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REPRODUCTIVE HIERARCHIES IN *ERODIUM*: EFFECTS OF VARIATION IN PLANT DENSITY AND RAINFALL DISTRIBUTION[1]

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Abstract. Reproductive hierarchies in even-aged plant monocultures often reflect the dynamics of intraspecific competition and, by their influence on effective population number, can alter significantly the relative importance of genetic drift in the evolution of plant populations. In experimental populations of *Erodium botrys* and *E. brachycarpum,* I examined the interactive effects of intraspecific competition and rainfall variability on the development of reproductive hierarchies in these annual species. Reproductive inequality within monocultures of both species increased with increasing plant density and plant productivity. Plant productivity, as measured by seed production, was determined by rainfall distribution. The magnitude of reproductive inequality was dependent on the interaction of sowing density and rainfall distribution. At the highest sowing density, reproductive inequality was greatest in populations that experienced early autumn precipitation and lowest in populations exposed to drought during flowering. In contrast, at the lowest sowing density there was no significant effect of rainfall pattern on reproductive inequality. Effective population number was relatively insensitive to increases in population density because of increased inequality in reproduction at higher population densities. Reproductive variance could be a major contributor to drift variance in dense populations of both *Erodium* species.

Key words: annual; coefficient of variation; drought; effective population number; Erodium; *fecundity distribution; genetic drift; intraspecific competition; N_e; population structure; reproductive hierarchies; size inequality.*

INTRODUCTION

In even-aged plant monocultures, pronounced hierarchies of size and reproduction often develop with a large number of small, low fecundity individuals and a few, very large plants that contribute the majority of offspring to the next generation (Obeid et al. 1967, White and Harper 1970, Gottlieb 1977, Solbrig 1981, Weiner 1985). Although most studies to date have emphasized ecological aspects of size hierarchies, a few investigators have examined the evolutionary implications of reproductive inequality (Gottlieb 1977, Levin 1978, Heywood 1986).

In a study focusing on the potential genetic basis for size hierarchies in populations of the annual *Stephanomeria exigua* ssp. *coronaria,* Gottlieb (1977) found no genotypic differences between large and small individuals. He pointed out that large variation in annual plant fecundity, caused by plastic growth responses to environmental conditions, can significantly reduce effective population number (N_e). As N_e decreases, genetic drift may become a primary evolutionary force for genetic change within populations (Wright 1931, Kimura and Crow 1963, Crow and Kimura 1970, Levin 1978). Heywood (1986) examined the potential impact of reproductive hierarchies on genetic drift in annual plant populations by calculating the contribution of variation in potential adult fecundity to drift variance. His analysis of data from several annual plant species indicated that fecundity variation among the reproductive plants in a population often accounts for the majority of the drift variance.

In addition to the recent interest in the evolutionary aspects of size and reproductive hierarchies, a growing number of studies have focused on the relative importance of intraspecific competition in the development of plant size variation (Weiner 1988). Harper (1977) proposed that development of size and reproductive hierarchies result from a "hierarchy of exploitation" or "asymmetric" competition (Begon 1984) wherein larger individuals within the population acquire resources "at the expense" of smaller, suppressed individuals. In contrast, early theoretical studies (Koyama and Kira 1956) indicated that variation in relative growth rate alone might be sufficient to create size hierarchies within even-aged monocultures. More recent individual-plant growth models indicate that the development of size hierarchies may depend on a complex interaction of growth rate, spatial distribution of individuals, and the degree to which competition is symmetric or asymmetric (Bonan 1988).

