Outplanting and Differential Source Population Success in *Lupinus guadalupensis*

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Abstract: *The choice of appropriate source populations is crucial for the success of outplanting attempts, but this choice is often based on assumptions regarding patterns of adaptation and distribution of genetic variability in natural populations. Although local adaptation is often assumed to exist, few data exist to support this model on smaller geographic scales, particularly in rare plant species. My study investigated the pattern of adaptation in populations of an annual, island endemic plant,* Lupinus guadalupensis, *on San Clemente Island, California. A reciprocal transplant experiment with three populations provided no evidence for local adaptation, but two source populations performed significantly better than the other at all sites. Desiccation and herbivory are the major factors causing mortality and reducing fruit production. The young rosettes are the most vulnerable life-cycle stage. Differences among natural population sites in vegetation community, dominant species, soil type, and parent material did not affect populations of* L. guadalupensis; *significant differences were not observed in either total fruit production or in the majority of fitness components. Success of outplanting into three introduction sites varied from the death of all plants before flowering or before fruits ripened to fruit production exceeding that at natural population sites. The results suggest that large populations are better sources of seeds for outplanting in* L. guadalupensis *and that outplanting is most successful in sites where plants are least subject to desiccation.*

Siembra en Sitios Externos y Fuentes Diferenciales de Exito Poblacional en *Lupinus guadalupensis*

Resumen: *La detección de fuentes apropiadas de poblaciones es crucial para el éxito de los intentos de siembra externa, pero esta opción se basa frecuentemente en suposiciones sobre patrones de adaptación y distribución de variabilidad genética en poblaciones naturales. A pesar de que frecuentemente se asume que la adaptación local existe, pocos datos soportan este modelo a escala geográfica pequeña, particularmente en especies raras de plantas. Investigué el patrón de adaptación en poblaciones de una planta anual endémica isleña,* Lupinus guadalupensis, *en la isla San Clemente, California. Un experimento de transplante recíproco con tres poblaciones, no aportó evidencia de adaptación local, pero dos poblaciones fuente se desarrollaron significativamente mejor que la otra en todos los sitios. La desecación y hervivoría son los factores mayores causantes de la mortalidad y reducción de la producción de frutos. Las rosetas jóvenes son los estados del ciclo de vida mas vulnerables. Diferencias entre sitios de poblaciones naturales en la comunidad de la vegetación, dominancia de especies, tipo de suelo y material parental no afectó las poblaciones de* L. guadalupensis; *no se observaron diferencias significativas en la producción total de frutos ni en la mayoría de los componentes del estado de las especies. El éxito de plantar en el exterior en tres sitios de introducción diferentes varió desde la muerte de todas las plantas antes de florecer hasta la muerte antes de que los frutos maduráran para producción, esto excedió los valores de sitios con poblaciones naturales. Los resultados sugieren que las poblaciones grandes son mejores fuentes de semillas para plantar* L. guadalupensis *en otros sitios y que el éxito de estas plantaciones es mayor en sitios donde las plantas son poco sujetas a la desecación.*

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Introduction

The effective management of endangered plant species requires information about the distribution of genetic variation and patterns of adaptation in natural populations. The widespread occurrence of intraspecific genetic variation for morphological traits in plant species was established by the common garden experiments of Turesson (1925) and others and led to the concept of the ecotype (Briggs & Walters 1969). Since the late 1960s, electrophoretic surveys of genetic variation have provided many examples of genetic differences among populations (summarized in Hamrick & Godt 1989). Because common garden studies are usually performed in artificial environments and because electrophoretic surveys assay presumably neutral genetic markers, it is difficult to assess the functional significance of the observed differences. These studies demonstrate, however, that populations of many species are sufficiently isolated that genetic differences can arise among them, and some of these genetic differences may be adaptive. Reciprocal transplant studies, such as those of Clausen et al. (1940), have demonstrated the adaptation of conspecific populations to their local environment, especially in wide-ranging taxa. Although the demonstration of adaptive differences is by no means universal in reciprocal transplant studies (e.g., Rice & Mack 1991), natural resources managers must confront the possibility of such local adaptation when considering outplanting to supplement existing populations or to initiate new populations. In the absence of experimental studies on target species, the choice of appropriate source populations relies heavily on assumptions about the distribution of genetic variation and patterns of adaptation. Although local adaptation is an appealing model, it may be relevant primarily to wide-ranging species occupying sites that clearly vary in climate, soil, and other variables (reviewed in Bradshaw 1984). It is questionable whether local adaptation of populations can be expected on smaller scales, where differences among sites may be minor. Alternative patterns include the absence of adaptive differences among populations and adaptive differences among populations that are independent of site (some populations perform better at all sites). Little information is available regarding local adaptation of plant populations on smaller geographic scales.

A related issue for effective management is the identification of suitable sites for outplanting attempts. Populations of rare and endangered species are often absent from apparently suitable habitat; this absence may be attributed to insufficient adaptation to various ecological factors that render a site either marginal or completely unsuitable to self-sustaining populations. Alternatively, low seed production and poor dispersal ability may retard the successful colonization of suitable sites. The correlation of ecological variables with distribution data may reveal potential habitat not currently occupied by populations of a species (Kellogg & Kellogg 1994), but the value of correlational data rests heavily on the measurement of all relevant ecological variables. Using preliminary experiments to test the suitability of habitat for introduction of populations of target species allows more effective use of valuable seed collections, especially if demographic data are collected for comparison with natural populations. Collection and analysis of demographic data permit both the identification of life-history stages that have a major impact on population growth and the identification of the biological causes of variation in these stages; these constitute vital information for conservation efforts (Schemske et al. 1994).

