

# DYNAMICS OF STRIPED VEGETATION PATTERNS AND WATER BALANCE IN THE CHIHUAHUAN DESERT

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## Abstract

Striped patterns of vegetation have been recognized in many parts of the world's drylands. They include plant populations established in parallel stripes perpendicular to the slope, alternating with bare zones. Following an initial description of this vegetation type in the Chihuahuan Desert of Mexico, a study of the water budget and of the dynamics of plant cover was carried out to test hypotheses on changes in pattern and the importance of the superficial water dynamics. Soil water measurements show the role of the top soil water budget in the functioning and maintenance of this pattern. The vegetation stripe receives an average of 1.5 to 2.5 times the annual rainfall due to run-on. This accounts for the density and diversity of the plant cover in spite of an arid environment. The studies on changes along the margins of the vegetation stripe confirm a slow upslope migration, related to surface water flow. This occurs via specialized pioneer species. It seems likely that the initiation of this pattern is linked to a slow geomorphological evolution of a slope initially occupied by a complex vegetation.

This type of pattern appears to be in stable equilibrium in relation to the existing environmental factors and results in the efficient utilization of water by vegetation in an arid environment.

## Introduction

The presence of particular vegetation patterns, corresponding to plant populations established in parallel stripes alternating with bare zones, has been reported in many parts of the arid and semi-arid regions of the world. Many studies deal with their description, their plant composition, and propose hypotheses for their establishment and origin (Boudet 1972 in Mali, Leprun 1979 in Mali and Burkina Faso, White 1970 in Niger, Worral 1959 in Sudan, Boaler and Hodge 1964 and Hemming 1965 in Somali; and outside Africa, in Jordan by White 1969, in Australia by Slatyer 1961 and Litchfield and Mabbutt 1962, in America by Ives 1946).

Various studies have emphasized the importance of the superficial water dynamics to justify the establishment and maintenance of such vegetation patterns (Slatyer 1961; Hemming 1965; White 1971; Leprun 1979; Mabbutt and Fanning 1987) but only Slatyer (1961) includes a quantitative study of the water balance. Greig-Smith (1979) and White (1971) propose two ways in which striped vegetation could establish: (1) a more or less homogeneous, dense plant cover evolves into stripe-like patches of dense vegetation cover with bare ground between the stripes; (2) bare ground or reduced plant cover develops vegetation stripes along natural obstacles which stop the run-off. More recently, Mabbutt and Fanning (1987) propose a relation between the occurrence of stripes and a change in plant cover associated with the slow geomorphological evolution of the slope.

