DUPLICATE

Plant adaptations in desert dunes

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Desert sand dunes are an unstable habitat in which plants suffer frequently from cover and exposure by sand moved by wind. Plants growing in a sandy habitat are adapted to specific stresses that differ from one habitat to another. The establishment of grasses that easily produce adventitious roots and rhizomes and develop new stems when covered by sand leads to a local decrease in wind velocity. Consequently, fine-grained particles are deposited, the amount of available water increases, and filamentous cyanobacteria become established. Aggregation of clay- and silt-sized particles by cyanobacterial filaments, and gelatinous polysaccharides excreted by their trichomes lead to trapping of these particles and to the formation of a microphytic crust. Consequent improvement of the soil moisture regime and increasing soil stability and fertility, through development of nitrogen-fixing cyanobacteria, lead to the development of different higher plant communities in the processes of plant succession. Destruction of the microphytic crust by trampling or during several consecutive dry years leads to wind erosion. Fine soil particles are carried away and only plants with thick bark on the roots or with special root anatomy may remain.

Plants of sandy or non-sandy habitats may function as an obstruction to the movement of sand (saltation and creeping) and cause accumulation of phytogenic hillocks at their leeward side. Such hillocks may vary from a few centimetres to a few metres in diameter and height. Some hillock plants produce adventitious roots and use resources that accumulate in the hillocks, while others remain limited to their original rhizosphere.

Introduction

Sandy soils and dunes are very common in many parts of the world's deserts. According to Rice (1988), one-tenth of the continental areas between the latitudes 30°N and S are covered by active sand deserts. In the desert areas of Israel (mean annual rainfall <200 mm), the sands constitute some 13% of the total area; in the Sinai (mean annual rainfall <100 mm), they cover 21% of the area (Danin, 1983); and in the Saharan Desert they cover 28% (Tsoar, 1982). Mobile sand is an extremely poor habitat for plant growth because it contains very small quantities of fine-grained particles, organic matter and nutrients, and in areas with low precipitation no plants grow on sands (Bagnold, 1941). In areas with a mean annual rainfall of 30 mm or more, plants may grow in rainy years, and in less extreme environments plant cover may be more prominent. When growing on sands the plants induce changes in the substratum by trapping fine-grained particles and adding organic material, thus improving the local edaphic conditions. Such changes may facilitate the subsequent establishment and growth of other plants.

The adaptations of various plants for survival and growth in sand deserts are the focus of this paper. Many examples will come from sands of Israel and Sinai, areas with which the

author is most familiar. In this region, sands occur along a climatic gradient between 6(mm mean annual rainfall at the Mediterranean coast and 10–20 mm in the southern coast area of the Gulf of Suez. Many of the species that play a role in the sandy ecosystems (Israel and Sinai have vicariant species in other sandy areas such as northern Africa an southern Africa. Such floristic similarities may imply similarities in the physical con ponents of the ecosystems.

Environmental stresses in the sand desert

In order to review plant adaptations to sand, one has to focus first on the environmenta stresses imposed by desert sands on plant life. The most important environmental stress i that of the moisture regime which is strongly affected by soil texture. Mobile sand i coarse-grained, composed of fine-to-coarse sand with a very low proportion of silt and cla) (Tsoar, 1974; Danin, 1978; Danin & Yaalon, 1982; Seely, 1991). Such a substratum has ; very low water-holding capacity (Kramer, 1969). The upper sand layers may become dr) soon after rain falls, thus limiting seed germination and seedling establishment. However much of the water is retained in deeper layers because of no runoff, deep and rapid penetration, small water losses through direct evaporation from the soil surface, and the mulching effect of the dry top sand layer (Chadwick & Dalke, 1965; Noy-Meir, 1973; Leistner, 1967; Zohary, 1973; Pavlik, 1980; Orshan, 1986; Seely, 1991). On the other hand, in dune areas where vegetation cover is minimal, some water is lost in recharging underground water reserves (Prill, 1968).

The high mobility of sand in strong winds leads to additional obstacles to plant life, i.e. coverage and sometimes burial of the entire plant in sites of sand accumulation, or exposure of roots in deflation sites. The mobility of smaller quantities of sand may interfere with germination or seedling establishment. Wind-borne sand particles and heavier particles moving in saltation may injure aerial parts of plants (Boyce, 1954). Nutrient content of the nearly-pure quartz deposits is very low (Ranwell, 1972). In many areas, trampling and overgrazing by large herds of domestic animals have a profound influence on plant life (Tsoar & Moller, 1986; Danin, 1987).

Habitat types of desert dunes

Many kinds of dunes have been characterised by their morphology (Cooper, 1958; Tsoar, 1974; Chapman, 1976; McKee, 1979, 1982; Tsoar & Moller, 1986). Their taxonomy is beyond the scope of the present chapter. Our observations of sands of Israel and Sinai (Danin, 1978, 1983; Kutiel et al., 1979/80; Danin & Yaalon, 1982; Kutiel & Danin, 1987) led us to distinguish a series of habitats, some of which are syngenetically related in processes of succession. It is necessary to deal with all the processes that the sand passes through from its accumulation through stabilisation, to erosion to see and understand the role of plants in this ecosystem. The habitats discussed here may be found in all dune types. Each of these habitats may be characterised by plants that are best adapted to the limiting factor or assemblage of such limiting factors that are imposed by that habitat. The first category of habitat is deep sand, over 5 m deep, where vegetation is influenced by sand properties alone.

(1) Sites of sand accumulation. These are the flanks of longitudinal dunes, the leeward side of barchan, barchanoid, and parabolic dunes, and the arms of star dunes (McKee, 1982).

(2) Sites of constant deflation including interdune areas and the windward side of dunes that are structured by unidirectional winds.

(3) Stable sand fields with little or no sand accumulation or deflation.

The second category is shallow sands, where vegetation is greatly influenced by properties of the underlying soil.

(1) Mobile sand covering sand fields. Occurs in areas where sand accumulation takes place in pulses. The old sand was influenced by geomorphological processes that led to a certain degree of stability.

(2) Sand covering hills or plains of hard or soft rocks. This is a habitat that supplies higher quantities of water than pure sand because of the higher water-holding capacity of the underlying strata (Danin, 1983).

