

SEED DISPERSAL OF DESERT ANNUALS

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Abstract. We quantified seed dispersal in a guild of Sonoran Desert winter desert annuals at a protected natural field site in Tucson, Arizona, USA. Seed production was suppressed under shrub canopies, in the open areas between shrubs, or both by applying an herbicide prior to seed set in large, randomly assigned removal plots (10–30 m diameter). Seedlings were censused along transects crossing the reproductive suppression borders shortly after germination. Dispersal kernels were estimated for *Pectocarya recurvata* and *Schismus barbatus* from the change in seedling densities with distance from these borders via inverse modeling. Estimated dispersal distances were short, with most seeds traveling less than a meter. The adhesive seeds of *P. recurvata* went farther than the small *S. barbatus* seeds, which have no obvious dispersal adaptation. Seeds dispersed farther downslope than upslope and farther when dispersing into open areas than when dispersing into shrubs. Dispersal distances were short relative to the pattern of spatial heterogeneity created by the shrub and open space mosaic. This suggests that dispersal could contribute to local population buildup, possibly facilitating species coexistence. Overall, these results support the hypothesis that escape in time via delayed germination is likely to be more important for desert annuals than escape in space.

Key words: desert annuals; dispersal kernel; escape in time and space; inverse modeling; *Pectocarya recurvata*; removal experiment; *Schismus barbatus*; seed dispersal; Sonoran Desert; species coexistence.

INTRODUCTION

Increased interest in spatial ecology has focused attention on the critical role seed dispersal plays in many aspects of plant population and community dynamics (Nathan and Muller-Landau 2000). Seed dispersal helps offspring escape competition with conspecifics and kin, reduce risk in spatiotemporally varying environments, and reach safe sites meeting specific biotic or abiotic habitat requirements (Venable and Brown 1993, Schupp and Fuentes 1995, Wenny 2001, Levin et al. 2003). It also influences abundance or persistence in gap phase or metapopulation dynamics (Hanski 2001, Premoli and Kitzberger 2005), rates of colonization and invasion (Cain et al. 2000, Neilson et al. 2005), gene flow and population differentiation (Levin 1981, Ennos 1994), and species coexistence and diversity (Tilman 1994, Snyder and Chesson 2004). Given that many of these effects are important to offspring fitness, seed shadows and dispersal morphology are under strong natural selection (Donohue et al.

2005). Measuring dispersal is more difficult than measuring most other plant life-history parameters (Bullock et al. 2006). Thus, empirical documentation of where seeds actually go has lagged behind other empirical aspects of plant demography and life history, despite the strong theoretical interest in dispersal.

Seed dispersal of desert annuals is of special interest because desert annuals have been increasingly investigated as model systems for understanding life-history evolution, the evolution of bet hedging, competitive interactions, source–sink dynamics, and species coexistence mechanisms (Venable and Lawlor 1980, Ellner and Shmida 1981, Venable and Brown 1988, Chesson and Huntly 1989, Gutterman 1994, Boeken and Shachak 1998, Kadmon and Tielborger 1999, Chesson 2000, Snyder 2006). Researchers are particularly interested in the partial substitutability of dispersal and dormancy as bet-hedging adaptations in spatially and temporally varying environments (Venable and Brown 1988, Snyder 2006). It has often been suggested that desert annuals rely more on dormancy than dispersal because precipitation is a dominant source of variability and it is easier to wait for favorable precipitation than it is to chance upon it via dispersal (Venable and Lawlor 1980, Ellner and Shmida 1981).

We are especially interested in knowing the role of seed dispersal in competitive coexistence with regard to

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spatial environmental variation in this system (Chesson 2000). How does the spatial scale of dispersal interact with the spatial scale of environmental heterogeneity to promote or reduce species coexistence in this community (cf. Snyder and Chesson 2004)? If species have different responses to the environment and seed dispersal is low enough, population density for a particular species will build up in local sites when and where it is favored (e.g., under shrub canopy vs. open in desert systems). This potentially contributes to species coexistence by increasing the strength of intraspecific competitive interactions relative to interspecific interactions. In contrast, if dispersal is high relative to the spatial scale of environmental heterogeneity, the effects of local buildup on competition may be weak (Chesson 2000). While various attempts have been made to document seed bank dynamics of desert plants (Philippi 1993, Pake and Venable 1996, Clauss and Venable 2000, Moriuchi et al. 2000, Arroyo et al. 2006), little is known quantitatively about dispersal distances and where seeds actually go.

One line of thinking, based on the argument above that dispersal is less useful in deserts, is that desert annual seed dispersal is quite limited. Desert annuals are known to have well-developed mechanisms for dispersal in time (dormancy) that can alleviate the need for dispersal in space, and surveys reveal a lower frequency of species with morphological structures favoring dispersal in desert plants than in nondesert plants (Ellner and Shmida 1981, Ehrman and Cocks 1996). An alternative expectation is that seed dispersal is widespread due to the open structure of the vegetation and the importance of precipitation runoff and wind in deserts (Mott and McComb 1974, Reichman 1984). Evidence for this expectation largely comes from the observance of seeds in places where wind or water is likely to have deposited them. There have not been explicit measurements of dispersal kernels for desert plants that could help resolve these conflicting expectations.

