

The dynamics of vegetation and sand mobility in arid regions of Tunisia

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This work, carried out in the pre-Saharan region of Tunisia, was designed to investigate the changing characteristics of sandy steppe during its progressive invasion by wind-borne sand from disturbed neighbouring zones (regressive evolution). In addition, the development of the vegetation in such regions after the disturbance had ceased has been determined (progressive evolution). The method consisted of studying differences in the main perennial species in the presence of mobile sand, in order to establish whether these species show special adaptations to the mobility of the sand and their role in sand fixation. Only two species show ability to tolerate sand accumulation and are thereby able to fix drifting sand. These are *Rhanterium sauveolens* Desf. and *Aristida pungens* Desf. The most effective mode of resistance to sand mobility (accumulation and deflation) appears to be a change in the vegetative growth, i.e. the formation of adventitious roots in the accumulated sand and the development of aerial structures at a level corresponding with the new soil surface.

Introduction

Intensified exploitation of the natural environment in arid regions is the cause of floristic changes, decreasing production, water and wind erosion. These processes may be reversible or not, depending on the intensity and duration of the disturbance. They have been the subject of much research (Noy-Meir, 1974; Le Houérou, 1962, 1969, 1977, 1981, 1986; MacMahon, 1981; Floret, 1981; Foret *et al.*, 1981; etc.) related to the dynamics of the vegetation and its environment, problems of stability and resilience, and of desert encroachment. One of the most spectacular aspects of ecosystem deterioration in arid regions is the movement of sand subsequent to a decrease in, or disappearance of, the plant cover (following clearing for cultivation, overgrazing, and other mismanagement practices).

The dynamics of vegetation in regions of drifting sand have been studied primarily on the coastal dunes of temperate regions (Boterenbrod *et al.*, 1956; Kuhnholz-Lordat, 1923; Willis *et al.*, 1959). The literature related to the adaptation of plants to the movement of sand in arid regions is much less abundant. For instance, Bowers (1982) has indicated adaptations of species to the dune environment in the U.S.A., especially the elongation of stems and roots. Dittmer (1959) also noted such adaptations in roots.

Plants growing where the sand is mobile must become adapted to a number of constraints in order to survive. (a) They have to be able to germinate under highly unfavourable soil moisture conditions (low quantity and/or transience) and at depths which may alter greatly. Once it has germinated, a seedling must, in turn, be able to grow sufficiently quickly to become established. (b) Seedlings must have a very fast rate of initial

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root elongation to compensate for the rapid drainage of water. (c) They must remain emergent above sand which tends to bury them. Local accumulations of the order of a decimetre are not unusual in a matter of days, or even hours. (d) Plants have to withstand the blast of sand particles which cause lesions, especially in plantlets. (e) They must withstand unearthing of the roots. (f) They must have a flexible root system enabling them to take advantage of water availability at all depths. (g) They have to be able to make very rapid use of slight, transitory water, and to tolerate water scarcity over very long periods. (h) They must be able to tolerate very low levels of nutrients in order to meet the low trophic level of the substrate.

This work was carried out in the pre-Saharan region of Tunisia in order to study the changes in steppe, initially in good dynamic condition, during its progressive invasion by wind-borne sand from disturbed neighbouring zones (regressive evolution). In addition, we have tried to determine the development of the vegetation in regions when disturbance has ceased, i.e. when protective measures have caused the deposition of sand to cease (progressive evolution).

The study region is located in the Tunisian Jeffara, a coastal plain separated from the Sahara by a relief of *cuestas* (Matmatas). The average annual rainfall is 150 mm (Fig. 1), with a 4-5-month hot-dry period. The average temperature is 20° (with occasional light winter frost). The soils are composed of relatively old wind-borne deposits, often covering an early Pleistocene (Villafranchian), eroded, calcareous hardpan or lime-crust. The vegetation of the sandy areas, and the processes contributing to its deterioration, have been described and mapped by Le Houérou (1959, 1969), Le Floc'h (1973), Floret & Pontanier (1982), Bendali *et al.* (1986) and Bendali (1987). The undisturbed steppe vegetation has a cover of 20 to 30%, comprising predominantly chamephytes, annual plants which develop from the autumn rains and persist until the end of the following spring. These chamephytes are quite numerous (Fig. 2) and the physiognomy is marked by the predominant species, *Rhanterium suaveolens*. Even when there is no great disturbance in neighbouring areas, a light film of sand is carried by heavy wind and accumulates in the form of small mounds around individual plants of certain perennial species which trap it (micro-nebkas: R.S. and S.V.B. in Fig. 2(a) and Table 1).