The present study examined the interactive influence of plant density and rainfall patterns on reproductive hierarchies in the introduced annual species *Erodium botrys* (Cav.) Bertol. and *E. brachycarpum* (Godr.) Thell. (Geraniaceae). Previous studies on the population bi-

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ology of both *Erodium* species indicate that both environmental and genetic factors contribute to observed variation in size and reproduction among individuals (Rice 1985, 1987*a, b*). I assessed the potential importance of intraspecific competition in the development of reproductive inequality in *Erodium* populations by growing populations at different densities. By simulating three different rainfall distribution patterns, I also was able to explore how year-to-year variation in the physical growth environment might alter *Erodium* reproductive structure. The degree to which reproductive inequality in these populations might reduce variance effective population number (N_e) was estimated by calculating the contribution of fecundity variance to the overall variance associated with genetic drift.

Methods

Seeds of *Erodium botrys* and *E. brachycarpum* were collected from four annual grassland sites (Beasley Flat, Lambing Pasture, Orchard Pasture, and Buck Pasture) at the University of California Hopland Field Station, Mendocino County, California. Seeds from the different populations were pooled for each species and mechanically scarified to break dormancy caused by seed coat impermeability to water (Rice 1985). In conjunction with a study on interspecific competition in *Erodium* (Rice and Menke 1985), I established experimental *Erodium* populations in 12 large (60 × 60 × 60 cm) plywood soil containers. Soil within the containers was a fine-loamy, mixed, mesic Ultic Haploxeroll obtained from the Buck Pasture seed collection site. To preserve gross structural characteristics of the profile, the soil was placed into the containers in 15-cm layers. Soil moisture within the containers was monitored with calibrated gypsum resistance blocks buried at depths of 9, 20, and 40 cm. Initially, the soil within the containers was covered by litter remaining from annual grassland sods transplanted to the containers during previous experiments. To prepare nine sowing plots (each 10 × 10 cm) within each container, blocks of soil (10 cm square by 5 cm deep) were removed, broken up by hand, and autoclaved to kill any resident seeds. This disaggregated soil, when placed back into the holes from which it had been taken, reasonably simulated natural soil disturbances that are often sites for *Erodium* colonization (Rice 1985, 1987*b*). Plots were separated by 10-cm buffer strips of undisturbed sod. Upon germination, these buffer strips were dominated by the annual grasses *Bromus mollis* L. and *Avena barbata* Brot.

To vary rainfall distribution, the soil containers were placed outdoors under an open-sided, clear plastic rain shelter (3 × 6 m) at the University of California, Davis, Yolo County, California. Although light quality was not altered by the shelter, light intensity was reduced by 20–25%. Outside temperatures did not differ significantly (maximum observed difference = 3°C) from those measured under the shelter. Four soil containers, providing a combined total of 36 sowing plots, were randomly selected for each of three watering treatments that simulated qualitatively different rainfall regimes: early germination, drought at anthesis, and no drought. Seeds were sown into all containers on 20 September 1980 (well before the onset of winter rains in early December). At this time the four soil containers within the "early germination" treatment were watered with the equivalent of 5 cm of rainfall to initiate germination. With the onset of winter rains in December, all 12 containers received 5 cm of water, and the rain shelter was removed. To simulate a year with low spring rainfall, the "drought at anthesis" treatment containers were recovered with the rain shelter on 1 March 1981.

Monocultures of each *Erodium* species were sown in 18 randomly selected plots distributed among the four containers within each watering treatment. As part of a separate study on interspecific competition in *Erodium* (Rice and Menke 1985), mixtures of the two species were sown in the remaining 18 plots of each watering treatment. The monocultures of both species were sown in 10 × 10 cm plots in a square grid pattern at 16, 36, and 64 seeds/dm^2. Previous observations at the Hopland Field Station (Heady 1958, Bartolome 1979) indicate that the above sowing densities encompass the usual range of field densities for *Erodium* seedlings. For each species there were three replicates of each density within each rainfall regime. Beginning in March, *Erodium* reproduction within the populations was censused weekly until seed production ended in May. An elongated style column, a structural component of the schizocarp, persists on the plant after seed (mericarp) dispersal. The number of style columns was used to estimate seed output per plant because normal seed set in both species is five seeds per schizocarp. I also was able to estimate rates of seed abortion because aborted seeds usually remain attached to the style column (Rice 1985).

