

Vegetation patterns related to environmental factors in a Negev Desert watershed*

L. Olsvig-Whittaker¹, M. Shachak² & A. Yair^{3**}

¹ *Section of Ecology and Systematics, Cornell University, Ithaca, NY 14853, U.S.A.*

² *Desert Research Institute, Ben Gurion University of the Negev, Sede Boquer, Israel*

³ *Department of Geography, Hebrew University, Jerusalem, Israel*

Keywords: Desert, Detrended correspondence analysis, Ecosystem, Microsites, Negev Desert, Ordination, Pattern analysis, Spatial heterogeneity, Species diversity, Vascular plants, Watershed

Abstract

Three strip transects, each ca 100 contiguous $0.5 \times 1 \text{ m}^2$ quadrats, were sampled during the spring bloom of March 1981 across four surface structural units of a Negev Desert research watershed at Sede Boquer, Israel. Presence of all vascular plants was recorded. Data were subjected to detrended correspondence analysis (DCA ordination), and resulting spatial patterns of species distribution and abundance were compared. Large-scale gradients of vegetation were related to differences in soil moisture availability among the four structural units. Where micro-scale vegetation patterns were important, these correlated with rock and crevice microtopography. Species richness was influenced by high numbers of therophytes on the dry upper slope of the watershed and their reduced importance on the lower three units. Relationships between vegetational patterns and known ecosystem properties of the watershed are discussed.

Introduction

In arid land ecosystems such as the Negev Desert (Israel), variation in soil moisture availability may be one of the most important causes of spatial

heterogeneity in plant communities (Evenari *et al.*, 1971). Previous studies conducted in a Negev Desert watershed at Sede Boquer have demonstrated that surface properties of rock and soil (e.g. relative cover percentages, rock surface structure, soil surface permeability) are the main factors controlling the spatial distribution of soil moisture at various scales (Yair, Sharon & Lavee, 1978, 1980). From this work a basic question has emerged: do the spatial patterns of distribution and abundance of the biotic communities (both plants and animals) in this watershed correspond to patterns of surface properties? This paper is one in a series of Sede Boquer studies on this question (see Yair & Danin, 1980; Yair & Shachak, 1982). The assumption that spatial patterns in the vascular plant community correspond to patterns in soil surface properties of the watershed is examined in the present study using ordination-based pattern analysis developed by R. H. Whittaker (Whittaker, Gilbert & Connell, 1979; Whittaker & Naveh, 1979; Whittaker, Niering & Crisp, 1979; Shmida & Whittaker, 1981).

* Nomenclature follows Zohary (1962).

** We thank the staff of the Desert Research Institute at Sede Boquer for facilities and field assistance in the execution of the transect work for this study. In particular, we wish to thank Dr Yitzchak Gutterman, Ms Jael Bar, and Mr Bert Boeken for their help in the field and identification of species. We also thank Dr Avinoam Danin for help with species identification. Computer analyses were conducted by the senior author at Cornell University, where we thank Mr Hugh Gauch, Jr., for advice and assistance with the computer programs, and his comments on interpretation of the data. We thank Dr Danin and Prof. Zev Naveh for advice and comment.

This paper is dedicated to the memories of the senior author's husband, Robert H. Whittaker, and father, Edward E. Olsvig, who anticipated and encouraged the early stages of this research.

Site description

The Sede Boqer research watershed is located in the northern Negev Desert of Israel, about 40 km south of Beersheva, at an altitude of 510 m (Fig. 1, inset). Average annual rainfall is 92 mm, with extreme recorded values of 34 and 167 mm. Rainfall is limited to winter (October–April) with the number of rain days varying between 15 and 42. Mean monthly temperatures vary from 9 °C in January to 25 °C in August (climatological data from Evenari *et al.*, 1971).

The study site (Fig. 1) covers an area of 1.1 ha on the north-facing hillside of a first order drainage basin. Local stratigraphy is Upper Cretaceous (Turonian of Arkin & Braun, 1965), represented by three limestone formations called (from top of slope to bottom): Netser, Shivta, and Drorim. Although similar in composition, these formations differ greatly in structural properties, which create four different meso-scale physical environments for the plant communities: (A) The upper part of the Netser formation, at the top of the watershed, is thinly bedded, densely jointed chalky limestone with very shallow, patchy soil. (B) The lower portion of the Netser formation is more massive, resembling the strongly step-like, crystalline limestone Shivta formation which lies underneath. Lower

Netser and Shivta should be considered one unit. The Drorim formation is subdivided into two structural units: (C) an upper unit of massive limestone with extensive bedrock outcrops, and (D) a lower unit which is densely jointed and covered with an extensive colluvial mantle (Yair & Danin, 1980; Yair & Shachak, 1982). These four structural units, in the sequence just given, will henceforth be referred to as Units A, B, C, and D.

Throughout the site, soil material is mainly loess (Yaalon & Dan, 1974) which is high in silt and sand (85–95%). The clay fraction forms a higher percentage (14.5%) of soil in joints and crevices than in the soil covering flatter bedrock surfaces (7–10%; Yair & de Ploey, 1980).

The vegetation of this region is considered to be a transition between the Irano-Turanian plant geographical region and the Saharo-Arabian region, with some Mediterranean components in the most mesic sites (Danin *et al.*, 1975; Yair & Danin, 1980). The watershed slope has a range of communities from semi-desert (10–30% perennial vegetation cover) on the rocky upper slopes, to some patches of true desert (less than 10% perennial cover) on the lower colluvium. Perennials include the shrubs and semishrubs *Artemisia herba-alba*, *Gymnocarpus decander*, *Hammada scoparia*, *Noaea mucronata*, *Reamuria negevensis*, and *Zygophyllum dumosum*