When increasing deposits of sand occur (due for example to clearing in neighbouring areas) the floristic variety decreases gradually [Figs 2(b),(c)]. This leads to the disappearance of a large number of perennials and annuals. Conversely, there is a spectacular development in one species, *Aristida pungens*. This exists even in regions which are constantly disturbed by the movement of sand dunes, and partially fixes them [A.P. in Fig. 2(d)]. Thus, in a same region, it is possible to note the spatial juxtaposition of these two types of vegetation steppe with *Rhanterium suaveolens* in the least disturbed regions,

Table 1. List of the main species involved in the dynamics of the sandy Jeffara plain (symbols on Fig. 2)

A.U.	<i>Argyrobium uniflorum</i> (Desf.) Jaub. & Spach	Leguminosae
A.P.	<i>Aristida pungens</i> Desf.	Graminaceae
A.C.	<i>Artemisia campestris</i> L. subsp. <i>glutinosa</i> (J. Gay) Batt.	Compositae
A.S.	<i>Atractylis serratuloides</i> Sieb.	Compositae
E.F.	<i>Echiochilon fruticosum</i> Desf.	Boraginaceae
G.D.	<i>Gymnocarpus decander</i> Forssk	Caryophyllaceae
H.S.	<i>Helianthemum lippii</i> (L.) Pers. var. <i>sessiliflorum</i> (Desf.) Murb.	Cistaceae
L.A.	<i>Linaria aegyptiaca</i> (L.) Dum.-Cours.	Scrophulariaceae
M.A.	<i>Malcolmia aegyptiaca</i> Spr.	Cruciferae
N.C.	<i>Nolletia chrysocomoides</i> (Desf.) Cass.	Compositae
P.A.	<i>Plantago albicans</i> L. subsp. <i>albicans</i> (L.) Le Houérou	Plantaginaceae
R.S.	<i>Rhanterium suaveolens</i> Desf. var. <i>suaveolens</i>	Compositae
S.V.B.	<i>Salsola vermiculata</i> L. var. <i>brevifolia</i> Maire & Weiller	Chenopodiaceae

