INDIVIDUAL DIFFERENCES IN PROGENY VIABILITY IN *LAVANDULA LATIFOLIA*: A LONG-TERM FIELD STUDY

CARLOS M. HERRERA[1]

Estación Biológica de Doñana, Consejo Superior de Investigaciones Científicas, Apartado 1056, E-41080 Sevilla, Spain

Abstract. Despite its potential importance as a source of fitness variation in natural plant populations, few studies have so far examined long-term patterns of individual differences in progeny viability under natural conditions. This paper reports on a six-year field study on the differences in progeny viability (defined here as the probability of seeds contributing an established, prereproductive juvenile to the population), and its two components (seedling emergence and seedling survivorship), for the Mediterranean evergreen shrub *Lavandula latifolia.* The main objectives of the study were (1) to assess whether individual plants actually differ in the viability of their progeny under natural conditions, and (2) to determine if naturally occurring levels of variation in viability may modify individual differences in fecundity. Seed progenies from 14 maternal parents belonging to one population were sown at 10 field sites differing broadly in habitat type and soil characteristics, and seedling emergence and survival subsequently were monitored for six years. Maternal parents differed significantly in progeny viability because of both differential seedling emergence and seedling survivorship, and variation in either of these parameters was not significantly related to maternal differences in seed size. Differences in seedling survivorship were more important than differences in seedling emergence as determinants of maternal variation in progeny viability. While individual differences in seedling emergence remained consistent across sowing sites, there was a strong parent × sowing site interaction on seedling survivorship, and the rank of maternal parents with regard to this variable varied erratically among sowing sites. A significant inverse relationship existed across maternal parents between seed production and progeny viability, which was not mediated by differences in seed size, thus suggesting a trade-off between the number and quality of the progeny produced by *L. latifolia* plants. Although maternal differences in seed production were about twice as important as differences in progeny viability in determining maternal differences in juvenile recruitment, viability differences should not be disregarded a priori as unimportant sources of fitness differences. Results of this study stress the importance of conducting long-term, direct field assessments of individual differences in progeny viability across a range of environments encompassing the conditions actually faced by the species.

Key words: Lavandula latifolia; *maternal differences; Mediterranean; parent × environment interaction; progeny viability; seedling emergence rate; seedling survivorship.*

INTRODUCTION

Individual differences in the number of descendants contributed to the next generation is an essential prerequisite for natural selection to operate, as this variance in fitness is what actually provides the ''opportunity for selection'' (Arnold and Wade 1984, Brodie et al. 1995). Variance in fitness may be partitioned into fecundity (number of independent offspring produced) and viability (the probability that each of these reaches adulthood) components (e.g., Endler 1986, Falconer 1989), hence the distinction between fecundity and viability selection often recognized in selection studies (e.g., Kalisz 1986, Stewart and Schoen 1987, Shykoff 1988, for plant investigations). In sexually reproducing plant populations, the opportunity for selection will simultaneously depend on the variance in number of seeds produced per individual (via both female and male functions, in the case of hermaphroditic species), on the between-individual variance in the average probability of seeds eventually reaching adulthood, and on the covariance (across individuals) between these two variables.

While there is a long tradition of investigations focusing on the causes and implications of individual differences in fecundity in natural plant populations (e.g., Janzen 1978, Solbrig and Solbrig 1984, Weller 1985, Scheiner 1987, Aarssen and Taylor 1992), individual differences in progeny viability *under field conditions* have been examined in detail much less frequently (but see, e.g., Thompson 1985, Waser and Price 1989, Campbell 1997, Ramsey and Vaughton 1998). Individual variation in some components of progeny viability (e.g., seed germination, seedling survivorship) has been quite often documented under greenhouse or

[1] E-mail: herrera@cica.es

artificial garden conditions (e.g., Schmitt and Antonovics 1986, Van Andel et al. 1988, Biere et al. 1989, Biere 1991*a*, Levin 1991, Delesalle and Blum 1994, Norman et al. 1995, Helenurm and Schaal 1996, Sakai et al. 1997, Husband and Gurney 1998, Culley et al. 1999). However, its actual importance as a determinant of fitness variation in natural plant populations, particularly in comparison with variation in fecundity components, remains largely unexplored. This represents a serious gap in our knowledge of the evolutionary mechanisms operating in natural plant populations, as certain processes influential on plant reproduction (e.g., pollination-dependent inbreeding depression) are well known for their capacity to generate differences in progeny viability and thus have the potential to become significant agents of viability selection. Unfortunately, conclusions from studies on patterns of progeny viability conducted under artificial conditions cannot safely be extrapolated to field conditions. Investigations that have simultaneously studied viability patterns under field and artificial conditions have frequently revealed important discrepancies (Montalvo 1994, Herrera 2000, and references therein). This has been most often found, for instance, in cases where inbreeding depression is an important determinant of progeny viability, whose magnitude is smaller under relatively benign greenhouse or garden conditions than in the harsher field conditions (e.g., Mitchell-Olds and Waller 1985, Dudash 1990, Eckert and Barrett 1994, Montalvo 1994, Koelewijn 1998, Ramsey and Vaughton 1998).

This paper reports on a 6-yr field study aimed at elucidating patterns of variation in progeny viability across maternal parents in the insect-pollinated Mediterranean shrub *Lavandula latifolia* (Labiatae). The study was prompted by two previous investigations on the evolutionary ecology of reproduction in this species (Herrera 1991, 2000). In one of these, I found that individual variation in flower production was the most important variable in explaining individual differences in seed production, while the contribution of differences in fruit and seed set was negligible (Herrera 1991). In the other study, different insect pollination regimes induced experimentally on plants gave rise to variation in both seed production and, principally, field-assessed progeny viability (Herrera 2000). To evaluate the selective potential of pollinators on *L. latifolia* plants (Herrera 1987*a, b,* 1988, 1995, 2000), it thus was critical to examine if individuals actually differ in the viability of their progeny under natural conditions, and if they do, to compare the magnitude of naturally occurring levels of individual variability in progeny viability with levels of variability in seed production. Specifically, the following questions will be addressed here. (1) Do *Lavandula latifolia* maternal parents differ in the average likelihood of their seeds producing an established juvenile plant under natural field conditions (termed ''progeny viability'' hereafter)? As defined here, progeny viability may be decomposed into the probability of the seed yielding an emerged seedling and the likelihood of this seedling surviving up to the juvenile stage, so I will also consider patterns of individual variation in each of these two components. (2) What is the relative importance of variation in seedling emergence and seedling survivorship in explaining individual differences in progeny viability? (3) Do differences between maternal parents in progeny viability, seedling emergence rate, and seedling survivorship remain consistent across environments? And (4) Is there some relationship across plants between maternal fecundity and progeny viability? In this paper I emphasize aspects related to individual variation, although I studied progeny viability and its components along a broad environmental gradient, and some results related to spatial variation will be presented. Patterns of variation in progeny viability and population recruitment at different spatial scales and their environmental correlates will be dealt with elsewhere.

METHODS

This study was conducted during 1992–1998 in the Reserva de Navahondona-Guadahornillos, Parque Natural de Cazorla-Segura-Las Villas (Jaén province, southeastern Spain; see Luque [1995] for descriptions of the vegetation). Mature seeds were collected in September–October 1992 from 15 previously marked *L. latifolia* shrubs at a population growing around the intersection of Arroyo Aguaderillos and the track joining Roblehondo and Hoyos de Muñoz. This was the same population used in the earlier study on individual variation in maternal fecundity (Herrera 1991), and the plants providing the seeds used here were the same used in the earlier investigation on the fecundity and viability consequences of different pollination regimes (Herrera 2000). The number of seeds produced by each plant was counted, and seeds from different plants were kept as separate batches in paper bags, held in the dark at ambient temperature until they were sown in the field in January 1993. One plant (No. 4) produced very few seeds in 1992, and was thus excluded from this study. To characterize individual differences in seed mass, a subsample of $N = 100$ seeds was taken from each batch, and seeds weighed individually to the nearest 0.01 mg.

