A Phytogeographical Analysis of Coastal Vegetation in the Yucatan Peninsula

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Journal of Biogeography is currently published by Blackwell Publishing.
A phytogeographical analysis of coastal vegetation in the Yucatan Peninsula

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ABSTRACT. Distribution patterns of 237 species belonging to sixty-three families of the coastal dunes of the Yucatan Peninsula were analysed. Cosmopolitan families like Gramineae, Compositae and Leguminosae are best represented. Other families are mainly tropical.

For a geographical synthesis the coast of the Yucatan Peninsula was divided into five natural sections according to differences in climate, substrate, water-table, distance to the sea and proximity of adjacent backdune vegetation. These factors explained the presence or absence of particular species which were related to the different physiognomy of the stabilized dune vegetation. The five sections are Campeche and Quintana Roo with a humid climate and West, Middle and East Yucatan where a semi-dry climate prevails. A higher floristic richness was found on the coasts facing the Caribbean Sea where hurricanes occur and neighbouring tropical rain forest influences the floristic composition of the dune vegetation.

The zonation of species along the sea-inland gradient showed differences in morphology and life history. The species attributes characterize the different habitat zones. Species adapted to salt-spray and exposure are widely distributed herbs with abiotic dispersal modes. The sheltered habitats of the dunes are densely covered by palms, trees with broad entire leaves, epiphytes and armed and succulent shrubs. These species show narrow distribution patterns and zoochorous dispersal modes. Herbs are most tolerant to saline habitats, whereas shrubs and trees thrive in the non-saline dune environments.

The flora of the sand dunes of the Yucatan Peninsula is equally characterized by two elements: (a) Caribbean species and (b) South Mexican and Central American species which together form the Meso-American element.

Introduction
The Yucatan Peninsula is a limestone rock projection between the Gulf of Mexico and the Caribbean Sea. The coast is 500 km long and belongs entirely to the United States of Mexico. It comprises Campeche, Yucatan and Quintana Roo States. The southern base of the peninsula extends to northern Guatemala and Belize (Fig. 1). The coastal sand dune flora of the Yucatan

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Peninsula is considered of special interest since it is the only part of the Mexican flora that shows clear relationships with the Caribbean flora (Millspaugh, 1896, 1898; Lundell, 1934; Miranda, 1958; Sauer, 1967; Rzedowski, 1978). Barrera-Marin (1964) considers the Yucatan Peninsula as a special biotic province because it is a separate physiographic unit with its own flora and fauna.

The principal feature that characterizes the coast of the peninsula is the complex mixture of mangroves and dune thickets, which is related to the combination of barrier islands and coastal lagoons. At the shallow edge of the lagoon opposite to its mouth there is a combination of mangrove and a saltmarsh-like vegetation. As both mingle with the dune thickets, they produce an interesting coastal vegetation complex.

Inland rain forests, which consist of combinations of tropical trees and shrubs with different heights and different composition according to the various climates (named selvas in Spanish) like the low deciduous, medium subdeciduous and medium evergreen rain forests (Miranda & Hernandez, 1963; Rzedowski, 1978) and ‘petenes’ (a mixture of mangrove and these kind of rain forests species) (Rico-Gray, 1982; Flores & Espejel, 1986; Olmsted, López-Ornat & Durán, 1983) are also important floristic sources to the coastal vegetation.

The coastal vegetation treated in this paper, refers specially to the dune system. In this case the word dune was used to homogenize the terms used in another paper (Moreno-Casasola & Espejel, 1986). Actually, in this biotic region (the Yucatan Peninsula) the word dune refers particularly to wave-deposited material known geomorphologically as beach ridge system.

Two aims regarding distribution of species were considered in this study: (1) to analyse the zonation of the Yucatan Peninsula dune system in relation to the species distribution and vital attributes (growth forms, modes of dispersal and specializations of leaves and stems); (2) to analyse phytogeographically the dune flora of the Yucatan Peninsula.

Regarding the last aim mentioned, all assumptions written in this paper are based on the floristic knowledge of the Yucatan Peninsula up to the 1985 publication of the Etnoflora Yucatanense (Sosa et al., 1985).

Description of the area

Climate

The mean temperature does not vary much during the year along the peninsula coast. The average monthly temperature of the coldest month (January) is 23°C and from May to September the temperature ranges from 25°C to 28°C. Yearly fluctuation of monthly temperature is lower than 10°C and no frost occurs (Fig. 2).

There is a high rainfall variability between the wettest and driest month. The peninsula receives 2000 mm of annual rainfall near the Guatemala border and this amount decreases to 600 mm toward the northwest corner (Progreso). There is a strong influence of frontal precipitation with strong northerly winds associated with certain polar outbreaks called ‘nortes’. A clear seasonality is shown; an anticyclonic cell centred just off the northwest corner of Yucatan makes March and April the driest months. This is the reason for the presence of a semi-arid climate in Celestun, Sisal and Progreso (West Yucatan) (Garcia, 1974; Mosiño & Garcia, 1981). In the rainy season (May–October) there is a tendency towards a double maximum; one in June and one in September–October. The June peak is related to the occurrence of hurricanes (Sands, 1960; García, 1964; Oreilana, pers. comm.). The strong winds involved in these cyclones have a damaging effect upon the...
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**Geology**

The southern part of the peninsula is early Jurassic. In that period it was connected with southeast Mexico, Central America and the Greater Antilles. During the later Jurassic and at the Cretaceous it was covered by water, but a new uplift started during the Miocene and proceeded from the south towards the north. The peninsula is still rising and some beaches in the northwest are only 100 years old (Sapper, 1945; Robles-Ramos, 1959).

