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DESERT ECOSYSTEMS: ENVIRONMENT AND PRODUCERS

❖ 4051

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INTRODUCTION

The purpose of this review is to examine present knowledge on structure and function of the ecosystems of deserts or arid lands, terms used synonymously here. It focuses attention on features distinctly characteristic of deserts, i.e. common to all or most of them but not to most other ecosystems. It explores the implications of these characteristics for systems analysis and simulation modelling of arid ecosystems, and reviews recent efforts in these directions. The evidence includes results from the rapidly ramifying recent studies in desert ecology, in particular those under the International Biological Program (IBP). Though subjects in desert ecology are being reviewed separately fairly frequently (11, 44, UNESCO Arid Zone Research series), reviews with an integrated approach, such as that by Ross (91) on arid Australian ecosystems, are still rare.

The desert ecosystem is first considered as a whole system, with a sketching out of its dominant diagnostics and some of their deducible consequences. These are then examined in detail with reference to the components of climate, soil, and plants, which bring in more factual evidence and some complicating effects. Sections on consumers (including man) and decomposers, and on feedbacks and modelling in arid ecosystems will be included in the next volume of this series.

Definitions and Characteristics of Arid Ecosystems

The classification used here is generally consistent with the terms and maps of Meigs as used by McGinnies et al (63):

Extreme arid (*E*)—less than 60–100 mm mean annual precipitation;

Arid (*A*)—from 60–100 mm to 150–250 mm;

Semiarid (*S*)—from 150–250 mm to 250–500 mm.

The higher limits refer to areas with high evaporativity in the growing season (e.g. subtropical summer rainfall regions). The limit between *A* and *E* corresponds roughly to the limit between diffuse natural vegetation and vegetation contracted to favorable sites only (67). The limit between *S* and *A* is roughly the drier limit

of diffuse dryland farming; the limit between semiarid and nonarid zones is where such farming becomes a reasonably reliable operation. In this review ecosystems of all three zones are considered, but with emphasis on the typical *A* zone. Life in extreme deserts is scarce and little known, while semiarid ecosystems often have some features of grasslands or woodlands.

There are three main obvious attributes of these arid ecosystems, one almost by definition, two others by correlation with the first: (*a*) precipitation is so low that water is the dominant controlling factor for biological processes; (*b*) precipitation is highly variable through the year and occurs in infrequent and discrete events; (*c*) variation in precipitation has a large random (unpredictable) component.

Let us now ignore the exceptions and define desert ecosystems as "water-controlled ecosystems with infrequent, discrete, and largely unpredictable water inputs."

What are the implications of this definition for the behavior of the system, in particular the patterns and dynamics of energy flow in it and the adaptive strategies of its organisms? What are the implications for our attempts to understand this behavior and to represent it by models (conceptual, graphical, and mathematical)?

Water-Controlled Ecosystems

Attribute *a* means that the rates of energy flows to and within the ecosystem are controlled by levels of available water, directly or indirectly. Energy flow in a radiation- or temperature-controlled ecosystem may be well represented and understood by a classical diagram (Figure 1a), in which energy transfer is controlled by energy levels in the donor and recipient components. Most important, the flow of energy into the ecosystem, photosynthesis, is controlled by the level of radiant and/or heat energy available to the plants. But Figure 1a would be a meaningless model for a desert ecosystem if it did not represent the levels of available water which (rather than energy levels) determine the rate of energy inflow. These levels could be introduced as external factors, but it would be more meaningful to draw up a water flow model alongside the energy flow model, utilizing the fact that water moves in the system through essentially the same compartments and paths as energy and carbon (Figure 1b). The most important link between the two is the fact that the water status of the plant, through the stomatal control mechanism, influences the rates of both photosynthesis (*A*, energy and CO_2 inflow) and transpiration (*T*, water outflow). Changes in plant water content are usually small compared to the transpiration flow, so that the latter is almost equal to water uptake from the soil. Hence both *A* and *T* are in effect controlled by available soil moisture. They are also dependent similarly on other factors influencing the stomata (light, temperature, air humidity) and on the amount of vegetation. Thus the water-controlled nature of arid ecosystems is essentially due to the tight coupling of energy inflow with water outflow, or indeed with water throughflow in the soil-plant-atmosphere path. Or the vegetation in an arid system may be regarded as a converter of a water inflow to an energy inflow. The critical factors for production are those determining the water inflow and the efficiency of the conversion.

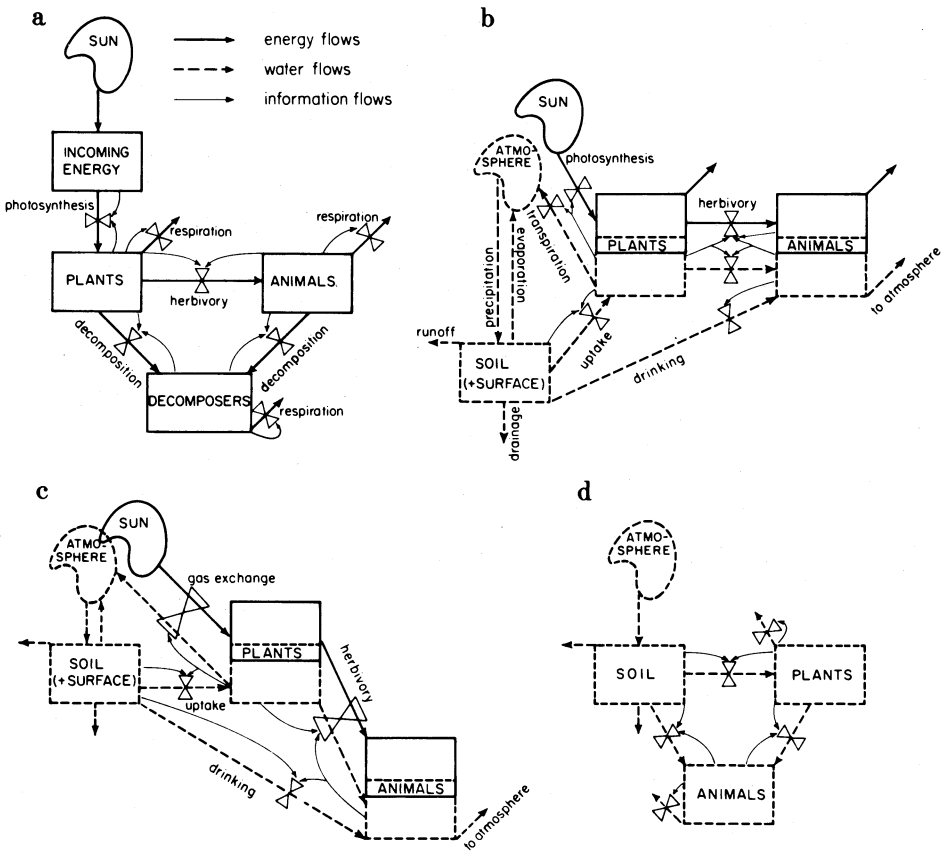


Figure 1 Compartment models of desert ecosystems: (a) Energy flow model; (b) Energy and water flow models combined (decomposers not shown); (c) Same, simplified; (d) Water flow model alone.

