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A Case Study of Energy, Water and Soil Flow Chains in an Arid Ecosystem

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Abstract. Little attention has been directed to the study of soil flow and the complex relationships among energy water and soil flow in terrestrial ecosystems. Soil plays an important role in arid ecosystems. After water soil is the second key factor in the development of an arid ecosystem since soil is the only part of the system capable of absorbing and storing water and nutrients during the hot and long summer period. The present work presents a case study of an ecological soil flow chain in an arid environment and analyses the relationship between this chain and the energy and water flow chains. The study was conducted at the Sde Boqer experiment site located in the northern Negev of Israel where average annual rainfall is 92 mn. Data collected during five consecutive years show that the soil movement process within the ecosystem studied cannot be considered as a purely physical phenomenon, but rather as a part of a complex system in which the burrowing and digging activity of Isopods and Porcupines plays an important role by providing disaggregated soil particles easy to remove by shallow flows. Although controlled by the spatial distribution of soil moisture the biological activity acts as a regulator of soil depth and thus of soil moisture. If this regulating role is deleted from the system a new ecosystem, more arid, can be expected to develop. It is therefore concluded that the study of state and flow variables of an arid ecosystem should consider altogether the water, soil, energy and mineral chains.

1 Introduction

Numerous recent studies deal with flow of energy and of minerals in ecosystems. The study of energy flow (Lindeman 1942; Odum 1957; Golley 1960) deals with the conversion of solar energy to organic matter by the producers and the transformation of the energy to the consumers and decomposers. The mineral flow studies are concerned with the movement of minerals from the abiotic elements to the biotic and vice versa (Cole et al. 1967; Likens and Bormann 1972; Burton and Likens 1975; Gosz et al. 1976). Except for some notable exceptions (Abaturov 1972; Lofty 1974; Rusek 1975), little attention has been directed to the study of soil flow and the complex relationships among energy, water and soil flow in terrestrial ecosystems. The inclusion of soil flow in the study of ecosystems is of great importance, especially in arid areas. After water, soil is the second key factor in the development of an arid ecosystem, since soil is the only part of the system capable of absorbing and storing water and nutrients for long periods. In the absence of sufficient soil, few higher plants can become established. Therefore, the input, output and the flow of the soil through processes of soil erosion and deposition must be considered as part of ecological flow chains. (In this study an ecological flow chain is defined as the flow of matter and/or energy controlled by biotic and abiotic elements.) Of particular interest are the spatial distribution of soil, its depth and its salt content. The latter indirectly influences the water holding capacity of the soils which, in an arid environment, controls the spatial distribution of plants and burrowing animals (Yair 1978). The activity of burrowing and digging animals contributes to the soil turnover within the physical structure of the ecosystem. Therefore, the study of the soil flow chain may contribute to current research on the role of consumer populations as regulators in the total ecosystem function (Kitchell et al. 1979).

The main purpose of the present paper is to present a case study of an ecological soil flow chain in an arid environment and to analyze the relationships between this chain and the energy and water flow chains. Special attention will be accorded to the spatial variability over limited areas of rainfall, runoff, soil moisture and their influence on the spatial distribution of soil turnover by animal activity, namely isopods and porcupines. The assumed relationships between the abiotic and biotic factors in the soil flow chain in the ecosystem under study are presented in Fig. 1.

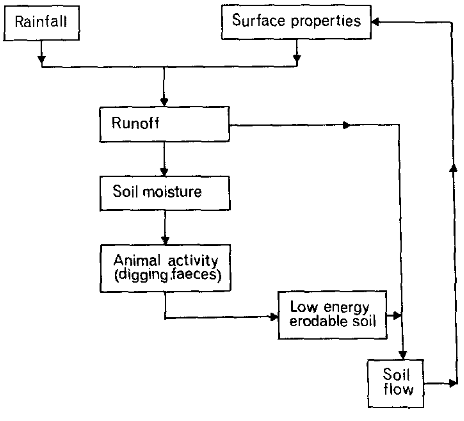

Fig. 1. Assumed relationships among abiotic and biotic variables in the soil flow chain in the Northern Negev Desert ecosystem

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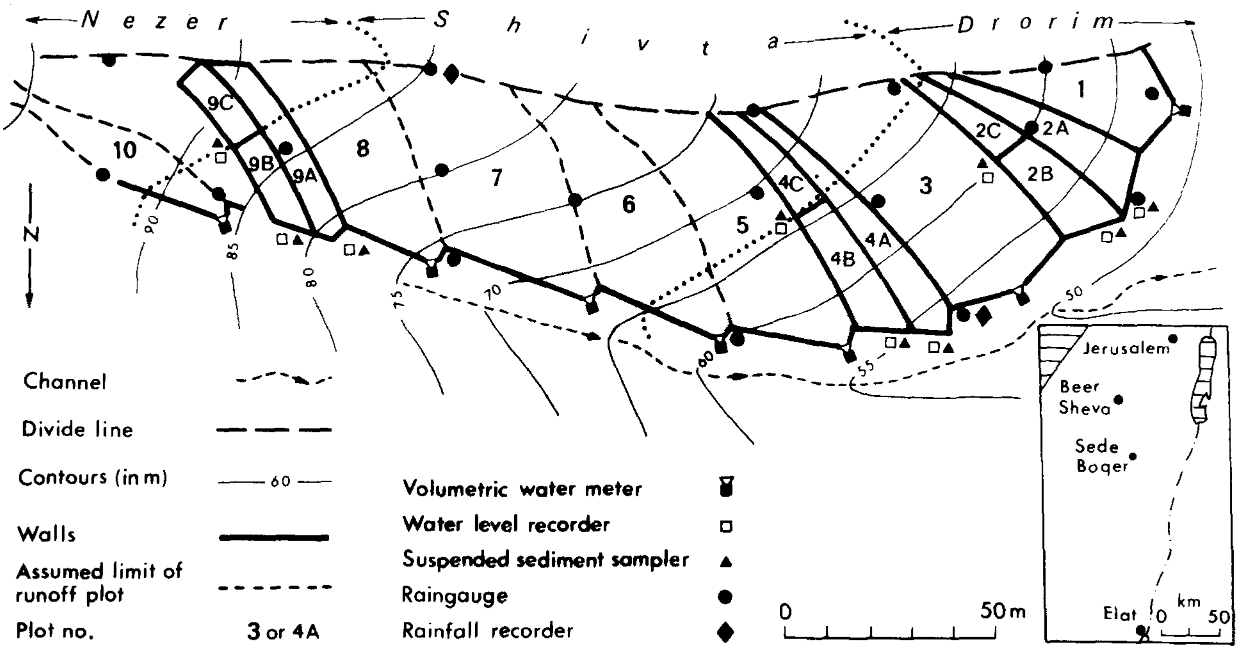

