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Seed Reserves of Desert Soils

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ABSTRACT

Soil and litter samples from Rock Valley and Silverbell were analyzed for their seed content with special attention to spatial distribution. In both sites, the seed content of the soil fell off sharply from the surface downwards; at the time of sampling, however, the surface 1 cm of soil contained more seeds of most species than were in the loose litter on the soil surface. At Silverbell, 18% of all seeds occurred below 5 cm; in Rock Valley the corresponding figure was 3%.

At Rock Valley most seeds were found under shrubs. At Silverbell this difference was less marked, and was reversed for two species of *Bouteloua*. Under certain shrub species at both sites, there was a significant reduction in seed population as one proceeded from the center to the periphery of shrub canopy.

Total seed populations are estimated at 427 m^{-2} in Rock Valley and 33097 m^{-2} in Silverbell. with biomasses of 5 kg. ha^{-1} and 83 kg. ha^{-1}, respectively.

INTRODUCTION

Numerous studies have been made of the seed reserves in arable soils and in improved grassland, but very little information is available on reserves in desert soils, either in North America or elsewhere. This project was initiated in 1971 to develop methods for estimating seed reserves, and to inventory the seed reserves of validation sites.

OBJECTIVES

This project has as its purpose to obtain estimates of the seed populations in the Desert Biome Validation Sites, and also to provide information on their spatial distribution.

METHODS

Fieldwork

The Jornada Validation Site and the Silverbell Validation Site were sampled for seed reserves in June, 1972, in order to test depth stratification, and seed distribution under different species of shrub and in open ground.

At the Jornada Validation Site, samples were taken from the playa, the playa fringe and the bajada zones. Replicate samples were taken in the open and under the canopies of *Prosopis glandulosa, Larrea divaricata, Ephedra trifurca, Yucca elata, Fallugia paradoxa,* and *Hilaria mutica.* At the Silverbell Validation Site, samples were taken in the open and under the canopies of *Larrea divaricata, Cercidium microphyllum, Ambrosia dumosa, Acacia constricta* and *Olneya tesota.* While approximately four replicates of the above samples were made, only one series of samples was made at Silverbell under the canopies of *Opuntia spinosa, Opuntia fulgida, Fouqueria splendens,* and *Cereus giganteus.* In November, 1971, samples were taken at Rock Valley in the open and under the canopies of *Lycium pallidum, Lycium andersonii, Ambrosia dumosa, Krameria parvifolia, Larrea divaricata,* and *Ephedra nevadensis,* representing the Mohave Desert.

In June, 1972, samples were collected at the Curlew Valley Validation Sites. Because the variables of depth, canopy type, and distance from canopy center were dealt with adequately in 1971, it was felt that elimination of sampling procedures

providing this type of information would increase project efficiency. To that end, replicate samples were collected under canopies of tussock grasses, *Artemisia tridentata*, *Atriplex confertifolia* and *Chrysothamnus nauseosus*, as well as in open sites at both the northern and southern sites in Curlew Valley. Each sample was a cubic decimeter in volume and was taken midway between the canopy center and its periphery.

Laboratory techniques

The laboratory techniques used in 1971, and described in the Progress Report for the year (Goodall, 1972), proved satisfactory, and were in the main continued in 1972, although minor adaptations were used for different soil types. Soaking in Calgon was not so necessary for coarse textured soils, because few aggregates were present. The soaking period was not eliminated, however, it was merely shortened.

Another feature of coarse textured soil was that a large quantity of mineral particles was retained in the flotation solution. Because a large amount of mineral particles increased the chance of trapping seeds and thereby causing them to sink, two successive flotations were used to reduce this potential source of error.

An additional flotation in zinc chloride solution of specific gravity 1.9 was applied to one half of the samples from each test site in order to check on the efficiency of flotation by the potassium carbonate solution normally used. No seeds were found in this additional flotation.

Tests of seed recovery for species occurring in Rock Valley showed that total seed recovery remained well over 90%. Because adequate supply of test seeds of plants occurring at Silverbell was not available to test their recovery, similar tests could not be run. However, seeds of the same genus, or otherwise similar to those found at Silverbell, were tested successfully, indicating that poor recovery is probably not a serious source of error in seed counts.

Seed identification

Field collections of additional seed species from Curlew Valley have been labeled and added to the seed herbarium. This collection is now virtually complete for Curlew Valley seeds. In addition, seeds of *Phlox gracilis* and *Veronica biloba* were obtained from plants grown from Curlew Valley soil taken undisturbed from the field and placed in a greenhouse.

The Rock Valley herbarium has grown from the addition of field samples collected and identified by Dr. S. Bamberg. James Nelson at the University of Southern California has also contributed some seed samples.

Although the seed herbarium at Logan is poorly supplied with seeds of plants at Silverbell, identifications of many seeds from that site have been made. James Reichman at Northern Arizona University helped greatly in these identifications by permitting use of his seed herbarium, as well as making several personal identifications.

Dr. W. G. Whitford has sent a preliminary collection of identified seeds from Jornada Validation Site.

Determination of bulk density

In order to extrapolate from actual seed counts of soil samples to seed reserves on an area basis, a determination of the bulk density of the surface 10 cm of soil at each site was necessary. These measurements were made on clods from soil samples. The clods were weighed, then dipped in paraffin. The volumes of the clods were determined by displacing water and correcting for the volume of the paraffin coating. The average bulk densities are:

Curlew Valley	1.68
Rock Valley	1.58
Silverbell	1.60

RESULTS AND DISCUSSION

Only the results of analysis of samples taken in 1971 in Rock Valley and in 1972 at Silverbell are included in this report. Analysis of the samples taken in 1972 at Jornada and in Curlew Valley are still incomplete.