For this study, we quantified effective seed dispersal in a desert annual community that has been intensively investigated with regard to long-term population dynamics (Venable and Pake 1999), species interactions (Pantastico-Caldas and Venable 1993), species coexistence mechanisms (Pantastico-Caldas and Venable 1993, Venable et al. 1993), bet hedging (Pake and Venable 1996, Venable 2007), and the physiological mechanisms underlying demographic variation (Angert et al. 2007, Huxman et al. 2008; G. A. Barron-Gafford, A. L. Angert, D. L. Venable, A. P. Tyler, K. L. Gerst, and T. E. Huxman, *unpublished manuscript*). Seed production was systematically suppressed in randomly assigned plots in order to measure seed dispersal across the plot borders. We estimated fine-scale dispersal from measurements of seedling densities in the following germination season as a function of distance from the border. Specifically, dispersal was estimated through inverse modeling involving the numerical integration over the

seed source area to obtain total seed rain expected at different distances from the border.

MATERIALS AND METHODS

Study site and species

This investigation was conducted on the northern flank of Tumamoc Hill at the Desert Laboratory of the University of Arizona in the Sonoran Desert, Arizona, USA (elevation 700 m) during December of 1993. Mean annual precipitation at this site is 300 mm with roughly half falling during the “summer monsoons” (July–September) and the rest scattered through October–April, with May and June typically being drier. The soils on this northern flank are sandy clay derived from igneous rock. The principal perennial species are *Larrea tridentata*, *Ambrosia deltoidea*, *Opuntia fulgida*, *O. phaeacantha*, and *Fouquieria splendens*. The principal winter annuals encountered in this year at the study site were *Pectocarya recurvata* (constituting 49% of the 18 360 seedlings censused), *Schismus barbatus* (32%), and *Bromus rubens* (13%). Other species that together represent 7% of the seedlings censused include *Cryptantha* spp., *Daucus pusilus*, *Spermolepis echinata*, *Eriastrum diffusum*, *Plantago insularis*, *Plantago patagonica*, *Sisymbrium irio*, *Stylocline micropoides*, and *Bowlesia incana*. These seedlings germinated in response to 2.8 cm precipitation on 15 November and were censused during the first week of December. Seedling mortality to this point was negligible (<5%). Analyses were done on *Pectocarya recurvata* and *Schismus barbatus* because these species accounted for 81% of the seedlings encountered and thus each had sufficient data for separate analysis. *Pectocarya recurvata* is native to the desert areas of Baja California and Sonora, Mexico, southeastern California, southern Arizona, and southern Nevada, USA. It has small, recurved seeds (0.95 ± 0.031 mg [mean \pm SE]; Pake and Venable 1996) with bristles suggestive of adhesive dispersal by animals (epizoochory; cf. van der Pijl 1972). *Schismus barbatus* is an introduced species native to Africa and Eurasia that has become widespread in arid regions in southwestern United States and northwestern Mexico. *Schismus barbatus* was first collected in Arizona in 1926 and became naturalized to the central part of the state by 1931 and the southern part by 1949. It was not known in California until 1935 (Burgess et al. 1991). *Schismus barbatus* has very small seeds (0.08 ± 0.0055 mg; Pake and Venable 1996), with no obvious dispersal adaptation other than small size and large number.

Experimental inhibition of reproduction and dispersal across boundaries

To quantify seed dispersal we utilized removal plots that were established in 1990 for a different field experiment. For this other experiment, reproduction of winter annuals had been inhibited each year since the spring of 1990 within large removal plots (10–30 m in diameter) by spraying the annuals with RoundUp

