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Freshwater Requirements of a Semi-arid Supratidal and Floodplain Salt Marsh

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ABSTRACT: When rivers are impounded, the reduction in downstream flow can produce important and often adverse effects, especially in the estuarine environment. One or more dams have been proposed for the Olifants River system in the Western Cape, South Africa. This estuary has an extensive area of salt marsh that was examined to see whether it required occasional flooding with freshwater to wash out accumulated salts. The dominant salt marsh species, *Sarcocornia pillansii*, occurred in supratidal and floodplain areas where the water table was shallowest, the soil moisture highest, and the soil electrical conductivity lowest. Aerial photographs and simulated runoff data showed that no flood had covered the floodplain during the previous 80 years. The data indicate that salt marsh plants use saline groundwater during the dry months of the year in order to survive, but use the short season winter rainfall period with low salinity conditions to grow and reproduce. This study demonstrated that live roots of *S. pillansii* reached the water table during the dry season. Tissue and soil water potentials, the relationship between vegetation cover, depth to the water table, and electrical conductivity of the groundwater support the conclusion that saline groundwater is the only source of water during the drier months of the year. Freshwater flooding of the river in winter may be important because it covers the supratidal area with less saline water and reduces the depth to the water table on the floodplain. This makes the groundwater more accessible to the halophytes growing on the floodplain.

Introduction

Supratidal and floodplain salt marsh forms 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 extraction of freshwater. The reserve is the quantity and quality of freshwater required to satisfy basic human needs, considering both present and future needs, and to protect aquatic ecosystems in order to secure ecologically sustainable development and use of the resource.

The freshwater requirements of the supratidal and floodplain salt marsh in estuaries forms part of the ecological reserve but little is known about the response of salt marsh plants to changes in salinity and the availability of water. This matter gained prominence when modifications to the normal flow of the Orange River on the border between Namibia and South Africa resulted in the collapse of the salt marsh near the mouth and a decrease in migrant bird numbers that threatened the Ramsar status of this unique wetland (http://www.environment.gov.za/PolLeg/Conventions/ramsarbriefing.htm). The Convention on Wetlands of International Importance (or commonly known as the Ramsar Convention) is an international treaty signed on February 2, 1971, in the Iranian city of Ramsar. The Council for Scientific and Industrial Research (Council for Scientific and Industrial Research 1991) identified the lack of back flooding by freshwater as the cause for the dieback of *Sarcocornia pillansii* (Moss) A.J. Scott, which was the dominant species in that salt marsh. Morant and O'Callaghan (1990) found the flooding of the vegetation by freshwater to be beneficial to *S. pillansii*.

Several authors have shown the importance of flooding in reducing the salinity content of floodplain and high marsh soils (Jolly et al. 1993; Neill 1993; Slavich et al. 1999b). Species distribution, germination, and growth in a salt marsh (especially xerohalophytes) are primarily determined by soil salinity and moisture (Pan et al. 1998; Sánchez et al. 1998; Egan and Ungar 2000; Noe and Zedler 2000; Álvarez Rogel et al. 2001). The proposal to extract more water from the Olifants River catchment through the building of more dams prompted an estuarine freshwater requirement study on the Olifants estuary that was undertaken in 1997 (Huizinga and van Niekerk 1997). This study highlighted that further work was required to determine the physiological and flooding requirements of the marsh plants. The main reason for this study was that the building of one or more dams would significantly reduce the number of floods that will reach the estuary.

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The initial hypothesis of the study was that supratidal and floodplain salt marsh requires occasional (at least one in two years) flooding by freshwater to wash out the accumulated salts in the surface soils. This hypothesis was rejected early in the study because an analysis of past and recent aerial photographs together with field observations indicated that even during relatively large floods, the floodplain in the lower reaches of the Olifants estuary is not inundated.

Since flooding did not appear important, a vegetation survey was conducted to determine zonation patterns and develop hypotheses as to the variables responsible for the observed plant distribution in the estuary. Data analysis and field observations suggested that abiotic factors determine the distribution of the vegetation. Seasonal analysis of vegetation and physical and chemical variables indicated that the depth from the surface to the water table had the greatest influence on vegetation distribution. Based on these results the following hypothesis was developed: *S. pillansii* extracts water from the less saline groundwater. To test this hypothesis the relationship between vegetation cover, depth to water table, and electrical conductivity of the groundwater was measured in the field. Soil and tissue water potential measurements were used to investigate water availability. Water level fluctuations were measured in boreholes to determine the origin of the groundwater. These experiments showed that the null hypothesis could not be rejected; the plants do use groundwater.

The question still remained whether the saline groundwater was the only source of water to these plants. The fact that the seeds and seedlings do not have direct access to the water table indicated that precipitation might be important, at least for some part of the life history of the salt marsh vegetation. The large quantity of root biomass in the surface soils also suggested the possibility that moisture added to the surface, probably as rain, is important in this system. The hypothesis tested was that a freshwater pulse from rain is important in lowering surface soil salinity to allow seedling establishment and water uptake by adult plants. Two cohorts of seedlings were monitored over a period of 21 months. The effect of rain on soil moisture, electrical conductivity, and soil and tissue water potential was investigated.

Study Location

The Olifants River estuary lies on the West Coast of South Africa (Fig. 1). It was selected as the study site since the South African Department of Water Affairs and Forestry required an estimate of the ecological reserve of the estuary before the proposed dam developments could proceed. The estuary is relatively pristine in terms of its ecological condition, it is one of the most important estuaries in South Africa (based on a botanical importance rating and an estuarine health index) and has large supratidal and floodplain salt marshes (Adams and Bate 1997; Coetzee et al. 1997; Turpie et al. 2002). Supratidal marshes occur above the intertidal marshes and do not receive daily tidal inundation, but are normally flooded during spring high tide and other associated high water levels. The tidal range for the estuary is approximately 1.3 m (Huizinga and van Niekerk 1997). The floodplain is the area adjacent to the supratidal area, elevated above the rest of the estuary and normally covered with water during large flood events. The permanently open Olifants River estuary is tidal for approximately 32 km upstream of the mouth with the highly variable river-estuary interface located 16 km upstream. The Olifants River forms the southern boundary of the Namib Desert and the annual rainfall never exceeds 250 mm. The combination of the cold Atlantic waters and the warm semi-arid environment causes a high incidence of fog.

