



Primary sand-dune plant community and soil properties during the west-coast India monsoon

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ABSTRACT

A seven-station interrupted belt transect was established that followed a previously observed plant zonation pattern across an aggrading primary coastal dune system in the dry tropical region of west-coast India. The dominant weather pattern is monsoon from June to November, followed by hot and dry winter months when rainfall is scarce. Physical and chemical soil characteristics in each of the stations were analysed on five separate occasions, the first before the onset of monsoon, three during and the last post-monsoon. The plant community pattern was confirmed by quadrat survey. A pH gradient decreased with distance from the shoreline. Nutrient concentrations were deficient, increasing only in small amounts until the furthest station inland. At that location, there was a distinct and abrupt pedological transition zone from psammite to humic soils. There was a significant increase over previous stations in mean organic matter, ammonium nitrate and soil-water retention, although the increase in real terms was small. ANOVA showed significant variation in electrical conductivity, phosphorus, calcium, magnesium and sodium concentrations over time. There was no relationship between soil chemistry characteristics and plant community structure over the transect. *Ipomoea pes-caprae* and *Spinifex littoreus* were restricted to the foredunes, the leguminous forb *Alysicarpus vaginalis* and *Perotis indica* to the two stations furthest from the strand. *Ischaemum indicum*, a C₄ perennial grass species adopting an ephemeral strategy was, in contrast, ubiquitous to all stations.

KEYWORDS

dunes, monsoon, plant community, soil chemistry, transect survey, west coast of India

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INTRODUCTION

There has been coastal sand grain deposition for as long as there has been river-sediment discharge and tidal oceans in the geological history of Earth. Until plants invaded land, there were no existent dune systems as are currently seen. Plant roots and contiguous microflora stabilise sand grains, forming a flexible natural barrier to encroachment by the sea. Primary coastal dunes are harsh environments. Plant nutrients are deficient (Lammerts & Grootjans 1997; Lammerts et al. 1999). High percolation rate and limited soil-water retention affect plant-water balance. Increased levels of low-affinity uptake mechanism of sodium (Na) may compete with potassium (K) uptake and upset osmotic balance (Salisbury & Ross 1978). Aeolian sand grains can extinguish seedlings by burial (Maun 2004) and, in the west coast India tropics, between summer

monsoons, intense solar radiation adversely affects photosynthesis, and thus carbon (C) cycles (Powles 1984), and desiccates plants.

Soil nutrients in natural ecosystems are spatially discrete at the macro-, meso- and micro-scales (Hodge 2006) and in primary coastal dunes, the distribution of deficient concentrations is as patchy (Olsson et al. 2002) as is the distribution of plants (Davy & Figueroa 1993; Jackson & Caldwell 1993). Maun (2009) describes deficiency and patchiness as consistent key factors of coastal primary dune ecosystems where organic matter (OM), in particular, is invariably low in concentration. Soil nitrogen (N) is described as the plant growth-limiting nutrient in primary dune soils in temperate regions (Tilman 1984; Willis 1989), and a low input of OM suggests that there is a similar limitation where it is rapidly turned over in tropical environments. Access to plant-available phosphorus (P) can be restricted in any soil, even where large concentrations may be

fixed (Brady 1974). Baldwin and Maun (1983) suggested that the primary source of P in dune soils is weathering of minerals that are found in very low quantities. Mineralisation of organic P from plant litter, and sorbed inorganic P complexed in OM (Bloom 1981; Gerke & Hermann 1992) also contribute to the available pool. Dissolved P concentrations often increase in anaerobic soils (Morris & Hesterberg 2010), a factor that may be important where monsoon rain can sustain soil saturation for long periods of time. Deficient minor and trace-element nutrients can also be limiting.

The west coast of India's summer monsoon weather system is the dominant climatic feature in the area, with rains usually beginning early in June. The annual mean precipitation on the Goa coast is 2770 mm, 2500 mm of which falls before the end of September. Night-time temperatures range from winter (Jan/Feb) $\sim 12^{\circ}\text{C}$ to summer (April/May) $\sim 27^{\circ}\text{C}$. Day-time temperatures are $\sim 30^{\circ}\text{C}+$ from November to May. Relative humidity (RH) increases from $\sim 50\%$ in winter to $\sim 72\%$ in early April. From mid-April until summer, occasional short and light localised showers can occur, more regularly as June approaches. Moisture-laden air annually carried northward over the Arabian Sea by summer winds that originate in an area of high pressure in the southern Indian Ocean fuels convection and storm cloud development, generating monsoon. The leading edge of the weather system generally arrives in the south of India in late May and reaches the Himalaya Range in the far north by mid-July. Heavy rains driven onshore by strong westerly winds (Fig. 1) are prevented from escaping onto the Deccan Plateau by the Western Ghats, a mountain range (average elevation 1200 m) that runs parallel to the coast from the tip of India to ca 270 km north of Mumbai. Instantly daytime temperatures are reduced by $\sim 10^{\circ}$ while relative humidity (RH) approaches 100%. Plant growth is regenerated in the dunes. Rains continue into September, gradually changing to less regular, often still heavy and at times prolonged, showers. Rainfall

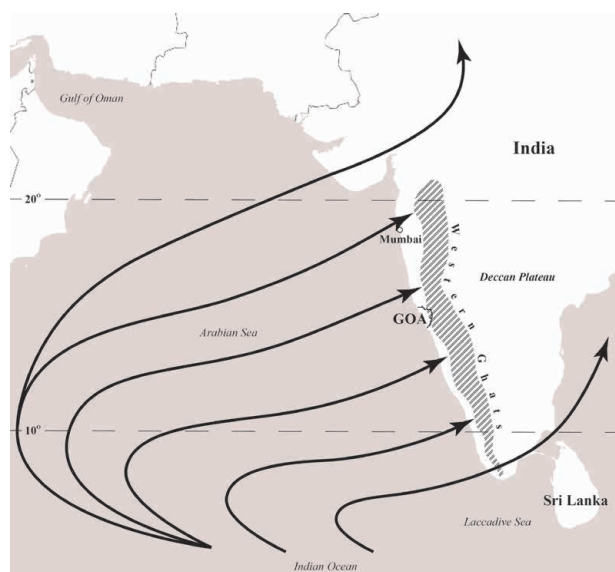


Figure 1. Annual passage of summer monsoon rains carried northerly from the Indian Ocean that fall on the west coast of the sub-continent.

after early November is rare. The dunes' shallow rooted plants rapidly wither and die, and even the deepest rooted species become severely stressed before monsoon returns.

