were planted in two cohorts, one week apart, so that individuals would be staggered in their development for use over the long field season. The greenhouse was maintained under natural day lengths. Approximately one month after planting, young plants were moved outside to acclimate to natural temperatures and full light intensities. Plants were maintained outside on campus and in the field until used in the experimental arrays in June, July, and August.

Experimental units consisted of field arrays of plants established at two sites in three years. Each array consisted of 19 individually potted, flowering plants arranged 0.5 m apart in an evenly spaced hexagonal pattern (Fig. 1). Ten to 15 arrays were haphazardly positioned throughout the native population at each site. Arrays were spaced 10–20 m apart to minimize direct pollinator flights between them. Flights between arrays were never observed and hybridization never

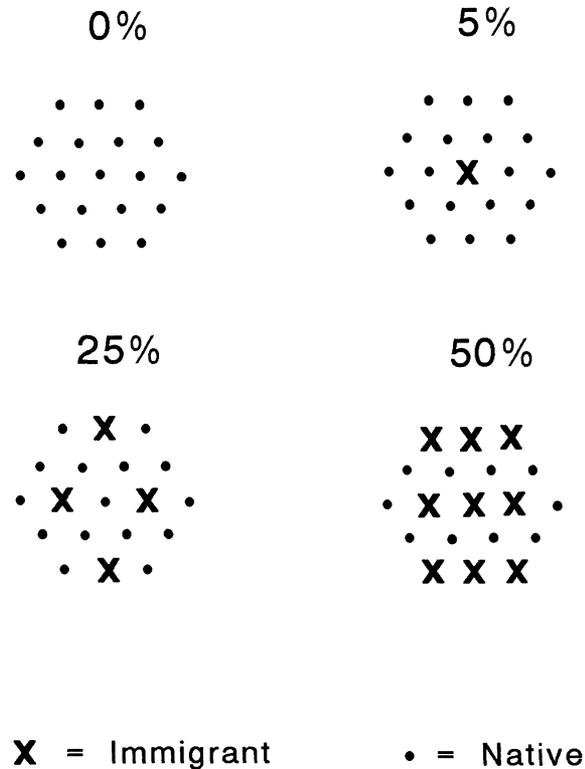


FIG. 1. Diagram of field array structure showing positions of native and immigrant plants in four immigrant frequency levels. Plants were separated by 0.5 m.

occurred in the 0% immigrant arrays, supporting the assumption that arrays were independent. Three to six replicate arrays were established for each frequency treatment level at each site. Subspecies were assigned “native” or “immigrant” status depending on the site; *G. c. capitata* was native at the inland site and *G. c. chamissonis* was native at the coastal site. The main treatment effect, frequency of immigrants, was randomly assigned to each array. The four frequency levels were: “0% immigrant” (0 immigrants and 19 natives), “5% immigrant” (1 immigrant and 18 natives), “25% immigrant” (4 immigrants and 15 natives), and “50% immigrant” (9 immigrants and 10 natives). Exact immigrant frequency levels were 0%, 5.26%, 21.05%, and 47.37%, respectively.

Each year plants were placed in field arrays for an eight- to 10-day period. Plants were selected for use in the experiment if they had one or more inflorescences with flower buds ready to open. Arrays were protected from mammalian herbivory by 0.5-m chicken wire and/or a 2-m, five-wire electric fence. Pollinators did not appear to be deterred by either barrier. Plants were watered twice daily while in the field. Since *G. c. capitata* inflorescences produce half as much pollen as *G. c. chamissonis* inflorescences (see below), *G. c. capitata* plants were maintained with two simultaneously blooming inflorescences throughout the experiment, while *G. c. chamissonis* plants were maintained with one. The result was that pollen grain ratios within the arrays reflected subspecies plant frequencies.

Due to seasonal constraints and first-year results, the man-

ner in which arrays were replicated varied slightly from year to year. In 1991 an additional factor, overall plant density, was crossed with the frequency factor. Because it did not have a significant effect on seed production or hybridization rate for either subspecies at either site (analysis not shown) plant density was not included in the design in subsequent years and is not considered further here. Also in 1991, two 10-day experimental trials were conducted at each site, the second immediately following the first. Treatment levels were reassigned to arrays for each trial. In 1992 the 25% immigrant frequency level was excluded due to a shortage of experimental plants and a second trial was conducted only at the coastal site. In 1993 a single experimental run was conducted at each site and consisted of a greater number of replicated arrays per frequency treatment than in previous years. Effects due to these relatively minor variations in array replication will be included in the analysis as variation among years.

To ensure that treatments were not overwhelmed by background populations, experiments were initiated near the end of the flowering period of the surrounding *Gilia* populations; late June at the inland and mid to late July at the coastal site. An actively flowering native *Gilia* population would have drastically altered the experimental immigrant frequencies. Therefore, the very few naturally occurring *Gilia* plants still in flower at the site during the experiment were trimmed of all open inflorescences. During experiments pollinator behavior was observed in each array (see Nagy 1995). When experimental inflorescences in an array had finished blooming, plants were moved back into the greenhouse where fruits matured. Fruits were collected when dry.