Because of this ongoing uplift many lagoons and sand ridges are not yet well established. There is a large variation in local topographical zonation complexes produced by an interaction of barrier islands and coastal lagoons that corresponds to the complicated mixture of mangrove species and dune thickets.

**Soils**

Calcareous soils dominate the whole peninsula. On the west and east coasts rocky limestone beaches, ‘caletas’, are frequent. The sandy soil on the beach is classified as a calcareous regosol or quarsipsament. The sand consists of more than 90% CaCO$_3$ all along the coast; abundant coralline elements because of the well-developed coral reefs. In general the coralline sands are fine, in Campeche and Yucatan the beaches have coarser sand with abundant small shell pieces.

Close to the lagoons the soil has a higher content of clay and organic matter. It is a hydro-morphic classified as gleysol or hidraquent. They are flooded during one half of the year (Wright, 1970; López-Ornat, 1983; Espejel, 1983, 1984, 1986a). Soil details are given in Espejel (1986b).

A striking physiographic feature of the peninsula is the absence of permanent rivers except at the southwestern and southeastern ends. Typical subterranean streams occur which are important to the vegetation since they emerge as fresh water springs at several points. Close to these springs differences in vegetation are found (Espejel, 1984; Moreno-Casasola & Espejel, 1986; Espejel, 1986a).

**Methods**

The coastal vegetation of the Yucatan Peninsula was surveyed through botanical collections and relevés from 1981 to 1984 (Espejel, 1984; Flores, 1984; Rodriguez, 1984). An overall synthesis including the Gulf of Mexico is presented by Moreno-Casasola & Espejel (1986).

About 600 specimens of phanerogams were collected on all sandy beaches and some limestone coastal areas. Vouchers are deposited in the herbarium XAL/YUC of INIREB at Mérida, Yucatan. Other collections used were: (1) Yucatan Peninsula islands (Flores, 1984) and

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**FIG. 2.** Climate of three sites of the Yucatan Peninsula (data taken from Dirección General de Geografía del Territorio Nacional, 1981).
other smaller collections of coastal systems in the Etnoflora Yucatanense project (Sosa et al., 1985) (2) the flora of Quintana Roo (Sousa & Cabrera, 1983), and (3) a survey by Castillo (1984) of the Tabasco and Campeche coasts. The latter two collections are deposited in the National Mexican Herbarium (MEXU) at the National University in Mexico City.

Nomenclature follows the Etnoflora Yucatanense (Sosa et al., 1985). A complete checklist with authorities is available on request.

The Yucatan Peninsula coast has been divided into five sections for a geographical synthesis. The sections correspond roughly with the political subdivision into Campeche, Yucatan and Quintana Roo; with Yucatan State divided into West, Middle and East Yucatan (Fig. 1). This division of areas is based on the differences in climate (mainly precipitation), orientation of the beaches (facing the Gulf of Mexico, the Yucatan Channel or the Caribbean Sea), the backdune vegetation (mangroves, low deciduous or medium subdeciduous rain forest), the presence of fresh water springs, width of the sand dune system and the sand coarseness. These were considered the most important factors determining the species distribution along the peninsula coast. To summarize the distributional patterns, a classification of the five geographical sections (Campeche, West, Middle and East Yucatan and Quintana Roo) using all 237 species was carried out. A polythetic divisive clustering was performed using TWINSPAN (Hill, 1979b) with default options.

In addition to the vegetation analysis (Espejel, 1984, 1986a; Moreno-Casasola & Espejel, 1986) several transects across the zonation on the coasts of Yucatan and Quintana Roo states were analysed floristically. In Fig. 3(a–c) three representative transects are presented. Each transect was laid down perpendicular to the shoreline across the stabilized zone. The inland limit of the transect was the mangrove or the tropical forest. The topography and percentage cover of the vegetation was recorded on every square metre along the transect. To correlate the vegetation gradient with the environmental zonation a species ordination using Detrended Correspondence Analysis (Hill, 1979a; Hill & Gauch, 1981) was performed. The vegetation data used have been described by Moreno-Casasola & Espejel (1986). Indirect gradient analysis was done with several morphological and biological characters as well as some environmental variables superimposed on the resulting diagram (Fig. 4).

A chi-square approach was used to test the null hypothesis that species attributes were related with the environment. The relationship between distribution patterns, environmental factors and species attributes such as mode of dispersal, growth form and leaf and stem morphology were statistically tested. Contingency tables were constructed for each pair of the features considered. Expected observations were estimated and the chi-square fitness test was computed. Yate’s correction factor was used when analysing 2×2 contingency tables with one degree of freedom.

