

11. Short-term water and energy flow in arid ecosystems

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Introduction

In desert ecosystems precipitation is low and largely unpredictable in its spatial and temporal distribution (Noy-Meir, 1973). The evaporation potential is high. Water redistribution on the surface of the landscape after a precipitation event involves complicated processes (infiltration, run-off, storage, drainage). Each arid landform has different surface and soil characteristics which affects water availability, hence the type of plant community occupying it. The dominant animal species of each plant community are fairly distinctive with respect to their responses to available water and plant biomass availability.

The objective of this chapter is to discuss the dynamic behavior of the biotic components of arid ecosystems in relation to water and energy flow between and within seasons. The growth responses of the different plant species occupying adjacent ecosystems in a watershed will be related to water availability and to heat energy levels. Growth and behavioral responses of groups of animals with contrasting adaptations to changing conditions of food and water availability will be discussed. Plant and animal litter redistribution and decomposition patterns will be discussed with respect to patterns of energy flow and climatic variation. Finally, general conclusions about desert ecosystem dynamics with respect to short-term water and energy flow will be stated.

Approach and methods

The major emphasis in this chapter will be on data and discussion of short-term water and energy flow in a northern Chihuahuan Desert watershed under study on the Jornada Experiment Station of New Mexico State University, which is 40 km north-northeast of Las Cruces, New Mexico. This watershed and the data it has produced on environmental driving forces (precipitation, soil water, radiant energy, and temperature) and biotic responses (plant productivity, animal population changes and microbial activity) for time intervals of weeks during the growing season are most familiar to the authors. However, data from other arid lands in North America (e.g. Wallace & Romney, 1972; Romney *et al.*, 1973) and other parts of the world (e.g. Evenari, Shannan & Tadmor, 1971) will be used in a comparative way and

Ecosystem dynamics

will be needed to draw general conclusions about short time-scale ecosystem dynamics of water and energy flow in deserts.

Water availability in the soil will be indicated by the level of water stored by soil volume. Plant water content will be an important variable for the animals. Energy in desert ecosystems will be considered in two basic ways: first, the radiant energy available and its capture and conversion to chemical or potential energy by the plants; second, the radiant energy which is absorbed, reflected, and conducted by the soil and air and converted to heat energy. The flow of chemical energy to animals and litter will be of considerable importance to the system. The importance of temperature effects on the dynamics of the ecosystem can be considered as it interacts strongly with water flow.

Results and discussion

Water dynamics and growth responses of producers

A Chihuahuan Desert system

To illustrate the dynamics of water and the response of plants to water in the different ecosystems of a Chihuahuan desert watershed, we will show data for precipitation, soil water storage, plant response and temperature. Precipitation totals for periods of consecutive days of precipitation and the water stored in the soil profile to a given depth will be shown. The changes in energy content (calories) of the leaves and fruits produced by the plants through the different seasons will be given. Minimum daily air temperatures are used as an expression of the energy (heat) budget of the system through time.

Precipitation was recorded using a weighing bucket rain gauge. Soil moisture storage was monitored using electrical resistant gypsum blocks and the bulk densities of the soils. Air temperatures were measured using hygrothermographs housed in standard weather instrument shelters. Data from two weather stations will be used, one located on the alluvial fans and the other in the basin.

Productivity estimates were based on harvest methods (Milner & Hughes, 1968) and dimensional analysis (Newbould, 1967). Details of methodology of measuring productivity of species is beyond the scope here, but are described in Ludwig, Reynolds & Whitson (1975) and Whitford (1974).

Alluvial fans (bajadas)

The upper alluvial fans are characterized by *Larrea tridentata*. The precipitation events are highly seasonal (Fig. 11.1). Storage of water in the profile on these alluvial fans follows the precipitation patterns. Response of *L. tridentata* follows the water storage patterns. When minimum air temperatures drop

Short-term water and energy flow

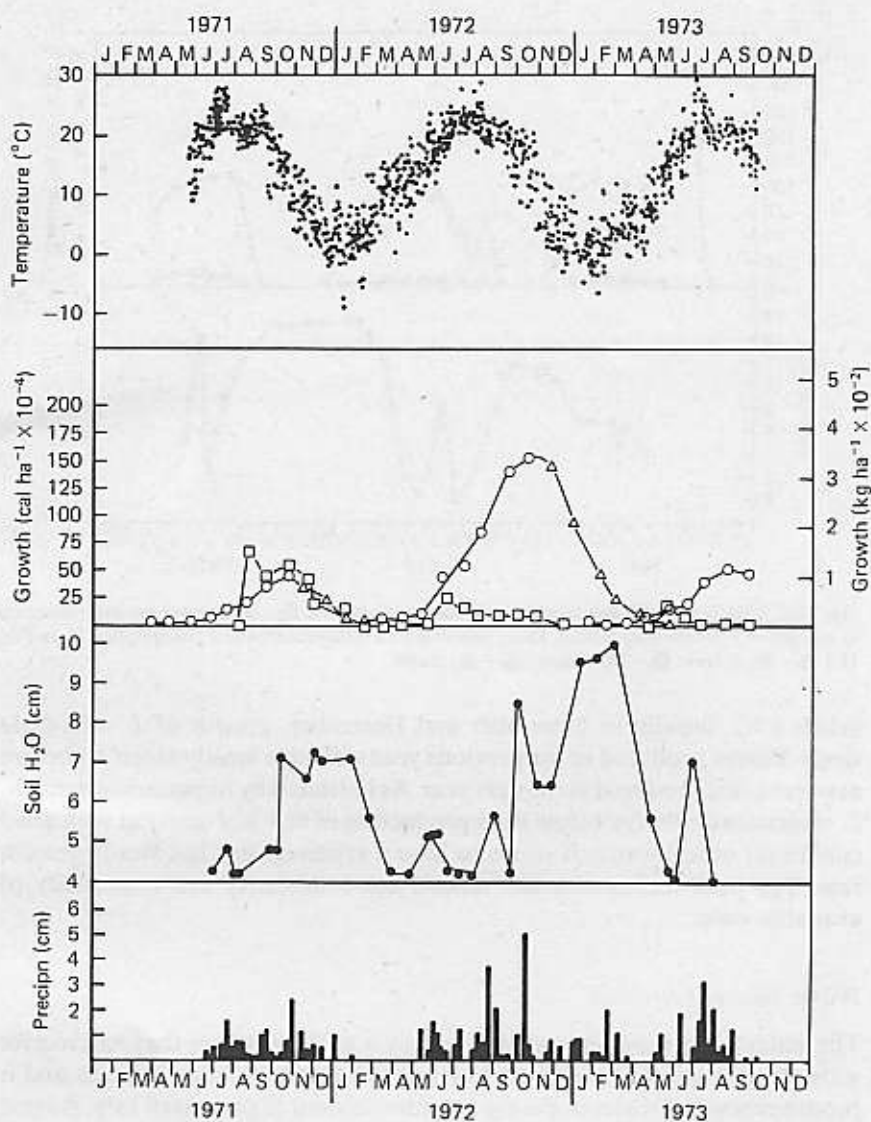


Fig. 11.1. Chihuahuan Desert alluvial fans (bajadas). Precipitation, soil water storage, growth responses of creosotebush (*Larrea tridentata*) and daily minimum air temperatures for 1971-73. \triangle - \triangle , Old leaves; \circ - \circ , new leaves; \square - \square , fruits.

Ecosystem dynamics

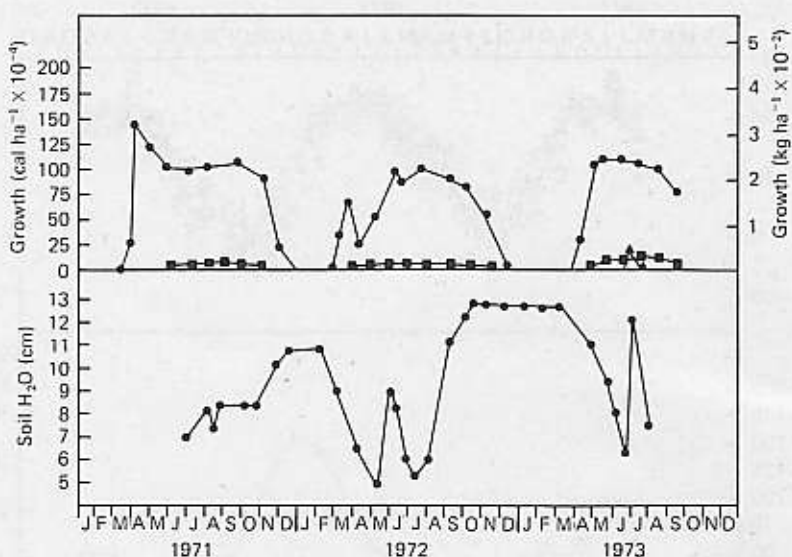


Fig. 11.2. Chihuahuan Desert larger water courses (arroyos). Soil and water growth responses of mesquite (*Prosopis glandulosa*). Daily minimum air temperatures and precipitation as in Fig. 11.1 ●—●, leaves; ■—■, shoots; ▲—▲, fruits.

below 0 °C, usually in November and December, growth of *L. tridentata* stops. Leaves produced in the previous year will have mostly fallen off before new leaves are produced in the next year. As indicated by its pattern of growth, *L. tridentata* is relatively slow in its production of new leaf material with good conditions of soil water. It seems to have a relatively low but steady growth rate. The peak leaf production reflects the consistency and seasonality of available water.

