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Coastal sand dune vegetation of Tabasco and Campeche, Mexico

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Abstract. Sand dune vegetation along the coast of the Mexican states of Tabasco and Campeche was sampled by means of 1501 relevés and the data were analyzed with classification and ordination programs. 36 community types were distinguished, which were grouped into 10 higher-order groups. The communities are described in a sequence reflecting the main vegetation zonation. Beach, embryo dune and foredune community groups include 12 community types, the sheltered zone includes 16 types and the fixed dunes 8 types. The ordination results reveal one main vegetation gradient corresponding to the increase in mean distance from the shoreline and elevation, and being covariant with species richness, mean vegetation cover and mean vegetation height.

Additional differences are related to the geographical transition between the Gulf and Caribbean coastal vegetation and environmental conditions, mainly type of sand, occurring in the study area. Siliceous sand and a Gulf climate are characteristic for most of Tabasco, and calcareous sand and a Caribbean-type climate are characteristic for Campeche.

Disturbance caused by coconut plantations, cattle grazing and tourism favours the invasion of ruderal species from waste places behind the dunes, which attain local dominance in the dunes described here. Consequently some separate community types had to be distinguished.

The distribution of community types is analyzed in the context of the transitions between calcareous and siliceous substrates in the study area.

Keywords: Classification; Community type; Invasion; Ordination; Ruderal species; Syntaxonomy.

Nomenclature: Sosa et al. (1985) for the Caribbean flora; Standley & Steyermark (1946-1977) for the Gulf of Mexico flora.

Introduction

Many coastal dunes in Mexico suffer from severe destruction by human activities, including agriculture (cattle ranching, coconut plantations), tourism (resort building, trampling) and oil industry. In some areas this has resulted in a complete destruction of the natural vegetation, with considerable economical damage in adjacent areas basically due to uncontrolled sand movement. Coastal dunes form complex systems of habitats for plants, due to the combined effects of steep environmental gradients. Important gradients are based on salinity, nutrients, humidity (due to spatio-temporal variations in the phreatic level), wind, and inundation (Ranwell 1972). Most of these gradients are related to the distance from the shoreline. At the shoreline, the effects of salt spray, wind and inundation are strongest, while decreasing gradually landward.

So far, studies on the coastal dunes of Mexico and Central America have mainly been floristical and / or phytogeographical (Gonzalez-Medrano 1972; Puig 1976; Espejel 1984). Synecological studies in this area include Poggie (1962), Bonet & Rzedowski (1962), Moreno-Casasola et al. (1982), Castillo (1984) and Moreno-Casasola & Espejel (1986).

Since most of these studies are of a local outlook and employ different methodologies, an integrated view of the structure, composition and functioning of the coastal vegetation of the Gulf of Mexico is still lacking. For the northern Gulf area (Tamaulipas and Veracruz) and the Caribbean (Peninsula of Yucatan) typologies have been elaborated by Moreno-Casasola & Espejel (1986). The present study, dealing with Tabasco and Campeche, and using the same methods, aims at completing the overall picture of vegetation and environmental gradients along the Atlantic coastline of Mexico.

Study sites

15 sites were chosen for detailed analysis, partly for reasons of accessibility, partly because at least their beach and foredune systems did not show signs of severe anthropogenic disturbance. These sites cover a length of

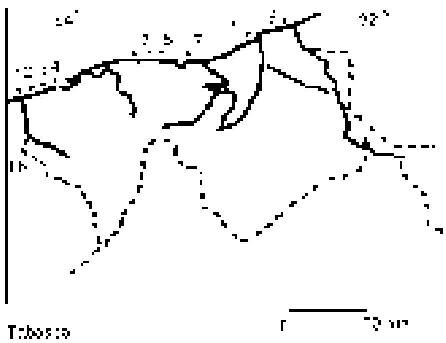
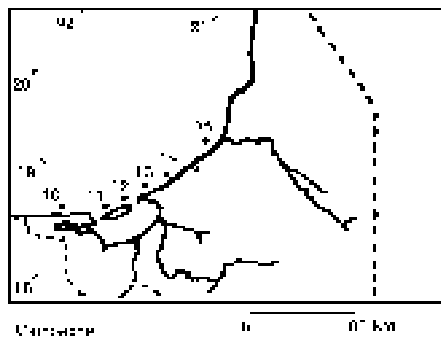


Fig. 1. Location of the study sites and climatological stations (See Appendix 1).
a. *Tabasco*: 1. Cuahtemozing; 2. Alvaris; 3. Pailevot; 4. Rancho Grande; 5. Ostion; 6. Las Flores; 7. Jalapita; 8. Vellizia; 9. La Estrella.
b. *Campeche*: 10. Emiliano Zapata; 11. Santa Rita; 12. Puerto Real; 13. Isla Aguada; 14. Isla (km 26); 15. Champoton (km 95).



17 km along the coast of the states of Tabasco and Campeche (Fig. 1), on a total of 520 km of coastline. The coastline of the eastern part of Campeche is formed by mangrove vegetation and is not included in this study. According to West, Psuty & Thom (1969) the coastal plain of western Campeche and Tabasco is of alluvial origin, formed by an active delta of several rivers combined. The coastal landforms present are products of sedimentary discharge of this delta system. The predominant coastal landform is a beach-ridge system, with occasional low sand dunes present at the inner or outer margins of these ridges. Sand is seldom accumulated up to dunes higher than 3 m above sea level. The beaches of Campeche consist mainly of white, calcareous shell-sand, while those of Tabasco consist of silicate sand; the transition between the two substrate types is gradual (West, Psuty & Thom 1969; Castillo 1984). Climatological data are available for six stations located near the study sites. Fig. 2 presents climate diagrams for two stations, one for each state (for location see Fig. 1).

The major climatic difference is in the amount and distribution of rainfall: Campeche receives less rain and has a longer dry season than Tabasco, the latter state being the wettest region of the Gulf. According to the Köppen system, the Tabasco climatic station can be classified as an Aw (tropical wet) climate, while the Campeche station represents an Am (tropical monsoon) climate (West, Psuty & Thom 1969). The predominating winds are NE, blowing mainly from November to February, frequently bringing a high amount of rainfall and low temperatures (the so-called 'Nortes'). During the dry season the predominating winds come from the SE. Hurricanes do hit the area regularly, and can have disastrous effects on the dunes and their vegetation (Poggie 1962; West, Psuty & Thom 1969).

Field methods

The vegetation was sampled using the relevé method of the Zürich-Montpellier School (Mueller-Dombois & Ellenberg 1974; Westhoff & van der Maarel 1978), using van der Maarel's (1979) ordinal transformation as a basis for subsequent analysis. Relevé size varied from 2 m × 2 m in the beach and grass zones, to 10 m × 10 m in the coastal thickets (Moreno-Casasola & Espejel 1986). A two-stage sample program was followed. The first stage resulted in a series of 1000 relevés, which were submitted to a complete analysis as the one described below. Then, based on the results of the first stage, a second round of sampling was undertaken to complete information on poorly defined types. At this stage another 501 relevés were added to the first set, so that the total data set consisted of 1501 relevés.

Data analysis

In this study we used classification as well as ordination methods to analyse the data structure. The main emphasis was on classification because of the typological nature of the study. Ordination was used in part to check whether the classification results reflect in an adequate way the main floristical gradients in the data set, and also to detect relations between some environmental factors and the composition and structure of the vegetation.

We used two different classification programs: TWINSPAN and FLEXCLUS. TWINSPAN (Hill 1979a), based on the method of indicator species analysis, and dividing up the relevés into groups through repeated dichotomization. This technique was used as a quick and efficient way to obtain an initial clustering of the 1501 samples. However, due to the absence of a formal stopping rule in the program, this resulted in groups of quite different internal heterogeneities. Therefore the TWINSPAN results were refined by means of the program FLEXCLUS (van Tongeren 1986), which uses relocative centroid sorting, RCS, (van der Maarel, Janssen & Louppen 1978) and subsequent relocation of relevés to homogenize clusters, followed by hierarchical fusion. RCS started with 63 TWINSPAN clusters, a number considered to be well above the expected final

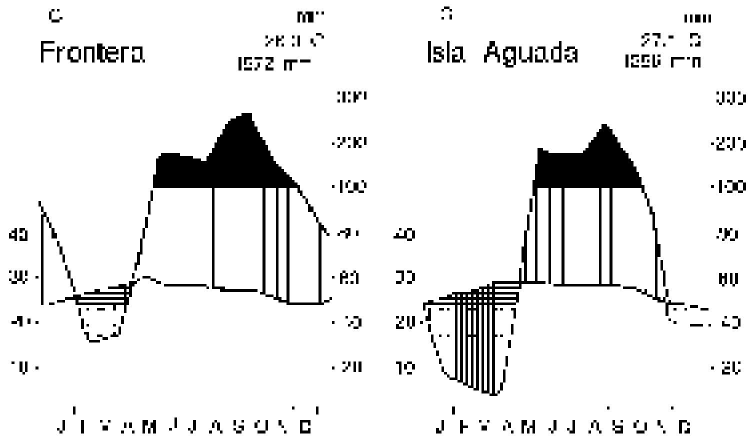


Fig. 2. Climate diagrams of the stations of Frontera (Tabasco) and Isla Aguada (Campeche) (Walter & Lieth).

number of groups. Relocation and fusion were continued until all clusters were sufficiently isolated (isolated being defined as having a higher average internal similarity than the similarity to its nearest neighbour). While using the Similarity Ratio (van der Maarel, Janssen & Louppen 1978) as a resemblance measure, this coincided with a maximal between-cluster similarity (fusion level) of 0.50. At this point 43 clusters remained, of which 36 had a size of seven samples or larger. The smaller (outlier) clusters were omitted from further analysis. The clusters defined thus were further used as the basic units of the typology discussed here, and are primarily defined on numerical criteria. They will be further referred to as community types.