In January 1993, maternal seed progenies were sown at 10 broadly spaced sites located in the same general region as the Aguaderillos site, ranging in elevation between 770 and 1645 m, and differing in habitat type and soil characteristics (Table 1). The two most distant localities (AT and CV) were 8.5 km apart, and the two closest ones (CV and CN) only 150 m apart. One of the sites (AP) was located ~30 m away from the plants that provided the seeds for the experiments. Sites were located in dense evergreen oak forest and scrubland, oak–pine mixed forest, and montane pine forest (Table 1). I replicated over 10 sites with maternal families from only one site as a way of sampling a broad range

TABLE 1. Main characteristics of the 10 experimental sowing sites.

Site†	Elevation (m)	Habitat type‡	Soil texture		
			Sand (%)	Clay (%)	Silt (%)
AT	770	OF	28.1 ± 4.4	43.9 ± 8.0	28.0 ± 5.2
AG	1030	OF	37.5 ± 5.4	34.4 ± 5.9	28.1 ± 3.7
HM	1080	OF	23.4 ± 6.0	40.7 ± 3.4	35.9 ± 4.0
AP	1200	MF	29.6 ± 4.8	37.5 ± 1.2	32.9 ± 5.2
CB	1210	MF	62.1 ± 6.0	8.4 ± 1.6	29.5 ± 4.5
TS	1245	OF	10.5 ± 2.3	61.2 ± 1.5	28.3 ± 2.3
RH	1400	MF	29.1 ± 6.5	42.1 ± 7.7	28.8 ± 1.5
CC	1465	PF	14.4 ± 1.6	46.6 ± 5.0	39.0 ± 4.0
CV	1640	PF	37.4 ± 4.2	17.8 ± 3.1	44.8 ± 3.6
CN	1645	PF	22.0 ± 2.4	55.6 ± 2.5	22.4 ± 2.6

Note: Soil texture data are mean ± 1 SD values for $N = 5$ samples of topsoil from each site.
† Sites (localities) are listed in increasing order of elevation and are coded as follows: AT, Arroyo de las Truchas; AG, Agracea; HM, Hoyos de Muñoz; AP, Aguaderillos-1; CB, Cuevas Bermejas; TS, Aguaderillos-2; RH, Roblehondo; CC, Collado del Calvario; CV, Correhuelas-Viejo; CN, Correhuelas-Nuevo.
‡ OF, dense Mediterranean evergreen oak (*Quercus rotundifolia*-dominated) forest and scrubland; MF, oak (*Quercus rotundifolia*)–pine (*Pinus nigra*) mixed forest; PF, montane pine (*Pinus nigra*-dominated) forest.

of environmental conditions. When selecting experimental sites, I deliberately avoided those with established *L. latifolia* populations, as a pre-existing seed bank could have interfered with my experimental sowings. Wild plants of *L. latifolia* existed within 100 m of all experimental sites except CN and CV (where the nearest individuals were 350 m away), thus corroborating the suitability of general environmental conditions of sowing sites for the persistence of this species.

At each site, 28 (14 maternal parents × 2 replicates) 30 × 30 cm plots were distributed over a surface of roughly 50 m², and randomly assigned to maternal parents. Each plot received 100 seeds from a single maternal parent, which were distributed as homogeneously as possible over the soil surface. To initially hold seeds in place, each plot was covered with a piece of dense fiberglass net, tightly affixed to the ground with nails. Nets were removed three months later, when seedlings started to emerge. For some plants I did not have sufficient seeds to fulfill the design, and one of the two replicates for these individuals was missing from some of the sites. A total of 252 plots were eventually established, instead of the 280 required by a perfectly balanced design, and 25 060 seeds were sown (rather than the 28 000 required by the design).

Experimental sites were visited every 10 days during February–July 1993, and plots examined for newly emerged seedlings. On each occasion, new seedlings emerged since the last visit were marked on one of the cotyledons with a small dot of fast-drying black ink. This procedure afforded a precise determination of the cumulative number of seedlings emerged per plot during the whole germination season (late April–early June in 1993). Simple repeated counts of seedlings present per plot would have underestimated emergences, as substantial short-term seedling mortality took place at some sites. Some additional seedlings ($N = 31$, all sites combined) emerged in the experimental plots in

1994, but their importance was negligible in comparison with the total number of seedlings emerged in 1993 ($N = 7580$, all sites combined). This indicates that seedling emergence failures did not reflect dormancy, but rather seed or pre-emergence seedling death. This study will consider only the data for the 1993 cohort. At the planting sites, seedlings of *L. latifolia* were found only inside or, very rarely, immediately adjacent to the plots, thus verifying that only the planted seeds were followed in the study.

After the 1993 seedling emergence period finished, experimental sites were monitored every three months until June 1994, and at progressively longer intervals until the completion of the study in late December 1998. In each inspection, the number of surviving seedlings was recorded for each plot. Seedlings alive by the end of the study were harvested, and fresh mass of aerial parts determined to the nearest 0.1 mg within 5 h of collection. By that time, sixth-year survivors had become well-established juveniles, and some of them would most likely have flowered for the first time 2–3 years after collection. The study was discontinued, however, upon realizing that the small number of surviving juveniles and its strongly imbalanced distribution among sites and maternal parents (see *Results* below) would preclude any statistical demonstration of maternal and site effects beyond the juvenile life history stage.

Data analysis

All statistical analyses were performed using the SAS statistical package (SAS Institute 1990*a,* 1996). Statistical significance levels of correlations involving maternal plant means (thus based on $N = 14$) were always evaluated by randomization (10 000 repetitions; routines written in SAS Macro Processing Language [SAS Institute 1990*b*]).

Progeny viability and seedling emergence.—The

significance of the effects of sowing site (Site) and maternal parent (Mother) on the probability of one seed yielding an emerged seedling (''seedling emergence rate'' hereafter) and eventually an established, 6th-year juvenile (''progeny viability,'' as defined here) was assessed by fitting generalized linear models to the data using procedure GENMOD. Individual plots ($N = 252$) were used as experimental units, and Site ($N = 10$ locations) and Mother ($N = 14$ plants) were both treated as fixed effects. Estimates of seedling emergence rate (seedlings emerged/seeds sown) and progeny viability (surviving juveniles/seeds sown) for each plot were modeled using logits and the binomial probability distribution. The overdispersion scale parameter, used to adjust likelihood ratio statistics, was estimated by the square root of the deviance of the model divided by its degrees of freedom (SAS Institute 1996).

Seedling survivorship.—Proportional hazards regression models (also known as Cox's regressions; Allison 1995) were used to study seedling survival patterns. This method was preferred over life table nonparametric methods or accelerated failure-time regression models because it makes no assumptions about the shape of the distribution of survival times (see, e.g., Fox [1993] and Allison [1995] for detailed descriptions of major failure-time analytical methods available). Computations were performed using procedure PHREG. As this implementation of Cox regression has no built-in capability for testing the effect of categorical covariates, I first created a dummy-coded design matrix for the effects of Site, Mother, and their interaction using GLMMOD procedure. Columns of this design matrix were then used as the independent variables in the PHREG procedure, and linear hypotheses of interest were tested using the appropriate TEST statements (Allison 1995). Tied data were handled using the Efron method (Allison 1995).