Fig. 2. Sede Boqer watershed study, showing the three geological formations, the 10 plots and the layout of the instrumentation

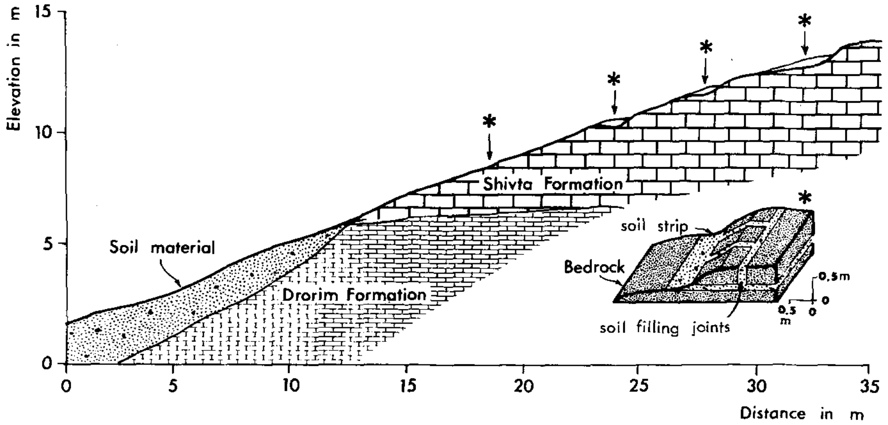

Fig. 3. Patterns of soil distribution in the Shivta and Drorim formations. * soil material in the Shivta formation

2 The Study Area

2.1 Climate

The study area is located in the northern Negev, some 40 km south of Beer Sheva (Fig. 2), at an altitude of 510 m. Average annual rainfall recorded over 30 years is 92 mm, with extreme values of 34 mm and 167 mm. Mean monthly temperatures vary from 9° C in January to 25° C in August. Average daily relative humidity attains 60–70% in wintertime and 40–50% during the hot summer months.

2.2 Topography, Geology and Soil Cover

The study area was limited to the north-facing hillside of a first order drainage basin, extending on one side of the channel (Fig. 2). The relative relief is 30 m. Length of slopes varies from 55 m to 76 m and mean slope gradient varies from 12% to 29.5%. The site extends over an area of 11,325 m^2. The local stratigraphy is Turonian, represented by the Drorim, Shivta and Netzer formations. Although the three formations are mainly composed of limestone rock (Arkin and Braun 1965), they create completely different environments. Rock strata of the Drorim formation are 10–30 cm thick and very densely jointed. The rock weathers into cobbles and boulders which cover most of the surface. The middle and lower parts of the slopes are covered by an extensive stony colluvial soil whose thickness at the slope base exceeds 250 cm. It is a desert brown loessial serozem (Dan et al. 1972). Repetitive wetting and drying cycles have produced a compacted topsoil crust. Vegetation covers 5–10% of the area and is quite uniformly spread. The characteristic plant association is that of *Artemisia herba alba-Gymnocarpos decander* (Danin 1972; Yair and Danin 1980).

The Shivta formation is a massive crystalline limestone. Stratum thickness is 30–80 cm forming a stepped topography. Jointing is spaced and bedrock is exposed over 60–80% of the surface. Soil material is found in two different adjoining environments (Fig. 3): (1) non-contiguous soil strips located at the base of bedrock steps; (2) joints and bedding planes of the surficial rock strata. The vegetation

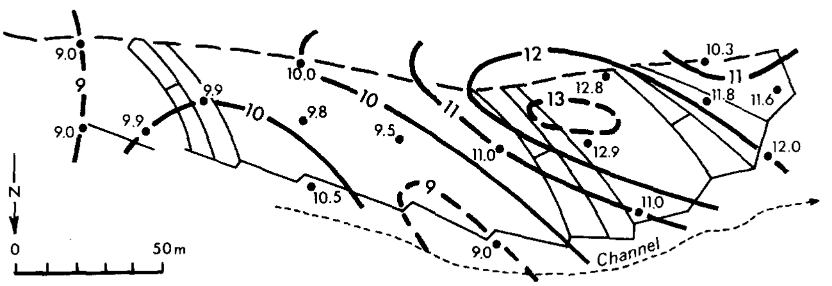

Fig. 4. An example of the characteristic spatial distribution of effective rainfall in the Sede Boqer watershed (5/4/77)

cover (5–10%) is concentrated along the soil strips and soil-filled joints. The characteristic plant association is that of *Vartemia iphionides-Origanum dayi* (Danin 1972).