There may be other couplings. Herbivory and carnivory usually involve transfer of both food (energy, C) and water from prey to consumer by the same process. In arid ecosystems the rate of food consumption may often be controlled by the availability of water, in the food or as surface drinking water, and by the water (and heat) balance of the animal (62). Thus secondary as well as primary energy flows are coupled to, and often dominated by, corresponding water flows (Figure 1c). Indeed, one is tempted to drop the energy model altogether and regard the water flow model as a self-sufficient representation of life processes in a desert ecosystem (Figure 1d). Most organisms are fairly homeohydric, so that the amount of water in any particular biological compartment is a good measure of the amount of living material in it; in poikilohydric organisms (seeds, microorganisms) water content is closely related to biological activity. Such a model would be structurally similar to

the energy flow model of an energy-controlled system (Figure 1a). Both have three trophic levels, flows between which are in general controlled by levels in donor and recipient compartments. The most significant difference is that in the water flow system the first trophic level, soil water, has no positive feedback control over its inflow comparable to the feedback from growing plants to photosynthesis.

This similarity highlights an important property of water as a limiting factor in an ecosystem; like energy, but unlike most nutrients, water is not recycled in the system but cascades through it (if we define an ecosystem locally rather than on a global scale). The amount of water recycled from plants and animals back to soil is negligible, and relatively little evaporated or transpired water is recycled locally (e.g. as dew). Most of it is lost from the local ecosystem by convection, to be precipitated in a distant ecosystem. Water is essentially a noncyclable, periodically exhaustible resource, replenished only by new input.

Thus even if our interest is in the trophic energy balance of the ecosystem or any of its subsystems, in an arid ecosystem study of this would be meaningless without considering its water balance as well. If we define a local ecosystem, including vegetation, animals, the root layer of the soil, and the canopy layer of the atmosphere, then the balance for any period is

$$P = R + \Delta S + D + E + \Delta V + T + \Delta A + L \quad 1.$$

where P = precipitation, R = runoff/runon (all horizontal flows across the boundaries), ΔS = change in soil (and surface) storage, D = drainage (vertical flow beyond the root layer), E = evaporation (from soil surface), ΔV = change in vegetation storage, T = transpiration, ΔA = change in animals storage, and L = evaporative losses from animals.

ΔV , ΔA , and L are usually negligible compared to the rest, and ΔS is small for periods of one or several years. The component driving the energy flow to the biotic subsystem is the amount of transpired water

$$T = P - R - D - E \quad 2.$$

Precipitation is the input or "driving variable." It is not controlled by factors within the local ecosystem, but its partition between the biologically active T and the "losses" R , D , E , and the partition of T in space and time and between organisms, to a large extent are controlled by such factors. The nature of the input is discussed first, then the factors affecting its partition.

DESERT CLIMATE: RAINFALL, THE MASTER INPUT

Systems with Discontinuous Input

While temperature, radiation, and nutrient input to ecosystems vary fairly continuously over the year, precipitation usually comes in discontinuous packages. In arid regions there are only 10–50 rainy days a year, occurring in 3–15 rain events or clusters of rainy days, of which probably no more than 5–6 (sometimes only one) are sufficiently large to affect biotic parts of the system.

Thus the input driving the system comes in "pulses" of very short duration relative to the periods of zero input between them. The response of the system, or any of its parts, to a single input pulse may itself be a pulse (Figure 2a). After a long

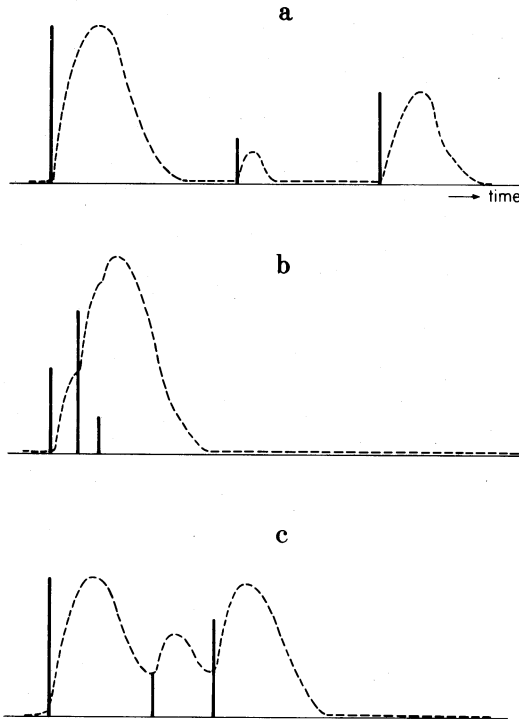


Figure 2 System response to input pulses: (a) widely separated, (b) clustered, (c) with intermediate spacing.

dry period the ecosystem (or most of it) is in some inactive steady state or "zero state." An effective rain event activates biological processes (in particular production and reproduction), and biomass of plants and animals builds up. These processes exhaust the ration of available water supplied by the rain. After a usually short growth period water becomes limiting and both processes and biomass decrease again to a steady state (which may or may not be equal to the previous one). The response of the system to a sequence of rain events depends on the time interval between events relative to the "relaxation time" of the system in response to the individual events. If the former is much larger (e.g. in hot deserts with aseasonal rain) the response will be a series of simple pulses (Figure 2a). If it is much smaller (rain events clustered, markedly seasonal rainfall, slow response, e.g. in cool, winter-rainfall deserts) the effects of the input pulses will accumulate to produce a single larger response pulse (Figure 2b); the total rain of the season may then be considered a single input pulse. In intermediate situations there will be a composite response of distinct but partially cumulative pulses (Figure 2c). The concept and techniques of impulse response used in engineering systems analysis may be applicable at least in the first two cases.

Since many physical and biological processes in deserts occur in fairly discrete pulses, and many responses are of a “trigger” type, Bridges et al (10) have proposed construction of simulation models of deserts in terms of discrete events and qualitative states rather than continuous processes and variables. This was applied, for instance, to models predicting the “phenological states” of plant types from weather conditions in the current and previous seasons.

Westoby (114) and Bridges et al (10) have also questioned the usefulness in deserts of the “level-regulating-flows” paradigm (Figure 3a) which is the now classical representation of each compartment in an ecosystem model. Instead, they suggest the “pulse and reserve” paradigm (Figure 3b). A trigger (e.g. a rain event) sets off a pulse of production (e.g. of annuals). Much of this pulse is lost rapidly by mortality or consumption but some is diverted back into a reserve (e.g. seeds). The reserve compartment loses only slowly during the no-growth period and from it the next pulse is initiated. The authors noted that: (a) flexible transition between an inactive resistant and an active (susceptible) state is highly adaptive in an intermittently favorable environment, (b) the prevalence of this pattern among desert organisms explains the long-term stability of the system despite its extreme short-term variabil-

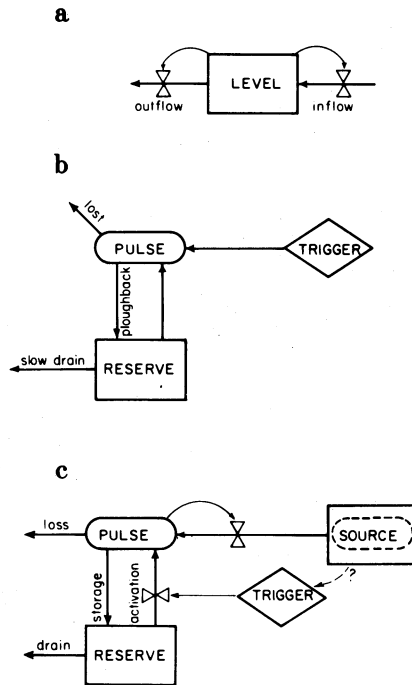


Figure 3 Graphical representations of a biological component in an ecosystem model. (a) The “level-controlling-flows” paradigm. (b) The “pulse-and-reserve” paradigm (from 10, 114). (c) Modified pulse-and-reserve module.

ity, (c) this stability will be endangered only by mechanisms causing overexploitation of the reserves or consistent prevention of backflow to reserves (which may be different from the mechanisms causing short-term variations), and (d) organisms at higher trophic levels must adapt either by adopting a pulse-reserve pattern themselves (e.g. insects), by utilizing reserves of other organisms (e.g. seed-eaters), or by flexible feeding habits, using whatever pulse or reserve is available at any time.

