THE ZONATION OF *SPOROBOLUS VIRGINICUS* (L.) KUNTH AND *DACTYLOCTENIUM AUSTRALE* STEUD. ON THE NORTHERN SHORES OF LISTER POINT, LAKE ST LUCIA

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INTRODUCTION

The St Lucia system on the Zululand coast consists of three large, shallow and saline lakes connected to the sea in the south by a narrow channel.

Lister Point is situated on the western shore of False Bay, the most north-easterly of the three lakes (Fig. 1).

While Lister Point receives an annual rainfall of 700 mm p.a. (Hutchenson, 1974) the main supplies of fresh water to False Bay are from the Hluhluwe and Nyalazi rivers in the south and Mzinene river in the north. Hell's Gates (see Fig. 1) acts as both the outlet channel for the fresh water entering the Bay and the inlet channel for brackish or saline water from the main lake system.

In times of severe drought when the inflow of fresh water to False Bay becomes negligible the brackish or saline water may flow into the Bay where it becomes concentrated through evaporation. As a result the salinity of the water varies greatly both spatially and temporarily. Salinities at Lister point have been recorded since 1966 and while the lowest reported was 14,3 ppt in June 1974 (I. M. Shaw, 1974, pers. comm.), the highest salinity known to have occurred in the whole St Lucia system - 110 ppt or three times that of sea-water - was reported from this point in October 1970 (Hutchenson, 1974).

The water level in the Bay also shows considerable fluctuations. These may be seasonal or on a short-term basis. The latter fluctuations are caused by internal seiche movements which in turn are subject to wind strength and direction.

Siltation is an important aspect of the hydrology of False Bay. Fresh water entering the system from the three rivers mentioned above carries large quantities of material in suspension. Fine silt and clay particles are carried into the Bay where they settle evenly over the whole basin, with the result that the Bay is shallow (average depth 1 m) and the shores very gently sloping (Kriel, 1966). Fluctuations in water level therefore cause alternating exposure and inundation of large areas adjacent to the shore.