3 Methods

3.1 The Water Flow Chain

The study of the water flow chain included the spatial distribution of rainfall, runoff and soil moisture content. Rainfall distribution was obtained by a dense network of 19 rain gauges and two rainfall recorders. The rain gauges were established along three lines: at the slope base, at mid-slope and along the local ridge divide of the watershed (Fig. 2). Rain gauges were read shortly after each storm. In order to obtain the effective rainfall amount intercepted on the ground surface, rain gauges having their orifice exactly parallel to the local sloping ground were used (Yair et al. 1978; Sharon 1980).

For the study of runoff the experimental site was subdivided into 16 plots draining the entire slope area of one half of a watershed (Fig. 2).

Soil samples for moisture analysis were collected a day or two after each rainstorm exceeding 2 mm and at subsequent intervals of one to two weeks. The samples were weighed initially and then oven dried to constant weight at 105° C. Two sets of measurements were conducted.The first related to the soil moisture content of the topsoil layer. It was based on 20 sampling points along a whole slope profile. The second set related to the variation of moisture content with soil depth at the following environments: joints, bedding planes and soil strips of the Shivta formation; colluvium at the base of the slope.

3.2 The Soil Flow Chain

The soil flow chain was studied as a combination of biotic and abiotic aspects.

3.2.1 Biological Aspects. In order to estimate the amounts and spatial distribution of easily erodible soil prepared by animals, a grid system was constructed over the study site. It consisted of 24 rows parallel to the rock strata. The study of the spatial distribution of *H. reaumuri* families was carried out once a year in September from 1973 to 1977. Previous studies of the life cycle, population dynamics and activity of *H. reaumuri* in an area located 3 km from the experimental site (Shachak et al. 1976; Shachak 1980) showed that the conditions of the faeces pile in September provided the necessary information on the establishment and survivorship of the families.

The total weight of loose soil produced by the isopods' activity was obtained by multiplying the number of families by an average weight of a faeces pile, based on 30 samples collected and weighed.

Hystrix indica feeds on underground geophyte bulbs which are buried at a depth of 4 to 12 cm. For feeding a porcupine digs a hole with its toes. The feeding sites of the porcupines are easily identified as small depressions, about 5 x 10 x 12 cm, with a mound of loose soil. The grid system for isopods served also for mapping the spatial distribution of porcupine activity. To estimate the amount of easily erodible soil produced by the procupines the procedure adopted for the isopods was used.

3.2.2 Abiotic Factors. The study of soil erosion processes was conducted in the field with the aim of obtaining quantitative data on the rate and spatial distribution of the material eroded from the runoff plots. Comparisons could then be made with the amounts of erodible material prepared in the same plots through biological activity.

The sediment samples were derived from the network of 16 runoff plots (Fig. 2). Those plots, equipped with a stage recorder, were also equipped with an automatic suspended sediment sampler, each containing 24,500-cc bottles. The first water sample was taken at the very beginning of the flow and the following samples, until the flow ended, at fixed intervals of 2.5 or 5 min. Samples collected were submitted to a standard concentration analysis.

4 Results and Discussion

4.1 The systematic and characteristic trends in the spatial variation in effective rainfall are given in Fig. 4. Analysis of the isohyetal map shows that rainfall distribution over the experimental site is strikingly non-uniform, varying from 12.9 mm to 16.6 mm. The observed differences in rainfall distribution within the small study area can be explained in terms of the geometric combinations among the following factors: local slope angle and aspect on the one hand, and the direction and inclination of falling raindrops on the other (Sharon 1980).

Figure 5 presents the characteristic trend of the lateral variation in runoff in a given rainfall. A negative correlation between the spatial distribution of rainfall and runoff production was found. Plot 7, located within the area of minimum rainfall, generated the highest runoff yield per unit area, whereas plots 1 to 3, extending over the area of maximum rainfall, generated the lowest runoff yield per unit area. On the basis of previous works (Yair 1974; Yair and Lavee 1976), the following explanation is proposed: plot 7 extends over the massive limestone of the Shivta for-

Plot no.	10	9	8	7	6	5	4	3	2	1
Rainfall (mm)	14.5	14.7	14.3	13.5	13.3	14.7	15.4	15.5	15.5	16.5
Runoff (mm)	0.8	0.9	1.9	2.9	1.7	1.8	0.5	0.5	0.5	0.5

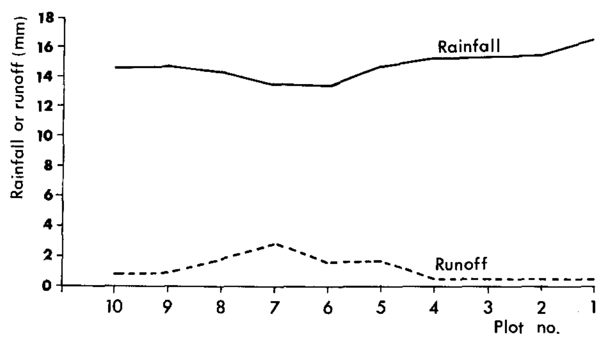

Fig. 5. An example of a typical lateral variation in rainfall-runoff relationship (5/12/74)

mation (Fig. 2) where extensive outcrops of smooth bare bedrock surfaces occur. The porosity of the crystalline limestone being very low, infiltration losses are reduced and the threshold amount of daily rainfall necessary to generate runoff is very low, on the order of 1–2 mm. Consequently, the frequency as well as the magnitude of runoff generation over such areas is relatively high. A different situation exists over plots 1 to 3. The whole of plot 1 and most of plots 2 and 3 extend over the Drorim formation characterized by a densely-jointed bedrock and a contiguous thick colluvial soil at the lower slope section. Infiltration capacities are much higher than those of the smooth bedrock outcrops. The threshold amount of daily rainfall needed to generate runoff over the colluvial mantle is 3–5 mm. As the frequency of daily rainfall events exceeding 3 mm is lower than that of 1–2 mm (Yair et al. 1978), runoff generation over the colluvium can be expected to be lower in its frequency and magnitude than over the Shivta formation.