Water courses (arroyos)

The water courses on alluvial fans occupy a position where they will receive water from run-off. *Yucca elata* occurs in the smaller water courses and it produces new leaf material during the summer rainfall periods of July, August and September (Smith & Ludwig, 1976). Reproduction is highly variable. When production of fruits is high, production of new leaves remains very low. Thus *Y. elata* shows a different strategy in water utilization and energy flow relative to new leaf production and reproduction than *Larrea tridentata*.

In the large arroyos, the soils are deeper with the profile extending to an average depth of 120 cm. Storage of water exceeded 12 cm during many of the seasons (Fig. 11.2). The growth data for *Prosopis glandulosa*, mesquite, shows that the leaf biomass produced at old nodes on old stems of this species

Short-term water and energy flow

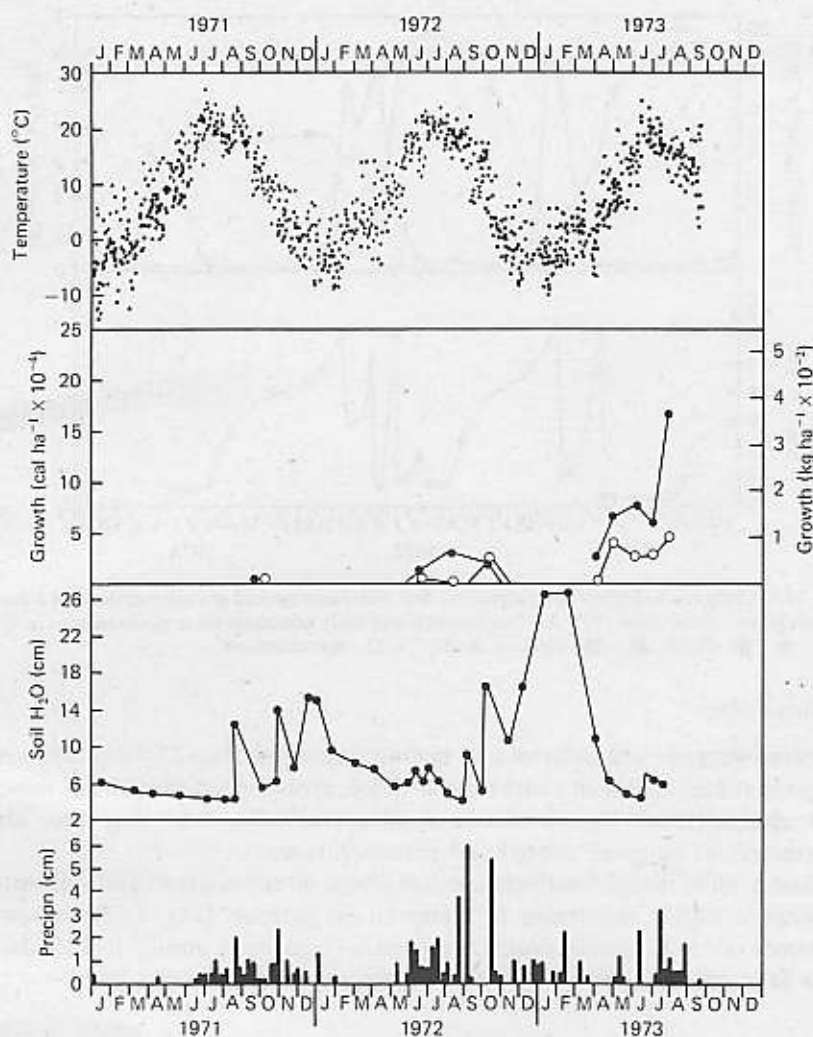


Fig. 11.3. Chihuahuan Desert alluvial flats. Precipitation, soil water storage and growth responses of small annual and perennial forbs, and daily minimum air temperatures for 1971–73. ●—●, Annual forbs; ○—○, perennial forbs.

is generally constant from year to year, but there may be some die-back in the months of May and June. In early April 1972, there was a frost and leaf biomass did not recover until June, since water storage was low until late May. Reproduction in *P. glandulosa* was essentially zero in 1971 and 1972, but a large quantity of fruits were produced in 1973. This same pattern is evident for the production of new shoots. In November, when minimum daily air temperatures drop below freezing, *P. glandulosa* loses its leaves. The reproductive response in *P. glandulosa* is similar to that of *Y. elata*.

Ecosystem dynamics

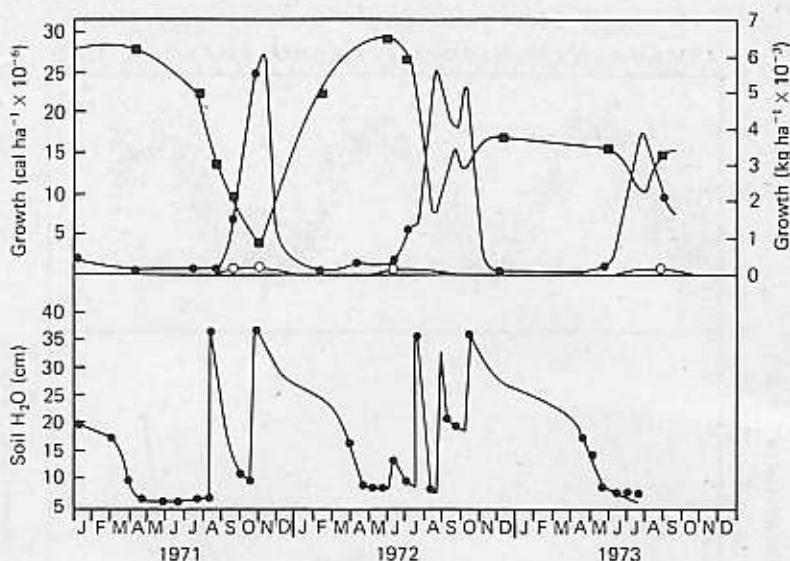


Fig. 11.4. Chihuahuan Desert basins (swales). Soil water storage and growth responses of tobosa grass (*Hilaria mutica*) for 1971–73. Precipitation and daily minimum air temperatures as in Fig. 11.3. ●—●, Green; ■—■, standing dead; ○—○, reproductions.

Alluvial flats

Alluvial flats are characterized by having slopes less than 2% and represent areas in the landscape of water run-on. These areas in the Chihuahuan Desert are characterized by *Flourensia cernua* (tarbush), but they are also characterized by small annual and perennial forbs.

Soil profiles in this landform average about 60 cm in depth and soil water storage is highly responsive to precipitation patterns (Fig. 11.3). In early summer of 1972, rainfall events triggered a response in annual forbs, which was followed by a peak in perennial forbs about two months later.

Basins (swales)

As one proceeds down the alluvial flat to areas with less than 1% slope, the soil texture changes to a clay loam. Swales in southern New Mexico are characterized by *Hilaria mutica* (tobosa grass). This large perennial grass has a deep and diffuse root system. Soils are deeper than on the alluvial flats (about 90 cm). Since these areas are lower on the watershed and have deep soils, they represent the system with maximum soil water storage. *H. mutica* is highly responsive to both temperature and the soil water. The dynamics of water utilization and energy accumulation by this species (Fig. 11.4) shows that its production is considerable. It reached a peak calorie content of over 25 Mcal ha⁻¹ in both 1971 and 1972.

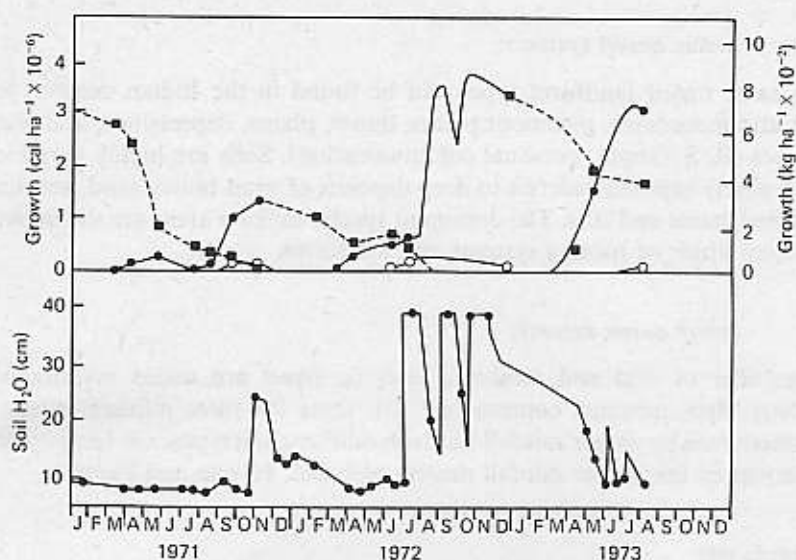


Fig. 11.5. Chihuahuan Desert sinks (playas). Soil water storage and growth responses of vine mesquite grass (*Panicum obtusum*) for 1971–73. Precipitation and daily minimum air temperatures as in Fig. 11.3. ●—●, Green; ■—■, standing dead; ○—○, reproductions.