A second, higher level classification was elaborated based on the 36 community types delimited. For this purpose a so-called centroid table was prepared, using within-group species frequency as a measure of relative importance. Species frequency values in each group were transformed to an ordinal scale with 1 for a frequency from 10 - 20 %, 2 for 21 -30 %, etc., to 9 for a frequency from 91-100 %. Species that did not reach a transformed value of 1 in any of the community types were excluded from further analysis at this level. The centroid matrix thus formed (36 types × 80 species) was again analyzed by RCS. This time a complete hierarchical analysis (without relocations) was performed. The results were evaluated using the SWOL criterion described by Popma et al. (1983). Fig. 3 shows the SWOL-values for the hierarchical analysis, indicating a numerically optimal solution of 10 type-groups (further called community groups or groups). The resulting typology is presented in Tables 1, 2 and 3.

The centroid matrix was ordinated by reciprocal averaging, RA, (Hill 1973), using the program DECORANA (Hill 1979b). Possible relationships between the composite floristical gradient(s) as defined by RA, and vegetation structure and topographical factors, were checked with Spearman's Rank Correlation. Variables included in the analysis were RA-axis scores for the community types (axis 1 to 4) and means for the relevés composing the community types for species richness, mean vegetation height, mean total cover, distance to the shoreline, inclination and height above sea level. Significant correlations were found only with RA axis 1 and 2 (Table 4, below).

Description of the community types

General remarks

Before describing the different vegetation types, some general observations concerning cluster structure need to be made. One of the most important is that virtually every community type seems to be defined by the dominance of one or two species rather than by a particular combination of species. There are two reasons for this phenomenon. First, the appearance of dominant plant species in most of the vegetation described here is very obvious in the field, and second, the use of a quantitative similarity measure (type Similarity Ratio, van der Maarel, Janssen & Louppen 1978) makes sure that this dominance is given a rather high weight in comparisons between samples. Furthermore, parts of the area have constantly been altered by human activities which has increased the phenomenon of local dominance of certain and the disappearance of other, naturally subdominant species. A few of these new dominants are ruderals which have attained dominance only under

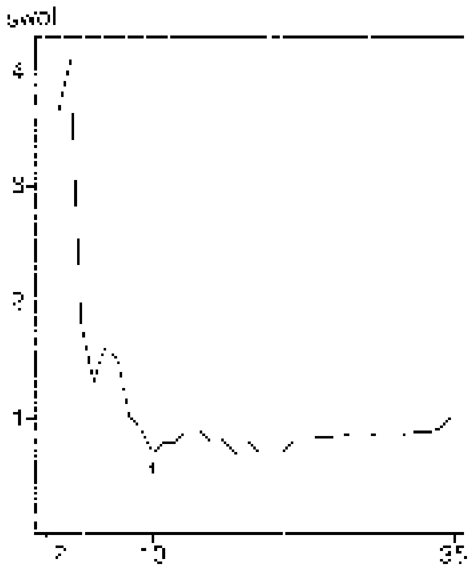


Fig. 3. SWOL coefficient for a hierarchical clustering by centroid sorting of the 36 community types.

these new conditions. This has resulted in the formation of several local floristic groupings which appear as casuistic co-occurrences of species at the same time and in the same environment, rather than as balanced communities.

A description of the community types following both the hierarchy of the typology, as well as the main vegetation zonation will now be presented. For this purpose the area has been subdivided in three broad zones which are correlated with the topography, from pioneer vegetation to stabilized vegetation which are shown in the profile. The distribution of each community type along this zonation is presented in Fig. 5 (further below).

The community types are indicated by numbers and the type-groups by letters, which symbols are also used in the synoptical tables 1, 2 and 3. The community types are named after the dominant species, which is quite evident in most groups. If several co-dominant species occur, the one most restricted to the community type is chosen. The type-groups are named after species that show a distributional optimum in the group. In general the same name was given to groups showing the same dominance and / or species composition as the ones reported by Moreno-Casasola & Espejel (1986).

Beach, embryo dune and foredune vegetation

Pioneer communities are formed by 12 community types. They are mostly found on the beach and developing embryo dunes which later on will become part of the foredune. Table 1 summarizes information on 695 relevés and 81 species.

Group A*: *Tournefortia gnaphalodes

Comm. 1: *Tournefortia gnaphalodes*

This group is formed by one community type only, which is one of the few beach pioneer communities dominated by shrubs. It is probably the structurally most complex and floristically most diverse pioneer community. Shrub-dominated pioneer communities on the beach are rather frequent in the Caribbean. *Tournefortia gnaphalodes* is a small evergreen shrub (70 - 100 cm tall) with succulent, whitish pubescent nanophyllous leaves and long (4-5 m) horizontal branches. Because of its growth form, this species is efficient in the retention of sand, thus forming both embryo dunes and foredunes. It is restricted to soils with a moderate to high $CACO_3$ content; hence its major distribution range is along the coast of the Yucatan Peninsula and the calcareous islands in the State of Veracruz. Under its canopy, frequent companion species are herbaceous pioneers like *Amaranthus greggii* and *Ipomoea pes-caprae*, *Sporobolus virginicus* and *Bidens pilosa*. Within the study area this community is restricted to three sites in Campeche, where it is found in the foredunes, often on gentle north slopes.

Group B: Okenia hypogaea

Comm. 2: *Okenia hypogaea*

A rare pioneer community, forming a group by itself, characterized by a high dominance of *Okenia hypogaea* (*Nyctaginaceae*), a shrub with nanophyllous, sticky leaves. The only frequent companion species is *Sporobolus virginicus*. It is not included in the *Sporobolus* group, because of the absence of *Ipomoea pes-caprae* and some other species. It is found in two sites of Tabasco only, where it occurs at the base of the foredune. *Okenia* is found only in Mexico and on the Florida Keys. Along the Gulf it is mainly distributed in the State of Veracruz, where it is frequently found growing on young primary dunes.

Group C: Sporobolus virginicus

This group is formed by 10 community types, all of them characterized by a high frequency of *Sporobolus virginicus* and the dominance of a particular pioneer species. These communities are mainly found in sites with high sand movement and / or salt spray, such as the beach, embryo dunes, foredunes and blowouts (Doing 1981, 1985; Moreno-Casasola & Espejel 1986), although they can persist in more stabilized sites. *Sporobolus virginicus* is a pantropical (Sauer 1967) perennial grass, 15 - 25 cm tall, with a capacity for fast vegetative spread by stolons. It has a superficial root system and sclerophyllous, nanophyllous leaves. It forms open communities, which are often the first colonizers of young, primary dunes. It is also found in a variety of humid slacks and in more stabilized communities in protected areas behind the foredunes, though much less frequent there. *Sporobolus virginicus* is one of the most widespread pioneer species and its communities are distributed along the coasts of the Gulf and the Caribbean.

Comm. 3: *Cakile edentula*

This ephemeral pioneer community is only found in the easternmost Campeche sites. The dominating species, *Cakile edentula*, is an annual, salt-tolerant species, 30 - 40 cm tall, with succulent, nanophyllous leaves. It grows scattered over the beach at the high-tide line, where it establishes during the rainy season. During the 'Norte' season, with strong winds and high tides, it may die off. According to Sauer (1967) this species is distributed along the Gulf, Caribbean and Antillean coasts. Structurally, this is an open, low community. Frequent companion species are *Sporobolus virginicus* and *Ipomoea stolonifera* and sometimes other salt-tolerants like *Salicornia bigelovii*.

