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Environmental factors controlling the vegetation zonation patterns and distribution of vegetation types in the Olifants Estuary, South Africa

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Abstract

The Olifants Estuary is one of only three permanently open estuaries on the West Coast and is ranked third in terms of conservation importance of all estuaries in South Africa. It has the largest supratidal (143 ha) and floodplain (797.1 ha) salt marshes in the country. Intertidal salt marsh covers 91.94 ha, reeds and sedges 60.05 ha and the submerged macrophyte *Zostera capensis* 47.72 ha. Correspondence analysis revealed intertidal, supratidal, floodplain and terrestrial plant community types within the studied estuary. The species composition of these communities was the same for the lower, middle and upper reaches of the Olifants Estuary, with the exception of the supratidal community type in the upper reaches that consisted of halophytes with a lower salinity tolerance range rather than the typical dense monospecific stands of *Sarcocornia pillansii*. The environmental variables that had the greatest influence on the distribution of the dominant salt marsh species, *S. pillansii*, included soil moisture, distance from the estuary, elevation above mean sea level, and depth to the water table. The most important ecological driver for salt marsh vegetation, especially along the arid West Coast of southern Africa, is moisture. The low rainfall and irregular occurrence of advection sea fog increases the importance of a shallow (<1.5 m) saline (<35 psu) water table in the floodplain as a source of moisture during dry periods.

Keywords: Olifants Estuary; Salt marsh; Soil; Vegetation; Water table; Zonation

1. Introduction

Supratidal and floodplain salt marshes form an integral part of many estuarine and coastal ecosystems. In many semi-arid areas, the natural functioning of estuaries is threatened because of freshwater impoundment. The South African National Water Act (Act 36 of 1998) states that an ecological reserve must be determined for rivers and estuaries prior to the abstraction of freshwater. The freshwater requirements of the supratidal and floodplain salt marsh in estuaries forms part of the estuarine reserve, but little is known about the response of salt marsh plants to changes in salinity and the availability of water.

The infrequent inundation of the supratidal and floodplain areas with water, the capillary rise from the brackish groundwater common to this area and the semi-arid climate of the West Coast region of South Africa with the resultant high evaporative demand results in the accumulation of salt in the surface soil. If these salts are not leached from the soils through flooding with relatively fresh water, as happened at the Orange River mouth (CSIR, 1991), these areas would become hypersaline and lead to the reduction in plant cover. The precipitation along the west coast of South Africa is spatially and temporally highly variable and is so low (50–200 mm $year^{-1}$) that rainfall has not been thought to play a role in leaching salts from the soil. The conservation value of this vegetation lies in the fact that halophytes are the only plants adapted to grow in these harsh environments and the loss of this vegetation would lead to the formation of bare, dry salt pans that are more easily eroded by wind and water.

The die-back of the floodplain salt marsh in the Orange River estuary was attributed to the lack of over bank flooding, due primarily to water impoundments altering the hydrological regime and mouth condition of the Orange River (Morant and O'Callaghan, 1990; CSIR, 1991; Bornman et al., 2004b). Several authors have shown the importance of flooding in reducing the salinity content of salt marsh soils (Zedler et al.,

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1986; Jolly et al., 1993; Neill, 1993; Slavich et al., 1999). To identify and quantify the importance of floods in the functioning of salt marshes in the Olifants Estuary, the spatial and temporal variation in vegetation and edaphic conditions were analysed. However, it became clear early in the study that no floods over the last 80 years have overtopped the banks of the estuarine floodplain. This raised several questions regarding the functioning of the floodplain salt marsh and the factors controlling it. To gain an understanding of the system and the possible factors that might influence the distribution of the vegetation, changes in the spatial and temporal edaphic gradients were tested. Noe and Zedler (2001) found that soil salinity and moisture predicted a very small portion of the spatial variation in vegetation and that other factors might be more important. Riehl and Ungar (1982) showed that amongst other variables, the level of the water table influenced the growth and distribution of salt marsh plants. Edaphic factors other than salinity have received very little attention, and although salinity and moisture might be the most important variable found in salt marshes, the relative importance of all edaphic factors still needed to be tested in different halophytic communities and systems (Pan et al., 1998).

The objectives of this paper were to investigate the spatial and temporal variations in vegetation cover and soil characteristics (pH, moisture, organic content, redox potential, particle size and electrical conductivity); to evaluate the relative importance of specific edaphic factors in explaining variation of species assemblages; to identify the ecological preferences of the dominant salt marsh species, *Sarcocornia pillansii*; and to determine the freshwater and flooding requirements of *S. pillansii*.

2. Materials and methods

2.1. Study site

The Olifants Estuary is located approximately 250 km north of Cape Town on the West Coast of South Africa (Fig. 1). The estuary is tidal for approximately 32 km upstream with the REI (River Estuary Interface) situated between 10 and 16 km upstream of the mouth (in the region of Soutpansklipheuwel; Fig. 1) (Morant, 1984). The mouth of the estuary is permanently open and its position is maintained by a rocky platform on the northern bank. According to data collected by the South African Weather Services, the study area received below average rainfall from 1998 until July 2001 (mean annual rainfall from 1986 to 2001 was 137.8 mm ± 10.41 mm SE). The Bulshoek irrigation barrage (with a capacity of 7.5×10^6 m^3) and the Clanwilliam Dam (with a capacity of 127×10^6 m^3) regulate flow into the estuary. The Olifants Estuary is one of the most important estuaries in the country based on its botanical importance rating (Coetzee et al., 1997), estuarine health index (EHI; Harrison et al., 1994a,b) and its conservation (ranked 3rd) and biodiversity importance (Turpie et al., 2002).

2.2. Vegetation analyses

The vegetation was analysed along ten transects (GPS coordinates of each transect are provided in Table 1 Supplementary material) during four field trips, i.e. November 1999, March 2000, July 2000 and November 2000. To capture possible variation in the vegetation and the physico-chemical characteristics of the soil along the length and breadth of the estuary, four transects, two on either side of the river, were placed in the lower reaches (Fig. 2), middle reaches (Fig. 4), and upper reaches (Fig. 6). Two of the transects in the upper reaches were destroyed during the building of a farm dam and were not included in this study. Vegetation cover was measured as percentage cover in a permanent quadrate (1 m^2) located every 20 m along the transect. In addition, four random quadrates were located around the permanent quadrate and the percentage cover estimated in each. The quadrates were used to determine whether seasonal changes in vegetation cover were occurring. The patchiness of the vegetation necessitated the use of random quadrates to establish a more accurate assessment of the percentage cover, species richness and diversity along each transect.