The characteristic variation of soil moisture content along a slope is presented in Fig. 6. Data were obtained following a rainstorm of 22 mm. The cumulative rainfall amount since the beginning of the rainfall season was 35.6 mm. A similar pattern of soil moisture distribution was obtained at the very beginning of the rainy season following a storm of 4.5 mm, as well as 3 weeks after the last storm of the year which amounted to 3.9 mm. Data analysis shows that the driest moisture regime prevails at the base of the colluvium, the wettest regime in the environment of joints and bedding planes of the Shivta formation and an intermediate one at the upper part of the colluvium and along the soil strips.

The relatively good water regime prevailing in the rock fissures and adjoining soil strips can be explained in the following terms: large joints and soil strips occur in the massive limestone where extensive outcrops of bare bedrock are responsible for frequent and relatively high magnitude water flow events. On its way downslope, part of the runoff water infiltrates into the soil strips. Thus, these two microenvironments collect, in addition to direct rainfall, an additional amount of water from surface flow. The good water regime results, therefore, from the relatively high input of water combined with the limited volume of soil material inside the joints. Furthermore, evaporation losses from the soil filling bedding planes are seriously reduced as the soil is not submitted to direct solar radiation, being covered by a rock block whose thermal conductivity is low. This is not the case of the soil strips where the soil, submitted to direct solar radiation, may lose its moisture content more quickly than in the joints.

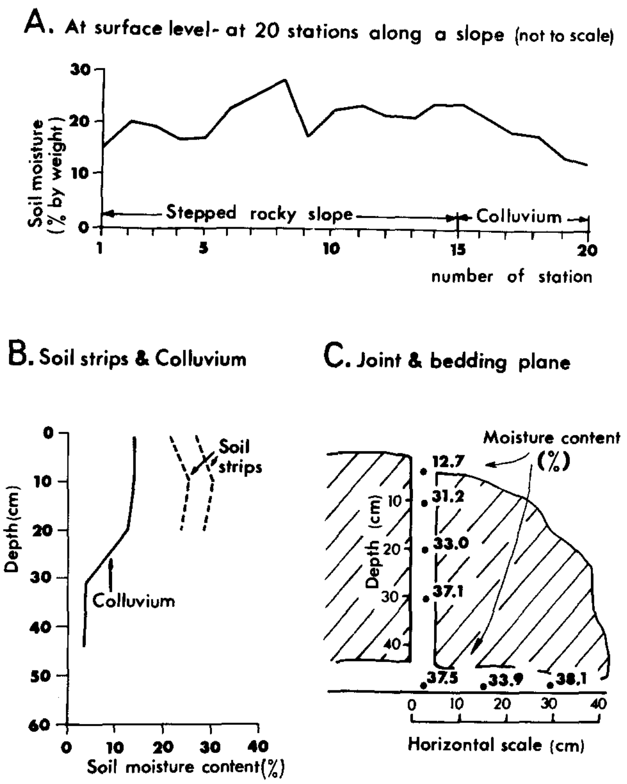

Fig. 6. Soil moisture content at surface level, soil strips, colluvium, joint and bedding plane following a rainstorm at 22 mm (26–27/12/77)

The low soil moisture content at the slope base, as well as the downslope decrease in moisture content in the colluvial part of the slope, can also be explained in terms of water input-soil volume. The depth of the colluvium increases gradually downslope. But, as indicated by the hydrological findings, the input of water decreases downslope due to higher infiltration losses in the upper part of the colluvium than in its lower part (Yair et al. 1980).

The spatial distribution of soil moisture is fully confirmed by the spatial distribution of plant associations. Yair and Danin (1980) show that the best water regime in the study area is that of rock fissures. This environment is characterized by high values for the number of species, species diversity, and percentage of Mediterranean species. The dry conditions prevailing at the slope base are clearly displayed by the low percentage of Mediterranean species and high percentage of Saharo-Arabian species.

The downslope worsening of the water regime along the colluvium is also indicated by the results of a detailed pedological study. An analysis of the soil profile along a trench dug into the colluvium shows that no calcium nodules appear at the upslope part of the trench. Such nodules can be observed at a depth of 50–60 cm in the central part of the trench. The depth of occurrence of the nodules decreases downslope where gypsum occurs as well at a depth of 30 cm. The catenary sequence described above indicates clearly a decrease in the rate of leaching in the downslope direction parallel to the decrease in the input of runoff water originated in the upper part of the slope (Yair 1981).