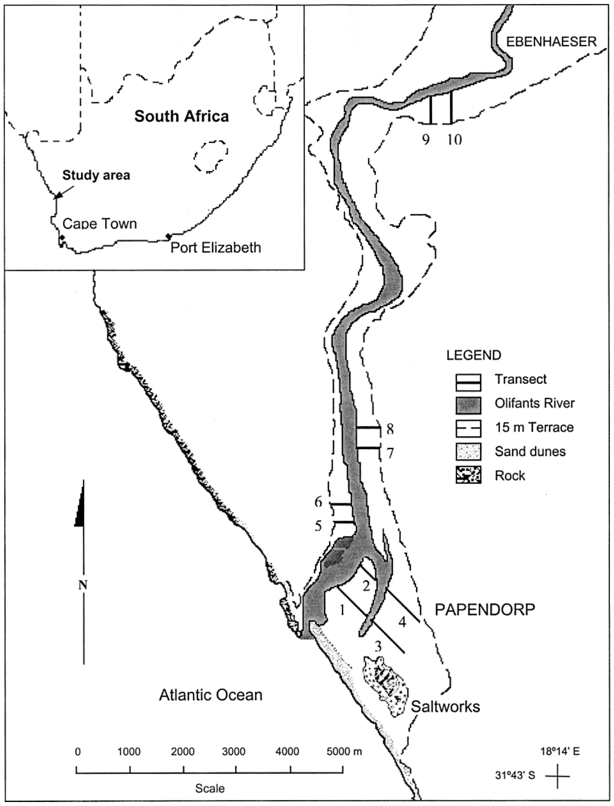

Fig. 1. Map of the Olifants River estuary showing the location of the 10 transects (Source: 1:50 000 Topographic map 3118 CA PAPENDORP).

Materials and Methods

SEASONAL STUDY

Ten permanent transects were established in the marsh areas along the estuary as depicted in Fig. 1. The profile and elevation above mean sea level for each transect was determined using a theodolite (Sokkisha TM 6). Vegetation changes were analyzed by determining the percentage cover in a permanent quadrat located every 20 m along the transect. Four random quadrats were located around the permanent quadrat, and the percentage cover determined in each. The permanent quadrats were used to determine whether seasonal changes in vegetation cover were occurring. The random quadrats were used to obtain a good assessment of the state of the vegetation. Four quadrats were chosen because there are many bare areas in the marsh (the statistics behind this are not shown but are reported in Bornman 2002).

Soil samples (approximately 400 g) were collected at 100, 200, and 300 m from the edge of the estuary along each transect. At each site samples were collected at three depths, 0–0.05, 0.05–0.15, and 1.0–1.2 m. Soil pH, redox potential, and electrical conductivity (EC) were determined in a field laboratory on the same day as sampling. Samples were sealed and transported to the laboratory where analyses of soil moisture, organic content, and particle size were undertaken. Soil characteristics were determined using the following methods: soil moisture content (Black 1965); organic content (Briggs 1977); electrical conductivity (Barnard 1990) using a YSI 30M/10 FT handheld conductivity meter; pH (Black 1965); redox potential (Barnard 1990) using a Metrohm AG9101 electrode; and particle size (Day 1965). A saturated paste was used to determine electrical conductivity; the amount of de-ionized water used to attain saturation was recorded for each sample (Barnard 1990). Seasonal data were collected during 4 sampling trips, November 1999, March 2000, July 2000, and November 2000. Climatic conditions in the study area were recorded by the South African Weather Services at the Lutzville weather station near Ebenhaeser (see Fig. 1).

POPULATION STUDY

The site for the population study was along Transect 7 (Fig. 1) and hence the soil properties measured there were similar to the conditions experienced by the seedlings. Two cohorts of seedlings were measured and counted in five permanent quadrats (1 m^2) during the 4 seasonal sampling trips as well as during July 2001 over a period of 21 mo. These were 5 new permanent quadrats and not the same as those used in the assessment of vegetation cover. Length measurements were made from the base of the stem to the live apical tip. The survivorship curves are presented based on counts of number of seedlings, and do not take into account death before or at germination. The large seedlings (50–60 mm initial height) germinated during 1998 and the smaller seedlings (10–20 mm initial height) during April 1999.

GROUNDWATER STUDY

Seasonal analysis of vegetation and physical and chemical variables indicated that the depth from the surface to the water table had the greatest influence on vegetation distribution and further groundwater investigations were needed. Water level fluctuations were measured in boreholes to determine the origin of the groundwater. During the field trip in July 2000, boreholes were sunk at 100, 200, and 300 m along Transects 1, 3, 5, 7, and 9. Boreholes were augered manually to a depth of 3 m. During borehole installation each color change and textural change in the soil was sampled and the depth of change noted. Soil textures were differentiated according to particle size composition. Borehole casings comprising 63 mm diameter PVC piping with a 1 m length of continuous slotted screen (0.2 mm slot openings) in the lower, capped end were placed down the holes. The removed soil was used to back-fill the bore space to the surface and clay material was packed around the borehole at the ground surface to prevent contamination of the deeper water by surface runoff. The boreholes were left to stabilize for 3 mo before monitoring began. Accurate water level measurements were taken using a modified moisture meter that displayed a signal as soon as the electrodes touched water. The length of the cord and the height of the casing protruding above the soil surface were noted. Groundwater electrical conductivity, salinity, and temperature were recorded using a YSI 30M/10 FT handheld conductivity-salinity-temperature meter.

In July 2001 the relationship between vegetation cover, depth to the water table, and electrical conductivity of the groundwater was investigated. Twenty-six additional sites were selected in the lower reaches of the estuary in both supratidal and floodplain areas. At each site, percentage vegetation cover (10 random quadrats), depth to the water table, and the electrical conductivity of the groundwater were recorded.