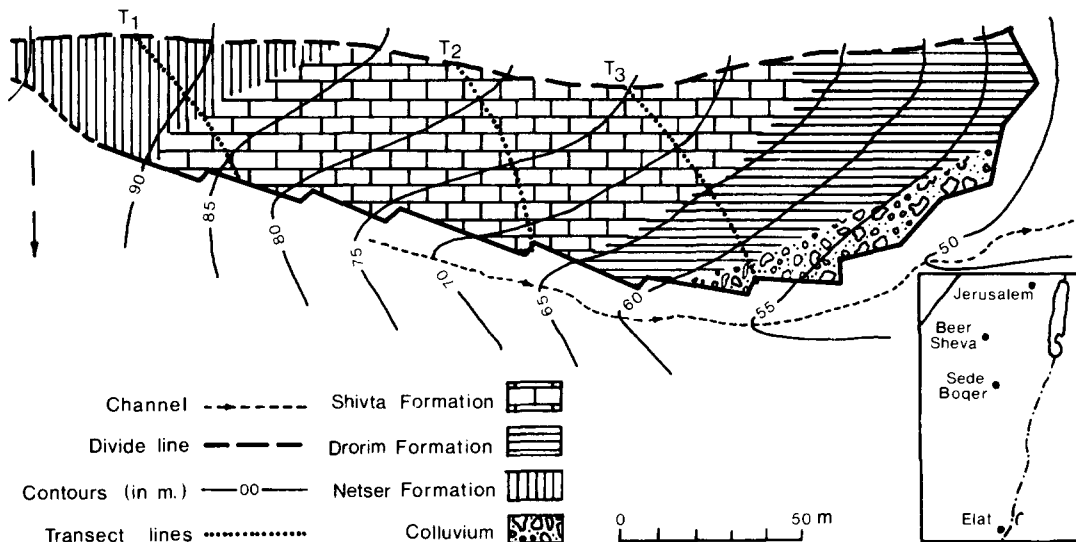


Fig. 1. Sede Boqer research watershed, showing the four major structural units: Netser (Unit A), Shivta (Unit B), Drorim (Unit C), and Colluvium (Unit D). Inset: Map of southern Israel, showing location of Sede Boqer. T1, T2, T3 are transects 1, 2, and 3, respectively.

as dominant species. In addition, during the rainy winter season, there is an assortment of annuals, geophytes, and hemicryptophytes (Table 1). Units A and D are both rich in annuals. Geophytes such as *Iris*, *Gagea*, *Ornithogalum*, *Scilla*, and *Tulipa* are a striking feature of Unit B and are important in the vertebrate ecology, nutrient cycling, water dynamics, and soil movement on the watershed slope (Yair & Shachak, 1982).

Methods

Pattern analysis, general methods

Most traditional measures of within-community patterns test contagion and species association on only one or two species at a time (e.g. Kershaw, 1957; Greig-Smith, 1964; Pielou, 1974). Since our present research is concerned with more general ecosystem patterns, we will confine our analyses to those parameters which integrate information from the whole flora thereby revealing major patterns of differentiation in the plant community. These measurements include species diversity statistics, for example, as well as the results of community ordination and classification.

The system of pattern analysis used in this study was developed over the past decade by R. H. Whittaker and other colleagues in our research group (see Whittaker, Gilbert & Connell, 1979; Whittaker & Naveh, 1979; Whittaker, Niering & Crisp, 1979; Olsvig(-Whittaker), 1980; Shmida & Whittaker, 1981). Previous studies have mostly concentrated on biologically induced patterns in shrubland mosaic vegetation, although such methods are equally appropriate to examining the kind of physically induced patterns which concern us here.

Field data for this type of pattern analysis is taken from a strip transect, i.e. a series of contiguous small plots. One hundred plots seem in practice to be the usual minimum sample size required for useful results. In each plot, presence or coverage of species is recorded, along with pertinent additional data.

Earlier studies by our group used reciprocal averaging (RA; Hill, 1973, 1974; Gauch *et al.*, 1977) as the main ordination method for pattern analysis. More recently we have used detrended correspondence analysis (DCA; Hill, 1979; Hill & Gauch,

1980), an improved version of RA. Both algorithms ordinate samples and species simultaneously, so that the final output matrix places samples with similar composition, and species with similar distribution in the samples, adjacent to each other (for details, see Gauch, 1982). However, with DCA the axes have been rescaled so that the difference in value between two sample scores reflects their relative difference in species composition. Because typically only the first and second DCA axes are ecological interpretable, we use only the first two axes scores for pattern analysis. Generally, vegetation differences evident in these scores are examined in one of two ways: 1) by a scatter plot of sample or species scores on the first two DCA axes (e.g. Fig. 2) or 2) by a plot of sample scores from a single DCA axis against sample position on the strip transect (e.g. Fig. 3). Such a plot of ordination position to real sample position has been termed an ordination 'trace' (Whittaker, Gilbert & Connell, 1979; Whittaker & Naveh, 1979; Whittaker, Niering & Crisp, 1979).

Sample to sample variations along a DCA ordination trace are a reflection of micro-scale variation in species composition. The meso-scale changes in vegetation, which may also be evident in the DCA trace, are more difficult to spot. If there is a major change in vegetation along the transect, it may be continuous. In this case, it will show on the first axis DCA trace as a relatively smooth trend of change in sample scores from one end of the transect to the other (Fig. 3B). In these circumstances, a regression line fitted to the trace will illustrate the meso-scale change quite well. The slope of the line, like the maximum difference in scores, reflects the degree of change along the derived coenocline. The regression coefficient, r , indicates the significance of the observed trend.

If the meso-scale change is an abrupt one, with two or more relatively homogeneous sets of samples (i.e. vegetation type patches) which are quite different from each other, the DCA trace will show clusters of sample scores with sharp score changes between sets. An extreme of this situation occurs when the between-patch variation forms a strong, repeating 'wave' in the DCA trace (e.g. Fig. 3C). This situation has been termed 'two-phase vegetation' (Whittaker & Naveh, 1979). In Figure 3C, clusters of samples in one microsite type (rock) have similar scores, which differ greatly from scores for the other microsite type (soil pockets). In such a

Table 1. Average frequency of occurrence of species.