Pulse and reserve modules of various organisms may be combined into a causal (information flow) diagram model of a desert ecosystem (114). Adaptation of Figure 3b to an energy/matter flow model requires some modification (Figure 3c): (a) an inflow to the pulse from a source (a pulse or a reserve of another component) and (b) the effect of both the trigger and the reserve level on the reserve-to-pulse initiation flow.

Systems with Stochastic Input

The master input to arid systems is not only discontinuous but also stochastic. The variation in timing and magnitude of precipitation events has a large random component. This creates special problems for climatologists trying to describe desert climate (inadequacy of averages), for hydrologists and ecologists trying to simulate it in models (inadequacy of deterministic input), and for organisms trying to live in it (optimization in an unpredictable environment).

It is useful to consider rainfall variation at several time-scales, attempting at each to separate some persistent components (pattern) from the random ones.

YEARS The increase in between-year variability with decreasing mean rainfall is well documented in all arid zones. This variation seems to be mostly random. Stories about cycles of good and drought years (with a half-period of 3, 5, or 7 years) are common in the folklore of arid zone people (and in some publications) but have rarely, if ever, been demonstrated statistically. Throughout Australia, Maher (65) found no such persistences and showed runs of wet and dry years to be only random, with a binomial distribution. McDonald (61) found no year-to-year autocorrelation in Arizona. He did detect fluctuations within a period of about 50 years [as found also in the Negev (94)] but these accounted for only 10% of the variation.

MONTHS There is more persistence in monthly variations. In some arid and semi-arid zones there are consistently timed rainy seasons in winter (mediterranean), summer (monsoonal), or spring and fall. In some, rainfall is aseasonal or erratic, i.e. randomly distributed throughout the year (parts of Australia and Sahara), and there are many intermediates between seasonal and erratic. Winter rain is generally the more reliable in areas where it is greater than or about equal to summer rain (e.g. in southeastern Australia), but the opposite is true in some of the mixed-season areas (61) and of course in summer rainfall areas.

DAYS There is a definite tendency of rainy days to occur in sequential runs, which may be expressed by a first-order Markov chain, with different probabilities of rain after rainy and dry days. Fitzpatrick & Krishnan (30) in central Australia found

persistence of wet and dry pentads (5-day periods) with a good fit to the Markov model.

WITHIN-DAYS The distribution of rain intensity at a scale of hours and minutes is important for accurate runoff prediction and is expressed by hydrologists as intensity-duration functions. In arid stations these seem to be parallel with (though lower than) those for humid stations (94).

Meteorologists have long recognized the need to supplement mean annual and monthly rainfall data in arid zones by tables of probabilities of different amounts of yearly, seasonal, and monthly rain, and of weekly and daily rain in different times of the year. Of the various functions which have been fitted to these distributions, the "incomplete gamma" (3, 87) and a Poisson-geometric distribution (31) have been most successful.

While stochastic input has been used in hydrological models (26), ecologists often simply use sequences of actual rainfall data or permutations of these. However, in the first simulation model of an arid ecosystem, Goodall (35, 36) did use stochastic input with a first-order Markov model for raindays and an empirical probability distribution of rain quantity per rainday. Repeated randomized runs then provided a distribution and thus confidence limits for outputs. The development of realistic stochastic models for rainfall at all time scales, and the estimation of their parameters for sites, will become increasingly important as ecosystem modelling emerges from a validation stage to a predictive and applicative one.

The main problem that randomness poses to desert organisms is in the adjustment of their responses to environmental signals so as to optimize growth and survival. In particular, what signals should be used to trigger the activation flow from reserve to an active pulse (e.g. germination, shoot-growth in perennials, breeding in animals) and how much of the reserves should be used? Secondly, when and how fast should the storage flow start? (e.g. seed setting, translocation to reserves). In a predictably seasonal environment any of a number of correlated signals (the first shower, temperature, photoperiod) may serve as indicator of the start of a growing season in which reproductive success is almost certain; there are also several reliable indicators of its approaching end. Organisms in such environments are likely to respond to any one of these simple signals and can commit all or most of their reserves to each seasonal pulse.

When timing and magnitude of rainfall are uncertain, full response to a simple signal (e.g. a light rain) may be premature and may severely decrease rather than increase the reproductive potential (particularly for short-lived organisms). In a study of optimal strategy in random environments with special reference to germination of annuals (19, 20), two main conclusions were drawn: (a) The optimal germination fraction (in general, reserve commitment fraction) decreases as the probability of an unsuccessful outcome increases; thus in highly uncertain environments the optimal strategy is one of cautious opportunism. In such environments, longevity of reserve forms is also of high adaptive value. (b) Growth is optimized by maximizing correlation between the external signals for activation and a successful outcome. In an uncertain environment, with low correlations between the vari-

ous signals and between signals and their outcomes (e.g. a desert), this requires organisms to process a larger amount of environmental information to regulate their responses (and to pay the cost of this processing and of missed opportunities due to cautious response).

Indeed, seed longevity and seed heterogeneity, which allows delayed or differential germination, are common in desert plants (52, and papers reviewed there). Many of them also have complex germination regulation mechanisms which attune their response rather finely to a precise combination of environmental factors or to a sequence of events (27, 38, 52, 74).

Spatial Variation in Rainfall

Imposed on the temporal variation, and interacting with it, is the spatial variation of rainfall, persistent and random, at all scales. Persistent differences occur not only at the regional scale but also at scales of 0.1–10 km. In particular, the orographic increase of rainfall with altitude (4) and the effects of direction and speed of wind, degree of slope, and rain angle on differences in rainfall between windward and leeward slopes should be important in hilly arid regions (25). In a 1 km² watershed in an extreme arid area Sharon (95) has reported an inverse orographic effect (valleys consistently receiving 40% more rain than ridges), probably related to local wind patterns.

Random spatial variation may be expressed by the lack of correlation in daily, monthly, or yearly rainfalls between two stations. The steepness at which this correlation decreases with distance depends on the size of rain systems and is an indicator of the spottiness of rainfall. It is greater for summer (thunderstorm) than for winter (cyclonic) rain (61), and seems to increase from humid to semiarid and to arid regions (96). For stations 50–200 km apart correlations are often very low even for seasonal or annual totals (61, 94). Daily rainfall is often localized at a much smaller scale. In several areas a considerable proportion of rainfall was found to come as thunderstorm “cells” of 3–8 km diameter, randomly distributed in space (31, 96) and discharging rain on a patch or a strip of land.

This frequently high spatial variation, both persistent and random, has obvious implications for interpolation of rainfall records and for input to hydrological models (26). It can hardly be ignored in ecological modelling in arid zones.