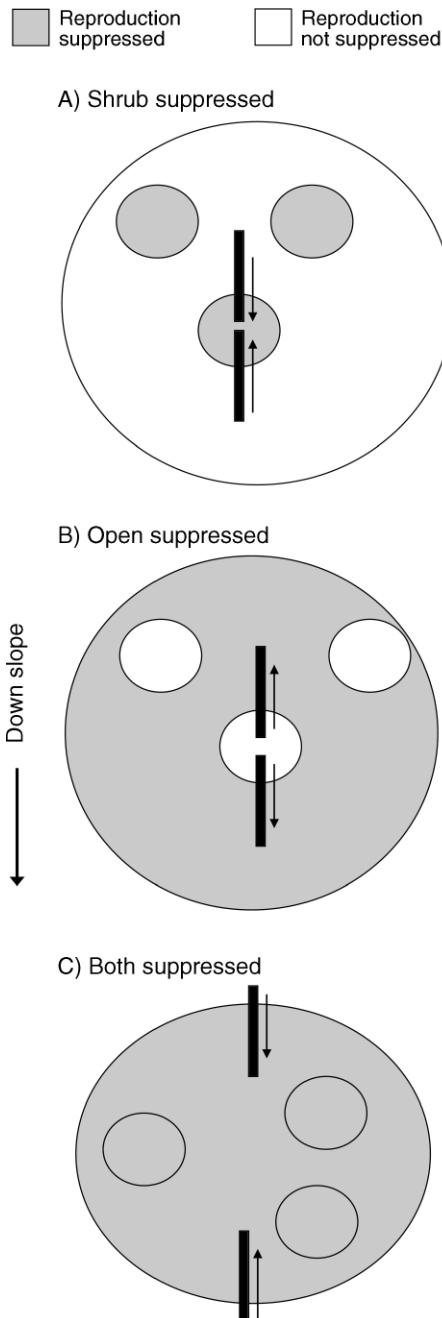


FIG. 1. Annual plant reproduction was suppressed within large removal plots (~30 m diameter). (A) Diagram of a plot in which annual plant reproduction was suppressed under shrubs (shrub-suppressed treatment). (B) Diagram of a plot in which annual plant reproduction was suppressed in the open, outside of shrub canopies (open-suppressed treatment). (C) Diagram of a plot in which all annual plant reproduction was suppressed (both under shrubs and in the open). Census transects were 0.1 m wide and 6–9 m long extending parallel to the slope ~1 m into the zone with no reproductive suppression (though extent into or out of shrubs was limited by the size of the shrub canopy). Half of the transects measured dispersal upslope and half downslope (indicated by small arrows pointing upslope or downslope). This investigation was conducted on the northern flank of Tumamoc Hill at the Desert Laboratory of the University of Arizona in the Sonoran Desert, Arizona, USA.

herbicide (Monsanto, St. Louis, Missouri, USA) prior to seed set. Plot boundaries were marked on the ground with paint and used consistently from year to year to guide spraying. Each year plants were repeatedly sprayed prior to reproduction until no living plants could be found. In the experiment there were four treatments (Fig. 1): (1) plots in which winter annual reproduction was suppressed under shrubs (shrub-suppressed plots), (2) plots in which winter annual reproduction was suppressed in the open, outside the crowns of shrubs (open-suppressed plots), (3) plots in which all winter annual reproduction was suppressed (both-suppressed plots), and (4) plots with no treatment (control plots).

In 1993 we censused seedling abundances within 28 transects at these plots. There were two transects per plot (one upslope and one downslope; Fig. 1), and a total of eight transects in the open-suppressed plots, six in the shrub-suppressed plots, 10 in the both-suppressed plots, and four in the control plots. Each transect (except the controls, which will not be considered further) extended from a zone in which reproduction was not suppressed across a painted border perpendicularly into a suppression zone. Each transect was 10 cm wide, extending roughly 1 m into the zone with no suppression. We carefully searched 5–8 m into the removal area, though seedling numbers generally declined to zero by 3–4 m. We recorded the numbers of seedlings of each species in each 10-cm interval along each transect. The transects ran parallel to a shallow slope that varied from 1.8° to 5° over the site, with the removal area on the downslope side for half of the transects and on the upslope side for the other half (Fig. 1).

Independent measurement of the residual seed bank on these plots showed that it was negligible. This was not surprising since we permitted normal germination but suppressed reproduction for the three years prior to this experiment. In addition, reproductive suppression began immediately following a three-year drought during which germination and low seed production had already reduced seed banks (Venable and Pake 1999). For these reasons we assumed that the residual seed bank that existed before the experiments did not contribute significantly to observed seedling densities. Specifically, our fitted models assume that all seedlings are the offspring of plants growing in the non-suppressed areas.

We analyzed seedling data for *P. recurvata* and *S. barbatus*, which together constituted 81% of observed seedlings. The densities of the other species were too low and sporadic to meet our model assumptions and give adequate fits. We do not report results for fits in cases in which seedling densities outside the suppressed area were exceptionally low (<2 seedlings/cm²), as fits did not converge in these cases. This left us with 20 transects for *P. recurvata* (six of both-suppressed, eight of open-suppressed, and six of shrub-suppressed) and 21 for *S. barbatus* (eight of both-suppressed, seven of open-

suppressed, six of shrub-suppressed). See Supplement 1 for data.

In the both-suppressed plots, we measured seedling densities on transects crossing the borders of the large 10–30 m diameter removal areas. For these cases we assumed a linear border, since any curvature was small relative to transect length. For the open-suppressed and shrub-suppressed plots, we measured seedling densities on transects crossing the borders of individual *Larrea* shrubs. In these cases we assumed a curved border with the target area being a circle in the shrub-suppressed treatments and the source area being a circle in the open-suppressed treatments. Diameters used in each case were the individual measured shrub diameter (0.9–2.3 m).

