

Ecology of Sonoran Desert Plants and Plant Communities

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Population Ecology of
Sonoran Desert Annual Plants

D. Lawrence Venable and Catherine E. Pake

Roughly 50% of the species in local floras in the Sonoran Desert are annuals, with 60% to 80% of these being winter annuals and the rest being summer or nonseasonal annuals (fig. 4.1; Venable et al. 1993). Deserts are ecosystems with a high level of environmental variation driven by rainfall (hot deserts have the highest coefficient of variation in interannual actual evapotranspiration of any of the earth's biomes; Frank and Inouye 1994). Desert annuals are highly responsive to these environmental fluctuations and play an important role in modulating that variation and passing it on to higher trophic levels (Went 1949; Beatley 1967; Patten 1975, 1978; Gutierrez and Whitford 1987). They are most appreciated in "good wildflower years" when the floral displays of the more showy species color the landscape. This often occurs in association with El Niño weather events that tend to result in higher than average winter precipitation in the southwestern United States. Desert annuals spend most of their lives as seeds and in some years may even be inconspicuous during their normal growing season due to low germination or little growth (e.g., Tevis 1958a). Their rapid dynamics appear to make them more sensitive to invasions and extirpations than perennials. Introduced species constitute a higher fraction of annuals than perennials in local floras (fig. 4.2). They may also be more readily lost, judging from the observation that three-fourths of the 27 possible extirpations in the Tucson Mountain flora (species not collected since 1950) are annuals (mostly winter). This is significantly more than expected given that annuals only make up 45% of the flora ($G = 9.87$, $P < .001$; data from Rondeau 1991). The seeds of

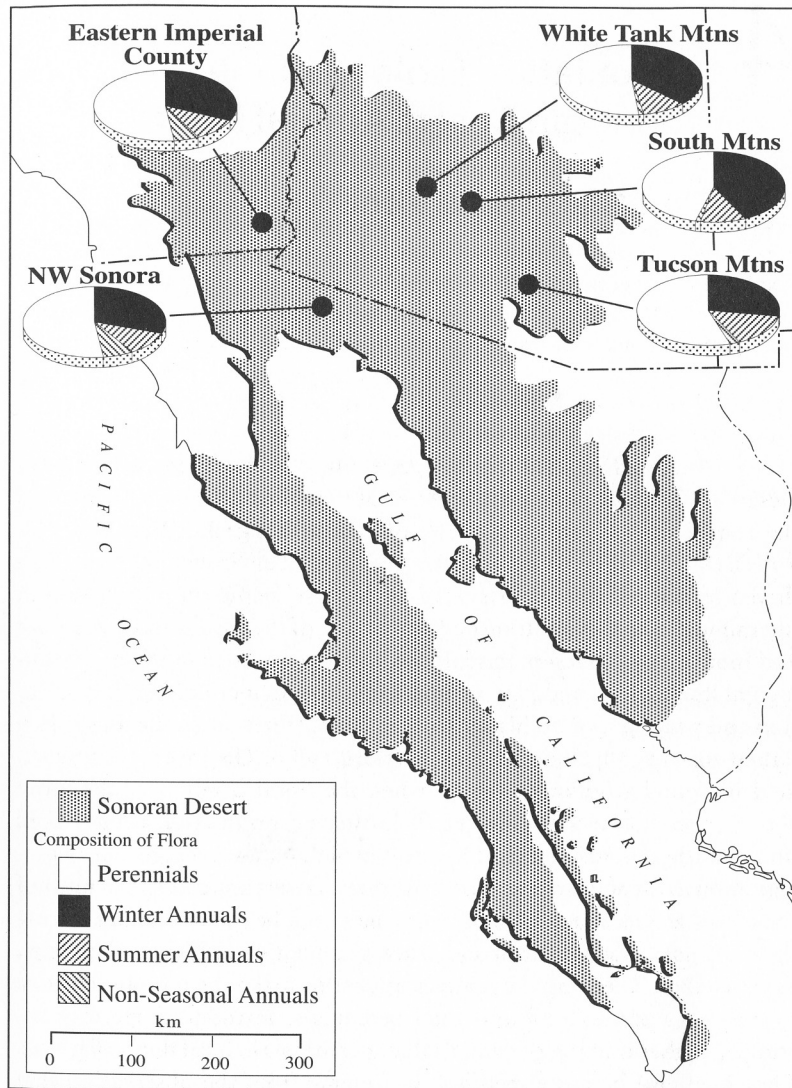


Figure 4.1 Map of the Sonoran Desert showing the proportion of perennials and annuals in five regional floras. Data taken from Keil (1973), Felger (1980, 1992), McLaughlin et al. (1987), Rondeau (1991), and Daniel and Butterwick (1992).

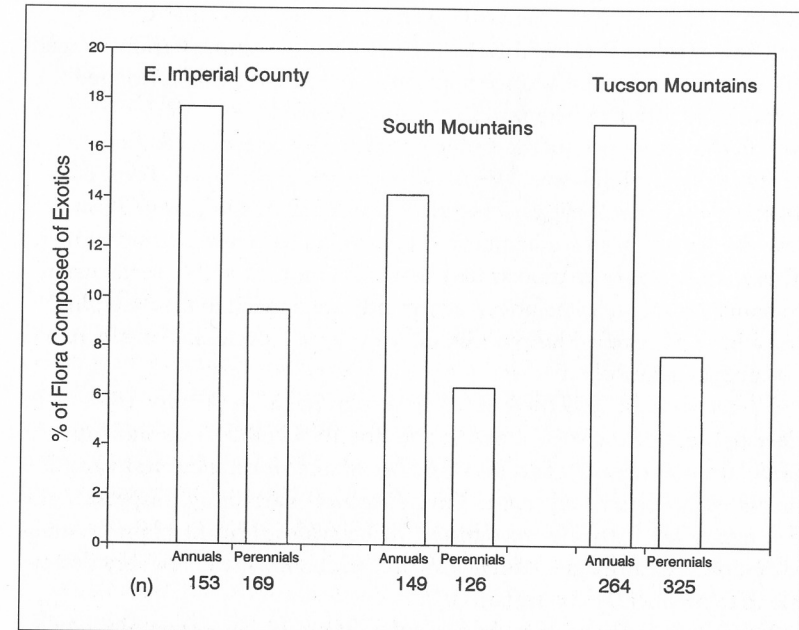


Figure 4.2 Percent of exotic species among the annual and perennial components of three regional floras in the Sonoran Desert. Annuals have a significantly greater proportion of exotic species than perennials in each case (East Imperial County, $G = 4.7$ [$P < .05$]; South Mountains, $G = 19.2$ [$P < .001$]; Tucson Mountains, $G = 12.0$ [$P < .001$]). (n) signifies the number of species.

desert annuals are a primary food source for ants and rodents and their vegetative bodies are important browse for grasshoppers, rabbits and larger grazing animals (Mares and Rosenzweig 1978; Rissing 1986). Annual plants and their fluctuations play a critical role in the population dynamics and species composition of these consumers (Brown et al. 1975, 1979, 1986; Inouye et al. 1980; Davidson et al. 1984, 1985; Samson et al. 1992). Because of the numerical and ecological importance of annual plants in deserts, an understanding of their population dynamics and species interactions is critical to understanding desert ecosystems.