Sinks (playas)

As one proceeds down the alluvial flats into a sink (basin or playa) the area is generally level and the soil texture is a clay with a hard pan at about 60 cm. The playa in our system is not saline and is characterized by a plant cover of *Panicum obtusum* (vine-mesquite grass). This perennial grass reproduces vegetatively by stolons and also sexually by seeds. It has diffuse root systems which remain relatively shallow due to the clay pan. Significant growth occurs when a series of large rainfall events keeps this basin under water for periods of up to a month (Fig. 11.5). Production of seeds by *P. obtusum* will follow good vegetative growth.

Australian desert systems

A desert region very similar to our Chihuahuan Desert is the area around Alice Springs, Australia. It is characterized by summer rainfall with an average yearly total of about 25 cm (Slatyer, 1962). It also is a region characterized by landforms similar to those found in the Chihuahuan Desert (M. A. Ross, personal communication). In the communities receiving run-on, such as mulga groves, productivity within the groves exceeded by five times that outside of the groves (900:180 kg ha⁻¹) following periods of heavy rainfall (Ross & Lendon, 1973).

Ecosystem dynamics

Indian desert systems

The same major landform types can be found in the Indian deserts: low hills and mountains, piedmont plains, dunes, plains, depressions, and water courses (R. S. Gupta, personal communication). Soils are highly variable – from nearly exposed bedrock to deep deposits of wind-blown sand, and finer textured loams and silts. The dominant species in these areas are shrubs with different kinds of rooting systems and life forms.

Israeli desert systems

A number of arid and semi-arid sites in Israel are under investigation (I. Noy-Meir, personal communication). Data for three different sites, all characterized by winter rainfall but with different soil types, are fairly typical examples of the winter rainfall deserts of Israel, Jordan and Egypt.

Sarayia site

This site, located on the north slope of a limestone hill southeast of Hebron, is at an altitude of 700 m. The average rainfall is about 250 mm, with most occurring between November and April. The soil is shallow (10–25 cm) and is over a hard fissured limestone material. The vegetation is characterized by summer deciduous shrubs and herbaceous plants. The shrubs cover about 3–4%, and are low in stature (20–35 cm).

The seasonal dynamics of growth for two shrubs (*Sarcopoterium spinosum* and *Artemisia herba-alba*) are shown in Fig. 11.6. *S. spinosum* green material (total minus woody) reaches a peak at about 135 kg ha⁻¹ in April. *Artemisia herba-alba* green biomass (total minus woody) reaches peak biomass in July at about 80 kg ha⁻¹. *Poa bulbosa* peaks at about 300 kg ha⁻¹ in March. Annual forbs and grasses peak rapidly in April at about 500 kg ha⁻¹.

Sde-Boqer site

This site is located on a plain with loess soils, which are increasingly saline below 50 cm. Average rainfall on this site is about 75 mm, occurring from October to April. Minimum air temperatures, about 2 °C, occur in January. The vegetation is characterized by a shrub cover of about 3–5%, the major shrub being *Hammada scoparia*. Other plant groups are annual and perennial forbs.

Maximum soil moisture storage is reached in the winter and spring months. However, maximum growth does not occur until temperatures reach the favorable growth levels in March and April.

The growth response of *Erodium hirtum* to precipitation inputs and soil

Short-term water and energy flow

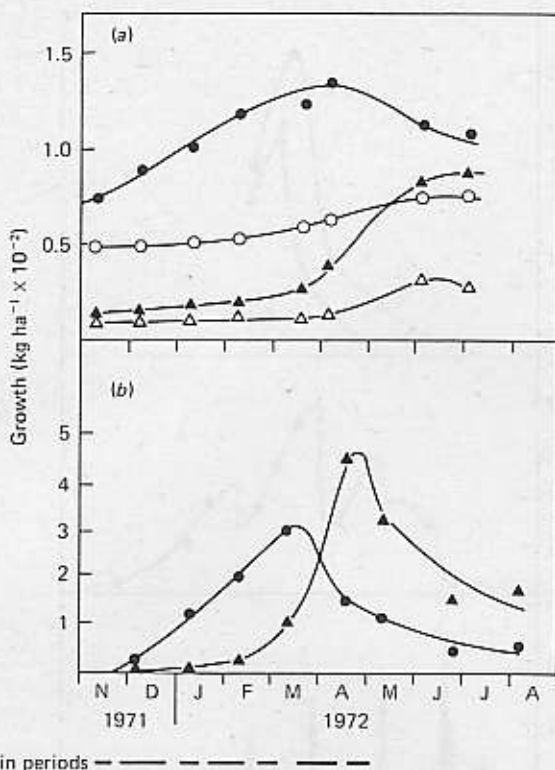


Fig. 11.6. Negev Desert Sarayia site. Seasonal growth dynamics for two shrubs (*Sarcopoterium spinosum* and *Artemisia herba-alba*), a perennial grass (*Poa bulbosa*) and annual forbs and grasses. Rainfall periods are indicated. Data provided by I. Noy-Meir (personal communication). (a) *Sarcopoterium*: ●, total; ○, woody. *Artemisia*: ▲, total; △, woody. (b) ●, *Poa bulbosa*; ▲, annuals.

moisture (% by weight) at 30–45 cm is shown in Fig. 11.7. This species is characterized by a maximum growth peak in April at about 320 kg ha⁻¹. The growth of annuals follows very closely that of *E. hirtum*, peaking at about 250 kg ha⁻¹ in April.

Migda site

This site is located on a plain of deep loess soils. Vegetation is dominated by annual grasses and forbs due to past grazing. The average rainfall for this area is 250 mm, with essentially all of it occurring between October and April. Mean January air temperature minima are about 6 °C. The peak biomass is reached in April for annual grasses and forbs at about 6000 kg ha⁻¹ (Fig. 11.8). After this there was no rain and the green biomass of annual grasses and forbs decreased rapidly to virtually zero by June 1.

Ecosystem dynamics

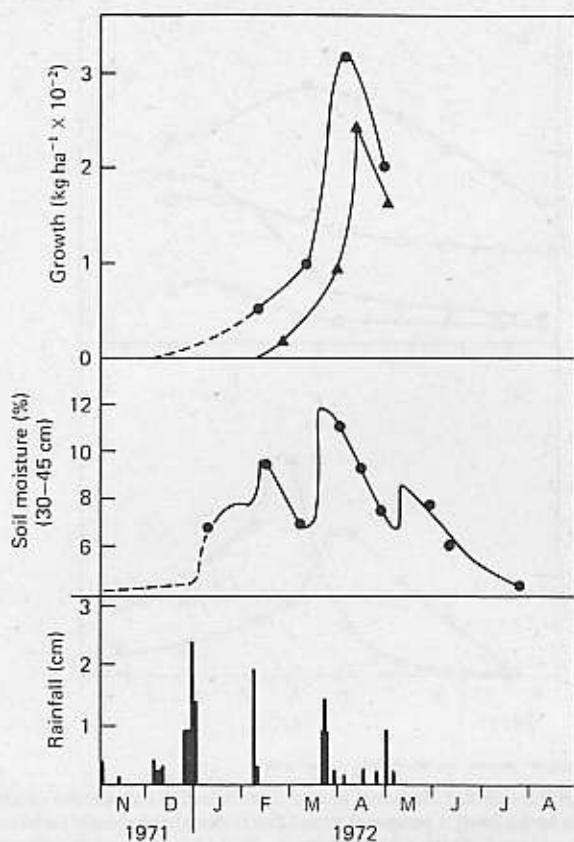


Fig. 11.7. Negev Desert Sde-Boqer site. Precipitation, percent soil moisture by weight and seasonal growth dynamics for *Erodium hirtum* and annual forbs and grasses. Data provided by I. Noy-Meir (personal communication). ● *Erodium hirtum*; ▲, annuals.

These three Israeli sites also illustrate the importance of soil depth on different landscape areas relative to the amount of soil moisture that is stored after precipitation inputs. The sites with the deepest soil had the maximum amount of biomass. Most species or species groups showed maximum biomass occurring in April, after soil temperature increased to allow maximum growth in March. This contrasts with the Chihuahuan Desert system where water inputs occur during the warm season. Here temperature regimes are adequate and the controlling factor of temporal biomass or energy flow dynamics is water input. In the Israeli deserts, the factor controlling temporal dynamics is largely temperature.

Short-term water and energy flow

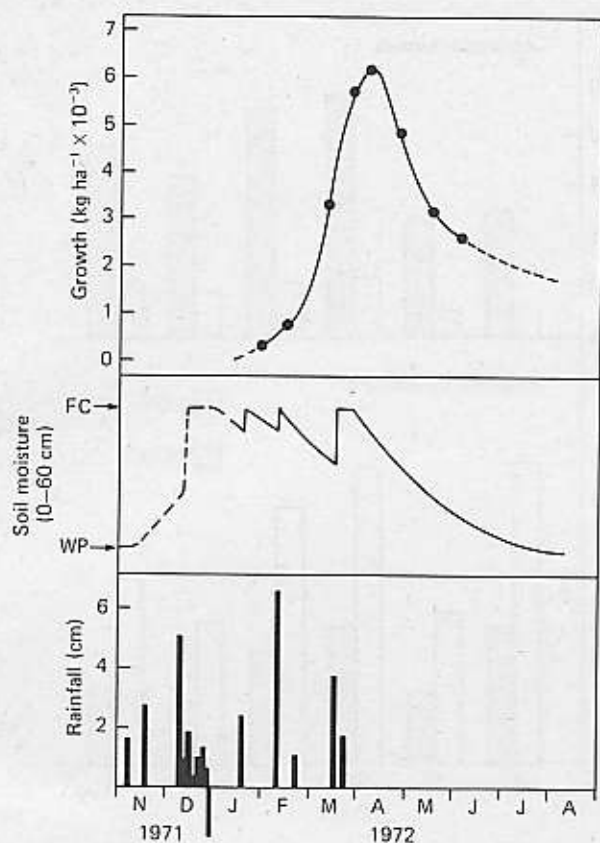


Fig. 11.8. Negev Desert Migda site. Precipitation, estimated soil water potential and seasonal growth dynamics for annual forbs and grasses. Data provided by I. Noy-Meir (personal communication). FC, field capacity; WP, wilting point.