The vegetation data collected every 20 m along each transect was handled using Correspondence Analysis (CA) to identify possible zonation patterns. Only the vegetation cover at 100 m, 200 m and 300 m along each transect were used in the Canonical Correspondence Analysis (CCA) to determine the influence of environmental variables on the vegetation patterns.

Aerial photographs, field observations and the transect data were used to construct a vegetation map of estuarine and floodplain vegetation of the Olifants Estuary (Fig. 1). A similar vegetation map was created from the earliest available aerial photographs (1942) to determine the changes that have occurred over time. These maps were digitised in ArcGIS™ version 9. A sample of each species recorded along the 10 transects was collected, pressed and identified. Taxon names follow Germishuizen and Meyer (2003) and a full list with authorities is supplied in Table 1. Voucher specimens are housed in the Ria Oliver Herbarium (PEU) of the Nelson Mandela Metropolitan University.

2.3. Soil analyses

Soil samples were collected at 100, 200 and 300 m from the edge of the estuary along each transect. At each site, samples were collected from three depths, i.e. 0–0.05 m, 0.05–0.15 m and 1.0–1.2 m. Four replicates of each sample were collected. Soil pH (measured in water), redox potential and electrical conductivity (EC) were determined in a field laboratory on the same day as sampling. Further samples were sealed and transported to the laboratory where analyses of soil moisture, organic content, and particle size distribution were ascertained. Details on the methods used to analyse the soils are found in the following sources: soil moisture content (Gardner, 1965), organic content (Briggs, 1977), electrical conductivity (The Non-Affiliated Soil Analyses Working Committee, 1990) using an YSI 30M/10 FT hand held conductivity meter, pH (Black, 1965), redox potential (The Non-Affiliated Soil Analyses Working Committee, 1990) using a Metrohm AG9101 electrode, and particle size (Day, 1965) using the hydrometer method.

Depth to the groundwater was determined by manually auguring down to the water table. The level of the groundwater

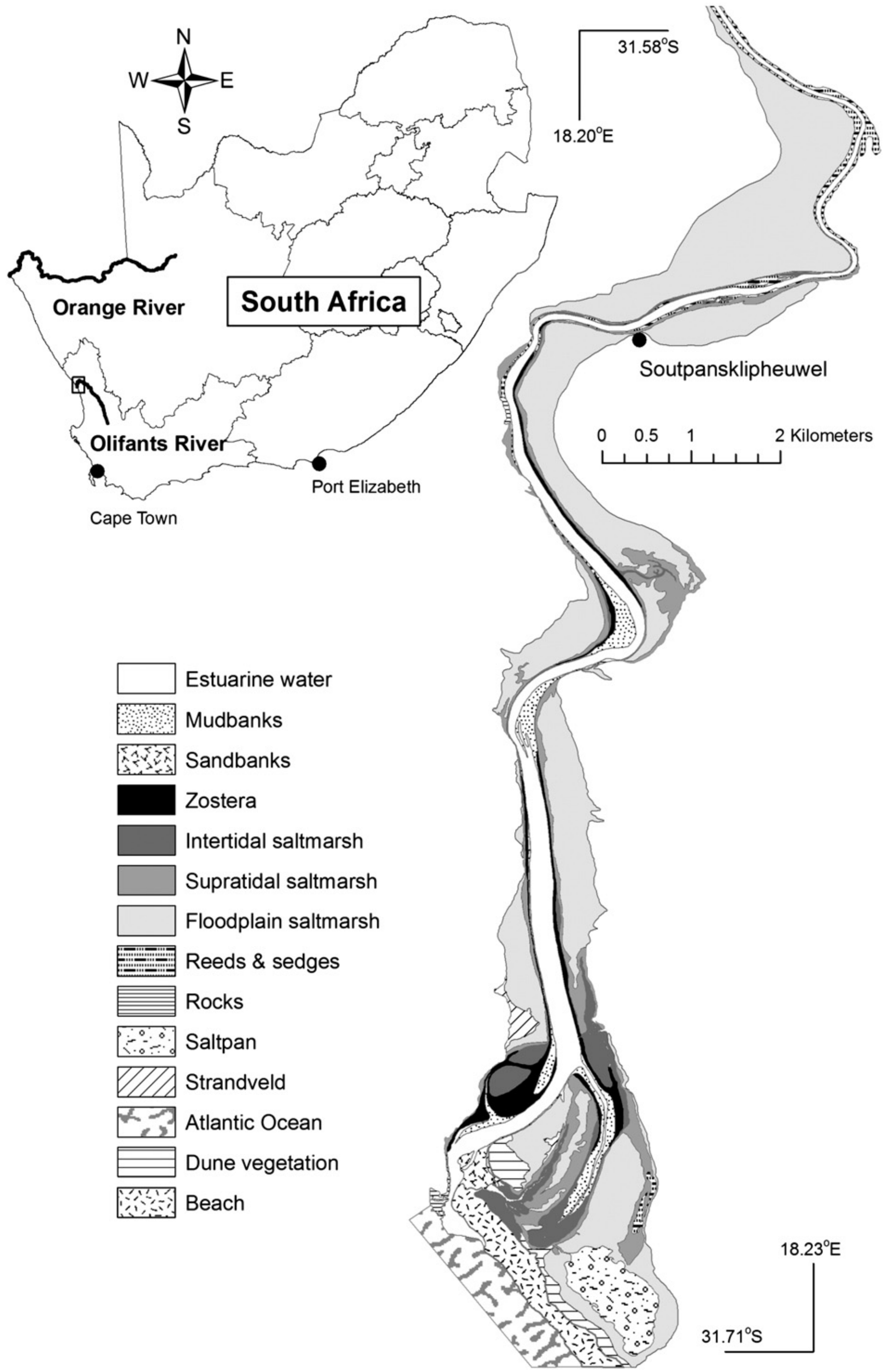

Fig. 1. Map of the Olifants River estuary on the West Coast of South Africa.

was measured using a modified moisture meter that displayed a signal as soon as the electrodes touched the water. Water table depth readings were taken at the same sites from where the soil samples were collected. Four replicate holes were augered at each site.