Comm. 4: *Salicornia bigelovii*

Although distinguished in the analysis as a separate community, it is doubtful whether this community is different from the former, as the main difference lies in dominance rather than in species composition. It is restricted to one site in Campeche and has not been reported as a community type from the Caribbean (Moreno-Casasola & Espejel 1986). The dominant *Salicornia bigelovii* is a salt-tolerant annual with succulent, nanophyllous leaves. The community is not only floristically similar to the *Cakile edentula* community, but also similar regarding its habitat and distribution.

Comm. 5: *Sesuvium portulacastrum*

A very common pioneer community forming embryo dunes and also inhabiting slopes (often northern) and crests of foredunes with considerable sand movement. The vegetation is low and open and develops mainly during the wet season. The dominant *Sesuvium portulacastrum* is decumbent, 20 - 30 cm tall, and has succulent, nanophyllous leaves. It has a pantropical distribution and is found along the Gulf and Caribbean coast. Frequent companion species (with low cover-abundance values) are *Ipomoea stolonifera*, *I. pes-caprae*, *Amaranthus greggii* and *Sporobolus virginicus*.

Comm. 6: *Amaranthus greggii*

This community is common in both states, although more frequent in Tabasco. It is characteristic of zones with large amounts of accumulated organic material (storm-tide line). It has its optimal vegetative develop-

Table 1. Synoptic phytosiociological table of beach, embryo dune and foredune community types in the states of Tabasco and Campeche. Growth form codes are: G: Grass; HE: Erect herb; HCl: Climbing herb; HP: Prostrate herb; HSu: Succulent herb; VCr: Creeping vine; S: Shrub; SU: Succulent; SCl, Climbing shrub; T: Tree.

Group code	A	B	C	C	C	C	C	B	C	C	C	C
Community number	01	02	03	04	05	06	07	08	09	10	11	12
No. of relevés *n*	019	008	011	013	098	102	056	011	074	092	086	025
Total no. of species *N*	24	05	07	07	24	15	30	02	31	40	49	30
Mean no. of species	05	02	04	04	03	03	04	05	03	04	04	05
Mean distance to shore (m)	15	17	09	09	19	23	24	01	22	27	27	35
Mean altitude (cm)	094	096	059	057	079	078	097	012	068	087	076	130
Mean slope (°)	01	06	01	04	03	03	01	03	01	02	03	01
Mean % external cover	80	92	67	82	78	82	75	05	68	73	75	85
Mean % bare sand cover	08	20	25	08	17	15	19	02	28	22	32	12
Mean height vegetation (cm)	126	045	035	057	027	024	031	006	026	028	035	044
Dominant growth form	S	HP	HE	HSu	HSu	HP	VCr	S	VCr	VCr	G	HE
No. of sites in Tabasco	0	2	0	0	8	8	6	8	9	6	8	4
No. of sites in Campeche	3	0	3	1	5	3	5	6	4	6	5	1
Tournefortia gnaphalodes	9	-	-	-	-	-	-	-	-	-	-	-
Okenia hypogaea	-	9	-	-	-	-	-	-	-	-	-	-
Cakile edentula	-	-	9	5	-	-	-	-	-	-	-	-
Salicornia bigelovii	-	-	2	9	-	-	-	-	-	-	-	-
Sesuvium portulacastrum	1	1	-	-	9	3	1	-	1	1	3	-
Amaranthus greggii	1	-	3	5	1	9	1	-	1	1	2	1
Canavalia rosea	2	-	-	-	-	-	9	2	-	2	-	4
Croton punctatus	-	-	-	-	-	-	4	9	1	1	2	1
Ipomoea pes-caprae	4	-	-	-	4	2	5	5	9	4	6	4
Ipomoea stolonifera	3	-	7	6	1	1	3	3	1	9	2	2
Sporobolus virginicus	2	6	8	9	4	4	6	5	5	7	9	7
Ambrosia artemisiifolia	-	-	-	-	-	-	1	1	-	-	-	9
Panicum amarum	1	1	-	-	-	-	3	2	1	2	1	3
Passiflora foetida	-	-	-	-	-	-	-	1	1	-	1	-
Andropogon scoparius	-	-	-	-	-	-	-	1	-	-	1	-
Bidens pilosa	3	-	-	-	-	-	-	-	-	-	-	2
Chamaesyce dioica	-	-	-	-	-	-	-	-	-	1	-	-
Coccoloba uvifera	-	2	-	-	-	-	-	-	-	-	-	-
Agave angustifolia	1	-	-	-	-	-	-	-	-	-	-	-
Chamaecrista chamaecristoides	-	-	-	-	-	-	-	-	-	-	-	1
Vigna luteola	-	-	-	-	-	-	-	2	-	-	-	1
Cenchrus tribuloides	1	-	-	-	-	-	-	-	-	-	-	-
Chamaesyce ammanioides	-	-	-	-	-	-	1	-	-	-	-	-
Commelina erecta	-	-	-	-	-	-	-	-	1	-	-	1

ment during the rainy season. Structurally it forms a species-poor, open and low herbaceous community. The dominant *Amaranthus greggii* is a plant with prostrate branching and microphyllous, mesophytic leaves, 20 - 30 cm tall. According to Sauer (1967) it is a Gulf endemic. Frequent companions are *Ipomoea pes-caprae*, *Sporobolus virginicus* and *Sesuvium portulacastrum*. Floristically this community shows a high similarity to the former community, but it occupies a quite different habitat.

Comm. 7: *Canavalia rosea*

This is a common pioneer community that is widely distributed over the whole dune system and not restricted to the foredune zone, although it is more common there. Structurally it is a low, open vegetation dominated by creeping herbaceous and graminoid life forms. The dominant species, *Canavalia rosea*, is a perennial creeping vine, with succulent, 5 - 10 m long stems with a modular growth habit. It has its major development during the rainy season, while it is almost completely leafless during the dry season. It has sclerophyllous, mesophyllous leaves and reaches a height of 30 - 40 cm. *Canavalia rosea* has a pantropical distribution (Sauer 1967) and is found along the whole Gulf and Caribbean coast. Companion species in this community are *Ipomoea pes-caprae*, *I. stolonifera*, *Croton punctatus*, *Sporobolus virginicus* and *Panicum amarum*.

Comm. 8: *Croton punctatus*

This common pioneer community, characteristic of (mostly northern and eastern) slopes, structurally presents a higher cover than all other communities of this group. The dominant species is *Croton punctatus*, which has a large ecological range and is found also in more stabilized zones behind the first dune rows and in areas of active sand movement inside the dune system. The fact that it is found on northern and southern slopes might indicate that this species is tolerant to sand movement (Moreno-Casasola 1986). According to Sauer (1967) *Croton punctatus is* a Gulf-Caribbean species; indeed, it is very abundant in all but one of the sites investigated. It is a perennial, evergreen and has microphyllous, very pubescent leaves. Frequent companion species in this community are *Ipomoea pes-caprae* and *Sporobolus virginicus*.

Comm. 9: *Ipomoea pes-caprae*

A very common pioneer community found at the base of the first dune row. This is a seasonally ‘moving’ community, extending its long succulent branches towards the shoreline during the rainy season, being pushed backward during the ‘Nortes’ season when high tides are frequent. For this reason it is often found as an almost monospecific stand. The dominant species has a growth form very similar to that of *Canavalia rosea*. *Ipomoea pes-caprae* is a pantropical species and is abundant along the whole Gulf and Caribbean coast. Frequent companion species are *Sporobolus virginicus* and *Ambrosia artemisiifolia*.

Comm. 10: *Ipomoea stolonifera*

A widely distributed pioneer community, extending landward from the foredunes. It is floristically more diverse and structurally more differentiated than the former community. The dominant *Ipomoea stolonifera* is a herbaceous, perennial evergreen species, with succulent, short stolons and mesophyllous leaves. It has a pantropical distribution (Sauer 1967) and is common along the Gulf and Caribbean coast. Often *Sporobolus virginicus* is present as a co-dominant, while *Sesuvium portulacastrum*, *Canavalia rosea* and *Panicum amarum* are frequent companions.

Comm. 11: *Sporobolus virginicus*

A pioneer community on young, primary dunes, characterized by the dominance of *Sporobolus virginicus*. Companion species are *Ipomoea pes-caprae* and *Sesuvium portulacastrum* (with low abundance). For a description of the dominant species see the group description.

Comm. 12: *Ambrosia artemisiifolia*

An uncommon community, characteristic of disturbed areas within stabilized and intermediate zones. Accompanying species belong to the pioneer group being the ones with the broadest distribution range within the local zonation. Structurally it is the most differentiated pioneer community. The dominant *Ambrosia artemisiifolia* is a herb, 50 to 100 cm high with an erect growth form. It presents lobulated, mesophytic, mesophyllous leaves. It is widely distributed, and not restricted to coastal habitats. In inland vegetation it is often characteristic of ruderal communities, as well as abandoned old fields. Along the coast this species is most abundant in Veracruz, while in the sites investigated it seems to be restricted mainly to Tabasco. *Bidens pilosa* also characteristic of ruderal communities, *Canavalia rosea*, *Ipomoea pes-caprae*, *Panicum amarum* and *Sporobolus virginicus* are frequent companions.

