Spatial and temporal variation of seed distributions in Sonoran Desert soils

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ABSTRACT. Samples taken in seventeen different microhabitats in the Sonoran Desert, NW of Tucson, Arizona (U.S.A.), revealed large variation in spatial (78-fold) and temporal (28-fold) patterns of seed distribution. Seed densities were lowest in normally dry washes and open areas between shrubs, were intermediate between shrubs, and were highest in artificial and naturally occurring depressions in the soil surface. There were microsites with high seed densities within microhabitats of low overall seed density. Differences between microhabitats were greatest during periods of high seed production and tended to disappear in seasons when rainfall was low.

Seed densities were not correlated with shrub canopy volume, but were correlated with the dimensions of microtopographic depressions. Seeds which were small, or round, tended to form higher density patches than large or long seeds.

Introduction

The spatial distribution and abundance of seeds in desert soils are important to the structure of plant communities and to animals that rely on seeds as a food resource (Brown, Reichman & Davidson, 1979). Studies of seed distributions in the Sonoran and Mojave Deserts of North America suggest that seeds are patchily distributed (Nelson & Chew, 1977; Reichman & Oberstein, 1977) and that these distributions are affected by foraging ants, birds and rodents (Pulliam & Brand, 1975; Reichman, 1979). In turn, various taxa of seed consumers may select and partition the seed resource is in relation to seed distribution (Brown *et al.*, 1979).

One method of analysing seed distributions is to investigate where plants occur, as they represent locations where seeds have survived to germinate. This, however, reveals only the final resting site of seeds that have survived a rigorous environmental sieve (Harper, 1977). Seeds that do not germinate have succumbed to a variety of depredations, including decomposition and consumption on the parent plants or in the soil.

As part of an investigation on desert granivores, hundreds of soil samples were taken from a range of microhabitats and from numerous seed traps placed in the ground. The investigation was designed to determine the variation in seed density: (1) between microhabitats; (2) through time; (3) within microhabitats (i.e. the degree of clumping); and (4) in relation to seed size and shape. Analysis of these data shows seed densities are highly variable in time and in space. In addition, seeds of differing morphologies exhibit distinct distribution characteristics.

Methods

Soil samples were taken from September 1974 to September 1976 within a 1 km² area approximately 40 km northwest of Tucson, Arizona, at the Silver Bell site previously (1970–72) used by the US/IBP Desert Biome project. The area consists of *Larrea* shrub flats.

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with interspersed individuals of the small shrub *Ambrosia*. Several other perennial shrubs and trees are present (e.g. *Cercidium*, *Acacia* and *Opuntia*) and a diverse and ephemeral community of annuals is produced following sufficient rainfall. The Sonoran Desert usually exhibits two distinct wet seasons, unpredictable summer thunderstorms and more gentle winter rains. Each rainy season produces a characteristic flora and most of the herbaceous plants function as annuals even if they are actually perennials.

Two main types of samples were gathered for analysis. Samples from a number of microhabitats were taken with a 39 mm diameter vial pressed into the ground to a depth of 2 cm. (Childs & Goodall (1973) noted that 89% of seeds occur in the upper 2 cm of desert soils.) A metal sheet was then carefully slipped over the opening of the vial and the contents of the vial placed in a labelled paper coin envelope. These samples will be designated as core samples. The second sampling procedure involved burying round (39 mm diameter) 30 ml plastic medicine cups (hereafter called traps) flush with the soil surface where they served as seed traps, catching seeds and other blown material (debris and soil) as well as small invertebrates. Granivores had access to the uncovered traps. The size of a trap was generally comparable to that of naturally occurring depressions in the area.