Spatial variation in rainfall (in addition to runoff redistribution and edaphic diversity) is one of the causes of patchiness in desert environments, affecting both species diversity and the adaptive behavior of organisms. It offers highly mobile organisms some compensation for the hazards of high and unpredictable temporal variability. Low spatial correlations mean that at a time of drought in one locality there is still a fair probability of favorable conditions in some other part of the region of which mobile organisms can take advantage. Opportunistic migration, “following the rains,” is indeed known for some birds (64) and large mammals (e.g. 75) in arid zones and may be obligatory for their survival. The inclusion of such nomadic populations in ecosystem models requires modelling at a regional rather than a local scale.

Other Climatic Factors

Radiation as such is often assumed not to be a limiting factor in deserts. This may require some caution in view of stomatal behavior of plants which often restricts photosynthesis to periods of low evaporativity (e.g. early morning), when radiation is also low.

Evaporativity (E_o = potential or free-water evaporation), correlated with radiation, temperature, wind, and air humidity deficit, is much higher than precipitation in arid climates in most periods. Being the "evaporative demand" on evaporation and transpiration, evaporativity has a significant effect on the water balance and biological processes tied to it. This is evident in vegetation differences between north- and south-facing slopes, and in many "drought-evading" behavioral adaptations of plants and animals which utilize the marked difference in E_o between day and night.

Temperature often influences plant and animal activities in deserts to an extent which requires modification of the earlier approximation that "deserts are water-controlled ecosystems," though temperature effects are usually in close interaction with the water factor. Rainfall seasonality in relation to temperature has a strong modifying effect on plant growth dynamics. When rain occurs in a warm season (low-latitude or summer-rainfall deserts, e.g. Northern Australia, Sahara, Sahel), both soil moisture and temperature are simultaneously optimal and an almost immediate and very rapid growth pulse follows (e.g. 92). Production is unlikely to be significantly affected by too high temperatures as long as sufficient moisture is available. Where rain or snow fall in a cold season (high-latitude or altitude winter-rainfall deserts, e.g. parts of Central Asia, Great Basin), root and shoot growth are almost completely inhibited by low temperatures until spring, even though moisture is available. Since evaporation losses are also low in winter one may assume as a first approximation that the cold season precipitation is stored until the growing season starts. However, the eventual utilization and production from this water may sometimes be reduced by after-effects of an extremely cold winter (13).

In arid zones where rain falls in a cool winter (mediterranean-type climates), growth is slowed but not fully inhibited by winter temperatures, often after being initiated in autumn. Hence in these deserts spring production is greatly enhanced by autumn rains.

The effects of temperature on growth may be partly compensated for by adaptation of plants to prevailing temperatures. Species from warm-season rainfall zones have higher optimal temperatures for photosynthesis, and in some species temperature acclimation occurs during the growing season (14, 103). In arid zones with two rainfall seasons, different sets of species germinate after summer rain and after winter rain, due to different temperature requirements for germination (71, 112).

THE SOIL: STORE AND REGULATOR IN THE WATER FLOW SYSTEM

A discussion of the role of the soil in arid ecosystems is inseparable from a discussion of the ecosystem water balance and its dynamics. The edaphic factors which are

often so prominent in arid zones operate almost always by modification of the water regime. The soil acts as: (a) a temporary store for the precipitation input, allowing its use by organisms; (b) a regulator controlling the partition of this input between the major outflows: runoff, drainage, evaporation, and uptake transpiration, and of the latter (biologically active) flow between different organisms.

Some aspects of these flows relevant in deserts are considered in order of increasing time lag after a rain event.

Infiltration, Runoff, and Horizontal Redistribution

Most of the water input (rain + runoff) at any point either infiltrates the soil or runs off the surface within minutes to hours. Interception by plants causes only minor evaporative losses in arid zones (due to low cover), but may, in conjunction with stemflow, create marked patterns of soil wetting under and around shrubs and trees (86, 99). Surface storage for more than a few hours occurs in deserts only in low sites receiving runoff, with low-permeability soils.

Detailed mathematical models of the infiltration/runoff partition at a point, with a resolution time of minutes, have been based on generalized flow equations (40, 41) or on explicit functions of time (15, 99). An approximation is provided by empirical functions relating daily runoff to daily rainfall (26, 106) and expressing the increase in runoff proportion with rain intensity for an area with given surface properties. Both types of functions have been used in models predicting runoff from whole watersheds in arid zones (15, 26, and others from the Tucson group).

Runoff from sandy and stony surfaces is usually lower than from clayey and silty ones, particularly if the latter are crust-forming (28). Cover of dead and living vegetation usually increases infiltration in arid zones (106) by reducing rain impact and probably some physical or chemical modifications of the surface (59).

Modelling and measurement of infiltration/runoff are mostly done either by soil physicists for uniform areas up to 1 m², or by hydrologists interested in the water output from the main channel of a large (1–100 km²) heterogeneous catchment. However, much of the ecological significance of these processes is at scales between 1 m² and 100 km², especially as they concern horizontal redistribution of water *within* the catchment. Even in a rain event producing no channel flow, runoff from some areas (sources) may become runoff to others (sinks) and infiltrate there. The infiltration input at any point may be much lower or higher than precipitation, depending on position in the landscape, surface properties, and vegetation. The ensuing spatial variation in soil moisture has significant effects on diversity and production in arid zones. These are widespread, but easiest to demonstrate in areas with regular microtopographical patterns, e.g. the mulga grove-intergroves (98, 84), gilgai plains (16), or furrowed fields. In extreme arid zones it is this redistribution which enables any vegetation to survive in the sink areas at all (51, 67, 119). Runoff models with emphasis on within-catchment redistribution are badly needed.

Vertical Redistribution, Storage Capacity, and Drainage

The movement of infiltrated water down the soil profile can be accurately described by a generalized flow equations model taking account of the relations between water

content, water potential (ψ), and conductivity in each layer (e.g. 40, 41). In most soils a more or less sharp and stable "wetting front" on which the concept of field capacity is based, is discernible for some time. Though it ignores the slow and often significant diffusion across the front (28), the wetting front is a useful abstraction for comparing vertical distribution in different soils from a single parameter: the storage capacity C_w , the difference in volumetric water content between soil at field capacity and "dry" soil. This parameter is 3–6% for sands, 7–15% for loams and silts, 15–25% for clays, and decreases linearly with stone content. The "depth of wetting" by a given rain P is P/C_w , hence proportionally larger for sandy and stony than for fine soils.

Therefore, in coarse-textured soils more water is generally lost by drainage (deep percolation) beyond the root zone. However, it is characteristic of the water balance in arid zones that the depth of wetting by prevalent rains is normally not greater than maximal rooting depth. Hence all soil moisture is evaporated or transpired, and layers beyond that depth are permanently dry (111, 43). Substantial drainage and groundwater recharge flows occur mostly in runon areas and channels and in unvegetated deep-wetting soils (e.g. dunes; 85). In most other sites in arid regions the term D in the water balance is zero or negligible.

Impermeable layers (e.g. of clay, marl) in the profile modify the vertical distribution by causing accumulation of water above them. However, in hard rocks and calcified horizons there often are enough cracks to allow (or even facilitate) the passage of water and roots, thus seemingly shallow soils on such substrates in arid zones may in fact be deep soils ecologically.