Transect surveys inland from the shoreline in dune systems have a long history (Cowles 1899; Callaway & Walker 1997). A general trend in plant succession is from a limited diversity of patchy, prostrate herbaceous dune-building species in near-shoreline severely nutrient-deficient primary dune soils, with fertility and diversity increasing through secondary dunes and into forest beyond. Organic matter increases and pH decreases in detectable gradients, sometimes over a considerable distance (Pennanen et al. 2001; Lane et al. 2008). Community structure and dynamics in primary dunes are complex and variable. Carboni et al. (2009) described, for example, mosaic pattern and Fenu et al. (2013) zonation pattern. The attributed driver mechanisms vary. Franks (2003) proposed a nucleation hypothesis to succession where a clumped distribution notable in dune systems might be explained by seed dispersal and germination in early life history. Seedling burial by wind-borne sand grains can contribute a considerable constraint and Lichter (1998, 2000) suggested that succession may not be the result of gradual soil development.

A herbaceous plant community zonation pattern in the flora of an aggrading primary coastal dune system in North Goa had been previously observed during monsoons. The zones were clearly identifiable in annually formed incipient berm, in 4–7 m high, 35–45 m wide primary grey dunes, and in leeward flats beyond. The soil nutrient status has been rarely investigated in detail on a short-term temporal basis in a tropical primary coastal dune, and compared with plant community pattern. To the best of our knowledge, this is the first such survey in the west-coast India monsoon. It was considered that where active plant growth coincides with the short-term monsoon event, there may be an opportunity to examine the influence soil factors may have on plant community structure. The hypothesis is that one (or several) of the soil physical and chemical characteristics of the system is the driver mechanism of the observed plant community zonation pattern.

1. MATERIALS AND METHODS

An interrupted belt transect (Fig. 2) was established before the onset of monsoon rains across an aggrading primary dune system on the coast of Goa, India ($15^{\circ}37'55''\text{N}$, $73^{\circ}43'22''\text{E}$) (Fig. 3). The selected line extended 175 m from mean high-water mark (MH-WM) to within 5 m of a banyan tree. The tree was 15 m in front of a wall that separated cultivated rice paddy 0.5 m below. The line avoided sparsely planted exotic cashew and coconut root zones and fallen palm fronds, which might augment nutrient concentrations in indigenous plant rhizosphere soils. Seven stations (St.) 2 m wide and 3 m long, and approximating the observed zones, were marked at 5, 20, 35 m from MH-WM in the foredunes, and at 65, 101, 138, and 175 m in the hind dunes.

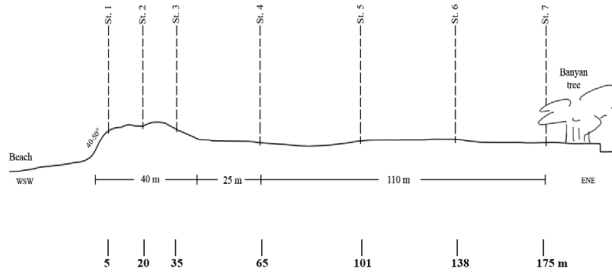


Figure 2. Transect line on Morjim (Goa) dune system indicating positions of sample sites (St. 1–7) in metres from mean high-water mark (MH-WM).



Figure 3. North Goa coastline indicating study-site location.

A grid quadrat (600 × 600 mm divided into 100 mm squares) survey of plant frequency was conducted when herbaceous plant biomass was estimated to be maximal, 111 days after monsoon onset. Five quadrats per station were placed by restricted randomisation (Greig-Smith 1983) and diversity and abundance of plant species rooted within each of the 36 inner grids recorded. Means are expressed as percentage frequency. Soil samples for chemical analysis were taken from rhizosphere soils ($n \geq 3$ plants sp^{-1}) to 20 cm depth and thoroughly mixed by hand to give a single homogeneous sample for each station. This was undertaken on five separate occasions (hereafter Series), the first before rains (0 day), three during (20, 67, 129 d), and the last post-rains (189 d), May to November 2010. Air-dried 100 g sub-samples were sieved to 2 mm to remove the large OM fraction. Sub-sample analyses followed procedures laid out by Singh et al. (2005). pH was measured in soil–water suspension in a 1:2 ratio (Elico L1 120 pH meter, ELICO Ltd., Hy-

derabad, India), electrical conductivity (EC) from the clear extract after pH measurement (Elico CM 180 conductivity meter), organic carbon (OC) by the Walkley and Black (1934) method, factored to give OM percentage by weight, available P_2O_5 by Brays method (Bray & Kurtz 1945) using Bray's No. 1 solution, potassium (K_2O) and Na by the ammonium acetate method from Hanway and Heidel (1952), and magnesium (Mg) and calcium (Ca) by a modified ammonium acetate method from Barvah and Barthakur (1997) (Elico flame photometer Unit 21). The available micronutrient iron (Fe) was assessed from foredune rhizosphere soils on one occasion only by the DTPA- CaCl_2 -TEA method (Lindsay & Norvell 1978) using an atomic absorption spectrophotometer AAS-EC Electronics Corps of India Element AS AAS 4139. Ammonium-N ($\text{NH}_4\text{-N}$) partial transect data for stations 4–7 only were obtained by titration procedures described in Indian Bureau of Mines (2004) and analysed by Italab Ltd., Madgaon, Goa, India. Further sets (St. 1–7) of samples were extracted during February and May of the following dry season and Na concentrations analysed.

