Patterns of plant species distribution on coastal dunes along the Gulf of Mexico

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ABSTRACT. Floristic data of coastal dunes along the Mexican coast of the Gulf of Mexico were collected from published sources, field work and herbaria. 467 species belonging to seventy-eight families in sixty-nine areas were included. The majority of families are mainly distributed in tropical regions, and are represented by few species. The few widespread families including Gramineae, Compositae, Leguminosae, Cyperaceae and Euphorbiaceae are well represented. Seven patterns of species distribution were found; they are mainly correlated with variation in sand composition (light-coloured siliceous, dark-coloured siliceous and calcareous), climatic factors (mainly amount of precipitation and minimal temperature), and stability of the dune systems. The composition of the flora was compared with that of the northern littorals of the Gulf of Mexico, Florida, the south-eastern coast of the U.S.A. and the Caribbean. The northern part of the Mexican Gulf coast is especially related to the northern American Gulf coast and the whole Mexican Gulf coast is related to the Caribbean.

Key words. Coastal dunes, plant dispersal, species distribution, Gulf of Mexico.

Introduction

The Mexican Gulf coast from the mouth of the Rio Bravo, at the northern border of the country, to Campeche in the south is approximately 1500 km long. This stretch of coast has narrow and wide beach ridge systems, long barrier beaches, complex dune systems and volcanic headlands.

Little has been published on its flora and vegetation. The best source available is Sauer (1967) but his survey does not cover the floristic and ecological variation in this huge complex. Between 1981 and 1984 we were able to study the vegetation of fourteen dune areas in Veracruz (Moreno-Casasola et al., 1988a, b) and five more in the south of Tamaulipas (García, 1985). In addition thirteen sites in Tabasco were documented by Castillo (1984). An overall synthesis including also the Yucatan Peninsula (Espejel, 1984) is presented by Moreno-Casasola & Espejel (1986).

Detailed distribution patterns cannot yet be elaborated for all the species, as many of them have only been collected in a few sites. However, the information from the areas we sampled, together with the floristic surveys available in the literature from other areas, are sufficient data to now attempt a geographical synthesis.

The aim of this work is to define distribution patterns for species collected and/or reported and to relate them with geographical and environmental factors which modify their distribution.

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Coastline and climate

The eastern Gulf coast of Mexico shows great environmental diversity. Climatically the north of Mexico has a semiarid steppe climate (BSx') with 500–800 mm of rain and occasional frost. There is rain all year round, with winter rains varying from 10.3% to 18% of total rainfall. Towards the south of Tamaulipas the climate type changes to a tropical humid one (Koppen Af and Am) with 1200–3500 mm of rain, a marked rainy season in the summer and with only 5.1–10.2% of annual rainfall in winter. The climate becomes drier again towards the Peninsula of Yucatan (Fig. 1a, b). Seasons are more marked by changes in precipitation than in temperature (DETENAL, n.d.; Rzedowski, 1978). The Gulf of Mexico and surrounding areas are influenced by periodic intrusions of cooler polar air during the winter months, that are locally called ‘nortes’. These are sufficiently common to modify the climatic characteristics of the cool season. Temperatures may drop as much as 10°C and the amount of rain falling during this season can represent 10–12% of the total annual precipitation. Usually twenty to twenty-five such frontal storms are experienced between October and March (Thom, 1967). They are accompanied by strong winds, creating high energy waves and are responsible for moving large quantities of sand in the dune systems (Poggie, 1962; Moreno-Casasola, 1982). There is also considerable variation in the water level. High water levels occur during the rainy season and may last through the ‘norte’ period (Thom, 1967). Flooding of beaches is frequent at this time. Hurricanes are another important climatic factor, causing substantial modification of the beach profile.

Littoral lagoons are very common particularly where poorly drained coastal plains come into contact with the sea. It is also a region with numerous rivers, transporting the riverine siliceous sand responsible for the dune buildup along the coast. Sand changes from light coloured siliceous sand with a certain degree of calcareousness (Fig. 1c) to dark-coloured sand in the central part of Veracruz, with less CaCO$_3$, ...

FIG. 1(a). Map of Mexico showing the precipitation in cm/yr. Taken from Rzedowski (1978).
FIG. 1(b). Map of Mexico showing the minimal extreme temperatures. Taken from Rzedowski (1978).

FIG. 1(c). Atlantic coast of Mexico showing type of beach sand. ↔ calcareous; †† siliceous; ⬤, both.
to light-coloured in the southernmost part of the Gulf, increasing its calcareous content until the Yucatan Peninsula, which is totally calcareous (Castillo, 1984; Espejel, 1984; Garcia, 1985; Puig, 1976; Sauer, 1967).

The major orientation of the littoral varies from an easterly exposure south to Veracruz then changing to northerly for the rest of the study area. Together with a change from a narrow continental shelf in the north to a wide one in the south, this results in great contrasts in exposure to the prevailing winds and waves (Sauer, 1967).

