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ABUNDANCE AND DISTRIBUTION OF SOIL MICRO-ARTHROPODS IN ROCK VALLEY, NEVADA

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ABSTRACT

Weekly observations throughout 1974 of the nature, density and distribution of soil arthropods in Rock Valley, Nevada, are reported, together with associated soil temperatures and moisture values. Density usually decreased at greater distances below the surface or away from the shrub base; however, density in the top 10 cm fell below that in the next 10 cm in June and September. In general, densities were highest in the winter months. Neither the size nor the species of shrubs affects the density of arthropods below them. Density is positively correlated with soil carbon concentration. Artificial watering confirmed the importance of soil moisture in controlling arthropod density, and changes in patterns of vertical distribution were associated with temperature changes. Increased soil salinity probably leads to a decrease in arthropod density. A more satisfactory model for calculating total numbers and biomass of arthropods present has been developed. Using these values and published measurements of oxygen consumption, calculations of total metabolism for various taxa and trophic levels of arthropods have been made. Approximately 0.2% of the total energy input involved in net primary productivity in the area was respired by detritivorous arthropods in 1974.

INTRODUCTION

This is the final report on work done during a three-year period, 1973 through 1975. An earlier report (Edney et al. 1975) referred to the distribution of arthropods during the first 26 weeks of 1974, and reached tentative conclusions concerning the effects of season, soil temperature, moisture and vertical and horizontal distances from shrubs, on arthropod numbers. The present report presents complete data on distribution for 1974 and deals with further work done during 1975 in the following areas: 1) reliability of extraction techniques; 2) seasonal changes in vertical distribution; 3) the effects of salt concentrations; 4) the relationship of soil carbon to arthropod distribution; 5) the effect of shrub size and further analysis of distribution patterns around shrubs; 6) the effects of various watering treatments; and 7) estimates of total metabolism.

The three-year program was initially undertaken as a contribution to the analysis of a desert ecosystem in Rock Valley, Nevada, and the results are in a form suitable for integration with other work in the same area. The significance of soil invertebrates in desert ecology has so far received very little attention, and the present investigation has produced the most detailed set of data on the subject presently available (stored under DSCODE A3UED01).

Some data on the effects of soil salinity are included in the present report. These were obtained in response to a need for information about the effects of undue salinity caused by energy generation (particularly geothermal energy). Although this work was not part of the original research plan, the data are included because of their general interest.

METHODS

The main techniques have already been described, but for convenience they are briefly repeated here, and a revised model for calculating total numbers is described. Most of the sampling was done by taking 1 liter of soil from each of three depth levels (0-10, 10-20 and 20-30 cm) at each of three distances from a shrub base; at the base itself, at the canopy margin and at three mean shrub radii from the base. Four species of shrubs, *Larrea tridentata*, *Ambrosia dumosa*, *Lycium andersonii* and *Krameria parvifolia*, were sampled once a week, between 9:00 and 10:00 a.m. Each sample was thoroughly mixed and two 500-ml subsamples were used for extraction of arthropods. Soil temperatures were measured weekly in the field in each sample position and samples were taken for gravimetric soil moisture determinations. Arthropods were extracted from the soil by modified Newell funnels (Newell 1955; Edney at al. 1974). For some experiments, additional sampling positions were used. These were at the usual three levels, but at one-half-radius distances from the shrub base. These positions are numbered 1A, 1B and 1C from above (Fig. 1). In earlier reports (Edney et al. 1974, 1975), in order to make the data compatible with those of Bamberg et al. (1974) for root biomass, it was assumed that positions 1, 2 and 3 represent the central one-third of the area covered by a shrub canopy (Zone A); positions 4, 5 and 6 represent the remaining two-thirds (Zone B); and positions 7, 8 and 9 represent the area between shrubs (Zone C). However, as a result of further intermediate samples, we now have a better picture of arthropod density profiles around shrubs and we know that size of shrub has no effect on arthropod density. Thus the total numbers and biomass of arthropods in the soil under a shrub, down to 30 cm, as well as in the intershrub areas, can be calculated by an improved method (as described in the "Results" section).

As regards extraction technique, Bender et al. (1972) report that in certain soils, extraction of arthropods by flotation may be up to ten times more efficient than extraction by standard Tullgren funnels. However, their results do not necessarily apply to all kinds of soil and, since flotation is very time-consuming when large numbers of samples are involved, we decided to use a funnel method which seemed to give satisfactory results. The following experiments were carried out to compare the efficiency of the two methods for our desert soils.

Tests were made with two sets of soils, both from under shrub canopies. For each test, six samples (five in one case) were extracted by both methods and the results compared. Soil for each test was homogenized for 15 min in a Patterson-Kelly twin shell lab blender running at 10-15 rpm and the soil was then separated into 200- and 20-cc aliquots.

The 20-cc samples were used for flotation. Each was placed in a vertical glass cylinder and blended with $MgSO_4$ (specific gravity 1.2). After agitation for several minutes, more $MgSO_4$ solution was added from below. The material floated off (containing arthropods) was filtered through cheesecloth and arthropods in the residue were counted. The benzene extraction procedure of Bender et al. (1972) was omitted because of interference by resin-like materials at the benzene-water interface. For the Newell funnel extraction, 200-cc aliquots were used. Extraction proceeded for 36 hr and the arthropods were collected in 70% ethanol. According to the results shown in Table 1, the Newell funnel method was 0.912 times as efficient as the extraction method for soil #1 and 0.862 times as efficient for #2 (giving a mean efficiency of 0.887). Variation between samples was large and differences between the means are not significant at the 5% level. Since there is no demonstrable difference in extraction efficiency, we have used uncorrected numbers derived from funnel extractions in expressing the results that follow. No claim is made that our data represent actual numbers present. Neither do we know whether extraction is equally efficient for all taxa. Further work on extraction efficiency is in progress.

Table 1. Comparison of two methods of extraction of arthropods from desert soils. Densities are in numbers per 200 ml soil

	Soil #1		Soil #2	
	Flotation	Funnel	Flotation	Funnel
N	5	6	6	6
Mean	928.33	846.54	510.71	440.17
S.D.	108.17	76.73	118.79	88.93
S.E.	27.04	31.33	44.90	36.30

RESULTS

Size of Shrub

Before calculating biomass and densities for the whole area, we must know whether the density of arthropods under the canopy of any shrub is constant, or is affected by absolute shrub size. The same question applies, of course, to areas between shrubs. In order to answer these questions, samples were taken at four distances: at 0, 0.5, 1.0 and 3 mean shrub radii from the base (positions 1, 1A, 4 and 7, respectively) all at 0-10 cm depth from six groups of *Larrea* shrubs, each group consisting of five individuals with widely different radii.

There was great variation between the numbers at different times of the year, as might be expected, and the number of samples in each group was rather small. Thus, in order to combine data from all groups, observations were standardized by calculating Z where $Z_i = (X_i - \overline{X})/s$, $\overline{X}$ is the mean density for all samples at one position and in one group, X_i is the actual density of sample (i) and s is the standard deviation for that group and position (Dixon and Massey 1969).

The results for position 1 (0-10 cm depth at shrub base) are shown in Figure 2, where standardized values are plotted against shrub radius and a regression line has been calculated. The slope of the line is $-0.0025\ Z \cdot cm^{-1}$, r is 0.089 and $P > 0.1$. In other words, there is no measurable effect of shrub size on density of arthropods in position 1. Table 2 shows the standardized values in relation to shrub radius from all four positions and the regression slopes and coefficients concerned. There is only one position, namely 7 (0-10 cm depth at 3 radii), at which any indication of a size effect is seen. Here the slope is $-0.0128\ Z \cdot cm^{-1}$, r is -0.46 and P lies between 0.02 and 0.01. The effect is small and is

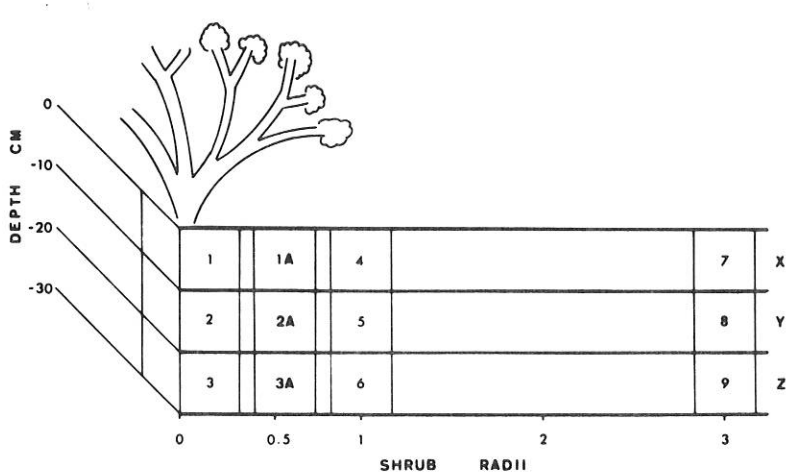

Figure 1. Diagram showing the dimensions and numbering of sample positions in relation to a shrub. 1, 2, 3 at the shrub base, 1A, 2A, 3A at 0.5 radii, 4, 5, 6 at 1 radius, and 7, 8, 9 at 3 radii from the base. X, Y and Z refer to levels 0-10, 10-20 and 20-30 cm, respectively.

significant only if the very largest intershrub spaces (9 m or above) are included. These are very rare, and we feel justified in assuming a uniform density throughout the intershrub area. This assumption is further justified below under "Densities in Relation to Shrub Species."

