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Patterns of development and succession of vegetated hummocks in slacks of the Alexandria coastal dune field, South Africa

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Abstract. Dune hummocks (small aeolian dunes formed by sand deposition in and around pioneer plants) are the smallest vegetated dune unit; they occur along the entire South African coastline but are poorly studied. Structural properties and distribution of the two main hummock-forming plants: *Arctotheca populifolia* (a pioneer species with fast growth rate and rapid turnover) and *Gazania rigens* (a later colonizer with slower growth) were investigated. A marked vegetation succession exists across the floor of the slack as a result of the migration of transverse dune ridges across the slack. *Arctotheca* hummocks were initiated on the newly exposed eastern margin of the slack, and were replaced about midway across the width of the slack by *Gazania* hummocks. Hummocks increased in size with distance from the eastern side of the slack. *Gazania* hummocks attain a greater vegetation height, support a greater vegetation complexity and mass, and attain a larger maximum size than *Arctotheca* hummocks. Succession, defined as both the replacement of plant species as well as site modification within the plants over time, was evident. Since the growth form and dynamics determine (1) the ability of plants to trap wind-borne soil and detritus, (2) the shape of the hummocks, and (3) the habitat complexity available to spiders and insects, the ecology of the hummocks is probably determined largely by the vegetation characteristics of the hummock-forming plants.

Keywords: Animal ecology; *Arctotheca populifolia*; *Gazania rigens*; Landscape ecology; Plant architecture.

Introduction

A variety of physical and biological processes are thought to interact to create and modify habitats available to animals. However, the patterns of development of habitats have rarely been studied and are poorly understood. Here, we investigate the development of a specific dune field habitat, dune hummocks. Dune hummocks are defined as small aeolian dunes formed by sand deposition in and around pioneer plants (e.g. Hesp 1989). The process whereby the hummocks develop is a combination of the growth and development of the plant which forms the hummocks, and the accumulation of soil around the plant which in turn stimulates further growth and increases sand-trapping ability. Knowledge of the development of hummocks has implications for dune field dynamics in terms of the trapping of sand by plants and the management of sand dynamics.

The presence of dune hummocks within slacks has been noted earlier (Ranwell 1958; Tinley 1985; McLachlan et al. 1987; van der Merwe 1989), and physical and biotic process on foredunes and embryo dunes have been fairly well documented (e.g. Forster 1979; Forster & Nicolson 1981; Hesp 1984; Doing 1985; Masson 1990; Masson & McLachlan 1990; van der Putten et al. 1993), while Hesp (1989) reviewed some processes involved in the initiation and development of incipient foredunes, including those of *Arctotheca populifolia* and *Gazania rigens*.

Site modification is a result of the changes in structural properties of the vegetation over time, including increased habitat and modification of the micro-environment (reduced wind speed and ameliorated temperatures). Besides a change in species composition of vegetation over time, the phenomenon of succession includes changes in the individual plants themselves (Price 1975; Bach 1990). Attributes of plants that change with succession include age, structural architecture, height and density, and nutritional and chemical quality (Bach 1990). Thus, although the hummocks investigated in this study were mono-specific, sites were nevertheless modified with hummock development.

Vegetation succession across the width of slacks has been well recorded (McLachlan et al. 1987; Young 1987); it is hypothesised that the distribution of *Arctotheca* and *Gazania* hummocks will change with distance from the newly exposed eastern margin of the slack. Because air flow velocities are reduced within and behind plants, wind-borne sand is deposited within and/or behind the vegetation (Hesp 1989). Since the hummocks grow and develop as the plants grow and accumulate sand, it is further hypothesized that the structural features of the hummocks will change with size.

The specific objective of this study is therefore to describe the structural development of *Arctotheca populifolia* and *Gazania rigens* hummocks, in the context of the successional pattern across the slack floor, and to test the hypothesis of a change in hummock structure (habitat development) with size.

Study area

Physiography and climate

The Alexandria coastal dune field is the largest unvegetated coastal dune field in southern Africa and one of the largest in the world (Tinley 1985). It stretches along the northern shore of Algoa Bay, from the mouth of the Sundays River in the west (33° 43' S, 25° 51' E) to Woody Cape in the east (33° 46' S, 26° 19' E) (Parker-Nance et al. 1991), covering an area of 120 km^2 (Fig. 1a). There is a trimodal, high-energy wind regime which results in sand being transported in three distinct directions. Since the prevailing wind is southwesterly, net sand movement is northeastwards, and the sand is transported parallel to the coast at a rate of 4 - 5 m/yr (McLachlan et al. 1982).