Following an initial description of this type of vegetation in the Chihuahuan

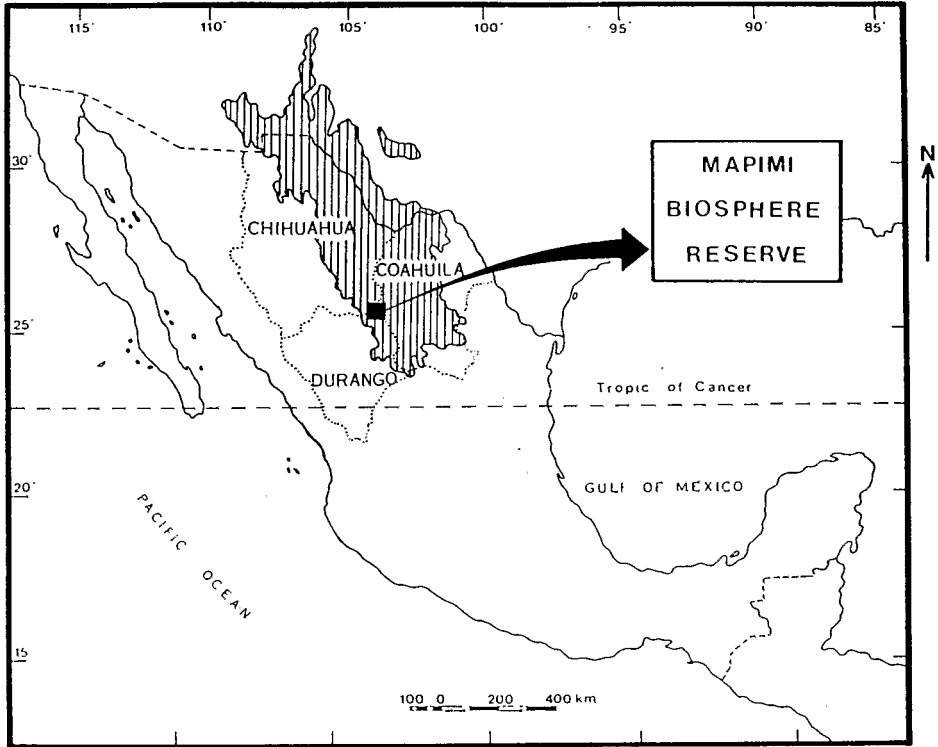


Fig. 1. Localization of Mapimi Biosphere Reserve (Durango, Mexico).

Desert of Mexico (Cornet *et al.* 1983), a study was carried out from 1982 to 1986 to consider the importance of the water balance on the dynamics of plant cover.

### The Study Area

The Mapimi Biosphere Reserve is located (Fig. 1) in the central part of the arid zone of Mexico at an average elevation of 1100 m. It has internal drainage. The Reserve covers some 160.000 ha between latitudes 26°29' to 26°52'N and longitudes 103°32' to 103°58'W. It forms part of the Chihuahuan Desert (Schmidt 1979). The climate is highland tropical arid (Cornet 1987) with an annual rainfall of 264 mm and a variation coefficient of 42% (recorded in Ceballos, 1956–1983, the nearest weather station). Most rains occur during summer, the rainfall from June through September being 71% of the annual total. The average annual temperature is 20.8°C; the average minimum temperature of the coldest month, January, is 3.9°C, and the average maximum of the warmest month, June, is 36.1°C.

The various soil types in the Reserve are mainly differentiated by their parent material and their way of deposition. Most substrates are alluvions and colluvions which are distributed in the landscape according to geomorphology (Delhoume 1987). The higher elevations with steep slopes are characterized by lithosols (FAO

1974) on hard rocks, and regosol on stony colluvions. The glacis or 'Bajadas' with gentle slopes have yermosols and xerosols on alluvions of fine to average texture which cover underlying indigenous limestones and marls. In the lower plains ('Playas') the soils originate from alluvions with a fine texture and variable levels of salinity; these are gypsic yermosol at the saline or sodic phase, or locally modal solontchaks.

The vegetation is a microphyllous desert matorral, and the dominant plant is *Larrea tridentata* with various facies differing in the abundance of crassulescent plants. These communities occur on slopes and their pediments, as well as on the higher glacis (Bajada superior); the intermediate glacis (Bajada inferior) are covered by a mosaic of vegetation: matorrals with *Larrea tridentata*, shrublands with *Prosopis glandulosa*, grasslands with *Hilaria mutica*. The striped vegetation is dominant here. The lower slopes and alluvial plains are occupied by steppe with tufted grasses and halophytes (*Hilaria mutica*, *Sporobolus airoides*, *Sueda* and *Atriplex* spp.). Nomenclature follows Correll and Johnston (1979).