2.4. Data analyses

The seasonal species and environmental data for each transect were analysed using CANOCO for Windows (version 4.0, Ter Braak and Šmilauer, 1998). The size of the data set made it impossible to analyse more than four transects at one time and, as a result, transects were grouped into the lower, middle, and upper reaches. CA was used to identify patterns in species distribution and cover. CCA was used to obtain an ordination of the vegetation data constrained by environmental variables. Monte Carlo permutation tests (999 permutations) were performed to assess the significance of the canonical axes showing the relationship between species and the selected environmental variables. The results of the CA and CCA were plotted as two-dimensional

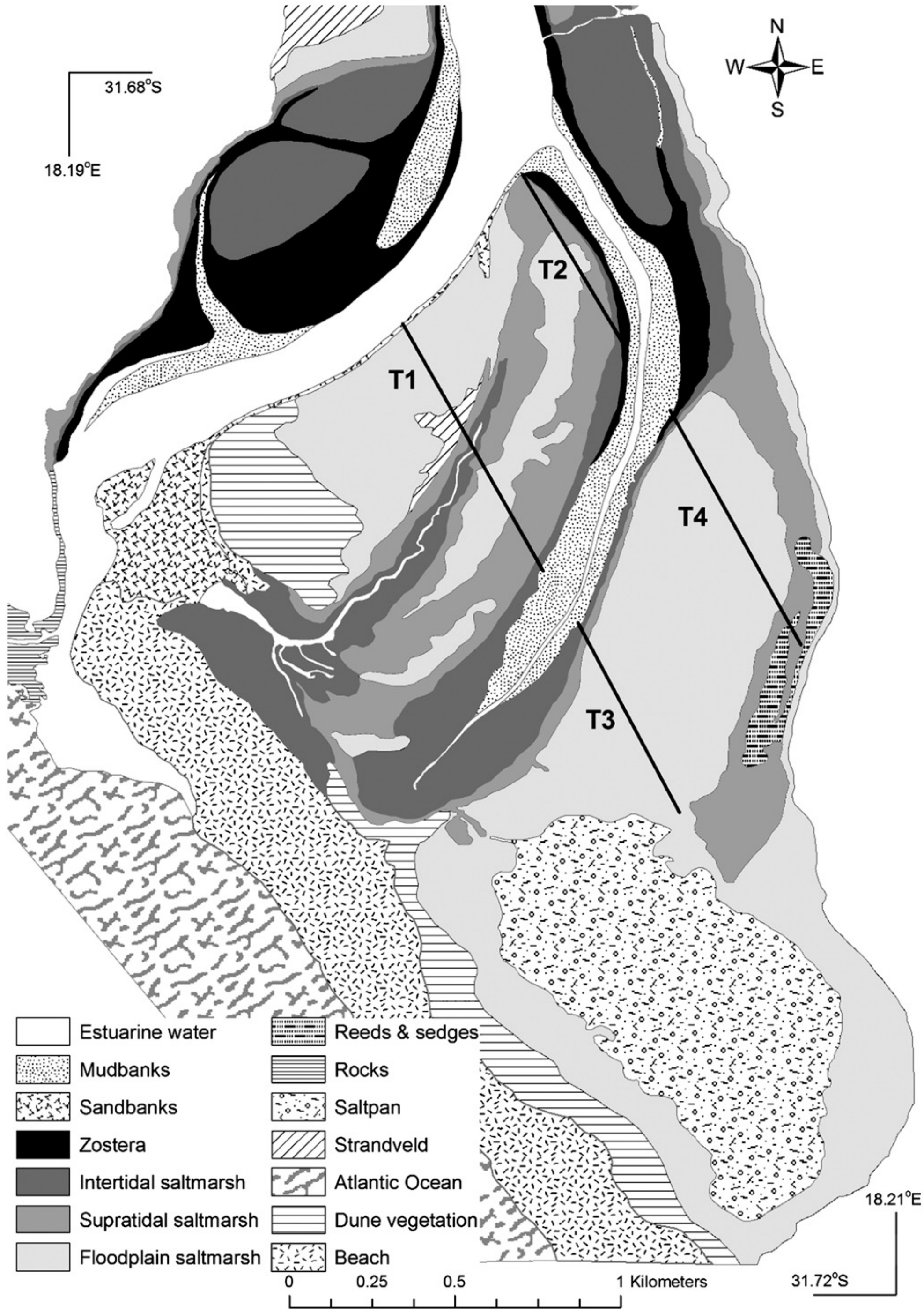

Fig. 2. Vegetation and habitat distribution of the lower reaches (T1–T4 = sampling transects).

graphs using CANODRAW version 3.1. The continuous environmental variables were plotted as arrows originating from the centre of the graph. Correlation statistical analyses were performed using Statistica, version 6 (StatSoft, 2002).

3. Results

3.1. Present vegetation distribution

The distribution of the different plant community types are depicted in Fig. 1 and the study site areas are enlarged in Figs. 2, 4 and 6. The dominant plant community was salt marsh with floodplain salt marsh making up 66% of the estuarine vegetation, covering 797.1 ha (Table 2). Supratidal salt marsh covered 143 ha (11.85%) and intertidal salt marsh 91.9 ha (7.6%) (Table 2). Reeds and sedges made up less than 5% of the vegetation cover and were restricted to freshwater seeps at the edge of the floodplain and along the banks of the estuary in the upper reaches (Figs. 1 and 6). The submerged macrophyte *Zostera capensis*, formed extensive beds in the lower reaches but it was restricted to a thin strip adjacent to the intertidal zone in the middle reaches of the estuary (Figs. 1, 2 and 4).