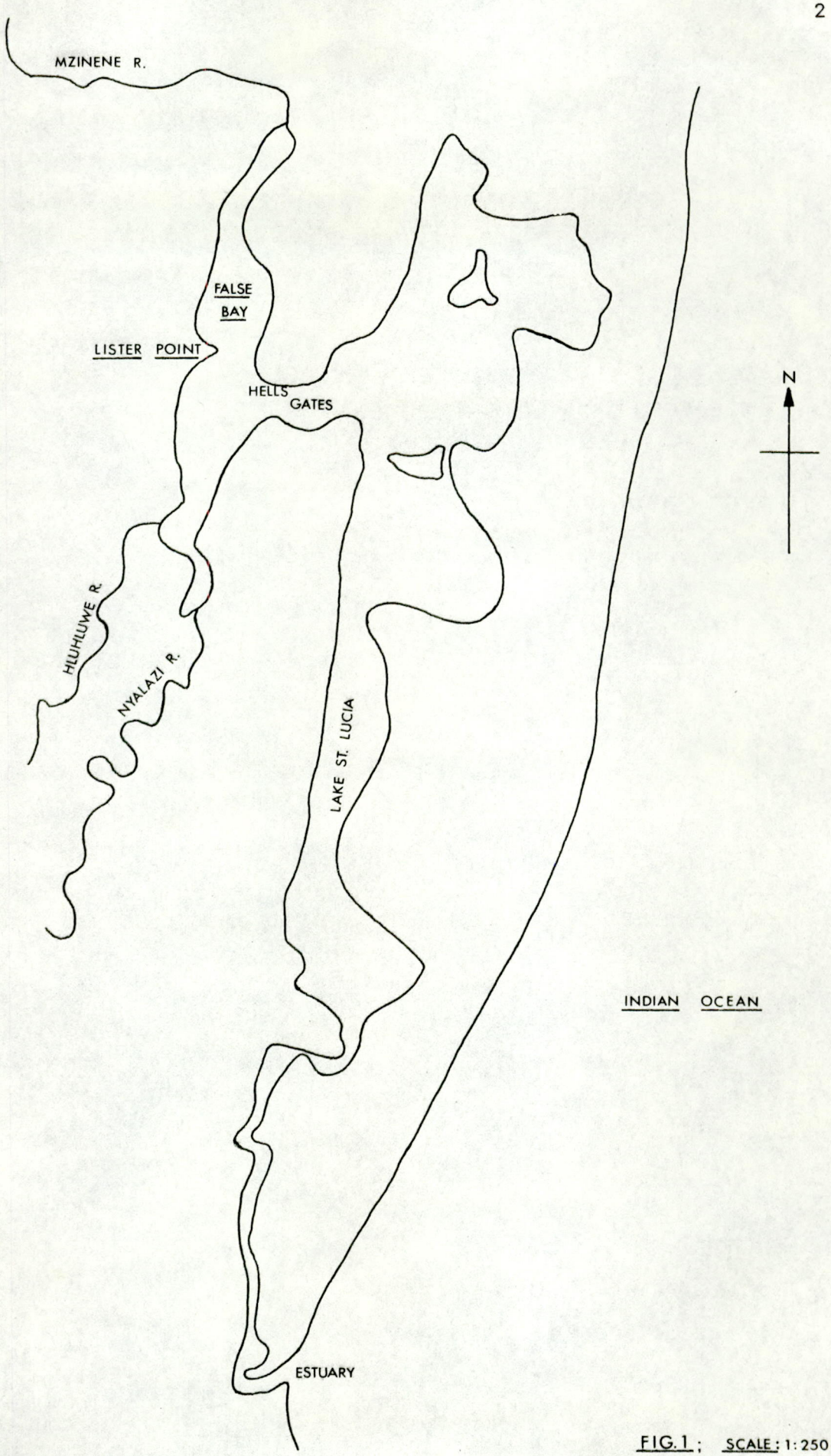


FIG. 1 ; SCALE : 1: 250 000

Soils at Lister Point other than the silt deposits of the immediate shoreline are derived from calcareous sandstone of marine origin and Cretaceous age (Truswell, 1970).

The general vegetation type at Lister Point is described by Bayer and Tinley (1966) as being "dry forest", and also as "secondary thicket and woodland (with Newtonia hilderbrantii)". Between this forest and the lake itself however, is a narrower strip (approximately 30 m wide) of grassland in which the dominant species are Sporobolus virginicus and Dactyloctenium australe.

Sporobolus occurs in pure stands near the water's edge. Inland of this community there is a sudden change to pure Dactyloctenium stands. The distribution of the latter grass extends into the forest vegetation.

The aim of this study was to record the zonation of Sporobolus and Dactyloctenium on the northern shores of Lister Point and to determine what factors influence it and the extent they do so.

SPOROBOLUS VIRGINICUS (L.) KUNTH

S. virginicus is a perennial grass characteristic of littoral areas in the Cape, Natal and Zululand and considered by Bews (in Meridith, 1955) to be the most important pioneer under saline conditions that occur beside coastal lagoons and estuaries.

Flowering shoots and adventitious roots are produced from the many nodes of long creeping stoloniferous rhizomes (i.e. each of these stems may travel both above and below the ground). These stolons branch repeatedly so that a single plant may cover several square metres.

Ward (1971) describes this grass as being intolerant of long hours of shade and unable to compete with other sand dune pioneers.

DACTYLOCTENIUM AUSTRALE STEUD.

D. australe is a stoloniferous perennial from the coastal areas of the Eastern Cape, Natal and Zululand. The flat stolons have long (20 - 30 cm), curving

internodes and flowering shoots and adventitious roots are produced at the nodes. While the stolons remain green and above ground for an indefinite period of time, they eventually die and decompose, so isolating the plantlets which have formed at the nodes.

D. australe is described by J. K. A. Chippindall (in Meredith, 1955) as being a good sand-binding grass which is sometimes a pioneer on sand dunes, "likes" shade and is of frequent occurrence on forest floors and margins.