Core samples and trap samples were taken in a total of seventeen microhabitats as follows (also see Table 1): core samples from under the NW (1) and SE (2) sides of large *Larrea*, under the NW (3) and SE (4) sides of small *Ambrosia* bushes, the interstices between the shrubs ('open-area core samples'; 5), dry washes (6), on the NW (7) and SE (8) sides of natural obstructions (< 25 mm × 100 mm), in naturally occurring depressions (9), and in areas showing extensive rodent digging (10). For another set of core samples the upper 2 mm of the soil (11) was separated from the remainder (2–20 mm; 12) to determine what fraction of the seeds occurred in the upper portion of a sample. Twenty-five traps were randomly placed in open areas between shrubs (13) and a single trap under the NW (14), NE (15), SE (16) and SW (17) sides of eight *Larrea* shrubs (i.e. total of eight traps for each direction). The dates of sampling and samples sizes are presented in Table 1. Each core sample in a microhabitat was located by tossing a small rubber ring over the shoulder and sampling where it landed. The prevailing winds are from the NW in the winter and SE in the summer, although they vary considerably.

In the laboratory, samples were weighed

TABLE 1. Microhabitats from which samples were taken, dates of sampling, and sample size for each date. The numbers of the microhabitats correspond to those in the text, Tables 2 and 3, and Fig. 1.

Microhabitat	Dates sampled	Sample size
1. NW of *Larrea* bush	Sept. 1974; March 1976	50 (Sept.); 25 (March)
2. SE of *Larrea* bush	Sept. 1974; March 1976	Same as no. 1
3. NW of *Ambrosia* bush	March 1976	50
4. SE of *Ambrosia* bush	March 1976	Same as no. 3
5. Open-area core samples	Sept., Dec. 1974; March June, Sept., Dec. 1975; March, June, Sept. 1976	50
6. Normally dry washes	Sept. 1974; March 1976	50
7. NW of obstruction (< 25 × 100 mm)	Sept. 1974; March 1976	50 (Sept.); 25 (March)
8. SE of obstruction	Sept. 1974; March 1976	50 (Sept.); 25 (March)
9. Natural depressions	Sept. 1974	25
10. Extensive rodent digging	Sept. 1974	25
11. Upper 2 mm	March 1976	50
12. 2 cm deep less upper 2 mm	March 1976	50
13. Open-area traps	Same as no. 5	25
14. Trap NW of *Larrea*	Same as no. 5	8
15. Trap NE of *Larrea*	Same as no. 5	8
16. Trap SE of *Larrea*	Same as no. 5	8
17. Trap SW of *Larrea*	Same as no. 5	8

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(after air drying for at least 2 weeks in the laboratory), and sieved to eliminate large debris. The remainder was floated in a saturated solution of K_2CO_3 (specific gravity = 1.56). The floating component, which contained the seeds and any other items of similar density, was decanted, washed with fresh water, and dried. The residue was searched under a dissecting microscope (at 10×) for seeds, which were removed and identified. Nelson & Chew (1977) have reported that this procedure is effective and accurate for extracting seeds from the soil. To determine the density of seeds in a sample, the number of seeds present was divided by the sample volume. To determine the density of seeds in the traps the number of seeds in a sample was divided by the volume of soil in each trap.