For the phytogeographical approach the flora list of the peninsula (only considering species occurring in coastal vegetation) was compared with other lists available for twenty nearby areas: Gulf of Mexico, Western Florida (Harper, 1914; Laessle, 1942); Louisiana (Breton Island) (Lemaire, 1961; Gould & Ewan, 1975); Texas (Padre Island) (Tharp, 1926; Correll & Johnston, 1970; Dahl & Goen, 1977; Judd, Leonard & Sides 1977); Tamaulipas (Poogie, 1962; Sauer, 1967; González-Medrano, 1972; García, 1985); Veracruz (Sauer, 1967; Moreno-Casasola et al., 1982; Moreno-Casasola, 1985); Tabasco and Campeche (Thom, 1967; Psuty, 1970; Castillo, 1984).

Central America: Belize atolls (Linhart, 1980); Guatemala (Standley, Steyemark & Williams, 1930).

Caribbean area: Florida (Kurz, 1942; Davis, 1942; Austin & Weise, 1972); Bimini Islands (Howard, 1950); Bahamas (Coker, 1905; Britton & Millspaugh, 1920; Cuba (Uphof, 1924; Seifriz, 1943; Samel, 1973; Borhidi, 1987); Jamaica (Fawcett & Rendle, 1936; Chapman, 1940; Steers, 1959; Asprey & Loveless, 1958; Adams, 1972; Percival, 1974); Cayman Islands (Sauer, 1982); Haiti–Dominican Republic (Ekman, 1929a, b, 1930; Moscoso, 1943; Howard, 1955); Puerto Rico (Britton & Wilson, 1923; Gleason & Cook, 1927; Cook & Gleason, 1928); Leeward and Windward Antilles (Beard, 1949); Danish West Indian islands (Børjesen, 1909); St Croix and Virgin Islands (Eggers, 1879); Navassa Island (Ekman, 1929c); West Indies (Hitchcock & Chase, 1917); Antilles (Howard, 1973); Antigua (Loveless, 1960); Barbados (Gooding, 1947; Randall, 1970); Nether-
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TABLE 1. Families (63) and number of species (240) present in the littoral of the Yucatan Peninsula. \( P = \) number of species in the whole peninsula; \( L = \) number of species in the littoral. In parenthesis the number of subspecies. *Introduced. †Very rare species, only one herbarium voucher collected on the dunes.

<table>
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Tablelands Antilles (Stoffers, 1956, 1987); Trinidad and Tobago (Domin, 1929; Marshall, 1934).

Although many of these sources are not entirely reliable regarding nomenclature, information on distribution and general characteristics of the species, most of the uncertainties involved could be interpreted on the basis of the recent sources.

**Results**

**Families and genera**

Almost one third of the families known from the Yucatan Peninsula are represented in the coastal sand dunes (Table 1). Most of these families are either pantropical or neotropical, but also cosmopolitan families like the Euphorbiaceae with 125 species in the peninsula and ten on sand dunes, Gramineae with thirty-three species on dunes out of the 183 and Compositae with sixteen out of the 111 species are well represented. Most of the species belong to the Leguminosae (251 species in total) which in the sand dunes (eighteen species) is also one of the best represented families.

A high percentage (12%) of exclusively coastal species is distinctive for the Yucatan Peninsula.

The palms are a special feature of the dune vegetation of the Caribbean area. A high proportion of the Mexican palms is found on the Peninsula (Quero, 1981); four genera with four species are restricted to sandy or rocky coastal environments. The absence of palms on the sand dunes of the Gulf of Mexico is worth noticing and was one of the features used to differentiate the Gulf and Caribbean regions (Moreno-Casasola & Espejel, 1986). The Palmae are not important regarding their number; however, they are physiognomically distinctive. The same is true for the Orchidaceae, the Bromeliaceae (with many epiphytes) and the Cactaceae (with eight genera and eight species occurring on coastal dunes). Species of these families were joined in the category ‘tropical growth forms’.

On the dry coasts (West Yucatan), tropical growth forms include only Bromeliaceae and Cactaceae since no palms occur there. Both the physiognomical dominance of these species and the abundance of epiphytes (Cactaceae, Bromeliaceae, Loranthaceae) and several lichens (not considered in this article) are outstanding in dry dune areas.

The absence of Pinaceae is an important differentiating characteristic of the sandy coasts of the Yucatan Peninsula if compared with the Caribbean islands, Florida and Belize. Pinus
caribaea does not occur in the coastal vegetation of Mexico though it is found on one inland site in Quintana Roo State (Chavelas, 1981; Flores & Espejel, 1986).

Only one genus is endemic to the Yucatan Peninsula: Enriquebeltrania with only one species E. crenatifolia. Its major distribution is in the west and east sand dunes of Yucatan State.

Distribution in the peninsula

Five geographical sections were selected due to the floristical differences and climate, distance to the sea, proximity of backdune vegetation, substrate and water-table factors. Also human disturbance, in the form of coconut plantations and recreation, affects the actual distribution of species. Floristic richness does not vary widely among sections but slight quantitative differences are important since they involve the presence or absence of species which determine the physiognomy of the dune vegetation.

Several species distribution patterns have been found. Most of the species of the beach, embryonic dunes, and foredunes occur all along the coast. One exception is Suaeda mexicana, a species of the northern part of the Gulf of Mexico which occurs only on beaches of dry West Yucatan within the study area.

1. Campeche Section. The climate is humid and warm. Coasts are sheltered from eastern hurricanes although 'nortes' might affect the vegetation. This sheltered position allows the development of large mangrove complexes. A variety of substrates is found including muddy flats, rocky and sandy beaches. All these characteristics of the Campeche coasts result in a rich coastal vegetation, which is threatened by disturbance.