To estimate reproductive hierarchies within the experimental populations, I used the coefficient of variation (CV) and unbiased Gini coefficient (Weiner 1985). Both statistics estimate the degree of inequality within a reproductive or size hierarchy and often are highly correlated (Weiner and Thomas 1986). The SAS General Linear Model procedure (Freund et al. 1986) was used to analyze treatment effects on statistics describing fecundity distributions (e.g., mean, variance, and CV). Mean and variance data were log transformed before analysis to eliminate heterogeneity of variances. Differences among treatment means were analyzed using the Student-Newman-Keuls multiple range procedure.

The ratio of variance-effective population number to actual population number at reproduction (i.e., N_e/N) is related directly to the CV of the reproductive distribution within the population (Heywood 1986). For each replicate, an estimate of N_e/N was calculated

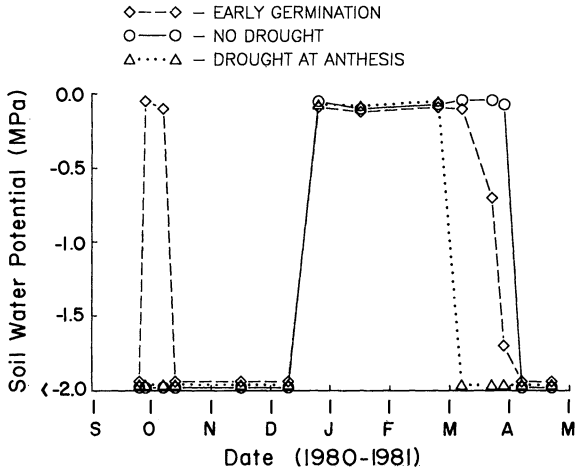

FIG. 1. Seasonal changes in soil water potential for the three rainfall regimes. Values are averages from measurements taken at 9, 20, and 40 cm soil depths. Redrawn from Rice and Menke (1985).

using the following equation provided by Heywood (1986):

$$N_e/N = 1/[(1 + F)(s_b^2/z_b^2) + 1],$$

where z_b and s_b^2 are the mean and variance of the frequency distribution of seed production among adults, and F is the fixation index measuring deviations from Hardy-Weinberg frequencies among adults. My calculations assumed a fixation index value of 1 because electrophoretic data suggest that both *Erodium* species are highly selfing (S. J. Novak, *personal communication*).

RESULTS

Changes in soil moisture within the soil containers indicated distinct differences among the rainfall regimes in the seasonal availability of soil water (Fig. 1). Recharge and depletion rates of soil moisture within the containers reasonably simulated rates measured in the field at Beasley Flat (Rice 1987*a*). During March and April, depletion of soil moisture within the "early germination" treatment occurred much earlier than in the "no drought" treatment, despite exposure to identical rainfall regimes since the previous October.

Average pre-reproductive mortality was <5% in the low density (16 seeds/dm^2) and moderate density (36 seeds/dm^2) populations. Mortality was slightly higher but still low (<10%) in high density (64 seeds/dm^2) populations.

Seed production was significantly higher in *E. brachycarpum* (mean ± 1 SE = 31.5 ± 5.6 seeds) than in *E. botrys* (17.5 ± 3.5 seeds), but species did not respond differently to rainfall or density treatments (i.e., no significant interactions involving species in Table 1A). However, there were significant interactive effects of density and rainfall treatment on seed number per plant (Table 1A); changes in density had a signif-

TABLE 1. Analysis of variance of the interactive effects of species identity, sowing density, and rainfall treatment on the average, variance, and CV of seed production per plant in *Erodium*. Data on average seed production and the variance in seed production were log transformed before analysis.