Species	Transect: Units:	1			2				3	
		A	INT	B	B ₁	B ₂	C	D	B ₁	B ₂
Therophytes										
<i>Aizoon hispanicum</i>		9.3								
<i>Anagallis arvensis</i>			16.6	5.1						
<i>Anthemis pseudocotula</i>			33.3		3.8		12.5			
<i>Biscutella didyma</i>		2.3								
borage sp.		2.3								
<i>Bromus</i> sp. A		9.3	16.6	10.3		3.8			2.0	24.0
<i>Bromus</i> sp. B				12.8						
<i>Calendula arvensis</i>									2.0	2.0
<i>Carrichtera annua</i>		7.0				11.5				4.0
composite sp.										
<i>Cuscuta</i> sp.		7.0	83.3	33.3	26.9	26.9	37.5	41.7		
<i>Cutandia memphatica</i>		34.9								
<i>Erodium desertorum</i>		18.6								
<i>Filago contracta</i>					11.5					
<i>F. desertorum</i>		34.9	33.3	2.6		19.2	29.2	20.8		
<i>Gymnarrhena micrantha</i>		14.0							4.0	
<i>Helianthemum ledifolium</i>										4.0
<i>Lappula sessiliflora</i>		2.3								
<i>Lathyrus pseudocicera</i> (?)		4.7								
<i>Linaria haelava</i>		2.3								
<i>Lophochloa pumila</i>		2.3			11.5	15.4	8.3	4.2		
<i>Matthiola livida</i>		39.5								
<i>Minuartia picta</i>		55.8								
<i>Ononis sicula</i>					3.8			4.2	2.0	
<i>Picris damasena</i>					3.8	3.8	20.8	62.5	28.0	28.6
<i>Plantago coronopus</i>									4.0	24.0
<i>P. ovata</i>		18.6				19.2	4.2			
<i>Pteranthus dichotomus</i>		7.0								
<i>Reboudia pinnata</i>		2.3		2.6						
<i>Scabiosa porphyromeura</i>					7.7					6.0
<i>Schismus arabicus</i>								4.2		2.0
<i>Senecio desfontanii</i> (?)		7.0		2.6			4.2	4.2	2.0	
<i>Stipa capensis</i>					3.8	19.2	16.7	12.5	8.0	26.0
<i>Trigonella arabica</i>		18.6					4.2			
<i>T. stellata</i>					7.7					
Total number of species		21	5	7	9	8	9	8	8	9
Average frequency (%)		14.3	36.6	9.9	8.9	14.9	15.6	19.3	6.5	13.4
Geophytes										
<i>Allium</i> sp.				2.6	11.5					
<i>Bellevalia desertorum</i>				2.6					2.0	
<i>Colchicum tuviae</i>				5.1						
<i>Crocus</i> sp. (?)		2.3		2.6					4.0	26.0
<i>Gagea chlorantha</i>					15.4					
<i>G. reticulata</i>		16.3		7.7	7.7	3.8	8.3			
<i>Iris edumea</i>					3.8					
<i>I. sisyrinchium</i>					3.8					
<i>I. regni-uzyae</i>									6.0	
<i>Ornithogalum narbonense</i>										2.0
<i>Scilla hanburyi</i>				2.6	3.8	11.5	8.3			6.0
<i>Tulipa montana</i>				10.3	11.5		25.0	41.7	2.0	4.0
Total number of species		2		7	7	2	3	1	4	4
Average frequency (%)		9.3		4.8	8.2	7.7	13.9	41.7	3.5	9.5

Table 1. (Continued).

Species	Transect: 1		2				3			
	Units:	A	INT	B	B ₁	B ₂	C	D	B ₁	B ₂
Hemicryptophytes										
<i>Anemone coronaria</i>						3.8			2.0	
<i>Carex pachystylis</i>			2.6							
<i>Centaurea aegyptiaca</i>							4.2			
<i>C. eryngioides</i>	4.7	33.3	71.8	26.9	23.1			10.0	2.0	
<i>Diplotaxus harra</i>	32.6		7.7	7.7	19.2	16.7	16.7	10.0	6.0	
<i>Erodium hirtum</i>	76.7	100	64.1	65.4	69.2	45.8	25.0	38.0	28.0	
<i>Haplophyllum tuberculatum</i>	2.3									
<i>Helianthemum</i> sp.	2.3		5.1			11.5	16.7	12.5		
<i>Launea nudicaulus</i>	60.5	33.3	30.8	7.7						
<i>Piptatherum mileacea</i>				3.8					4.0	
<i>Ranunculus asiaticus</i>						8.3				
<i>Scorzonera judaica</i>	44.2	16.6	10.3				29.2			
Total number of species	7	4	7	4	5	4	5	6	3	
Average frequency (%)	31.9	45.8	27.5	26.9	25.4	21.9	17.5	12.8	12.0	
Chamaephytes										
<i>Artemisia herba-alba</i>	51.5	50.0	61.5	61.5	69.2	75.0	83.3	26.0	40.0	
<i>Asparagus stipularis</i>								2.0	2.0	
<i>Astragalus sanctus</i>	20.9		23.2	3.8	3.8	8.3	8.3	4.0	10.0	
<i>Echinops polyceras</i>				3.8				2.0	4.0	
<i>Ephedra aphylla</i>								8.0		
<i>Gymnocarpus decandrum</i>	4.7		46.2	34.6	30.8	29.2		18.0	22.0	
<i>Hammada scoparia</i>	7.0									
<i>Helianthemum kahiricum</i>	34.9	100	64.1	15.4	3.8	20.8	8.3	4.0		
<i>H. ventosum</i>		16.6	23.1	3.8		16.7	45.8	8.0	18.0	
<i>H. vesicarium</i>	9.3		41.0	11.5	11.5	58.3	75.0	16.6	6.0	
<i>Limonium pruinosum</i>			2.6							
<i>Noaea mucronata</i>			23.1	19.2	46.2	33.3	66.7	32.0	28.0	
<i>Paronychia syriaca</i>								4.0		
<i>Pituranthos tortuosus</i>								2.0		
<i>Reamura negevensis</i>	23.3	16.6	12.8	23.1				6.0	2.0	
<i>Salvia lanigera</i>							8.3			
<i>Stachys aegyptiaca</i>				7.7				2.0	6.0	
<i>Varthemia iphionoides</i>						4.2			2.0	
<i>Zygophyllum dumosum</i>	23.3								2.0	
Total number of species	8	4	9	10	6	8	7	14	12	
Average frequency (%)	21.9	45.8	33.1	18.4	27.6	30.7	42.2	9.6	11.8	
Total species, all life forms	39	13	30	30	21	24	21	31	27	

situation, the trend of change in vegetation from one end of the transect to the other is relatively insignificant compared to the microsite differences.

Pattern analysis, *Sede Boqer*

For this study, three separate transects of contiguous ($0.5 \times 1 \text{ m}^2$) plots were laid out on the north-facing slope of the watershed, during March 1981. Although our major interest was in the nature of the

transition between geological/structural units, the character of the watershed made it impossible to include all four structural units in a single transect without changing other important factors, such as slope or aspect. Therefore, two parallel transects, each intersecting two or more structural boundaries, were used. Transect 1 extended for 88 quadrats within watershed study plot 10 (Fig. 1); there were in this area only 44 m between crest and wadi, of which roughly half were in Unit A and half in Unit

B. Transect 2 included 100 quadrats, beginning in Unit B and ending in Unit D, within study plot 5. The additional transect 3 was entirely within Unit B, study plot 7, and was included to compare patterns entirely within one structural unit against patterns which occur when two or more units are encountered. Each transect began on the upper slope of the watershed, and extended to the wadi. In each quadrat, the presence of all vascular plant species was recorded. In addition, field notes on topography and visual and probe estimates of soil depth were recorded for each quadrat. DCA ordination was done for each transect separately. Ordinations combining all three transects were also conducted, but added no new information.