I describe experiments investigating patterns of adaptation in natural populations and the suitability of habitat in an annual island endemic, *Lupinus guadalupensis* E. Greene (Fabaceae; Guadalupe Island lupine), with a highly restricted distribution. As part of an effort to increase its numbers on San Clemente Island and to preclude federal listing as a threatened or endangered species, a series of studies is being undertaken to investigate genetic variability, life-history characteristics, and adaptation in natural populations of this species. My objectives were (1) to determine the life-cycle stages at which population growth is limited and to identify the factors limiting population growth, (2) to determine whether populations are adapted to their local environment or whether there are adaptive differences among populations that are independent of site, and (3) to assess the prospects for introduction of this species to sites where it has not historically occurred on San Clemente Island.

Methods

The Study Species

Lupinus guadalupensis is a winter annual herb endemic to San Clemente Island, California, and Guadalupe Island, Mexico. Seeds germinate in November and December with the onset of winter rains, rosettes grow through winter, and bolting occurs in February. Plants flower in March and April and die in May. They are generally found in annual grassland and maritime desert scrub communities. On San Clemente Island *L. guadalupensis* is known from fewer than 20 sites, located primarily in the central plateau of the island above elevations of 250 m; it appears to be extremely rare on Guadalupe Island, where the author of the most recent flora (Moran 1996) has observed only six plants at four sites over the last 40 years (R. Moran, personal communication). Because of its limited distribution, few populations, and threat from Navy activities, *L. guadalupensis* has been listed federally as a Category 2 candidate species (Skinner & Pavlik 1994). (*Editor's note*: In 1995 the U.S. Fish

and Wildlife Service arbitrarily removed all of nearly 4000 species from the Category 2 list of candidates for endangered or threatened listing.)

Reciprocal Transplant Experiment

Seeds were collected in May 1995 from three populations distributed across the central range of the species (Fig. 1); each population contained at least 50 individuals and produced several hundred seeds. Seeds were collected from 50 plants chosen haphazardly across areas of similar size in each population. The following site descriptions include associated species used by Kellogg and Kellogg (1994) and J. Stone (personal communication), soil descriptions from the U.S. Soil Conservation Service (1982), and geology from Olmstead (1958).

The Larkspur Canyon site is an annual grassland vegetation community dominated by *Avena barbata*, *A. fatua*, and *Bromus diandrus*. Other common taxa include *Amsinckia menziesii* var. *intermedia*, *Dichelostemma capitatum*, *Lactuca serriola*, *Nassella pulchra*, *Plagiobothrys* spp., *Sanicula arguta*, *Sonchus* spp., and *Viola pedunculata*. Soils are described as Chinapoint cobbly clays, and the parent material is Tertiary andesite. In 1995 several thousand individuals of *L. guadalupensis* were distributed across an area of approximately 200 × 600 m.

The Tombstone Road site is an annual grassland vegetation community dominated by *Avena barbata* and *Atriplex semibaccata*. Other common taxa include *Achillea millefolium*, *Bromus madritensis* ssp. *rubens*, *Calystegia macrostegia* ssp. *amplissima*, *Erodium* spp., *Hordeum* spp., *Lasthenia californica*, *Nassella pulchra*, *Opuntia littoralis*, and *Salsola tragus*. Soils are described as Eelpoint clay, and the parent material is Tertiary dacite. In 1995 several thousand individuals of *L. guadalupensis* were distributed across an area of approximately 200 × 350 m.

The Box Canyon site is a maritime desert scrub (cholla phase) vegetation community dominated by *Calystegia macrostegia* ssp. *amplissima*, *Lotus argophyllus* ssp. *argenteus*, *Opuntia littoralis*, *O. oricola*, and *O. prolifera*. Other common taxa include *Lupinus bicolor* and *Mirabilis californica*. Soils are described as Ustalfs-rock outcrop complex, and the parent material is Tertiary andesite and dacite. In 1995 several hundred individuals of *L. guadalupensis* were distributed across an area of approximately 20 × 50 m.

The experiment was designed as a reciprocal transplant (complete factorial design), with seeds from the Larkspur Canyon, Tombstone Road, and Box Canyon populations planted into each of these three sites. An additional blocking factor was included within sites (Fig. 2). Sets of 150 seeds (3 seeds from each of 50 mothers from a source population) were the experimental units. Five blocks (nuisance factor), each consisting of three adjacent 1 × 2-m plots, were chosen haphazardly at each site over the area from which seeds were collected. The three adjacent plots in each block were randomly assigned to sets of seeds from different populations. The seeds composing each experimental unit were randomly assigned to locations in a 10-cm grid in
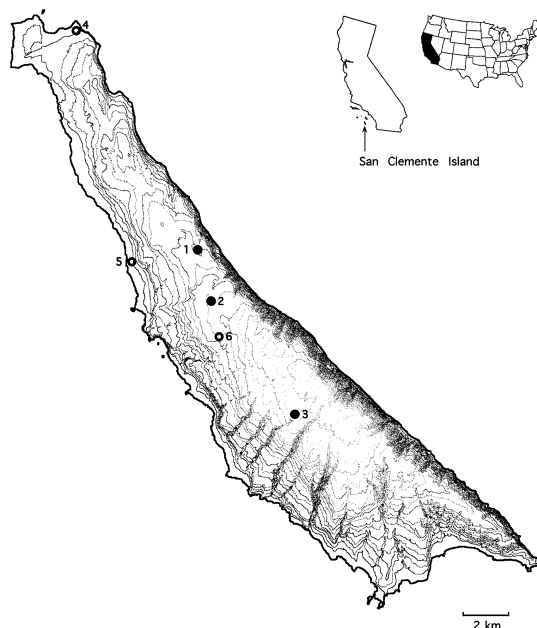