Table 1
List of species, families and abbreviations used in the text and the figures

Species	Family	Abbreviation
Conyza scabrida DC.	Asteraceae	Cony_sca
Cotula coronopifolia L.	Asteraceae	Cotu_cor
Didelta carnosa (L.f.) Aiton var. *carnosa*	Asteraceae	Dide_car
Oncosiphon suffruticosum (L.) Källersjö	Asteraceae	Onco_suf
Pteronia glabrata L.f.	Asteraceae	Pter_gla
Senecio sarcoides C. Jeffrey	Asteraceae	Sene_sar
Atriplex cinerea Poir. subsp. *bolusii* (C.H. Wr.) Aellen	Chenopodiaceae	Atri_cin
Chenolea diffusa Thunb.	Chenopodiaceae	Bass_dif
Salsola zeyheri (Moq.) Bunge	Chenopodiaceae	Sals_zey
Sarcocornia '*perennis*' sensu auct. austroafr.	Chenopodiaceae	Sarc_per
Sarcocornia pillansii (Moss) A.J.Scott	Chenopodiaceae	Sarc_pil
Euphorbia sp. L.	Euphorbiaceae	Euph_sp.
Frankenia repens (P.J. Bergius) Fourc.	Frankeniaceae	Fran_rep
Delosperma crassum L.Bolus	Mesembryanthemaceae	Delo_cra
Drosanthemum delicatulum (L.Bolus) Schwantes	Mesembryanthemaceae	Dros_del
Drosanthemum diversifolium L.Bolus	Mesembryanthemaceae	Dros_div
Drosanthemum parvifolium (Haw.) Schwantes	Mesembryanthemaceae	Dros_par
Malephora framesii (L.Bolus) H.Jacobsen & Schwantes	Mesembryanthemaceae	Male_fra
Mesembryanthemum crystallinum L.	Mesembryanthemaceae	Mese_cry
Mesembryanthemum nodiflorum L.	Mesembryanthemaceae	Mese_nod
Psilocaulon dinteri (Engl.) Schwantes	Mesembryanthemaceae	Psil_din
Ruschia glauca L.Bolus	Mesembryanthemaceae	Rusc_gla
Vanzijlia annulata (A.Berger) L.Bolus	Mesembryanthemaceae	Vanz_ann
Oxalis pes-caprae L.	Oxalidaceae	Oxal_pes
Limonium equisetinum (Boiss.) R.A.Dyer	Plumbaginaceae	Limo_equ
Lycium cinereum Thunb.	Solanaceae	Lyci_cin
Lycium tetrandrum Thunb.	Solanaceae	Lyci_tet
Zygophyllum morgsana L.	Zygophyllaceae	Zygo_mor
Asparagus capensis var. *litoralis* Suess. & Karl	Asparagaceae	Aspa_cap
Juncus kraussii Hochst. subsp. *kraussii*	Juncaceae	Junc_kra
Triglochin striata Ruíz & Pav.	Juncaginaceae	Trig_str
Phragmites australis (Cav.) Steud.	Poaceae	Phra_aus
Sporobolus virginicus L.Kunth.	Poaceae	Spor_vir
Zostera capensis Setch.	Zosteraceae	Zost_cap

3.2. Changes in vegetation over time

Most of the changes that have occurred in the distribution of estuarine vegetation over the last 60 years took place in the dynamic lower/mouth reaches of the estuary. Approximately 8 ha of "Die Eiland" have eroded on the south bank. This has been replaced by 8 ha of mud and eelgrass (*Z. capensis*) on the north bank of the main channel (Fig. 2). The blind arm is slowly silting up and in 1942 there were 28 ha of water in this area that now consists of mud and intertidal salt marsh. There has been an increase in the area covered by reeds and sedges in the middle to upper reaches of the estuary. The 1942 photograph showed 15 ha of bare mudflat that is now colonized by reeds. During the course of this study there was no change in species cover along all 10 transects with the exception of the terrestrial succulent annuals that germinated and grew in response to the winter rainfall and died-back before the onset of summer.

Table 2
Area (in hectares) covered by different plant community types and habitat units in the Olifants Estuary

Estuarine plant community types and habitat units	Area (ha)	Percentage (%)
Water area	227.86	
Mudbanks	54.53	
Sandbanks	22.47	
Zostera capensis	47.72	3.95
Intertidal salt marsh	91.94	7.60
Supratidal salt marsh	143	11.85
Floodplain salt marsh	797.10	66.00
Reeds and Sedges	60.05	4.97
Other habitat units		
Salt pan (at mouth)	56.79	
Strandveld (on floodplain)	10.44	
Dune vegetation (at mouth)	29.81	

Percentages indicate the percentage area covered by that plant community type compared to the total estuarine plant area (1139.8 ha).

3.3. Structure and zonation of vegetation

3.3.1. Lower reaches (Fig. 2)

Canonical analysis grouped the species into three distinct communities, i.e. intertidal, supratidal and floodplain, and terrestrial (Fig. 3). The terrestrial community occurred mainly in Transects 1 and 2 on "Die Eiland". The other two communities were typical of the vegetation of the lower reaches of the estuary. The intertidal area was small (1–10 m) and divided into different zones. *Sarcocornia* '*perennis*', *Triglochin striata* and *Cotula coronopifolia* grew mixed closest to the water, followed by a band of *Chenolea diffusa*.

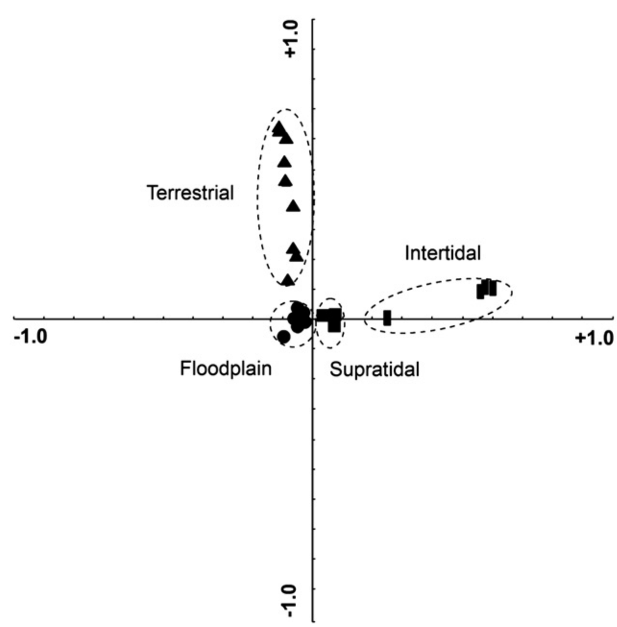

Fig. 3. CA ordination for the lower reaches.