Rock Valley

Depth distribution: The distribution of seeds with depth (to 10 cm) is shown in Table 1. It will be noted that four species have no identification, while two others are identified only to genus. It is hoped that germination tests will enable these uncertainties to be reduced. In Table 1, for each depth, both the number of samples in which seed of the species in question was found, and the total number of seeds counted, are recorded. In the case of the surface litter samples, the whole was analyzed, and hence the counts refer to 100 cm^2 per sample. In the deeper samples,

a sub-sample of 100 g of air-dry soil was analyzed; hence the count must be multiplied by the bulk density and by the thickness (in cm) of the soil layer in order to arrive at an area estimate. The last two columns of the Table give the number of samples to 10 cm in which the seeds were recorded at one or more depths, and an estimate of the mean number of seeds in these samples in an area of 1 dm^2. Only samples which were complete for all depths have been included in these calculations. The total number of such samples was 71.

Table 1 suggests strongly a marked difference in seed concentration with depth, and this indication was confirmed by statistical tests. In Table 2, seed counts for eight of the more abundant species are recorded for all complete sets of samples (i.e., those where figures were available for all four depths of soil). In each case, a X^2 test showed great heterogeneity. Furthermore, the depth distribution for the different species does seem to follow the same pattern; the 8 x 4 table including all these data gives a X^2 value of 34.88 with 21 degrees of freedom, with $P<.05$ This heterogeneity derives from the fact that, unlike other species, no seeds of *Oryzopsis hymenoides* were found below 1 cm; without this species, the X^2 value becomes 20.33 with 18 degrees of freedom, so that the attenuation of seed concentration with depth can be regarded as uniform for the other species.

The surface litter, even where present, fairly consistently contained fewer seeds than the top 1 cm of soil. Table 3 shows the number of sample pairs in which this relation holds, for each of the more abundant species. The only exception seems to be *Larrea divaricata*; seeds of which were usually more numerous in the litter.

In Table 4, the overall distribution of seeds by depth is given for the more abundant species, and for the whole seed population. It will be seen that three quarters of the total seed population are found within 1 cm of the surface, and only 3% are deeper than 5 cm.

Sample location: Comparisons of samples taken in the interspaces between shrubs and under canopies of different shrub species, are presented in Table 5. The number of shrubs or interspace areas in each category where seeds of the species in question were recorded is shown, and also the number of 100 cm^2 samples (to 10 cm depth, including litter). The seed quantities recorded are estimates of those contained in such a 1-litre volume of soil, obtained by multiplying the numbers actually found in subsamples of 100 g by the bulk density and thickness of the soil layer represented.

Table 1. Seed distribution depth at Rock Valley DSCODE——A3UGE22

Species	Surface Litter		0-1 cm		1-2 cm		2-5 cm		5-10 cm		All Depths	
	Sample where present	Seeds counted	Sample where present	Seeds counted	Sample where present	Seeds counted	Sample where present	Seeds counted	Sample where present	Seeds counted	Sample where present	Seeds counted
Amsinckia tesselata	2	4	3	3	0	0	2	2	0	0	6	3.0
Astragalus lentiginosus	0	0	4	5	4	8	2	6	3	3	6	12.1
Chaenactis carphoclinia	4	6	11	16	1	1	0	0	1	1	15	2.7
Chorizanthe rigida	0	0	1	2	0	0	0	0	0	0	1	3.2
Cryptantha circumscissa	4	16	7	17	2	5	1	2	0	0	8	7.5
C. micrantha	0	0	0	0	1	1	0	0	0	0	1	1.6
C. nevadensis	1	1	1	3	0	0	0	0	0	0	2	2.9
C. pterocarya	1	1	0	0	1	1	0	0	0	0	2	1.3
C. recurvata	4	9	3	5	1	2	1	2	0	0	6	4.9
Descurainia pinnata	5	8	17	43	10	18	5	7	1	1	22	6.6
Eriogonum maculatum	0	0	0	0	0	0	1	1	0	0	1	4.7
E. trichipes	1	1	4	4	1	1	0	0	0	0	6	0.7
E. spp.	0	0	1	1	0	0	0	0	0	0	1	1.6
Euphorbia spp.	0	0	2	2	1	1	2	2	2	2	3	10.0
Festuca octoflora	6	23	26	42	11	29	6	14	5	7	36	7.1
Gilia spp.	0	0	2	2	0	0	0	0	0	0	2	1.6
Grayia spinosa	0	0	2	2	0	0	0	0	0	0	2	1.6
Ipomopsis polycladon	2	2	2	2	2	2	0	0	1	1	7	1.9
Krameria parvifolia	0	0	1	1	0	0	0	0	0	0	1	1.6
Larrea divaricata	12	67	6	22	3	4	3	3	3	3	14	10.4
Lycium andersonii	3	30	8	27	1	1	2	3	0	0	10	8.8
L. pallidum	1	1	0	0	0	0	0	0	0	0	1	1.0
Mentzelia obscura	0	0	3	4	2	11	1	1	2	2	3	14.7
Oryzopsis hymenoides	1	1	4	30	0	0	0	0	0	0	5	9.7
Pectocarya spp.	5	10	3	10	0	0	0	0	0	0	8	3.8
Phacelia fremontii	0	0	1	1	1	1	1	1	0	0	3	2.6
Phacelia vallis-mortae	2	3	5	9	3	5	0	0	0	0	7	3.6
Stephanomeria exigua	0	0	0	0	0	0	1	1	0	0		4.7
Streptanthella longiros.	3	15	3	14	2	3	2	3	0	0	6	9.3
Stylocline microporoides	1	1	0	0	0	0	0	0	1	1	2	4.5
Tridens pulchellus	1	2	0	0	0	0	0	0	0	0	1	2.0
Species A	1	1	2	2	0	0	0	0	0	0	3	1.4
Species B	1	4	1	6	0	0	0	0	0	0	1	13.5
Species C	0	0	1	1	0	0	0	0	0	0	1	1.0
Species D	1	2	2	11	1	4	2	3	0	0	2	19.5

Table 2. Seed Distribution by Depth at Rock Valley.