**Methods**

Floristic lists of sixty-nine localities along the Gulf coast are used in the present analysis (Fig. 2), collected from Castillo (1984), García (1982), García (1985), Gonzalez-Medrano (1972), Lot-Helgueras (1971), Moreno-
Plants on coastal dunes in Gulf of Mexico

Casasola et al. (1982), Moreno-Casasola & Espejel (1986), Moreno-Casasola et al. (1988a, b), Poggie (1962), Puig (1976), Sauer (1967) and Vazquez-Yanes (1971). Species localities were completed by checking herbarium specimens deposited at MEXU.

An intensive vegetation analysis was carried out in the nineteen sites along the coast, trying to include the different types of dune systems. Every topographical unit found was sampled by using relevés which varied in size from 2×2 m to 10×10 m. Smallest sizes were used when sampling open, pioneer vegetation surrounded by sand, grassland and slacks. Medium and tall thickets were sampled using 10×10 m quadrats. Cover estimations were made using an ordinal scale from 1 to 9 (Westhoff & Maarel, 1978). Relevés were subjected to the classification and table structuring program TABORD (Maarel et al., 1978). Community types for the region based on the obtained classification were defined. For a detailed description see Moreno-Casasola et al. (1982) and Moreno-Casasola & Espejel (1986). Transects across the zonation were also analysed in the nineteen areas of Tamaulipas and Veracruz. Each transect was laid down at right angles to the shore from the high tide-line through the embryo dunes, foredunes and the stabilized zone. The transect was ended when a very disturbed area was met (mainly through grazing) or a different system (coastal lagoon, mangrove or a floristically rich, tall tropical forest). At every square metre along the transect the change in elevation was measured and the percentage cover of the vegetation was estimated. Four of these transects will be used to represent plant zonation and types of dune systems in the region.

Data from the vegetation analysis was also subjected to detrended correspondence analysis (Hill, 1979; Hill & Gauch, 1981). Sample ordination is reported in Moreno-Casasola & Espejel (1986). In this paper a species ordination was made using these same vegetation data covering the Gulf area.

Results

The zonation and morphology of the vegetation found along the coast will be exemplified through the following transects:

A. In the south of Tamaulipas (Fig. 3), barrier beaches are common, with the Gulf to the east and coastal lagoons to the west. They have narrow or wide beaches, a low ridge parallel to the shore which slopes slowly towards the lagoon or salt marshes (Garcia, 1985; Gonzalez-Medrano, 1972; Puig, 1976; Sauer, 1967). Common species on the foredune are the tall grass *Uniola paniculata*, smaller ones such as *Sporobolus virginicus*, *Panicum geminatum*, *Cenchrus* spp., small shrubs like *Croton punctatus* and *Chamaecrista chamaecristoides* and the creeping vines *Ipomoea pes-caprae*, *Ipomoea stolonifera* and *Canavalia rosea*. The leeward slope and flat depression are commonly occupied by *Lippia nodiflora*, *Fimbristylis* spp., *Dactyloctenium*

![FIG. 3. Vegetation profile from Bocatoma, Tamaulipas (Garcia, 1985).]
aegyptium, Palafoxia texana var. robusta, Acacia farnesiana, Turnera ulmifolia, etc. Close to the lagoon Conocarpus erecta is very frequent.

B. In the area of Tecolutla, in the north of the state of Veracruz, one can find narrow beaches with wide low, beach ridges. The ground water table is near to the surface and in some localities (i.e. Riachuelos) humid slacks, rich in species, are frequent. The transect from El Raudal (Fig. 4) shows a narrow beach with creeping vines Ipomoea pes-caprae and Ipomoea stolonifera, the grass Sporobolus virginicus which penetrates into the sheltered zone behind the first dune ridge, as well as isolated individuals of Cakile edentula and Chamaesyce ammaniaoides. Low shrubs like Bidens pilosa, Palafoxia lindenii, Crotalaria incana are common. Farther back Randia laetevirens and Dalbergia brownei form tall, dense thickets.

C. South of Nautla, volcanic hills which form part of the Sierra de Naolinco (Eje Volcanico Transversal), exist near the coast, forming a complex mosaic of cove beaches between basalt headlands. Enormous dune systems in different degrees of stabilization are found in this area. Dark, heavy siliceous sand derived from volcanic rocks predominates (Sauer, 1967; Moreno-Casasola et al., 1982). Numerous rivers provide material for dune building; the dunes can sometimes be 20 m high (Fig. 5).

Along Veracruz and Tabasco the more important sand binders are low shrubs and creeping vines: Croton punctatus, Palafoxia lindenii, Acacia sphaerocephala, Sesuvium portulacastrum, Ipomoea pes-caprae, Canavalia rosea. Among the grasses present are Sporobolus virginicus, which is particularly abundant in wide, flat beaches; Andropogon scoparius var. littoralis mainly in overwashed areas or zones with sand movement, and Panicum amarum, found frequently on fore-dunes in Tabasco (Castillo, 1984). The shrubs grow forming large patches of one or more species. They cover the sand more homogeneously than the vines but are less extensive on the beach.