(3) Sand covering salt marshes (Batanouny & Batanouny, 1968, 1969; Danin, 1981a, 1983). Water is sufficient, but has a high osmotic component.

(4) Sand covering wadis in gravel plains (Danin, 1974, 1983; Rudich & Danin, 1978).

Plant adaptations to environmental stresses in desert dunes

In previous accounts of plant adaptations to sands, little attention was given to the different habitats that exist in the desert sand dune ecosystem. I prefer to organise the present account under subheadings relating to the principal habitats listed above. Each habitat imposes different stresses on plant life and I wish to focus on the special plant adaptations that appear to mitigate those stresses.

Deep sands

Adaptations to sand accumulation
The plant best representing adaptations to sites where sand accumulates in deserts is *Stipagrostis scoparia* (Trin. & Rupr.) de Winter (Poaceae). Its diaspores are one-seeded, wind-dispersed and armed with three plumose awns. Winds scatter the diaspores and they accumulate in sites where wind velocity is low, such as leeward sides of dunes or phytogenic hillocks. Sand accumulating in these sites covers the diaspores to various depths, where they are ready for germination. After 2 successive rainy days in sandy areas east of the Suez Canal we observed, in 1968, mass germination of S. scoparia that resulted in seedling establishment all over the area of mobile sands. This is comparable to the germination of *Ammophila breviligulata* Ferland. (Poaceae) on coastal dunes after heavy showers supplied humidity and stability to the ground (Gimingham, 1964). Stems of S. scoparia covered with sand give rise to adventitious roots from the nodes. In many aspects it functions like *Ammophila arenaria* (L.) Link, which has been more extensively dealt with in the literature (Greig-Smith et al., 1947; Olson, 1958; Gimingham, 1964; Hesp, 1981; Danin & Yaalon, 1982; Gehu, 1985). *Stipagrostis scoparia* has a short-lived stem and root system that not only tolerates sand burial, but requires it. Stem branching is rather limited. Many stems that bear inflorescences give rise to one branch below the inflor-escence, thus keeping the number of branches rather low. The plagiotropic rhizomes do branch at their tips into two to four branches that in time lead to an increase in the diameter of the tuft. Dead stems remain straight and function as a wind break for some time. Later they lie on the sand and protect it from wind erosion for a few years. Removal of sand cover from the plant or cessation of sand accumulation leads to its death (Danin, 1983). After establishment of a seedling, sand begins to accumulate on the leeward side of the plant (Hesp, 1981). Rhizomes grow into the sand, new aerial stems sprout, and a phytogenic hillock develops (Fig. 1), as described for S. pungens (Desf.) de Winter (Bendali, 1987). Very few plant species accompany S. scoparia in the mobile dunes except for a few annual grasses in relatively rainy areas during the winter (Danin, 1978).

Similar adaptations are shown in other sandy deserts by S. acutiflora (Trin. & Rupr.) de Winter in Egypt, S. pennata (Trin. & Rupr.) de Winter in Iran (Zohary, 1973), S. pungens in southern Tunisia (Bendali, 1987), S. sabulicola (Pilger) de Winter, S. cf. namaquensis
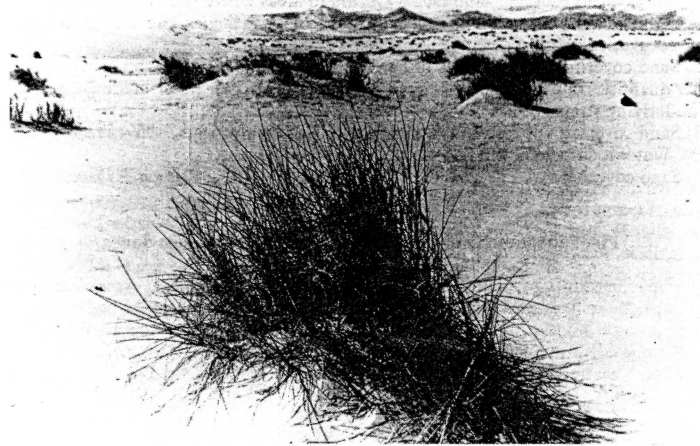
takes place during a 'pulse' of several consecutive rainy days when sand is relatively stable and wet enough to induce germination. Such 'pulses' of precipitation are the principal driving forces in ecosystems of extreme deserts (Noy-Meir, 1973, 1974). Perennial grasses that germinate and establish themselves withstand sand accumulation by producing adventitious roots and plagiotropic rhizomes after being covered with sand. By producing denser vegetation the plants locally decrease wind speed and lead to accumulation of finer sand particles in the phytogenic hillock around them. Reduced wind speed decreases water losses by direct evaporation from the sand surface (Tsoar & Moller, 1986) and
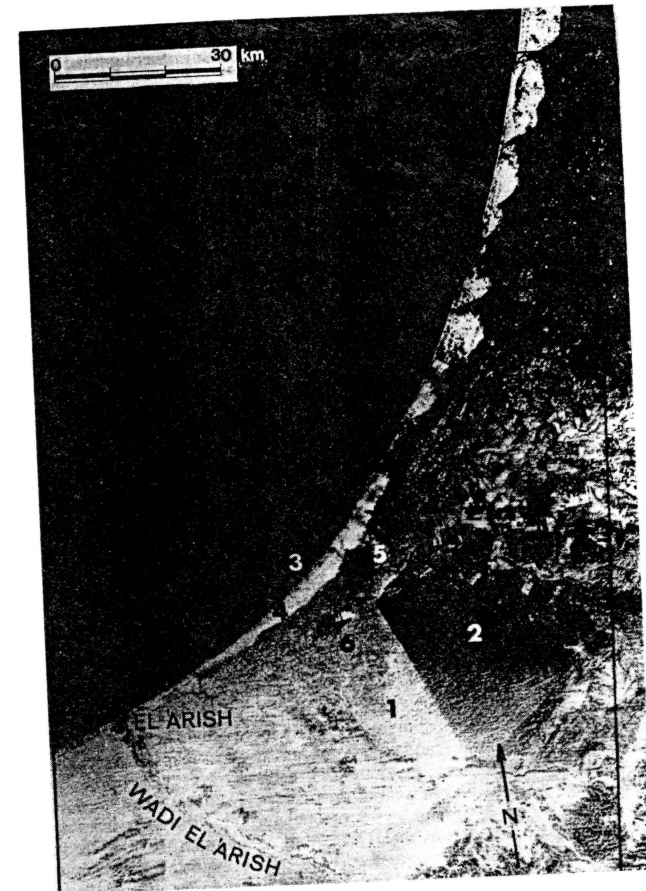

Figure 1. Phytogenic hillocks around *Stipagrostis scoparia* tufts in western Sinai.