### Description of the striped vegetation pattern

Patterned vegetation is found mainly at the intermediate level along the toposequence, between the matorral with *Larrea tridentata* in the upper part and *Hilaria mutica* grasslands lower down. The dense vegetation stripes follow isohypses. Their width varies from 20 to 70 m and their length from 100 to 300 m; the broadest stripes are in the lower part of the toposequence. The ratio of vegetated stripes to bare zones varies from 24 to 30%. A zonation can be found within each vegetation stripe, and five zones can be described (Cornet *et al.* 1983). Figure 2 shows the zonation across a strip of vegetation and the distribution of the major species. Starting from the higher zone downwards, we find: (1) a transition zone with bare ground and very light plant cover, averaging 4.4%; (2) a border zone, almost flat, with a ground surface deposit of fine material which forms polygonal cracks, and is colonized by a sparse, low vegetation characterized by *Tridens pulchellus*; (3) a zone which in its lower part carries a dense layer of *Hilaria mutica* in 15 to 60 cm high tufts under a dense shrub canopy of 1.0 to 1.5 m high, almost exclusively made up of *Flourensia cernua*. The *Hilaria* grass layer covers to a larger or smaller extent the entire stripe; (4) a floristically more diverse, shrubby zone, from 1.5 to 2.5 m high consisting of *Prosopis glandulosa*, *Aloystia gratissima*, *Lippia graveolens* and *Parthenium incanum*, followed by an open shrubland with fewer species, mainly older *Prosopis* and few *Acacia constricta* covering the *Hilaria mutica* herb layer and fading into a rim of old dying tufts of *Hilaria* and a few trees; (5) a zone of bare ground with a few Cactaceae and remnants of dead shrubs. This zonation was similar in all the observed stripes but the width of zones was variable.

The soil did not show any discontinuities of marked heterogeneity within the whole unit, except for some minor variation in the top soil in relation to the plant cover (Delhoume 1987). The soil profiles of the bare area were the same as within the stripes (Table 1), but there were small differences in the thickness of the horizons. The organic carbon content of the top soil layer is close to 2%; the

Table 1. Soil analysis in a vegetation stripe (after Delhoume 1987).

| Depth<br>(cm) | Layer   | Texture (%) |      |      | pH  | Organic<br>carbon<br>(%) | Total<br>nitrogen<br>(%) | C/N  | Exchange<br>capacity<br>(meq %) | Conductivity<br>(mS.cm <sup>-1</sup> ) | CaCO <sub>3</sub><br>(%) |
|---------------|---------|-------------|------|------|-----|--------------------------|--------------------------|------|---------------------------------|--|--------------------------|
|               |         | Clay        | Silt | Sand |     |                          |                          |      |                                 |  |                          |
| 0-3           | A 11    | 15.9        | 42.3 | 41.8 | 8.1 | 1.96                     | 0.052                    | 37.7 | 27.5                            | 1.00                                   | 12.2                     |
| 6-14          | A 12    | 28.0        | 16.2 | 55.8 | 8.5 | 0.53                     | 0.053                    | 10.0 | 22.2                            | 0.80                                   | 12.8                     |
| 25-33         | B 21    | 33.1        | 15.2 | 51.7 | 7.7 | 8.31                     | 0.056                    | 5.5  | 21.3                            | 0.60                                   | 22.4                     |
| 48-58         | B 22    | 24.1        | 31.2 | 44.7 | 8.2 | 0.23                     | 0.033                    | 7.0  | 19.6                            | 1.00                                   | 22.0                     |
| 71-79         | II B 23 | 39.4        | 42.4 | 18.2 | 8.4 | 0.21                     |                          |      | 21.3                            | 0.75                                   | 33.7                     |
| 97-105        | II B 3  | 37.4        | 48.0 | 14.6 | 8.8 | 0.19                     |                          |      | 18.5                            | 2.00                                   | 36.7                     |
| 130-140       | II C    | 41.0        | 24.7 | 34.3 |     |                          |                          |      |                                 |  |                          |

Table 2. Variation in organic carbon content and C/N ratio of the soil of the vegetation stripe as compared to bare areas (after Delhoume 1987).

| Layer | Vegetated area   |      | Bare ground      |     |
|-------|------------------|------|------------------|-----|
|       | Organic carbon % | C/N  | Organic carbon % | C/N |
| A11   | 1.96             | 37.7 | 0.55             | 7.1 |
| A12   | 0.53             | 10.0 | 0.45             | 6.7 |
| B21   | 0.31             | 5.5  | 0.30             | 6.0 |

organic matter is very little humified (C/N ratio close to 40) and originates from periodic litter fall. This is apparently rapidly mineralized since the A<sub>12</sub> layer has an organic carbon content and a C/N ratio close to those found in unvegetated zones (Table 2).

