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Transgressive dunefield landforms and vegetation associations, Doña Juana, Veracruz, Mexico

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ABSTRACT: Transgressive dune fields often comprise a multiplicity of landforms where vegetation processes largely affect landform dynamics, which in turn, also affect vegetation processes. These associations have seldom been studied in detail. This paper examines four separate landform types in a complex coastal transgressive dunefield located in the central Gulf of Mexico, in order to assess the relationships between dunefield habitat, local environmental factors, vegetation associations and landform evolution. Topographic surveys using tape and clinometer were conducted in conjunction with vegetation survey transects at four locations across the Doña Juana dunefield. Vegetation surveys allowed the estimation of relative plant cover of each plant species found along the transects. A large variety of landforms were found at the Doña Juana Dunefield: deflation plains, gegenwalle (counter) ridges, transverse dune trailing ridges, blowouts and parabolic dunes, aklé (fish-scale shaped) dunefields and precipitation ridges, with plant species associations developing on these different landforms equally variable. Flood tolerant species were located in the lower parts (deflation plain and gegenwalle ridges) whereas the older and dryer parts were covered by coastal matorral shrubs. Burial-tolerant species were dominant in the most mobile areas (blowouts and aklé dunefield and margin). The dune trailing ridge, with relatively milder conditions, showed the highest richness, with no dominant species. A dual interaction was found such that colonizing species both create and affect topography, and in turn, topography determines vegetation association and succession patterns. In coastal dunes, the vegetation and abiotic environment (namely the different landforms and the inherent microenvironmental variability) interact tightly and generate a complex and highly dynamic biogeomorphic system where substrate mobility and colonization processes reinforce one another in positive feedback. Copyright © 2010 John Wiley & Sons, Ltd.

KEYWORDS: coastal dunes; geomorphology; colonizing species; heterogeneity; Veracruz, Mexico

Introduction

Transgressive dunefields are large-scale, mobile, partially, and fully vegetated coastal dunefields that, when active, migrate transversely, obliquely or alongshore depending on the regional wind regime (Gardner, 1955; Hesp and Thom, 1990; Hesp *et al*, 1989). They often comprise a multiplicity of landforms and landform units especially when parts of, or a significant portion of the dunefield is being colonized by vegetation. While the literature describing geomorphological processes on coastal dunes is quite abundant (Cooper, 1958; 1967; Davies, 1980; Hunter *et al*., 1983; Garcia Novo, 1997; Borowka, 1990; Hesp and Thom, 1990; Lubke, 2004), and there are plentiful studies dealing with vegetation processes in dune environments (Salisbury, 1952; Ranwell, 1972; van der Maarel 1993a, 1993b; Hesp, 2004; Bakker *et al*., 1990; Martínez and Psuty 2004; Lubke and de Moor, 1998; Garcia Novo *et al*., 1997; Moreno-Casasola *et al*., 1998; Martínez *et al*., 1993) few authors have looked to integrate the information from these two areas of study (Paul, 1944; Olson, 1958; Pluis and De Winder, 1990), particularly so in transgressive dunefields.

Geomorphology and vegetation dynamics are naturally interrelated and affect each other considerably. Apart from a very few studies on the evolution of transverse dunes into parabolic dunes (Tsoar and Blumberg, 2002; Duran *et al*., 2005), very little research has been conducted on transgressive dunefield vegetation colonization processes, and the role of vegetation in transforming active (mobile) deflation plains, sand sheets and dune types (e.g. barchans, transverse and aklé (fish-scale or network) dunes) into new or other dune types. In addition, limited work (Borowka, 1990; Hesp, 2004; Kim and Yu, 2009) has been carried out on the relationships between colonizing or pioneer species, dune landform evolution, vegetation species presence/absence, plant associations, successional trends and dunefield habitat and landform type, and especially so in tropical coastal transgressive dunefields.

It has long been demonstrated that environmental heterogeneity (such as a variety of landforms) largely affects plant species distribution owing to variations in microenvironmental conditions and the specific responses of plants to this variability (Ranwell, 1972; Cutler *et al.,* 2008; Flinn, 2007). Usually, vegetation studies that sample the vegetation mosaic of highly heterogeneous environments fail to describe in detail such heterogeneity (see, for instance, van der Maarel 1993a and 1993b; Castillo and Moreno-Casasola, 1998). In turn, geomorphological studies commonly fail to analyze the role of vegetation in landform variety (Kim and Yu, 2009). Nevertheless, a few studies have shown the mutual impact of the biotic and abiotic elements of coastal dunes ecosystems (Stallins and Parker, 2003; Martínez *et al*., 2001). The comprehension of this mutual interplay between landforms and vegetation processes is fundamental to fully understand the dynamics of coastal dune ecosystems.

In the following, we examine four separate landform types in the Dona Juana transgressive dunefield in order to assess the interrelationships between dunefield habitat, local environmental factors, vegetation associations and landform evolution. We attempt to explore to what degree spatial landform heterogeneity is driven by vegetation colonization and dynamics, and then subsequent landform evolution. In this sense, our study site offered a good opportunity given its highly heterogeneous landscape.

Methods

We have utilized vertical aerial stereographic photographs from several periods, 1973, 1980, 1994, 1995, and 2004 to map vegetation and morphological changes in the dunefields. The 1973 to 1995 photography is a scale of 1 : 50 000. The 2004 colour aerial photographs are at a scale of 1 : 10 000 and provide high resolution imagery for detailed mapping of landform units. These maps were then field checked in 2000, 2004 and 2007 to provide further temporal quantitative and qualitative data on dunefield and vegetation changes. We utilized geomorphological mapping techniques outlined in Goudie *et al*. (1990) and mapped dunefield landform units (Hesp *et al*., 1984) to produce a detailed geomorphological map of the area. Topographic surveys using tape and clinometer were conducted in conjunction with 1 m^2 to 5 m^2 vegetation survey quadrats (depending on the vegetation present and landform scale) along transects at four locations across the Doña Juana dunefield in 2007. Non-contiguous quadrats (5 m^2) were utilized in dense, tall vegetation. Previous vegetation survey tests indicate that little bias is introduced by varying quadrat size given the relatively uniform nature of the coastal mattoral. Vegetation surveys were performed by estimating relative plant cover of each plant species found in each of the quadrats. The relative importance of species comprising each landform unit (Figure 10 later) was determined by calculating the ratio between the relative frequency (the proportion of quadrats where the species *x* is occurring per the total number of quadrats across the profile), and the relative cover (proportion of percentage cover of each species per total percentage cover of all species across the profile) (Krebs, 1989).