(Nees) de Winter and *S. lutescens* (Nees) de Winter in Namibia (Louw & Seely, 1982; Yeaton, 1988), *Uniola paniculata* L. in North Carolina (Wagner, 1964), and in the Euro-Siberian and Mediterranean sands by *A. arenaria* (Gehu, 1985).

Artemisia monosperma Delile in Israel and north-eastern Sinai, functions as a dominant in the second stage of phytogenic sand stabilisation (Danin, 1978; Danin & Yaalon, 1982). It needs light for germination (Koller *et al.*, 1964) and germinates only in sites where there is some sand cover. These conditions are found between hillocks of *S. scoparia* where wind velocity is low. *Artemisia monosperma*, with its denser crown, decreases wind velocity more efficiently and also leads to accumulation of fine sand around the plants. It also has the ability to develop adventitious roots from sand-covered stems. In addition, it resists sand deflation, as will be discussed later. In time it leads to formation of stable sand fields where sand mobility is minimal (Danin, 1978). In these sites eolian silt and clay are trapped, thus leading to amelioration of water regime and soil stability. The amelioration is displayed by increasing species diversity and phytomass production of ephemeral species. Filamentous cyanobacteria are found at this stage at the soil surface or slightly below the surface; they are responsible for the increasing stability and better moisture regime. Their role in sand stabilisation is further discussed later. The quantity of *A. monosperma* decreases from north to south with a decrease in the amount of annual rainfall leading along the Israeli–Egyptian border (Fig. 2). In the northern (dark) section of area 2 in Fig. 2 all the formerly active longitudinal dunes are covered with a community dominated by *A. monosperma* and *Panicum turgidum* Forssk. Towards the south, in a lighter coloured area, there are very few *A. monosperma* plants and instead there are longitudinal dunes with *S. scoparia* as the principal plant. This seems to indicate that as long as *A. monosperma* is within the area of its optimal growth, sand will be arrested and will be covered with relatively dense vegetation. A similar situation, with *A. monosperma* as the leading species that follows the pioneer grass, is found in moister parts of Israel (Kutiel *et al.*, 1979/80; Danin & Yaalon, 1982).

In conclusion, the first important stage that the dune ecosystem has to pass to proceed with biogenic stabilisation is germination of plants in the exposed and mobile sand. This

Figure 2. LANDSAT imagery of the border area between south-western Israel and north-eastern Sinai (1973). 1, Reworked sand, vegetation destroyed; 2, sand, vegetation intact; 3, date palm plantations; 4, shifting coastal sands; 5, sandy–loamy area covered by orchards; 6, fenced area of Israeli settlements where destruction of vegetation ceased (courtesy of NASA, from Danin, 1983).

creates the specific germination niche required for other species. Species with higher plasticity which withstand coverage and exposure of roots establish themselves and lead to more stability in the site and replacement of the pioneer plants. Finer air-borne particles are trapped and the mobile dune becomes a sand field. In a comprehensive study of dust content in desert soils small amounts were found in mobile sands and larger amounts at the surface of stabilised sands (Gerson *et al.*, 1985).

Adaptations to sand deflation

The most prominent feature of plants that grow in areas where sand is constantly removed by wind in Israel and Sinai is their exposed taproots (Danin, 1983). The most common and dominant species have roots with corky bark, i.e. *Convolvulus lanatus* Vahl and *A. monosperma*. Roots of *Cornulaca monacantha* Delile (like many other lignified Chenopodiaceae) have internal active phloem and xylem elements (Fahn *et al.*, 1986), thus enabling transportation activity even when the root is exposed. It is assumed that the protection of the xylem and phloem from external desiccation enables these drought-resistant species to withstand the principal stress of this habitat. There are sites where the exposed root of the shrub is 1–2 m long. These species are accompanied by a few others also adapted to root exposure. In northern Sinai sandy areas (cf. Danin, 1983, fig. 4 no. 6), there is a large deflation area with many plants with exposed roots and only a small area of a mobile sand accumulation. The interdune 'deflation' areas, dominated by these species, have the coarsest soil texture; their fine-grained components have been removed by wind.

A somewhat similar situation is found in Mediterranean sands where *A. monosperma* develops with exposed roots. Elsewhere, other species that are better adapted to root exposure become dominants: *Moltkiopsis ciliata* (Forssk.) I.M. Johnston, *Echiochilon fruticosum* Desf. and *Scrophularia hypericifolia* Wydl.

Stable sand fields

This type of habitat is assumed to be the long-term situation in sandy areas with mean annual rainfall >100 mm. To become stable the area has to support vegetation that will be dense enough to locally protect the ground from being eroded by wind, a situation not found in extremely dry areas. In Israel and north-eastern Sinai the plant communities that achieve this phase are mostly dominated by *A. monosperma*. After its establishment and replacement of the pioneer grass *S. scoparia*, the population of *A. monosperma* becomes denser, as far as the local water regime (depending on rainfall and soil texture) allows. In the sequence of communities during dune succession this community is the richest in number of species, life forms, and phytomass production (Danin, 1978).