Measurements of soil physical properties were conducted, without repetition, during the course of the study. Sand grain particle size, an estimate of aggregation, was measured by gently passing air-dried 50 g samples ($n = 3$) from each station through nested 1003, 500, 250 and 52 μm sieves (Cheetham et al. 2008), after first removing the large OM fraction above 2 mm. Proportions were derived gravimetrically. Soil water content samples ($n = 5$ from each station, homogenised) were extracted 1 h and 4 days after rain to 20 cm depth. Percentage water was determined gravimetrically after drying at 105°C for 6 h. Silt–clay fraction was assessed by water column suspension using the hydrometer method (Singh et al. 2005). Rainfall data were obtained from India Meteorological Department station, Panjim, Goa, situated on the coast 21 km south of the research site.

A correlation matrix was constructed of mean chemistry data (5 temporal datasets × 9 variables), soil physical properties and plant distribution over the transect length. Further examination was made of variation between the five temporal datasets within each of the chemistry variables and correlated with rainfall figures cumulated up to and including each of the sampling dates. Graphics were drawn in Microsoft Excel 2007 (USA). Gradient analysis and analysis of variance (ANOVA) where pairwise comparisons were made by Tukey's Honestly Significant Difference (HSD) test at $P = <0.05$ (Hsu 1996) were carried out in Minitab 16 (Minitab Inc., USA). ANOVA was applied to spatial- and temporal-scale data. Canonical correspondence analysis (CCA) and de-trended canonical correspondence analysis (DCCA) were carried out in the CANOCO v4.51 package (Microcomputer Power, Ithaca, NY). The length of the longest gradient from DCCA was 2.7, suggesting there was no need for a DCCA over a CCA. Using the nomenclature of CANOCO, the plant species × location (i.e. distance of the transect stations from the strand) data matrix was compared with study-period mean soil chemistry × location data matrix (as “environmental variables”). Plant species data were $\log(x+1)$

transformed and down-weighted for rare species, ensuring that the ordination was not dominated by the most common species, nor overly influenced by the rare species. Pearson's correlation coefficient was used to relate patterns of plant and soil chemistry data over the transect and applies to all references to correlation in the text. Pearson's was also used as a test where CCA indicated association. Simpson's index of diversity (1-D) was used as a measure of species diversity over distance in the plant community.

2. RESULTS

2.1. Plant community

All of the plant species encountered were prostrate. A 100% frequency was found only in the ubiquitous grass species *Ischaemum indicum*, at the furthest inland station, all other recorded frequencies indicating a patchy distribution. Table 1 further suggests plant zonation, with *Ipomoea pes-caprae* and *Spinifex littoreus* restricted to the foredunes, the leguminous forb *Alysicarpus vaginalis* and *Perotis indica* to the two stations furthest from the strand. Ten of the 13 species recorded were

Table 1. Plant species rooted frequencies in 7 stations on the transect

	St. 1	St. 2	St. 3	St. 4	St. 5	St.6	St.7
Distance from strand (m)	5	20	35	65	101	138	175
Species	%	%	%	%	%	%	%
<i>Spinifex littoreus</i> (Burm.f.) Merr. (Poaceae) (P;C)	13.75 (±9.5)	37.50 (±14.1)	-	-	-	-	-
<i>Ipomoea pes-caprae</i> (L.) R.Br. (Convolvulaceae) (P;C)	56.25 (±9.4)	2.50	10.42	-	-	-	-
<i>Digitaria adscendens</i> (H.B.K.) (Poaceae) (P;C)	12.50	1.25	-	1.25	-	-	-
<i>Launaea fallax</i> Jaub. & Spach (Asteraceae) (B/P; C)	2.50	-	-	1.25	6.25	1.25	-
<i>Cyperus arenarius</i> Retz. (Cyperaceae) (P)	1.25	6.25	21.25 (±2.8)	48.75 (±8.9)	3.75	15.00 (±7.2)	-
<i>Digitaria stricta</i> Roth. (Poaceae) (A)	-	-	-	-	-	2.50	-
<i>Waltheria indica</i> L. (Sterculiaceae) (P)	-	-	-	8.75	51.25 (±15.6)	15.00 (±9.5)	-
<i>Dactyloctenium aegyptium</i> L. (Poaceae) (A;NR)	-	-	-	-	12.50	20.00 (±8.7)	21.25 (±5.7)
<i>Zoysia matrella</i> (L.) Merr. (Poaceae) (P;C)	-	-	-	-	53.75 (±10.9)	55.00 (±17.1)	28.75 (±13.0)
<i>Panicum repens</i> L. (Poaceae) (P;C)	-	-	-	-	5.00	-	-
<i>Alysicarpus vaginalis</i> L. (Fabaceae) (P;NR)	-	-	-	-	-	12.50	27.50 (±17.9)
<i>Perotis indica</i> L. (Poaceae) (A)	-	-	-	-	-	-	1.25
<i>Ischaemum indicum</i> (Houtt.) Merr. (Poaceae) (P)	8.75	61.25 (±4.7)	71.25 (±5.78)	68.75 (±15.0)	33.75 (±16.5)	75.00 (±14.8)	100.00
Simpson's Index of Diversity (1-D)	0.646	0.595	0.871	0.596	0.745	0.774	0.646

SD in parenthesis. Overall Simpson's Index of Diversity (1-D) = 0.816. A = annual, B = biennial, C = clonal, NR = nodal rooting, P = perennial.

perennials, seven clonal in habit. All eight Poaceae species were C_4 (Waller and Lewis 1989), five were clonal perennials, and one of the three annuals, *Dactyloctenium aegyptium*, was nodal-rooting. All perennials except *I. indicum* were rooted deeply, particularly genets of *I. pes-caprae* (Duvall 1992) and *S. littoreus* in the foredunes. Simpson's index of diversity (1 - D) was characteristic of coastal dunes, low in stations and overall (Table 1).

