Productivity of Desert Ecosystems

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Primary production in desert ecosystems is limited by precipitation, nutrient availability (especially nitrogen), and the species' production potential. Plant biomass provides food for consumers that occupy several trophic levels. The resultant transfer of energy and nutrients is also water-limited as are rates of decomposition and activities of decomposer organisms. (Accepted 20 February 1981)

Desert or arid regions, which currently cover an estimated 20–30% of the earth's land area, are increasing at an alarming rate as a result of both natural causes (prolonged drought) and man's activities (overgrazing, overcultivation). The creation of new deserts or desert-like conditions (termed desertification) seriously reduces the land's productivity and, in some cases, completely destroys it. To better understand the degree of the desertification process, a greater knowledge of the structure and function of native desert ecosystems is needed. Such information is being provided by scientists throughout the world from individual research programs and as part of combined task forces such as the International Biological Program (IBP) (Goodall and Perry 1979).

The only syntheses of information pertaining to productivity at the ecosystem level are the comprehensive reviews by Noy-Meir (1973, 1974). This summary, which builds upon these reviews, incorporates new information on primary and secondary productivity, decomposer activities, and nutrient cycling. The roles of consumer organisms in desert regions are emphasized since physiological processes of plant productivity in arid zones were recently reviewed by Fischer and Turner (1978). Coverage here is restricted primarily to tropical and sub-tropical deserts in which low precipitation (less than 250 mm per year) is coupled with high temperature at least part of the year.

PRIMARY PRODUCTION

Deserts are typically characterized as regions of low productivity. Noy-Meir's summary of annual above-ground net primary production suggests production varies from 30 to 300 g dry wt $\cdot$ m^{-2} $\cdot$ yr^{-1} in arid zones. Recent values reported in Table 1 are in general agreement with this earlier synthesis. The new production values cover a rather extensive range due to seasonal and year-to-year variation in precipitation, and the diversity of habitats that have been studied in desert ecosystems. The lowest observed production (2.6 g dry wt $\cdot$ m^{-2} $\cdot$ yr^{-1}) occurred in a dune community during a dry year; in a subsequent wet year, production increased nine-fold (Seely and Louw 1980). The highest observed production (816 g dry wt $\cdot$ m^{-2} $\cdot$ yr^{-1}) oc-

curred in a large arroyo that received extensive run-on water during a wet year in the Chihuahuan Desert (Ludwig and Smith 1978). The average production over a four year period was 180 (bajada) and 137 (playa) g dry wt $\cdot$ m^{-2} $\cdot$ yr^{-1}. The largest year-to-year variation in above-ground production occurs for annual species in the Mojave and Sonoran Deserts and perennial grasses in the northern Chihuahuan Desert.

Net primary production also depends upon the degree of habitat utilization by consumer organisms. Pearson (1965) found that production by a previously grazed desert grassland community was only 79% of the above-ground biomass produced at a site that had been protected from grazing for 11 years. However, because below-ground production was significantly greater at the grazed site, total production in the latter exceeded that of the protected site.

Water Availability

Water availability is the key environmental factor limiting production in arid zones. So intimately is energy flow coupled to and controlled by water availabil-

Table 1. Annual above-ground net primary production (ANPP) of desert communities.

Desert or Locality	Community Type	Years Studied	ANPP (g dry wt$\cdot$m$^{-2}\cdot$yr^{-1})	Reference
Idaho	Desert Grassland	1	98/123*	Pearson (1965)
Mojave	Desert Scrub	1	32	Soholt (1973)
Sonoran	Variety (3)	1	92 to 129	Whittaker and Niering (1975)
Mojave	Desert Scrub	2	14/43†	Bamberg, et al. (1976)
Algeria, Negev & Syria	Variety (5)	1 to 3	25 to 238	Evenari, et al. (1976)
Chihuahuan	Variety (6)	4	30 to 816	Ludwig and Smith (1978)
North America	Variety (4)	1 to 5	14 to 251	Szarek (1979)
Namib	Dune	2	2.6/24†	Seely and Louw (1980)