It is widely believed that delayed germination and long-lived seed banks play an important role in the population dynamics of desert annuals. Yet little work has been done to quantify nongerminating seed fractions of

desert annuals in natural environments (but see Nelson and Chew 1977; Reichman 1984; Price and Reichman 1987 for documentation of seed-bank densities). Long-lived seeds and species-specific germination requirements have been hypothesized to explain observed fluctuations in population densities, especially the sudden appearance of species following one or more years of absence (Went 1949; Juhren et al. 1956; Tevis 1958a, 1958b; Shreve and Wiggins 1964). More recently, the germination of a few species has been studied in well-controlled tests in growth chambers. These studies have demonstrated that a fraction of viable seeds usually remains dormant, even under apparently ideal germination conditions (Baskin et al. 1993; Philippi 1993a, 1993b; S. Adondakis and Venable, unpublished data).

Desert annuals and their seeds have played an important role in the development of theories about adaptation to variable environments, the population dynamic functions of dispersal and dormancy, and variance-mediated species coexistence. Environmental variability, dispersal, and dormancy are generally recognized to be widespread in plant communities, biologically significant in a variety of contexts, and not very amenable to experimental investigation.

In this paper we review some results on population dynamics of desert annuals from our research conducted at the Desert Laboratory. We have documented the conditions under which desert winter annuals have emerged since 1982. We have also documented the survival and reproduction of emerging seedlings over this period. In this research we have measured population dynamic properties critical to evaluating some theoretical issues for which desert annuals have been used as examples. We have documented germination fractions for different species in several years. Investigations of shifts in interspecific interactions, in concert with information on seed-bank dynamics, have shed light on mechanisms of species coexistence in this community. We have also partitioned the sources of seedlings into local reproduction, seed bank, and dispersal and measured seed dispersal distances.

The Desert Laboratory Site

The study area for the long-term plots and competition studies is a gently sloped alluvial plain at 725 m elevation northwest of Tumamoc Hill. Other results come from work done further east, from the northeastern base of

Tumamoc Hill extending around to the northwest side. The Desert Laboratory property has been ungrazed by livestock since 1907 (Bowers and Turner 1985; Burgess et al. 1991), and our study sites are dominated by *Larrea tridentata* (creosote bush), which may be joined by *Ambrosia deltoidea* (triangle-leaf bursage), *Krameria grayi* (white ratany), *K. parviflora* (range ratany), *Opuntia fulgida* (jumping cholla), *O. phaeacantha* (prickly pear), and *Fouquieria splendens* (ocotillo) (Bowers and Turner 1985).

The Long-Term Plots

In the autumn of 1982, research was initiated on the demography of desert winter annuals along a 250-m transect through the previously mentioned gently sloped creosote flat. Fifteen permanent plots (0.10 m² each) were placed in random positions in the open along this transect. Plots have been visited each year following each rainfall event, and censuses have been taken if germination occurred. Generally, plots had censuses taken four to six times a season for emergence, survival, and reproduction. This sampling scheme gave sample sizes of hundreds (occasionally thousands) of individuals for most species in most years. Data were collected by mapping on acetate sheets placed with fixed coordinates over plexiglass mapping tables. Maps were later digitized to record spatial coordinates, germination and death dates, and fecundity of individual plants. Estimates of seed-bank dynamics were obtained from soil cores (28 per year) collected from 1982–1986 and 1989–1996 (180 cores per year).

More than 30 species of winter annuals have been found on these plots with the most common species being *Plantago patagonica* (Indian wheat) and *P. insularis* (Plantaginaceae), *Schismus barbatus* (Poaceae; introduced from the arid Middle East), *Erodium texanum* (native) and *E. cicutarium* (filaree; introduced from the Mediterranean; Geraniaceae), *Evax multicaulis*, *Stylocline micropoides*, *Monoptilon bellioides* (Mohave desert star), *Eriophyllum lanosum* (woolly daisy; Asteraceae), and *Pectocarya recurvata* (Boraginaceae).

We now understand many basic aspects of the population dynamics of these species. Germination typically occurs from October through January (fig. 4.3). Plants grow and reproduce until late March to early May when a combination of high temperatures (> 35°C) and drought results in death (fig. 4.3). High temperatures can be associated with either mortality or high rates of plant growth, depending on rainfall. Thus mortality or

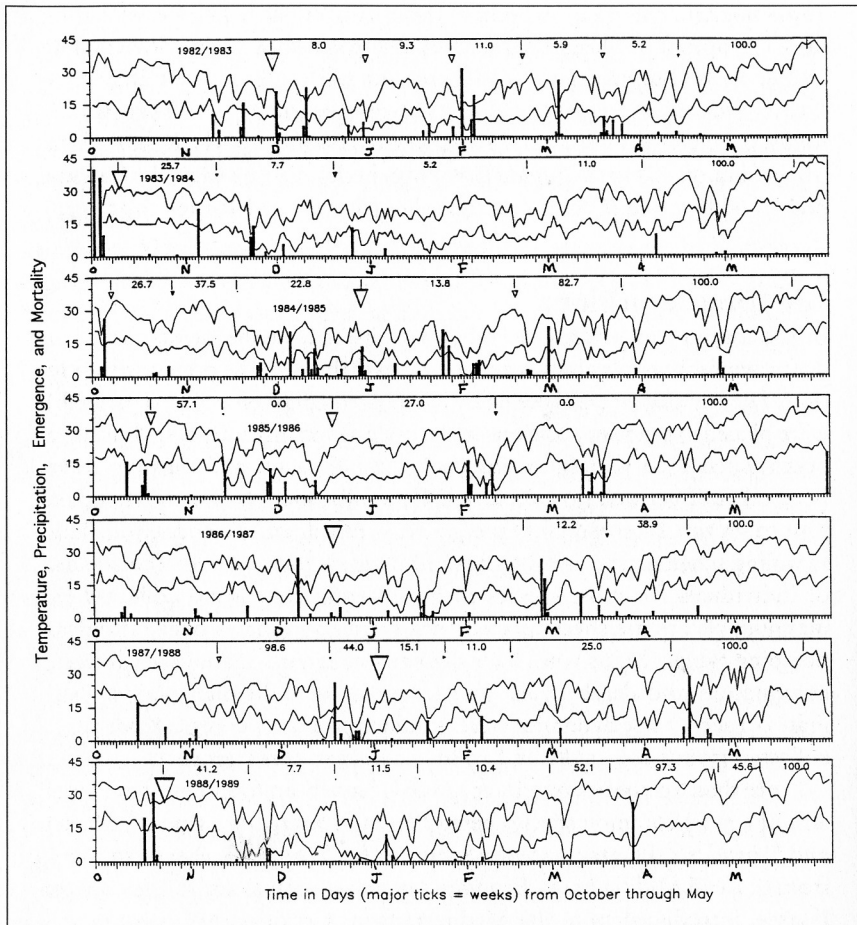


Figure 4.3 Weather, emergence, and mortality of winter annuals on the long-term plots at the Desert Laboratory from 1982–1989. Solid lines indicate daily max/min temperatures ($^{\circ}\text{C}$). Solid bars indicate daily rainfall (mm). Down-pointing arrows indicate emergence, with the size of the arrow being proportional to the percentage of the total year's emergence that occurred at that census. The numbers across the top of each year's graph indicate the average per capita mortality between the dates indicated by the ticks, expressed on a per month basis, for plants alive at the beginning of each interval.