Vegetation of the sheltered zone behind the foredune

These communities are usually dominated by graminoid, herbaceous or low shrub species and are located in more protected areas behind the foredune. They include 16 community types of which only 10 have been described earlier.

Group D: Bidens pilosa

This group, formed by 9 communities, is characterized by two types of species. The first type includes *Passiflora foetida*, *Bidens pilosa* and *Ambrosia artemisiifolia*, ruderal species that have invaded the dunes, mainly in disturbed patches. They can be considered as indicators of human activities (trampling, grazing, clearing of vegetation). The other type includes mainly coastal pioneer species that form the community types of the *Sporobolus* group we have just described. Communities of these species can be considered as a transitional group establishing in more protected areas behind the foredune, where most of the human activities take place. In the community ordination (Fig. 5) this group occupies an intermediate position between the beach and foredune communities and the coastal thicket, and it shows structural and floristical affinities with both. It includes the community type *Suriana maritima* that is found both as a pioneer thicket and in the more protected areas behind the foredune. Furthermore it appears to be strongly related to group E, *Croton punctatus*.

The species that name the community types in the present group are not at all restricted to it; at most they show their optimum here. Most communities in the *Bidens* group are herbaceous, with scattered patches of shrubs. Generally, they have broad distributions ranges. Table 2 summarizes information for 500 relevés and 77 species.

Comm. 13: *Suriana maritima*

This community is found on gentle (often eastern) slopes and flat zones behind the foredune, exclusively found on calcareous substrates in the easternmost sites of Campeche, where it reaches the northern limit of its distribution. The community forms part of the pioneer thicket. *Suriana maritima* is a strongly ramified shrub (1 - 3 m tall), evergreen, with mesophytic, pubescent, nanophyllous leaves; it has a pantropical distribution. Frequent companion species in this community are *Bidens pilosa*, *Ipomoea stolonifera* and another shrub, *Scaevola plumieri*.

Comm. 14: *Scaevola plumieri*

A community of low shrubs, found in Campeche sites only, and characteristic of the flats behind the foredune with a somewhat irregular topography. The dominant *Scaevola plumieri*, widely distributed in the Caribbean, is a low evergreen shrub (1 - 1.5 m tall) with succulent, mesophyllous, yellowish green leaves. It forms often monospecific patches and has a pantropical distribution (Sauer 1967). Frequent companion species are *Bidens pilosa* and *Panicum amarum*, and occasionally other woody shrubs like *Ernodea littoralis*, *Coccoloba uvifera* and *Randia laetevirens* appear with low abundance values; they are characteristic of the thicket zone.

Comm. 15: *Passiflora foetida*

The *Passiflora foetida* community, characterized by the dominance of *P. foetida*, is very similar to the next one, *Bidens pilosa*. Both communities occupy flat zones, frequently grazed by cattle, presenting a low and dense herbaceous cover. Both are frequent outside the coastal system in disturbed areas. *P. foetida* is a pantropical climbing perennial herb with lobed, mesophytic, microphyllous leaves, conspicuous flowers and edible fruits.

Comm. 16: *Bidens pilosa*

The *Bidens pilosa* community differs from the previous type only in the dominance of *B. pilosa*. It tends to dominate in more humid areas. *B. pilosa* is an erect herb, with mesophytic, microphyllous leaves, 30 - 60 cm tall, growing in patches; it has a Gulf-Caribbean distribution. Moreno-Casasola & Espejel (1986) report a *Bidens pilosa* type in Yucatan, restricted to disturbed beaches, but with different accompanying species.

Comm. 17: *Panicum amarum*

This is the most common community type extending from the crest of the first dune row into the flat zones behind it, frequently found in both Tabasco and Campeche. Its dominant, *Panicum amarum*, is distributed over the whole vegetation zonation. It enters pioneer vegetation, where it acts as an efficient sand retainer. This is mostly seen in Tamaulipas and on the southeastern coast of the USA (Dahl & Goen 1977; Garcia 1987; Moreno-Casasola & Espejel 1986). *Panicum* is a deep rooting, tall grass (40 - 90 cm) growing in dense tussocks with erect, mesophyllous leaves. It has a pantropical distribution (Sauer 1967). Frequent companions are *Ipomoea pes-caprae*, *I. stolonifera* and *Sporobolus virginicus*.

Comm. 18: *Chamaecrista chamaecristoides*

A community found on slopes and flat zones from the second dune row until the stabilized zone, both in Tabasco and Campeche. Structurally it is a low shrub community with a high cover formed by low erect herbaceous, graminoids and low shrub growth forms. *Chamaecrista chamaecristoides* is a small deciduous leguminous shrub (0.50 - 1 m) with leptophyllous, mesophytic leaves, reported to be endemic for the Gulf of Mexico (Sauer 1967). In Veracruz it is found mainly on sites with considerable sand movement being considered a very efficient substrate-stabilizing species (Moreno-Casasola 1986). Frequent companions are *Croton punctatus*, *Bidens pilosa*,

Group code	D	D	D	D	D	D	D	D	D	E	E	E	E	E	E	E
Community number	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28
No. of relevés *n*	26	63	44	66	70	67	23	29	16	12	11	13	41	07	07	07
Total no. of species *N*	31	48	52	43	41	44	18	32	21	17	17	20	35	11	20	14
Mean no. of species	6	6	7	6	5	6	4	6	6	6	6	6	6	4	7	8
Mean distance to shore (m)	20	32	41	42	34	57	27	60	40	44	52	73	62	73	60	88
Mean altitude (cm)	125	134	082	120	102	127	124	130	075	044	150	091	070	040	086	041
Mean slope (°)	03	02	03	03	04	05	15	03	04	00	11	00	02	00	00	00
Mean % external cover	92	89	92	94	82	91	86	87	98	96	85	94	92	89	85	94
Mean % bare sand cover	03	07	01	05	15	06	10	09	01	05	17	03	08	04	13	01
Mean height vegetation (cm)	214	126	051	077	082	065	120	047	138	099	090	116	098	103	065	093
Dominant growth form	S	S	HCl	HE	G	SU	SP	HE	S	HE	S	S	G	G	G	S
N of sites in Tabasco	9	0	5	5	7	4	0	1	0	0	1	1	3	1	1	1
N of sites in Campeche	3	5	2	3	3	3	1	2	1	1	1	0	2	0	0	0
Suriana maritima	9	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Scaevola plumieri	3	9	-	-	-	1	5	1	-	-	-	-	-	-	-	-
Passiflora foetida	2	1	9	4	1	3	-	2	1	5	6	6	5	4	7	1
Bidens pilosa	6	4	5	9	2	5	5	4	6	-	3	2	2	1	-	8
Panicum amarum	3	4	6	7	9	3	3	4	7	-	1	-	1	-	1	-
Chamaecrista chamaecristoides	-	1	-	1	-	9	1	2	-	-	6	-	-	-	-	7
Agave angustifolia	-	-	-	-	-	-	9	-	-	-	-	-	-	-	-	-
Ambrosia hispida	2	1	-	-	-	-	-	9	-	-	-	-	-	-	-	-
Pithecellobium keyense	-	-	-	-	-	-	-	-	9	-	-	-	-	-	-	-
Borrichia frutescens	-	-	-	-	-	-	-	-	-	9	-	-	-	1	1	-
Porophyllum nummularium	-	-	-	-	-	-	-	-	-	-	9	-	-	-	-	-
Eupatorium odoratum	-	-	-	-	-	-	-	-	-	9	-	9	-	9	5	4
Andropogon scoparius	-	-	2	-	-	2	-	2	4	-	4	3	7	9	-	2
Dactyloctenium aegyptium		-	-	-	-	-	-	-	-	-	-	2	-	-	9	-
Crotalaria incana	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	9
Ipomoea pes-caprae	1	1	4	6	3	3	2	-	1	1	-	3	3	-	5	1
Sporobolus virginicus	1	3	5	3	5	2	2	4	-	9	-	-	4	-	-	1
Ipomoea stolonifera	5	2	3	1	3	3	2	5	1	-	2	-	5	1	2	4
Canavalia rosea	3	3	4	5	2	2	-	4	3	-	-	-	-	-	-	-
Cenchrus tribuloides	1	-	-	-	-	-	1	-	1	-	2	-	-	-	-	-
Gomphrena decumbens	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Vigna luteola	4	1	2	1	-	-	-	-	2	-	-	8	1	-	1	-
Croton punctatus	-	1	3	5	1	6	-	2	8	4	6	4	6	4	5	7
Ernodea littoralis	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Randia laetevirens	-	1	-	-	-	-	1	-	-	-	3	-	-	-	-	-
Coccoloba uvifera	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-
Cuscuta americana	-	1	-	-	-	-	-	3	1	-	-	-	-	-	-	-
Phaseolus acuminatus	-	1	-	-	-	-	-	1	-	-	-	-	-	-	-	-
Amaranthus greggii	-	-	1	1	1	-	-	-	-	-	-	-	-	-	-	-
Commelina erecta	-	-	-	1	-	2	-	1	-	-	5	-	-	-	-	-
Panicum maximum	-	-	-	-	-	1	-	-	-	-	2	-	-	-	-	-
Fimbristylis spathacea	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	-
Oenothera drummondii	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1	2
Waltheria indica	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-
Dalbergia brownei	-	-	-	-	-	-	-	-	5	-	-	-	-	-	-	-
Solidago scabrida	-	-	-	-	-	-	-	1	-	5	-	6	2	4	-	4
Paspalum vaginatum	-	-	-	-	-	-	-	-	-	-	-	3	5	2	-	5
Iresine celosia	-	-	-	-	-	-	-	-	-	-	3	-	-	-	-	-
Ambrosia artemisiifolia	-	-	-	-	-	-	-	-	-	-	-	1	-	-	1	-
Cyperus articulatus	-	-	-	-	-	-	-	-	-	-	-	6	2	-	4	-
Cyperus ligularis	-	-	-	-	-	-	-	-	-	-	-	2	-	-	2	-