*grazed/ungrazed site
†dry/wet year at same site

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November 1981

ity that Noy-Meir (1973) suggested a reasonable estimate of productivity could be determined from a linear regression analysis of these two variables. However, the relationship between production and precipitation is modified by factors such as the intensity, frequency, and timing of precipitation, topography, vegetation density, and edaphic conditions. Noy-Meir (1973) estimated that 25–75 mm of annual precipitation was needed to sustain the vegetation of arid ecosystems, and that precipitation amounts above this zero-yield threshold would increase production by 0.5-2 mg dry $wt^{-1} \cdot g^{-1}$ water. Similar analyses have since been conducted for the North American deserts by Webb et al. (1978). These investigators reported that minimum water requirements of 38 and 170 mm of annual precipitation were necessary for sustaining the perennial vegetation of the hot and cold deserts, respectively. Production/water use efficiencies above these zero-yield thresholds were 0.3 and 1.1 mg dry $wt^{-1} \cdot g^{-1}$ water, respectively.

In years with abundant rainfall, the above-ground production contributed by species of annual plants may constitute one-half of the total community production (e.g., Evenari et al. 1976, Szarek 1979). Their contribution to community production varies according to the microhatitat in which they occur. During years with low precipitation, winter-active annuals growing below the canopy of small trees and shrubs in the Sonoran Desert produced nearly twice the biomass on an areal basis than plants growing in the interspaces (Halvorson and Patten 1975, Patten 1978). The production was nearly equal in these two microhabitats during years with abundant rainfall. Finally, it should be noted that in some communities, e.g., the saltbush (Atriplex) community of the Negev Highlands and the saltbush-sagebrush (Artemesia) community of the Great Basin Desert, production by native annual species appears to be insignificant unless the habitat is disturbed.

Productivity Potential

The accumulation rate of plant biomass is limited by the productivity potential per unit foliage (or stem) biomass. Stem succulent species, e.g., cacti, have the lowest relative growth rate since they are evolutionarily adapted to minimize transpiration. Opuntia inermis, which

heavily infested eastern Australia in the 1920s, has a maximum growth rate of 0.043 g dry $wt \cdot g^{-1} \cdot day^{-1}$ under optimum conditions for young cladophylls (pads) (Osmond et al. 1979). This productivity potential, estimated from the rate of CO_2 assimilation, is at least 3- to 5-fold greater than that of older cacti growing in desert habitats (e.g., Nobel 1977). Indeed, incremental growth rates decrease markedly with age (Hastings and Alcorn 1961). The arido-active creosote bush (Larrea tridentata) has a maximum observed relative growth rate of 1.44 g dry $wt \cdot g^{-1}$ leaf dry wt per growing season (Cunningham et al. 1979). The production rate of this species appears to be inversely related to the leaf retention time (Syvertsen and Cunningham 1977), which is normally 12 months for field-grown plants (Burk 1970). Other arido-passive shrub and tree species have relative growth rates, which range from 0.94 to 1.20 g dry $wt \cdot g^{-1}$ leaf dry wt per growing season (Szarek 1979).

At the community level, total above-ground standing live biomass is more frequently measured, and relative production rates, computed on the basis of g standing biomass per year, are 0.17–0.49 for arido-active shrubs of the Negev Highlands (Evenari et al. 1976); ca. 0.26 for the dominant arido-passive saltbush and winter-fat (Ceratoides lanata) shrubs of the Great Basin Desert (Calwell et al. 1977); and 0.11–0.46 at four sites generally dominated by arido-passive shrub species in the North American deserts (Szarek 1979).

Biomass Allocation

Though the roots of plants native to hot deserts extract a maximum of moisture from the soil, their biomass is relatively low. Winter-active annuals have the lowest root/shoot ratios, with values ranging from 0.2–0.5 (Noy-Meir 1973). Since this earlier review, a consistent root/shoot ratio of 0.2 has been observed during vegetative growth of eight Mojave Desert annuals and may represent the minimum root investment for optimum growth (Bell et al. 1979). For perennials in hot deserts, the root/shoot ratio varies according to species, but in the majority of cases it is less than one (e.g., Barbour 1972) and correlates strongly with the above-ground biomass of the species (Wallace et al. 1974).