Various distribution patterns occur within the stabilized dunes. The main distribution area of the Campeche thicket species is the Gulf coast; their southern limit is where the soil becomes calcareous (Castillo, 1984; Moreno-Casasola, 1985). Examples are Ambrosia artemisiifolia, Randia laetevires (which occur inland in Yucatan but never on sand dunes) and Coccoloba humboldtii. The latter, which is restricted to Southern Mexico, is found only among the coconut plantations of Campeche.

2. West Yucatan is the driest area of the peninsula. The presence of backdune mangroves and low deciduous rain forest produces a combination of xeromorphic species, shrubs and trees. Human disturbance is increasing but the sparse natural vegetation has not yet disappeared.

Some of the endemic and South Mexican species are characteristic of West Yucatan: Cordia globosa, Trianthema portulacastrum, Stenocereus laevigatus, Sarcostemma clausum, Matelea yucatanensis, Suaeda mexicana

3. Middle Yucatan has also a dry climate but the dune thickets are different from the other semi-arid sites. The natural border of the dune vegetation is mainly mangrove but also some narrow strips of low deciduous forest occur. The presence of freshwater springs is the most distinctive feature and it allows rain forest species to establish and mingle with dune vegetation.

The endemic, South Mexican and Central American tropical rain forest species are abundant here: Anthurium tetragonum var. yucatanensis, Hippocratea celastroides, Manilkara achras, Mammillaria gaumeri, Phoradendron vernicosum.

4. East Yucatan shows a transition between semi-arid and humid climates. The border of the dune vegetation is either tropical rain forest (especially medium high subdeciduous rain forest) or mangroves. Freshwater springs are common as well as highly saline flat areas which resemble saltmarshes. The transitional situation and the neighbourhood of several vegetation types might account for the high diversity of this section.

East Yucatan is peculiar because of the occurrence of many species which ordinarily occur in the adjacent tropical rain forest. The intermediate localization and the variety of vegetation types surrounding the coasts of the east section of Yucatan may explain the high presence of all the phytogeographical elements, especially the endemic and Central American: Hyperbaena winzerlingii, Prosopis juliflora (North American, only in East Yucatan dune thickets), Pseudophoenix sargentii (North Caribbean palm species with a discontinuous distribution on the peninsula).

5. Quintana Roo is an area with a warm and humid climate. Hurricanes constitute an active ecological factor of greater importance here than elsewhere in the peninsula. The backdune mangroves and inland rain forests (medium high evergreen rain forest) makes this section floristically the richest. Rocky beaches ('caletas') and freshwater springs also increase
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environmental and floristic diversity. Due to the homogeneity of the dune systems and the large extent of coconut plantations no smaller subsections were considered, so the whole Quintana Roo coast was considered as one unit.

*Strumphia maritima* and *Eritalis fruticosa* are two Pan-Caribbean species which mainly occur on limestone substrates and are found only in Quintana Roo.

The following species have a disjunct distribution in Campeche and Quintana Roo: *Eleocharis cellulosa*, *Pouteria campechiana*, *Morinda royoc*, *Stenotaphrum secundatum* (introduced).

The Central American species *Diospyros*

![FIG. 3(a). Zonation of species in a sand ridge system of West Yucatan. 1=1-3, 2=4-5, 3=7-9 of Braun-Blanquet cover-abundance scores.](image-url)
FIG. 3(b). Zonation of species in a sand dune system of East Yucatan.
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Species attributes along sea-inland gradients

Qualitative differences within the peninsula's dune flora become clear with the zonation analysis. According to coastal sand dune studies of the world the zonation is usually very clear and floristic and environmental gradients are often obvious. The Yucatan Peninsula vegetation is not an exception. As Moreno-Casasola & Espejel (1986) noted, there is a clear zonation of vegetation across the sand dune topography: beach, embryonic dunes, foredunes, sheltered zone, internal and stabilized ridges (tops and slacks) and humid area close to mangrove vegetation.

Most pioneer species of beaches, embryo dunes and foredunes occur all along the peninsula coasts. On the other hand, the thicket species of stabilized dunes have different dis-
FIG. 4. Species ordination (DCA) in which axis 1 reflects the gradient from the beach to the inner dunes. Axis 2 reflects a transition of tree and shrub vegetation from the humid zones to the herbaceous and succulent vegetation of saline habitats. ★ = Beach, ( = sheltered habitats, ▲ = dune tops, o = moist slacks, ■ = saline humid slacks.
Distribution ranges and local areas differ in their thicket flora (see vegetation profiles in Figs. 3a–c).

The first profile (Fig. 3a) represents the dry sites of West Yucatan. Thicket species include many succulents and thorny species but palms are absent. Fig. 3(b) shows a typical zonation of East Yucatan with thickets dominated by the three common palms (*Thr雀nax radiata*, *Coccothrinax readii* and *Pseudophoenix sargentii*) and the endemic *Enriquebeltrania crenatifolia* and Pan-Caribbean species like *Coccoloba uvifera*. In the narrow beaches of Quintana Roo the seashore mangroves are common and combinations of both vegetation types are outstanding. The dune area (strip) is so narrow that the typical foredune species *Suriana maritima* mingles with the mangrove tree *Conocarpus erecta* (Fig. 3c).