growth is sometimes high in the autumn (if plants emerge early) or in the spring, but neither is high in the cool winter months (fig. 4.3). These winter annuals do well in terms of growth and reproduction in El Niño years (1982/83, 1986/87, 1990/91, 1991/92, and 1994/95) and worse in dry years. However, exceptions exist and species have individualistic responses to temporal variation (fig. 4.4, Venable et al. 1993). The total number of seedlings of all species emerging has varied by two orders of magnitude over the 15-year period (1982–1997). Populations tend to increase following El Niño events (fig. 4.5), though the details vary from species to species (fig. 4.6). Desert annual populations were high during the early 1980s but crashed in 1989/90, the third year of the late '80s winter drought (1987/88–1989/90). Populations recovered in the period from 1991/92 to 1992/93 after low-density, high-fecundity seasons in 1989/90 and 1990/91 (fig. 4.4; fig 4.5; fig 4.6). They remained high through 1994/95 but dropped again during the mid-1990's drought due to low germination survival and fecundity in 1995/96 and 1996/97.

It is interesting to contemplate how these patterns observed at the Desert Laboratory might vary over broad geographic areas. Personal observations and preliminary results from a lower-elevation, drier study site near Gila Bend, Arizona, plus published accounts from other studies suggest that there are overriding regional patterns, probably produced by regional winter frontal storm systems. Published accounts of year-to-year variation in annual plant densities, biomass, or reproduction for sites in Nevada or southeastern California (Nelson and Chew 1977; Beatley 1969) correspond fairly well to winter precipitation records taken at the Desert Laboratory in Tucson (Venable, personal observation). Yet many details of desert annual population dynamics appear to vary, sometimes dramatically, on a scale of tens to hundreds of miles or along short elevational, slope, or aspect gradients. Frontal systems may drop different amounts of rain at sites only a few miles apart resulting in sites with missing or extra germination cohorts (Venable, personal observation). Also, late cohorts may be missing from some sites where a heavy early rain apparently depleted the seed bank of most nondormant seeds. Plant populations that reliably experience different weather regimes are also likely to have ecotypic differences. Germination and flowering times have been documented to be more flexible in dry Lower Colorado Valley or Mojave Desert sites than at our Desert Laboratory site. For example, rains before September or after January result in only negligible germination at the Desert Laboratory, but

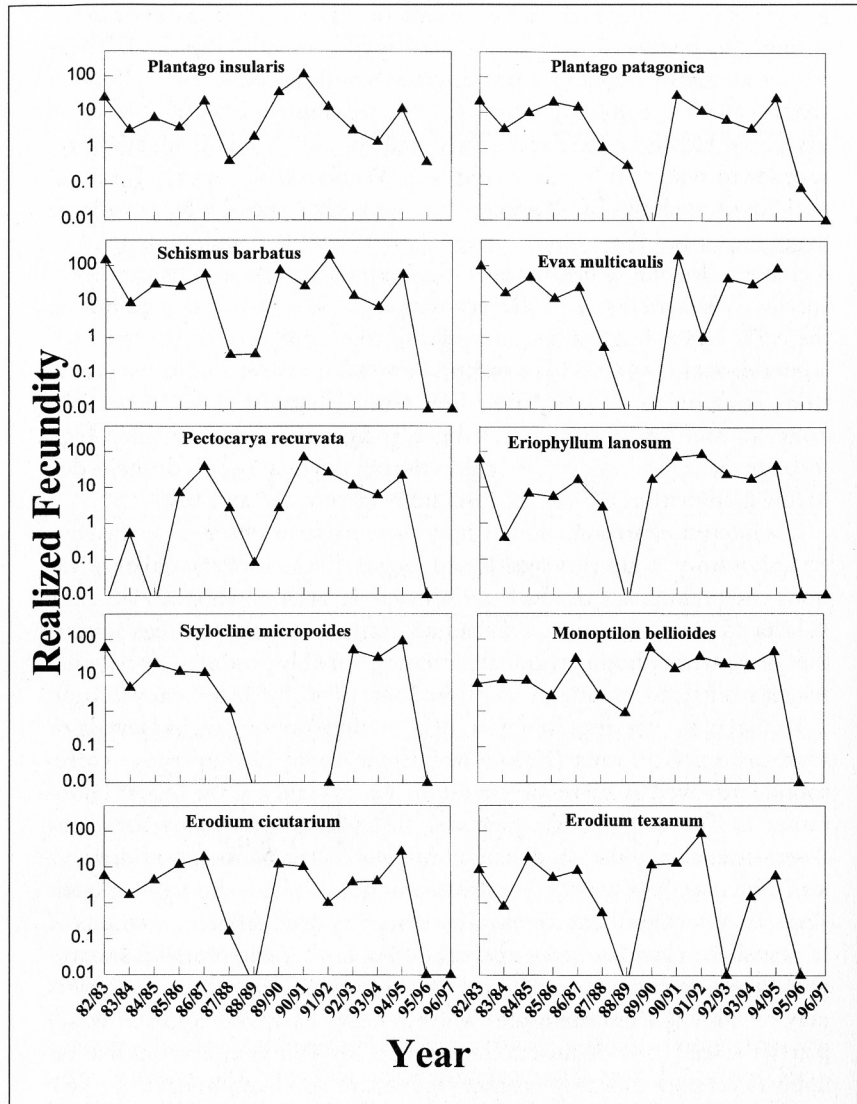


Figure 4.4 Realized fecundity (average survival [from emergence to maturity] \times average fecundity [seed per adult]) for 10 species of winter annuals on the long-term plots at the Desert Laboratory for each year from 1982/83–1996/97.