Soil Temperature and Moisture

Soil temperature was measured by YSI telethermometer immediately before samples were taken (between 9:00 and 10:00 a.m. daily). Figure 3 shows the monthly means at two depths, —5 and —25 cm; readings at all lateral positions being averaged to represent the temperature at each depth. As might be expected, the results show a rise in soil temperature during the summer months. They also show seasonal changes in the direction of the mean temperature gradient (warmer or cooler near the surface). Figure 3 also shows soil moisture, each point representing the mean for all positions at each level for all species for all weeks in each month. Soil moisture was generally lower in the summer than at other times and lower near the surface than elsewhere, except duing the fall months and in July, when precipitation occurred. The relationships of these data to arthropod density are considered below.

Densities in Relation to Shrub Species

Densities of all arthropods by shrub species and month are shown in Figure 4. As the previous report suggested, there is no clear, constantly maintained species effect. The March value for *Krameria* is surprisingly high and both *Krameria* and *Lycium* appear to have higher densities than the other two species in November, and perhaps in December. However, analysis of variance shows that when the data for 1974 are taken as a whole (Table 3) there is no effect of species, but there are strong effects of relative distance (in terms of radii) and of depth, apart from the effects of the covariates, temperature, moisture and time of year. The conclusion is that the lumping together of values for all species is justified.

Patterns of Distribution around Shrubs

Previously reported data for lateral distribution were based on samples from 0, 1 and 3 radii from the shrub base. There was a need for finer discrimination than this and, consequently, during 1975, samples from more intermediate distances were taken. Five *Larrea* shrubs were used and samples were taken on five days during the period of June through December at distances of 0, 0.5, 1.0, 1.5, 2.0, 2.5 and 3.0 radii; no account being taken of actual shrub size. The results are shown in Table 4 and graphed in Figure 5. It is clear that there is a progressive, apparently linear, decrease in arthropod density from the base to about 1.4 radii, beyond which densities remain constant.

As a result of this additional information, a better model for calculating total numbers can be developed. Each 1-liter sample had a depth of 10 cm, vertical sides and, therefore, a top surface area of 100 cm^2. Other samples were 0.5 liter and, therefore, their surface was 50 cm^2. Thus, the total density of arthropods in numbers per cm^2 is known at several distances from the shrub base. This value falls off linearly to 1.447 radii and remains at a constant low level at greater distances. If we assume that positions 1, 2 and 3

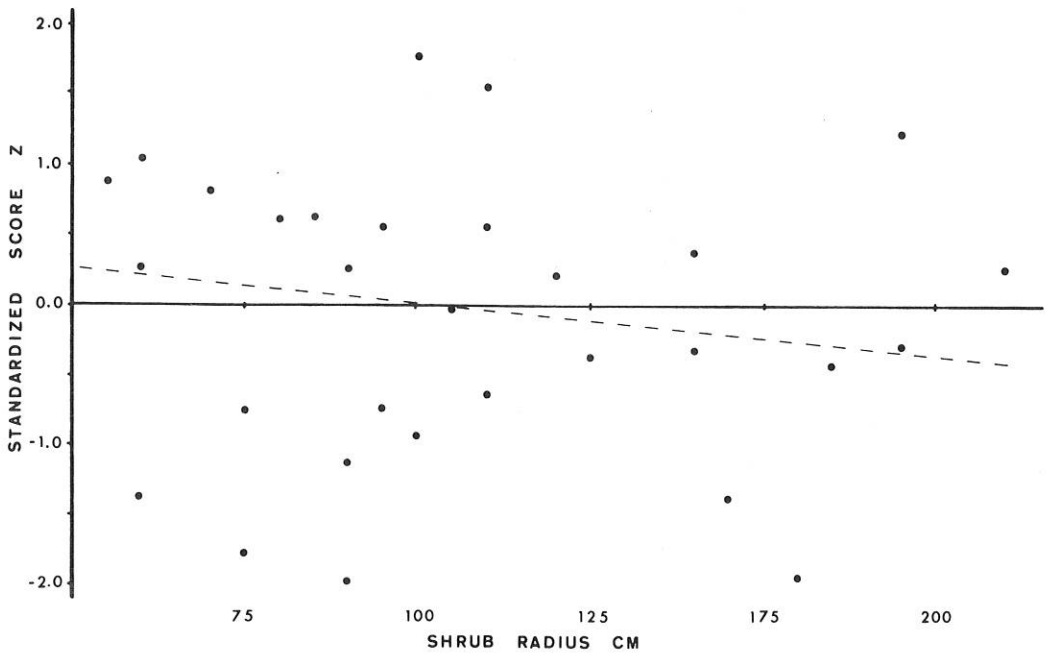

Figure 2. The regression of standardized scores (Z numbers derived from arthropod densities) at position 1, on shrub radius. The slope is 0.0025 $Z \cdot cm^{-1}$, r is 0.089 and $P >> 0.1$. Thus, there is no demonstrated effect of radius on density at position 1.

represent densities at 0 radii, that 4, 5 and 6 represent 1 radius and that 7, 8 and 9 represent > 1.45 radii, then each set of nine samples can be used to calculate the best fit for a linear regression from 0 to 1.447 radii. Thus, $y = ax + b$, where y is density of arthropods in numbers per cm^2, x is distance from the shrub base in centimeters, a is the slope of the line and b is the y-intercept calculated from the regression.

The numbers of mites in the area of influence of any one shrub may then be calculated by setting up a double integral in polar coordinates as follows:

$$\text{no. of mites} = \int_0^{2\pi} \int_0^{R} x\,(ax + b)\,dx \cdot d\theta \qquad (1)$$

where R in centimeters is 1.447 times the mean shrub radius and θ is the angle in radians through which the function is rotated (2π in this case). Solving this double integral gives the expression $1/3\,\pi\,x^2y$. Dimensional analysis then shows that the expression is in $(cm^2)\cdot(n\cdot cm^{-2})$, or n, the number of mites.

Plant species and shrub size have no effect, so that we can deal with average shrubs and derive an estimate of total numbers of arthropods per hectare as follows. From data given by Ackerman et al. (1975b), the weighted mean radius of a shrub is 0.3053 m, and the mean density of shrubs is 8904/ha. The present data show that the influence of a shrub on arthropod numbers extends to 1.447 times its own radius, and further calculation then shows that shrubs influence 54.59% of the total area, leaving 45.41% unaffected. Equation 1 gives the number of arthropods in the area influenced by an average shrub and, from this, the total number of arthropods in such influenced areas, per hectare, can be obtained. The number of arthropods per hectare in the uninfluenced areas can also be obtained from densities at a distance of 3 radii from a shrub base (i.e., positions 7, 8 and 9). Finally, the sum of these two numbers gives the total numbers of arthropods per hectare.

Arthropod Densities and Biomass

In order to arrive at total biomass in terms of dry mass per unit area, further measurements and manipulation of the data are required. First, estimates were obtained for the mean dry mass of individual mites belonging to each family. These masses were determined by weighing mites that had been dried at 60 C for 48 hr after prior preservation in alcohol. The mites were weighed in groups on a Cahn microbalance to the nearest 1.0 μg. Since each group of mites was weighed as a single batch, no reliability estimates for the mean individual masses can be given. The results are shown in Table 5. Multiplying the mean dry mass by the mean population density gives an estimate of the biomass for each family.

The insect orders, Collembola and Coleoptera, were represented by several families with different individual sizes, and the proportion of the total insect populations represented by each family varied considerably throughout

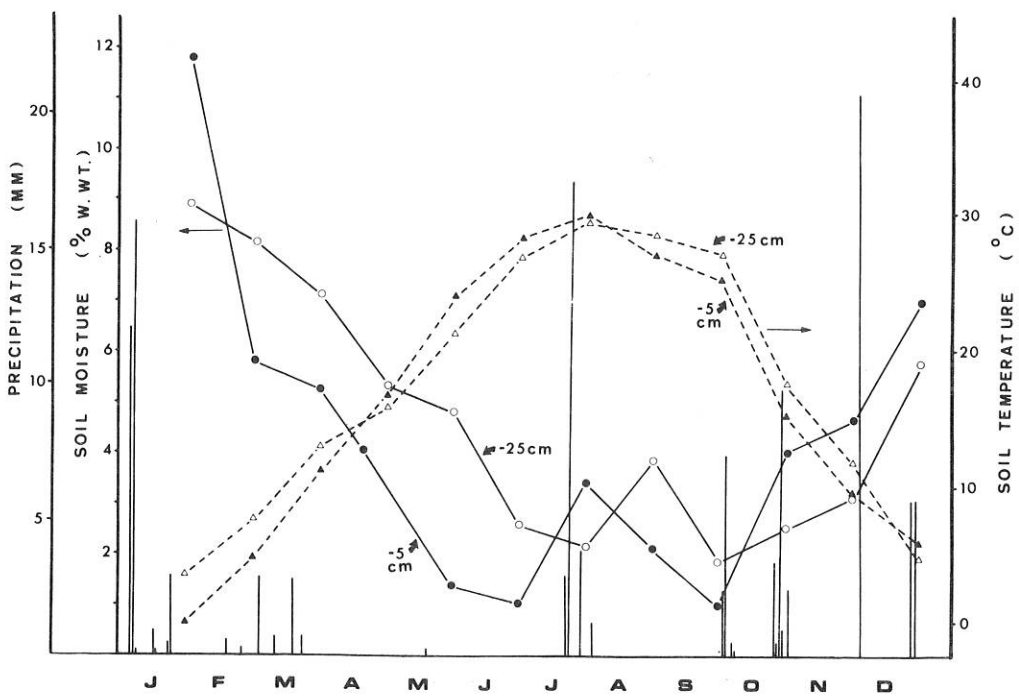

Figure 3. Abiotic data during 1974. Solid and open triangles: mean monthly soil temperatures between 9:00 and 10:00 a.m. at depths of 5 and 25 cm, respectively, averaged for positions 1, 4 and 7. Solid and open circles: soil moistures at corresponding depths. Vertical lines: precipitation.