Mean seed production and hybridization rate were measured for each subspecies in each array. A subsample of up to five plants per subspecies per array were randomly chosen to measure seed production. For these plants fruits and seeds were counted, and mean number of seeds per fruit was calculated for each inflorescence. For plants in which more than one experimental inflorescence was collected, one average seed set value was calculated. A subsample of up to 10 plants per subspecies per array was used to estimate hybridization rate (plants that produced no seed were excluded from the subsample). Hybrids between these subspecies can be readily identified by visual inspection of flower color. F_1 hybrids have a flower color intermediate to the pale and dark purple flower colors diagnostic of the inland and coastal subspecies, respectively. Scoring hybrids by flower color was 97% accurate, as confirmed by a discriminant analysis based on a variety of vegetative and floral characters (DISCRIM procedure; SAS Institute 1988, unpubl. data). All progeny from each plant were grown in the same 80-mm square pot in the greenhouse under low nutrient levels, 16-h days and temperatures of 15°C/35°C (min/max) to promote rapid flowering. Postgermination mortality was very low (less than 10%). Seeds from each experiment were germinated, raised, and scored the following season to allow the necessary after-ripening period. On the order of 10 to 50 progeny were scored per plant, more than 21,000 progeny in all. Hybridization rate was calculated as the number of hybrid progeny divided by the total number of progeny scored for a plant.

Statistical Analysis.—The effects of immigrant frequency, site, and year on seed production and hybridization rate were

analyzed with analysis of variance. For both variables, the array is considered the experimental unit. Therefore, seed production and hybridization means were calculated by subspecies and array. Array means were calculated from plant means when more than one inflorescence was sampled per plant. Mean seed production was square-root transformed to meet the assumptions of the analysis. Frequency level “0% immigrant” was not included in the hybridization rate analysis because no hybrids were expected or observed. The hybridization data were highly skewed and could not be transformed to meet the assumptions of analysis of variance; therefore, the ranks of hybridization rates were analyzed (Conover and Iman 1981; Potvin and Roff 1993; N. Willits pers. comm.).

The experimental design was not fully factorial; except for the 50% immigrant treatment, subspecies frequencies were not replicated at each site. Because the immigrant subspecies is expected to be relatively rare following migration, it was always assigned frequencies 0, 5, 25, and 50%; natives were never assigned frequencies less than 50%. Therefore, analyses were done separately by site and subspecies, resulting in four two-way fixed effects analyses of variance (each with year and frequency factors). For both dependent variables, type III sums of squares were tested and Tukey's Studentized Range Tests were used to detect differences between factor levels when main effects were significant (GLM procedure; SAS Institute 1988). To test if hybridization rate differed between sites, a Kruskal-Wallis chi-square approximation test (NPAR1WAY procedure; SAS Institute 1988) was conducted on the unranked hybridization rates for the 50% immigrant frequency treatment. Data were pooled across years.

Greenhouse Experiment

Rationale.—If pollinators visit immigrants and natives randomly, pollen mixtures carried by bees are likely to reflect actual subspecies frequencies in the arrays. Any variation among treatments in seed production or deviation from expected hybridization rates could be attributed to postpollination factors such as incompatibility, pollen competition, or selective seed maturation. However, pollinator behavior was influenced by immigrant frequency and native versus alien status in these experiments (Nagy 1995). Likewise, other factors may affect seed production and hybridization rate in mixed populations. To separate the effects of nonrandom pollinator behavior from postpollination dynamics, hand pollinations were done in the greenhouse using pollen mixtures that reflected pollen availability within the field arrays. These hand pollinations, therefore, mimicked a situation in which pollination in a field array was random with respect to subspecies.

Design.—Using seeds collected from the field during the previous season, 60 plants of each subspecies were raised in the greenhouse in the fall of 1992. Plants were moved regularly to homogenize greenhouse environmental effects. Twenty plants of each subspecies were assigned as experimental mothers, and 40 as members of a pollen donor pool. As the experimental plants began to flower, the first five inflorescences to develop were randomly divided among five pollination treatments: (1) pure native pollen (pollen from

the same subspecies as the recipient); (2) 5% immigrant pollen (a mixture of one part immigrant pollen and 19 parts native pollen); (3) 50% immigrant pollen; (4) pure immigrant pollen; and (5) no pollen at all. All five pollen treatments were replicated on each experimental plant. The greenhouse pollen treatments "0% immigrant," "5% immigrant," and "50% immigrant" each correspond to field array frequency treatments of the same name. The "100% immigrant" treatment was not represented in the field, and the "25% immigrant" field array frequency level was not represented in the greenhouse. Pollen mixtures were created by collecting freshly dehiscent anthers from 20 haphazardly selected members of the pollen pool and mixing them thoroughly in a microcentrifuge tube with a fine paint brush. Treatment levels were determined by adding different numbers of anthers from each subspecies. Anther samples taken from the pollen donor pool revealed that the subspecies produce significantly different amounts of pollen ($t_{34} = 4.39$, $P < 0.0001$); the coastal subspecies produces almost exactly two times as much pollen per anther as the inland subspecies. Therefore, in making a 50% pollen mixture, two inland anthers were used for every coastal anther. Fresh pollen mixtures were made from the pollen pool two to three times per pollination session.

Pollinations were conducted daily between 22 February and 17 March 1993. Prior to the pollinations, experimental inflorescences were trimmed to five to 10 flowers and emasculated by plucking predehiscent anthers from flower buds to prevent self-pollination. Nonexperimental inflorescences were removed from all experimental mothers to minimize the potential for resource competition among inflorescences. After flowers opened, pollen was applied to receptive stigmas with a paint brush; the "no pollen" treatment was treated with a clean brush. Flowers were pollinated daily, from when the stigma became receptive until it was dry and withered (ca. three days). Fruits were harvested over the course of the next six weeks as they matured. Seed production and hybridization rate were measured as for plants from the field study, for all five pollination treatments on all maternal plants.