WATER POTENTIAL STUDY

Soil and tissue water potential (Ψ) measurements were made using a WP4 Dewpoint PotentiaMeter (Decagon Devices, Inc). All measurements were made in the field immediately after sampling in the vicinity of Transect 3 and 7 (Fig. 1). Soil samples were collected from 4 depths: 0.0–0.05, 0.05–0.15, 0.2–0.3, and 1.0–1.2 m. Plant tissue samples were taken and their Ψ measured immediately. No root Ψ measurements were made because the root system consisted of a single woody taproot and numerous fine roots, both of which would require time to prepare, making the readings inaccurate. Measurements of Ψ were made before the rainy season in July 2001, during a rain event, and one week after the rain had stopped. This was done to determine the influence of rain on the vegetation, soil characteristics and availability of water.

STATISTICAL ANALYSIS

The seasonal species and environmental data for Transect 7 were analyzed using CANOCO for Windows (version 4.0, 1997). Detrended canonical correspondence analysis (DCCA) was used to obtain an ordination of the vegetation data constrained by environmental variables. The analysis included each sampling as a separate variable; the value for each quadrat was not an average across seasons. Only results for Transect 7 are used as the data set was too large for the program to handle. Monte Carlo permutation tests (999 permutations) were performed to assess the significance of the canonical axis showing the relationship between species and the selected environmental variables. The result of the DCCA was plotted as a two-dimensional graph using CANODRAW (version 3.1, 1997). The environmental variables were plotted as arrows originating from the center of the graph. The origin represents the mean value of each separate variable and the direction of the arrow line represents an increase in the value of that particular variable.

A correlation analysis was run using Statistica (version 5.5 1999 and version 6, 2002, Statsoft Inc.) on all variables tested at all sites over the four sampling periods (n = 1439). Variables included in the analysis were: date of sampling (to determine if any variables changed over time); transect number (increasing upstream, to identify variables related to distance along the estuary); distance inland from the estuary; depth below the soil surface (soil samples were collected at three depths); percentage soil moisture; soil electrical conductivity, soil pH; soil redox potential; percentage soil organic content; percentage vegetation cover; percentage sand fraction in the soil and the percentage clay fraction in the soil. The correlation matrix included in the results is for all transects because the data from Transect 7 alone, did not reveal much, as the sample size was too small.

The relationships between soil and tissue water potential, rooting depth, groundwater depth, electrical conductivity, and rainfall were assessed using ANOVA. One-way and two-way ANOVAs were used to determine significant differences among means. When a significant difference was found, a Post Hoc comparison of means was run using Tukey's Honest Significant Difference Test to determine differences between individual means. All ANOVA and correlation statistical analyses were run using Statistica.

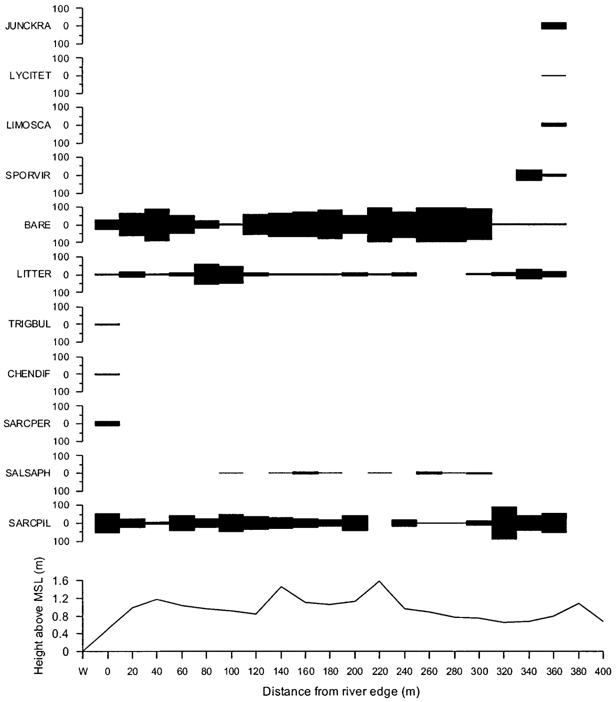

Fig. 2. Kite diagram showing the typical distribution of salt marsh plants in the Olifants River estuary during November 1999. The start of the transect is denoted by o along the x-axis. The level of the estuary was denoted by a W for water or MSL. The y-axis indicates percentage cover. Plant names are abbreviated as follows: SARCPILL = *Sarcocornia pillansii*; SALSAPH = *Salsola aphylla*; SARCPER = *Sarcocornia perennis*; CHENDIFF = *Chenolea diffusa*; TRIGBUL = *Triglochin bulbosa*; SPORVIR = *Sporobolus virginicus*; LIMOSCA = *Limonium scabrum*; LYCITET = *Lycium tetrandrum*; and JUNCKRA = *Juncus kraussi*. Other abbreviations: litter = organic litter; bare = bare ground.

Results

SEASONAL STUDY

The kite-diagram in Fig. 2 shows a typical distribution of salt marsh plants from the water edge inland. The intertidal area of the estuary is small (less than 2 m in width) and species such as *Sarcocornia perennis* (Mill.) A. J. Scott, *Chenolea diffusa* Thunb., and *Triglochin bulbosa* L. are dominant in this zone. The supratidal areas that occur beyond the intertidal zone consist mostly of dense monospecific stands of *S. pillansii*. The floodplain is nor-