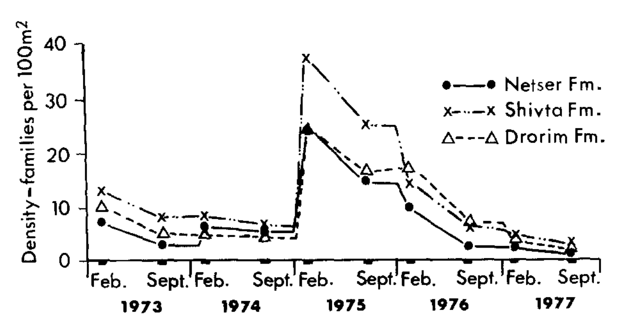

Fig. 7. Fluctuations in the density of isopod families (*H. reaumuri*) in the three rock units in the Sede Boqer watershed

4.2 The Soil Flow Chain

4.2.1 Biological Factors, Isopods and Porcupines. The changes in the density of *H. reaumuri* families through time from September 1973 to September 1977 in the three rock units of the experimental site are shown in Fig. 7. The reasons for such changes are not understood at present.

The highest average density of isopod families, both of settlers and successful families, was recorded for the Shivta formation. They were 15.3 and 8.9 families per 100 m^2, respectively. The lowest average densities were in the Netzer formation with 9.9 for settling and 5.2 for successful families per 100 m^2. The average densities for the Drorim formation were intermediate: 11.7 for settling and 6.4 for successful families per 100 m^2. The same pattern of density distribution can be seen when the densities of total settlers and successful families per row are compared (Fig. 8). Most of the rows with high average density are located in the Shivta outcrops.

The non-uniform spatial abundance of the isopod population is assumed to depend on the following factors: energy, soil depth and soil moisture content. The latter factor provides the burrows with a high water vapor pressure necessary for the survival of the isopods (Shachak 1980). As shown previously (Shachak et al. 1976), energy is not a limiting factor since the isopods consume only 0.6% of the available energy. The high population density in the Shivta formation cannot be explained either by the soil depth alone, as much deeper soils are found in the colluvium at the lower part of Drorim slopes. It therefore appears that the abundance of isopod families in the study area can be explained principally in terms of the spatial distribution of soil moisture content as described above (Shachak 1980). This relationship explains the high population density of

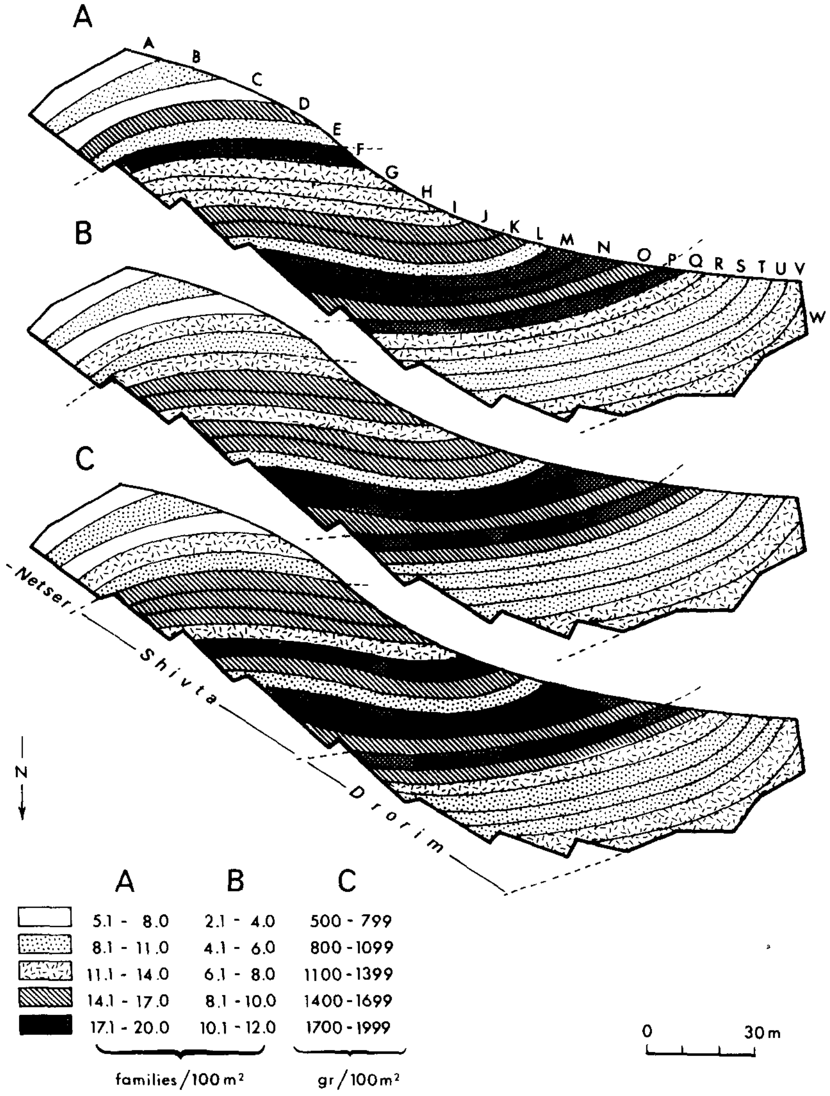

Fig. 8. Average abundance of desert isopod *H. reaumuri* families and amounts of easily erodible soil produced by their burrowing activities (1973–1979).
A Average annual density of settlers (families established in February).
B Average annual density of successful families (survived from February to September).
C Average annual amount of easily erodible soil produced by the isopods

Table 1. Average annual low energy erodible sediment production by the desert isopod, *H. reaumuri*. g/100 m^2 (1973–1977). (Average ± S.D.)

Rock unit	Successful families	Unsuccessful families	Total settlers
Shivta	1,351 ± 275	255 ± 61	1,605 ± 302
Drorim	978 ± 181	205 ± 57	1,182 ± 212
Netzer	695 ± 293	177 ± 75	812 ± 362

isopods in the favorable microenvironments represented by the rock fissures of the Shivta formation, as well as the low population density in the Netzer formation where the shallow soil dries quickly. The Drorim formation, with its colluvial cover, represents an intermediate environment in terms of soil moisture.