D. In the southern part of the state of Veracruz the coast has an east–west direction. This area, as well as Tabasco and Campeche, has narrow beaches with small sand ridges parallel to the coastline. Veracruz terminates with the mass

![Vegetation profile from El Raudal, south of Tecolutla, Veracruz.](image-url)
FIG. 5. Schematic cross-sectional profile of a dune system in the central part of Veracruz showing some of the dominant plants of major communities.
of the Sierra de Los Tuxtlas. Here the coast shows cliffed headlands of lava flows that penetrate into the coast and break the continuous beaches. Sontecomapan, at the mouth of the lagoon bearing the same name, has a narrow beach covered mainly with *Ipomoea stolonifera* (Fig. 6); the frontal part of the foredune has a dense thicket of *Randia laetevirens*, *Psychotria erythrocarpa* and *Coccoloba barbadensis*.

In Tabasco and western Campeche light-coloured siliceous sand replaces dark siliceous sand, and the calcareous elements become increasingly important towards the Caribbean, although they have been present all along the Gulf sands but in a lesser quantity. Together with the region of Los Tuxtlas, these areas constitute the rainiest zone of the Gulf coast; extensive mangrove forests are found along the littoral (Castillo, 1984; Sauer, 1967; Thom, 1967). The coastal plain is a large complex of coalescent delta deposits of active and abandoned river channels. Between the river mouths, fairly straight quartz sand beaches are continuous; generally the beach is backed by a low beach ridge system (Castillo, 1984; Sauer, 1967). The vegetation is very similar to that found in the south of Veracruz.

In the eastern part of Campeche calcareous sand of marine origin predominates. Physiognomically and floristically the area is very similar to the dune systems of the Peninsula of Yucatan (Castillo, 1984; Espejel, 1983, 1984; Moreno-Casasola & Espejel, 1986; Moreno-Casasola & Gaos, 1988; Sauer, 1967) and other Caribbean areas (Asprey & Robbins, 1953; Gooding, 1947; Randall, 1970; Samek, 1973).

Towards the Caribbean, grasses and vines decrease in importance. *Sporobolus virginicus* and *Cenchrus echinatus* come down to the beach but they are abundant only in more protected areas. Vines are found intermingled with other species but they do not form dense patches. The main species on embryo dunes and foredunes are shrubs 1–3 m tall, *Suriana maritima*, *Tournefortia gnaphalodes* and *Scaevola plumieri* being the most important. *Coccoloba uvifera* appears occasionally as a beach pioneer.

Beach species show a change in the dominance of growth forms associated with a geographical gradient. Rhizomatous growth forms are found in low dunes in the north of Mexico. Stoloniferous growth forms take over in the central Gulf region, alternating with low shrub growth forms. Finally, in the Caribbean taller shrub forms predominate. Family dominance also changes. Beach shrub pioneers along the Gulf coast belong mainly to the Leguminosae, Compositae, Euphorbiaceae and Rubiaceae, which are among the more common families. In the Caribbean pioneer shrubs belong to the Boraginaceae, Goodeniaceae, Polygonaceae and Simaroubaceae.

![Vegetation profile from Sontecomapan, in the south of the state of Veracruz.](image)
I. Family representation

Field studies and work by other authors gave a list of 467 angiosperms, belonging to seventy-eight families and 266 genera. These numbers will almost certainly increase with further floristic surveys and identification of unknown herbarium specimens. Forty-eight of the families have all or most of their members distributed in the tropics. Twenty-seven families have a world-wide distribution and three have mostly temperate elements. The following families are well represented: Gramineae 77 spp.; Leguminosae 61 spp. (Mimosoidea 19, Caesalpinioidea 5 and Papilionoidea 37); Compositae 43 spp.; Cyperaceae 23 spp.; Euphorbiaceae 25 spp.;
Rubiaceae 14 spp.; Amaranthaceae 11 spp.; Verbenaceae and Celastraceae 9 spp.; Boraginaceae and Solanaceae with 8 spp. each; Chenopodiaceae, Apocynaceae and Asclepiadaceae, with 6 spp. each; Malvaceae with 5 and Capparidaceae, Convolvulaceae and Cruciferae with 4. Of the other families two are represented in Mexico by only one species with a coastal distribution (Sauer, 1967): Batidaceae and Goodeniaceae.

Nineteen of the well-represented families mentioned above are widely distributed and only five of them are mainly distributed in the tropical regions.