Statistical Analysis.—Fixed effects repeated measures analysis of variance with subspecies as a between-subject factor (two levels) and pollen treatment as a within-subject factor (five levels) was conducted on seed production and hybridization rate (GLM procedure; SAS Institute 1988). This analysis is identical to a split plot design (split = subspecies, plant = block) but provides an indication of dependence among inflorescences within plants. Any lack of independence was compensated for by using a Huynh-Feldt adjusted P -value. Mean seeds per fruit was $\ln(x+1)$ transformed to meet the assumptions of the analysis. Hybridization rate, however, was highly skewed and could not be transformed adequately. Therefore a nonparametric Friedman's test was conducted by employing the repeated measures analysis used above on the ranks of plant hybridization rates (N. Willits, pers. comm.). Only the three treatments involving immigrant pollen were included in this analysis. Again, Huynh-Feldt adjusted P -values were used so that within-plant correlation would be corrected for. Multiple contrasts were tested to detect differences between pollination treatments for both variables (GLM procedure, REPEATED CON-

TRAST; SAS Institute 1988) and significance levels were Bonferroni-corrected for multiple comparisons (Rice 1989). To compare seed production by the two subspecies following pollination with mixed pollen loads, the "proportion of maximum seed set" was calculated for both the 5% and 50% immigrant pollen treatments and both subspecies. For each subspecies, seed production for the 5% and 50% pollen treatments was divided by the 0% immigrant treatment seed production mean. Seed production proportions were analyzed in one-way fixed effects analyses of variance (subspecies factor, separate analyses for 5% and 50% immigrant treatments) to test for differences between subspecies in relative seed set. No transformation of the data was needed.

Field Pollen Supplementation Experiment

Rationale.—Migration by pollen will likely result in a small number of pollination events by immigrant pollen on native stigmas. The success of immigrant pollen will depend on environmental factors, competitive interactions with native pollen, and compatibility with native gynoecia. To realistically simulate migration by pollen, hand pollinations were made in the field using nonnative pollen and naturally growing, native plants. The purpose of this experiment was to confirm the potential for long-distance migration by pollen, as well as to confirm that reproductive mechanisms observed in the greenhouse are important under field conditions.

Design.—During May and June of 1992, while native plants were flowering in the field, pollen from greenhouse-grown plants was applied to flowers at both sites. Forty plants at the inland site and 99 plants at the coastal site were haphazardly selected. Inflorescences were assigned at random to either an "immigrant pollen supplementation" treatment or a "control" (no pollen addition) group. For approximately 20 of the inland plants two inflorescences were selected per plant; one received immigrant pollen and the other was the control. Because of inflorescence limitations during the experiment it was impossible to nest both pollen addition and control treatments within all experimental plants. Therefore, for the remaining 20 plants at the inland site and all of the plants at the coastal site, single inflorescences on separate plants were used for either of the two treatments. Plants and inflorescences were labeled with tape but were otherwise undisturbed and unprotected from natural pollination. When inflorescences were fully open, those assigned to the nonnative pollen treatment were dusted thoroughly with immigrant pollen. The treatment was repeated on the same inflorescences two days later. Fruits ripened in the field and were collected when mature. Seed production and hybridization rates were measured exactly as described above.

Statistical Analysis.—Within each site, immigrant-pollinated and naturally pollinated groups were analyzed for differences in seed production. Mean number of seeds per fruit was calculated for each inflorescence and data were natural-log transformed to meet the assumptions of the analysis. A one-way fixed effects analysis of variance on seeds per fruit was conducted with pollination treatment (immigrant vs. no pollen) as the factor (GLM procedure; SAS Institute 1988). For the nonnative pollen supplementation treatment, the proportion of offspring classified as hybrid (hybridization rate

TABLE 1. Analysis of variance on seed production in the field over a range of immigrant frequencies and years. Two-way fixed effects analyses using Type III sums of squares were conducted separately for subspecies and sites. Data are square-root transformed. Overall analysis of the model for the coastal subspecies at the coastal site was not significant.

Source of variation	df	SS	F	P
Inland ssp. in inland site:				
Year	2	0.45	8.06	< 0.001
Frequency	3	0.14	1.63	0.20
Year × frequency	4	0.23	2.03	0.11
Error	42	1.18		
Inland ssp. at coastal site:				
Year	2	0.43	2.26	0.13
Frequency	2	0.92	4.85	< 0.02
Year × frequency	2	0.22	1.13	0.34
Error	24	2.29		
Coastal ssp. at inland site:				
Year	2	7.26	12.16	< 0.001
Frequency	2	0.61	1.03	0.37
Year × frequency	3	1.79	2.00	0.13
Error	35	10.44		
Coastal ssp. at coastal site:				
Year	2	0.93	2.43	0.10
Frequency	3	0.51	0.88	0.46
Year × frequency	3	0.60	1.04	0.38
Error	42	8.04		

for each inflorescence) was compared between sites (i.e., subspecies). A Kruskal Wallis test (NPAR1WAY procedure WILCOXON option; SAS Institute 1988) was conducted on the hybridization rate data since it could not be transformed to meet the assumptions of parametric analysis. In addition, a log-likelihood ratio *G*-test (Zar 1984) was conducted on the numbers of plants that matured any hybrid seed at the two sites to determine if coastal site plants were more or less likely to mature hybrid offspring than inland plants following pollination with immigrant pollen.

RESULTS

Field Array Experiment

Seed Production.—Immigrant seed production was significantly affected by immigrant frequency only for the inland subspecies at the coastal site (Table 1). As an immigrant, the self-incompatible inland subspecies produced fewer seeds per fruit when at low frequencies (Fig. 2). A Tukey's test detected significant differences between the 5% immigrant frequency level and the 25% and 50% levels (Fig. 2). Seed production by immigrants at the inland site was not significantly affected by changes in frequency (Table 1, Fig. 2). At neither site was native seed production significantly affected by immigrant frequency (Table 1), although there was a trend for native seed production to decline with increasing immigrant frequency at both sites (Fig. 2). Seed production by both natives and immigrants varied significantly among years at the inland site, but not at the coastal site (Table 1). There was no significant frequency-by-year interaction at either site for either subspecies, indicating that the frequency effect on immigrant seed production did not vary significantly among years.