Species	Number of Seeds in Samples of Equivalent Weight				
	0-1 cm	1-2 cm	2-5 cm	5-10 cm	X^2 *
Chaenactis carphoclinia	14	4	0	1	25.84
Cryptantha circumscissa	17	5	2	0	29.0
Descurainea pinnata	41	17	7	1	56.42
Festuca octoflora	79	27	13	6	104.60
Larrea divaricata	22	4	3	3	53.38
Lycium andersonii	27	1	3	0	64.61
Oryzopsis hymenoides	30	0	0	0	90.00
Streptanthella longirostris	14	3	3	0	22.80

* Significance limit of X^2 for $P = .01$ is 12.84

Table 3. Distribution of Seeds in Litter and Surface Soil at Rock Valley

Species	Number of Samples Without Litter but with Seeds in the Surface Soil	Samples with Litter	
		More seeds in surface soil than in litter	Fewer seeds in surface soil than in litter
Chaenactis carphoclinia	3	7	2
Cryptantha circumscissa	-	4	3
Descurainia pinnata	5	10	2
Festuca octoflora	7	18	3
Larrea divaricata	2	2	10
Lycium andersonii	1	5	1
Oryzopsis hymenoides	2	2	1
Streptanthella longirostris	1	1	2

Table 4. Proportion of seeds at different depths at Rock Valley

Species	Percentage of total seeds at: Surface	0-1 cm	1-2 cm	2-5 cm	5-10 cm
Astragalus lentiginosus	0	22	28	33	17
Chaenactis carphoclinia	24	56	16	0	4
Cryptantha circumscissa	40	43	12	5	0
C. recurvata	56	19	13	12	0
Descurainia pinnata	12	55	23	9	1
Festuca octoflora	11	56	20	9	4
Larrea divaricata	68	22	4	3	3
Lycium andersonii	49	44	2	5	0
Mentzelia obscura	0	13	69	6	12
Oryzopsis hymenoides	3	97	0	0	0
Pectocarya spp.	48	48	0	4	0
Phacelia vallis-mortae	18	53	29	0	0
Streptanthella longirostris	43	40	9	8	0
Species D	10	58	20	15	0
All species	29	46	14	8	3

Table 5. Estimates of seed numbers per sq. dm under different shrub species, Rock Valley

Canopy Species:	Between shrubs	*Ephedra nevadensis*	*Lycium andersonii*	*Lycium pallidum*	*Ambrosia dumosa*	*Krameria parvifolia*	*Larrea divaricata*
No. of canopy individuals:	5	1	3	4	4	2	5
No. of 1 sq. dm samples:	5	4	9	12	12	5	19
Seed species							
Chaenaetis carphoclinia	0	0	0	0.7	0.3	0.2	2.5
Cryptantha circumscissa	0	0.4	0	0	0	0.3	2.7
Descurainia pinnata	0.3	0	5.2	3.9	1.1	0.3	4.3
Festuca octoflora	0.3	1.8	3.6	1.6	3.0	15.9	6.9
Larrea divaricata	0	0	0	0	1.5	0	6.5
Lycium andersonii	0	0	6.7	2.5	0.3	0	0.2
Oryzopsis hymenoides	0	0	0	0	1.1	2.6	1.2
Streptanthella longirostris	0	0	0	0.2	0.1	1.0	2.5
Other species	0.4	0.5	3.2	3.1	4.7	12.8	2.1
Total, all species	1.0	2.7	18.7	12.0	12.1	33.1	28.9

The density of seeds of all species in the soil under different types of canopy was compared for the more abundant seed species by analysis of variance. Only sample sets in which all soil depths were represented were included in the analysis. The estimates of seeds dm^{-2} at different soil depths were summed; these figures were subjected to a square-root transformation, and the variance due to canopy type was separated from that between different canopies of the same type.

The results are reported in Table 6. In the five areas sampled outside shrub canopies, only four seeds were found in a total of 500 cm^2. Under shrub canopies the average number in this area would have been 72. This difference is highly significant. There is some evidence that certain shrub species are more likely than others to have high seed concentration beneath them -- the figures range from 1.25 seeds per 100 cm^2, in one shrub of *Ephedra nevadensis* studied, to 10.57 as an average for four shrubs of *Larrea divaricata*. The differences between individual shrubs, however, are such that these differences in average seed population did not reach significance. Similar analyses were performed for the different seed species but no significant effects emerged -- doubtless because of the small numbers in most cases.

Table 6. Total seed population per sq. dm under different shrub canopies, Rock Valley*

Source of variation	d.f.	SS	MS	F	P
Bare ground vs. shrubs	1	50.6160	50.616	10.60	<.05
Between shrub species	6	28.6384	4.773	1.47	>.05
Within canopy types	18	58.2765	3.2375		
Total	25	137.5309			

*Analysis of variance (after square root transformation)

Position under shrub canopy: Comparisons were also made between the seed populations (totalled over all depths) in soil at different distances from the center of a shrub canopy. Samples were taken within 10 cm of the center, between 20 and 30 cm from it, and so forth at intervals of 20 cm between sample centers. The results are tabulated in Table 7.