Mohave desert systems

Data describing Mohave desert dynamics of water and energy flow are available from IBP studies at a Rock Valley site in Nevada. The stem production of two Mohave desert shrubs (*Ambrosia dumosa* and *Krameria parvifolia*) are given in Fig. 11.9, for six different zones in 1971 and 1972 (Romney *et al.*, 1973). *A. dumosa* reached a peak biomass of new stems in Zone 22 of only about 3 kg ha^{-1} in 1971. This contrasts sharply with 1972 when it reached a peak stem production of about 10 kg ha^{-1} in Zone 22.

The biomass of these two shrubs indicates that for this winter rainfall desert, temperature is also the critical factor in determining peak biomass. Biomass peaks in the spring of the year were very similar to the Israeli sites.

Ecosystem dynamics

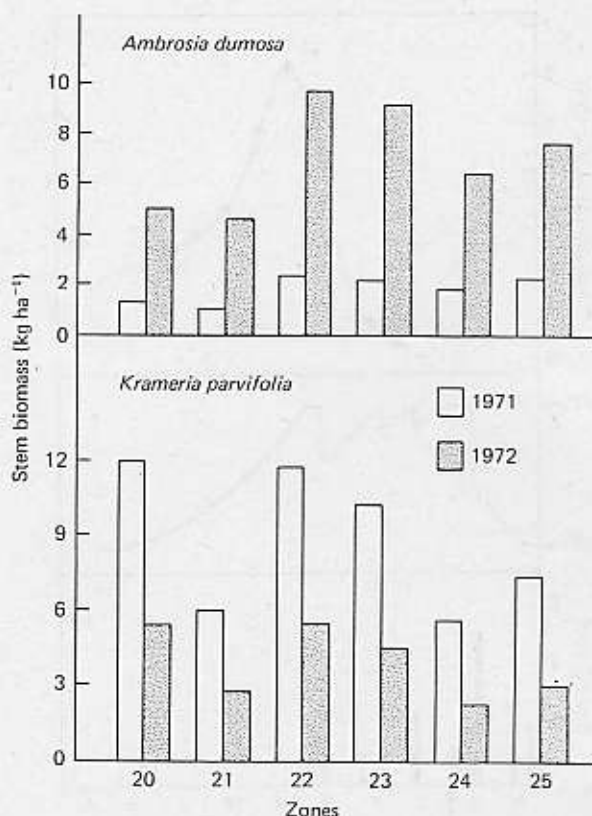


Fig. 11.9. Mohave Desert Rock Valley site. Dry stem production by two shrubs (*Ambrosia dumosa* and *Krameria parvifolia*) in six homogeneous zones. Data provided by S. A. Bamberg and F. B. Turner (personal communication).

Tunisian desert systems

In an area called the Pre-Saharan Zone of Tunisia, there are similarities of different landforms in relationship to other desert ecosystems (C. Floret, personal communication). Their plains can be divided depending on whether the substrate is calcareous, or gypsum. Dune areas may be stable or mobile and various kinds of depressions may occur. These areas may be flooded with salt or fresh water. Plant species with quite different characteristics occur on these different geomorphic landscapes.

Comparison of producers in desert ecosystems

Peaks in new biomass production

The peaks of new biomass produced in different years and seasons for selected species or species groups from different desert landscapes and regions across the world are shown in Table 11.1. Comparing the southwestern United States deserts on equivalent alluvial fan landscapes and comparing *Larrea tridentata* with *Krameria parvifolia*, we see that in *L. tridentata* peak production occurs in the fall whereas in *K. parvifolia* peak production occurs in the spring. Peak production of new shoots in the Chihuahuan Desert is about 200 kg ha⁻¹ in 1971, whereas in *K. parvifolia* in 1971 it was 12 kg ha⁻¹, indicating the difference in production. Of course, it would have been better to compare the same species in these two deserts. Both species occur in both deserts, but comparable growth data were not available.

In comparing annual forb production in the three different deserts (the Chihuahuan and Mohave in North America, and an Israeli site), we can see that in a year of good growth such as 1972 (precipitation above average in all three regions), that peak production in the Chihuahuan Desert was about 55 kg ha⁻¹. In the Mohave Desert, a maximum production occurred in the spring at about 7.5 kg ha⁻¹. This compares with the peak production in the Israeli Sde-Boqer site of 250 kg ha⁻¹. In comparing these results, the Israeli site was recently grazed (I. Noy-Meir, personal communication) and shrub cover is low (3–4% v. 15–20% in the United States). The response of annuals in a disturbed area is likely to be greater.

Rates of productivity

Another way of comparing different ecosystems is to compare their rates of productivity during periods of maximum growth when water storage (availability) is at a maximum.

In order to calculate rates of production with reasonable accuracy, estimates of biomass must be made at relatively short intervals and based on the time interval of maximum (near-linear) growth.

The relative rates of production for the two shrubs and the annuals in our Chihuahuan Desert and Noy-Meir's Sde-Boqer site are given in Table 11.2. Since caloric data is not available from both sites, product rates are in terms of biomass, with rates over the time interval indicated.

The production rates of *Larrea tridentata* exceeds *Hammada scoparia*, however, it must be stressed that the rates are given on an area basis, thus if the density and biomass of *L. tridentata* is greater than *H. scoparia*, this could account for the difference. However, using standing biomass estimates to calculate productivity rates also assumes that turnover rate (death) and

Table 11.1. Production peaks of new biomass in categories for selected species or species groups in different years and seasons from certain desert landscapes and regions

Desert	Precipitation (mm)	Landscape	Species or group	Category	Year	Season	Biomass (kg ha ⁻¹)	
Chihuahuan, USA	197	Alluvial fans	<i>Larrea tridentata</i>	Shoots	1971	Autumn	200	
	395				1972	Autumn	707	
	235				1973	Summer	265	
				Fruits	1971	Summer	150	
					1972	Spring	93	
					1973	Spring	120	
Mohave, USA		Alluvial flats	Annual forbs and grasses	Shoots	1971	Autumn	2	
					1972	Summer	55	
					1973	Spring	550	
		114 (1972)	Alluvial fans	<i>Krameria parvifolia</i>	Stems	1971	Spring	12
		1972				Spring	6	
						1971	Spring	6
Sde-Boqer, Israel		Alluvial fans	Annual forbs and grasses	Shoots	1972	Spring	7	
	160				1972	Spring	350	
					<i>Hammada scoparia</i> <i>Erodium hirtum</i>	1972	Spring	320
						1972	Spring	250

Short-term water and energy flow

Table 11.2. Rates of production for shrubs and annuals in two desert sites in 1972

Desert	Species or group	Component	Production rates (kg ha ⁻¹ day ⁻¹)	Interval
Chihuahuan	<i>Larrea tridentata</i> Annuals	Green shoots	4.6	June–September
		Above-ground	2.3	July–August
			6.9	
Sde-Boqer	<i>Hammada scoparia</i> Annuals	Green shoots	1.2	April–June
		Above-ground	4.5	February–April
	Annuals	Above-ground	4.2	February–April
				9.9

consumption (by all animals) are not significant effects (over the time interval considered).

The rates given in Table 11.2 cannot be considered as estimates of net primary production, since they only consider the rates of biomass increase of certain plant components. Root biomass is not considered. In the shrubs, biomass increments of the older woody parts was not used. Further, these rates in terms of kg ha⁻¹ day⁻¹ cannot be multiplied by the number of days in the year to obtain total annual production since these rates are averaged only over the time of maximum growth.

Growth and behavioural responses of animals

Factors affecting short-term responses

Energy flow through consumer populations in a desert ecosystem may best be summarized by examining the major groups of organisms consuming specific portions of the producer species rather than considering individual species. The relative amounts of seed production and herbage varies from one year to the next depending on the timing and intensity of rainfall events as has been shown in the previous sections. In addition, the availability of seeds of a specific type and rate of production of fresh green vegetation may vary greatly even within one season depending on the timing and intensity of rainfall. The time of year when seeds and/or herbage of a particular type are available to consumers largely determines the behavioural and/or physiological responses of these populations. Thus, years with identical total rainfall and total primary productivity may result in very different productivities of animal species.

Ecosystem dynamics

Irrespective of the taxon, the rate of energy flow through consumers is largely a function of availability of suitable sources of energy and therefore ultimately a function of the past climate.