The climate is warm temperate with a bimodal winter rainfall pattern, with peaks in early and late winter (Heydorn & Tinley 1980).

Slack topography

The hollows between dune ridges where the water table is near the surface are defined as slacks (e.g. Ranwell 1959). They occur in the Alexandria coastal dune field as a result of deflation (Hesp 1986). Dune hummocks are prevalent in the slacks in the western margin of the dune field.

Along the western 10 km of the dune field a series of 37 sparsely vegetated slacks is found (Fig.1b), comprising 0.1% of the total dune field area (van der Merwe & McLachlan 1991). The slacks lie ca. 50 m landwards of the drift line, and most are connected to the beach via a pebble berm ca. 2 m above sea level (McLachlan et al. 1996). The average length of the slacks is 200 m in a north-south direction, with an average width of 50 m in an east-west direction. The area of a typical slack is 18 794 m^2, of which 47% is mad e up by the slack floor (McLachlan et al. 1987).

The slacks are separated by dune ridges which migrate eastwards across the slack floor at rates of 5-7 m/yr, creating a well-defined succession westwards across the width of the slack. This corresponds roughly to a 5-yr time scale for an average slack floor width of 30 - 40 m (McLachlan et al. 1987; Burkinshaw 1990). Since the slack floor is constantly being exposed at the east end and buried at the west end, the chronology of hummock succession is set out in space.

Slack interstitial environment

Since the water table is within 1 m of the slack floor, the slacks correspond to Ranwell's (1959) definition of a wet slack. The floor is often damp due to capillary action from the ground water table (Illenberger 1988). Van der Merwe & McLachlan (1991) recorded that sand in the slack is loosely packed and well-aerated, and well- to very well-sorted. The overall mean sand grain size is 173µm, wit h no significant differences in sand particle size along the width or length of the slack. The mean organic content of the sand is 0.69%, and decreases linearly with depth and with distance from the seaward margin (Lubke 1983; van der Merwe & McLachlan 1991).

Slack vegetation

Slack vegetation is comprised largely of grasses and herbs with succulent leaves which are mostly wind- and water-dispersed, and exhibit sympodial growth or have stolons to enable them to advance in front of accumulating sand (Lubke & Avis 1988). Ground cover in the slacks averages 10%, and plants rarely exceed 0.5 m in height. Young (1987) identified 21 plant species, of which 12 are common and exhibit succession across the width of the slack. McLachlan et al. (1987) identified three vegetation zones within slacks in this area: (1) the *Sporobolus* zone along the eastern margin, (2) the *Gazania* hummock zone along the central and western sides of the slack, where plant diversity is higher and hummocks occur, and (3) the *Psorolea* zone, a sheltered zone in the landward western corner of the slack.

Dune hummocks

The two main hummock-forming plants in the Alexandria coastal dune field are the tufted composite species *Arctotheca populifolia* (Berg.) T. Norl. (dune cabbage), a primary colonizer with a fast growth and rapid turnover (Fig. 2), and *Gazania rigens* (L.) Gaerth var. *uniflora*, a later colonizer with slower growth. Both species are members of the family Asteraceae and display similar phenological patterns. Flowering and production of seeds and fruits, as well as seed germination and seedling establishment, occur throughout the year (Young 1987).

Arctotheca forms mini-hummocks around seedlings of 1 cm high, and has limited vertical growth with extensive horizontal growth. *Gazania* exhibits a vertical, multi-shoot growth with limited horizontal growth (Fig. 2). Percent plant cover on *Gazania* hummocks is typically 50 - 80 %, while cover is 20 - 50 % on *Arctotheca* hummocks. Thus, *Gazania* is aerodynamically four times rougher than *Arctotheca*, and so traps more wind-borne materials (Hesp