METHODS AND MATERIALS

1. COLLECTION OF FIELD DATA AND SAMPLES

1.1 Selection of study areas

Two 1 m wide sites which ran from the water's edge, through the grass communities to the edge of the dry forest vegetation were selected for this study.

Site 1 (Plate 1) incorporated a dry littoral pool enclosed by a low bank which had been colonised by S. virginicus, while Site 2 (Plate 2) ran across a mud flat as yet not colonised by any vegetation.

The two lines forming the outer boundaries of each of these sites (i.e. those running from the shore to the forest) were used as transect lines, such that transects one and two were made at Site 1 (Plate 1a) and transects three and four at Site 2 (Plate 2a).

1.2 Determination of transect profiles and species distribution

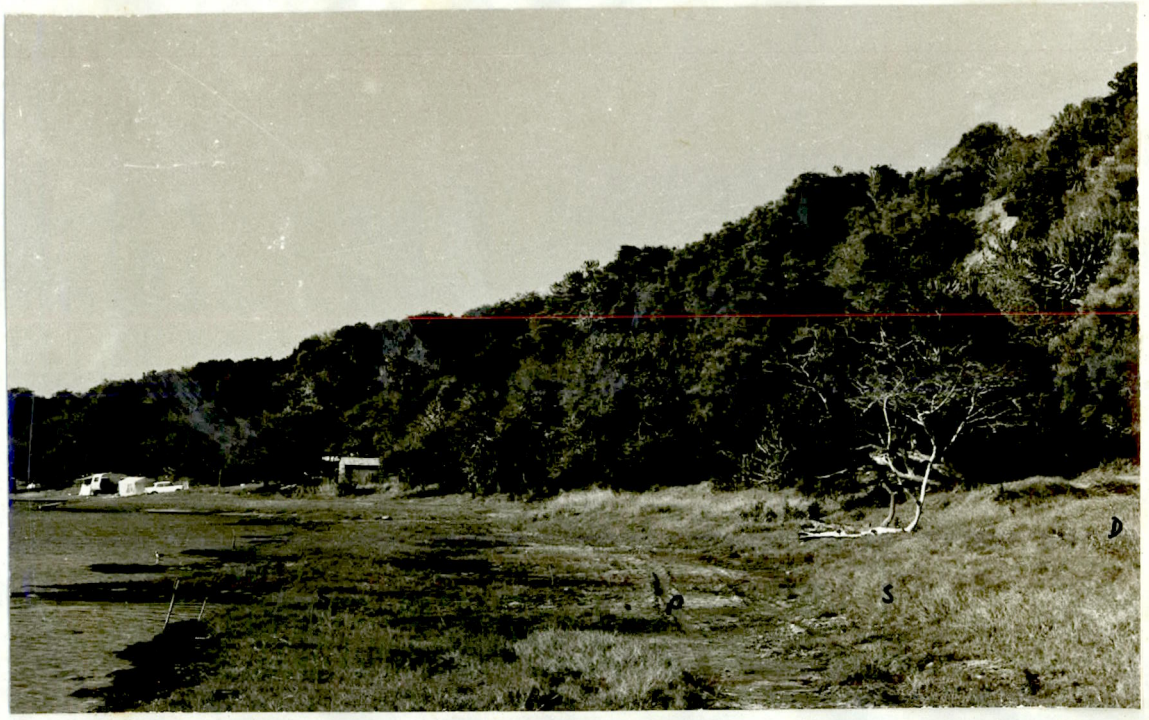
The profile of the lake shore along each transect was surveyed using an Abney Level and the distribution of Sporobolus and Dactyloctenium determined by the line intercept method.

For this latter determination the presence or absence of the two species was noted in points spaced at 5 cm intervals along the transect. The frequency of occurrence of each species per 0,5 m of the transect line was then calculated using the following formula:

$$\text{Freq.} = \frac{\text{No. of occurrences/0,5 m}}{\text{No. of points/0,5 m}} \quad .$$

1.3 Collection of soil and plant samples

Soil samples were taken from each transect at approximately 2 m intervals using a core borer. The top 15 cm of each core (10 cm wide) was collected and a second sample was taken at the maximum depth at which grass roots were present in the core. In those bare areas where neither grass was present the second sample was taken from a depth of 45 - 55 cm. All second samples are hereinafter referred



↑PLATE 1 General view at Site 1

←PLATE 1a Site 1 showing position of transects.