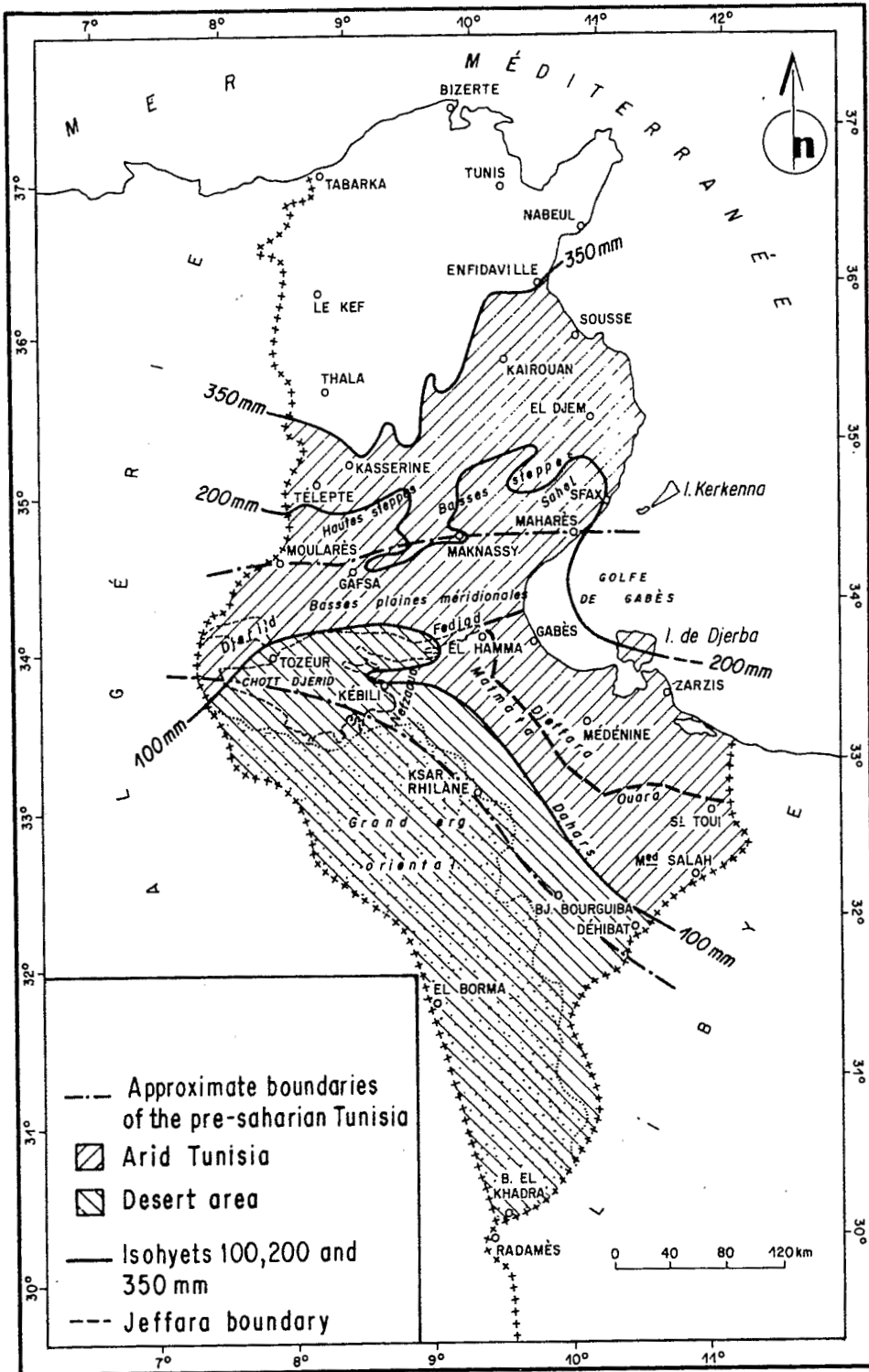


Figure 1. Location of study area in presaharian Tunisia.