Survivor size.—The distribution of survivors' fresh mass was very skewed to the right and departed significantly from normality, but became normalized after logarithmic transformation. The effects of Mother, Site, and their interaction on this variable were thus assessed by fitting a general linear model to the log-transformed seedling mass data using procedure MIXED and restricted maximum likelihood estimation. Individual plots were used as experimental units, and effects were all treated as fixed.

RESULTS

Progeny viability

For all sites and mothers combined ($N = 252$ plots), mean per-plot progeny viability from sowing (January 1993) up to the end of the study (December 1998) was 0.0163 ± 0.0392 juveniles/seed (mean $\pm$ 1 SD; this notation will be used throughout unless otherwise stated), or less than two juveniles per each 100 seeds sown. There was, however, substantial variation around this average value among maternal parents (Fig. 1A) and sowing sites, and both sources of variation were statistically significant ($\chi^2 = 32.0$, df $= 13$, $P = 0.002$, for maternal parent; $\chi^2 = 388.5$, df $= 9$, $P \ll 0.0001$, for sowing site). Mean progeny viability for individual plants, computed on a per plot basis for all sites combined, ranged between 0.007 ± 0.0036 and 0.028 ± 0.0134 juveniles/seed. Among sowing sites (all mothers combined), progeny viability ranged between 0 and 0.080 ± 0.0127 juveniles/seed.

No seedling survived up to the end of the study at three sites, and the number of survivors was negligible at three further sites. The Site × Mother interaction effect on progeny viability thus could not be estimated, and its statistical significance could not be tested directly by including such an interaction among the independent terms of the generalized linear model. Indirect evidence, however, suggests that such interaction, although weak, probably exists. For the model with Site and Mother as the sole main effects, the sources of variation left out, which necessarily include the interaction effect, were marginally significant (scaled $\chi^2 = 261.3$, df $= 229$, $P = 0.070$; goodness-of-fit test for the model with Site and Mother as the only effects).

Components of viability: seedling emergence and survivorship

Mean seedling emergence rate, averaged across plots for all sites and mothers combined, was 0.302 ± 0.214 emerged seedlings/seed. When a saturated model was fitted (Model A in Table 2), the effect of Site on seedling emergence was highly significant, that of Mother was barely significant, and the interaction Site × Mother was far from significance, with a P value close to unity. This last result allows one to accept safely the null hypothesis that individual differences in seedling emergence remained consistent across sowing sites. Eliminating the interaction term from the model (Model B in Table 2) had no consequence for its overall fit to the data, but the significance of the Mother effect increased substantially. Mean seedling emergence rates for individual plants, computed on a per plot basis for all sites combined, ranged between 0.218 ± 0.147 and 0.384 ± 0.256 emerged seedlings/seed (Fig. 1B). Mean seedling emergence rate for the different sowing sites (all mothers combined) ranged between 0.032 ± 0.034 and 0.542 ± 0.109 seedlings/seed.

Survivor and cumulative hazards function estimates for emerged seedlings, all mothers and sites combined, are shown in Fig. 2A. Only 5.5% of seedlings remained alive six years after emergence. Most mortality took place during the first few months after emergence. The cumulative hazards curve (= the negative log-survivor function) tended to progressively level off, thus revealing an overall decrease over time in seedling mortality risk. This decrease, however, was not steady, as hazards rate peaked in summer every year. Detailed presentation of data on the seasonality of mortality
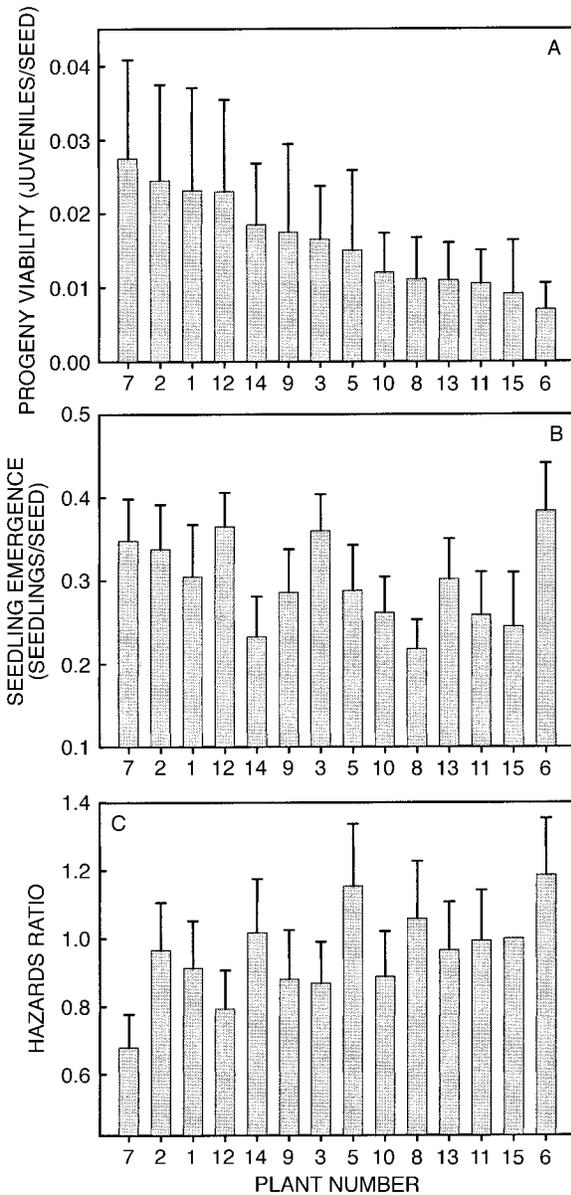
FIG. 1. Variation among maternal parents in progeny viability (= proportion of experimentally sown seeds leading to an established juvenile plant), seedling emergence rate (= proportion of seeds producing a seedling), and seedling mortality hazards ratio for the six-year period following emergence. Maternal parents are plotted on the horizontal axis in decreasing order of progeny viability. In panels (A) and (B), bars denote mean per-plot values computed over all sites combined, and vertical segments represent the standard error of the mean. In panel (C), bars represent the hazards ratio estimates (with respect to plant number 15), obtained by exponentiating the corresponding regression parameters from a Cox regression model having maternal parent and sowing site as regressors. Error bars represent the upper confidence limits of estimates.

rates is omitted, yet the summer increases in hazard rate corresponding to 1993 and 1994 were intense enough to show up in Fig. 2A.

Seedling survivorship varied significantly among both maternal parents ($\chi^2 = 60.5$, df = 13, $P \ll 0.0001$) (Figs. 1C, 2B) and sowing sites ($\chi^2 = 153.1$, df = 9, $P \ll 0.0001$). Individual differences in the mortality rate of seedlings during the first two summers after emergence were largely responsible for longer term differences in survivorship (Fig. 2B). Variation among sites in the survival prospects of seedlings was extreme. While all emerged seedlings died within one year of emergence at the three sites with the highest hazards ratio, two sites still had 14% of seedlings alive six years past emergence.

