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ADAPTATIONS IN ARID ECOSYSTEMS

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Soil moisture - d.  
Rainfall - d.  
Soil - nutrients - d.

The information on adaptations in animals and plants to arid conditions is very extensive. However, the structure and functioning of the whole ecosystems with its producers, consumers and decomposers is hardly known. For that reason it is very difficult to give a short overview of the situation, only details with special relevance to this study will be touched upon.

Limiting factors

Precipitation

The limiting factor of predominant importance in arid and semiarid zones is the scanty rainfall. The distribution of the arid zone and vegetational cover is determined by precipitation (Fig. 1.1). Detailed maps of precipitation as well as of the number of humid days were published in connection with the Sahel (Matlock & Cochrum, 1974). For West Africa it is stated that the average annual precipitation decreases 1 mm per kilometre in proceeding northward from the southern forests toward the Sahara. However, this kind of disjointed information gives a false picture of the ecological reality, which is characterized by variability and irregularity of precipitation. This variability increases when the precipitation decreases. An important fact is that this variation occurs in both time and space.

The variation of the precipitation in time has been fairly well studied. It must be pointed out, however, that long-term series are needed in order to provide a correct picture of the situation. In many cases such series are lacking in the developing countries. Development projects have failed for neglect of the temporal variation in precipitation (Talbot, 1971). Not only the annual and monthly variation but also the micro-variation is of ecological importance. The amount and distribution in time of the showers are critical for the primary production. It is well known from North Africa that rainfalls of less than about 5 mm in 24 hours in summer or 48 hours in winter have no



ditions have also been taken into account in investigations of the ecosystems in southern Tunisia (Wagner, 1975). Every village has grazing grounds – sometimes up to 25 km distant – scattered over an extensive area. The inhabitants deem this dispersal as providing some guarantee against drought. This is a kind of rain insurance. In chapters 3 and 5 of this volume, dealing with the social aspects, other social systems are described which were developed to compensate for local droughts.

#### Soil nutrients

The soils in arid and semiarid areas have characteristics that put limitations on the ecosystems. The soils are formed by processes where water has played a limited role. As a result of this, the soils are not leached, but owing to evaporation have an accumulation of soluble salts (especially sodium salts) near the surface. Charley & West (1975) have shown that the nutrient patterns in the semidesert ecosystems of Utah are dominated by the individual shrubs both in the vertical and horizontal planes. From a fertility point of view plant nutrients are readily available. However, the amount of certain nutrients is very limited, especially the essential nutrients nitrogen and sometimes phosphorus. This lack of nutrients is associated with the lack of organic components in the arid soils because of the rapid decomposition processes. Bazilevich (1974) has brought together information on the reserves of nitrogen in litter, steppe or desert matting in the world ecosystems. The figures taken from her paper will illustrate the very important difference between different climatic regions (Table 1.1).

Table 1.1. Nitrogen content in litter of ecosystems in different climatic zones (modified from Bazilevich, 1974).

Region	N t km <sup>-2</sup>
Polar	106.2
Boreal	76.0
Subtropical	
Humid	18.0
Semiarid	10.5
Arid	3.0
Tropical	
Humid	8.6
Semiarid	5.7
Arid	1.2

These very important facts are not always properly understood when Western agricultural technology is applied to tropical and dry areas.

#### Adaptations by plants and animals

The irregular changes between a short period with water and limited nutrients and a long period of dryness present animals and plants in arid areas with special problems. The larger animals, including man, have avoided the difficulties by migration; the sedentary species have solved the problem in two different ways. The larger group consists of the ephemerals, appearing in active form during humid conditions and surviving during the dry period as inactive stages (seeds, eggs). Both plants and animals occur in this group, the members usually being small in size. The second group consists of larger organisms provided with special mechanisms for resisting drought conditions. There are many different types of adaptations among the plants. Some plants can reduce the green biomass by a factor of 4–20 (Orshan & Diskin, 1968). Other plants are also adapted for reducing evaporation by modifications in the surface. Surface structures may also be used for collection of water (dew or fog). Many plants have reserves of moisture and nutrients. The adaptations in arid plants have been well described by Kassas (1966) and Evenari *et al.* (1971). Schmidt-Nielsen (1972) has given an overview of the different physiological adaptations in desert animals.

Of great interest in this connection is the C<sub>4</sub> photosynthesis pathway which was recently summarized by Black (1971) in an important review. This method of photosynthesis is twice as effective (increase of biomass per time unit) as the earlier known C<sub>3</sub> pathway. Plants with the C<sub>4</sub>-system occur especially in tropical areas. The method seems especially adapted for plants where water resources are scarce and limited in time. "Most of the plants in the grazing lands of arid and semiarid Western India belong to C<sub>4</sub> high photosynthesis capacity ones" (Pandeya, 1974). Andrews *et al.* (1974) point out that during warm seasons grasses with C<sub>4</sub> assimilation dominate the American prairie. Caldwell (1974), however, found that there was no difference in assimilation efficiency between C<sub>3</sub> and C<sub>4</sub> plants in cold desert areas. He investigated communities dominated by shrubs featuring C<sub>3</sub> and C<sub>4</sub> photosynthesis. These different ways for the photosynthesis need to be studied intensively. There are good grounds for believing that the results will be of practical value in promoting productivity in arid areas.