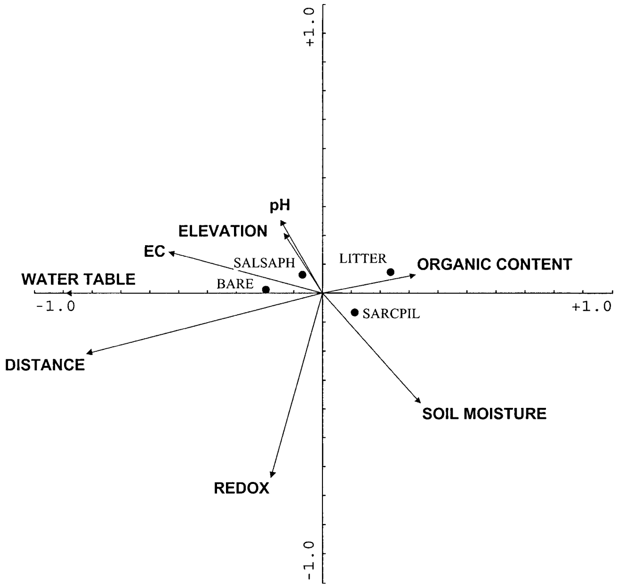

Fig. 3. Ordination diagram based on a Detrended Canonical Correspondence Analysis of seasonal species and environmental data for Transect 7. The eigenvalues of axis 1 (horizontally) and axis 2 (vertically) are 0.37 and 0.03, respectively. The scale marks along the axis apply to the quantitative environmental variables that are indicated by the arrows. EC = Electrical conductivity of the soil; water table = depth to water table; Distance = distance from the waters edge inland; Elevation = height above sea level; pH = soil pH; organic content = soil organic content; soil moisture = soil moisture; redox = redox potential (Eh); SARCPIL = *Sarcocornia pillansii*; SALSAPH = *Salsola aphylla.*

mally situated ca. 1 m higher than the supratidal zone, and the vegetation is sparse with *S. pillansii* and *Salsola aphylla* L.f. dominant. In all transects, a high percentage of bare ground and litter made up the total area of the floodplain. Salt marsh species that can be considered more terrestrial, and less salinity tolerant, were found at the outer edge of the floodplain where, presumably, freshwater runoff from the slopes surrounding the estuary decreases the soil salinity. The profile of Transect 7 (Fig. 2) is the result of numerous sediment deposition and erosion events that have occurred during past flooding over many years. Sediment profiles obtained by drilling showed an intricate and complex floodplain geomorphology. Core profiles no more than 1 m apart have been found to differ substantially and this can be attributed to the different sediment types (clay/sand) carried by the rivers and tributaries feeding into the estuary (Bornman 2002).

The results of a DCCA are shown in Fig. 3. A Monte Carlo permutation test of the trace (sum of eigen values of all canonical axis; 999 permutations) confirmed the overall significance of the canonical ordination ($p < 0.001$). The first canonical axis (horizontal) describes 88% of the variation of the species-environment relation. This axis was negatively correlated with depth to the water table, distance from the estuary, and soil electrical conductivity. The strongest negative correlation (-0.84) was between the first canonical axis and depth to the water table. Soil moisture and soil organic content was positively correlated to the first DCCA axis. *S. pillansii* occurred at a closer than average distance from the estuary, at lower than average EC, and at shallower than the average water table depth. *S. aphylla,* on the other hand, had the highest weighted averages for EC and elevation growing in soil with high EC and in highly elevated areas where the water table was deep. Bare ground had the highest weighted average for depth to the water table; in areas where the water table was very deep there was bare ground.

The correlation analysis for the vegetation cover and environmental variables tested over a period of 21 mo for all transects ($n = 1439$) showed significant correlations for most of the variables tested (Table 1). The strongest and most important in relation to freshwater in the floodplain were the percentage soil moisture that increased with depth and EC of the soil that decreased with depth. The percentage cover of *S. pillansii* increased with an increase in soil moisture content.

The monthly rainfall during the study period is shown in Fig. 4. During July 2001, 102 mm of rainfall was recorded which was the same as the total rainfall recorded during the year 2000 and only 3.2 mm less than the total rainfall for 1999. Only 9.5 mm of rainfall were recorded for November 1999, yet it had a more pronounced influence on the surface and subsurface soil moisture, although not significantly so ($p > 0.05$, $n = 12$), than the 102 mm recorded during July 2001. Average soil moisture and soil EC values for the different sampling depths in Transect 7 can be seen in Figs. 5 and 6. Surface and subsurface soil moisture was significantly higher in November 1999 and July 2001 ($p < 0.05$, $n = 12$; Fig. 5). No significant difference ($p > 0.05$, $n = 12$) was recorded in the percentage soil moisture at groundwater level (1.0–1.2 m). The EC of the surface soils were significantly lower during November 1999 and July 2001 ($p < 0.05$, $n = 12$; Fig. 6). Although the EC in the surface soils during July 2001 was lower than the drier months, it was not significantly lower than the EC recorded during July 2000 ($p > 0.05$, $n = 12$). No significant difference was apparent in the EC of the soils of the different sampling dates for the subsurface soils or the soils at the level of the groundwater ($p > 0.05$, $n = 12$).

POPULATION STUDY

The survivorship curve of large and small seedlings is shown in Fig. 7. There was a steady de-

TABLE 1. Correlations among vegetation and physical and chemical variables for all 10 transects over the four sampling periods (Date of sampling (Date), transect number (Trs), distance inland from the river edge (Dist), depth of sampling below the soil surface (Depth), percentage soil moisture (% Moist), soil electrical conductivity (EC), soil pH (pH), soil redox potential (Redox), percentage soil organic content (% OC), percentage vegetation cover (% Veg), percentage sand fraction of the soil (% Sand) and percentage clay fraction of the soil (% Clay). Significant correlations, r, are those for $p < 0.05$; $n = 1{,}439$).

	%Moist	EC	pH	Redox	%OC	%Veg	%Sand	%Clay
Date	0.14	0.07	0.25	0.34	0.08	—	—	—
Trs	0.09	—	−0.11	0.32	0.19	—	0.49	0.52
Dist	—	—	—	0.11	—	−0.06	0.09	0.21
Depth	0.37	−0.56	—	0.18	−0.45	—	−0.28	—
% Moist		−0.14	−0.06	0.14	0.22	0.24	—	0.18
EC				−0.14	0.23	0.09	0.24	—
pH				−0.36	—	—	−0.16	−0.19
Redox					−0.05	−0.13	0.19	0.3
%OC						0.10	0.23	0.2
%Veg							−0.08	—
%Sand								0.52
%Clay								

crease in the number of small seedlings between November 1999 and November 2000 and then a sharp decrease between November 2000 and July 2001. The decrease in the number of small seedlings (Fig. 7) is reflected in a significant increase ($p < 0.05$, $n = 12$) in average seedling height (Fig. 8). This effect is most likely the result of the smaller seedlings (in the small seedling cohort) dying before the larger ones. Further comparison between Figs. 7 and 8 show that the large seedlings survived better than did small seedlings.