Fitting an individual dispersal kernel from the population dispersal distribution

In each transect seedling densities changed approximately sigmoidally at the exclusion border (Appendix B: Fig. B1). We used this data to infer the average dispersal kernel for individual plants under the assumption that an area with reproductive plants can be well approximated as one continuous area source with constant seed production per unit area (a reasonable assumption when individual reproductive adults are sufficiently small and evenly distributed). Seeds arriving at a given distance, w , from the exclusion border include seeds coming from plants at distance w on the edge of the border plus seeds from all plants at distances, $z > w$ on the other side of the border. While there is just one point on the border at distance w from a dispersed seed in the exclusion zone, there is an arc of points on the other side of the border at any distance $z > w$, and the length of this arc increases with z (Fig. 2). Expected seedling density at different positions relative to an exclusion border can be calculated from a known individual-plant dispersal kernel appropriately integrated over the entire area of the seed source (the area on the other side of the border). Our problem was the inverse: to infer the parameters of a dispersal kernel that best generated the observed pattern of seedling densities along transects perpendicular to the border.

To find the individual-plant seed dispersal kernels most consistent with the observed spatial pattern of seed densities (dispersed from many plants), we first derive the spatial patterns that would be expected under different dispersal kernels. We calculated such expectations for points at different distances inside or outside borders separating areas with reproductive plants from those without reproductive plants. This was done for the case of straight-line borders as well as for circular borders. We assume that individual reproductive adults are sufficiently small and common that an area with reproductive plants can be well approximated as one continuous area source with seed production F per unit area, rather than a set of individual plant point sources.

Let $p(z)$ be the distance distribution, or one-dimensional individual plant seed dispersal kernel, such that

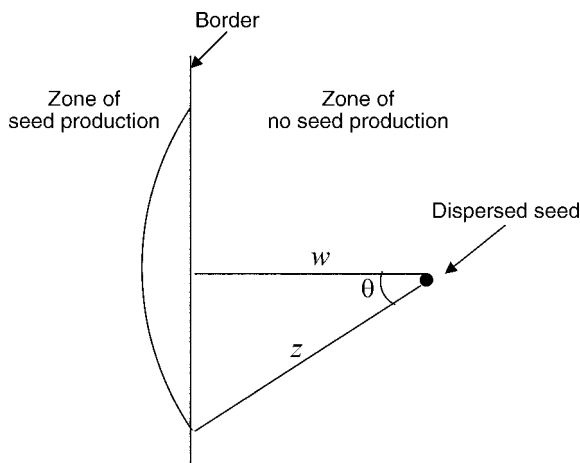


FIG. 2. A seed at distance w from the border has an arc of seed sources at distance $z > w$, and the length of this arc (and thus the number of seed sources) increases with z . This is the case of a straight-line border; circular borders were also considered.

$p(z)dz$ is the probability of a seed landing in an annulus of width dz a distance z from its source plant. Note that this is equal to $2\pi z$ times the two-dimensional dispersal kernel giving the probability of a seed landing in a unit area.

Suppose there is a straight-line border separating an area with reproductive plants from an area without such plants. Let w be the distance from this border, with positive values representing distances beyond the border (on the side where there are no reproductive plants) and negative values representing distances inside the border (in the area with reproductive plants). Then the total seed rain per unit area with a straight-line border varies with w as

$$S_{\text{straight}}(w) = F \begin{cases} \frac{1}{\pi} \int_w^\infty \arccos\left(\frac{w}{z}\right) p(z) dz & w > 0 \\ 1 - \frac{1}{\pi} \int_{-w}^\infty \arccos\left(\frac{-w}{z}\right) p(z) dz & w < 0 \\ \frac{1}{2} & w = 0. \end{cases}$$

The derivation of these integrals is quite straightforward. In Fig. 2, at a distance z from the point where a seed has landed in the exclusion zone ($w > 0$), a proportion $2\theta/2\pi$ of a circle around that seed is contained within the area where seeds are produced. θ is equal to $\arccos(w/z)$. Thus, the proportion of the circle that is located in the zone of seed production is $\arccos(w/z)/\pi$. $F \times p(z)$ is equal to the total seed rain going distance z from a plant producing F seeds and thus also equal to total seed rain arriving from a plant at distance z to a point. If all the points at distance z from an arrival location are producing F seeds per unit area,

we need only integrate $F \times \arccos(w/z)/\pi \times p(z)$ from w to infinity to obtain total seed rain arriving. The other parts of the equation for seedling density as a function of distance from a linear border can be derived similarly.