Evaporation and the Inverse Texture Effect

Evaporation from the soil may be simulated by the same flow model used for infiltration and redistribution (41). When the surface is wet evaporation is close to the demand E_o , but as the top layers dry out desiccation of deeper layers slows down progressively. The upper 5 or 10 cm are mostly dry within 5–25 days in arid climates and plants have little chance to extract water from this layer. It takes many weeks for evaporation to dry out the 10–30 cm layer, so that roots can effectively compete with it there. For many months there is little direct evaporative loss from beyond 30 cm (34, 85, 86). Thus the total evaporation loss E is proportional to the storage capacity of the top 20 or 30 cm; it will be considerably lower from sandy, gravelly, and rocky soils than from fine soils (2). Also, E will be higher if a given rainfall is distributed over more events. In general, a higher proportion of rain will evaporate in summer (higher E_o) than in winter; therefore summer rains are considered "less effective" than winter rains.

Vegetation cover reduces radiation and wind speed at the soil surface and hence reduces evaporation. Once established, a leafy plant thus controls to some extent the loss of its own resource, as well as creating a favorable microenvironment for other plants and animals. The proportion of the area thus affected is small in arid ecosystems, but may be ecologically significant.

Movement of vapor along soil temperature gradients can be important in dry soils under high daily radiation (90). The main effect is a nocturnal upward flow of

moisture to the surface (66) causing subterranean dew. A similar seasonal flow should occur in autumn, but possible biological effects have not yet been demonstrated.

Condensation of atmospheric moisture as dew is common in coastal deserts, but much less common inland. Whether its absorption by higher plants in the hours before re-evaporating contributes significantly to their water balance is controversial (e.g. 66, 28). It certainly allows a morning pulse of photosynthesis in lichens and algae (54) and is utilized also by animals. According to Walter (111), fog is a useful supplement to soil moisture for plants in the Namib desert, and in parts of the South American coastal desert vegetation depends almost entirely on "combing" moisture out of the fog.

The fact that in arid zones evaporation from upper layers, rather than drainage from deeper ones, causes the largest loss of soil moisture, is the main cause of the "inverse texture effect." In humid climates sandy and rocky soils are considered dry (due to low C_w) and carry relatively poor vegetation. In arid and semiarid climates throughout the world they usually support taller and denser perennial vegetation than do finer soils than it does on fine ones (101, 77). The balance point between the advantage of coarser texture (less E) and its disadvantage (more D) occurs somewhere between 300 and 500 mm rainfall. Thus the inverse texture effect is really diagnostic of arid and semiarid ecosystems as defined above. Other factors contributing to the inverse texture effect are the lower runoff from coarse soils (105) and the reduced evaporation from a stony surface.

Transpiration and Water Uptake By Roots

The total amount of water taken up and transpired by plants (T) depends mostly on what remains after the unavoidable losses by runoff, drainage, and surface evaporation, and also on the rate of uptake from the 5–40 cm layer, in competition with evaporation. The rate of water flow through the soil-plant-atmosphere path depends on the difference in ψ between soil and atmosphere and on the resistances between them, among which the stomatal resistance, r_s , is most frequently dominant. Plants are able to regulate r_s (and hence the flow) rather tightly in response to changes in water demand (E_o) and supply (ψ in soil); this mechanism is essential for optimization of water use in arid conditions. Increased soil resistance due to drying around roots seems to be usually compensated for by root growth (H. P. Van Keulen, personal communication; 86).

Whether transpiration (and growth) is a linear or a step function of soil water content has long been controversial. It is now clear that the shape of the curve depends on E_o and root density (21, 99), or actually on the effectiveness of the plant in adjusting water supply to demand. Over a wide range T may be linear with soil water potential (69). While in crop plants zero transpiration or wilting point is reached at -10 to -30 bars, an ability to use soil moisture down to -100 (or -150) bars seems to be common for arid zone perennials, xerohalophytes, sclerophyllous shrubs, and grasses (69, 99, 115, 47). Local differences in root density and uptake are yet another source of horizontal and vertical patterns in soil moisture

dynamics about which little is known and which could be important in arid communities (86).

Water Balance Models

A number of dynamic models of the overall ecosystem water balance have recently been developed. WATBAL (60) calculates weekly changes in soil moisture storage (S) assuming $(E + T)/E_o$ to be a step function of S ; it was tested with moderate success on an arid grassland (115). A model developed by Specht (102) originally for perennial evergreen vegetation computes a monthly balance, assuming a linear relationship and the regulation of transpiration by the vegetation for year-long water availability. Model NEGEV (93) included a water balance subroutine which considered daily runoff, evapotranspiration (linear with S), and vertical redistribution between layers, based on the field capacity assumption. All these models are consciously simplistic, in using crude empirical approximations for most processes, in not separating evaporation from transpiration (processes which differ in controlling factors and in ecological significance), and in not considering root growth to different layers (important in annual communities). T and E were separated in models by Ross & Lendon (92) and Tadmor & Van Keulen (unpublished); the latter also modelled root growth. Basic models of soil water flow (e.g. 41) could be applied to ecosystem water balance once an uptake-transpiration term was included (76).

There are at present few data on comprehensive water balance dynamics of natural arid and semiarid ecosystems to validate even the simpler models. Separation of evaporation from water uptake, and of the vertical and horizontal components of the latter, presents some technical difficulties but is essential for a real understanding of desert systems. Some detailed studies have been done in central Australia (98, 115); a number of fairly comprehensive ecosystem water balance studies are now under way in arid Australia, Israel, and the USA.

Salinity and its Effect on Water Relations

Many fine and some medium textured soils in deserts have a horizon where soluble salts (mostly NaCl, some sulfates) accumulate. The origin of the salt (apart from hydromorphic saline depressions not considered here) may sometimes be the parent material; in deserts within 50–150 km of a coast there is a large input of air- and rain-borne salt (118). Accumulation is due to the lack of deep percolation and leaching in deserts; the depth of maximum accumulation varies between 10 and 100 cm, depending on the normal depth of wetting [(thus on rainfall, infiltration, and texture (105, 117)]. The water stored in this horizon is often a significant proportion of the total moisture store. Its water potential is lower due to the addition of an osmotic component to the matric potential. Therefore, this water can be used by plants only insofar as they reduce their internal ψ , or couple water uptake to salt uptake ("salt exclusion" mechanisms may be useful in wet saline soils, but not in dry ones). To prevent salt from accumulating indefinitely in the active tissues there must be a salt outflow by excretion or by accumulation in special organs. Xerohalophytic plants growing on dry saline soils indeed have high internal osmotic potentials and efficient mechanisms for salt uptake, transport, and secretion (e.g. 37). The

salinity factor has so far been neglected in models of arid ecosystems, which for many deserts is hardly justifiable.

DESERT VEGETATION: CONVERTING WATER TO ENERGY

The Distribution of Soil Water in Space, Time, and Water Potential: An Opportunity for Niche Diversification

Soil water in deserts is far from being a single homogeneous resource; it is highly diversified in several dimensions. The water stores in different soil layers differ widely in the frequency at which they are filled, in the rate at which they are emptied by evaporation, and in the types of energy investment needed to gain access to them (Figure 4). Plants with different time strategies, root systems, and other special mechanisms have adapted to utilize each of them. The dominant type in each site will be the one which has the largest competitive advantage in the utilization of the largest store there. Usually there will be enough water in other stores to allow types with specialized niches, overlapping partly or not at all with that of the dominant, to coexist in the same site.