2.2. Silt/clay, soil-water and sand-grain particle size

Soil silt/clay fraction was negligible up to St. 7 where there was a three- to six-fold increase that, in real terms, remained very low (Fig. 4). There was a significant positive correlation of silt/clay with mean P_2O_5 , NH_4-N , Mg, OM and K_2O (Table 2). Soil water content assessment (Fig. 5) indicated higher levels of retention in the two stations furthest inland. Correlation indicated significant similarity in the two datasets (Table 2), 1 h after rain and 4 d after rain. There was significant correlation

of 1 h mean and highly significant correlation of 4 d mean soil water content with OM (Table 2). A significant negative correlation was found between $< 52 \mu m$ sand-grain particle size data (Fig. 6) and 1 h soil water content, and a significant positive correlation between 250–500 μm sand-grain particles and 1 h soil water (Table 2). The two sand grain fractions made up $> 97.5\%$ of the matrix overall. Rubification of the soil was clearly observed at St. 7, a transition from psamment inceptisol to humic mollisol soil (USDA NRCS n/d) occurring in just 1 to 2 m of transect length.

2.3. Soil chemistry characteristics

Mean pH (Fig. 7a) followed a general trend towards acidity after an initial slight increase in St. 2 on the crest of the foredunes, and decreased sharply in the last station where the variation over time was greatest. There was an overall increase in mean acidity by almost one order of magnitude (range pH 5.4–7.2). Analysis indicated a transect-wide pH gradient across the system (mean pH = $6.953 - 0.006 * t$) where mean pH was calculated over the sample time points (Series 1–5) and $t =$

Table 2. Significant Pearson's correlations between silt/clay, soil H2O and nutrients (n=5)

Variables	r	P
Silt/clay & OM % d.w.	0.919	0.014
Silt/clay & NH_4-N	0.966	0.004
Silt/clay & P_2O_5	0.860	0.031
Silt/clay & Mg	0.925	0.012
Silt/clay & K_2O	0.883	0.024
H ₂ O 1 h & H ₂ O 4 d	0.765	0.045
H ₂ O 1 h & OM	0.738	0.038
H ₂ O 4 d & OM	0.990	<0.001
H ₂ O 1 h & $<52 \mu m$	-0.861	0.030
H ₂ O 1 h & 250-500 μm	0.820	0.045

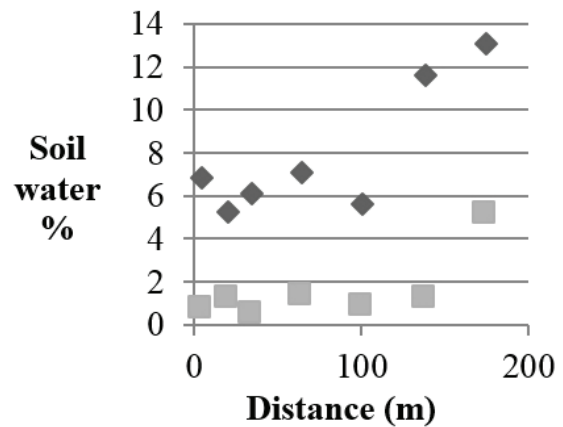


Figure 5. Soil water retention in transect stations. (♦ = 1 h, □ = 4 d after rain)

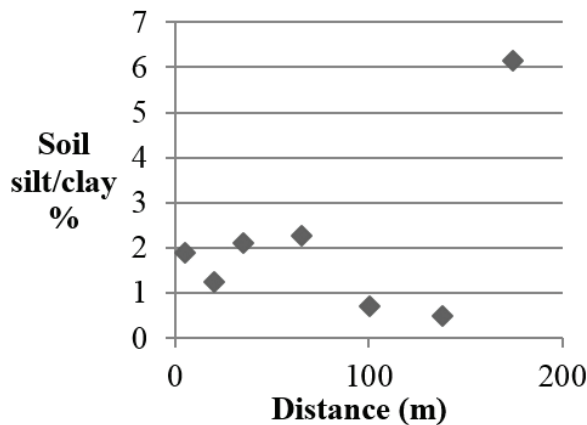


Figure 4. Silt/clay fraction in transect stations.

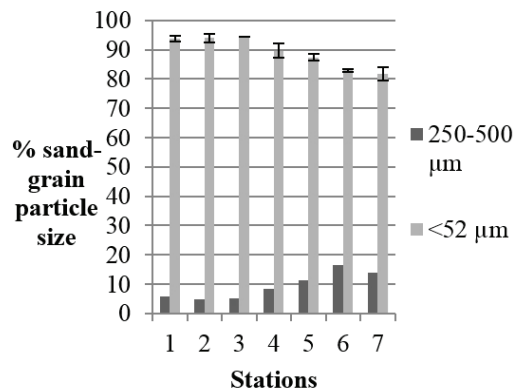


Figure 6. Mean sand-grain particle sizes, $> 97.5\%$ of the matrix. Error bars are SD of three replicates.

