

Porcupine disturbances and vegetation pattern along a resource gradient in a desert

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Received January 9, 1991 / Accepted in revised form May 17, 1991

Summary. In the Negev Desert, Israel, the Indian crested porcupine, *Hystrix indica*, digs similar sized, discrete, elongated pits ($257 \pm 21.3 \text{ cm}^3$; $n=144$) while foraging for below-ground plant storage organs. In these digs, soil moisture content is higher than in the surrounding soil matrix. The digs disturb population and community structure due to porcupine consumption or damage of 18 species of plants, and repopulation by 55 plant species. Over the past 14 years we have studied dig dynamics on a rocky hillslope with three distinct habitats as regards soil moisture content. Midslope soil moisture is the highest, decreasing towards upper and lower slope. We have counted a total of 6,609 digs in the area: 2141 on the upper, 3211 in the middle and 1257 on the lower part of the slope. The number of digs at midslope is significantly higher than on the other parts of the slope (ANOVA; $P < 0.0001$). There is a significant ($P < 0.05$) correlation between the mean number of porcupine digs and the cumulative rainfall amount for the 2 years prior to dig formation. To study plant repopulation in digs, all plants in 144 digs along the slope and from equal sized plots in the undisturbed soil matrix were collected. In all, 288 samples with 20 584 plants were collected, 2042 from the matrix and 18,542 from digs. Of the 55 species, we focused on the abundance patterns of *Filago desertorum*, *Picris cyanocarpa* and *Bromus rubens*, which made up 69.5% of all the individuals in the digs and 68.3% in the matrix. Our results showed that all three species increased in abundance in the digs as compared to the matrix. *F. desertorum* density increased by a factor of 2.9, *P. cyanocarpa* by 9.5 and *B. rubens* by 12.0. There were species-specific responses in abundance to the location of the digs along the moisture gradient. The only species whose abundance responded to the moisture gradient was *F. desertorum*. *P. cyanocarpa* demonstrated peak abundance in the location with the poorest moisture regime, while *B. rubens* showed peak abundance at the

intermediate part of the moisture gradient. We suggest a scheme for integrating the increase in density and the species-specific responses to the digs along a water gradient based on R.H. Whittaker's view of individual species abundances along an environmental gradient.

Key words: Annual plants – Disturbance – Negev Desert – Porcupine – Resource shift

Disturbances in the natural environment affect the dynamics of populations, communities and ecosystems. They are important and widespread phenomena in nature (e.g., Sousa 1984; Pickett and White 1985). Discreteness and disruption are concepts used in defining disturbances. Disruption may be abiotic, by "Changing resources, substrate availability or physical environment" (White and Pickett 1985) or biotic by the "killing, displacement or damaging of individuals that... creates an opportunity for new individuals to become established" (Sousa 1984). A wide variety of biotic and abiotic disruptions have been studied and reported (White 1979). However, a framework that integrates diverse ecological processes defined as disturbances is lacking (Pickett and White 1985; Turner et al. 1989). The difficulty in erecting a simple but effective theoretical framework results from several factors:

1. Disturbances are highly variable in size, uncontrolled and capricious (O'Neill et al. 1986; Shugart and West 1981).
2. Disturbances are usually controlled by factors other than those controlling repopulation processes. For example, tree gaps may be caused by wind, while repopulation is controlled by light intensity (White 1979; Lieberman et al. 1989; Veblen 1989; Whitmore 1989).
3. Disturbances are variable in size and location and organismal responses are species- and site-specific (Veblen 1989; Lieberman et al. 1989).