The principal geomorphologic process that takes place in a site where deflation and accumulation is minimal is enrichment of the soil surface with fine-grained particles (Danin, 1978; Danin & Yaalon, 1982; Danin *et al.*, 1989). Air-borne silt and clay, originating from adjacent desert areas (Yaalon & Ganor, 1973; Yaalon & Dan, 1974), are deposited and trapped by the vegetation. Once the silt and clay content of the top layer reaches 1·5–2%, cyanobacteria may be found (Danin *et al.*, 1989). Their quantity increases with time after their first establishment and with increasing amounts of fine-grained components in the soil. Table 1 and Fig. 3 present the results of analyses of 18 crust samples in sites with stable and mobile dunes in the western Negev, sampled (September 1988 and March 1989) some 50 km west of Beer Sheva (Danin, unpubl. data). The area was under grazing before 1948 and was protected for some 40 years from cutting by humans and grazing by domestic animals (Noy-Meir & Seligman, 1979). The site's exact age could not be established. The parameters for linear regression of organic matter to soil components, and levels of significance, are presented in Table 2.

The data presented in Table 2 may be interpreted as feedback processes that take place in these sands. When passing a certain threshold of silt plus clay content in the ground, cyanobacteria establish themselves in the soil and increase sand stability by inducing an aggregation of soil particles. Bar-Or & Danin (1989) found different mechanisms that

contribute to the aggregation of soil particles. These are: (1) attachment of particles to binding sites along the cyanobacterial cell walls; (2) adhesion to the mucilaginous sheath or slime layer that is produced by several species of cyanobacteria in the crust; and (3) mechanical binding of the particles by the three-dimensional network of filaments.

When dampened by rain some phototactic cyanobacteria move out of their sheaths and above the thin layer of soil covering them. A similar phototaxis is known in cyanobacterial mats in other habitats (Gabai, 1985; Richardson & Castenholz, 1987). Once exposed and wet for a sufficient length of time, the filaments produce a new mucilaginous sheath. These new components of the microphytic crust may attract additional fine soil particles that become fixed by one or more of the three modes described above. Hence, soil texture changes in close proximity to the filaments. An improved moisture regime with increasing proportions of fine-grained particles enables increasing amounts of cyanobacteria to develop. Scanning electron micrographs of soil (from one of the old sites of Table 1) display sand, silt and clay particles tightly bound by cyanobacterial filaments and mucilage (Figs 4, 5).

Cyanobacteria found in the western Negev were mostly filamentous, of the genera *Microcoleus*, *Scytonema* and *Schizothrix*; globular components, such as *Nostoc* sp., were found as well. Some of these cyanobacteria have mucilaginous sheaths that attach strongly to soil particles (Fig. 5). When a crust is well developed, nearly no soil particles can be removed by winds. The role of a cyanobacterial crust in prevention of erosion in sandy soils in the southern part of the central United States was demonstrated by Booth (1941). He found several types of crust populated by species of the genera *Microcoleus*, *Scytonema*, *Schizothrix* and *Porphyrosiphon* in different stages of succession. He attributed the resistance of the crust to erosion by water to the binding of surface particles of soil by cyanobacteria into a non-erodible layer. Later investigators, such as Marthe (1972) and Bailey *et al.* (1973), experimentally achieved soil aggregation by cyanobacterial inoculates.

A similar situation with cyanobacteria from the same genera was described in less sandy soils in Arizona (Fletcher & Martin, 1948). One of the important modes of adaptation of cyanobacteria to this environment is their being poikilohydric. They actively grow during the winter after being sufficiently moistened by rain. Their resistance to low water

Table 1. *Results of granulometric analysis of cyanobacterial crust from the western Negev along the Israel–Egypt border (Danin, A., unpubl. data)*

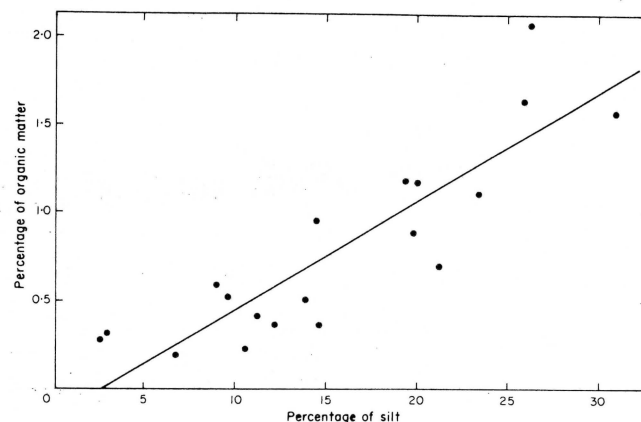| Per cent of silt + clay	Per cent of organic matter	Relative age of stabilisation
15·8	0·52	Young
30·6	2·05	Very old
13·0	0·59	Old
20·4	0·36	Old
35·4	1·56	Old
25·4	0·69	Very old
21·8	0·95	Very old
17·2	0·41	Young
11·0	0·22	Young
26·6	1·17	Old
24·2	0·88	Old
18·2	0·50	Old
8·6	0·19	Old
32·6	1·62	Very old
4·3	0	Mobile sand
23·6	1·17	Very old
16·0	0·36	Old
29·6	1·10	Old

Figure 3. Scatter diagram of relationships between silt content and percentage of organic material in cyanobacterial crusts from the western Negev. Coefficient of correlation $r = 0.879$; $p \ll 0.0001$ (see Table 2).

Figure 4. Scanning electron micrograph of the surface of a cyanobacterial crust on stable sand from the western Negev (bar = 0.1 mm).

Figure 5. Silt-sized quartz grain bound to the crust by polysaccharide threads derived from a cyanobacterial sheath (bar = 0.01 mm).

potentials (Brock, 1975), high temperatures (Buzer et al., 1985), and avoidance of intense solar radiation by growing below or among soil particles (Levy & Steinberger, 1986), ensure their presence in crusts during long dry periods between rains.

Cyanobacteria in young crusts are green and found below a thin protective layer of sand or silt; in time they develop above the ground and become dark coloured due to pigments that protect the cells from photo-oxidative death (Abeliovich & Shilo, 1972).

Their development is limited to the stage in the geomorphologic sequence when the amount of fine-grained particles is sufficient to retain a certain amount of water annually. Protection from erosion promotes an increase in the number of plant species. *Nostoc* species are known as nitrogen fixers and their establishment and dense growth may also improve the nutrient regime (Fletcher & Martin, 1948; Rychert & Skujins, 1974; Loeftis & Kurtz, 1980). Comprehensive reviews concerning cyanobacteria living in soils of desert and semi-desert areas in most continents are those of Friedmann & Galun (1974) and Starks et al. (1981).