Floristical zonation and gradual changes are also clear from an ordination obtained by detrended correspondence analysis (Fig. 4). Axis 1 (eigenvalue 0.636) shows that species are arranged along the main gradient from beach to stabilized dunes; and axis 2 (eigenvalue 0.354) represents the differences between the fresh and saline water-table.

The distribution of growth forms is related to the ordination diagram. With some exceptions, all species at the right-hand side of axis 1 are herbs. Axis 1 shows the transition from annual herbs and/or succulents of the beach towards the foredune species (in the middle of the diagram) being partly perennial herbs but mainly succulent shrubs. The latter tolerate salt spray and exposure (*i.e.* *Suaeda linearis*, *Cakile edentula*, *Sesuvium portulacastrum*). The species of the sheltered zone which tolerate less salt-spray are mainly herbs, and found in the middle of the ordination space. On the left corner of the diagram thicket species of stabilized zones are concentrated; these are mainly spiny, succulent shrubs, epiphytes, climbers, trees and palms intolerant to salt-spray.

Axis 2 shows a gradient from species that tolerate a saline water-table (mangroves and beach species) toward species that grow around fresh-water springs (Fig. 4).

In addition, a geographical gradient is reflected along the diagonal from the upper left corner where the dry thicket species and some endemics (*i.e.* Cactaceae and Agavaceae) and salt marsh species considered typical of the dry Yucatan coast are localized; while most of the species exclusive to the warm and humid Caribbean Sea coast are found towards the bottom of the left margin.

In the zonation diagrams it can be seen that in habitats where extreme environmental factors dominate (beach and mangrove) the floristic diversity decreases. The opposite situation occurs in protected habitats (sheltered and stabilized dunes).

Relationships between species life history and morphology are clear (Fig. 5 and Table 2).

Salt spray and exposure permit only herbaceous species to occur. In disturbed habitats (ruderal zones) creepers and vines play an important role. When dunes have been stabilized the vegetation becomes more complex and shrubs, trees and species with typical tropical growth forms (cactaceous, palms, agave-like and bromelia-like species) dominate the landscape. Especially epiphytes and succulent armed shrubs are abundant on the dune tops while in the slacks small trees and palms thrive.

Saline conditions are found at the beaches but especially at the edge of the coastal lagoon. Species response to salinity is expressed by tissue modifications like succulence of stem and leaves and by an increment of pubescence. The occurrence of these characters is more frequent among habitats with saline influence and exposure.

The presence of species with thorns and reduced or absent leaves indicate frequent water stress.

**Relationships between floras**

The species of the sand dunes of the Yucatan Peninsula show twelve patterns of distribution. As might be expected, some phytogeographical elements show a maximal representation in some parts of the peninsula coast.

To illustrate some important distribution patterns of the dune vegetation of the Yucatan Peninsula, narrow or restricted distribution ranges are shown in Fig. 6. The twelve distribution ranges along the peninsula coasts are (Fig. 7):

1. The coastal endemic element. Sixteen endemic species are confined to the peninsula coast. They make up only 6.7% of the dune flora throughout the area surveyed (Table 3). Most of the Cactaceae are endemics and occur on the dry
coasts of Yucatan State. Many of them are described in Standley (1930). The endemic palm *Coccothrinax readii* is closely related to *Coccothrinax jamaicensis* (Quero, 1980) and other species of the West Indies. Because of the fairly recent origin of the peninsula and the ongoing uplift movement, it seems likely that all are neo-endemics. However, Bonet & Rzedowski (1963) mention that *Cenchrus insularis* is present on the sand keys of the coral Alacran reef situated in front of Yucatan State and noted that it might be a palaeoendemic species due to its disjunct distribution (in the Alacran Reef, Colombia and Brazilian coasts).

2. The South Mexican element. Species belonging to this element are found in the southern part of the peninsula and adjacent Northern Guatemala and Belize (Standley et al., 1930; and on the Belize atolls (Linhart, 1980). The majority of these species occur in rain forests, mainly low deciduous rain forest (Standley, 1930; Flores & Espejel, 1986). This element is best represented in East Yucatan and Quintana Roo with eleven and fourteen species, respectively, out of the total nineteen species.

3. Central American element. These species have a narrow distribution in Central American rain forests. Many of these species occur where fresh-water is available: individuals of some species have been established on stabilized sand dunes, and species like *Manilkara achras* and *Pouteria campechiana* are only found where