Species diversity

Most diversity indices, such as the Shannon-Wiener, combine different diversity parameters, leading to ambiguous results if the component parts are not responding in the same way to environmental patterns. For this reason, it is useful to examine separately the basic components of diversity.

Within a site, diversity parameters include 1) species richness on the micro-scale (point or quadrat species richness); 2) species richness on the meso-scale (site floristic richness or alpha diversity *sensu* Whittaker, 1972, 1977); 3) the degree of change in species composition along a coenocline or environmental gradient within the site; and 4) total site heterogeneity. Both terms 3) and 4) have been called *beta diversity* (Whittaker, 1975) when applied to standard coenocline data, and *pattern diversity* when applied to within-site transect data (Whittaker & Naveh, 1979). However, change in species composition along a single ordination-based coenocline is a derivation, i.e. an abstraction which does not usually reflect the full compositional variation of the data set. Therefore term 4) will be distinguished in this paper as *site heterogeneity*. Only 3), the turnover of species along the derived coenocline, will be termed *beta* or *pattern diversity*.

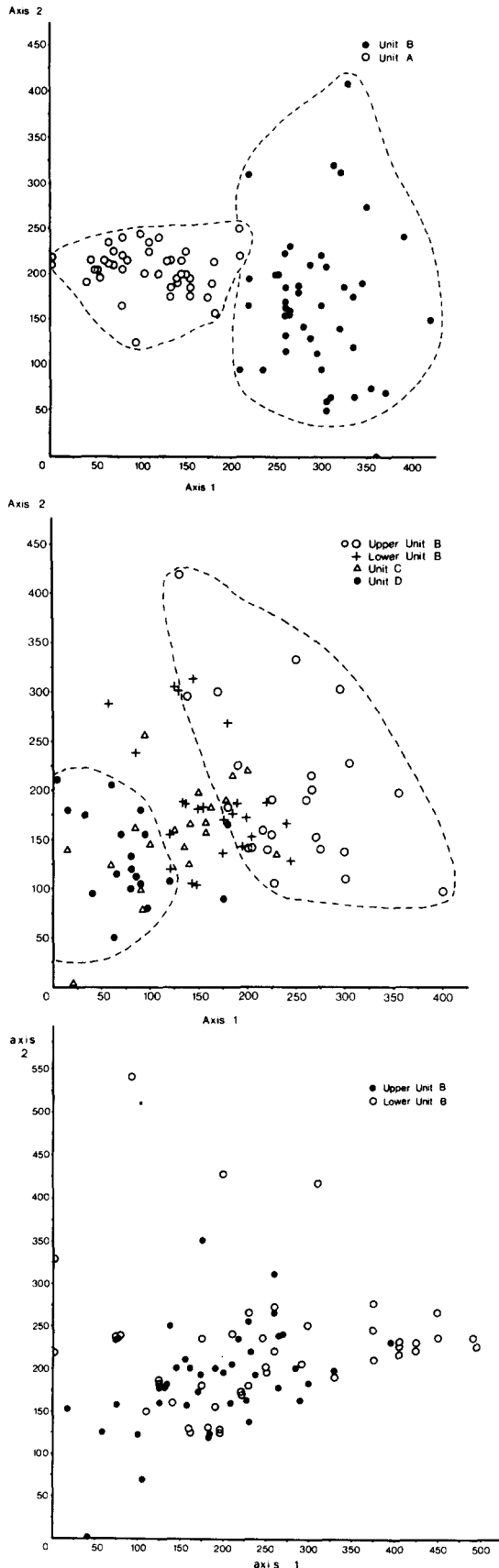
The following methods were used to obtain the four diversity parameters discussed above:

1. Point diversity, \bar{S} , was determined as the average number of species in a 0.5 m² quadrat, averaged over 10 quadrats per structural unit, per transect.
2. Alpha diversity, S_c , was determined as the total number of species in each structural unit of each transect, or the combined species richness. Since the value of S_c is clearly dependent on sample size, and comparisons are valid only between sample sets of equal size, an additional statistic was used. S_{c10} was the combined species richness of 10 quadrats per structural unit. It was used as a check on trends observed in S_c .
3. Pattern diversity, or species turnover on a coenocline, can be determined using a number of different indices (Gauch, 1982; Wilson & Mohler, 1982). Turnover of species along a coenocline can be quantified in half-changes (HC), or 50% changes in species composition (Whittaker, 1960; Gauch & Whittaker, 1972). Wilson & Mohler (1982, 1983) propose the Gleason (G) as the compositional turnover occurring if all change were concentrated in a single species whose abundance changed 100%. 'For example, a 1 G coenocline might consist of three species, two of which change from 50% to 0% relative abundance as the third species changes from 0% to 100% relative abundance.' DCA ordination provides a third index, the number of SD units, or average standard deviations of species distributions, which is used to scale the ordination axis length and correlates with species turnover (Hill, 1979; Hill & Gauch, 1980; Gauch, 1982). In the present study, we used three calculations of HC values: 1) Whittaker's graphical estimate, 2) Wilson & Mohler's refinement of that estimate (the GRADBETA program; Wilson & Mohler, 1982, 1983), and 3) Hill's formula:

$$HC = 2.568 \sqrt{EV/(1 - EV)}$$
 where HC is the number of half-changes, and EV is the eigenvalue of the DCA ordination axis selected for the coenocline (M. O. Hill, personal communication).

Gleason values were obtained using Wilson & Mohler's GRADBETA program, and were analyzed on the basis of 10 composite samples from each transect. The composite samples were formed by dividing the DCA ordination coenocline in 10 equal units, and pooling all samples in each unit.

SD units were obtained directly from the DECORANA ordination output of each transect.



4. Site heterogeneity was calculated by S_c/\bar{S} for each structural unit. The same caveat about sample size discussed for S_c applied here, and therefore $S_c 10/\bar{S}$ was also calculated. An alternative, visual demonstration of site heterogeneity, was the ordination trace (Fig. 3), which provided information on the range of sample scores as well as their pattern of distribution.