In periods of water stress, feeding preferences of consumers may be shifted to provide adequate water for maintenance. If adequate water is unavailable, the viability of the population is reduced. Therefore, in order to understand the flow of energy and water through consumers over short periods, we suggest that only when the minimum physiological requirements for water are met is a population capable of acquiring the extra energy needed for reproduction. If there are insufficient water sources, increased mortality serves to reduce energy flow through a taxon.

Factors affecting water and energy flow in consumers

Seed consumers

Most species of heteromyid rodents are capable of maintaining water balance on a seed diet without resorting to free water or green vegetation (Schmidt-Nielsen, B. & Schmidt-Nielsen, K., 1952; Chew, 1965). Although some authors (Beatley, 1969; Bradley & Mauer, 1971) claim that the reproductive success of heteromyids is a function of the availability of vegetation with good moisture content, Whitford (1976) suggests that survivorship and recruitment is a function of caloric content of forage, not its succulence. Non-heteromyids require varying amounts of succulent vegetation or insect food to meet their water requirements (MacMillen, 1964). Energy flow through desert rodent populations appears to be a function of precipitation resulting in abundant food supply which has been suggested by French *et al.* (1974) as the primary factor limiting population growth.

Whitford (1976) summarizes four years of intensive study on rodent communities of the Chihuahuan Desert, which showed that density and biomass of cricetid rodents responded rapidly to rainfall that exceeded the long-term average, but that heteromyid rodent biomass showed significant change only following a drought period when seed supplies were scarce, thus reducing the availability of energy sources and metabolic water (Fig. 11.10). As this model shows, variation in rainfall above the minimum physiological needs for 'water independent' (heteromyids or other species with similar physiological traits) species has little effect on their density and biomass. Establishment and survival of 'non-water independent' species depends on patches of favorable habitat which provides their water needs during drought periods. The amount of precipitation to meet their minimum physiological needs is greater than that of heteromyids and exceeds the long-term average rainfall of the most arid deserts. For example, Turner (1972, 1974) reported only one species of *Peromyscus* at the Rock Valley Site in Nevada, which

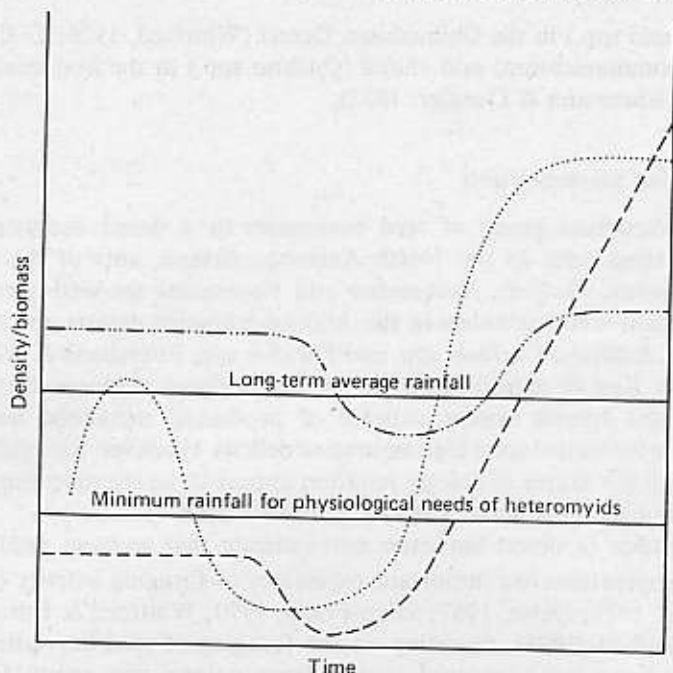


Fig. 11.10. A generalized scheme showing the relationship between rainfall and density or biomass of Chihuahuan Desert rodents, based on data in Whitford (1976). — · — · —, Heteromyids; ---, cricetids; ····, annual rainfall.

occurred at extremely low density ($< 0.1 \text{ ha}^{-1}$) even during a year which exceeded average rainfall ($< 100 \text{ mm yr}^{-1}$) by a factor of two. We submit that this model may be generally applicable to rodent populations in other deserts of the world. The dominant rodents in the African and Eurasian deserts, jerboas (*Jaculus* spp.) and gerbils (*Taterillas* and *Tatera* spp.) and in the Australian deserts, *Notomys* spp, possess physiological adaptations similar to kangaroo rats (Kirmiz, 1962; MacMillen & Lee, 1967; Chew, 1965).

In these deserts, as in the North American deserts, stability of rodent biomass will be a function of the amount of rainfall. This model suggests that fluctuations in numbers and biomass will increase as rainfall amounts approach the minimum physiological requirements for these 'water independent' species. 'Non-water independent' rodent species will make up significant parts of the rodent biomass only in those areas that are marginal deserts or that have recently undergone desertification.

The density and biomass of some species like woodrats (*Neotoma* spp.) is limited by habitat. *Neotoma* spp. build nests in areas which supply ample succulent food and nest building materials such as *Yucca* spp. and prickley

Ecosystem dynamics

pear (*Opuntia* spp.) in the Chihuahuan Desert (Whitford, 1976; C. Grenot, personal communication) and cholla (*Opuntia* spp.) in the Sonoran desert (Brown, Liebermann & Dengler, 1972):

Seed-harvesting ants

Another important group of seed consumers in a desert ecosystem are seed-harvesting ants. In the North American deserts, ants of the genera *Pogonomyrmex*, *Pheidole*, *Novomessor* and *Veromessor* are seed-harvesters. The dominant seed-harvesters in the African-Eurasian deserts and *Messor* spp. and in Australia *Chelaner* spp. and *Pheidole* spp. Ettershank & Whitford (1973) and Kay & Whitford (1975) present indirect evidence that some harvester ant species appear capable of producing metabolic water to compensate for water loss at high saturation deficits. However, the availability of seeds and the degree of colony satiation appear to be the most important regulators of foraging activity in Chihuahuan Desert species.

Most studies of desert harvester ants indicate that ambient and/or soil surface temperatures are important regulators of foraging activity (Shaeta & Kaschef, 1971; Delye, 1967; Szlep-Fessel, 1970; Whitford & Ettershank, 1975). Whitford (1978), reporting on the foraging of seed-harvesting ants (*Pogonomyrmex* spp.), showed that a large colony size group forager, *Pogonomyrmex rugosus* (> 1000 foragers per colony) harvested intensively in a year with high annual production following a drought but was nearly inactive during the subsequent year in which annual plant production was also high. Species that were individual foragers with small colony size (< 1000 foragers per colony) foraged with equal intensity during both years. Thus, precipitation appears to affect seed removal by harvester ants in two ways: production of a seed resource and, if excess seeds are available, group foraging colonies may store sufficient seeds to eliminate the necessity for surface activity in the following year.

When we estimated the energy flow through the various seed consumers in the Chihuahuan Desert, the rodents and ants exhibited reciprocal behavior in terms of energy flow: for example, in 1971, rodents, 1241 kcal ha⁻¹; ants, 0.9 kcal ha⁻¹; birds, 3.1 kcal ha⁻¹; and in 1972, rodents, 270 kcal ha⁻¹; ants, 12 kcal ha⁻¹; birds, 4.0 kcal ha⁻¹. These estimates show that in terms of energy flow, ants and birds are much less important than rodents in a Chihuahuan Desert ecosystem, which is probably true for other desert ecosystems as well. Seed-harvesting ants are not affected by short-term drought as are rodents, hence are able to respond quickly to abundant seeds following a drought. Although harvester ants required only an estimated 12 kcal ha⁻¹ for maintenance and growth in 1972, they harvested approximately 71 kcal of seeds.

Short-term water and energy flow

Table 11.3. *Arthropod biomass (g dry wt ha⁻¹) for time periods specified and for arthropod groups indicated. (Data are from Whitford, 1971, 1972, 1973, 1974). Blank spaces indicate data not collected or samples not processed*

Arthropod	1971		1972		1973		1974	
	May	August	May	August	May	August	May	August
<i>Playa</i>								
Shrub dwelling	17.2	54.6	3.1	175.7	8.9	57.7	—	—
Lepidoptera and								
Hymenoptera	—	—	—	3.2	5.6	1.1	2.0	0.2
Orthoptera	—	—	—	48.0	98.0	51.0	0.0	0.8
<i>Bajada</i>								
Shrub dwelling	19.9	21.9	46.6	7.6	68.8	12.3	—	—
Lepidoptera and								
Hymenoptera	—	—	—	0.1	0.3	0.3	0.9	0.5
Orthoptera	—	—	—	10.0	25.0	100.0	0.0	0.0

Seed-eating birds

The avifauna of a desert region must be considered in two parts: (a) the breeding or resident population and (b) migrants or transient populations. While the resident populations may be important as rate regulators in the system, the transients are potentially of greater importance in energy flow and as exploiters of excess resources.

In the Chihuahuan Desert, resident birds are primarily insectivores and even the granivorous black-throated sparrow consumes some insects during the breeding season and at times of water stress (R. J. Raitt, personal communication). The productivity of resident birds is directly a function of moisture availability and insect productivity is the ultimate factor (Raitt & Pimm, 1976). The generalized model proposed for rodents (Fig. 11.10) is also applicable to birds. Resident birds behave like heteromyid rodents in that insufficient moisture during the breeding season results in reproductive failure but the adults exhibit normal survivorship. Rainfall close to the long-term average allows reproduction and maintenance of a relatively stable bird population. Excess moisture produces large blooms of annuals, and hence seeds in excess of those that can be exploited by rodents and ants allowing migrant seed-feeding birds such as lark buntings and horned larks to enter the system to exploit this resource during the non-growing season (Raitt & Pimm, 1976). Hence their impact on the system is like that of cricetid rodents.