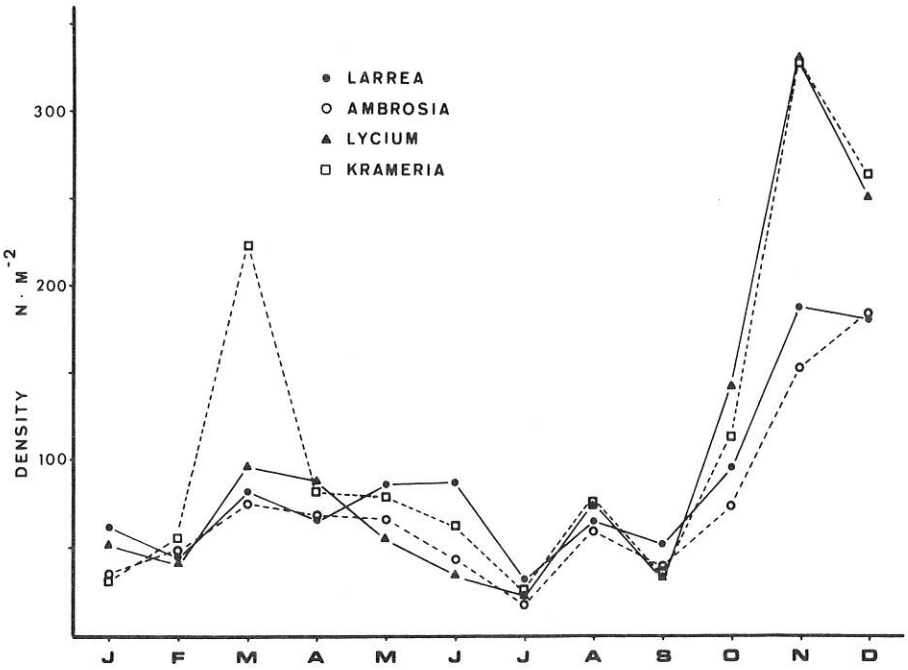

Figure 4. Density of soil arthropods associated with four shrub species.

the year. To overcome this problem, the mean mass of individuals of each family and the frequency with which each family occurred, were used to calculate a weighted mean mass for collembolans and for coleopterans for each month throughout the year (Table 6).

Data obtained in these ways for densities and biomass of each main arthropod group are shown as monthly means through the year 1974 in Table 7. These data refer only to the top 30 cm of soil, but as other results show (Edney et al. 1975 and the present report), numbers decrease rapidly down to 30 cm, and samples from below this level would probably not add much to the totals.

Table 7 shows that the total number of insects was always less, usually very much less, than the total number of mites; however, because the insects concerned were heavier than the mites, there was generally a greater biomass of insects than of mites. The only exceptions to this are in October and November, when there was an enormous increase in mite numbers. In Figure 6, essentially the same data are shown in summary form, including means and standard deviations; the latter being based on weekly totals not shown in Table 7. Combining these data with the abiotic data shown in Figure 3 permits the following observations.

In 1974, densities were low during the winter; they increased in March (perhaps as a result of a temperature rise), but declined thereafter (perhaps as a result of a fall in soil moisture) to a low level in the summer months. Densities then increased strongly, to a peak for the year in November (perhaps as a result of rain and increasing soil moisture). In a general way, soil arthropod density seems to correspond with soil moisture, but may be influenced by temperature (as in January and February) when soil moisture was abundant, but temperatures were low. There is an interesting correlation between the small peak in August 1974 and soil moisture. This was almost certainly the result of rains that occurred in the last part of July (see Fig. 3). The May peak in biomass is largely due to coleopteran larvae.

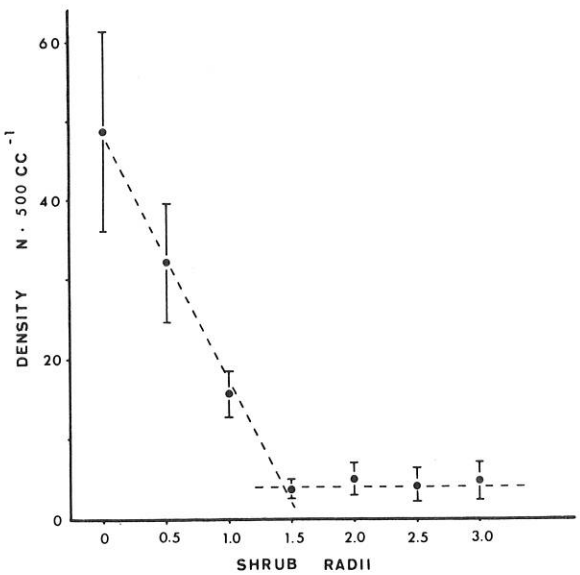

Figure 5. Distribution of arthropods around a shrub. Columns represent mean densities ± one standard error, in samples taken at indicated distances from the shrub base.

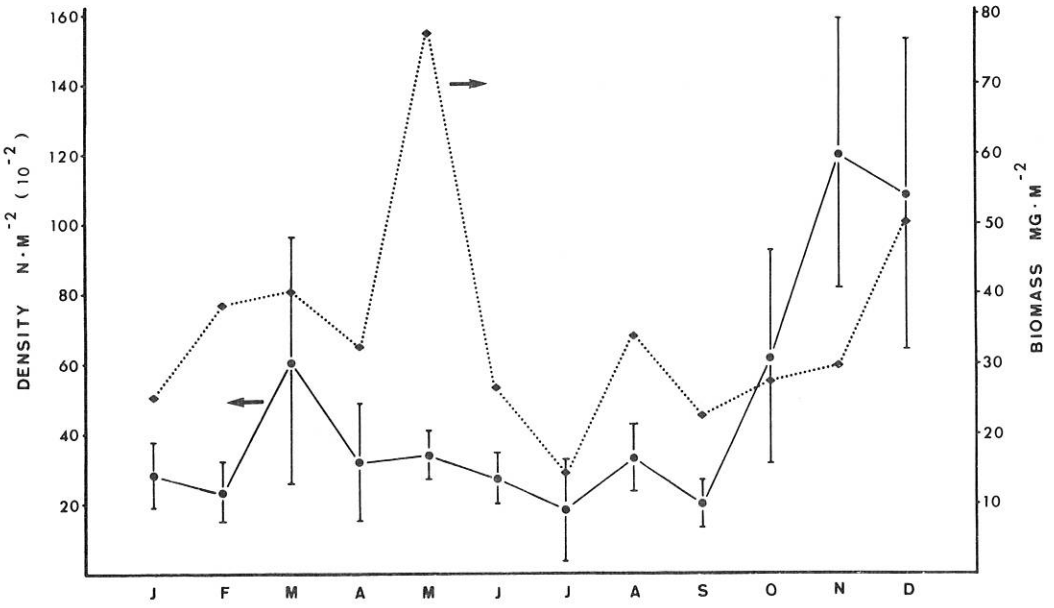

Figure 6. Density (solid line) and biomass (dotted line) of all arthropods by month in 1974. Standard deviations are based on weekly means for each month. Further explanation in text.