KEY: S_1 - Sporobolus virginicus community on low bank;
P - Dry littoral pool;
S - S. virginicus community;
D - Dactyloctenium australe community.

PLATE 2 General view near Site 2 (arrowed).

PLATE 2a Site 2 showing position of transects.

KEY: M - Exposed mud flat;
S - Sporobolus virginicus community;
D - Dactyloctinium australe community.

to as those taken at "maximum root depth".

Samples of the aerial parts of each grass species were also taken at approximately 2 m intervals from both Sites 1 and 2.

Immediately on collection of the samples, all dead material was removed and the fresh weight of the living material determined with a triple beam balance. At least 15 g of each sample was collected.

1.4 Determination of water table depth and free soil water salinity

The holes resulting from the removal of soil samples were bored to a maximum depth of 1 m. After 12 hours the depth from the soil surface to that of the water accumulated within the holes (i.e. the water table depth) was measured and the salinity of this water (i.e. the free soil water) was determined with an A and O optical salinometer.

One month later, both above parameters were remeasured along transect two. Since some holes along each of the other three transects had collapsed by this date no other measurements were taken.

2. ANALYSIS OF FIELD SAMPLES

2.1 Soils

Soil samples from one transect of each site were used. They were air-dried, ground and passed through a 0,5 mm sieve before any analysis was performed.

2.1.1 Salinity

The method used to determine the salinity of the soil from the respective sample points provided comparative data for the sodium chloride (NaCl) in the soils rather than absolute values of the salt (NaCl) content.

50 g of air-dried soil were placed in a plastic bottle containing 100 ml of distilled water. The bottle was stoppered and shaken vigorously by hand for 2 min before being placed on a mechanical oscillator for 30 mins.

The bottles were then left to stand for at least 2 hrs or until all soil particles had settled. The salinity of the supernate was determined with an

A and B optical salinometer.

2.1.2 Mechanical properties

The mechanical properties of the soils which were investigated were the silt and clay content. Two methods were used in this determination.

(a) Method I

The Bouyoucos hydrometer method for silt and clay was used for all soil samples analysed.

This method involves firstly, the dispersion of the soil and secondly, the grading of the dispersed particles into size groups. The former is carried out by means of a high speed mixer while the latter is determined by the differential rate of sedimentation of soil particles.

The rate of sedimentation is dependent mainly on the size of the soil particles and so the separation of silt and clay fractions of the soil by this method is in accordance with Atterberg's classification of soil particles accepted by the International Society of Soil Science in 1913. In this classification clay particles are considered to be those particles which exhibit Brownian movement in aqueous suspension and are smaller than 0,002 mm. Silt particles on the other hand do not exhibit Brownian movement and range in size from 0,002 mm to 0,02 mm (Baver, 1956).

The procedure followed in this experiment is described in Appendix I.

(b) Method II

Since particle size is the main factor determining the rate of sedimentation, inefficient dispersal of the soil particles will produce erroneous results.

One of the most important factors which may affect dispersal is organic matter. This acts, particularly when present in large amounts, by cementing primary soil particles together to form aggregates.

A second important factor is the effect of particle charge. Clay particles possess a negative surface charge and this potential must be kept above a certain

critical level in order to prevent floculation. The removal from the soil of floculating ions is therefore required for complete dispersal.

The degree to which these factors, and a third, calcium carbonate particles, affected the results obtained by Method I was determined by a second method.

Calcium carbonate was removed with hydrochloric acid and organic matter with hydrogen peroxide. The floculating ions were removed by successive washings of the soil samples. The silt and clay content was then determined by the hydrometer method. Only the top 15 cm samples from transect one were used in this analysis. The full procedure is described in Appendix II.