In the Negev Desert, Israel, the Indian crested porcupine, *Hystrix indica*, digs similar sized, discrete, elon-

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gated pits ($\sim 300 \text{ cm}^2$) while foraging for below-ground plant storage organs (Yair and Rutin 1981; Gutterman 1982, 1987). In these pits, soil moisture content is higher than in the surrounding soil matrix due to runoff water accumulation. Thus, porcupine disturbances alter the water regime, a dominant factor in the desert (Yair and Rutin 1981; Gutterman 1988). In addition, there is a disruption of population and community structure as a result of the consumption or damage of 18 species of geophytes and hemicryptophytes (Gutterman 1987, 1988). The porcupine disturbance thereby creates the opportunity for colonization by many species of plants (Gutterman and Herr 1981; Gutterman 1988, 1989). We supposed that since porcupine disturbances are similar in size and are controlled by a biotic factor, foraging behavior (Yair and Shachak 1982), they are less capricious than disturbances such as tree gaps and fires that are controlled largely by abiotic factors. In addition, we assume that repopulation of the digs by annual plants is controlled mainly by one factor, water availability (Gutterman 1987). Thus, we should be able to determine spatial and temporal patterns in porcupine digs and plant repopulation along a water gradient. We postulated that the intensity of porcupine disturbances and abundance of plant species that respond to pits should differ in relation to water availability. However, the disturbances and species responses should exhibit a general pattern along a soil moisture gradient.

To test our assumption, we studied porcupine disturbances and their repopulation by annual plants along a slope exhibiting a soil moisture gradient. In this study, we present a case study of the relationship among porcupine disturbances, soil moisture content and the abundance of annual plants. We then suggest a scheme whereby disturbance is viewed as producing a shift in resource availability along a gradient. Our generalization is based on the view of Whittaker (1956; 1967) that there are species-specific responses in abundance along an environmental gradient. The responses are such that at a low level of resources, an increase in resources may bring about an increase in abundance. However, at high resources, biotic factors such as new competitors or predators may overcome the positive effect of the resources and the net response will be a decrease in abundance.

Study area

Location and habitats

The study area is located at Sede Boqer in the Central Negev Highlands (Fig. 1). The climate is that of a temperate desert, i.e., cool winter and hot summer months (Evenari et al. 1983). Annual rainfall is highly variable, with a mean of 93 mm, minimum of 25 mm and maximum of 167 mm over the past 35 years.

In relation to porcupine activity on the slope, three distinct habitats can be defined by geological formations and plant associations. They are Netsar, Shivta and Drorim which are located on the upper, middle and lower parts of the slope, respectively. The upper habitat

is of chalky limestone with very patchy and shallow soil. The characteristic plant association, *Hammadetum scopariae lepidosum*, covers 5–8% of the area. The middle habitat is of massive limestone with stepped topography. Soil cover is limited to soil strips at the base of rock terraces with very extensive bare bedrock areas. The plant association is *Vartemia iphionides-Origanum dayi* and covers 10–15% of the area. In the lower habitat, the soil cover is extensive, thick and stony. *Artemesia herba alba - Gymnocarpus decander* define the plant community and cover 5–10% of the area (Danin 1972).

Due to their surface properties, the three habitats differ in their soil moisture content. This creates a soil moisture gradient. Midslope soil moisture is the highest, decreasing toward the upper and lower slopes (Yair and Lavee 1982, 1985).

The organisms

In this study we concentrate on four species: one animal, *Hystrix indica*, and three annual plant species, *Bromus rubens*, *Picris cyanocarpa*, and *Filago desertorum*.

Hystrix indica. This porcupine is widely distributed in South Central Asia and is found throughout Israel in mediterranean as well as desert habitats. *H. indica* is probably the only large mammal (body mass $\sim 14 \text{ kg}$), in the Negev that feeds principally on below-ground plant storage organs, tubers, rhizomes corms and bulbs (Alkon and Saltz 1986; Gutterman 1982, 1987). The animals are nocturnal, emerging from their dens at night and moving $2.8 \pm 0.7 \text{ km}$ nightly while foraging (Saltz and Alkon 1989). The most commonly consumed below-ground storage organs on the slope are: *Erodium hirtum*, *Colchicum tunicatum* and *Bellevalia desertorum* (Gutterman 1982) which are buried at a depth of 4–12 cm. In order to reach the below-ground storage organs, *H. indica* disturb the soil by digging elongated depressions ($\sim 12 \times 5 \text{ cm}$ and 5 cm deep) (Yair and Rutin 1981).