Figure 1. Location of transplant sites (closed circles: 1, Larkspur Canyon; 2, Tombstone Road; 3, Box Canyon) and introduction sites (open circles: 4, Northwest Shore; 5, Spray; 6, Arizone) of L. guadalupensis *on San Clemente Island, California. Contour lines represent 100-foot elevation intervals.*
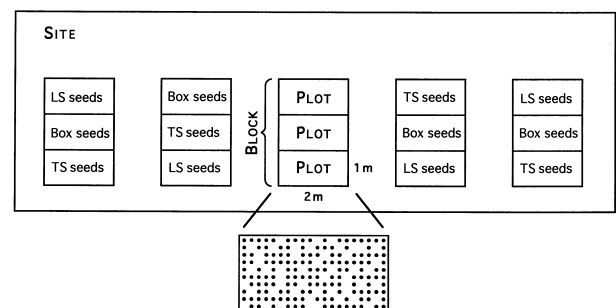

Figure 2. Experimental design in the reciprocal transplant experiment. Sets of 150 seeds (3 seeds from each of 50 mothers from a source population) were the experimental unit. Sets of seeds from Larkspur Canyon (LS), Tombstone Road (TS), and Box Canyon (Box) were randomly assigned to adjacent plots within each of five blocks per site. Seeds were sown randomly in a 10-cm grid within plots.

each plot, avoiding cells consisting of bare rock. Every block therefore consisted of 150 seeds representing each of the three populations, for a total of 450 seeds per block. A total of 2250 seeds (5 blocks $\times$ 3 plots/block $\times$ 150 seeds/plot) was planted at each site, for a grand total of 6750 seeds for the entire experiment.

Seeds were planted 12–14 December 1995 to coincide with winter rains. Sets of seeds were weighed, and seeds were individually scarified with a serrated knife the evening before planting to encourage high germination. Seeds were planted 1 cm deep, covered with loose soil, and marked with plastic toothpicks. Mishandling of seeds resulted in fewer than 150 seeds being planted in some plots. All plants were harvested 29 April–3 May 1996, when fruits were mature but had not yet dehisced.

Introduction Experiment

Seeds collected in May 1995 from the Box Canyon population were planted in three sites in which *Lupinus guadalupensis* did not historically occur. Two of these (Spray and Arizone Road) were identified as potential habitat based on their physical characteristics (Kellogg & Kellogg 1994); the third (Northwest Shore) was included to determine whether other habitats might also support populations of *L. guadalupensis.*

The Northwest Shore site is a maritime desert scrub–sand dune community dominated by *Ambrosia chamissonis* var. *bipinnatisecta*, *Astragalus nevinii*, and *Hordeum* spp. Other common taxa include *Abronia umbellata*, *Astragalus miguelensis*, *Atriplex* spp., *Eriophyllum nevinii*, and *Mesembryanthemum* spp. Soils are described as sand dunes, and the parent material is recent sand deposits (eroded marine sediments; A. Yatsko, personal communication).

The Spray site is a maritime desert scrub (lycium phase) vegetation community dominated by *Atriplex* spp., *Bergerocactus emoryi*, *Hemizonia clementina*, and *Lycium californicum*. Other common species include *Amblyopappus pusillus*, *Eschscholzia ramosa*, *Mesembryanthemum* spp., *Opuntia prolifera*, and *Suaeda taxifolia*. Soils are described as Westshore silt loam, and the parent material is Tertiary andesite.

The Arizone site is an annual grassland vegetation community dominated by *Avena barbata*, *Bromus* spp., and *Calystegia macrostegia* ssp. *amplissima*. Other common taxa include *Achillea millefolium*, *Dichelostemma capitatum*, *Gnaphalium* spp., *Lasthenia californica*, and *Viola pedunculata*. Soils are described as Eelpoint clay, and the parent material is Tertiary dacite. This site is similar to the Tombstone Road site and is only a few hundred meters from a natural population of *Lupinus guadalupensis*.

Sets of 150 seeds (3 seeds from each of 50 mothers from the Box Canyon population) were the experimental units. At each site, five haphazardly chosen plots of

1×2 m were planted with a set of 150 seeds. Seeds were randomly assigned to locations in a 10-cm grid in each plot, avoiding cells consisting of bare rock. A total of 750 seeds (5 plots $\times$ 150 seeds/plot) was planted at each site, for a grand total of 2250 seeds for the entire experiment.

Seeds were planted 3–4 January 1996. Sets of seeds were weighed, and seeds were individually scarified with a serrated knife the evening before planting to encourage high germination. Seeds were planted 1 cm deep, covered with loose soil, and marked with plastic swordpicks. All plants were harvested 29 April–3 May 1996, when fruits were mature but had not yet dehisced.

Data Collection and Analysis

Semi-monthly surveys of germination, survival, and growth were conducted at all six sites. Germination, early leaf production, bolting, flowering, number of inflorescences, and number of ripe and aborted fruits were recorded. In addition, signs of herbivory and desiccation were noted. The presence of *Rhizobium* nodulation on roots was noted when plants were harvested.