In the North American cold desert (Great Basin), the majority of communi-

ty biomass is below-ground. The dominant shrub species include shad-scale (Atriplex confertifolia) and winter-fat, which have root/shoot ratios of 7 and 4, respectively (Caldwell et al. 1977). As much as 25% of the shad-scale root system is replaced annually, and below-ground productivity comprises more than 75% of total plant productivity. The high turnover of roots may be important for extending the duration of photosynthesis into the dry season (Caldwell and Camp 1974). There is increasing evidence that the maintenance of large root systems in cold desert species is facilitated by seasonal acclimation in root respiratory capacity (Holthausen and Caldwell 1980).

Irrigation of desert species increases production until soil texture, soil salinity, and nutrient levels (especially nitrogen and phosphorus) become limiting. Short-term irrigations should be restricted to months when temperatures are optimum for growth. Hodgkinson et al. (1978) demonstrated that early summer watering, even when supplemented with nitrogen fertilization, failed to stimulate shoot elongation or any dry weight increase in the spring-active shrubs of shad-scale. Bamberg et al. (1976) and Cunningham et al. (1979) have reported similar relationships between the time of watering and growth responses of other desert perennials. Long-term irrigations significantly increase above-ground biomass, which ultimately stabilizes at a new equilibrium (Evenari et al. 1977). Year-long irrigation of cultivated apricot trees (Prunus armeniaca) increased peak biomass approximately 2-fold, with a 5-fold greater relative production of reproductive biomass. When creosote bush receives supplemental water, the biomass allocated to vegetative structures is proportionately greater than that allocated to reproductive structures (Cunningham et al. 1979).

Extensive studies conducted in the Mojave Desert demonstrate that the biomass allocation of the community is dependent upon the year-to-year variation in precipitation (e.g., Turner 1973, 1974). Site-wide community production and biomass allocation has been studied for more than 30 winter-active annuals and 7–9 perennials of nearly equivalent community importance. The percentage of root biomass was not significantly different between wet and dry years. The percentage of leaf and flower biomass generally decreases, whereas those of stem and fruit biomass increase during wetter years. With optimum growth con-

ditions, the reproductive biomass of annuals can even exceed that produced by perennials. The latter allocated nearly 85% of their total production to photosynthetic tissue during the dry year of 1974, and only 4% to reproductive tissue.

Unfortunately, sufficient information is not yet available to predict the environmental and biological control of primary production in desert ecosystems. The bar-day formulation, which describes the time-accumulated drought stress during vegetative growth, adequately predicts the potential carbon gain of cultivated apricot trees and aridoactive shrubs of the Negev Desert (Schulze et al. 1980). The stress-degree day formulation, which describes the time-accumulated temperature stress during reproduction, accurately predicts the reproductive yield of annual crop species (Idso et al. 1980). Both formulations warrant validation with native species of other desert ecosystems. The greatest progress in modeling primary production has come from the extensive studies of creosote bush. A simulation model is in a heuristic stage (Cunningham and Reynolds 1978), although there has been no attempt to compare model predictions with field data.

CONSUMER ORGANISMS

A relatively large amount of net production in desert ecosystems goes into storage or reproductive organs and, thus, provides food for consumers. Most studies on desert consumers have centered on "grazing herbivores" which represent the first or primary consumer level, or on the activities of detritivores; little is known about the energetic efficiencies or productivity of higher trophic level organisms. Because xeric environments typically have fewer component populations, dominant species generally have a high trophic importance. Hence, a thorough understanding of the energetics of a dominant species can provide considerable information on community energy flux in general.

Invertebrate Herbivores

A portion of the food web of the grasshopper *Trimerotropis pallidipennis*, an important herbivore in the Sonoran Desert, is diagrammed in Figure 1. The complex feeding and predator-prey relationships illustrated here can also exist in desert ecosystems in which the energy

base and the higher trophic levels contain fewer species. A case in point is the Namib Desert dune ecosystem which, in addition to the above, for the most part lacks decomposer microorganisms and important detritivore groups such as termites, millipedes, and isopods (Seely and Louw 1980). In this particular ecosystem, the grazing food chain and the detritus food chain parallel one another, with the energy ultimately consumed by the higher trophic level organisms being derived principally from the detritus.