The vegetation is the major cause for changes in some analytical characteristics and physical properties of the top soil; the plants, due to periodic litter fall, induce a higher organic matter content which, in addition to a larger amount of roots, produces a fine-structured soil with increased permeability. However, these differences are restricted to the upper 30 cm, below which the soil characteristics are not different.

### The soil water budget

The soil water content was monitored from 1983 to 1986 from a transect along the slope, across a vegetation stripe. Pipes for the use of a neutron probe were set in each of the main zones: in bare gravelly areas upslope, in the pioneer fringe, at various levels within the vegetation stripe and in bare ground below the stripe. Measurements were made every 10 days during the rainy season and every month in the dry season. In order to estimate run-off which could not be directly measured, the soil moisture was determined on several occasions before and after the rains to assess the amount stored by infiltration at each site.

Figure 3 shows the changes in soil water for the four zones before and after a shower of 31.8 mm on July 5th, 1984 and Fig. 4 the changes over one year, 1985. In the bare zone the depth of moisture infiltration and the stored quantity of water are very low because of the rather low permeability of the ground. Sheet run-off is important, so that whatever the intensity of the showers, the depth reached by moisture is less than 70 cm and the soil stays moist for only short periods. The unfavorable water budget prevents the plants from colonizing the bare zone, so that it acts as a water catchment area.

In the pioneer zone, the low slope angle and the cracks in the ground surface, slow down the run-off water and favor infiltration (Fig. 3). This zone receives incoming fine soil particles and run-on water from upslope. The run-on is stored in the soil, mainly in the upper part of the vegetation stripe. The moisture depth increases up to a maximum of 120 cm and the stored water allows for continuous growth between showers (Fig. 4). The vegetation stripe receives an average of 1.5