Because the seed data are highly skewed and highly kurtotic, distribution free (non-parametric) statistics were used to determine differences between sampling areas. Because non-parametric statistics were used, variances rather than standard deviations are presented with the means in Tables 2 and 3. A Mann-Whitney U-statistic was used for pairwise comparisons and Kruskal-Wallis rank sum tests were used for one way ANOVA (Hollander & Wolfe, 1973). Pearson product-moment correlation coefficients were calculated for data on depression size and seed density and Spearman rank correlations were used for comparisons of the orders of seed densities between sampling dates (Sokal & Rohlf, 1981). Ratios of the variance to mean number of seeds were used as an index of the degree of clumping of the seeds and a chi-squared-test was used to test the significance of the ratios (Greig Smith, 1957).
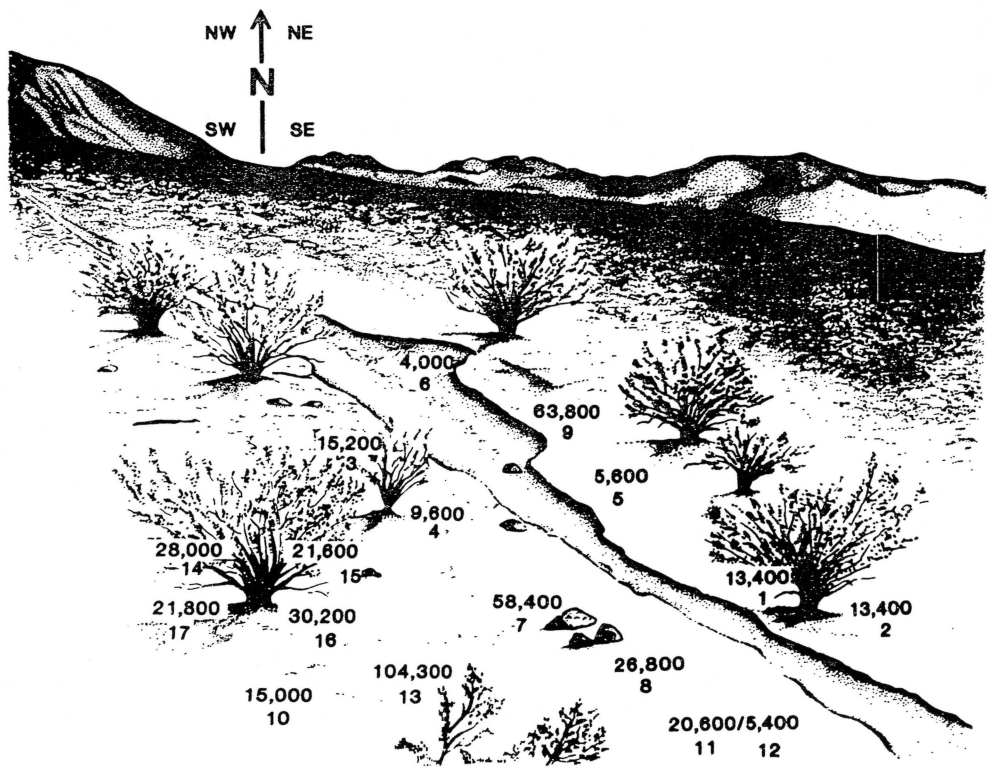

FIG. 1. Average seed densities per m² in seventeen microhabitats. The numbers under each value correspond to those in the Methods section and in Table 1. The values are extrapolated from numerous smaller samples as though they were for a square metre but are not meant to imply that these densities actually occur over the entire square metre.

Results

Fig. 1 offers a general characterization of seed densities without details of variation between sampling periods, within microhabitats, or for seeds of different sizes. The data are discussed in more detail below. The data are presented as though they were the values for an entire square metre, but were extrapolated from samples of a much smaller size. The Figure is not meant to suggest that there are actual square metres with as many seeds in them as are represented in the Figure. Details of sample size and dates of sampling are in Table 1. The numbers in parentheses next to microhabitat designations correspond to those in the methods section and Table 1.

Variation between microhabitats

Tables 2 and 3 present the average number of seeds/cm^3 of soil from various microhabitats for a number of dates. The tables also indicate those samples that are statistically indistinguishable from each other (see table legends). There are large differences between some sites, with the lowest average values occurring in core samples from open areas (5) and in the normally dry washes (6; Tables 2 and 3). The highest seed densities were associated with what might be considered wind shadows, where seeds blow and then fall into microsites where the wind was not likely to reach and move them again. These included open-area traps 13; (the highest values recorded), naturally occurring depressions (9), and microsites adjacent to small obstructions (7 and 8). Almost three-quarters of the seeds in the core samples were located in the upper 2 mm of samples 2 cm deep (1.03 seeds/cm^3 in the upper 2 mm [11] and 0.27 seeds/cm^3 in the remainder of a 2 cm deep sample [12]; Table 3). The values for core samples from an area that exhibited extensive rodent foraging (10) were somewhat higher than the average for open areas, but still much less than some of the highest values (Table 3). No statistically significant differences were found between mean seed densities on the four sides of the *Larrea* (14–17) so the data for traps around the shrubs were pooled for comparisons and calculations (Tables 2 and 3).

There were, however, differences between traps under the bushes (pooled, 14–17) and the traps placed in the open (13) during 1974 and 1975. These differences disappeared in 1976 (Table 2).