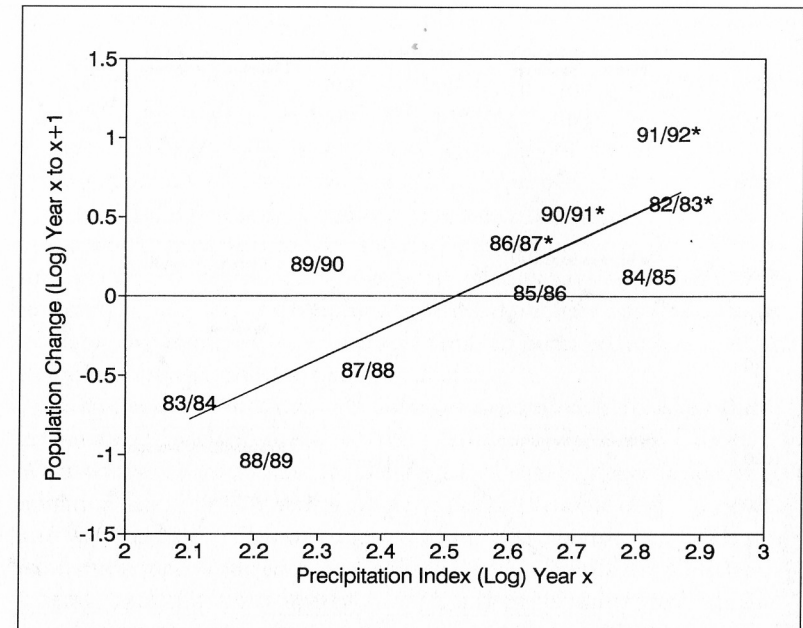


Figure 4.5 The total population of all desert annuals on the long-term plots at the Desert Laboratory tends to increase following years of higher winter precipitation. The precipitation index is total precipitation from November through February of each year. Population change is calculated as $\log(N_{x+1}) - \log(N_x)$, where N_x is the number of seedlings emerging in year x . Asterisks indicate the population increases that followed El Niño events. $R^2 = 0.68$, $P < .0025$.

may produce large cohorts at drier, more variable sites (e.g., Tevis 1958a; Beatley 1967; Venable, unpublished data from Gila Bend).

Germination Fractions, Seed Size, and Environmental Variation

Seed-bank dynamics and germination behavior of desert annuals in natural habitats are relevant to a variety of ecological and evolutionary issues beyond desert ecology per se. Germination behavior of desert annuals has been used as a model system for understanding adaptations to variable

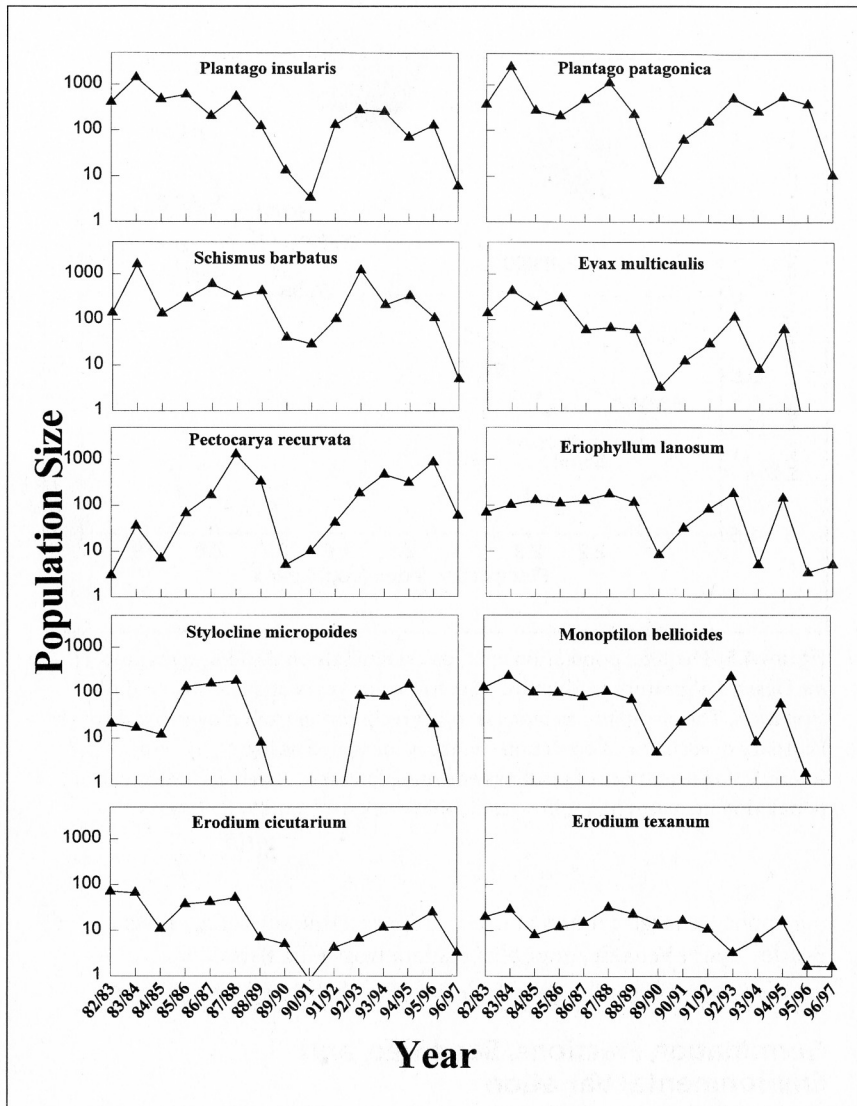


Figure 4.6 Population size (number of seedlings emerged) for each of 10 species of winter annuals on the long-term plots at the Desert Laboratory for each year from 1982/83–1996/97.

environments. Theoretical studies have shown that fractional germination for desert annuals can result in the adaptive reduction of temporal variation in fitness commonly called bet hedging (Cohen 1966; MacArthur 1972; Venable and Lawlor 1980; Ritland 1983; Bulmer 1984; Leon 1985; Philippi and Seger 1989; Venable and Brown 1988; Venable 1989). Delayed germination of a fraction of a plant's progeny buffers it from the consequences of near or complete reproductive failure in unfavorable years, but it may also reduce success in favorable years by sacrificing opportunities to reproduce. While desert annuals have been useful to evolutionary ecologists for developing theories about how adaptation should occur in variable environments, very little empirical data has been collected in a way suitable for testing such ideas.

To that end, we have quantified the fractions of viable seed banks that germinated in each of three years for 17 species at the Desert Laboratory. We used these data to look for the predicted negative correlation of germination fraction with demographic variance (Venable et al. 1993; Pake and Venable 1996). This was done by sifting and counting the viable seeds from soil samples (180 each year, collected with a stratified randomization scheme, each 5.4 cm diameter \times 2.5 cm deep; viability determined by visual inspection of embryo/endosperm as in Pake and Venable 1996). These samples were always collected after the winter germination season but before new seeds dispersed in the spring. Densities of emerging seedlings were obtained from 48 nearby quadrants so that germination fractions could be calculated as seedlings/m² \div (seeds + seedlings)/m². We calculated fitness variance as the year-to-year variance in reproductive success of seeds that germinate (survival \times mean fecundity of survivors for each of nine species using 10 years of demographic data). We found that the species whose germinating seeds experienced greater variance in per capita reproductive success had lower germination fractions (fig. 4.7). This is the first study to use long-term data on population dynamic variance to test the prediction from bet-hedging theory that selection should lead to lower germination fractions in species with higher variance in success (Cohen 1966). Philippi (1993b) found a similar but less-direct result. Seeds of *Lepidium lasiocarpum* collected from sites with lower mean rainfall had lower germination fractions in growth chamber experiments.