Older crusts in our area support cushiony mosses such as *Pterygoneurum* sp. and *Aloina* sp. Such mosses trap clay, silt and sand particles (Danin & Yaalon, 1981) and increase stability and microsite diversity. The only places where sand is available for wind erosion are where tunnelling animals (Danin, 1978) or the activity of man, domestic animals, or

natural game (Danin, 1987) break the microphytic crust. Such damage is naturally repaired by regrowth of cyanobacteria in the rainy season.

In addition to the microphytic crust, stable sand fields support plants adapted to desert conditions with sand as the supporting soil. Such a soil has low moisture-holding capacity that varies with soil texture (Kramer, 1969). Many species have a well developed root system that enables them to obtain water from a relatively large volume of soil (Zohary & Fahn, 1952; Orshan, 1986; Seely, 1988). The low nutrient status of sand has been reported by Ranwell (1972) and by Seely & Louw (1980). Ranwell (1972) suggested that in coastal areas, the increasing diversity of plant species with time is related to input of nutrients with

Table 2. *Relation of organic material (%) in the cyanobacterial crust with soil texture. The equation is: microphytic biomass = aX + b, where X = percentage of soil component, r = coefficient of linear regression, p = level of significance, a and b factors in the equation (based on Danin, A., unpubl. data)*

X	r	p	a	b
Silt + clay	0.878	0.0001	0.051	−0.237
Silt	0.879	0.0001	0.059	−0.143
Clay	0.546	0.01	0.143	1.326

the tide. I suggest that in desert sand fields it is the trapping of air-borne dust and the increasing activity of cyanobacteria that play a similar role to the tide in coastal situations.

A common morphological feature found in many annual and small perennial plants growing in this habitat, in desert and coastal areas, is a layer of sand on above-ground parts. Typical examples are *Ifloga spicata* (Forssk.) Sch. Bip., *Fagonia arabica* L. and *Fagonia glutinosa* Delile, which have glandular hairs or other means by which sand grains stick to the plant surface. The sand layer may reduce physical injuries caused by air-borne sand or silt particles. Plants with such sand protection occur in various sandy habitats and are not restricted to stable sand fields. In Israel and Sinai they are not common in habitats such as those mentioned earlier.

Sand covering other substrates

When sand depth above an already existing soil is <5 m, the roots of many species are anchored in the substratum and sand plays a different role to the one discussed in the previous section.

Mobile sand covering sand fields

Mobile dunes covering a sand field or interdune deflation plains, as described earlier, have two principal zones: (1) a barren zone where plants are killed by moving sand, and (2) a vegetated zone at the foot of mobile dunes. In the latter zone the amount of sand slipping from the dune covers the ground at a rate that does not kill the plants. A new habitat is formed that supports denser and taller vegetation than on the sand field or the dune. Plants are constantly covered by sand and must be able to produce adventitious roots. The large individuals and the high density they achieve may be interpreted as a result of their exploiting larger amounts of water in their rhizosphere than plants of the sand field. The additional water supply they have is assumed to be from the ground below the dune, where the dune plants do not reach. This layer may be charged by vertical water movement in dune areas as reported by Prill (1968). Apart from having deep root systems and the ability to produce adventitious roots, plants growing here have no special adaptations. In north-western Sinai, in areas where the deflation sites were dominated by *C. lanatus* and the dunes by *S. scoparia*, plants typical of moister areas, such as *A. monosperma* and *Scrophularia hypericifolia*, succeed very well in this habitat.

Sand covering hills or plains of hard or soft rocks

This is a habitat that supplies higher quantities of water than pure sand because of the high water-holding capacity of the overlain strata (Danin, 1983). Higher quantities of water occur in this habitat than in lithosols because of the mulching effect of the sand cover (Fig. 6). Plants growing here have to survive constant coverage and removal of sand from their above-ground parts. This habitat is restricted to areas where the amount of mobile sand is not sufficient to create a deeper mantle over the hills. The vegetation in this habitat depends on the quality of the overlying strata. In north-western Sinai, west of the Mitla Pass, a series of three to four plant communities develops in such a situation above limestone hills (Danin, 1983, fig. 43). Where sand depth is >3 m, vegetation of mobile sand develops: *S. scoparia* and *S. acutiflora* in patches, as described earlier. Sites where sand depth is 1–2 m are populated with stands of *Retama raetam* (Forssk.) Webb. The most common habitat of this species in the Sinai Desert is *wadis* where additional water accumulates in the ground. In sands, *R. raetam* grows in a diffuse pattern in monospecific stands (Monod, 1931; Danin, 1983). Its crown may be free or nearly totally covered with sand. Total burial for a long time causes death, but if sand does not cover the whole plant it may survive cycles of accumulation and deflation down to the limestone, where the principal rhizosphere of the plant occurs.

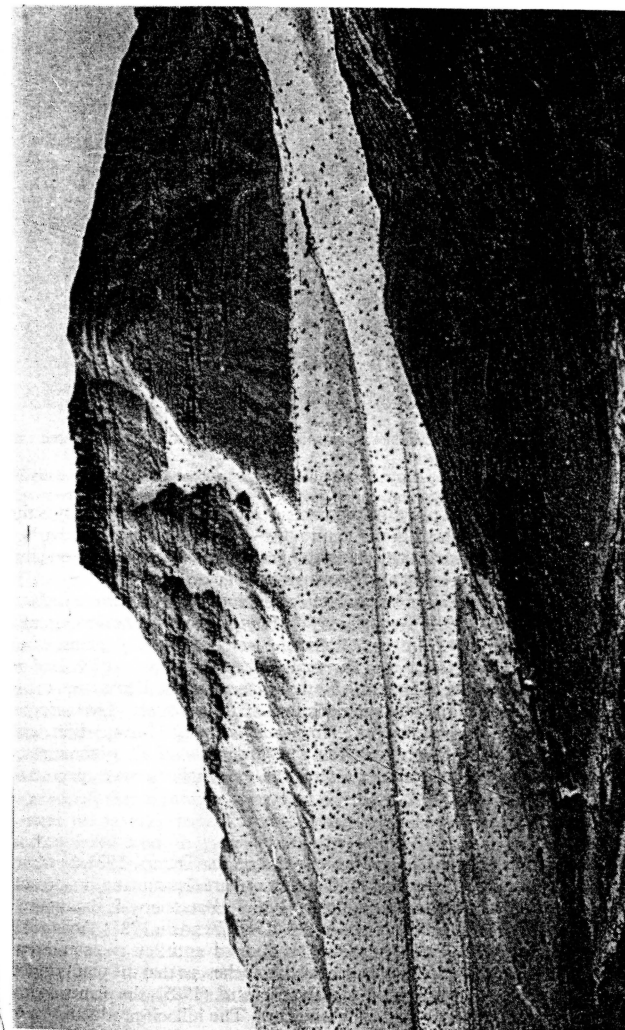In sites where the depth of sand is 10–70 cm, there is a community dominated by