In the same way, we derived equations for seedling density as a function of distance from the border of a circular area within which or outside which reproduction was suppressed. First consider a circular area within which there are no reproductive plants and outside which there are reproductive plants producing seeds at density F per unit area (like our shrub reproduction suppression treatment). Let R be the radius of the circle and w be the distance from the border of the circle, with positive values representing points outside the circle and negative values points inside the circle. Then the total seed rain per unit area varies with w as

$$S_{\text{circleempty}}(w) = \begin{cases} 1 - \frac{1}{\pi} \int_w^{2R+w} \arccos \left[\frac{(R+w)^2 - R^2 + z^2}{2(R+w)z} \right] p(z) dz & w > 0 \\ \int_{2R+w}^{\infty} p(z) dz & \\ -\frac{1}{\pi} \int_{-w}^{2R+w} \arccos \left[\frac{R^2 - (R+w)^2 - z^2}{2(R+w)z} \right] p(z) dz & w < 0 \\ \frac{1}{2} & w = 0. \end{cases}$$

If instead there are no reproductive plants outside a circular area, only within it (as in our open-suppressed treatment), then the total seed rain per unit area at a point a distance w from the border (with positive values representing points outside the circle and negative values points inside) is

$$S_{\text{circlefull}}(w) = \begin{cases} \frac{1}{\pi} \int_w^{2R+w} \arccos \left[\frac{(R+w)^2 - R^2 + z^2}{2(R+w)z} \right] p(z) dz & w > 0 \\ \int_0^{2R+w} p(z) dz & \\ -\frac{1}{\pi} \int_{-w}^{2R+w} \arccos \left[\frac{R^2 - (R+w)^2 - z^2}{2(R+w)z} \right] p(z) dz & w < 0 \\ \frac{1}{2} & w = 0. \end{cases}$$

To fit the dispersal kernel, $p(z)$, we searched for the function providing the best fit to the observed seed rain

at distances w from borders of areas where reproduction was suppressed. Specifically, we searched for the kernel that maximized the likelihood of the observed seed density at distance w , $R(w)$, under Poisson errors. (The Poisson was superior to the normal as a model of the residuals.) This is exactly analogous to previous inverse modeling of seed, seedling, and pollen dispersal kernels in tree stands in which individual adult plants are treated as point sources (Ribbens et al. 1994, Tufto et al. 1997, Clark et al. 1998). The MATLAB code (MathWorks, Natick, Massachusetts, USA) used for fitting the dispersal kernels is provided in Supplement 2.

We fit 1-D exponential, 2-D exponential, generalized exponential (Ribbens et al. 1994), gamma, 2-D Gaussian, inverse power (Clark et al. 2005), lognormal (Greene et al. 2004), Wallace (Wallace 1966), Weibull (Greene et al. 2004), Student t (“2Dt”; Clark et al. 1998), and a one-parameter version of the Student t (with p set at 1) dispersal kernels to all of our transect data using maximum likelihood. Usually several kernels gave very similar-looking curves with similar likelihood values (Appendix A). Some kernels failed to converge on some of the data sets, suggesting a poor fit. The 1-D exponential kernel and one-parameter version of Student t kernel (Clark et al. 2004) converged well in all cases and had consistently high likelihood values. The one-parameter Student t had slightly better likelihood values (average: 76.0764 vs. 77.366 for 1-D exponential). Thus, we report results for maximum likelihood fits of the one-parameter Student t kernel assuming a Poisson error distribution. That is, we fitted the probability, $p(z)$, that a seed goes a distance z with the function

$$p(z) = \frac{2z}{u \left(1 + \frac{z^2}{u} \right)^2}.$$

The mean dispersal distance under this distribution is $\Gamma(1.5)\Gamma(0.5)\sqrt{u} \approx 1.571\sqrt{u}$, the median is \sqrt{u} , and the 95th percentile is $\sqrt{19u} \approx 4.359\sqrt{u}$.

Subsequent to fitting these curves, a split-split-plot ANOVA was conducted with SAS Proc MIXED (SAS Institute, Cary, North Carolina, USA) on the natural log of the fitted dispersal parameter (u) to test for differences between species, reproductive inhibition treatments (shrub-suppressed, open-suppressed, and both-suppressed plots), and slopes. Slope was treated as discrete (upslope vs. downslope), then reanalyzed as a continuous variable using the actual mean slopes. Satterthwaite’s approximate degrees of freedom were calculated for the appropriate error terms (resulting in fractional degrees of freedom). Reproductive inhibition treatments were assumed to be assigned to larger sampling units in a completely randomized fashion. One uphill slope and one downhill slope were measured within each larger sampling unit, and species were measured within each slope.