The surface layer (0–2 cm) water is too transient a pulse to be used by vascular plants. However, in many arid zones it is utilized by algae and lichens, which become photosynthetically active upon wetting. The lifetime of the 10–30 cm store

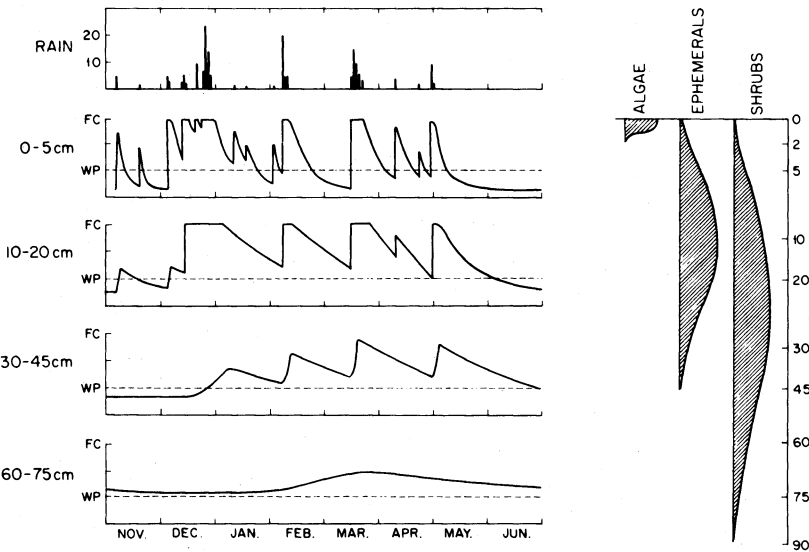


Figure 4 Left: Seasonal dynamics of soil moisture in different layers (schematized from data from desert shrubland on loessial plain; WP, FC – apparent “wilting point” and “field capacity” moistures). Right: Vertical distribution of activity of plant types (scale distorted to fit left part).

is just long enough for fast-growing ephemerals (annuals and herbaceous perennials) to take up most of it before it evaporates and to complete a significant production pulse and reproductive cycle. They utilize also part of the 2–10 cm store, which is important for germination and establishment, but they can hardly depend on it alone for reproduction unless there is a sequence of rain events. Many ephemerals, once established, can use water also from the 30–60 cm layer, and in certain soils and in the absence of shrubs, even down to 120 cm. However, in these layers (and deeper ones if they receive moisture) shrubs have the advantage of maintaining a deep perennial root system. These stores, only slightly affected by evaporation, are a more stable reserve resource which can be used at a slow and well-regulated rate to maintain perennial structures, and possibly some level of photosynthesis, during long dry periods. However, while trees and shrubs specialize in using the deeper stores for drought survival, many of them have not given up the production pulse from the 10–30 cm layer. They usually have an extensive and fairly dense horizontal root system there (in addition to deeper vertical roots), augmented in wet periods by deciduous rootlets. There is strong competition for the water in this layer between direct evaporation, ephemerals, and shrubs (particularly shrub seedlings) and between different species of each type. The long-term composition of the vegetation at each site in the desert is mainly determined by the terms of this competition.

The relative advantages of different types and species depend on the site characteristics which affect the vertical distribution of available moisture (or moisture-period probabilities), in particular, rainfall distribution and soil texture. Frequent very light rains (0.5–4 mm) will benefit only surface cryptogams. A number of light rains of 10–20 mm at intervals of a few weeks, which just maintain available moisture in the top 30 cm, will be highly advantageous for ephemerals. They also will enhance shrub growth, but shrub survival depends on the replenishment of the deeper reserve at least once every 1–2 years by 40–100 mm falling in a short period (or a period of low evapotranspiration).

The effect of texture on the moisture profile is no less important. In clayey, silty, or loamy soils with high water capacity most desert rains do not penetrate beyond 30 cm, thus favoring plants with shallow roots and rapid growth pulses, particularly ephemerals. In sandy, gravelly, or rocky soils, where capacity is lower, less water will be stored in this zone and much will percolate deeper, shifting the advantage to deep-rooted perennials (111, 77).

Texture also affects the form of relationship between water content and water potential. In sand it becomes very steep below –15 bars so that relatively little additional water becomes available between –15 and –50 (or –150) bars. In loams, and even more so in clays, the curve is such that the amount of this marginal water is far from negligible compared to the normal available water. In these soils there is an advantage to plants which can reduce their internal ψ (by osmotic potential or negative turgor) and take up water from soil well beyond –15 bars.

Soil salinity increases the relative proportion of marginal water and thus enhances the effect of fine texture in favoring plants able to extract potential water at low ψ , particularly by salt throughflow. Tolerance to high concentrations of specific ions is also required (9, 68). These requirements are met by a specialized group of

xerohalophytes, both annuals (mostly summer-growing Chenopodiaceae) and shrubs (Chenopodiaceae, Zygophyllaceae, Tamaricaceae).

Another specialization is induced by soil heterogeneity, in particular, stoniness. In a rocky or stony soil, moisture is very unevenly distributed in the profile, being concentrated in soil pockets and fissures, at soil-rock interfaces, and under stones (28). This favors plants with flexible "exploring" roots, capable of penetrating cracks, following tortuous paths, and expanding whenever a favorable pocket is found. Some desert perennials are able to develop such roots, while others are apparently restricted to homogeneous soils. Still others seem to be specifically adapted to the moisture regime of a certain combination of soil layers (e.g. sand upon loam, loess upon chalk).

The importance of the space-time stratification of soil moisture and of the corresponding adaptive stratification of root systems and cycle durations of different plants has been recognized by desert ecologists (49, 111, 77, 28). This multidimensional partitioning of the most important resource allows the coexistence of a number of plant species and types in every site, which in turn affects animal diversity. It also allows a more complete and efficient utilization of this resource for primary production. While the general principles are well understood, the interactions are often complex and many phenomena not fully explained. The application of simulation modelling to this central problem in the desert system would be useful.

Problems of Water Use Efficiency

Primary production (A) in arid ecosystems depends on the part of water input used by plants (T) and on the efficiency (A/T) of its use for energy and CO_2 fixation. In an analysis of crop yields and water use in arid (high radiation and evaporativity) conditions, de Wit (116) found a good fit to a linear relation $A = gT/E_o$ or $A/T = g/E_o$ (see also 104); i.e. efficiency is inversely related to average evaporativity in the growing season, where g is a species constant more or less independent of climate and moisture. The theoretical explanation was that when radiation (and E_o) is high, photosynthesis is saturated and invariant, while transpiration continues to increase. Another interpretation is that in these conditions the two processes are perfectly coupled, i.e. their rates depend on the same resistances to gas diffusion in the stomatal pathway (mostly r_s itself). Any regulation of r_s by external and internal factors will not affect the ratio A/T , which will be equal to the ratio of the demands for photosynthesis (g , expressing the photosynthetic capacity) and transpiration (E_o). Only the introduction of substantial additional resistances, which affect A and T differently, will cause decoupling and deviation from this relationship.

The main prediction of the de Wit equation (lower yield per unit water transpired at higher E_o) has not been directly tested in natural arid communities. The often observed "lower effectiveness" of rain in summer and in low latitude deserts is consistent with it (but may also be caused entirely by higher evaporation losses). Decreases in the A/T ratio during summer and at midday have occasionally, but not consistently, been found in gas exchange measurements (14, 53).