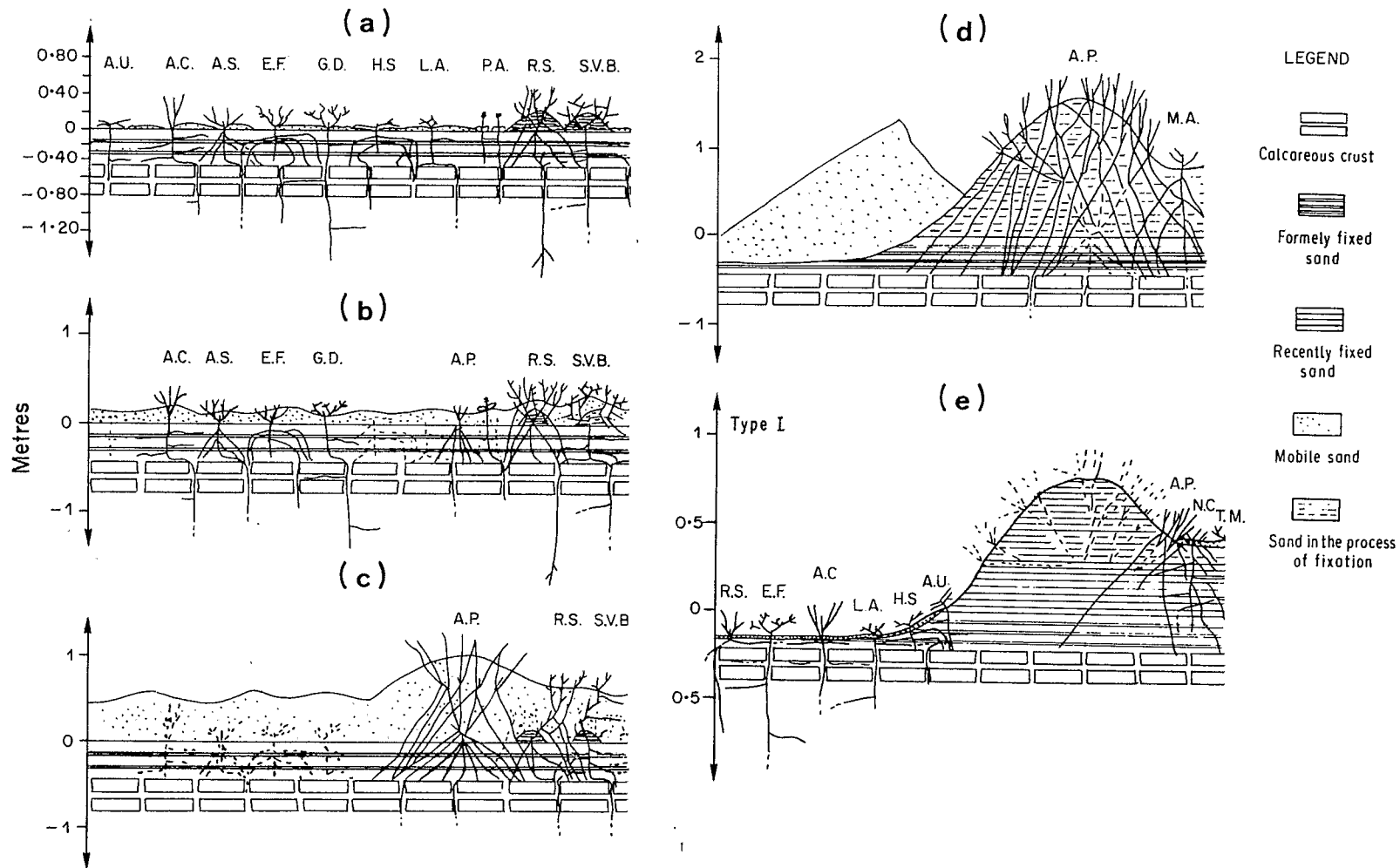


Figure 2. The dynamics of vegetation and sand mobility in the Jeffara Plain. A.U., A.C., etc.—see Table 1.

and populations of *Aristida pungens* in wind corridors. These occur when the wind encounters an obstacle which causes the deposition of the suspended sand. In regions benefiting from long-term protection, *Aristida pungens* dies out and species of the initial *Rhanterium suaveolens* steppe can grow again [Fig. 2(e)].

We investigated this by studying the differences in behaviour of the main perennial species in the presence of mobile sand, asking the following questions: Do these species show special adaptations? What is their role in sand fixation? To what extent do fixing species facilitate the establishment of other species? and, is it possible to apply models of succession as described in the literature (Clements, 1916, 1936; Drury & Nisbet, 1973; Connell & Slatyer, 1977; Noble & Slatyer, 1980; etc.)?

Material and methods

The ecological groups and plant communities of all the species which are linked to sand accumulation, sand veil, deflation, have been described by Le Houérou (1959, 1969). The principal species involved are listed in Table 1 and are shown in Fig. 2. We have tried to explain the behaviour of these plants through a study of their structure. Authors who have tried to link plant response and structure have concentrated primarily on trees (Halle & Oldeman, 1979; Halle, Oldeman & Tomlinson, 1978; Edelin, 1977, 1984). The growth diagrams of the trees studied have also been adapted to graminaceous plants (Jeannoda-Robinson, 1977). We have tried to use the terminology developed by these authors in defining the architectural units of the chamephytes we studied (Fig. 3). *Module*: an axis which expresses the whole sequence of aerial differentiation. *Architectural diagram*: sequence of modules, emitted in a determined order. *Reiteration*: partial duplication (adaptive or traumatic) of the architecture, modifying the module hierarchy.

Study of the root system is also indispensable in defining functional units. Thus, we have tried to classify the various species as a function of this criterion. Fifteen samples of the aerial parts of each of these species, taken both from the undisturbed steppe and from regions undergoing burial by sand, were observed *in situ* and tagged. The growth of the shoots was measured over one year on a station protected from large herbivores. The

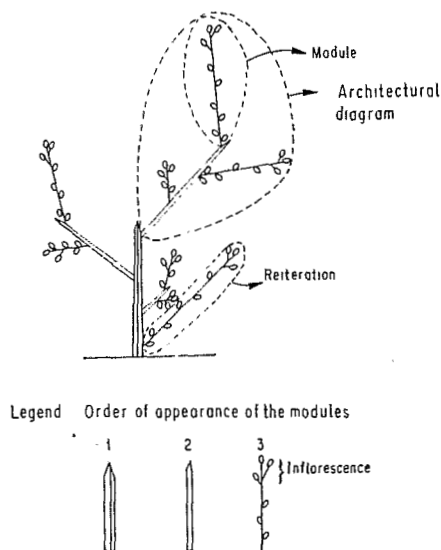


Figure 3. Definition of architectural units.