Plant-dwelling arthropods

Population growth in plant dwelling arthropods appears to vary as a function of plant water potential and phenology of the host plant (Table 11.3). Changes

Ecosystem dynamics

in insect biomass on shrubs like *Prosopis glandulosa* and *Larrea tridentata*, follow periods of growth of new leaves. Most of the shrub-dwelling insect biomass is made up of sucking insects (Psyllidae, Membracidae, Miridae) which depend upon the quality of phloem sap and cell sap for their maintenance and growth. Shrub productivity varies directly with rainfall (Table 11.1, Figs. 11.1–11.5). Thus, herbivorous insect biomass varies with rainfall.

Plant exudate and honeydew feeders

Energy flow through animal populations which feed on plant exudates and/or honeydew is obviously tied to plant water status. Most of these consumers are either social insects which have a variety of ways to integrate short-term fluxes in energy availability and/or water stress, or insects like the dipterans, which avoid stress in the egg stage and are capable of rapid development to the adult stage given favorable environmental conditions.

Colony densities of exudate/honeydew feeding ants reach 77 ha^{-1} and many of these species forage most of the year (Schumacher & Whitford, 1974). The high colony densities suggest that exudate/honeydew feeders are important but as yet unevaluated consumers.

Domestic stock

Cattle and similar consumers respond directly to moisture availability, and thus, to new growth per unit time. Thus, energy flow through these populations does not exhibit the time lags evident in the seed consumers. Cattle grazing probably has an effect on energy flow through insect foliage consumers. Insects exhibited peak activity with a lag of about three weeks after initial growth response of grasses and forbs to rainfall. A similar response was noted in the Sahara by Cloudsley-Thompson (1964). Reduction of standing live grasses and forbs by cattle grazing probably limited energy flow through foliage-consuming insects to some degree. The intensity of grazing on our study area was not as severe as that reported by Cloudsley-Thompson (1964) where grazing by domestic stock denuded the area, thus effectively eliminating herbivorous insects.

Predators

Data on energy flow through predators in any ecosystem is difficult to obtain. During the peak of the drought cycle in a Chihuahuan Desert ecosystem arthropod predators exceeded the biomass of herbivorous insects on *Prosopis glandulosa* and *Larrea tridentata*. However, the biomass of arthropod predators did not respond as rapidly to increased productivity following the onset of rains as did the herbivorous insects (Whitford, 1971, 1972, 1973, 1974).

Short-term water and energy flow

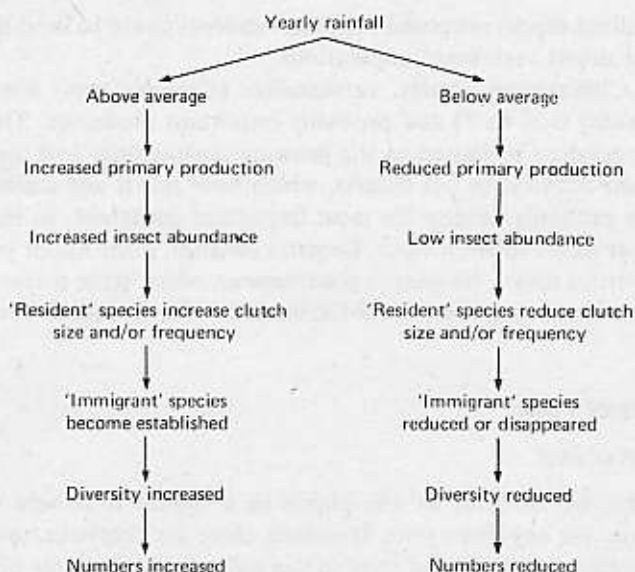


Fig. 11.11. A scheme showing the relationship between rainfall, density and diversity of desert lizard communities, based on data in Whitford & Creusere (1977).

In discussing the interrelationships of arthropods in the Sahara, Cloudsley-Thompson (1968) suggested that a high proportion of carnivores is characteristic of desert fauna. He suggests that seasonal cycles of abundance are related to rain events and that in the non-rainy season these animals exhibited reduced activity.

In our studies (Whitford, 1971, 1972, 1973, 1974) mid-summer predatory species accounted for nearly 50% of the arthropod biomass. Many of the predatory arthropod species are known to be long-lived. The low turnover of many species of desert predatory arthropods and high turnover of most herbivorous insects probably accounts for this apparent paradox in relative biomass.

Whitford & Creusere (1977) discuss the short-term changes in numbers and biomass of a desert lizard community. Seasonal activity periods of adult and hatchling lizards were longer during dry years than wet years. During wet years adults and juveniles of most species exhibited allochronic activity. Densities and biomass of most resident species varied directly with changes in productivity and relative abundance and activity of arthropods.

Whitford & Creusere (1977) present the following model for the relationship of lizard productivity to rainfall (Fig. 11.11). In lizards, as in insectivorous birds, rainfall below a certain critical level results in insufficient insects for normal reproduction, hence a drop in numbers and biomass with a time lag of one to two years after the drought event. These relationships suggest that

Ecosystem dynamics

the generalized model proposed for desert rodents could be modified slightly to fit most desert vertebrate populations.

In the Chihuahuan Desert, rattlesnakes (*Crotalus* spp.) are abundant (approximately 0.25 ha^{-1}) and probably important predators. Their importance as predators is limited to the growing season since low temperatures restrict their activity. In hot deserts, which have few if any freezing nights, snakes are probably among the most important predators. In the Algerian Sahara near Beni-Abbes, a viper, *Cerastes cerastes*, is the major predator on the herbivorous lizard, *Uromastix acaanthinurus*, which is the major vertebrate herbivore in that ecosystem (Grenot & Vernet, 1972; Grenot & Vernet, 1973).

Dynamics of litter

Production of litter

The production of litter by the plants in a system is closely tied to the productivity for any given year. However, there are delays in turnover from growth to standing dead and then to the soil surface. In some plant groups (e.g., annuals) this turnover may be very rapid. In contrast, many of the wood stems of shrubs may persist in the canopy as standing dead for many years.

We used litter collectors under selected shrubs to obtain data on the dynamics of litter production by *Larrea tridentata* (Fig. 11.1). The changes in biomass of the stems and leaves produced as litter follow very distinct patterns. After growth is reduced due to either cool autumn temperatures (1972) or summer drought (1973), older stems and leaves are shed. This differs from previous reports on litter production in this species (Burk & Dick-Peddie, 1973), which indicate that the abscission of stems occurs during periods of rapid growth, rather than after major growth. Slight phasing was also found in the loss of stems and leaves by Oechel, Strain & Odening (1972).

The dynamics of litter produced by the two perennial grasses, *Hilaria mutica* and *Panicum obtusum*, which occur within the swale and playa ecosystems, respectively, are shown in Figs. 11.4 and 11.5. The patterns in 1971 are quite similar for both species, based on data obtained by area harvesting of litter biomass. The peaks in July reflect a decrease in standing dead material produced by growth in 1970. With the summer rains, there was decomposition of some of the litter material, but an increase occurred again in the autumn, following late summer growth. In the winter, there was some decomposition again since precipitation did occur during this period.

Role of detritivores and decomposers

Of all of the sources of energy available to consumers, detritus, of all categories, is probably the most constant since it certainly represents the greatest percentage of the productivity for any given year. There is little known

Short-term water and energy flow

about the litter consumers in North American desert ecosystems. The information which is available is based on studies in very different deserts (Wallwork, 1972*a, b*; Wooten & Crawford, 1974, 1975; Haverty & Nutting, 1974*a, b*; 1975*a, b*, 1976; LaFage, Nutting & Haverty, 1973; Haverty, LaFage & Nutting, 1974; Haverty, Nutting & La Fage, 1975; McBrayer, Mamolito & Franco, 1975; Johnson & Whitford, 1975; Crawford, 1976). Wallwork (1976) summarizes the available literature. The studies on the activities of detritivores in other arid lands of the world have been largely limited to studies of termites (Lee & Wood, 1971*a, b*; Boullion, 1970) and studies on breakdown of animal dung (Anderson & Coe, 1974; Ferrar & Watson, 1970).

Wallwork (1972*a*) found that microarthropods were extremely scarce even in moist desert microhabitats and was forced to limit his study to the microarthropods of the litter of juniper trees, the only site where they occurred in significant numbers in Joshua Tree Monument. This has been substantiated by the studies of Edney, McBrayer, Franco & Phillips (1974, 1975). In survey studies in the Chihuahuan Desert we found microarthropods only in the soil and buried leaf litter of a large arroyo (Whitford, 1973). The micro-arthropods were predominately mites varying in density from zero to 31 individuals per 100 g soil between June and August. Further, Wallwork (1976) concludes from his studies in 1972 and those of Wood (1971) that microarthropods reach their highest densities in winter, and that in the Mohave Desert, a smaller population peak is observed in spring. These findings and those of Wood (1971) and Wallwork (1972*a*) strongly suggest that microarthropods are much less important in litter breakdown in deserts than are other arthropod groups.

