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Environmental filtering and plant functional types on Mexican foredunes along the Gulf of Mexico¹

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Abstract: Ecological theory suggests that environmental filtering (the survival or elimination of species in the community in response to environmental constraints) is a key process in the species assemblages of communities. Environmental filters, such as sand movement and soil salinity in coastal dunes and beaches, may result in shared ecological tolerances and functional types, independently of phylogenetic and evolutionary history. In 19 beach–foredune sites located along the coast of the Gulf of Mexico we studied plant functional composition and diversity of vascular plants. Functional groups were determined with a classification analysis. Relative importance values and diversity indices of species and functional groups were compared with ANOVA tests. We distinguished 5 groups: a group of species tolerant to soil salinity and burial, most abundant on accreting beaches; a group of species tolerant only to burial, which were abundant on all coasts; and 3 groups that lacked specific responses to burial and soil salinity and were most abundant on stable and erosive coasts. Accreting foredunes showed the lowest species richness and functional diversity, because only a few species were tolerant to burial and soil salinity. In the foredune environment, sediment dynamics and geomorphological processes act as environmental filters that largely determine the floristic and functional composition of the community.

Keywords: coastal dune, environmental filters, functional diversity, plant traits, sedimentary dynamics, species diversity.

Résumé : La théorie écologique suggère que le filtrage environnemental (la survie ou l'élimination d'espèces dans la communauté en réponse aux contraintes environnementales) soit un processus clé des assemblages d'espèces dans les communautés. Les filtres environnementaux comme le mouvement du sable et la salinité du sol dans les dunes côtières et les plages peuvent conduire à des tolérances écologiques et des types fonctionnels partagés, indépendamment de l'histoire phylogénétique et évolutive. Dans 19 sites d'avant-dunes - plages le long de la côte du golfe du Mexique, nous avons étudié la composition fonctionnelle des végétaux et la diversité de plantes vasculaires. Les groupes fonctionnels ont été déterminés par une analyse de classification. Les importances relatives et les indices de diversité d'espèces et de groupes fonctionnels ont été comparés avec des tests d'ANOVA. Nous avons distingué 5 groupes d'espèces : 1) tolérantes à la salinité du sol et à l'ensevelissement, plus abondantes sur les plages en accrétion; 2) uniquement tolérantes à l'ensevelissement, abondantes sur toutes les côtes; 3-5) n'ayant pas de réponses spécifiques à l'ensevelissement et à la salinité du sol, plus abondantes sur les côtes stables et celles en érosion. Les avant-dunes en accrétion présentaient les plus faibles richesses en espèces et diversité fonctionnelle puisque seulement quelques espèces étaient tolérantes à la salinité du sol et à l'ensevelissement. Dans les environnements d'avant-dunes, la dynamique sédimentaire et les processus géomorphologiques agissent comme des filtres environnementaux déterminant en grande partie la composition floristique et fonctionnelle de la communauté.

Mots-clés : diversité d'espèces, diversité fonctionnelle, dune côtière, dynamique sédimentaire, filtres environnementaux, traits des plantes.

Nomenclature: Cronquist, 1981.

Introduction

One of the focal topics in ecology is identification of the mechanisms that determine the species composition and structure of natural communities. Ecological theory has suggested environmental filtering as a key process to explain this (Keddy, 1992). Environmental filtering refers to the survival and persistence of certain species in the community and the elimination of others in response to environmental constraints. This filtering reduces the variety of trait values and reflects shared ecological tolerances (Cornwell, Schwillk & Ackerly, 2006; Kraft, Valencia & Ackerly, 2008; Mayfield, Boni & Ackerly, 2009), and shared structural and functional attributes, independently of the phylogenetic and

evolutionary history of the species involved. These groups of species are known as functional types or groups (Westoby, 1999; Wilson, 1999; Duckworth, Kent & Ramsay, 2002). Environmental filtering leads to the coexistence of a suite of species (functional types) on a given site (Cornwell, Schwillk & Ackerly, 2006). Functional traits can thus be used to interpret and predict community behaviour and ecosystem functioning (Díaz & Cabido, 2001).

The functional type approach has been applied in a diverse array of ecosystems, such as temperate forests (Wramneby *et al.*, 2008), grasslands (Phoenix *et al.*, 2008), tussock tundras (Chapin *et al.*, 1996; Bret-Harte *et al.*, 2008), tropical rain forests (Condit *et al.*, 2000), and along moisture gradients (Zelnik & Carni, 2008). In coastal dune plants, Shao, Shugart, and Hayden (1996) used Plant Functional Types (PFTs) to assess the response of barrier

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island vegetation to climate change, while García-Mora, Gallego-Fernández, and García-Novo (1999; 2000) followed this approach to describe the responses of foredune plants to environmental stress and disturbance. Stallins (2002; 2005), Stallins and Parker (2003), and Miller, Gornish, and Buckley (2010) related PFTs with the movement of sediments and modification of dune topography. Feagin and Wu (2007) used PFTs to study plant succession and the response to disturbance regimes of different PFTs. Finally, Zunzunegui *et al.* (2005) focused on how PFTs responded to water stress. In coastal ecosystems, the extreme abiotic factors of the communities closest to the sea, such as soil salinity and substrate mobility (Maun, 2004) may represent environmental filters constraining survival and persistence of individuals bearing specific “response traits” while leading to the local extinction of those unable to thrive in this environment (Keddy, 1992; Carboni, Santoro & Acosta, 2010).

In dynamic coastal ecosystems, these functional groups may change as the successional sequence takes place (Feagin & Wu, 2007), and they are also determined by the spatial and temporal variability of the geomorphological processes to which beach–foredune vegetation is closely related (García-Mora, Gallego-Fernández & García-Novo, 1999; Hesp & Martínez, 2007; da Silva *et al.*, 2008). Geomorphological processes are determined by the local sediment budget. Depending on the balance of erosion / stability / accretion processes, the beach–foredune complex will be, respectively, erosive, stable, or accreting, and the constraining environmental conditions will vary accordingly. Because tolerance to burial by sand and to soil salinity varies among species, it is reasonable to expect that the different types of coastal sedimentary dynamics (erosive, accreting, or stable) will play an important role in the plant functional types that thrive in the beach–foredune environment (García-Mora, Gallego-Fernández & García-Novo, 1999; Feagin & Wu, 2007).