Other aspects of desert annual life histories may also reduce variance in ways that should increase fitness. Seed size is one such trait. A larger-seeded plant is likely to produce fewer seeds in favorable years than a

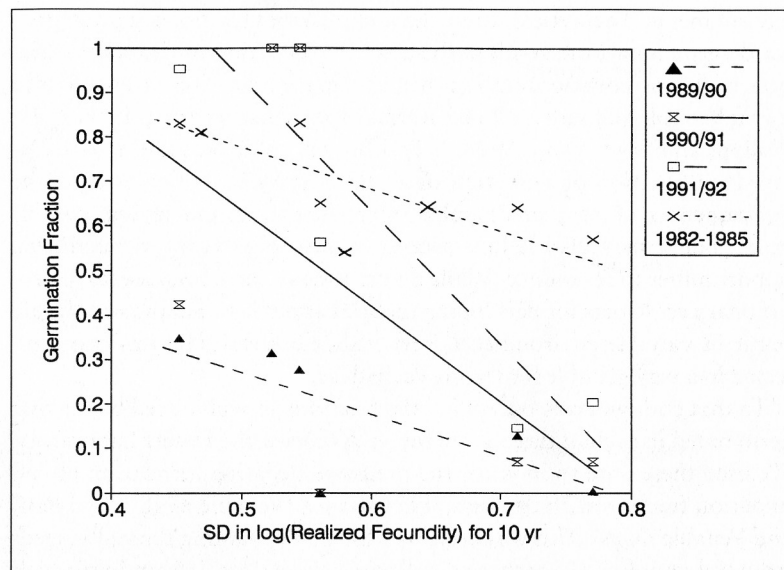


Figure 4.7 Germination fractions of desert winter annuals were lower for species that experienced greater year-to-year variance in reproductive success. Germination fractions are graphed for field data collected at the Desert Laboratory in 1989/90, 1990/91, and 1991/92 and for the average of data collected at the Desert Laboratory from 1982–1985.

small-seeded one (given similar amounts of nutrients and energy available for reproductive allocation). However, large seed size means more maternal provisioning, which may buffer seeds from some negative effects of dry years, as originally posited by Baker (1972; see Venable and Brown 1988 for the theoretical arguments regarding bet hedging). In our system, we found that smaller-seeded species have a higher variance in reproductive success (Spearman $r = -0.7448$, $P < .0001$; Pake and Venable 1996). Thus our results are consistent with the idea that larger seed size buffers plants from variance in arid environments (see also Venable and Brown 1988).

By reducing the variance experienced by a desert annual, larger seed size should also modify the strength of natural selection for delayed germination. Thus theoretical studies have suggested a positive correlation be-

tween germination fraction and seed size (Venable and Brown 1988), and this pattern is also highly significant in our data (Pake and Venable 1996). A positive correlation between germination fraction and seed size has also been reported in a comparative study of species of British plants (Rees 1993).

Species Coexistence

Another line of inquiry for which the population dynamics of desert annuals has had an impact on general ecological concepts is the theory of species coexistence mechanisms promoted by environmental variance. Desert annuals are frequently cited as an example of a system in which temporal variation may promote species coexistence (Shmida and Ellner 1984; Ellner 1987; Chesson and Huntley 1988, 1989; Chesson 1994). Again, few empirical results are available to test the ideas. Since the pioneering works of Hutchinson (1961) and Grubb (1977), ecologists have been aware that temporal environmental variation may promote species coexistence of organisms with different “temporal niches.” More recently, the importance of resistant life-history stages, such as seed banks, for temporal-variance-mediated species coexistence has been recognized (Chesson and Huntley 1988). Temporal heterogeneity is a factor that might be expected to be very important in promoting coexistence in desert annuals, since deserts are the biome with the greatest coefficient of variation among years in actual evapotranspiration (Frank and Inouye 1994).

One frequently suggested annual-plant scenario with the population dynamic elements necessary for variance-mediated coexistence involves persistent seed banks and species-specific germination responses to environmental variation (Chesson and Huntley 1989). Persistent seed banks are necessary to buffer populations against extinction in unfavorable conditions (i.e., to “store” population inputs from favorable years). Species-specific germination responses provide opportunities for species to bounce back from rarity by occasionally escaping competition with abundant species. Another related scenario (Venable et al. 1993; Pake and Venable 1995) involves germination fractions that are correlated with reproductive success (predictive germination). Predictive germination, with year-to-year variation in survival and fecundity that is not completely correlated among species, increases the coexistence-promoting properties of variable environments. These theoretical scenarios make specific predictions about

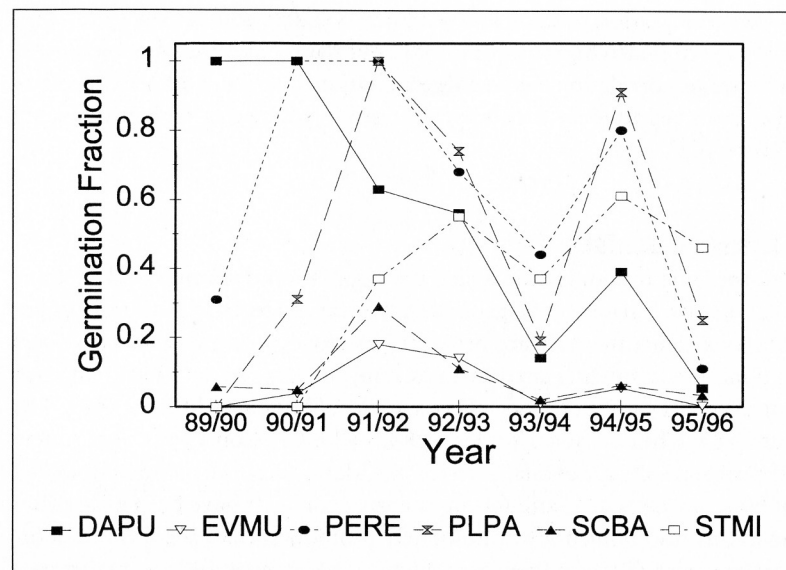


Figure 4.8 Graph of germination fraction of six species of desert winter annuals on permanent plots at the Desert Laboratory in seven years, illustrating species-by-year interaction. DAPU = *Daucus pusillus*; EVMU = *Evax multicaulis*; PERE = *Pectocarya recurvata*; PLPA = *Plantago patagonica*; SCBA = *Schismus barbatus*; STMI = *Stylodine micropoides*.

the dynamics of seeds in the soil and about shifts in the relative abundance and relative performance of species over time. Such predictions can be tested with data from desert annuals (Venable et al. 1993).