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**FIG. 5.** Relative abundance of thirty species attributes over six zones along the sea–inland gradient of the Yucatan Peninsula dunes.
<table>
<thead>
<tr>
<th>Species</th>
<th>Modes of dispersal</th>
<th>Growth form</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Biotic O (E)</td>
<td>Abiotic O (E)</td>
<td>Herbaceous O (E)</td>
<td>Shrubs and trees O (E)</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Species</td>
<td>237</td>
<td>91</td>
<td>96</td>
<td>124</td>
</tr>
<tr>
<td>Restricted</td>
<td>133</td>
<td>58** (51)</td>
<td>38** (53)</td>
<td>58</td>
</tr>
<tr>
<td>Wide</td>
<td>105</td>
<td>37** (40)</td>
<td>52** (42)</td>
<td>64</td>
</tr>
<tr>
<td>Sea influenced</td>
<td>64</td>
<td>21</td>
<td>(26)</td>
<td>32</td>
</tr>
<tr>
<td>Sheltered</td>
<td>174</td>
<td>70</td>
<td>(70)</td>
<td>64</td>
</tr>
<tr>
<td>Saline</td>
<td>31</td>
<td>10</td>
<td>(12)</td>
<td>14</td>
</tr>
<tr>
<td>Brackish</td>
<td>155</td>
<td>58</td>
<td>(59)</td>
<td>69</td>
</tr>
<tr>
<td>Non-saline</td>
<td>52</td>
<td>23</td>
<td>(20)</td>
<td>13</td>
</tr>
<tr>
<td>Moist</td>
<td>113</td>
<td>44</td>
<td>(43)</td>
<td>50</td>
</tr>
<tr>
<td>Dry</td>
<td>125</td>
<td>47</td>
<td>(48)</td>
<td>46</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Species</th>
<th>Morphology of stem and/or leaves</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Succulence: pubescence or thorns</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Texture: leathery or mesic</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Leaves</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Entire O (E)</td>
<td>O (E)</td>
</tr>
<tr>
<td></td>
<td>Compound</td>
<td>Reduced or absent O (E)</td>
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<tr>
<td>Species</td>
<td>237</td>
<td>104</td>
</tr>
<tr>
<td>Restricted</td>
<td>133</td>
<td>63</td>
</tr>
<tr>
<td>Wide</td>
<td>105</td>
<td>41</td>
</tr>
<tr>
<td>Sea influenced</td>
<td>64</td>
<td>44*</td>
</tr>
<tr>
<td>Sheltered</td>
<td>174</td>
<td>60*</td>
</tr>
<tr>
<td>Saline</td>
<td>31</td>
<td>16</td>
</tr>
<tr>
<td>Brackish</td>
<td>155</td>
<td>69</td>
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<tr>
<td>Non-saline</td>
<td>52</td>
<td>19</td>
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<tr>
<td>Moist</td>
<td>113</td>
<td>42</td>
</tr>
<tr>
<td>Dry</td>
<td>125</td>
<td>62</td>
</tr>
</tbody>
</table>

Restricted distribution = Endemic, South Mexican, Central American, Pan-Caribbean, North Caribbean, North American and Gulf; Wide distribution includes all the others. Sea influenced = Beach and sheltered zones; Sheltered category are the rest. Saline habitat = Humid zone; Non-saline habitat = slacks and the rest are brackish. Moist zone = the beach, the slacks and humid zones and Dry zones = all the others.

* = significant differences between observed and expected values (P<0.005), ** = significant differences between observed and expected values (P<0.05).
Coastal vegetation in the Yucatan Peninsula

FIG. 7. Number of species belonging to the twelve phytogeographical elements of the Yucatan Peninsula as a whole and in five geographical sections described in the text. En=Endemic, Sm=South Mexican, Ca=Central American, Pc=Pancaribbean, Nc=Northcaribbean, Na=North American, Gu=Gulf of Mexico, At=Atlantic, Nt=Neotropical, Pt=Pantropical, Co=Cosmopolitan, In=Introduced. Broken lines show joint distribution patterns: M=Meso American and C=Caribbean.

TABLE 3. Percentage of endemics in the littoral of the Yucatan Peninsula

<table>
<thead>
<tr>
<th>Section</th>
<th>No. species</th>
<th>No. endemics</th>
<th>% Endemics</th>
</tr>
</thead>
<tbody>
<tr>
<td>Campeche</td>
<td>147</td>
<td>6</td>
<td>4.1</td>
</tr>
<tr>
<td>West Yucatan</td>
<td>157</td>
<td>7</td>
<td>4.5</td>
</tr>
<tr>
<td>Middle Yucatan</td>
<td>146</td>
<td>8</td>
<td>5.5</td>
</tr>
<tr>
<td>East Yucatan</td>
<td>149</td>
<td>9</td>
<td>6.0</td>
</tr>
<tr>
<td>Quintana Roo</td>
<td>189</td>
<td>7</td>
<td>3.7</td>
</tr>
<tr>
<td>Total</td>
<td>237</td>
<td>16</td>
<td>6.7</td>
</tr>
</tbody>
</table>

non-saline water is present (Middle Yucatan and Quintana Roo). Although their presence could be due to human introduction (both species are edible), they thrive particularly there because the occurrence of fresh-water springs. In Middle Yucatan twenty-four and in Quintana Roo twenty-five of the thirty-three Central American species are present.

The two Caribbean elements show a clear maximum in Quintana Roo with forty-seven of all fifty-three represented.

4. Pan-Caribbean (including the small islands forming the Leeward and Windward West Indies, the north coasts of South America, Central America and Belize). These species are common on sand dunes on most of the Caribbean Islands. Many of them have been used in the classification of the Caribbean sea-shore vegetation and play an important role in dune dynamics. One of them, *Hippomane mancinella*, is also widespread along the tropical American

east coast but its absence on the Yucatan Peninsula is remarkable. It is not obvious whether the absence of this species is due to dispersal or ecological barriers. According to Guppy (1917) and Ridley (1930) this species is dispersed by ocean drift and fruits have been recorded along several Caribbean and American beaches.