Different studies have shown that, frequently, plant functional diversity increases with species diversity (Lloret & Vila, 2003). However, this does not seem to hold true for coastal dune vegetation. For instance, in the harsh beach–foredune–coastal dune environment, plant diversity ranges from low to moderately high but the plant community is functionally redundant, with taxonomically different species exhibiting similar ecological functions (Moreno-Casasola, 1986; Moreno-Casasola & Espejel, 1986; Hesp, 1988; Lawton & Brown, 1993; Naeem, 1998; da Silva *et al.*, 2008). When sedimentary dynamics change and the coastline becomes stable, environmental conditions may be improved (less substrate mobility), resulting in higher species diversity (Hesp, 1988; da Silva *et al.*, 2008). Nevertheless, functional diversity may sometimes not increase, as some attributes (*i.e.*, tolerance to soil salinity and burial) are progressively lost because of competitive replacement of tolerant species by more effective competitors (García-Mora, Gallego-Fernández & García-Novo, 1999; Martínez, Vázquez & Sánchez-Colón, 2001; Carboni, Santoro & Acosta, 2010).

In this paper, foredune vegetation along the Gulf of Mexico (Mexico) is examined to compare and contrast the occurrence and dominance of different PFTs in relation

to foredune dynamics. Specifically, the objectives of this study were 1) to identify those PFTs occurring on Mexican foredunes along the Gulf of Mexico; 2) to examine whether foredune sedimentary dynamics affected species and functional diversity; and 3) to determine if the abundance of particular traits can be related to the sedimentary dynamics of the beach–foredune environment. Our working hypotheses were that a) the constraining conditions of the beach–foredune environment would select functional groups where tolerance to burial by sand and soil salinity are predominant features; b) species and functional diversity would be higher in eroding foredunes, because a mixture of merely coastal and inland species would coexist; and c) attributes such as tolerance to burial would be more abundant on accreting beaches, where burial by sand is a recurring disturbance. We also hypothesized that dispersal by ocean currents would be a recurring trait in those species tolerant to soil salinity (Woodell, 1985).

Methods

STUDY AREA

The coastline of the Gulf of Mexico is highly diverse, with coastal forms ranging from small dunes with narrow sandy beaches to large and high dunes with wide sandy beaches. The climate may be tropical humid, with a mean annual temperature of 25 °C and total average yearly precipitation of 2150 mm, or sub-tropical semi-humid, with a mean annual temperature of 22 °C and a total average yearly precipitation of 1000 mm (Martínez, Valverde & Moreno-Casasola, 1992). The rainy period occurs mostly during the summer and early fall (June to September). In the winter (November to February), strong northerly winds favour along-shore sand movement. Tourism and urban development along the coast are also highly variable in density and intensity. The vulnerability of coastal dunes along the Mexican Gulf of Mexico varies depending on the local geomorphological dynamics and the intensity of human impact (Martínez *et al.*, 2006).

The vegetation patterns of coastal dunes along the Gulf of Mexico have been studied by Moreno-Casasola (1988), Moreno-Casasola and Espejel (1986), and Castillo and Moreno-Casasola (1998). Moreno-Casasola and Espejel (1986) found that coastal dune vegetation along the Mexican coast of the Gulf of Mexico can be grouped into 3 large regions: Northern Gulf, Central Gulf, and Caribbean. Sand is siliceous in the Northern and Central Gulf regions, and it is calcareous in the Caribbean region. In the Northern Gulf region, *Ipomoea imperatii*, *I. pes-caprae*, *Uniola paniculata*, and *Panicum amarulum* are the dominant species. In the Central region, both *Ipomoeas*, *Canavalia rosea*, *Croton punctatus*, *Chamaecrista chamaecristoides*, and *Palafoxia lindenii* abound (the last 2 are Mexican endemics; *Chamaecrista* is found along the Gulf of Mexico and at some locations in the Pacific, whereas *Palafoxia* is exclusive to the Central Gulf region). Also, relatively tall shrub (*Coccoloba barbadensis*, *Chrisobalanus icaco*) and tree species (*Diphyssa robinoides*, *Cedrella odorata*, and *Bursera simaruba*) are found in the Central Gulf of Mexico region. In the Caribbean region, species such as *Tournefortia gnaphaloides*, *Cakile maritima*, and *Cocotrinax* sp. are very abundant.

FIELD SAMPLING

Nineteen beach–foredune locations were selected along the coast of the Gulf of Mexico according to their morpho-sedimentological features (accretional, stable, or erosional) (Carter, 1995). The locations covered 902 km of coastline from the state of Tamaulipas to the state of Tabasco (Figure 1). There were 2 restrictions to this selection. First, the coastal city of Veracruz was not considered because its coastline is totally urbanized, the beach is narrow and artificially maintained, and there are practically no foredunes or natural vegetation left. Secondly, the coastline between the city of Veracruz and Coatzacoalcas was not sampled because of its volcanic features, with scarce sandy beaches and no foredunes. In each of the selected locations we had from two to four 200- to 300-m segments where vegetation was sampled (Figure 1). Thus, we had a total of 47 plots distributed along the 19 study sites (16 accreting, 16 stable, and 15 erosive).

Foredune sedimentary dynamics were inferred qualitatively at each site. Accreting beach–foredunes ($n = 16$) were those with evident sand input, and with newly developed embryo dunes (nebkas) around litter or vegetation stems. The beach at these locations was wide (> 30 m), and abundant nebkas were observed. Foredunes with evidence of erosion ($n = 15$) had cliffs on the dune

face, plants with undermined roots, and new blowout development. The beach in these locations was < 10 m wide and totally lacked nebkas, or any evidence of sand accumulation. Finally, foredune systems were considered “stable” when neither evident accretion nor erosion was noticed according to the above-mentioned features ($n = 16$). The potential alternation of accretion and erosion was evaluated through subsequent visits to the study sites. In general, we observed that the sedimentary dynamics (erosive or accreting) remained the same during different periods throughout the year. Furthermore, more recent studies (Jiménez-Orocio, 2010) analyzed long-term changes in the coastline by means of comparing aerial photographs from different dates. These studies confirmed our field assessment of sedimentary status. Jiménez-Orocio (2010) found long-term erosion or accretion in the same study sites we had, which coincided with our qualitative assessment. Hence, although we did not measure sand movement at each site, we had indirect evidence of the overall accretion–erosion processes at the coast.