Results

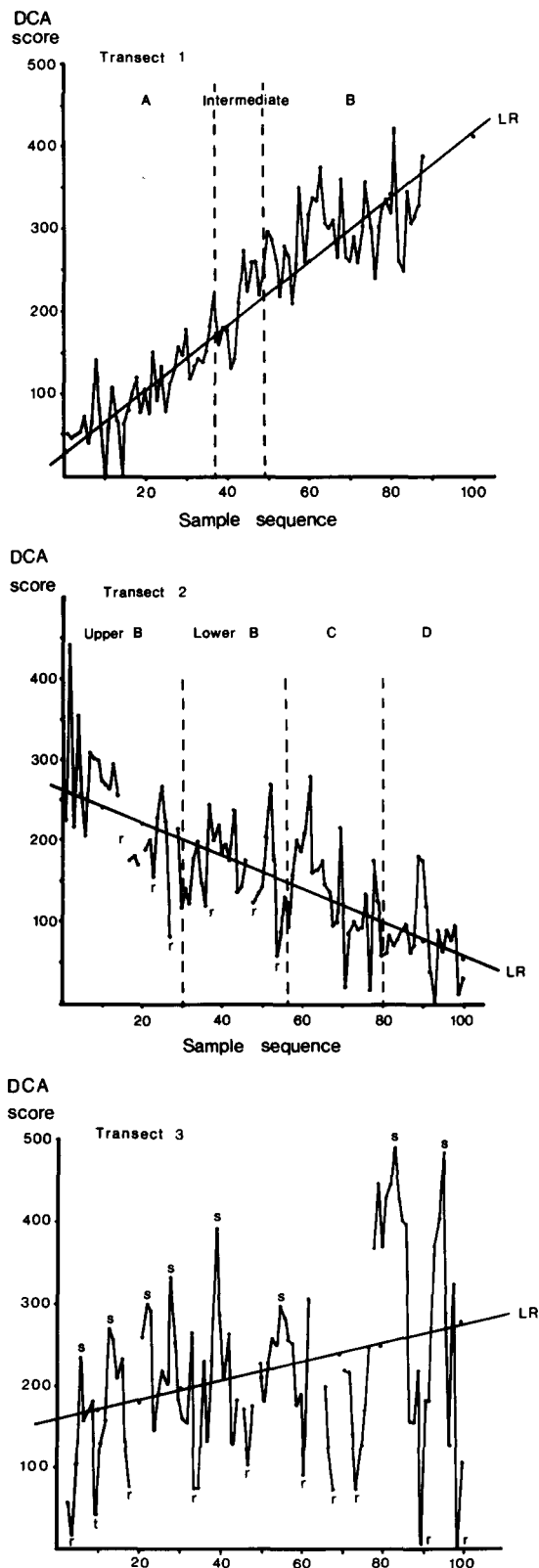
DCA ordination: scatter plots

Scatter plots of sample scores from DCA axes 1 and 2 (Fig. 2) showed definite separation of samples from the four structural units. However, the discreteness of this separation varied, depending on the structural units involved. There was complete separation between samples from Units A and B (Transect 1, Fig. 2A), but overlap between Units B, C, and D (Transect 2, Fig. 2B). When only one structural unit was involved (Unit B, Transect 3, Fig. 2C), there was little meso-scale differentiation between top and bottom of the slope. Thus, at least in Unit B, slope position did not seem important in within-unit differentiation of vegetation.

DCA ordination: sample score traces

The DCA traces for the three transects (Fig. 3) provide information about pattern on both the micro-scale and meso-scale. Only Transects 1 and 2 showed a major change in vegetation (as indicated in the first axis of DCA ordination) from one end of the transect to the other. The slope of the regression line through sample points was steepest (indicating greatest meso-scaling change in vegetation) on Transect 1, i.e. the transition from Unit A to B. Note that this transect also showed the clearest separation of samples on the scatter plots of Figure 2. In contrast, Transect 3 (Fig. 3) showed no significant meso-scale change in vegetation.

Fig. 2. Scatter plots for first two axes of DCA sample ordinations. (A) Transect 1: Unit A (Upper Netser) to Unit B (Lower Netser and Shivta). (B) Transect 2: Unit B (Shivta) to Units C (Upper Drorim) and D (Lower Drorim). (C) Transect 3: Unit B. On Transect 3, samples were equally divided between Upper and Lower Shivta. Axis lengths are scaled in SD units of DCA ordination.



Transect 3, confined to structural unit B, was meant to test the relative importance of meso-scale patterns (especially position on the watershed slope) versus micro-scale patterns. As observed above, meso-scale differentiation did not seem important within the unit. Instead, the greatest contrast in sample scores reflected micro-scale conditions: the lowest value generally corresponded to rock crevice samples, and the highest to vegetation on thin surface soil (Fig. 3C). Thus, within Unit B, the most important differentiation of vegetation was caused by the physical micro-scale structure of the substrate. It should be noted that this is also physically much more heterogeneous than the other three units, with sharp contrast between the properties of rock outcrop and crevice (Fig. 4). Hence relatively greater microsite differentiation of vegetation is not surprising.

Point species diversity

The species richness obtained as an average of 10 quadrats within each transect segment (structural unit) is presented in Table 2. Unit A has by far the greatest total species richness, with an average of 8.4 species per 0.5 m². Separation of growth forms shows that this is mainly due to the large number of annual therophytes and hemicryptophytes in Unit A.

Alpha diversity

The total number of species in each structural unit (Tables 1 and 2) is affected by the number of samples from each. Since there is some variation in sample size among the four units, these data must be treated with caution. At every scale, however, the species richness of Unit A is much greater than that of other units (Table 2). This is mainly due to the large number of annuals (therophytes) in Unit A. These samples were taken in a high rainfall year, however, when the annual flow was rich. A low rainfall year might not produce the same results.

Fig. 3. DCA traces of first axis sample ordination scores. (A) Transect 1: Units A to B. (B) Transect 2: Units B, C, and D. (C) Transect 3: Unit B only. Abbreviations: LR = linear regression line through DCA trace; r = rock outcrop, s = soil pocket or crevice. Axis 1 is the sample sequence on the transect; Axis 2 is the sample score on the first DCA ordination axis.