WATER POTENTIAL STUDY

It was difficult to quantify the presence of fine roots through the soil profile. Live root material was none-the-less found above and below the surface of the water table. The surface soil water potential (Ψ_{soil}) during the drier months of the year was extremely low (Table 2). It was only at groundwater level (1.0–1.2 m) that Ψ_{soil} was higher than the Ψ_{tissue} of *S. pillansii.* Rainfall significantly increased the Ψ_{soil} in the surface areas to a level higher than the Ψ_{tissue} of *S. pillansii* ($p < 0.05$, $n = 4$). The rainfall also affected the Ψ_{soil} of the deeper sediments by significantly decreasing it ($p < 0.05$, $n = 4$). No significant difference in Ψ_{tissue} was recorded before, during, and after the rain ($p >$

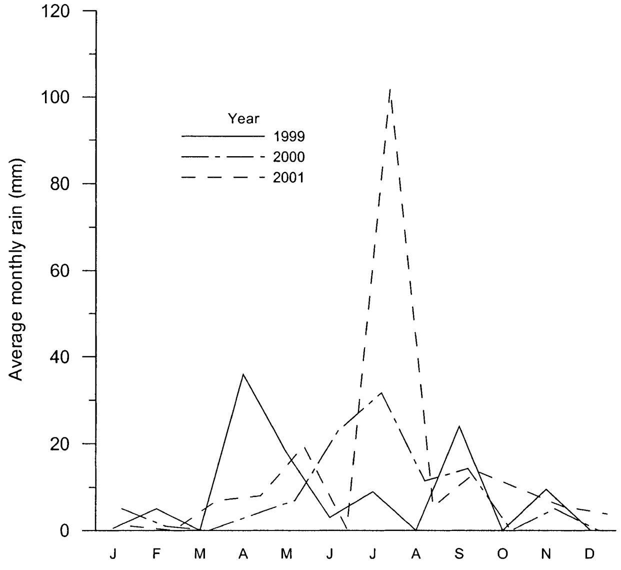

Fig. 4. Average monthly rainfall data for the years 1999, 2000, and 2001, measured by the South African Weather Service at the Lutzville weather station.

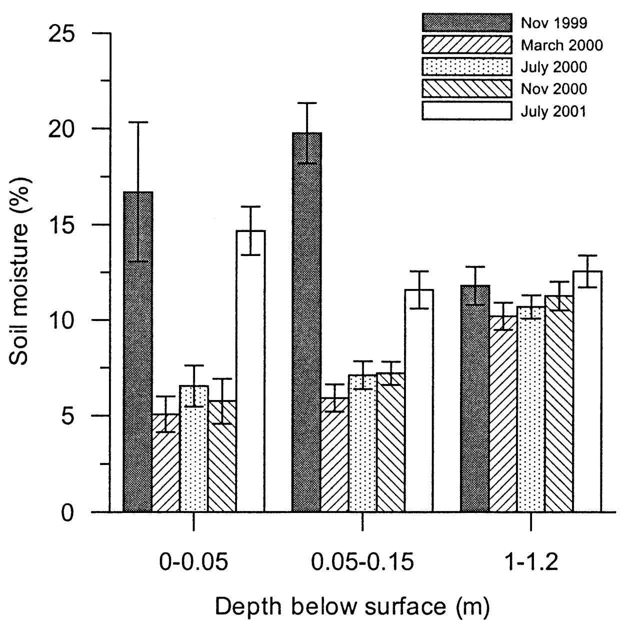

Fig. 5. Percentage soil moisture (mean ± SE) at three different depths along Transect 7 over a period of 21 months (data at 100, 200, and 300 m distance from the waters edge were combined for the respective depths).

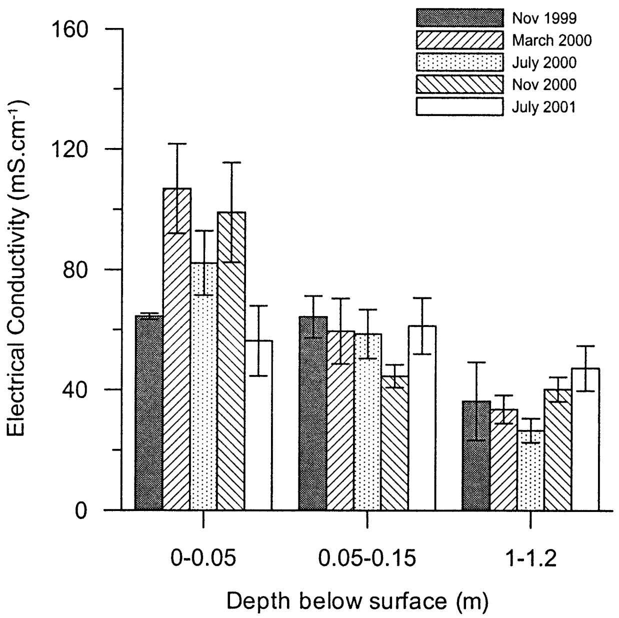

Fig. 6. Electrical conductivity of the soil (mean ± SE) at three different depths along Transect 7 over a period of 21 months (data at 100, 200, and 300 m distance from the waters edge were combined for the respective depths).