Variance-to-mean ratios for the seed data ranged from less than 1 to 3 for most core samples (5) and traps under shrubs (13–17) to as high as 17 in June 1975 for the open traps (13; Tables 2 and 3). Dozens of samples from certain microhabitats (open traps [13], natural depressions [9], and obstructions [7, 8]) had few seeds while a few samples had hundreds of seeds. Even though the average seed densities in the open areas were relatively low, the high variance in mean seed density suggests that there were specific patches which have extremely high densities.

The greatest differences between microhabitats occurred during 1974 and 1975 following a period of relatively high productivity (as determined by the standard deviation of average rainfall for the area; see Brown, 1975). In the period preceding March 1976, rainfall and production were low and many of the differences between microhabitats during the previous year and a half disappeared (Tables 2 and 3). Thus, it appears that the greatest heterogeneity in the spatial distribution of seeds may occur during periods when seed density is high.

Variability in time

Seed densities varied significantly within microhabitats between sampling dates. For example, densities in open-area traps (13) varied over 25-fold through the sampling periods. The traps under *Larrea* shrubs (14–17) followed a seasonal pattern similar to that exhibited by the open-area traps (13) but the variation was much less pronounced and showed a lag in 1976. Random core samples in the open (5) exhibited average seed densities that were strikingly stable through time (Table 2). Microhabitats that exhibited low densities in 1974 also had low densities in 1976. Conversely, microhabitats that had high densities in 1974 (the open traps [13] and the NW and SE sides of obstructions [7, 8]) showed statistically significant reductions in seed densities by March 1976 (see double asterisks in Table 3; Mann-Whit-

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TABLE 2. Values for the mean number of seeds/cm^3 of soil (x) and variance (v). Statistically indistinguishable values share a lower case letter (a, b or c for comparisons within a microhabitat between dates, i.e. within rows; x, y or z for comparisons within a date between microhabitats, i.e. within columns; Kruskal-Wallis rank sums, $P < 0.05$). There were no differences between directions for the shrub traps, so they were pooled for comparisons with the other two microhabitats. Numbers associated with the microhabitats correspond to those in Table 1. Those values with asterisks have variance/mean ratios that differ statistically from 1, suggesting that they are highly clumped. All of the traps were washed out in December 1975.

Microhabitats	Sept. 1974	Dec. 1974	March 1975	June 1975	Sept. 1975	Dec. 1975	March 1976	June 1976	Sept. 1976
1. Core samples (x)	0.56	0.09	0.32	0.26	0.25	0.29	0.31	0.23	0.18
(v)	(0.28)	(0.03)	(0.20)	(0.05)	(0.06)	(0.05)	(0.08)	(0.05)	(0.05)
Microhabs.	c	a	bc	bc	bc	c	bc	bc	b
Dates	y	y	x	x	y		y	y	y
13. Open traps (x)	4.82*	3.13*	9.15*	20.28*	1.48		0.84	0.73	0.90
(v)	(8.53)	(6.86)	(27.77)	(354.95)	(0.83)		(0.25)	(0.44)	(0.52)
Microhabs.	c	c	c	d	b		ab	ab	ab
Dates	z	z	y	y	z		z	z	z
14—17. Shrub traps (x)		1.68	1.67	2.85*	0.66		0.52	0.96	0.55
(v)		(1.77)	(0.90)	(6.45)	(0.36)		(0.07)	(0.72)	(0.43)
Microhabs.		b	b	b	a		a	a	a
Dates		z	z	z	y		yz	z	yz

TABLE 3. Average number of seeds/cm^3 of soil (x) and variances (v) in samples from various microhabitats. Some of the data are repeated from Table 1 to allow comparisons within the two dates. Within dates, microhabitats that are statistically indistinguishable share a lower case letter (a, b or c for 1974; w, x, y or z for 1976; Kruskal-Wallis rank sums; $P <$ 0.05). The numbers associated with the microhabitats correspond to those in Table 1. Data for traps from the four compass directions around shrubs were pooled for all directions for 1976. Those values with an asterisk (*) have a variance/mean ratio significantly greater than 1, suggesting the seeds are highly clumped. Those microhabitats marked with a double asterisk (**) show a statistically different value between the two dates (Mann-Whitney U-statistic, $P <$ 0.05).