Source of variation	df	Mean square	*F*	*P*
A. Average number of seeds per plant				
Species	1	6.1855	80.02	.0001
Density	1	25.5760	330.86	.0001
Rain	2	3.0580	39.56	.0001
Species × density	1	0.0698	0.90	.3473
Species × rain	2	0.0938	1.21	.3071
Density × rain	2	0.4991	6.46	.0036
Species × density × rain	2	0.0317	0.41	.6660
Error	42	0.0773		
B. Variance in number of seeds per plant				
Species	1	17.4785	32.72	.0001
Density	1	12.8347	24.03	.0001
Rain	2	29.5189	54.26	.0001
Species × density	1	4.4511	8.33	.0061
Species × rain	2	0.9385	1.76	.1850
Density × rain	2	0.4706	0.88	.4219
Species × density × rain	2	0.0531	0.10	.9056
Error	42	0.5342		
C. Coefficient of variation for seeds per plant				
Species	1	2.34	0.01	.9061
Density	1	47 859.58	287.97	.0001
Rain	2	6891.80	41.47	.0001
Species × density	1	2214.17	13.32	.0007
Species × rain	2	252.11	1.52	.2312
Density × rain	2	3706.91	22.30	.0001
Species × density × rain	2	229.22	1.38	.2629
Error	42	166.19		

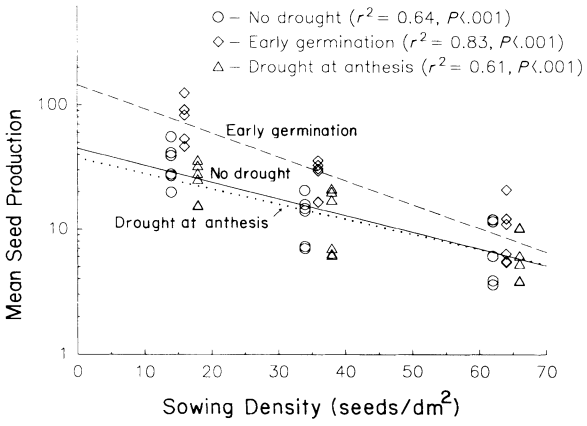

FIG. 2. Influence of sowing density on mean seed production per plant in *Erodium* populations experiencing different rainfall distribution patterns.

icantly stronger effect on seed production in the "early germination" treatment than in the "no drought" or "drought at anthesis" treatments (Fig. 2; ANCOVA, $P < .01$). Density responses of the "no drought" and "drought at anthesis" treatments were not significantly different from each other (ANCOVA, $P > .50$). Considering main effects alone, an overall decrease in seed production per plant with increasing density suggests that competition increased with density (Fig. 2, Table 1A). In addition, the significant main effect of rainfall distribution indicates that overall plant productivity, as measured by seed production, was higher in the "early germination" treatment (Fig. 2, Table 1A).

Variance in *Erodium* seed production per plant, averaged across both density and species, differed significantly among rainfall treatments (Table 1B). Reproductive variance in the "no drought" treatment (113.7 ± 32.0) was intermediate between high variance in early germinating populations (642.8 ± 125.1) and relatively low variance in plants exposed to drought during flowering (67.1 ± 17.7). Species identity and density had an interactive effect on reproductive variance (Table 1B, Fig. 3); reproductive variance in *E. botrys* populations decreased (ANCOVA, $P < .01$) with increasing density, while variance in *E. brachycarpum* did not respond significantly to changes in density.

Reproductive hierarchies as measured by the CV of seed output were affected by interactions of density with species identity and density with rainfall treatment (Table 1C). In the species × density interaction (Fig. 4A), there was significant crossing interaction so that reproductive hierarchies were more pronounced in *E. botrys* at low density while hierarchies in *E. brachycarpum* were more developed at high density. Averaged across species, the density response differed among rainfall treatments (Fig. 4B); increases in reproductive hierarchy with density were larger in *Erodium* populations germinating early (ANCOVA, $P < .001$). There was also an indication that reproductive hierarchies in the "no drought" treatment responded more strongly to increasing density than populations exposed to drought during flowering (ANCOVA, $P = .06$).