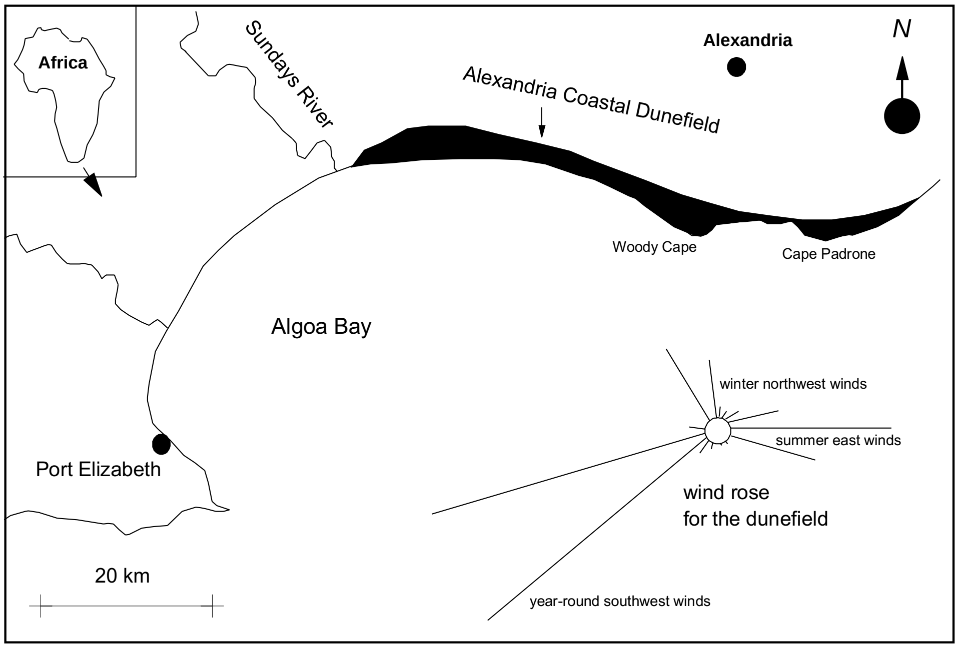

Fig. 1a. Locality map of the study area showing the position of the Alexandria coastal dune field on the northern shore of Algoa Bay. The wind rose arms are plotted in the upwind direction. (Modified from Illenberger & Rust 1988.)

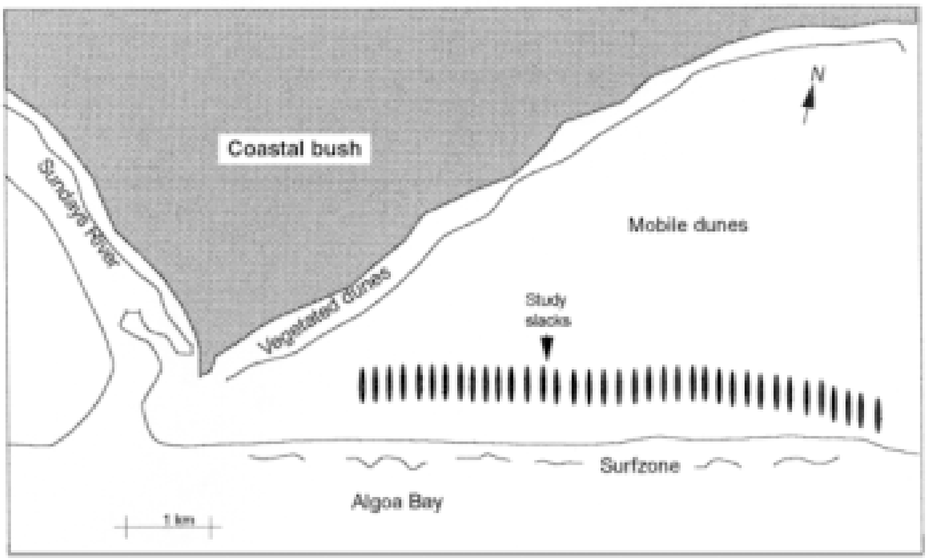

Fig. 1b. Schematic map of the study area, showing the position of the slacks in the dune field.

1986).

Arctotheca populifolia forms low, semi-circular mounds, with high temperatures near the surface, greatest sand volume per wet plant weight, and low to moderate detritus trapping ability. On the other hand, *Gazania rigens* hummocks are high, narrow, conical to elongate mounds with low surface temperatures, less sand volume to wet plant weight, and high detritus production and trapping ability (Hesp 1986).

Methods

Nine typical hummocks of each *Arctotheca populifolia* and *Gazania rigens* were selected to cover the size range from two adjacent slacks ca. 6 km east of the Sundays River. The topography of the two slacks and relative positions of the hummocks were recorded with a dumpy level in early March 1994 (Fig. 1c) .