Table 2. Standardized values ("Z" scores) for density against shrub radius

Date (1975)	Radius (cm)	Sample position (in radius units) 0	0.5	1	3
4-28	55	0.896	-0.012	-0.040	0.147
	85	0.641	1.806	0.094	1.028
	105	-0.015	0.047	1.779	0.440
	140	0.386	-0.774	-0.647	0.294
	155	-1.908	-1.067	-1.186	-1.909
6-2	75	-0.749	-1.033	-0.580	1.737
	90	1.967	0.090	-0.580	0.401
	110	-0.632	-1.033	-1.159	-0.935
	140	-0.303	1.661	0.773	-0.267
	170	-0.283	0.314	1.545	-0.935
8-20	80	0.262	0.973	0.233	0.571
	95	-0.719	-1.037	0.233	-1.214
	110	1.569	-0.931	-0.155	1.643
	145	-1.373	1.396	1.397	-0.500
	185	0.262	-0.402	-1.708	-0.500
9-24	60	0.277	-0.555	-0.180	-0.303
	80	-0.605	-0.185	-0.424	1.971
	90	-1.109	-1.481	-0.914	-0.682
	100	1.790	1.110	-0.424	-0.682
	125	-0.353	1.110	1.942	-0.303
10-27	60	1.050	0.954	-0.631	-0.928
	75	-1.759	-0.678	1.663	1.650
	95	0.562	-0.804	0.516	0.619
	110	0.562	-0.929	-1.204	-0.928
	160	-0.415	1.456	-0.344	-0.413
11-12	60	-1.365	1.845	1.278	0.950
	70	0.813	0.231	-0.365	-0.346
	100	-0.929	-0.692	-1.095	1.382
	120	0.232	-0.923	-0.913	-0.778
	170	1.249	-0.461	1.095	-1.209
Slope		-0.0025	-0.0003	0.0004	-0.0128
(r) Corr. coeff.		-0.0913	-0.0092	0.0151	0.4602
N		30	30	30	30
P		>>0.1	>>0.1	>>0.1	0.01 - 0.02

Table 3. Analysis of variance of the arthropod density data for the whole of 1974

	Degrees of freedom	F	p
Mean	1	1.266	0.261
Plant species	3	1.730	0.159
Relative distance	2	7.528	0.001
Depth	2	186.538	0.000
Species - distance	6	1.018	0.412
Species - depth	6	1.976	0.066
Distance - depth	4	23.020	0.000
Sp. - dist. - depth	12	0.792	0.659
Covariate - temperature	1	18.294	0.000
Covariate - moisture	1	38.769	0.000
Covariate - time	1	186.049	0.000

Table 4. Distribution of soil arthropods around shrubs (numbers per 500 ml soil)

Date (1975)	Distance from shrub base in radii 0	.5	1.0	1.5	2.0	2.5	3.0
6-18	67	39	15	6	6	10	4
10-29	23	18	15	5	2	2	1
11-12	44	28	14	1	3	1	3
11-21	24	18	8	1	1	0	2
12-3	85	58	26	6	13	14	14
$\bar{X}$	48.6	32.2	15.6	3.8	5.0	5.4	4.8
S.D.	27.1	16.8	6.5	2.6	4.8	5.7	5.3
S.E.	12.1	7.5	2.9	1.2	2.1	2.5	2.4

Seasonal Changes in Vertical Distribution of Populations

In an earlier report (Edney et al. 1975), three-dimensional graphs were presented to show densities in relation to distance and depth during the first half of 1974. Data for the whole year are now presented and it is indeed apparent that systematic changes in population distribution do occur (Table 8 and Figure 7). Level 0-10 cm had a very high proportion (from 71 to 94%) for certain weeks in January and February. This fell to as low as 21% for a week in July and again in September, but rose towards the end of the year. Distributions at other levels also varied; level 10-20 cm having a maximum during September, level 20-30 cm during June and September. Whether or not these changes are due to vertical migrations or to differential births and deaths cannot be said for certain. The organisms move quite rapidly and diurnal vertical migrations have been reported by Pande and Berthet (1975) and by McBrayer et al. (in press); however, further work on this problem is necessary.

Table 5. Mean dry weights of individual arthropods

Taxon	Number in batch	Mean individual mass (micrograms)
Oribatei	27	6
Acaridae	7	1
Nanorchestidae	7	7
Caeculidae	6	76
Tydeidae	21	1
Caligonellidae	7	15
Bdellidae	5	5
Trombidiidae	5	117
Collembola		
Entomobryidae	7	15
Sminthuridae	7	17
Onychiuridae	7	2
Poduridae	7	3
Coleoptera (larvae)		
Curculionidae	15	46
Tenebrionidae	3	1839
Cleridae	4	731

Distribution of Soil Carbon

To obtain an indication of the amount of food available to arthropods, carbon contents of soil samples throughout the year 1975 were measured using Walkley's (1947) method. For these measurements, samples from 0.5 radius from the shrub base were included, as well as the usual distances of 0, 1 and 3 radii. Samples were taken once each month from one shrub of each of the usual four species. The results are shown in Table 9, where each entry is a mean of eight samples, two from each shrub species. The overall results are quite consistent with arthropod densities. Thus, there is always a fall in carbon content with distance from the shrub base, and a much wider fluctuation of carbon contents in upper than in lower levels. Some of this probably reflects litter fall during the summer months, although litter itself was excluded from the samples. A comparison of dry weight of arthropods (from Table 7) with the weights of carbon in Table 9, shows that the arthropods themselves contribute but insignificantly to the total carbon present. There is a distinct drop in carbon content during November and December, and it is possible that this may be related to the enormous increase in mite numbers at that time, but whether carbon is a limiting resource cannot be said.

Some of these carbon values may be compared statistically with arthropod distributions that were used to determine the density profile around shrubs (see "Patterns of Distribution around Shrubs" above), for we have data for both variables for comparable weeks during 1975. When this is done, for 20 comparison points, a linear regression of densities on carbon values gives: $y = 33.95x - 11.9$, where y is number of mites per 500 ml and x is percent soil carbon. The correlation coefficient, r, is 0.89, and $P < 0.01$.

Table 6. Subdivisions of Collembola and larval Coleoptera by month throughout 1974

	J	F	M	A	M	J	J	A	S	O	N	D
COLLEMBOLA					percent of total numbers present							
Entomobryidae	0.0	.014	.149	.375	.444	.417	.128	.648	.875	.015	.003	0.0
Sminthuridae	.206	.383	.289	.500	0.0	.004	.045	.099	.031	.018	.023	.009
Onychiuridae	.689	.531	.333	.125	.556	.333	.767	.242	.078	.955	.956	.973
Poduridae	.105	.072	.228	0.0	0.0	.166	.060	0.0	.016	.012	.017	.018
					weighted mean mass							
(mg)	.0052	.0078	.009	.014	.008	.008	.005	.012	.014	.003	.003	.002
COLEOPTERA (larvae)					percent of total numbers present							
Curculionidae	.905	.925	.875	.902	.292	.200	.583	.059	0.0	0.0	.909	0.0
Tenebrionidae	.095	.027	.014	.042	.521	.400	.167	.471	.500	.750	0.0	1.0
Others	0.0	.048	.111	.056	.167	.400	.250	.470	.500	.250	.011	0.0
					weighted mean mass							
(mg)	.217	.127	.148	.160	1.094	1.037	.517	1.212	1.285	1.562	.050	1.839

Table 7. Numbers·m^{-2} (not underlined) and biomass in mg·m^{-2} (underlined) by month through 1974 for various taxonomic groups of arthropods

	J	F	M	A	M	J	J	A	S	O	N	D
Oribatei	511.7	684.2	956.9	329.9	420.3	435.3	167.1	413.8	394.0	620.3	970.4	974.9
	2.05	2.74	3.83	1.32	1.68	1.74	0.67	1.66	1.58	2.48	3.88	3.90
Acaridae	101.2	29.7	314.9	208.6	102.3	2.8	17.1	3.2	1.1	2.5	20.5	136.6
	0.10	0.03	0.31	0.21	0.10	0.01	0.02	0.01	0.01	0.01	0.02	0.01
Nanor-chestidae	43.9	265.2	363.8	203.7	387.3	483.2	139.5	374.9	217.6	514.8	495.1	277.7
	0.31	1.86	2.55	1.43	2.71	3.38	0.98	2.62	1.52	3.60	3.47	1.94
Caeculidae	1.4	13.6	13.6	4.5	3.6	6.7	3.3	5.0	23.8	7.6	24.2	6.6
	0.02	0.20	0.20	0.07	0.05	0.10	0.05	0.08	0.36	0.11	0.36	0.10
Tydeidae	179.3	225.5	1485.9	566.7	539.8	231.5	232.9	1312.7	766.8	3134.8	8290.4	9270.4
	0.18	0.23	1.49	0.57	0.54	0.23	0.23	1.31	0.77	3.13	8.29	9.27
Caligonellidae	4.2	20.1	29.5	51.2	162.9	205.8	108.1	204.0	187.2	190.1	181.0	158.3
	0.06	0.30	0.44	0.77	2.44	3.09	1.62	3.06	2.81	2.85	2.72	2.37
Bdellidae-Cunaxidae	25.0	103.9	210.6	118.6	130.1	176.0	95.2	192.3	90.3	155.1	136.4	104.1
	0.13	0.52	1.05	0.59	0.65	0.88	0.48	0.96	0.45	0.78	0.68	0.52
Erythraeidae	66.4	35.1	96.4	26.4	60.6	31.9	12.1	17.4	6.5	10.5	5.9	10.7
	0.73	0.39	1.06	0.29	0.67	0.35	0.13	0.19	0.07	0.11	0.06	0.12
Trombidiidae	6.5	51.3	30.1	11.3	20.1	13.3	1.2	7.7	2.5	20.0	42.3	21.4
	0.76	6.00	3.52	1.32	2.35	1.56	0.14	0.90	0.29	2.34	4.95	2.50
Other mites	296.2	265.3	911.6	638.4	383.4	244.5	123.6	247.9	181.3	222.8	327.9	194.3
	1.78	1.59	5.47	3.83	2.30	1.47	0.74	1.49	1.09	1.34	1.97	1.17
Collembola	818.8	242.9	167.8	11.7	10.1	13.8	155.2	158.3	107.6	684.3	431.0	844.7
	4.26	1.90	1.42	0.48	0.08	0.10	0.72	1.85	1.48	1.78	1.12	1.78
Heteroptera	38.3	72.5	122.4	111.8	102.4	47.7	68.0	76.9	30.3	71.9	98.5	69.5
	0.50	0.94	1.59	1.45	1.33	0.62	0.88	1.00	0.39	0.93	1.28	0.90
Coleop. larvae	66.8	169.6	120.5	125.9	57.1	12.6	14.9	15.6	7.3	5.4	17.2	13.9
	14.46	21.61	17.79	20.12	62.47	13.08	7.70	18.91	9.38	8.44	0.86	25.56