Table 7. Total seed population at different distances from the center of a shrub canopy, Rock Valley

Canopy Species	0-10 cm. No.of Samples	0-10 cm. Seeds per sq. dm.	20-30 cm No.of Samples	20-30 cm Seeds per sq. dm.	40-50 cm No.of Samples	40-50 cm Seeds per sq. dm.	60-70 cm No.of Samples	60-70 cm Seeds per sq. dm.
Ephedra nevadensis	1	4.6	1	0	1	0	1	6.3
Lycium andersonii	3	19.87	3	23.57	2	10.63	1	7.9
L. pallidum	4	24.95	3	7.87	4	5.15	1	0
Ambrosia dumosa	4	22.93	4	3.18	3	12.43	1	9.4
Krameria parvifolia	2	12.15	1	15.8	1	53.1	1	76.2
Larrea divaricata	6	38.67	5	41.64	4	31.63	4	19.45

The very patchy distribution found seemed to call for a non-parametric test in this case, to ascertain whether there were common patterns in the distribution of particular seed species in relation to the shrub base. Rank-sum tests were used, applied to the rank order of samples at different distances from the canopy center. The samples could be ranked, of course, only where the species occurred in at least one of the series, and consequently the number of rankings available differed from species to species; moreover, the number of samples in the series depended on the size of the shrub under which it was taken. The data are consequently very irregular. The results of these tests are shown in Table 8, where data for seed of a given species have been combined for all shrub canopies, irrespective of species. Since the number of samples under a canopy varied, it was necessary to treat series of three samples and series of four samples separately, which accounts for the partial overlap between the upper and lower parts of the Table. The penultimate column shows $\underline{W}$, the coefficient of concordance between the rankings (Kendall, 1962). None of these values of $\underline{W}$ reaches significance according to Kendall's tables; the results consequently fail to support the view that the order of seed quantities, in samples taken from the canopy center outwards, follows a common pattern. However, possibly more interesting than concordance among the different rankings for a species is the question whether all seed species under a given shrub tend to be concentrated towards the base; agreement between rankings would seem less biologically meaningful than a test of trend in this sense. To answer this question, it would be valuable to combine data for sample series of different numbers, which cannot well be done when the coefficient of concordance is employed. For this purpose a different type of non-parametric test was used.

Table 8. Tests of concordance: Rankings of seed populations at different distances from the center of a shrub canopy, Rock Valley

Seed Species	No. of Canopy Individuals	No. of Samples Per Canopy	W	P
Descurainea pinnata	4	4	.133	.80
Festuca octoflora	5	4	.080	.88
Chaenactis carphoclinia	2	4	.633	.65
Cryptantha circumscissa	3	4	.778	.22
Streptanthella longirostris	2	4	.900	.04
Oryzopsis hymenoides	3	4	.651	.31
Larrea divaricata	4	3	.214	.65
Descurainea pinnata	9	3	.004	.99
Lycium andersonii	2	3	3.500	.65
Festuca octoflora	9	3	.159	.36
Chaenactis carphoclinia	4	3	.019	.98
Cryptantha circumscissa	4	3	.250	.65
Oryzopsis hymenoides	4	3	.438	.37

For each sequence of samples at different distances from a shrub center, the estimated seed densities were ranked. The probability of each possible ranking was calculated on the assumption of random distribution, and these probabilities were summed for all rankings which, on the alternative hypothesis of a decreasing density from the center outwards, were not more improbable than that observed. These probabilities, P_i, derived from different sample sequences, were then combined. Where the number of possible values of the probability for each set is large (where it can be treated as continuous), the appropriate method for doing this, due to Fisher (1963), is to calculate:

$$X^2 = -2 \sum_{i}^{n} \ln P_i$$

which is distributed as a X^2 variable with n degrees of freedom on the null hypothesis of no trend. In the present instance, however, the probabilities may take only a small number of values, and as shown elsewhere (Goodall, 1966) the Fisher method then over-estimates the combined probability. Accordingly, an exact combinatorial method was used. This method enabled data sets with different numbers of samples, and many ties, to be combined without loss of information. The results are given in Table 9. It is clear that under *Larrea divaricata* and *Lycium pallidum* there is a definite tendency for seeds to be concentrated towards the shrub base, but that this does not apply to the other shrub species.

Table 9. Effect of position under a shrub canopy on seed density, Rock Valley

Shrub Species	Number of Canopy Individuals	Number of 1 sq.dm. Samples	Number of Rankings	Signi-ficance*
Ambrosia dumosa	4	12	19	.25
Krameria parvifolia	1	4	14	.82
Larrea divaricata	5	19	25	.03
Lycium andersonii	3	9	14	.50
Lycium pallidum	4	12	18	.015

*Probability of observed rankings on the null hypothesis, against the alternative hypothesis of a trend from the center outwards.

Estimate of total seed population: In order to obtain an estimate of the total seed population of the area we should have estimates of the proportion of the area under shrub canopies, and the proportion at different distances from the shrub center. These estimates could then be combined with the estimate of seed population density to give figures for quantity of seed in the area as a whole. Data on numbers of shrubs of different sizes have been collected in the course of the Rock Valley study, but are not available in the requisite form at the time of writing.

Meanwhile, approximate figures may be derived from the cover estimates given in the progress report for the Rock Valley Validation Site for 1971 (Turner, 1972). Taking the total shrub cover of 19.3% from this report, and the populations of seed of different species found under shrubs and in bare areas, overall estimates of population may be obtained on the assumption that the shrub species do not differ in the seed populations they harbor.

Conversion of these population figures to biomass estimates requires values for the average weight of a seed. These are given in Table 10. Many of these figures were based on a very small number of seeds -- sometimes only a single seed -- so they are not to be regarded as highly accurate.