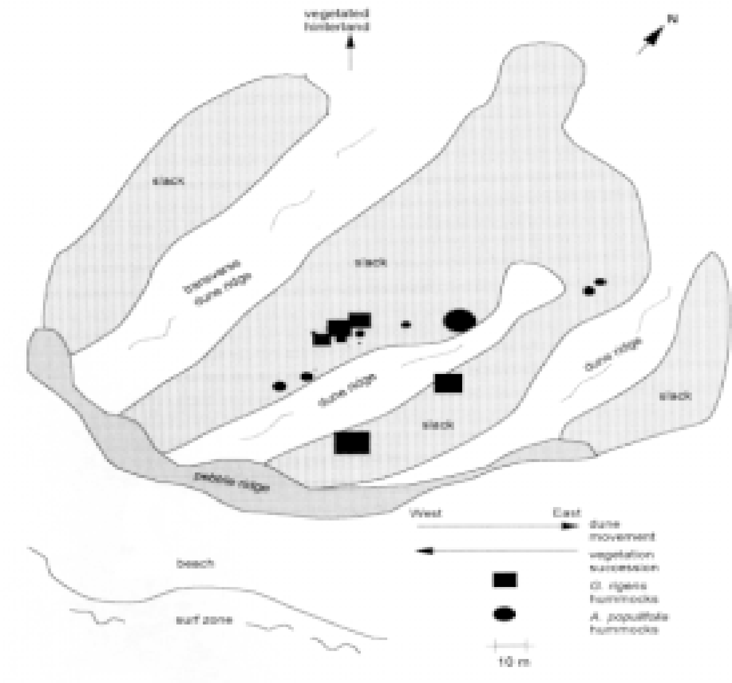

Fig. 1c. Diagrammatic representation of the study slacks, including the position of the study hummocks. The size of the symbols is proportional to the hummock sand volume.

Hummock shape

The shape of the hummock mounds was determined by erecting a frame of poles around the perimeter of the hummock, and stretching strings between the poles. The string was marked at 5-cm intervals, and positioned horizontally with a spirit level. Distance from the string to the soil surface of the hummock was recorded at 5-cm intervals to the nearest cm, once across the entire length of the hummock, and at three equidistant transects across the width. The profiles of smaller hummocks were recorded at one or two transects across the width, depending on the size.

From these detailed measurements, sand volume of the hummocks was estimated via integration of the area under the curves (Prof. P.R. Hall, Dept. of Mathematics and Appl. Mathematics, University of Port Elizabeth, pers. comm.). Basal area (the two-dimensional area occupied by the base of the hummock) was estimated by assuming the hummock was ovoid, and applying the equation:

$$\text{Area (m}^2) = 2 \times \text{length (m)} \times 2 \times \text{width (m)} \times \pi \qquad (1)$$

Hummock vegetation

The vegetation characteristics of each hummock were determined in order to demonstrate differences between the hummocks. Percent vegetation cover of the entire hummock was estimated as the proportion of points on a 10cm × 10 cm grid of 1 m^2 that coincided with plant structures ('point-intercept method'; Mueller-Dombois & Ellenberg 1974). On hummocks larger than 1 m^2, the grid was moved several times to estimate plant cover on the entire hummock surface.

The mean (average of five random measurements) and maximum vegetation height was recorded. Above- and below-ground vegetation (collected by clipping and sieving through a 1-mm mesh, respectively) was oven-dried at 60°C for 48 h to obtain dry mass values. The number and mass of individual stems from each hummock was recorded.

Regressions of the vegetation characteristics and hummock basal area were calculated from the data collected from the range of hummocks. Regressions of length versus dry and wet mass of leaves, and the number and length of leaves on individual stems were obtained. Regressions for leaf length versus leaf area (McLachlan et al. 1996) were incorporated to obtain estimates of leaf area : dry stem mass.

Arctotheca populifolia:

Leaf area (cm^2) = – 3.14 + 0.19 × leaf length (mm); $r = 0.96$, $n = 38$, SE = 2.32.

Gazania rigens:

Leaf area (cm^2) = –0.41 + 0.06 × leaf length (mm); $r = 0.91$, $n = 49$, SE = 0.48.

Leaf surface area versus vegetation dry mass was calculated by first determining the leaf area for a range of dry stem weights, and then applying the

Fig. 2. An example of a medium-sized *Gazania rigens* hummock (foreground) with a small *Arctotheca populifolia* in the background. Note the denser, more erect growth of *Gazania.* (Photo: J.J. Watson.)

formula to the dry weight of each stem collected from the hummocks, and then adding the total leaf area for the total above-ground vegetation mass. Since the hummock volume had already been determined, and vegetation mass was directly measured, regressions for total leaf surface area per hummock volume could be computed.

Hummock sand volume was probably the most accurate reflection of hummock size (basal area represents only a two-dimensional indication of the hummock profile, and so cannot account for the large differences in hummock shape between the two species). This was used to test hypotheses regarding the relationship between hummock size and vegetation features.