Table 8. Changes in vertical distribution with season (percentage of total found at each level)

	Week (of the year)	0-10 cm	10-20 cm	20-30 cm
JAN	2	90.8	5.3	3.9
	3	91.1	7.9	1.0
	4	74.4	10.6	14.0
	5	78.0	13.7	8.3
FEB	6	94.1	2.2	3.7
	7	77.4	15.4	7.2
	8	81.2	12.6	6.2
	9	71.4	23.0	5.6
MAR	10	80.6	12.9	6.5
	11	69.5	18.8	11.7
	12	90.9	6.3	2.8
	13	86.0	9.5	4.5
APR	14	85.2	10.6	4.2
	15	84.8	10.9	4.3
	16	51.5	31.2	17.3
	17	76.7	7.6	15.7
MAY	18	64.6	21.6	13.8
	19	58.7	19.0	22.3
	20	26.8	46.9	26.3
	21	42.7	42.2	15.1
	22	30.9	53.0	16.1
JUNE	23	25.5	51.5	23.0
	24	35.1	34.9	30.0
	25	21.7	50.4	27.9
	26	37.9	30.0	32.1

	Week	0-10 cm	10-20 cm	20-30 cm
JULY	27	42.7	31.8	25.5
	28	45.5	30.9	23.6
	29	20.1	32.6	47.3
	30	61.8	15.3	22.9
AUG	31	66.6	17.3	16.1
	32	45.7	33.1	21.2
	33	46.1	41.5	12.5
	34	38.3	40.5	21.2
	35	26.4	49.5	24.1
SEPT	36	21.0	47.7	31.3
	37	23.4	53.9	22.7
	38	28.5	43.3	28.1
	39	32.2	40.7	27.1
OCT	40	72.5	16.7	10.8
	41	70.9	23.9	5.2
	42	42.3	46.5	11.2
	43	80.0	14.0	6.0
	44	80.5	13.6	5.9
NOV	45	89.3	7.5	3.2
	46	86.5	10.8	2.7
	47	89.4	7.8	2.8
	48	90.6	6.8	2.6
DEC	49	83.7	12.2	4.1
	50	78.0	17.0	5.0
	51	81.5	11.3	7.2

Table 9. Soil carbon content (percent dry weight) in Rock Valley. Monthly means from soil below four shrubs, one of each species

Month	Sample week	POSITION 1	2	3	1A	2A	3A	4	5	6	7	8	9
Jan	2	1.994	0.796	0.718	-	-	-	1.040	0.564	0.485	0.523	0.427	0.402
March	12	1.110	0.667	0.605	-	-	-	0.637	0.571	0.459	0.393	0.456	0.533
Apr	16	1.637	0.983	0.572	1.129	0.785	0.649	0.786	0.410	0.494	0.452	0.350	0.330
May	21	1.646	0.653	0.497	1.062	0.404	0.406	0.811	0.282	0.317	0.297	0.321	0.345
June	25	2.199	0.816	0.618	1.222	0.723	0.557	0.723	0.453	0.436	0.341	0.292	0.404
July	31	1.990	0.883	0.679	1.620	0.851	0.608	0.835	0.579	0.366	0.369	0.380	0.387
Aug	36	2.206	1.564	1.432	1.764	1.081	0.924	1.034	0.655	0.586	0.355	0.330	0.367
Sept	40	2.740	1.352	1.140	1.348	0.806	0.633	1.149	0.317	0.489	0.368	0.357	0.339
Oct	44	1.884	1.263	1.049	1.292	0.791	0.740	0.887	0.494	0.487	0.267	0.295	0.285
Nov	48	1.231	0.836	0.620	1.056	0.646	0.628	0.888	0.559	0.482	0.413	0.423	0.380
Dec	51	2.279	1.429	0.966	1.899	1.053	0.692	1.237	0.694	0.517	0.532	0.409	0.387

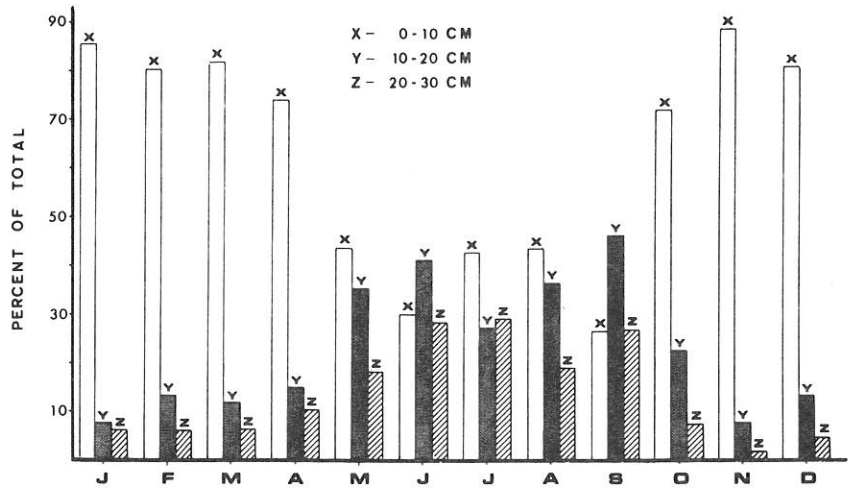

Figure 7. Vertical distribution of all arthropods by month. X, Y and Z are the three levels from above downwards. Level X contains the highest proportion in most months, but there are more arthropods in level Y than elsewhere in June and again in September.

The Effect of Watering on Arthropod Density

The relationship of arthropod density to abiotic factors over periods up to a year is difficult to define. In order to help in such interpretations, field experiments were carried out in which the effects of various watering regimes were measured, the aim being to observe the effects of differences in total amount and frequency of application, and the time relations of any such effects. Water was applied from above the plots by "Rainbird" sprinklers and three water regimes were used as follows: 1) *repeated application* -- five 10-m-radius plots were watered for a duration of 0 (control), 0.5, 1.0, 2.5 or 5 hr, twice a week for two weeks. Soil samples were taken from 0-10 cm depth at the usual three distances, immediately before each treatment (day 0) and on days 4, 7, 11, 14, 21 and 28 following treatment; 2) *single application* -- five plots were watered for 0, 0.5, 1.0, 2.5 and 5 hr on a single occasion; samples were taken as in #1; 3) *single application, early sampling* -- watering was the same as in the second treatment, but samples were taken on days 0, 1, 2 and 3, to detect any early effects.

Ideally, treatments 2 and 3 should have been combined in one experiment, but the need for data about early effects was apparent only after the results of 1 and 2 had been analyzed. Treatment 3 took place some four months later when the climate was quite different, so that treatment 3 should be treated as a separate experiment. In fact, if the results from treatment 3 are plotted on the same graph as those from treatment 2, the combined data give a consistent pattern with a peak on the third day, but we cannot be sure that this would have occurred when treatments 1 and 2 were being applied.

Samples were taken from shrubs all within 3-5 m from the center of the circle, to ensure that, as far as possible, all samples (within each treatment group) would have had similar amounts of water. Measurements of the amount of water applied showed that 1-hr sprinkling delivered about 31 mm ($n = 54$; $\overline{X} = 31$; SE = 2.0, range: 7.0-80.5). This is equivalent to 3.1 ml water·cm^{-2}. For comparison, the maximum precipitation during one event in 1974 was 21 mm, and total rainfall in 1974 was 130.1 mm (Turner et al. 1975). Two samples of soil, each 500 cc, were taken from each position as required; samples being taken always from the north side of shrubs because the prevailing southerly wind tended to concentrate the water there.

The results are shown in Tables 10a-c, and those for the 5-hr applications and the control (0) applications (for position 1 only) are graphed in Figures 8a-c. In general, they show that watering results in an increase in arthropod density.

For the repeated applications (treatment 1), densities usually increased to maxima on day 14. No samples were taken between days 11 and 14 or between days 14 and 21, so that the precise time of the peak is not known.

On day 7 in treatment 1, densities at all positions are lower than on days 4 or 11. This strange inconsistency prompted us to look more closely at the original abiotic data and it appeared that on this day, samples were taken at 12:45 p.m. onwards rather than at the usual 9:00 to 10:00 a.m., and the corresponding soil temperatures (taken as usual immediately before each sample) show very high readings on that day (28-34 C compared with 25-27 and 24-27 C on the previous and succeeding days).