Organisms living in arid conditions are characterized by specific properties. These features have been reviewed by Noy-Meir (1974). He pointed out that organisms in an arid ecosystem have to meet the following five conditions:

1. Tolerance of extreme conditions.
2. Ability for rapid recovery. High growth rates, rapid successions of development stages, and high fecundity.
3. Adaptation of pulse-reserve transitions. "The problem then is how to regulate timing and intensity of these transitions when incidence and duration of good periods is wholly of partly random". In desert plants special delay and trigger mechanisms are at work.
4. Flexible and opportunistic feeding habits. Studies of the diets of desert animals have shown a wide dietary range and ability to switch between different types of food.
5. Nomadic migrations. Large-scale movements are probably the most important adaptation in mammals – including man – and birds for utilizing the resources of the arid zones.

To these five groups of characteristics mentioned by Noy-Meir (1974) a sixth group may be added.

6. Special distribution patterns. The organisms in dry areas are not only rare and dispersed over large distances but they show a characteristic distribution pattern which is pronounced on silty and clay soils, but not on sandy soils. The perennial plants are clumped together, the exposed interspaces being without higher plants (Norton, 1975). This spacing is very important as the perennial plant can use water from a large area. The infiltration rate is high beneath the perennials but mostly low at the interspace. At the interspace an algal crust may be formed which has a low infiltration rate and the precipitation is flushed away. The desert landforms also tend particularly to form closed basins both large and small. Such basins collect rainwater and dew and favour clumped perennial vegetation (Jewitt, 1966). The spacing between the species and also specimens may be caused by antibiotics (Odum, 1971). The root exudates may be toxic to other species, but in some cases also to the same species.

The spacing is also important for the transport of airborne nutrients which are deposited and caught in the vegetation. The role of airborne nutrients has been very little studied, but it may be assumed that this transport is of importance and that it does not only have adverse effects, such as soil erosion (Rapp, 1974), but also favourable effects, such as increased productivity in sedimentation areas (Lundholm, 1975).

Noy-Meir (1974) has also described certain weak points in these arid ecosystems. He mentions the following four areas where disturbances may cause extensive changes:

1. Susceptibility to damage of reserves. Any factor which drastically increases the mortality of the resistant reserve forms (seeds or eggs) or the disappearance of the reserves of nutrients to be used for rapid response to pulse transitions will be dangerous.

Rodents and ants are very important in the ecosystems in southern Tunisia, as during some years they may consume up to 75 % of the seeds of the dominating plant species (G. Novikoff, pers. comm.). In the same way, grazing, which prevents seed setting or the build-up of belowground reserves of nutrients in grasses, may have very sizable effects. Franclet & Le Houérou (1971) reported from Tunisia rodent densities corresponding to a grazing pressure of 1.3 sheep per hectare.

2. Susceptibility to lagging components. As pointed out, it is important that the changes in population size of the different organisms follow the environmental changes. If some species lag in the response to these changes — for example, if a consumer continues to breed — the whole system may be destabilized. Introduced species may frequently produce this effect; examples of this are rabbits and sheep in arid Australia (Noy-Meir, 1974).

3. Low density, biomass and productivity. The irregular distribution pattern of the species requires extensive areas if the species are to survive. If sufficient areas are not available, species may be lost to the ecosystem. An important factor is whether species abundance and distribution ranges are influenced by neighbouring ecosystems.

4. Susceptibility to topsoil erosion. "Due to low plant cover, erosion forces are high in arid and semiarid regions. In many of these regions a thin topsoil layer (5–10 cm) is critical for the plant establishment and growth" (Noy-Meir, 1974).

Rapp (1974) has shown the extent of soil erosion. Novikoff (1975) has stressed both the biotic and abiotic factors influencing the different erodibility of soils. Lundholm (1975) has pointed out the characteristics and importance of dry deposition in relation to the ecosystems, with the concomitant transport of nutrients and hazard of accumulation of toxic substances.

### Stability of ecosystems

The earlier ecological hypothesis about diversity-stability and a close correlation between these two concepts is now strongly questioned (Holling, 1973; Goodman, 1974; May, 1974; Margalef, 1974; Noy-Meir, 1974). It was formerly believed that the tropical humid forest with many different species was very stable but that the arid ecosystem or arctic areas with few species were unstable. In connection with the arid zone the term fragile was used frequently. The background to this discussion has been the human impact on the different ecosystems. Now it has turned out that the tropical humid forests are very sensitive to human actions.

The rather confused discussion has partly been caused by the fact that there are many different kinds of stability. To clarify this, Holling (1973) and Noy-Meir (1974) have suggested that the concepts of resilience and persistence be used. Resilience refers to the probabilities of qualitative changes and an ecosystem with high resilience has a large variation, but it springs back to its former structure. It has high plasticity around an average. Persistence refers to the ability of a system to remain constant under the environmental influences, and high persistence means a small variation.

Orians (1975) has pointed out that the analyses of the stability-diversity problems so far have dealt with variations in time and not in space and that the analytical problems in dealing with both time and space are formidable, but that such work has started. Murdock (1975) has suggested, based on model studies, that increased stability might be achieved by spatial diversity. In the real world this is what the nomads have created with their system of subsistence economy. An important variable in this spatial diversity in the arid zones is uneven distribution of precipitation.

There is a certain antagonism between the two concepts. Some arid ecosystems have high resilience but low persistence. The humid tropical forests have high persistence but low resilience.

The crucial question is the resilience of the arid and semiarid ecosystems and their ability to recover from the impact of man. Noy-Meir (1974) is of the opinion that the arid ecosystems in Asia and Africa have shown a high degree of resilience when the nomadism with its strong human impact was developed.

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