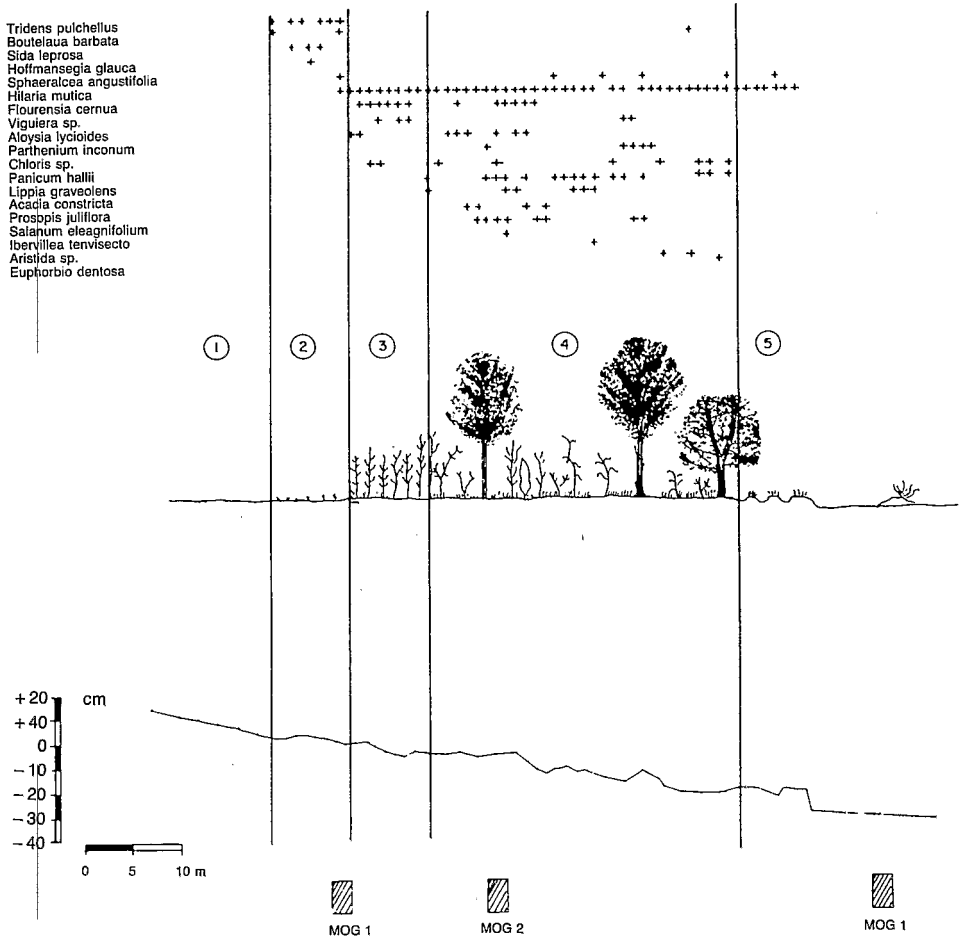


Fig. 2. Section across a vegetation stripe showing the distribution of plants, the surface level profile and the localization of the soil sites studied 1 – Bare area, transit zone; 2 – Deposit area, pioneer zone; 3 – Screen of *Flourensia cernua*; 4 – Dense bushy area, stripe zone; 5 – Downhill bare zone.

to 2.5 times the annual rainfall, due to run-on. This explains the density and diversity of the plant cover in spite of the arid environment.

Run-on does not reach, or can only occasionally reach the lower part of the stripe where the plants become sparse and receive only rain water. Prolonged water stress during the dry years results in the death of the shrubs, and later of the *Hilaria mutica* tufts. The bare zone below the stripe is similar to that above the stripe with reduced infiltration and sheet flow.

### Vegetation dynamics

The dynamics of the vegetation stripe were studied in a grid of permanent quadrats located at the upper and lower limits, comprising in the upper part a 2 m-wide

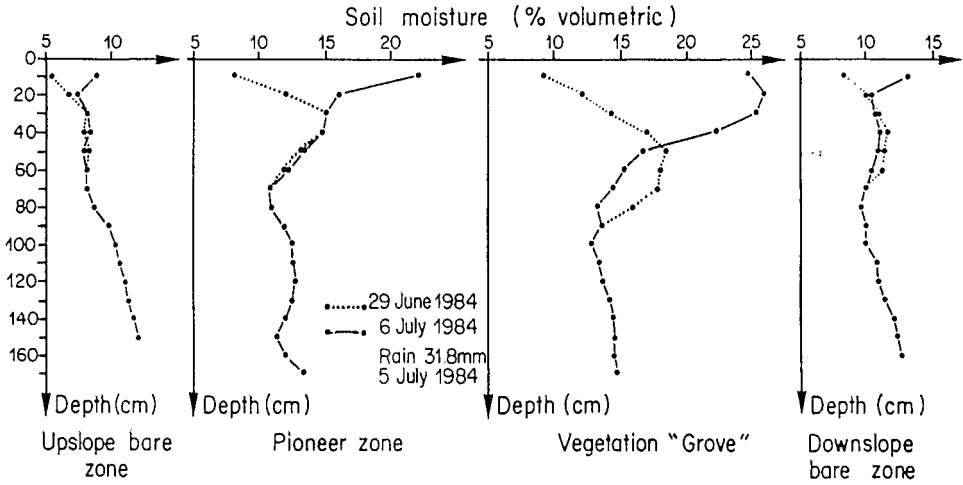


Fig. 3. Change in soil moisture in the four zones of the vegetation stripe before and after a shower of 31.8 mm on July 5th, 1984.