Microhabitats		Sept. 1974	March 1976
1.	NW of *Larrea* (x)	0.74 b	0.53 y
	(v)	0.36	0.35
2.	SE of *Larrea* (x)	0.81 b	0.39 y
	(v)	0.86	0.17
3.	NW of *Ambrosia* (x)		0.76 y
	(v)		0.42
4.	SE of *Ambrosia* (x)		0.48 y
	(v)		0.13
5.	Open core samples (x)	0.56 a	0.31 y
	(v)	0.18	0.08
6.	Washes (x)	0.30 a	0.09 x
	(v)	0.27	0.01
7.	NW of obstructions (x)	4.13 c **	0.49 y
	(v)	36.84*	0.76
8.	SE of obstructions (x)	3.33 b, c**	0.35 y
	(v)	22.75*	0.12
9.	Natural depressions (x)	3.19 b, c	
	(v)	36.36*	
10.	Foraged area (x)	0.75 b	
	(v)	0.64	
11.	Surface (x)		1.03 w
	(v)		1.85
12.	Below (x)		0.27 y
	(v)		0.16
13.	Open traps (x)	4.82 c **	0.84 z
	(v)	8.53*	0.25
14—17.	Shrub traps — pooled (x)		0.52 y, z
	(v)		0.09

ney U statistic, P always $<$ 0.05 for comparisons between the two dates for any pair of values). Although absolute seed densities changed between the two sampling periods, a Spearman Rank correlation test indicated that the order of microhabitats, in terms of seed densities, was nearly identical between the two periods ($r = 0.77$, $n = 7$, $P <$ 0.05).

Another indication of variability in transient material through time is amount of

soil that accumulated in traps in various periods. For example, the 3 month period of March 1975 to June 1975 yielded an average sample weight (soil from open-area traps) of 3.5 g, whereas the subsequent 3 month period produced an average sample weight of 36 g. The average number of seeds per trap during these two periods were 72 and 34.8 respectively, and calculations indicate that there were no significant correlations

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between the number of seeds in a trap and the weight of the sample (i.e. the amount of soil in the trap). The variation in soil accumulation does suggest, however, that material being moved by wind and water will exhibit a high degree of variation through time. The absence of any relationship between seed and soil accumulation in the traps could be caused by a number of factors such as rodent foraging in the traps, decreased wind velocity and soil movement during the interval, or differences in seed production between the two periods.

Variability within microhabitats

Seed densities are likely to vary even within microhabitats, as some accumulate few seeds while others garner many seeds, forming large clumps. The exact location of a microhabitat, or its dimensions, should dictate, to some degree, its seed trapping characteristics. For example, Nelson & Chew (1977) indicated that seed density under Mojave Desert shrubs was correlated with the volume of the shrub. No such correlations were evident in the present study. Seed density data from traps under the eight *Larrea* bushes (14–17), and from core samples taken from under twenty-five *Larrea* bushes (1, 2) and twenty-five *Ambrosia* bushes (3, 4) yield correlations with shrub volumes of −0.04, 0.16 and 0.13 respectively, none of which are statistically significant.

There does appear to be a relationship between the dimensions of smaller wind shadows (i.e. soil depressions) and seed density. Reichman (1981) reported significant correlations (ranging from 0.79 to 0.91) between soil depression features such as perimeter, volume, depth, surface area, and longest dimension and the number of seeds contained in the depression. Regression calculations on these data (obtained in the same area as the current study) predict that the average number of seeds in a depression the size of the traps used in this study should be approximately 5.96 seeds/cm^3 of soil. The actual value is 5.18 seeds/cm^3, within 15% of the predicted value. This is important, as it suggests that the traps function similarly to natural depressions that are the same size as the traps. Because soil surface depressions

appear to be important factors in accumulating seeds, I estimated the area of the soil surface covered by depressions deep enough to accumulate seeds approximating the highest densities found. To do this, I calculated the per cent of core samples taken in the open which equalled the average number of seeds in the open traps. This yielded a value of 2.5%, which serves as an estimate of the area covered in the past by depressions approximating the size of the traps.