Sand volume of the hummocks was approximated by recording the height, width and length of the hummock and assuming that the hummocks had a tetrahedral pyramid shape. Volume was then determined by the formula:

$$\text{Volume (m}^3) = \text{length (m)} \times \text{width (m)} \times \text{height (m)} \times 1/3 \qquad (2)$$

Vegetation succession

Changes in abundance of the six most abundant plant species were recorded across 10 line transects spaced 10 m apart across the width of the slack, roughly midway between the pebble berm and the landward margin. The width of the slack floor was then divided into four zones of equal width, with zone 1 representing the eastern margin, and zone 4 the western part of the slack. The width of any plant species that overlapped or intercepted the transect line was recorded to the nearest mm. The accumulated length occupied by a species out of the total transect length was expressed as the percent cover for that species (the ‘line-intercept method’; Mueller-Dombois & Ellenberg 1974).

The basal areas of the *Arctotheca populifolia* and *Gazania rigens* hummocks across the width of the slack were recorded in order to determine if there was an increase in hummock size with time. Eight line transects were placed at 10 m intervals across the width of the central portion of the slack, and the length and width of all hummocks lying along the transects was recorded. The size-frequencies of the hummocks in each zone were calculated. Areas of the hummocks were estimated by the equation:

$$\text{Area (m}^2) = 1/2 \times \text{length (m)} \times 1/2 \times \text{width (m)} \times \pi \qquad (3)$$

In order to identify the differences in structural properties of the two different species of hummocks, regressions of vegetation characteristics and surface area versus hummock volume were determined and compared (Zar 1984).

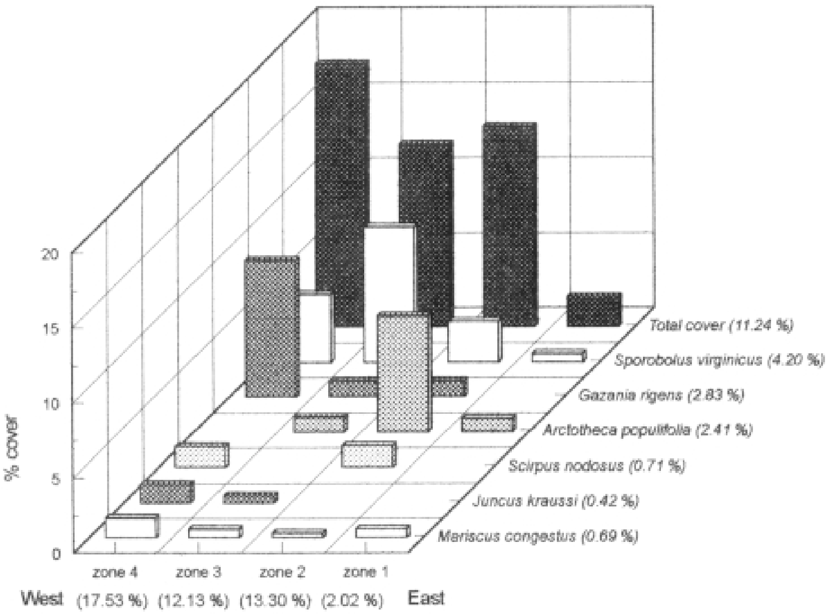

Fig. 3. Vegetation cover for the dominant plant species within four vegetation zones across the width of the slack. Values in parentheses represent the total percent cover for each zone within the slack (*x*-axis) and the average percent cover for each species across the width of the slack (*z*-axis).

Results

Vegetation succession

The composition of plant species changed across the width of the slack (Fig. 3). Zone 1 supported a low diversity and abundance of plants. *Arctotheca populifolia* was the most abundant species in zone 2 (7.8 % cover of the transect length), *Sporobolus virginicus* had the highest percent cover in zone 3 (9.0 % cover of the transect length), and *Gazania rigens* was the most abundant species in zone 4 (9.1 % cover of the transect length).

Total vegetation cover increased with distance from the eastern perimeter, from just over 2 %, to nearly 18 % on the western fringe. Over 80% of *Arctotheca* occurred in zone 2 (with about 10% each in zones 1 and 3), while the bulk of *Gazania* was recorded in zone 4 (over 80 %, with ca. 10 % each in zones 2 and 3). *Mariscus congestus* occurred in all zones, *Juncus kraussi* in zones 3 and 4, and *Scirpus nodosus* in zones 2 and 4, all with a low percent cover.