The demographic characteristics of the three natural populations were investigated by means of the performance of seeds planted into their home sites (in the reciprocal transplant experiment). The total number of fruits produced per plot was compared for the three populations with a one-way analysis of variance (ANOVA). To determine whether the life-cycle stages at which population growth is limited varied among populations, additional comparisons were conducted for survival between successive life-cycle stages and for reproductive components of fitness (inflorescence production per flowering plant, number of fruits initiated per inflorescence, and number of fruits ripened per initiated fruit). These analyses were repeated with the number of plants per plot as a covariate because of variation among plots in the number of surviving plants, but the covariates were not significant and their use caused only minor changes in probability values associated with site differences. All proportions were arcsin-transformed before analysis.

The reciprocal transplant experiment was analyzed in two ways. First, overall differences among populations were tested with two-way ANOVAs using site of planting, source of seeds, site-by-source interaction, and block (nested within site) as main effects. These ANOVAs were performed for the total number of fruits produced per plot and also for fitness components. The effect of site was tested over the block mean squares (MS) because blocks were nested within sites. The effect of seed source was tested over the error MS or over the site-by-source interaction MS if the latter was significant (there was no replication within blocks; Sokal & Rohlf 1981). Second, the hypothesis that populations are locally

adapted was tested by contrasting the relative performance of seeds planted in home sites with their relative performance when planted in foreign sites by means of a one-way ANOVA. Relative performance was calculated separately for each block ($n = 5$) at each site ($n = 3$) as the ratio of fruit production for a seed source to the average fruit production of the other two seed sources. A set of ratios was calculated and separately analyzed for each of the three source populations. Ratios were square-root-transformed before analysis.

The overall success of outplanting in the three introduction sites was assessed by contrasting the fruit production of plots at each introduction site with the fruit production of Box Canyon seeds averaged across the natural population sites. To determine the causes of differential success at the introduction sites, additional comparisons of each introduction site and natural sites were conducted for survival between successive life-cycle stages, inflorescence production per flowering plant, number of fruits initiated per inflorescence, and number of fruits ripened (expressed as a proportion of initiated fruits).

Results

Reciprocal Transplant Experiment

The total number of fruits produced per plot was significantly affected by seed source ($F = 5.13$, df = 2,24, $R^2 = 0.804$, $p = 0.0140$; Table 1, Fig. 3), with fruit production higher for seeds from Larkspur Canyon ($\overline{x} = 157.1$, SE = 39.6, $n = 15$) and Tombstone Road ($\overline{x} = 156.9$, SE = 26.0, $n = 15$) than from Box Canyon ($\overline{x} = 89.6$, SE = 24.8, $n = 15$). Blocks differed significantly ($F = 4.40$, df = 12,24, $p = 0.0010$), but there was no additional effect of planting site ($F = 3.37$, df = 2,12, $p = 0.0689$).
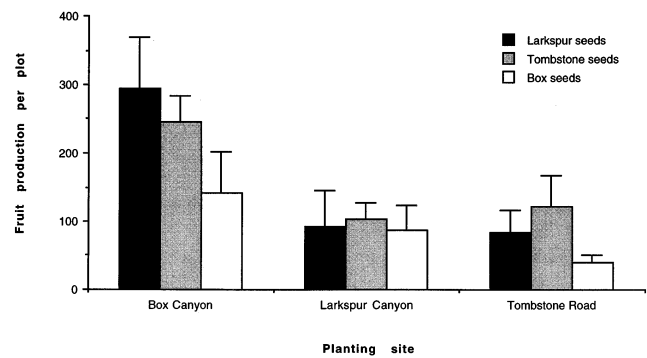

Figure 3. Fruit production per plot for seeds planted in a reciprocal transplant design at Larkspur Canyon, Tombstone Road, and Box Canyon. Fruit production was standardized to 150 seeds for plots in which a different number of seeds was planted. Error bars are +1 SE (n = 5 plots).

The principal fitness components that contributed to differences among seed sources in total fruit production were the number of inflorescences produced per plant ($\overline{x} = 1.92$, SE = 0.14, $n = 15$ for Larkspur Canyon; $\overline{x} = 2.23$, SE = 0.21, $n = 15$ for Tombstone Road; $\overline{x} = 2.08$, SE = 0.26, $n = 14$ for Box Canyon; Table 1) and the proportion of initiated fruits that ripened successfully ($\overline{x} = 0.70$, SE = 0.04, $n = 15$ for Larkspur Canyon; $\overline{x} = 0.74$, SE = 0.04, $n = 15$ for Tombstone Road; $\overline{x} = 0.62$, SE = 0.05, $n = 13$ for Box Canyon). There were no significant differences in plant mortality among the three seed sources, but a significant block effect occurred for nearly every fitness component (Table 1).

When the relative performance of seeds planted in their home and foreign sites was compared, no significant difference was obtained for Larkspur Canyon seeds

Table 1. Effect of planting site, seed source, site-source interaction, and block on components of fitness and on total fruit production per plot of *Lupinus guadalupensis* in the reciprocal transplant experiment.