Table 2. Synoptic phytosiociological table of community types occurring in the sheltered dune zone in Tabasco and Campeche. Additional species: *Metopium brownei*: 1 in Comm. 14; *Chamaesyce dioica*: 1 in Comm. 16; *Okenia hypogaea*, *Tribulus cistoides*: 1 in Comm. 19; *Trachypogon gouinii*: 1 in Comm. 20; *Serjania racemosa*: 1 in Comm. 21; *Croton glandulosus*: 1 in Comm. 26.
Growth form codes are: G: Grass; HE: Erect herb; HCl: Climbing herb; HP: Prostrate herb; HSu: Succulent herb; VCr: Creeping vine; S: Shrub; SU: Succulent; SCl, Climbing shrub; T: Tree.

Passiflora foetida, *Panicum amarum* and *Ipomoea stolonifera*.

Comm. 19: *Agave angustifolia*

A community found only in one site in Campeche, where it occurs behind the foredune, on northern and southern slopes. *Agave angustifolia* is a true succulent rosette plant, about 1 m high. It has very thick megaphyllous ascendent leaves with spiny margins. The community is structurally characterized by succulent growth forms like *Opuntia stricta* var. *dillenii*, *Acanthocereus pentagonus* and frequent companion species are *Bidens pilosa*, *Scaevola plumieri* and *Panicum amarum*. This community type is very common in the northern part of the Yucatan peninsula (Moreno-Casasola & Espejel 1986), and the floristic composition of the present type is sufficiently similar to consider it as the same type.

Comm. 20: *Ambrosia hispida*

A community of disturbed sites, typical where shrub communities have been cleared. In the Yucatan Peninsula it is frequent in open sheltered areas as well as on disturbed sites (Moreno-Casasola & Espejel 1986). The vegetation is very low, open and herbaceous. The dominant *Ambrosia hispida* is a species reported to be widely distributed along the coast of the Yucatan peninsula (Espejel 1984), being a prostrate creeper, with mesophytic, nanophyllous leaves. Frequent companion species are *Panicum amarum*, *Bidens pilosa*, *Canavalia rosea*, *Sporobolus virginicus*, and *Ipomoea stolonifera*.

Comm. 21: *Pithecellobium keyense*

A closed shrub community forming a fringe between the *Coccoloba* thicket and the herbaceous vegetation behind, was only found in one site of Campeche. Its local distribution seems to be limited through intensive grazing of the adjacent herbaceous vegetation. The dominant is an evergreen, spiny shrub (1 - 2 m) with sclerophyllous, nanophyllous leaves. It has a neotropical distribution and is reported as a matorral forming species along the coast of the Yucatan Peninsula (Moreno-Casasola & Espejel 1986). Frequent companion species are *Croton punctatus*, *Panicum amarum* and *Bidens pilosa*.

Group E: Croton punctatus - Passiflora foetida

A group formed by seven community types all characterized by the presence of *Croton punctatus* and *Passiflora foetida*. Most of these communities are poorly represented in the regional typology and are present only in one or two sites. They will only be listed here:

- three herbaceous communities: *Eupatorium odoratum* (24), *Borrichia frutescens* (22) and *Andropogon scoparius - Eupatorium odoratum* (26);
- two graminoid communities: *Andropogon scoparius - Croton punctatus* (25) and *Dactyloctenium aegyptium* (27); and
- two small-shrub communities: *Porophyllum nummularium* (23) and *Croton punctatus* (28).

They all share species, sometimes with a high cover value, which are not typical dune species, notably *Eupatorium odoratum*, *Paspalum vaginatum* and *Solidago scabrida*. Table 2 gives a summary of the composition of these types. The species characterizing these communities are in general species tolerant of heavy grazing.

Comm. 25: *Andropogon scoparius* - *Croton punctatus*

This is the only more widely distributed community type in this group. The leading species *A. scoparius* is a tufted grass, 50 - 100 cm tall, which is very common in the mobile dunes areas of Veracruz.

Vegetation of fixed dunes

This vegetation includes medium and tall shrubs, locally called matorrales. Stabilized communities are divided into five groups, all of them dominated by a spiny shrub typical of matorrales or coastal thickets. *Randia laetevirens*, one of the most common species throughout the Caribbean, is present in almost all of the groups. Only two community types (29 and 30) are found in most of the sampling sites. The others seem to

Table 3. Synoptic phytosiociological table of community types of fixed dunes in Tabasco and Campeche. Additional species: *Hibiscus pernabuscensis*: 1 in Comm. 31; *Paspalum vaginatum*: 2 in Comm. 32; *Metastelma pringleii*: 1 in Comm. 34; *Tribulus cistoides*: 1 in Comm. 35; Growth form codes are: G: Grass; HE: Erect herb; HCl: Climbing herb; HP: Prostrate herb; HSu: Succulent herb; VCr: Creeping vine; S: Shrub; SU: Succulent; SCl, Climbing shrub; T: Tree.

Group code	F	F	F	G	H	H	I	J
Community number	29	30	31	32	33	34	35	36
No. of relevés *n*	159	64	10	14	12	08	07	09
Total no. of species *N*	85	43	17	21	19	21	15	22
Mean no. of species	06	05	04	06	05	07	08	10
Mean distance to shore (m)	060	059	030	041	093	121	049	034
Mean altitude (cm)	144	164	220	119	108	150	086	171
Mean slope (°)	05	05	02	01	00	00	05	10
Mean % external cover	097	096	099	097	095	088	100	098
Mean % bare sand cover	02	03	00	04	03	13	00	01
Mean height vegetation (cm)	254	115	142	200	182	092	230	171
Dominant growth form	T/S	S	SCl	S	T/S	S	S	S
N of sites Tabasco	7	5	1	1	1	0	0	0
N of sites Campeche	3	3	1	1	1	1	1	2
Coccoloba uvifera	9	-	3	2	2	1	9	9
Randia laetevirens	4	9	6	8	2	-	9	2
Caesalpinia bonduc	-	-	9	-	-	-	-	-
Psychotria erythrocarpa	-	-	-	1	8	-	-	-
Chrysobalanus icaco	-	-	-	-	-	9	-	-
Ernodea littoralis	1	-	-	-	3	9	9	-
Borrichia frutescens	-	-	-	-	-	-	9	-
Vigna luteola	1	-	-	-	1	1	-	8
Lantana involucrata	-	-	-	-	-	-	8	7
Gomphrena decumbens	-	-	-	6	-	-	-	7
Chamaecrista chamaecristoides	1	1	1	-	3	8	-	1
Bidens pilosa	2	2	3	4	5	-	-	5
Panicum amarum	3	2	1	5	2	3	-	2
Scaevola plumieri	1	-	-	4	-	-	4	-
Iresine celosia	2	1	3	1	-	-	-	-
Andropogon scoparius	-	2	-	-	5	6	-	1
Sporobolus virginicus	1	1	-	-	-	1	-	-
Ipomoea stolonifera	1	2	-	-	2	5	-	-
Canavalia rosea	1	1	1	-	-	-	5	-
Passiflora foetida	1	1	3	-	-	1	4	4
Waltheria indica	1	-	1	1	1	2	-	-
Chiococca coriacea	1	2	-	3	-	-	-	-
Conocarpus erecta	-	-	-	-	-	-	4	-
Metopium brownei	1	-	-	4	-	-	-	2
Croton punctatus	-	1	-	-	-	-	2	-
Agave angustifolia	-	1	3	-	-	-	-	-
Dalbergia brownei	-	1	2	-	-	-	-	-
Panicum maximum	-	2	1	-	-	-	-	-
Ipomoea pes-caprae	-	-	1	-	-	-	4	1
Dactyloctenium aegyptium	-	-	-	4	-	1	-	1
Commelina erecta	-	-	-	5	-	-	-	3
Phaseolus acuminatus	-	-	-	5	-	-	-	-
Porophyllum nummularium	-	-	-	-	-	2	-	3
Acanthocereus pentagonus	-	-	-	-	-	1	-	3
Cenchrus tribuloides	-	-	-	-	-	-	-	2
Ambrosia hispida	-	-	-	-	-	2	-	-
Cuscuta americana	-	-	-	-	-	3	-	-
Fimbristylis spathacea	-	-	-	-	-	3	-	-
Trachypogon gouinii	-	-	-	-	-	2	-	-