Bromus rubens L. This plant is a winter annual which inhabits the Saharo-Arabian, Irano-Turanian and Mediterranean regions of Israel. *B. rubens* germinates during winter rains, reaching a height of 10–30 cm. It flowers during April and May, and scatters its dispersal units during June and July. It is common throughout the Negev (Feinbrun-Dothan 1978).

Picris cyanocarpa Boiss. This plant is a winter annual (13–20 cm) inhabiting the east Saharo-Arabian region of Israel, mainly located in wadis in the central and southern Negev. This plant is rare in most habitats. Germination is during winter and flowering is in March–April (Feinbrun-Dothan 1978).

Filago desertorum Pomel. This is a small winter annual, 5–8 cm, which inhabits the Saharo-Arabian and Western Irano-Turanian regions of Israel. *F. desertorum* is a common winter annual in the Negev, which germinates

during winter and flowers during February–April (Feinbrun-Dothan 1978).

Methods

Patch formation

Once a year, before the rainy season, we counted the number of porcupine digs on a rocky slope ($\sim 11000 \text{ m}^2$) in the Negev Desert, Israel (Fig. 1). We counted digs for 14 years (1973–1986), at three locations, the upper, middle and lower parts of the slope. The best soil moisture regime is at midslope, decreasing towards the upper and lower slopes. Altogether, we counted the digs at ten plots. Each plot is a lateral strip parallel to the rock strata, from the water divide to the channel (Fig. 1). This method was chosen in order to minimize soil moisture variation at a given plot (Yair and Lavee 1982, 1985). At the upper slope four plots with areas of 348, 456, 411 and 433 m^2 were sampled. At midslope, three plots of 520, 528 and 396 m^2 were sampled. At the lower slope three plots of 472, 524, and 564 m^2 were sampled. All the data were scaled to digs/100 m^2 .

Plant repopulation

In order to determine the significance of the digs for plant repopulation, we collected the plants from digs and undisturbed soil matrix

at the same ten plots where we noted patch formation. In the spring of 1989 we collected all the plants from 108 samples (54 digs and 54 matrix) on the upper slope, and 90 samples (45 pits and 45 matrix) from the middle and lower slopes. We chose digs with more than 50% annual-plant cover indicating high population size (Guterman et al. 1990). We collected all the plants from a dig and from a nearby undisturbed area of the same size and shape as the pit. We identified all the species and calculated the abundance of each species per sample.

Results

Patch formation

Over the past 14 years we have counted a total of 6609 digs in the area; 2141 on the upper, 3211 in the middle and 1257 on the lower part of the slope. We found no significant differences in patch size along the slope (ANOVA; $P > 0.2$). The average patch size is $257 \pm 21.3 \text{ cm}^3$. There are significant differences in the density of digs among locations and years (Two-way

Table 1. Average density of porcupine disturbances (digs/100 m^2) at three locations on a hilly slope in the Negev Desert. $n = 14$ years

Year	Location		
	Upper	Middle	Lower
1973	20.5	34.3	14.3
1974	2.3	4.8	3.4
1975	10.2	24.3	10.1
1976	7.2	18.0	5.6
1977	1.5	1.8	1.4
1978	2.5	2.6	2.4
1979	4.2	4.7	4.9
1980	17.0	22.4	8.1
1981	11.7	14.4	9.2
1982	12.4	19.7	4.8
1983	19.7	47.9	12.7
1984	9.9	16.5	2.6
1985	0.5	5.0	0.3
1986	5.3	5.2	1.5

