Part 5: Subzonobiome VII (rIII) of the Extremely Arid Deserts of Middle Asia: the Biome Group Middle Asia

H. Walter et al., *Ecological Systems of the Geobiosphere*

5.0 General

Compared with the subtropical deserts of zonobiome III, conditions in these middle-Asian deserts, with no greater rainfall, are less extreme. For the vegetation this is partly because after a process of hardening, the plants enter a period of quiescence, and water losses through winter dryness are minimal. Furthermore, precipitation in winter accumulates as snow, so that in spring water from the thaw can seep deeply into the soil and is stored there. Apart from the Mohave desert in North America and the Andean desert of South America, which have been described in Vol. 2, this type of desert is found only in Asia, where it covers a vast area (Fig. 5.1).

The Eurasian desert can be divided into four biome groups:

1. The Caspian Lowland with the northern, Kazakhian deserts with mainly summer rainfall (biome II in Fig. 5.1). These we have already discussed.
2. The Turanian deserts (biome I in Fig. 5.1) which lie further south and have less cold winters with winter rainfall. This western part of the great Asiatic desert region is described in the Russian literature as "Middle Asia" (*Srednaya Azia*), while the eastern part is known as Central Asia (*Zentralnaya Azia*).
3. The Central Asian deserts have rainfall only in summer (biome III in Fig. 5.1) and are quite distinct floristically from the Turanian deserts.
4. The high plateau deserts of the eastern Pamirs and Tibet (Biome IV in Fig. 5.1) at 4000 m NN, where even the summer is very cool.

South of the Middle Asian deserts of Turania lie the deserts of Iran and southern Afghanistan, to which we will return in Vol. 4, in the context of ZB IV in Europe and the middle East.

These Eurasian deserts of the temperate climatic zone resemble those of ZB III in many ways; the plant cover, for example, is very scanty and there is usually no zonal vegetation because nearly all the soils are raw soils (syrozems).

As in all arid regions, the soils are alkaline because there is no leaching of calcium carbonate; rather, as a result of evaporation from the surface, soluble ions are moved in the capillary water to the surface. Water below a depth of 1 m is, however, not affected by capillary forces, but remains stored in the soil, unless it is taken up by the roots of plants.

Again, as in ZB III, the commonest pedobiomes are lithobiomes (stone deserts, gravel deserts), psammobiomes (sand deserts), halobiomes (salt deserts) and amphibiomes (floodplain soils of foreign rivers which flood periodically).

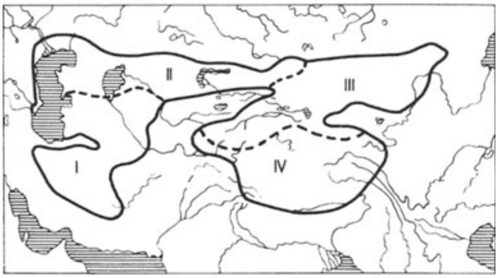

Fig. 5.1. Biome group of the Eurasian deserts. *I* Irano-Turanian; *II* Kazakho-Dsungarian; *III* Central Asian; *IV* Pamiro-Tibetan. The Turanian part north of the Kopet Dagh (see Fig. 5.2) is known as Middle Asia

In these deserts, likewise, it is the clay soils that are the driest biotopes; sandy soils are relatively moister, and rocky crevices without any superficial drainage are the most favourable biotopes. Wet soils become saline at the surface due to accumulation of readily soluble salts. In extreme cases a firm salt crust can form on the surface (see Vol. 2, pp. 220–223).

Middle Asia includes the great basin between the Caspian Sea in the west and the huge Tien Shan and Pamiro-Alai mountain systems in the east. Its southern border is formed by the Kopet Dagh (Fig. 5.2) and further east by the northern foothills of the Hindu Kush and the mountain chains of the Pamirs. The geological history of Middle Asia begins with the receding of the Tethys Sea. During the Tertiary, formation of the massive mountains to the south and east of the Turanian depression took place, separating this area from the rest of Asia. One consequence is that the climate has been arid since the Miocene. During the Pleistocene there was repeated and major glaciation in the mountains, and the river system of the Amu-Darya developed. At the end of the Apsheron regression in the late Pliocene, this river emptied into the Caspian Sea, forcing a way between the Great and Little Balkhans near to the present city of Krasnovodsk. Subsequently, it filled the entire basin of the Central Karakum with the products of weathering of the mountains, while constantly changing its course as it flowed across the area between the Kopet Dagh in the south and the Trans-Unguz area in the north. The Unguz escarpment was for a time the right bank of the Amu-Darya (Fig. 5.2).

These alluvial layers, which were deposited in arid conditions and partially redistributed by the

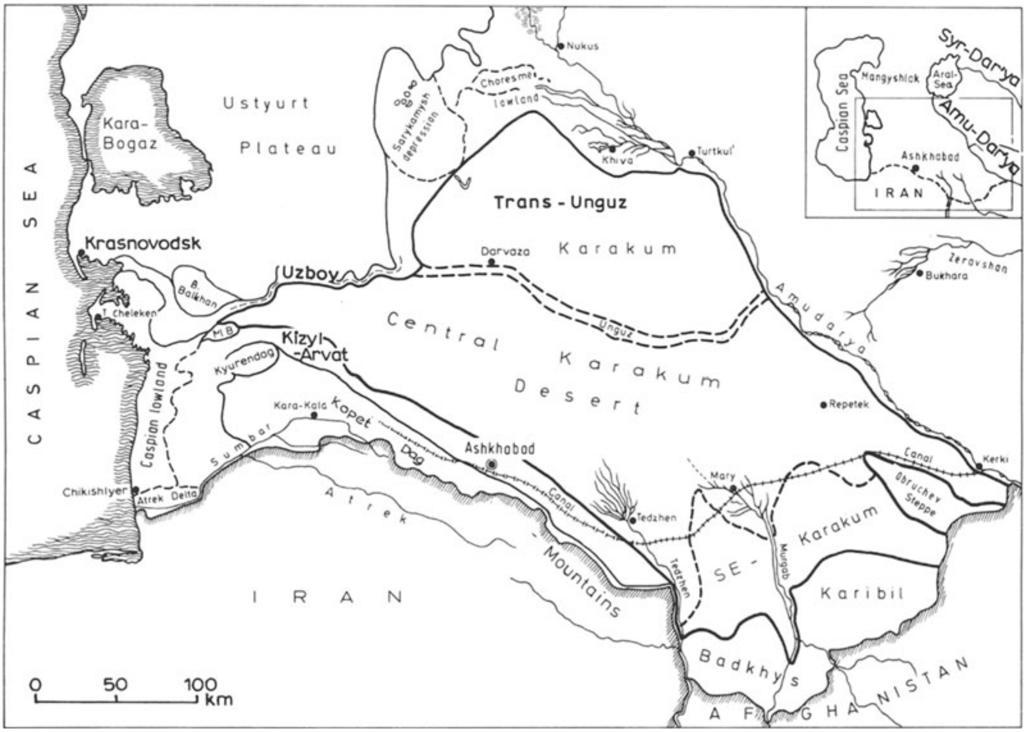

Fig. 5.2. Map of Turkmenistan with the Karakum *(outlined)* and neighbouring regions (from Walter 1976)

wind, form the most recent surface of the central Karakum, for the last transgression of the Khvalynic Sea affected only the western part as far east as Kizyl-Arvat.

The lower course of the Amu-Darya was, however, pushed continuously to the east by the delta deposits of the rivers Tedzhen and Murgab coming directly from the south. Finally, in the second half of the Pleistocene, the Amu-Darya broke through to the north to reach the Aral Sea and became established along its present course. The delta region was, however, repeatedly shifted. At times one arm in the delta emptied into the currently dried out Sarykamysh Depression, filling it with water. Today this is dry, but then a fresh water lake was formed, which later found an outlet through the Uzboi River into the waters of the last transgression of the Caspian, the Khvalyn Sea. The water level of the Khvalyn Sea lay considerably above the level of the present Caspian Sea. It sank during the ensuing period, however, so that the Atrek River, coming from the Kopet Dagh in the southwest of the region, was able to build a broad delta into the Caspian Sea.

The mouth of the Amu-Darya in the Aral Sea was later pushed even further east by deposits in the delta area. The western arm of the river dried up and so, too, did the Sarykamysh Lake, leaving only a few small salt lakes behind. The Uzboi today is stagnant. The lakes along its course are not remnants of the former river, but rather undrained depressions fed laterally from groundwater and then slowly becoming enriched with salts.

The present form of the relief in the sand deserts is due to wind action. In dry areas sand is readily blown away; firm sand layers at the surface are broken up by loose sand being blown against them.

The Turanian Desert is divided into two large sand deserts:

1. The Kyzylkum (Turkish *kyzyl* = red; *kum* = desert) between the Syr Darya and the Amu-Darya.
2. The Karakum (Turkish: *kara* = black) in which the plant-covered sand surface has a dark colour.

This desert has been investigated in great detail and will therefore be discussed here at some length. The separation in the Tertiary of the Turanian depression from the rest of Asia led to the development of a distinct flora with many endemic species and even genera which occur only in this region and are dominant.

5.1 The Climate

The Turanian Lowland lies in the transitional zone between the dry, subtropical air masses of the Arabian-South Iranian region and the continental, temperate air masses to the north. This transitional zone has, climatically, an arid mediterranean character. Mediterranean cyclones bring precipitation both in the winter and spring with a maximum in March. The summer months are rainless and very hot (Fig. 5.3).

Annual precipitation is only 80–100 mm, although at the foot of the Kopet Dagh rainfall rises to about 200 mm. Mean annual potential evaporation is about 1500 mm: in the interior of the desert it is more than 2500 mm, while on the coast of the Caspian Sea, where air humidity is greater, it is only 1000 mm.

Annual incident solar radiation is 543–585 kJ cm^{-2}, being in December only a fifth of the July value. The Siberian high pressure system invades Middle Asia 12 to 23 times during a winter, and absolute minimum temperatures reach about –26° C. Frost and thaws alternate, however, so that, unlike Kazakhstan, there is no continuous snow cover. The temperature may fall by 25° C within a short time, causing frost at the same time as heavy falls of snow. Late frosts can occur in April, endangering cotton crops. Under the influence of the large body of water, the climate on the banks of the Caspian Sea is more temperate: the winters are less cold, while summer temperatures are 3–5° C lower. The humidity even in August is 30–40% higher than further inland and this makes the climate very sultry.

The southwestern district with the Atrek Delta is protected by the Kopet Dagh from the northeasterly winds, so that the climate is almost subtropical. Olives, figs, almonds and pomegranates, as well as date-palms (*Phoenix*) and *Citrus* spp. can be cultivated, although even here the absolute minimum is –10° C.

5.2 The Soils

Typical soil profiles develop more readily in these deserts than in those of the subtropical zone. This is due partly to the effect of the water from the melting snow in spring and also because during the cold winters, decomposition of organic litter takes place slowly, and there is a slight accumulation of humus.

Several different soil types are found in Middle Asia. These include dark serozems (= seroburozems) on the outcropping rock of the Ustyurt Plateau. These have stony or gravelly upper horizons with compaction and salination at a depth of 5 to 15 cm. The humus content is 0.7–1.0%. Light serozems are found above loess and carry an ephemeral vegetation. The upper horizon has a relatively high humus content of 1.0–1.5%; it is thoroughly wetted in spring, but completely dry in summer. Gypsum precipitates in the form of fine threads are present in the upper horizon, gypsum crystals at greater depths.

We will return to the sandy soils which cover 80% of the surface, the takyry, the solonchak soils with their halophytic vegetation and the allu-

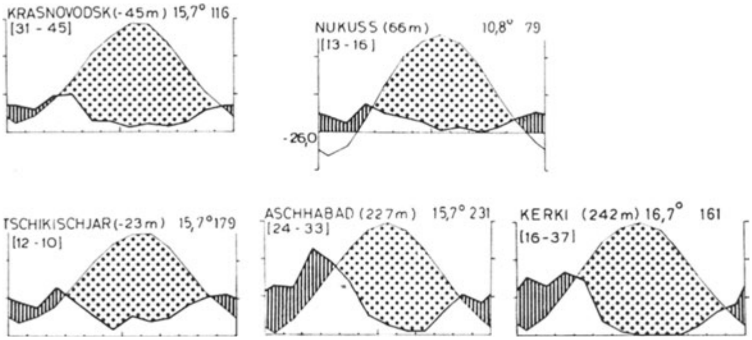

Fig. 5.3. Climatic diagrams from the regions bordering the Karakum: Krasnovodsk on the Caspian Sea, Nukus in the Amu-Darya delta, Chikishlyer in the Atrek delta, Ashkhabad at the foot of the Kopet Dagh, and Kerki on the Amu-Darya (extreme right in Fig. 5.2) (from Walter 1976)

vial meadow soils of the flood plains and delta areas. The remaining soils are raw soils, that is, syrozems.

5.3 The Producers

The vegetation shows great variations, depending on which pedobiome is dominant in any particular desert region. On the Ustyurt Plateau, a Hamada-like desert region, the biogeocoenosis complexes of lithobiomes predominate.

It would be going too far to catalogue the different plant communities, especially since they have not been investigated ecophysiologically. It should simply be pointed out that there are transitions to *Artemisia maritima* halophytic communities.

Areas with relatively good ground cover are used for grazing, especially with Karakul sheep. An important fodder plant is the annual *Ceratocarpus arenarius* (Chenopodiaceae) which lasts until autumn and has a dry weight production of 500 kg ha^{-1}. On gypsum-containing soil this vegetation also occurs extrazonally, outside the desert climatic zone.

The extensive sand deserts and the floodplains of the Amu-Darya are described in detail in Section 5.9.

5.3.1 Halobiomes or Salt Deserts

This halophytic vegetation is usually limited to moist depressions and the area around salt lakes. A distinction is made between salt pans (*shory*) and takyres. The salt pans are very extreme biotopes. They arise in undrained depressions with a high groundwater level. The saline groundwater which rises by capillary action to the soil surface, evaporates, forming swollen crusts which contain, besides NaCl, calcium sulphate. The high salt concentration in the centre of the salt pan prevents any plant growth. Here, as in the Caspian Lowland, the first pioneer species is *Halocnemum strobilaceum,* which appears at the edge of the saltpans where the salt concentration is lower, and forms cushions with a cover of about 25%. The shoots of this perennial chenopodacean are reminiscent of *Salicornia.* Around the small salt pans which occur scattered though the Karakum desert in hollows with high groundwater the following zonation is found with decreasing salt content of the soil: (1) *Halocnemum strobilaceum,* (2) *Seidllitzia rosmarinus,* (3) *Halostachys caspica* with *Limonium suffruticosum* and as accompanying plants also *Kalidium caspicum* and other Chenopodaceae or the salt-secreting grass *Aeluropus litoralis.* Blown sand may accumulate around the plants, which then crown little piles of sand. This happens, for example, with *Halocnemum,* and the result is a Nebka landscape (see Vol. 2). Table 5.1 shows the salt content for some halophytes.

In the next, less saline zone, *Suaeda* and *Salsola* species are dominant and so is *Petrosimonia. Anabasis salsa* and *Artemisia maritima* occur even higher up. Apart from the last-mentioned species, these are all euhalophilic stem or leaf succulent Chenopodeaceae. The zonation, which is related to the salt content of the soil, is usually very clearly marked (Fig. 5.4).

5.3.2 The Takyry

The first takyry to be studied in detail were those of Middle Asia. Takyry are, typically, clay-floored depressions which fill with water during the rainy season. During the dry period the water evaporates and the floor becomes cracked. They

Table 5.1. Na and Cl content of the organs and litter of three halophytes as a percentage of dry weight (after Bazilevich et al. 1972)

Plant parts	*Halocnemum strobilaceum*		*Kalidium caspicum*		*Salsola turcomanica*	
	Na	Cl	Na	Cl	Na	Cl
Annual shoots	5.37	10.05	10.05	8.63	5.90	11.06
Old shoots	2.08	1.68	1.46	1.28	—	—
Roots	1.65	2.09	2.84	1.93	1.04	1.19
Litter	3.10	5.18	—	—	—	—

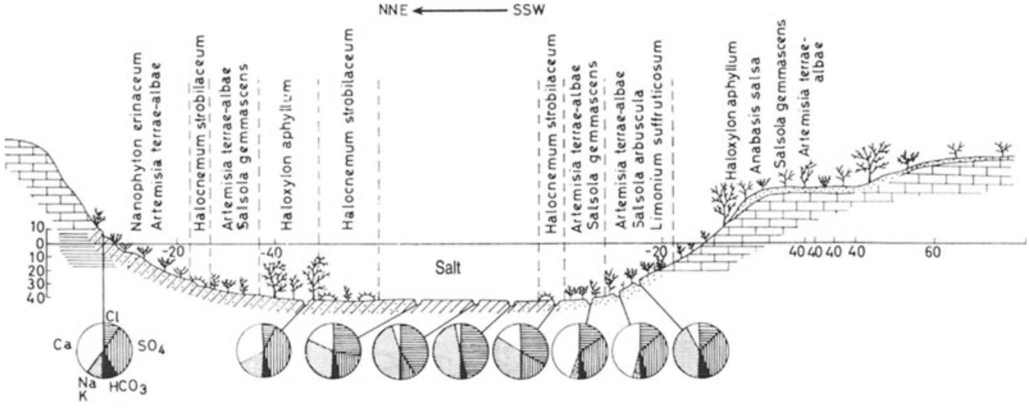

Fig. 5.4. Zonation of the salt pan Kaundy on the Mangyschlak peninsula in Middle Asia. Height in the profile is magnified 20-fold. *Numbers* on the zero line show the height of the surface in m. *Circles* show the percentage of salt ions in the watery soil samples. In the *centre* there is only NaCl; towards the periphery the percentage of sulphates and soluble carbonates increases (from Walter 1968)

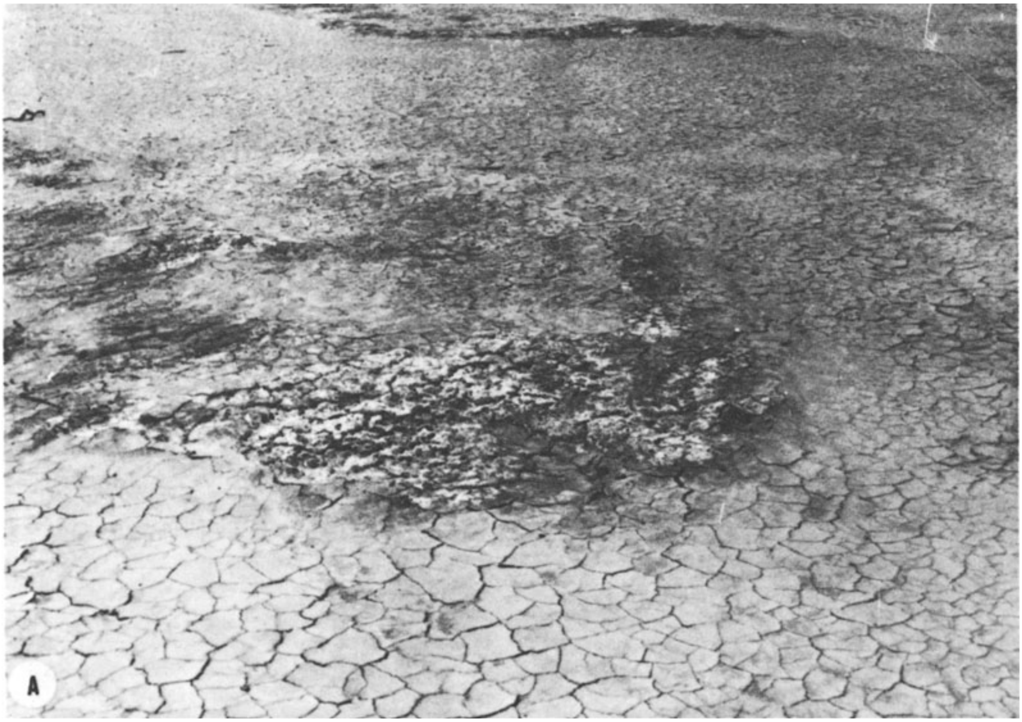

Fig. 5.5. Dry takyr with algal mat (photo L.E. Rodin)

may form both on small areas of clay and also over larger areas of what we call deluvial deposits (Fig. 5.5).

Deluvial deposits are formed as a result of sporadic floods following rainfall or the melting of snow. Products of weathering on illuvial slopes are swept along by the flood waters: while the coarser material, stones and gravel, is redeposited on the slopes, the finer sand and clay particles are carried to the foot of the slope or across gently inclined ground where the water fans out and evaporates. These sand and clay deposits form takyry. Such events may occur several times in spring and are the origin of the takyry at the foot of the Kopet

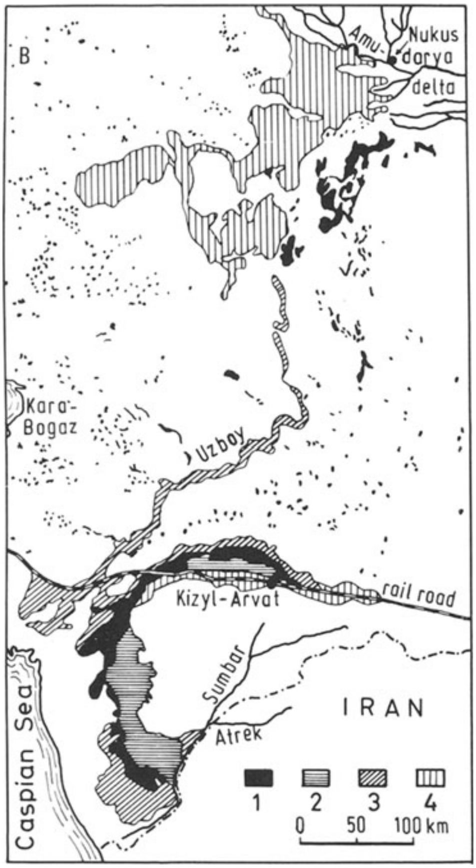

Fig. 5.6. Distribution of takyr soils in Turkmenistan. *1* algal takyry on solonchak soils; *2* lichen takyry on solonchak soils; *3* takyry with siero-burozem soils; *4* areas of scattered small takyry (after Rodin 1954, from Walter and Box 1983)

Dagh. Similarly, the delta region of the Amu-Darya receives muddy elluvial deposits when the snows melt in spring and summer. The inundated areas dry out quickly, leaving an upper crusty layer of very dense clay.

Figure 5.6 shows the distribution of takyry in central Middle Asia.

The takyry are flooded either only in spring or sometimes several times during the year, but the water is not able to sink very far into the heavy, dried-out clay. Instead, it evaporates; the soil dries out and cracks into more or less regular polygons. When the ground is again flooded, the clay swells and the cracks close. On such areas, where the soil is wetted only superficially, homeohydrous, rooting plants are unable to establish themselves. The vegetation thus consists only of poikilohydrous algae and lichens. These communities of algae (Deserti-Algeta) and lichens (Deserti-Licheneta) are probably the oldest type of land vegetation, typical perhaps of pre-Devonian times when there were no higher plants.

The vegetation of the takyry has been studied by Rodin (1954, 1956, 1961, 1963). Blue-green algae of the genus *Phormidium* (32 species) are the most important on the clayey takyry, along with *Microcoelus vaginatus.* A total of 147 species were identified: 92 Cyanophyta, 38 Chlorophyta, 5 Xanthophyta and 12 Bacillariophyta. A detailed list is to be found in Gollerbakh et al. (1956). In puddles of standing water it is primarily the *Zygnema* species which develop.

The algae form a film several millimetres in thickness on the surface. The production of dry weight is 0.5–1.0 (up to 1.4) t ha^{-1}. Growth occurs not only as a result of flooding but also after wetting by rain. All of these plants are able to withstand complete desiccation or can survive in a resistant form. This microflora is also ephemeral in character, developing only temporarily in shallow pools 5–10 cm deep which form wherever the microrelief is slightly uneven. The water in such pools warms up to temperatures well above 20° C, which greatly promotes the growth of the Cyanophyta. As a result of the uptake of CO_2 for photosynthesis, the water becomes slightly alkaline. Since these blue-green algae absorb atmospheric nitrogen, the proportion of nitrogen in their dry substance is high, namely, 4.5%.

Lichens grow on those higher parts of the relief which are not flooded but are nevertheless moist. The most important species are *Diploschistes albissimus, D. scruposus* and *Squamaria lentigera* together with species of *Collema, Aspicilia* and *Psora.* Their phytomass reaches a dry wt. of 0.5 to 1.0 t ha^{-1}.

Since the surface of the takyry is subject to constant changes resulting from sedimentation, the inundated areas are constantly changing position. Thus the algal and lichen communities are in a constant dynamic state, replacing each other whenever the distribution of the water changes.

The most important decomposers are the soil fungi, which are primarily Dermatiaceae *(Stemphylium, Macrosporium, Alternaria, Cladosporium)* and also *Aspergillus* but seldom *Penicillium.* In addition there are actinomycetes and bacteria. One of the fungi, *Stemphylium algophagum,* has been shown to kill algae growing near to it (Litvinov 1956).