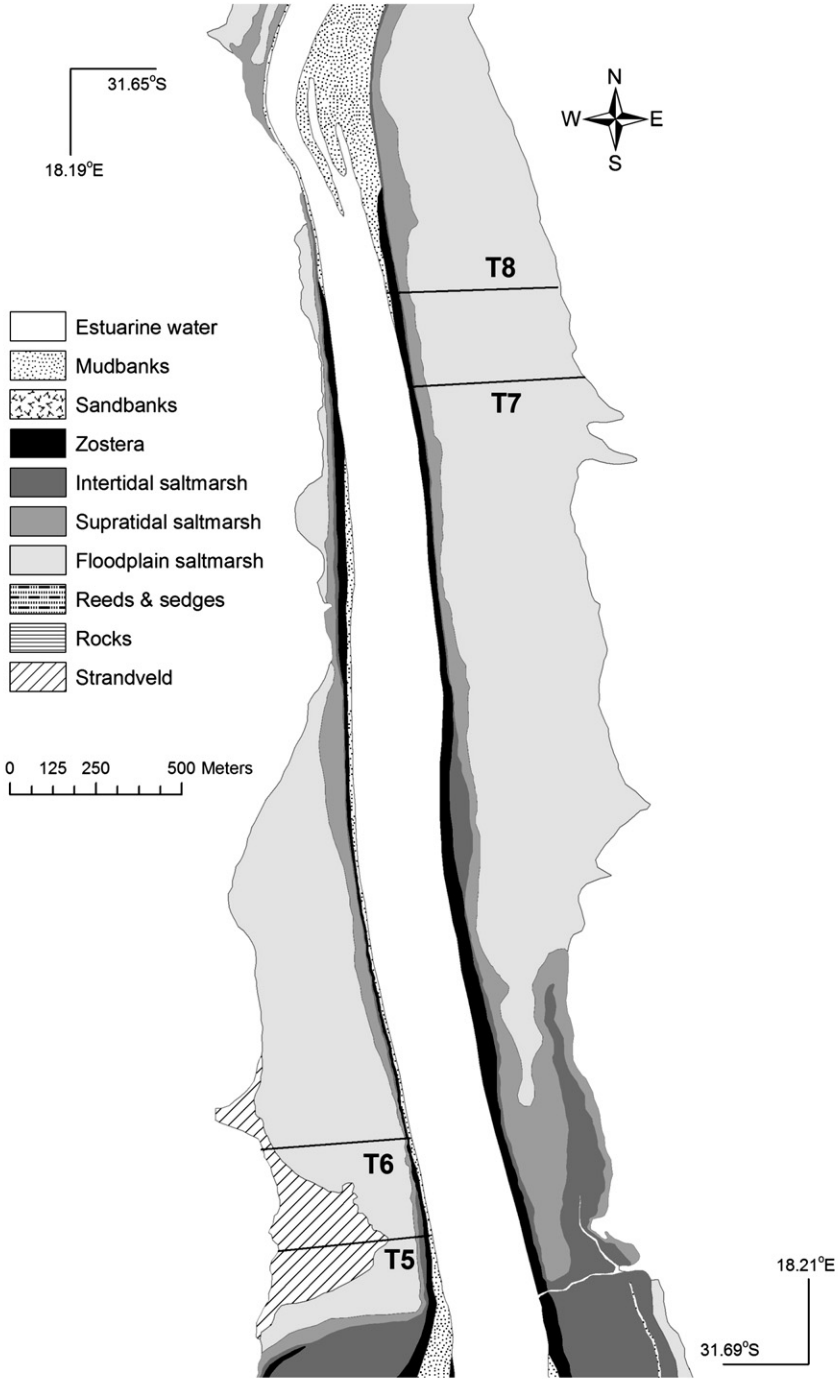

Fig. 4. Vegetation and habitat distribution of the middle reaches (T5–T8 = sampling transects).

Limonium equisetinum, normally associated with the outer fringe of the intertidal area, had the highest cover in the supratidal zone and was also present in the wetter areas of the floodplain. The small supratidal zone was dominated by dense monospecific stands of *S. pillansii* and associated large quantities of organic litter. *S. pillansii* was also the dominant plant on the floodplain, although its cover was greatly reduced. The species variable that had the greatest cover on the floodplain was bare ground. Other species commonly found on the floodplain included *Salsola zeyheri*, *Frankenia repens*, *L. equisetinum*, the annual *Mesembryanthemum nodiflorum*, *Lycium tetrandrum* and *L. cinereum*.

3.3.2. Middle reaches

The vegetation in the middle reaches was made up of four habitats (Fig. 4), such as intertidal, supratidal, floodplain, and terrestrial (Fig. 5). The terrestrial species were restricted to the upper section of Transects 5 and 6 (Fig. 4). Transects 7 and 8 were more typical of the vegetation found in the middle reaches and were very similar to the structure found in the lower

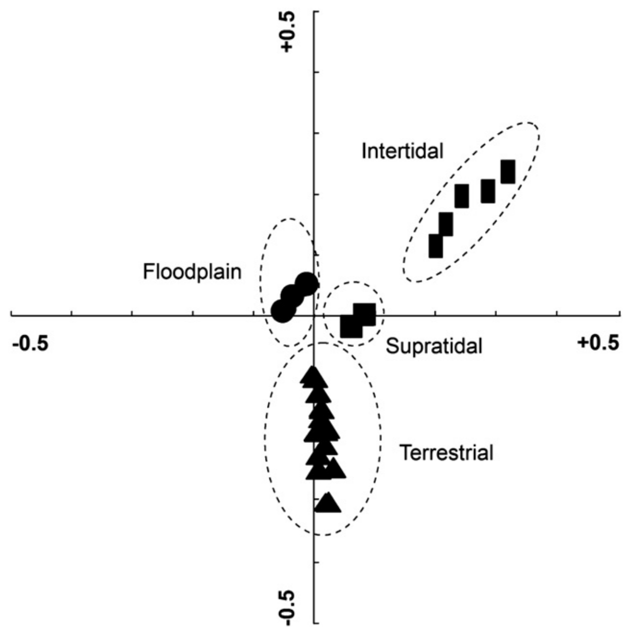

Fig. 5. CA ordination for the middle reaches.

reaches. The small intertidal zone (1–2 m in width) consisted out of *S.* '*perennis*', *T. striata* and *C. coronopifolia*, followed by a band of *C. diffusa* and further up into the supratidal zone, dense clumps of *L. equisetinum*. The supratidal zone consisted of dense monospecific stands of *S. pillansii* and large quantities of organic litter. The floodplain consisted largely of bare ground with *S. pillansii* the dominant species and *Salsola* sp. as co-dominant. The annual, *M. nodiflorum*, was common on the floodplain after the winter rainfall.