Sizes and shapes of individual seed species

Because of the extreme variability of the seed data it is difficult to make specific points concerning individual seed species, seed sizes and shape, and their propensity for occurring in specific microhabitats. Generally, because smaller particles can be moved by low wind velocity, they tend to move farther and more frequently than larger particles (Bagnold, 1941). Reichman (1981) has shown that small seeds are more likely to occur in large clumps than are large seeds. In the current study, however, correlation matrices for samples within a microhabitat do not show a trend for similar sized seeds to occur together in the same sample.

The size characteristics of seeds differ between microhabitats (Fig. 2). I used the eleven most common species (these totalled over 95% of all seeds in the samples) to construct histograms illustrating the frequency of seeds of different sizes in the samples from various microhabitats (Fig. 2). Two of the species remain unidentified, but have weights of 0.46 and 1.73 mg. Among those identified (and their weights) are *Astragalus nuttallianus* (1.08 mg), *Astragalus wootoni* (1.26 mg), *Bouteloua* spp. (0.51 mg), *Erodium cicutarium* (7.4 mg), *Larrea tridentata* (2.29 mg), *Lotus tomentellus* (1.34 mg), *Lupinus* spp. (1.41 mg), *Plantago insularis* (0.93 mg) and *Schismus barbatus* (0.06 mg). Weights for *Larrea, Plantago* and *Erodium* were taken from Reichman (1976).

Seeds from class 1 (0–0.25 mg; primarily *Schismus*) and class 6 (1.26–1.50 mg) were by far the most abundant in the traps and soil samples (Fig. 2). The smallest seeds were highly represented in the core samples from
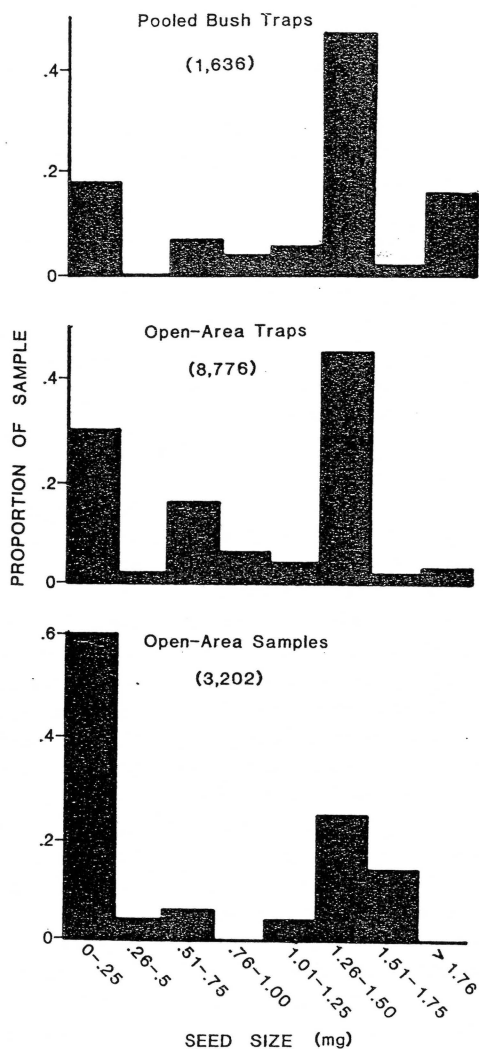
FIG. 2. The per cent of the total number of seeds from pooled shrub traps, open traps, and open core samples in eight weight categories. The data are pooled for all dates the samples were taken. The numbers in parentheses are the total number of seeds in the pooled samples from each microhabitat. See Table 1 for details of microhabitats and sampling dates.

the open areas (5) between shrubs, while large seeds from class 6 were the most abundant in traps, either in the open or under shrubs (13–17; Fig. 2). Note that traps under the *Larrea* shrubs (13–17) contained many seeds from the largest size class (17.5%), which includes *Larrea* seeds. Data from the extensive March 1976 samples show that traps under bushes (14–17), traps in the

open (13), and core samples from washes (6) had a preponderance of seeds from class 6. Most of the other microhabitats (e.g. samples from under *Larrea* [1, 2] and *Ambrosia* [3, 4], and from around obstructions [7, 8]) exhibited distributions indistinguishable from the open samples (i.e. smallest size class dominant; Fig. 2).