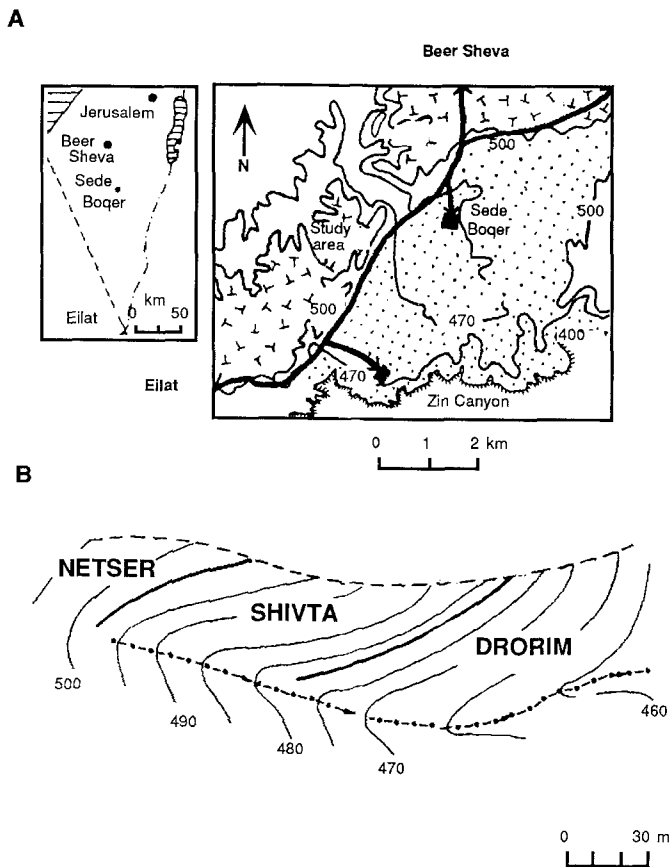


Fig. 1A, B. The study area. **A** Location of Sede Boqer. — paved road — rocky area — loessic plain — contour line elevation (m). **B** Topography of the study site indicating the three habitats: Netser, Shivta and Drorim (upper, middle and lower slope, respectively). — divide line — channel — contour line elevation (m) — boundary between habitats

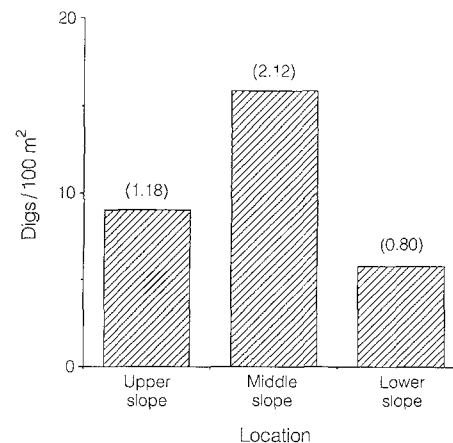


Fig. 2. Spatial distribution of porcupine digs along the rocky slope. Digs are the average for 14 years (1973–1986). Number in parenthesis is SD

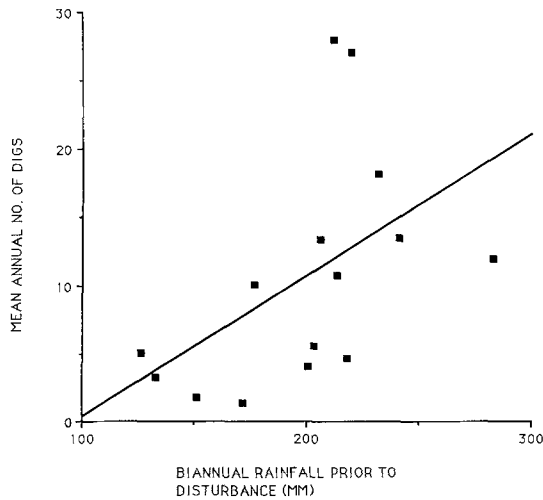


Fig. 3. Relationship between rainfall in previous 2 years and number of porcupine digs. $y = -9.97 + 0.10x$; $R = 0.51$; $P < 0.05$

ANOVA; $P < 0.0001$). In spite of the variation in densities of digs from year to year (Table 1), a general pattern in space emerged (Fig. 2). The number of digs in the middle part of the slope is significantly higher than on the other parts of the slope (ANOVA; $P < 0.0001$). This pattern was noted almost every year (Table 1). As for the temporal pattern, we found a significant correlation between the rainfall in the 2 years prior to the disturbance and the annual number of digs (Fig. 3). This may be explained by the reestablishment and growth characteristics of *Erodium hirtum* which is the main geophyte consumed by the porcupine on the study slope (Gutterman 1982; Boeken 1986; Boeken and Gutterman 1989).