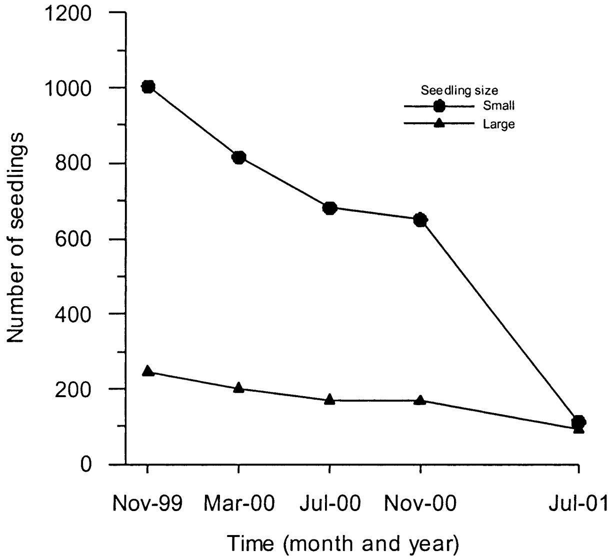

Fig. 7. Survivorship curve of small and large seedlings in the field over a period of 21 months.

0.05, n = 4). A significant decrease in surface Ψ_{soil} was measured one week after the rain had stopped ($p < 0.05$, n = 4). An increase in Ψ_{soil} from 0.05 m and deeper only occurred after the rain had stopped. No significant change ($p < 0.05$, n = 4) in Ψ_{soil} occurred at water table level (1.0–1.2 m) during the study. Table 3 indicates an increase in percentage cover of *S. pillansii* with a decrease in water table depth. *S. pillansii* cover was also higher where the EC of the groundwater was low.

Groundwater Study

The water table fluctuation measured at 200 m from the estuary at Transect 7 is shown in Fig. 9. No clear fluctuations were measured between tides during specific events but large differences in water level were noted between neap, spring, and an extra high spring tide. The extra high spring tide was recorded when a normal spring high tide coincided with a flooding river and large swell caused by storm events at sea. These findings indicate that the water level in the open water portion of the estuary affects the groundwater level beneath the supratidal and floodplain marshes.

Discussion

Species diversity on the supratidal and floodplain areas of the Olifants River estuary is very low, with only 2 species (*S. pillansii* and *S. aphylla*) making up 90% of the vegetation cover (Fig. 2). Of the two species, *S. pillansii* is the most dominant. The low rainfall, high evaporative demand, and hypersaline soils result in low vegetation cover and extensive bare areas. Krüger and Peinemann (1996) found the lower the soil salinity in coastal plain areas, the higher the percentage cover and number of species present.

Depth to the water table appears to be the most important variable affecting the distribution of *S. pillansii*. Where the water table was deepest (> 1

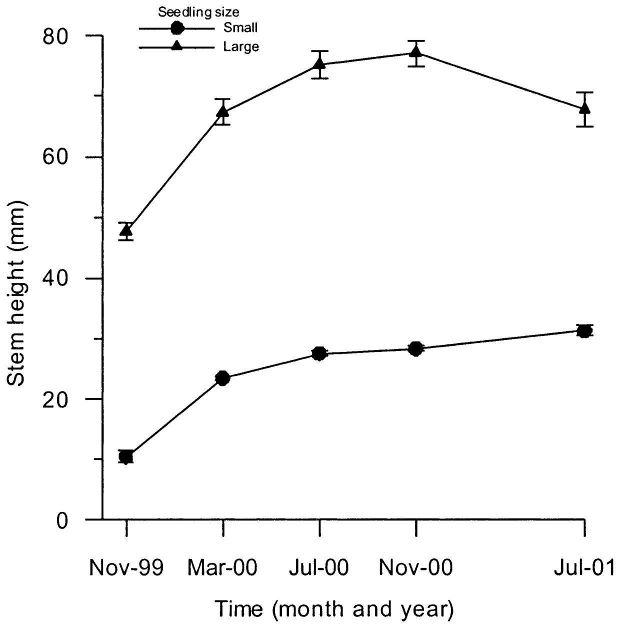

Fig. 8. Growth in terms of height of small and large seedlings in the field over 21 months.

TABLE 2. Tissue and soil water potential (MPa) readings (mean ± SE) before, during, and after the seasonal rain (July 2001; n = 4).

Time	*S. pillansii*	Soil depth (m)			
		0.0–0.05	0.05–0.15	0.20–0.30	1.0–1.2
Before	−8.18 (0.13)	−40.18 (0.84)	−7.54 (0.21)	−6.59 (0.23)	−4.71 (0.16)
During	−8.15 (0.13)	−0.92 (0.17)	−5.04 (1.23)	−11.16 (0.38)	−5.77 (0.6)
After	−8.01 (0.12)	−21.77 (1.27)	−7.49 (0.42)	−6.23 (0.29)	−4.39 (0.27)

m), bare ground was found to make up the greatest area. Cantero et al. (1998), Pan et al. (1998), and Cisneros et al. (1999) found similar results where the distribution of salt marsh vegetation depended on the depth to the water table and the salinity of the groundwater that in turn controlled the edaphic salinity.

The increase in soil moisture and decrease in soil EC with depth indicated the existence of a water table. The groundwater was less saline than the overlying soil layers and was very shallow (1.1 ± 0.13 m, n = 26) with an extremely variable EC. The positive correlation between *S. pillansii* cover and soil moisture, suggests that the plants extend their roots to where the soil had the highest moisture content, i.e., at the level of the water table. The depth of the water table varied greatly throughout the supratidal and floodplain areas depending on the soil elevation. Where it was shallowest, the percentage cover of *S. pillansii* was highest.