Population and biomass estimates for each of the more important species are combined in Table 11. In view of the way these estimates were derived, no error figures are attached to them; better estimates with errors will be available at a later stage. The total mass of seeds estimated amounts to 5 kg. ha^{-1}.

Table 10. Mean weight of individual seeds: Rock Valley DSCODE——A3UGE21

Species	Seed Weight (mg)	Species	Seed Weight (mg)
Amsinckia tesselata	1.99	*Larrea divaricata*	6.63
Astragalus lentiginosus	3.17	*Lycium andersonii*	2.21
Chaenactic carphoclinia	0.32	*L. pallidum*	14.00
Chorizanthe rigida	0.57	*Mentzelia obscura*	0.30
Cryptantha circumscissa	0.14	*Oryzopsis hymenoides*	1.72
C. micrantha	0.02	*Pectocarya* spp.	0.41
C. nevadensis	0.24	*Phacelia fremontii*	0.22
C. recurvata	0.37	*P. vallis-mortae*	0.64
Descurainia pinnata	0.15	*Streptanthella longirostris*	0.24
Erigonum maculatum	0.39	*Stylocline micropoides*	0.21
E. trichopes	0.10	*Tridens pulchellus*	1.00
Festuca octoflora	0.37	Species A	0.27
Gilia spp.	0.98	Species B	0.10
Grayia spinosa	0.25	Species C	0.05
Ipomopus polycladon	0.75	Species D	0.02
Krameria parvifolia	97.10		

Table 11. Seed reserves in Rock Valley

Species	Per sq. m	
	Population	Biomass (mg. air-dry weight)
Chaenactis carphoclinia	12.0	3.84
Cryptantha circumscissa	11.0	1.54
Descurainia pinnata	71.9	10.79
Festuca octoflora	129.8	48.03
Larrea divaricata	25.7	170.39
Lycium andersonii	31.3	69.17
Oryzopsis hymenoides	15.8	21.18
Streptanthella longirostris	12.2	2.93
Other species	117.2	171.11*
Total	426.9	498.98

*For this figure a mean seed weight of 1.46 mg was used, derived by weighting the figures in Table 10 for different species with their relative overall abundance.

Silverbell

Depth distribution: As at Rock Valley, samples were taken to test the distribution of seeds with depth on the Silverbell site. Table 12 gives the counts of seeds found, presented in the same way as Table 1 for Rock Valley. The number of unidentified seeds is much greater here than in the Rock Valley samples, but again it is hoped that germination tests during 1973 will enable many of these uncertainties to be resolved. Again, the last two columns of Table 12 give the numbers of samples, complete to 10 cm, in which each seed species was found (out of a total of 71 such samples), together with the mean quantity in such samples. It will immediately be noted that seeds are very much more abundant at this site than in Rock Valley.

The variation in seed density with depth is presented in Table 13. In all species there are significant differences with depth, and in most a progressive decline in deeper soil layers. *Euphorbia chamaesyce* appeared at first to be an exception, for one of the samples included no fewer than 344 seeds of this species between 2 and 5 cm. This large number appears to be due to the chance inclusion of a cache of seeds collected by a rodent or insect. If this exceptional sample is excluded the decrease in density with depth is continuous in this species, as in most of the others. Even with this correction, however, the depth distribution differs from species to species. If the data in Table 13 are analyzed as a contingency table, the X^2 value is 613 for 39 degrees of freedom, with a very high significance. This is in contrast with the results for Rock Valley, where only one species (*Oryzopsis hymenoides*) deviated from the norm by not appearing below the immediate sub-surface. At Silverbell, on the other hand, several species--*Astragalus nuttalliana*, both *Ferocactus* species, and the unidentified species designated as C -- all occur in quantity below 5 cm.

As in Rock Valley, a good proportion of samples are bare of litter, and where litter is present it usually contains fewer seeds of most species than does the surface 1 cm of soil (Table 14). This comparison would doubtless vary greatly with the time of year, these samples having been collected in June.

The distribution of seeds with depth is further illustrated in Table 15, in terms of proportions. For the four aberrant species mentioned above (*Ferrocactus* and *Astragalus nuttalliana*, and Species C), over 25% of the total seed population are to be found below 5 cm, whereas the figure for the other species averages 5%, and almost half the buried seeds occur in the top 1 cm of soil.

Sample location: Comparisons of samples taken in inter-shrub areas, and under shrub canopies, are presented in Table 16, in the same fashion as for Rock Valley in Table 5.