II. Species ordination

The species ordination gave the following results (Fig. 7). Axis 1 reflects a transition from species growing on the beach, embryo dunes and foredunes, through species from humid and wet slacks, towards the central part of the graph where species from grasslands and low scrub appear, and ending with the species of tall thickets on the left side. Axis 2 shows a gradient from species in humid and wet slacks with fresh water, to those growing in brackish conditions. Furthermore, there is a diagonal transition starting on the upper right corner (1), where species only found in Tamaulipas are present (a few also in the Caribbean – see next section); these areas have mainly light-coloured siliceous sands with an important calcareous element; precipitations range from 700 to 1200 mm. In the central part appear species whose distribution range includes central Tamaulipas, Veracruz, Tabasco and part of Campeche (2). They grow mainly on siliceous sand (light and dark), with a higher calcareous content only in the extreme ranges of their habitat, and with higher precipitation. Finally, in the left and bottom left of the ordination space (3) appear species only found in the central part of Veracruz, growing on dark siliceous sand, in complex dune systems that offer protected areas, and with precipitation similar to the ones found in the former case. Slack species distribution is not so clear as species depend on the presence of a superficial ground water table.

III. Species distribution patterns

The analysis of species presence along the sixty-nine localities produces the following coastal distribution patterns (Fig. 8). It should be noted that some species have broader ranges among inland communities. (a) Species which are only found in Tamaulipas and the northern part of the state of Veracruz. The area has a precipitation ranging from 700 mm in the north to 1500 mm in the south. Freezing temperatures are common, especially in Tamaulipas. Fig. 1(b) shows the geographical distribution of the areas in which a minimum extreme of 0-5°C is registered, producing frosts during winter months. The southern limit of this zone coincides with the southern range limits of the species belonging to this group.

\[Acalypha\ radians\]
\[Agonandra\ obtusifolia\]
\[Bacopa\ monnieri\]
\[Celtis\ iguanaea\]
\[Condalia\ hookeri\]
\[Condalia\ lycioides\]
\[Eleocharis\ interstincta\]
\[Eustoma\ exaltatum\]
\[Forestiera\ texana\]
\[Lycium\ berlandieri\]
\[Palafoxia\ texana\ var.\ robustum\]
\[Psychotria\ hebeclada\]
\[Salicornia\ virginicus\]
\[Uniola\ paniculata\]

Sauer (1967) mentions the presence of \[U.\ pancilata\] for one site in Tabasco, well south of this zone, but Castillo (1984) was unable to find it there. MEXU has one specimen collected in Dos Bocas, Tabasco. It would seem to be a small population separated from the main distribution area.

(b) Species with a disjunct coastal distribution, found both in the region mentioned above and

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**FIG. 8.** Patterns of plant species distribution along the Gulf coast. (a) Species only found in Tamaulipas and north of Veracruz. (b) Species found in Tamaulipas, north of Veracruz and the Peninsula of Yucatan. (c) Species found from central Tamaulipas to southern Veracruz. (d) Species only found in the complex dune systems of central Veracruz. (e) Widely distributed species, except on the drier areas of Tamaulipas and the Peninsula of Yucatan. (f) Caribbean species with their northern distribution limit in Veracruz or in Tabasco and Campeche. (g) Widely distributed species, both in the Gulf and the Caribbean.
and on the Yucatan Peninsula. Precipitation in both area varies from 700 to 1500 mm; mean temperature is not very different. The north of Mexico has siliceous sand mainly, but the calcareous constituent is important; sands on the Peninsula are highly calcareous. Many of the species found in both areas extend on the West Indies. Some of the species (*) are also present in the calcareous islands in front of the port of Veracruz, although they are absent on the mainland from the same geographical region. The species placed in this group are predominantly coastal species, i.e. strictly confined to seashore habitats (sensu Sauer, 1967).

Atriplex arenaria  
Caesalpinia bonduc*  
Cakile lanceolata  
Capparis flexuosa  
Capparis incana  
Coccoloba uvifera*  
Heliotropium curassavicum  
Lycium carolinianum  
Panicum amarulum  
Philoxerus vermicularis  
Scaevola plumieri  
Sophora tomentosa  
Suaeda linearis  

C. bonduc has been recorded as isolated individuals in two areas of central Veracruz.
(c) Species found mainly from the central part of Tamaulipas to central and southern Veracruz. They inhabit mainly riverine siliceous dune systems with precipitation of 1000–2500 mm. They are absent from the driest parts of Tamaulipas. Some of them are common in humid and wet slacks. Many of them are classed as primarily inland species, because their borders reach the coast as marginal parts of extensive interior distributions (sensu Sauer, 1967).

Acacia cornigera  
Acacia farnesiana  
Casearia nitida  
Croton glandulosus  
Fimbristylis castanea  
Hydrocotyle bonariensis  
Indigofera suffruticosa  
Iva asperifolia  
Phyllanthus niruri  
Psidium guajava  
Turnera ulmifolia

(d) Mainly inland species only found in the complex sand dune systems of central Veracruz. The group includes a few important coastal species (Palafoxia lindenii). The sand is dark and siliceous. These are mainly grassland and thicket species: many of them are commonly found in other types of inland vegetation, but three of them are endemics* (Ackerman, 1986; Turner & Mollis, 1976). Dune systems in this area include many microenvironments in different stages of succession. They offer areas with higher soil moisture and nutrient levels, protected from salt spray and strong winds, thus allowing the establishment of species characteristic of evergreen and seasonal tropical forests.