The Region

Veracruz State lies in the Gulf of Mexico, and is centered around 19° to 21°N (Figure 1). The climate is tropical humid with a 1200 mm rainfall, the majority of which falls in the summer months (June to September) (Moreno-Casasola, 1988, 1997; Martinez *et al*., 1997, 2007; Perez-Villegas 1989). The mean annual temperature is 24°C, and the mean annual humidity is greater than 75% (Fernandez-Eguiarte *et al*., 1989). Hurricanes only occasionally impact the coastline directly, but the margins of hurricanes frequently affect the coast. Winter storms are common from October to February and can reach speeds of 80–100 km h^{-1}. The dominant wind direction is from the north, but moderate to strong easterly and southerly winds occur at times (Figure 1). Significant sand movement takes place between October and April (the dry season) when strong (>40 km h^{-1}) northerly winds associated with the passage of cold fronts (‘nortes’) occur (Martinez *et al*., 1997). Surfzones are generally moderate to high energy, intermediate and dissipative types.

Figure 1. Location of Veracruz State, Mexico and the Doña Juana dunefield. On the right side is a sand rose indicating wind resultants and resultant drift direction (RDP) for the region. The darker black lines indicate wind direction and sand transporting potential, while the thin black line indicates the net direction and vector magnitude that sand transporting winds would blow in.

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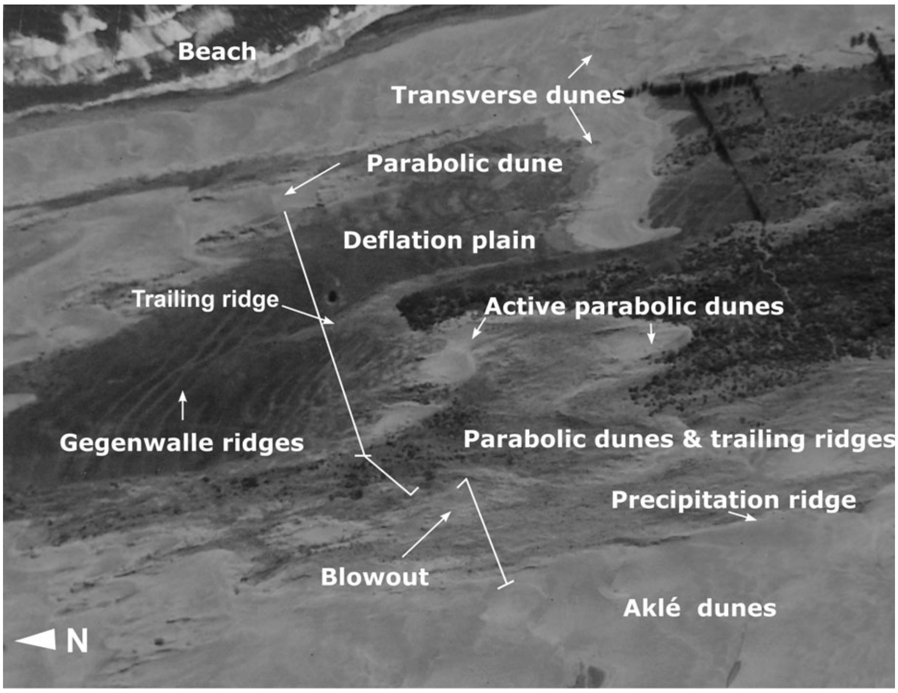

Figure 2. Vertical aerial photograph of the southern portion of the dunefield indicating the survey line and dune types.

The Doña Juana Dunefield

The dunefield is one of several large transgressive dunefields north of Veracruz city in Veracruz State, Gulf coast, Mexico. It is centered on 19° 2′ 02″ N, 96° 18′ 47″ W. Figure 1 illustrates the location of the dunefield. The dunefield is typical of many in the region, and typical of many elsewhere, comprising a large-scale active dunefield, deflation plains, and multiple, local landform units.

Figures 2 and 3 display an unrectified vertical aerial photograph and geomorphological map of the dunefield respectively. The dunefield migrates alongshore and obliquely onshore and has two salients building eastwards towards or onto surfzone/nearshore reefs. In general, along a north to south line, the system displays the following series of landforms extending from the beach inland: a narrow sand sheet, sand ribbons and coarse granule mega-ripple field, a small transverse and aklé dunefield along the coastal fringe, a deflation plain separating this easternmost small dunefield from another more western one which builds downwind into a more extensive, and significantly larger aklé dunefield. Towards the southern end of the dunes, the dunes become more transverse and are the largest dunes in the system. The active dunefield is bordered by a high precipitation ridge (Figures 2 and 3). An older, more extensive, vegetated transgressive dunefield lies landward of the active one and comprises long straight and sinuous ridges. In places these have formed in association with a hummocky, somewhat chaotic dunefield and may be trailing ridges as described by Hesp and Martinez (2008); in other places they are separated by deep swales and may be multiple precipitation ridges.

Figure 4 illustrates the topographic cross-section and landform types surveyed across the eastern portion of the dunefield. The formation and geomorphology of each of these is outlined below.

Gegenwalle Ridges, Transverse Dune Trailing Ridges, Blowouts and Aklé Dunefield Margin/Precipitation Ridge

In the following we briefly explain the origin and formation of each of the landform types examined in the dunefield. We have added the Spanish translation of these units because currently, the terminology does not exist in this language.

Gegenwalle ridges (Contra cordón)

Gegenwalle (literally ‘counter ridge’) ridges were first described by Paul (1944). They are formed where pioneer plants colonize the downwind edge of an active deflation basin or plain (*planicie de deflación* or slack), particularly following flooding of the plain. They may form immediately upwind of individual parabolic dunes or transverse dunes, or extensively across the front of an advancing dunefield (Pye, 1983; Martinho *et al*., 2006). They are ‘counter ridges’ because they are typically formed when the wind blows either offshore or opposite (counter) to the dominant onshore or down-dunefield winds. When this occurs, sand is transported off the dunes back onto the deflation plain or basin and trapped in the marginal vegetation, forming a ridge (in much the same way as foredunes form). David *et al*. (1999) describes ‘dune track ridges’ which may be the same landform.