Character	n	R^2	Site[a]	Source[a]	Site-source interaction[a]	Block[a]
Survival[b]						
germination	45	0.759				0.0008
1 leaf	45	0.776			0.0241	0.0022
8 leaves	45	0.720				0.0040
bolting	44	0.742	0.0081			0.0434
flowering	44	0.563				
fruit initiation	44	0.660				0.0254
fruit maturation	43	0.656				
Inflorescences per plant	44	0.845		0.0068		0.0001
Initiated fruits per inflorescence	44	0.631			0.0365	
Ripe fruits per initiated fruit	43	0.799		0.0331		0.0050
Total fruits per plot	45	0.804		0.0140		0.0010

[a] *Probability values less than 0.05 are listed.*
[b] *Survival values are expressed as proportions relative to the previous life-cycle stage.*

($F = 2.63$, df $= 2,12$, $R^2 = 0.305$, $p = 0.1131$), Tombstone Road seeds ($F = 0.46$, df $= 2,12$, $R^2 = 0.071$, $p = 0.6408$), or Box Canyon seeds ($F = 0.72$, df $= 2,12$, $R^2 = 0.107$, $p = 0.5060$).

The mass of seeds sown for this experiment varied for the three source populations ($F = 521.42$, df $= 2,42$, $R^2 = 0.961$, $p < 0.0001$). Sets of 150 seeds from Box Canyon were significantly heavier ($\overline{x} = 7.65$ g, SE $= 0.02$, $n = 15$) than sets of seeds from Tombstone Road ($\overline{x} = 6.97$ g, SE $= 0.02$, $n = 15$) and Larkspur Canyon ($\overline{x} = 6.84$ g, SE $= 0.02$, $n = 15$). Average seed masses were 51.03 mg, 46.5 mg, and 45.6 mg for these seed sources, respectively.

Introduction Experiment

No plants survived through the rosette stage to bolting at Northwest Shore (Table 2, Fig. 4). Although there was no difference in early seedling survival, germination and survival of rosettes were significantly lower than at natural sites. The poor overall performance of plants at this site is largely attributable to highly variable seed germination among plots and to desiccation and herbivory of rosettes. Mortality caused by herbivory was not significantly different than at natural sites ($F = 1.92$, df $= 1,18$, $R^2 = 0.096$, $p = 0.1833$) nor was mortality caused by desiccation ($F = 2.01$, df $= 1,18$, $R^2 = 0.100$, $p = 0.1732$). No data are available regarding *Rhizobium* nodulation at Northwest Shore due to early desiccation.

No plants produced ripe fruits at Spray (Table 2, Fig. 4). Germination and seedling and rosette survival were not significantly different at Spray than at natural sites. Beginning with bolting, however, survival was significantly worse at every subsequent stage, largely due to desiccation. Mortality caused by herbivory was not significantly different than at natural sites ($F = 0.05$, df $=$
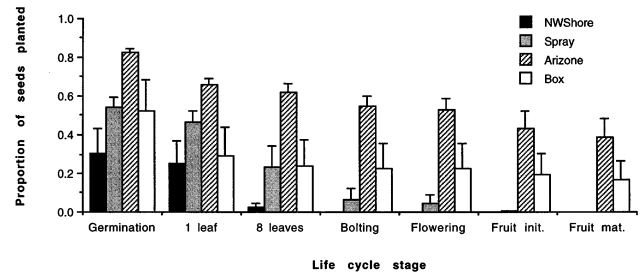

Figure 4. Survival of plants through successive life-cycle stages at three introduction sites, expressed as a proportion of total seeds planted per plot. Because seeds from the Box Canyon populations were used in this experiment, their survival at the Box Canyon site is included for comparison. Error bars are +1 SE (n = 5 plots).

$1,18$, $R^2 = 0.003$; $p = 0.8191$), but mortality caused by desiccation was significantly higher at Spray ($F = 4.91$, df $= 1,18$, $R^2 = 0.214$; $p = 0.0398$). In addition, plants at Spray initiated few fruits, and, due to desiccation, none of these ripened successfully. All plants at this site had *Rhizobium* nodules.

In contrast, plants at Arizone performed better than those at natural sites, with total fruit production per plot at Arizone ($\overline{x} = 220.2$, SE $= 59.0$, $n = 5$) exceeding total fruit production per plot at natural sites ($\overline{x} = 89.9$, SE $= 25.2$, $n = 15$; $F = 5.53$, df $= 1,18$, $R^2 = 0.235$; $p = 0.0302$; Table 2, Fig. 4). The only significantly different component of fitness was survival to the eight-leaf stage, for which plants at Arizone performed significantly better ($\overline{x} = 0.94$, SE $= 0.02$, $n = 5$) than plants at the natural sites ($\overline{x} = 0.62$, SE $= 0.06$, $n = 15$; $F = 9.48$, df $= 1,18$, $R^2 = 0.345$; $p = 0.0065$). Mortality caused by her-

Table 2. Performance of Box Canyon seeds of *Lupinus guadalupensis* at three introduction sites.[a]

Character	Northwest Shore		Spray		Arizone	
	$\overline{x} \pm SE$	p	$\overline{x} \pm SE$	p	$\overline{x} \pm SE$	p
Survival[b]						
germination	0.30 ± 0.16	0.0180	0.54 ± 0.05		0.83 ± 0.02	
1 leaf	0.76 ± 0.09		0.85 ± 0.04		0.79 ± 0.04	
8 leaves	0.08 ± 0.03	0.0004	0.45 ± 0.18		0.94 ± 0.02	0.0065
bolting	0.00 ± 0.00	<0.0001	0.11 ± 0.09	<0.0001	0.88 ± 0.03	
flowering	—		0.71 ± 0.04	0.0001	0.97 ± 0.02	
fruit initiation	—		0.05 ± 0.05	0.0043	0.76 ± 0.10	
fruit maturation	—		0.00 ± 0.00	0.0002	0.88 ± 0.02	
Inflorescences per plant	—		1.08 ± 0.08		1.29 ± 0.09	
Initiated fruits per inflorescence	—		0.14 ± 0.14	0.0162	3.14 ± 0.45	
Ripe fruits per initiated fruit	—		0.00 ± 0.00	0.0010	0.62 ± 0.04	
Total fruits per plot	0.00 ± 0.00	0.0035	0.00 ± 0.00	0.0035	220.2 ± 59.0	0.0302