Table 5.2. Runoff and wetting of the soil on a 1200 m^2 takyr area in the Karakum (after Bogdanov 1954)

Day	Rainfall (mm)	Original state of surface	Runoff after rain (mm)	Depth of water layer (mm)	Runoff (m^3)	Depth of soil wetted (cm)	Water taken up by soil (mm)
13 March	1.9	Dry		None		1.5	–
20 March	3.6	Dry	3.0	0.13	0.16	4	0.47
21 March	8.8	Wet	2.8	4.0	4.8	6	2.0
17 April	15.7	Dry	2.9	9.6	11.6	9	3.2
18 April	2.7	Wet		None		–	–

Table 5.3. Biomass and chemical composition of the takyr vegetation (after Rodin 1954)

Zone	Total organic mass (dry wt.) (phytomass) (kg ha^{-1})	Annually decomposed organic mass (kg ha^{-1})	Nitrogen content of decomposed organic mass (kg ha^{-1})	Ash content (kg ha^{-1})
I Low-lying areas with clay salt-soils and few ephemerals	100	100	1.5	6–7
II Raised areas with soil algae or soil lichens, few ephemerals	300	300	9–10	20–22
III a Scattered patches with ephemeral vegetation (transitional zone)	1200–1600	1200–1600	20–30	90–140
b *Artemisia* semi-desert with ephemerals on serozems	12,000	10,000	90	475

As a result of evaporation at the edges of pools, the salts contained in the water accumulate, so that halophytes such as *Salsola* and *Suaeda* settle here. The roots of these plants loosen up the clay so that the soil can be wetted more deeply and the takyr becomes covered with vegetation in such places. The process is further encouraged by the rodent *Allactaga elater* which throws up little mounds of soil. Higher plants can also establish themselves more easily on abandoned termitaria (*Hodotermes angerianus*), on ant-heaps (*Cataglyphis* spp.) or on the 3–10 cm high cones formed by the wolf spiders (*Lycosa* spp.), each with a crater at the top.

Measurements of the extent of run-off and wetting of the soil in the Karakum are summarized in Table 5.2. In this region the takyrs cover only small areas. Here an ecological series can be seen that is often at the same time a succession, and serves as an example of a biogeocoenosis complex:

Raw soils (syrozems) with algae → Takyr-syerozems with lichens → Typical syerozems with ephemerals

Table 5.3 shows the phytomass and its chemical composition in the three stages.

5.3.3 Deserts with Ephemeral Vegetation

This type of vegetation is typical of the areas of light serozem soils above loess at the foot of the northern slopes of the Kopet Dagh and other parts of Middle Asia (Figs. 5.7–5.9).

The main species growing on this soil, which is wetted only in spring, are *Poa bulbosa* and *Carex pachystylis*. In addition there are many annual ephemerals such as *Holosteum, Erodium, Arenaria, Papaver, Delphinium, Nigella, Capsella, Erophila* and *Bromus* as well as ephemeroids including *Ranunculus severzovii* with its white-haired leaves and rhizomes, *Eranthis* and *Allium*. The growing season is brief, although it varies in length from year to year. In years when rainfall is good the plants reach a height of 10–20 cm, in dry years they are dwarfed, only 1–2 cm in height.

The ephemeral desert vegetation can be used as grazing for 3 months of the year. Productivity of dry wt. is 0.5–2.5 t ha^{-1}. In summer the plants

Fig. 5.7. Desert with ephemerals growing on loamy soil in southwest Turkmenistan in spring (photo M.P. Petrov)

Fig. 5.8. Vegetation profile at the peak of flowering in a desert with ephemeral vegetation. The ephemerals and ephemeroids root only in the uppermost soil layers that dry out completely in summer (after Korovin 1961)

above the ground are completely dead. Their roots attain a depth of little more than 20 cm, for only the upper soil layers remain wet for any length of time in spring, both field capacity and also wilting point of loess being relatively high.

5.3.4 The Sand Desert of Central Karakum

General and the Hydrography of the Karakum

This sand desert has been studied in great detail. As early as 1912, a research station was established at Repetek (38°34'N and 63°1'E, elevation 190 m NN) in the southeastern Karakum region, on the first railway line from Krasnovodsk on the Caspian Sea to Ashkhabad, Bukkhara and Samarkand. Ecological investigations have been conducted since that time and it is thus not surprising that *from an ecological point of view the Karakum is the most thoroughly studied desert in the world.* It serves as a useful example of how a biome can be subdivided ecologically down to the smallest unit. The results of these many years of research have been published in several different works, all in Russian. These include a collection of papers edited by Kunin (1955), a volume on the geography *Turkmenistan* by Kunin (1969), the works of Rodin (1954, 1956, 1961, 1963) and the two-volume monograph of Korovin (1961/62).

The Karakum, a desert with an area of 350,000 km^2, is part of zonobiome VII and within this is ascribed to subzonobiome VII(rIII) of the temperate deserts. It belongs to the biome group of the Middle Asian or Turanian deserts and, together with the less well-researched Kyzylkum, to the biome complex of sand deserts. The desert is part of the large Aral-Caspian (Turanian) Depression (see Fig. 5.2).

We have already touched briefly on the geological history of this region (pp. 234, 235). The largest river, the Amu-Darya, 2,600 km long and

Fig. 5.9. Profile of vegetation growing on loess slopes of the foothills in a desert with ephemeral vegetation. Here there is some summer rain and several perennial species therefore occur: *1 Carex pachystylis; 2 Poa bulbosa* var. *vivipara; 3 Ranunculus pinnatifidus; 4 Scaligeria alloides; 5 Haplophyllum perforatum; 6 Phlomis thapsoides; 7 Ixiolirion tataricum; 8 Gentiana olivieri;* and *Eremostachys labiosa* in the middle (without a number) (after Korovin 1961)

with a catchment area of 465,000 km^2, exerts a dominant influence over the Karakum.

The source of the river is the Vrewski Glacier at 5000 m NN in the southern Pamir. Here the river bears the name Pyandzh (Panji) and becomes known as the Amu-Darya only after joining with the Vakhsh, which rises in the western Pamir. The Pyandzh and Vakhsh account for 80% of the total runoff. Within the catchment area 400 glaciers and perpetual snow fields (firns) are known.

At Kerki, somewhat north of the Afghanistan border where the Amu-Darya reaches the Karakum, the mean flow is 2000 cumec (= m^3 s^{-1}), and when the river is in flood this may reach 6000 to 8000 cumec. Mean width of the river is 1–1.5 km, but when in flood it is 3 km wide. As it flows across the northern Karakum a great deal of its water seeps into the ground. This forms a subterranean lake beneath the whole Karakum. This flows slowly in the direction of the Caspian Sea, but very little water is actually discharged into the Caspian. The greatest water loss from the Amu-Darya is due to diversions to irrigated areas along the lower course of the river and in the delta region. As a result, today the Aral Sea receives very little water and it dries out rapidly.

The high water period lasts, with several peaks, for 4 to 5 months. It starts to fall at the end of July; the lowest level is reached in January when the river even receives water from the groundwater. Each year, 200 million tonnes of sediment are carried by the river as far as Kerki and this is deposited on the irrigated areas and in the delta region.

The second largest river in the southeast of Karakum is the Murgab. It is fed primarily by melting snow in spring. The Tedzhen River in the south is longer than the Murgab (1100 km), but it carries less water. Its source is in the mountains of Afghanistan. The water in these two rivers, in as far as it is not used for irrigation, seeps into the groundwater of the Karakum.

The Karakum is by no means a waterless desert, for groundwater at a relatively shallow depth means that it is possible to obtain water at any point. The groundwater is, of course, mostly saline, but on it float lenses of freshwater. The latter collect beneath sand dunes after rain and can be tapped by means of wells. An annual rainfall of 100 mm over the 350,000 km^2 area of the Karakum amounts to 35 km^3 of water. Part of this is lost through evaporation from the surface and through transpiration by plants; part seeps into the sand of the naked dunes and reaches the groundwater. The rate of this increment to the groundwater has been estimated to be 30 cumec. The following rough computation of the annual runoff to the groundwater has been made on the basis of the available data (Kumin 1955):

Infiltration from the Amu-Darya riverbed	150 m^3s^{-1}
Rainwater seepage in Barchan areas	30 m^3s^{-1}
Underground runoff from the Kopet Dagh	20 m^3s^{-1}
Infiltration from the Murgab River	17 m^3s^{-1}
Infiltration from the Tedzhen River	4 m^3s^{-1}
Seepage from hillocks or from takyry	1 m^3s^{-1}
Mean total increment to groundwater	222 m^3s^{-1}

The following estimate of losses can also be made. The data are unreliable, but serve as a rough guide:

Evaporation from wet salt pans	165 m^3s^{-1}
Loss of groundwater through transpiration	57 m^3s^{-1}
Total loss of groundwater to the atmosphere	222 m^3s^{-1}

According to this rough calculation, no significant quantity of groundwater should reach the Caspian Sea, a conclusion which is confirmed by observation and experience.

The various alluvial soils have different degrees of permeability. In general, however, the groundwater moves very slowly from east to west, although losses through capillary rise and evaporation occur where the groundwater rises to within a metre of the surface. In some places the roots of plants reach the groundwater at 5–10 m depth and water is lost by transpiration.

Since the river sediments were deposited under arid conditions, temporary, larger or smaller salt lakes were constantly formed, only to dry out or be filled again with fresh sediments. Thus varying quantities of salts, mainly NaCl and Na_2SO_4, are trapped in the loose sediments. As it moves, the groundwater dissolves these salts so that it is always saline to some extent, the exact concentration of salts varying greatly from place to place. A mixing of the different groundwater streams occurs either not at all or only to a limited degree. As a result, the salt content of water from different springs is very different and unpredictable. The same is true of water from boreholes.

The springs at salt pans are typically very saline. This is because the salts which accumulate through evaporation are dissolved when the pans fill with water in spring and this salty water seeps into the ground. The groundwater beneath Barchans (wandering dunes) is, however, always very low in salts and is thus good drinking water.

As much as 50–70% of the rain in the Karakum area falls in the first 2–3 months of the year. In the Barchan areas the rain water sinks completely into the loose sand. Only a small portion evaporates from the surface, another part remains trapped by the sand as capillary water, but most of the water sinks gravitationally to the groundwater and, since it has a lighter specific weight, collects in the form of a lens on its surface. A freshwater lens is asymmetrical, rising only slightly above the groundwater surface, but sinking more deeply into the groundwater, just as an iceberg projects little above the surface of the sea. Mixing with the saline groundwater takes places to a very limited extent. These freshwater lenses can be tapped by way of wells or boreholes; if water is removed too rapidly, saline groundwater may flow into the wells. The formation of freshwater lenses is furthered by overgrazing and trampling by livestock since the plant cover is destroyed and open areas of sand are formed with small dunes.

Artificial freshwater lenses are also deliberately produced by the inhabitats of areas where there are large takyry. Water will remain standing as a thin layer above the impervious clay and there is no storage of water in the soil (p. 239). Beneath the clay of a takyr there is, however, usually a layer of sand. If the clay layer is deliberately broken open, the water can enter and is stored in the sand. To do this on a large scale, the water flowing as a broad sheet across a takyr is led by very shallow ditches (with the lower wall on the slope side) to the deepest part of the takyr. Here a larger depression is created with several rings of small well shafts dug down to the sand layers. The rainwater which collects in the depression during the rainy season passes into the wells and penetrates from the shaft sideways into the sand above the saline groundwater. In this way a freshwater lens is formed that is protected from evaporation. During the drought period this water can be used both as drinking water and for watering livestock and even for maintaining small vegetable gardens. The water is drawn from the same wells that were used to collect it.

A rainfall of 10 mm over 1 km^2 of takyr surface amounts to 10,000 m^3 of water that can be stored in wells. Since a karakul sheep requires 1.5 m^3 of water per year, this quantity of water is sufficient for a herd of 6000 sheep. In the sand desert 6 ha of grazing is required per sheep. This means that, given a watering place with a capacity of 10,000 m^3 of stored water, 36,000 ha of grazing land can be made accessible. The surface of the takyr on which water collects should be kept as free of plants as possible, for sand accumulates around the plants and obstructs the flow of water to the well, while the plants also cause loss of water through transpiration.

A freshwater lens formed beneath such wells is shifted slightly by movement of the groundwater, but only by a few metres per year. Where there is no great volume of sand above the groundwater, that is, where the groundwater is at a depth of 3–4 m, the wells are arranged in a row, parallel to the direction of groundwater flow. Water is led to the first and when this is full, to the next and so on. Likewise, during the drought period, the wells are used one after the other, each being first exhausted of its store of freshwater. It is of course always necessary to adjust to local conditions.

No accumulation of freshwater occurs beneath areas of sand with a vegetation cover. The surface of these sands is somewhat compacted, while the upper layers of soil contain a certain amount of humus and have a relatively high field capacity, that is, they retain more water than does barren sand, which is to the advantage of the plants. In years with high rainfall the ephemeral vegetation develops more abundantly and the perennials form stronger shoots, so that water uptake is greater. If a surplus of water remains, it replenishes the capillary water in the deeper layers of sand and this is available to deeper-rooting woody plants in dry years.

A striking phenomenon on the northwestern border of the Karakum is the occurrence of *freshwater lakes* in the western part of the Uzboi River valley where otherwise only bitter-salt lakes are found. The shores of these salt lakes are desert-like and only a few hygro-halophytes are able to survive. These lakes are produced by standing groundwater which reaches the surface and evaporates. The level of the lake is maintained by the throughflow of groundwater, but the salt concentration continually rises. Along the shore the ground surface is wetted by the capillary fringe, but the water evaporates at the surface, leaving a white salt crust.

The situation in the freshwater lakes is more complicated. Reeds, tamarisks and poplars grow along their shores. They are found in valleys of the former tributaries of the Uzboi. They often extend for 10 km or more and are fed by groundwater, but not by the salty groundwater from the Karakum side. Since these lakes are not far from the Ustyurt Escarpment and the Great Balkhan, it may be assumed that water from the higher rainfall on the mountains finds its way to the freshwater lakes through fissures. Some water from these fissures flows, either above or below the ground, from the lakes into the Uzboi valley. These lakes are thus formed not by standing, but by slowly flowing water. Although evaporation is about 2 m a^{-1} there is always a certain amount of runoff, which prevents an increase in salt concentration.

The depression at the foot of the Kopet Dagh in the south is relatively well supplied with water. At the foot of the mountains there are numerous springs. Water can also be won from the scree fans by means of gallery wells (*kanats*)[9]. The outcropping rocks of the mountains are highly fissured limestones of the Lower Cretaceous; water percolates readily into this rock and is then fed to the springs at the foot of the mountains. Many small and larger oases have existed here for a long time.

Conditions become noticeably less favourable west of Kyzyl-Arvat. Here there are areas of bare clay into which rain barely penetrates. The landscape has the general appearance of *"bad lands"*, there is no plant cover and numerous small erosion channels furrow the slopes of the cone-shaped mountains. Contrary to widespread opinion, however, such *slopes are hardly eroded at all.* The dried loam surface is very resistant to erosion. Rainwater runs off superficially, slightly muddied by the loam, and sinks in only when it reaches the plain. It is for this reason that this area of the Karakum has large freshwater lenses above the groundwater. The barrenness of the slopes greatly increases runoff. Thus this region does not suffer from lack of water.

Recently, more efficient utilization of the water has been made possible by the construction of numerous dams. Groundwater should be collected as close to the foot of the mountains as possible, where it has not yet mixed with the salty groundwater of the Karakum.

There are also very deep groundwater streams in the Karakum region carrying water under pressure; artesian wells are, however, rare. Of far greater importance for land exploitation is the Karakum Canal which roughly follows the original course of the old Amu-Darya at the foot of the southern mountains; it is constantly being extended. For the first 37 km this canal uses the

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[9] These are nearly horizontal wells used to intercept at a higher level the downward-flowing groundwater on slopes, especially in valleys. The water can be used to irrigate terraces built just below the wells.

widened Bosaga-Kerki Canal then, after a further 9 km, it unites with the Kelif-Uzboi depressions, which are part of the Afghan river Balach. It continues for 80 km in this channel, forming a reservoir with a capacity of 350 million m^3. It then cuts across a section of the Karakum and reaches the delta of the Murgab at the railway station Sachnet. The canal continues by way of Mary to the town of Tedzhen and is there led into the river of the same name. Up to this point the canal has a length of 600 km. Water is led into the canal from the Amu-Darya without any dams. The maximum rate of flow into the canal is 300 cumec.

The new oasis on the sandy-loamy plain of the Obruchev steppe permits the growing of fodder for intensive cattle-raising. Irrigation in the delta area of the Murgab and the Tedzhen allows better utilization of the arable areas because the Amu-Darya has its high-water level in summer, at a time when the Murgab and Tedzhen are at their lowest. The canal ensures a steady supply of drinking water and provides a waterway for the transport of goods. The same applies to other sections along the Kopet Dagh. There is a danger of salinization by water seeping from the canal.

The Climate of the Karakum

The macroclimate has already been discussed. The climatic diagrams in Fig. 5.3 are for stations which lie on the edge of the Karakum. Figure 5.10 shows mean values of climatic observations made for 50 years for the climate at the research station Repetek, fluctuations in rainfall and the temperature maxima and minima for each month of the year. Furthermore, it can be seen from the climatogram (Fig. 5.10 D) that the winter rainfall was very high in some years. In 1968/69, for example, it was 200 mm in all. This allows the reserves of freshwater in the deeper sand layers to be replenished.

The warm season, that is, with mean daily temperature above 5° C, lasts from February to the beginning of December, the hot period with daily means above 29° C, from the end of April to the end of October. The absolute maximum is 50° C, the absolute minimum −31° C; mean daily fluctuations in temperature are 20–25° C, the mean number of rainy days is 32. In 1917 rainfall was only 24.3 mm; in 1953, however, it was 230 mm. Fog, dew or hoar frost were recorded on 50 days, but are of no ecological importance.

Total solar radiation is 672 kJ cm^{-2} of which one-third is diffuse radiation. The reflection (*albedo*) from bare sand accounts for 25–26% of the total radiation, that from sand with a plant cover for 20–22%. The microclimate close to the soil is very much hotter around midday.

The Soils

In this psammobiome the soils are sands which are often loose and readily shifted, forming the following types of dune:

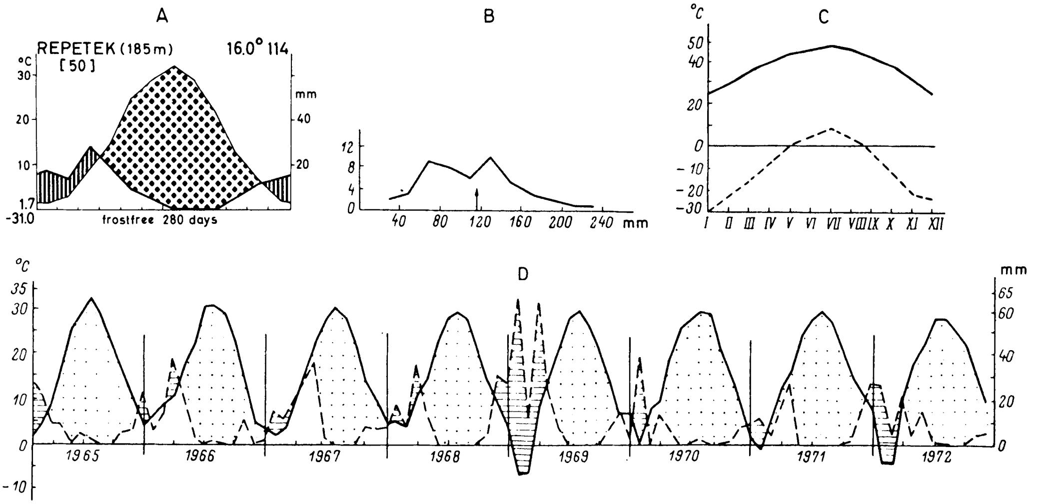


Fig. 5.10. Climatic data for the station at Repetek for the years 1913–1917 and 1926–1970. *A* climatic diagram. *B* Rainfall (*arrow* indicates mean annual value). *C* Absolute maxima and minima of temperature 1951–1972. *D* Climatogram for 8 years showing the unusually high rainfall of more than 200 mm in 1968/69 (after Rodin 1954, from Walter and Box 1983)

1. Low sand hillocks (*nebkas*) which form around shrubs when the wind diminishes locally and sand is deposited around them.
2. Individual *Barchans* or crescent-shaped dunes which may be shifted more than 100m per year by the wind. The windward side has a gentle slope of 12–15°, whereas the leeward side has a steep slope of 30–35°.
3. Barchan fields are found in large areas of sand such as the delta of the Amu-Darya, along its banks or around oases. The sand masses are very large and therefore move very slowly, but as a result of winds blowing from different directions, the actual crests of the dunes are constantly shifted.
4. Barchan chains are typical of regions with outcroppings of loose sandstone. The edges of the Barchans join together laterally so that the crest of the resulting chain forms a long, winding line running perpendicularly to the direction of the wind. These dune chains can reach a height of 30 to 40m, but are usually about 5 to 15m high. If the wind blows continuously from a given direction, the sand mass will migrate about 5 to 15m annually and may cover entire villages and railway lines.
5. Sand ridges are especially widespread in the Karakum. Their length is 10 to 100 times their width or height. They vary in length from 100m to several kilometres, in height from 5 to 60m and in width from 10 to 100m and more. Their orientation is mostly in a north-south direction. The sand of these ridges is firm and covered with vegetation so that the ridges are immobile. In some places, however, sand can be blown out of them to form Barchans. This gives rise to a terrain of sand ridges and hillocks.

The type of movement caused by wind depends on the size of the sand grains: sliding or rolling, depending on wind speed, for diameters of 0.5 to 1mm, bouncing or skipping for diameters of 0.25 to 0.5mm, and streaming with no ground contact for diameters of 0.05 to 0.25mm. The form of the ripple marks depends also on the grain size, being larger as the size of the grains becomes larger. In the Karakum the ripple marks are 0.5 to 3cm high and 6 to 20cm apart; for coarse sands they are 8 to 10cm high and 40cm apart.

The wind direction in the Karakum is determined by the Pamiro-Alai mountain ranges. In summer the wind blows from the northwest towards the mountains, while in winter it blows from the southeast away from the mountains. The Barchans are thus shifted back and forth, with a net movement towards the northwest; this is 4 to 4.7m annually at Kerki.

Chemically, the sands are composed of 50% silica, up to 10% feldspar and up to 4% calcite, with considerable quantities of mica as well.

About 80% of the total area of the Karakum carries some vegetation; only 5–10% has little or none (mobile sands). The rest consists of takyry and saltpans scattered in depressions; here the wind has removed the sand, exposing layers wetted by groundwater, and a salt crust forms at the surface.

Detailed investigations have been made of the water content of sandy soils on dune ridges (Nechayeva et al. 1979). These have confirmed that the desert vegetation is well supplied with water, even in summer.

The Producers

The flora of the sand desert includes some 350 species, of which 56% are endemic. The vegetation of the Turanian region has evolved under arid conditions and in almost complete isolation since the Tertiary. This has led to the development of a unique flora which we will describe in some detail.

a) Trees with Definite Trunks

Ammodendron conollyi (Leguminosae), the sand acacia, is an important tree on slightly mobile sands. It reaches a height of 4–9m, with a trunk diameter of 6–30cm and a trunk height of 1–3m. The upper parts of the lateral, second- to sixth-order branches die back annually and are replaced by new branches from renewal buds.

The silvery, pinnate leaves are reduced to a pair of leaflets 30mm long and 3mm wide. The tip of the rachis is spiny. Long, first- to third-order shoots are produced only in favourable years. These reach a length of 150cm and form the crown. Long trunk shoots can be produced from dormant buds. The showy flowering racemes are reddish-violet.

The formation of the root system is shown in Fig. 5.11. While the shoot of a first-year seedling grows to only 10–20cm in height, the root penetrates 70–100cm deep into the ground. In the second year the root increases its length to only 120cm but forms long, horizontal, lateral roots, which supply the plant with water after each rainfall. Even in old plants the main root does not

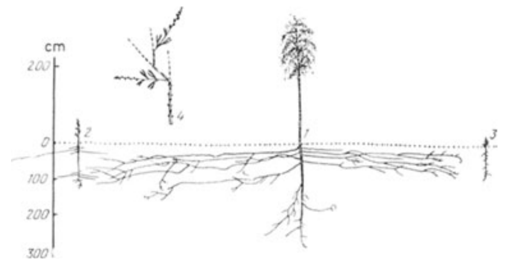


Fig. 5.11. *Ammodendron conollyi: 1* small tree, 10 years old, with root system; *2* 2-year old plant; *3* 1-year-old plant; *4* branching of shoot (after Petrov 1966, from Walter 1976)

reach deeper than 3m. The trees live to be 50 years old.

In the open stands of sand acacia there are about 75 trees ha^{-1}. The aboveground phytomass is about 0.57t ha^{-1}. The age structure of such a stand is as follows:

Age in years	Number (%)
1	6
2	2
3–5	11
6–10	18
11–15	9
16–20	6
21–25	3
26–30	2
>30	1
Dead	42

This species tolerates both covering and uncovering by sand. In the former case, it forms long trunk shoots, and in the latter, adventitious roots.

Eremospartum flaccidum (Leg.) is another endemic of similar importance, but this tree grows to only 5m with a trunk height of 2m. In a normal stand there are about 40 trees ha^{-1} with a phytomass of 60kg ha^{-1}.

Calligonum eriopodum (Polygonaceae) grows to 6m (trunk 1.5m) and is the only tree belonging to an otherwise well-represented genus to which we will return.