Rain (November 1999 and July 2001) significantly increased the soil moisture and decreased the soil EC in the surface soil layers. The influence of rain is critical in the germination, establishment, and ultimate survival of salt marsh plants (Rose 1996; Gul and Weber 1998; Noe and Zedler 2001a,b). The rainfall data showed that only 9.5 mm were recorded during November 1999. The large change in soil characteristics during this month could be due to the fact that sampling occurred very shortly after the actual rainfall event. Noe and Zedler (2001a) established that the daily variability in rainfall affects the daily and weekly variability of soil salinity and moisture, and that this variability would be lost in monthly sampling. The effect of the 102 mm rainfall event in July 2001 was very similar to that recorded during November 1999. A possible explanation could be that even a small amount of rainfall will affect the properties of the surface soil layers and, irrespective of the amount of rainfall that falls, it affects only the surface and subsurface (0–0.15 m) soil and its impact is very short lived. The surface soils (0–0.05 m) of the floodplain and supratidal areas had a high clay content (~30%), which appears impermeable to water, because the rainwater pools on the surface and evaporates before infiltrating into the soil. Soil with high clay (10–20%) and low sand content has a higher water holding capacity resulting in higher moisture and salinity being measured before and after rain compared to other soils (Noe and Zedler 2001a). Rain had little influence on the soil moisture and EC values in the deeper layers. Glasshouse studies have shown that *S. pillansii* would not be able to grow in soils with ECs as high as that found in the surface soil of Transect 7 during the drier months (Bornman 2002). The rain lowered the surface soil ECs within the range (< 80 mS cm^{-1}) in which *S. pillansii* can grow.

TABLE 3. Correlations between depth to groundwater (depth), percentage cover of *S. pillansii* (% vegetation), and the electrical conductivity of the groundwater (EC) (Significant correlations, r are those for $p < 0.05$, n = 26).

Variables	Depth	% Vegetation	EC
Depth	1		
% Vegetation	−0.87	1	
EC	—	−0.43	1

The steady decline and eventual sharp decrease in the small seedling population can be attributed to the low rainfall the area received during 2000 and up to July 2001. The small seedlings were rooted in the surface layers, which, although they remained moist enough to ensure survival during the drier months, had an EC level much higher

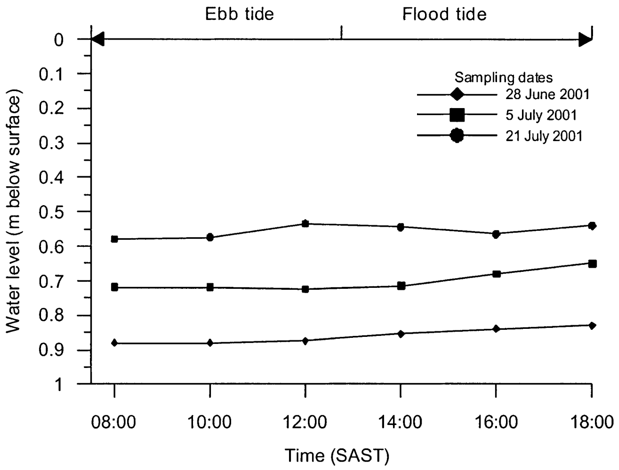

Fig. 9. Water levels measured at the 200 m borehole in Transect 7. Measurements were made during neap tide (June 28, 2001), spring tide (July 5, 2001), and an extra high spring tide (July 21, 2001).

than their tolerance (< 80 mS cm^{-1}) level. Seedling recruitment by high marsh perennial plants is limited by high soil salinity (Ungar 1991; Shumway and Bertness 1992; Khan and Ungar 1997), although the presence and uptake of Na^+ ions enhances the growth and survival of most halophytes in dry soil with decreased soil water potential (Dodd and Donovan 1999). Several annual plant species in the supratidal marsh have been found to germinate in winter after rainfall lowers the soil salinity and moisture, but they senesce by late summer when soils are hypersaline and dry (Callaway et al. 1990; Noe and Zedler 2001a). Unlike the annuals, the perennial halophytes are dependent on the next winter rainfall in order to survive. The larger seedlings showed fewer deaths due to the lower salinity of the subsurface layers into which they were rooted. The height of the surviving small seedlings increased significantly with time ($p < 0.05$, n = 1005 decreasing to 113), possibly due to the death of the smaller seedlings rather than to the growth of the survivors. The absence of a significant increase in the size of the large seedlings as the drought progressed was also observed in a glasshouse study where the seedlings under water stress stopped growing along their main axis and concentrated growth in the side branches (Bornman 2002). Live roots were found at the water table indicating that the larger plants were possibly using moisture from groundwater.

This was confirmed by the water potential study, which showed that only the soils at groundwater level have water potentials high enough for *S. pillansii* to use during the drier months. Similar results were recorded by Donovan et al. (1996) where, during the drier months, the only available soil moisture was from the deeper soil layers or from the groundwater. The results also showed the influence of rain in increasing $\Psi_{\text{surface soil}}$ to make the water in the surface available to both the adult plants and seedlings. The influence of rain on the surface soil is, however, short lived and $\Psi_{\text{surface soil}}$ returned to a level lower than that of the plants within one week after the rain stopped. Young and Nobel (1986) found that Ψ_{soil} of the surface sediment (0–0.05 m) in the Sonoran Desert returned within 8 days to its level before being watered. The Ψ_{tissue} of *S. pillansii* remained the same throughout the study, and Morales et al. (2000) suggested that this is a way of reducing leaf water losses, because cuticular transpiration is lower. The presence of large concentrations of roots in the surface soil is an indication that the plants do use water from the surface when its Ψ_{soil} is high enough. Flanagan et al. (1992) and Donovan and Ehleringer (1994) found that the shallow roots of *Chrysothamnus nauseosus* were not active in water transport during the dry season, eliminating shallow soil capacitance and allowing a more rapid equilibration with the deeper, moist soil layers. The decrease in Ψ_{soil} noted at the 0.2–0.3 m depth of this study during rainfall indicates the leaching of salts from the surface layers. This indicates that the rainwater might have infiltrated the soil to a deeper depth (0.2–0.3 m) than indicated by Figs. 5 and 6. This could be because no measurements were taken at that particular depth during the seasonal study. Tobe et al. (2000) and Noe and Zedler (2001a) also recorded the leaching down of salts from the surface layers as a result of rain.