There was a remarkable Mother $\times$ Site interaction effect on the hazards function ($\chi^2 = 605.0$, df = 106, $P \ll 0.0001$), thus denoting that differences between
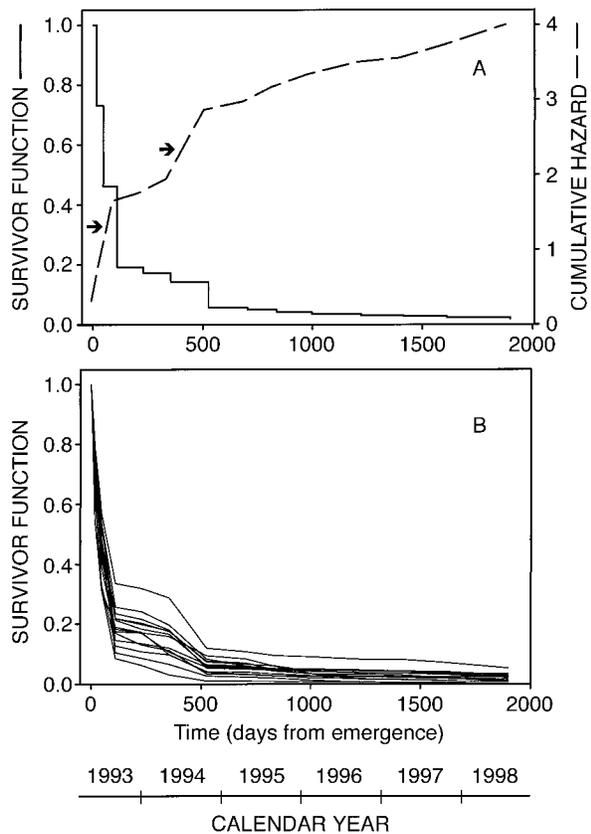

FIG. 2. (A) Survivor (continuous line) and cumulative hazards (broken line) function estimates for *Lavandula latifolia* seedlings, all maternal parents and sowing sites combined ($N = 7580$ seedlings). Confidence limits of the survivor function are too narrow to be shown. The hazard function is the derivative (slope) of the cumulative hazards function shown here, and the two arrows denote the peaks of the hazards function that took place during the first two summers following seedling emergence (1993 and 1994). (B) Seedling survivor function estimates plotted separately for the different maternal progenies.

TABLE 2. Likelihood ratio tests for the effects of sowing site (Site) and maternal parent (Mother) on the seedling emergence rate (emerged seedlings/seeds sown) of *Lavandula latifolia* seeds experimentally planted in the field.

	Model fit				Significance test		
Model	Scaled χ^2	df	P	Effect in model	df	χ^2	P
A	110.5	121	0.743	Site	9	267.8	≪0.0001
				Mother	13	23.3	0.038
				Site × Mother	108	77.3	0.989
B	214.7	229	0.742	Site	9	326.7	≪0.0001
				Mother	13	34.2	0.0011

Notes: Model B differs from the saturated Model A in that the interaction effect has been dropped. A generalized linear model was fitted to the data, using the binomial distribution and logits as link function.

maternal parents in seedling survivorship did not remain consistent across sites. The magnitude of this inconsistency can be appreciated in Fig. 3. For any given maternal parent, the survivorship of its seedlings relative to the survivorship of other plants' seedlings varied dramatically across sites. Depending on sowing site, seedlings of any given maternal parent could be either the locally most successful (lower ranks) or unsuccessful (higher ranks) (Fig. 3).

Survivor size

Size differences between surviving juveniles should be incorporated into a realistic assessment of progeny viability. Unfortunately, however, a comprehensive analysis of patterns of variation in final juvenile size was precluded by the fact that survivors occurred in only seven sites, and almost all of them (96%, $N =$

FIG. 3. Inconsistency across sowing sites in the hazards ratio of seedling progenies from different maternal parents, illustrating the strong Plant × Site interaction effect on seedling survivorship. Hazards ratios were obtained separately for each maternal parent at each sowing site, and the values obtained transformed to within-site ranks to facilitate comparisons (lower ranks corresponded to relatively lower seedling mortality risks). In the graph, each line connects the data points for different plants at the same site, and different lines correspond to different sites. On the horizontal axis, plants are arranged in order of decreasing progeny viability, for consistency with Fig. 1.

415) were concentrated in only four sites (AG, CB, CC, HM). Restricting the analysis to the data for these four sites, the Mother ($F_{13,351} = 4.06$, $P \ll 0.0001$; range of maternal means = 0.63–3.02 g), Site ($F_{3,351} = 5.90$, $P = 0.0006$; range of site means = 1.08–2.32 g), and Mother × Site interaction ($F_{30,351} = 4.11$, $P \ll 0.0001$) all had statistically significant effects on log survivor fresh mass.

Relationships among viability and its components

Maternal differences in seedling survivorship were more influential on variation in progeny viability than differences in seedling emergence. A multiple regression was run with progeny viability as the dependent variable, and seedling emergence rate and hazards ratio as independent ones. The relative importance of the two independent variables was then assessed by comparing their standardized, and thus scale-free, partial regression coefficients. The partial regression coefficient for seedling emergence rate (± 1 SE, determined by bootstrapping) was 0.195 ± 0.288, while that for the hazards ratio was -0.627 ± 0.297.

There was no evidence that progeny viability ($r = 0.036$, $N = 14$, $P = 0.91$), seedling emergence rate ($r = 0.136$, $N = 14$, $P = 0.66$), or seedling hazards ratio ($r = -0.292$, $N = 14$, $P = 0.31$) was correlated with mean survivor fresh mass, thus suggesting that maternal variation in juvenile size was unrelated to variation in other parameters influencing viability. This result, however, must be taken with some reservations, as maternal means for survivor size are based on relatively few data from only four sites, and thus are not strictly comparable to maternal means for other parameters that were based on data from the whole set of sowing localities.

Fecundity, seed mass, and viability

Mean seed mass differed significantly among maternal parents ($F_{13,1386} = 7.84$, $P \ll 0.0001$; range of maternal means = 1.18–1.53 mg). Individual differences, however, accounted for only 6.1% of total variance in seed mass, while variation within maternal progenies accounted for 93.9%. Individual variation in
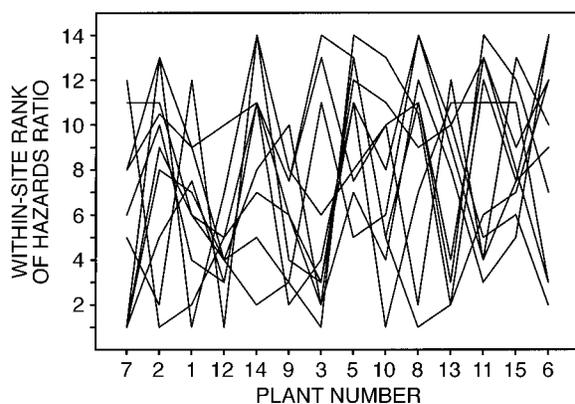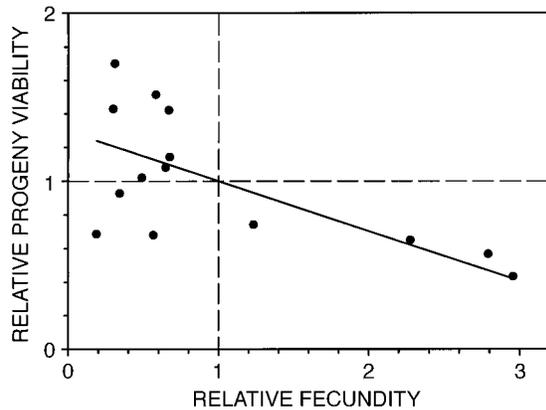
Fig. 4. Covariation across maternal parents of estimates of relative fecundity and relative progeny viability for the 1992 reproductive season. Relative estimates were computed by dividing seed production and mean progeny viability values for each plant by the mean value for the whole set of experimental plants. (Dashed lines at $y = 1$ and $x = 1$ thus denote the population mean values for the two variables.) The continuous line is the major axis regression fitted to the data ($y = 1.299 - 0.299x$).

mean seed mass was not significantly related to differences in either mean seedling emergence rate ($r = 0.076$, $N = 14$, $P = 0.80$), seedling hazards ratio ($r = 0.181$, $N = 14$, $P = 0.54$), or progeny viability ($r = -0.440$, $N = 14$, $P = 0.12$). Plants also differed significantly in their degree of variability in seed mass ($F_{13,1386} = 11.65$, $P \ll 0.0001$; Levene test for relative variability), but this variable (as measured with the coefficient of variation; range $= 17.6–33.2$) was not correlated with seedling emergence rate ($r = -0.268$, $N = 14$, $P = 0.35$), seedling hazards ratio ($r = -0.177$, $N = 14$, $P = 0.55$), or progeny viability ($r = -0.149$, $N = 14$, $P = 0.61$).