The fluctuation and uncertainty of available resources and the stresses imposed by the harsh environmental conditions require consumers in desert ecosystems to be both opportunistic and flexible in their feeding behavior. Grazing herbivores consume a variety of plant species and plant parts with their preferences depending upon the season and the state of the vegetation. More specialized small herbivores such as desert rodents, whose diet consists predominantly of seeds, still consume the green portions of shrubs and succulents, and even small invertebrates. The diets of desert carnivores are mixed to such an extent that "omnivory" more accurately describes their mode of feeding. Shifts in food preferences obviously reflect food availability, but may also be dictated by the water, salt, and nutrient needs of the animal (Noy-Meir 1974). The alkali grasshopper, *Anconia integra*, a common herbivore species of halophytic plant communities in the Sonoran Desert, exhibits a marked shift in food preference from *Atriplex canescens* (four-winged saltbush) to *Suaeda Torreyana* (seep-weed) during hot summer months,

suggesting selection of a more concentrated source of calories and possibly water (Burkhart 1978). Similarly, the collared peccary *(Tayassu tajacu)* feeds on a mixed diet of cacti, tubers, and dry browse, but eats the succulent prickly pear cactus almost exclusively during dry periods to help maintain a positive water balance (Schweinsburg 1969, Zervanos and Hadley 1973).

Important invertebrate primary consumers in desert ecosystems include ants, grasshoppers, and other herbivorous insects. Ant colonies having densities of 2,000–4,000 colonies per hectare (ha) were observed at study sites in the Chihuahuan Desert, making them the most numerous insect present with the possible exception of termites (Schumacher and Whitford 1976). Harvester ants will remove a significant fraction of the seeds produced in a given year (Tevis 1958, Mott and McKeon 1977, Brown and Davidson 1977, Ludwig and Whitford in press) and, in so doing, can influence both species diversity and individual plant numbers in a desert community (Brown et al. 1979a). Grasshopper foraging activities can also have a significant impact on productivity in arid regions. Burkhart (1978) estimated that the alkali grasshopper, *Anconia integra,* consumed 2.6% of the perennial net primary productivity of a saltbush community in the Sonoran Desert. When production of litter during feeding was included, total vegetation removed equaled a maximum of 5.2% of the net primary productivity. In a similar study conducted in the Mojave Desert, Mispagel (1978) found that the grasshopper *Bootettix punctatus,* which feeds exclu-
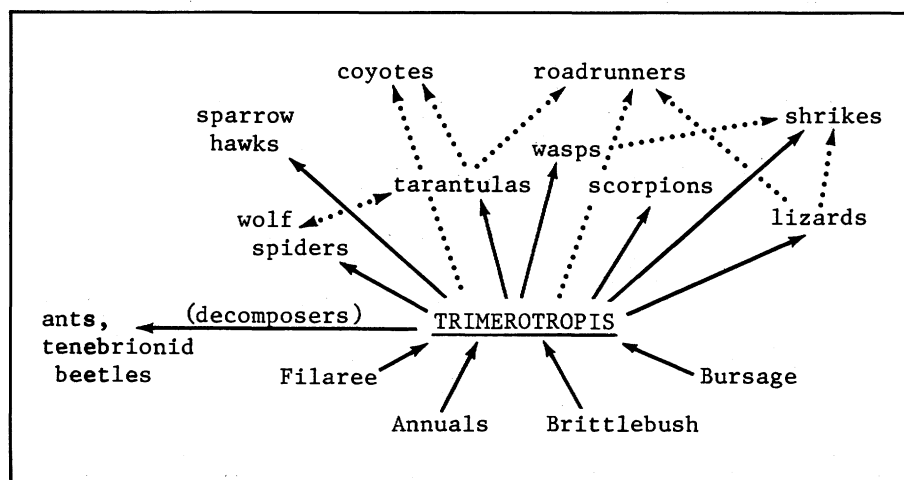

Figure 1. Partial food web for the grasshopper *Trimerotropis pallidipennis* in the Sonoran Desert. Arrows indicate direction of energy and nutrient transfer. Solid lines indicate preferred food items of the grasshopper and its principal predators. Dotted lines indicate infrequent or presumed predators and predator-prey relationships between representatives of the higher trophic levels.