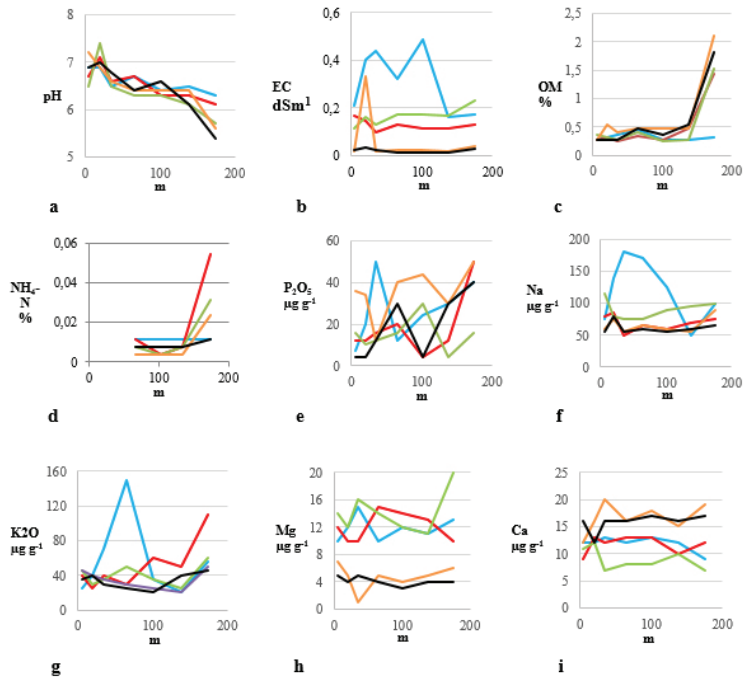


Figure 7. Scatter diagrams of soil chemistry analyses. St. 1–7 distances from MH-WM: 5, 20, 35, 65, 101, 138 and 175 m. Time-series sample retrieval: — 0 day; — 20 d; — 67 d; — 129 d; — 189 d.

locations along the transect. The mean absolute % error (MAPE) was 1.820, mean absolute deviation (MAD) 0.119 and mean squared deviation (MSD) 0.019; all accuracy measures indicate a robust fit (Hobai 2009). There were no other similarly clear gradients. Electrical conductivity (Fig. 7b) varied throughout the monsoon, particularly in St. 2–5 where the maximum range (0.49 dS m⁻¹) exceeded SD in the period prior to the onset of monsoon rains. Days 129 (Series 4) and 189 (Series 5) concentrations were comparatively low. OM (Fig. 7c) was <0.5% in St. 1–6, and up to 4 × higher (range maximum 2.12%) in St. 7 after the onset of rain. A pattern similar to OM was shown in the partial data set of NH₄-N (Fig. 7d), low and even distribution of plant-growth limiting concentrations (mean 0.01%) in St. 4–6 with a sharp increase in St. 7 (mean 0.03%, range up to 0.06%) where there was a reduction on cessation of rains. Canonical correspondence analysis (Fig. 8) and correlation (Table 3) indicated a transect-wide significant negative association between pH and OM and between pH and P₂O₅. The pH and OM in the partial St. 1–3 transect, however, showed no significant relationship, yet in the partial St. 4–7 transect, there was a significant negative correlation. Interestingly, there was no significant correlation between partial transect St. 4–7 NH₄-N and OM (Table 3). Plant-available P₂O₅ (Fig. 7e) concentrations were notably variable both spatially and temporally. There was nevertheless a negative correlation of mean P₂O₅ with mean pH and a highly significant positive correlation with mean OM (Table 3). The greatest variation in Na levels (Fig. 7f) was in St. 3 on the back-slope of the foredunes and in St. 4, high levels recorded prior to rains (up to range maximum 180 μg g⁻¹),

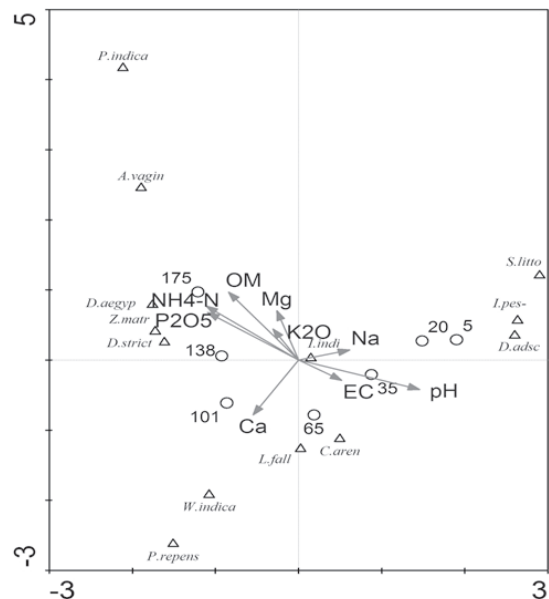


Figure 8. CCA triplot showing ordination of plant species (triangles), transect stations locations (circles) and mean soil chemistry data (arrows). For full list of species names, see Table 1. The two axes jointly explain 70.9% of the variation.

rapidly leached to comparatively low levels (mean < 55 μg g⁻¹) after the onset of monsoon rain. There was no significant correlation of mean Na with EC over the transect length. Levels of Na concentrations in samples collected during the following hot, dry months of February and May (Fig. 9) indicated a significant correlation ($r = 0.872$; $P = 0.010$) between the two

Table 3. Spatial-scale correlations between mean soil chemistry characteristics over 7 stations

Variables	r	P	
pH & OM	-0.813	0.047	
pH & P ₂ O ₅	-0.887	0.022	
pH & OM	-0.593	n/s	(St. 1-3)
pH & OM	-0.948	0.007	(St. 4-7)
OM & NH ₄ -N	-0.731	n/s	(St. 4-7)
OM & P ₂ O ₅	0.959	0.005	
OM & Mg	0.811	0.048	
K ₂ O & Mg	0.877	0.025	

n/s = non-significant

data sets, and ANOVA indicated significant difference ($F = 25.1$; $P = 0.001$). The May data set mean was 30.2% lower than that recorded in February. There was no correlation between the dry season data sets and monsoon season mean data. K₂O (Fig. 7g) showed greatest variability in St. 4 where pre-monsoon maximum range was singularly high at > 150 µg g⁻¹. Canonical correspondence analysis indicated that there was association between K₂O and Mg (Fig. 7h), confirmed by significant correlation (Table 3). There was no significant correlation between Ca (Fig. 7i) and any other variable. ANOVA indicated a spatial (i.e. distance of stations from the MH-WM) effect on three of the variables, pH ($F = 15.98$; $P < 0.001$), OM ($F = 12.96$; $P < 0.001$) and NH₄-N ($F = 8.83$; $P = 0.001$). Canonical correspondence analysis confirmed that there were no soil chemistry patterns consistent with plant community zonation structure over the length of the transect excepting an indication of *I. pescaprae*, *S. littoreus* and *Digitaria adscendens* constraint to Na-rich foredune zones.