The absence of fruit germination on the beach led Guppy to suggest that the intervention of land-crabs (or goats) may be necessary, and that germination could only occur after the fruit has gone through a digestive tract. He mentioned a wider occurrence for this species than it actually has; the species was not mentioned in the floras of Florida, Texas, Veracruz and Yucatan. Seeds have been collected in Florida (Gunn, 1968), Carolina (Gunn, Dennis & Paradine, 1976) and in Quintana Roo (Gunn, Andrews & Paradine, 1976-82; and myself). Viability has not been recorded by any of them. This supports Guppy’s suggestion.

5. The North Caribbean element. It includes species which mainly occur in Florida, on the Bahamas Islands, Cuba, Puerto Rico, Haiti, Republique Dominicana and Jamaica and grow on warm humid places. *Pseudophoenix sargentii* is one example of this distribution type (Quero, 1981).

6. The North American element. These species which occur in the coastal salt marshes of North America usually grow in the transition zone between beach and mangrove where the vegetation often resembles a salt marsh. This element is most important in the semi-dry sites: West Yucatan, with all seven species represented (Fig. 7); it is also well represented in Middle and East Yucatan where it mainly occurs at the flat edges of coastal lagoons.

7. The Northern Gulf of Mexico element. These species occur mainly in similar habitats as described above in Texas and Tamaulipas but they are absent on the Pacific Ocean coasts. In the peninsula, the Gulf element is best represented in West Yucatan.

8. The tropical Atlantic element is represented by a single species, *Scaevola plumieri*, which occurs on both the American and African tropical coasts of the Atlantic Ocean.

The Neotropical and Pantropical elements are the most common elements in the sand dune flora. Both occur maximally in Quintana Roo.

9. The Neotropical element. The forty-four species that constitute this element mainly occur on the eastern coasts of tropical America.

10. The Pantropical element. The forty-nine species are mainly beach species, mangroves and weeds.

11. The Cosmopolitan element. It includes four species which also occur on temperate coasts.

12. Introduced species. This group includes five cultivated species; *Cocos nucifera* is planted over large areas. *Casuarina equisetifolia* is rare, the others are species escaped from adjacent cultivation fields.

Analysis of species distribution and modes of dispersal

Relationships between species distribution and modes of dispersal are clear (Fig. 5 and Table 2). Results are in agreement with the general knowledge that sea and lagoon species are long-distance dispersed. The few wind-dispersed species dominate in sheltered and ruderal habitats. The ones found in ruderal habitats are also often dispersed by animals. Zoochorous species are more frequent on the stabilized dunes.

Species with narrow distribution ranges are found on the stabilized dunes, whilst wide-distributed species occur on exposed habitats. The cosmopolitan species occur along roads and paths and the introduced species are planted on beaches and sheltered areas.

With the recent construction of roads, many ruderals have colonized the road embankments and new species have appeared. These new species are not necessarily ruderal, *Typha domingensis*, a species of inland ponds, was recently collected in a destroyed dune area with several fresh-water springs.

Discussion and Conclusions

On the basis of the following coincident models, the distribution of dune vegetation along the peninsula’s coasts is analysed.

An explanation for actual patterns and processes in dune vegetation has been proposed by Guevara (1982). It regards availability of propagules, vital attributes of species and natural and anthropogenic disturbance. Sauer (1982) parallels the evolutionary and biogeographic...
patterns and states that propagule dispersal, a largely ‘positive force’, is constrained by the environment, understood as a ‘negative force’. The result is a series of ‘steady states’ in the vegetation which define the dunes as a ‘permanent dynamic ecotone’ (Sauer, 1975). Disturbance is considered an important factor for the maintenance of species richness in this steady state vegetation through differentiation in the ‘regeneration niches’ of species (Grubb, 1977) or ‘establishment niches’ as Cramer (1985) described for rising sea-shores.

**Propagule availability**

The actual occurrence of beach species depends on random factors of migration and introduction (Moreno-Casasola, 1985). The wide distribution of beach species reflects the absolute climatic limits they can withstand (Ranwell, 1972). This can be demonstrated on the extreme beach environment where the species assemblage in the seed drift (Gunn et al., 1976–82) is much richer than the beach communities actually established.

Adjacent coastal and inland tropical forest vegetation are the main source of available species to establish in fixed sand dunes if proper conditions are found (see general model of Noble & Slatyer, 1980; Guevara, 1982). *Manilkara achras* is an example of a species from the evergreen tropical forest occurring in the sheltered dune slacks where fresh water is available. Examples of species from adjacent Caribbean island coasts are the shrub species *Erialthis fruticosa* and *Strumphia maritima*, occurring on fixed dunes in eastern Quintana Roo under the same climatic and soil conditions as in their main distribution area.

**Disturbance**

It is generally considered that diversity in plant communities is maintained in part as a result of recurrent disturbances by outside forces (Loucks, 1970; Grubb, 1977; Huston, 1979). After local intense anthropogenic disturbance establishment of exotic species may occur in the dunes (an example is the inland aquatic species *Typha dominguensis*).