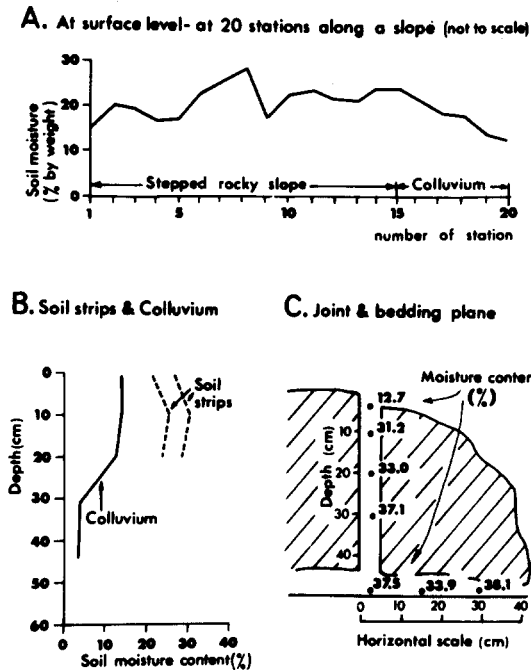


Fig. 4. Soil moisture on the Sede Boquer watershed slope. (A) Percentage surface soil moisture from Unit B (Shivta) at left, to Unit D (Colluvium) at right. Note high variation in Unit B soil moisture, and the steady decline in soil moisture through the colluvium. (B) Contrast in soil moisture between Colluvium and soil strips (crevices) of Unit B. Note the increase in soil moisture with depth in Unit B, with a maximum at 10 cm depth. (C) Pattern of soil moisture within crevices of Units B and C. Note that the soil accumulated under rock in the horizontal bedding plane has the highest soil moisture (37.5–38.1%). Data from A. Yair & M. Shachak.

Spatial heterogeneity

S_c/\bar{S} is dependent on the total number of samples used to calculate S_c . Therefore both S_c of whole structural units and $S_c/10$, the combined richness over 10 samples per unit, are presented in Table 2A. In both cases, the highest values for spatial heterogeneity occurred in Unit B, and the lowest in Unit D. This trend seems due to the relatively low point diversity of Unit B. However, it is not simply related to the reduction in annual species which occurs in Unit B, since the same trends are observed when S_c/\bar{S} and $S_c/10/\bar{S}$ are calculated without annuals (Table 2B).

Pattern diversity

Five indices of pattern diversity are presented for the three transects (Table 2B). Three of these indi-

ces, the Whittaker measure of half-change (HC), Wilson & Mohler's refinement of Whittaker's index, and Wilson & Mohler's Gleason index (G), show the same trend: highest values for Transect 2 and lowest values for Transect 3. Apparently pattern diversity is directly correlated to the number of structural units represented in the coenocline.

Hill's eigenvector estimate of half-change $HC(EV)$, shows the reverse trend. Since the first three indices require compositing of samples, we checked the effect of making composite samples on $HC(EV)$ as well. The same trend was observed as before. DCA ordination SD lengths correlated with $HC(EV)$ on composite samples, but not on original samples. We must conclude that both $HC(EV)$ and the SD units are unreliable estimates of pattern diversity defined as species turnover along a gradient.

Patterns of soil moisture

The information currently available about soil moisture and related parameters, based on published and ongoing studies of the Sede Boquer watershed, is presented in Table 2 and Figure 4. Soil moisture following rainfall is highest in Unit B, and equally low in Units A and D; electrical conductivity, primarily reflecting salinity, shows an inverse relationship (Table 3). Spatial heterogeneity, as previously discussed, seems related to relatively high moisture conditions, although species richness (including annuals) is not.

Figure 4A clearly shows the high variability of soil moisture within the rocky slope area (Units B and C) compared to a steady decline in soil moisture within the colluvium (Unit D). Where soil has accumulated within crevices of Unit B, there is a marked increase in soil moisture with depth (Fig. 4C) providing an improved moisture resource for those plants which can reach it. Even at the surface, the soil of Unit B and C contains more moisture than the colluvium of Unit D (Fig. 4B).

Discussion

Correlations

At the Sede Boquer watershed, geological surface structure is correlated with most aspects of vegetation, including patterns of species richness and

Table 2. Species and pattern diversity.

A. Species diversity and spatial heterogeneity								
Transect:	1		2				3	
Units:	A	B	B ₁	B ₂	C	D	B ₁	B ₂
1. Point diversity, \bar{S} (.05 m ²)								
with therophytes	8.4	6.5	4.4	4.2	5.2	4.9	2.2	4.1
without therophytes	5.1	5.8	3.4	3.5	4.2	3.8	2.1	2.1
2. Alpha diversity, 10 quadrats combined, $S_c/10$ (5 m ²)								
with therophytes	32	21	16	14	17	15	12	20
without therophytes	12	19	12	10	12	10	12	11
All quadrats in unit, S_c								
with therophytes	39	30	30	21	24	21	31	27
without therophytes	17	23	21	13	15	13	24	19
In entire transect								
with therophytes	54			47			40	
without therophytes	30			31			28	
3. Spatial heterogeneity, S_c/\bar{S}								
with therophytes	4.6	4.6	6.8	5.0	4.6	4.3	14.1	6.6
without therophytes	3.3	4.0	6.2	3.7	3.6	3.4	11.4	9.0
$S_c/10/\bar{S}$								
with therophytes	3.8	3.2	3.6	3.3	3.3	3.1	5.4	4.9
without therophytes	2.4	3.3	3.5	2.9	2.9	2.6	5.7	5.2
B. Pattern diversity								
Transect:	1		2				3	
Whittaker's <i>HC</i>		2.7			4.4			2.2
Wilson & Mohler's <i>HC</i>		3.0			4.8			1.9
Wilson & Mohler's Gleasons		3.1			6.1			2.9
Hill's <i>HC(EV)</i>								
on composite samples		3.4			3.7			4.2
on original samples		2.9			2.5			3.8
DCA ordination SD units								
on composite samples		420			443			495
on original samples		517			471			503

composition. A general summary is presented in Table 3. The reasons for these correlations are complex, but seem founded in a basic hydrogeological feature of the Negev, and probably many other deserts as well: the pattern of runoff generation. If the environment for the desert community were uniform, flat, and comprised only of even-texture soil (a loessal plain comes close to this ideal), then the spatial distribution of soil moisture would correlate with the spatial distribution of rainfall. But in a desert on rocky hillsides, with patches of rock alternating with patches of soil, the situation is quite different. The rocky patches generate runoff, while the soil patches absorb the water. Therefore, the distribution of soil moisture will be dependent on the distribution and ratio of rock surface to soil

volume. High soil moisture can be predicted where the rock/soil ratio is high and surface properties can be considered the controlling factors determining the spatial distribution of soil moisture. This relationship may be expressed by a formula:

$$\text{relative soil moisture} = \int \left(\frac{SA_{\text{rock}}}{SA_{\text{soil}}} \times \frac{1}{\text{soil depth}} \right)$$

where *SA* is surface area.