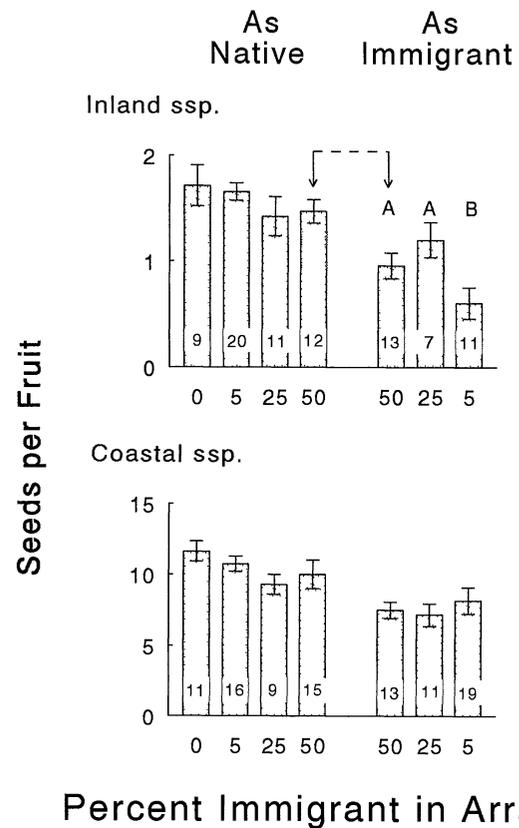


FIG. 2. Mean seeds per fruit (\pm SE, *n* within bar) for field experiment presented by subspecies. Charts are split between native and nonnative sites. Shared letters indicate nonsignificant differences between frequency levels where analysis of variance revealed significant main effects (see Table 1). For the 50% immigrant frequency treatment, means between sites were significantly different for the inland subspecies (arrows), but not for the coastal subspecies (see text).

To test for the effect of site on seed production, 50% arrays were compared between sites. The three-way fixed effects analysis of variance (year, site, subspecies factors) revealed a significant site-by-subspecies interaction ($F_{1,41} = 8.89$, $P < 0.005$) indicating that the subspecies responded differently to the two sites. Therefore, the subspecies were tested separately. The inland subspecies produced significantly more seeds per fruit as a native than as an immigrant in the 50% arrays ($F_{1,19} = 11.23$, $P < 0.003$; Fig. 2 arrows); no other effects were significant in the inland subspecies analysis. The coastal subspecies produced slightly more seeds as a native than as an immigrant in 50% arrays, but the difference was not significant (Fig. 2; model $F_{5,22} = 2.17$, $P = 0.09$).

Hybridization Rate.—Only the coastal subspecies matured hybrid seed. None of the plants native to the inland site matured hybrid seed in any of the field arrays. Therefore, only the coastal subspecies was analyzed for hybridization rate. At the inland site, the hybridization rate for the immigrant was relatively high, but did not vary significantly with frequency or year (Fig. 3, Table 2). At the coastal site, however, hybridization rate for the native was lower (Fig. 3) and varied significantly with both immigrant frequency and year independently (Table 2). Hybridization rate increased with

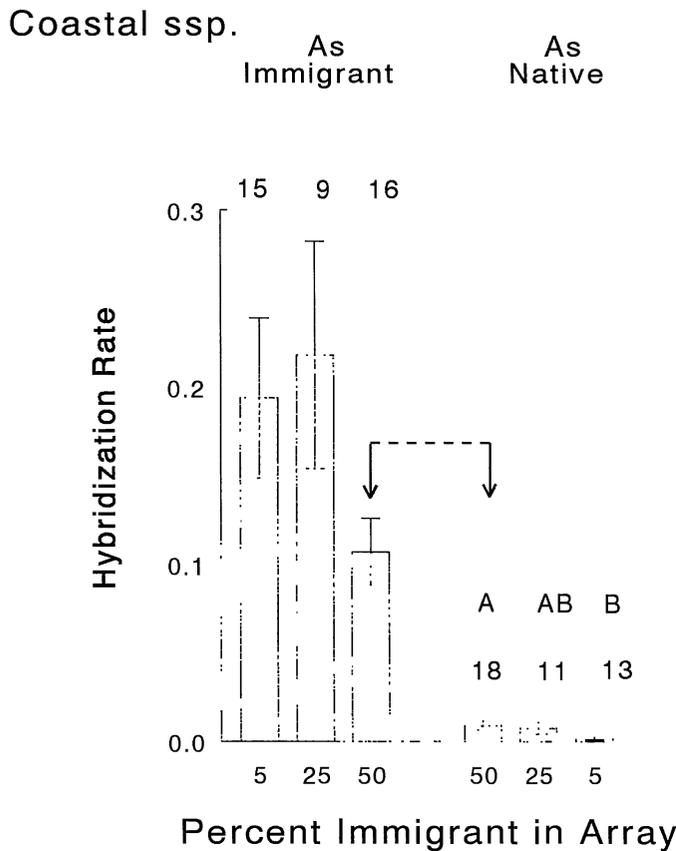


FIG. 3. Mean hybridization rates (\pm SE, n above bar) of coastal subspecies for field experiment presented by site. Shared letters indicate nonsignificant differences between frequency levels where analysis of variance revealed significant main effects (Table 2). For the 50% immigrant frequency treatment, means between sites were significantly different (arrows, see text).

increased immigrant frequency (Fig. 3), and Tukey multiple comparisons showed that hybrid seed production differed significantly between 5% and 50% immigrant treatments. Within the 50% immigrant treatment level, hybridization rate was much greater at the inland site than at the coastal site ($\chi^2 = 18.73$, $df = 1$, $P < 0.0001$).