Figure 6. Sand covering limestone hills in northern Sinai. Note the prominent vegetation cover on the sand as compared with the poor cover on limestone slopes.
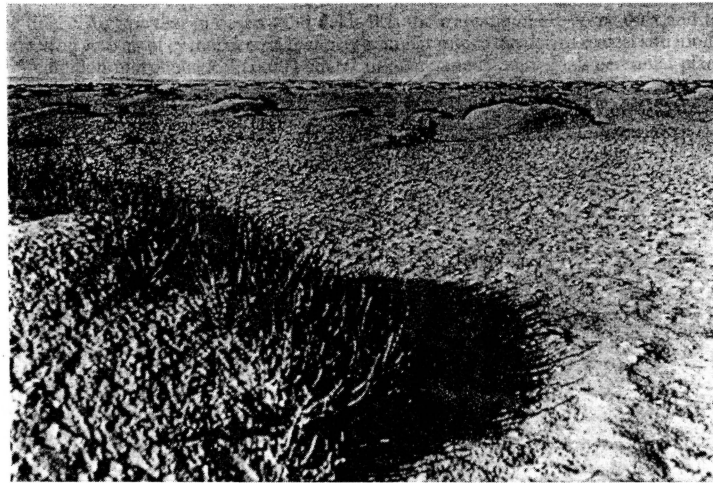
Figure 7. Hillocks at the leeward side of *Halocnemum strobilaceum* plants on a sand-covered salt marsh, northern Sinai.

Anabasis articulata (Forssk.) Moq. A prominent botanical feature of this community is the presence of a locally endemic semi-shrub in the community—*Astragalus camelorum* Barbey (Danin, 1976). It is not clear what enables the development of particular species there, but the sand depth screens out all species not as tall as the maximal sand cover.

A typical microhabitat that develops in this habitat is the phytogenic hillock, or 'nebka' (Batanouny & Batanouny, 1968, 1969; Bendali, 1987). Phytogenic hillocks develop as a result of sand accumulation around plants rooting in the overlain soils. The plants often produce adventitious roots which grow into the accumulated sand and which lead to creation of a wind-protected microhabitat used by various animals. There are many species that are capable of forming phytogenic hillocks: *A. articulata*, *Gymnocarpos decander* Forssk., *Calligonum comosum* L'Her., *Hammada salicornica* (Moq.) Iljin, and *Panicum turgidum*. Most of these hillocks result from sand accumulation above the surface of the entire area, others consist of subsurface soil from the once-higher surface, protected by plants from wind erosion.

Sand covering salt marshes

Salt marshes are a common feature of coastal areas in deserts (Danin, 1981*a*). Many hydrohalophytes trap saltating and creeping sand and finer particles moving in aerosols and this leads to the formation of phytogenic hillocks (Fig. 7) (Batanouny & Batanouny, 1968, 1969; Chapman, 1976; Danin, 1983; Evenari *et al.*, 1985; Bendali, 1987). According to Batanouny & Batanouny (1968, 1969) the plants produce adventitious roots and new branches into the accumulated soil which replace buried branches, so that the plants 'float' above the covering sands. In most cases studied by Evenari *et al.* (1985), the plants do not produce adventitous roots into hillock soil, only branches. The hillock-producing halophytes studied by Evenari *et al.* (1985) were *Nitraria retusa* (Forssk.) Ascherson, *Zygophyllum album* L.f., *Limonium axillare* (Forssk.) Kuntze, *Aeluropus lagopoides* (L.) Twaites, and *Halocnemum strobilaceum* (Pallas) MB.

Huge areas of wet coastal saline soil in Namibia south of Walvis Bay are covered by a

Figure 8. *Salvadora persica* forming hillocks in south-eastern Sinai, near Ras Nusrani. Note the exposed trunks and stems at the northern, windward size of the plants.

nearly monospecific community of *Salsola notholensis* that forms hillocks >2 m high. There are no successional changes in hillock communities dominated by *Halocnemum strobilaceum* in northern Sinai, nor by *S. notholensis* in Namibia; therefore we can conclude that those hydrohalophytes do not 'float' but are well anchored in the wet, saline soil. In eastern Sinai, inland from the salt marshes, the glycophytic tree *Salvadora persica* L. produces phytogenic hillocks up to 10 m high (Fig. 8) (Danin, 1983; Evenari *et al.*, 1985). It is assumed that its roots reach non-saline water. In a similar way date palms planted near salt marshes may become substantially covered with sand while still being able to use the high water table (Fig. 9).

Batanouny & Batanouny (1968, 1969) mention some 30 species that form hillocks, belong to several life forms, and grow in different habitat types. The hypothesis they presented, that the ability to produce phytogenic hillocks is an adaptation to desert dunes, seems to be only partially true. Many hydrohalophytes produce no roots into the accumulated sand, in contrast with phytogenic hillocks in non-saline habitats. Edaphic conditions in sandy areas, with *S. scoparia*, *A. monosperma* or other sand-binding plants, change as a result of plant activity but saltmarsh vegetation, such as that illustrated in Fig. 7, will not change as a result of small hillocks accumulated around the hydrohalophytes. The principal limiting factor of this habitat, the occurrence of salty water close to the surface, will not change as a result of plants growing there. It seems to me that the principal adaptation of the above-mentioned halophytes is to withstand a wet and saline rhizosphere and not to trap sand; the latter process may be regarded as a by-product and not as a main adaptation.