Table 12. Estimated seed distribution by depth, Silverbell DSCODE——A3UGE42

Species	Litter		0-1 cm			1-3 cm			2-5 cm			5-10 cm			All depths	
	Sample	Seeds.	Sample	Seeds.	Seeds per sq. dm	Sample	Seeds	Seeds per sq. dm	Sample	Seeds.	Seeds per sq. dm	Sample	Seeds	Seeds per sq. dm	Sample where present	Estimated mean seeds per sq. dm
Amsinckia tesselata	2	2	1	1	1.6	1	1	1.6	0	0	0	0	0	0	4	1.3
Astragalus nuttalliana	1	1	11	13	1.9	16	18	1.8	9	11	5.85	4	4	8	27	5.01
Boerhaavia spp.	10	39	11	26	3.78	5	7	2.24	3	3	4.8	2	2	8	22	5.55
Bouteloua aristidoides	17	451	28	967	55.25	20	73	5.84	8	55	32.98	8	16	16	43	58.30
B. barbata	15	193	39	492	20.18	17	63	5.92	11	73	31.82	16	28	14	40	41.38
B. sp.	0	0	2	2	1.6	1	1	1.6	0	0	0	0	0	0	3	1.60
Crytantha sp. 1	1	1	2	2	1.6	1	1	1.6	2	2	4.8	1	1	8	5	4.68
C. sp. 2	0	0	2	4	3.2	0	0	0	1	2	9.6	1	1	8	4	6.00
Eriochloa spp.	2	2	0	0	0	0	0	0	1	1	4.8	0	0	0	3	2.27
Euphorbia chamaesyce	6	8	23	68	4.72	16	38	3.79	11	361	157.49	2	2	8	33	58.38
E. hyssopifolia	0	0	3	20	10.66	3	10	5.32	2	3	7.2	1	1	8	3	23.47
Ferocactus sp. 1 = sp. A	2	7	12	31	4.13	11	15	2.18	6	11	8.78	4	6	12	19	9.55
Ferocactus sp. 2 + sp. B	4	43	6	99	26.4	7	64	14.62	6	67	53.57	7	60	6856	11	100.49
Franseria spp.	11	18	2	3	2.13	3	3	1.6	1	1	4.8	1	1	8	16	2.53
Larrea divaricata	3	3	2	3	2.13	0	0	0	0	0	0	0	0	0	5	1.56
Lepidium medium	0	0	1	1	1.6	0	0	0	0	0	0	0	0	0	1	1.60
Lesquerella gordoni	0	0	0	0	0	0	0	0	1	1	4.8	0	0	0	1	4.80
Pectocarya spp.	17	45	40	111	4.43	17	25	2.35	5	6	5.76	5	6	96	50	6.79
Phacelia spp.	0	0	0	0	0	1	1	1.6	0	0	0	0	0	0	1	1.60
Plantago insularis	0	0	2	3	2.4	0	0	0	0	0	0	0	0	0	4	1.20
Sphaeralcea spp.	0	0	2	2	1.6	1	1	1.6	0	0	0	0	0	0	3	1.60
Strephanomeria spp.	0	0	1	1	1.6	0	0	0	0	0	0	0	0	0	1	1.60
Thelypodium lasiophyllum	0	0	1	1	1.6	0	0	0	0	0	0	0	0	0	1	1.60
Species C	4	5	28	58	3.31	31	48	2.46	16	28	8.4	13	16	9.84	47	9.30
Species D	0	0	15	32	3.41	16	18	1.79	5	5	4.8	5	5	8	25	5.76
Species E	2	52	10	54	8.46	9	46	8.18	10	67	32.16	1	1	8	19	28.51
Species F	2	8	15	18	5.76	3	5	2.66	2	4	9.6	1	1	8	5	14.40
Species G	0	0	5	12	3.84	3	3	1.6	2	4	9.6	0	0	0	4	10.80
Species H	0	0	1	1	1.6	0	0	0	0	0	0	0	0	0	1	1.60

Table 12. Continued

Species	Litter		0-1 cm			1-3 cm			2-5 cm			5-10 cm			All depths	
	Sample	Seeds	Sample	Seeds	Seeds per sq. dm	Sample	Seeds	Seeds per sq. dm	Sample	Seeds	Seeds per sq. dm	Sample	Seeds	Seeds per sq. dm	Sample where present	Estimated mean seeds per sq. dm
Species I	0	0	2	2	1.6	0	0	0	0	0	0	0	0	0	2	1.60
Species J	0	0	1	1	1.6	0	0	0	0	0	0	0	0	0	2	1.60
Species K	0	0	0	0	0	0	0	0	1	1	4.8	0	0	0	1	4.80
Species L	0	0	0	0	0	0	0	0	1	1	4.8	1	1	8	2	6.40
Species M	0	0	0	0	0	0	0	0	0	0	0	1	1	8	1	8.00
Species N	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1.00
Species O	0	0	2	2	1.6	1	1	1.6	0	0	0	0	0	0	2	2.40
Species P	1	1	0	0	0	1	1	1.6	0	0	0	0	0	0	1	2.60
Species Q	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1.00
Species R	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1.00
Species S	1	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1.00
Species T	0	0	0	0	0	1	1	1.6	0	0	0	0	0	0	1	1.60
Species U	0	0	0	0	0	1	1	1.6	0	0	0	0	0	0	1	1.60

Table 13. Seed distribution with depth, Silverbell

Species	Number of seeds at depth				X^2 (*)
	0-1 cm	1-2 cm	2-5 cm	5-10 cm	
Astragalus nuttalliana	13	18	3	4	10.35
Boerhaavia spp.	26	7	3	2	38.79
Bouteloua aristidoides	694	71	49	16	2637.34
B. barbata	313	66	26	26	863.25
Euphorbia chamaesyce†	67	34	17	1	78.55
E. sp.	5	9	1	1	26.00
Ferocactus sp. A	33	15	10	6	26.63
Ferocactus sp. B	99	63	69	59	13.61
Pectocarya spp.	103	20	5	7	201.83
Species C	44	46	27	16	19.76
Species D	29	16	5	5	31.66
Species E	55	49	64	2	52.67
Species F	18	5	4	1	24.43
Species G	37	13	3	-	75.42

*At .01 Significance level X^2 = 11.34
At .001 Significance level X^2 = 16.27

†Without one sample area which included a cache of 344 seeds at 2-5 cm

Table 14. Distribution of seeds in litter and surface soil, Silverbell

Species	No. of samples without Litter but with seeds in the surface soil	Samples with litter	
		More seeds in surface soil than in litter	Fewer seeds in surface soil than in litter
Astragalus nuttalliana	4	7	--
Boerhaavia spp.	5	3	8
Bouteloua aristidoides	15	12	13
B. barbata	19	13	6
Euphorbia chamaesyce	11	12	2
E. hyssopifolia	3	--	--
Ferocactus sp. A	5	5	2
F. sp. B	--	7	--
Pectocarya spp.	11	22	6
Species C	7	8	1
Species D	10	18	1
Species E	5	3	1
Species F	--	4	--
Species G	3	--	--