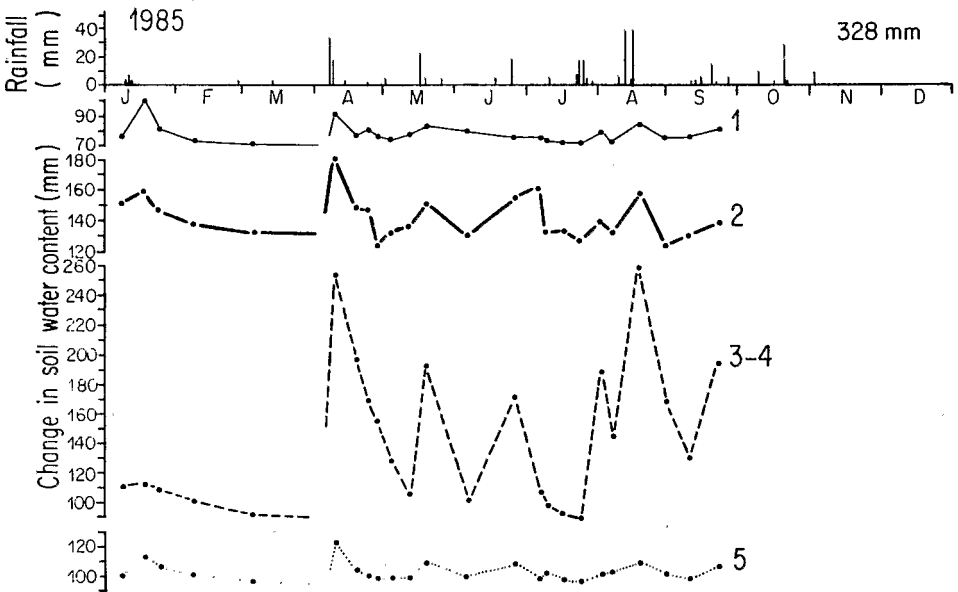


Fig. 4. Changes in water stored in the ground during the 1985 rainy season. 1: Upslope gravelly zone; 2: pioneer deposit zone; 3-4: vegetated zone; 5: downslope bare zone.

and 10 m-long strip of 320 quadrats of 0.25 by 0.25 m, and in the lower part a 2 × 8 m strip of 256 quadrats. It was monitored from 1982 to 1986 in order to determine the encroachment or retreat of the vegetation, and to ascertain the changes of frequency of various species.

Rainfall was low in 1982 and 1983, average in 1984 and above average in 1985

Table 3. Pioneer zone above the vegetation stripe: changes in the occurrence of the main species (from 320 permanent quadrats) through time.

| Main species              |                                  | 1982 | 1984 | 1986 |
|---------------------------|----------------------------------|------|------|------|
|                           | <i>Tridens pulchellus</i>        | 233  | 252  | 252  |
| Other perennial grasses   | <i>Hilaria mutica</i>            | 3    | 5    | 25   |
|                           | <i>Panicum hallii</i>            | 3    | 10   | 16   |
|                           | <i>Pappophorum mucronulatum</i>  | 1    | 11   | 37   |
|                           | <i>Trichachne californica</i>    | 15   | 3    | 0    |
|                           | <i>Trichloris crinita</i>        | 16   | 24   | 36   |
| Perennial pioneer species | <i>Hoffmanseggia densiflora</i>  | 112  | 182  | 97   |
|                           | <i>Sphaeralcea angustifolia</i>  | 70   | 69   | 75   |
|                           | <i>Sida leprosa</i>              | 56   | 43   | 31   |
|                           | <i>Argythamnia neomexicana</i>   | 67   | 83   | 36   |
|                           | <i>Bahia absinthifolia</i>       | 51   | 45   | 14   |
|                           | <i>Haplopappus heterophyllus</i> | 1    | 8    | 24   |
| Young woody plants        | <i>Flourensia cernua</i>         | 29   | 18   | 22   |
|                           | <i>Prosopis glandulosa</i>       | 0    | 5    | 6    |
|                           | <i>Larrea tridentata</i>         | 2    | 1    | 8    |
|                           | <i>Castella texana</i>           | 0    | 2    | 3    |
|                           | <i>Opuntia leptocaulis</i>       | 3    | 3    | 8    |

and 1986. The width of the upper pioneer zone dominated by *Tridens pulchellus* changed from 10 m in 1982 to 10.75 m in 1984 and to 11.75 m in 1986.