One may expect desert plants to have adaptations which increase the efficiency of water use for either seed production or survival-maintenance, by increasing g ,

reducing E_o , or decoupling photosynthesis from transpiration. Very common are "behavioral" adaptations in which the plant uses stomatal control on A and T so that both activities occur mostly (or exclusively) in seasons, days, or hours of low E_o . Decreases in rates of gas exchange during summer and at midday have been observed in several desert perennials (14, 29, 47). The reduction of leaf surface in dry periods is another mechanism of adaptation (80). In many desert plants E_o of periods when most A and T occur is probably much lower than the average E_o . The major limitation is that photosynthesis cannot occur at night when E_o is lowest.

This is overcome in succulents, particularly desert cacti, by "adaptive decoupling" using the crassulacean acid metabolism (107, 108, 83). The capacity to fix and store large quantities of CO_2 in the dark allows these plants a separation in time of the light-requiring processes of photosynthesis from CO_2 uptake. The latter occurs at night, when E_o and T are very low, while in dry periods gas exchange during the day is negligible. Thus high overall A/T ratios may be achieved.

Behavioral restriction of transpiration to periods of low E_o will result in slow, but efficient growth. This will be advantageous for plants with a water reserve to which they exclusively have access (e.g. in deeper layers, under rocks). However, for plants in a competitive situation (e.g. shallow-rooted plants), where the water supply is exhausted also by direct evaporation or by other species, selection will favor unrestricted, rapid, though inefficient, transpiration (20). Most desert ephemerals have apparently adopted the latter strategy, while many shrubs have specialized in slow and regulated use of exclusive water stores (102). This also requires an ability to survive for long periods at low levels of activity.

High photosynthetic capacity (g), as a possible mechanism for higher water use efficiency (at given E_o), is characteristic of plants with the C_4 photosynthetic pathway, many of which occur in arid zones (82). Though higher A/T have been found in C_4 plants in gas exchange measurements over short periods (100, 14), annual production (absolute or per unit water) in semiarid communities dominated by them does not seem to be much higher than in those dominated by C_3 plants (J. K. Marshall, personal communication; 14). Possibly the lower intrinsic efficiency (g) of the latter is compensated for by stricter behavioral restriction of activity to low E_o . The adaptive value of higher g in C_4 plants may not be so much in higher productivity per se, but in the ability to produce at all in periods and latitudes with high E_o where they have the advantages of high light saturation and flexible temperature acclimation (14).

Adaptive decoupling of photosynthesis from transpiration by an increased mesophyll resistance to water flow may be important in some desert shrubs in which photosynthesis levels are maintained while transpiration decreases drastically after midday (53). On the other hand, desert plants usually avoid any decoupling which reduces efficiency; e.g. cuticular transpiration is usually very low (79, 100).

Ecological Types and Pulse-Reserve Strategies in Desert Plants

In attempting to apply the pulse-reserve paradigm (10, 114) to desert plants one may ask what is the reserve by which each species survives dry periods, and how does each species regulate the transfer between the reserve and the active pulse. This

question is related to the distinction of the ecological types of desert plants (28, 51, 111, 119). The types differ in the degree to which their activity is geared to rainfall pulses and in their kinds of reserves: whether water or energy, internal or external, above or below ground.

POIKILOHYDRICS These plants maintain all structures under extreme changes in hydration; their activity pulses are perfectly in phase with moisture pulses. Transition between active and reserve forms involves only rapid and reversible biochemical changes upon wetting and drying. This group includes algae and lichen, which are very common on soil and stones in deserts (32, 54), and a few ferns and higher plants (111).

EPHEMERALS These are plants which during dry periods maintain no photosynthetically active parts but only a special resistant reserve form, from which a new pulse is initiated and which is in turn replenished from it. The transfer between the two may involve a certain lag in the response to rainfall, but the growth pulse is still closely tied to transients of available moisture in the upper (5–30 cm) soil layer. These species are often referred to as “drought evaders” and are a majority in the flora of most deserts. Two subtypes are:

(a) *Annuals* The only reserve of annuals is seeds, which store energy and nutrients but not water and hence depend on external water for reactivation. Both activation (germination) and storage (seed setting) are irreversible once triggered. Reserve biomass is small compared to peak active biomass, the latter building up mostly from its own production.

(b) *Perennial ephemeroïds* (geophytes and hemicryptophytes) Storage organs of these plants (bulbs, rhizomes) often contain water reserves, as well as a reserve of carbohydrates and protein which may be comparable in magnitude to peak vegetative biomass. Hence active biomass can be built up rapidly upon the first signal of a rainy season, and flowering can be independent of rainfall. Reactivation and storage flows may be more flexible and reversible than in annuals. Strategies in this group vary in the degree and timing of reserve commitment and in the timing of the storage flow (e.g. throughout the growth period or only towards its end).

DROUGHT PERSISTENTS This group includes all perennials which maintain some photosynthesis throughout dry periods; they must have reserves of both water and energy to account for inevitable transpiration and respiration losses of the active tissues.

Sizeable energy and nutrient reserves in woody parts above and below ground are an adaptation of trees and shrubs generally, but those in arid zones require also an external or internal water reserve. The many special adaptations of these true xerophytes have been the subject of many morphological, physiological, and ecological studies (e.g. reviewed in 79). They vary in the level of activity maintained in drought and hence in their dependence on reserves.

(a) *Fluctuating persistents* Many desert shrubs reduce photosynthetically active biomass and transpiring surface considerably during dry seasons by shedding most leaves or stems or by replacing them with smaller, denser leaves with lower gas exchange rates (80, 28, 51, 23, 24). The root system is also reduced by shedding rootlets in the dry upper layer. Thus, while a residual activity is maintained, water and energy losses are low and relatively small water reserves (in soil and perhaps in wood) are sufficient.

(b) *Stationary persistents* In other desert shrubs and trees the green biomass is maintained at a nearly constant level throughout the year. These require a larger and more reliable water reserve, as well as tight control of cuticular and stomatal transpiration, high A/T efficiencies (e.g. by decoupling), and tolerance of low internal water potential and of high internal temperatures resulting from suppression of transpiration. All or most of these are characteristics of the two main types of true drought-enduring plants.

Evergreen shrubs may be sclerophyllic (*Larrea*, *Acacia*), leafless with green stems ("retamoid"), or xerohalophytes with semisucculent leaves (many chenopods). Many of them have been shown to take up water from soil beyond -100 bars, and/or to have specialized root systems. These attributes enable them to utilize slowly and efficiently external water reserves in deep, saline, or rocky layers, that are not available to other plants.

Succulents, typically the cacti of American deserts, often have fairly shallow root systems and thus little external water reserves. Instead they accumulate a large internal water reserve, from which the green cortex (and some activity) is maintained during droughts.

There are indications that in both evergreens and succulents, even though the green biomass fluctuates only little, most net production occurs during the short favorable periods (78, 83); thus most production must be translocated to reserves. In these and other desert perennials ephemerals and fluctuating persistents, translocation, storage, and mobilization of reserve materials must be important. Little is known about these processes and how they are regulated; even the form and location of the main energy reserves are often not fully identified. The expected seasonal changes in reserves were detected in some plants (22, 48) but not in others (78, 103).