For feeding and burrowing, *H. reaumuri* consume large quantities of mineral soil, 25 to 48 mg/individual/day (Shachtak et al. 1976). Mineral soil is not digestible, thus the defaecation of the isopods consists mainly of soil material. They remove the faeces pellets with the maxillipeds and drop them outside the burrow on the soil surface at a distance of up to 25 cm (Shachak 1980).

The average annual production of faeces by isopods per row in the study area is given in Fig. 8c. Out of the total average annual production, about 82% was produced by successful families. As indicated in Table 1, the highest average annual production is in the Shivta formation. The lowest is in the Netzer formation and an intermediate value in the Drorim formation.

The annual amount of easily erodible sediment produced by the isopods depends on the number of families formed in February and their survival throughout the summer. A marked annual variation was recorded in the density of isopods before and after pair formation. In the five generations studied, the density before pair formation varied from 914 to 75 isopods/100 m^2 in the Shivta formation, from 637 to 63 isopods/100 m^2 in the Drorim formation, and from 572 to 41 isopods/100 m^2 in the Netzer formation. However, in the five generations studied, the average annual density before and after pair formation was usually the highest in the Shivta formation.

Increase in family size occurs in May when 80–90 offspring hatch from the brood pouch of the female in the family burrow. As a consequence of the parental care, the mortality of hatchlings is very low. From June to September most of the available sediment is produced. Decrease in population size occurs from June to September due to mortality of whole families. Out of the total number of isopods that hatch in May, 63–89% die by September. The lowest average mortality is in the Shivta area – 68%.

To summarize, the production of low-energy erodible sediment by isopods is highly dependent on their population dynamics. The amount of erodible material produced per season (February to September) depends on the number of families formed in February during the pair formation stage and the survival of the young from May to September. Thus, the annual amount of easily erodible sediment (Es) produced by the isopod population can be calculated by the following equation:

$$Es = Ps \cdot Ms \cdot Mf \cdot W_1 + Ps \cdot Ms(1 - Mf) W_2$$

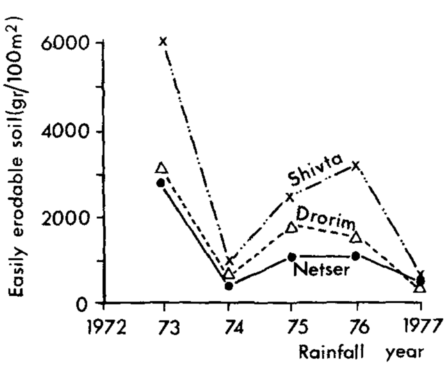

Fig. 9. Annual variation in the amounts of easily erodible soil produced by the digging activities of porcupines (*H. indica*) in the three rock units

where: Es – annual production of low-energy sediment; Ps – total number of females at the onset of pair formation; Ms – survival of females during pair formation (%); Mf – survival of families during growth stages (%); W_1 – average weight of available sediment produced by a successful family; W_2 – average weight of available sediment produced by an unsuccessful family.

It can be seen that the differences in the production of low-energy erodible sediment in the study area result from the differences in the population variables Ps, Ms and Mf.

In contrast to the isopods, which live in the study site, the porcupines are treated as an input variable. No data are available on the population dynamics, home range and foraging strategy of porcupines. Thus, the only data presented in this paper are concerned with indirect evidence of their activity.

Figure 9 illustrates the annual variation in the amount of easily erodible sediment produced by the digging activity of porcupines in the study area. The amounts produced vary greatly from one year to the next. Although the temporal changes show the same trend in the three rock units, the production per unit area is not spatially uniform. As was true of the isopods (Fig. 8), the highest production was noted in the Shivta outcrops, followed by the Drorim and Netzer formations. More detailed data on the spatial variation in the easily erodible sediment are given in Fig. 10.

As already stated for the isopods, the difference between the Shivta and Drorim formations is in fact more pronounced than it appears in Figs. 9 and 10 when considering that soil occurrence in the Shivta area is far more limited than in the Drorim area.

The distinct site selection process used by the porcupines is directly related to the spatial distribution of geophytic bulbs on which they feed. The geophytic bulbs in question are of Mediterranean origin. They are, therefore, especially abundant in the rock fissures of the Shivta formation where a good water regime prevails. Thus both isopod and porcupine populations are strikingly more active in the Shivta formation than in the Drorim and Netzer formations.

Altogether, during the study period, porcupines and isopods contributed on the average 4,160 g/100 m^2/yr in the Shivta outcrops, 2,650 g/100 m^2/yr in the Drorim outcrops, and only 2,000 g/100 m^2/yr in the Netzer outcrops. However, the relative contribution of the two populations is not equal; on the average, porcupines produced more easily erodible soil per unit area than isopods.