Field work took place at the end of the rainy season, in September. In each location, plant species composition was recorded by sampling two 10×25 -m plots that were randomly located on the seaward slope of the foredune (between the seaward vegetation limit and the foredune crest), avoiding the inclusion of secondary dunes or any other inland vegetation. The longest axis was laid parallel to the shore. In each plot, relative cover of each species (0–100%) and percentage of bare sand (0–100%) were estimated. Plant species were collected, identified, and deposited at the XAL herbarium (Instituto de Ecología, AC, Xalapa, Veracruz, Mexico). Relative Importance values were calculated by adding relative frequency (proportion of plots where a species occurred) and relative cover (proportional cover per species, relative to plant cover [all species] per plot). The result was then divided by 2 in order to produce a maximum value of 1, which facilitated comparisons between species and study sites (Brower & Zar, 1977).

PLANT FUNCTIONAL TYPES

Because the functional attributes to be used to determine plant functional types must be linked to the functional response of interest (Leishman & Westoby, 1992; Chapin *et al.*, 1996; Díaz & Cabido, 1997; Fonseca & Ganade, 2001; Lavorel & Garnier, 2002), we selected a set of traits that fits our case study species, which were rather different from those considered in other similar studies (García-Mora, Gallego-Fernández & García-Novo, 1999; Feagin & Wu, 2007). Thus, due to their significance for exposed coastal environments along the shorelines of the Gulf of Mexico, we selected burial resistance, dispersal by sea water, soil salinity resistance, and type of below-ground structures as the traits that determined functional groups. These traits were selected because only those plants with a certain set of attributes are able to thrive in the beach-dune environment, with sand input, the possibility of dispersal by ocean currents, inundations, and substrate mobility. Burial by drifting sands is the prime factor that limits plant growth on coastal foredunes (Moreno-Casasola,

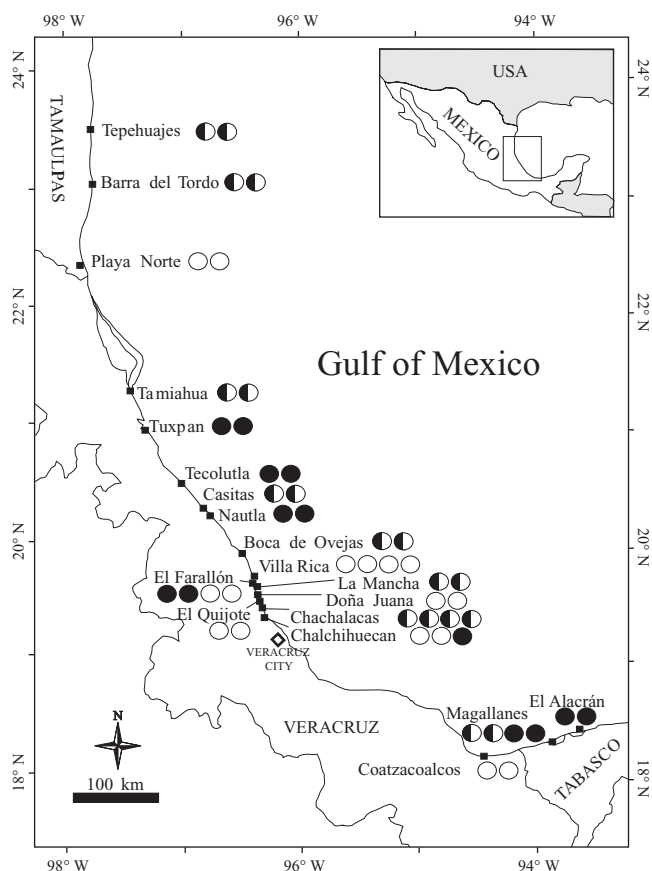


FIGURE 1. Location of the study sites along the Gulf of Mexico. Filled circle = eroding foredunes; blank circle = accreting foredunes; and half-filled circle = stable foredunes. The number of sampled plots is indicated by the number of circles in each location.

1986; Maun & Perumal, 1999), and coastal dune plants are tolerant to and are even stimulated by burial (Martínez & Moreno-Casasola, 1996; Maun, 1998; Gilbert, Pammenter & Ripley, 2008). Similarly, soil salinity is a dominant feature of the beach and foredunes in which species are able to thrive (Woodell, 1985; Maun, 1998; Wilson & Sykes, 1999) by means of several tolerance mechanisms (such as salt accumulation in plant tissues) and also by taking advantage of dispersal by ocean currents (Harris & Davy, 1986a). Below-ground traits were selected because they are considered to be useful for erosive conditions (Maun, 1998).

In addition, we considered the very dynamic nature of the vegetation growing on coastal dunes as complementary attributes to be considered in the functional type analysis. The recurring disturbances that constantly take place in these environments lead to repeated local extinctions of populations (García-Mora, Gallego-Fernández & García-Novo, 1999). Hence, the floristic composition of these plant communities is the result of their disturbance history, species availability, and the life history attributes of the species colonizing and reproducing successfully in that particular environment. Based on the above, we considered growth form (herb, vine, shrub) as an additional trait. Herbaceous species are better able to thrive after recurring disturbances than woody shrubs and trees (Castillo & Moreno-Casasola, 1998) and hence growth form can be used as a proxy to infer tolerance to recurring disturbances (Table I). Vegetative reproduction and growth form were considered relevant attributes because they are helpful in responding to disturbance events (*i.e.*, burial, recolonization after erosion) (Harris & Davy, 1986b; Maun, 1998; Klimesova & Klimes, 2007). We did not distinguish between life histories of our study species, because there is only 1 annual species in our study site (*Triplasis purpurea*). This was not sufficient to use life history as an attribute determining functional traits.