The distinctions between active and reserve biomass and between the patterns of production and translocation in different types should therefore be important elements in models of arid ecosystems. They are of consequence in the modelling not only of primary production but also of herbivory and its effect on long-term production potential (109). An interesting aspect is the analysis of the different pulse-reserve strategies as optimized strategies in different environments.

Primary Productivity and Biomass in Arid Lands

An examination of data from various arid regions shows that the average annual net above-ground primary production varies between 30 and 200 g/m² in the arid zone and between 100 and 600 g/m² in the semiarid zone (e.g. 17, 81, 73, 88, 12, 113, 55, 8). Estimates of below-ground production are scarce, but are given in some

of the Russian papers. It seems that total production may be 100–400 g/m² for arid, 250–1000 g/m² for semiarid communities.

These data, as well as some which directly relate productivity to precipitation (56, 111), suggest that a fair proportion of variation in productivity (Y) in arid ecosystems could be accounted for by a linear regression on precipitation:

$$Y = b(P - a) \quad (Y = 0 \text{ if } P < a)$$

where a may be interpreted as the total of "ineffective precipitation" or water losses (evaporation and runoff) and b as the average water use efficiency of the community. The "zero-yield intercept" a is between 25 and 75 mm/year. The efficiency b is between 0.5 and 2 (mg dry matter/g water) [or (g/m²)/mm] for above-ground production, from which one may estimate it to be 1–6 mg/g for total production. This is considerably lower than the A/T values of 5–50 mg/g measured for individual desert plants over periods of hours by gas exchange measurements (14, 29, 53, 100), but similar in magnitude to efficiencies reported for irrigated crops in arid climates over a growing period (68, 104). Apparently adaptations of desert plants for more efficient water use just compensate for energy losses due to the irregularity of the water supply.

The accumulation of standing live plant biomass and the turnover rate (productivity/biomass) in deserts depend on the dominant type. In ephemeral communities there is 100% turnover of shoots (and of root biomass in annuals) during the growth period of 2–5 months. The numbers for net annual production are equal to peak biomass (mean biomass has little meaning). In fluctuating perennials annual foliage production may be 50–95% of peak foliage biomass (81), but when stems and roots are included, production is probably only 20–40% of biomass, which in communities where this type is dominant amounts to 150–600 g/m² above ground or 400–2500 g/m² total (12, 73, 88, 113). These turnover rates are higher than in forest or tundra (88). In arid and semiarid communities of stationary drought-persistent trees, shrubs, and cacti, annual production may be only 10–20% of a standing biomass of 300–1000 g/m² above ground (e.g. 17), i.e. possibly 600–4000 g/m² including roots.

The distribution of biomass between roots and shoots also differs greatly between life forms. The root/shoot ratio of crop plants and trees is often observed to increase in dry conditions (probably a mechanism for adjustment of water supply to demand). However, not all desert plants have high root/shoot ratios. In many desert winter annuals it is apparently not much higher than in nondesert annuals (0.2–0.5). In perennials ratios of below-/above-ground biomass should be interpreted carefully, as the fractions include not only active roots and shoots but also reserve organs (wood, rhizomes); the ratio may often reflect mostly the distribution of the latter. For perennial grasses and forbs in arid and semiarid regions, ratios between 1 and 20 have been reported (89). For shrubs it is usually between 1 and 3, but in the cold deserts of Central Asia values of 6–12 are common (e.g. 58). On the other hand, in some shrubs in semiarid Australia (45, 12) ratios as low as 0.2–0.3 have been found. It seems that a high below-/above-ground ratio is not a characteristic of desert vegetation generally; it may be more closely related to certain life forms or to temperature regimes than to aridity.

Reproduction and Population Dynamics in Desert Plants

A major problem of desert plants is how to regulate time and intensity of flowering, seed-setting, dispersal, and germination so as to maximize successful reproduction in an environment where periods suitable for each of these processes are short and uncertain. As discussed above, seed longevity and a cautiously opportunistic strategy, with seed diversification and maximum utilization of environmental signals, are expected and usually found in desert annuals (18, 19, 38, 52, 74). Other adaptations of this group are the ability to produce some seeds (at least one per plant) even when conditions allow only limited vegetative growth, high seed yields in favorable conditions, and dispersal mechanisms which allow both continued occupation of safe microhabitats and search for new ones (27, 28, 52).

Desert perennials differ in that successful reproduction may occur less frequently, without endangering the population (depending on life expectation). Seed longevity is less critical and the seeds of some desert shrubs are viable for only a few months. Germination of some perennials follows a strategy of trial-and-error almost every year; in others it depends on climatic sequences which occur only once in several years (39, 28, 70), and which are presumably correlated with high probability of successful establishment. In some arid shrub and tree communities in Australia and Israel germination seems to occur only after death or disturbance of the mature population.

There are few detailed studies of plant population dynamics in arid zones. Summarizing 40 years of observation at Koonamore on Australian shrub communities recovering from grazing, Hall, Specht & Eardley (39) found irregular fluctuations superimposed on both the increasing trend and the eventual steady state. These fluctuations, with periods of 2–5 years, seemed to be mostly in response to sequences of dry and wet years. In some populations turnover was fairly rapid, while in others there was no change in 40 years!

These features make the definition of succession and climax in desert communities problematic. Kassas (50) distinguishes successional changes in desert vegetation from seasonal and accidental (due to random climatic fluctuations) changes. Thus the climax is defined to include these irregular fluctuations in composition. Succession (i.e. long-term trends) in deserts is usually allogenic in response to geomorphological processes (50, 5); autogenic succession occurs in dune stabilization and in the formation of mounds around shrubs. Changes in human and stock pressure may induce drastic successional or degradational trends in arid communities, as documented for instance in North America (42).

Competition and Other Interactions Between Plant Populations

Two opposite views on the importance of competition in arid communities are possible (33): (a) the harsh environment controls density so that competition rarely has a chance to occur; (b) there is intense competition for the scarce limiting resource—water. Assumption *a* may be true where the environment is not only arid but also extremely unstable, i.e. the frequency of catastrophes is high in relation to population growth rate (extreme deserts, erodible surfaces). In many arid communi-

ties, periods between disasters appear to be long enough for densities to build up to levels where intense competition for water does occur. In mature arid shrub communities root systems may occupy most of the area even where canopy is only 3–5%. Evidence for within-species competition is the regular spatial pattern sometimes observed in desert shrub populations (e.g. 110); in other cases evidence may have been obscured by habitat microheterogeneity. Mortality due to competition for water has been indicated in desert annuals populations (7).

Competitive inhibition of shrub seedlings by mature shrubs, to a distance 5 times the canopy radius, has been demonstrated by Friedman (33). Many phenomena in the distribution of species and communities in arid and semiarid zones can be explained only by assuming strong between-species competition for water (e.g. 111). The yield of forage grasses and forbs in semiarid rangelands is inversely related to density of woody perennials (e.g. 6).

Some desert shrubs produce allelopathic substances that inhibit germination and growth of other species, but the significance of this in the field cannot always be proved (72). Salinization of the soil surface by salt accumulating and excreting halophytes, with consequent inhibition of nonhalophytes, is apparently common (16, 57).

Positive effects of shrubs and trees on other plants, as expressed in spatial association, are also often observed in deserts (1, 72). The microenvironmental modifications involved are partly atmospheric (reduction of radiation, temperature, wind, and evaporativity) and partly edaphic (increased organic and nutrient contents, accumulation of windblown sand and silt). Other mechanisms are concentrations of windblown seeds and protection from grazing.

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