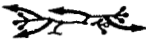

1 \ 2	Basal	Basitonic	Rarely foreseeable	Acrotonic
Vertical	 <i>Artemisia campestris</i>	 <i>Rhanterium suaveolens</i> <i>Aristida pungens</i>		 <i>Thymelaea microphylla</i> <i>Atractylis serratuloïdes</i>
Growth upright as they bloom				 <i>Echiochilon fruticosum</i> <i>Nolleha chrysocomoïdes</i>
In any form but constant			 <i>Salsola vermiculata</i> <i>Linaria aegyptiaca</i>	 <i>Malcolmia aegyptiaca</i>
Unprecise or sub-horizontal			 <i>Argyrolobium uniflorum</i>	 <i>Helianthemum sessiliflorum</i> <i>Gymnocarpus decander</i>

Figure 4. Classification of aerial systems.

underground systems of at least three individuals of each species were laid bare in pits by spraying water under pressure. The root systems were drawn *in situ* and, later, in the laboratory after excavation.

Results

Aerial system

Figure 4 shows a classification of the species as a function of their modules and ramification. This classification does not indicate the existence of any true adaptation to sand accumulation, or to fixing sand. Thus, the species whose modules grow vertically either have a structure which does not rise (basitonic), or else have modules in the distal position (acrotonic) which are weaker than at the base. The size reached during a growing period is certainly one of the most important criteria for judging a species' ability to withstand sand accumulation. Table 2 shows a classification of the species as a function of the average size of their growth units after elongation. For most species, the average elongation remains relatively small.

Root system

Similarly, the classification of species according to their root morphology is based on their ramification and reiteration. The length of roots could not be measured, however. Instead, emphasis was placed on the direction of growth (tap or horizontal) and on the number of roots (Fig. 5). Species whose taproot is duplicated at a distance from the collar retains a functional taproot that is longer than that of species whose taproot is reiterated near the neck. In addition, species with short taproots have dense root ramifications near the

Table 2. Classification of species according to the average size of the growth units after elongation (growth observed from 1 September 1984 until 31 August 1985)

Size (cm)	Species
0-10	<i>Argyrobium uniflorum</i> <i>Echiochilon fruticosum</i> <i>Gymnocarpos decander</i> <i>Helianthemum sessiliflorum</i> <i>Plantago albicans</i> <i>Linaria aegyptiaca</i> (<i>Malcolmia aegyptiaca</i>)* (<i>Nolletia chrysocomoides</i>)
10-20	<i>Salsola vermiculata</i> <i>Rhanterium suaveolens</i> <i>Aristida pungens</i> <i>Atractylis serratuloïdes</i>
20-40	<i>Artemisia campestris</i> (<i>Rhanterium suaveolens</i>) (<i>Salsola vermiculata</i>)
40	(<i>Aristida pungens</i>)

* In parentheses: species observed in the part of the station that became sanded-up.

Horizontal ramifications	Tap root	Distal reiteration (long tap root)	Proximal reiteration (Short tap root)	Reiteration near the collar (several tap roots)	Without tap root
Numerous		<i>Artemisia campestris</i> (Salsola verm)	<i>Nolletia chrysacomoides</i>	<i>Atractylis serrulata</i>	
Moderately numerous		<i>Salsola vermiculata</i>	<i>Echiochilon fruticosum</i> <i>Argyrobium uniflorum</i> <i>Helianthemum sessiliflorum</i> (Plantago albicans)	<i>Rhanterium suaveolens</i>	
In small numbers		<i>Gymnocarpus decander</i> <i>Linaria aegyptiaca</i> <i>Thymelaea microphylla</i>	<i>Molcaimia aegyptiaca</i>		<i>Aristida pungens</i>

Figure 5. Classification of root systems.

surface. It is difficult to say which system makes best use of the drifting sand substrate. Resistance to baring may be greater in species with long tap roots replicated relatively far from the collar. The ability to form adventitious roots is a factor of major importance in resistance to sand. The taproots of *Rhanterium suaveolens* which are duplicated from the neck are like adventitious roots.