Haloxylon ammodendron (aphyllum) (Chenopodiaceae), the black *saksa'ul* (= with black wood) is the most important tree. Trees of 50 to 70 years and, in exceptional cases of 100 years, reach a height of 5–9m and a trunk diameter of 24–28cm. The tree is leafless and the assimilating shoots die at the end of the growing season. Branching is sympodial. Secondary increase in thickness takes place abnormally from several cambia.

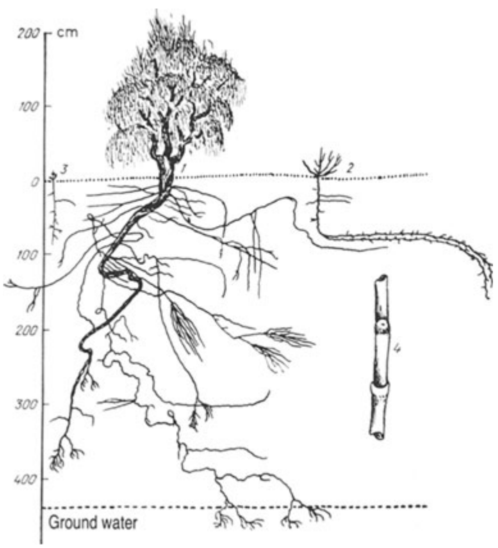


Fig. 5.12. *Haloxylon ammodendron* with root system: *1* a plant about 10–15 years old; *2* a 2-year-old plant; *3* a 1-year-old plant; *4* part of a vegetative shoot (from Petrov 1967, from Walter 1976)

The root system is shown in Fig. 5.12. The growth form may be shrubby or aborescent, depending on local conditions. Large individuals develop when the roots reach groundwater at a depth of 4–5m, sometimes at even more than 7m. This gives rise to dense thickets which are used for firewood. This species tolerates slightly saline water. The young shoots provide good fodder for camels and sheep throughout the year. Figure 5.13 shows the distribution of the phytomass in profile.

b) Shrubs (up to 6m tall without trunk)

Haloxylon persicum (Chenopodiaceae), the white *saksa'ul* is the characteristic plant of the Karakum. Together, this species and *Carex physodes* form the most common plant community on immobile sand. The shrub reaches a height of 3–5m, with a trunk of only 10–20cm. The long shoots, with small scale-like leaves, have a length of 50cm, of which the outer 10 to 20cm die back annually. The flowers are found on short shoots, only 1 to 3cm long (Fig. 5.14). The root system is shown in Fig. 5.15. The shrubs reach an age of over 30 years. They are eaten

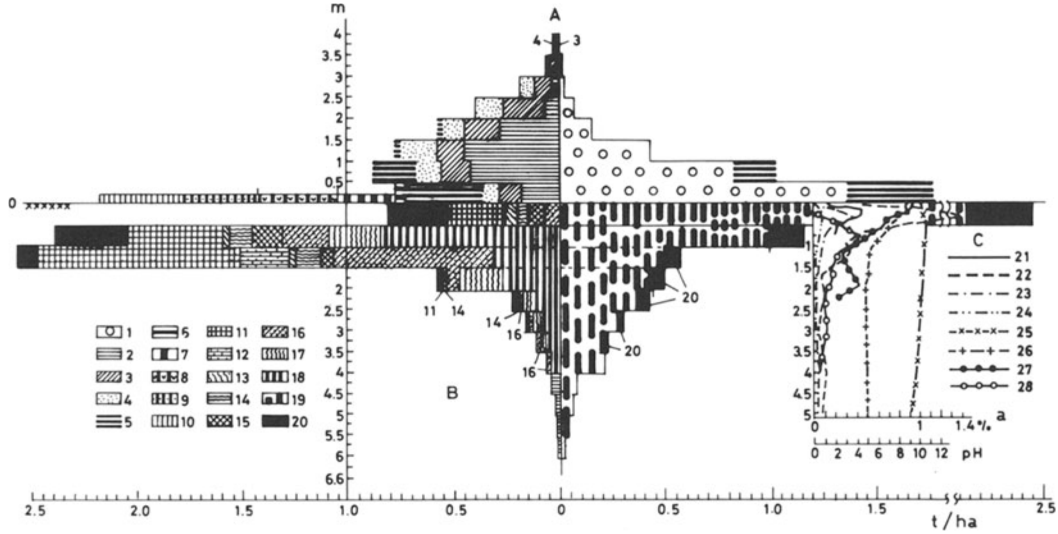


Fig. 5.13. Quantitative distribution with height aboveground and with depth in the soil of the phytomass of *Haloxylon ammodendron (= aphyllum)* in the biogeocoenosis with *Carex physodes,* above groundwater at a depth of 7 m. *A* aboveground phytomass: *1* trunk; *2* branches more than 1 cm thick; *3* inner branches; *4* shoot from the previous year; *5* dead branches in the crown; *6* dead wood on the ground, including *7* more than 7 cm in diameter; *8* 3–5 cm in diameter; *9* 1–3 cm in diameter; *10* less than 1 cm in diameter. *B* belowground phytomass: *11–18* are lateral roots, subdivided by diameter as follows: *11* less than 0.5 mm; *12* 0.5–1 mm; *13* 1–2 mm; *14* 2–4 mm; *15* 4–10 mm; *16* 10–20 mm; *17* 20–40 mm; *18* more than 40 mm; *19* taproot; *20* dead roots. *C* Composition and moisture content of the soil: *21* % humus; *22* % dry wt; *23* % Na; *24* % Cl; *25* pH; *26* % CO_2 *27* water content on May 5th and 28th, water content on July 2nd. The taproot of *Haloxylon* reaches the capillary fringe of the ground water

readily by sheep but rejuvenate easily from stump sprouts. This saksa'ul forms open stands with 120–150 individuals ha^{-1} and produces 0.4–0.5 t ha^{-1} of firewood and up to 0.2 t ha^{-1} of green fodder (Fig. 5.16).

Calligonum (Polygonaceae) is a genus which, in Turkmenistan, is represented by 55 species, only one of them a tree. Their cylindrical leaves fall early, leaving the shrubs bare (Fig. 5.17). Photosynthesis is carried on by annual shoots which are densely clustered (Fig. 5.18). These develop from axillary buds which branch even before elongation and are discarded during the dry season. The sympodial shoot system is shown in Fig. 5.18 (below). The taproot can reach groundwater provided this is no deeper than 3.5 m. Water is otherwise obtained by means of horizontal roots which can reach a length of up to 20 m.

The number of shrubs on firm sand is 100 to 300 per hectare, on mobile sand only 50 to 100 per hectare. The annual growth of the shoots amounts to 25 to 100 kg ha^{-1}. The most important species are *Calligonum caput-medusae* (height up to 2.5 m) and *C. setosum* (height 1.2 m). The age structure of a stand of *C. setosum* on drifted sand in the southern part of the central Karakum was as follows:

Age in years	Number (%)
1	8
2	3
3–5	1
6–10	14
11–15	20
16–20	41
>20	11
Dead	2

It is obvious that reproduction by seeds occurs only in favourable years. A shrub produces about 14,200 small nuts.

Salsola richteri (Chenopodiaceae) forms shrubs 1.5 to 2 m tall, of which the upper 20–30 cm long, flower-bearing parts die back annually.

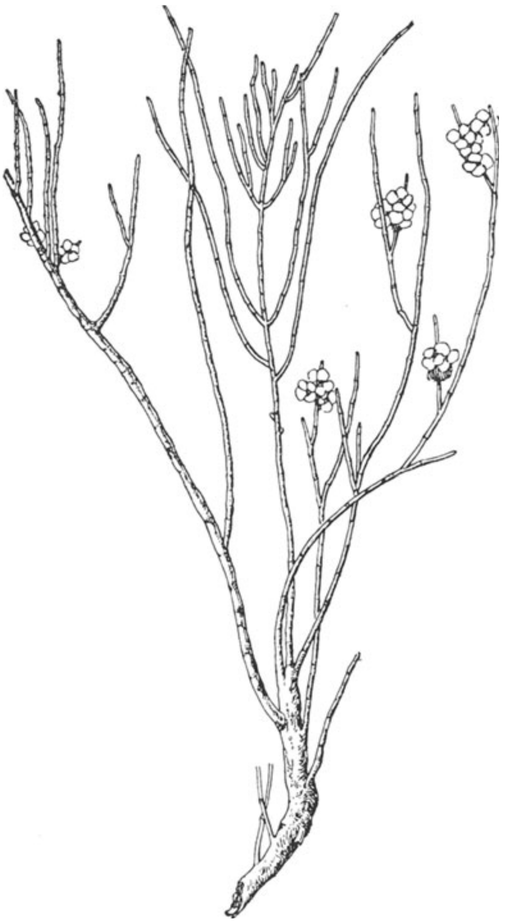


Fig. 5.14. *Haloxylon persicum:* part of a vegetative branch *(centre)* and fruiting branches *(right* and *left)* (after Petrov, from Walter 1968)

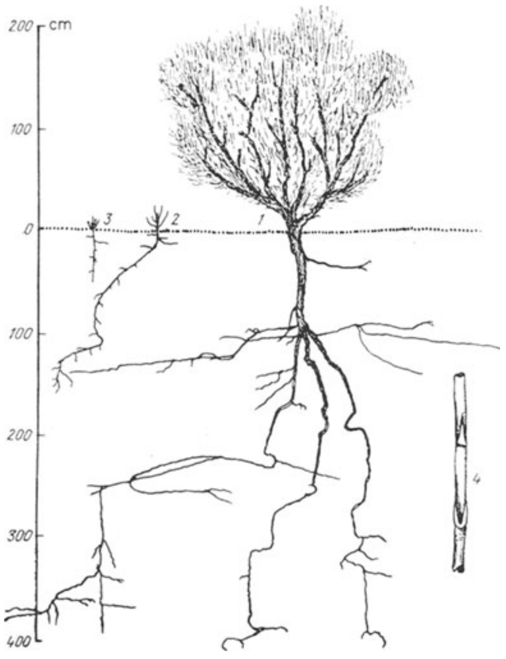


Fig. 5.15. *Haloxylon persicum 1* plant 10–15 years old; *2* a 2-year-old plant; *3* a 1-year-old plant; *4* part of a vegetative shoot with scaly leaflets (after Petrov, from Walter 1968)

Photosynthesis occurs by means of brachyblasts which develop at the base of perennial shoots and have already been dropped before the fruits are ripe. In good years, the shrubs grow primarily vegetative shoots, in dry years primarily generative shoots. The roots reach a depth of 3–4 m. This species is one of the subdominants. There are 25–100 individuals ha^{-1}. The annual aboveground growth can be 30 kg ha^{-1}.

Other important shrubs are the following: *Salsola arbuscula* (height 1 m) with a slight trunk (10 cm high), and other *Salsola* species; *Aellenia subaphylla* (Chenopodiaceae); the lightly foliated *Astragalus paucijugus,* and *Ephedra strobilacea* (height 1–2 m). The last species can live to be 100 years old and occurs either as individual shrubs or in stoloniferous form (Fig. 5.19). On slightly mobile sands it forms dense stands of 400–500 individuals per hectare with an annual growth of 0.4–0.5 t ha^{-1}. It is a valuable fodder plant.

c) Semi-shrubs

These include the endemic *Smirnovia turkestana* (Leg.) with small, summer-deciduous leaflets: various *Artemisia* spp., *Astragalus* spp. and small *Salsola* spp.

d) Herbaceous Species (forming many synusiae)
Carex physodes, with its long underground rhizomes, is the most important turf-forming species on immobile areas of sand with hillocks in the Karakum. The number of shoots reaches 600–700 m^{-2}. The total phytomass, with rhizomes, is 3.6–7.8 t ha^{-1}. The underground mass is 10–18 times greater than the aboveground mass. This species, known as *rang* and also *ilak,* is the most important forage for sheep and is eaten readily in both the green and dried state. Its mode of growth is shown in Fig. 5.20. The species *C. physodes*

Fig. 5.16. Typical vegetation of the central Karakum with *Haloxylon persicum* shrubs (photo Petrov, from Walter 1968)

Fig. 5.17. *Calligonum arborescens* along a railroad embankment 5 km from the Amu-Darya River (photo E.A. Bessey, from Walter 1976)

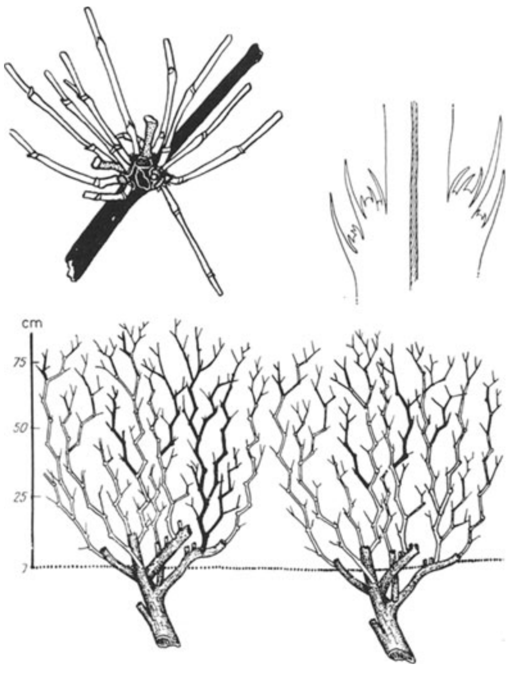


Fig. 5.18. Shoot structure in *Calligonum. Above left* 1-year-old, green, dense shoot on a 4-year-old branch of *C. rubens;* the leaves are only small scales. *Above right* longitudinal section through a lateral shoot bud, with primordia for lateral shoots. *Below* formation of new shoots *(black)* after a wet spring (old branches removed), in *C. setosum;* note the sympodial shooting structure (after Nechayeva, from Walter 1976)

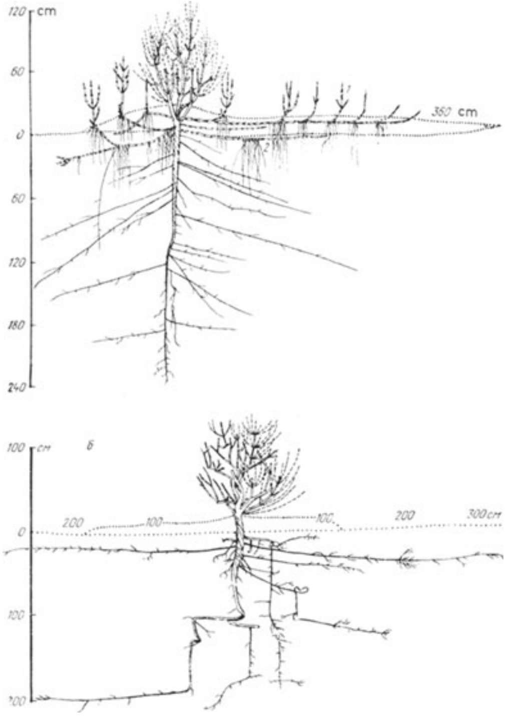


Fig. 5.19. *Ephedra strobilacea. Above* root system and formation of runners on a 10-year-old plant, the sand substrate of which has been blown out: *right* a young runner; *left* runner 2–3 years old. *Below* trunk-forming, roughly 20-year-old plant, the sand substrate of which was blown away during the juvenile stage (after Nechayeva, from Walter 1976)

found on sandy soil is closely related to *C. subphysodes* which grows on sandy grey earths and to *C. pachystylis (C. hostii)* found on loess soils of the foothills.

C. physodes was considered to be a poikilohydrous species but this has since been shown to be incorrect. The leaves die in May, but remain on the plant until September or even the following spring. Only the rhizomes, with active meristems at a depth of 2–3 cm, survive the drought period and the winter. The plants grow to a height of 15–40 cm. The scarcely branched rhizomes lie at a depth of 12–20 cm. The main root mass is found 7–22 cm below the soil surface, but some roots penetrate to 120 cm. In April, after it rains, numerous 0.3–1 cm long, white ephemeral rootlets form around the base of the runners. When the soil dries out again after 5–15 days, they die. There are, however, also longer, thin, but also short-lived roots.

C. physoides comes into leaf immediately after the first rain in autumn; the earliest date recorded was the 20th October; the latest the 20th November. It then lasts through the winter. The growing season varies from 90 to 215 days. The yield of dry mass is strongly correlated with the quantity of rain falling from November to May: 70 kg ha^{-1} for 50 mm rain, 160 kg ha^{-1} for 140 mm. Even under the most favourable conditions, however, the highest yield does not exceed 200 kg ha^{-1}. After a single dry year, the yield in the next year is relatively good; after 2 consecutive dry years it is low. As a result of its very extensive rhizomes, this species is a very successful competitor with the spring ephemerals and the seedlings of woody species. In dry years it definitely suppresses the others. It is a very useful species for sand stabilization. On slightly mobile sand it can advance 0.5 to 1 m in a year. On highly mobile sand the primary colonizers are the perennial

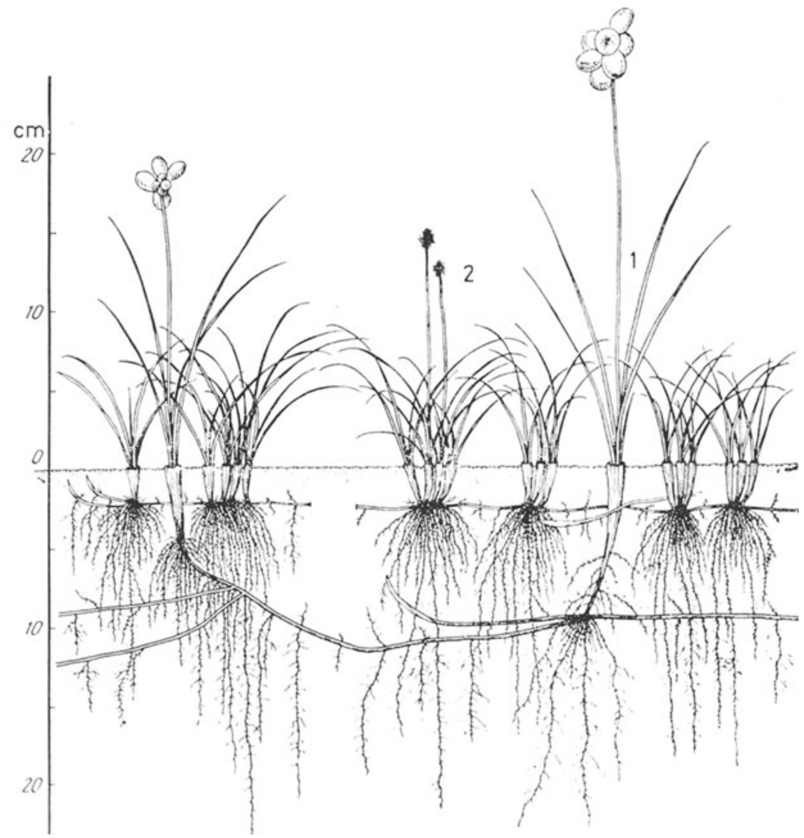


Fig. 5.20. *Carex physodes* with deep-lying rhizomes *(1)* and, for comparison, *Carex pachystylis (2)* growing in the *Poa bulbosa* – Carices association of the Badkhyz region (after Nechayeva, from Walter 1976)

species *Heliotropium arguzoides* and *Tournefortia sogdiana* (both Boraginaceae). Their production reaches 45 to 94 g m^{-2}, which is probably related to the lack of competition.

The most important stabilizer of shifting sand is *Aristida karelinii,* to which we return on pp. 257, 258. The spring geophytes are also represented by many species in sand areas but are not as important as on loess soils. The most noteworthy are *Allium* spp., *Gagea* spp., *Tulipa sogdiana, Rhinopetalum arianum, Eremurus inderiensis* (all Liliaceae), *Iris longiscapa, I. songarica,* the araceous *Emimium lehmannii,* and some dicotyledons with bulbs such as *Rheum turkestanicum;* the umbellifer *Schumannia karelinii* and the 1-m-tall *Dorema sabulosa. Cistanche flava* (Orobanchaceae), which parasitizes *Calligonum* species on the shifting sands, is also interesting. A plant which weighs 7 to 10 kg may consist of up to 94% water.

e) Annual Species

These are represented by 143 species, of which 98 are spring ephemerals and 45 are summer annuals. Only 24 occur in large numbers. The winter annuals, species of the genera *Ceratocephalus, Alyssum, Meniocus, Veronica,* are actually spring ephemerals. Others last until May; these include various Poaceae, Caryophyllaceae, Papaveraceae such as *Hypecoum,* Brassicaceae, Fabaceae, Geraniaceae, Boraginaceae and Asteraceae. We drew attention in Volume 1 (p. 154) to the changes in species composition from year to year. The longer a species need for its fruit to mature in spring, the deeper its roots penetrate, though a depth of 20 cm is seldom exceeded. Only the summer annuals, which germinate in the spring and grow on into the summer, are able to develop roots which penetrate to a depth of 70 cm. In favourable years the summer annuals scarcely develop. The chenopods *Agriophyllum*

Table 5.4. Aboveground phytomass (kg) and the proportion represented by annual shoots

	Above-ground phytomass	Annual shoots (%)
Trees		
[a] *Ammodendron conollyi*	8 kg	6
[a] *Eremosparton flaccidum*	2 kg	6
[a] *Haloxylon aphyllum*	152 kg	8
Shrubs		
[a] *Haloxylon persicum*	18 kg	8
Haloxylon persicum (NW)	5.9 kg	8
Salsola arbuscula	0.8 kg	12
Calligonum rubens	3.8 kg	15
C. setosum	2.3 kg	15
[a] *Ephedra strobilacea*	8.6 kg	19
Ephedra strobilacea (NW)	3.8 kg	20
Dwarf-shrubs		
Limonium suffruticosum	550 g	20
Semi-shrubs		
Convolvulus erinaceus	650 g	31
Astragalus longipetiolatus	330 g	32
Salsola orientalis	170 g	32
S. gemmascens	160 g	33
Mausolea eriocarpa	280 g	34
Smirnovia turkestana	545 g	35
Small semi-shrubs		
Artemisia kemrudica	150 g	39
A. kemrudica (NW)	90 g	37
Reaumuria turkestanica	120 g	62
Aellenia glauca	90 g	65
Acanthophyllum stenostegium	40 g	65
Convolvulus korolkovii	30 g	70

([a] = major species collected in the vicinity of Repetek Station by Togyzayev unpublished) (NW = NW Turkmenistan)

latifolium and *Horaninovia ulicina* can spread on highly mobile sands; that is, in the absence of competition. They germinate between 1st March and 6th April, produce three long roots and, as a result of their xeromorphic structure, last for 6 months.

Summing up, it can be said that the woody plants form the most important component of the vegetation. They are characterized by long annual shoots (1–2.5 m) and by aphylly or microphylly, which results in a small total transpiring surface, despite the denseness of the vegetation. The leaf area index lies considerably below 1. This is understandable because the woody species must survive the drought season. They can reduce water losses further by dropping the small leaves or by the dying-back of transpiring shoots. The fact that transpiration values both per dm^2 of leaf area and per g fresh weight are often very high for desert plants, especially during the favourable season, is not a reflection of their adaptation to desert conditions. To assess the water balance of plants it is more important to estimate the *rate of transpiration per unit area of ground surface* covered by the individual plant or by plant communities. Only then can water loss be related to precipitation. It must be borne in mind, however, that a varying proportion of the rainfall is lost to the atmosphere by evaporation, depending on the nature of the soil.

Table 5.4 shows the mean values for aboveground phytomass (dry wt.) of fully grown plants of different species and also the percentage of this represented by their annual soots. These figures should provide a general idea of the size of the plants and of approximate aboveground production.

The corresponding values for winter annuals are less than 1 g, for summer annuals between 0.3 and 33.6 g, and only for the long-lived annuals, *Salsola paulsenii* and *Horaninovia ulicina* (both Chenopodiaceae) does the phytomass (dry wt.) reach 128 to 500 g.

Ecological Studies on Individual Plants

Transpiration measurements by the quick weighing method, with cut branches, were made in the Karakum by Vasilyev (1931) and by Arcichovski and Opsipov (1931). The experiments of Vasilyev aroused considerable interest because of the high values reported, especially that for the endemic *Smirnovia turkestana*. Kokina (1935) checked these values a few years later and was able to show that they were two to three times too high. Kokina assumed the reason for the over-estimation to be the use of twigs of only 0.5 g and an insufficiently long exposure period (1 min). The most important of Kokina's results is shown in Table 5.5.

The highest transpiration values are attained in June, but the daily maximum is reached by 10 to 11 h. With increasing drought in summer, a reduction in transpiration becomes noticeable. The leaf area is also reduced. It can be seen that, relative to the values for June, the transpiration rate at the end of July had dropped to 76.6–95.8% and in September to 42.2–66.6%.

Nevertheless, the water supply to the plants of the Karakum desert must be regarded as good,

Table 5.5. Transpiration values [g (g fresh wt.)$^{-1}$ h^{-1}] in June, in the morning, according to Kokina (1935) and Vasilyev (1931)

Species	Kokina	Vasilyev
Smirnovia turkestana	1.075	2.93
Ammodendron conollyi	0.876	1.99
Haloxylon aphyllum	0.305	0.87
Haloxylon persicum	0.281	0.43
Salsola subaphylla	0.073	0.20

even during the drought period. This is confirmed by measurement of water deficit made by Bobrovskaya (1969, 1971). The deficits obtained are lower than those typical of steppe species. The deficits for desert species, measured in the field, do not exceed 25%, while sublethal values are in the range 43–53%. Thus the threat of water shortage does not normally exist.