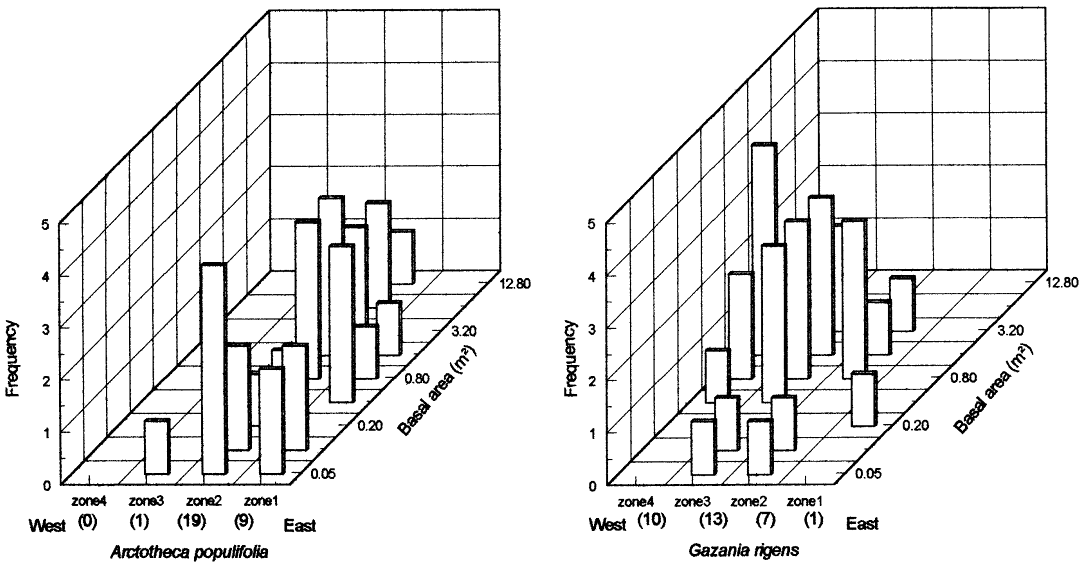

Fig. 4. Size-frequency of hummock dunes within each vegetation zone across the width of the slack. Values in parentheses are the numbers of hummocks within each zone. Note that the *z*-axis is scaled exponentially.

Table 1. Regression equations calculated from structural properties of dune hummocks. SE = standard error of the estimate, r = correlation coefficient, n = number of observations. For all regressions $P < 0.05$.

Dependent variable	Equation	SE	n	r
Arctotheca populifolia hummocks				
Leaf area (cm^2)	$122.04 + 0.01 \times$ volume (cm^3)	465.58	9	0.98
Basal area (cm^2)	$1\,755.90 + 0.10 \times$ volume (cm^3)	710.91	9	0.96
Vegetation dry mass below-ground (g)	$-\ 43.65 + 1.70 \times 10^{-3} \times$ volume (cm^3)	42.25	9	0.99
Vegetation dry mass above-ground (g)	$16.67 + 1.52 \times 10^{-3} \times$ volume (cm^3)	70.33	9	0.98
No. of stems	$-1.10 + 1.75 \times 10^{-4} \times$ volume (cm^3)	9.07	9	0.98
Hummock height (cm)	$7.32 + 5.40 \times 10^{-5} \times$ volume (cm^3)	5.77	9	0.92
Vegetation height (mm)	no significant regression			
Leaf area (cm^2)	17.26 x stem dry mass (g)$^{0.60}$	0.35	31	0.86
Leaf area (cm^2)	$-24.13 + 2.11 \times$ above-ground veg. dry mass (g)	150.73	9	0.99
Gazania rigens hummocks				
Leaf area (cm^2)	$2\,071.96 + 0.04 \times$ volume (cm^3)	355.79	9	0.95
Basal area (cm^2)	$5\,631.93 + 0.08 \times$ volume (cm^3)	507.21	9	0.94
Vegetation dry mass below-ground (g)	$53.46 + 2.20 \times 10^{-3} \times$ volume (cm^3)	356.82	9	0.88
Vegetation dry mass above-ground (g)	$69.03 + 2.79 \times 10^{-3} \times$ volume (cm^3)	212.56	9	0.97
No. of stems	$77.07 + 6.63 \times 10^{-4} \times$ volume (cm^3)	137.22	9	0.82
Hummock height (cm)	$4.82 + 8.50 \times 10^{-5} \times$ volume (cm^3)	5.08	9	0.98
Vegetation height (mm)	129.85 + 2.10 x 10^{-4} $\times$ volume (cm^3)	32.11	9	0.89
Leaf area (cm^2)	$25.60 \times$ stem dry mass (g)$^{0.73}$	0.21	31	0.96
Leaf area (cm^2)	$7.22 \times$ above-ground veg. dry mass (g)$^{0.99}$	0.14	9	0.99