3.3.3. Upper reaches

The upper reaches of the Olifants Estuary had four recognisable communities (Fig. 6), including intertidal, supratidal, floodplain and terrestrial/disturbed vegetation (Fig. 7). The intertidal area consisted of *S.* '*perennis*', *T. striata* and *C. coronopifolia*. The supratidal zone consisted of *Sporobolus virginicus*, *Juncus kraussii* and *Conyza scabrida*. The floodplain area was made up of alternating bands of *S. pillansii* and *S. zeyheri*. The middle section of Transect 10 was ploughed in the past in an attempt to farm on the floodplain. This disturbance resulted in the formation of a separate terrestrial community with *Malephora framesii* as the dominant species.

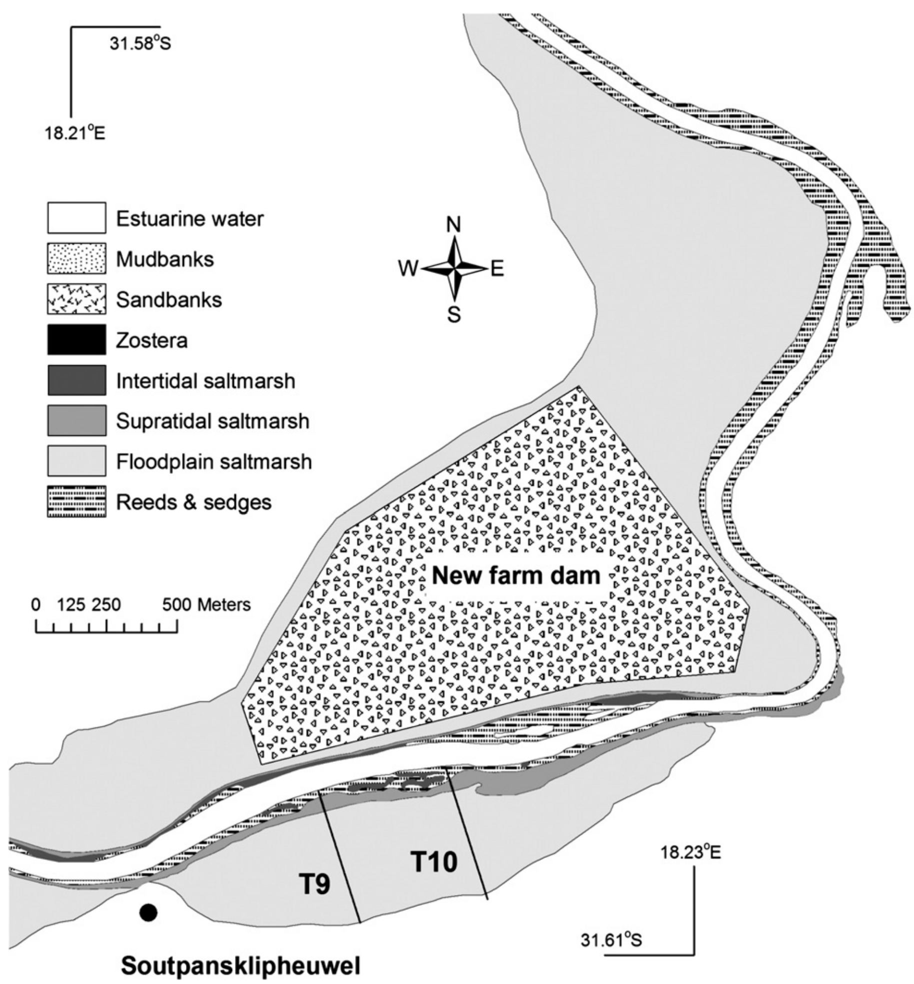

Fig. 6. Vegetation and habitat distribution of the lower reaches (T9 and T10 = sampling transects).

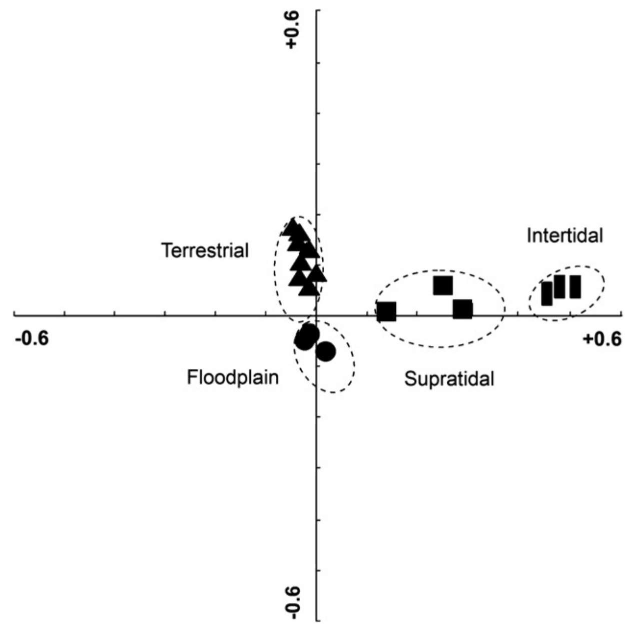

Fig. 7. CA ordination for the upper reaches.

3.4. Influence of environmental variables on vegetation distribution

3.4.1. Lower reaches

In Fig. 8 the first canonical axis accounted for 58% of the species–environment relation (Table 2 Supplementary material). This axis was positively correlated to elevation above MSL and depth to the water table (Table 3 Supplementary material). The second canonical axis accounted for 86.9% of the variation and was positively correlated to depth to the water table (Tables 2 and 3 Supplementary material). The strongest correlations were between the first canonical axis and elevation above MSL (0.92) and the second canonical axis and depth to the water table (0.72) (Table 3 Supplementary material).

Fig. 8 indicates that the terrestrial community occurred in the more elevated areas of the salt marsh further away from the estuary, where the salinity of the soil would be lower. *S. pillansii* was the dominant supratidal and floodplain salt marsh species that grew in low-lying areas characterised by a shallow water table and clay soils that had a high salinity and moisture content.