Table 15. Proportion of seeds at different depths, Silverbell

Species	Percentage of total seeds at Surface	0-1 cm	1-2 cm	2-5 cm	5-10 cm
Astragalus nuttalliana	1	16	23	36	24
Boerhaavia spp.	32	34	9	12	13
Bouteloua aristidoides	17	62	5	11	5
Bouteloua barbata	11	48	6	21	14
Euphorbia chamaesyce	3	41	21	32*	3
Euphorbia hyssopifolia	0	45	23	11	21
Ferocactus sp. A	4	29	13	27	27
Ferocactus sp. B	4	14	9	30	43
Pectocarya spp.	14	52	10	7	17
Species C	1	18	17	33	30
Species D	1	35	19	17	28
Species E	9	18	17	53	4
Species F	11	40	11	27	11
Species G	0	61	18	21	0
All species	13	37	11	21	18

*Sample with cache of these seeds omitted

Seeds of the two *Bouteloua* species are significantly more abundant in the open areas than under shrubs (though the one specimen of *Opuntia fulgida* sampled harbored a large number), but for other seed species the tendency is in the opposite direction. In Table 17 are analyses of variance separately for *Bouteloua* and for other seed species.

Position under shrub canopy: As in Rock Valley, comparisons were made between the total seed population per unit area (combining all depths) at different distances from the center of a shrub canopy. The results will be found in Table 18. They were subjected to concordance tests, as shown in Table 19, series of three, four and five samples from the shrub center being combined for each species of seed where that species occurred somewhere in the series.

As at Rock Valley, these tests showed no significant agreement between the rankings for a given seed species under different canopies, and the exact test of trend was applied, combining different seed species under a given canopy species. The results are shown in Table 20.

Under *Ambrosia dumosa*, *Larrea divaricata*, and *Olneya tesota*, a significant trend was shown, but under *Cercidium microphyllum* there was none.

Table 16. Estimates of seed numbers per sq. dm under shrub species, Silverbell

Canopy Species	Open	*Ambros. dumosa*	*Larrea divar.*	*Cercid. microph.*	*Olneya tesota*	*Opunt. spino.*	*Cereus gigan.*	*Fouqueria splendens*	*Acacia constr.*	*Opuntia fulgida*
No. of canopy Individuals	4	3	4	3	3	1	1	1	1	1
No. of 1 sq. dm samples	4	8	14	15	14	3	3	4	3	3
Seed species										
Astragalus nuttalliana	1.2	2.4	1.4	1.5	0.7	3.7	0.5	3.9	2.1	8.5
Boerhaavia spp.	2.8	3.1	1.0	3.5	1.4	0	0	0	0	0
Bouteloua aristidoid.	250.5	46.0	20.1	2.7	1.1	1.1	34.1	0	2.1	215.0
B. barbata	96.8	36.7	21.0	5.4	1.3	1.6	1.1	2.4	5.7	17.8
Euphorbia chamaesyce	5.6	8.7	0	.8	2.7	1.1	3.2	1.2	8.3	661.1
E. hyssopifolia	0	0	7.8	0	0	0	0	0	0	23.5
Ferocactus sp. A	0.4	0.2	0.8	.4	5.0	19.9	1.6	0.8	3.2	0
Ferocactus sp. B	0	0	1.9	.2	74.6	0	0	4.8	0	2.7
Pectocarya sp.	2.8	7.3	4.9	5.2	6.5	4.3	1.1	0	1.6	6.9
Species C	1.6	0.6	1.7	1.7	2.3	2.7	3.7	1.5	1.6	6.4
Species D	4.0	1.6	4.2	7.4	4.7	21.9	16.0	0.8	3.2	14.4
Species E	2.4	0	1.9	15.3	22.8	0	0	0	0	8.0
Species F	0	0	0	0	5.1	0	0	0	0	0
Species G	0	0	0.5	0	0	0	0	0	0	36.8
Other species	0.8	38.9	1.0	1.8	2.6	0.4	5.9	5.0	25.8	67.3
Total, all species	368.8	145.5	68.2	42.9	130.8	56.7	67.2	19.6	53.6	1068.3

Table 17. Analysis of variance, total seed populations per sq. dm, under different canopies

Species	D.F.	S.S.	M.S.	F.
Bouteloua spp				
Bare ground vs. shrubs	1	334.30	334.30	7.30*
Treatments: Bare ground	1	126.67	126.67	
Treatments: Under shrubs	1	2.21	2.21	
Between different shrubs				
Untreated area	8	236.21	29.53	
Treated area	3	222.37	74.12	
Within same canopy type and treatment	7	320.63	45.80	
Other species				
Bare ground vs. shrubs	1	29.36	29.36	
Treatments: Bare ground	1	12.92	12.92	
Treatments: Under shrubs	1	5.00	5.00	
Between different shrubs				
Untreated area	8	417.80	52.23	3.25
Treated area	3	65.02	21.67	
Within same canopy type	7	112.41	16.06	

*P < 0.05

Table 18. Total seed population at different distances from the center of a shrub canopy, Silverbell