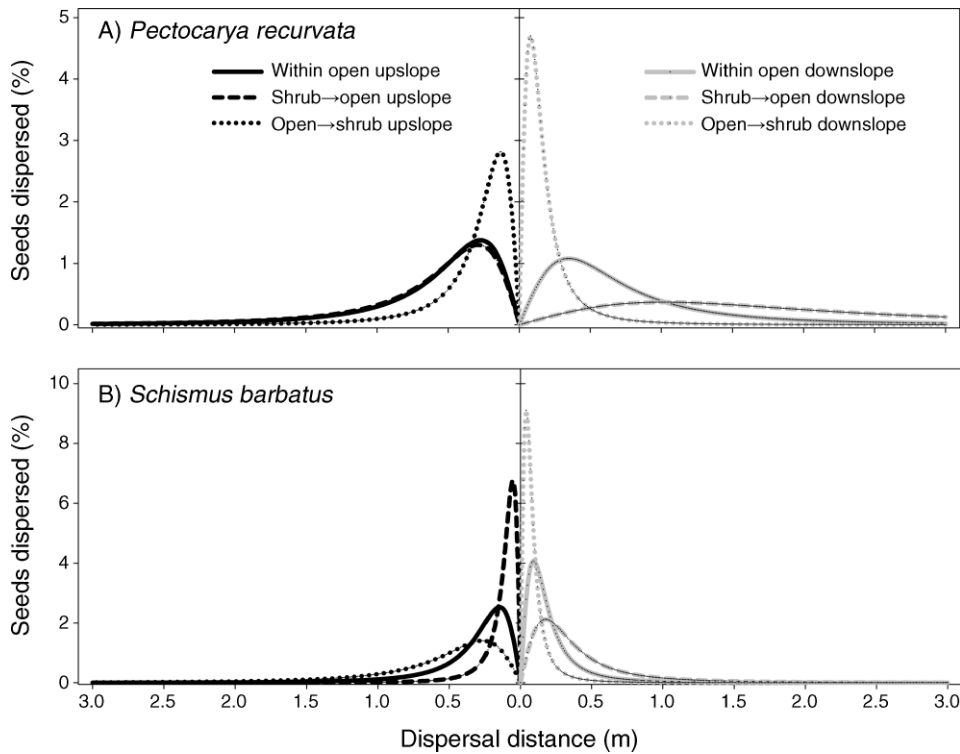


FIG. 3. Graphs of the fitted one-dimensional Student *t* seed dispersal kernels (i.e., radially integrated distance distributions) for (A) *Pectocarya recurvata* and (B) *Schismus barbatus*. Curves are for dispersal from under shrub canopy to the open, open to shrub, and within open areas extending upslope (toward the left of the graph) and downslope (toward the right of the graph). Though the total number of seeds at a distance peaks some distance away from the source (as shown here), the number of seeds arriving per unit area declines monotonically with distance from the source.

RESULTS

The population dispersal curves gave a good fit to the raw data for both species (Appendix B: Fig. B1). Seeds of *Pectocarya recurvata* and *Schismus barbatus* traveled short distances on average, with most seeds traveling less than a few meters (Fig. 3; Table 1).

Most of the variance in the fitted dispersal parameter is explained by significant differences among species, removal treatments, and the interaction of slopes with

removal treatments (Appendix B: Table B1A). When slope is coded as a continuous variable, the main effect of slope becomes more significant than the interaction of slope with removal treatment (Appendix B: Table B1B). This indicates that average slope differences among removal treatments (treatment averages: both, 5°; open, 4.3°; shrub, 1.8°) were causing the interaction of slope with removal to mask the true slope effect in the first analysis. Seeds go farther downhill than uphill, and

TABLE 1. Log-transformed dispersal parameter, $\ln(u)$, of the Student *t* kernel (Clark et al. 1999), for the different removal treatments and slopes for *Pectocarya recurvata* and *Schismus barbatus*.

Treatment, by species	Upslope dispersal					Downslope dispersal				
	$\ln(u)$	SE	Dispersal distance (m)			$\ln(u)$	SE	Dispersal distance (m)		
			Median	Mean	95%			Median	Mean	95%
<i>P. recurvata</i>										
Both	7.71	0.67	0.47	0.74	2.06	8.19	0.67	0.60	0.94	2.62
Open	7.83	0.59	0.50	0.79	2.18	10.35	0.59	1.77	2.77	7.70
Shrub	6.28	0.68	0.23	0.36	1.01	5.23	0.68	0.14	0.22	0.60
<i>S. barbatus</i>										
Both	6.49	0.52	0.26	0.40	1.12	6.84	0.67	0.31	0.48	1.33
Open	5.54	0.67	0.16	0.25	0.69	7.67	0.59	0.46	0.73	2.01
Shrub	4.52	0.68	0.10	0.15	0.42	3.93	0.68	0.07	0.11	0.31

Note: This investigation was conducted on the northern flank of Tumamoc Hill at the Desert Laboratory of the University of Arizona in the Sonoran Desert, Arizona, USA.

distance traveled increases with the magnitude of the drop in slope (increase in $\ln(u)$ with each additional degree of downhill slope = 0.35). The adhesive *P. recurvata* seeds traveled farther on average than the small-sized *S. barbatus* seeds, which have no obvious dispersal adaptation (Appendix B: Table B2). Removal treatments differed, mainly due to lower dispersal on average from open to shrub habitats. Dispersal from shrub to open was higher than within open habitats, but this was not significant with Tukey-Kramer adjusted pairwise comparisons (Appendix B: Table B2).