Relatively aridity may be generated by a low $SA_{\text{rock}}/SA_{\text{soil}}$ ratio, as in Unit A of this watershed, or it may be generated by great soil depth, as in the colluvium of Unit D. In contrast, where $SA_{\text{rock}}/SA_{\text{soil}}$ ratio is high and soil depth is generally low,

Table 3. Summarization of results.

Structural unit	A	B	C	D
	Upper Netser	Lower Netser-Shivta	Upper Drorim	Lower Drorim
Structure	thin soil cover, fine-grained	massive, blocky, step-like	rock outcrop	colluvial accumulation
Transition to lower unit	sharp	gradual	gradual	--
Internal (micro-scale) heterogeneity	weak	strong	intermediate	weak
% soil moisture (Yair & Danin, 1980) after rainfall event	low, 15%	high; 25–30% in soil strips, to 38% in crevices	intermediate, 20–25%	low, 10–15%
EC (salinity) mMHO/cm (Yair, unpublished data)	high, 3.9	low; 0.4–0.7 lower Netser, 0.4–0.5 Shivta	low, 0.4	high, 5
Species richness				
Annuals	high	low	low	low
Hemicryptophytes	high	high	low	low
Geophytes	low	high	high	low
Shrubs	low	high	high	high
Spatial heterogeneity (pattern diversity)	low	high	intermediate	intermediate
Animal activity	low	intermediate-high; concentrated in Shivta	intermediate	low

as in the step-like Unit B, a relatively mesic environment is created (Table 3 and Fig. 4). This relationship seems important at all scales of environment. On the micro-scale, variation in this ratio determines the high degree of heterogeneity in Unit B (Fig. 4A). Soil moisture, salinity (Yair & Danin, 1980), and texture differ greatly between the soil in crevices and the soil strips on flat bedrock in this unit. On the macro-scale, the landscape, this same relationship may be as important as rainfall in determining aridity. For example, studies by Yair in Ramat Hovav, which is north of Sede Boqer and receives more rain, indicate that the soil is actually more arid than at the Sede Boqer watershed. This situation is apparently caused by the absence of the runoff-generating Unit B-type rock (Shivta formation).

Life forms

The results suggest that the strength of apparent vegetation response to water regime is strongly affected by the life forms of the plant species involved. Species in this site may be conveniently divided into four major groups: therophytes, hemicryptophytes, geophytes, and chamaephytes, each distinctive in its distribution pattern.

Desert therophytes in the Negev Highland exploit the top centimeters of the soil, and are abundant only in favorable years (Loria & Noy-Meir, 1979) when surface soil moisture is relatively high during the growing season. Moisture conditions of the surface soil vary less spatially than they do temporally (A. Carnelli, unpublished data). Hence spatial heterogeneity of therophytes as a response to the surface structure of their environment may be relatively low, although countered by biologically caused patterning (Ellner & Shmida, 1982).

Hemicryptophytes are larger than therophytes, on the average, and, with their deeper rooting systems, will probably be more affected by spatial heterogeneity of soil moisture below the top centimeters. These species also show more patterning (for example, are more frequent in the Unit B crevices, averaging 0.4 individuals per plot, than in the soil strips, where they average 0.1 individual per plot). This is probably related to the greater heterogeneity of the total soil moisture which they can exploit.

From our data, both therophytes and hemicryptophytes seem at a disadvantage in this site when interacting with chamaephytes and geophytes. The richness and frequency of therophytes in particular seems inversely related to that of the latter three

groups (Table 1). Previous studies (Friedman *et al.*, 1977) have indicated suppression of certain annual species by *Artemisa herba-alba* in Negev vegetation, which could explain the reduced importance of therophytes in Units B, C and D.

Chamaephytes can exploit deeper soil for moisture than the other species reach. This group predominates in the upper colluvium (Unit C), where moisture resources are more limiting. Likewise, chamaephyte frequency (Table 1) is high in Unit B. Here, clay accumulation in the bedding plains beneath rocks (Yair & de Ploey, 1979) makes the available moisture harder to extract, but there is less evaporation loss. Because of larger root volume and reduced osmotic potential, the perennial groups may extract this moisture more successfully than therophytes. Thus, through competition for water and through physical limitation, the therophytes may be limited to the shallow soil strips in this unit.

Geophytes generally are the most mesic group of the four discussed here, belonging primarily to the Mediterranean component of the flora (Zohary, 1962). Most desert geophyte species are restricted to relatively mesic locations, such as Units B and C as seen in Table 1. This particular aspect of vegetation pattern also affects other ecosystem functions. In this area, porcupines (*Hystrix indica*) are a major herbivore predator of geophytes (Yair & Lavee, 1981; Yair & Shachak, 1982). Their activity is therefore concentrated in those relatively mesic areas of Units B and C where geophytes are found. Porcupine digging loosens soil, which increases erosion from these areas but also enhances water infiltration. This in turn maintains the relatively high moisture and low salinity which the geophytes require. Hence a self-reinforcing mechanism is generated, which helps to maintain the existing vegetation pattern (Yair & Lavee, 1981; Yair & Shachak, 1982).

Transition zones

Our original hypothesis about relationships between the plant community and its environment were only partly substantiated. Surface structure, the ratio of rock to soil in particular, seems the most important factor determining the spatial pattern of the vegetation. However, the correlation is far from perfect.

The transition in vegetation from the topmost

Unit A to the next structural unit downslope, B, is quite sharp (Fig. 2A). (Note that there is no overlap between samples from Units A and B in the two dimensional plot.) However, the change in vegetation composition from Unit B through Units C and D is continuous, as demonstrated in Figure 2B.

These patterns may result from the amount and importance of runoff input from the upslope unit to adjoining downslope areas. Unit A, with a slow $SA_{\text{rock}}/SA_{\text{soil}}$ ratio, is a net 'holder', i.e. generates little runoff, while Unit B is a net 'mover', with high runoff generation (Pomeroy, 1974; Shachak, 1983). Input of the small amount of runoff from Unit A to Unit B probably has little impact on growth conditions, since Unit B is the most mesic unit in any case. The runoff input from Unit B to the xeric Units C and D, on the other hand, is high (Yair *et al.*, 1978, 1980) and probably has a strong influence on the vegetation. In other words, runoff from a xeric, therefore saline unit (holder) to a more mesic, less saline unit (mover) has little influence and hence the transition between the two units will be sharp and the units functionally independent. Runoff input from a more mesic unit to a relatively xeric unit, in contrast, raises the moisture availability in the lower unit to a degree proportionate to the amount of runoff received. This runoff will be distributed in the lower unit in the form of a moisture gradient (Fig. 4A) along which vegetation change will be gradual.