November 1981

sively on the creosote bush, *Larrea tridentata,* consumed from 0.8 to 1.9% of the host plant's annual leaf biomass. Mispagel hypothesized that grazing by *Bootettix* may actually be beneficial to the physiology of *Larrea* as a result of the reduced transpiratory surface area caused by the defoliation (*Larrea* typically drops some of its older leaves during the driest months) and the apparent stimulatory effect on new growth caused by pruning prior to the onset of late summer rains. Millipedes, termites, and isopods also feed on live plant material; however, their primary trophic function is associated with the "detritus food chain" and will be discussed in the section on decomposers.

Vertebrate Herbivores

Most vertebrate herbivores are conspicuous and probably important components of natural desert ecosystems. However, quantitative data on biomass and percentage utilization of community primary productivity are available for only a few species. Grazing by herbivorous lizards has only a minor effect on energy flow. A Mojave Desert population of chuckwallas *(Sauromalus obesus)* consumed approximately 9 megacal · $ha^{-1} \cdot yr^{-1}$, which is less than 1.5% of the estimated net primary productivity of this community (Nagy and Shoemaker 1975). Birds are important primary consumers through their seed harvesting activities, although very few species are specialized granivores (Brown et al. 1979b). In the Sonoran Desert, species which are for the most part "resident granivores" include the mourning dove *(Zenaidura macroura),* the ground dove *(Columbigallina passerina),* the house finch *(Carpodacus mexicanus),* Gambel's quail *(Lophortyx gambelii),* and the black-throated sparrow *(Amphispiza bilineata).* Other resident species such as Abert's towhee *(Pipilo aberti)* and the curve-billed thrasher *(Toxostoma curvirostre),* which are primarily insectivorous, will consume large quantities of seeds during winter months when insect numbers are reduced. The seed-harvesting process is also strongly influenced by the arrival of large mixed-species flocks of finches into desert regions during the winter.

The grazing impact of mammalian herbivores in arid regions has been intensively studied. Merriam's kangaroo rat *(Dipodomys merriami)* in southeastern Arizona consumed only 1.2% of the total net primary production (5,700 megacal

$ha^{-1} \cdot yr^{-1}$) and up to 9.8% of total available production (Chew and Chew 1970). This same species in the Mojave Desert consumed 6.9% of the total net production (1,400 megacal $ha^{-1} \cdot yr^{-1}$) and 10.7% of the total available production (Soholt 1973). Although these values represent only a small proportion of the total net primary production, *D. merriami's* preference for seeds (75% of total diet) may have a great impact on the production of a single plant species. Thus, ants and rodents, the two principal granivores in desert ecosystems, may together consume most of the seeds produced (Brown et al. 1979b). Indeed, it has been demonstrated experimentally that the two taxa compete and inhibit each other when they occur together, and the each taxon is able to harvest more seeds and increase in numbers when the other is excluded (Reichman 1979, Brown et al. 1979a). Despite the heavy seed consumption by rodents, Reichman (1979) proposed that by reducing seed densities in clumps, thus reducing potential competition between subsequent seedlings, and by burying seeds in microhabitats which may enhance germination, rodent foraging activities may also have a positive effect on the plant community.

Whereas herbivorous rodents are primarily seed-eaters, desert hares and rabbits are the primary mammalian consumers of annuals, including grasses. Jack rabbits *(Lepus californicus)* in the Mojave Desert metabolized (assimilation minus urinary energy losses) 65% of the energy contained in spring annuals, but only 18% of the energy available in the shrub browse and dry annuals that constituted their winter diet (Shoemaker et al. 1976). An 80% efficiency of assimilation was found for the collared peccary *(Tayassu tajacu)* fed prickly pear cactus (Zervanos and Hadley 1973). Furthermore, they estimated that a herd of 25 peccaries would consume approximately 20% of the annual production of prickly pear in their home range.