Each trait was evaluated as follows: tolerance to burial and soil salinity were assessed by consulting the literature reporting greenhouse experiments (*i.e.*, Martínez, Valverde & Moreno-Casasola, 1992; Martínez, Moreno-Casasola & Vázquez, 1997) or studies providing a review of these responses (López-Rosas, 1999). Dispersal by ocean currents was determined through field observations in which we observed propagules of different species (seeds,

branches) in the debris located at the high tide water level. Finally, below-ground structures, vegetative reproduction, and growth form were observed directly in the field. Each functional attribute of each species was evaluated with binary values (1 present, 0 absent). We are aware that this approach is extremely simplified, since plants are not either “salt tolerant” or “salt intolerant”, nor are they either “sand burial resistant” or “sand burial intolerant”. Certainly, there are different levels of tolerance that are not reflected in our binomial categories. In spite of this drawback, we chose to narrow the levels in our functional attributes to only 2 because, for many species, the lack of available information does not warrant a larger set of categories. Thus, we think that until more information is generated for our study species, this was an acceptable option to test our hypotheses.

DATA ANALYSIS

Once each species was assigned a binary value in every functional trait, the PFTs were obtained by assembling groups of species according to their biological traits (Keddy, 1992; Lavorel *et al.*, 1997). These groups were generated by means of a Ward-type ascending hierarchical classification analysis (Relative Euclidean distance) applied on the matrix data of plant biological traits (48 species \times 6 traits) (PC-Ord). The different groups were selected based on the resulting dendrogram and similarity values reported with this analysis.

Once we had PFTs defined, we examined the relative occurrence of PFTs in each plot and at each site in order to test the response of foredune PFTs to sedimentary dynamics. We thus calculated the relative cover of each functional type by adding the relative percent cover of all the species within each group per site and then averaging such cover for all the sites with similar sediment dynamics. By doing this we were able to test if the relative abundance of each PFT was related to foredune sedimentary dynamic types. We also created a matrix with the abundance of each trait in each plot by multiplying the plant species data matrix (plant cover per species) by the traits data matrix (traits per species). Differences in the relative occurrence for all groups and traits among sedimentary dynamic types were analyzed using one-way ANOVA, followed by a multiple comparison Bonferroni test in those cases where significant effects of sedimentary types were detected. When variables did not have a normal distribution we used non-parametric Kruskal–Wallis tests.

DIVERSITY INDICES

For each sampled plot, diversity was calculated based on 2 criteria: species and functional traits. Species composition was analyzed through species richness (S: number of species per plot) and species diversity, which was calculated with the Shannon diversity index (H') (Magurran, 2004). The functional components of diversity (diversity related to functional traits) (Díaz & Cabido, 2001) were estimated through a) species richness in each functional group; b) functional richness (FR); and c) functional composition (FC). Functional richness was defined as the total number of PFTs per plot. Functional composition, the presence and relative abundance of PFTs per plot, was defined as the Shannon diversity

TABLE I. List of traits and description of their assessment in response to the most dominant constraining factors on foredunes.

Traits	Class description	Constraint factor
Burial resistance	Present <i>versus</i> absent	Sand input
Dispersal by sea water	Present <i>versus</i> absent	Linear habitat
Salinity resistance	Present <i>versus</i> absent	Sea-water and sea-spray
Below-ground structure	Shallow fibrous <i>versus</i> deep and thick	Substrate mobility
Vegetative reproduction	Present <i>versus</i> absent	Exposure to stress (disturbance intensity)
Growth form	Herbaceous <i>versus</i> shrub, tree	Recurring disturbances

index of PFTs for each plot and calculated from the cover estimations per trait as follows:

$$H' = -\sum p_i \log_2 p_i$$

p_i being the sum of the relative plant cover values for all species belonging to PFT_{*i*}.

A one-way ANOVA, followed by a multiple comparison Bonferroni test, was performed to test for differences between diversity indices calculated for each location with different sedimentary dynamics. Again, we used non-parametric Kruskal–Wallis tests when our variables did not have a normal distribution.

Results

COMMUNITY COMPOSITION AND STRUCTURE

We found a total of 50 vascular species belonging to 23 Families (Appendix I). Of these, Poaceae, Fabaceae, and Asteraceae had the largest number of species (12, 6, and 5, respectively). Two Mexican coastal dune endemic species (*Chamaecrista chamaecristoides* and *Palafoxia lindenii*) were recorded in 7 and 12 sites, representing, respectively, 27 and 46% of all sampled sites. In contrast, and coexisting with the endemics, 4 exotic species (*Casuarina equisetifolia*, *Arundo donax*, *Cynodon dactylon*, and *Cocos nucifera*) were observed growing on the foredune area of 17 locations (65% of the study sites). *Casuarina equisetifolia* and *Cocos nucifera* were not used for the data analysis because they were deliberately introduced by humans, and their cover was rather low in our plots.

Species composition and relative abundance varied significantly among the foredunes located on beaches with different sedimentary dynamics. Specifically, species richness and diversity were significantly lower on accreting foredunes than on stable or eroding foredunes (Table II). Beach and foredune pioneer species showed the highest relative importance values on all foredune types (Figure 2). However, the ranking between them was different: on accreting foredunes *I. pes-caprae* was clearly dominant (importance value was higher than 70%), followed by *Croton punctatus* and *Palafoxia lindenii* and then *S. portulacastrum* and *S. virginicus*. In contrast, 3 species, *C. punctatus*, *S. virginicus*, and *I. pes-caprae*, were

co-dominant on stable foredunes, but their importance values were much smaller (45%). Species typical of mobile dunes (the Mexican endemics *Palafoxia lindenii* and *Chamaecrista chamaecristoides*) were also relatively important on these stable beaches. Dominant species on eroding foredunes were slightly different: *C. punctatus*, followed by *I. imperati* and *S. virginicus*. *Ipomoea pes-caprae* was also found on these foredunes, but with a much lower importance value (25%). *Palafoxia* had a significantly reduced importance, and *Cenchrus echinatus*, a typically inland species, had an increased importance.

IDENTIFICATION OF PLANT FUNCTIONAL RESPONSE GROUPS

We distinguished 5 groups according to the cluster classification of the traits × species matrix (Figure 3). The cluster classification of the traits and species was independent of taxonomic affiliation. At the first division level, the analysis separated species according to their growth form, and thus herbs and woody species were located in different groups; most woody species (except for the 2 endemic shrubs) belong to Group 5. Herbaceous species were further grouped according to their tolerance to sand burial (Groups 1 and 2 were tolerant, and Groups 3 and 4 were not). Those species tolerant to burial were additionally separated according to their tolerance to soil salinity and dispersal by ocean currents. Finally, based on the presence of below-ground structures, species not tolerant to burial were further divided into 2 more groups (3 and 4).