2.1.3 Calcium carbonate

The amount of calcium carbonate in the soil samples was determined, using a Collins Calcimeter.

2,5 g of soil was treated with 10 ml of dilute (1 : 3) HCl and the volume of carbon dioxide (CO_2) evolved measured. The calcium carbonate present in the soil was then calculated in the following manner.

The known volume of CO_2 was converted to that at STP using the following formula:

$$\frac{P_1V_1}{T_1} = \frac{P_2V_2}{T_2}$$

where V_1 = Volume of CO_2 evolved;
P_1 = atmospheric pressure at the time of measuring V_1 ;
T_1 = temperature at the time of measuring V_1 ;
P_2 = standard pressure (760 mm);
T_2 = standard temperature (273°C);
V_2 = volume of CO_2 at STP.

Then if 44 g of CO_2 occupy 22,4 l at STP then x g CO_2 occupy (V_2) l.
And since 100 g $CaCO_3$ would produce 44 g CO_2 then y g of $CaCO_3$ would produce x g of CO_2.

y g of $CaCO_3$ is therefore the amount of $CaCO_3$ in 2,5 g of soil.

The above experiment was repeated three times for each soil sample taken from transect 1.

It should be noted that a method such as this which assigns all carbonates present in the soil to calcium carbonate may be extremely inaccurate, especially in soils with a relatively large amount of cations present. There are, however, two main factors justifying its use in this case. Firstly, the high calcium carbonate content of the St Lucia soils is made up to a large extent of mollusc shell fragments so that the amount of any other carbonates present will not have much affect on the final results. Secondly the determination of calcium carbonate present in the soil is essential in order to make the necessary corrections to a determination of organic matter by ignition. This is necessary because on ignition of a soil sample, any calcium carbonate present will likewise be ignited, resulting in its dissociation to calcium oxide and carbon dioxide which is then liberated in the gaseous form.

2.1.4 Organic carbon

The amount of organic carbon in the soils was determined by loss of weight on ignition.

This method determines the amount of organic matter present in the soil, together with any gases which may have been present or were formed by the action of the very high temperatures, e.g. carbon dioxide, formed from combustion of any carbonates present in the soil.

Soil samples were dried in an oven at 105°C to drive off any water present, and then cooled in a desiccator.

Exactly 5,000 g of oven-dried soil was then weighed into vitreosels capsules. The capsules were then transferred to a furnace at 550°C and left for 4 hrs, cooled in a desiccator and reweighed.

The loss of weight should correspond to the weight of organic matter present plus any gasses given off.

There is however, considerable disagreement between authors as to the temperature and length of time required to completely combust calcium carbonate. The temperatures, for example, range from 350°C (Jackson, 1958) to 950°C (White &

Wetzel, 1973). The samples in the capsules were therefore ignited at 950°C and the consequent loss of weight determined.

Replicate samples of some soils were removed after ignition at 550°C and after ignition at 950°C and tested in a Collins calcimeter for production of carbon dioxide.

The reaction of calcium carbonate on combustion is:

$$CaCO_3 + (Heat) \longrightarrow CaO + CO_2$$

$$100 \longrightarrow 56 + 44 .$$

(The above figures refer to the molecular weights of the substances.)

Therefore, $\frac{44}{100}$ of the original weight of calcium carbonate present in the soil is lost as carbon dioxide on ignition, while $\frac{56}{100}$ is retained as calcium oxide. To obtain the corrected value for the loss of organic matter on ignition, therefore, $\frac{44}{100}$ of the weight of calcium carbonate present in the sample is subtracted from the original value for the loss of weight on ignition.

For example:- $$I^1 = I - (C \times \frac{44}{100})$$

where I^1 = the weight of organic matter present;

I = total loss of weight on ignition, i.e. loss after 550°C plus loss after 950°C;

C = weight of calcium carbonate present in the soil sample.

2.2 Plant Samples

2.2.1 Determination of dry weight, and of the sodium (Na^+), potassium (K^+), calcium (Ca^{++}), magnesium (Mg^{++}) content

The plant samples collected at Lister Point were dried in a forced draught oven at 60°C for 5 days. They were then cooled in a desiccator and weighed.