The potential osmotic pressure (π^*) increases from spring through the drought period by about 1.5- to 2-fold; that is, the osmotic potential decreases. This leads to the formation of smaller, more xeromorphic summer leaves or to the shedding of transpiring organs (See Walter 1972b; Walter and Stadelmann 1974).

It is the view of some Russian ecologists that the scanty precipitation in the Karakum is not sufficient, at these high transpiration rates, to guarantee the plants the necessary water supply. It is therefore assumed that additional water finds its way into the soil through condensation of water vapour in the air or through the groundwater. It is suggested that the condensation takes place in temporarily cooler layers of soil.

Blagoveshchenskiy (1954b) conducted appropriate experiments in the Karakum and also further north at Lake Balkhash. After 5 years he was able to demonstrate small increments in soil water of a few tenths to 1% which might be attributed to condensation (see Walter 1968). These experiments are not convincing. There can be no doubt that a temperature-determined vapour pressure gradient in the soil will cause diffusion and condensation of water. With sufficiently sensitive methods it must be possible to demonstrate this. *An ecologist, however, is more interested in how large this condensation would be in relation to the water requirements of the plants.* All measurements of condensation have given values which are too small to be of any ecological significance.

In his measurements of the water content of sandy soils, Miroshnichenko (1975b) did not take account of the fact that the distribution of water beneath the plant cover is very uneven.

It is indeed questionable whether it is necessary to assume a special water source for the water supply of the plants. Careful investigation has shown that wherever plants are growing in the desert, there is readily available water in the region of the roots. This may come from rain which fell in wet years and, being sufficiently deep to be protected from evaporation, remained stored for many years and is sufficient to meet the water needs of the scanty vegetation. *The high transpiration rates of the leaves, measured per dm^2 of leaf area, are not, on their own, a reflection of the water utilization in mm of the plant cover.* In such calculations account must be taken of the very low leaf area index of desert plants (see biogeocoenose, p. 257).

In fact, more recent studies (Nechayeva 1975) have shown that the amount of water consumed by the vegetation in mm per unit area is significantly lower than the amount present in the soil. The plants of biocoenosis I, growing on drifted sand, lost a total of only 37.4mm by transpiration during the growing season. The small trees of *Ammodendron conollyi* showed the highest water consumption (21.6mm, 57% of the total), followed by the shrubs of *Calligonum arborescens* (13.7mm, 36.6%). All the *Aristida karelinii* plants together used only 2.1mm (5.7%), although their daily transpiration per gram fresh weight is, at 20–21g, very high.

At the beginning of the growing season, 83mm of water was stored in the upper 2m of sand in biogeocoenose, I. During the growing season, 49mm was lost through evapotranspiration, leaving 34mm in the autumn. The rain water stored in the soil is thus entirely adequate to cover the transpiration of the plants.

The situation in biogeocoenose II, with *Haloxylon persicum* and *Carex physodes,* is somewhat less favourable. Here 47mm was lost through transpiration. Of this, the shrubs used 30mm (64%), *Haloxylon* alone used 16mm, *Carex physodes* 17mm. Here the water supply in the upper 2m of soil was 62mm at the beginning of the growing season, the loss was 54mm, so that 8mm remained in the soil by autumn. Thus even in this case the water supply was adequate.

The situation in biogeocoenose III is different. This biogeocoenose includes *Haloxylon ammodendron* stands in the dune valleys, which also have a light undergrowth of *Carex physodes* and some halophytic summer annuals. The daily transpiration rate per gram of fresh weight is very high here also: *Haloxylon ammodendron* 7–9 g, *Ephedra strobilacea* 4–4.5 g, *Carex physodes* 15–16 g, summer annuals such as *Suaeda* 2–3 g or *Kochia* 5–6 g. When transpiration is calculated per unit area of surface, the shrubs are found to be responsible for the greatest losses. The total transpiration was 149 mm, that of the shrubs 138 mm (92.5%). *Haloxylon* alone accounted for 108 mm, with the light *Carex* stand needing only 10.6 mm (7%).

At the beginning of the growing season, 76 mm of water was stored in the upper 2 m of the sandy soil. This falls far short of the quantity lost through transpiration. In the dune valleys, however, *Haloxylon* can reach the capillary fringe of the groundwater with its deep roots and can largely cover its transpiration requirement through uptake from the groundwater. If its water requirement were entirely met by groundwater, then the requirement of the other plants (41 mm) would easily be met by the water in the upper 2 m of soil; indeed, some would be left for the use of *Haloxylon.*

These data clearly show that the water supply of all sand-desert plants can be met by rain water stored in the soil and that there is no need whatever to suggest the occurrence of special condensation processes or the uptake of water from the air by shoots.

Further confirmation that desert plants do not suffer from water shortage is provided by the work of Sveshnikova (1975), which has been translated into English. Some of his data are reproduced in Table 5.6. This has also been published in a summary of the research done at Repetek between 1965 and 1969 (Anonymous 1975).

The water deficits of the species of the Karakum are always low and lie far below the experimentally determined lethal values. Moreover, potential osmotic pressure (– osmotic potential) is continuously high only for the halophytes, *Haloxylon* spp. and *Salsola.* For the other species, only the maximum value during the drought is higher. Transpiration rates, per gram of fresh weight, are quite different. As is normal, the values are lower for the larger woody plants than for the semi-shrubs and herbs. The values are reduced during drought. The values of relative transpiration, compared with evaporation from an open water surface, are usually given as 1/4 to 1/18. The ephemerals, which root only in the top soil layers where there is sufficient water in spring, show no special adaptations.

For ecosystem research, however, the water losses of the entire soil-water supply, in mm, are more important. These are low, as we have seen, because the density of the plant cover is low and the plants have adapted to the meagre water supply by reducing their transpiring leaf areas. Many species, such as *Calligonum* spp. and *Eremosparton,* are leafless; others, like *Salsola* and *Astragalus* species, have small leaves, while in *Acan-*

Table 5.6. Data on the water budgets of dominant species in the Karakum Desert, Repetek (Sveshnikova 1975)

Growth forms and species	Transpiration level [mg (g fresh wt.)$^{-1}$ h^{-1}]		Water content (% of fresh wt.)	Osmotic potential (bar)		Water deficit (% of water saturation)	
	Max.	Typical		Min.	Max.[a]	Natural	Sublethal
Trees and shrubs							
Haloxylon ammodendron	670	100–400	62–80	–58	–46	14	47–50
Haloxylon persicum	850	100–700	50–66	–58	–38	21	48–53
Calligonum caput-medusae	780	100–500	60–76	–41	–16	19	45–48
Salsola richteri	760	100–400	55–76	–56	–31	24	46–48
Ammondendron conollyi	810	100–600	51–76	–50	–24	19	43–46
Semi-shrubs							
Astragalus paucijugus	1540	680–770	63–83			23	45–49
Smirnovia turkestana	2600	600	57–81			33	50–66
Herbs							
Aristida karelinii	930	240					
Heliotropium arguzioides	1750	780	52–89			33	50–67
Carex physodes	2760	600					

[a] Values at optimal water availability (juvenile values still lower).

thophyllum the leaves have been reduced to thorns and *Smirnovia* drops its leaves early.

It has been found that in the case of *Haloxylon ammodendron* 19% of the rain is intercepted by the crown, 14% runs down the trunk. The corresponding values for *H. persicum* were 16% and 9%. The water that runs down the trunk can penetrate along the tap root more deeply into the ground than elsewhere. This makes it easier for roots to grow deeper, especially in wetter years, and thus to reach the groundwater. The continued existence of the tree is then assured even in drought years.

Investigations on photosynthesis have shown that the plants of the Karakum have a positive net CO_2 assimilation throughout the summer, providing further evidence of a satisfactory water balance. Data for plants of the Karakum are shown in Table 5.7 and of the Kyzylkum in Table 5.8.

Table 5.7. Data for the gas exchange of Karakum Desert plants (Voznesenskiy, 1975)

Species	Intensity of apparent photosynthesis [mg CO_2 (g dry wt.)$^{-1}$ h^{-1}]		Productivity of photosynthesis [mg CO_2 (g dry wt.)$^{-1}$ day^{-1}]		Optimum temperature for apparent photosynthesis	Respiration intensity	
	Average	Max.	Average	Max.	(°C)	(°C)	[mg CO_2 (g fresh wt.)$^{-1}$ h^{1})
Ammodendron conollyi	7.6	20	110	160	22–35	30	1.2
Haloxylon ammodendron	7.1	10	80	100	10–30	33	1.2
Haloxylon persicum	6.1	10	55	85	10–45	30	1.1
Salsola richteri	6.0	18	120	160	20–30	30	0.6
Calligonum caput-medusae	5.8	12	80	125	25	30	0.7
Ephedra strobilacea	2.3	4	30	35	5–20	—	—
Astragalus paucijugus	14	22	170	240	15–23	35	0.7
Aristida karelinii	21	52	250	460	30–40	32	1.6
Heliotropium arguzioides	8.6	24	170	215	15–30	35	1.1
Carex physodes	14	29	205	220	17–30	—	—

Table 5.8. Data for the gas exchange of Kyzylkum Desert plants (Voznesenskiy 1975)

Species	Intensity of apparent photosynthesis [mg CO_2 dm^{-2} h^{-1})		Productivity of photosynthesis (mg CO_2 dm^{-2} day^{-1}) (maximal)	Optimum temperature for apparent photosynthesis	Respiration intensity	
	Average	Max.		(°C)	(°C)	[mg CO_2 (g fresh wt.)$^{-1}$ h^{1}]
Salsola orientalis	10	23	200	15–35	22–25	1.1
Calligonum aphyllum	25	32	300	—	22–25	1.3
Atraphaxis seravschanica	—	24	—	20–35	22–25	1.6
Aellenia subaphylla	20	22	270	15–35	22–25	0.5
Eurotia eversmanniana	—	40	—	15–35	22–25	0.9
Artemisia turanica	30	50	400	—	22–25	0.4
Alyssum desertorum	—	47	200	20–30	15	0.9
Malcolmia africana	—	27	230	25–30	15	0.6
Astragalus filicaulis	20	51	310	15–30	—	—
Ferula assa-foetida	28	30	340	—	22–25	0.8
Veronica campylopoda	—	25	—	30	15	0.3
Lamium amplexicaule	—	24	150	25	22–25	0.9

Since they have an adequate water supply, all species in the sand desert are photosynthetically active throughout the growing period. Double-peaked curves or a marked decrease in photosynthetic rate after a maximum during the morning have not been observed. In all the woody plants there is a rather flat peak around midday, whereas for the herbs there is a sharp maximum.

The highest values for CO_2 assimilation were recorded for *Smirnovia turkestana* (Leguminosae), which also typically has a high transpiration rate, in the grass *Aristida karelinii* and in the large umbelliferan *Ferula litwinowiana.* Of these, *Aristida* is the only C4 plant, the other two are both C3 plants. CO_2 assimilation is very low in the gymnosperm *Ephedra* and also in *Eminium lehmannii* (Araceae) and *Rheum turkestanicum.*

All desert species are of course sun-plants and utilize the full intensity of daylight. They are also adapted to higher temperatures. The optimum for CO_2 assimilation lies between 20 and 30°C; for *Haloxylon* it is even 45°C. Only *Ephedra* has a low optimum temperature between 5 and 20°C, and is thus able to assimilate even on cold days in winter.

The daily rate of production per gram of dry weight is very high in ephemerals which have a short growing period, very much lower in perennial species; total annual production per unit weight is more or less the same in these two groups of plants.

These observations all show that the various plant types of the Karakum desert are well adapted to the environmental extremes to which they are exposed in the summers of this very hot sand desert.

The Biogeocoenoses and Synusiae

In the Karakum, psammophytic biogeocoenose complexes predominate and can be regarded as the zonal vegetation. Within this, island-like, there are takyr biogeocoenose complexes on clay and halophytic biogeocoenose complexes on saline soils. Each complex consists of a series of biogeocoenoses which correspond to plant associations.

a) Psammophytic Biogeocoenose Complexes

The sand sea of the Karakum, with its characteristic vegetation, stretches in endless monotony over hundreds of kilometres from the Unguz southwards to the Kelif Uzboi (see Fig. 5.2). This comparison to a sea is especially appropriate in that the surface is not smooth but undulating in appearance. The sand waves are either elongated, low sand ridges or irregularly distributed dunes with sparse plant cover. The changing relief, with raised areas and with depressions or lower-lying plains between them, gives rise to a particular pattern in the vegetation, from the more poorly covered hilltops to the denser vegetation of the lower-lying areas. This biogeocoenose complex is thus in effect a catena (Fig. 5.21), as follows:

1. The highly mobile tops of the dunes carry only a few pioneer species.
2. On the upper part of the slopes the sand is less mobile, so a number of typical woody plants can form sparse stands and stabilize the sand.
3. The sand of the lower part of the slopes is immobile: the white saksa'ul with many accompanying species forms a dense vegetation.
4. In the lower parts of the relief the sand is covered in addition by the sand sedge, *Carex physodes.*
5. There are also valley-like hollows which will be discussed separately.

The boundaries between 1 and 2, as well as between 3 and 4, are indistinct. Thus it is more practical to distinguish only two biogeocoenoses: I, an Ammodendretum aristidosum on mobile sand and II, a Haloxyletum persici on immobile sand. The open and scattered vegetation of the desert is, in general, very difficult to subdivide into sharply delimited communities. The varying relief gives rise to a certain mosaic structure.

The areas with shifting dunes, individual barchans and barchan fields, found around the research station at Repetek and along the Amu-Darya, form a special vegetationless biogeocoenose.

The series 1 to 4 in Fig. 5.21 represents an ecological gradient or successional sequence on sands of decreasing mobility. The first pioneer species to appear on highly mobile sand is *Aristida karelinii.* The larger grass, *Elymus giganteus,* has its southern limit around Lake Aral.

Aristida karelinii forms clumps from 0.8 to 2.6 m. The orthotrophic shoots grow from the end of February to the beginning of December; blooming continues from the end of April until October, but is at a minimum during the summer drought. The fruiting stems and leaves die in autumn; the main stalks survive the winter and develop again in the spring. The stalks grow for 2 or

Fig. 5.21. Profiles along a catena (ecological-pedological series) in the hilly sand region of the central Karakum: *1* pioneer stand on mobile sand of dune ridges, with *Aristida karelinii, Tournefortia* etc.; *2* upper dune slope with still mobile sand and shrubs such as *Ammodendron conollyi; 3* lower slope with hardly mobile sand supporting *Haloxylon persicum* (not shown) and herbs (such as *Dorema, Astragalus); 4* sand completely covered by a closed turf of *Carex physodes* beneath *Haloxylon* (not shown)

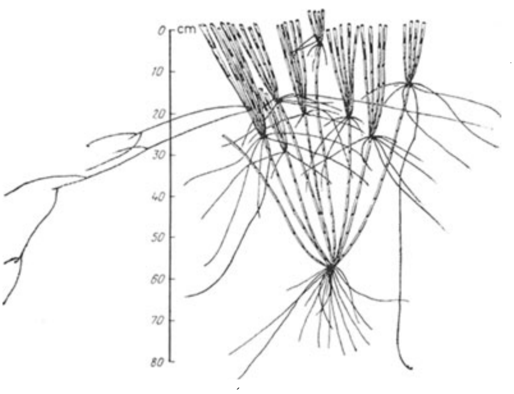


Fig. 5.22. *Aristida karelinii.* Formation of adventitious roots at a higher level after being covered by sand. Earlier level of sand surface was at a depth of 55 cm, the later level at 20–30 cm (after Nechayeva, from Walter 1976)

3 years, the whole clump for 15 to 20 years. This species tolerates being covered by blown sand, continuing to grow until it re-emerges (Fig. 5.22). The root system is very extensive in the sand. The 40 to 350 adventitious roots grow out radially and reach a length of 10 to 15 m. They penetrate up to 2.2 m deep into the ground, but most are found in the first 15–60 cm. The root tips are thickly covered with root hairs to which sand grains adhere. The root cortex dies early, and only the guiding central cylinder remains. It is surrounded by a loosely fitting sheath, made up of dead rhizodermis, with the root hairs and the attached sand grains. The same phenomenon is found in the *Aristida* spp. of Namibia (Vol. 2, p. 129; Walter 1939). This structure forms a sort of protective sheath for the roots once the sand dries out. Both the sand-covered shoots and the extensive root system help to stabilize the sand and other species are then able to establish themselves.

The aboveground phytomass of the *Aristida* stands reaches 6.3–8.9 t ha^{-1} and the total phytomass reaches 12.2–17.3 t ha^{-1}. The number of clumps can reach 3800 to 6400 per hectare. Table 5.9 shows the age structure of populations in the protected area near Repetek and in grazed areas. This grass is not readily eaten, but can be used as emergency forage for sheep in winter.

A second, smaller species is *Aristida pennata* (height 40–50 cm, clump diameter 40–80 cm). It is found more on small mobile sand patches in the hilly parts of the Karakum. The occurrence of this species on grazed areas is a certain sign of overgrazing. The still smaller *Aristida plumosa* grows only on immobile sand.

The next pioneer species, after *Aristida karelinii,* are *Heliotropium arguzioides* and *Tournefortia sogdiana* (both Boraginaceae). These spread very quickly, the first by means of horizontal roots with adventitious shoots at a depth of

Table 5.9. Age structure of *Aristida karelinii* stands on mobile barkhan stands in the central Karakum Desert (from Nechayeva et al. 1973)

Age (in years):	1	2–3	4–5	6–10	11–15	Dead
Protected area						
Number of plants	1843	493	345	588	193	290
Percentage	49	13	9	16	5	8
Grazed areas						
Number of plants	2583	1620	655	768	440	283
Percentage	41	26	10	12	7	4

20 cm, and the second by means of underground runners at a depth of 10 cm. These species also tolerate covering by sand. They are especially typical in blown-out depressions. Their roots reach to a depth of 1 to 2 m. Both species hold the sand together in summer, after the annual species of the open stands, *Agriophyllum latifolium* and *Horaninovia ulicina* (both Chenopodiaceae), have died. *Heliotropium* and *Tournefortia* provide summer forage. The phytomass of such stands is 1.2–1.4 t ha^{-1}, of which 18–33% of the total is represented by accompanying species.

If once sand movement is reduced, seedlings of woody species can often gain a foothold in the shelter provided by the grass clumps. With this begins the stage represented by open shrub and tree stands on only slightly mobile sands. The following species are important, with usually only 10–12 species on any particular site.

Woody plants: *Ammodendron conollyi, Eremosparton flaccidum, Salsola paletzkiana, S. richteri, Smirnowia turkestana, Ephedra strobilacea, Calligonum arborescens, C. caput-medusae, C. eriopodium, C. densum, C. erinaceum, C. microcarpum, Astragalus ammodendron* and, singly, *Haloxylon persicum.*

Perennial herbs: *Aristida karelinii, Convolvulus erinaceus, C. divaricatus, Acanthophyllum elatius, A. korolkovii, Artemisia diomoana, Heliotropium arguzioides, Tournefortia sogdiana, Dorema sabulosum.*

Annual Herbs: *Agriophyllum latifolium, A. minus, Horaninovia anomala, H. ulicina, H. minor, Corispermum lehmannianum, C. papillosum* and *Cutandia memphitica.*

Normally only 10–12 species occur simultaneously.

This biogeocoenose can be seen as comprising two synusiae, one on highly mobile sand with *Aristida* and associated species, and a second on slightly mobile sand with *Ammodendron* and its associated species; there might even be considered to be a third synusia with ephemerals.

The sand is so well bound by the shrubs that the white saksa'ul (*Haloxylon persicum*) becomes dominant and *Carex physodes* also invades.

The Haloxyletum persici is the most important plant community and has been described in detail by Rodin (1963). It is limited to deep, slightly hilly sands with little or no serozem formation. This is the most structured community in the Karakum, and the following strata and synusiae can be distinguished:

Upper stratum: this is composed of low trees and tall shrubs, with a height of 2.5–4.5 m and a cover of 20–30%. The dominant species is *Haloxylon persicum* (300–600 ha^{-1}). Subdominants are *Salsola richteri, Calligonum arborescens, C. eriopodum, Ephedra strobilacea* and, limited to blow-out scars, *Ammodendron conolloyi.*

Middle shrub stratum: usually 1–1.5 m tall, composed of individual *Astragalus paucijugus, A. unifoliatus, Smirnowia turkestana,* and several *Calligonum* spp. but only two or three of these in any one stand.

Semi-shrub stratum: 30–50 cm high, with four or five of the following: *Convolvulus erinaceus, C. divaricatus, Haplophyllum* spp., *Mausolea eriocarpa, Artemisia badkhysi var. arenicola, A. lobulifolia* and *Acanthophyllum* spp.

Herb stratum: Korovin (1961/62) identified a total of 130–140 herbaceous species for the entire Karakum region, of which 46.5% are ephemeral and 19% are perennial. The most important perennial is *Carex physodes,* generally considered to be an ephemeroid. It has a cover of 30–40%, rarely 60–70%. Ephemerals are very numerous, often appearing in groups which represent the seedling foci of the previous year. Especially common are *Arnebia decumbens* (Borag.), *Koelpinia linearis* (Comp.), *Papaver pavonium, Senecio subdentatus, Cutandia linearis, Bromus* *tectorum, Eremopyrum orientale, E. buonapartis, Schismus arabicus, Trisetum cavanillesii* (all Gram.), *Amberboa turanica* (Comp.), *Erodium oxyrrhynchum Isatis emarginata, I. trachycarpa, Acantholepis orientalis* (Comp.), *Euphorbia densa, Scabiosa olivieri, Astragalus* spp., *Spirorrhynchus sabulosus* (Cruc.) and *Malcolmia* spp.

In individual stands there are usually no more than 30–35 species, according to site samples which have been made (Nechayeva 1954b).

With a greater plant cover on the sands, the water situation for the plants deteriorates. The vegetation-less Barchan fields store about 50% of the rainwater, so that a freshwater reserve of groundwater forms beneath them. Where groundwater comes close to the surface, as at the base of the barchans, stands of reeds (*Phragmites*) may be found in the middle of the dunes.

Even the pioneer species on the tops of the dunes do not suffer from shortage of water. The pure sand contains at most 1.5–2% of grain sizes less than 0.01 mm. It has a wilting point of less than 1% water content, while the water content at a depth of 75 cm is always 1–3% while at 2 m even 3–5% and occasionally 5–7%. The clumps of *Aristida karelinii,* the roots of which penetrate a large column of soil, can easily survive the summer drought.

As a result of decomposing plant litter, the percentage of finer particle sizes reaches 3% during the sere represented by woody plants on easily mobile sand. In addition, there is 0.5% humus. Under the shrubs some activity by soil organisms becomes noticeable.

In the next successional stage on the stable sands, the proportion of finer particles is as much as 4–4.5% and the humus content also higher. An actual soil (a loose serozem) is beginning to form. This is true to an even greater extent in the *Haloxylon persicum – Carex physodes* community (Fig. 5.23).

The ash content of the litter supplies the soil mainly with calcium. The ash content of *Haloxylon* is 17.3%, of which only 6.7% is water-soluble. Similar ash content is found in the other woody species. The litter of the herbs also contributes considerable organic material. The nitrogen content of the soil rises to five or six times that of dune sand, while the phosphorus content doubles. The soil surface becomes somewhat compacted, and the water-holding capacity of the upper soil layers increases. A larger fraction of the rain water is stored at lesser depth, and, especially in wet years, relatively less water is stored at greater depths. The annual precipitation varies between 24 and 172 mm, while the potential evaporation is 1500 to 2000 mm. The water in the deeper layers is taken up by the roots and so, in the absence of adequate replacement, the soil underneath dries. Its water content becomes only 1.5–2 times the hygroscopic amount and is thus not usable. Even so, the precipitation should be sufficient to cover the needs of the vegetation (p. 254).

In dry years the woody plants and perennial herbs reduce their transpiring surfaces considerably, and the ephemerals barely develop at all. They exercise a certain buffering effect on the water balance which, cybernetically considered, represents a regulatory circuit with negative feedback.

Where especially dense stands of *Carex physodes* develop, very little water penetrates to deeper layers. This is especially true if a thick cover of moss (*Tortula desertorum*) is formed. This occurs mostly outside the central Karakum. In such cases the summer water supply of the higher plants is endangered and they usually die. The opinion is often expressed in the Russian literature that the succession is proceeding towards this as a final lichen-dominated stage. This purely theoretical consideration is, however, unlikely to obtain in natural conditions, for it does not take account of the burrowing activities of the large numbers of rodents, nor of the trampling by large herds — in former times wild game, now herds of sheep. Closing of the plant cover is prevented by these animals (pp. 265, 268).

Biogeocoenose III with *Haloxylon ammodendron* is scattered throughout the sandy regions, and is limited to the valley-like, deeper depressions and hollows (Fig. 5.24). It is encountered more often outside the central Karakum, when layers of loam intervene between the sand strata. When these layers are at not too great a depth and water accumulates above them, the black saksa'ul, *Haloxylon ammodendron (= aphyllum)* often occurs alongside *Haloxylon persicum. H. ammodendron* has a wide ecological range. It occurs mostly on loamy soils and is much less sensitive than *H. persicum* to salt, although it is not found on solonchak soils. It forms dense thickets on soils with shallow groundwater tables.