Large domestic mammals grazing on arid vegetation consume between 5–75% of the total primary production (Noy-Meir 1974). These species can have a detrimental effect on plant production and reproduction if their numbers and energy requirements surpass the range's capacity to support them. This is especially true in arid regions where long periods of drought have greatly reduced the plant biomass from the previous production pulse, forcing the herbivores to turn to limited plant reserves (Noy-Meir 1974).

Carnivores

Desert carnivores include certain insects, arachnids, lizards, snakes, insectivorous birds, larger birds of prey, and a variety of small- to medium-sized mammals. Few of these species, however, are strictly carnivorous; the majority exhibit a mixed diet that includes plant materials. Arachnids are perhaps the most important carnivorous group among the invertebrates and are likely to be responsible for transfering significant amounts of energy from the herbivore to the higher consumer trophic levels. In North American deserts, scorpions and spiders maintain sufficiently dense and stable populations to be significant in energy transfer. Scorpion communities are usually composed of 5–13 species with one species numerically dominant. At a desert sand dune site in the Mojave Desert, Polis (1980) found maximum total densities for the scorpion, *Paruroctonus mesaensis,* exceeded 40 individuals/100 m^2, and surface density on a given night was often greater than 20/100 m^2. Although this species was observed to feed on 95 different species of prey, scorpions of the same species were the most important diet item in terms of ingested biomass (Polis 1979). Spider densities are typically higher than those of scorpions in desert habitats having a greater plant assemblage; a desert creosote community averaged 24,900 individuals/ha or approximately 250 spiders/100 m^2 (Chew 1961). Because most scorpions and many spiders are active burrowers, they are also important in mixing and aerating desert soils, which improves plant stability and productivity.

DECOMPOSERS

Decomposition in desert ecosystems results from both abiotic and biotic processes, with water again the controlling factor. Desert soils contain most functional and taxonomic groups of microorganisms (Ghabbour et al. 1980, Vollmer et al. 1977, Went and Stark 1968). However, their activities are limited to periods when moisture is adequate, especially when the decomposition of litter and wood at or near the surface is considered. As a result, dry litter can accumulate to such an extent that it exceeds the above-ground living biomass. Weathering and erosion by wind are responsible for the disappearance of much of this above-ground litter and the standing dead material of annual plants.

The moisture limitation on microbial activity in arid ecosystems has enhanced the importance of decomposition by detritus-feeding arthropods such as nematodes, termites, isopods, acarids, and millipedes. The life history patterns, general distribution, and trophic roles of these desert detritivores have been recently reviewed by Crawford (1979). In certain warm-desert regions, nematodes are at least numerically dominant (Freckman and Mankau 1977), but quantitative data on their role in soil energetics are lacking. Termites, where they are abundant, have a significant impact on energy flow and nutrient cycling. Density estimates for two sites in the Chihuahuan Desert were 61 and 440 colonies/ ha, with each colony consisting of 5,000–10,000 individuals (Johnson and Whitford 1975). Although portions of yucca logs and cow dung were preferred forage items, extensive consumption of dead annuals by termites occurred in late fall when microclimatic conditions were more favorable for surface feeding at night. Termites also consume significant amounts of standing wood (Haverty and Nutting 1975) and are responsible for the removal of considerable creosote bush leaf litter, especially older leaves, which apparently contain lower levels of anti-herbivore allelochemics (Fowler and Whitford 1980). Overall, it has been estimated that subterranean termites consume about 50% of the net annual production at the Chihuahuan Desert study sites (Johnson and Whitford 1975) and over 90% of the fallen dead wood in the Sonoran Desert (Nutting et al. 1975).