Greenhouse Pollination Experiment

Seed Production.—Seed production declined significantly as native pollen was diluted with immigrant pollen for both subspecies (Fig. 4). Repeated measures analysis of variance on seed production with subspecies as the between-subject factor and pollination treatment as the within-subject factor revealed a significant subspecies-by-pollination interaction ($F_{4,36} = 56.10$, $P < 0.0001$), indicating that subspecies responded differently to the pollination treatments. Therefore, subspecies were analyzed separately. For both subspecies pollen treatment significantly affected seed production (inland subspecies $F_{4,76} = 33.31$, $P < 0.0001$; coastal subspecies $F_{4,68} = 61.58$, $P < 0.0001$). Significant differences in seed production between pollination treatments were seen for both subspecies at the Bonferroni-corrected significance level of $P = 0.005$ for multiple tests (Fig. 4). To test for differences

TABLE 2. Analysis of variance on ranks of coastal subspecies hybridization rates in the field over a range of immigrant frequencies and years. Two-way fixed effects analyses using Type III sums of squares were conducted separately by site. Inland site model was not significant.

Source of variation	df	SS	F	P
At inland site (as immigrant):				
Year	2	570.59	1.86	0.17
Frequency	2	142.34	0.46	0.63
Year \times frequency	3	191.88	0.42	0.74
Error	34	5216.95		
At coastal site (as native):				
Year	2	746.98	4.29	< 0.02
Frequency	2	1082.26	6.22	< 0.005
Year \times frequency	2	176.16	1.01	0.38
Error	33	2871.96		

in the degree of seed set reduction between subspecies, the proportion of maximum subspecies seed set was compared between subspecies for both the 5% immigrant and 50% immigrant pollen mixture treatments. Subspecies differed markedly in relative seed production within the 5% immigrant pollen treatment based on a one-way fixed effects analysis of variance ($F_{1,38} = 7.25$, $P < 0.01$) with the inland subspecies showing a 48% reduction in seed production, relative to the 0% immigrant pollen treatment, while the coastal subspecies showed only a 7% reduction (Fig. 4). For the 50%

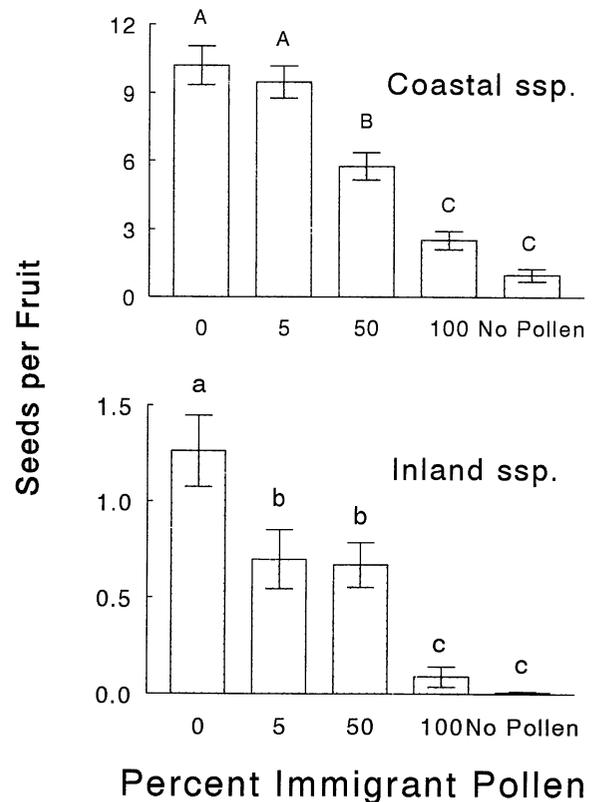


FIG. 4. Mean seeds per fruit (\pm SE, coastal ssp. "no pollen" $n = 18$, otherwise $n = 20$) for greenhouse pollination experiment. Shared letters indicate nonsignificant differences among frequency levels within subspecies.

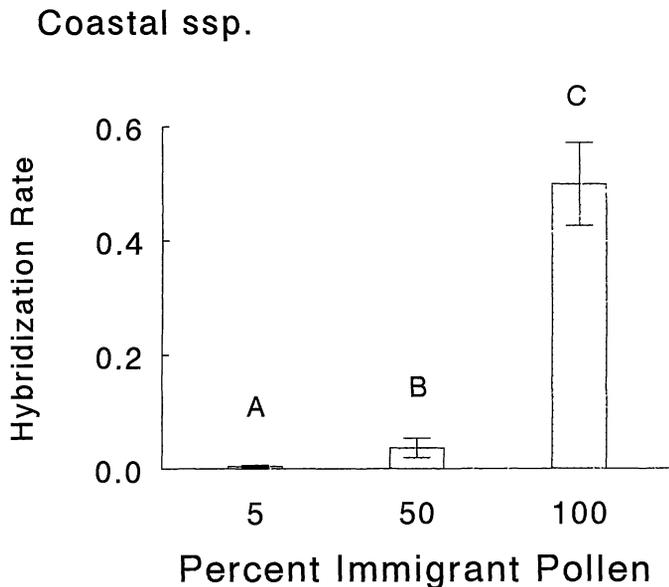


FIG. 5. Mean hybridization rates (\pm SE, "100" treatment $n = 19$, otherwise $n = 20$) of coastal subspecies for greenhouse experiment. Shared letters indicate nonsignificant differences between frequency levels.

pollen mixture treatment, subspecies did not differ in relative seed production ($F_{1,38} = 0.10$, $P = 0.75$); both showed about a 50% drop (Fig. 4). Differences between seed production rates by each subspecies in the 100% immigrant pollen treatment are discussed with respect to hybridization rate (see below).