In conclusion, pattern analysis has effectively demonstrated relationships between spatial patterns of vegetation, surface structure, and movements of soil and water in this Negev Desert watershed. The pattern analysis approach developed by Whittaker to describe vegetation has proven effective in describing these relationships, and has been useful as a heuristic method for the detection of correlations upon which future research in this watershed project can be based. Conversely, the necessity of obtaining environmental information for the interpretation of vegetational pattern analysis is equally clear.

References

- Arkin, Y. & Braun, M., 1965. Type sections of Upper Cretaceous formations in the northern Negev. Geol. Surv., Stratigraphic Section 2A. Jerusalem.

- Danin, A., Orshan, G. & Zohary, M., 1975. The vegetation of the northern Negev and the Judean Desert of Israel. *Isr. J. Bot.* 24: 118–172.
- Ellner, S. & Shmida, A., 1982. Why are adaptations for long range seed dispersal rare in desert plants? *Oecologia* 51: 133–134.
- Evenari, M., Shanan, L. & Tadmor, N., 1971. The Negev: the challenge of a desert. Harvard University Press, Cambridge, Massachusetts. 343 pp.
- Friedman, J., Orshan, G. & Ziger-Cfir, Y., 1977. Suppression of annuals by *Artemisia herba-alba* in the Negev Desert of Israel. *J. Ecol.* 65: 413–426.
- Gauch, H. G., 1982. *Multivariate Analysis in Community Ecology*. Cambridge Univ. Press, Cambridge. 298 pp.
- Gauch, H. G. & Whittaker, R. H., 1972. Coenocline simulation. *Ecology* 53: 446–451.
- Gauch, H. G., Whittaker, R. H. & Wentworth, T. R., 1977. A comparative study of reciprocal averaging and other ordination techniques. *J. Ecol.* 65: 157–174.
- Greig-Smith, P., 1964. *Quantitative Plant Ecology*, 2nd ed. Butterworths, London. 256 pp.
- Hill, M. O., 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.* 61: 237–249.
- Hill, M. O., 1974. Correspondence analysis: a neglected multivariate method. *J. Roy. Stat. Soc. Ser. C* 23: 240–254.
- Hill, M. O., 1979. DECORANA – A FORTRAN program for detrended correspondence analysis and reciprocal averaging. Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853.
- Hill, M. O. & Gauch, H. G., 1980. Detrended correspondence analysis, an improved ordination technique. *Vegetatio* 42: 47–58.
- Kershaw, K. A., 1957. The use of cover and frequency in the detection of pattern in plant communities. *Ecology* 38: 291–299.
- Loria, M. & Noy-Meir, I., 1979. Dynamics of some annual populations in a desert loess plain. *Isr. J. Bot.* 28: 211–225.
- Olsvig(-Whittaker), L., 1979. Pattern and diversity analysis of the irradiated oak-pine forest, Brookhaven, New York. *Vegetatio* 40: 67–78.
- Pielou, E. C., 1974. *Population and Community Ecology: principles and methods*. Gordon & Breach, New York. 424 pp.
- Pomeroy, L. R., 1974. *Cyclings of Essential Elements*. Dowden, Hutchinson & Ross, Stroudsburg, Pennsylvania. 373 pp.
- Shachak, M., 1983. Some aspects of the relationship between experimental scale and ecosystem properties. Submitted to *Oecologia*.
- Shmida, A. & Whittaker, R. H., 1981. Pattern and biological microsite effects in two shrub communities, southern California. *Ecology* 62: 234–251.
- Whittaker, R. H., 1960. Vegetation of the Siskiyou Mountains, Oregon and California. *Ecol. Monogr.* 30: 279–338.
- Whittaker, R. H., 1972. Evolution and measurement of species diversity. *Taxon* 21: 213–251.
- Whittaker, R. H., 1975. *Communities and Ecosystems*, 2nd ed. Macmillan, New York. 385 pp.
- Whittaker, R. H., 1977. Evolution of species diversity in land communities. *Evol. Biol.* 10: 1–67.
- Whittaker, R. H., Gilbert, L. E. & Connell, J. H., 1979. Analysis of two-phase pattern in a mesquite grassland, Texas. *J. Ecol.* 67: 935–952.
- Whittaker, R. H. & Naveh, Z., 1979. Analysis of two phase patterns. In: Patil, G. P. & Rosenzweig, M. L. (eds.), *Contemporary Quantitative Ecology and Related Ecometrics*, pp. 157–165. *Stat. Ecol. Ser. 12*. International Cooperative Publishing House, Burtonsville, Maryland.
- Whittaker, R. H., Niering, W. A. & Crisp, M. D., 1979. Structure, pattern, and diversity of a mallee community in New South Wales. *Vegetatio* 39: 65–76.
- Wilson, M. V. & Mohler, C. L., 1982. GRADBETA – A FORTRAN program for measuring compositional change along gradients. Section of Ecology and Systematics, Cornell University, Ithaca, New York 14853.
- Wilson, M. W. & Mohler, C. L., 1983. Measuring compositional change along gradients. *Vegetatio* (in press).
- Yaalon, D. H. & Dan, J., 1974. Accumulation of loess derived deposits in the semidesert and desert fringe areas of Israel. *Zeitschr. für Geom. N. P.* 20: 91–105.
- Yair, A. & Danin, A., 1980. Spatial variation in vegetation as related to the soil moisture regime over an arid limestone hillside, northern Negev, Israel. *Oecologia* 47: 83–88.
- Yair, A. & de Ploey, J., 1979. Field observations and laboratory experiments concerning the creep process of rock blocks in an arid environment. *Catena* 6: 245–258.
- Yair, A. & Lavee, H., 1981. An investigation of source areas of sediment and sediment transport by overland flow along arid hillslopes. In: *Proc. Florence Symp. Erosion and Sediment Transport Measurement*, pp. 433–446. IAHS Publ. 133.
- Yair, A. & Shachak, M., 1982. A case study of energy, water, and soil flow chains in an arid ecosystem. *Oecologia* (in press).
- Yair, A., Sharon, D. & Lavee, H., 1978. An instrumented watershed for the study of partial area contribution of runoff in an arid area. *Zeitschr. für Geom. Suppl. B* 29: 71–82.
- Yair, A., Sharon, D. & Lavee, H., 1980. Trends in runoff and erosion processes over an arid limestone hillside, northern Negev, Israel. *Hydrol. Sci. Bull.* 25: 243–255.
- Zohary, M., 1962. *Plant Life of Palestine*. Ronald Press, New York. 262 pp.