In treatment 2 there is another similar anomaly on day 14, when all arthropod densities appear to fall to near zero. On this day too, samples were taken after midday, from 1:50 p.m. onwards, and the mean soil temperature was 31 C (a maximum of 35 C was observed), while mean temperatures for the previous and subsequent days were 25.5 and 26.5 C, respectively. It appears that the arthropods moved downwards, away from the high surface temperatures, in the middle of the day, and this in turn emphasizes the importance of taking samples at the same time each day and also shows that short-term vertical movements, occasioned by temperature changes, must be taken into consideration when assessing the overall results of these experiments.

For single applications (treatment 2) results again show a strong effect of watering, but the densities peak earlier as might be expected. Most maximum densities are higher after longer waterings.

When earlier sampling was done, again after single applications (treatment 3), densities increased at most positions; the increases being greater after longer periods of watering. Absolute maximum numbers, which varied from about 20 to about 90 per 500 cc soil, usually decreased from position 1 outwards. Fairly consistently, maxima were reached on the second or third day after application and had begun to decline by the fourth day. In earlier experiments using one application (treatment 2), densities were sometimes higher on the seventh than on the fourth day, but climatic conditions were different in the two experiments which were separated by two months. Thus, comparisons between the effects of different amounts of watering within one experiment are useful, while comparisons between experiments carried out at different times are less reliable.

An interesting, and somewhat unexpected, relationship appears when "relative" concentrations of soil moisture and arthropod densities are compared (i.e., concentrations and densities at positions 1, 4 and 7 in any one set of samples). It then is seen that in 80 out of 88 comparisons, arthropod density was higher at position 1 than elsewhere, but in 30 out of 80 available cases, soil moisture was, in fact, lower at position 1 than elsewhere, and in 41 cases out of 80, soil moisture was higher at position 7 than elsewhere. Thus, there is certainly no simple correlation between soil moisture and densities in such relative, lateral comparisons. There is, of course, a strong correlation between soil moisture and absolute densities, as the main results discussed above show. It is likely that in all these experiments, uneven results are due in part to the uneven effects of watering by Rainbird sprinklers, but the possibility of short-term temperature effects should also be considered.

The Effects of Salinity

In order to approach the problem of the effects of salinity on soil arthropods, soil from Rock Valley was sterilized by heating, moistened to bring it to 5% dry weight water content, amended with various quantities of salt, inoculated with mites from Rock Valley soil, and incubated at 25 C for two weeks. After this, the arthropods were separated from the soil and counted. Three soil samples (230 g) were used at each salt concentration. The latter are expressed in Table 11 in terms of mass of salt per mass of soil and in conductivity in terms of mmho·cm^{-1}. The constitution of the salt used was 78.7% sodium chloride, 14% sodium sulphate, 6.7% $CaCl_2$ and 0.6% $MgCl_2$.

The results are shown in Table 11. The mean density of arthropods shows a strong, negative, linear correlation with salinity (in mmho·cm^{-1}), with a correlation coefficient (r) of —0.9899. However, the standard errors of the means themselves (shown in Table 11) are very high, and there is no significant difference (at the 5% level) between any of the first four means. The last two means are significantly different from each other and from any other mean. This experiment should be looked upon as preliminary, and the results as very tentative. Further work is clearly called for before any firm statements about the effects of salt on soil arthropods can be made.

Soil Arthropod Metabolism

Calculation of soil arthropod metabolism was undertaken as a means of comparing function in the Mohave Desert

Table 10a. Arthropod densities in numbers (not underlined) per 500 ml soil, and soil moistures (percent dry weight of soil; underlined numbers). Watering by applications of approximately 3 mm·hr^{-1} on days 0, 4, 7 and 11; sampling on the days indicated. Each entry is a mean of two samples

Date (1975)	Day #	Duration of each watering: 5 hr Positions 1	4	7	2.5 hr Positions 1	4	7	1 hr Positions 1	4	7	0.5 hr Positions 1	4	7	Control (No watering) Positions 1	4	7
7-17	0	7.0	5.5	4.5	7.0	5.5	4.5	7.0	5.5	4.5	7.0	5.5	4.5	7.0	5.5	4.5
														1.80	2.22	1.94
7-21	4	31.0	13.0	4.5	11.5	4.5	2.5	13.0	18.0	4.5	29.5	4.0	6.0			
		8.42	8.78	7.16	6.14	5.41	5.67	1.44	2.32	2.48	1.74	1.48	3.17	1.35	1.45	1.38
7-24	7	23.5	12.0	1.5	4.5	2.5	0.5	3.0	2.5	2.0	7.0	0.5	1.0	1.5	2.0	1.0
		5.49	6.36	4.92	1.23	1.87	4.19	1.65	2.36	3.25	1.30	1.56	2.10	1.26	1.86	1.73
7-28	11	58.0	33.5	16.5	60.0	43.5	20.5	22.0	9.5	5.0	15.0	8.0	4.0	15.0	6.5	5.0
		3.70	5.24	5.09	2.85	2.24	4.91	1.80	1.15	2.28	2.19	3.16	2.85	1.60	2.05	2.08
7-31	14	64.5	51.5	28.5	38.0	13.0	11.5	29.0	16.0	4.5	24.5	5.0	12.0	12.0	8.5	1.5
		3.29	4.22	5.88	2.85	1.74	2.29	1.21	1.54	1.94	1.18	1.50	2.31	0.77	1.13	1.35
8-7	21	33.5	17.0	7.5	20.0	3.5	3.5	19.0	2.5	1.0	11.0	4.0	4.0	8.0	10.0	2.0
		0.98	1.36	2.47	1.22	1.12	1.78	1.35	2.04	1.97	1.03	1.02	1.62	1.44	1.79	1.85
8-14	28	18.0	26.5	12.5	6.5	4.5	7.0	9.0	7.0	3.5	5.5	2.0	4.5	16.5	8.5	6.5
		2.46	2.50	2.33	1.48	1.57	1.82	0.99	1.28	1.59	1.54	1.43	1.49	1.28	1.19	1.45

Table 10b. As in 10a, except that watering occurred once only, on day 0

Date (1975)	Day #	5 hr Positions 1	4	7	2.5 hr Positions 1	4	7	1 hr Positions 1	4	7	0.5 hr Positions 1	4	7	Control Positions 1	4	7
6-19	0	28.0	10.5	3.5	28.0	10.5	3.5	28.0	10.5	3.5	28.0	10.5	3.5	28.0	10.5	3.5
														1.28	1.35	1.61
6-23	4	61.0	27.5	4.5	50.0	14.0	7.0	6.0	1.5	1.5	34.5	9.5	1.5	8.5	3.5	2.5
		6.62	4.51	5.43	3.97	4.55	3.65	1.06	1.61	1.99	2.10	2.07	2.32	1.53	1.81	1.68
6-26	7	51.5	16.5	3.5	57.0	15.0	0.5	20.0	8.0	4.0	0.5	3.0	6.5	6.5	6.0	7.0
		5.35	4.59	3.40	3.48	4.66	6.37	1.47	2.44	3.24	2.46	1.76	1.67	2.05	1.46	1.74
6-30	11	41.0	23.5	4.0	39.5	21.5	36.0	19.5	5.5	5.5	22.0	4.0	3.0	7.0	2.5	2.0
		2.91	3.25	2.82	3.85	2.94	1.92	1.72	1.86	2.28	2.06	2.29	2.46	1.86	2.23	2.22
7-3	14	2.0	4.0	3.5	31.0	17.0	7.0	8.0	2.5	2.0	6.5	2.5	3.5	4.5	0.5	1.0
		2.15	2.42	3.17	2.74	3.07	3.30	2.27	1.58	1.93	2.11	2.30	2.17	1.36	1.51	2.02
7-10	21	36.5	11.0	5.5	12.0	6.5	4.0	5.5	7.0	4.5	9.0	4.0	0.0	8.0	1.5	1.0
		1.69	1.74	1.45	1.60	1.73	2.11	1.41	2.12	1.93	2.20	1.00	1.75	1.21	1.69	2.03
7-17	28	30.5	5.5	1.0	19.5	9.0	2.0	12.5	3.0	5.0	9.0	6.5	4.0	7.0	6.5	3.5
		1.32	1.19	1.68	2.30	2.33	2.29	1.24	1.07	1.70	2.33	1.93	2.61	1.64	1.76	1.59

Table 10c. As in 10b, except that samples were taken on days 0 through 4

Date (1975)	Day #	5 hr Positions 1	4	7	2.5 hr Positions 1	4	7	1 hr Positions 1	4	7	0.5hr Positions 1	4	7	Control Positions 1	4	7
10-20	0													28.0	15.0	10.5
														2.25	1.33	1.69
10-21	1	32.0	8.0	6.5	38.5	40.0	7.5	72.0	38.5	9.5	60.0	14.0	12.5			
		12.91	10.10	10.38	10.21	11.85	11.65	3.07	6.26	5.01	6.20	2.81	4.26			
10-22	2	47.5	25.0	10.5	39.5	18.5	6.0	31.0	14.5	23.5	69.0	19.5	10.0			
		10.30	9.70	8.22	9.13	9.04	8.44	1.67	1.72	4.86	3.48	3.67	3.92			
10-23	3	89.5	39.0	19.0	76.5	64.5	32.5	27.0	31.5	10.5	49.5	38.0	22.5	27.0	16.0	11.0
		8.91	9.08	8.44	9.95	9.45	9.82	4.45	2.71	6.60	2.30	1.58	4.47	1.87	2.16	3.01
10-24	4	65.5	26.0	10.5	74.5	80.0	27.5	43.5	31.5	10.0	29.5	15.5	4.5			
		8.57	8.84	7.79	7.42	7.60	9.38	3.37	2.55	3.39	4.66	4.31	4.92			

with that in other intensively studied ecosystems. Calculations are based on estimates of density and biomass using weight-specific metabolism regressions from the literature (Table 12). Metabolic rate is temperature dependent and soil temperature was measured weekly at —5, —15 and —25 cm (Edney et al. 1975). Since densities are reported on a monthly basis, we used the mean monthly temperature (recorded between 9:00 and 10:00 a.m. each day) at each depth and a Q_{10} of 2 to predict monthly metabolism. Thus, the metabolism estimates are step functions rather than being continuous.