Larger seeds were relatively more abundant near the surface (11) than at depth (12) in soil samples. In March 1976, seeds from class 6 made up 88% of the seeds in samples taken from the upper 2 mm of soil while this size class made up only 7.5% in samples from 2 mm to 2 cm deep (with class 1 making up 53% of the seeds in these deeper samples). Seeds of all sizes were in high densities in early 1975 and this produced peak seed densities in the traps at that time. By 1976 seed densities were low and the differences between microhabitats had essentially disappeared (Tables 2 and 3). The small seeds of *Schismus*, however, remained fairly abundant in the random open-area samples (5) through the rest of the study, generating size distributions skewed toward small size classes (Fig. 2).

Discussion

Before discussing specific data presented in this study it is pertinent to note that the variation exhibited in seed distributions causes severe problems with data acquisition and analysis. Hundreds of samples and thousands of hours of laboratory work were required to get the data presented herein. The data were treated non-parametrically to avoid some of the problems with data that are not distributed normally (see Nelson & Chew, 1977, for a discussion of similar problems). The data were so highly skewed and kurtotic that standard transformations (square root and log) were insufficient. In addition, the data represent a mixed Poisson distribution such that the variance increases with the mean, making comparisons of variance/mean ratios difficult. These problems should be considered when looking at past studies dealing with seed distributions and when designing future studies.

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data presented in this paper is the tremendous
spatial and temporal variability in seed den-
sity. There are 25-fold differences in average
seed densities between various microhabitats
for all sampling periods (Tables 2 and 3) and
14-fold differences between microhabitats in
any one sampling period (Tables 2 and 3).
Nelson & Chew (1977) noted similar variation
in seed densities in the Mojave Desert. They
also found that average seed densities were
higher under shrubs than in the open spaces
between shrubs, a result also obtained in the
current study (Tables 2 and 3). The data
indicate, however, that there are specific
microhabitats in the open (e.g. traps [13–
17], depressions [9], obstructions [7, 8])
where average seed densities are highest,
higher than under bushes.

The seed densities are highly variable in
time as well as space. Bush traps and open-
area core samples varied 5- and 6-fold res-
pectively, while open-area traps exhibited
a 28-fold difference between dates. Table 2
shows the variation between sampling periods
in average seed densities for three micro-
habitats. The data also indicate that depres-
sions in the open (9, 13) are much more likely
to exhibit high variation through time than
random soil samples (5) or samples from
traps under shrubs (14–17).

The distribution of sizes of seeds is dis-
tinct for traps and core samples from various
microhabitats (see Fig. 2 and Results sec-
tion). This is primarily due to the presence or
absence of the tiny seeds of *Schismus barba-
tus*. At times of high density all sizes tended
to accumulate in the traps, but by 1976 many
of the clumps were gone (Tables 2 and 3).
Schismus, however, remained at a fairly high
density in the random open samples, but not
the traps, through the remainder of the study,
producing the positively skewed distribution
in Fig. 1 for the open samples. This suggests
that after a burst of production, seeds readily
move about, accumulating in traps or depres-
sions.

It is pertinent to ask what causes the
spatial and temporal variation in the distri-
bution of seeds. Several factors are obviously
important, including the location and produc-
tion regime of the parent plants, dispersal
factors such as wind and water, microtopo-
graphic features, and granivore foraging.

The location of the producing plant would
certainly affect subsequent seed distributions,
and parent plants also greatly affect seed
distribution by their absolute seed production
rates. Tables 2 and 3 show that the greatest
differences in seed densities in time or space
occur during periods of especially high overall
seed densities. When seed production is low,
many of the differences between micro-
habitats and sampling periods disappear.