In the Doña Juana dunefield, these ridges are extensive (Figure 3), and, in fact, are the largest suite of gegenwalle ridges in the entire State of Veracruz transgressive dunefields. They have particularly developed here due to the migration across a long deflation plain of a single transverse dune which split downwind into two portions. As new transverse and other mobile dunes evolve upwind, the plain and ridges is likely to be destroyed.

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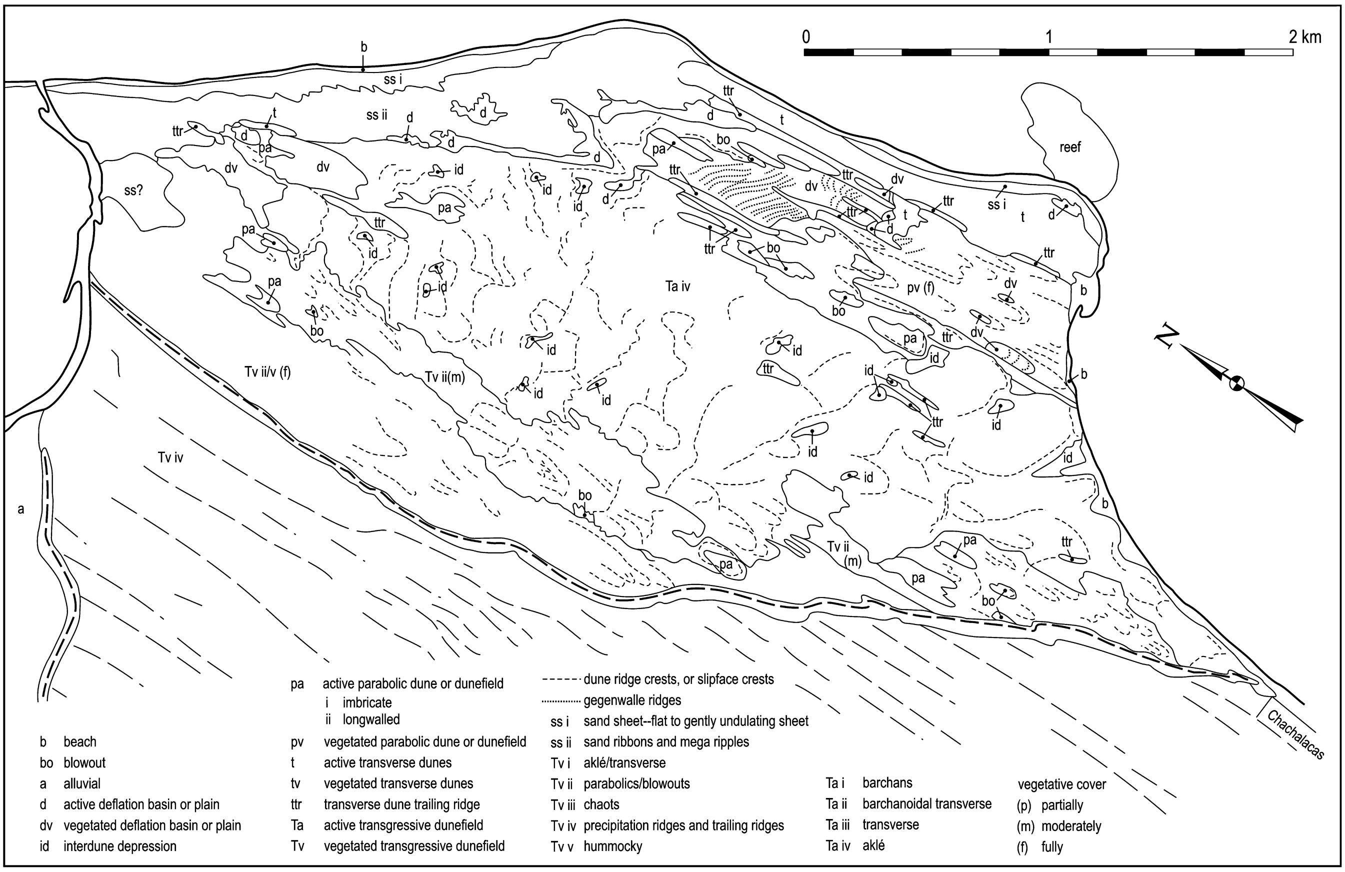

Figure 3. Geomorphological map of the Doña Juana dunefield mapped from unrectified vertical aerial photography.

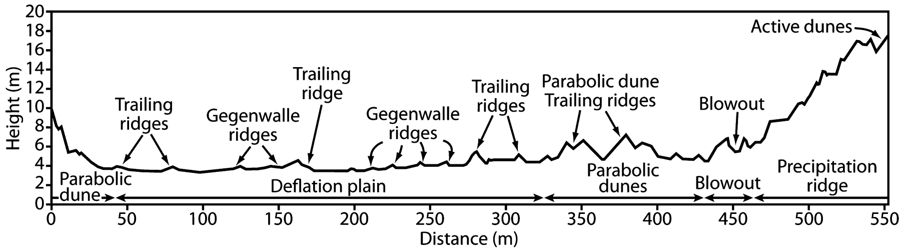

Figure 4. Topographic cross-section across the dunefield illustrating the geographical relationship of the vegetation transects to each other. The transect begins on the western trailing ridge of a parabolic dune, extends across the deflation plain containing deflation flats, gegenwalle ridges and transverse dune trailing ridges, across a blowout and parabolic dune, and up the eastern margin of the aklé dunefield margin/precipitation ridge.

In the Veracruz dunefields, field surveys indicate that *Phyla nodiflora* is the first pioneer plant which colonizes the newly formed moist to wet deflation plain (Figure 5a). *Eleocharis* then colonizes the incipient ridges, and *Croton* may also propagate on the ridges where they are relatively high. *Fimbristilis spadicea and F. spathacea,* eventually appear and *Hydrocotyle bonariensis* and *H. umbellata* colonize the adjacent plain. Sometime later, *Sporobolus virginicus* also colonizes the ridges. Figure 5b illustrates older, fully vegetated gegenwalle ridges in the survey area.

Transverse dune trailing ridges (Cordón de arrastre de dunas transversales)

The transverse dune trailing ridges are formed in the Veracruz transgressive dunefields by vegetation colonization of the lateral margins of active transverse, barchanoidal transverse, and aklé (fish-scale) dunes (*Escamas de pescado*; aklé = 'dune networks' of Cooke *et al.*, 1993). For simplicity, all trailing ridges formed from these dune types are referred to as transverse dune trailing ridges (Hesp and Martinez, 2008).