Although the Gini coefficients calculated from the experimental populations were not analyzed parametrically, Spearman rank correlations were calculated between population CVs and Gini coefficients. Similar to results reported by Weiner and Thomas (1986), there was a strong positive correlation ($r_s = 0.95$; $P < .001$) between the CV and the Gini coefficient.

Using CV values of reproductive distributions, I calculated the ratio between effective population number (N_e) and an idealized population (N), in which gamete production among members is equal, for each of the experimental populations. The range of values of N_e/N were 0.20–0.83 for *E. botrys* and 0.15–0.84 for *E. brachycarpum*.

DISCUSSION

The overall decrease in *Erodium* reproduction with increasing sowing density suggests that, under all rainfall regimes, the intensity of competition increased with plant density. While a negative relationship between individual reproduction and density indicates that competition is occurring, corresponding changes in the reproductive hierarchy of the population provide further insight into the competitive process. Resource preemption models of competition based on asymmetric or one-sided interactions predict that, for a specified period of growth, size inequality should increase with density (Weiner and Thomas 1986). This prediction is based on the assumption that the hypothesized asymmetric interactions of pre-emptive competition begin sooner within higher density populations. In contrast, symmetric or two-sided resource depletion competition models developed by Weiner and Thomas (1986) predict that size inequality should either decrease or stay the same with increasing density. Weiner (1986) further argues that competition for light is inherently asymmetric while competition for belowground re-

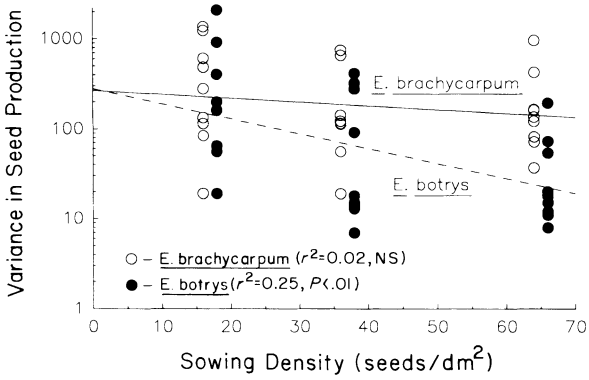

FIG. 3. Differences between *Erodium brachycarpum* and *E. botrys* in the response of variance in seed production per plant to changes in sowing density.

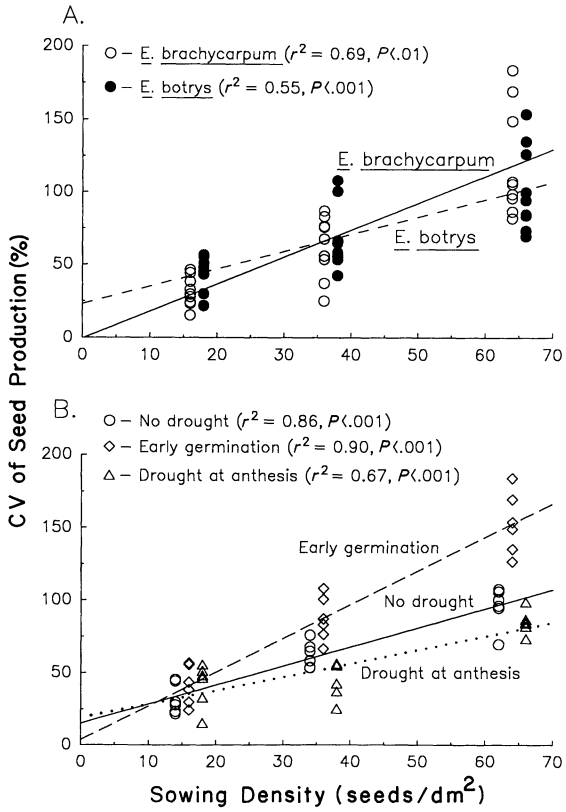

FIG. 4. (A) Effect of sowing density on the development of reproductive hierarchies (CV of seed output per plant) in *Erodium brachycarpum* and *E. botrys*. (B) Effect of sowing density on the development of reproductive hierarchies in *Erodium* populations experiencing various rainfall patterns.