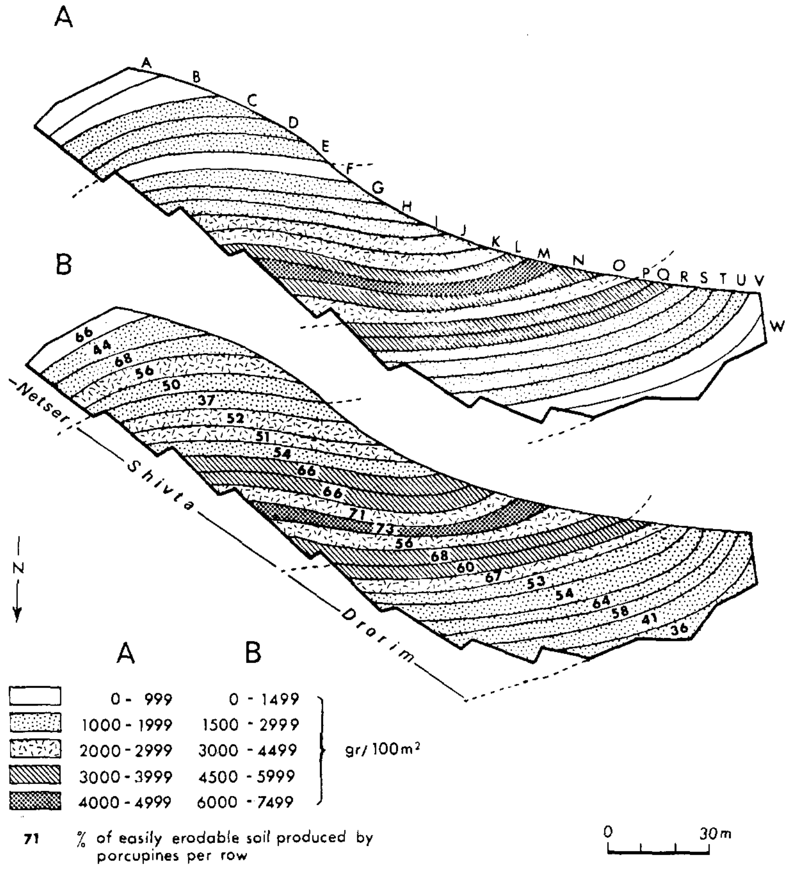

Fig. 10. Spatial distribution of easily erodible soil produced by animal activity.
A Average annual erodible soil produced by porcupines (*H. indica*).
B Average annual erodible soil produced by porcupines and isopods (*H. reaumuri*)

4.2.2 Abiotic Factors. The importance of the easily erodible soil in the process of soil flow under field conditions is supported by two phenomena. The first is the variation of sediment concentration during a flow event; the second is a comparison of the spatial distribution of soil amounts actually eroded from the plots to the amounts of easily erodible soil found in the plots.

A positive linear relationship has been obtained in many studies relating sediment concentration to runoff discharge. It was explained by the fact that with increasing discharge, an increase in flow velocity and erosive power is noted. In the present study area no relationship between sediment concentration and runoff discharge is observed (Yair et al. 1980). In fact, the highest concentrations are recorded at the initial runoff when flow energy is low. At peak flow, when flow energy is at maximum, concentration figures vary from low to very low. The high concentration at the initial runoff may be explained by the existence of the disaggregated soil material of biotic origin lying on the surface. This material is very vulnerable to splash and runoff erosion. Following the evacuation of the available sediment and the formation of a protective water layer (Palmer 1963), sediment concentration decreases despite the increase in runoff energy. Such a process clearly indicates that the increased runoff energy is not very efficient in destroying the soil's crust, being below the threshold flow velocity needed to detach the silty and sandy particles.

A strikingly non-uniform sediment contribution by the slopes was obtained. The three plots, numbered 7 to 9, supplied 88% of the total amount of sediment delivered by the drained area. The sediment contribution by the other plots, which cover altogether 64.6% of the surface, amounted to 12% only, and varied from 0.5% to 4.3% for individual plots.

Table 2. Comparison of the amounts of soil actually eroded from the plots in the storm of 24.11.72 (18 mm rainfall) with the amounts of easily erodible soil prepared by isopods and porcupines

Plot	Surface Properties			Sediment		
	Area (m^2)	Slope length (m)	Slope gradient (%)	B Easily erodible soil (g/m^2)	I Actually eroded soil (g/m^2)	
1	590	55	27.0	10.6	No data	
2	890	63	27.5	20.7	2.5	0.12
3	1,830	68	28.5	42.1	5.3	0.13
4	1,025	72	29.0	61.6	9.2	0.15
5	1,230	72	29.5	43.6	4.2	0.10
6	1,250	70	25.0	90.3	13.7	0.15
7	1,520	70	24.0	84.2	133.5	1.59
8	1,050	63	26.0	57.0	80.6	1.41
9	1,440	75	17.5	22.4	39.4	1.76
10	510	76	11.5	22.1	9.9	0.45

Such differences in the supply of sediment are far beyond the differences recorded in the runoff yields of the plots and in their topographic properties such as plot area, length of slope and mean slope gradient (Yair 1974). A comparison between the spatial distribution of easily erodible soil (Table 2; Fig. 10B) and the pattern of soil erosion shows a great similarity and suggests the existence of a link between the two patterns. The accelerated erosion ob-