Persistent seed banks are produced by most (probably all) members of our desert annual community (Pake and Venable 1996). Statistical analysis of the germination fraction data described above shows that germination fraction varied significantly among years, with individual species responding differently in different years (species \times year interaction; fig. 4.8; Pake and Venable 1995). Thus, the basic conditions for variance-mediated coexistence seem to be met in this community. Also, we have shown that germination fractions were higher in years when reproductive success was higher, suggesting that germination fraction is cued to conditions corre-

Table 4.1 Some statistically significant differences ($p < .05$) in species' performances that reveal shifts in hierarchies associated with temporal variation (either natural or simulated year-types).

Plots in different years,
all at low density

1990/91: PERE > SCBA, PERE > PLPA

1991/92: SCBA > PERE, PLPA > PERE, SCBA > PLPA

Plots in year-types simulated by varying density,
all under dry conditions

Low density: PLPA > PERE

Medium density: PERE > PLPA, PERE > SCBA

High density: SCBA > PERE, SCBA > PLPA

Source: Adapted from Pake and Venable (1995).

Note: PERE = *Pectocarya recurvata*; PLPA = *Plantago patagonica*; SCBA = *Schismus barbatus*.

lated with future prospects for reproduction (Pake and Venable 1996; cf. Cohen 1967 and Rice 1985). As mentioned above, a positive relationship between germination fraction and reproductive success suggests a role for the variation experienced by germinated seedlings in species coexistence.

To test for such shifts in reproductive success of species among years, we conducted a demographic field experiment with three winter annuals: *Plantago patagonica*, *Pectocarya recurvata*, and *Schismus barbatus* (Pake and Venable 1995). In this experiment we determined the extent to which species performance hierarchies shifted among years, among simulated year-type factors (water addition/removal and density manipulation), and between shrub and open habitats (the major contributor to local spatial variation). Seedlings were mapped in replicated plots in shrub and open habitats, and in different years, densities, and moisture levels, and their per capita survival and reproductive success were determined. The relative performance of these species shifted significantly as we experimentally varied the factors that are important components of the natural year-to-year environmental variation (table 4.1). For example, under low-density, dry conditions, *Plantago* outperformed *Pectocarya*; at medium-density, dry conditions, *Pectocarya* outperformed both *Plantago* and *Schismus*; while at high-density, dry conditions, *Schismus* outperformed both *Pectocarya* and *Plantago*. In 1990/91 at low density, *Pectocarya* outperformed both *Schismus* and *Plantago*, yet in 1991/92 at low

density, *Plantago* and *Schismus* outperformed *Pectocarya*, and *Shismus* outperformed *Plantago*. Thus, the relative success of competing species shifts under real and simulated temporal variation. Significant shifts in performance hierarchies were not found between shrub and open habitats, suggesting that this spatial component of environmental patchiness may be less important than the temporal components, at least under the conditions investigated here. These experiments represent an attempt to use population dynamic approaches to investigate plant competition in undisturbed natural habitats. Our results so far indicate that variance-mediated coexistence mechanisms are likely to be important in the species diversity of desert annuals (Venable et al. 1993; Chesson 1994; Pake and Venable 1995, 1996).

Community ecologists are well aware that a great variety of factors may potentially contribute to species coexistence in a given system (Tilman and Pacala 1993). In the research described above, we have attempted to explore the population dynamic components required by one potentially important factor for desert annuals: temporal variance. Spatial heterogeneity is also an important source of desert annual species diversity, with the standard gradients of slope, aspect, soil type, moisture, and nutrients contributing at a variety of scales (Shreve and Wiggins 1964)⁵. The mosaic pattern of open area and perennial cover, as well as microtopographic variation, also contribute at a local scale (Shmida and Whittaker 1981; Samson 1986). Another likely factor contributing to the coexistence and species diversity of desert annuals is the species-specific behavior of grazers and seed predators (Brown et al. 1979; Pacala and Crawley 1992).

Partitioning of Seedling Sources

While understanding the role of seed banks is clearly important to our understanding of desert annual population dynamics, we would also like to know the role of seed dispersal. Seed dispersal is another understudied aspect of plant population dynamics with many important consequences, including persistence and coexistence in variable environments. Since seed dispersal and seed-bank dynamics are both difficult to measure in natural populations, little good population dynamic data exists on their consequences for any plant species. To attack this problem, we have performed a variety of removal experiments in natural populations of desert annuals at the Desert Laboratory. The goal of these experiments was to determine

the proportion of the seedlings emerging in each of three years that came from *in situ* reproduction the previous year, delayed germination from prior years, or dispersal.

In the spring of 1991 (and in each subsequent year), we used a herbicide to inhibit reproduction of desert annuals either solely under shrubs, solely in open sites, both, or neither. This was carried out in replicated randomized-block removal experiments with replicated removal treatment areas roughly 10 m in diameter. During the following germination season (autumn 1992), we measured seedling emergence in small plots within the larger removal areas. These plots were either "natural" (uncovered and unbordered) or "seed bank" (small, bordered plots from which plants were removed and which were covered with a fine-mesh organza cloth during the seed dispersal season). Pairs of natural and seed-bank plots were located in shrub and open habitats in each of the larger removal areas representing the factorial combinations of reproduction inhibition. Comparison of seed bank and natural plots in the control areas (with no removal) determines the relative contribution from first-year germination and delayed germination. Comparison of shrub or open removal areas to control areas (with no removal) indicates the role of seed dispersal between the two habitat types. This process was repeated in each of the subsequent two years, but was not quite finished for the second year at the time of this writing.

During the first year in which we measured the results of these manipulations, 1992/93, the Sonoran Desert experienced the third favorable winter of high precipitation following the late 1980s drought (fig. 4.4; fig. 4.5; fig. 4.6). During the second year, 1993/94, germination season rainfall was low and early. Some noteworthy shifts occurred in seedling abundances between these years (data taken from unmanipulated plots). Two annual grass species increased considerably (*Schismus barbatus* and *Bromus rubens*) while the forbs either remained constant (*Plantago patagonica*, *Pectocarya recurvata*) or declined (*Stylocline micropoides* and *Eriastrum diffusum* [miniature wool star]; fig. 4.9). Data from seed-addition plots indicate that the dramatic decline in *Eriastrum* seedling density was due to low germination in the second year (0.5% germination vs. 26% the previous year). This was probably due to the low precipitation during the autumn germination season. Despite these shifts in abundance of species, partially due to differences in germination response, within species the relative densities in shrub and open sites did not shift between years. The