Noy-Meir (1974) has stated that microbial decomposition of litter and wood at or near the soil surface must be limited to the short periods when this layer is moist (after rain or dew), and O'Brien (in Whitford, 1974) has shown that active microbial decomposition occurs only when soils are moist and temperatures moderate.

Since microbial decomposition is limited by moisture near the soil surface and microarthropods and the other litter consumers appear to be considerably affected by moisture, termites, which are largely independent of soil moisture, appear to be the most important litter consumers in hot desert ecosystems. Johnson & Whitford (1975) showed that subterranean termites consumed 7.9 ± 2.8 and 1.2 ± 0.4 kg ha⁻¹ during July and August in two Chihuahuan Desert communities. They estimated the input of detritus in one system at 10.3 ± 10^6 cal ha⁻¹ and termite consumption at 3.4 ± 10^6 cal ha⁻¹. This one group of detritivores accounted for more than 50% of the net primary production of these Chihuahuan Desert ecosystems. These estimates of energy flow through a consumer group that appears to be relatively independent of rainfall (as long as litter is buried below the soil surface) suggest that termites may be the most important consumers in hot desert ecosystems.

Conclusions

In setting out our original objective to discuss the dynamic behavior of the biotic components of desert ecosystems in relation to short-term water and energy flow, we had hoped some underlying principles about the short-term dynamics of deserts would emerge. We knew that we would have to rely heavily on our own data which limits the scope. Even when other data were kindly provided for study, that deep intuition associated with a thorough knowledge of your own desert site was missing. It will need the data and intuitions of many more desert ecologists before a real integration of the principles of short-term dynamics in deserts can emerge.

In spite of the above dissatisfaction, our data and discussion does quantify and test, in a sense, some hypotheses put forth earlier by desert ecologists. Our conclusions regarding some of these hypotheses are as follows.

- (1) The quantity of available water is not only affected by precipitation inputs, but by the soil characteristics and the position of an ecosystem in the landscape. Our data on water storage shows that, of the ecosystems considered, the water courses on the alluvial fans have the greatest total and temporal storage, followed by swales. The lowest storage was found for the alluvial fans themselves (see Figs. 11.1–11.5).
- (2) The season of precipitation inputs, hence water availability, greatly affects the growth responses of the different species occupying the various ecosystems. Winter or late summer rainfall will not trigger as large a pulse of production as spring or early summer rainfall, when temperature conditions are nearer to optimum. Also, the reproductive response of some species is related to this seasonality in complex ways.
- (3) The sequencing of favorable and unfavorable moisture conditions also strongly influences productivity of certain desert plants. For example, our data show that annuals will attain a much higher level of production if a series of favorable growth seasons occur in sequence. The first production peaks may represent the maximum that can be obtained because of limiting seed reserves. If this is followed by a second favorable growth season, the production peaks will be orders of magnitude higher due to a larger, new seed reserve being available (see Bridges *et al.*, 1972; and Noy-Meir, 1973, for a discussion of the pulse-reserve strategy in desert plants).
- (4) The response strategy of annual plants (perhaps ephemerals in general whether annual or perennial) appears to be characterized by the saying, 'Hurry before it's too late'. The data for annuals in two sites show relatively high rates of productivity following significant water inputs. Maximum growth and production of annuals occurs within one to two months after initiation of growth.
- (5) The response strategy of evergreen, perennial shrubs appears to be

Short-term water and energy flow

characterized by the saying, 'Slow and steady wins'. The data for two shrubs in two sites shows the interval of maximum production to be about four months. The total (peak) production of new shoot material may be equivalent to, or exceed, the peak of the annuals because of this longer growth period. These values for shrub production do not account for the large amounts of energy going into secondary growth of old stems and roots.

- (6) The past disturbance of desert regions by domestic animals makes present comparisons of short-term energy flow difficult. Present 'openness' with respect to shrub cover may in some areas be due to past grazing. Production of annuals appears to be greater in open areas.
- (7) The ecological efficiencies of two desert sites characterized by two shrubs and annual grasses and forbs is less than 0.5%. This follows previous estimates of ecological efficiency for deserts (Whittaker, 1975). Since the values reported are minimum estimates, the total (Lindemann) ecological efficiency would probably be about double that given.
- (8) The seed consumer community in a desert ecosystem is composed of granivorous rodents and birds and harvester ants. The impact of each component of the seed consumer community is dependent on the immediate past climatic history of the system. Variation in rainfall amounts above the minimum physiological requirements of 'resident' vertebrates results in only small changes in biomass and numbers but rainfall amounts below that minimum result in significant reduction in numbers.

Migratory granivorous birds exploit seed sources following periods of greater than average precipitation when seed production exceeds the amounts used and stored by resident granivores.

- (9) Arthropods that feed on live vegetation or on plant honeydew/exudates account for a small portion of the energy flow through the ecosystem and are directly dependent on the water status of the host plants.
- (10) In hot desert regions, we suggest that termites are the single most important consumer group, processing more than 50% of the primary productivity. Since termites of a variety of families inhabit the hot desert areas of the world (Krishna & Weesner, 1970) it is probable that this is generally true. However, physiological differences in termites in other deserts may restrict foraging to periods of enhanced soil moisture.
- (11) Decomposition by microorganisms is soil moisture dependent and thus considerably variable. Microbial decomposition and mineralization of fecal material in and around subterranean galleries of social insects may be more constant and thus of greater importance.

Ecosystem dynamics

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References

- Anderson, J. M. & Coe, M. J. (1974). Decomposition of elephant dung in an arid, tropical environment. *Oecologia*, **14**, 111–25
- Beatley, J. C. (1969). Dependence of desert rodents on winter annuals and precipitation. *Ecology*, **50**, 721–4
- Bouillon, A. (1970). Termites of the Ethiopian region. In: *Biology of termites*, vol. 2 (ed. K. Krishna & F. M. Weesner), pp. 153–280. Academic Press, New York.
- Bradley, W. G. & Mauer, R. A. (1971). Reproduction and food habits of Merriam's kangaroo rat, *Dipodomys merriami*. *Journal of Mammalogy*, **52**, 479–507.
- Bridges, K. W., Willcott, C., Westoby, M., Kickert, R. & Wilken, D. (1972). *Nature: a guide to ecosystem modelling*. Minneapolis: IBP Ecosystems Modelling Symposium American Institute of Biological Sciences Meeting (presented paper, available from authors).
- Brown, J. H., Lieberman, G. A. & Dengler, W. G. (1972). Woodrats and cholla: dependence of a small mammal population on the density of cacti. *Ecology*, **53**, 310–13.
- Burk, J. H. & Dick-Peddie, W. A. (1973). Comparative production of *Larrea divaricata* Cav. on three geomorphic surfaces in southern New Mexico. *Ecology*, **54**, 1094–102.
- Chew, R. M. (1965). The water metabolism of mammals. In: *Physiological mammalogy – mammalian reactions to stressful environments*, vol. 2 (ed. W. V. Mayer & R. A. Van Gelder), pp. 43–178. Academic Press, New York.
- Cloudsley-Thompson, J. L. (1964). The insect fauna of the desert near Khartoum: seasonal fluctuation and the effect of grazing. *Proceedings of the Royal Entomological Society, London*, **A39**, 41–6.
- Cloudsley-Thompson, J. L. (1968). The Merkhayat jerbels: a desert community. In: *Desert biology* (ed. G. W. Brown), pp. 1–20. Academic Press, New York.
- Crawford, C. S. (1976). Feeding-season production in the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). *Oecologia*, **24**, 265–76.