Analyses of the five temporal data sets within each of the chemistry variables are an indication of the changes that have occurred in soil chemistry over the time period. There was (Table 4) significant positive correlation between pH and EC, between pH and K₂O, between EC and Na and between NH₄-N and K₂O. There was significant negative correlation between EC and OM and between Ca and Mg, and between OM and K₂O, suggesting K₂O is not complexed in OM. There was no significant correlation between EC and K₂O, nor between OM and Na, an indication that Na is also not complexed in OM. ANOVA showed that (a) EC: Series 1 was significantly greater than ($F = 8.07$; $P = 0.015$), and Series 5 significantly less than, Series 2, 3 and 4; b) P₂O₅: Series 4 was significantly greater than Series 3 ($F = 13.61$; $P = 0.003$) and differences in the other three series non-significant; (c) Ca: Series 4 and 5 were significantly greater than Series 1, 2 and 3 ($F = 12.40$; $P < 0.001$); (d) Mg: Series 4

Table 4. Correlations of transect variables in soil chemistry analyses over time, Series 1-5

Variables	r	P
pH & EC	0.992	0.026
pH & K ₂ O	0.929	0.022
EC & OM	-0.943	0.016
EC & Na	0.962	0.009
EC & K ₂ O	0.876	n/s
Ca & Mg	-0.975	0.005
NH ₄ -N & K ₂ O	0.920	0.027
OM & Na	-0.853	n/s
OM & K ₂ O	-0.878	0.050

n/s = non-significant. Data retrieval time points: 0, 20, 67, 129, 189 d.

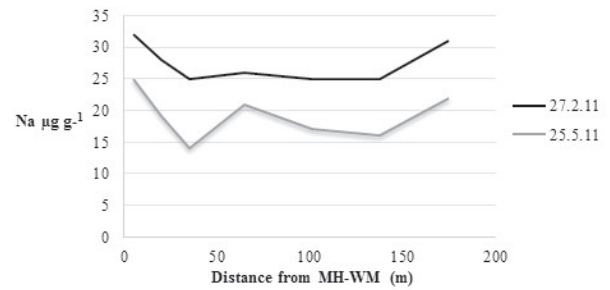


Figure 9. Sodium concentrations during the dry season. St. 1–7: 5, 20, 35, 65, 101, 138 and 175 m from the strand.

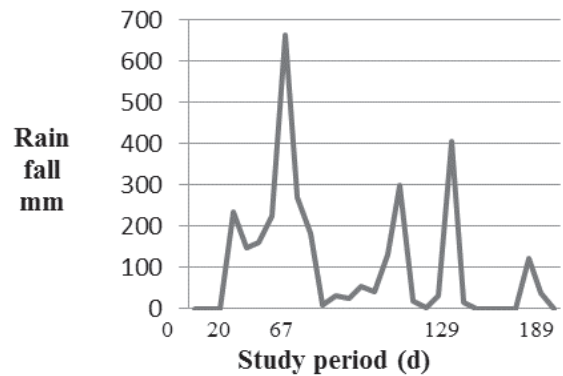


Figure 10. Rainfall over the study period, data set at 7 d intervals.

and 5 were significantly less ($F = 35.37$; $P < 0.001$) than Series 1, 2 and 3; and (e) Na: pre-monsoon Series 1 was significantly greater ($F = 7.08$; $P < 0.001$) than the four following series. There was no significant correlation between rainfall (Fig. 10) and any of the soil chemistry factors.

3. DISCUSSION

Despite the primary system ostensibly being simple, the survey results suggest considerable complexity. The plant community was composed of dune-building species, with CCA clearly supporting the initial observation of a zonal distribution pattern. Whether *I. pes-caprae*, *S. littoreus* and *D. adscendens* restriction to foredunes corresponds to the Na vector in CCA that indicates enrichment in the region, or not, is inconclusive. The Na data were inflated by the very high concentrations recorded before the onset of rain and ensuing increase in plant growth activity, and as the first two species are common in foredunes of tropical systems (Duvall 1992), genotypic characteristics cannot be discounted. On the mobile seaward face, the clonal perennial grass *D. adscendens* was established, but not in any of the other stations. This may be the first report of the occurrence. Excepting *I. indicum*, only two further species, *Launaea fallax* and *Cyperus arenarius*, were recorded in the foredune region, the remaining species variably occupying the stations in the behind-dune region only. *Launaea fallax*, *C. arenarius* and *Walteria indica* appeared intolerant of the higher nutrient status of St. 7 and the forb *A. vaginalis* was restricted to the last two stations. *Digitaria stricta* and *Perotis indica*, two of the annual grasses, were each recorded in one station only, both at very low frequency. The ubiquitous perennial *I. indicum* appeared to struggle on the seaward dune face but was established in all other stations. Inexplicably there was a lower frequency indicated at St. 5. A number of the perennial herbaceous species displayed considerable plasticity, particularly the shallow-rooted *I. indicum*, which has adopted an ephemeral lifestyle. Plant physiology (62% of the community are fine-leaved C_4 grasses, 77% are perennials, 46% clonal species) indicates adaptation to hostile conditions such as high winds that increase transpiration, mechanical damage from abrasion, intense radiation and elevated Na concentrations. Sodium concentrations can affect zonation (Mariko et al. 1992; Wilson & Sykes 1999) but here there was no clear indication of correlation with plant community structure. Plant zonation has also been attributed to sand-particle aeolin movement and consequent seedling burial (Moreno-Casasola 1988 and references therein; Dech & Maun 2005). The distribution of fine $<52 \mu\text{m}$ sand-grain particles in this system indicates considerable surface mobility, significant aggregation occurring only beyond 101 m from MH-WM. Wind-blown sand over the beach certainly irritates sun-bathers at times!