Haloxylon ammodendron is an alkali-halophyte; that is, it has a high ash content (22.5% of dry wt.) with a high proportion of sodium but little chloride and sulphate. The soil receives about 252 kg ha^{-1} of ash elements a year

Fig. 5.23. Spring phenophase in the Karakum near Repetek: *Haloxylon persicum* shrub and *Carex physodes* with very swollen utriculli (photo by Petrov, from Walter 1968)

Fig. 5.24. A dense stand of black saksa'ul *(Haloxylon ammodendron)* in a depression of the sand desert with brackish soil above groundwater. The ground is densely covered with *Carex physodes*. The large bunch grass in the foreground is *Lasiagrostis (Stipa) splendens* (photo Petrov, from Walter 1976)

from the litter (4.5 t ha^{-1}), which leads to a certain salination. As a result, the accompanying plants are often halophytes, for instance *Tamarix* spp.; these are also limited to places where there is groundwater. In the central Karakum there are only small stands of the black saksa'ul in the depressions of the dune regions. In the Trans-Unguz Karakum, *Haloxylon ammodendron* stands with a dense cover of *Tortula desertorum* occur.

The biogeocoenoses with *Haloxylon ammodendron* are less common in the sand desert. This species develops much better when its roots reach groundwater. In the river valleys there are dense forest-like stands with heights up to 14 m and trunk diameters of 1 m. The number of trees and larger shrubs can reach 2500–5000 ha^{-1}. The phytomass is estimated as 55 t ha^{-1} and the primary production as 10.5 t ha^{-1} (Rodin 1961). Most of the trees are chopped down for firewood, but some replanting does occur.

The Haloxyletum ammodendri is thus clearly related both to the floodplain biogeocoenose complex and also to the takyr biogeocoenose complex on solonchak with high groundwater. The *Haloxylon ammodendron* stands are characterized by an especially distinct mosaic structure. Beneath the tree crowns there are specific synusiae which have been studied, mainly in the Kyzyl Kum Desert (Rotshild 1960). The microclimate under the trees is much milder and less extreme because of shading, wind protection and the accumulation of snow in winter. The soil is also affected. It contains more humus and nitrogen, as a result of continuous availability of litter but it also contains more salts, set free during the decomposition of the litter. This leads to formation of solonetz and to compaction. Species such as *Carex physodes* and *Artemisia* are not found under the tree crowns. In their place appear certain characteristic species (Chenopodiaceae) which are more hygrophilic, nitrophilic and halophilic; that is, they have a more ruderal character. Burrows of *Rhombomys opimus* are common under the trees and make the mosaic structure more complicated. Ephemerals are often especially dense where water drips down from the tree canopy.

The special characteristics of the microbiotopes under *Haloxylon persicum* and other shrubs are not so distinct but are still clearly visible. These also represent especially suitable habitats for animals.

b) Takyr Biogeocoenose Complexes

In the true sand desert there are only small takyry. They occur in places where the upper layers of sand have been blown away, exposing firm, clayey, geologically older strata. Water collects on these areas after heavy rains and they are covered shallowly before the water evaporates. The temporarily wetted soil is a suitable biotope for the takyr algal communities.

These communities can represent the starting point for an ecological gradient which can also correspond to an ecological succession (see p. 240). Such a succession is a typical example of a biogeocoenose complex.

There is more runoff from a takyr when the snow melts than on rainy days. The melting of a 33-mm-thick snow cover in March 1948 yielded a runoff of 16.6 mm. Runoff from a dry takyr commences when about 3 mm of rain has fallen, from a wet takyr somewhat sooner. Before runoff begins, however, the cracks in the 2–3-cm-thick surface crust must close completely. On the takyry at the foot of the Kopet Dagh, which are less clayey, the runoff is somewhat less, even though the slope is slightly greater.

At some places in the takyr the water remains standing for longer and the soil is wetted to a greater depth. This enables ephemerals, which have a taproot, to establish themselves. Areas of erosion, where the sediments are loosened and deeper, and also piles of sand blown from nearby dunes, are good seedbeds for seeds washed down from the slopes. In a 6-cm layer of soil which had been deposited in an erosion channel, 31,000 seeds were found per m^2 (Rodin and Sukhoverko 1956). Only seedlings of species suited to this habitat survive and grow. The first are usually *Salsola turcomanica, Halimocnemis mollissima, Lepidium perfoliatum* and *Malcolmia africana.* These are followed by the annual grasses, *Hordeum leporinum* and *Eremopyrum orientale,* with their fine felt-like root systems, and finally also *Poa bulbosa.* These plants hasten the process of soil formation and semi-shrubs appear. *Artemisia* spp. and the very characteristic alkali-halophyte *Anabasis salsa.* The organic mass amounts maximally to 3 t ha^{-1}, one-third above the ground and two- thirds below (Rodin 1961). Soil algae remain numerous. Slight salinization usually occurs and this brings about changes in the vegetation.

More widespread than these true takyry are takyr-like areas where the clay crust is not as thick and so they carry a halophyte vegetation.

c) Halophyte Biogeocoenose Complexes

In the lowest-lying parts of the sand-desert relief, the groundwater may be so near the surface that this is always kept wet by the capillary fringe. As a result of the high evaporation, the salts contained in the groundwater accumulate and form a solonchak soil. Saltpans (*shory*) form and around these there is a clear zonation of plant communities. We can combine these into a biogeocoenose complex corresponding to an ecological series along a gradient of decreasing salt concentration (with increasing depth to the groundwater) from the centre of the saltpan to the periphery (see also p. 238). Sometimes salt-excreting grasses also occur, usually *Aeluropus litoralis*.

Sand blown from neighbouring dune areas collects around all the shrubby species of this complex. The dunes formed around *Halocnemum* remain small (0.5 m high), but much sand accumulates around the rapidly growing *Tamarix* shrubs and around *Nitraria*, which is indigenous to the area (Blagoveschenskyi 1955). Thus around the salt pans there may develop a "nebka" landscape, as it is known in North Africa (Vol. 2, p. 394); that is, heaped dunes occur at regular intervals, and from their crests emerge the shoot tips of the covered shrubs. The shrubs root in the groundwater. If the wind blows from one direction only, as it does between the Balkhan Mountains, then the dunes gradually take on the shape of long ridges, roughly parallel to the direction of the wind.

These heaped dunes provide a suitable habitat for non-halophilic herbs. *Haloxylon ammodendron* stands are often found around the edge of such saltpan depressions (Fig. 5.24). The dunes also harbour a specific fauna and thus form microecosystems. Characteristic for the true halophytes of this complex is the constantly high content of sodium and chlorine in their transpiring parts (Bazilevich et al. 1972) and in their litter (Table 5.10). These are thus typical chloride halophytes.

The phytomass of this biogeocoenose is not high: *Halocnemum* 1.76 t ha^{-1}, of which 59% is roots (litter: 0.515 t ha^{-1}); *Kalidium* 1.38 t ha^{-1}, of which 75% is roots (litter: 0.7 t ha^{-1}).

Sodium and chlorine, in the form of NaCl, return to the soil with the litter and can lead to salinization of the soil. The main salinization of these wet sites occurs, however, through the evaporation of capillary water at the surface, leaving salts behind. These salts contain a much larger fraction of sodium chloride than does the litter, in which more potassium, calcium and magnesium are found. Thus the salts coming from the litter are more favourable for plant growth than those coming from the groundwater. There is even a certain desalinization by the litter. The halophytes indeed actually prepare the soil for the ephemerals by their ability to collect windblown, salt-free sand.

Ecological Subdivision of the Karakum Desert

This desert has been so thoroughly studied that it is possible to subdivide it to the smallest ecological units, the synusiae. This is shown in the diagram on p. 264.

5.4 The Consumers

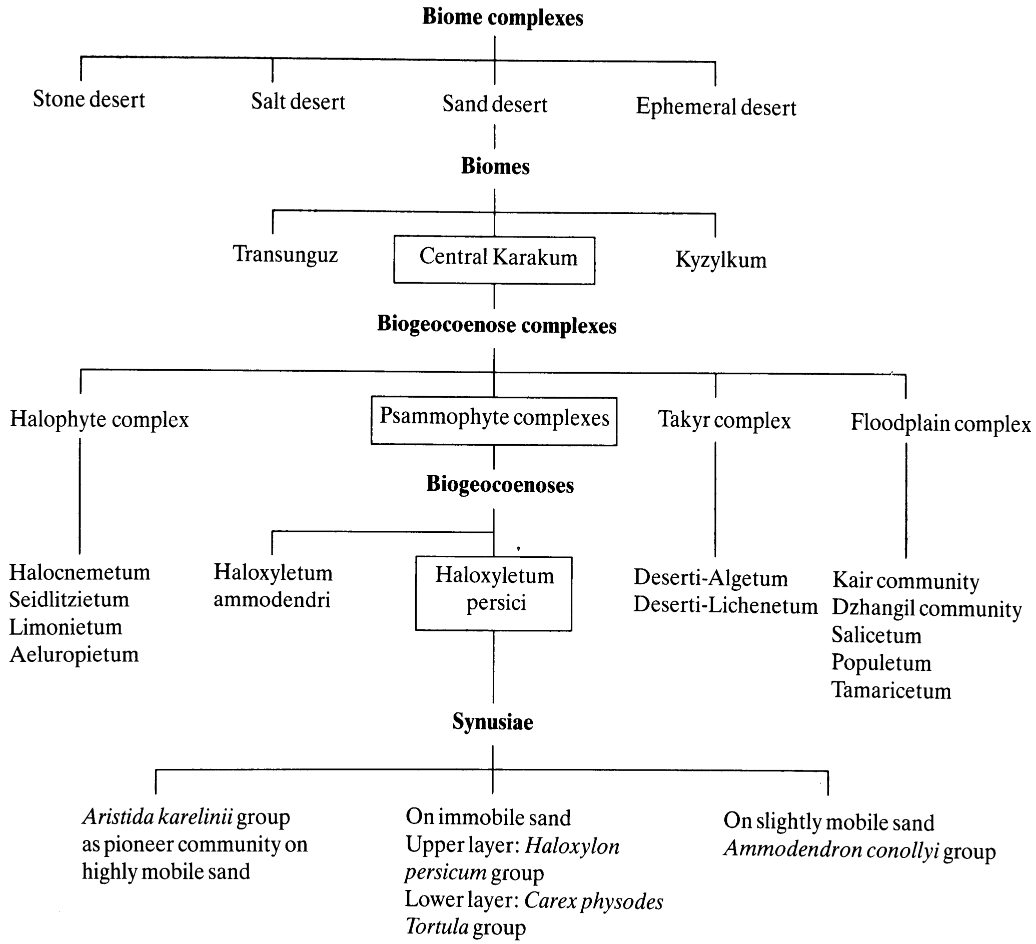
General

In the research conducted in the Karakum, much attention has been directed to the fauna as an important part of the ecosystem.

Turkmenistan is a region that has been settled since the Neolithic. In the course of its history,

Table 5.10. Content of sodium and chlorine (in percent) in the dry matter of various portions and litter of *Halocnemum strobilaceum, Kalidium caspicum,* and *Salsola turcomanica* (from Bazilevich et al. 1972)

Parts studied	*Halocnemum strobilaceum*		*Kalidium caspicum*		*Salsola turcomanica*	
	Na	Cl	Na	Cl	Na	Cl
Annual shoots	5.37	10.05	10.05	8.63	5.90	11.06
Older shoots	2.08	1.68	1.46	1.28	—	—
Roots	1.65	2.09	2.84	1.93	1.04	1.19
Litter	3.10	5.18	—	—	—	—



great empires have been repeatedly established and have fallen. Under these conditions, the original animal populations could not remain undisturbed. Animals which were important for hunting as well as the large carnivores which threatened their numbers, were decimated both in the settled areas on the border and in the desert itself. The large game herds mentioned in old chronicles, with thousands of saiga antelopes, tarpans (wild horses) and kulans (wild asses), have disappeared. To protect herds of livestock, the carnivores were also exterminated, upsetting the balance in the ecosystem. The rodents profited from the elimination of carnivores and birds of prey and today they are the most numerous mammals. Arthropods, as a result of their small size, were not greatly disturbed.

On hot summer days the sand desert gives a totally dead impression as far as animals are concerned; they are neither to be seen nor heard. Apart from the noise of the wind, the desert is silent. This appearance is, however, deceptive. Since the ground surface heats up to 60° C, in extreme cases even 80° C, during the day, and since the air is extremely dry, almost all animals seek shelter underground in burrows where it is cool and the air almost saturated with water. As a result, the animals lose relatively little water, which is important for survival in an area with so few watering places. Indeed, many animals meet their water requirements instead by eating water-containing parts of plants rather than by drinking. Metabolic water, formed during respiration, is also important.

Since it is cool at night and the air is relatively moist, total water loss when the animals are above ground is relatively low. Fluid excretion of these animals is quite small. Thus, like the plants, the animals show special adaptations to the rigorous conditions to which they are exposed in the desert.

The ecological roles of the animals in the Karakum are very varied (Kunin 1955; Rodin 1961):

a) The herbivores, as consumers, feed at the cost of the plant matter produced, while the carnivores eat the herbivores and thus regulate their numbers.
b) Hoofed mammals break up the sand surface and thereby prevent crusting and compaction of the soil.
c) Through burrowing, animals such as rodents and ants redistribute the upper layers of sand.
d) Animals affect the propagation of plants by distributing seeds and fruits, epi- or endozoochorously, as well as by pressing them into the ground under foot, thereby greatly facilitating germination.

The importance of animals as consumers in an ecosystem is less quantitative than qualitative. The total quantity of plant matter consumed is small, but as a result of the damage done to seeds and fruits of certain species, the animals affect the competitive relations of the plants and prevent any single species from attaining absolute dominance. At the same time, the numbers of rapidly reproducing herbivores are held in check by carnivores. There are thus many interdependent regulatory circuits by which the equilibrium of the system is maintained. Regrettably, these complex interrelationships have not yet been adequately investigated. Rodin (1961) has reviewed what is known of the changes effected by animals to the vegetation of western Turkmenistan.

The animals are limited to particular biogeocoenoses: for example, one reptile, one mammal and three bird species occur only in association with *Haloxylon ammodendron,* as is described very clearly by Zaletayev (1976). He points out that 65% of the seedlings of this species are found growing on the mounds of soil left by burrowing rodents. The loosened soil is probably a good germination site, and there is no competition from other plants. On the other hand, the larvae of the beetle *Turcmenigena varentzovi* are quite destructive, since they live in the lowest part of the trunks of old trees and make it easier for the fungus *Poria desertorum* to infect the wood. This fungus destroys the wood so that trunks 30 to 45 years old usually fall over. The sand hummock which arose around the tree is blown out and forms a hollow instead. *Carex physodes* settles on such sites and a levelling of the ground then follows. Animals often effect a series of microsuccessions in this way, giving rise to continuously changing microbiotopes.

Mammals in the Protected Area at Repetek

The area at Repetek, which has been protected since 1928, covers 34,000ha. Of these, 18,000ha have *Haloxylon persicum – Carex physodes* sand vegetation on small, only slightly mobile sandhills, on which *Aristida karelinii* and *Ammodendron conollyi* also grow. The region of shifting dunes with dune valleys makes up 14,000ha, and the remaining 2000ha represent lower-lying sand areas occupied by *Haloxylon ammodendron* stands.

In this relatively undisturbed area about 200 species of vertebrate were identified (29 mammals, 23 reptiles, and more than 140 birds). The invertebrates have not yet been studied in detail, but more than 1000 species of insects have been counted (Kuznetzov, in Resources 1975).

A detailed description of the mammals is given by Stalmakova (1955).

Insectivora

The most important representative of this group is the long-eared hedgehog, *Hemiechinus auritus.* This fairly common species lives in old rodent burrows under blown-out shrubs. In its search for food it may cover a distance of 5km in a single night. Its prey consists of reptiles and various arthropods.

The shrews, *Diplomesodon pulchellum* and *Crocidura suaveolens* also belong to this group and have a similar way of living.

Chiroptera

The bats (*Vespertilio* spp.) need shelter during the day, but this is lacking in the desert. They therefore live in the vicinity of the research station and can be found under the roofs of the houses and in other parts of the buildings. Five hundred individuals were counted in 1948.

Rodentia

The rodents are the largest group in the sand desert and are of great ecological importance.

The slender-fingered ground squirrel, *Spermophilopsis leptodactylus,* is found everywhere, though not in great numbers. Its diet consists of graminoids and herbs, but it disdains the halophytes. It generally forages within 100 to 150m of its burrow, but if the plant cover is very sparse, it may extend its range to 200–300m. This rodent tolerates relatively high temperatures and can leave its burrow during the day. It seeks shelter underground only when the heat becomes very intense, or during rainfall. It feeds mainly on the fruits of *Calligonum,* on the herbaceous ephemerals, and the bulbs of the ephemeroids. The latter are found by smell, even at a depth of 7–9 m. The same habit is shown by other rodents. Rodin mentions that there are areas which are free of *Allium, Tulipa* and *Iris,* although these are places where these plants would normally be expected to occur. That this is a consequence of the feeding activity of rodents is suggested by the many burrows in which remains of bulb sheaths have been found.

The porcupine *Hystrix hirsutirostris* lives in dense *Haloxylon ammodendron* stands and often covers as much as 9 km a night in search of food. Its diet consists of *Nitraria* fruit on saline areas, but otherwise of bulbs of *Tulipa* and the roots of *Ferula.*

The jerboas are represented by three species. *Dipus sagitta* leaves its burrow only at night and closes the opening with sand during the day. Its range extends up to 1 km from its burrow. When escaping predators it may clear 2 m in a single jump before quickly burying itself in the sand. Its main enemies are owls. Jerboas feed on the fruits and assimilating branches of shrubs, on the fruits and shoots of herbs, and on insects. This is also the diet of the desert jerboa *Eremodipus lichtensteinii,* which is found sporadically everywhere. *Paradipus ctenodactylis* is a widespread species which occurs in large numbers but is always restricted to a shrub vegetation, provided slightly mobile sands are present for it to build a burrow. The burrow reaches down into the wet sand layers, while the entrance is always covered with dry sand. It feeds on those shrubs which grow on such open sand areas, such as *Ammodendron* and *Calligonum* species, *Salsola richteri, Astragalus paucijugus* and *Haloxylon persicum.* This jerboa gnaws off branches, starting at the bottom of the shrub and moving upwards to a considerable height. This damage to the shrubs then leads to the blowing away of the sand. This species hibernates for 37 to 78 days, at a time when no *Haloxylon* fruits are available. Arousal from hibernation occurs in spring, when the temperature in the burrow at 2–2.5 m depth begins to rise; this is also the time when *Haloxylon* comes out again.

The vole, *Ellobius talpinus,* occurs only in the southeastern Karakum close to oases. It was, however, also observed in 1940–1943 at Repetek, where it fed on the roots of the shrubs *Haloxylon* and *Ammodendron.*

Rhombomys opimus is probably the most important and widely distributed rodent. In September 1938, 1600 individuals per km^2 were counted in the Haloxyletum ammodendri, but in the Haloxyletum persici there were only 39, while in blown-out dunes just 2. Counts made on a sample 5-ha plot between 1936 and 1950 showed numbers to fluctuate from 0 to 135. Places colonized by *Carex physodes* were most densely settled, 7000 burrow entrances being counted per hectare. The passages of the burrows run at a depth of 50 cm directly beneath the rhizomes of *Carex physodes,* where the water content of the sand does not fall below 0.5% and the temperature varies only between 18° and 35°C. The nesting chamber is at a depth of 80 to 120 cm. Here the humidity is over 80% and the temperature never exceeds 30°C. Food-storage chambers (70 cm long by 50 cm wide) are constructed, and here the food brought into the burrow is eaten. *Rhombomys* selects as sites for its burrows places where there is a supply of food, and lives in families which consist of the two parents and the 13 to 16 young from the last two litters. When foraging, the animals go only a few metres from their burrows. The burrows of individual families are joined with those of other families over an area of 1.5–2 ha. If food is plentiful, the young remain with their families for up to a year, otherwise they wander off after about 4 months. This rodent is active all year round and hordes food for the winter. In summer the animals leave the burrows in the early morning and in the evening; in winter, on fine days, they leave around midday. Their diet consists of various parts of the saksa'ul: in summer, when the branches contain more salt, only the fruit is eaten. In addition, both fresh and dried parts of the available herbs are eaten, above all the rhizomes of *Carex physodes.* In the dune valleys there may be one burrow per m^2 and from each of these it is possible to recover 1 kg hay. The hay consists of up to 90% *Carex physodes* rhizomes. This species disappears from such areas and is replaced by annual grasses, such as *Bromus tectorum, B. macrostachys* and *Eremopyrum orientale* (Rodin 1961). Up to 1.2 t of soil are thrown up by the burrowing. This loose soil is easily blown away by the wind, preventing the establishment of a surface covering of *Carex* and mosses (see p. 260).

In addition to *Rhombomys,* the gerbil *Meriones meridianus* is also common. This rodent inhabits plant-covered sands in the winter, but moves in spring into dune valleys to build burrows under plants or, less frequently, in open sand. The diet consists of fruits, seeds and, to a lesser extent, herbaceous plant parts. *Meriones meridianus* hinders attempts at afforestation with saksa'ul, since it easily finds the seeds which have been set out in the soil.

The red-tailed gerbil, *Meriones erythrourus,* is sparsely distributed in the protected area at Repetek. It seems to be extending its range, however. Indeed, since 1942 it has been found in the storage sheds at the research station, where it steals seeds and fruits intended for sowing. In the process it has adapted itself to new foods, such as *Elaeagnus* fruits and cotton seeds. The animals reproduced so rapidly that control measures became necessary.

Even though these rodents are mobile, they are often strictly limited to particular phytocoenoses. Thus, although *Meriones erythrourus* and *Rhombomys opimus* occur in the same part of the sand desert, they never settle in the same plant community (Rodin 1961). This is true also for the other rodents.

The soil is enriched with various organic materials as a result of the rodents' burrowing (urine, faeces, corpses, plant remains), while the soil structure is destroyed and loosened up. The piles of earth thrown up around burrows increase both the microrelief and soil erosion. The redeposited soil often has a higher salt content, having come from deeper soil layers. On sandy areas around abandoned rodent colonies the first plants to reinvade after abundant rains are ruderal species, followed by *Bromus tectorum.*

A series of ecophysiological investigations have been made on rodents (Stalmakova 1954). The summer is an especially difficult period because of the lack of water-rich food. The juicy organs of the succulent halophytes contain so much salt at this time of the year that the rodents will not eat them. They must subsist on dry food, such as seeds, dry leaves and stems, and a few somewhat juicier bulbs and roots or on the rhizomes of *Carex physodes.*

Stalmakova (1954) determined the water balance of the following species: *Spermophilopsis leptodactylus, Dipus sagitta, Meriones meridianus* and *Rhombomys opimus.* The animals were in water balance in spring when juicy vegetation is available. This was true also for *Meriones* in the autumn, since this species feeds on juicy *Salsola* at this time. In summer, however, water intake was consistently less than water loss and the animals must be making good this deficiency from water produced by oxidation of carbohydrates and fats obtained with the food. If this should be insufficient, then body fat or protein is respired and the animals lose weight.

As a result of the strained water balance, the rodents in the Karakum reproduce only during the short favourable period in March and April. In wetter steppe areas, these species generally have two or three reproductive periods each year. *Citellus fulvus,* which is found only in the northwestern Karakum, hibernates as soon as the herbaceous plants dry up in summer.

Lagomorpha

The desert hare (*Lepus tolai*) is an important species at Repetek. It is very mobile, even though it has its storage chambers in burrows, usually in plant-covered sands. In spring it feeds on the fresh leaves and stalks of herbs; at other times it feeds on the bark of large shrubs such as *Ammodendron conollyi, Eremosparton flaccidum, Calligonum arborescens* and *Astragalus paucijugus.* It does not eat *Haloxylon* or *Salsola* species. Even at the low density of two or three animals per km^2, it can cause great damage. Near *Haloxylon ammodendron* stands, all *Ammodendron* and *Eremosparton* shrubs show signs of gnawing. Young shrubs are bitten off completely. Stabilization of the dune sands is impeded because the plants which are used for this purpose happen also to be the favourite food of this species.

Carnivora

Of the Mustelidae, the weasel (*Mustela nivalis*) was found only once, and then next to the burrow of a ground squirrel (*Spermophilopsis leptodactylis*). The marbled polecat (*Vormela peregusna*) on the other hand, is widespread. This species seems to feed primarily on the large *Rhombomys opimus.*

Among the canines, the wolf (*Canis lupus desertorum*) was never seen at Repetek, although it does occur in winter in the Karakum. This is probably because there are too few watering places at Repetek. Jackal is also found only close to the oases along the Murgab and the Amu-Darya. Within the protected area at Repetek the most common carnivore is the fox (*Vulpes vulpes flavescens*). It eats small mammals, birds, reptiles and also sand-cockroaches (*Anisogamia tamerlana*), scorpions (*Liobuthus kessleri*), camel spiders *(Galeodes fumigatus)* and wolf spiders (*Tarantula bergsonii*). The stomach of one fox killed in the dune region contained 12 wolf spiders and two scorpions. In autumn and winter, foxes try to catch chickens from the settlement around the research station.

Among the cats, a spotted wildcat (a subspecies of *Felis sylvestris*) is very common in blown-out sand areas near *Haloxylon* stands, where many birds make their nests. In 1940, it was found that these wildcats destroyed half of the nests of the lesser whitethroat (*Sylvia curruca*), the nightingale (*Erythropygia*), the dark broad-tailed warbler (*Scotocera platyura*), the turtle-dove (*Stretopelia turtur*), as well as of *Rhodespiza obsoleta.* During the day, the cats lie up in shallow ditches next to shrubs. The sand cat (*Felis margarita thinobius*) was seen only once, as were the tracks left by a desert lynx.