Size distribution of hummocks

Arctotheca populifolia hummocks were most numerous and attained a maximum basal area (6.9 m^2) in zone 2 (Fig. 4). Only one small hummock was recorded in zone 3, and none in zone 4 (the western part of the slack). There was some overlap in zone 2 between the hummocks of *Arctotheca* and *Gazania*, although the former were more abundant (19 compared to 7). Larger *Gazania* hummocks were about equally numerous in zones 3 and 4, but achieved a maximum size (9.7 m^2) only on the western fringe of the slack.

There was a clear replacement of species of hummock-forming plants across the width of the slack, with no *Arctotheca* hummocks recorded in zone 4, while *Gazania* hummocks dominated zones 3 and 4. Furthermore, there was an increase in maximum hummock size (and more larger hummocks), with increasing distance from the eastern edge of the slack (Fig. 4).

Structural properties

Table 1 shows regression equations of vegetation characteristics and hummock basal area versus hummock sand volume. There were clear patterns of development across the size range of hummocks, with basal area, number of stems, hummock and vegetation height, vegetation mass, and leaf surface area increasing with sand volume. Hummock basal area versus sand volume was similar for the two species, but the two hummock-forming species showed large differences. *Gazania* hummocks supported at least 3 × the leaf surface area and number of stems than *Arctotheca* hummocks of equal volume. The maximum vegetation height of *Gazania* hummocks was almost double, while vegetation mass and hummock sand height were also all largely greater for *Gazania* than for *Arctotheca* hummocks of the same volume.

These relationships were all significantly linear with volume, and significantly linearly correlated with each other, except percent cover for both species, and vegetation height for *Arctotheca* hummocks (Tables 2 and 3).

Table 2. Correlation coefficients (significant at the 95 % confidence level) between structural properties of *Arctotheca populifolia* hummocks. Dashes indicate that the correlation was not significant.

	Volume	Leaf area	Basal area	Below-gr. veg.	Above-gr. veg.	No. of stems	Hummock height	Veg. height
Leaf area	0.98							
Basal area	0.96	0.96						
Below-ground vegetation	0.99	0.98	0.97					
Above-ground vegetation	0.98	0.99	0.96	0.97				
No. of stems	0.98	0.99	0.96	0.98	0.99			
Hummock height	0.92	0.96	0.90	0.90	0.97	0.96		
Vegetation height	-	-	-	-	-	-	-	
% cover	-	-	-	-	-	-	-	-

Table 3. Correlation coefficients (significant at the 95 % confidence level) between structural properties of *Gazania rigens* hummocks. Dashes indicate that the correlation was not significant.

	Volume	Leaf area	Basal area	Below-gr. veg.	Above-gr. veg.	No. of stems	Hummock height	Veg. height
Leaf area	0.95							
Basal area	0.94	0.92						
Below-ground vegetation	0.88	0.98	0.87					
Above--ground vegetation	0.97	0.99	0.93	0.97				
No. of stems	0.82	0.94	0.80	0.91	0.89			
Hummock height	0.98	0.94	0.98	0.90	0.97	0.80		
Vegetation height	0.89	0.85	0.94	0.81	0.88	0.68	-	
% cover	-	-	-	-	-	-	-	-

Discussion

Plant species were replaced in a characteristic order across the width of the slack, as predicted by the Clementsian (1914) view of succession. The zonation of vegetation was similar to that reported by McLachlan et al. (1987). Vegetation cover increased from east to west across the slack, as the initial colonizer *Arctotheca populifolia* gave way to *Gazania rigens* and *Sporobolus virginicus*. Total vegetation cover was greater than is considered typical of these slacks (2-10%), largely due to the high abundance of *Sporobolus virginicus*.

Wind and sand movement are probably the major factors controlling distribution and establishment of plant communities on coastal foredunes (Lubke 1983; Masson 1990). The importance of salt spray in limiting dune vegetation has been documented (Lubke & Avis 1982; Pammenter 1983), whereas soil factors have been regarded as probably being of secondary importance (Lubke 1983), since dune species show a great range of tolerance to soil quality. In the particular case of species replacement across the width of the slack (where salt spray is likely to be the same), the driving force for succession is most likely site modification by previous colonizers.