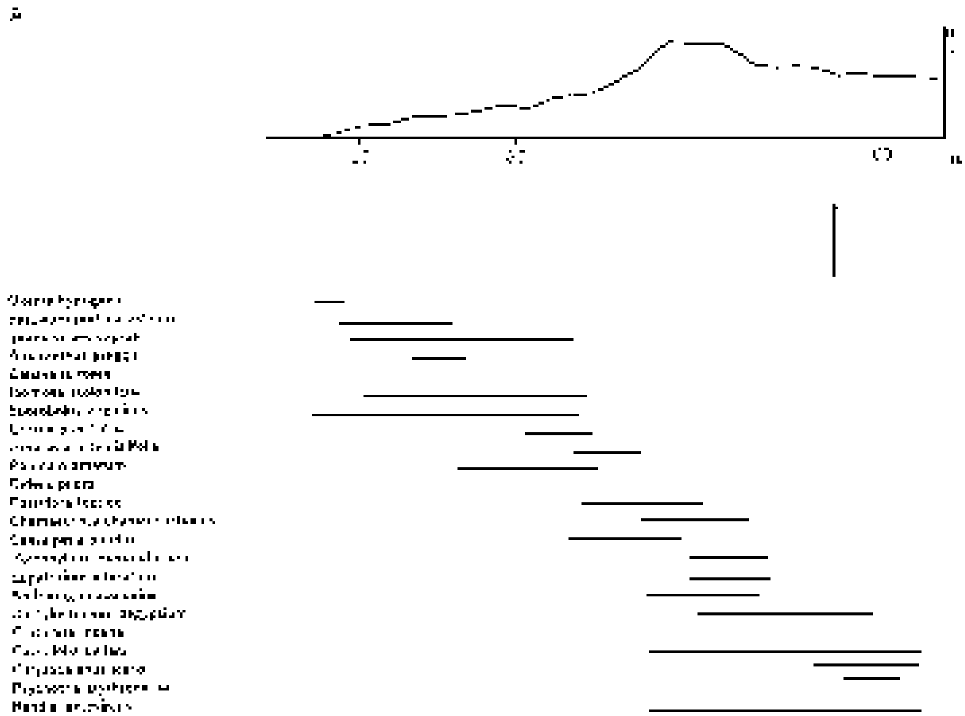


Fig. 4. A. Vegetation profile in Tabasco showing the distribution of community types.

be variants of the same type (richer in species) or resemble matorral types found in the Caribbean (Moreno-Casasola & Espejel 1986). The coastal thicket in this area appears like a transition between the matorral flora of the Gulf and that of the Caribbean coast, which is very different (Moreno-Casasola 1988). It should also be remembered that the fixed dunes have suffered continuous disturbance, mainly where the matorral establishes. The synoptic table (Table 3) presents the resulting centroid classification of these groups. A total of 283 relevés and 93 species were included.

Group F: Randia laetevirens

This group, consisting of three matorral communities, is characterized by the presence of *Randia laetevirens*. It also shows low values for several of the species found in disturbed areas (*Bidens pilosa*, *Iresine celosia* and *Passiflora foetida*), and for a few pioneer species that are able to inhabit stabilized areas behind the foredune. The remnant coastal vegetation in some of these areas forms a very narrow strip.

Comm. 29: *Coccoloba uvifera*

This is the most common stabilized matorral community in both states. It forms the border between the dune system and either deciduous forest (or rather forest remnants), mangrove vegetation or coconut plantations. There is a clear dominance of *Coccoloba uvifera*, reaching 2.5 m. In the original table this group included 159 relevés, which show a high diversity of shrub species, most of them with low frequency, such as *Metopium brownei*, *Lantana involucrata*, *Scaevola plumieri*, *Caesalpinia bonduc* and *Psychotria erythrocarpa*. In the Tabasco sites the understory is usually formed by *Randia laetevirens*, while in the Campeche sites many of the Caribbean species already mentioned, are found in this stratum. This makes it a structurally more complex community than the previous ones. *Coccoloba uvifera* is a neotropical, highly ramified, deciduous shrub, 2 - 6 m tall, without spines and with sclerophyllous, mesophyllous leaves.

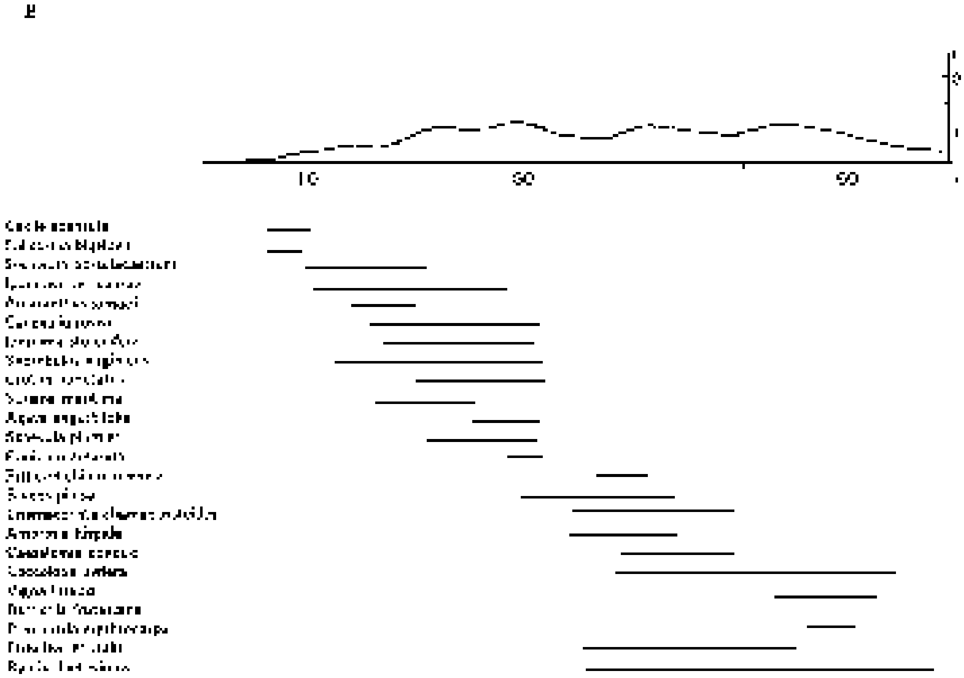
Comm. 30: *Randia laetevirens*

This is a common matorral community in both states, characteristic of the stabilized old dunes, in flat sites or on gentle (southern and western) slopes. In the zonation it often forms a transition zone between the herbaceous or small shrub communities of the *Bidens pilosa* group and the most stabilized communities of *Coccoloba uvifera*. *Randia laetevirens*, an evergreen shrub with very spiny branches and sclerophyllous, nanophyllous leaves, is always dominant in this type. Other shrub species attain only low frequency values: *Chiococca alba*, *Ernodea littoralis*, *Dalbergia brownei*.

Comm. 31: *Caesalpinia bonduc*

A rare matorral community found in two study sites

Fig. 4. B. Vegetation profile in Campeche showing the distribution of community types.



only, where it grows close to the foredune at the highest mean elevation recorded. The dominant *Caesalpinia bonduc* is a spiny shrub with nanophyllous leaves that forms long, lateral branches that spread over a canopy of *Randia laetevirens* or other shrub species. It is also found bordering low deciduous forest in stands with a more open structure.

Group G: Psychotria erythrocarpa

Comm. 32: *Psychotria erythrocarpa*

This community, found only in two sites of Tabasco with a total of 14 relevés, forms a group by itself because of its peculiar species composition, mainly the dominance of *Psychotria erythrocarpa* (together with *Randia laetevirens*). *P. erythrocarpa* is a minor component of the matorral of the Gulf coast (Tamaulipas and Veracruz). *P. erythrocarpa* is a small deciduous shrub with mesophytic, mesophyllous leaves. It forms a more or less closed canopy below which an understory of *Randia laetevirens* is common; other shrubs present are *Chiococca alba*, *Metopium brownei*, *Coccoloba uvifera* and *Scaevola plumieri*.