Table 3 shows, for the same zone, the changes in number of occurrences of the main species in 320 permanent quadrats. There was a small increase in *Tridens pulchellus* (233 to 252) as a consequence of the colonization of the upper bare ground and a decrease toward the lower end of the pioneer zone. Figure 5 shows the change in frequency of the species in relation to the distance from the edge of the vegetation stripe in 1982, 1984 and 1986.

The other species can be divided into two groups: (1) the perennial pioneer species, chamaephytes and hemicytrophytes but not grasses, in addition of *Trichachne californica*, which are only present within the pioneer zone and whose frequency decreases; (2) the perennial grasses and the shrubs in the stripe, whose frequency increases. As a whole, the frequency of low, pioneer species (*Tridens pulchellus*, *Argythamnia neomexicana*, *Bahia absinthifolia*, *Sida leprosa*) which colonise empty spaces increases in the upslope margin whereas their frequencies decrease in the lower part. There these plants are replaced by larger species coming from the stripe such as tufted perennial grasses (*Hilaria mutica*, *Trichloris crinita*) and shrub seedlings (*Flourensia cernua*, *Prosopis glandulosa*) (Fig. 6).

In the lower part of the vegetation stripe no obvious regression of the vegetation cover could be observed, except for the formation of gaps in the *Hilaria mutica* cover, after isolated tufts had died. The retreat of the vegetation may occur irregularly during drier years.

The result is consequently an up-slope migration of the pioneer zone and of the upper part of the stripe, related to the inflow of rain water and a colonization of the fringe which benefits from water inflow and siltation. The advance is made



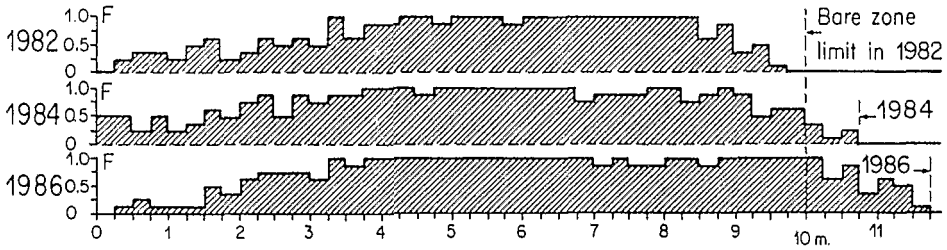


Fig. 5. Changes in frequency (F: 0–1) of a pioneer species (*Tridens pulchellus*) in the up-slope margin of a vegetation stripe.