Short-term water and energy flow

- Delye, G. (1967). Recherches sur l'écologie, la physiologie, et l'ethologie des fourmis du Sahara. PhD Thesis, Université d'Aix-Marseille.
- Edney, E. V., McBrayer, J. F., Franco, P. J. & Phillips, A. W. (1974). *Distribution of soil arthropods in Rock Valley, Nevada*. US/IBP Desert Biome Research Memorandum RM 74-32. Utah State University, Logan.
- Edney, E. B., McBrayer, J. F., Franco, P. J. & Phillips, A. W. (1975). *Abundance and distribution of soil microarthropods in Rock Valley, Nevada*. US/IBP Desert Biome Research Memorandum RM 75-29. Utah State University, Logan.
- Ettershank, G. & Whitford, W. G. (1973). Oxygen consumption of two species of *Pogonomyrmex* harvester ants (Hymenoptera: Formicidae). *Comparative Biochemistry and Physiology*, **46**, 605-11.
- Evenari, M., Shannan, L. & Tadmor, N. H. (1971). *The Negev: the challenge of a desert*. Harvard University Press, Cambridge, Massachusetts.
- Ferrar, P. & Watson, J. A. L. Termites associated with dung in Australia. *Journal of the Australian Entomological Society*, **9**, 100-2.
- French, H. R., Maza, B. G., Hill, H. O., Aschwander, A. P. & Kaaz, H. W. (1974). A population study of irradiated desert rodents. *Ecological Monographs*, **44**, 45-72.
- Grenot, C. & Vernet, R. (1972). Les reptiles dans l'écosystème au Sahara occidental. *Compte Rendu des Séances de la Société de Biogéographie*, **433**, 96-112.
- Grenot, C. & Vernet, R. (1973). Ecologie animale - sur une population d'*Uromastix acanthinurus* Bell isolée au milieu de Grand Erg Occidental (Sahara algérien). *Comptes Rendus hebdomadaires des Séances de l'Académie des Sciences, Serie D*, **276**, 1349-52.
- Haverty, M. I. & Nutting, W. L. (1974a). Density, dispersion, and composition of desert termite foraging populations and their relationship to superficial dead wood. *Environmental Entomology*, **45**, 480-6.
- Haverty, M. I. & Nutting, W. L. (1974b). Natural wood consumption rates and survival of a dry wood and a subterranean termite at constant temperatures. *Annals of the Entomological Society of America*, **77**, 153-7.
- Haverty, M. I. & Nutting, W. L. (1975a). Natural wood preferences of desert termites. *Annals of the Entomological Society of America*, **68**, 533-6.
- Haverty, M. I. & Nutting, W. L. (1975b). A simulation of wood consumption by the subterranean termites, *Heterotermes aureus* (Snyder), in an Arizona desert grassland. *Insectes Sociaux*, **22**, 93-102.
- Haverty, M. I. & Nutting, W. L. (1976). Environmental factors affecting the geographical distribution of two ecologically equivalent termite species in Arizona. *American Midland Naturalist*, **95**, 20-7.
- Haverty, M. I., LaFage, J. P. & Nutting, W. L. (1974). Seasonal activity and environmental control of foraging of the subterranean termite, *Heterotermes aureus* (Snyder), in a desert grassland. *Life Sciences*, **15**, 1091-101.
- Haverty, M. I., Nutting, W. L. & LaFage, J. P. (1975). Density of colonies and spatial distribution of foraging territories of the desert subterranean termite, *Heterotermes aureus* (Snyder). *Environmental Entomology*, **4**, 105-9.
- Johnson, K. A & Whitford, W. G. (1975). Foraging ecology and relative importance of subterranean termites in Chihuahuan Desert ecosystems. *Environmental Entomology*, **4**, 66-70.
- Kay, C. A & Whitford, W. G. (1975). Influences of temperature and humidity on oxygen consumption of Chihuahuan Desert ants. *Comparative Biochemistry and Physiology*, **52**, 281-6.
- Kirmiz, J. P. (1962). *Adaptation to desert environments: a study on the jerboa rat and man*. Butterworth, London.

Ecosystem dynamics

- Krishna, K. & Weesner, F. M. (1970) (eds.). *Biology of termites*, vol. 2. Academic Press, New York.
- LaFage, J. P., Nutting, W. L. & Haverty, M. I. (1973). Desert subterranean termites: a method of studying foraging behaviour. *Environmental Entomology*, **2**, 954-6.
- Lee, K. E. & Wood, T. G. (1971a). *Termites and soil*. Academic Press, New York.
- Lee, K. E. & Wood, T. G. (1971b). Physical and chemical effects of soils of some Australian termites and their pedological significance. *Pedobiologia*, **11**, 376-409.
- Ludwig, J. A., Reynolds, J. F. & Whitson, P. D. (1975). Size-biomass relationships of several Chihuahuan Desert shrubs. *American Midland Naturalist*, **94**, 451-61.
- MacMillen, R. E. (1964). Population ecology, water relations, and social behaviour of a southern California semi-desert rodent fauna. *University of California Publications in Zoology*, **71**, 1-59.
- MacMillen, R. E. & Lee, A. K. (1967). Australian desert mice: independence and exogenous water. *Science*, **518**, 383-5.
- McBrayer, J. F., Mamolito, G. E. & Franco, P. J. (1975). *The functional relationships among organisms comprising detritus-based food chains at Rock Valley Site*. US/IBP Desert Biome Research Memorandum RM 75-30. Utah State University, Logan.
- Milner, C. & Hughes, R. E. (1968). *Methods for the measurement of the primary production of grasslands*. IBP Handbook No. 6. Blackwell, Oxford.
- Newbould, P. J. (1967). *Methods for estimating the primary productions of forests*. IBP Handbook No. 2. Blackwell, Oxford.
- Noy-Meir, I. (1973). Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25-51.
- Noy-Meir, I. (1974). Desert ecosystems: higher trophic levels. *Annual Review of Ecology and Systematics*, **5**, 195-214.
- Oechel, W. C., Strain, B. R. & Odensing, W. R. (1972). Tissue water potential, photosynthesis, ¹⁴C-labelled photosynthate utilization and growth in the desert shrub *Larrea divaricata* Cav. *Ecological Monographs*, **42**, 127-41.
- Raitt, R. J. & Pimm, S. L. (1976). Dynamics of bird communities in the Chihuahuan Desert, New Mexico. *Condor*, **78**, 427-42.
- Romney, E. M., Hale, V. Q., Wallace, A., Lunt, O. R., Childress, J. D., Haaz, H., Alexander, G. V., Kinnear, J. E. & Ackerman, T. L. (1973). *Some characteristics of soil and perennial vegetation in northern Mojave desert areas of the Nevada Test Site. Los-Angeles: UC-38 Biomedical and Environmental Research TID-4500*. Clearinghouse for Scientific & Technical Information, Springfield, Virginia.
- Ross, M. A. & Lendon, C. (1973). Productivity of *Eragrostis eriopoda* in a mulga community. *Tropical Grasslands*, **7**, 111-16.
- Schmidt-Nielsen, B. & Schmidt-Nielsen, K. (1952). Water metabolism of desert rodents. *Physiological Review*, **32**, 135-66.
- Schumacher, A. & Whitford, W. G. (1974). The foraging ecology of two species of Chihuahuan Desert ants: *Formica perpilosa* and *Trachymyrmex smithii neomexicanus* (Hymenoptera: Formicidae). *Insectes Sociaux*, **21**, 317-30.
- Shaeta, M. N. & Kaschef, A. H. (1971). Foraging activities of *Messor aegyptiacus* Emery (Hymenoptera: Formicidae). *Insectes Sociaux*, **18**, 215-25.
- Slatyer, R. O. (1962). Climate of the Alice Springs Area. *CSIRO Land Research Series No. 6*, pp. 109-28.
- Smith, S. D. & Ludwig, J. A. (1976). Reproductive and vegetative growth patterns in *Yucca elata* Engelm. (*Liliaceae*). *Southwestern Naturalist*, **21**, 177-84.
- Szlep-Fessel, R. (1970). The regulatory mechanism in mass foraging and the recruitment of soldiers in *Pheidole*. *Insectes Sociaux*, **17**, 232-44.

Short-term water and energy flow

- Turner, F. B. (1972). *Rock Valley Validation Site Report*. US/IBP Desert Biome Research Memorandum RM 72-2. Utah State University, Logan.
- Turner, F. B. (1974). *Rock Valley Validation Site Report*. US/IBP Desert Biome Research Memorandum RM 74-2. Utah State University, Logan.
- Wallace, A. & Romney, E. M. (1972). *Radioecology and ecophysiology of desert plants at the Nevada Test Site*. United States Atomic Energy Commission Monograph, TID-2594.
- Wallwork J. A. (1972a). Distribution patterns and population dynamics of the microarthropods of a desert soil in southern California. *Journal of Animal Ecology*, **41**, 291-310.
- Wallwork, J. A. (1972b). Mites and other microarthropods from the Joshua Tree National Monument, California. *Journal of Zoology*, **163**, 91-105.
- Wallwork, J. A. (1976). *The distribution and diversity of soil fauna*. Academic Press, New York.
- Whitford, W. G. (1971). *Jornada validation site report*. US/IBP Desert Biome Research Memorandum RM 71-4. Utah State University, Logan.
- Whitford, W. G. (1972). *Jornada validation site report*. US/IBP Desert Biome Research Memorandum RM 72-4. Utah State University, Logan.
- Whitford, W. G. (1973). *Jornada validation site report*. US/IBP Desert Biome Research Memorandum RM 73-4. Utah State University, Logan.
- Whitford, W. G. (1974). *Jornada validation site report*. US/IBP Desert Biome Research Memorandum RM 74-4. Utah State University, Logan.
- Whitford, W. G. (1976). Temporal fluctuations in density and diversity of desert rodent populations. *Journal of Mammalogy*, **57**, 351-69.
- Whitford, W. G. (1978). Structure and seasonal activity of Chihuahuan Desert ant communities. *Insectes Sociaux*, **25**, 79-88.
- Whitford, W. G. & Creusere, F. M. (1977). Seasonal and yearly fluctuations in Chihuahuan Desert lizard communities. *Herpetologica*, **33**, 54-65.
- Whitford, W. G. & Ettershank, G. (1975). Factors affecting foraging activity in Chihuahuan Desert harvester ants. *Environmental Entomology*, **4**, 689-96.
- Whittaker, R. H. (1975). *Communities and ecosystems*, 2nd edn. Macmillan Publishing Co., New York.
- Wood, T. G. (1971). The distribution and abundance of *Folsomides deserticola* (Collembola: Isotomidae) and other microarthropods in arid and semi-arid soils in southern Australia. *Pedobiologica*, **11**, 446-68.
- Wooten, R. C. Jr & Crawford, C. S. (1974). Respiratory metabolism of the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). *Oecologia*, **17**, 179-86.
- Wooten, R. C. Jr & Crawford, C. S. (1975). Food, ingestion rates and assimilation in the desert millipede *Orthoporus ornatus* (Girard) (Diplopoda). *Oecologia*, **20**, 231-6.