The method used for estimating biomass has been described above. Results of metabolism calculations are shown in Figure 9. Community metabolism tended to correspond to seasonal temperature changes although that of component groups did not. There was no correlation with either population density ($r = -0.16$) or biomass ($r = -0.40$). Beetle larval metabolism was bimodal and reflected growth of individuals. They accounted for two-thirds of community metabolism in April and May while the actual amount of CO_2 respired doubled. This was during a period when larval numbers fell by approximately one-half but their individual weights increased by a factor of seven. The high productivities and metabolic rates are to be expected, for laboratory-reared *Eleodes armata* larvae increased in size by up to 250% in one month (McBrayer et al. 1975). The smallest *E. armata* larvae for which respiration was measured averaged 7.83 mg live weight or ~ 2.35 mg dry weight, which is 2.2 times larger than the average weight of beetle larvae field-collected in May. The laboratory-reared larvae had a measured metabolic rate of 3.02×10^{-1} cal·mg^{-1}·hr^{-1} compared to 5.63×10^{-1} cal·mg^{-1}·hr^{-1} estimated for the free-living larvae, which were less than half their size. Annual metabolism for the group was 83.6 cal·m^{-2}.

Collembolan metabolism was at its lowest in May when both density and biomass were at their lowest values, but when individuals were relatively large. Metabolism increased to an August maximum. The slight increase in June is due only to increasing temperature, for size of individuals and density remained virtually constant. During July, mean individual size decreased by 40%, and both density and total metabolism of the group increased by a factor of 10. August metabolism was nearly double that of July while density remained constant. Biomass more than doubled, however, while mean soil temperature declined. Thus, the maximum metabolic rate was due to an increase in biomass and only secondarily to summer soil temperatures. Annual collembolan metabolism totaled 67.74 cal·m^{-2}.

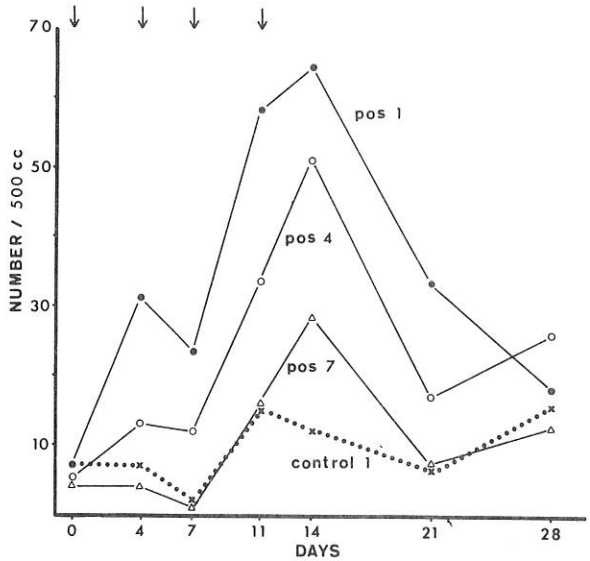

Figure 8a. Density of arthropods in level X (0-10 cm) following watering for 5 hr on each of the days indicated by an arrow above. Positions 1, 4 and 7 indicated by solid circles, open circles and triangles, respectively. The dotted line represents densities at position 1 in the control plot which was not watered. This should be compared with the position-1 data (solid circles) for the 5-hr watering treatment. It is not a control for the other positions.

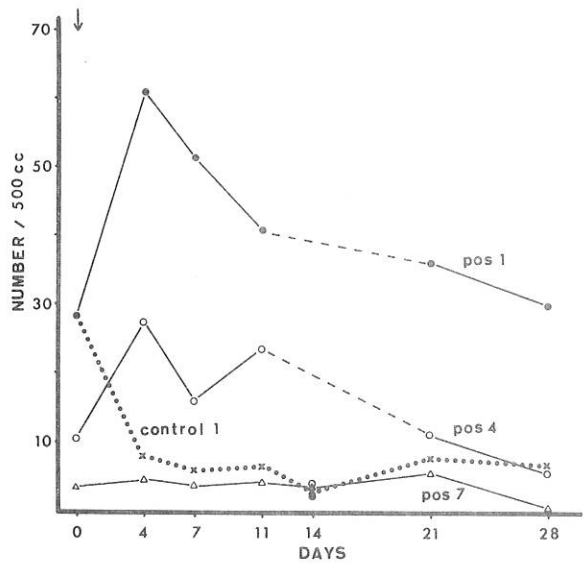

Figure 8b. As in Figure 8a, except that watering occurred only once, on day 0. The spuriously low numbers on day 14 are probably due to a different sampling time (see text).

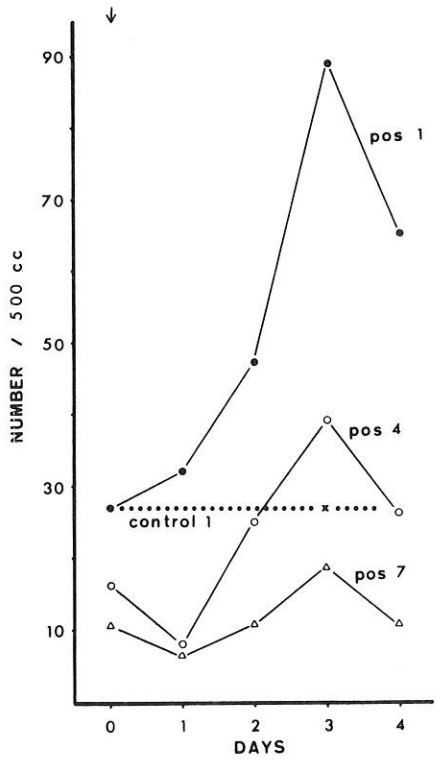

Figure 8c. As in 8b, except that sampling was done on days 0 through 4.

Table 11. The effect of soil salinity on arthropod density

Salinity		Number of arthropods per 250 ml soil		
$g \cdot kg^{-1}$	conductivity ($mmho \cdot cm^{-1}$)	$\bar{X}$	S.D.	N
0	0.77	339.7	169.2	3
0.333	3.05	289.0	29.4	3
0.667	5.57	261.3	70.1	3
1.555	11.59	213.0	81.9	3
3.999	24.70	87.3	18.6	3
6.666	36.70	20.0	20.4	3

Table 12. The rate of metabolism in various taxonomic groups of soil arthropods is given by $Y = ax^b$, where Y is nl $O_2 \cdot hr^{-1}$; a and b are constants; X is the mean dry weight (μ g) of one organism. Regressions have been adjusted to 20 C from the original sources by using a Q_{10} of 2.0

Taxon	a	b	Authority
Collembola	2.46	0.75	Dunger 1968
Saprophagous mites	0.14	0.93	Webb 1969
Predatory mites	1.76	0.72	Webb 1970
Beetle larvae	1.49	0.60	Reichle 1971

