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Original article

Soil disturbance by soil animals on a topoclimatic gradient

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Abstract

We measured the area and volume of soil disturbed by various groups of animals at three sites on a topoclimatic gradient in the Judean Desert, Israel. Both the area and volume of soil disturbed by animals correlated with the cumulative precipitation of the winter rain season. Rodent activity accounted for most of the soil disturbance at all sites except for June 2001, when the volume of soil transported to the surface by ants in the construction of nest chambers accounted for most of the soil volume moved at the intermediate rainfall site. The aggregate stability of soil ejected from animal excavations was significantly lower than that of undisturbed soil during and immediately following the winter rain season, but not during the following dry seasons. The quantities of soil moved by ants in the Judean Desert were comparable to quantities moved by ants in the Chihuahuan Desert of North America.

1. Introduction

One of the most important challenges in the ecology of desert ecosystems is understanding the relationship between rainfall (either individual rain events or seasonal rainfall) and ecosystem processes. Most desert ecosystem research has been based on the pulse–reserve conceptual model [7]. This model emphasizes the importance of rainfall as a trigger that initiates a pulse of biological activity. The duration of the pulse should be a function of the amount and distribution of rainfall. This relationship should be examined for a variety of ecosystem processes and taxa topoclimatic gradients. One successful approach was to examine the relationship between rainfall as a trigger and its role in maintaining a pulse of biological activity [8,9].

Soil disturbance by animals is an important ecosystem process that was recognized as early as the nineteenth century [2]. There is rich literature on soil disturbance by a variety of animal species [5,6,11,12]. Virtually all the studies cited in these reviews were autecological and most of the studies focused on a single ecosystem process or soil property that was affected by the species studied. To evaluate the importance of faunal pedturbation in desert ecosystems, it is necessary to consider all types of soil disturbance by the assemblage of animals living in the ecosystem. We designed an experiment of faunal pedturbation on a topoclimatic gradient to evaluate the relationship between pulse duration and amount of rainfall, and to evaluate the contribution of soil disturbances to soil properties and ecosystem processes.

2. Methods

The study sites were located in the Judean Desert in Israel, which is a rain-shadow desert occupying the east-facing slopes of the Judean Mountains. The eastern border of this desert is the Dead Sea, which is approximately 390 m below sea level. The mean annual rainfall decreases on a west-to-east gradient from approximately 620 mm in the west to less

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Table 1
Study sites and site characteristics of the Judean Desert topoclimatic gradient in Israel

Study site	Elevation (m)	Slope angle and aspect	Mean annual rainfall (mm)	Mean annual temperature
Maale adumim	450	15° S facing	450	15 °C
Mishor adumim	320	11° S facing	260	17 °C
Kalia	–60	12° S facing	110	20 °C

than 100 mm at the easternmost point. Study plots were established at three sites along this topoclimatic gradient (Table 1).

The frequency of occurrence, abundance and turnover (occurrence of pits which are filled with organic matter and then covered by soil) of faunal pedturbations was measured in permanent plots randomly located at each site. Three circular plots of 10 m in radius were established at permanent center posts. All measurements described were of fresh soil disturbances. Soil disturbances were identified and assigned to the appropriate species or taxon. For each disturbance, we recorded depth, diameter of opening, height and average diameter of ejected soil mound.

We measured differences in aggregate stability of ejected soil, and disturbed soil was compared with soil less than 1 m from the disturbance. Aggregate stability was measured by a modified wet sieving technique [3].

Organic matter collected in soil pits was sampled by collecting the contents from animal-produced soil pits in areas adjacent to the study plots. The collections were made four times during the year: in August during the summer dry season, in January and February during the winter rain season, and in June at the end of the winter, wet season. Because of the unstable political situation in the western region of the Judean Desert, we were unable to visit our study plots at Maale Adumin after February 2001. Within each study plot, all pits were tracked to determine the density and species composition of plants that germinated.

The data from each site on the topoclimatic gradient in Israel was evaluated by Repeated Measures Analysis of Variance of biological activities along the study period.

3. Results

Total area of soil disturbed by animals was not related directly to the average annual rainfall at the site but there was a relationship between average annual rainfall and volume of soil ejected from soil disturbances (Fig. 1). At the intermediate rainfall site, there was significantly less soil disturbance in February, the mid-point in the winter rain season, than in August and June, during the rainless summer months (Fig. 1). In February 2001, there was high plant cover of annuals and no soil disturbances were visible. At the Maale Adumin site, the field measurements were made approximately two weeks after a 47.5 mm rainfall. At the most arid site, soil disturbance was significantly greater during August at the beginning of the study than during the following summer or winter ($P < 0.05$) (Fig. 1).