Hybridization Rate.—In the greenhouse, as in the field, only the coastal subspecies matured hybrid seed. The hybridization rate for the coastal subspecies varied significantly among the three mixed-pollen treatment levels (model $F_{2,38} = 81.17$, $P < 0.0001$, Fig. 5), and all three levels were statistically distinct at the $P = 0.02$ level (Bonferroni corrected for multiple tests, Fig. 5). The coastal subspecies hybridization rate increased in proportion to the amount of immigrant pollen applied; hybridization in the 50% mixture was 10-times the rate in the 5% mixture. The less than 100% hybridization rate in the 100% immigrant pollen greenhouse treatment suggests there was some extra-experimental pollination (likely self) in the greenhouse. Contamination with self-pollen likely occurred before or during emasculation, despite efforts to prevent it.

Field Pollen Supplementation Experiment

Seed Production.—Pollen immigration to the inland site resulted in reduced seed production by natives, but pollen immigration to the coastal site did not affect native seed production. Analysis of variance revealed significant differences in seed production at the inland site between the immigrant pollen supplementation treatment and control inflorescences ($F_{1,38} = 4.29$, $P < 0.045$). Untreated control inflorescences produced more seeds per fruit ($\bar{x} = 2.10 \pm 0.24$ SE, $n = 10$) than inflorescences treated with additional immigrant pollen ($\bar{x} = 1.42 \pm 0.11$ SE, $n = 30$). At the coastal site, immigrant pollen supplementation did not affect seed

production by the native ($F_{1,97} = 0.01$, $P = 0.93$). Seed set by the control group ($\bar{x} = 10.27 \pm 0.50$ SE, $n = 43$) was nearly equal to that in the immigrant supplementation group at the coast ($\bar{x} = 10.06 \pm 0.37$ SE, $n = 56$).

Hybridization Rate.—Hybridization rates following supplementation with immigrant pollen were very low. No hybrid offspring were matured by inland plants ($n = 30$) and the hybridization rate at the coastal site was only 0.43% ($\bar{x} = 0.0043 \pm 0.002$ SE, $n = 56$). The Kruskal-Wallis test detected a nearly significant difference in hybridization rate between the sites ($Z = -1.87$, $P < 0.065$). However, the log-likelihood ratio G -test indicated plants at the coast were much more likely to mature hybrid seed than plants inland ($G_3 = 24.19$, $P < 0.001$).

DISCUSSION

In this study, I have identified a number of factors important to successful introgression between these two closely related subspecies. These factors, both ecological and biological, include: immigrant frequency, pollinator behavior, the physical environment, self-compatibility and cross-compatibility, between the subspecies. The importance of these factors varies between sites and subspecies. The dynamics of gene flow between sites will depend on interactions among these factors. It is important to remember that migrants must first survive to flowering for factors discussed here to be relevant. It is also likely that following natural migration immigrants will be very rare in a flowering population relative to natives, and so special attention should be given to the reproductive consequences of rarity here.

Reproductive Dynamics Following Controlled Pollination

Dilution of same-species pollen by immigrant pollen significantly reduced seed production for both subspecies. This is strong evidence that both subspecies are limited in their ability to use immigrant pollen. However, the pattern of seed production decline differed between the two subspecies. Seed set in the coastal subspecies declined proportionately to the pollen mixture: a 5% immigrant pollen mixture caused a 7% decline in seed production relative to the 0% immigrant pollen treatment; a 50% pollen mixture caused a 44% decline. These results indicate a limited compatibility between coastal plants' female function and inland pollen. In contrast, seed production by the inland subspecies was greatly reduced by even small quantities of coastal pollen: both the 5% and 50% immigrant pollen mixtures caused seed set to decrease by approximately 50%. This result suggests not only limited cross-subspecies compatibility, but also some type of an "inhibitory" effect on *G. c. capitata* seed production by *G. c. chamissonis* pollen. This could occur either through blocking of inland pollen germination or tube growth, or possibly through superior intersubspecies pollen tube competition and ovule preemption by infertile coastal pollen (followed by zygote inviability or embryo abortion). Some of these mechanisms have been documented in other studies (Grun 1961; Waser 1978; Lloyd and Yates 1982; Rathcke 1983; Hill and Lord 1986), and several studies have found active inhibitory effects of foreign pollen on female fitness (Sukhada and Jayachandra 1980; Feinsinger et al. 1986). This is the first ex-

ample of strong inhibitory or preemptive effects involving such small amounts of foreign pollen and between such closely related taxa. The fact that the 50% immigrant pollen treatment does not show an even greater seed set reduction than the 5% treatment argues for a proximal and general inhibitory effect (as opposed to zygote death or embryo abortion). If ovules were preempted by immigrant pollen and then lost, we would expect a negative relationship between the amount of immigrant pollen applied and seed produced. The results reveal no such quantitative relationship, but instead suggest a qualitative effect of the presence of immigrant pollen. The precise mechanism for the inhibitory effect of coastal pollen on inland seed set is unknown and deserves further study.