Artiodactyla and Perissodactyla

When the ephemerals develop in spring, wild pigs (*Sus scrofa*) move from the floodplain forests of the Amu-Darya far into the sand areas. Their tracks were observed in Repetek, where they had dug up bulbs of *Emimium lehmannii.* They do not remain continuously in the region.

Another ungulate is the Zheiran gazelle (*Gazella subgutturosa*). Normally there are only a few in Repetek, but their numbers increase in October when the gazelles migrate. They remain in the Haloxyletum persici, where they eat the dry leaves of *Carex physodes,* or in the dunes, where they feed on *Heliotropium arguzioides.* At the beginning of March most of them leave the area again. Those that remain seek shelter in the dense *Haloxylon* stands or sleep during the day under shrubs in the dune valleys. They do not need free water despite the fact that they live on dry sedge leaves and do not eat the juicy shoots of the saksa'ul.

Only 100–200 years ago, before firearms came into general use, there were large herds of antelope, including the saiga antelope, *Saiga tatarica,* and of the mouflon, *Ovis orientalis oreal.* The same applies to the kulan, *Equus hemionis.* Even at the beginning of the century, herds of up to 1,000 were present in southern Kazakhstan in the Lake Balkhash region. Today they have probably been completely eliminated from the region, and small herds occur only in eastern Iran.

These large wild herds certainly had a major ecological effect. The trampling of such herds breaks up the sand surface and prevents growth of *Carex physodes* and mosses, thus decreasing the production of sand vegetation. As a result, the expected final successional stage (p. 260) could never be reached, since the *Carex*-covered areas were the main grazing grounds of the herds. Today the grazers are replaced by man's domesticated animals. These are primarily flocks of sheep. Turkmenistan is the home of the karakul sheep, which yields the well-known black pelts. Karakul skins have become today one of the most important export commodities from this dry region.

When grazing is too heavy, the plant cover is completely degraded, whereas light grazing actually enhances it. Partially degraded areas can recover when protected from further grazing, but where there is no grazing at all, a soil crust of mosses, lichens and algae develops and less rain water sinks into the soil; the whole plant cover becomes poorer as a result. *The presence of large grazing animals is a necessary condition for maintaining the productivity of the ecosystem* (Nechayeva 1979).

Other Vertebrate Groups at Repetek

Detailed studies have been made both of the other vertebrate groups and the invertebrates (Nechayeva 1975).

In the whole of Turkmenistan 60 species of bird have been identified, 25 of which are found at Repetek; 13 of these are nesting migratory birds. Twenty-one species of bird nest in the forest-like *Haloxylon ammodendron* stands, where 11 reptile and 19 mammal species also occur. In the areas of mobile sands with partial plant cover, the numbers are 12 bird, 11 reptile and 15 mammal species.

The bird species found permanently in all three biogeocoenoses are as follows: *Corvus corax, Dendrocopos leucopterus, Aquila chrysatus, Buteo rufinus* and *Athene noctua.* The most common migratory birds are *Lanius excubitor, Sylvia curruca, Oenanthe isabellina* and *Circaetus gallicus.* Only one species (*Parus major*) can always be found in the *Haloxylon ammodendron* stands, but five species nest here (*Hippolais languida, H. caligata, Rhodospiza obsoleta, Sylvia cantillans* and *Upupa epops). Caprimulgus aegyptius* nests in the Haloxyletum persici, *Passer simplex* in the mobile sand. Nesting in both *Haloxylon* stands are *Scotocerca inquieta, Galerida cristata, Passer ammodendron, Streptopelia turtur, Cercotriches galactotes* and *C. europaeus, Podoces panderi* and *Sylvia nana* nest in both mobile and plant-covered sands.

All the polyphagous and herpetophagous species are found in all three biogeocoenoses.

After the breeding season, and especially in winter, many entomophagous birds eat the fruits and seeds of the desert plants. This is especially true for the species in the mobile sands. Carnivorous birds are important in limiting the numbers of the rodents.

There are 40 species of reptile in Turkmenistan; of these, 18 have been found at Repetek. Four of these species inhabit all three biogeocoenoses: two geckos, *Gymnodactylus russowi* and *G. caspius,* the "arrow-snake" *Psammophis lineolatus,* and *Varanus griseus.* Seven reptile species are found only in the mobile sand: *Phrynocephalus interscapularis, P. mystaceus, Crossobamon eversmanni, Teratoscincus scincus, Eryx miliaris, Eremias scripta* and *E. grammica.* The following are found in the stands of the two *Haloxylon* species: *Agama sanguinolenta, Eremias intermedia* and *E. lineolata, Echis carinata, Coluber tyria, C. karelini,* and the tortoise *Testudo horsfieldi.* The tortoises are among the most important herbivores because there can be as many as 100 ha^{-1}. A tortoise will eat each day several hundred grams of young shoots in the inflorescences of the ephemerals. Even though these animals are active for only 2.5–4 months, the damage they cause is clearly visible. During their active season, the tortoises lay 10–15 eggs in the sand. Embryonic development is completed after 3 months, but the young tortoises do not appear on the surface until the following spring and they are then the prey of many carnivores, including carnivorous birds. As soon as the herbaceous vegetation dries out, the tortoises burrow into the sand and disappear for 8 to 10 months.

Most of the other reptiles are carnivorous, especially the snakes, species such as *Thaphlometopon lineolatum, Eryx miliaris* and *E. tataricum:* these greatly reduce the rodent populations. The snakes use the underground tunnels of the rodents for access to their prey, but also for winter dormancy. The same is true also for the monitor, *Varanus griseus,* which grows to a length of 1 m and a weight of 2.5 kg. It hunts young tortoises and other lizards. These latter are also carnivorous as, for example, the extremely quick-moving species of the genus *Eremias.*

Agama lizards live high in the branches of the shrubs in summer but quickly descend and disappear into rodent burrows when danger approaches. Their most striking characteristic is an ability to change their skin colour, being blue when caught.

Invertebrates at Repetek

Only those species closely associated with the woody plants have been studied in any detail. Even for these, however, we have to limit ourselves to a brief account.

Representatives of many groups of arthropods are found in the crowns of *Haloxylon ammodendron.* Most of these are phytophagous and include representatives of the following taxa: Collembola, Orthoptera, Psocoptera, Hemiptera Homoptera including Auchenorrhyncha, Psylloidea, Aleurodoidea, Aphidoidea, Coccoidea, Hemiptera, Heteroptera, Thysanoptera, Coleoptera, Lepidoptera and Cecidomyiidae as well as trombidiform mites. One group, the Araneae (spiders) is carnivorous and in July, this group makes up 35.8% of the invertebrate zoomass in the canopy. Insect galls are very numerous. *Mesopsocus hyemalis* (Psocoptera) feeds on the fungi and algae on tree trunks and in February constitutes 9% of the total invertebrate zoomass on *Haloxylon.* The number of cicadas rises in October to 130,000–150,000 ha^{-1}. The caterpillars of butterflies are also very common, accounting for 50–80% of the zoomass.

Sandflies are dangerous to man, transmitting parasites such as *Leishmania* from rodents. Camping close to areas inhabited by rodents is not to be encouraged. The danger of malaria, however, exists only around the oases. Scorpions and tarantulas are poisonous; ticks often carry viruses.

There is a rich invertebrate soil fauna. Carnivores include the scorpions and pseudoscorpions as well as spiders. Phytophagous and detritivorous groups include the Tromboformes, the Thysanoptera, the larvae and adults of beetles and the larvae of Diptera.

Plant litter is a main source of food for the soil fauna. As a result, the soil fauna underneath tree crowns is quite different from that between the trees, where *Carex physodes* grows and produces almost no litter. Many invertebrates are restricted to the litter of *Haloxylon,* especially the larvae of many beetles which feed on detritus. Their numbers can reach 40,000 ha^{-1}. The larvae alone make up 30–40% (3–6 kg ha^{-1}) of the total mass of the soil fauna. They are most commonly found at a depth of 50–100 cm. Many larvae feed on the finer roots of the trees.

Among animals which spend most of their time underground, the most noteworthy are the brightly coloured ants of the genus *Camponotus* and the soil cicadas of the genus *Pentasteridius*. Termites are, however, rare in *Haloxylon* stands. The large termite (*Hodotermes angerianus*), which builts termitaria 50–70 cm, sometimes even 100 cm in height, is restricted to the foothills of the Kopet Dagh. Termites do occur on takyry, mostly close to depressions with dense marsh vegetation. Ants also inhabit takyry. They are partially seed-eaters but also carnivores. In general, the number of animal species on the takyry is relatively small, because of the low plant productivity. Tables 5.13 and 5.14 give data on the zoomass of the different animal groups.

5.5 The Decomposers

Data on soil flora are to be found in Nechayeva (1984). Novichkova-Ivanova (1978) describes the soil algae, but these belong, of course, not to the decomposers, but to the microproducers. Cyanophytes make up 50% of these algae, of which *Nostoc punctiforme, N. paludosum* and *Cylindrospermum muscicola* assimilated atmospheric nitrogen at the rate of 7.7 mg N per 100 ml of soil in 45 days. The algal mass (dry wt.) in the ephemeral stands (*Carex physodes, C. pachystylis, Poa bulbosa*) is about 15 mg m^{-2}. The algae inhibit soil erosion. They promote the growth of decomposers, whether bacteria, fungi or invertebrates.

The following parasitic or saprophytic fungi have been found on litter and humus: 25 *Peronospora* spp., 2 *Albugo* spp., 100 ascomycetes, 72 ustilaginales and uredinales, more than 100 basidiomycetes and many Fungi Imperfecti. More details are to be found in the tables of the original work (see also Nechayeva and Kaplina 1978).

Little is known about the decomposition and mineralization of the organic remains of plants and animals in the sand desert. Decomposition is initated by the microfauna; by saprophages which break up plant parts and partially consume them and also by coprophages and necrophages, which do the same to the excrement and corpses of animals. The mineralizing activities of the fungi and bacteria begin simultaneously. Because of the high summer temperatures, hardly any humus is formed. Since the litter of the halophytes, especially the Chenopodiaceae, always contains large amounts of soluble salts (ash content 22–32%), these accumulate in the soil and can result in salinization. For true halophytes the salts are usually sodium chloride and sulphate; for alkali-halophytes, of which *Haloxylon ammodendron* (ash content 22.5%) is one, the concentration of sodium ions outweighs those of chloride and sulphate together by a wide margin. These are compensated in the cell solution by ions of organic acids, often oxalic acid. Since the organic acids are oxidized to carbon dioxide, the sodium in the soil accumulates in the from of carbonate and the soil becomes strongly alkaline. This can result in the formation of solonetz.

Within the protected area of Repetek, 13 species of fungi were isolated from the rhizosphere and 14 species from the surrounding soil. Half of these were *Penicillium* species.

Soil bacteria are very numerous: 3 to 8 million g^{-1} dry soil. *Pseudomonas* and *Bacillus masentericus* were especially common, but *Azotobacter* and *Clostridium* occurred also, as well as Actinomycetes.

5.6 Quantitative Ecosystem Research

The most complex of the biogeocoenoses of the sand desert at Repetek is the *Haloxylon ammodendron* – *Carex physodes* community, in which the roots of *Haloxylon* reach to the groundwater. In such a stand the canopy cover of is 30%, ground cover 90%; the latter is due to *Carex physodes* growing between the trees. It is unable to grow beneath the crowns, because the litter of the *Haloxylon* as an alkali-halophyte is too alkaline. In *Haloxylon persicum* stands, however, *Carex physodes* grows well everywhere, because the crowns of this species cover a very small area and the litter is low in Na^+.

Data on the phytomass of the *Haloxylon ammodendron* – *Carex physodes* biogeocoenose are shown in Table 5.11 and litter production in Table 5.12. *Haloxylon* contributes 70% to the aboveground litter, the other shrubs 20%, *Carex physodes* 1% and the moss *Tortula desertorum* also 1%. Most of the litter from *Haloxylon* lies beneath the crowns, resulting in a mosaic structure of the herbaceous layer.

Net production is put at 7.47 t ha^{-1} a^{-1}. This is of the same order as the annual litter production of 7.41 t ha^{-1} a^{-1}. Of this, the assimilating organs make up 1.27 t (17%), the woody parts 0.64 t (8%) and the dead roots 5.56 t. *Haloxylon* accounts for 64% of the production, *Carex* for 12%.

Table 5.11. Amounts of phytomass (t ha^{-1} dry wt.) in *Haloxylon ammodendron – Carex physodes* communities (from Miroshnichenko 1974, p. 333)

Fraction of phytomass	*Haloxylon ammodendron*	*H. persicum*	*Ephedra strobilacea*	*Calligonum setosum*	*C. caput-medusae*	Other shrubs	*Carex physodes*	Ephemerals and forbs	Total phytomass	% of total
Green shoots	0.72	0.05	0.24	0.007	0.012	0.01	0.2	0.04	1.279	4.12
vegetative	0.63	0.025			0.01					
growing	0.06	0.018	0.24	0.007		0.01	0.02	0.04		
flowering	0.03	0.07			0.002					
Perennial parts	5.14	0.12	0.51	0.10	0.133	0.03	0	0	6.033	19.44
biennial branches	0.34	0.02	0.1	0.06	0.01		0	0		
branches < 1 cm diam.	0.51	0.03			0.025	0.03	0	0		
branches > 1 cm diam.	1.38	0.03	0.2	0.03	0.021		0	0		
trunks	2.91	0.04	0.21	0.01	0.077		0	0		
Live aboveground phytomass	5.86	0.17	0.75	0.107	0.145	0.04	0.2	0.04	7.312	23.56
Roots and rhizomes	9.53	0.27	0.84	0.24	0.22	0.05	8.23	0.044	19.424	62.57
very fine roots (< 0.5 mm)	1.17	—	0.05	0.004	0.01		1.54			
fine roots (0.5–4 mm)	0.5	—	0.05	0.006	0.02	0.05	5.29	0.044		
medium roots (4–20 mm)	1.28	—	0.14	0.04	0.02		0			
large roots (> 20 mm)	6.58	—	0.60	0.19	0.17					
rhizomes	0	0	—	0	0	0	1.4	0		
Total living phytomass	15.39	0.44	1.59	0.347	0.365	0.09	8.43	0.084	26.736	86.13
Dead branches in crown	0.57	0.01	0.04	0.04	0.16	0.01	0	0	0.83	2.67
Total aboveground phytomas (alive + dead)	6.43	0.18	0.79	0.147	0.305	0.05	0.2	0.04	8.142	26.23
Annual aboveground litter	0.72	0.037	0.02	0.005	0.014	0.01	0.2	0.04	1.046	3.37
Perennial branches	0.05	0.002	0.01	0.001	0.002	0.01	0	0		
Annual shoots	0.67	0.035	0.01	0.004	0.012		0.02	0.04		
Litter (total lying)	1.42	0.04	0.28	0.03	0.06	—	0.01	0	1.830	5.89
small twigs (1 mm)	0.38	0.01	0	0	0.02	—	0.01	0		
medium twigs (1–3 mm)	0.04	0.01	0	0.01	0.005	—	0	0		
large twigs (> 3 mm)	0.36	0.01	0.25	0.01	0.025	0	0	0		
branches	0.27	0.01	0.03	0.01	0.009	0	0	0		
Dead wood (lying)	0.59	—	0.01	0	0	0	0	0	0.600	1.94

Table 5.12. Annual litter (t ha^{-1}) for the *Haloxylon ammodendron – Carex physodes* biogeocoenose (Repetek 1969–1972, from Rodin 1977)

Plant parts	*Haloxylon ammodendron*	Shrubs	*Carex physodes*	Ephemerals	*Tortula desertorum*	Algae	Total	
							t ha^{-1}	%
Annual shoots and leaves	0.67	0.176	0.20	0.040	0.09	0.03	1.206	16
Branches	0.21	0.090	—	—	—	—	0.300	5
Trunks	0.24	0.100	—	—	—	—	0.340	5
Underground parts	2.10	0.420	2.90	0.044	0.10	—	5.564	74
Total (t ha^{-1})	3.22	0.786	3.10	0.084	0.19	0.03	7.410	
Total (%)	43	11	42	1	3	1	100	

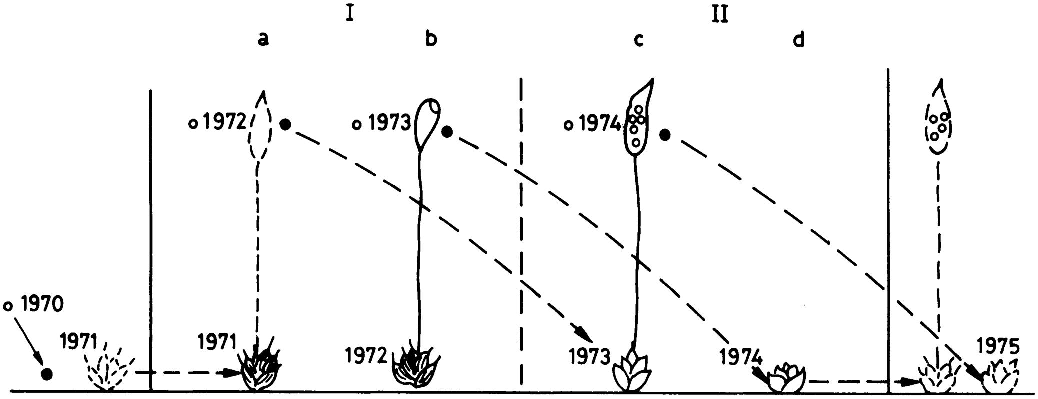


Fig. 5.25. *Tortula desertorum* synusia with plants of different ages (*a–d*) in the spring of 1974. An "o" before the number of the year means "in the autumn of that year"; – – – are parts already dead or not yet formed (1975); *I* slow-growing plants; *II* fast-growing plants (from Walter and Box 1983)

The moss synusia with *Tortula desertorum* is also important. The gametophyte grows for at least 3 years. The developmental cycle is shown in Fig. 5.25. Besides reproduction by spores, there is also vegetative reproduction by means of gemmae on the rhizomes; this represents an adaptation to adverse conditions in the desert. The production of the mosses is estimated to be 0.2 t ha^{-1}, while the phytomass of the algae which are always present (mostly cyanophytes) is put at 0.03 t ha^{-1}. The phytomass of the algae is turned over many times during the course of a growing season, so the production can be considerable; indeed, production of the algae and mosses together can amount to 3% of the total for the biogeocoenosis and on open sites without *Carex physodes* these synusiae can produce a dry weight of 20 g m^{-2}.

Ash analyses of species of different ecological groups are presented in Figs. 5.26 and 5.27. Annually, 0.5 kg m^{-2} of the litter falls to the ground beneath *Haloxylon ammodendron;* this is the equivalent of 70 g m^{-2} of ash. This gives rise during decomposition to the following quantities per m^2:

Na_2CO_3	42 g	$MgCO_3$	26 g
K_2CO_3	32 g	NaCl, KCl	4 g
$CaCO_3$	27 g	$CaSO_4$	4.4 g

Beneath *Haloxylon persicum* the salinization is much less. The quantities formed per m^2 are as follows:

Na_2CO_3	8 g	$MgCO_3$	18 g
K_2CO_3	18 g	NaCl, KCl	1.7 g
$CaCO_3$	40 g	$CaSO_4$	3.9 g

In this case it is primarily calcium that accumulates, the accumulation of alkaline elements being far less (Miroshnichenko 1978).

Data on the number of consumers per hectare and on their zoomass in kg ha^{-1} are given in Table 5.13. Table 5.14 shows seasonal changes in zoomass in the crowns of *Haloxylon ammoden-*

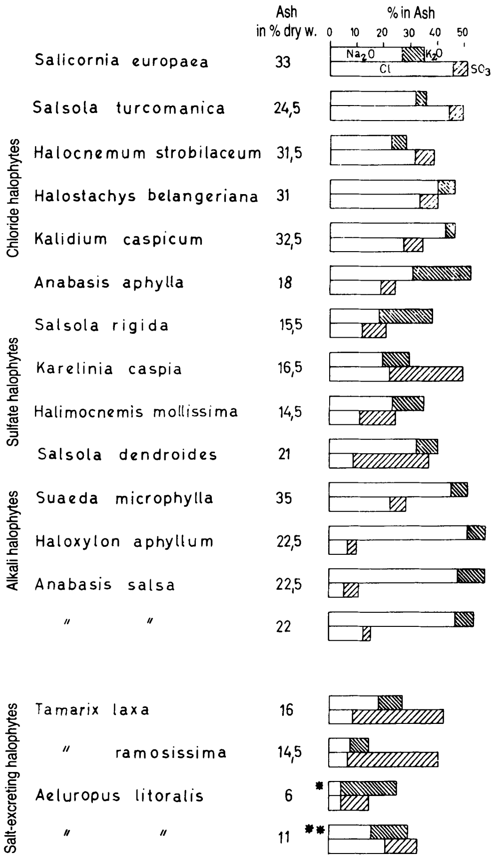


Fig. 5.26. Ash analyses of halophytes. The meaning of the different blocks is explained in the figure for *Salicornia*. Values for *Aeluropus* calculated on the basis of SiO_2 ash:* sample with 65% SiO_2 in the ash; ** sample with 36% SiO_2 in ash. This diagram was constructed from data of Rodin (1961) (from Walter 1968)

dron. For further details, see Walter and Box (1983).

Tables 5.15 and 5.16 relate to the vegetation of the takyry and the Solonchak soils.

5.7 Subdivision of Middle Asia into Biomes

The following biomes can be distinguished:

1. The Ustyurt Plateau with the former Mangyshlak Peninsula.
2. Caspian Coastal Depression.
3. Sumbar-Atrek valley with delta.
4. Trans-Unguz-Karakum.

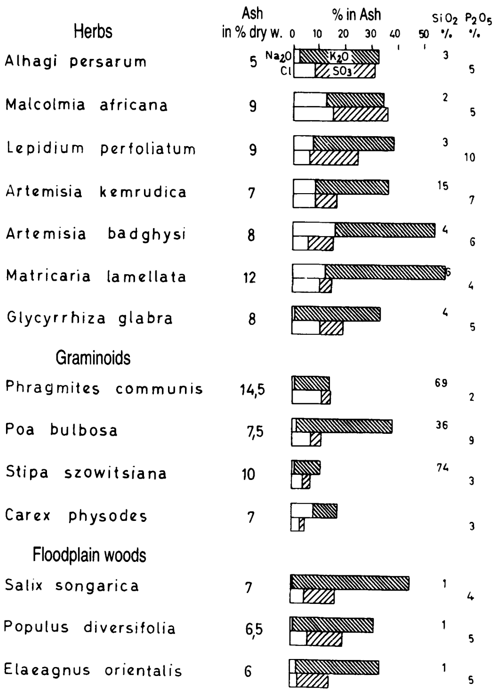


Fig. 5.27. Ash analyses of non-halophytes, computed from data of Rodin (1961) (from Walter 1968). Explanation of the blocks is shown for *Alhagi* (above)

5. Central Karakum.
6. Southern Karakum with the Tedzhen and Murgab deltas and also the northern slopes of the Kopet Dagh.
7. South-eastern Karakum with the Karibil-Badkhis elevation and the Obruchev steppe, which is today a storage dam.
8. Kyzyl-Kum, east of the Amu-Darya.
9. Amu-Darya delta region with the Sarykamysh Depression and the valley of the Uzboi River.
10. The orobiomes of the great mountain systems.

5.8 Orobiome VII (rIII) of Middle Asia

5.8.1 The Kopet Dagh Mountains

The Turanian basin is bordered in the south by the Kopet Dagh mountains. This range is built of layers of Cretaceous formation and consists of three longitudinal ridges: the northern (up to 1000m), the middle (up to 2000m), and the

Table 5.13. Number of individuals per hectare and zoomass in kg ha^{-1} for vertebrates in the protected area (III represents the *Haloxylon ammodendron* – *Carex physodes* biogeocoenose of Kuznetzov, in Rodin 1977)

Biogeocoenose	Mammals		Birds		Tortoises		Other reptiles	
	Number	Mass	Number	Mass	Number	Mass	Number	Mass
I (mobile sand)	4.3	0.3	0.8	0.02	—	—	41.0	0.21
II (immobile sand)	7.0	0.7	1.4	0.05	0.4	0.3	19.0	0.10
III (hollow)	16.4	1.4	2.6	0.06	0.6	0.5	24.8	0.8

Table 5.14. Seasonal variation in zoomass (kg ha^{-1}) in the canopy of *Haloxylon ammodendron* and in the soil (from Rodin 1977)

	February	April–May	July	October
Invertebrates in tree crowns	2.8	10.1	1.2	1.9
Invertebrates in the soil under crowns	7.0	15.0	?	8.5
Invertebrates in the soil between crowns	?	1.5	?	?

Table 5.15. Production of takyr vegetation (after Rodin 1954)

Zone	Phytomass (t ha^{-1})	Primary production (t ha^{-1} a^{-1})	Nitrogen (kg ha^{-1})	Ash (kg ha^{-1})
I	0.1	0.1	1.5	6–7
II	0.3	0.3	9–10	20–22
IIIa	1.2–1.6	1.2–1.6	20–30	90–140
IIIb	12	10	90	475

I = Lowest-lying areas, with clay deposition; soils saline; only soil algae.
II = Somewhat higher areas, with soil algae or lichens; few ephemeral seed-plants.
IIIa = Transition zone with patchy ephemeral vegetation.
IIIb = *Artemisia* semi-desert with rich ephemeral vegetation on sierozem.