Plant repopulation

In the 288 samples collected, we noted 20 584 plants. In the matrix samples we found 2042 plants while in the digs we found 18 542 individuals. Three species, *Filago desertorum*, *Picris cyanocarpa*, and *Bromus rubens* comprised 69.4% of all individuals (69.5% in the digs and 68.3% in the matrix). In this paper, we focus on the abundance patterns of these three species in disturbed and undisturbed areas along the slope.

Filago desertorum. Figure 4a shows significant increases in *F. desertorum* densities in the digs compared to the matrix in all three locations along the slope (Two-way ANOVA; $P < 0.002$ for locations as well as for the digs). As to the pattern along the slope, differences in densities of *F. desertorum* in the matrix are not significant ($P = 0.27$). However, *F. desertorum* density was significantly higher in the digs at midslope than in those at the upper or lower slope ($P < 0.002$).

Picris cyanocarpa. As shown in Fig. 4b, *P. cyanocarpa* was found at significantly higher densities in the digs compared to the matrix at all three locations along the

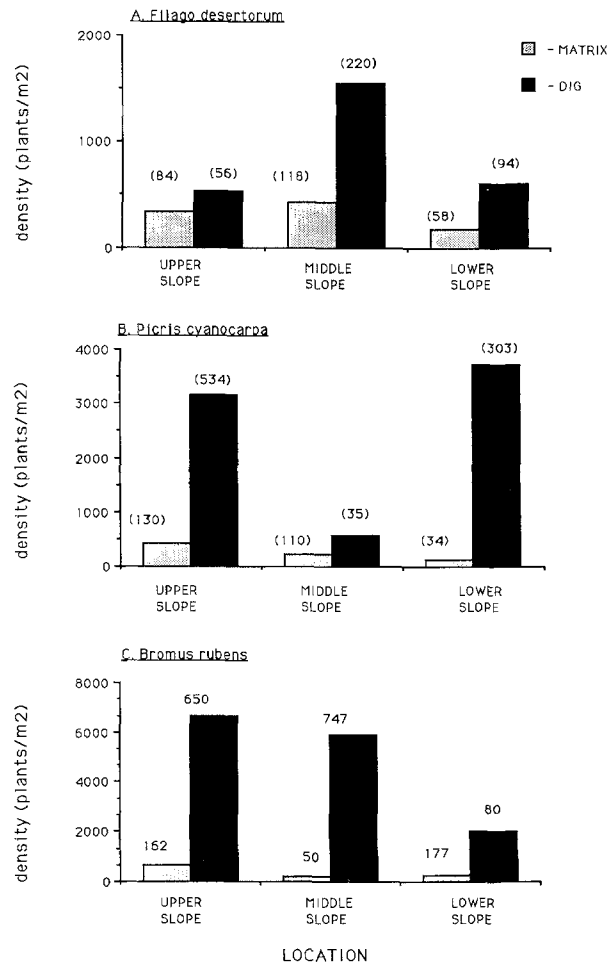


Fig. 4. Spatial distribution of **A** *Filago desertorum*, **B** *Picris cyanocarpa* and **C** *Bromus rubens* in 144 porcupine digs and 144 matrix samples along a slope. Number in parenthesis is SD

slope (Two-way ANOVA; $P < 0.01$ for locations and digs). As with *F. desertorum*, the densities in the matrix along the slope were similar ($P = 0.24$). However, in contrast to *F. desertorum*, in the digs *P. cyanocarpa* density was lowest at midslope as compared to upper and lower slope ($P < 0.001$).

Bromus rubens. As shown in Fig. 4c, *B. rubens* was also found at significantly higher densities in the digs as compared to the matrix at all three locations along the slope (Two-way ANOVA; $P < 0.01$ for locations and digs). *B. rubens* differed from the other species in that the densities in the matrix along the slope showed significant differences between the upper and middle slope ($P < 0.05$). In the digs, the significant differences are between the lower slope and the other parts of the slope ($P < 0.05$ in both cases).