Group 1 contained important dune builder species such as *Ipomoea pes-caprae*, *Sesuvium portulacastrum*, and *Uniola paniculata*, as well as species that are tolerant to burial by sand (*I. stolonifera*, *Canavalia rosea*, *Sporobolus virginicus*, *Okenia hypogaea*, and *Amaranthus greggii*). Four are creeping vines and the rest are erect; *Okenia* is the only annual. *Arundo donax*, an exotic species found on European coastal dunes (García-Mora, Gallego-Fernández & García-Novo, 1999), was also associated with this group. Group 2 included herbs and the 2 endemic shrubs that are tolerant to sand burial and have vegetative reproduction and shallow fibrous below-ground structures (10 species) but no specific adaptations to soil salinity. These are all species typical of foredunes and inland coastal dunes (stabilized and mobile), all located far from the maritime influence (soil salinity) (Moreno-Casasola & Espejel, 1986). Two relevant shrubby species were included in Group 2: *Croton punctatus*, a very good dune builder, and *Chamaecrista chamaecristoides*, the most important dune stabilizer on the mobile dunes of Veracruz (Moreno-Casasola & Espejel, 1986). Additional species are either dune fixer herbs (*Oenothera drummondii*, *Palafoxia lindenii*, and *Trachypogon plumosus*) on active dunes or species typical of grasslands from both active or semi-mobile dunes (*Cnidosculus texanus*, *Schizachyrium scoparium*, *Palafoxia texana*, *Pectis satirejoides*, and *Triplasis purpurea*). Herbs without any specialized traits for the dune environment were grouped together in Group 3 (8 species). Group 4 contained herbaceous species that are able to reproduce vegetatively and have a spreading below-ground network of rhizomes but lack any specific response to the beach–foredune

TABLE II. Mean values of species and functional diversity in study sites with different foredune sedimentary dynamics. Different letters indicate significant differences between dynamic type at $P < 0.05$ (one-way ANOVA followed by a multiple comparison Bonferroni test). S = species richness; H' = Shannon diversity index; FR = functional richness (number of functional types); FC = functional composition (presence and relative abundance of plant functional types per plot). N = number of total species registered in each foredune type. *** $P < 0.001$.

Dynamic type	n plots	N species	Species diversity		Functional diversity	
			S	H'	FR	FC
Accreting	16	15	3.8 ^a	1.38 ^a	2.38 ^a	0.79 ^a
Stable	16	38	9.4 ^b	2.69 ^b	3.94 ^b	1.54 ^b
Erosive	15	38	8.0 ^b	2.47 ^b	3.60 ^b	1.49 ^b
P			***	***	***	***

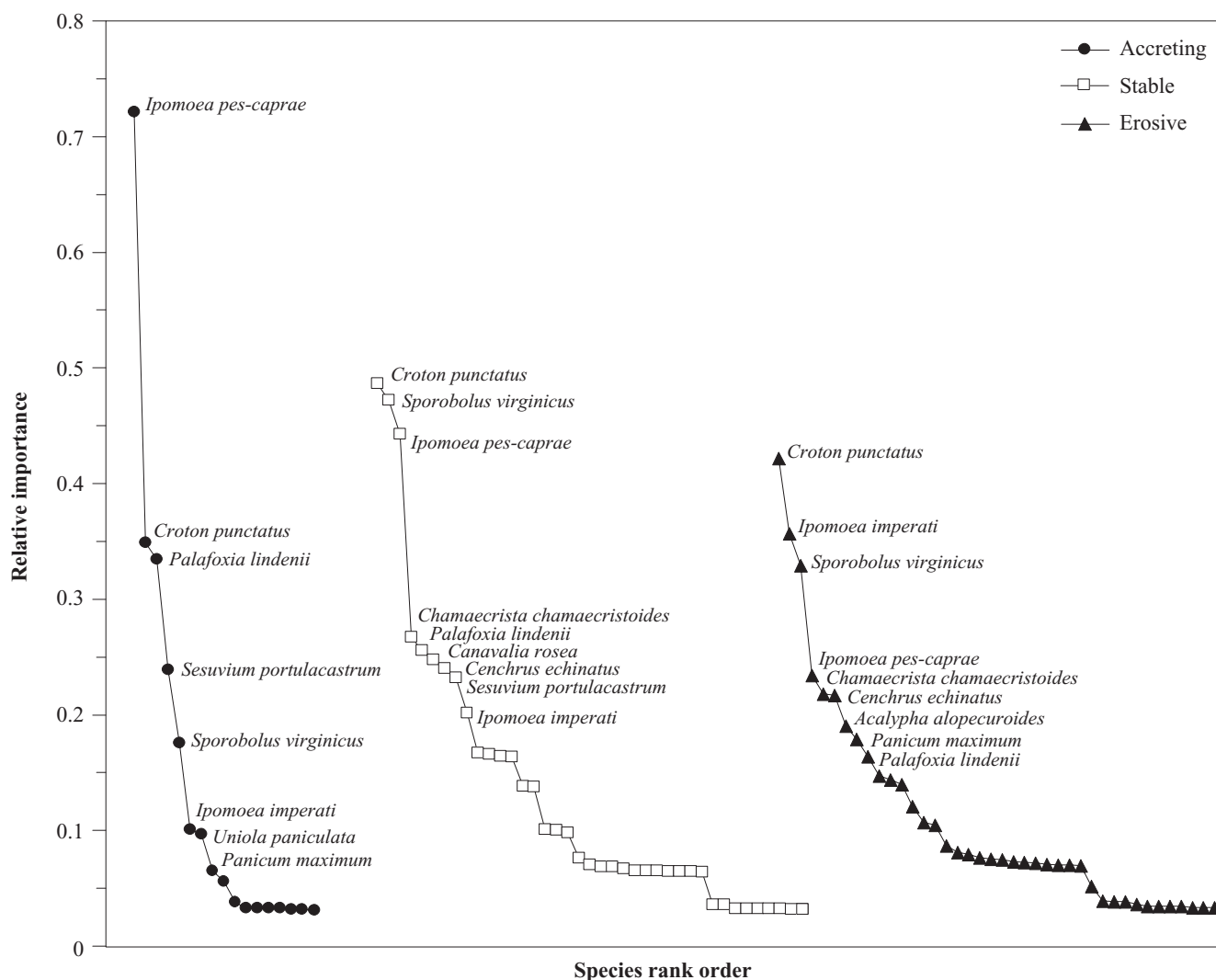


FIGURE 2. Ranking of species occurring on foredunes with different sedimentary dynamics, in terms of the relative importance values of the species.

environment (14 species). Species of Group 4 are not able to withstand soil salinity and burial by sand and seldom occur on mobile dunes. Finally, shrubs or trees species with a below-ground network of rhizomes were allocated to Group 5 (7 species).