Table 5.16. Productivity of succulent halophytes on solonchak with a cover of 10% (after Bazilevich et al. 1972)

Species	Phytomass (t ha^{-1})	Roots (t ha^{-1})	Primary production (t ha^{-1} a^{-1})
Halocnemum strobilaceum	1.76	1.04	0.5–0.7
Kalidium caspicum	1.38	1.04	0.5–0.7

southern (up to 3000 m), which forms the boundary with Iran. Since these ridges run parallel to the direction of the westerly winds which bring rain, rainfall scarcely increases with altitude: precipitation at the base of the mountains as well as at 1500 m NN is 200 mm. Temperature and thus potential evaporation do, however, decrease with altitude, so that the climate is less dry at higher altitudes.

The sequence of altitudinal belts is somewhat different in the eastern and western Kopet Dagh. In the western part of this mountain range, at 400 m NN, there is an ephemeral desert with *Carex pachystylis* and *Poa bulbosa*. Between 400 m and 600 m NN there is an *Artemisia ciniformis* semi-desert. From 600 m NN to the lower peaks the ephemerals are joined by the Compositae *Cousinia* and *Centaurea*, while along small streams are found thickets of *Rubus turcomanicus, Ulmus campestris, Malus pumila, Prunus cerasifera, Crataegus, Rosa* spp., *Vitis vinifera, Ficus carica.* In deeper ravines grow *Pistacia vera* and *Juglans regia.* All the slopes are heavily over-grazed and eroded.

The eastern part of the range is even more dry. The ephemeral desert, with *Agropyron* and *Artemisia* spp., extends from 800 to 1200mNN; in ravines there are thickets of *Celtis caucasica* and *Acer turcomanica.* In higher positions *Berberis turcomanica* occurs and still higher *Lonicera bracteolaris.* Above this belt lies montane steppe, extending up to 1600–1800mNN, with *Festuca sulcata, Stipa* spp. and *Agropyron trichophorum,* together with the ephemeroids *Poa bulbosa* and *Carex pachystylis.* Above 1800mNN these are joined, especially on rocky soil, by more and more dwarfed cushion plants (*Astragalus, Onobrychis, Acantholimon*) as well as by creeping *Juniperus.* In ravines, on protected sites, *Juniperus* can, however, reach a height of 6–12m.

5.8.2 The Tien Shan Mountains and the Pamiro-Alai System

The mountain systems to the east, which form part of the great mountain ranges of Central Asia, are far more complex. Figure 5.28 shows the pattern of the mountain chains and the basin landscapes. The mountains to the north and east of the Fergana basin form the Tien-Shan system, while those south of the basin form the Pamiro-Alai system (see Fig. 7.7).

The mountain peaks in the north reach altitudes of over 4000mNN, but towards the east and south they rise to over 7000mNN. All westerly slopes receive heavy rainfall which increases with altitude due to cooling as the moisture-laden air moves up the slopes. They have thus a pattern of altitudinal forest belts typical of a humid climate. Immediately adjacent to these, however, in places with a different aspect, are arid, treeless belts because on such slopes rainfall increases little in higher positions. This gives rise to a very

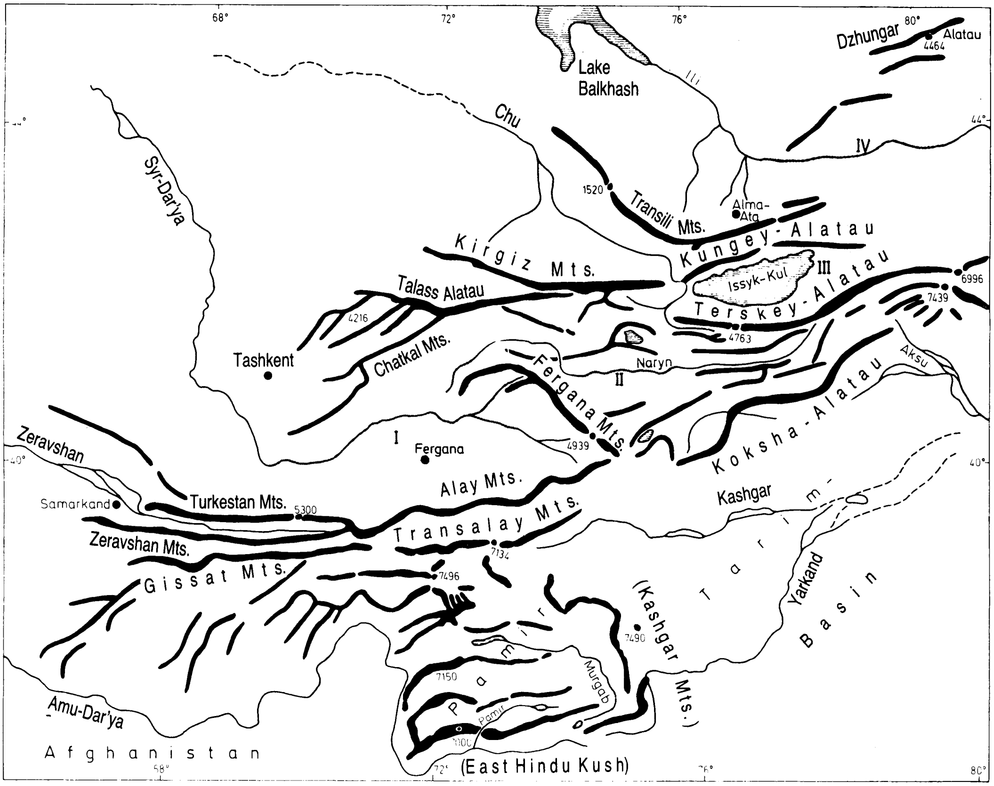


Fig. 5.28. Sketch map of the Middle Asian mountain ranges with data on altitude. Basins are indicated by *grey shading: I* Fergana Basin; *II* Naryn Basin; *III* Issyk-Kul' Basin; *IV* Ili Basin. To the north of these basins is the Tien Shan system and to the south is the Pamiro-Alai system (see also Fig. 7.7) (after Korovin, from Walter 1974)

complicated mosaic in the mountain vegetation, which has been thoroughly investigated. Reviews of this work are to be found in Korovin (1961, 1962) and Stanyukovich (1973a, b).

Vykhodtzev (1956) compared the altitudinal belt series of 18 mountain chains and came to the conclusion that in middle Asia there are no two mountain chains with the same series of altitudinal belts. The altitudinal belts with forests of wild fruit trees are especially interesting; indeed, these mountains are the primary source of almost all central European fruits and vines. We will limit ourselves here to a brief description of these altitudinal belts.

a) Arid Altitudinal Belt Series of the Talass-Alatau

This mountain chain belongs to the western Tien-Shan and reaches a height of more than 4000 m NN. The side chains, which extend southwest towards Tashkent, run out in the desert.

The Talass Alatau is especially exposed to the dry winds from the desert. The orographic snowline lies between 3450 and 4000 m NN, but even between 2000 and 3000 m NN snow patches remain until June, or even longer on northerly slopes or in the shade of rocks. In inner mountain valleys temperature minima of −44 to −47°C are recorded. Differences in aspect have a very marked effect in these mountains, which lie between 42° and 43° latitude.

According to Kultiasov (1955), there are the following altitudinal belts:

1. Ephemeral desert (semi-desert) (Fig. 5.29).
2. Herb-rich steppes with isolated shrubs.
3. *Juniperus semiglobosa* open woodland.
4. Subalpine belt with giant umbellifers, *Prangos* and *Ferula.*
5. Alpine steppes: the number of alpine species increases with altitude until finally they alone remain.

Pavlov (1980), who spent many years doing research in the western Tien-Shan, emphasized the absence of a forest belt, a consequence of the aridity of the climate. Even the stands of the arborescent *Juniperus semiglobosa* are too open to

Fig. 5.29. Foothills of the Chatkal Mountains near Tashkumyr (western Tien Shan). Semi-desert above marl with *Zygophyllum megacarpum* and *Salsola montana* as dominants. Other plants found here include *Atraphaxis pyrifolia* (Polygonaceae), *Jurinea bucharica, Rheum maximowiczii* and *Serratula aphyllopoda.* Bushes of *Sophora griffithii* are found in places (photo by V.N. Pavlov)

constitute a forest belt. The woody species all occur in small or open stands in locally moist biotopes. Along rivers are found *Populus tadshikistanica, P. talassica,* four *Salix* spp. and also *Betula pendula* with four other *Betula* spp. and an appropriate herbaceous vegetation. On moist slopes and in ravines one does find small stands of deciduous trees with *Acer, Ulmus* and even the walnut, *Juglans regia.* Such stands, however, cover barely 0.5% of the area of the particular altitudinal belt. The wild fruit trees, apple (*Malus siviersii*), plum (*Prunus sogdiana*) or *Crataegus* spp. are somewhat more tolerant. *Juniperus* spp. are even less demanding and are found even at altitudes of 1600–2400 m NN. They usually form very loose, open stands and only grow more densely on shady northern slopes. By 3100 m NN they are reduced to very low cushions. *Abies semenovii* and *Picea schrenkiana* are even more rare, both occurring only on steep northerly slopes up to altitudes of 2800 m NN.

A more detailed description of the different forms of this vegetation has been made (Pavlov 1980). Although he distinguished up to ten altitudinal belts, Pavlov has pointed out that these differ so widely on the different mountain ranges and on different aspects that no single subdivision fits all situations. The most striking feature is that, in the absence of a forest belt, the montane steppes are gradually replaced by alpine mats; at first sight, this appears quite impossible to someone with experience of central Europe. To understand this, it must be appreciated that steppe species require only 4 consecutive months of warmth together with a good water supply for their development; the other 8 months can be either cold winter months or a dry summer period.

Figure 5.30 shows schematically the climatic conditions for each altitudinal belt of these arid mountains. In the lower belt 1, the favourable growing period is interrupted by summer drought. Besides ephemeral species, there are only perennial xerophilic shrubs, that can survive a drought period and exploit the favourable conditions prevailing in autumn; this the steppe plants are unable to do. Belts 2 and 3 are suitable for montane and subalpine steppe, provided

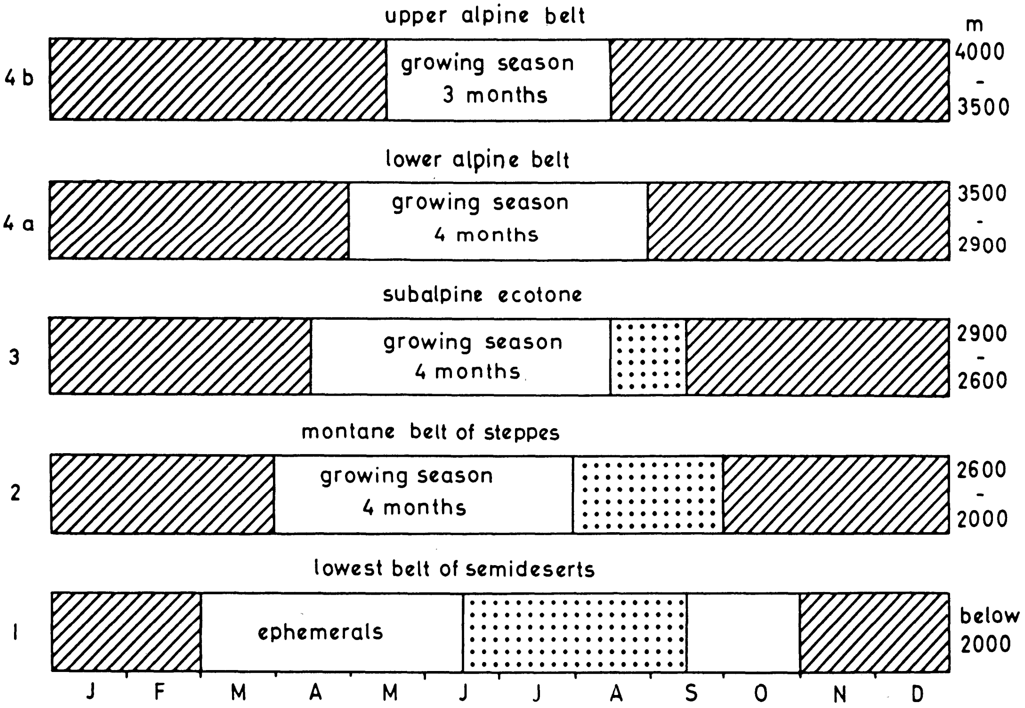


Fig. 5.30. Schematic representation of the altitudinal belts in the Tien Shan, showing the decrease in length of growing season with increasing altitude. *White* growing season; *dotted* drought period for plants; *hatched* winter dormancy. See text for further explanations (from Walter 1975)

there is no competition from woody species (open stands, shrubs). In belt 4, too, the growing period is long enough for steppe species, but the summers are so cool that competitors in the form of alpine species also occur. Their numbers increase with altitude and in belt 5, where the growing period lasts only 3 months, they become dominant.

The following example serves to illustrate ecological conditions at 3000 m NN. This was a high montane steppe on a 30° slope. The soil profile was as follows (only the lower limit of the horizons is given):

A_0	2–3 cm	Steppe felt
A_1	10–12 cm	Dark grey to brown, loose and friable, loamy, intensively rooted
B_1	35–40 cm	Grey-brown, dense
B_2	80–100 cm	Brown-grey, whitish calcareous precipitates, very effervescent, very compacted at 35–45 cm, plate-like.

The water content of the soil falls in August from 20% to 10%. The soil is mainly wetted in spring from the melting snow.

Vegetation: the most important plants are bunch grasses, 20–25 cm tall, such as *Festuca sulcata, Helictotrichon desertorum, Koeleria gracilis* and *Bromus turkestanicus:* these are joined by 10–20 cm tall herbs such as *Potentilla hololeuca, Artemisia aschurbajevii, Geranium saxatile* and *Veronica campylopoda.* The number of species on 100 m^2 is 20. *Kobresia* forms thick swards with 85% cover on fine-grained soils with ample water. In such cases the number of species drops, being only 12 to 18.

The following plot sample shows the composition of an alpine steppe meadow at 2950 m on a 20° southern slope:

Upper herb stratum (20–40 cm): 3 *Festuca sulcata,* 3 *Helictotrichon desertorum,* 1 *Hordeum brevisubulatum,* 1 *Poa attenuata.*

Middle herb stratum (10–20 cm high): + *Potentilla hololeuca,* 1 *Artemisia aschurbajevii,* 1 *Rhodiola heterodonta,* r *Myosotis suaveolens,* r *Potentilla tephroleuca.*

Lower herb layer (up to 10 cm): 3 *Kobresia schoenoides,* + *Veronica campylopoda,* 1 *Tulipa dasystemon,* r *Oxytropis immersa,* r *Aconitum rotundifolium,* r *Pachypleurum alpinum.*

The mixed composition of the high mountain steppes, derived from typical steppe elements and true alpine species, as well as montane xerophytes, is very characteristic.

The subalpine meadows with alpine elements are found on well-wetted places, mostly underneath snow patches and in snow valleys.

The snow valleys are characterized by leached, acidic (pH 3.5), permanently wet soils, which contain 10–12% humus and 25–30% organic matter. The roots go down 25 to 30 cm, some 1 m, but the upper 20 cm dries out considerably. Thus the situation is different from the snow valleys in the Alps, where the plants root only a few centimetres deep.

b) Altitudinal Belt Series with a Conifer Belt

These are found in the northern Tien Shan, for example, in the Trans-Ili and the Kungei Mountains north of Lake Issyk-Kul. In all mountains of the arid zone between 40° and 44°N, the differences between the northerly and southerly aspects are so marked that the altitudinal belts do not encircle the mountain; the southern slope is quite different from that on the northern face. Conifer forests are found only on the northerly slopes or in moist ravines above the montane steppes. There is also an aspen forest belt with an undergrowth of grass at 1100–1200 m NN; this forms a 300–600-m-wide transitional zone between areas of arid and more moist climate. Within this transitional forest steppe zone, montane steppe is found on slopes where the soil is deep, while rocky outcrops carry spruce (Fig. 5.31).

Above this, on northerly slopes, begins the conifer belt with *Picea schrenkiana;* at its upper limit at 2900–3100 m NN, the trees are wind-blown and stunted in form (Fig. 5.32). The trees may reach a height of 50 m and a trunk diameter of 120 cm, but more usually, trees of 100–150 years have a height of only 20–30 m (Fig. 5.33).

Besides spruce, the fir, *Abies semenovii,* is also found here. This species has ecological requirements similar to spruce, but does not occur at quite such high altitudes. It is a more southerly ecotype of *Abies sibirica,* which has its southernmost limit in the Dzungarian Alatau (NE corner in Fig. 5.28).

At their aridity border the conifer forests form a Piceetum nudum; that is, there is no undergrowth, showing that the trees entirely deplete the soil water.

A few deciduous species also occur in the *Picea schrenkiana* stands; these are *Populus tremula, P.*

Fig. 5.31. Altitudinal belt of forest steppe on a southerly slope in the intermediate zone between arid and humid altitudinal belts: mountain steppe on the slopes with deep soils; spruce stands on the rocky outcrops. Trans-Ili-Alatau, south of Alma Ata (photo M. Succow)

laurifolia, Betula tschanschanica, Sorbus tschanschanica and 38 different shrubs. In the undergrowth there are ferns, Pyrolaceae, *Goodyera repens, Coralliorhiza, Adoxa, Arctous alpina, Impatiens parviflora, Galium boreale, Geum urbanum, Poa nemoralis, Coeloglossum viride* and Middle Asian species of the genera *Aquilegia, Astragalus, Aegopodium* and *Carum.* In openings, tall forbs such as *Doronicum, Aconitum* and *Trollius* appear. Mosses common to conifer forests are also found in these forests.

The wild apple, *Malus sieversii,* is found below the conifer forest belt on northern slopes and higher up on southern slopes. The wild apple stands on the northern slopes of the Trans-Ili Alatau above Alma Ata (from the Kazak: *Almaty* = place of apples) are well known. Even today, when five-sixths of the forests have been destroyed, they still cover 5000 ha. Just how marked the effect of aspect is, emerges clearly from the sketch-map in Fig. 5.34. These forests occur mainly on northern slopes below 1400 m NN; a very few trees are found above this altitude on southern slopes. The time of flowering is in May (Fig. 5.35). *Malus sieversii* is genetically very close to the cultivars of apples grown in the west.

When the apples are ripe, the local people from Alma Ata collect thousand of tonnes of fruit from the forests. The apples are usually sliced and dried in the sun or used to make jam, as are also the wild apricots.

Meadows also occur within the conifer forest stands but only locally, on permanently wet sites in basins or on humus-rich mountain soils on gen-

Fig. 5.32. *Picea schrenkiana* at the upper forest limit (2000–2500 m NN) on rock and rubble slopes of the Trans-Ili-Alatau (photo V.N. Pavlov)

tle northern slopes. These meadows are mowed regularly once a year and are reminiscent of the European wet meadows with the grasses *Dactylis glomerata* or *Brachypodium pinnatum.* In somewhat drier places they resemble the herb-rich meadow steppes with *Phlomis* and *Helictotrichon pubescens* (Arystangaliyev 1956).

Figures 5.36–5.38 show three typical stand profiles while Fig. 5.39 is of the *Kobresia* montane meadows with a species of edelweiss (*Leontopodium*). All four profiles are from the Kungei Alatau, which runs between the Trans-Ili mountains and Lake Issyk-Kul. Figure 5.40 shows the subalpine belt with the steppe element *Phlomis.*

c) Altitudinal Belt Series with a Deciduous Forest Belt

In those mountains which have an altitudinal belt with a deciduous forest climate, that is, not too cold winters and moist summers, several species of maple are found: *Acer turkestanicum, A. pubescens, A. regelii, A. semenovii, A. turcomanicum.* The first two are forest-forming and *A. turkestanicum,* close to *A. laetum,* is very widespread. The maple occurs together with the walnut, *Junglans,* but extends right up to the alpine belt. The stands are usually open and contain solitary specimens of several wild fruit trees (Fig. 5.41). The latter are, however, more common in the Pamiro-Altai mountains of Tadzhikistan. As an example of mountains with a deciduous forest belt we describe the Hissaro-Darwaz mountains which have a moist, temperate climate.

These two mountain chains, together with the Peter the Great Chain, form a high arc open to the west on the border of the western Pamir (Fig. 7.7). Here air masses coming from the west are trapped, producing orographic rainfall on the windward slopes. The result is that the middle elevations receive 1000 mm and a climate prevails which is suitable for deciduous forests. The snowline is between 3700 and 4000 m NN and the

Fig. 5.33. *Picea schrenkiana* at lower levels of a valley floor (photo V.N. Pavlov)

glaciated area covers several hundred km^2. The climate is indeed mediterranean, with mean temperatures in January above 0° C, although heavy frosts do occur occasionally.

The altitudinal belts on favourable slopes are as follows:

750–1500 (1700) m. The original ephemeral desert belt with considerable *Agropyron (Elytrigia) trichophorum* and scattered wooded patches of *Amygdalus bucharica, Crataegus pontica, Cotoneaster racemiflora, Pistacia vera, Cercis griffithii, Ziziphus jujuba* and *Punica granatum.* Through the interference of man, however, the woodlands have been reduced to a few scattered remains. The plant cover today consists mainly of *Agropyron* with *Hordeum bulbosum* and *Poa bulbosa,* while *Cynodon dactylon* and *Andropogon ischaemum* occur on unploughed ground. These are joined by the especially widespread ephemerals *Vulpia myuros, Aegilops triuncialis, Bromus macrostachys* and *B. oxyodon. Junglans regia, Platanus* and *Populus,* together with the tall grasses *Erianthus* and *Phragmites,* are found in floodplains.

1500–2800 m. Deciduous forest belt with many tree and shrub species, including, in the lower part, species adapted to a warm habitat, such as *Junglans regia, Acer turkestanicum* and *Vitis hissarica* in the upper stratum; in the second stratum *Prunus divaricata, Crataegus turkestanica, Cerasus mahaleb, Malus sieversii, Celtis caucasica;* on rocky sites *Juniperus seravschanica;* beneath these are many shrubs. In the herbaceous layer are found *Dactylis glomerata, Aegopodium tadzhicorum, Impatiens parviflora* and on open sites *Inula grandis* and *Prangos pabularia.* These forests have also suffered greatly from man's presence, but there are still some closed forests of *Juglans regia* with trees of 15 to 20 m height and with many accompanying species. *Acer turkestanicum* (13–15 m tall) dominates above 2300 m NN. On rocky sites the species is no longer *Juniperus seravschanica,* but *J. semiglobosa* and *J. turkestanica. Betula* and *Populus* are found along watercourses, and *Rosa divina* is abundant on open sites. Meadows with *Polygonum coriarium, Ligusticum discolor* also cover large areas.

2800–3400 m. Subalpine meadow belt, with mountain steppes, prostrate *Juniperus* and cushion plants on rocky ground. Precipitation drops rapidly at the high-

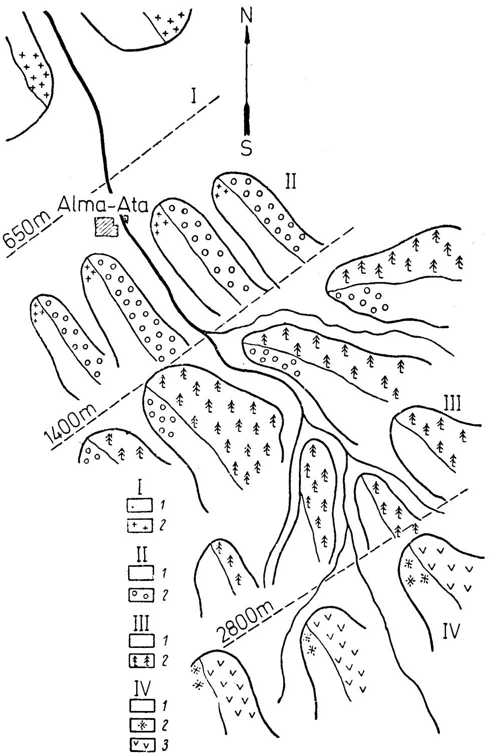


Fig. 5.34. Sketch map showing the distribution of wild apple forests above Alma Ata. *I* semi-desert belt; *1* ephemeral on SW slope; *2* with *Artemisia; II* desert-steppe belt: *1* with Agropyron, 2 with wild apple woodlands; *III* steppe and forest belt: *1* Festuceto-Stipetum; *2 Picea* (forest on NE slopes); *IV* high mountain belt: *1* alpine steppes and meadows; *2* prostrate *Juniperus; 3* small *Salix* species

est elevation. The moist meadows consist of *Alopecurus seravschanicus* with *Poa pratensis, Festuca rubra* and many forbs (*Geranium saxatile, Ligularia thomsonii, Astragalus andaulgensis,* often *Rumex ulsenianus*). *Polygonum coriarium* dominates among the tall herbs. Cushion plants (*Astragalus lasiosemius, Onobrychis echidna*) are not widespread, but rather accompany the steppes.

3400–3800m. Belt of the eucryophilic mats, often with *Polygonum hissaricum,* plus *Kobresia* swards with *Carex* species. *Festuca coelestis, F. sulcata* and *Poa litwinowiana* occur in patches of steppe.

Koroleva (1958) has published numerous plot samples and a vegetation map (1.5cm = 1km).