The structural attributes of the hummocks correspond to descriptions by Hesp (1986), who characterized *Arctotheca* foredunes as low, semi-circular mounds, with high surface temperatures, less plant weight per sand volume, and a low to moderate detritus trapping ability. In contrast, *Gazania* foredunes are high, narrow mounds with low surface temperatures, greater plant weight per sand volume, and a high detritus trapping ability.

In addition to vegetation succession, hummock size increased with increasing distance from the recently exposed eastern margin of the slack. Small *Arctotheca* hummocks were common on the eastern margins, larger *Arctotheca* and small *Gazania* hummocks co-occurred in the central portion, and large *Gazania rigens* hummocks predominated on the western parts of the slack floor, where they were subject to inundation by the slipface of the advancing transverse dune.

The reasons for the differences in distribution of *Arctotheca* and *Gazania* hummocks within the slack are not clear. Both plant species are wind-dispersed, and hummocks originate shortly after the retreating dune exposes new sections of the slack floor. Development is terminated after 5 - 7 yr (depending on the width of the slack) when they are smothered by advancing dunes. Although the development of *Gazania* hummocks is only terminated when the hummock becomes smothered by the advancing dune, most *Arctotheca* hummocks senesce before this event. Nematode involvement has been implicated in the die-out of *Ammophila breviligulata* dune hummocks along the north and mid-Atlantic coasts of the United States (Seliskar 1995), although no data are available on the possible involvement of pathogenic nematode species for the Alexandria coastal dune field.

Conclusions

Both vegetation succession defined as the characteristic replacement of species (the replacement of *Arctotheca populifolia* hummocks with *Gazania rigens* hummocks), and succession within the mono-specific hummocks themselves defined as site modification (increased sand volume and structural mass and habitat complexity) over time have been demonstrated.

The structural features of hummocks within the slack were very different for the two plant species. The shape of the hummocks is dependent on the vegetation around which the sand accumulates (Hesp 1981, 1989). *Gazania* has an erect growth form and is thin-leaved compared to the more prostrate growth form of *Arctotheca*. The increased plant height reduces the wind flow velocity, resulting in lower wind speeds in *Gazania* vegetation. A consequence of this is that the hummock dunes themselves are higher, and the basal width is narrower (Hesp 1989). This relationship was evident across the size range of hummocks, where both the vegetation height and hummock dune height were consistently greater for *Gazania* hummocks. This suggests an increased amount of resources and spatial niches available for fauna on the later colonizer.

The vegetation properties of the hummock-forming plants determine the ability to trap wind-borne materials (such as sand, detritus and seeds), the shape of the hummock dunes (Hesp 1981, 1989), and influence the composition of insect (Murdoch et al. 1972; Southwood et al. 1979; Boonsma & van Loon 1982) and spider fauna (Lowrie 1948; Duffey 1968). Thus, whereas sand movement is the key process controlling slack ecology as a whole (McLachlan et al. 1996) – since advancing and retreating transverse dune ridges smother and expose the slack floor respectively– the ecology of hummocks formed within the slacks is probably more immediately determined by the vegetation characteristics of the hummock-forming plants.

Hummocks provide an ideal study-ground for ecologists interested in exploring relationships between an increase in area of an ecosystem and corresponding changes in resources and community structures. Since an increase in hummock size results in a simple linear increase in resources, with no changes in plant species composition, successional processes can be investigated without the usual confounding factors. This is of special interest for animal ecologists, who need to consider the influence of the vegetation on the distribution of species.

This study has an important implication for the conservation of dune ecosystems. Since hummocks formed by different species of plants offer different resources and habitats for animals, they are likely to harbour at least some animals not common to all hummocks. Furthermore, since different species of plants produce hummocks with distinct vegetation characteristics, microclimates and organic trapping ability, there is likely to be little redundancy in ecological functioning. Thus all hummocks should not be managed as ecologically similar units. The conservation of a representation of all species of hummock-forming plants is required for the maintenance of biodiversity in coastal dunes.

In addition, since sand movement plays such an important role in slack ecology, it is essential that the integrity of the sand dynamics be maintained. For example, dunes should not be stabilized to facilitate tourist developments, and off-road vehicles should not be allowed access to dune systems.

Although the Alexandria coastal dunefield is largely within a proclaimed nature reserve, there is considerable illegal driving of off-road vehicles into the slacks, and this increasing. This study supports the rigourous protection of these hummocks on the basis of both sand stabilization and biodiversity conservation.

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