Acacia macracantha  
Amphilopium paniculatum  
Andropogon glomeratus  
Andropogon muelleris*  
Cissus sicyoides  
Coccoloba barbadensis  
Eleocharis cellulosa  
Erigeron myrionactis  
Lantana camara  
Palafoxia lindenii*  
Tecoma stans  
Trachypogon gouini*  
Schrankia quadrivalvis

(e) Species which constitute important elements of the coastal vegetation and are widely distributed along the coast, except in the dry regions of the north of Tamaulipas and Yucatan Peninsula. This group includes both coastal and inland species.

Ambrosia artemisiifolia  
Chamaecrista chamaecristoides  
Commelina erecta  
Metastelma pringlei  
Psychotria erythrocarpa  
Randia laetevirens

C. chamaecristoides has been reported as an endemic coastal species of the Mexican Gulf (Sauer, 1967). However, Percival (1974) recorded it in the Jamaican coastal scrub, although it is not mentioned in other coastal descriptions of the West Indies.

(f) Species which have their northern distribution limit in the south of Veracruz (†), or in Tabasco and Campeche. They are very common Caribbean elements of the Peninsula (Espejel, 1984, 1986). They inhabit areas with calcareous
sand and a tropical humid climate. The ones marked with an asterisk are found in the islands off the port of Veracruz. Coastal species are the more widely distributed in this group.

Ambrosia hispida  
Chamaesyce buxifolia*†  
Jacquinia aurantiaca†  
Lantana involucrata  
Suriana maritima*  
Tournefortia gnaphalodes*

(g) Finally there is a group of species widely distributed throughout the Gulf and Caribbean coast. They include beach pioneer, humid and wet slack plants as well as shrubs. A few of them are absent from Quintana Roo (*) for no apparent reason. They are mainly coastal species.

Bidens pilosa*  
Canavalia rosea  
Chiococca alba  
Croton punctatus*  
Cyperus articulatus*  
Fimbristylis spadicea*  
Fimbristylis spathacea  
Ipomoea pes-caprae  
Ipomoea stolonifera  
Philoxereus vermicularis  
Sesuvium portulacastrum  
Sporobolus virginicus  
Uniola paniculata

Other important beach pioneers as well as a climber abundant in the thickets are present from the north of Tamaulipas to Yucatan (except O. drummondii that does not go further south than Tabasco), except for the central region of Veracruz. This pattern closely resembles the latter and does not seem to be correlated with any obvious physical factor. There is not enough information to consider it as a distinct pattern, although it is worth mentioning it.

Amaranthus greggii  
Oenothera drummondii  
Okenia hypogaea  
Passiflora foetida

IV. Comparison with other regions

The floristic composition and zonation of the Mexican Gulf coast will now be compared with that of nearby regions.

1. Northern Gulf Coast, including Texas, Mississippi, Louisiana and the west coast of Florida (Dahl & Goen, 1977; Gould & Ewan, 1975; Judd, Leonard & Sides, 1977; Lemaire, 1961; Penfound & O’Neil, 1934; Pessin & Burleigh, 1941; Tharp, 1926). The similarity with Tamaulipas is high and still more pronounced when comparing with the barrier islands of Texas. There are common species to both areas from different zones in the dunes. Among shared beach plants are:

Cakile edentula  
Cakile geniculata  
Croton punctatus  
Ipomoea pes-caprae  
Ipomoea stolonifera  
Oenothera drummondii  
Philoxereus vermicularis  
Sesuvium portulacastrum  
Sporobolus virginicus  
Uniola paniculata

Among the species from humid slacks and beaches with a shallow ground water table and/or halophytes are:

Batis maritima  
Distichlis spicata  
Fimbristylis castanea  
Hydrocotyle bonariensis  
Panicum repens  
Salicornia bigelovii

Among the species from grasslands and thickets are:

Eragrostis elliotii  
Eragrostis secundiflorus  
Eupatorium betonicifolium  
Monantochole littoralis  
Opuntia stricta var. dillenii (as O. dillenii)  
Panicum amarum  
Physalis viscosa  
Pluchea purpurea  
Triplasis purpurea

Some of the important constituents of the coastal scrub in the Gulf are not reported for this area: Randia laetevirens, Citharexylum spp., Chiococca alba, etc.