We do not need to go into great detail in discussing the low mountains south of Dushambe. These are drier and their vegetation is similar to that of the Kopet Dagh: 300–900m: desert with dwarf shrubs and ephemerals. 900–1700m: considerably degraded vegetation with *Poa bulbosa* and *Carex pachystylis* and individual *Amygdalus* and *Pistacia* 1700–2300m: belt with open *Juniperus* stands and *Rosa kokanica* (after removal of the *Juniperus*), plus small fragments of deciduous woodland.

d) The Forests of Wild Fruit Trees in Middle Asia

In his great work on the wild fruit trees of Tadzhikistan (695 pages with 81 tables and many distrubition maps) Zaprygayeva (1964) lists the following species: *Juglans regia, Pistacia vera, Amygdalus spinosissima, A. bucharia, A. vavilovii, Celtis caucasica, Ficus carica, Berberis heterobotrys, B. oblonga, B. multispinosa, B. integerrima, B. nummularia, B. kaschgarica, Ribes meyeri, R. janczewskii, R. heterotrichum, R. villosum, R. malvifolium, Cotoneaster hissarica, Pyrus bucharica, P. regelii, P. tadshikistanica, P. cajon, Malus sieversii, Sorbus tianschanica, S. turkestanica, S. persica, Crataegus pontica, C. turkestanica, C. altaica, C. hissarica, C. songorica, Rubus caesius, Fragaria bucharica* (of no economic importance), *Prunus sogdiana* (related to *P. cerasifera,* the Alych plum), *P. divaricata, P. domestica* (probably escaped from cultivation), *Aflatunia* (related to *Cerasus*) *ulmifolia* (no economic importance), *Cerasus verrucosa, C. tadshikistanica, C. erythrocarpa, Padus mahaleb, Rhus coriaria, Ziziphus jujuba, Vitis vinifera, Hippophaë rhamnoides, Elaeagnus angustifolia* (economically unimportant), *E. orientalis, E. songarica, Punica granatum* (wild, related to the garden form), *Diospyros lotus, Vitex agnus-castus.*

As a consequence of the arid climate, Middle Asia is a very impoverished refuge of Tertiary forests. These have survived only in the wettest parts of the mountains. This applies especially to the deciduous forests, in which there is a fairly large number of species. In the following list of the genera, the number of species is given in parentheses:

Abelia (1; Caprifoliaceae), *Acer* (5), *Aflatunia* (1; Rosaceae), *Alnus* (1), *Armeniaca* (8; apricot), *Atraphaxis* (1; Polygonaceae), *Berberis* (6), *Betula* (10), *Cerasus* (4; morello cherry), *Cotoneaster* (5), *Crataegus* (11), *Euonymus* (3), *Exochorda* (2; Rosaceae), *Fraxinus* (3), *Grossularia* (1), *Jasminum* (1), *Juglans* (2), *Lonicera*

Fig. 5.35. Flowering *Malus* on 11th May near Alma Ata. The hilltop behind at 1000 m NN. In the background, high montane spruce forest belt followed by snow-covered mountain peaks (photo M. Succow)

Fig. 5.36. Transect of *Brachypodium* meadow-steppe on the Kungey Alatau. *1 Brachypodium pinnatum; 2 Phleum phleoides; 3 Ranunculus polyanthemus; 4 Pedicularis dolichorrhiza; 5 Campanula glomerata; 6 Lathyrus pratensis; 7 Dactylis glomerata; 8 Helictotrichon (Avena) pubescens; 9 Thalictrum simplex.* (after Arystangaliyev 1956, from Walter 1974)

Fig. 5.37. Transect of *Dactylis* meadow steppe on the Kungey Alatau. *1 Dactylis glomerata; 2 Brachypodium pinnatum; 3 Silene commutata; 4 Pedicularis dolichorrhiza; 5 Thalictrum simplex; 6 Stachyopsis lamiiflora; 7 Ranunculus polyanthemus* (after Arystangaliyev 1956, from Walter 1974)

Fig. 5.38. Transect of *Phlomis* meadow steppe on the Kungey Alatau. *1 Phlomis oreophila; 2 Trollius dschungaricus; 3 Helictotrichon pubescens; 4 Euphorbia alatavica; 5 Polygonum nitens; 6 Aegopodium alpestre; 7 Papaver croceum; 8 Brachypodium pinnatum; 9 Alchemilla sibirica* (after Arystangaliyev 1956, from Walter 1974)

Fig. 5.39. Transect of *Kobresia* mountain meadow on the Kungey Alatau. *1 Kobresia capilliformis; 2 Allium atrosanguineum; 3 Myosotis suaveolens; 4 Euphorbia alatavica; 5 Erigeron aurantiacus; 6 Primula algida; 7 Potentilla nervosa; 8 Geranium saxatile; 9 Cerastium tianschanicum; 10 Papaver croceum; 11 Leontopodium campestre; 12 Alchemilla sibirica* (after Arystangaliyev 1956, from Walter 1974)

Fig. 5.40. Subalpine *Phlomis oreophila* meadow (2400 m) in the Kirgiz Mountains (photo V.N. Pavlov)

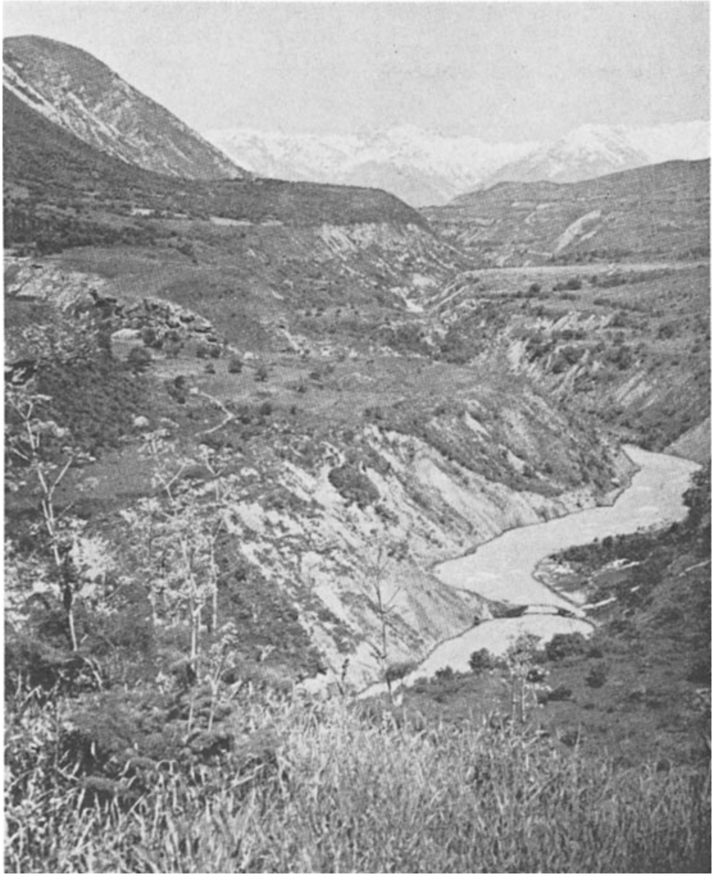


Fig. 5.41. Belt of deciduous forest on the western Tien Shan showing individual groups of *Juglans, Malus, Prunus divaricata* in the midst of steppe communities with *Agropyron trichophorum* and *Hordeum bulbosum* and large umbellifers. In the *left foreground* is *Ferula tenuisecta* or else *Prangos pabularia* (photo V.N. Pavlov)

(15), *Malus* (3; apple), *Mespilus* (1), *Prunus padus* (1; bird cherry), *Planatus* (1), *Populus* (9), *Prunus* (2), *Pyrus* (5; pear), *Rhamnus* (1), *Ribes* (1), *Rubus* (4), *Sorbaria* (1; Rosaceae), *Sorbus* (2), *Spiraea* (1), *Thelycrania* (2; Cornaceae), *Viburnum* (1), *Vitis* (2). There are also many species of *Amygdalus* (almond), *Rosa* and *Salix*.

The large number of species of wild fruit trees is very striking; in some cases they form veritable orchards of wild fruit (Figs. 5.35 and 5.41). For thousands of years these wild fruits of Middle Asia have been subjected to deliberate or chance selection and cultivation. This is true also for the wild vine which, according to Popov, should be classified not as *Vitis sylvestris* but as *Vitis vinifera*.

The wild walnut trees are usually thought all to be subspecies of the very polymorphous *Juglans regia* which includes forms with thick- and thin-shelled nuts. Some, however, would prefer to introduce a second species, *Juglans fallax*. The walnut is very widely distributed in the mountains of Middle Asia (Fig. 5.42). It often occurs as solitary, old trees in river valleys and ravines, but shady forest stands also occur (Korovin 1961, 1962).

Table 5.17 shows climatic data for the *Juglans* forests at 1433 m NN in the Chatkal mountains which run southwest from the Talass-Alatau. It can be seen that the climate is moderately warm and the winters not very cold. It is mildly continental with a rainy spring and although the summer (July-August) is dry, total annual rainfall is high, at 1000 mm. The walnut shows a certain degree of cold-resistence. Rejuvenation by seed is good (840–6000 seedlings ha^{-1}). The trunks of old trees are up to 1 m in diameter.

The soils are brown forest soils, rich in humus, sometimes with a bleached horizon. They remain moist until the beginning of July, then dry out

Fig. 5.42. Walnut stand on the Fergana Mountains: *left* old *Juglans fallax* tree; *centre Lonicera* and *Rosa* bushes; *right* small *Prunus divaricata (cerasifera)* trees (photo V.N. Pavlov)

Table 5.17. Climatic data for the *Juglans regia* forest belt of the Chatkal Mountains in Middle Asia (from Korovin 1962)

Month	Jan.	Feb.	Mar.	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.	Year
Mean temperature (°C)	- 3.4	- 2.0	1.9	8.7	12.1	17.5	17.5	20.6	14.0	8.4	3.3	1.9	9.5
Minimum temperature (°C)	-20.7	-15.1	-13.5	-1.6	-2.9	-2.2	-2.2	5.2	0.7	-10.0	-13.4	-16.2	-20.7
Precipitation (mm)	56	113	203	193	92	32	32	0.3	13	143	69	75	995

quickly so that the underbrush wilts. There is a snowdrop phenophase in spring.

The roots of *Juglans* penetrate to 3.5 m, so that the supply of water in summer is guaranteed, especially as the habitats are usually shady slopes, furrows or ravines. In these forests there is only a tree stratum, the shrub layer is thin and the undergrowth strikingly sparse; this is due to the presence in the leaf litter of the quinone, Juglon (5-hydroxy-1,4-naphthoquinone).

The undergrowth consists of: *Brachypodium sylvaticum, B. pinnatum, Festuca gigantea, Melica altissima, Agropyrum caninum, Poa nemoralis, Bromus benekeni, B. inermis, Carex polyphylla, Archangelica decurrens, Conioselinum latifolium, Ligusticum discolor, Aegopodium podagraria, Crepis sibirica, Alliaria officinalis, Impatiens parviflora, Lamium album;* in addition there are other Middle Asian species of *Cerastium, Melandryum, Senecio, Allium, Polygonatum* and *Arum.*

In floodplain stands there are many lianas, also *Vitis vinifera,* and abundant *Impatiens parviflora.* Most stands are 60 to 90 years old and the trees have trunk diameters of 35–65 cm. The number of trunks can be as much as 120 to 150

Fig. 5.43. Open tree stands in northern Afghanistan at 1500 m NN with *Pistacia vera* and the flowering ephemeroid *Eremurus olgae.* On the *extreme right,* the large-leaved *Inula grandis* (photo H. Freitag)

ha^{-1}. The yield of nuts varies from 3 to 32 kg per tree (Popov 1940).

An important wild fruit tree that is also cultivated is *Pistacia vera.* It belongs, however, to the semi-desert belt of wooded fields. These are wooded areas in which the trees are widely separated. The rainfall is so light that only the upper layers of soil are wetted. The roots therefore have a wide horizontal spread in all directions, so that the stand is actually closed. The trees utilize all the available water, except in spring when there is a certain surplus. This is exploited by ephemerals or ephemeroids (usually with bulbs) which have a short growing period (Fig. 5.43). Such wooded areas are thus ecologically completely different communities from savannas (see Vol. 2, ZBII), even if the grass cover in spring makes them appear superficially similar. In savannas there is sharp competition between woody plants and grasses (Vol. 2, p. 129). In the wooded fields, however, the ephemerals exploit an existing ecological niche, as does the spring vegetation of ephemerals and geophytes in the deciduous forests of ZB IV. For this reason, the arid wooded fields should not be regarded as "pseudosavannas" or as "semi-savannas" as some Russian authors do.

e) Altitudinal Belts on the Northern Slopes of the Hindu Kush

The vegetation typical of Middle Asia extends southwards as far as Hindu Kush (Breckle 1973; Freitag 1971). We show several photographs of this region. Figure 5.44 shows the ephemeral desert, Fig. 5.45 the *Juniperus* wooded fields, Figs. 5.46 and 5.47 the lower alpine, thorny cushion-plant area; Fig. 5.48 shows the alpine belt with *Kobresia* turf. Afghanistan will, however, be dealt with together with Iran in Volume 4.

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A mass of data is available on phytomass and annual litter from the different altitudinal belts of individual mountain ranges. The appropriate tables are to be found in Walter and Box (1983), pp. 184–191. Here it is intended to give only a brief summary.

Zlothin (1971) investigated the vegetation of the high plateaux at 3000–4000 m NN of the arid central part of Tien Shan (Table 5.18). The measurements were made on very different soils and the values for phytomass, annual litter production and zoomass accordingly vary considerably.

Fig. 5.44. Semi-desert with ephemeral vegetation at 450 m NN on loess hillsides in mid-March in northern Afghanistan; heavily over-grazed. In the *foreground on the right* are burrows of steppe rodents (photo H. Freitag)

Fig. 5.45. Wooded field in June at 1900 m NN in northern Afghanistan with *Juniperus seravschanica,* bushes of *Ephedra equisetina* and a geophyte-rich, relatively dense herbaceous layer (photo H. Freitag)

Fig. 5.46. Subalpine *Cousinia* semi-desert in central Afghanistan, west of Bamian at 3300 m NN with thorn-cushion plants, *Acantholimon, Astragalus* and *Onobrychis* as well as Chenopodiaceae and *Cousinia* (photo S.-W. Breckle)

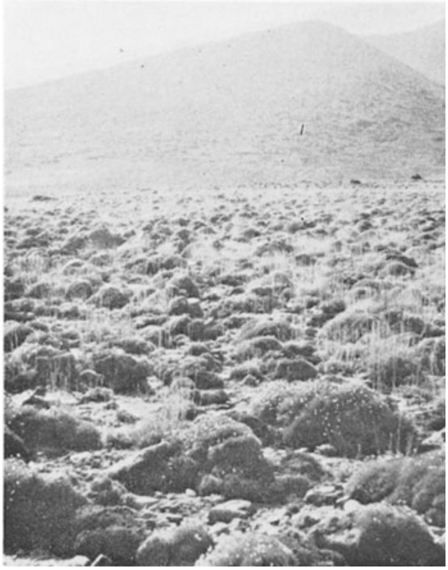

Fig. 5.47. A close-up of the *Acantholimon* thorn-cushion plants shown in Fig. 5.45 (photo H. Freitag)

The table gives data only for the dominant species which make up 50–90% of the phytomass (cover in % in parentheses).

Some data for a *Malus* stand in Trans-Ili-Alatau are shown in Table 5.19. For the same stand data are also available on nitrogen, phosphorus and potassium. Similar data are also given for 18 high mountain vegetational types.

Popov (1975) gives the phytomass of various altitudes:

1. *Bothriochloa ischaemum* dry steppe on light chestnut earth
2. *Stipa capillata – Agropyron repens – Festuca sulcata* mountain steppe on dark chestnut earth
3. *Dactylis glomerata* herb-rich (40 species) grassland on deep chernozem
4. *Phlomis oreophila – Poa angustifolia* high mountain grassland (70 species) on deep mountain humus soil
5. *Phleum phleoides – Alchemilla – Aegopodium alpestre* subalpine grassland on subalpine humus soils (Table 5.20).

Primary production (air dried) of grassland at 1900–1950 m NN in the years 1969–1972 was between 0.87 and 1.46 t ha^{-1}, depending on rainfall (Malinovski 1975).

Fig. 5.48. *Leucopoa* steppe at Koh-i-Baba at 4000 m NN: dense *Kobresia* turf next to an erosion furrow with water from the melting snow (photo S.-W. Breckle)

Table 5.18. Data on biomass for high plateaux of the Central Asian Tien Shan

	Phytomass	Litter	Zoomass
High montane steppes (3700–3300 m NN)			
Festuca tianschanica (15%)[a]	8.8	3.5	3.0
Saussurea leucophylla (5–20%)[a]	6.3	2.0	0.01
High montane salt desert (3200–3000 m NN)			
Limonium + *Reaumurea* (< 5%)[a]	3.0	0.9	0.003
Semidesert (30%)[b] (3300–3100 m NN)			
Artemisia + *Oxytropis* (10–20%)[a]	4.2	1.3	0.03
Marsh (approxiamtely 100%)[b] (3700–3300 m NN)			
Carex melanantha	13.3	8.8	0.07
Cryophilic cushion plants (10%)[b] (4000–3000 m NN)			
Dryadanthe tetrandra	16.8	2.9	0.03
Wet turf (60%)[b]			
Kobresia capilliformis	43.4	8.7	3.00

[a] Percentage cover of the species.

[b] Percentage of total ground cover.

Table 5.19. Data on phytomass ($t\ ha^{-1}$) and production ($t\ ha^{-1}\ a^{-1}$) in a *Malus sieversii* stand; values for belowground phytomass are shown in parantheses (after Malinovsky 1975)

	Total phytomass	Annual increase	Litter	Net increase
Tree layer				
Malus	88.6 (36.7)	5.82 (1.77)	4.79 (1.36)	1.03 (0.41)
Crataegus	17.8 (7.4)	1.22 (0.33)	0.79 (0.16)	0.43 (0.17)
Shrub layer	0.8 (0.35)	0.32 (0.15)	0.32 (0.15)	— —
Herbaceous layer	16.3 (12.4)	7.50 (3.74)	7.50 (3.74)	— —
Total stand	123.5 (56.8)	14.86 (5.99)	13.40 (5.41)	1.46 (0.58)

Table 5.20. Phytomass and litter layer ($t\ ha^{-1}$) of meadow biogeocoenoses (see text for meaning of stand numbers) in the Kirgiz Mountains of the northern Tien Shan (after L.I. Popov, L.P. Lebedeva, R.I. Ionov, and I.G. Korneyeva, in Malinovsky 1975)

Stand No.	Elevation (m)	Phytomass			Total organic matter
		Above-ground	Below-ground	Litter layer	
1	1200	4.34	64.84	1.40	70.58
2	1500	2.78	46.20	1.58	50.56
3	2000	2.89	42.36	2.95	48.20
4	2300	2.15	30.59	2.30	35.04
5	2400	2.68	29.54	3.43	36.65

5.9 Pedobiomes: Amphibiomes of the Floodplains of the Amu-Darya

The Karakum desert is bordered to the east by the Amu-Darya River. This river comes down in flood for 4–5 months in spring and early summer. The water level begins to fall at the end of July and reaches its lowest point in January. Wide areas remain inundated for up to half a year. On these, various sediments are deposited — gravel, sand or clay in constant alternation, depending on the rate of flow of the water. These form the soils of the very extensive floodplains.

In arid areas, wet soils normally become salinated. This does not occur where the soil is flooded every year, for then the salt crusts that form at the surface are repeatedly washed away. In the floodplain, five stages of silting can be distinguished. Moving from the riverbank, these are:

1. Ka'ir Areas. These are river alluvions and are the most low-lying areas, where fresh sedimentation or large-scale shifting of soil occurs annually. They carry a sparse vegetation of pioneer plants. A vast number of seeds ($100–500\ m^{-2}$) start to germinate on the fresh deposits as soon as the water level drops and the soil is exposed. On sand, seedlings of *Typha pallida* develop, on clay sediments those of *Calamagrostis dubia.* If these plants are not destroyed by the next flood, they continue to grow, but in time, tall grasses such as reeds (*Phragmites*) and wild sugar cane (*Saccharum spontaneum*) become dominant, so that stage 3 is reached.

2. Floodplain Meadows. This stage lies somewhat higher than stage 1. It is a zone of less mobile soil, where the water flows more slowly, depositing fine sediments evenly as is typical of delta areas. Such soils become covered with meadow communities of *Cynodon dactylon* and *Puccinel-*

lia distans or, where there is salination, by *Aeluropus litoralis* with ruderal species such as *Peganum harmala, Alhagi persarum;* in addition there are species such as *Poa bulbosa* var. *vivipara* and *Cardaria draba.* Here, too, the reeds, *Phragmites communis, Ph. isiaca* eventually become dominant.

Reeds cover an area of 300,000–600,000 ha in the delta region of the Amu-Darya and on the shores of the Aral Sea, extending far into the shallow water. The local population is entirely dependent on the exploitation of *Phragmites.* It serves as year-round pasturage and the young shoots are used as hay. The reeds are also used to construct dwellings and as firewood, their caloric value being higher than that of wood. They are used to reinforce roads and paths and even tombstones are made of *Phragmites.* Hunting within these habitats is also very important as a source of meat and furs.

The soils are peaty, muddy, or meadow-like swampy soils, but can occur in both brackish and non-brackish varieties. The reed stands vary from very dense stands, usually 3–4 (exceptionally up to 6) m tall, with an annual production of 25 t ha^{-1} of dry matter, to low, quite open stands which are under water for long periods.

3. *Jangil.* This is the name given to the next highest level, which carries impenetrable thickets of reeds and other tall grasses, such as *Saccharum spontaneum* and *Erianthus purpurascens;* the former is found only in places where the groundwater table is never lower than 1.5–1.75 m. The tall grasses often form the 2–4 m tall upper layer; beneath them grow dense stands of species such as *Glycyrrhiza glabra, Equisetum ramosissimum* and the camel-thorn, *Alhagi.* All these plants have underground rhizomes and can tolerate being covered with mud to a depth of 10–15 cm, or even 30–40 cm in the case of *Saccharum.* The rhizomes develop each time at a higher level (Kerbayev 1964).

4. *Floodplain Shrub Thickets.* This is the next level, where the floodwaters are no deeper than 1 m above the soil. Closed stands of *Salix songarica* and *S. wilhelmsiana* may develop without undergrowth. The soil surface is covered with a litter layer of leaves and twigs on which an algal film of *Scytonema* forms. Where flooding is rare, salinization takes place and a scrub of salt-excreting *Tamarix* species develops with halophytic undergrowth.

5. *Tugai.* This is the name given to the floodplain forests of Middle Asia. Typically, they grow on slightly raised areas, which stand under water for only a short time. The soils are usually sandy loams or loamy sands. The most important tree species are *Populus diversifolia* (known as *turanga*) and *P. pruinosa* (known as *petta*). The trees reach an age of 35–40 years and a height of 13–15 m. The reserve of wood is 90–200 m^2 ha^{-1}. The lower tree storey is formed of willows (*Salix*) with *Elaeagnus orientalis* in drier places. The shrub stratum contains *Tamarix* spp. and *Halimodendron halodendron* on slightly brackish soils. The lianas are very abundant and reach to the crowns of the trees; these are *Clematis orientalis, Cynanchum sibiricum* and *Asparagus persicus.* The herb layer has fewer species and varies with soil wetness, the salt content of the soil and the availability of light on the forest floor.

Undisturbed floodplain forests are seldom found, since the wood requirements of the local population are great. The forests that remain are open and park-like, and support many ruderal species.

Where the soil is seldom flooded but the groundwater is at times high, salination occurs. Stands of *Tamarix* bushes develop with a halophytic undergrowth. These thickets form a transition to the Haloxyletum ammodendri, which is also found in the sand desert, in places where the roots reach to the groundwater.

The phenology of the floodplains in the middle course of the Amu-Darya is as follows. In the middle course of the river, the frost-free period lasts a mean of 216 days (190–246), between the end of March and the beginning of November. At the beginning of April the floodplain turns green. Vigorous growth sets in at the end of April. *Glycyrrhiza* flowers in the first half of May, before it is overshadowed by the grasses. The dominant colour at the beginning of June is reddish, a result of the flowering of *Tamarix* and the abundant fruits of *Glycyrrhiza.* Only in mid-July do the tall grasses flower one after the other. They create a silvery white coloration. *Erianthus* and *Phragmites* flower in the first half of August. The last phenophase of the ripening grasses is characterized by a dark yellow tone.

In the floodplain forests the flowering of the poplars gives rise to the first striking phenophase. Development on the wet soils of the floodplain is a month behind that in the sand desert.

Productivity of the floodplains is greatly enhanced by the good water supply. The only data available for the floodplain forests are those on phytomass. Reed stands 2 m in height in the middle course of the Amu-Darya have been estimated to have a total phytomass of 106–133 t ha^{-1}; the belowground phytomass is double that above the ground (Gladyzhev 1969). More details are to be found in Walter and Box (1983, pp. 95–101; see also references there to further literature).

5.10 Zonoecotone to the Deserts of Central Asia

The deserts of the Dzungarai in northern Sinkiang can be regarded as transitional to the deserts of Central Asia. Floristically they have much in common with the deserts of Kazakhstan and Middle Asia and climatically they are intermediate between Middle and Central Asia. We return to this region in Part 6.