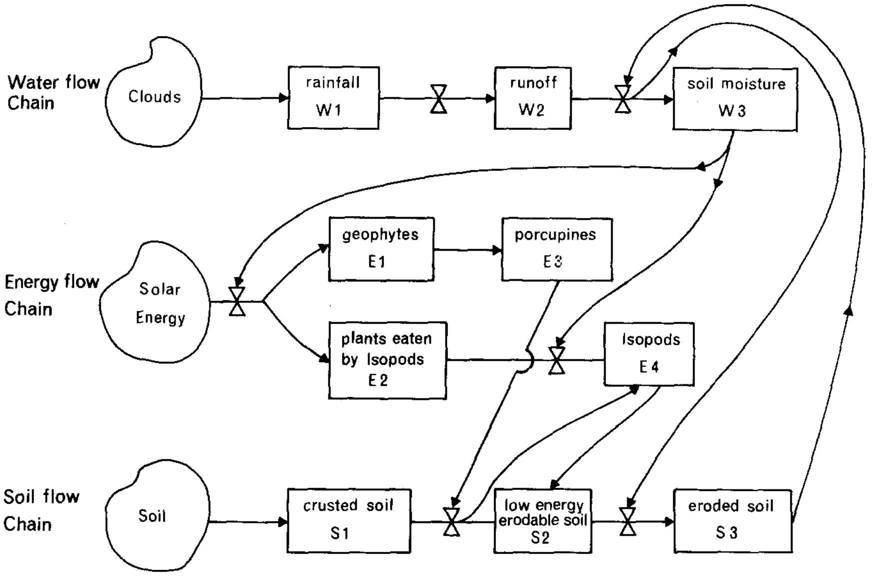

Fig. 11. Summary diagram of our present knowledge of the relationship among water, energy and soil flow in the Sede Boqer watershed ecosystem (see Table 3)

Table 3. Matrix of relationships among the variables in the water, energy and soil flow chains in the Sede Boqer watershed ecosystem (see Fig. 11). 0 = no direct relationship; 1 = direct relationship

		Water flow chain			Energy flow chain				Soil flow chain		
		W_1	W_2	W_3	E_1	E_2	E_3	E_4	S_1	S_2	S_3
Water flow chain	W_1	0	1	1	1	1	0	0	1	1	1
	W_2	0	0	1	1	1	0	0	0	0	1
	W_3	0	0	0	1	1	0	1	1	0	1
Energy flow chain	E_1	0	0	1	0	0	1	0	0	0	0
	E_2	0	0	1	0	0	0	1	0	0	0
	E_3	0	0	1	1	0	0	0	0	1	1
	E_4	0	0	1	0	1	0	0	0	1	1
Soil flow chain	S_1	0	1	1	0	0	0	0	0	0	1
	S_2	0	1	1	0	0	0	0	0	0	1
	S_3	0	1	1	0	0	0	0	0	0	0

served on plot 7, which extends wholly over the Shivta formation, and on plots 8 and 9, whose lower parts are on the same formation, can be explained as follows: in the Shivta formation extensive rock outcrops generate, per unit area, a relatively high runoff coefficient. Runoff, moving orthogonally to the rock terraces, gains in energy at the base of the terraces where runoff hits the disaggregated, loose and easy to remove soil prepared by the activity of the isopods and porcupines. Under such conditions the ratio of actually eroded soil amount (I) to the amount prepared through biological activity (B) is higher than 1, indicating that probably most of the latter amount was removed in addition to soil of nonbiotic origin.

In the Drorim and Netzer outcrops erosion processes are less intense. This can be explained by the combination of the following factors characteristic of both formations: (1) the amounts of easily erodible soil are limited (Fig. 10B); (2) rock outcrops are densely jointed, less extensive and less contiguous, generating therefore less runoff per unit area; (3) surface roughness is high. Flow velocity may therefore be expected to be slow and of limited erosive power. Under such conditions, the ratio I/B is very low (10 times lower than in the Shivta formation), indicating that most of the easily erodible soil was not removed from the area and was probably integrated into the colluvial part of plots 2 to 6.

5 Theoretical Implications

The present study has shown that the soil movement process within an arid ecosystem cannot be considered as a purely physical phenomenon, but rather as part of a complex system which includes the interaction among the three ecological flow chains presented in Fig. 11. The theoretical implication of such a conclusion is that the study of state and flow variables in an arid ecosystem should consider altogether the water, soil, energy and mineral chains. The research can be conducted on three different levels:

- interaction among different variables within each of the ecological flow chains;
- the study of a single flow chain;
- the whole of the ecosystem.

These three levels were included in the present study and their relationships are presented in the matrix in Table 3. The matrix shows clearly the six interdisciplinary and the three disciplinary topics dealt with. It also draws attention to the role that should be attributed to the various factors in the structure and function of the ecosystem studied, i.e., the role of consumers as regulators of the soil movement process. Such an approach supports the trend expressed in current research that the role of consumers should be shifted from energy flow towards the regulation of the nutrient cycling (Kitchell et al. 1979) and towards the various ecological flow chains. Finally, the analysis of the matrix allows the identification of the feedback mechanisms which are most important in the understanding of any ecosystem. Whereas in previous works (O'Neill et al. 1975) the role of consumers as regulators was mainly limited to the nutrient cycling process, it appears that in the present study area the role of the consumers is by far more complex, controlling in fact the whole ecosystem, as indicated by the following example.

The soil moisture regime in the study area is controlled by the combination of the spatial distribution of runoff generation areas with that of soil volume and depth. On the basis of data obtained it clearly appears that an increase in the extent of soil cover, due to a decrease or a total arrest in the production of easily erodible soil by biological activity, would result in the reduction of bedrock outcrops. Following such a process, an overall decrease in the soil moisture regime should be expected, especially in the outcrops of the Shivta formation, leading to a decrease in the spatial distribution of the most favorable conditions for the activity of both isopods and porcupines. In this sense, although this activity is closely controlled by the soil moisture regime, it regulates at the same time the soil moisture regime itself through the production of easily erodible soil whose erosion limits the soil volume and maintains the extensive bedrock surfaces responsible for a high input of water.

The above conclusion clearly implies that if the regulating role of the consumers is deleted from the soil flow chain, one should expect a basic change in the whole ecosystem. The new ecosystem can be expected to be more arid, less productive and less diverse. Examples of such degraded ecosystems do exist in the vicinity of the experimental site.

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