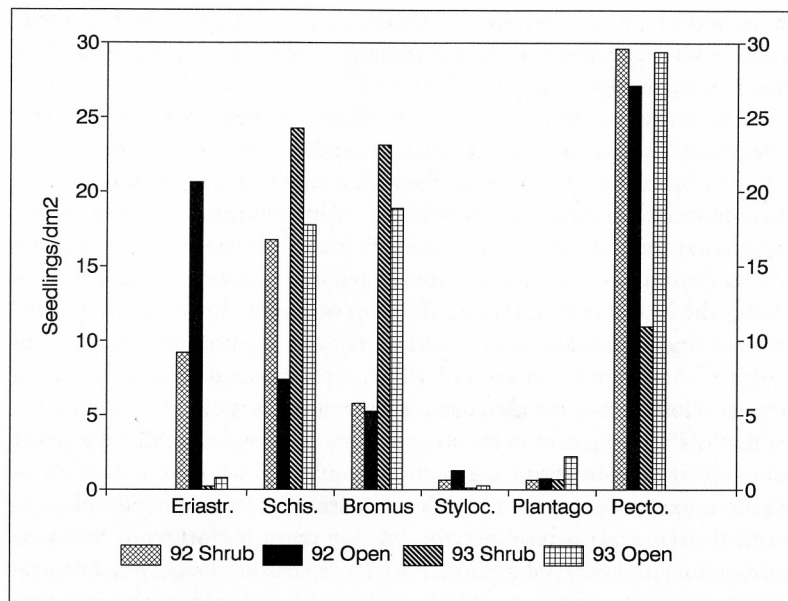


Figure 4.9 Densities of seedlings emerging in shrub and open habitats for two years in the seedling source experiment at the Desert Laboratory. Eriastr. = *Eriastrum diffusum*; Schis. = *Schismus barbatus*; Bromus = *Bromus rubens*; Styloc. = *Stylocline micropoides*; Plantago = *Plantago patagonica*; Pecto. = *Pectocarya recurvata*.

two grasses were consistently more abundant under the shrubs. *Eriastrum*, *Stylocline*, and *Plantago* were somewhat more abundant in the open in both years (and *Pectocarya* was exceptional in shifting from more abundant under shrubs in the first year to more abundant in the open the second year; fig. 4.9).

Dispersal was usually a less important source of seedlings than delayed germination (as predicted for desert annuals by Ellner and Shmida [1981]; fig. 4.10). Nonetheless, the shrub and open habitats have a source-sink relationship that differs in direction for different species: the habitat in which a species occurs at lower density usually has a greater fraction of its seedlings originating from dispersed seeds (e.g., lower density and more immigration under the shrubs for *Eriastrum* and *Stylocline* and in the

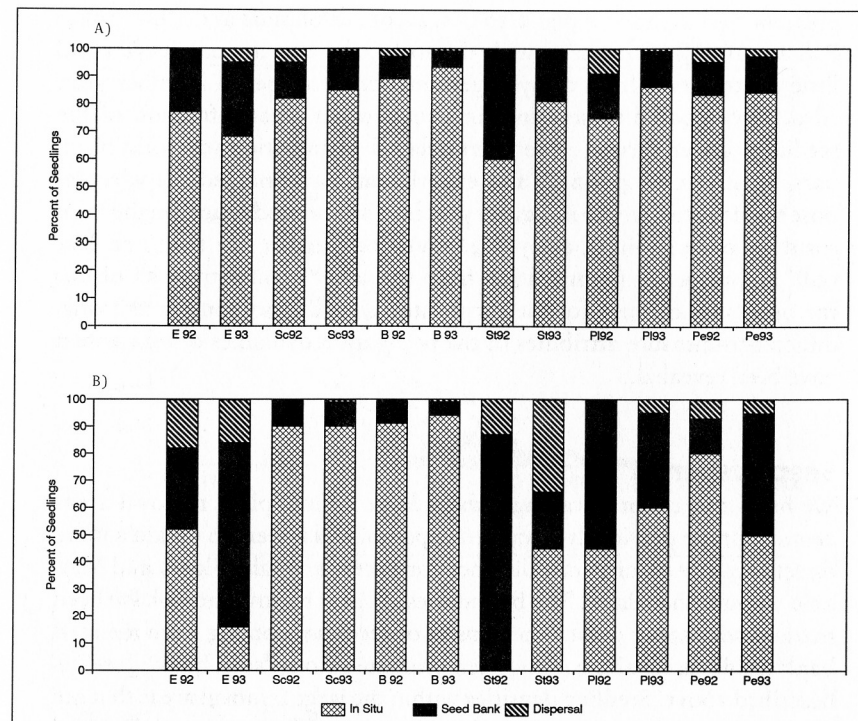


Figure 4.10 Partition of seedling origin into *in situ* reproduction, delayed germination, and immigration in two years in the seedling source experiment at the Desert Laboratory. (A) Open habitats; (B) Under shrubs. E = *Eriastrum diffusum*; Sc = *Schismus barbatus*; B = *Bromus rubens*; St = *Stylocline micropoides*; Pl = *Plantago patagonica*; Pe = *Pectocarya recurvata*.

open for the two grasses [fig. 4.10A vs. 4.10B; cf. Shmida and Ellner 1984; Pulliam 1988]). Compared with the forbs, the two annual grasses had little contribution from delayed germination or dispersal in either year. Also, as compared to seedlings in open sites, a greater fraction of the seedlings under shrubs came from delayed germination (cf. solid black bars, fig. 4.10A vs. 4.10B). These experiments have enabled us to decompose the densities we see in a given year into *in situ* production (in the local shrub or open habitat), delayed germination (seeds more than one year old), and dispersal (immigration from the other habitat type: shrub for the open sites or open for the shrub sites). In this way some interesting, difficult-to-measure attributes of the population dynamics of this system have been revealed.

Seed Dispersal

We have also taken advantage of the large annual plant removal areas created for the previously discussed experimental system to obtain a more direct measure of dispersal distance for desert annuals (Flores and Venable, unpublished data). The boundaries of these removal areas have been marked with spray paint. The density of seedlings coming from the seed bank inside removal areas has been estimated from "seed-bank plots" as described above. Seedling densities within the large removal areas that are greater than the background seed-bank density are due to seed dispersal across the borders. To estimate dispersal distances, we have taken censuses of seedlings in transects that run perpendicular across these borders. A blurred, sigmoidal gradient of seedling densities is found along such transects (e.g., fig. 4.11). Densities along these transects represent dispersal curves for the population of plants outside the removal border. These can be converted to dispersal curves for individual plants using the fact that the population dispersal curve is the integral (or sum) of the dispersal curves of all the plants from the border outward. The dispersal curve in figure 4.11 is for all annual plants together and indicates a rapid decline in seed number with distance. The estimated rate of decline in seed numbers is -4.0 (seeds \times seed $^{-1} \times$ meter $^{-1}$). This is quite low among published estimates of dispersal rate (the average exponential dispersal rate for herbaceous plants without dispersal mechanisms was -2.75 in the studies reviewed by Willson [1993]).