DISCUSSION

Dispersal distances and differences between species and treatments

The mean dispersal distance for *Pectocarya recurvata* averaged 0.70 m overall or 1.48 m considering only dispersal within open sites. This is similar to the values reported by Willson (1993) for herbaceous plants with morphological adaptations for wind dispersal, which averaged 0.92 m, and somewhat greater than that of herbaceous species with no apparent dispersal mechanism, which averaged 0.49 m. (Willson [1993] did not summarize data for species with morphological structures aiding adhesive dispersal by animals.) Mean dispersal distance for *S. barbatus* averaged 0.29 m (0.43 m within open sites), which is lower than any of Willson's (1993) means. However, these should not be considered fixed species values. Local dispersal is likely to vary spatially and temporally, even within a restricted geographic area. Our treatment means varied considerably with slope and habitat. Mean *P. recurvata* dispersal distance from our transects ranged from 2.77 m for downslope dispersal from shrubs to 0.22 m for dispersal upslope into shrubs, and *S. barbatus* treatment means ranged from 0.72 m for downslope dispersal out from shrubs to 0.11 m for downslope dispersal into shrubs. Nonetheless, we must conclude that the majority of these desert annual seeds do not travel very far. This view is reinforced by comparison of our values with those given by Willson for trees; on average trees disperse more than an order of magnitude greater distances (Willson 1993).

Seeds of *P. recurvata*, which has adaptations for adhesive dispersal, moved farther on average than seeds of *S. barbatus*, which have no apparent adaptation for dispersal. While this might initially seem intuitive, it is unlikely that adhesion was involved in the movement of most *P. recurvata* seeds over these short distances. Most adhesive seeds do not manage to attach to passing animals, and passive dispersal by falling from the parent followed by secondary dispersal via wind or water is more typical. Seed movement along our fine-scale transects was greater in the downslope than upslope direction, and movement distance increased with the inclination of the slope, further suggesting the dominance of passive dispersal aided by gravity. Thus it

would have been reasonable to expect the lighter *S. barbatus* seeds to have moved farther.

The greater movement of seeds from shrubs to open, and within the open, than from open sites to shrubs could have a variety of causes. The surfaces beneath shrubs at our site were not usually elevated above the surrounding open areas, as sometimes occurs in desert habitats. It is possible that seed removal by granivores was higher under shrubs, as has been reported at some sites (e.g., Kelt et al. 2004). However, shrub vs. open foraging preferences of granivores have been shown to be species-specific (Brown 1988), and other studies have documented that the materials that accumulate under desert shrubs and trees sometimes provide a refuge for seeds (e.g., Aerts et al. 2006). Alternatively, the area under shrubs could represent a relative "dead zone" for dispersal vectors such as wind or animals and litter buildup under shrubs could also inhibit the passive movement of seeds.

Methodological advances

In this study we quantified ultimate dispersal distance from a boundary that we created by inhibiting seed production for several years on one side of a linear boundary. Our boundaries were created by spraying an herbicide to inhibit reproduction of otherwise intact plants on one side of an arbitrarily determined boundary in a previously unbounded population. This setting closely approximates what can be expected for continuous natural populations (i.e., this is neither a natural habitat boundary nor has the soil topography or perennial vegetation been altered in any way). This approach combines the strengths of techniques that directly measure distance (for we have directly measured a minimum dispersal distance from the boundary) with the greater naturalism of other inverse modeling approaches. Previous inverse modeling estimates of seed dispersal have dealt only with point sources (individual reproductive plants) and thus were impractical for use with many herbaceous plants. Here we show how numerical integration can be used to apply the same techniques to plants that are essentially continuously distributed within particular mapped areas of our study site. This provides a new technique for the empirical study of seed dispersal with considerable potential for high-density herbaceous plants.

Seedling shadow vs. seed shadow

We measured what Pleasants and Jurik (1992) have called the "seedling shadow." Measuring seedling positions guarantees that we have located the final seed destination following all dispersal activities. However, measuring the distance of seedlings from parents is an indirect way of measuring the distance seeds move from parents, and these could differ for a variety of reasons. If seeds or seedlings are systematically eaten or die at certain dispersal distances, seedling distances would be a biased measure of seed dispersal distances. Still, seedling

distances represent “effective dispersal distance,” i.e., the distances moved by seeds that were successful at reaching the next life-history stage. If seeds that move different distances have systematically different dormancy times, such that they disperse differently through time, seedling distances would be a biased estimate of seed distances, unless the population was in temporal equilibrium with as many old seeds coming out of dormancy as new ones going in. We do not think that either of these phenomena was likely to be systematically biasing our results. Seeds moving within open habitat are mostly traveling small distances and the target sites where they arrive are fairly homogeneous, differing systematically from the source sites only in the inhibition of annual plant reproduction. Also, we do not expect density-dependent seedling mortality as seedlings were just over two weeks old at the time of censusing; only trace levels of mortality (<5%) had occurred on nearby mapped plots used in a different set of experiments. We have no reason to expect differential dormancy at different distances, either. Thus the seedling shadow is likely to give a good representation of the seed shadow, but with some caveats for shrub/open dispersal (discussed in *Dispersal distances and differences between species and treatments*).