2. Florida (Davis, 1942; Harper, 1914; Kurz, 1942). Both regions share mainly pantropical beach pioneers (I. pes-caprae, I. stolonifera, S. portulacastrum and S. virginicus), as well as other beach pioneers with more restricted dis-
tributions: *Uniola paniculata*, *Philoxereus vermicularis*, etc. Some elements from the Caribbean pioneers and thickets are also common: *Chamaesce beuxifolia*, *Scaevola plumieri*, *Tournefortia gnaphalodes*, *Caesalpinia crista*, *Coccoloba uvifera*, *Lantana involucrata*, etc., mainly in the northern Mexican coast. Some thicket species from Veracruz are also found in Florida:

- *Ambrosia artemisifolia*
- *Bursera simaruba*
- *Eugenia axillaris*
- *Heliotropium curassavicum*
- *Lantana camara*
- *Randia laetevirens* (as *R. aculeata*)
- *Rivina humilis*
- *Waltheria indica*

3. South-eastern Coast of the United States (mainly North and South Carolina as well as Georgia). The following works were consulted: Bellis (1980), Burk (1962), Cooper (1971) and Stalter (1974, 1986). Few species are shared. Among the beach species are *Cakile edentula*, *Ipomoea stolonifera*, *Sporobolus virginicus*, *Uniola paniculata*, *Oenothera drummondii*, *Croton punctatus*. Other species found behind the foredune and in humid areas are:

- *Andropogon glomeratus*
- *Bacopa monnieri*
- *Cenchrus tribuloides*
- *Cynodon dactylon*
- *Distichlis spicata*
- *Euphorbia ammannioides*
- *Fimbristylis spadicea*
- *Hydrocotyle bonariensis*
- *Lippia nodiflora*
- *Panicum amarum*
- *Physalis viscosa*
- *Triplasis purpurea*

None of the important shrub and vine species of the coastal thicket are common to both areas.

4. West Indies (Asprey & Robbins, 1953; Chapman, 1944; Gleason & Cook, 1926; Gooding, 1947; Loveless, 1960; Randall, 1970; Percival, 1974; Samek, 1973; Sauer, 1982; Seifriz, 1943; Stoddart, 1962; Uphof, 1924). The highest number of common genera and species are found between the Gulf and West Indies.

Among them are many of the pantropical species already mentioned as well as several of the elements also distributed in Florida. Others are:

**Beach and foredune species:**
- *Canavalia rosea*
- *Heliotropium curassavicum*

**Slacks and humid areas:**
- *Fimbristylis spadicea*
- *Fimbristylis spathacea*
- *Hibiscus tiliaceus*
- *Suaeda linearis*

Dry areas where plants do not reach the water table and thickets:

- *Acacia farnesiana*
- *Andropogon glomeratus*
- *Centrosera virginianum*
- *Cnyza canadensis*
- *Crossopetalum latifolium*
- *Crotalaria retusa*
- *Cynodon dactylon*
- *Dalbergia ecastaphyllum*
- *Echites umbellata*
- *Eragrostis ciliaris*
- *Flaverya linearis*
- *Indigofera suffruticosa*
- *Iresine celosia*
- *Paspalum vaginatum*
- *Phyllanthus niruri*
- *Randia laetevirens* (as *R. aculeata*)
- *Rhynchosia minima*
- *Tecoma stans*
- *Tephrosia cinerea*
- *Thespesia populnea*
- *Turnera ulmifolia*
- *Vigna luteola*
- *Waltheria indica* (syn. *W. americana*)

5. Caribbean Coast of Mexico (Espejel, 1983, 1984; Lundell, 1934; Miranda, 1958; Moreno-Casasola & Gaos, 1988; Sauer, 1967; Tellez & Sousa, 1982). There are many common species to the Gulf and Caribbean coasts of Mexico. Among them are species belonging to the distribution patterns shown in Figs. 8a–g. Throughout the Gulf and Caribbean beaches one can find many pioneers widely distributed:

- *Amaranthus greggii*
- *Canavalia rosea*
- *Cenchrus echinatus*
- *Fimbristylis spadicea*
Plants on coastal dunes in Gulf of Mexico

**Fimbristylis spathacea**
**Heliotropium curassavicum**
**Ipomoea pes-caprae**
**Sesuvium portulacastrum**
**Sporobolus virginicus**

As well as other species from drier areas in the dunes:

- *Bouteloua repens*
- *Bumelia retusa*
- *Bursera simaruba*
- *Centrosema virginianum*
- *Chiococca alba*
- *Chrysobalanus icaco*
- *Dactiloctenium aegyptium*
- *Eragrostis domingensis*
- *Eupatorium odoratum*
- *Opuntia stricta var. dillenii*
- *Waltheria indica*

In humid areas one can find:

- *Cyperus articulatus*
- *Eleocharis caribea*
- *Lippia nodiflora*

Other species are shared in part of their distribution ranges (distribution pattern in Fig. 8b).

**Discussion and Conclusions**

**Species distribution patterns**

Patterns of species distribution show that, in general, the Gulf coast vegetation can be divided into two large groups: one present on the northern part of the country (Tamaulipas, north Veracruz – between 20 and 21° N latitude – and partly the islands off the port of Veracruz) and another one on the rest of the Gulf (central and southern Veracruz, Tabasco and southern Campeche). These differences include the communities belonging to the beaches and the different zones of the dunes – foredune, slacks and stabilized areas. There is a change not only in species distribution but also in dominance of certain species, which in some regions constitute community types. Classification results showed fifty-nine types for the Gulf area, i.e. *Amaranthus greggii* type, *Canavalia rosea* type, *Chamaecrista chamaecristoides* type, *Fimbristylis castanea–Chamaesyce dioica* type, *Randia laeveis* type, etc. (Moreno-Casasola & Espejel, 1986).