RESPONSE OF PFTs TO FOREDUNE DYNAMICS

We observed that the relative occurrence of PFTs differed according to foredune dynamics (Figure 4). Group 1 showed the highest cover values on accreting foredunes. The proportion of Group 1 species was almost double that recorded on stable or erosive coasts ($F_{2,46} = 7.769$; $P = 0.001$). The relative abundance of Group 2 showed no significant differences among foredune sedimentary dynamic types ($F_{2,46} = 1.546$; $P = 0.224$). Groups 3, 4, and 5 showed the lowest proportional cover on accreting foredunes but were more abundant on stable and erosive coasts (Group 3: $F_{2,46} = 5.210$, $P = 0.009$; Group 4: $F_{2,46} = 9.375$, $P < 0.0001$; Group 5: $F_{2,46} = 3.748$, $P = 0.031$).

Species richness in each functional group (Rg) also differed among foredune dynamic types (Figure 5)

(Group 1: $F_{2,46} = 4.028$, $P = 0.025$; Group 2: $F_{2,46} = 5.396$, $P < 0.008$; Group 3: $F_{2,46} = 3.459$, $P = 0.040$; Group 4: $F_{2,46} = 10.842$, $P < 0.0001$; Group 5: $F_{2,46} = 3.812$, $P = 0.030$). In all cases, stable foredunes had higher species richness per functional group than accreting foredunes and were relatively similar to erosive dunes. Also, in all cases, Group 1 included the largest number of species. Accreting dunes had significantly lower species richness in functional groups 3, 4, and 5. In contrast, the mean relative abundance of each trait was highest on accreting foredunes (Table III). Stable and erosive foredunes had similar lower relative abundance values in all the studied traits, but in general, accreting foredunes showed the lowest relative cover of all traits that we considered in this study.

SPECIES AND FUNCTIONAL DIVERSITY OF FOREDUNE COMMUNITIES

Significant differences were observed in terms of species richness and diversity indices between accreting foredunes and the other 2 sedimentary dynamics types (Table II). Accreting foredunes had the lowest values of

species richness and species diversity, whereas stable and erosive foredunes had double the species richness and diversity. Similarly, functional diversity indices differed significantly between accreting foredunes and stable or erosive foredunes (Table II). Accreting foredunes had the lowest values in terms of the occurrence of different functional groups per plot (FR). Likewise, stable and erosive foredunes had larger relative presence and abundance of functional groups (FC). Species richness and diversity, as well as functional diversity, were lowest on accreting foredunes.

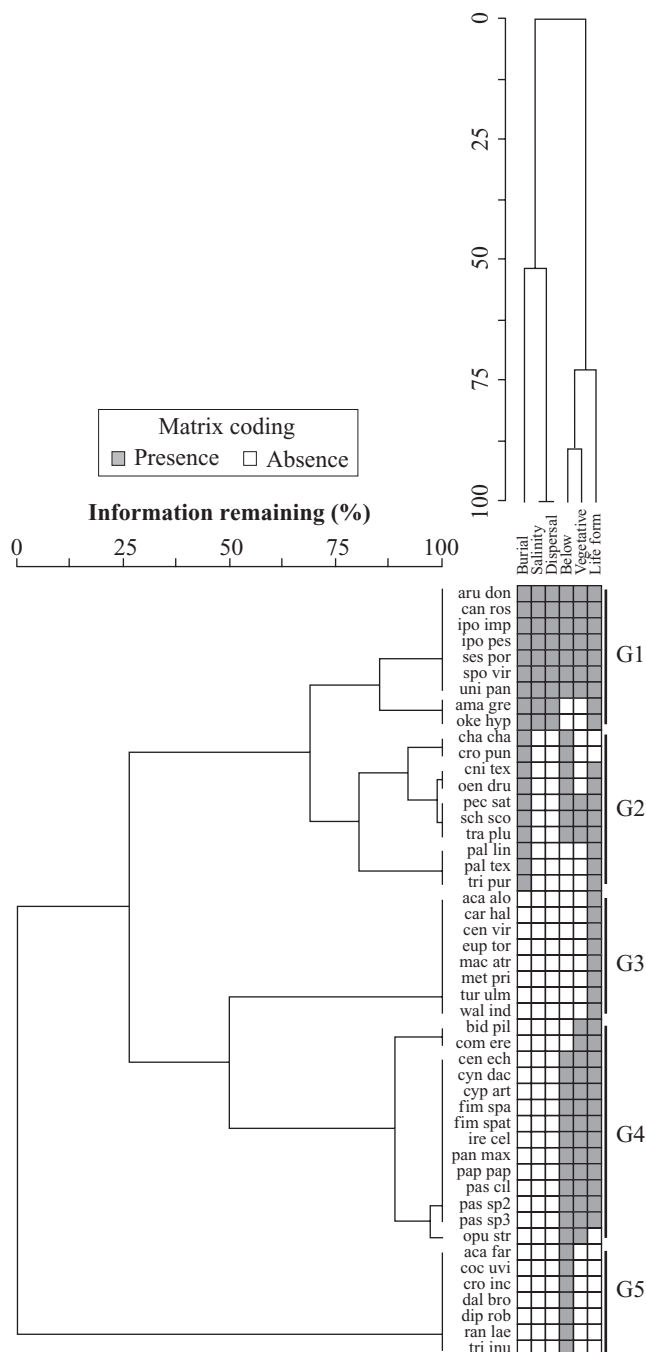


FIGURE 3. Cluster analysis with the species classified according to their functional traits. Full species names can be found in Appendix I.