During the drier months the surface soil moisture remained relatively high (5–6%) despite the fact that it rained less than 147.6 mm in 19 months. Onkware (2000) showed that non-saline and low salinity soils were dependent on precipitation to recharge their moisture supply, but that hypersaline soils maintained high moisture levels throughout the year because they received moisture from groundwater. The large water potential gradient that existed between the surface soil and the soil at water table level may result in the movement of saline water up from the groundwater to the surface.

Evaporative discharge from groundwater has been found to be much less in highly saline soils and Thorburn et al. (1992) attributed this to low soil permeability and low hydraulic conductivity. Diffusive discharge from the shallow water table will still take place and result in the concentration of salts in the surface layer (Krüger and Peinemann 1996; Tobe et al. 2000). It is only the temporary effect of rain that makes the surface soil layers, with their high organic content, suitable for plant growth. *Atriplex nummularia* (Slavich et al. 1999a) and *Eucalyptus largiflorens* (Jolly and Walker 1996; Slavich et al. 1999b) were found to use shallow water sources derived from rainfall for most of the year, but during the drier times used saline groundwater.

The availability of water seems to be the limiting factor for these plants, the salinity of the water source being of secondary concern. High moisture levels in saline soils ameliorate salt stress and promote plant development in comparison to soil with lower soil moisture content (Ungar et al. 1979; Onkware 2000). Low moisture has been found to limit biomass and production on non-saline soils and salinity was found responsible for low production in the hyper-saline soils (Onkware 2000).

The origin of the groundwater is important in the maintenance of estuarine supratidal and floodplain vegetation. This study clearly indicated an estuarine source. The groundwater was saline and fluctuated with the tides. The fluctuation of the water table inside the floodplain is far from sinusoidal even though its variation is forced by an essentially sinusoidal tide. Tidal fluctuations in unconfined aquifers usually do not occur in the form of a simple sinusoidal wave (Carr and van der Kamp 1969; Nielsen 1990; Serfes 1991; Jiao and Tang 1999). This could be due to damping and time lag (Carr and van der Kamp 1969; Jiao and Tang 1999), distance (Yim and Mohsen 1992; Raubenheimer et al. 1999), or very low hydraulic conductivities of the unsaturated zone (Serfes 1991). This could also explain the large variation between tidal events. The water table level always approached the highest level rather than the lowest of a particular tidal event. The intertidal slope of the estuary could be acting as a nonlinear filter that causes the water table to rise abruptly and drop off slowly compared to the near-sinusoidal tide that drives it (Nielsen 1990). The inland water table was found to be at a higher elevation than mean sea level and is probably due to the formation of a seepage face around low tide. The elevation difference was also recorded by Nielsen (1990) and Yim and Mohsen (1992), but this was found not to influence the water table fluctuation (Raubenheimer et al. 1999).

From the point of view of the Water Act (36) of 1998, it becomes clear that flooding events where water overtops the banks is not critical for the survival of salt marsh vegetation along the Olifants estuary although the groundwater in the unconfined aquifer is influenced by the hydrology of the estuary. Any changes in the hydrology of the estuary may reduce groundwater recharge, resulting in a drop in the water table. In the lower reaches of the Olifants estuary, the water table level is not likely to be affected by the river inflow due to the strong influence of the ocean, but it could become more saline. Flooding of the estuary itself by freshwater therefore remains an important event for the salt marsh, as it probably lowers the salinity in the supratidal areas and decreases the depth to the water table in the floodplain. The importance of rare, large freshwater flooding events cannot be overlooked. These events are probably important in controlling pulses of plant establishment and long-term community dynamics. The last large flood that breached the sand spit at the mouth through the central arm (Fig. 1) occurred in 1925 before the building of the Clanwilliam dam in 1932 (Council for Scientific and Industrial Research 1984).

Floods are also important in the Olifants estuary as they flush out accumulated sediments; dilute nutrients introduced by agricultural return flow and prevent reed and water hyacinth encroachment (Adams and Bate 1997; Huizinga and van Niekerk 1997). Baseflow is important in maintaining a longitudinal salinity gradient. The reduction in the mean annual runoff in the catchment has already resulted in saline intrusion in the estuary (Huizinga and van Niekerk 1997).

If dam construction proceeds the design of the dam must allow for some freedom in planning the required releases and operating procedures. Water releases should take place during the winter months, thereby simulating natural conditions. A single release of water should be maintained for several days over a spring tidal cycle. The combined effect of the water release and spring high tide must be such that it raises the water level in the estuary sufficiently to cover the supratidal areas with low salinity water and also decreases the depth to the water table in the floodplains. The consequences of not providing this water are potentially that the floodplain will become bare of vegetation with all the associated problems of desertification.

The likelihood of planned discharges coinciding with higher water levels in the estuary is unfortunately small and the continued monitoring of the salt marsh vegetation will be important in identifying salt marsh deterioration. The resilience of the vegetation means that unfavorable conditions might only manifest itself through the vegetation once it is too late. Simple monitoring of the water table depth and salinity in the boreholes set up during this study should give adequate warning of any change in the groundwater hydrology. The dependence of *S. pillansii* plants on the groundwater means that recolonization through seeds will not be an effective rehabilitation process if the groundwater becomes hypersaline. The removal of the vegetation will also alter the physical and chemical character of the soil and, as a result, rehabilitation will be difficult as was found in the Orange River estuary. The loss of vegetation in the Orange River estuary was attributed to a lack of overbank flooding (Council for Scientific and Industrial Research 1991). However salinzation of the groundwater may also be a reason that would need further investigation.

Conclusions

The highest percentage vegetation cover was recorded in low-lying areas on the floodplain and was related to the depth to the water table. The high salinity of the surface soil makes it unsuitable for plant growth and, as a result, the plant roots extend down to the less saline groundwater where a suitable water potential gradient exists between the soil and the roots. The plants appear to use this resource only as a source of moisture to maintain essential metabolic processes to survive the drier months of the year. The single large pulse of freshwater during rain is essential for the survival of the vegetation on the floodplain salt marsh. The rainfall event, if large enough, will trigger seed germination, seedling growth, and allow the mature plants to access the fresher water accumulating on the soil surface.

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