Field observations indicate that pioneer plants (*Croton punctatus, Palafoxia lindenii* and *Ipomoea pes caprae* –the latter closest to the beach) initially establish on, or near the basal flank (leading corner) of the transverse dune slipface. The plants then grow up, and colonize the mid to upper portions of the slipface flank or outside lateral margin. As the transverse dune continues to migrate downwind, other plant species (e.g. *Chamaecrista chamaecristoides*) stabilize and hold the outside flank or dune margin, while the inside portion of the newly forming ridge begins to erode. With time, additional plant species (*Shizachyrium scoparium; Trachypogon plumosus, Randia laetevirens and Acacia farnesiana*) colonize the outside flank furthering the stabilization process. The transverse dune migrates further downwind, leaving a marginal trailing ridge in its wake. The pioneer species (usually either *Croton* or *Chamaecrista*) colonize the ridge crest, the

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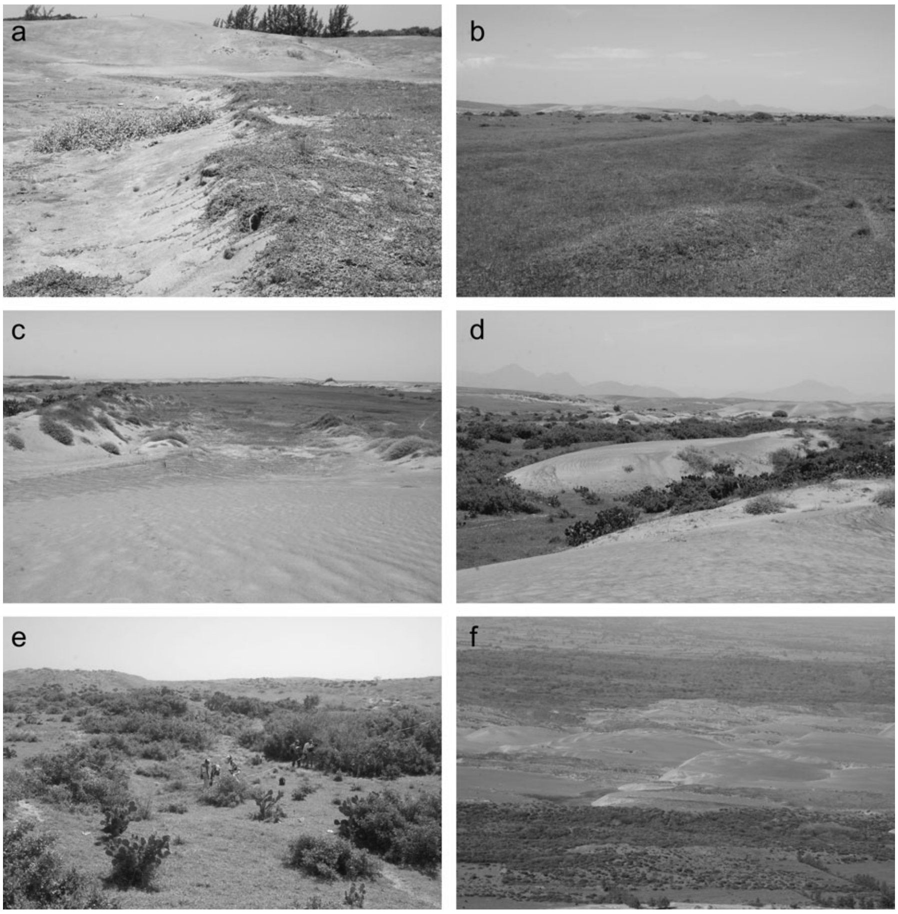

Figure 5. View of (5a) a new gegenwalle ridge forming at the active margin of the deflation plain; (5b) the gegenwalle ridges in the surveyed transect; (5c) the surveyed transverse dune trailing ridge on the left and its companion ridge; (5d) General view of the blowout/parabolic dune region in the transect area; (5e) detailed view of the mattoral region; and (5f) aerial view of the eastern precipitation ridge of part of the active transgressive dunefield in the transect area.

inside margin of the ridge, and may also colonize a portion of the lower dune stoss face and/or interdune region. Further shrub and tree species (*Lantana camara, Gliricidia sepium* and *Tabebuia rosea*) may propagate in the older, more upwind portions of the ridge. Where a transverse dune is an isolated feature, trailing ridges may form on each margin of the dune (Figure 5c). The ridges are formed in a similar way to parabolic dune trailing ridges (Hesp, 2000).

Blowouts and parabolic dunes (voladuras y dunas parabólicas)

Blowouts are saucer, bowl, cup or trough shaped depressions formed by wind erosion of a pre-existing substrate (McKee, 1979; Hesp and Hyde, 1996). They are common in all dune landscapes, and often develop in coastal transgressive dunefields where (i) vegetation begins to colonize mobile dunes, stabilizing some parts, and thereby allowing the development of blowouts (and sometimes parabolic dunes – Tsoar and Blumberg, 2002) in adjacent non-vegetated areas; (ii) greater aridity/higher wind speeds result in blowout development as the vegetation on a stabilized dunefield starts to decline.

Parabolic dunes are U and V-shaped or upsiloidal dunes with depositional lobes (the advancing front), trailing ridges and a deflation basin or plain contained within the ridges (Cooper, 1958, 1967) (see Figure 2). Blowouts do not have trailing ridges (cordón parabólico de arrastre) while parabolic dunes do (Hesp, 2000).

In the Veracruz dunes, active blowouts may be found forming in virtually any part of the dunefield, and therefore the species surrounding, or colonizing the erosional landform may vary considerably. For example, near the beach, pioneer species typical of the foredune (e.g. *Sesuvium, Ipomoea,* and *Croton*) may be most common. The latter species, together with *Chamaecrista* and *Palafoxia* also occur as pioneers in multiple places in the dunefield anywhere active sand deposition is occurring (Figure 5d and 5e).