Wind, water and animals appear to be the
important dispersal factors in the desert.
Although actual airborne dispersal is not
likely to be important (Burrows, 1973,
1975), movement near the ground is sig-
nificant (Bagnold, 1941). The wind blows
almost every day as the desert heats up,
and afternoon velocities are usually suf-
ficient to move soil and the seeds it con-
tains. Sheet flooding or surface runoff can
be especially significant. In one heavy
thunderstorm at another study site all of the
seed traps were filled with soil in minutes,
whereas it might take months to fill them
with wind-blown material. Seed size and
shape also are reflected in dispersal pat-
terns. Seeds which are small or round tend
to move farther and occur in higher density
clumps than seeds which are large or long
(Reichman, 1981).

One of the most important factors determ-
ining the distribution of seeds is the nature
of the surface microtopography (Harper,
Williams & Sagar, 1964; Mott & McComb,
1974; Thompson & Grime, 1979; Roberts,
1981; Pavone & Reader, 1982). Seeds may
move across the soil surface and into the soil
like pebbles in a stream. Just as the surface
of a stream bottom serves to slow down the
flow of water and generate eddies, soil de-
pressions do the same for wind, causing it to
drop its load of soil and seeds in specific
types of microsites. These sites then accumu-
late soil and seeds until they fill up and no
longer serve as traps (Reichman, 1981). Al-
though it is obvious how depressions fill
up with seeds and other debris, it is not
clear how the depressions are formed. Per-
haps frost heaving, or even animal tracks,
are important factors in determining micro-
topography and, hence, seed distributions.

The highest seed densities in this study
were recorded from locations that would

generate eddies or wind shadows, such as traps, depressions and small obstacles. These microsites would produce conditions of near zero wind velocity, causing the wind to give up its load. Other surface features, such as shrubs of various sizes, would also slow the wind, while open, relatively smooth areas would not do so. Variation in microtopography thus would generate a wind velocity gradient and help explain the seed density pattern seen in Tables 2 and 3 with seed densities lowest in open core samples, intermediate in shrub samples, and highest in open traps and depressions. Note that although seed densities averaged across all sampling periods are higher in core samples from under shrubs than from core samples in the open, the reverse is true for shrub and open traps. This suggests that while the average seed densities might be highest under shrubs, the transient population of seeds is greatest in the open, yielding the possibility of extremely high densities in small, discrete wind shadows.

Animals are an important factor in determining seed densities and distributions. Rodents forage on specific seed sizes or in specific microhabitats for seed patches (Brown *et al.*, 1979; Reichman, 1979; O'Dowd & Hay, 1980). Ants are known to concentrate on the most abundant small seeds (Davidson, 1977; Whitford, 1978), and birds, in concert with other granivore taxa, can substantially affect seed densities during periods of low production (Soholt, 1973; Pulliam & Brand, 1975).

Seed densities and distributions, in turn, are important to future generations of plants. Evolutionary pressures related to dispersal qualities (size, shape; Harper, Lovell & Moore, 1970) will also affect germination success and resistance to desiccation. Evolutionary trade-offs must be made between numerous factors relating to dispersal, germination, seedling competition, and predator avoidance. For example, small seeds might be able to work into the interstices between soil particles to 'hide', but small seeds also cluster together, and in these large clusters would be more subject to predation (Reichman & Oberstein, 1977) and crowding (Inouye, 1980; Inouye, Byers & Brown, 1980).

Harper (1977) discusses the environ-mental sieve that seeds must go through to reach their final destination, but many unexamined features of the sieve remain. For example, we know less about the impact of birds on seed densities and distributions than we know about ants and rodents, and little is known about decomposition of seeds in the soil by microorganisms. What we do know is intriguing and suggests that in open areas such as deserts tremendous variation in seed densities and distributions occur and are related to characteristics of the seeds and the physical environment. This heterogeneity is important to the entire community through the relationships between seeds, germination and seedling competition, plant populations, and seed predation by granivores.

Acknowledgments

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