sources, such as water and nutrients, may be more symmetric. However, recent modeling efforts by Miller and Weiner (1989) indicate that the conclusions of Weiner and Thomas (1986) hold only under uniform spatial distribution of individuals within a population. In populations with nonuniform spatial arrangement, increases in size inequality with density could occur even if competition was completely symmetric (Miller and Weiner 1989). Although the results reported here cannot directly measure the relative importance of shoot and root competition, the observed increase in *Erodium* reproductive inequality with density probably reflects asymmetric competitive interactions because the experimental populations were planted in a uniform pattern. The interactive effects of species identity and sowing density on reproductive hierarchies also suggest that there may be interspecific differences in *Erodium* in the relative intensity of asymmetric competition. The causes for this interspecific difference are unclear, however, because both species are very similar in morphology and growth rates (Rice 1984).

In addition to density effects, the growth environment of the *Erodium* populations under the different rainfall regimes had significant effects on reproductive inequality. The higher mean seed output overall in the "early germination" treatment suggests that the potential productivity within this treatment was greater than in the "no drought" and "drought at anthesis" treatments. Within the "early germination" treatment, this higher productivity may have resulted from a combination of increased time for growth and warmer growing conditions during seedling development. For both symmetric and asymmetric competitive interactions, models predict that size inequality should be greater in more fertile or productive environments (Weiner 1985). For asymmetric competition, however, greater size inequality in more productive environments should be more pronounced at higher densities because plants in productive environments should grow more quickly to the point where asymmetric competitive interactions become significant. For both *Erodium* species, greater reproductive inequality in the more productive, "early germination" treatment is most apparent at higher plant densities. These results, along with results reported above on the general increase of reproductive inequality with density, suggest competitive asymmetry in these populations.

Inferences obtained from this investigation on reproductive hierarchies in *Erodium* should be tempered by the fact that the experimental populations used in this study represent a small subset of the gene pool of both species. Variation within a single species for the response of size inequality to changes in plant density was demonstrated by growth chamber studies on *Danthonia caespitosa* (Quinn and Hodgkinson 1983). In material collected from *D. caespitosa* populations arrayed along a latitudinal gradient, coefficients of variation for shoot mass per plant in response to density variation differed significantly among populations. Similar studies on size and reproductive hierarchies in several populations of the introduced annual *Bromus tectorum* also suggest that the quantitative impact of density on size or fecundity distributions may depend on the population being studied (K. J. Rice and R. N. Mack, *unpublished manuscript*).

The potential evolutionary implications of asymmetric competition on fecundity distributions in *Erodium* can be illustrated by plotting N_e against sowing density (Fig. 5). Increased inequality in reproduction with increasing sowing density (N) can act to decouple changes in plant density from changes in N_e; often N_e will not increase as quickly as might be expected from changes in N. In fact, as N increases, N_e may change little or may even decrease. In the present study, for example, the difference between 36 seeds/dm^2 and 64 seeds/dm^2 represents an increase of 78% in N. Averaged across rainfall treatments, the corresponding increase in N_e was calculated to be only 12% for *E. botrys*, while N_e for *E. brachycarpum* actually decreased by 11%. Focusing on early germinating populations of both species provides an even more striking comparison (Fig. 5). For the same 78% increase in N, reproductive