On the whole the Gulf coastal flora shows the strongest relation with the Caribbean coastal flora, including the West Indies and the Yucatan Peninsula (sharing more than 100 species). About 15% of these species are only shared by the north of Mexico and the Caribbean (pattern 8b) and are mainly coastal beach pioneers and thicket species. Physiognomy between both areas is quite different as these species grow as isolated individuals in Tamaulipas. Amongst the other species shared (Fig. 7), they are mainly beach pioneers of wide distribution, many secondary species, including grasses (*Cenchrus* spp., *Bouteloua repens*, *Dactyloctenium aegyptium*, *Commelina erecta*, *Eupatorion odoratum*, *Asclepias curassavica*, etc.), thicket species (*Chiococca alba*, *Bumelia retusa*, *Chrysobalanus icaco*, *Malvaviscus arboreus*, *Bursera simaruba*, etc.) and a few species from humid habitats (*Cyperus articulatus*, *Lippia nodiflora*, *Eleocharis caribea*, *Hibiscus tiliae*es, etc.).

There is also a change in growth form along this latitudinal gradient, mainly on beach and foredune communities. Sand binding plants with rhizomatous growth forms are found in the dunes of the southeastern U.S.A. and north of Mexico; stoloniferous forms take over in the central Gulf region, together with low shrub growth forms, while taller shrubs predominate in the Caribbean.

Davies (1972) distinguishes two growth forms that are important in influencing accretion and stabilization of dune sand: the rhizomatous (with the tussock forming *Ammophila* as an example) and the stoloniferous (with long stolons creeping over the sand surface like in *Ipomoea* and *Canavalia*). A third growth form can be distinguished, exemplified by low and tall shrubs which are found growing right down to the back of the beach. They are able to accumulate sand and initiate a stabilizing process, i.e. *Chamaecrista chamaecristoides*, *Croton punctatus*, *Palafoxia lindenii*, *Coccoloba uvifera* (Gleason & Cook, 1926; Moreno-Casasola, 1986).

This change in growth forms, together with the decrease in the number of annuals, reflects the way in which tropical plants are able to expose growth renewal buds in warmer frost-free climates; and secondly, conditions of reduced exposure to wind – with lower rates of sand movement and waves, when compared with temperate ones (Barbour, De Jong & Pavlik, 1985; Davies, 1972).
Species dispersion and availability

Beaches have many more species in common than other dune zones. Humid and wet slacks also have common species, but their richness as well as presence of these habitats is very varied. These species appear in the central part of the ordination graph (Fig. 7), which represents species with a distribution range that includes most of the Gulf coast. On the other hand, thicket composition and richness is different even among nearby dune systems. Several factors are important in limiting species distribution. The interpretation of patterns must embrace species arrival – and as a consequence species availability – as well as temporal and spatial variability as essential features of community dynamics.

Distribution patterns in which coastal species – those species that are confined to seashore habitats – predominate (Fig. 8b, f, g) show broader geographical ranges and species are shared by many coasts including the Caribbean, south-eastern coast of U.S.A. and Gulf regions. Some of the species are pantropical and also occur in Africa and Australia. These species, adapted to the environmental conditions of the seashore, are not restricted by climatic differences along the coast. They inhabit warm areas in the Gulf with annual precipitations ranging from 500 to more than 3000 mm. Many of them show little preference for particular soil types. Few are restricted to siliceous sands and humid climates: *Palafaxia lindenii* and *Chamaecrista chamaecristoides*, while others only appear on calcareous soils: *Tournefortia gnaphalodes* and *Scaevola plumieri* (Fig. 7).

The presence or absence of these species from particular beaches depends first of all on the arrival of propagules. This reflects in the absence of a particular species that is present in close-by beaches. Many beach species produce buoyant and impermeable seeds which may float for months. Guppy (1917), Ridley (1930) and Gunn & Dennis (1976) have reported many diasporas of beach species floating on sea water. They have pantropical distributions (*Canavalia rosea*, *Ipomoea pes-caprae*, *Sesuvium portulacastrum*, etc.). The tiny seeds of grasses and other families do not seem to float for significant lengths of time (Sauer, 1967, in Davies, 1972), and may travel by other means, i.e. birds. The broad picture of distribution suggests that they do not disperse so successfully, although some like *Sporobolus virginicus*, *Fimbristylis spathacea*, *Lippia nodiflora*, also have pantropical distributions. Other coastal species have more restricted distributions (Sauer, 1982), i.e. *Opuntia stricta var. dillenii*, *Croton punctatus* which appear in the West Indies and east coast of America, *Fimbristylis spadicea* in the West Indies and both coasts of America. Other species widely distributed in the Gulf and Caribbean are weedy species which produce numerous small, easily dispersed seeds, i.e. *Iresine celosia*, *Bidens pilosa*, etc.