Species diversity was low in all stations, and variable, typical of primary dune systems (Ranwell 1972; Maun 2009), indicating, according to some evidence, long-term ecosystem instability (de Mazancourt et al. 2013; Yadav & Mishra 2013). The data suggest plant/plant facilitation, or at least non-competitiveness, where correlations between frequencies of *I. pes-caprae* and *D. adscendens* in St. 1-4, *L. fallax* and *W. indica* St. 4-6, and *D. aegyptium* with *Zoysia matrella* St. 5-7 were significantly positive. The plants are affected by observed wind-shear that contributes to the general prostrate habit, a common strategy that helps reduce transpiration and therefore desiccation

(Huang & Fry 1999; Ripley & Pammenter 2004). Plant cover was visibly patchy, even in the higher frequency St. 7 region, contributing to soil evapo-transpiration.

Analyses of mean soil chemistry revealed that the only clear gradient across the system was pH, a feature commonly found in studies of coastal dune systems (Lichter 1998; Gormally & Donovan 2010). Other gradients often reported over more extensive systems, e.g. OM, $\text{NH}_4\text{-N}$ and salinity (Maun 2009; Gilliam & Dick 2010), showed no clear delineation in the current study. OM and $\text{NH}_4\text{-N}$ concentration remained very low up to St. 7 where there was a sharp increase, in real terms still deficient (c.f. Willis & Yemm 1961, Lammerts & Grootjans 1997), yet sufficient to support a 33% increase in plant frequency over the previous station. The data suggest OM is the principal limiting factor in the system (Sprengel-Liebig Law of the Minimum; see van der Ploeg et al. 1999). Kachi & Hirose (1983) suggested that low supply of inorganic N in a Japan coastal dune system was attributable to restriction of mineralisation and nitrification of OM by low water-holding capacity of sand. The circumstances may be different in monsoon-rain-saturated soils, however, as indicated by a lesser availability pre- and post-monsoon, perhaps a result of desiccation in hot, dry winter-season sands. The negative transect-wide correlation of pH with OM conforms to common soil chemistry activity where microbial OM degradation activity increases acidity (Brady 1974; Yan et al. 1996), a sharp increase in OM/ $\text{NH}_4\text{-N}$ concentration and soil water retention coincident with similarly sharp increase in soil acidity at Station 7. The non-significant relationship between pH and OM in St. 1-3, where pH was greater than neutral, and increasing acidity in St. 4-7 where a negative correlation was highly significant, supports this feature. The OM levels recorded up to St. 7 were similar to results found in south India by Karthikeyan and Selvaraj (2009), 0.12-0.67% (range 0.18-0.34% in the current study), as were P_2O_5 levels, 15.5-53.6 $\mu\text{g g}^{-1}$ (range 4.2-50.0 $\mu\text{g g}^{-1}$ in the current study). The negative correlation of pH with P_2O_5 and CCA, indicating a positive correlation of mean OM with P_2O_5 , suggests that a large proportion of plant-available PO_4 may be complexed in OM. This would not be bound directly to humic molecules however, but metals, particularly Fe and aluminium (Al) complexed in the humic substances (Gerke 2010). There was also significant positive correlation of OM, and P_2O_5 to a lesser extent, with silt/clay content. Correlations between silt/clay and both OM and $\text{NH}_4\text{-N}$ were highly significant. What proportion of silt/clay (around 2% in total in St. 1-6 and slightly $> 6\%$ in St. 7) might be flocculated with OM particles cannot be ascertained. At the recorded EC range 0.02 to $> 0.35 \text{ dS m}^{-1}$, the Sumner et al. (1998) nomogram suggests clay particles might rather be dispersed. Monsoon rain wetting-drying cycles may have a considerable effect on the dynamics of flocculation/dispersal.

Sodium is often equated with EC and here there was correlation between the two on the temporal scale. High salinity is described as a major limiting factor in plant growth in coastal dune systems (Wilson & Sykes 1999) and indeed a general halophyte adaptation is demonstrated by reduced biomass

production and plants remaining prostrate, as was apparent here. Levels at which NaCl become toxic vary with plant species. Sahrawat et al. (2009) found that salt-sensitive pigeonpea (*Cajanus cajan* (L.) Millsp) was adversely affected at EC 0.83 dS m⁻¹, far greater than levels recorded here. Detrimental effects are often related to osmotic potential reversal affecting water relations, particularly in germination and development at seedling stage (Rozema et al. 1985). Sodium has also been shown to affect reduction in plant-available ammonium in some soils (Wali et al. 2003; Green et al. 2008). The Na concentration in coastal dunes in some reports was similar to that found here, e.g. 92 µg g⁻¹ in rhizosphere soils of *Distichlis spicata* (L.) Greene on a Californian dune system (Allen & Cunningham 1983). During the monsoon rains, mean concentrations were relatively low (< 55 µg g⁻¹), even in the foredune region (75 µg g⁻¹; range 55–115 µg g⁻¹), and anomalously lower still in the analysis of samples from the following dry season. The ratio of ΣK₂O/Ca/Mg:Na of 3.3, calculated from mean data, and no significant spatial scale correlation between EC and Na, suggests there is comparatively little saline-induced stress (Munns & Tester 2008) to the halophyte plants in this dune habitat, and little detriment to plant growth. The OM and Na temporal correlation is included in Table 4 even though not significant since each is placed in a significantly different group in ANOVA, suggesting Na is not complexed in OM.