Discussion

Patterning of patch formation

Temporal. Pits are formed by porcupines digging in search of food in the form of below ground storage

organs. Year-specific patch abundance may be related to rainfall. In arid lands, temporal changes in primary production are related to rainfall amount (e.g. Rosenzweig 1968; Schmida et al. 1986). If we assume that porcupine foraging intensity is related to plant production, then the density of patch formation through time should respond to rainfall. We found a significant correlation between the mean number of porcupine digs and the cumulative rainfall amount for the 2 years prior to patch formation (Fig. 3). Thus we can assume that temporal variation in the density of digs is indirectly controlled by rainfall through its effect on plant production.

Spatial. The high density of digs at midslope cannot be explained by the rainfall pattern since rainfall is similar at the three locations. However, the differences in density along the slope may be understood by relating the dig abundances to the results of hydrological and botanical studies carried out in the area.

Yair and Lavee (1982, 1985) and Tenbergen (1986) studied patterns of soil moisture content and above-ground phytomass along slopes in and near the study area. The spatial distribution of soil moisture and plant phytomass are similar to the distribution pattern of porcupine digs. There are higher soil moisture content and phytomass at midslope than on upper or lower slope. Due to the apparent similarity in the spatial pattern of soil moisture content, phytomass distribution and patch density, we propose that soil moisture controls phytomass productivity which affects porcupine foraging activity that produces the observed pit pattern.

Hydrological investigations (Yair and Lavee 1982, 1985) in the study area showed that soil moisture along the slope is controlled by direct rainfall and surface runoff water. The main differences in soil moisture content along the slope are explained by differences in runoff infiltration at any given location. Gravity and the distribution of rocks and soil along the slope control the generation, redistribution and infiltration of runoff along the slope creating the pattern of soil moisture content (Yair and Lavee 1982). Soil moisture increases from the top of the slope to about midslope and decreases from there to the slope base. This is the same pattern as found for patch formation (Fig. 2). Thus, the ultimate factor controlling the pattern of patch formation along the slope is the variability in the amount of runoff infiltration among upper, middle and lower slope.

Repopulation pattern

A topic that has received little attention in the literature is the variation in responses of an individual species to disturbances along an environmental gradient (Veblen 1989). We discuss the variable repopulation responses of three annual species, *F. desertorum*, *P. cyanocarpa* and *B. rubens*, to porcupine disturbances along a soil moisture gradient. Our results showed that all three species increased in abundance in the digs as compared to the undisturbed soil matrix. There were species-specific responses in abundance to the location of the digs along

the moisture gradient. The only species whose abundance responded to the moisture gradient was *F. desertorum*. *P. cyanocarpa* demonstrated peak abundance in the location with the poorest moisture regime, while *B. rubens* showed peak abundance at the intermediate part of the moisture gradient. There are two questions concerning repopulation. One refers to the changes in plant abundance in the digs compared to the matrix. The other question refers to the effect of the patch location along the water gradient on species abundance.

We suggest a scheme for integrating the increase in density and the species-specific responses to disturbances along a resource gradient. Our explanation is based on the view of Whittaker (1956, 1967) concerning the properties of changes in abundance of a species along an environmental gradient. Whittaker suggested that species abundance along a gradient is in the form of a bell-shaped curve, which is species-specific. The bell-shaped curve results from the pattern that at low levels of resources, an increase in resources may bring about an increase in abundance. However, at high levels of resources, biotic factors such as new competitors and/or predators may overcome the positive effect of the resources and the net response will be a decrease in abundance.