[a]*Performance at each introduction site was tested against the performance of seeds from Box Canyon at the three natural sites. Only probability values less than 0.05 are listed.*
[b]*Survival values are expressed as proportions relative to the previous life-cycle stage.*

bivory was not significantly different than at natural sites ($F = 0.83$, df = 1,18, $R^2 = 0.044$, $p = 0.3732$), nor was mortality caused by desiccation ($F = 1.89$, df = 1,18, $R^2 = 0.095$, $p = 0.1860$). Overall, desiccation of unripe fruits reduced fruit production by 38.2% (SE = 0.04, $n = 5$) at Arizone, which was not significantly different than at natural sites ($\overline{x} = 38.3\%$, SE = 0.05, $n = 13$, $F = 0.01$, df = 1,16, $R^2 = 0.001$, $p = 0.9141$). *Rhizobium* nodulation occurred in only 68.6% of the plants at Arizone, and there was significant heterogeneity among plots ($\overline{x} = 66.39$, $p < 0.0001$). Nodulated plants produced significantly more fruits per plant ($\overline{x} = 4.02$, SE = 0.21, $n = 131$) than plants without nodules ($\overline{x} = 1.06$, SE = 0.30, $n = 63$) in the four blocks in which both types were present ($F = 36.29$, df = 1,186, $R^2 = 0.320$, $p < 0.0001$).

Factors Limiting Population Growth

There was no significant difference in the number of fruits produced per plot among the populations at the three natural sites ($F = 0.25$, df = 2,12, $R^2 = 0.039$, $p = 0.7777$), and sites did not vary in fitness components except for the number of fruits initiated per inflorescence (Table 3, Fig. 5). The major causes of mortality appeared to be desiccation and herbivory by *Apantesis proxima* (Arctiidae; Mexican tiger moth). Desiccation resulted in the death of 42.2% of plants overall before fruit production in natural sites, with significantly lower mortality at Box Canyon ($\overline{x} = 0.1176$, SE = 0.0538) than at Larkspur Canyon ($\overline{x} = 0.5044$, SE = 0.1104) or Tombstone Road ($\overline{x} = 0.6452$, SE = 0.0786; $F = 10.38$, df = 2,12, $R^2 = 0.634$, $p = 0.0024$). Herbivory resulted in the death of 25.2% of plants overall, with no significant difference among sites ($F = 1.40$, df = 2,12, $R^2 = 0.189$, $p = 0.2850$).

Desiccation and herbivory reduced fruit production in addition to causing mortality at earlier stages. Desiccation of plants before all fruits were ripe reduced fruit
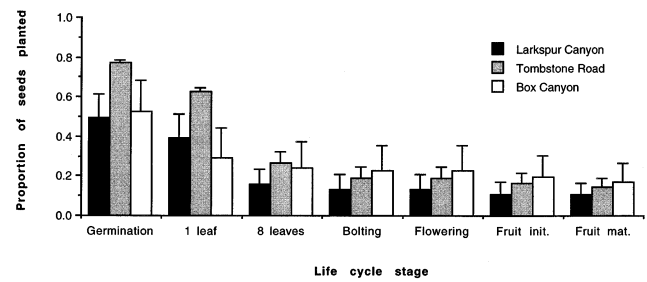

Figure 5. Survival of plants through successive life-cycle stages at three natural population sites, expressed as a proportion of total seeds planted per plot. Results are shown only for seeds collected from the same site in the previous year. Error bars are +1 SE (n = 5 plots).

production by 33.3% overall, with no significant difference among sites in the proportion of dessicated fruits per plant ($F = 0.99$, df = 2,11, $R^2 = 0.152$, $p = 0.4036$). Herbivory of ripe fruits by rodents reduced fruit set in one plot.

With the exception of one block in Box Canyon, all but one or two plants per block had *Rhizobium* nodules. In this particular block 24.3% of plants were not nodulated. Nodulated plants produced significantly more fruits per plant ($\overline{x} = 3.36$, SE = 0.27, $n = 106$) than plants without nodules ($\overline{x} = 2.06$, SE = 0.47, $n = 34$) in this block ($F = 5.67$, df = 1,138, $R^2 = 0.039$, $p = 0.0186$).