Sand covering dry water courses (wadis)

Plants in *wadis* also may form hillocks. The most prominent of all in this habitat in the Negev and Sinai is *Tamarix aphylla* (L.) Karsten. This is a tropical tree that in Israel and
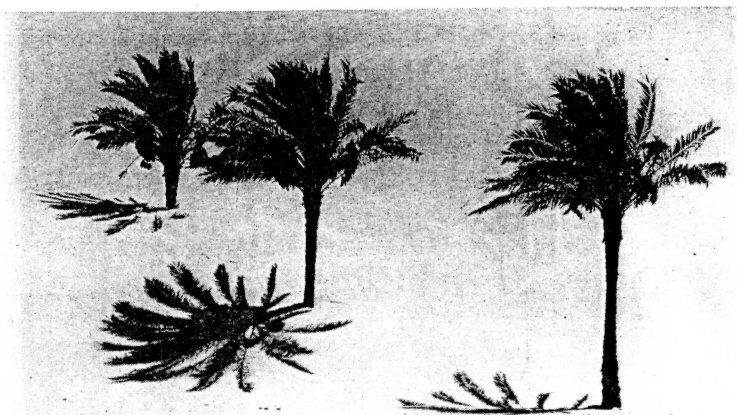
Figure 9. Three date palms, planted near a salt marsh in northern Sinai and partially covered by mobile dune.

Sinai germinates in *wadis* of hot desert areas after rare events of summer rains (Danin, 1981*b*). When growing free of human interference in sites with a high water table, this tree may become >10 m high. When growing in an area where sand displacement by wind is a common event, plants may form hillocks 5–7 m high. In Nahal Arava, southern Israel, where such hillocks are found, there are rather dense stands of *Calligonum comosum* and *Haloxylon persicum* Bunge that function as wind breaks and do not allow the development of 'creeping' hillocks like those of *S. persica* in the alluvial fans of the southern Sinai coastal area. Similar situations, with denser hillocks of *T. aphylla* and *T. nilotica* (Ehrenb.) Bunge, occur in south-western Sinai in large *wadis* in the catchment area of the Gulf of Suez (e.g. Wadi Gharandal and Wadi Sudr; Danin, 1983).

Utilisation of dew and fog water in sand deserts

Water deficiency in sand deserts led several authors to search for sources other than rainfall for plants growing in extreme deserts. Vaadia & Waisel (1963) studied direct absorption of dew water by several desert plants and concluded that the amounts were negligible. They assumed that xerophytes, because of their thicker cuticles, are less adapted than mesophytes to rapid foliar absorption of water at night. *Trianthema hereroensis* Schinz, growing in the fog zone in Namibia, is one of the few desert plants found to efficiently use fog water (Louw & Seely, 1982).

It seems that a more general process by which plants obtain water in the sandy deserts is the use of water condensing near the sand surface. Jackson (1973) found diurnal variation in water content of the surface soil under field conditions. Marshall & Holms (1979) further explained this variation as 'thermally induced moisture flow; nocturnal cooling by radiation from the ground surface is often observed to cause an early morning accumulation of moisture in a rather thin layer near the surface of the soil'. Louw & Seely (1982) sprayed tritiated water on the top 1 cm of soil near *S. sabulicola* and found efficient

water absorption by the plant. It seems that the use of dew water (through quick absorption by superficial root systems) may be an important adaptation of some desert dune plants.

Comparison between plants of desert and coastal dunes

The term 'coastal dunes' is confusing to a certain extent. There are coastal dunes in wet countries such as Norway or Britain and in dry ones such as Egypt or Namibia. In dry countries, a distinction and separation between the two types is rather difficult. The geological and geomorphological set-up of the coastal area has a lot of influence on the ecological conditions and hence on the plants growing there (Danin, 1981*a*). Let us separate in this discussion the vegetation of the dunes from that of the interdune habitats.

The principal differences between plants of desert dunes and of coastal dunes in moister areas is that in many coastal dune systems, plants have to withstand the stress of salt spray or inundation in addition to that of sand mobility (Oosting & Billings, 1942; Boyce, 1954; Barbour *et al.*, 1973; Chapman, 1976). Desert sand plants do not suffer from salt spray or inundation. Coastal dunes are populated with plant species different to those of the desert. As opposed to the large proportion of grass species (Poaceae) in desert dunes (as reviewed above), the pioneer community in coastal dunes of East London, South Africa, is rich in species from Asteraceae, Goodeniaceae, and only a small proportion is Poaceae (Burns & Lubke, 1986). A similar situation is found in sandy coasts of California but with plants from other families (Barbour *et al.*, 1973). Chapman (1976) indicated that plant succession on coastal dunes of Europe and North America is mainly of hemicryptophytes and the climax is of phanerophytes. In northern Israel it starts with perennial grasses, continues with chamaephytes and the climax is of phanerophytes (Kutiel *et al.*, 1978/79; Danin & Yaalon, 1982). In southern Israel and northern Sinai stable sands are dominated by chamaephytes with very few phanerophytes. Mobile sands in deserts are dominated by grasses, whereas stable ones are populated by chamaephytes. In Namibia, the semi-stable inland dunes are dominated by grasses with only a very small proportion of chamaephytes.

In moister coastal areas the rates of plant-dependent processes are higher, and the accumulation of organic matter as humus during plant succession is marked. *Ammophila arenaria* is the principal species that is adapted to accumulating sand in the coastal dunes of Israel, north-east Sinai (Danin, 1983, 1987; Danin & Yaalon, 1982), most of the Mediterranean countries, the British Isles and western Europe (Ranwell, 1972; Corre, 1975; Chapman, 1976; Gehu, 1985; Doing, 1986). It has rather similar adaptations to accumulating sand to those of *Stipagrostis* species, i.e. it has perennial but short-lived stems, roots that develop from buried nodes and rhizomes that grow into the embryonic dune or hillock that is accumulated at its leeward side.