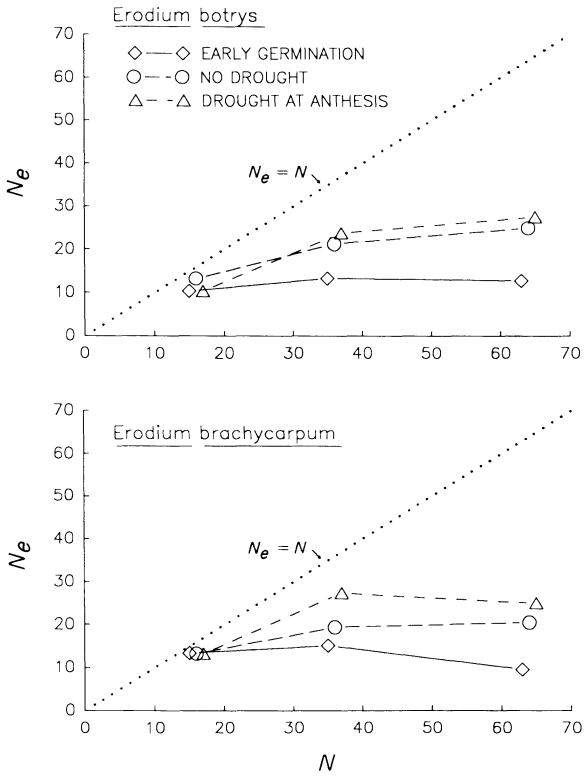

FIG. 5. Effects of variation in *Erodium* sowing density and rainfall distribution on the relationship between effective population number (N_e) and sowing density (N). Estimates of N_e were calculated from formulae provided by Heywood (1986).

inequality in high density populations reduced the predicted N_e by 4% in *E. botrys* and 36% in *E. brachycarpum*. Whether this insensitivity of N_e to changes in population density commonly occurs in other plant species is difficult to determine because of the lack of relevant studies on changes in reproductive inequality over varying population densities. However, results from an agronomic study on the distribution of grain yield per plant in maize suggest the generality of this phenomenon. Comparing reproduction at a low (5 plants/m^2) and high (20 plants/m^2) planting density, Edmeades and Daynard (1979) found that the CV for kernel production increased from 9.9 to 114.9 seeds per plant, respectively. For this 400% increase in plant density, the corresponding increase in N_e calculated from these CV values is only 74% (assuming total outcrossing, i.e., $F = 0$). This increase in N_e is even less if some inbreeding occurs; if one assumes total inbreeding in these maize populations (i.e., $F = 1$), the calculated increase in N_e is only 10%.

For all high density *Erodium* populations examined, values of N_e/N were <0.5 (assuming $F = 1$). Values of $N_e/N < 0.5$ indicate that variance in potential fecundity among adults makes a greater contribution to drift variance than does the variance due to gamete sampling (Heywood 1986). Actual values of N_e/N depend, in part, on the value chosen for the fixation index and in *Erodium* probably are somewhat <1. Qualitatively, however, the results indicate that hierarchies in reproductive output might have a strong impact on the magnitude of genetic drift in dense populations of both *Erodium* species.

The ranges of N_e/N values found in this study for populations of *E. botrys* (0.20–0.83) and *E. brachycarpum* (0.15–0.84) are comparable to the range reported by Heywood (1986) in a survey of 37 different annual plant species. Given that the experimental *Erodium* populations in this study were derived from only four populations within a single region, the wide range of N_e values observed in response to changes in density and rainfall distribution underscores the sensitivity of N_e to environmental variation.

The demonstrated role of reproductive inequality in reducing N_e in *Erodium* and other annuals (Gottlieb 1977, Heywood 1986), coupled with the observation that reproductive hierarchies in annual populations are common (White and Harper 1970, Weiner 1985), suggest that genetic drift should be an important force of evolution in many annual plant populations. For a balanced view of plant microevolutionary processes, additional work is needed on how reproductive hierarchies, and thus the potential for genetic drift, are influenced by the interaction of resource availability and intraspecific competition.

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