Discussion

ENVIRONMENTAL FILTERING AND FUNCTIONAL GROUPS

Environmental filtering may be studied by comparing traits and plant functional types in response to specific environmental constraints. The 48 vascular plant species that we found were grouped into 5 functional types, independently of their phylogenetic origin and biogeographic history, according to their responses to environmental filters (Lavorel *et al.*, 1997; Lavorel & Garnier, 2002; Mayfield, Boni & Ackerly, 2009), especially sedimentary dynamics and soil salinity.

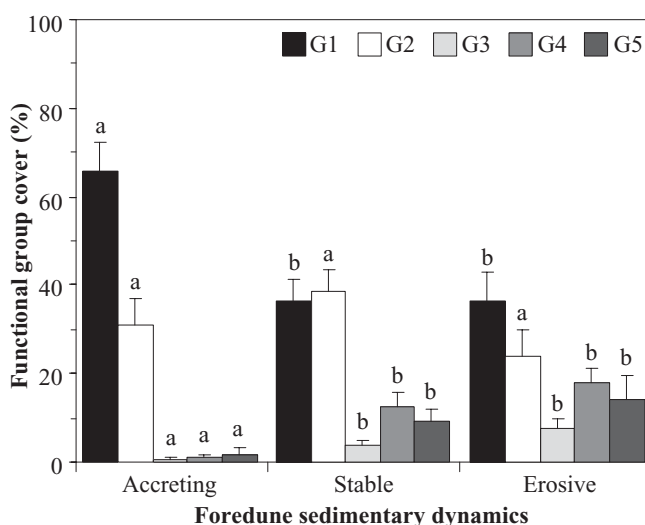


FIGURE 4. Mean relative cover of each functional group on foredunes with different types of sedimentary dynamics. For each functional group, different letters indicate significant differences among sedimentary dynamic types at $P < 0.05$ (one-way ANOVA followed by a multiple comparison Bonferroni test).

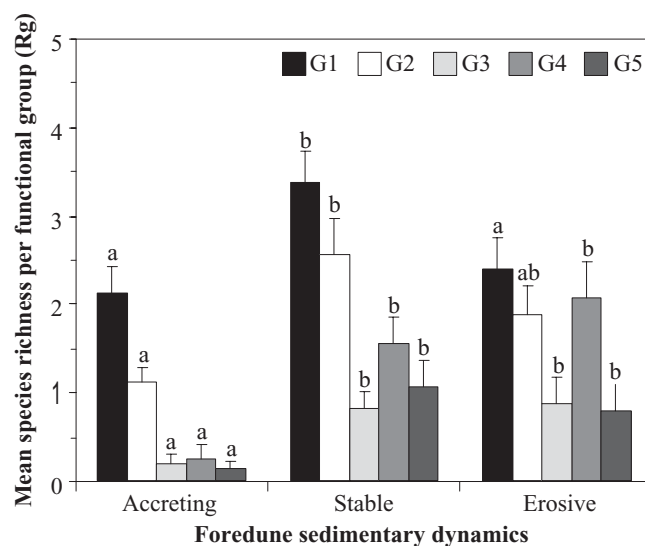


FIGURE 5. Mean species richness per functional group in foredunes with different sedimentary dynamic types. For each functional group, different letters indicate significant differences among sedimentary dynamic types at $P < 0.05$ (one-way ANOVA followed by a multiple comparison Bonferroni test).

Classification in terms of functional groups enabled us to distinguish 2 groupings according to their tolerance to burial. The first grouping, species in groups 1 and 2, contained mostly pioneer species (Moreno-Casasola, 1986) that are tolerant to sand burial and thus grow almost exclusively on coastal dunes, including foredunes and inland mobile dunes. Group 1 was composed of 9 species (19% of all the species found in our sampling) (Figure 3). All are herbs, tolerant to sand burial and soil salinity; all are dispersed by ocean currents; and most reproduce vegetatively and have a spreading below-ground network of rhizomes (López-Rosas, 1999). They are all typical of the beach–foredune environment (Moreno-Casasola & Espejel, 1986). The second large grouping comprised Groups 3, 4, and 5 and included species typical of inland environments as well as of stabilized dunes and swales (Castillo & Moreno-Casasola, 1998).

The functional types of coastal dune vegetation observed in this and other similar studies (Shao, Shugart & Hayden, 1996; García-Mora, Gallego-Fernández & García-Novo, 1999; Stallins, 2002; Feagin & Wu, 2007) are unique to each location. However, they all converge in the importance of 2 attributes: tolerance to soil salinity and to sand burial. This is not surprising since these are the 2 environmental constraints that typify the coastal setting (Moreno-Casasola, 1986; Maun, 1998; Wilson & Sykes, 1999). In this sense, it has been shown that foredune plants have the ability to tolerate burial and soil salinity; in fact, the growth of some species is even stimulated by these otherwise limiting conditions (Woodell, 1985; Hesp, 1991; Martínez, Valverde & Moreno-Casasola, 1992; Maun, 1998; Martínez & Moreno-Casasola, 1996; Maun, 2004). Additionally, along-shore geographic variation in geomorphological features, substrate mobility, and exposure to soil salinity also determines species composition and abundance, as was observed by García-Mora, Gallego-Fernández, and García-Novo (1999) and da Silva *et al.* (2008).

PLANT FUNCTIONAL TYPES AND FOREDUNE DYNAMICS

We found that the composition and relative abundance of the functional groups were associated with foredune dynamics. As expected, in all conditions of sedimentary dynamics, species from groups 1 and 2, which are tolerant to sand burial and soil salinity, were always the most

abundant functional groups because, after all, all locations were on the coast. As expected, tolerance to burial was a more abundant trait on accreting foredunes, where sand supply (and burial) is more intense. Finally, the relative abundance of groups 3, 4, and 5 was higher on stable foredunes, where substrate mobility was minimal and thus species lacking adaptations to this environmental constraint were able to colonize. Only below-ground attributes showed no significant differences between foredune types, and this was probably because these attributes are common in a variety of habitats, including both inland coastal communities, such as coastal matorrals, and tropical rain forests. Therefore, this rooting system is not considered a unique attribute of plants that occur in a coastal environment.