The Na, K, Ca, Mg content of the samples was determined by atomic absorption spectroscopy using solutions of plant ash.

The procedure used to obtain these solutions is described in Appendix III.

3. DETERMINATION OF ASPECTS RELATING TO THE SALINITY TOLERANCE OF SPOROBOLUS AND DACTYLOCTENIUM

3.1 Germination

To determine the most suitable conditions under which the effects of salinity on germination could be tested, seeds collected at Lister Point were germinated under a variety of environmental conditions. These are listed below.

(1) In soil in the greenhouse under normal day-night conditions (May-June 1974) with temperatures ranging between 35°C (day) and 10°C (night).

(2) At 30°C in both total darkness and 24 hrs light.

(3) At 20 - 25°C in both total darkness and 24 hrs light.

(4) On a laboratory bench receiving about 2½ hours of morning sunlight. Temperatures about 20 - 25°C.

The latter conditions were found to be most suitable (see Results and Discussion: D).

The percentage germination was then determined in distilled water, tap water and each of the following salt (NaCl) solutions:- 5, 10, 15, 20, 30, 40, 60, 80 and 110 ppt.

4 x 50 seeds were used for each treatment. Each group of 50 seeds was placed in a plastic petri dish containing 30 g of acid purified sand saturated with the respective solution.

The sand was preferred to filter paper since a larger volume (± 10 ml) of solution could be used so reducing the effect of increased salt concentration resulting from evaporation. Saturation of the sand was maintained by using an extremely fine spray of distilled water. Even though the surface of the sand was not allowed to dry out it was only necessary to use the spray once or in some cases twice during this experiment.

The percentage germination was determined once it was considered that no further seeds would germinate.

Those seeds treated with a salt solution which did not germinate were transferred to tap water. Germination which occurred after transference was calculated as a percentage of the original total seeds used (i.e. of 200).

3.2 Inundation of seedlings with salt water

Three-month-old seedlings (± 2 cm high) were inundated with varying concentrations of saline water.

Each of two sets of 20 Sporobolus seedlings were inundated to a depth of 0,5 cm with one of the following solutions:- distilled water, 10, 20, 30, 40, 60 and 80 ppt NaCl.

Owing to the low germination of Dactyloctenium seeds only nine seedlings were used in this experiment. They were divided equally between solutions of 10, 20 and 30 ppt NaCl.

The progress of all seedlings was observed over a period of 14 days. At the end of this period, those Sporobolus seedlings surviving, were harvested. Their fresh weight, dry weight, Na^+, K^+, Ca^{++} and Mg^{++} content was then determined.

A further 40 seedlings were harvested before the experiment started and treated in the same manner.

For the full procedure used in this experiment refer to Appendix IV.

3.3 The presence of salt glands in the leaves

For this investigation leaves of Dactyloctenium were obtained from a seedling which had been inundated with a 10 ppt salt solution in the previous experiment (Exp. 3.2). Sporobolus leaves were obtained from two separate communities of adult plants growing in Umgeni sand. One community was watered with a strong saline solution before removal of leaves and the other with tap water.

Sections of the leaves, 10μ thick, were cut and then stained with Safranin/fast green.

Appendix V contains the full procedure used in sectioning and staining these leaves.

RESULTS AND DISCUSSION

A. FIELD DATA

(i) Transect profiles

The profiles of transects 1 and 2 (Site 1) are illustrated in Figures 2a and 3a.

The transects were positioned at right angles to the shore and ran from the water's edge (height 0 cm).

From these profiles it can be seen that a low bank, approximately 10 cm high and 4,5 m wide, runs in front of a shallow depression, which in transect 1 falls below the level of the lake. This depression forms an impermanent littoral pool which is flooded at high lake levels. The depression extends from approximately 4,5 m to 10,5 m from the shore line and thereafter the land rises steadily to 107 cm above lake level, 18 m from the shore line.

Figures 4a and 5a illustrate the profiles of transects 3 and 4 (Site 2) respectively.