Table 4 Supplementary material indicates that soil moisture increased with depth (as a result of the shallow water table) and that the soil at depth was less saline than on the surface. The strong positive correlation between the water table and elevation indicates that the water table in the lower reaches followed the contours of the floodplain.

3.4.2. Middle reaches

In Fig. 9 the first canonical axis accounted for 63% of the species–environment relation (Table 2 Supplementary material). The strongest correlations were between the first canonical axis and percentage soil moisture (0.58), distance from the estuary (−0.69) and elevation above MSL (−0.73) (Table 5 Supplementary material). The terrestrial community occurred in elevated areas on the floodplain, further away from the estuary (Fig. 9). These soils were characterised by low moisture, salinity and clay content. The supratidal and floodplain communities preferred soils that have higher moisture content.

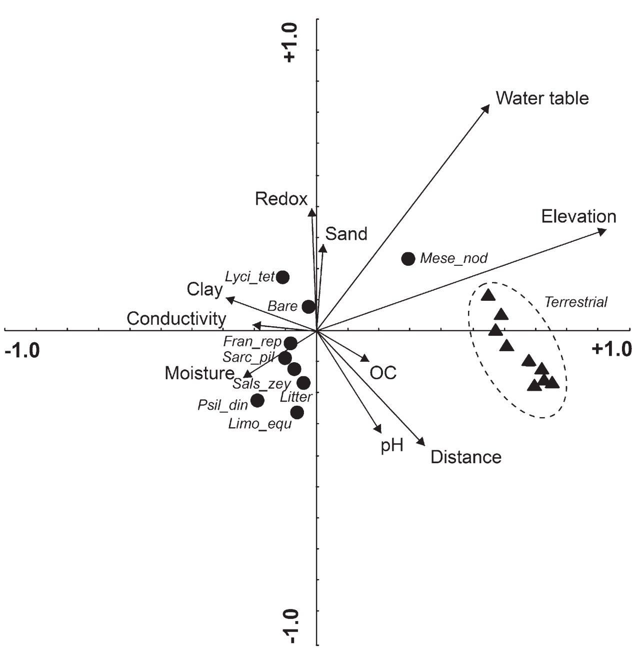

Fig. 8. CCA ordination for the lower reaches (Triangles = terrestrial community and circles = supratidal and floodplain salt marsh. Abbreviations: Mese_nod = *Mesembryanthemum nodiflorum*; Lyci_tet = *Lycium tetrandrum*; Fran_rep = *Frankenia repens*; Sarc_pil = *Sarcocornia pillansii*; Sals_zey = *Salsola zeyheri*; Psil_din = *Psilocaulon dinteri*; Limo_equ = *Limonium equisetinum*; bare = bare soil; litter = dead plant material).

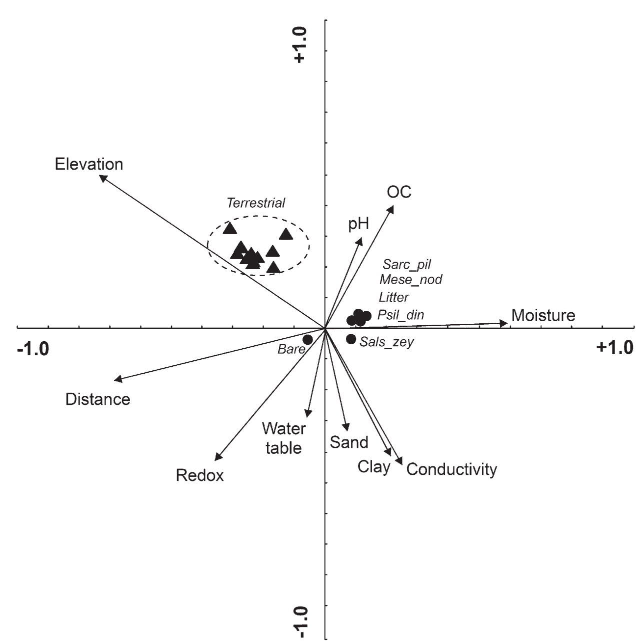

Fig. 9. CCA ordination for the middle reaches (Triangles = terrestrial community and circles = supratidal and floodplain salt marsh. Abbreviations: Mese_nod = *Mesembryanthemum nodiflorum*; Sarc_pil = *Sarcocornia pillansii*; Sals_zey = *Salsola zeyheri*; Psil_din = *Psilocaulon dinteri*; bare = bare soil; litter = dead plant material).

These soils characteristically also had a higher clay and salinity content and were located in areas closer to the estuary and at a lower elevation than average (Fig. 9). Table 6 Supplementary material also indicates that the soil of the elevated areas on the salt marsh, favoured by the terrestrial community, had a lower salinity and moisture content. Elevation above MSL was also negatively correlated to the depth to the water table indicating that the elevated areas had a deeper water table (Table 6 Supplementary material). Soil moisture increased and soil electrical conductivity decreased with depth, indicating the presence of less saline groundwater. As in the lower reaches, the surface soils had a higher sand fraction and the deeper soils contained more clay. The higher the elevation the lower the clay content of the soil.

3.4.3. Upper reaches

In Fig. 10, the first canonical axis accounted for 61% of the species–environment relation and had the strongest correlations with percentage soil moisture content (−0.58), Soil EC (−0.47), distance from the estuary (−0.61) and the soil clay fraction (−0.53) (Tables 2 and 7 Supplementary material). The second canonical axis described 80% of the variation and was positively correlated to elevation above MSL (0.76) (Tables 2 and 7 Supplementary material). The floodplain community occurred in areas that had a high soil clay, moisture and EC content (Fig. 10). These areas were located further from the estuary and at elevations higher than the average, which is opposite to the lower and middle reaches. The terrestrial community was restricted to soils closer to the estuary that had a lower moisture, clay and salinity content (Fig. 10). The water