Millipedes are also conspicuous detritivores in parts of the Chihuahuan Desert. One of the most common species, *Orthoporus ornatus,* feeds on dead plant material, superficial tissue of desert shrubs, sand, and parts of arthropods (Wooten and Crawford 1975). Crawford (1976) measured densities of *O. ornatus* of 1302 individuals/ha and further estimated that this species ingests at least 0.24% of the community's net primary production. This percentage is well below that estimated for termites, but is comparable to consumption values reported for millipedes in other ecosystems. In the Negev Desert, Israel, the isopod *Hemilepistus reaumuri* is a saprovore, herbivore, and a microbivore (Shachak et al. 1976). Populations of this species, which achieved a summer maximum density of 5–18 isopods/m², consumed 1.1–4.3% of the available plant material and 0.5–5.4% of the organic matter in the soil crust annually (Sha-

chak et al. 1976). The pulmonate snail *Sphincterochila zonata,* which also feeds on the tightly packed soil crust in the Negev Desert, consumes 0.6–6% of the annual net primary production of algae present on the soil surface (Shachak and Steinberger 1980). Millipedes, isopods, and snails, by ingesting organic matter and inorganic soil particles, may alter the substrate in such a manner to influence the rate of decomposition by microbes and, hence, indirectly affect plant productivity through the release of nutrients. Because soil is a standard part of their diets, Crawford (1979) has also suggested that these animals may be reservoirs and dispersal agents for fungi and other decomposition-associated microorganisms.

In the Namib Desert dune ecosystem, the formation of detritus results from the ephemeral life of the dune grasses and the abrasive action of surface winds (Seely and Louw 1980). Once formed, the detritus degrades slowly and becomes an important energy source for a variety of tenebrionid beetles which replace termites, isopods, and millipedes as the principal decomposers in this desert community (Seely and Louw 1980). Another unique feature of this dune ecosystem is the apparent absence of microbial decomposition. Instead, degradation of the cellulose-rich detritus is accomplished by endogenous cellulose enzymes contained in the digestive tracts of the beetles.

NUTRIENT CYCLING

Nutrients are essential for maintaining the continuity and stability of all ecosystems. In arid regions, nutrient levels may limit plant productivity as does moisture availability. Nitrogen appears to be the key limiting nutrient in most hot deserts, while in arid regions of Australia, phosphorus levels are also often insufficient (Charley and Cowling 1968). Seely and Louw (1980) found both minerals to be deficient in the dune sands of the Namib. Deficiencies in essential nutrients result from a combination of low decomposition rates, short-term periods of rapid growth after precipitation that exhaust nutrients faster than they can be replaced, and intrinsically low nutrient content of the soil in some regions.

Nitrogen fixation by soil algae and bacteria probably provides a major input of nitrogen in most desert ecosystems. Annual nitrogen fixation by algal lichen crusts in the Great Basin Desert was estimated at 10 to 100 kg N ha⁻¹ yr⁻¹

(Rychert and Skujins 1974). Blue-green algae (*Anabaena* and *Nostoc* spp.) perform a similar function in the desert west of Alexandria, Egypt (Ghabbour et al. 1980). In the latter study, it was further demonstrated that inoculation of the soil with microfauna (Protozoa, Nematoda, etc.) stimulated nitrogen and organic carbon fixation under certain combinations of moisture and temperature. An exception to the usual pattern is found in the Namib Desert dune ecosystem where significant algal components are absent. Here the major source of nitrogen is apparently derived from uric acid excreted by the tenebrionid beetles that forage on the accumulated detritus (Seely and Louw 1980). Symbiotic fixation by leguminous and other naturally occurring plants may be significant in some warm-desert communities, but these processes thus far have received little quantitative study (Noy-Meir 1974).

The nutrient supply in arid regions is confined largely to the upper surface (0–5 cm); lower soil layers are typically "nutrient poor" due to low decomposition and leaching rates. As a result, large quantities of nitrogen are lost to the atmosphere via erosion and volatilization, leaving only a small percentage available to roots of higher plants. Nutrient return via litter and dead plants is also strongly localized around the plants (Garcia-Moya and McKell 1970). The concentric pattern of nutrients and microbial activity that results may be an important factor limiting the establishment and growth of other plant species in the spaces between the permanent vegetation (Muller 1953).

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