In addition, the climatic factors as hurricanes and ‘nortes’ enhance high richness in dune systems through niche creation and delivery of propagules (Stoddart, 1969; Sauer, 1967). The Gulf region, with its complex dune system, is extremely rich and the Yucatan Peninsula, if compared with other Caribbean dune systems, is relatively rich (Moreno-Casasola & Espejel, 1986). Together with Malaysia these two regions form the most important centres of plant diversity on sea-shores (Sauer, 1982).

The floristic composition and vegetation structure of the dunes is also influenced by other climatic factors. The xerophytes developed adaptive strategies for arid conditions and only occur in the semi-dry Yucatan. The salinity of the ground water is one of the most important limiting factors in the Peninsula’s dune zonation. mainland species of the humid rain forests do not tolerate salinity, and are restricted to the surroundings of the freshwater springs. On saline and flooded soils salt marsh and mangrove species develop (Espejel, 1986b). The absence of *Uniola paniculata* is explained by the lack of sand accretion (cf. Wagner, 1964).

**Species attributes and zonation**

The clear floristic zonation in the peninsula’s dune system changes gradually from one habitat to another; the pattern of species presence and cover is zoned into bands parallel to the shore, as is usually the case on sea-shores (Richmond & Mueller-Dombois, 1970; Ranwell, 1972; Doing, 1981, 1985; Stoddart & Fosberg, 1981; Barbour, De Jong & Pavlik, 1985; among others). The floristic composition along the gradient is modified by the establishment of randomly arrived propagules and soil development during primary and secondary succession (Guevara, 1982; Moreno-Casasola, 1985). In the more limiting environment of the beaches, species occurrence is mainly determined by climate and edaphic factors. On the fixed dunes, where soils and vegetation are more complex, vital attributes of species play a more important role.

The species occurring in different habitats along the sea–inland gradient are characterized by different modes of dispersal (Table 2). The abiotically dispersed species are those of the beach and humid zones. The species on stabilized dunes are adapted to zoochorous dispersal; by birds (Ridley, 1930; Linhart, 1980; Snow, 1981) or by other animals like bats, foxes or crabs (Guppy, 1917; Howard, 1950). An example is the absence of *Hippomane man*
cinella, which appears to need animal scarification of its seeds for germination (Guppy, 1917).

The dune species along the zonation show that they have developed different adaptive strategies for their establishment and perpetuation. Little is known about the seed germination and the physiology of the species studies. Nevertheless, the modification of the plant tissues will be considered as a result of physiological responses. These can be expressed as adaptive strategies that allow species to thrive. The development of thorns and succulent tissues (Table 2, Fig. 5) shows that they are related to the species on fixed dunes in habitats where drought or salinity play an important role in community composition.

The growth form is also considered a vital attribute as it describes growth rate and size at maturity (Noble & Slatyer, 1980). In Fig. 5 and Table 2 the species subjected to similar environmental constraints have similar adaptive features; i.e. most of the species are herbs (erect, runners, creeper and vines) where constant disturbance prevails (beaches and roads or paths across the sheltered zones). All the perennials (tropical growth forms, trees and shrubs) occur in the sheltered zones of the dune.

**Phytogeography**

The considerable amount of endemic species found on the dunes of the peninsula (6.7%) is in accordance with the findings of Rzedowski (1978). One of the endemics, *Enriquebeltraniana crenatifolia*, forms a community type of its own. *Coccothrinax readii* and *Mammillaria gaumeri* also are common endemic coastal species (Moreno-Casasola & Espejel, 1986). There are clearly fewer endemics, however, if compared with other coastal dune vegetation, such as in Cuba (Borhidi, 1987), where an extremely high number of endemics is mentioned, or on the peninsula of Baja California, where 30% of the species are endemics (Johnston, 1977, 1982), or in Israel, where endemics are reported to comprise 12.8% of the dune flora (Auerbach & Shmida, 1985).

Several authors have suggested that the major biogeographical element in the peninsula coastal flora was the Caribbean (Millsapgh, 1896, 1898; Standley, 1930; Lundell, 1934; Miranda, 1958; Barrera-Marin, 1964). Two other authors mention the importance of American species (Sauer, 1967; Rzedowski, 1978). Indeed, the Caribbean element is really important but the two mainland distribution patterns – the South Mexican together with the Central American (Meso-American) – are equally important as the Caribbean element.

**Acknowledgments**

I am deeply indebted to all collaborators of the Etnoflora Yucatanense project, especially Victoria Sosa, Rafael Lira and Victor Rico-Gray. Fuensanta Rodriguez from the Faculty of Science of the National Mexican University has been a helpful friend during the field work. I appreciate the comments on this paper by Eddy Van der Maarel, Colin Prentice, Hugo Sjörs and Graciela Rusch. Profile drawings were done by Pauli Snoeijjs. This research was possible thanks to the CONACYT project PBCBNA-005 238, Centro de Recursos Bióticos de la Peninsula de Yucatán, the Swedish Institute and the Institute of Ecological Botany of the Uppsala University.

**References**


Barrera-Márin, A. (1964) la Peninsula de Yucatán como Provincia Biótica. Tesis Doctoral, Instituto Politécnico Nacional Mexico, D.F.


Coastal vegetation in the Yucatan Peninsula


Sands, R.D. (1960) A study in the regional dynamic climatology of Mexico with precipitation as the correlative factor. Ph.D. dissertation, geography, Clark University, U.S.A.