Seeds from plants producing larger seed crops were less likely to contribute an established juvenile to the population eventually, and this effect was independent of individual differences in mean seed size. For all sites combined, mean progeny viability was inversely related across plants to maternal fecundity (total number of seeds produced) ($r = -0.648$, $N = 14$, $P = 0.009$), and this negative correlation persisted after partialling it on mean seed mass (partial $r = -0.568$, $N = 14$, $P = 0.043$). The relationship is illustrated in Fig. 4 in terms of relative fecundity (RF) and relative viability (RV) estimates, obtained by dividing seed production and mean progeny viability for each maternal parent by the respective means for the whole set of plants.

Maternal differences in fecundity were about twice as important as differences in progeny viability in determining individual variation in juvenile recruitment to the population. Estimates of the relative contribution of juveniles (RCJ) to the population for the 1992 reproductive event were obtained for each maternal parent by multiplying seed production by mean progeny

viability, and then dividing the values obtained by the mean for the set of plants. The relative importance of RF and RV as determinants of individual differences in RCJ was then assessed using the standardized partial regression coefficients in a multiple regression of RCJ on RF and RV (fitted without intercept term). The coefficients (± 1 SE, determined by bootstrapping) for RF and RV were, respectively, 0.741 ± 0.082 and 0.366 ± 0.064.

DISCUSSION

Progeny viability and its components

Results of this study indicate that *L. latifolia* plants differ in the inherent capacity of their seeds to produce seedlings in the field. This agrees with earlier laboratory tests of germinability of seed progenies from the same maternal parents used here (seeds collected in 1991), which demonstrated significant individual differences (range of laboratory seedling emergence rates $= 0.45–0.98$ seedlings/seed; Herrera 2000; C. M. Herrera, *unpublished data*). Individual differences, however, did not remain consistent between the field and the laboratory. The correlation between field (1992) and laboratory (1991) values was weak and only marginally significant ($r = 0.481$, $N = 14$ plants, $P = 0.075$).

Maternal differences in seedling survivorship mainly originated from differential mortality during the first two summers after emergence. This was not unexpected, as the dry and hot summer characteristic of the Mediterranean climate represents a stressful period for perennial plants in general (e.g., Tenhunen et al. 1990, Duhme and Hinckley 1992). Similar seasonal patterns have been reported for other southern Spanish woody plants (*Phillyrea latifolia,* Herrera et al. 1994; *Lavandula stoechas,* J. Herrera 1997), the vast majority of whose seedlings died of desiccation during the first summer after emergence. Differential ability to withstand summer water stress most likely underlies observed differences between *L. latifolia* maternal parents in seedling survivorship. Some results of this study suggest, however, that the mechanisms involved are probably very complex. In contrast to seedling emergence rate, for which no Mother × Site interaction was found, variation among progenies in seedling survivorship was remarkably inconsistent among sites, with any given maternal progeny falling among either the best or the worst ones at surviving, depending on the site. This suggests that a number of distinct traits are possibly involved in the ability of seedlings to withstand summer (e.g., stomatal control, dehydration tolerance, leaf-pubescence levels, root-system development; Kramer 1983), the effectiveness of each of them being strongly context dependent.

Maternal variation in progeny viability has been assessed here over a six-year period. Despite this long duration, however, none of the surviving juveniles had

flowered for the first time by the end of the study. In the study region, *L. latifolia* plants generally reproduce for the first time at age 7–9 yr, and the life-span of individuals that reproduce at least once during their lifetime is 25–32 yr (C. M. Herrera, *unpublished data*). Precise estimates of progeny viability would thus have required a much longer study duration, and starting the study with an even larger number of seeds sown in order to end up with an acceptable number of survivors. One additional limitation of this study, also related to the extended life-span of *L. latifolia* plants, is that progeny viability and maternal fecundity estimates both refer to a single reproductive episode. There is evidence suggesting, however, that patterns of seed-to-juvenile viability documented in this study reflect patterns of viability up to the reproductive stage, at least for the particular seed cohort studied. First, the shape of the cumulative hazards curve for all progenies combined, and the survivor function estimates for the different progenies, both suggest that subsequent mortality would have been too low to alter substantially the patterns of survivorship established during the first two years after emergence. And second, there is no reason to suspect that maternal differences in the size of survivors could have subsequently cancelled or substantially altered the patterns of viability documented in this study, since survivor size and viability were unrelated across maternal progenies.

The finding that maternal differences in seed size were unrelated to differences in either progeny viability or any of its components contrasts sharply with many studies reporting important effects of within-population variation in seed mass on both germination levels and seedling vigor (e.g., Cideciyan and Malloch 1982, Howe and Richter 1982, Marshall 1986, Wulff 1986*b*, Mazer 1989, Biere 1991*a*, Herrera et al. 1994). Differences between *L. latifolia* plants in mean seed mass, although statistically significant, were quantitatively small, and only a minimal proportion of total variance was accounted for by maternal variation. Although many studies have documented substantial contributions of within-plant variation to total variance in individual seed mass, the value found here for this *L. latifolia* population (93.9%) probably represents one of the highest figures ever reported (e.g., Stanton 1984, Antonovics and Schmitt 1986, Mazer et al. 1986, Wulff 1986*a*, Hendrix and Sun 1989, Obeso and Herrera 1994). Given the small among-individual variance in seed mass, possible effects of this variable on maternal differences in progeny viability would likewise be small, and failure to detect them could simply be due to insufficient statistical power. In any case, however, results of this study for *L. latifolia* (see also Herrera 2000) should warn us of the risks of uncritically using differences in easily measured seed mass as a surrogate for maternal differences in offspring vigor or viability (see also Roach and Wulff 1987 for a similar conclusion).
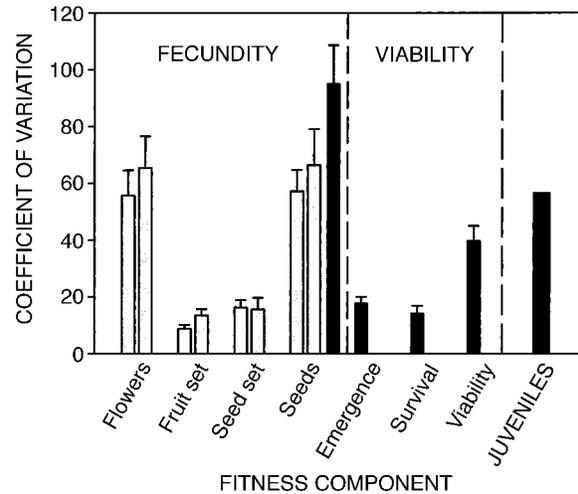

FIG. 5. Coefficient of variation of plant means (100 × SD/mean) for various fitness components of the *Lavandula latifolia* Aguaderillos population. Error bars are +1 SE, obtained by bootstrapping. Estimates represented with bars of the same shading refer to the same individual plants and reproductive seasons: gray bars, 1984 and 1986 (based on Herrera 1991; data for the two years are shown as two separate estimates for each component); solid bars, 1992 (present study). The estimate for ''Juveniles'' lacks a standard error because values for that parameter were estimated for each plant by multiplicatively combining seed production, seedling emergence, and seedling survival values, rather than actually measured. Variables shown and original measurement units are as follows: Flowers = total number of flowers produced; Fruit set = proportion of flowers setting fruit; Seed set = proportion of initial ovules setting seed in each fruit; Seeds = total number of seeds produced per plant; Emergence = probability of a seed producing a seedling when sown in the field; Survival = seedling hazards ratio (relative to plant no. 15); Viability = probability of one seed producing one juvenile; Juveniles = estimated number of juvenile plants contributed to the population per maternal parent.