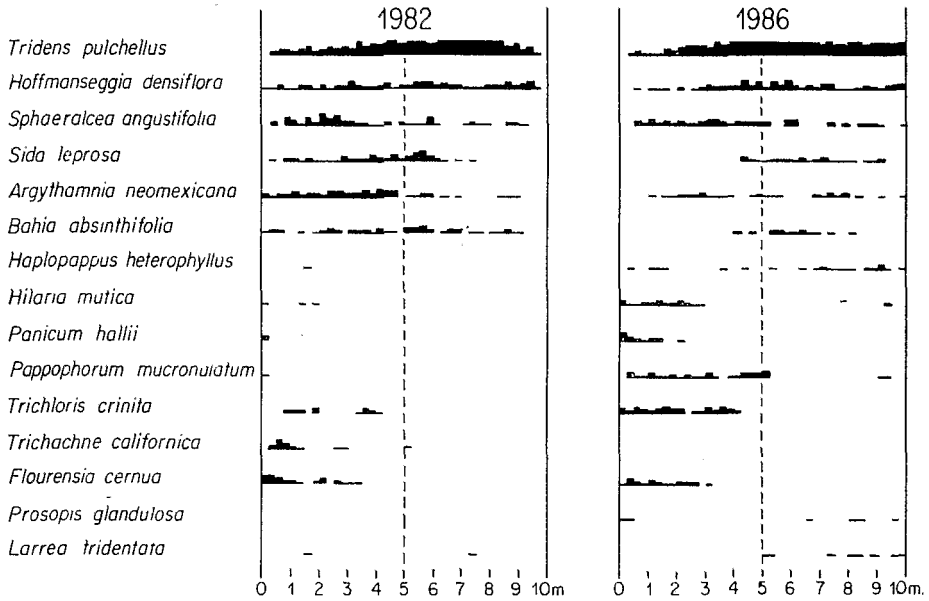


Fig. 6. Changes in distribution and frequencies of the main species in the up-slope margin from 1982 to 1986.

by plants which improve the soil properties and enable the establishment of more demanding species.

### Discussion and conclusion

The plant community studied in the Mapimi Biosphere Reserve is similar to vegetation reported from Africa or Australia which have similar climatic, geomorphological and edaphical characteristics:

- an arid or semi-arid climate with few but high intensity rains;
- a gentle (0.25–1.0%) but regular slope;
- soils with low permeability and a relative abundance of fine particles producing intense sheet run-off.

Under these conditions, vegetation tends to concentrate into dense stripes perpendicular to the slope, a pattern which corresponds to the optimal interception of run-off water. This general response of the vegetation to sheet run-off and run-on water is accentuated by the pattern's secondary properties: silt deposition, shading effects, organic matter accumulation and root penetration.

The soil water measurements show the paramount role of the top soil water budget in the functioning and maintenance of this pattern of plant cover. The studies of changes along the margins of the vegetation stripes confirm a slow up-slope migration of the stripes; they demonstrate that the movement is related to water flow and occurs via specialized species. In the upper part of the vegetation stripes pioneer plants occur, which may belong to various plant communities, as has been noted by many authors (Worrall 1959; Boaler and Hodge 1962; White 1970; Wickens and Collier 1971). Although stripe migration generally exists, it can be very slow, especially where the vegetation stripe interferes with the formation of a hard pan in the soil (Litchfield and Mabbutt 1962; Mabbutt and Fanning 1987). The rate of migration can sometimes be boosted by incoming aeolian sands (Worrall 1959).

It has been suggested that this vegetation pattern originates either from the progressive degradation of a more or less uniform plant cover under a worsening climate or soil degradation (White 1971; Greigh-Smith 1979), or from the rehabilitation of previously bare zones (White 1971; Boudet 1972). Field observations at the limit between the matorral and the striped vegetation show that the phenomenon develops at present within the studied zone through a slow regressive evolution of the slope. The development of vegetation stripes seems a consequence of this evolution of land forms, linked with initiation of sheet flow. This was also reported by Mabbutt and Fanning (1987) from Australia. The regressive evolution of the drainage lines leads to their progressive attenuation on the lower slope, and to the replacement of the gullies by sheet flow. The plants which were growing along the drainage axis (*Hilaria mutica*, *Flourensia cernua*, *Prosopis glandulosa*) build-up into local dense clumps and the vegetation becomes structured so that it forms an obstacle that stops run-off and prevents the matorral growth lower down. This pattern never derives from a previously homogeneous cover through the influence of man. Man's intervention by overgrazing and wood cutting destroys the pattern and creates bare zones with irregular woody clumps, which are not big enough to stop run-off. Moreover, observations by Toutain and De Wispelaere (1979) in northern Burkina Faso have shown that the vegetation stripes remain remarkably stable when no longer exploited in spite of a drought over the last 15 years. The hypothesis that this pattern derives from previously bare areas after degradation (Boudet 1972) and local aeolian sand deposits, could be valid if the dominant winds and the slope had the same direction, or if the vegetated clumps were re-oriented by run-off. However, this was not observed.

The conclusion is that this vegetation pattern apparently derives from the geomorphological evolution of the slopes in the arid or semi-arid zones on soils with a lower permeability. It represents an equilibrium under the existing environmental conditions and results in an efficient use of water by plants in this environment, enabling the continuation of biomass production and maintenance of floristic diversity.

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