Aklé dunefield margin/precipitation ridge

The principal active dunefield comprises predominantly aklé dunes, and some large transverse dunes (Figures 2 and 3). It is bordered on both the western and eastern margins by partially vegetated precipitation ridges. The western ridge is the more ‘classic’ type described by Cooper (1958, 1967) where sand ‘precipitates’ or rains down into the shrub and forest margin, primarily building upwards, and slowly westwards as the active dunes pile up against the vegetation. Such ridges are, however, primarily formed not only by this classic process – i.e. sand precipitation (suspension, saltation and avalanche) into vegetation (Thom *et al.*, 1992), but also solely by plant colonization of dunefield margins. In the latter case, as the dunefield builds upwards and downwind, it has a clearly defined, non-vegetated marginal slope. Portions of this edge or marginal slope of the dunefield may be colonized by various plants (e.g. *Croton punctatus, Chamaecrista*

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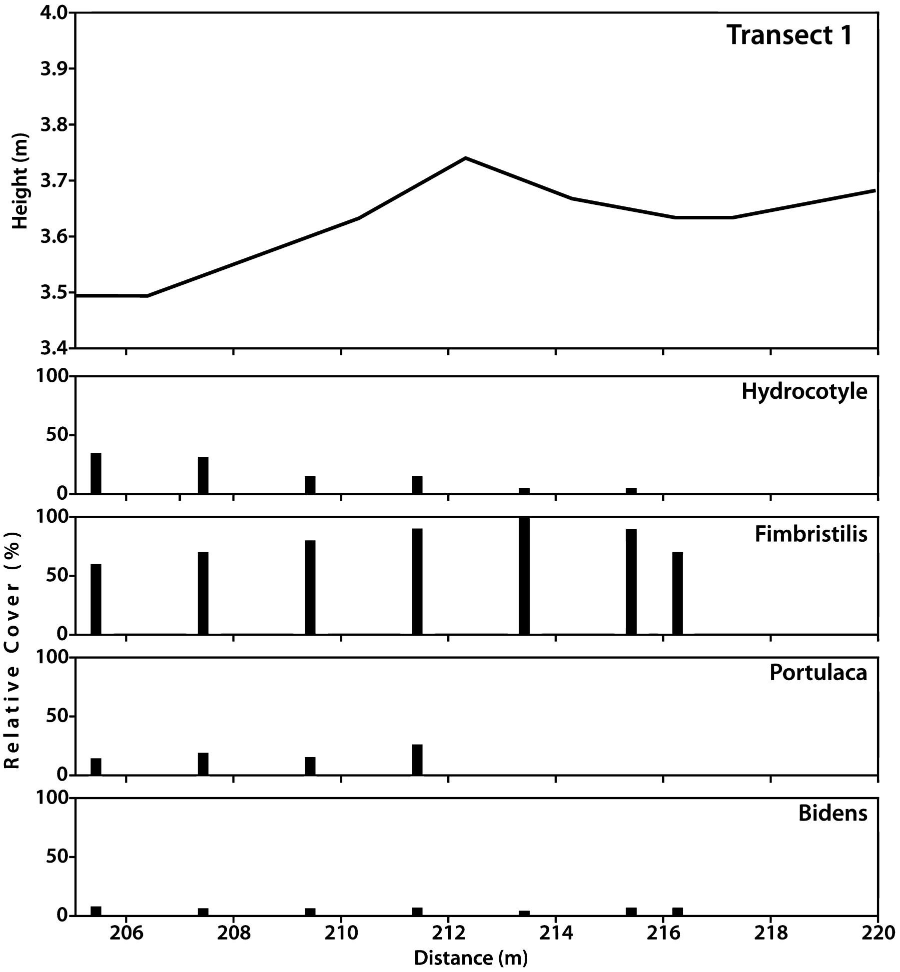

Figure 6. Topographic and vegetation survey of the gegenwalle ridge and deflation plain transect 1.

chamaecristoides and Palafoxia lindenii). Such plant colonization leads to further sand deposition and the formation of discrete nebkha (discrete, semi-circular to pyramidal dunes formed within a plant), nebkha chains and fields, and larger areas of vegetated dunes. This in turn, leads to vertical accretion of the ridge. The eastern margin of the dunefield is principally forming by this latter method – it is both the active dunefield margin and it is actively being colonized and partially stabilized by vegetation (see Figure 5f).

Cross-Dunefield Morphology and Vegetation Associations

Deflation plain and gegenwalle ridges

Figure 6b illustrates a portion of the deflation plain containing the gegenwalle ridges and inter-ridge deflation plain. There is a clear distinction visible between the vegetation covering the flat versus the ridges largely due to the more intense green color of the plants growing in the deflation flats compared to the ridges. Figure 10 shows the detailed topographic survey and vegetation cover across one ridge and adjacent plain.

On this transect, *Fimbristylis spadicea* dominates the plain and ridge but displays a 20 to 30% lower cover on the ridge crest which is slightly dryer and ~25cm higher than the surrounding plain. *Hydrocotyle bonariensis* displays a greater dominance on the lower ridge slope and plain. All species present are tolerant of wet conditions and of inundation. At the time of survey the water table was 35 cm below the plain surface, but observations show that at times the inter-ridge deflation flats are completely inundated. Note that by this stage/age *Phyla nodiflora, Eleocharis* and occasionally *Croton* (the initiating plants) have now disappeared.

Transverse dune trailing ridge

Figure 7 illustrates the transverse dune trailing ridge in the cross-section area. The ridge is relatively low, around 1·5 m high, and slightly asymmetric. Figure 11 illustrates the topographic profile and vegetation cover. These ridges are normally initiated by either *Ipomoea*, *Croton* or *Chamaecrista* (or combinations of these) establishing on either side of the basal slope (in the case of *Ipomoea*) or the crest. In many portions of the dunefield, *Chamaecrista* seedlings initiate stabilization on dry ridge crests. Other species (*Rinchosia, Cenchrus*) then typically spread upwards onto, or establish on the dune ridge once the transverse dune has migrated downwind and *Ipomoea*, *Croton* or *Chamaecrista* have effectively stabilized the ridge. At this site, *Hydrocotyle, Cyperus* and *Sporobolus* are most common on the adjacent flat where they tolerate wetter conditions. *Bidens* is co-dominant on the crest with *Chamaecrista*, and then in relatively high percentage cover on the lowermost slopes adjacent to the deflation plain (see Figure 5). A variety of other species are present on the upper slopes and crest region. If the ridge crest was the first portion of the original transverse dune colonized (as has been observed