Fecundity and viability

The inverse relationship across plants between fecundity and progeny viability found in this study emphasizes the need for considering both viability and fecundity effects in plant reproduction studies. For the *L. latifolia* population studied, maternal variation in seed production is mainly due to differences in the total number of flowers produced, while the influence of individual differences in fruit and seed set is negligible (Herrera 1991). This is because flower production is much more variable among plants than the other two components (Fig. 5), and because negative covariances across plants between fecundity-related fitness components (which could mitigate the overwhelming influence of variance in flower production) are unimportant (Herrera 1991: Table 5; see also Mazer 1989 for analogous results in *Raphanus raphanistrum*). As a consequence, individual variability in maternal fecundity is of roughly the same magnitude as variability in flower production (Fig. 5). The situation for variability in progeny viability is different. Variability in

progeny viability is well above the rather low variability levels of each of its two components (seedling survivorship and seedling emergence; Fig. 5), presumably because individual differences are enhanced by a positive covariance between these two components across individuals (Fig. 1B, C). In addition, the inverse relationship between seed production and progeny viability makes maternal variability in the number of juvenile plants contributed to the population to be much lower than would be expected from considerations based on fecundity alone.

These considerations lead to two important conclusions for the *L. latifolia* population studied, namely (1) knowledge of maternal differences in progeny viability is essential to understand differences among maternal parents in their contribution of juvenile plants to the population; and (2) maternal differences in progeny viability tell us more about individual variation in actual reproductive success (progeny recruited) than differences in such popular parameters as fruit or seed set. The lack of comparable studies precludes any assessment of the generality of these results, although other investigations likewise point to the importance of viability effects under natural conditions. In a field study of *Gilia achilleifolia,* Schoen (1983) found that differences in seedling survivorship accounted for most differences in the net reproductive rate of plants differing in the number of generations of selfing. Waser and Price (1989), in their long-term field study of the effects of outcrossing distance on reproductive success of *Ipomopsis aggregata,* found that offspring viability was more strongly affected by outcrossing distance than seed set.

The inverse relationship across *L. latifolia* plants between fecundity and mean progeny viability seems to represent the first field-documented instance of a trade-off between progeny number and progeny quality independent of seed size. Aarssen and Clauss (1992) found a negative relationship between seed production and percent germination for some genotypes of *Arabidopsis thaliana,* but tests were done in growth chambers and individual differences in seed size apparently were not accounted for. I hypothesize that the relationship found here between progeny viability and fecundity actually reflects an inverse relationship between progeny viability and flower number, mediated by differential proportions of self and cross pollinations of plants differing in flower number. Although *L. latifolia* is self-compatible, outcross pollination results in greater fruit and seed set relative to self pollination (Herrera 1987a; C. M. Herrera, *unpublished data*), and pollination regimes increasing the frequency of cross pollinations lead to more numerous and more viable progeny (Herrera 2000). The results of numerous studies (e.g., Hessing 1988, De Jong et al. 1992, 1993, Robertson 1992, Barrett et al. 1994, Harder and Barrett 1995, Snow et al. 1996, Rademaker and de Jong 1998), suggest that the proportion of geitonogamous pollinations will increase with the number of simultaneously open flowers on *L. latifolia* plants. As individual variation in total flower production during the whole flowering period and daily flower number are closely correlated in this species (C. M. Herrera, *unpublished data*), one would expect mean levels of inbreeding depression in seed progenies to increase with flower production, thus ultimately leading to the negative relationship between progeny viability and seed production found here. Under this hypothesis, the fecundity–viability trade-off found in *L. latifolia* would thus be an example of the "dilemma of geitonogamous pollination" (Hessing 1988), wherein increases in fitness derived from flower production are partly compensated by decreased fitness of individual offspring.

Concluding remarks

Focusing on individual differences in progeny viability, and doing it using a long-term, field-based perspective, as was done here, is an unusual methodological combination in evolutionary ecological studies of plant reproduction, most of which are conducted under artificial conditions and over relatively short periods. As an illustrative example, consider Husband and Schemske's (1996) review of patterns of inbreeding depression in plants. Because of the extreme scarcity of field investigations, these authors had to confine their review to studies performed in greenhouse or other artificial conditions, and even these suffered from a shortage of data on progeny survivorship because of the prevalence of short-term studies. The short duration of most investigations on patterns and processes involved in the recruitment of plant populations has been recently documented by Clark et al. (1999). The important discrepancies frequently found between results of studies conducted in the field and under artificial conditions, and between short- and long-term investigations, have recurrently led some authors to call attention to the decisive importance of conducting studies of sufficient duration in the field for obtaining biologically realistic information on the occurrence and actual importance of a variety of processes directly influential on the evolution of plant reproduction (Waser and Price 1989, Montalvo 1994, Herrera 1998, 2000, Ramsey and Vaughton 1998, Clark et al. 1999). Based on the results of the present investigation, I would further add that explicit consideration of variation in progeny viability over a range of *natural* environments is one further essential element if reasonable degrees of ecological realism and evolutionary perspective are to be achieved.

Differences among individuals within a single population are evolutionarily relevant because they are the raw material on which natural selection acts, as emphasized in the *Introduction,* but also because variation itself may be the end product of natural selection (Wilson 1998), an aspect that has received little, if any, consideration by plant evolutionary ecologists. On the

other hand, inconsistency among genotypes in their response to environmental factors (i.e., parent × environment interactions), have been documented for a variety of fitness components whenever some effort has been made to look for them (e.g., Heywood and Levin 1984, Schmitt and Antonovics 1986, Biere et al. 1989, Biere 1991b, Delesalle and Blum 1994, Stratton 1995, Stratton and Bennington 1998). Consideration of a broad range of conditions thus seems an essential requisite for any realistic assessment of individual differences and their importance. This is clearly supported by the strong parent × environment interactions for long-term seedling survivorship found in this study. As there are no comparable data available, it is not possible to know whether this extreme context dependence is a characteristic of *L. latifolia* or of the life stage involved, but the finding serves at least to emphasize the importance of testing individual differences in progeny viability across a range of environments encompassing the conditions naturally faced by the species.

Some of the acknowledged limitations of this investigation (e.g., the fact that none of the juveniles had still reproduced by the end of the study) were ultimately related to the small number of eventual survivors, and its extremely unbalanced final distribution among sites and maternal parents. These limitations occurred in spite of having initially sown some 25000 seeds, and exemplify the "frustrations [that] await those attempting to measure fitness of perennial plants in nature" (Waser and Price 1989:1107). Although the limitations of this study restrict the interpretations of its results, they do not detract from the value of attempting to gather information on plants other than short-lived species and conducting long-term studies in the field that can "illuminate the real variability experienced by organisms on a microevolutionary time scale" (Waser and Price 1989:1107).