Canopy Species	0-10 cm		20-30 cm		40-50 cm		60-70 cm		80-90 cm	
	No. of Samples	Seeds per sq. dm	No. of Samples	Seeds per sq. dm	No. of Samples	Seeds per sq. dm	No. of Samples	Seeds per sq. dm	No. of Samples	Seeds per sq. dm
Cercidium microphyllum	3	45.57	3	35.53	3	52.35	3	34.13	3	47.24
Larrea divaricata	4	75.2	3	37.13	4	64.75	3	94.73	0	--
Ambrosia dumosa	3	151.87	3	88.53	2	52.00	0	--	0	--
Olneya tesota	3	177.8	3	145.4	3	112.93	3	140.93	2	49.9
Opuntia spinosior	1	68.8	1	75.6	1	25.6	1	0	0	--
Cereus giganteus	1	76.8	1	46.4	1	78.4	1	0	0	--
Fouqueria splendens	1	19.2	1	11.2	1	20.8	1	27.2	0	--
Acacia constricta	1	40.4	1	61.6	1	52.8	1	0	0	--
Opuntia fulgida	1	251.6	1	163.2	1	2764.8	1	0	0	--

Table 19. Tests of concordance: Rankings of seed populations at different distances from the center of a shrub canopy, Silverbell

Species	No. of canopy Individuals	No. of samples Per canopy	W
Astragalus nuttalliana	5	5	.218
Boerhaavia sp.	3	5	.305
Bouteloua aristidoides	5	5	.107
Bouteloua barbata	3	5	.281
Euphorbia chamaesyce	2	5	.338
Ferocactus sp. A	2	5	.417
Ferocactus sp. B	2	5	.321
Pectocarya sp.	5	5	.210
Species C	5	5	.293
Species D	4	5	.153
Species E	3	5	.544
Astragalus nuttalliana	7	4	.125.
Boerhaavia sp.	5	4	.021
Bouteloua aristidoides	6	4	.297
Bouteloua barbata	4	4	.172
Euphorbia chamaesyce	5	4	.091
Ferocactus sp. A	4	4	.083
Ferocactus sp. B	4	4	.017
Pectocarya sp.	7	4	.214
Species C	8	4	.246
Species D	5	4	.078
Species E	3	4	.573
Astragalus nuttalliana	12	3	.002
Boerhaavia sp.	5	3	.031
Bouteloua aristidoides	10	3	.085
Bouteloua barbata	8	3	.014
Euphorbia chamaesyce	10	3	.009
Ferocactus sp. A	7	3	.354
Ferocactus sp. B	3	3	.636
Pectocarya sp.	12	3	.022
Species C	12	3	.292
Species D	8	3	.094
Species E	4	3	.250

Total seed populations on the Silverbell site: Again, as with Rock Valley, estimates of areas of different annuli under shrub canopies, and areas between shrub canopies, would be needed for combining with estimates of the seed populations in these categories of area to obtain accurate estimates of the seed population of the site as a whole, in view of the fact that the population densities often decrease from the center of a shrub outwards. Data for numbers of shrubs of different sizes were not available at the time of writing, so use was made of data for shrub cover included in the 1972 Progress Report for the Silverbell Validation Site (Thames, 1972). Seed weights are given in Table 21. Table 22 estimates the reserves of seeds in the untreated area as a whole at 33,091 m^{-2}, weighing 8.1311 g.

Table 20. Effect of position under a shrub canopy on seed density, Silverbell

Shrub Species	Number of Canopy Individuals	Number of 1 sq. dm Samples	Number of Rankings	Significance*
Ambrosia dumosa	3	8	9	.005
Cercidium microphyllum	3	15	24	.50
Larrea divaricata	4	14	29	.025
Olneya tesota	3	14	26	.004

*Probability of observed rankings on the null hypothesis, against the alternative hypothesis of a trend from the center outwards.

Table 21. Mean weight of individual seeds, Silverbell DSCODE A3UGE41

Species	Seed Weight (mg)	Species	Seed Weight (mg)
Amsinckia tesselata	1.99	*Thelypodium lasiophyllum*	0.10
Astragalus nuttalliana	1.20	Species C	1.50
Boerhaavia spp.	0.60	Species D	1.33
Bouteloua aristidoides	0.24	Species E	0.11
B. barbata	0.12	Species F	0.40
B. spp.	0.80	Species G	0.93
Cryptantha spp. 1	0.18	Species H	0.10
C. spp.2	0.07	Species I	0.10
Eriochloa spp.	1.90	Species J	0.40
Euphorbia chamaesyce	0.12	Species K	0.40
E. hyssopifolia	2.28	Species L	0.65
Ferocactus spp. 1=species A	0.46	Species M	0.40
Ferocactus spp. 2=species B	1.26	Species N	1.83
Franseria spp.	1.70	Species O	0.30
Larrea divaricata	6.63	Species P	0.10
Lepidium medium	0.10	Species Q	14.10
Pectocarya spp.	0.41	Species R	1.10
Phacelia spp.	0.50	Species S	1.00
Plantago insularis	1.27	Species T	1.40
Sphaeralcea spp.	0.50	Species U	1.10
Stephanomeria spp.	0.31		

Table 22. Seed reserves at Silverbell

Species	Per sq. m	
	Population	Biomass (mg)
Astragalus nuttalliana	130	157
Boerhaavia sp.	268	161
Bouteloua aristidoides	21,805	5,233
B. barbata	8,583	1,030
Euphorbia chamaesyce	521	63
E. hyssopifolia	21	48
Ferocactus sp. A	88	40
Ferocactus sp. B	213	268
Pectocarya sp.	311	127
Species C	167	250
Species D	422	562
Species E	325	36
Species F	14	6
Species G	23	21
Other Species	206	309*
Total	33,097	8,311

*For this figure a mean seed weight of 1.50 mg was used, derived by weighting the figures in Table 12 for the different species with their relative overall abundance.

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