Morphological reaction of species to sand accumulation

Overall reactions to the accumulation of sand can be summarized as follows: (a) Some species show no particular reaction, viz. *Argyrobium uniflorum*, *Echiochilon fruticosum*, *Gymnocarpus decander*, *Helianthemum sessiliflorum*, *Thymelaea microphylla* and *Plantago albicans*. All these have an acrotonic architectural diagram, and relatively short shoots. Among these species, behavioural distinctions should be differentiated: the root systems of *Echiochilon fruticosum*, *Helianthemum sessiliflorum* and *Argyrobium uniflorum* tend to reiterate one or more taproots after the accumulation of sand. The main taproot of *Gymnocarpus decander* and *Thymelaea microphylla*, on the other hand, remains large, despite the accumulation of sand; (b) In *Artemisia campestris* subsp. *glutinosa*, *Salsola vermiculata* var. *brevifolia* and *Rhanterium suaveolens* (Fig. 6), the original plant is separated into several functionally independent units following moderate (layered) sanding. The functional units of *Artemisia campestris* and *Salsola vermiculata* are composed of aerial reiterations connected with horizontal roots through sections of the taproot [Fig. 6(a) and (b)]. The functional units of *Rhanterium suaveolens* are connected with new taproots which are, in reality, adventitious roots [Fig., 6(c)]; (c) In these last three species, therefore, aerial and root reiterations reveal themselves capable of acquiring a functional autonomy within a relatively short time. The plant seems in this way to renew itself entirely by adapting to sand accumulation.

Aristida pungens resembles *Rhanterium suaveolens* but, since the root system is strictly adventitious, roots appear at the base of the new modules [Fig. 6(d)]. Thus, the module

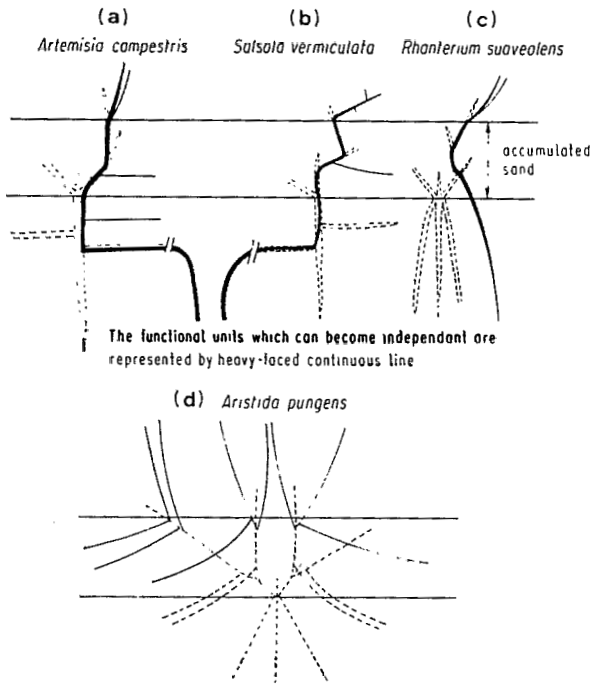


Figure 6. Reaction of four species to the accumulation of sand.

(runner) rooted can make use of light rain. This improves its resistance to sand accumulation, thanks to a greater length of shoot. When sand accumulation is continuous, it leads, in *Aristida pungens*, to an inclination of the stems towards the periphery of the tuft, to the appearance of new adventitious roots, and to the growth of vigorous reiterations which check and trap the sand, causing the formation of a small mound (Fig. 7).

The continuing rejuvenation of *Aristida* stops when wind-borne sand ceases to accumulate. When the deposit of sand decreases, the centre of the plant dwindles and the plant diminishes until it dies. This can be observed in areas which have long been protected from grazing. The species growing in undisturbed *Rhanterium suaveolens* steppe once again becomes competitive and can recolonize the station.