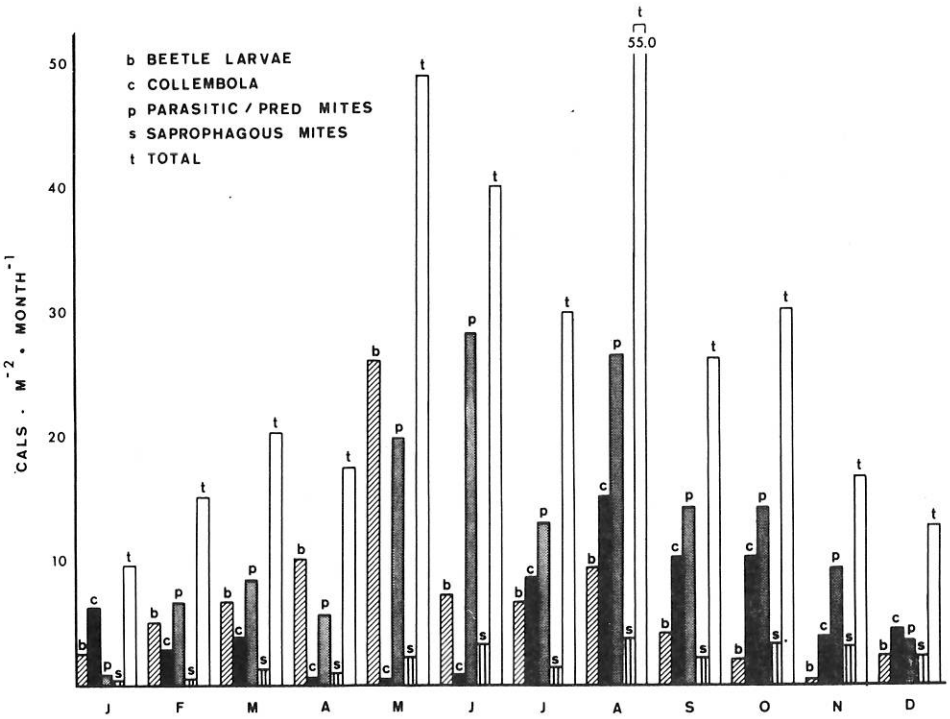

Figure 9. Monthly metabolism of soil arthropods at Rock Valley, Nevada, in 1974: b = beetle larvae, c = collembolans, p = predatory-parasitic mites, s = saprophagous mites, t = total.

Metabolism of mites is treated as a function of population density and temperature only, since it is calculated on the basis of the mean annual weight of individuals in each taxon. Saprophagous mites respired 24.80 cal·m^{-2} during the year, apportioned according to: Oribatei, 4.85 cal (20%); Tydeidae, 7.16 cal (29%); Nanorchestidae, 12.62 cal (51%); and Acaridae, 0.17 cal (< 1%). Minimum respiration was calculated in January for all groups, and this corresponded to minimum populations except for Oribatei. Metabolism peaks occurred in June (due to Nanorchestidae), in August (Oribatei) and in October-November (Tydeidae).

The remaining mites are considered to be predators and include five families plus a catchall group of Prostigmata which were not identified further. The latter group contributed only 0.04% of the annual respiration attributed to predatory mites. The total group respired 151.64 cal·m^{-2} annually, apportioned according to: Caligonellidae, 69.30 cal (46%); Trombidiidae, 31.23 cal (21%); Bdellidae, 29.95 cal (20%); Erythraeidae, 12.29 cal (8%); and Caeculidae, 8.82 cal (6%). All are predatory-parasitic on insects and other arthropods (Krantz 1970). Caligonellids reached their greatest abundance in summer and early fall; hence their large contribution to group metabolism. Bdellids were abundant throughout the year and the remainder were primarily winter-spring organisms.

The predatory mite group contributed nearly half of the total soil invertebrate metabolism. This compares with < 25% in deciduous forest (McBrayer et al. 1974). It is likely that many of these species should be excluded when considering decomposer food chains since some are known to be parasitic on larger herbivorous insects and vertebrates.

For purposes of rough calculation, it can be assumed that litter production is only slightly less than net primary productivity (NPP), because the portion consumed by herbivores and the amount converted to permanent standing crop are small. Based on an estimated NPP for 1974 of 19.8 g·m^{-2} (Ackerman et al. 1975a, 1975b), and assuming an energy equivalent for plant litter material of 4.3 kcal·g^{-1} (Golley 1961), the three detritus-feeding soil arthropod groups respired about 0.2% of the annual energy input.

The contribution of ground-dwelling detritivores, such as isopods, ants and others, to litter turnover has not been considered here, but it is evident that inclusion of these species would bring our figures more in line with those previously reported.

DISCUSSION

The original aims of the present program were to identify and study the main biotic and abiotic relationships of desert soil arthropods and to measure productivity. These aims have been achieved only in part and, as usual, the work has uncovered as many problems as it has solved.

Two tasks have been completed: 1) a fairly rapid technique has been developed for extracting arthropods from desert soils with an efficiency not significantly different from that obtained by flotation; and 2) the numbers of most groups of arthropods have been measured as they varied through a year and as they are affected by the presence of four common species of desert shrubs. The precision with which the second aim has been achieved is not great, largely because of the very low numbers of individuals present in most soil samples. This, combined with high variation, leads to the possibility of large errors. Further, when the data are converted to numbers or biomass, the necessary multiplication may lead to large absolute errors.

It is interesting to compare the present values with those obtained by other workers in similar and dissimilar situations. A summary of the available data is shown in Table 13, and it appears that the present (Mohave Desert) values span those from an Australian desert (Wood 1971). The Russian values (Krivolutsky 1968) are for oribatids only and are not, therefore, comparable. The present numbers, however, never reach those reported for a Californian pine forest by Price (1973). In general, the present numbers correspond well with expectations based on the few studies available.

Our estimates of the part played by soil invertebrates in the decomposer food chain (they respired only 0.2% of the annual energy input in terms of net primary production), are lower by an order of magnitude than the values of 1-8% obtained for deciduous forest by Witkamp (1971) and McBrayer et al. (1974), but here again the possible error is large, and our data omit several large species. Further, the balance between decomposers and herbivores may be very different.

Our results leave no doubt about the general form of the distribution of arthropods in the soil around shrubs. Arthropod density does not appear to be affected by shrub species, and it is interesting to find that shrub size does not affect density either (the density of arthropods near the base of a shrub, for example, is the same no matter what the size of shrub). There may be a small decrease in density at the center of the largest interspaces, but any error introduced in this way would be swamped by sampling errors, and we assumed a uniform distribution throughout areas between shrubs.

Of interest is the relation of densities to abiotic features. In general, densities are higher in winter than in summer, and the same is true of soil moisture values. But temperature, of course, also varies, and without further work it is impossible to say how these two factors interact in their influence on arthropod density. Some suggestions in this regard have been referred to above.

The results of the artificial watering experiments show that an increase in soil moisture causes an increase in absolute numbers of arthropods, but the precise relationship is not clear, because comparison of densities with soil moisture over short distances at any one place or time shows that the two are not even correlated, let alone causally related. Other modifying factors (perhaps temperature again) must be at work.

Table 13. A comparison of soil arthropod densities in various environments

Habitat	Number per square meter	Description	Authority
California pine forest	222,000	Total microfauna, wet and dry seasons	Price (1973)
Various forest soils	154,600 - 834,500	Total arthropods	Various authors in Wallwork (1970)
Lowland grasslands	32,000 - 298,000	Acari and Collembola	Wallwork (1970)
Australian desert	2,000 - 3,000	Microarthropods	Wood (1971)
Russian desert	250	Oribatids only	Krivolutsky (1968)
Mesic hardwood forest	60,000 - 120,000	Total soil arthropods	McBrayer et al. (1974)
Mohave desert	1,000 (minimum - July) 13,000 (maximum - Nov.)	Total soil arthropods	Present study

A very interesting indication that arose indirectly from the watering experiments is that temperature seems to play a large part in short-term distribution patterns. Distributions in all positions in the top 10 cm declined strongly on two days when samples were taken after noon rather than in the morning, and soil temperatures varied accordingly. Vertical migration probably explains these results. Such movements are already known or suspected (Pande and Berthet 1975; McBrayer et al., in press), but in circumstances very different from our own (forest soils). It will be interesting to follow up this lead with further experiments in controlled conditions.

According to the present results, seasonal differences in vertical distribution profiles also exist. This conclusion is based on samples taken always at the same time of day, but temperature distributions and absolute levels vary from season to season, and it is possible that the apparent seasonal migrations are in part due to immediate, short-term responses to local temperature or humidity gradients.

One of the reasons for doing studies such as this is that they provide an information base against which effects of environmental disturbances may be measured. Thus, the present study may provide a control for future measurements of the effects of pollution on desert soil arthropods. This is not the place to enlarge on such matters, but we have included in this report the results of some preliminary work on salinity tolerance -- a question that has already arisen in connection with geothermal power generation. There is evidence of a large adverse effect of salinities of 24 mmho·cm^{-1} (about 0.07 M NaCl equivalent), and a suggestion of effects at much lower levels, but the problem awaits further analysis.

One aspect of the problem that is of great interest concerns the trophic relationships of the arthropods involved in the study. The fact that variations in soil carbon correspond more closely with density than do any other abiotic factors studied is indeed interesting and could be explained if soil carbon is a measure of food availability and if the latter is limiting. But, here again there is very probably an interaction between soil carbon, moisture and temperature in determining the amount of food available, and this should be the subject of further study. Pande and Berthet (1975) showed that soil carbon may be important in vertical distribution, but again in an environment different from ours. Apart from this, too little is known at present about the trophic habits of all species concerned to permit generalization.

There has not been much previous work on desert soil arthropods. In fact, the present work, although incomplete in many ways, is the only large-scale survey of the field. Techniques have been established and information obtained. Several interesting relationships have been proposed, and problems needing further work have been defined. One aspect that certainly merits further attention concerns the trophic relationships and general ecological significance of desert soil arthropods. This will be a difficult field to explore, but one from which results of considerable biological interest may be expected, in relation to both fundamental and applied problems.

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