Group H: Andropogon scoparius - Chamaecrista chamaecristoides

This group includes two matorral communities with a restricted distribution, characterized by the presence of the grass *Andropogon scoparius*, common throughout the Gulf coast, as well as by the virtual absence of *Randia laetevirens* which is present in almost all other thicket communities. This is a matorral group rather poor in species, found farthest from the shoreline.

Comm. 33: *Chrysobalanus icaco*

A rare matorral community found on the old dunes of only two sites. It occupies the space between patches of *Coccoloba uvifera* stands. The community type is occasionally found along the Gulf coast, but is more common along the Caribbean; the accompanying species change throughout its distribution range. The dominant *Chrysobalanus icaco* is common throughout the West Indies; it is a 2 - 4 m tall shrub, with sclerophyllous, microphyllous leaves. Frequent companion species in this area are *Bidens pilosa*, *Andropogon scoparius*, *Ernodea littoralis* and *Chamaecrista chamaecristoides*.

Comm. 34: *Ernodea littoralis - Andropogon scoparius*

A rare shrub community located only at the site of Isla Aguada, Campeche, bordering coconut plantations. The type is commonly distributed in the Caribbean, although accompanying species are different there. The dominant is a small shrub, 70 - 100 cm tall, with sclerophyllous, nanophyllous leaves. It grows in patches together with *Chamaecrista chamaecristoides* and *Ipomoea stolonifera*.

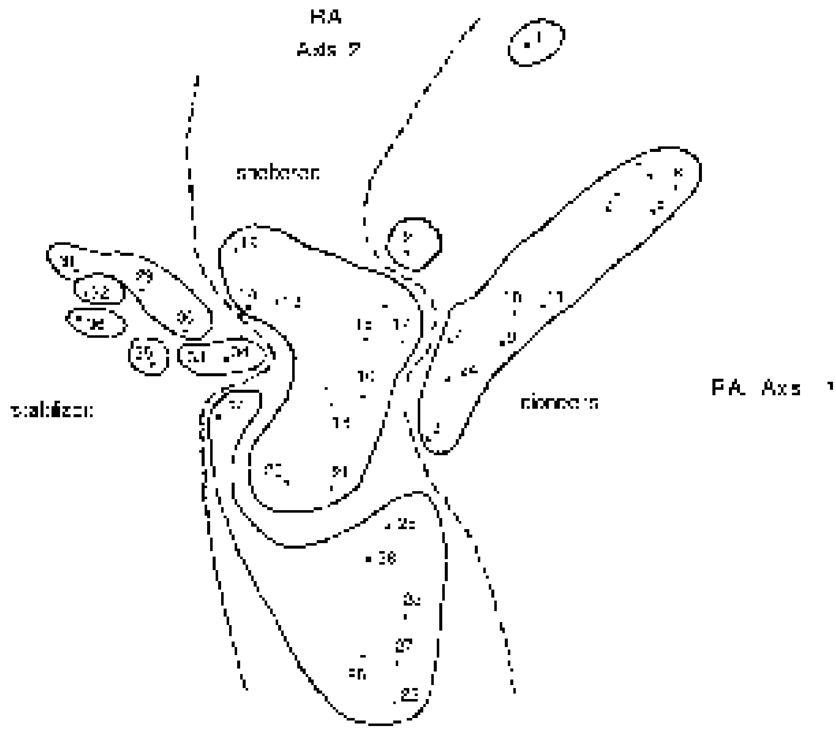


Fig. 5. Ordination of community centroids, with type-groups superimposed. The ordination graphs show the same gradient found for other dune areas: a stabilization gradient from the beach toward the thickets.

Group I: Ernodea littoralis

Comm. 35: *Ernodea littoralis - Borrichia frutescens*

A very dense matorral found only at one site in Campeche where it occurs in a very flat stabilized zone. It is a very diverse tall matorral with a high frequency of several species, including *Coccoloba uvifera*, *Randia laetevirens* and *Lantana involucrata*.

Group J: Coccoloba uvifera

Comm. 36: *Coccoloba uvifera - Vigna luteola*

Found in two sites of Campeche. This type is characterized by the climbing vine *Vigna luteola*, but structurally dominated by *Coccoloba uvifera*. It may also be considered a variant of the *Coccoloba* community (29) with *Gomphrena decumbens* as a differentiating species. *Randia laetevirens* occurs only with low values and one may say it is replaced by *Lantana involucrata*.

Ordination of community types

The RA ordination of the community types as presented in Fig. 5, shows one main ordination axis which is clearly related to a stabilization gradient. The more extreme pioneer communities are found at the right side of the diagram, first herbaceous types and then scrub types, with the sheltered groups in the middle, and the stabilized thicket communities on the left side. The second axis separates some communities found in the sheltered areas, the lowermost representing the *Croton* group with some ruderal species; this floristical deviation may be related to effects of grazing.

Correlation between ordination scores and topographical and vegetational structural variables (Table 4) confirms that floristic variation is mainly related to the zonation (mean distance to the shoreline, elevation) and that the same holds true for general development of vegetation: increase in vegetation diversity (measured as mean species richness), mean vegetation cover and

Table 4. Means of six factors for the relevés composing the community types were correlated with scores on RA axes 1 and 2 using Spearman Rank Correlation. Only significant correlations are shown; all values significant at $P < 0.001$, except 0.36 ($P < 0.05$).

	Axis 1	Axis 2
Species richness	0.56	0.62
Distance shoreline	0.54	0.73
Altitude	0.64	
Mean total cover	0.73	
Mean vegetation height	0.80	
Inclination		0.36

mean vegetation height across the zonation. The only correlation value adding to the interpretation of axis 2 is inclination, but this concerns only a weak correlation.

Distribution of community types

Table 5 presents data on the representation of the various community types and the groups in the 15 sites. The general picture is that most of the pioneer communities, represented in the top of the table, are distributed over most sites, both the Tabasco and the Campeche sites. The first four pioneer communities, however are restricted to one to three sites, and three of them to Campeche sites. Of the 16 communities of sheltered areas only three are found in most of the sites. No less than nine communities occur in one to three sites, about equally many restricted to Tabasco and to Campeche. Two of the eight communities of fixed dunes are found throughout the study area, six are restricted in their occurrence, three of which are confined to Campeche.

All communities belonging to the *Croton punctatus* group (E), characteristic of the grazed and disturbed sites, are restricted to one or a few sites.

General discussion

The general interpretation from the community descriptions regarding the communities' position towards the zonation is summarized in Fig. 4. In both areas, Tabasco and Campeche, the zonation is clearcut and similar. Communities occurring in both areas have roughly the same position in the zonation and for communities missing in either area there are replacement types.

From the floristic-geographical point of view the region of Tabasco and Campeche is a very interesting area of the eastern coast of Mexico, where two floristic coastal groups merge (Moreno-Casasola 1988). Environmental conditions also change: Tabasco being the wettest region of the Gulf coast, mostly with silicate sand and Campeche with considerable less rain, a longer dry season and calcareous sand. There is also a physiognomical change related to this transition, i. e. from a low herbaceous and vine cover predominating in Tabasco, to beach thickets so typical of Caribbean beaches (Espejel 1984; Moreno-Casasola & Espejel 1986).

Generally, the pioneer communities are more widely distributed than the communities of the more sheltered dunes (which confirms the results presented earlier by Moreno-Casasola & Espejel 1986). Of the communities of sheltered dune zones relatively more are restricted to either area, which we relate to the differentiating effect of the substrate: calcareous sand in Campeche (with comm. 13, 14, 20, 34, 35 and 36) versus siliceous sand in Tabasco (with comm. 22, 24, 26, 27, 28).

The isolated occurrence of a type in Tabasco may indicate the southeastern end of a Gulf distribution, as with the *Okenia hypogaea* and *Amaranthus greggii* comm., the same situation in Campeche may point to the beginning of a Caribbean distribution, as with the *Tournefortia gnaphalodes* and *Suriana maritima* comm.

The topography of the dunes of Tabasco and Campeche is simple; usually there is only a low beach-ridge system, similar to the ones found in the Caribbean and in parts of Tamaulipas. For this reason two common dune environments: active dunes and humid to wet dune slacks, are almost missing. Species commonly found in these particular habitats are found only as scattered populations in Tabasco, e. g. *Lippia nodiflora* and *Cyperus articulatus*.

For the habitats represented well in the study area (beach, embryo dunes, sheltered and fixed dunes) the floristic classification gives numerous groups as a result of local changes in species composition; in most stands of these types only a few species occur. Physiognomically the communities of dry dunes are more uniform; together they differentiate the dunes from the rest of the littoral.