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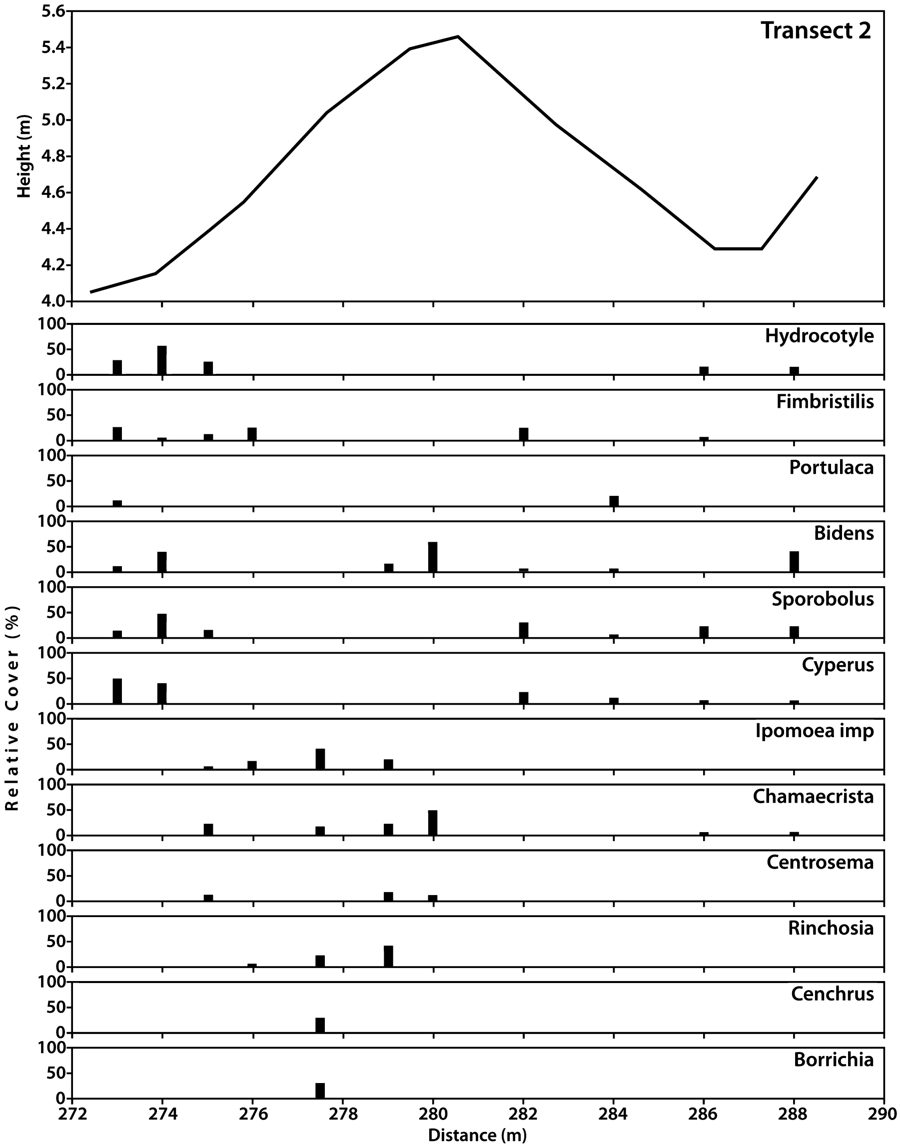

Figure 7. Topographic and vegetation survey of the transverse dune trailing ridge transect 2.

downwind where the ridge is initially forming), then the crest area is the oldest vegetated portion, and this may explain why there are a greater number of species here, as this region has been stabilized longer than the mid to lower slopes.

Parabolic dunes

Figure 5e illustrates the older, mostly stabilized parabolic dune region. Figure 8 shows a detailed topographic and vegetation transect across this area. The topography is complex and hummocky, principally comprising partially overlapping parabolic dune trailing ridges.

The site increases in age from left to right, such that ridge 1 where the vegetation survey started still displayed bare sand on the upper eastern slope and crest, and was partially colonized by *Randia*. To the immediate west, ridge 2 was older and significantly more stable. The dominant species are *Randia laetevirens*, *Acacia farnesiana, A. cornigera* and *Lantana camara*, which are typical of the coastal dune matorrals (later successional stage) where there is little sand movement or deposition. These species are the first colonizers of the lower-dryer parts. Once their cover is relatively high (>50%) a coastal matorral is formed and new matorral and tropical rain forest tree species (such as *Diphysa robinoides* and *Bursera simaruba*) colonize the area. At the site, the water table was 80 cm below the lowest dune swale base and conditions are considerably dryer than in the other sites described above. In addition, the site is generally older relative to the previous sites, and displays a more advanced successional stage.

Eastern precipitation ridge

Figure 5f illustrates the eastern active margin or precipitation ridge of the principal active dunefield, and Figure 9 shows the topography and vegetation cover up the ridge slope. There is an active blowout near the base of the ridge, and the central erosional basin has very little vegetation presence or cover. *Chamaecrista* is common here on the margins of the blowout due to its ability to colonize depositional areas (450–470 m region). The ridge crest is also typically first colonized by *Chamaecrista*, while the lower to mid flanks are typically colonized by *Croton*. *Opuntia* also occurs on the mid flanks. Both *Chamaecrista* and to a lesser degree *Croton* are tolerant

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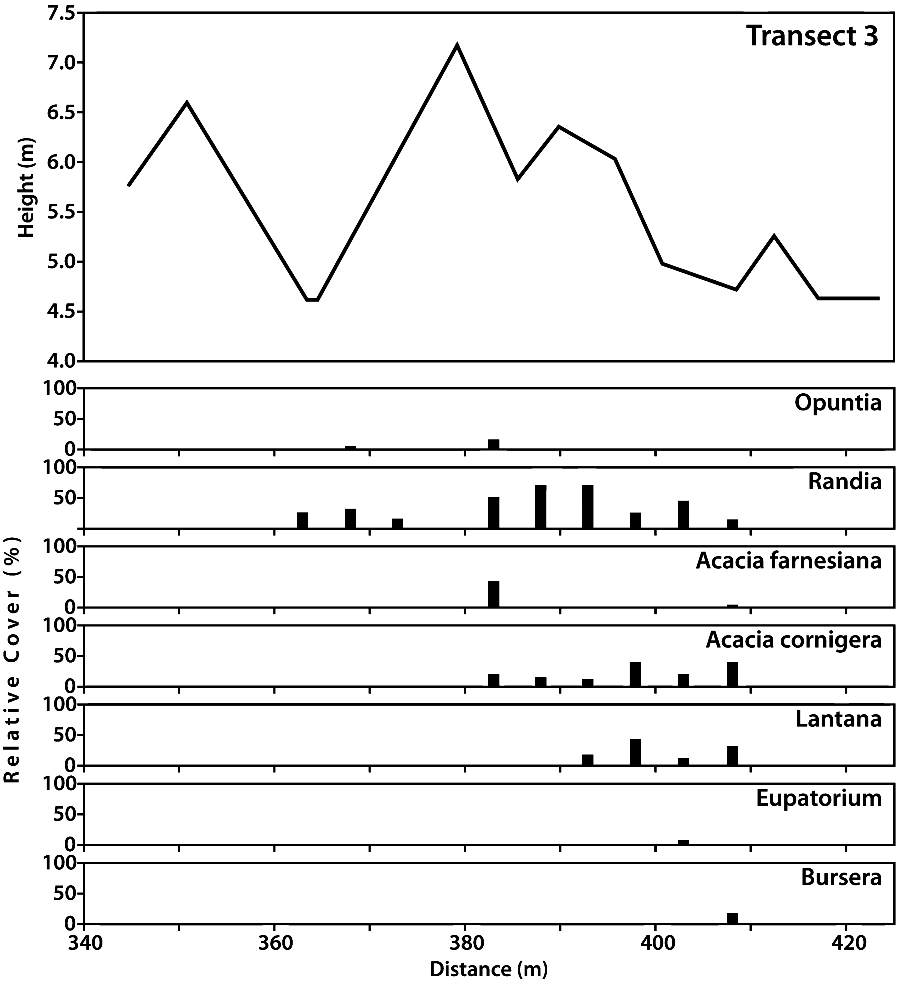