By incorporation of disturbance into Whittaker's scheme, the changes in species abundance due to disturbance may be viewed as a shift in the species position along the resource gradient (Fig. 5). The response of the individual species to disturbance is dependent on: the initial resource base in the matrix (R_1), the changes in the resource due to disturbance (D_1 , D_2 and D_3), and the species-specific abundance curve. The response in abundance differs depending on whether the initial resource level in the matrix is related to the ascending or descending part of the curve. If the initial resource amount on the matrix is low (R_1) then, in accordance with the changes in the resource caused by the disturbance and the biotic responses, the species abundance may increase or decrease. At low changes (D_1), abundance will increase (A_2). At an intermediate level of resources (R_3) the species abundance should reach its maximum (A_3). At high levels of resource (R_4) the abundance may decrease

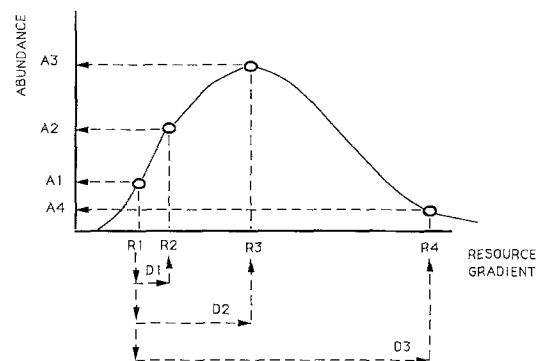


Fig. 5. The relationship among disturbance, resources and species abundance. *A*, Individual species abundance; *D*, Disturbance in terms of shift in resource amount; *R* Resource amount. (See text for explanation)

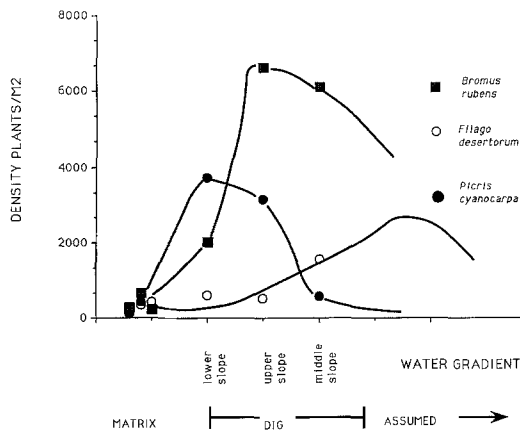


Fig. 6. The supposed species-specific responses of plants to porcupine disturbances along a moisture gradient (see text for further explanation)

(A4). This idea is in accordance with hypotheses proposed by Peet et al. (1983), Connell (1978) and Grime (1979) on the relationship between species diversity and disturbance. The hypotheses suggest that species richness will be greatest in communities experiencing some intermediate level of disturbance (Pickett and White 1985). Our suggestion is that the same response to some intermediate level of disturbance should hold true for species abundance (Fig. 6).

The pattern that we suggest in Fig. 6 is in accordance with the geographic range of the three species along the rainfall gradient. On a geographical scale, the distribution of the three species is on a gradient from 50–600 mm average annual rainfall (Zohary 1962). *P. cyanocarpa*, which is naturally found in its greatest abundance in the more arid zones, has its peak density in the digs at the driest location. In contrast, *B. rubens*, a mediterranean species, whose peak abundance is in the wettest zone of the geographical gradient had its highest response in the digs of the wetter locations of the slope. *F. desertorum*, whose peak geographic abundance is in the Irano-Turanian zone, which is intermediate in reference to the geographical water gradient, responded the least to the increase in water amount in the digs.

Disturbances of the same size and location differ in their biological effects (abundance) on different species. Therefore, we suggest that when studying disturbances we must look at the intensity of the shift in resources caused by the disturbance and the individual species responses in abundance. This approach was recently suggested by Lieberman et al. (1989) and Canham (1989) in the studies of disturbances in the form of tree gaps in the forest canopy. Lieberman et al. (1989) argued that studies should be shifted from the comparison of gaps with non-gaps to the continuum of light levels. This approach is similar to the one we used in interpreting species responses to porcupine disturbances. We view species responses to porcupine disturbances not as matrix versus dig but as continuous changes on a water gradient. The intensity of the shift in water resources brought about different species responses which could be interpreted in accordance to Whittaker's classic work (1956).

Acknowledgements. We wish to thank Steward T.A. Pickett for commenting on our manuscript and Sonia Rozin for her help. This is publication no. 117 from The Mitrani Center for Desert Ecology and no. 78 from the Unit for Ecophysiology and Introduction of Desert Plants.

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