LITERATURE CITED

Aarssen, L. W., and M. J. Clauss. 1992. Genotypic variation in fecundity allocation in *Arabidopsis thaliana.* Journal of Ecology **80**:109–114.
Aarssen, L. W., and D. R. Taylor. 1992. Fecundity allocation in herbaceous plants. Oikos **65**:225–232.
Allison, P. D. 1995. Survival analysis using the SAS System. A practical guide. SAS Institute, Cary, North Carolina, USA.
Antonovics, J., and J. Schmitt. 1986. Paternal and maternal effects on propagule size in *Anthoxanthum odoratum.* Oecologia (Berlin) **69**:277–282.
Arnold, S. J., and M. J. Wade. 1984. On the measurement of natural and sexual selection: theory. Evolution **38**:709–719.
Barrett, S. C. H., L. D. Harder, and W. W. Cole. 1994. Effects of flower number and position on self-fertilization in experimental populations of *Eichhornia paniculata* (Pontederiaceae). Functional Ecology **8**:526–535.
Biere, A. 1991a. Parental effects in *Lychnis flos-cuculi.* I: Seed size, germination and seedling performance in a controlled environment. Journal of Evolutionary Biology **3**:447–465.
Biere, A. 1991b. Parental effects in *Lychnis flos-cuculi.* II: Selection on time of emergence and seedling performance in the field. Journal of Evolutionary Biology **3**:467–486.
Biere, A., R. Cappers, and V. Van Andel. 1989. Quantitative and qualitative aspects of fecundity in *Lychnis flos-cuculi.* Acta Botanica Neerlandica **38**:203–218.
Brodie, E. D., A. J. Moore, and F. J. Janzen. 1995. Visualizing and quantifying natural selection. Trends in Ecology and Evolution **10**:313–318.
Campbell, D. R. 1997. Genetic and environmental variation in life-history traits of a monocarpic perennial: a decade-long field experiment. Evolution **51**:373–382.
Cideciyan, M. A., and A. J. C. Malloch. 1982. Effects of seed size on the germination, growth and competitive ability of *Rumex crispus* and *Rumex obtusifolius.* Journal of Ecology **70**:227–232.
Clark, J. S., B. Beckage, P. Camill, B. Cleveland, J. Hillerislambers, J. Lichter, J. McLachlan, J. Mohan, and P. Wyckoff. 1999. Interpreting recruitment limitation in forests. American Journal of Botany **86**:1–16.
Culley, T. M., S. G. Weller, A. K. Sakai, and A. E. Rankin. 1999. Inbreeding depression and selfing rates in a self-compatible, hermaphroditic species, *Schiedea membranacea* (Caryophyllaceae). American Journal of Botany **86**:980–987.
De Jong, T. J., N. M. Waser, and P. G. L. Klinkhamer. 1993. Geitonogamy: the neglected side of selfing. Trends in Ecology and Evolution **8**:321–325.
De Jong, T. J., N. M. Waser, M. V. Price, and R. M. Ring. 1992. Plant size, geitonogamy and seed set in *Ipomopsis aggregata.* Oecologia (Berlin) **89**:310–315.
Delesalle, V. A., and S. Blum. 1994. Variation in germination and survival among families of *Sagittaria latifolia* in response to salinity and temperature. International Journal of Plant Science **155**:187–195.
Dudash, M. R. 1990. Relative fitness of selfed and outcrossed progeny in a self-compatible, protandrous species, *Sabatia angularis* L. (Gentianaceae): a comparison in three environments. Evolution **44**:1129–1139.
Duhme, F., and T. M. Hinckley. 1992. Daily and seasonal variation in water relations of macchia shrubs and trees in France (Montpellier) and Turkey (Antalya). Vegetatio **100**:185–198.
Eckert, C. G., and S. C. H. Barrett. 1994. Inbreeding depression in partially self-fertilizing *Decodon verticillatus* (Lythraceae): population-genetic and experimental analyses. Evolution **48**:952–964.
Endler, J. A. 1986. Natural selection in the wild. Princeton University Press, Princeton, New Jersey, USA.
Falconer, D. S. 1989. Introduction to quantitative genetics. Third edition. Longman, Harlow, UK.
Fox, G. A. 1993. Failure-time analysis: emergence, flowering, survivorship, and other waiting times. Pages 253–289 *in* S. M. Scheiner and J. Gurevitch, editors. Design and analysis of ecological experiments. Chapman and Hall, New York, New York, USA.

Harder, L. D., and S. C. H. Barrett. 1995. Mating cost of large floral displays in hermaphrodite plants. Nature **373**: 512–515.

Helenurm, K., and B. A. Schaal. 1996. Genetic and maternal effects on offspring fitness in *Lupinus texensis* (Fabaceae). American Journal of Botany **83**:1596–1608.

Hendrix, S. D., and I. F. Sun. 1989. Inter- and intraspecific variation in seed mass in seven species of umbellifer. New Phytologist **112**:445–451.

Herrera, C. M. 1987*a*. Components of pollinator ''quality'': comparative analysis of a diverse insect assemblage. Oikos **50**:79–90.

Herrera, C. M. 1987*b*. Componentes del flujo génico en *Lavandula latifolia* Medicus:polinización y dispersión de semillas. Anales del Jardín Botánico de Madrid **44**:49–61.

Herrera, C. M. 1988. Variation in mutualisms: the spatiotemporal mosaic of an insect pollinator assemblage. Biological Journal of the Linnean Society **35**:95–125.

Herrera, C. M. 1989. Pollinator abundance, morphology, and flower visitation rate:analysis of the ''quantity'' component in a plant-pollinator system. Oecologia (Berlin) **80**:241–248.

Herrera, C. M. 1991. Dissecting factors responsible for individual variation in plant fecundity. Ecology **72**:1439–1448.

Herrera, C. M. 1995. Microclimate and individual variation in pollinators: flowering plants are more than their flowers. Ecology **76**:1516–1524.

Herrera, C. M. 1997. Thermal biology and foraging responses of insect pollinators to the forest floor irradiance mosaic. Oikos **78**:601–611.

Herrera, C. M. 1998. Long-term dynamics of Mediterranean frugivorous birds and fleshy fruits: a 12-yr study. Ecological Monographs **68**:511–538.

Herrera, C. M. 2000. Flower-to-seedling consequences of different pollination regimes in an insect-pollinated shrub. Ecology **81**:15–29.

Herrera, C. M., P. Jordano, L. López-Soria, and J. A. Amat. 1994. Recruitment of a mast-fruiting, bird-dispersed tree: bridging frugivore activity and seedling establishment. Ecological Monographs **64**:315–344.

Herrera, J. 1997. Effects of disturbance on the reproductive potential of *Lavandula stoechas,* a Mediterranean sclerophyllous shrub. Ecography **20**:88–95.

Hessing, M. B. 1988. Geitonogamous pollination and its consequences in *Geranium caespitosum.* American Journal of Botany **75**:1324–1333.

Heywood, J. S., and D. A. Levin. 1984. Genotype–environment interactions in determining fitness in dense, artificial populations of *Phlox drummondii*. Oecologia (Berlin) **61**: 363–371.

Howe, H. F., and W. M. Richter. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. Oecologia (Berlin) **53**:347–351.

Husband, B. C., and J. E. Gurney. 1998. Offspring fitness and parental effects as a function of inbreeding in *Epilobium angustifolium* (Onagraceae). Heredity **80**:173–179.