The scale of seed dispersal in desert annuals and its ecological implications

The results from our fine-scale transects support the suggestion of Ellner and Shmida (1981) that seed dispersal in desert plants is low. Ellner and Shmida’s (1981) hypothesis was based principally on an adaptive scenario: the amount and timing of rainfall is a dominant and variable environmental factor for desert plants, yet the spatial scale of rainfall is larger than the dispersal distances most plants can achieve with any reliability. Thus, plants may be more successful dispersing in time via seed dormancy, reducing selection for dispersal structures. These authors also point out that deserts have open canopies that often provide abundant safe sites for germination near the parent. This contrasts with the disturbance-driven pattern of establishment, which often occurs for plants of closed vegetation and selects for higher dispersibility (Venable et al. 1998).

Another point of view suggests that seed dispersal in the desert via sheet wash or wind is widespread, potentially involving many seeds and great distances (Mott and McComb 1974, Reichman 1984). Ellner and Shmida (1981) mention a case in which all of the seeds from a dense stand of *Aspergularia diandra* on a slope in the Negev were washed away by heavy rains. It has even been suggested that antidispersal adaptations sometimes evolve in desert plants, partly to anchor against such seed loss (Zohary 1962). Indeed, seeds of desert winter annuals can be found where plant litter accumulates in clumps or even in lines at the edges of sheet flow. The distribution of such patches of seeds and seedlings suggests that dispersal in sheet flow can take seeds

considerable distances (>10 m). In a both-suppressed treatment (different from the ones used for the transects reported here) some patches of seedlings were encountered 12 m from the nearest upslope border. Most of these patches were associated with spaces between rocks, depressions in which water or small fallen branches accumulate and act as leaf litter traps. The most frequent category was between rocks, while the largest patches were found below shrubs. At our Desert Laboratory site such dramatic seed movement does not seem to happen frequently in most plots, though it is typical of a few exceptional plots not included in this study. The occurrence of such long-distance dispersal appears to be quite variable in space, depending on local runoff conditions, which are determined by surface microtopography and soil water penetration. Occasional heavy rains may increase the importance of sheet wash, generating high temporal variation as well.

The idea that dispersal in desert plants is limited and the idea that seeds move widely via sheet wash may not be as contradictory as they first seem. Our data indicate that at our study site, most seeds travel very limited distances in the year of study. Yet some seeds at other times and places may travel greater distances via sheet wash, and adhesion to animals moves others long distances also. This would be consistent with other plant studies that indicate different dispersal processes occurring at different spatial scales and rare long-distance events with particularly variable spatial and temporal occurrence (Clark et al. 1999, Cain et al. 2000, Higgins et al. 2003). Thus the answer to the population dynamic question “where do the great majority of seeds go?” may be “a few meters away at best.” We have previously documented considerable delayed germination in these and other species in this guild of desert annuals at this study site (Moriuchi et al. 2000, Adonakis and Venable 2004, Venable 2007). Escape in time via delayed germination is likely to dominate over escape in space for these species. However, some processes such as gene flow and colonization may be influenced more by rare long-distance travel, and the tails of dispersal distributions for desert annuals may be quite long. The historical colonization and rise to dominance of *Schismus barbatus* in a few decades of the 20th century would seem to have been unimpeded by the low mean mobility of seeds. The relative importance of these two patterns is likely to vary widely across sites and years.

The low mean dispersal of desert annuals is likely to have important implications for species coexistence. Despite potential infrequent long-distance dispersal, the bulk of seeds travel quite short distances relative to patterns of spatial heterogeneity operating on the scale of shrub/open habitat or greater. Thus local population buildup is likely to be a feature of desert annual communities. We have previously demonstrated for this system that species respond to the physical environment in different ways (Pantastico-Caldas and Venable 1993,

Venable and Pake 1999, Angert et al. 2007). Thus low dispersal potentially contributes to species coexistence by creating negative covariance between local population growth and local population density and thereby stronger intra- as opposed to interspecific competitive interactions (Chesson et al. 2005). This potentially has a “very powerful role in promoting species coexistence in the presence of spatial variation” (Chesson 2000:231).

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APPENDIX A

Best-fit parameters for all dispersal kernels (*Ecological Archives* E089-127-A1).

APPENDIX B

ANOVAs, main effects, and fits to raw data (*Ecological Archives* E089-127-A2).

SUPPLEMENT 1

Seedling counts for each dispersal transect (*Ecological Archives* E089-127-S1).

SUPPLEMENT 2

MATLAB code for determining best-fit parameters and graphing dispersal kernels to a dispersal transect data set (*Ecological Archives* E089-127-S2).