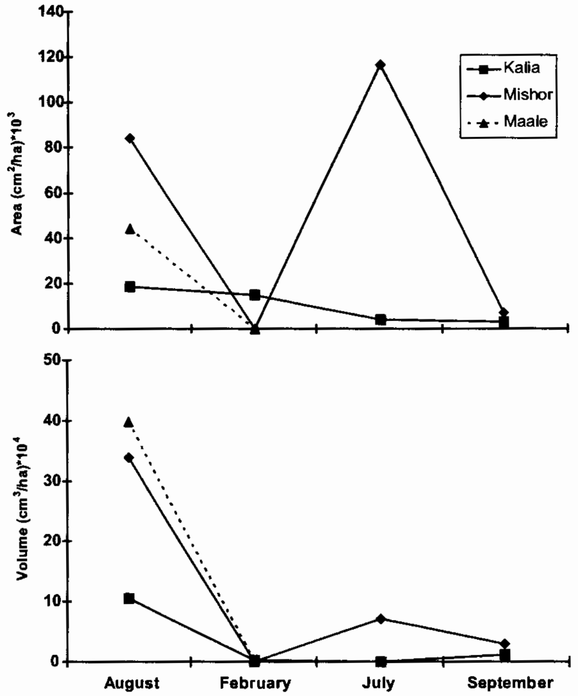

Fig. 1. Total area of disturbance and volume of soil ejected at the different sites during the study period.

At the driest site on the gradient, rodent excavations and burrows accounted for most of the soil disturbance (Table 2). At the intermediate rainfall site, ant nest mounds accounted for between 30% and 96% of the soil disturbance. Soil disturbance by invertebrates contributed only a small fraction to the total area of soil disturbed (Table 2).

The largest differences in soil aggregate stability classes were during and immediately following the rainy season (February and June) (Table 3). There were larger differences in aggregate stability of undisturbed soil compared to soil ejected from excavations by animals at the driest site than at the other sites.

4. Discussion

Although there was a relationship between average annual rainfall and soil disturbance by animals, that relationship was not the same for area of soil disturbed and

Table 2
The percentage of contribution to the total area of soil disturbed by animals reported by functional groups, for each month and site: 1 is Kalia—average annual rainfall of 110 mm; 2 is Mishor Adumin—average annual rainfall of 260 mm; and 3 is Maale Adumin—average annual rainfall of 450 mm

Month	8	8	8	2	2	2	6	6	6	9	9	9
Site	1	2	3	1	2	3	1	2	3	1	2	3
Rodent excavations	79.2	67.5	59.0	67.8	aaa [a]	aaa	94.8	3.0	–	89.8	76.8	0.0
Ant mounds	2.2	27.3	1.1	2.7	aaa	aaa	0.0	96.3	–	2.4	7.2	–
Ant Lion pits	0.05	0.61	0.0	0.0	aaa	aaa	0.0	0.0	–	0.9	0.0	–
Rodent burrows	17.3	4.5	39.9	29.3	aaa	aaa	0.0	0.0	–	0.0	12.4	–
Spider holes	0.3	0.0	0.04	0.0	aaa	aaa	4.0	0.0	–	1.3	0.8	–
Termite holes	0.0	0.1	–	0.3	aaa	aaa	1.2	0.6	–	5.6	2.8	–

[a] aaa indicates nearly total cover by herbaceous plants and absence of soil disturbance by animals.

Table 3
Comparison of aggregate stability classes of soil ejected from excavations by rodents or ant nest mounds. Unds—undisturbed soil; eject—soil ejected from excavations

Month	Kalia		Mishor		Maale	
	Unds	Eject	Unds	Eject	Unds	Eject
August	5.3	4.7	3.7	2.3	5.3	5.3
February	6.0	4.9	2.6	1.6	5.7	3.0
June	6.0	4.6	3.3	1.3	–	–
September	5.3	4.3	3.6	2.6	–	–
January	3.6	3.3	3.3	1.6		

quantity of soil ejected by animals. Rodents produced most of the soil disturbance at the sites and rodent excavations have relatively small surface area compared to depth. This accounts for the differences in surface area disturbance and soil ejected from disturbances. In the Chihuahuan Desert, rodent activity accounted for most of the soil surface area disturbed by animals [4] and soil disturbance patterns were similar to those reported here. Most of the seasonal differences were a function of the activity patterns of ants and spiders in the two deserts.

Because ants transport soil from depths of up to 2 m or more, soil removed from construction of storage galleries and chambers in nests is a more important contributor to pedogenesis and soil profile development than rodent activity. At the intermediate rainfall site, ants transported an average of 92.4 kg ha^{-1} of soil from the soil profile to the soil surface. This quantity of soil transport is slightly greater than the largest quantities of soil moved by ants in the Chihuahuan Desert (21.3–85.8 kg ha^{-1} y^{-1}) [11]. Average annual precipitation at the Chihuahuan Desert sites is 250 mm with 60% as summer rainfall compared with the Mishor Adumin 260 mm winter rainfall. Maximum soil movement by ants at the Kalia site was 0.58 kg ha^{-1} y^{-1}. The small amount of soil turnover by ants at the driest Judean Desert site supports the relationship between rainfall, productivity and density of ant colonies [1].

This study documented a relationship between differences in aggregate stability of soil ejected by animal excavations and undisturbed soil and rainfall. Soil aggregate formation requires growth of soil microbes in the surface soil [10]. During the long dry period (April to October), there is undoubtedly high mortality of bacteria and fungi in the surfacial soils of the Judean Desert. When initial winter rains stimulate growth of the soil microflora, soil aggregates can reform. Soil that is excavated by animals is exposed to sunlight and desiccation, which cause mortality of soil microflora. This accounts for the significantly lower aggregate stability of the ejected soil compared to the undisturbed soil. Reduced aggregate stability of ejected soil makes the soil volume more susceptible to wind and water erosion and contributes to spreading subsoil transported by animals across the landscape.

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