Discussion

Factors Limiting Population Growth

Desiccation and herbivory are the major factors limiting population growth, both by causing mortality before

Table 3. Performance of seeds of *Lupinus guadalupensis* at three natural population sites on San Clemente Island.[a]

Character	Larkspur Canyon $\overline{x} \pm SE$	Tombstone Road $\overline{x} \pm SE$	Box Canyon $\overline{x} \pm SE$
Survival[b]			
germination	0.49 ± 0.12	0.77 ± 0.02	0.52 ± 0.16
1 leaf	0.71 ± 0.08	0.82 ± 0.04	0.47 ± 0.02
8 leaves	0.44 ± 0.12	0.42 ± 0.08	0.67 ± 0.03
bolting	0.77 ± 0.09	0.67 ± 0.09	0.93 ± 0.04
flowering	1.00 ± 0.00	1.00 ± 0.00	1.00 ± 0.00
fruit initiation	0.79 ± 0.11	0.79 ± 0.07	0.90 ± 0.04
fruit maturation	0.89 ± 0.10	0.91 ± 0.03	0.92 ± 0.04
Inflorescences per plant	2.55 ± 0.73	2.68 ± 0.45	2.90 ± 0.92
Initiated fruits per inflorescence	1.53 ± 0.23	2.18 ± 0.13	3.08 ± 0.30[c]
Ripe fruits per initiated fruit	0.71 ± 0.10	0.57 ± 0.05	0.73 ± 0.11
Total fruits per plot	93.0 ± 53.1	122.2 ± 45.2	142.1 ± 60.6

[a] Only seeds collected from the same site in the previous year were used.
[b] Survival values are expressed as proportions relative to the previous life-cycle stage.
[c] The value for Box Canyon is significantly higher than the values for the other two populations (p = 0.0017).

successful fruit production and by reducing fruit production of surviving plants. The most vulnerable part of the life cycle of *L. guadalupensis* is survival of young rosettes: on average, only about half of the seedlings survived to the eight-leaf stage. The overall average number of fruits produced per plot was 119.1 (SE = 29.0) for seeds planted in their home sites. Fruits usually contain five to seven ripe seeds, giving approximately a five-fold increase in the number of seeds produced over the number planted. This cannot be interpreted as a measure of population growth for 1 year because seeds were scarified before planting (natural germination would probably have been lower and ungerminated seeds are susceptible to predators or pathogens), but it indicates that this species has the potential to increase in numbers.

Differences among Natural Population Sites

The natural population sites used in this study are located within 10 km of each other but differ in vegetation community, dominant species, soil type, and parent material. These differences do not appear to affect populations of *L. guadalupensis*. When seeds were planted in their home sites, significant differences among sites were not observed in total fruit production or in the majority of fitness components. In addition, the reciprocal transplant experiment failed to reveal a significant site effect for total fruit production or for the majority of fitness components. Desiccation and herbivory were the major causes of mortality and reduced fruit production at all sites, with a significant difference observed only for mortality caused by desiccation before fruit production; *Rhizobium* nodulation was found for most plants at all sites (except for Northwest Shore, where plants died before the presence of nodules could be determined). In contrast, success varied considerably among blocks within sites.

Pattern of Adaptation of Populations

The reciprocal transplant experiment provided no evidence of local adaptation of populations. First, there was no significant interaction among planting site and source of seeds on total fruit production per plot in the two-way ANOVA. Second, direct tests of whether seeds performed best at their home site indicated that there were no significant differences. In contrast, this experiment provided strong evidence that some populations are generally better adapted than others, regardless of the site in which they were planted. Seeds from the Box Canyon population produced on average only 57% as much fruit as the other populations. These differences in fruit production can be interpreted as phenotypically detectable variation in fitness. Because *L. guadalupensis* is an annual, and the entire life cycle of this annual plant was censused, fruit production is a close approximation

of fitness. The fitness component that contributed most to differential fruit production—the number of inflorescences produced per plant—indicates that plant size rather than survival varied among source populations. Differences in plant size probably result from general growth rate differences that were not so extreme as to cause differences in mortality in response to herbivory or desiccation.

A comparison of seed mass in the three source populations excludes a common ecological explanation for their differential performance. Maternal effects operating through seed mass are associated with increased fitness in the congeneric *L. texensis* (Helenurm & Schaal 1996) as well as in plants generally (Roach & Wulff 1987). Seeds from Box Canyon, however, were 10% heavier on average than seeds from the other two populations, but they performed worse at all sites. Thus, the differential performance of material from different source populations is unlikely to be caused by differences in seed mass. It is also unlikely that differences in micronutrients stored in seeds are responsible for the differences among source populations because no differences in appearance or survival were apparent early in the life cycle. Moreover, seeds from all sources performed well at Box Canyon (Fig. 3), so this site is unlikely to be deficient in essential micronutrients. Genetic differences among populations are the most likely cause of the observed differences in fruit production.

Although several reciprocal transplant studies have demonstrated an apparent lack of local adaptation and even cases of maladaptation of populations in various plant species (Antonovics & Primack 1982; Cheplick 1988; Rapson & Wilson 1988; Rice & Mack 1991), there are few examples of species in which some source populations appear to have higher fitness at all sites. In *Amsinckia grandiflora* one population outperformed others in germination at all planting sites in 1996 (although not in previous years) with no apparent correlation to seed mass (B. Pavlik, personal communication). Recent reciprocal transplant experiments with *Quercus douglasii* have also suggested that some populations perform better than others at all planting sites (K. Rice, personal communication).

Genetic Drift in Natural Populations

The observed pattern of adaptation, in which some populations were generally better adapted than others, may be a consequence of genetic drift. Genetic drift can be a more powerful evolutionary force than selection in small and isolated populations and can thus cause the fixation of alleles that reduce fitness. Box Canyon is the smallest of the three populations used in the reciprocal transplant experiment, and the area over which plants have been found is small, suggesting that this site cannot support a large population. Genetic drift would be ex-

pected to have the greatest impact on allele frequencies in this population, including the fixation of deleterious alleles at some loci.