Only the coastal subspecies matured hybrid seed. This result reveals that a unilateral incompatibility exists between these two subspecies; inland pollen fertilizes coastal ovules and produces hybrid seed, but coastal pollen is infertile on inland stigmas. The hybridization rate seen in maternal plants of the coastal subspecies was only about 10% of that expected based on the mixture of pollen applied. (The less than 100% hybridization rate for the coastal subspecies in the 100% immigrant pollen treatment suggests there was some extra-experimental pollination. However, if hybridization rates are adjusted for this source of error, they are still only 20% of expected.) This supports the conclusion drawn from the seed production results that cross-compatibility is incomplete; that is, that some fertility barrier exists between inland subspecies male function and coastal subspecies female function as well.

In Grant's (1950) extensive work on *G. capitata*, he observed incomplete and biased compatibility between these two subspecies, but not to the degree measured here. Although not previously reported in the Polemoniaceae, the evolution of unilateral incompatibility between self-compatible pollen donors and self-incompatible pollen recipients has been described thoroughly in the Solanaceae (Grun 1961). The genetic basis for this type of incompatibility is unclear, but does not appear to be controlled by self-incompatibility S-alleles (Lewis and Crowe 1958; Grun 1961; Whalen and Anderson 1981). One hypothesis for the evolution of a unilateral barrier in this direction is that natural selection has acted to prevent the breakdown of the self-incompatibility system by favoring genes that impart reproductive isolation from self-compatible taxa (Grun and Radlow 1961). Interestingly, unilateral incompatibility between these two subspecies was not observed by Grant during his work on the systematics and genetics of the entire *G. capitata* complex (Grant 1950, 1956). It is possible, however, that the specific reproductive mechanisms observed here are unique to the study populations and not a general feature of the two subspecies. Grant did document large amounts of variation in breeding system within the species complex (Grant 1950, 1956).

Influences of Immigrant Frequency on Seed Production

Immigrant frequency will play a critical role in successful gene establishment through seed production only following migration to the coastal site. The immigrant at the coast, the inland subspecies, is self-incompatible and unable to use native pollen, as observed in both field experiments and in the

controlled mixture crosses. So, when the inland subspecies is a rare immigrant at the coast, it has few mates. Application of coastal pollen under both greenhouse and field conditions revealed an inhibitory effect on inland subspecies seed production. Low seed production by immigrants at the coast is also likely exaggerated by low pollinator visitation to immigrants, especially when they are rare, and the high degree of foraging constancy pollinators display (Nagy 1995). Every mechanism studied in these experiments will have a negative effect on seed production by immigrants at the coastal site.

Seed production by immigrants at the inland site was not significantly affected by immigrant frequency. Three of the four mechanisms that contribute to poor immigrant seed production at the coast are less important at the inland site. First, the coastal subspecies is self-compatible. Therefore, a rare or lone individual can set seed through self-pollination. Second, although compatibility is not complete, the coastal subspecies is able to mature viable hybrid seed using pollen from the inland subspecies. And third, seed production by the coastal subspecies is not inhibited by pollination by the inland subspecies. These three factors apparently reduce frequency-dependent effects on immigrant success and outweigh the fact that pollinators also display foraging constancy and discriminate against immigrants at the inland site (Nagy 1995).

Native female function was not significantly affected by immigrant presence or frequency at either site, although there was a slight trend for reduced seed production by natives as immigrant frequency increased. At the inland site, the combination of a larger number of compatible mates, and the promotion of assortative mating by pollinator foraging behavior seems to outweigh the potential effects of seed set inhibition and incompatible pollination presented by immigrants. This conclusion is supported by the fact that the inhibitory effect *was* observed in the field when pollen was applied by hand, but *not* when insects deliver the pollen. If the coastal subspecies is little affected by the presence of the inland subspecies when it is at the inland site, it is even less so at home. A large number of highly compatible mates, in concert with preferential pollinator visitation, make it even less likely that limited compatibility with the inland subspecies will adversely impact *G. c. chamissonis*' seed production.

Influences of Immigrant Frequency on Hybridization

The highest rate of hybridization observed in the field was by the coastal subspecies at the inland site. Because only the coastal subspecies can mature hybrid seed, gene flow into the inland population can only occur through hybrid seed production by immigrants. However, immigrants at the inland site matured hybrid seed at a rate much less than expected based on the relative availability of inland pollen in the field arrays. In addition, the rate of native pollen use by immigrants at the inland site did not vary significantly with immigrant frequency. It was expected that rare immigrants would mature more hybrid seeds than less rare immigrants because they were surrounded by a higher proportion of natives. This trend was found (Fig. 3), but was not significant. High within-site variation in hybridization rate (array mean ranges: 0–60% for each of the 5% and 25% treatments, and 2–23% for the 50% treatment) at the inland site likely obscured detection

of a significant effect. The overall low immigrant hybridization rate observed in the field is consistent with the greenhouse results that indicate an incomplete compatibility between the subspecies; even when equal portions of the two pollen types are applied to a coastal subspecies' stigma, the hybridization rate is much less than 50%. However, because pollinators visit natives preferentially (Nagy 1995), the ratio of subspecies pollen carried by pollinators in the field should be native biased. The consequence of this would be a higher hybridization rate than expected based on immigrant frequency levels. The fact that the hybridization rate in the field was greater than that measured in the greenhouse suggests that pollen mixtures carried by insect pollinators did have a greater proportion of native pollen than expected. This interpretation is strengthened by the fact that greenhouse plants were emasculated prior to experimental pollination; field plants were not. Because the coastal subspecies is capable of autogamy, the availability of self-pollen in the field would tend to reduce its hybridization rate, irrespective of visitation frequency. All evidence, therefore, points to pollinator behavior as a mechanism for creating heavily native-biased pollen mixtures.