Data describing relationships between K₂O, Ca and Mg have proved complex and not easily explained. Canonical correspondence analysis and correlation indicate association of Mg with OM, but stronger with silt/clay, suggesting the mineral resource may be complexed more in silt/clay. Further, there is greater significant correlation of K₂O with silt/clay than with OM, suggesting K⁺ is also complexed to a greater extent in silt/clay. This interpretation is supported by a significant K₂O and Mg correlation. Yet there was a significant positive correlation between OM and the silt/clay fraction, suggesting a high degree of flocculation rather than the dispersion suggested above. High K₂O concentrations accumulated in the soil as a result of leaching by early heavy rains may have had an antagonistic effect on the uptake of Ca and Mg (Jakobsen 1993). There was negative correlation between K₂O and OM and positive correlation between K₂O and NH₄-N on the temporal scale that seems anomalous where NH₄-N is derived from OM. There was no significant correlation between Ca and any other factor. Calcium ions help clay particles to flocculate by neutralising negative charges, thus reducing the repulsive forces between them, and form a “bridge” between humic acids and clay aggregates (Muneeer & Oades 1989). However, Fe- (mean 8.36 µg g⁻¹ in foredune soils) and Al- (not analysed) oxides are also strong flocculants, and can reduce the available surface area for adsorption of OM onto clay particle (Six et al. 2002). An interesting phenomenon from analyses of Ca and Mg is a clear temporal interchange in the last two time-series. ANOVA indicated significant differences between datasets ($F = 5.14$; $P = 0.043$), the juxtaposition possibly the result of decreasing rainfall and leachate rates (Amezketta 1999; Bronick & Lal 2005) as monsoon rains abated.

The calculation of Ca:Mg concentration ratios, however, shows 1:1 in the first two Series, 1:1.7 in Series 3, and 3.5:1 and 3.35:1 in Series 4 and 5, respectively. Dontsova and Norton (2001) described a greater Mg component as having a dispersion effect on clay particles.

Mean spatial P₂O₅ data were found to be significantly correlated with OM that belies extensive variation over time, on occasions deficient, as low as 4 µg g⁻¹, at other times attaining plant nutrient-sufficiency levels of 40 µg g⁻¹ (Bagyaraj & Balakrishna 2003) and more within stations, even within the same time-series. Phosphates released from Ca and Fe in clay and loam soils can be substantial (Pierre & Parker 1927; Brady 1974) but are limited in a tropical primary dune psammite matrix (Sato et al. 2009). Low Ca concentrations and no significant correlation between Ca and P₂O₅ indicates that little plant-available PO₄ was sequestered from this resource. Rather, the discussion above suggested PO₄ is sequestered from labile sources hydrolysed from OM-Fe (Al) complex, and to a lesser extent flocculated/dispersed silt/clay fraction, although comparative station by station data of silt/clay content is not available. This singularly large P₂O₅ variation is interesting and should perhaps be investigated further. If it is a general trend in soil PO₄ availability, it may have a considerable implication in plant nutrition, particularly where, as is the case in primary sand dunes, there is high dependence upon arbuscular mycorrhiza fungal symbiosis (Koske et al. 2008).

Soil chemistry data at the temporal scale describes pattern, and thus difference between or similarity in, the transect in each of the time-series. It was surprising to find no significant correlation between rainfall and EC where a relationship was anticipated. It may be that the statistic is suspect, the accumulated precipitation data employed not representative of a soil-water effect on soil chemistry. EC was significantly correlated with Na but ANOVA suggested that the temporal patterns of change differed. Pre-monsoon (Series 1: day 0) EC was significantly greater than post-monsoon (Series 5: d 189), pre-monsoon significantly greater than Series 2 (d 20) and 3 (d 67) and Series 3 and 4 (d 129) significantly greater than Series 5. However, Na was significantly greater only in Series 1, Series 2–5 being relatively stable. Change in EC also correlated significantly with pH but there were no significant ANOVA differences between series, suggesting that the patterns of change over time may be similar to each other. The correlation between EC and K₂O was non-significant, and there were no significant ANOVA differences, suggesting K salts have little effect on EC. EC was further correlated with OM, here negatively, but with no significant ANOVA differences. Interpretation is difficult to define where there seems to be little difference in the OM series over distance, St. 1–6 ranging from 0.02–0.05%, and ANOVA indicated distance was the primary influencing factor. Either EC was highly variable and OM was not, or OM, even though in such small concentration, was also highly variable over time. The time-scale used, which was too coarse, did not indicate where the variability may lie. K₂O was significantly correlated with pH, and again ANOVA indicated a non-significant differ-

ence, suggesting that increasing acidity may be affecting K⁺ nutrient availability. OM and NH₄-N were grouped together in ANOVA as might be expected, N having derived from OM. However, the K₂O and NH₄-N correlation was significantly positive whereas the K₂O and OM correlation was significantly negative. Again the statistic is not open to clear interpretation where NH₄-N data were gained from transect region St. 4–7 only. The spatial correlation above has shown distinct pH and OM polar opposites between regions St. 1–3 and St. 4–7 however, and the data may suggest a partitioning of the two. The topographical differences are obvious.

Levels of soil water content 1 h and 4 d after rain showed strongly similar pattern over the transect, both increasing in St 7. Correlation with OM was significant in both instances, strongly so in the 4 d data, indicating, as might be expected, OM was influential in moisture retention after percolation. Negative correlation of soil water content with 52 µm sand-grain particle size and positive correlation with 250–500 µm particle size seems to be at odds where percolation through the larger size might have been anticipated to be the greater. This may be explained by water-retentive OM being instrumental in sand grain aggregation (Six et al. 2004).

The study has shown no clear relationship between plant community pattern and soil chemistry data, and revealed no confirmation of what the driving force of zonation might be. Detailed soil analyses in stations along the transect over both time and distance have, however, indicated partition in below-ground factors between fore- and behind-dunes regions and further partition, so sharp that it might be termed a 'pedoecotone', at St. 7 where soil-type changed, pH decreased sharply, and soil-moisture retention, nutrient concentrations and plant frequency increased. This may be the first stage in pedogenesis in this ecosystem. Importantly neither partition was wholly evident from plant frequency and diversity analyses alone.

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