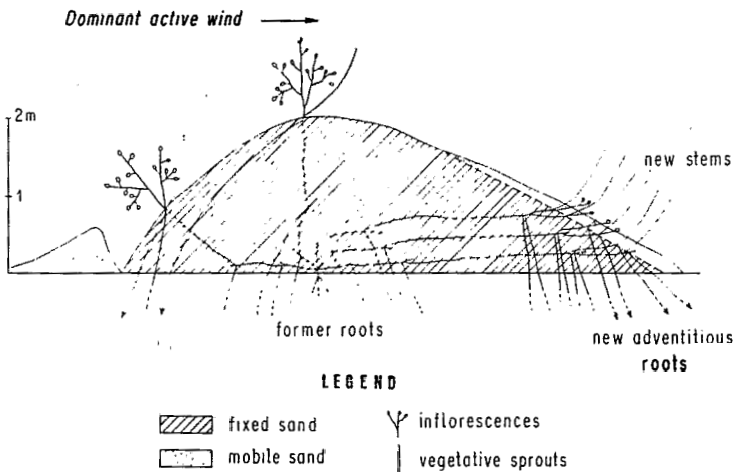


Figure 7. Sand accumulation by *Aristida pungens*.

Discussion and conclusion

Only two species show ability to tolerate sand accumulation and thereby fix drifting sand. These are *Rhanterium suaveolens* and *Aristida pungens*. In the former, aerial structures and roots are reproduced near the surface of the soil, within the limits of moderate (layered) sanding. This species predominates in the majority of undeteriorated sandy areas of Tunisia (average annual precipitation between 100 and 200 mm), where the winds carry relatively large quantities of sand at certain periods of the year. This species determines the physiognomy of the steppe by accumulating and fixing hillocks of sand.

Aristida pungens sends out runners at all levels and these may reach a length of 100 cm in one season. In consequence, the species can maintain the density of its structures after accumulation of sand, partly through constantly renewed adventitious roots which provide it with water from reserves in the accumulated sand. When *A. pungens* predominates, following the disappearance of *Rhanterium*, it is able to create sand hillocks up to 2 m.

The phytosociological units of these formations and their dynamics have been described by Le Houérou (1959). Generally speaking, the spatial succession corresponds to the interpenetration of two metastable ecosystems. These are more or less in equilibrium with the conditions of sand mobility and with the quantities of sand which cross them. They are: (a) the *Rhanterium suaveolens* steppe, which corresponds to an aeolian geomorphology appearing in the form of a wind-borne film with micronebkas; (b) the *Aristida pungens* formation, which includes nebkas, dunes in the process of becoming fixed, and small barkhanes, in which mobile sand covers more than 50% of the ground.

There are, of course, intermediates between these two types. This temporal succession appears to agree with spatial successions observed in the field (Le Houérou, 1959, 1969; Bendali *et al.*, 1986; Bendali, 1987). Other types of disturbance act together with sand mobility to complicate the process of successions: periods of drought cause a drastic reduction in plant cover and favour wind erosion, and grazing plays the same role, reducing the aerial structures of the grazed plants selectively.

The data gathered clearly reveal a number of distinct directional changes in floristic composition over time. Wind-borne sand and surface organic matter accumulate and are fixed around tufts of vegetation, thereby creating conditions favourable to the development of species which are less well adapted to moving sand. In this case, there is a succession of the allogenic type (Tansley, 1949) with facilitation, in the sense given to the term by Clements (1916) and by Connell & Slatyer (1977). When accumulation is slow enough, the hillock shows alternating layers of sand and organic material under the shrub. A good turnover of organic matter favours autogenic succession (Le Houérou, 1986).

The most effective mode of resistance to sand accumulation and deflation appears to be a change in vegetative growth, i.e. the formation of adventitious roots and the development of new aerial structures (reiterations) at a level corresponding with the new soil surface. In some species (*Salsola vermiculata* var. *brevifolia*, *Rhanterium suaveolens*, *Artemisia campestris*), aerial reiterations are connected to new roots and form functional units which may correspond to what Watson & Casper (1984) call 'Integrated Physiological Units'. These appear to be more or less autonomous in their use of water and nutrients, important for units which escape burial by sand.

Reiteration requires release from architectural constraints, and corresponds to a phenotypic plasticity. This plasticity constitutes adaptation to sand mobility. Because of genetic constraints, the slightest abrupt change in one environmental parameter should condemn a species to disappearance. Sand mobility, however, challenges a plant's most essential characteristic: the division between aerial parts and underground parts. The vegetation at the level of the soil changes the relation between the plants and the ground. Considered in this light, it may be wondered whether reiteration is an adaptation to sand mobility, or whether it is an original aspect of a plant's response imposed by mobile sand.

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