At the coastal site, the only site where natives were capable of maturing hybrid seed, there was a significant effect of immigrant frequency on the production of hybrid seed by the native; increased immigrant frequency increased the hybridization rate, as expected. The overall hybridization rate by natives, however, was extremely low, even lower than the low hybridization rate observed in the controlled pollen mixture experiment. At this site, the incomplete compatibility between the coastal subspecies and inland pollen, and the inflated representation of native pollen in the field caused by pollinator preference for native flowers, will both act to reduce the production of hybrid seed. But even though pollinators display an overall discrimination against immigrants, pollen export by immigrants to natives is proportional to their frequency in the population.

Site Comparisons

Seed production and hybridization rates differed markedly between sites in the 50% immigrant treatment arrays (the only treatment replicated in both sites). Both ecological and environmental factors could have caused these differences. The inland subspecies produced significantly more seeds at home than away. This may be largely due to preferential pollinator visitation to the native plants. At the coastal site, pollinator behavior will both deprive the immigrant of needed visitation and bias pollen loads heavily with native pollen. Coastal pollen is infertile on inland stigmas and inhibits seed production by the inland subspecies. It is also possible that environmental factors adversely affected the inland subspecies' seed production at the coast. The inland subspecies suffered greatly at the coast during the field array experiment, even given the short period it was exposed to the local environment. Strong coastal winds battered the taller *G. c. capitata*, and fog frequently matted its small, densely packed flowers, possibly rendering them less receptive to pollen delivered by pollinators, which were apparently undeterred by the weather. In addition, pollen in the small, wet immigrant

flowers may have been less accessible to pollinators, accounting in part for the exceptionally low rates of successful pollen export to the coastal native. On the other hand, seed set by the coastal subspecies in the 50% arrays seemed insensitive to site; seed production was slightly, but not significantly reduced at the inland site. Because the coastal subspecies is self-compatible, it may be less sensitive to pollinator discrimination. And while this subspecies did show developmental responses to the radically different environmental conditions inland (changes in leaf shape, thickness and anthocyan content, inflorescence elongation, and flower size; pers. obs.), it did not display any observable reproductive difficulties. The rates of hybrid seed production by the coastal subspecies in the 50% immigrant arrays were significantly different between sites. The coastal subspecies matured significantly more hybrid seed as an immigrant at the inland site than when at home. This is probably due, again, to native-biased pollen loads caused by the pollinators' preference for natives. This general pollinator behavior (observed at both sites) would tend to increase hybrid seed production by the coastal subspecies at the inland site, but reduce it at the coastal site. The difference in hybridization rates between the sites could also be a function of the environmental factors described above that inhibit immigrant pollen export at the coastal site, thereby potentially lowering the hybridization rate.

Probability of Successful Introgression

All the factors discussed above suggest that natural migration by the coastal subspecies to the inland site will likely result in almost full female fertility by way of selfing, outcrossing among immigrants, and outcrossing with natives. In contrast, male fertility will be low, since immigrant pollen deposited on unreceptive native stigmas will be lost. Reproductive success of the native inland subspecies will be largely unaffected by the presence of migrants from the coast. Pollinator constancy to natives was especially high at the inland site (Nagy 1995), so immigrant pollen may be too rare in pollen loads to inhibit seed production by natives (no evidence for the inhibition effect was observed in the field). Native pollen will, however inefficiently, fertilize immigrant ovules. Introgression may therefore proceed through the production of a few hybrid seeds, accompanied by larger numbers of pure immigrant seeds produced by the self-compatible immigrants at the inland site. Hybrid individuals are fertile, self-compatible, and suffer less stringent barriers to survival and potential reproduction than do immigrants (Nagy 1995). Migrant frequency (a function of both immigrant number and native population size) will have little impact on the process of introgression at the inland site. Gene migration inland, therefore, is likely to proceed relatively quickly with no special disadvantage suffered by rare immigrants.

Migration by members of the inland subspecies to the coast may be much more difficult, especially when the immigrant is rare. The female fitness of immigrant individuals will be low due to the inhibition of seed production by native pollen, cross-incompatibility, self-incompatibility, and environmental stress. Male fitness will also be low due to inefficient pollen export to the native. However, both male and female

fitness for the immigrant will increase with its representation in the population. This means immigrants to the coast will have a better chance of successful introgression if they arrive in large numbers and/or migrate into a small population. Native fitness will remain high through outcrossing and selfing, with some pollen being lost to incompatible immigrant stigmas. And, although the production of hybrid seed by the coastal native will be low, it will increase as immigrant frequency increases. Introgression is likely to proceed through infrequent pollination events of the native by the immigrant and perhaps some pure immigrant seed production. Both processes are frequency-dependent and thus more effective in small native populations or if immigrant numbers are high. Therefore, for a variety of biological, ecological, and environmental factors, natural gene flow and introgression into the coastal population is likely to be slow or inefficient.

In addition to serving as a model system, the dynamics described here may very well reflect the actual, historical process of introgressive evolution between *G. c. capitata* and *G. c. chamissonis*. A third subspecies, *G. c. tomentosa*, appears to be a stabilized hybrid between *G. c. capitata* and *G. c. chamissonis* (Grant 1950). This study uses present-day evidence of ecological and reproductive processes to predict a probable scenario for the evolution of this third subspecies. Grant (1950) documented numerous introgressive populations in western-central California, and observed intermediate populations occurring in both habitat types. The results discussed here suggest that the initial hybridization events leading to the evolution of *G. c. tomentosa* were in all likelihood results of migration by coastal *G. c. chamissonis* into inland *G. c. capitata* populations.

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