DIVERSITY AND FOREDUNE DYNAMICS

In studies similar to ours, Stallins (2002) and Carboni, Santoro, and Acosta (2010) observed that species diversity is lower on coastal dunes owing to the intensity of natural disturbances such as sand burial. Diversity is locally reduced because the extreme abiotic factors in communities closest to the sea represent a filtering mechanism that is too strong for incoming species lacking the particular traits required to occur and grow in the coastal environment. When environmental filters from a harsh environment are relaxed, then higher species diversity is expected because of the less severe environmental filter (Carboni, Santoro & Acosta, 2010).

Conclusion

Species composition within a community, or a functional group, is influenced by the history of species arrivals, environmental conditions, and the functional groups that can fill the available niches (Law & Morton, 1993; Díaz *et al.*, 1999; Watkins & Wilson, 2003). In the foredune environment, sediment dynamics, soil salinity, and geomorphological processes play an important role in the functional composition of the community. The extreme abiotic factors represent an environmental filter that leads to converging functional traits that assemble a community of physiologically and ecologically persisting and coexisting species.

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TABLE III. Mean relative cover (%C) of each trait per plot among sedimentary dynamics types. For each trait (row) a different letter indicates a significant difference at $P < 0.05$ between foredunes with different sedimentary dynamics (one-way ANOVA followed by a multiple comparison Bonferroni test). * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; - $P > 0.05$.

Traits	<i>P</i>	Accreting	Stable	Erosive
		%C	%C	%C
Burial	***	97.8 ^a	75.7 ^b	61.4 ^b
Salinity	**	65.7 ^a	39.0 ^b	34.9 ^b
Dispersal	**	65.7 ^a	39.0 ^b	34.9 ^b
Below-ground	-	88.1	81.1	78.5
Vegetative	*	66.7 ^a	47.7 ^b	48.2 ^b
Life form	*	88.5 ^a	65.2 ^b	66.4 ^b

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APPENDIX I. List of species considered in the study, including life form, habitat, and foredune dynamics of habitats where each species is located in the field. Life form: T = tree; H = herb; V = vine; SC = subshrub. Habitat: R = selva; Sh = shrubland; F = flooding zone; B = beach; G = grassland; D = dune. Presence of species on foredune with different sedimentary dynamics: A = accreting; S = stable; E = erosive. ** = endemic species; # = exotic species.

Species	Life form	Habitat	Foredune dynamics		
			A	S	E
<i>Acacia farnesiana</i> (L.) Willd.	T	R		+	+
<i>Acalypha alopecuroides</i> Jacq.	H	G	+	+	+
<i>Amaranthus greggii</i> S. Watson	H	B		+	
# <i>Arundo donax</i> L.	H	B	+	+	+
<i>Bidens pilosa</i> L.	H	G		+	+
<i>Canavalia rosea</i> (Sw.) DC.	V	B	+	+	+
<i>Cardiospermum halicacabum</i> L.	V	G		+	
# <i>Casuarina equisetifolia</i> L.	T	D	+	+	+
<i>Cenchrus echinatus</i> L.	H	G	+	+	+
<i>Centrosema virginianum</i> (L.) Benth.	V	Sh		+	+
** <i>Chamaecrista chamaecristoides</i> (Colladon) Greene	SC	D		+	+
<i>Cnidoscolus texanus</i> (Muell. Arg.) I.M. Johnston	H	G		+	
<i>Coccoloba uvifera</i> L.	T	G		+	+
# <i>Cocos nucifera</i> L.	T	B			+
<i>Commelina erecta</i> L.	H	G, D	+	+	+
<i>Crotalaria incana</i> L.	S	G	+	+	+
<i>Croton punctatus</i> Jacq.	SC	D, B	+	+	+
# <i>Cynodon dactylon</i> (L.) Pers.	H	G		+	+
<i>Cyperus articulatus</i> L.	H	F			+
<i>Dalbergia brownii</i> (Jacq.) Urban	V	Sh			+
<i>Diphysa robinoides</i> Benth.	SC	R			+
<i>Euphorbia torrida</i> DC.	H	B		+	+
<i>Fimbristylis spadicea</i> (L.) Vahl	H	F, B		+	
<i>Fimbristylis spathacea</i> Roth	H	F, B		+	
<i>Ipomoea pes-caprae</i> (L.) R. Br.	V	D, B	+	+	+
<i>Ipomoea imperati</i> (Vahl) Griseb	V	D, B	+	+	+
<i>Iresine celosia</i> L.	H	Sh			+
<i>Macroptilium atropurpureum</i> (Sessé & Mociño ex DC.) Urban	V	G		+	+
<i>Metastelma pringlei</i> A. Gray	V	G		+	+
<i>Oenothera drummondii</i> Hook.	H	B		+	
<i>Okenia hypogaea</i> Schldl. & Cham.	H	B	+	+	+
<i>Opuntia stricta</i> Haw. var. <i>dillenni</i> (Kerr Gawler) Benson	SC	Sh			+
** <i>Palafoxia lindenii</i> A. Gray	H	D	+	+	+
<i>Palafoxia texana</i> DC.	H	D		+	
<i>Panicum maximum</i> Jacq.	H	G	+	+	+
<i>Pappophorum pappiferum</i> (Lam.) Kuntze	H	G		+	+
<i>Passiflora ciliata</i> Dryander	V	R, B			+
<i>Paspalum</i> sp. 1	H	G		+	
<i>Paspalum</i> sp. 2	H	G		+	
<i>Pectis saturejoides</i> (Miller) Schultz-Bip.	H	G			+
<i>Randia laetevirens</i> Standley	SC	R		+	+
<i>Sesuvium portulacastrum</i> L.	H	B	+	+	+
<i>Sporobolus virginicus</i> (L.) Kunth	H	B, F	+	+	+
<i>Schizachyrium scoparium</i> (Michaux) Nash	H	G	+	+	+
<i>Trachypogon plumosus</i> (Humb. & Bonpl. ex Willd.) Nees	H	G		+	+
<i>Triplasis purpurea</i> (Walter) Chapm.	H	G		+	
<i>Trixis inula</i> Crantz	SC	Sh		+	+
<i>Turnera ulmifolia</i> L.	H	Sh			+
<i>Uniola paniculata</i> L.	H	B	+		
<i>Walteria indica</i> L.	H	G			+