The presence of a peculiar group of widely distributed species frequently found on disturbed sites, particularly *Ambrosia artemisiifolia*, *Bidens pilosa* and *Passiflora foetida,* contributes to the floristic variety of the dune communities. These species are commonly found inland as weeds and ruderal species. They are also found as accompanying members of sand dune community types elsewhere in the Gulf and Caribbean, but in the regions described here, especially in Tabasco, they attain local dominance and constitute own community types. This can be interpreted as a response to a very high level of human disturbance here.

Table 5. Distribution of community types: number of relevés for each type is indicated for each of the 15 study sites in Tabasco: Cu = Cuahtemozin; Al = Alvaris; Pa = Pailevot; Ra = Ranchray; Os = Ostion; Fl = Flores; Ja = Jalapita; Ve = Vellizia; Es = Estrella; Campeche: EZ = E. Zapata; SR = Santa Rita; PR = Puerto Real; IA = Isla Aguada; IK = Isla km 26; CH = Champoton.

Study site Group / Comm.	Cu	Al	Pa	Ra	Os	Fl	Ja	Ve	Es	EZ	SR	PR	IA	IK	Ch
Pioneer communities															
A 1	-	-	-	-	-	-	-	-	-	-	-	3	-	11	5
B 2	-	1	-	-	7	-	-	-	-	-	-	-	-	-	-
C 3	-	-	-	-	-	-	-	-	-	-	-	-	2	1	8
C 4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	13
C 5	-	8	7	2	13	15	9	1	10	9	1	-	8	13	2
C 6	2	13	13	10	23	11	13	1	-	2	-	-	-	10	6
C 7	7	2	12	5	-	10	2	-	-	6	4	-	4	2	2
B 8	12	6	2	2	-	10	7	10	15	13	20	2	3	6	-
C 9	6	7	8	1	1	4	1	7	10	7	8	-	7	7	-
C 10	-	5	5	2	-	28	5	11	-	5	2	9	3	3	14
C 11	6	8	7	3	2	9	-	8	23	5	-	5	7	1	2
C 12	12	16	3	-	-	-	-	-	2	-	-	-	-	10	-
Communities of the sheltered zone															
D 13	-	-	-	-	-	-	-	-	-	-	-	-	5	3	18
D 14	-	-	-	-	-	-	-	-	-	-	11	10	17	13	12
D 15	4	-	-	6	-	2	17	-	8	3	-	-	4	-	-
D 16	16	-	16	8	-	-	14	-	5	1	-	-	4	2	1
D 17	5	9	12	6	-	9	1	5	1	1	-	-	10	-	11
D 18	12	7	8	-	-	-	13	-	-	1	14	-	5	-	-
D 19	-	-	-	-	-	-	-	-	-	-	-	19	-	-	-
D 20	-	-	-	-	-	-	-	-	-	-	-	-	13	-	11
D 21	-	-	-	-	-	-	-	-	-	16	-	-	-	-	-
E 22	-	-	-	-	-	-	-	-	12	-	-	-	-	-	-
E 23	8	-	-	-	-	-	-	-	-	-	-	-	3	-	-
E 24	-	-	-	-	-	-	-	-	13	-	-	-	-	-	-
E 25	-	-	-	-	-	-	3	21	11	2	-	-	4	-	-
E 26	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-
E 27	-	-	-	-	-	-	-	-	7	-	-	-	-	-	-
E 28	-	-	-	-	-	-	-	7	-	-	-	-	-	-	-
Communities of the fixed dunes															
F 29	12	13	14	13	11	24	6	-	-	7	5	8	26	8	12
F 30	16	12	2	-	5	-	12	-	-	-	-	8	6	-	3
F 31	-	-	-	-	7	-	-	-	-	-	-	3	-	-	-
G 32	-	1	-	-	-	-	-	-	-	-	-	-	-	-	13
H 33	-	-	-	-	-	-	5	-	-	-	-	-	7	-	-
H 34	-	-	-	-	-	-	-	-	-	-	-	-	8	-	-
I 35	-	-	-	-	-	-	-	-	-	-	7	-	-	-	-
J 36	-	-	-	-	-	-	-	-	-	-	-	-	2	7	-

The thicket vegetation of the sheltered and especially of the stabilized areas appears also as a transition, i. e. between the coastal thickets of the Gulf and those of the Caribbean. Some of the dominating species reach their distribution limit here, or their accompanying species change. Also, variation in such divergent factors as soil development, on places where succession proceeds, degree and type of disturbance, availability of propagules (fruit production and dispersion, formation of seed banks) and attributes of the species that allow them to reach, colonize and reproduce successfully in an area (Doing 1981; Guevara 1982), make that thickets are very variable communities, that differ from site to site (Moreno-Casasola 1988).

Only a few community types are exclusive to the dunes of the study area, notably some types of the *Bidens* group: *Passiflora foetida* and *Panicum amarum*.

The floristic variation within the study area can also be indicated by summarizing the distribution of all 190 species encountered in any of the dune relevés; only 70 species or 37 % are shared by Tabasco and Campeche, 57 species were only found on Tabasco dunes and 63 only on Campeche dunes.

The following species distribution patterns along the coast may be discerned:

1. Gulf species, disappearing towards the Caribbean. Examples are: *Casearia nitida*, *Cissus sicyoides*, *Cytharexyllum berlandieri*, *Paspalum geminatum*, *Phoradendron tamaulipense*, *Serjania racemosa*, *Verbesina persicifolia*.
2. Caribbean species reaching their northern distributional limit in Campeche: *Agave angustifolia*, *Ambrosia hispida*, *Metopium brownei*, *Suriana maritima*, *Tournefortia gnaphalodes*. Some species of this group have some isolated localities in the northern Gulf of Mexico: *Scaevola plumieri*, *Coccoloba uvifera*.
3. Tabasco species (only few): *Brachiaria mutica*, *Vernonia cinerea*.
4. Campeche species (only few): *Oenothera laciniata*, *Cydista diversifolia*.

Appendix 1. Description of localities

a. *State of Tabasco*. Narrow beaches, low beach-ridge dune systems, 80 - 300 m wide, mostly siliceous sand. Usually coconut plantations behind the dunes.

1. Cuahtemozing, at Barra de Tonala (18 ° 13' N, 94° 06') near the River Tonala. The dunes are used for grazing. The beach is littered with material washed ashore (trunks, water lilies, plastic, etc.)
2. Alvaris, 30 km east of site 1 (18° 15' N, 94° 05' W); coconut plantations. Some recreation and grazing activities.
3. Pailevot, 30 km west of Barra Santa Ana (18° 17' N, 93° 55' W); coconut plantations. Local recreation, grazing and fishing activities.
4. Rancho Grande, 4 km from the detour to La Noria (18° 18' N, 93° 53' W); coconut and pepper plantations. Very flat terrain; coconuts come down almost to the beach.
5. Ostion, between Barra Tupilco and Barra Chiltepec (18° 26' N, 93° 35' W), with coconut plantations; fishing activities.
6. Las Flores, also between Barra Tupilco and Barra Chiltepec (18° 26' N, 93° 21' W), with coconut plantations; fishing activities.
7. Jalapita, east of Barra Chiltepec (18° 26' N, 93° 0' W); recreation activities including installations.
8. Vellizia, km 68 on the road from San Pedro and San Pablo to Frontera (18° 32' N, 92 45' W); disturbed area, cutdown and at the time of sampling lacking woody vegetation.
9. Estrella, east of Barra Frontera, close to Pico del Buey (18° 40' N, 92° 45' W), coconut plantations. No ridges, covered by herbaceous species; grazing and accumulation of material washed ashore.

b. State of Campeche: narow beaches, low ridge dune systems 20-500 m wide, mostly calcareous sand.

10. Emiliano Zapata, east of Barra San Pedro and San Pablo (18° 33' N, 92° 10' W), on the detour to Nuevo Progreso, coconut plantations, fishing activities; accumulation of material on the beach.
11. Santa Rita, 4 km west of Ciudad del Carmen (18° 07' N, 91° 37' W), oil-drilling installations.
12. Puerto Real, 30 km. east of Isla del Carmen, 3 km from Barra Puerto Real (18° 07' N, 91° 34' W); recreation activities.
13. Isla Aguada, 10 km west of Campeche (18° 45' N, 91° 30' W); access through coconut plantations.
14. Isla 26 km east of Isla Aguada, between Sambacuy and Champoton (19° 0' N, 91° 28' W); very narrow, without dunes.
15. Champoton, 95 km east of Isla Aguada, between Sabancuy and Champoton (federal road to Campeche- 19° 02' N, 90° 02' W); coconut plantations.

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