Secondly, microenvironmental gradients on the beach play a major role is selecting the array of available propagules (*sensu* Guevara, 1986), thus determining local floristic composition. Their establishment depends on their ability to cope with local conditions of soil moisture, soil temperature and salinity, soil pH, salt spray, nutrient availability, sand movement, herbivory, many of which vary according to beach exposure. Only a small set of species is adapted to survive and reproduce under beach conditions.

Many of the important dune species of more stabilized areas are component species of other vegetation types or secondary growth. In the different associations of the semi-evergreen seasonal forest studied in Tamaulipas by Puig (1976), *Coccoloba barbadensis*, *Psychotria erythrocarpa*, *Randia laetevirens*, *Chiococca alba*, *Eugenia capuli*, *Citharexylum berlandieri*, *Karwinska humboldtiana* and *Bursera simaruba* are among the important constituents of the tree layer. In the shrub layer *Rhatoma uragoga*, *Tecoma stans*, *Acacia farnesiana*, *Psidium guajava*, *Casearia nitida*, *Cestrum nocturnum*, *Lantana camara*, *Malvaviscus arboreus*, *Pluchea purpurascens* are found. In the deciduous communities *Bromelia pinguin*, *Cissus sicyoides*, *Pisonia aculeata*, *Acacia corningera*, *Celitis iguanaea* are common. A similar situation can be found among the species reported by Novelo (1978) for the evergreen and semi-evergreen seasonal forest at La Mancha in Veracruz. All these species are frequent elements of the stabilized dune vegetation of Tamaulipas and Veracruz (García, 1985; Moreno-Casasola et al., 1982; Moreno-Casasola & Espejel, 1986; Puig, 1976).

It is frequent to find one of these particular
species widespread in a dune system, common enough to constitute a community type (i.e. *Acacia farnesiana*, see Moreno-Casasola & Espejel, 1986), and absent from nearby areas with similar physical conditions. The general littoral distribution ranges of these species is more affected by climatic (precipitation and minimal temperatures) and edaphic factors (siliceous or calcareous sand). Their distribution in dune systems under the same climatological conditions seems to depend more on particular environmental conditions of the system. These can be very heterogeneous, differing in the degree of exposure to wind, salt spray and sand movement, topography, soil conditions and geological age. When a dune system starts to stabilize, colonization must come from propagules dispersed from surrounding areas or other stable parts of the dune system.

Accessibility of sites for propagule arrival is an important factor in the colonization of these areas. Seeds from tropical forest species tend to be rather large and are dispersed by animals, gravity and sometimes wind. Secondary species have small, easily dispersed seeds. For the latter type, as well as for beach species, dispersion over larger geographical areas is easier, thus increasing their distribution ranges (*Crotalaria incana, Indigofera suffruticosa*). Seeds from tropical forests can arrive easily at nearby dune systems, and once they become established persist as part of the thicket communities on dunes. Propagule availability differs among the species mentioned and many times influences the floristic composition of a patch.

‘Random’ arrival of propagules from nearby vegetation as well as differences in spatial and temporal conditions for their establishment is a determinant of species composition. Many of these species from tropical forests are found in the large, complex dune systems of central Veracruz (Fig. 7). This last point implies presence of sheltered areas (from wind and salt spray), with a certain accumulation of organic material and higher water retention. Even where background physical conditions are relatively uniform across a site, opportunities for recruitment, growth, reproduction and survival vary spatially, reflecting variation in the intensity of biological interactions, resource availability and microclimato logical conditions. Restrictions on dispersion as well as environmental conditions where they can successfully establish have produced thicket communities that are very variable in species composition and richness. Thus, distribution patterns are more restricted geographically and are closely correlated with complexity of the dune system.

The following general hypothesis can be extracted from this analysis: There is a higher and more constant availability of propagules for beach colonization than for stabilized areas, but only a restricted group of species are able to establish successfully because of severe environmental restrictions; these produce more homogeneous distribution patterns. In contrast, stabilized areas have a lower and more heterogeneous availability of propagules depending more on neighbouring vegetation, but there is a high diversity of environments, thus allowing an increment in species diversity and variability in species composition.

**Acknowledgments**

This research received support from CONACYT 005223. I am grateful to S. Castillo and F. Rodriguez for their help throughout the work. I also want to thank M. Kellman and J. Rzedowski for their critical revision of the manuscript. I am indebted to S. Guevara and E. van der Maarel for the fruitful discussions.

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**Appendix 1**

Localities shown on the map in Fig. 1.

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<td>Las Flores, east of Ostión</td>
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Source: 1, Sauer (1967); 2, Gonzalez-Medrano (1972); 3, Puig (1976); 4, García (1985); 5, Poggie (1962); 6, García (1982), Moreno-Casasola et al. (1982), Moreno-Casasola & Espejel (1986), Moreno-Casasola et al. (1988a, b); 7, Vazquez-Yanes (1971); 8, Lot (1971); 9, Castillo (1984); 10, García (1982).