Stability of the sandy areas in coastal situations of moister countries is achieved by complete cover of the area by phanerogamic vegetation. In several areas with coastal dunes in the Eastern Cape, South Africa, i.e. near Port Alfred and Alexandria, precipitation dunes develop (Cooper, 1958) at the contact zone of the mobile dune system and the 'coastal thickets' (*sensu* Lubke *et al.*, 1988). There are a few woody species from the thickets, such as *Brachylaena discolor* DC., which are able to grow above the accreting sand, thus forming large hillocks. These were termed 'ascending accretion dunes' (Tinley, 1985). The shrubs or trees that build such dunes grow to several dozen metres in height, preventing further movement of the entire dune system inland. In coastal areas of South Africa with a high rate of sand accretion and high-energy winds, grasses growing on the mobile dunes play only a minor role in stabilising the sand. I assume that the high series of phytogenic dunes is responsible for most stabilisation processes. It seems that the high quantity of available water and deep roots anchored in mature soils enable *Brachylaena* and other trees and shrubs to create these precipitation dunes parallel to the coast.

Cyanobacteria develop in coastal dunes (Van den Ancker *et al.*, 1985; Nokrian, 1988; de Winter *et al.*, 1989), but their role in the final stages of succession is not so crucial as it is in desert ecosystems. Mosses also contribute to the stabilisation of coastal dunes as discovered in Europe (Chapman, 1976) and in Australia (Moore & Scott, 1979). Moss species were found to grow 3–4 cm a year and emerge from a sand layer that covered them. Mosses contribute to the microphytic crust of desert climax communities but they do not play a role in the successional processes of dune stabilisation.

When the comparison of coastal vs. desert dunes is expanded to the interdune area, one has to take into consideration the salinity, quantity, duration and depth of underground water. The quantity of rainfall in the area is of great significance as it influences not only the moisture regime but also the soil salinity (Danin, 1981*a*). In European slacks (interdune depressions) aquatic plants such as *Potamogeton* and *Zanninchellia* occur where free freshwater is available all the year round. Other slacks where the soil is damp for a long time have *Juncus*, *Salix*, *Carex* and *Scirpus* species (Chapman, 1976). In the coastal zone of Israel, where there is the appropriate geomorphological situation (such as Akko–Haifa area) there are interdune salt marshes dominated by *Arthrocnemum*, *Sarcocornia*, *Limonium* and *Tamarix*. A similar situation is described by Corre (1975) from Camargue in southern France.

Sandy areas along the coast of Israel that are not influenced by a high water table (most of the area) are covered by seral communities influenced by the type of substrate beneath the sand and by the climatic conditions (Danin & Yaalon, 1982). There is a park woodland of *Ceratonia siliqua – Pistacia lentiscus* and related seral communities in the northern part of the country, and shrubland in the southern area.

In northern Sinai, north-east of El ʻArish, the coastal sandy desert area is not influenced by saline water. Due to geomorphological conditions there is a high water table of freshwater that is used for date palm cultivation (Danin, 1983). Much of the terrain between El ʻArish and Port Said has large areas where the salty water table is close to the surface. The interdune salt marshes are dominated by the hydrohalophytes *Halocnemum strobilaceum*, *Arthrocnemum macrostachyum* (Moric.) Moris Delponte, *Sarcocornia* spp. and *Suaeda* spp. whereas depressions where water is less salty are dominated by *Juncus arabicus* (Ascherson & Buchenau) Adamson and *Phragmites australis* (Cav.) Steudel (Danin, 1983). In drier areas, such as along the Gulf of Suez, the sand dunes are devoid of vegetation whereas, as a result of underground flow of fresh or saline water, the interdune areas are covered with coastal halophytic vegetation (Danin, 1981*a*, 1983; Evenari *et al.*, 1985). The dominants in these salines are *Halocnemum strobilaceum*, *Arthrocnemum macrostachyum*, *Nitraria retusa*, *Limonium axillare* and *Suaeda vermiculata* J. F. Gmel.

Conclusions

The most important factors affecting plant distribution in desert dunes are the amount of available water and the degree of sand stability. Sources of water are firstly rain, secondly condensation of water in upper soil layers, and thirdly moisture retained in soils or rocks below the sand but in a water table shallow enough for roots of some plants to reach.

Fresh and mobile sand is a poor habitat, devoid of plants. In areas where the amount of annual rainfall is less than 20–30 mm nearly no plants are found in regular years; they may develop in exceptionally wet years. Above the 20–30 mm threshold, perennial grasses germinate following a few consecutive rainy days when wet sand is somewhat stable. These grasses, mostly of the genus *Stipagrostis*, are capable of growing above accreting sand. Forming biogenic hillocks, the plants create obstruction to wind, decreasing wind velocity enables local deposition and trapping of fine-grained particles transported via aerosols. An amelioration of the water regime in areas with more than a certain threshold of water input leads to development of filamentous cyanobacteria. By growing among the sand grains and by adhering to them, cyanobacteria form a crust in which sand and finer particles are

aggregated. This crust decreases much of the sand mobility. The common occurrence of a cyanobacterial crust in areas with 80–200 mm mean annual rainfall in Israel and its absence from the eastern dunefields of Namibia may be a result of a higher input of water condensation in the Israeli sands. A few events of water condensation leading to wetting of the top 1 cm layer of sand in the Negev may be considered as an important source of water. In Namibia, the amount of rainfall together with condensation is probably too low for the development of cyanobacterial crust. The less mobile sand among hillocks of the pioneer *Stipagrostis* supports additional species of *Stipagrostis* and other taxa. These species are adapted to semi-stable or slightly mobile dunes and replace the pioneer vegetation. In areas where a cyanobacterial crust develops, communities that are poorly adapted to sand mobility take over the pioneer vegetation.

Trampling by domestic animals in overgrazed areas is the main cause for breaking of the protective effect of the cyanobacterial crust. Reworking of the sand leads to wind erosion and death of sensitive plants. A substantial decrease in water input through rainfall and condensation may lead to similar results.

For a greater understanding of the role of plants and microorganisms in sand stabilisation and adaptation of these organisms to desert dunes, comprehensive studies of moisture and nutrient regimes are needed. Combined surveys of sand deserts from phytosociological, microbiological and ecological viewpoints may lead us to a better appreciation of these ecosystems.

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