Husband, B. C., and D. W. Schemske. 1996. Evolution of the magnitude and timing of inbreeding depression in plants. Evolution **50**:54–70.

Janzen, D. H. 1978. Seeding patterns of tropical trees. Pages 83–128 *in* P. B. Tomlinson and M. H. Zimmermann, editors. Tropical trees as living systems. Cambridge University Press, Cambridge, UK.

Kalisz, S. 1986. Variable selection on the timing of germination in *Collinsia verna* (Scrophulariaceae). Evolution **40**: 479–491.

Koelewijn, H. P. 1998. Effects of different levels of inbreeding on progeny fitness in *Plantago coronopus*. Evolution **52**:692–702.

Kramer, P. J. 1983. Water relations of plants. Academic Press, Orlando, Florida, USA.

Levin, D. A. 1991. The effect of inbreeding on seed survivorship in *Phlox*. Evolution **45**:1047–1049.

Luque, P. 1995. Mapa de vegetación del Parque Natural de las Sierras de Cazorla, Segura y Las Villas. Agencia de Medio Ambiente, Junta de Andalucía, Sevilla, Spain.

Marshall, D. L. 1986. Effect of seed size on seedling success in three species of *Sesbania* (Fabaceae). American Journal of Botany **73**:457–464.

Mazer, S. J. 1989. Family mean correlations among fitness components in wild radish: controlling for maternal effects on seed weight. Canadian Journal of Botany **67**:1890–1897.

Mazer, S. J., and D. L. Gorchov. 1996. Parental effects on progeny phenotype in plants: distinguishing genetic and environmental causes. Evolution **50**:44–53.

Mazer, S. J., A. A. Snow, and M. L. Stanton. 1986. Fertilization dynamics and parental effects upon fruit development in *Raphanus raphanistrum*:consequences for seed size variation. American Journal of Botany **73**:500–511.

Mitchell-Olds, T., and D. M. Waller. 1985. Relative performance of selfed and outcrossed progeny in *Impatiens capensis*. Evolution **39**:533–544.

Montalvo, A. M. 1994. Inbreeding depression and maternal effects in *Aquilegia caerulea,* a partially selfing plant. Ecology **75**:2395–2409.

Norman, J. K., A. K. Sakai, S. G. Weller, and T. E. Dawson. 1995. Inbreeding depression in morphological and physiological traits of *Schiedea lydgatei* (Caryophyllaceae) in two environments. Evolution **49**:297–306.

Obeso, J. R., and C. M. Herrera. 1994. Inter- and intraspecific variation in fruit traits in co-occurring vertebrate-dispersed plants. International Journal of Plant Sciences **155**:382–387.

Rademaker, M. C. J., and T. J. de Jong. 1998. Effects of flower number on estimated pollen transfer in natural populations of three hermaphroditic species: an experiment with fluorescent dye. Journal of Evolutionary Biology **11**: 623–641.

Ramsey, M., and G. Vaughton. 1998. Effect of environment on the magnitude of inbreeding depression in seed germination in a partially self-fertile perennial herb (*Blandfordia grandiflora,* Liliaceae). International Journal of Plant Sciences **159**:98–104.

Roach, D. A., and R. D. Wulff. 1987. Maternal effects in plants. Annual Review of Ecology and Systematics **18**: 209–235.

Robertson, A. W. 1992. The relationship between floral display size, pollen carryover and geitonogamy in *Myosotis colensoi* (Kirk) Macbride (Boraginaceae). Biological Journal of the Linnean Society **46**:333–349.

Sakai, A. K., S. G. Weller, M. L. Chen, S. Y. Chou, and C. Tasanont. 1997. Evolution of gynodioecy and maintenance of females: the role of inbreeding depression, outcrossing rates, and resource allocation in *Schiedea adamantis* (Caryophyllaceae). Evolution **51**:724–736.

SAS Institute. 1990*a*. SAS/STAT user's guide. Version 6. Fourth edition. SAS Institute, Cary, North Carolina, USA.

SAS Institute. 1990*b*. SAS Guide to macro processing. Version 6. Second edition. SAS Institute, Cary, North Carolina, USA.

SAS Institute. 1996. SAS/STAT software: changes and enhancements through Release 6.11. SAS Institute, Cary, North Carolina, USA.

Scheiner, S. M. 1987. Size and fecundity hierarchies in an herbaceous perennial. Oecologia (Berlin) **74**:128–132.

Schmitt, J., and J. Antonovics. 1986. Experimental studies of the evolutionary significance of sexual reproduction. III. Maternal and paternal effects during seedling establishment. Evolution **40**:817–829.

Schoen, D. J. 1983. Relative fitnesses of selfed and outcrossed progeny in *Gilia achilleifolia* (Polemoniaceae). Evolution **37**:292–301.

Shykoff, J. A. 1988. Maintenance of gynodioecy in *Silene acaulis* (Caryophyllaceae): stage-specific fecundity and viability selection. American Journal of Botany **75**:844–850.

Snow, A. A., T. P. Spira, R. Simpson, and R. A. Klips. 1996. The ecology of geitonogamous pollination. Pages 191–216 *in* D. G. Lloyd and S. C. H. Barrett, editors. Floral biology. Studies on floral evolution in animal-pollinated plants. Chapman and Hall, New York, New York, USA.

Solbrig, O. T., and D. J. Solbrig. 1984. Size inequalities and fitness in plant populations. Oxford Surveys in Evolutionary Biology **1**:141–159.

Stanton, M. L. 1984. Developmental and genetic sources of seed weight variation in *Raphanus raphanistrum* L. (Brassicaceae). American Journal of Botany **71**:1090–1098.

Stewart, S. C., and D. J. Schoen. 1987. Pattern of phenotypic viability and fecundity selection in a natural population of *Impatiens pallida.* Evolution **41**:1290–1301.

Stratton, D. A. 1995. Spatial scale of variation in fitness of *Erigeron annuus.* American Naturalist **146**:608–624.

Stratton, D. A., and C. C. Bennington. 1998. Fine-grained spatial and temporal variation in selection does not maintain genetic variation in *Erigeron annuus.* Evolution **52**:678–691.

Tenhunen, J. D., A. Sala Serra, P. C. Harley, and R. L. Dougherty. 1990. Factors influencing carbon fixation and water use by mediterranean sclerophyll shrubs during summer drought. Oecologia (Berlin) **82**:381–393.

Thompson, J. N. 1985. Postdispersal seed predation in *Lomatium* spp. (Umbelliferae): variation among individuals and species. Ecology **66**:1608–1616.

Van Andel, J., R. A. Wesselingh, and H. J. Van Donk. 1988. The performance of progeny groups from two populations of *Phyteuma nigrum,* with particular reference to the chance of survival or extinction. Acta Botanica Neerlandica **37**:165–169.

Waser, N. M., and M. V. Price. 1989. Optimal outcrossing in *Ipomopsis aggregata*: seed set and offspring fitness. Evolution **43**:1097–1109.

Weller, S. G. 1985. The life history of *Lithospermum caroliniense,* a long-lived herbaceous sand dune species. Ecological Monographs **55**:49–67.

Wilson, D. S. 1998. Adaptive individual differences within single populations. Philosophical Transactions of the Royal Society, London B **353**:199–205.

Wulff, R. D. 1986*a.* Seed size variation in *Desmodium paniculatum.* I. Factors affecting seed size. Journal of Ecology **74**:87–97.

Wulff, R. D. 1986*b.* Seed size variation in *Desmodium paniculatum.* II. Effects on seedling growth and physiological performance. Journal of Ecology **74**:99–114.