Figure 8. Topographic and vegetation survey of the parabolic dune transect 3.

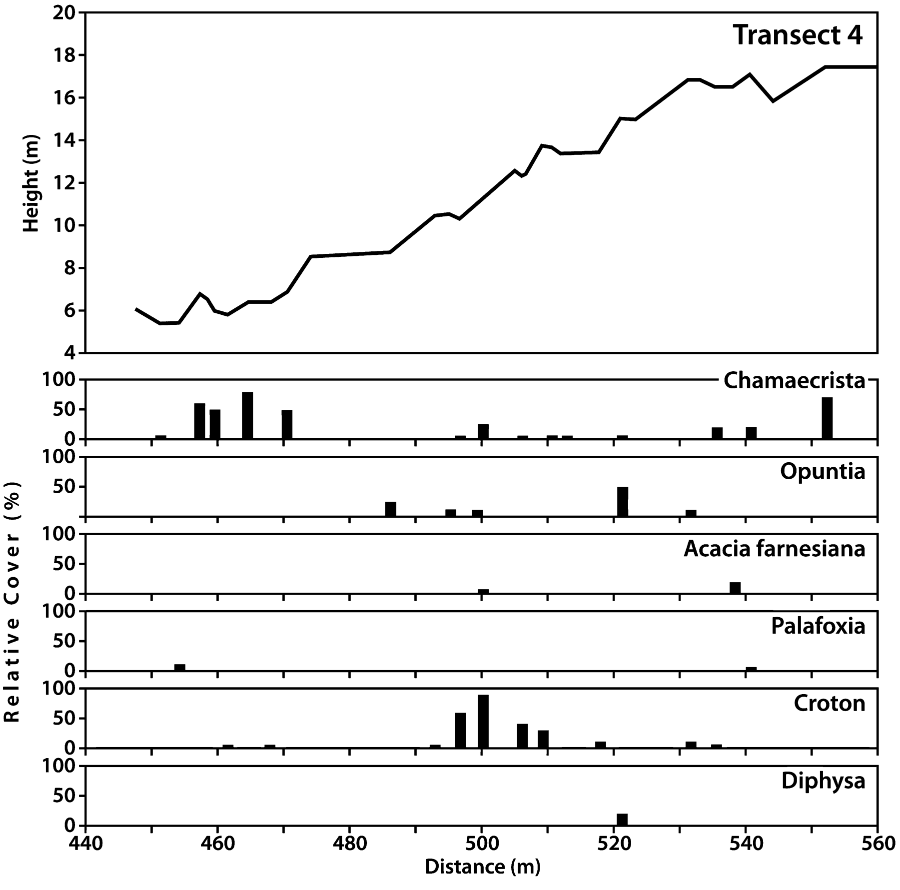

Figure 9. Topographic and vegetation survey of the precipitation ridge transect 4.

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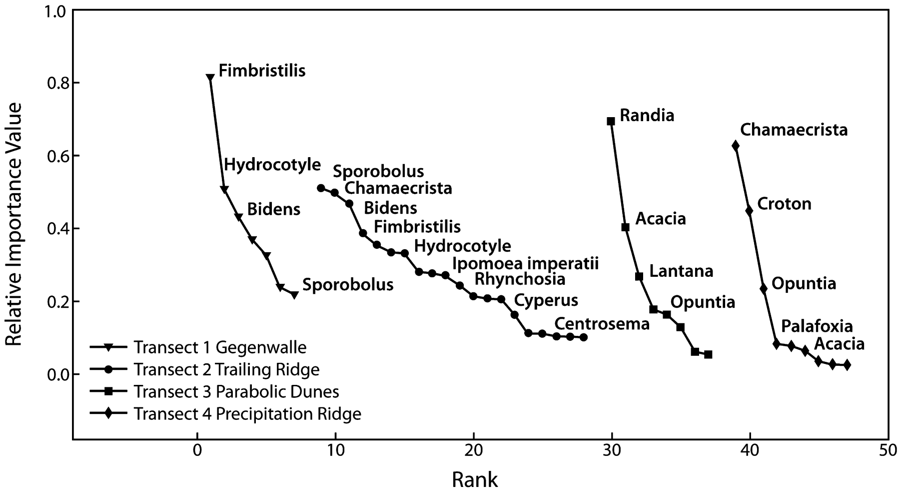

Figure 10. Relative dominance of vegetation species comprising each transect. The top species is the most dominant, and the steepness of the curves illustrates the importance of each species relative to the other species occurring in each profile.

of active sand transport and deposition and dryer conditions (Moreno-Casasola, 1988, Martínez and Moreno-Casasola, 1996).

Species Dominance and Landform Type

Figure 10 indicates the species for each transect (and includes all species found). The relative importance of species comprising each landform unit was determined by calculating the ratio between the relative frequency and the relative cover (see Methodology section) (Krebs, 1989). The steepness of the curves in Figure 10 illustrates the importance of each species relative to the other ones occurring in each profile. For example, in Figure 10, transect 2 has the flattest curve, while transects 3 and 4 have the steepest curves. This indicates that all the species in transect 2 have relatively low importance, while in transects 3 and 4, the highest one or two species have high importance relative to the other species.