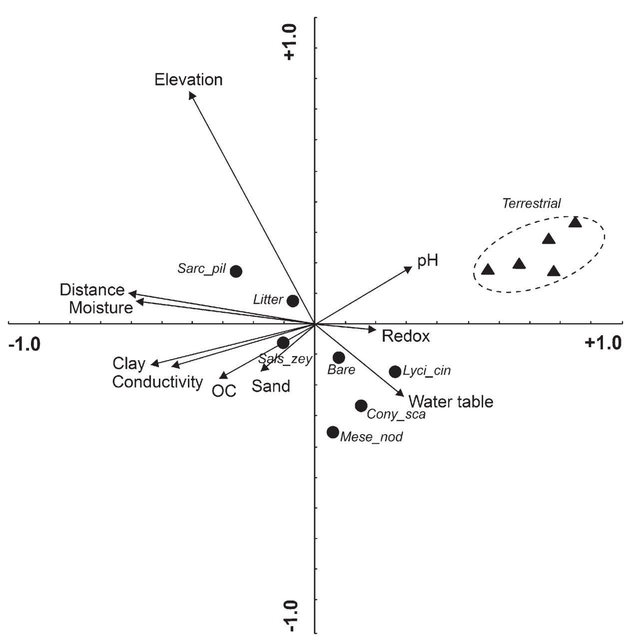

Fig. 10. CCA ordination for the upper reaches (Triangles = terrestrial community and circles = supratidal and floodplain salt marsh. Abbreviations: Mese_nod = *Mesembryanthemum nodiflorum*; Lyci_cin = *Lycium cinereum*; Sarc_pil = *Sarcocornia pillansii*; Sals_zey = *Salsola zeyheri*; Cony_sca = *Conyza scabrida*; bare = bare soil; litter = dead plant material).

table closer to the estuary was deeper than the more elevated areas further inland. Soil moisture increased and soil electrical conductivity decreased with depth, indicating the presence of less saline groundwater (Table 8 Supplementary material). The surface soils had a higher sand fraction whereas the wetter less saline soils at depth consisted mostly out of clay. Elevation above MSL and the soil clay content increased with distance from the river, whereas the depth to the water table decreased inland (Table 8 Supplementary material).

4. Discussion

The Olifants Estuary is a large permanently open estuary and seven of the nine estuarine plant community types identified by Colloty et al. (2002) occur here with only the subtropical swamp forest and mangrove communities that are absent. The dominant vegetation was salt marsh, making up more than 85% of the total vegetation cover of the estuary and surrounding floodplains. The large intertidal salt marsh areas are important, as only 18% of South African estuaries are permanently open with intertidal salt marsh and they can thus be considered rare. The Olifants Estuary also has the largest supratidal/floodplain salt marsh in South Africa. On parts of the floodplain Strandveld was present that had a high species richness of more terrestrial species. Overall the salt marsh had naturally low species diversity as these highly saline areas generally have few competitors.

Analysis of past and present aerial photographs indicated very little change in the vegetation cover and structure of the floodplain over the last 60 years. This could be a result of reduced flooding. The last large flood that breached the sand spit through the central arm (blind arm) in the mouth region occurred in 1925 before the construction of the Clanwilliam dam in 1932 (Morant, 1984). The blind arm appeared to be slowly silting up because of a lack of flushing in that area. Changes in the cover of the reeds were mostly related to the last flooding event. Increased sediment and nutrient run-off from agricultural activities on the banks could also have created favourable conditions for reed expansion in the upper reaches. The species cover along the 10 transects showed no temporal or spatial variation over the study period except for the Strandveld annuals, e.g. *M. nodiflorum*, *Vanzijlia annulata* and *M. framesii* that germinated and grew in response to the winter rainfall and died-back before the onset of summer.

The vegetation of the Olifants Estuary consisted of four community types, i.e. intertidal, supratidal, floodplain and terrestrial. These communities were restricted to specific zones related to distance from the estuary water channel. The intertidal zone occurred closest to the estuary, followed by the supratidal zone, the floodplain and lastly the terrestrial community. The CA ordination for the lower and middle reaches revealed that *S. pillansii* was well separated from the rest of the floodplain community and therefore placed in a community of its own, i.e. supratidal, although *S. pillansii* was the dominant species in both these zones. *L. equisetinum* appears to behave in a similar manner in the lower reaches where the highest concentration of this species was found in the supratidal zone, but it was also present in the floodplain with a similar percentage cover to the rest of the floodplain species. The only difference between these community types were that the supratidal zone consisted out of dense monospecific stands of *S. pillansii*, whereas the highest coverage of the floodplain area was bare ground, interspersed with clumps of *S. pillansii* and *S. zeyheri*. The annual *M. nodiflorum* was also restricted to the floodplain, but was only present after the winter rainfall. The Strandveld vegetation that fringed the estuary was also present in certain elevated areas of the floodplain.

Lycium tetrandrum and *L. cinereum* was limited to a narrow elevation band (elevated areas or levees) and its peak occurrence fell between the broader areas of wetland and terrestrial vegetation. The vegetation composition of the supratidal area in the upper reaches was different due to drier soil caused by a lack of high tide induced overbank flooding and wave spray. This zone was occupied by a community consisting of the halophytes *S. virginicus* and *J. kraussii* and the terrestrial species *C. scabrida*. This study showed that these species were less tolerant of high salinity soils and groundwater.

The dominant salt marsh species of the Olifants Estuary, *Sarcocornia pillansii,* had the highest percentage cover in areas where the soil moisture was high and the water table shallow. These areas were also characterised by a clayey surface soil that had a high salinity content. The shallow less saline groundwater acts as a source of “fresher water” to these halophytes (Bornman et al., 2004a). The terrestrial community were located in areas of the floodplain were the water table was deep and were the capillary rise of the saline groundwater was less likely. The soils in which this community occurred were characterised by low moisture and salinity and had a higher fraction of sand than the rest of the floodplain. In the lower and middle reaches, the areas conducive to the growth of *S. pillansii*, were located closer to the estuary and at low elevation above MSL. In the upper reaches on the other hand, *S. pillansii* were located in the more elevated areas further away from the estuary than the terrestrial community. This was due to the water table being closer to the surface in the elevated areas (Bornman et al., 2004a) resulting in a higher soil moisture content.

It would appear from these data that the environmental variable that has the most influence on S. *pillansii* is moisture. The large salinity tolerance range of *S. pillansii* (0 psu to 70 psu) (Bornman, 2002) shows that this plant can survive in a range of soil salinity as long as there is sufficient moisture available. In most of the estuary the more moist soils were located in areas where the water table was shallowest (<1.5 m). The saline groundwater cannot be used as a water source by the terrestrial species because of their narrower salinity tolerance range, restricting this community to areas were the soils was less saline, but also drier.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2008.05.002.

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