Three features of the reproductive biology of *L. guadalupensis* would accentuate the impact of genetic drift in small populations. First, seed dispersal occurs through explosive dehiscence of fruits upon desiccation, resulting in dispersal distances of up to approximately 1 m. Populations are thus probably well isolated with respect to seed dispersal, and inbreeding due to mating between relatives may be expected to occur. Second, some individuals of *L. guadalupensis* are autogamous in the greenhouse (K. Helenurm, unpublished data), suggesting that some self-fertilization may occur in natural populations. Self-fertilization would further limit gene flow among populations. Moreover, inbreeding and selfing decrease effective population size (Crawford 1984; Caballero & Hill 1992), making drift an even more potent force in small populations and overriding the purging of deleterious alleles by selection that would otherwise be expected under inbreeding. Third, the variance in fruit production of individuals was high, ranging from 1.0 to 29.9 times greater than the mean fruit production of plants growing in their home sites in this experiment ($\bar{x} = 3.79$, SE = 0.45, $n = 14$); effective population size is reduced when the variance in reproduction is higher than the mean (Heywood 1986).

To evaluate the hypothesis that genetic drift has played an important role in the evolution of these populations, other expectations of genetic drift can be tested. Because genetic drift causes the loss of genetic variation, small populations of *L. guadalupensis* would be expected to have less genetic variability than larger populations. Moreover, because genetic drift is a stochastic process, deleterious alleles would be expected to be fixed at different loci in different small populations. Thus, the progeny of interpopulational crosses would be expected to carry beneficial alleles at more loci than would progeny of intrapopulational crosses, and thus to exhibit higher fitness.

Prospects for Outplanting

The success of populations introduced to new sites ranged from the death of all plants before flowering (Northwest Shore) or before fruits ripened (Spray) to fruit production greater than at natural population sites (Arizone; Fig. 4). The failure of the population at Northwest Shore was caused by a combination of low seed germination, herbivory, and desiccation; the failure of the population at Spray can be attributed primarily to desiccation. The timing of seed planting and rainfall may have contributed to the lack of successful fruit production at Spray. This site experiences earlier desiccation than Arizone, probably due to more wind, higher salt concentration, and lower plant biomass (J. Stone, per-

sonal communication). After planting, rain occurred sporadically starting in mid-January. Had seeds been planted earlier or had rain been more frequent in early 1996, many plants at this site might have completed their life cycle and produced ripe fruits. Clearly, among-year differences in rainfall will affect the success of populations, and it is possible that the Spray site may support considerable fruit production in some years. This year's results, however, strongly suggest that Spray is a marginal habitat at best, and that Northwest Shore is not appropriate for *L. guadalupensis*.

The success of plants at Arizone demonstrates that the date of planting at the introduction sites in this experiment did not preclude successful fruit production. Plants at Arizone outperformed plants at natural population sites in spite of a lower rate of *Rhizobium* nodulation. Limited dispersal of *L. guadalupensis* seeds is probably responsible for the sparsity of populations in the grassland community of San Clemente Island.

Implications for Management

The choice of appropriate source populations is crucial for the success of outplanting attempts. Although populations with greater genetic variation are generally considered superior sources of seeds for outplanting (because genetic variation is a prerequisite for future adaptation and may affect immediate fitness), local adaptation of populations could doom outplanting strategies based on surveys of genetic variation alone. The possibility of local adaptation is thus a troubling concept for the management of species for which extensive experimental data are unavailable (most target species). Although local adaptation may be likely in widespread species in which distant populations experience considerably different biotic and abiotic environments, it is possible that species with restricted distributions exhibit little local adaptation. The data reported here for *L. guadalupensis*, an island endemic found in different vegetation communities, suggests that local adaptation is unimportant in determining population growth. In contrast, genetic differences among populations appear to cause differential performance at all sites, making certain populations superior choices for outplanting. These results should be interpreted as reason to avoid certain source populations but to use several seed sources for outplanting attempts, rather than to use seeds from only one, best seed source. The use of material from only one source population would probably restrict the genetic variability available for outplanting, and thus might decrease the long-term survival of introduced populations.

Although seed mass is clearly not relevant, population size may be a reliable predictor of the performance of source populations. If a survey of genetic variation reveals that small populations of *L. guadalupensis* (including Box Canyon) are genetically less variable than large

populations (including Larkspur Canyon and Tombstone Road), this would support the hypothesis that genetic drift has had a strong impact on current fitness and that larger populations are better choices as seed sources for outplanting.

Analysis of the reciprocal transplant experiment showed that blocks varied significantly in overall fruit production and in most fitness components, but that there was no additional effect of planting site except for one component of survival. This suggests that seeds should be sown in many areas within a target site to increase the probability of success at that site. Alternatively, the sowing of seeds in few blocks at a large number of suitable sites may be as efficient a use of seeds as sowing them in many blocks at fewer sites.

Although a variety of sites have been identified as potential habitat for *L. guadalupensis* (Kellogg & Kellogg 1994), their suitability appears to vary based on desiccation of plants in these localities. The choice of target sites in grassland communities, especially if chosen in conjunction with rainfall and soil moisture data, may increase the success of outplanting efforts. Differences in life-history characteristics, however, may occur among natural populations. If plants from some populations flower earlier, and consequently have a shorter life cycle, their use in outplanting may permit the introduction of *L. guadalupensis* into apparently marginal sites such as Spray. A broad survey of natural populations in a common garden experiment is necessary to reveal genetic variation that may allow the use of more sites for outplanting.

Acknowledgments

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