In transects 1 (gegenwalle ridge), 3 (parabolic dunes) and 4 (precipitation ridge) there is a clear dominance of *Fimbristilis, Randia* and *Chamaecrista* respectively, whereas in transect 2 (trailing ridge) there are no clearly dominant species. The community is more diverse, probably because the transverse dune trailing ridge is formed at the same time as the deflation plain is formed and therefore the species which occur in each environment are closely co-located and colonizing adjacent landform units, especially where the trailing ridges are low as in this example. In addition, it may be that environmental conditions are somewhat milder there (higher moisture and nutrient contents; lower temperature and substrate mobility) for a broader number of species. In transect 4 (precipitation ridge), the habitat is highly stressful in the active blowout and on the mid to upper active slope and crest of the precipitation ridge. Thus, only the most tolerant species (*Chamaecrista* and *Croton*) achieve relatively high cover and frequency values, while the others remain with low relative importance values. Transect 3 traverses an older stabilized parabolic dune system. Our observations indicate that these dunes would have been initially stabilized by species such as *Chamaecrista, Palafoxia* and *Croton,* which are then replaced by the mattoral species such as *Randia* and *Acacia*.

The figure clearly shows a separation of the landform units based on species dominance (the highest relative importance), despite the state of succession.

Discussion and Conclusion

The Doña Juana Dunefield is remarkably diverse and highly variable across a relatively short distance. In an area of a few tens to hundreds of metres, it is possible to find parabolic dunes, transverse dunes, trailing ridges, blowouts, large-scale aklé dune-dominated dunefield, precipitation ridges and gegenwalle ridges. Plant species associations developing on these different landforms are equally variable.

Our results are in accordance with earlier studies (Hesp, 1991; Moreno-Casasola 1997; Acosta *et al*., 2005; Kim and Yu, 2009), where the topographic-environmental mosaic resulted in a vegetation mosaic as well. However, in contrast with the above-mentioned studies, we have described the topographic variability of the site with greater detail and thus, show how this affects vegetation. We found that there is a dual interaction: colonizing species create and affect topography, and in turn, topography, and the temporal changes that take place as a landform unit may continue to form or build, determines vegetation association and succession patterns.

Spatial heterogeneity is well known to affect plant species and their distribution owing to different microenvironmental conditions and specific tolerance of plants to them (Moreno-Casasola, 1988; Hesp and Martinez, 2007; Flinn, 2007; Cutler *et al.,* 2008). However, it has seldom been shown that plants may themselves affect and even generate different landforms as is the case in coastal dunes. Several earlier studies reveal a mutual impact of the biotic and abiotic elements of a community (Cowles, 1898; Farrow, 1919; Clements, 1928; Lee, 1995). For instance, Stallins and Parker (2003) and Martínez *et al*. (2001) showed such interplay in different successional stages and El-Bana *et al*. (2002) found the same mutual interaction between plants, nebkhas and mircoenvironmental conditions. Furthermore, it has also been shown that biotic processes affect the spatial distribution of soil properties (Isermann, 2005; Zheng *et al*., 2008; Maun, 2009).

It is well known that only a few plant species are able to adapt to, or survive in an environment dominated by sand deposition (Maun, 1998, 2009) and eventually, as sand accumulates around them, they produce different landforms (nebkhas, gegenwalles, transverse dunes and parabolic dune trailing ridges, for example), which would not exist in the absence of plants. These species vary geographically, but share their responses to the abiotic environment (Garcia-

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Novo, 1997; Maun, 1998; Gallego-Fernandez and Martínez, in revision). In contrast, trailing ridges and precipitation ridges are created as the dune system, or individual dunes move downwind. In this case, plants colonize and propagate into an already existing landform (e.g. a transverse dune, a parabolic lobe, the active margin of a dunefield), and eventually stabilize it creating new landforms. Without the plants, the marginal dunefield ridge would continue to move and in time, it would change into a deflation plain as it migrated downwind. The trailing and precipitation ridges are created due to the interaction of the dunefield with vegetation and unless they are stabilized by plants, they do not remain as such over time.

Once the landforms are created, the environmental factors associated with the development of that landform begin to control successional patterns (Kellman and Kadin, 1992; Maun and Perumal, 1999; Martinez *et al*., 2001; Stallins and Parker, 2003; Dech and Maun, 2005). Different landforms offer different environmental conditions and thus, species will vary according to their own specific tolerance (Garcia-Novo, 1997; Maun 1998). Plant–plant interactions (such as facilitation) also play a significant role in coastal dune vegetation dynamics (Martínez, 2003; Martínez and García-Franco, 2004; Martínez *et al*., 2004). Once covered and stabilized by vegetation, these plant-generated landforms will remain largely unchanged until sand becomes mobile due to vegetation disruption, owing to human activities, climate change or natural disturbances.

In conclusion:

(i) A multitude of landform units occur in this tropical coastal transgressive dunefield over a relatively short distance, and this structure may be more common in tropical dunefields compared to temperate dunefields (cf Hesp, 2004).

(ii) Four landform types and their vegetation cover have been described for the first time from one dunefield in Vearcruz State. Their highly variable cover and species presence/absence are related to the dynamics of the dunefield position, and subsequent evolution. For example, gegenwalle ridges develop on a flat deflation plain which experiences a high water table to seasonally flooded environment. Over time, slight variations in elevation (ridge verses plain) determine successional changes or plant colonization processes. Highly mobile substrates and dry to seasonal drought conditions occur in the parabolic dunes and precipitation ridges leading to a completely different suite of colonizing species, and different set of final successional species.

(iii) In this dunefield, a dual interaction exists: colonizing species both create and affect topography, and in turn, topography determines vegetation association and succession patterns.

(iv) In coastal dunes, the vegetation and abiotic environment interact tightly, and generate a complex and highly dynamic biogeomorphic system where substrate mobility and colonization processes reinforce one another in positive feedback.

(v) In three cases here (gegenwalle ridges, transverse dune and parabolic trailing ridges) and the landforms owe their existence and largely their morphology to plant colonization processes. Without the plants, which are responding to specific environmental conditions, the landforms could not exist. Once colonized, changes in nutrient status, moisture, etc. may drive further successional change; however, inundation by sand at various levels (slight to intense) may also be the dominant abiotic factor driving subsequent change.

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