This predictable and low rate of seed dispersal is not the whole story for

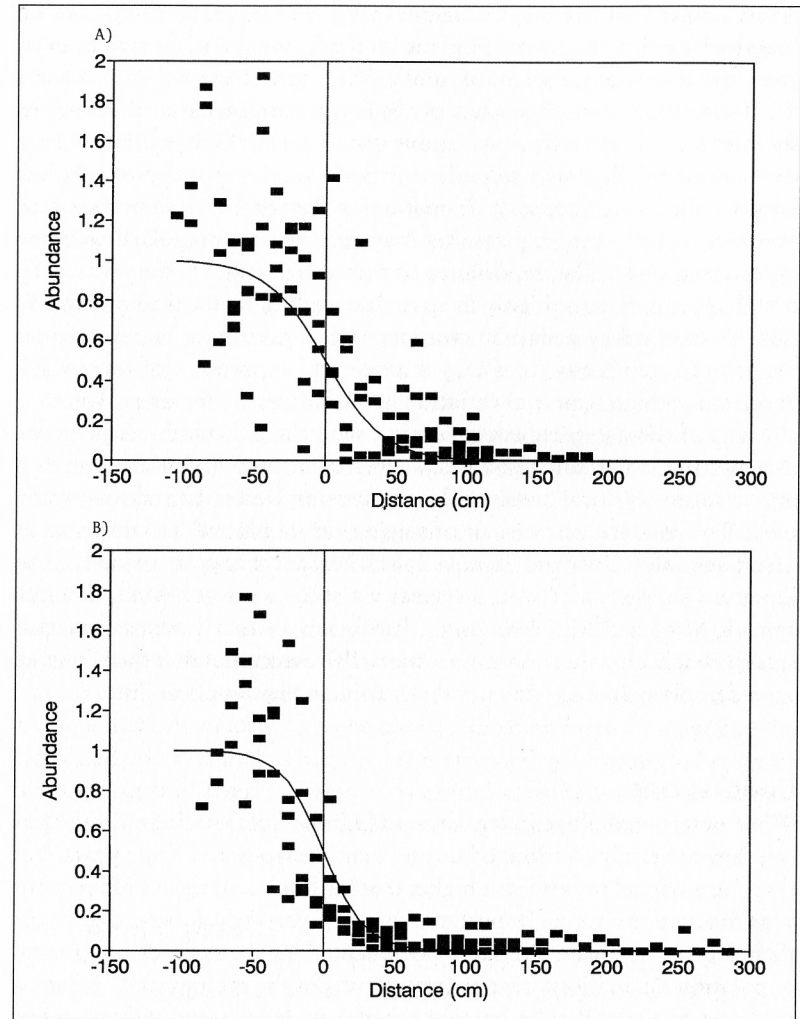


Figure 4.11 Seed dispersal across an annual plant removal boundary. The abundance of emerging seedlings of all species is plotted against distance from the boundary. (A) Dispersal down a gently sloped bajada; (B) Dispersal up a gently sloped bajada.

desert winter annuals. High densities of desert annual seedlings can be found where tiny fragments of plant litter accumulate in clumps or even lines that represent the edges of rainfall sheet flow. It would appear from the distribution of such patches of seeds and seedlings that dispersal in sheet flow can take seeds considerable distances. We find seed-laden litter deposits on the downhill side of 10 m wide total-removal plots. At our Desert Laboratory site, such dramatic seed movement does not seem to occur frequently in most plots. Yet it appears to occur regularly in a few exceptional plots. The importance of such long-distance sheet wash dispersal appears to vary highly in space, depending on local runoff conditions determined by surface microtopography and soil water penetration. Occasional very heavy rains may increase the importance of sheet wash and generate high temporal variation in seed dispersal distances. The conclusions of these experiments, together with those from the experiment that partitioned seedling sources, suggest that seed dispersal is often a minor source of local seedling density on our Desert Laboratory study plots. This is consistent with prior suggestions of limited seed dispersal in desert annuals (Ellner and Shmida 1981). Yet, another point of view in the literature suggests that seed dispersal via sheet wash (or wind) is widespread (Mott and McComb 1974; Reichman 1984). It seems from our studies that both points of view are partially correct, but that there may be considerable spatial and temporal variation in their applicability.

Conclusions

While desert annuals represent around half the flora of the Sonoran Desert, they are easily overlooked during many seasons and some years. Yet they are a critical resource for higher trophic levels and their wide year-to-year fluctuations are an important source of variation for the organisms that depend on them. We have documented 15 years of desert annual population fluctuations in an ongoing study of the ecology and evolution of desert annuals. Besides gaining a better understanding of how desert annuals respond to variation in weather between years, we have documented germination fractions of desert annuals in natural field sites. Delayed germination is greater for those species that experience more year-to-year demographic variation, as predicted by life history theory, and larger-seeded species experience less year-to-year variation in reproductive success. These are the first long-term plant population dynamic data

to confirm these theoretical predictions for bet hedging. Desert annuals also appear to have many properties necessary for temporal-variance-mediated species coexistence. These include delayed germination, with germination fractions varying among years in different ways for different species. Also, there is a correlation between a higher germination fraction for a given species and the years in which it has higher reproduction. Competitive hierarchies shift among years, densities, and moisture levels, which should contribute to temporal-variation-based coexistence. Dispersal may be a less important source of seedlings than delayed germination for desert annuals. Both vegetation cover and open habitats appear to provide population sources and sinks for different species that have a habitat preference for one or the other. While seed dispersal of desert annuals appears often to be quite limited, at certain places and times seeds may travel considerable distances in sheet flow during heavy rains.

Desert annuals provide a tractable system for studying many aspects of plant population and community ecology in variable environments. Since they are small, working with many of them is easy. By virtue of being annuals, their vegetative life cycle is short and they have the many convenient properties that attract researchers to short-lived plants. They occur as persistent dominant members of relatively undisturbed natural communities. Thus, their responses to temporal variation can be easily studied in nature. Also, since water availability is an important limiting factor, causes of population fluctuations may be less obscure than for some plant populations and communities. The long-term availability of protected research stations like the Desert Laboratory is critical to our growing understanding of the population and community ecology of desert annuals.

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5 Form and Function of Cacti

Park S. Nobel and Michael E. Loik

Perhaps no other image of the Sonoran Desert is as enduring as that of the saguaro cactus (*Carnegiea gigantea*). The saguaro and other cacti are uniquely adapted to the characteristic droughts and thermal extremes of the region. Precipitation rarely exceeds 300 mm per year, and a particular location may not receive any rainfall for many months. High temperatures can reach 70°C at the soil surface, and temperatures below 0°C can occur for up to 30 days per year. Various animals can escape the harsh extremes of the physical environment of the Sonoran Desert, but plants are sessile and therefore must tolerate the extended periods of drought and extremes of temperature.

The approximately 140 species of cacti native to the Sonoran Desert are exclusively perennial stem succulents (Shreve and Wiggins 1964). Their primary physiological adaptation to drought is the utilization of Crassulacean acid metabolism (CAM), in which stomatal opening and CO₂ uptake occur mainly at night, when air and tissue temperatures are cooler than during the daytime (Nobel 1988). This results in less water loss and a higher water-use efficiency (mass of CO₂ taken up per mass of water lost) than for C₃ or C₄ plants (Nobel 1991). Morphological adaptations of cacti to drought and temperature extremes include stem succulence and orientation, ribs and tubercles, spines and apical pubescence, shallow roots, and association with "nurse plants." This chapter will review such features related to the form of cacti and how they function to increase survival in the often harsh environment of the Sonoran Desert.