A low mud flat (maximum height 5 cm) extends 8 m inland from the water's edge. Beyond this the shore rises gradually to 173 cms, 20 m from the shore line. The last 0,5 m of both transects is flat and may represent an old shore line.

(ii) Species distribution

The difficulties involved in counting numbers of plants of stoloniferous grasses mitigated against the use of parameters such as abundance. Thus the quadrat size was reduced to a point and the frequency of the species estimated for 0,5 m units along the length of the transect.

Sporobolus was the only coloniser of the low bank at Site 1; indeed, in both transects (Figs. 2a/b and 3a/b), Sporobolus attained highest frequency here, suggesting that conditions were more favourable for its establishment on the low-lying area. However, further inland in the shallow depression there was no colonisation by either species, suggesting that height above water level was not

TRANSECT 1

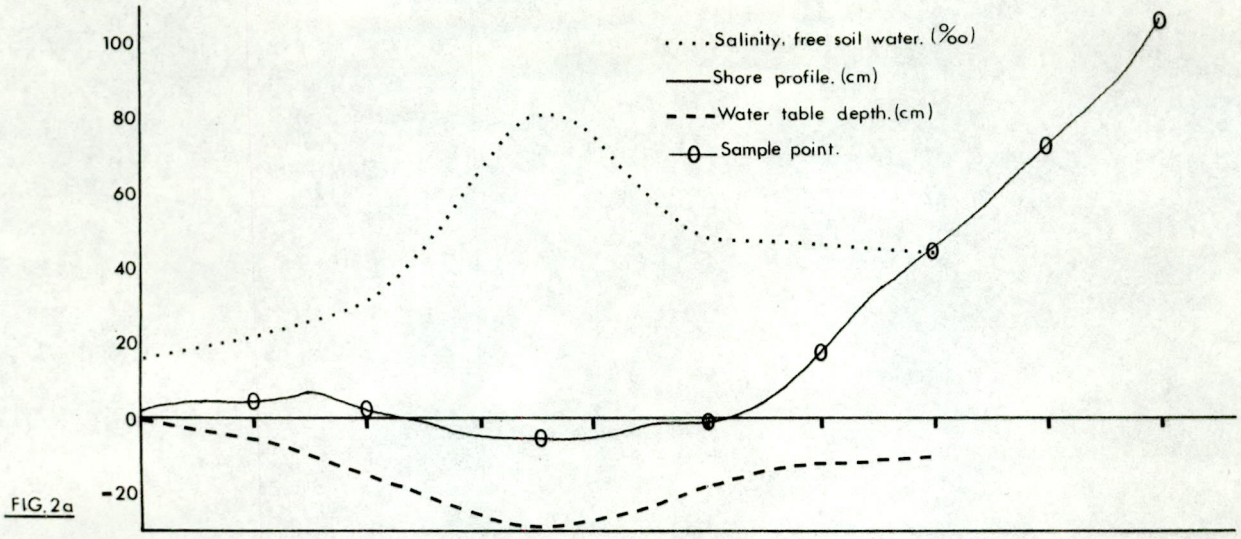


FIG. 2a

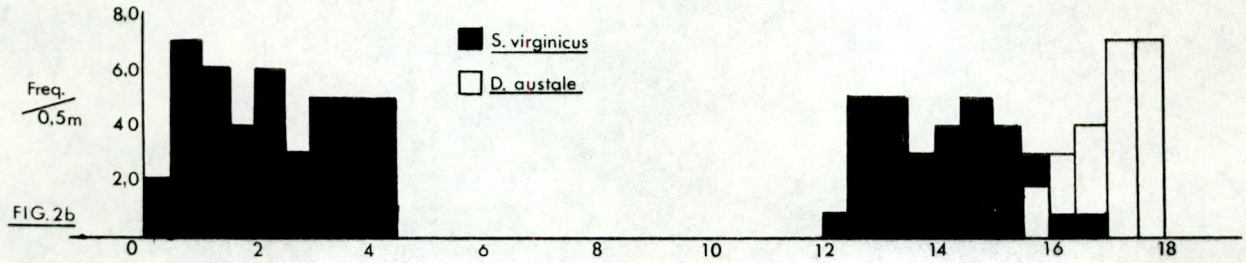


FIG. 2b

TRANSECT 2

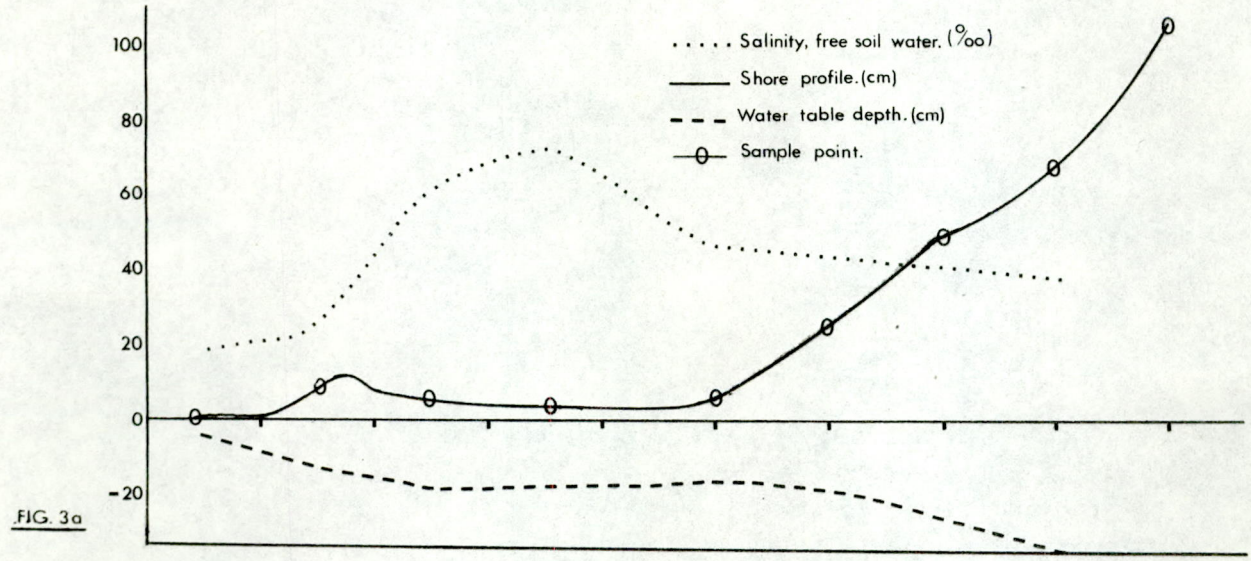


FIG. 3a

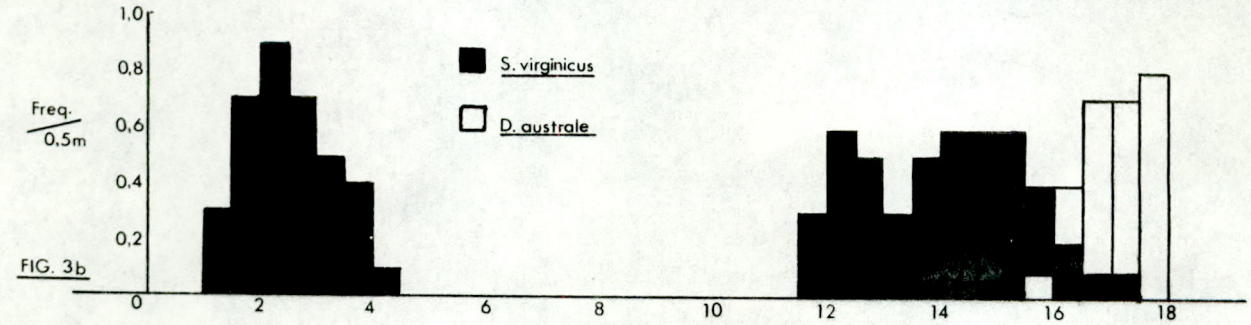


FIG. 3b

Distance from shore line. (m)

TRANSECT 3

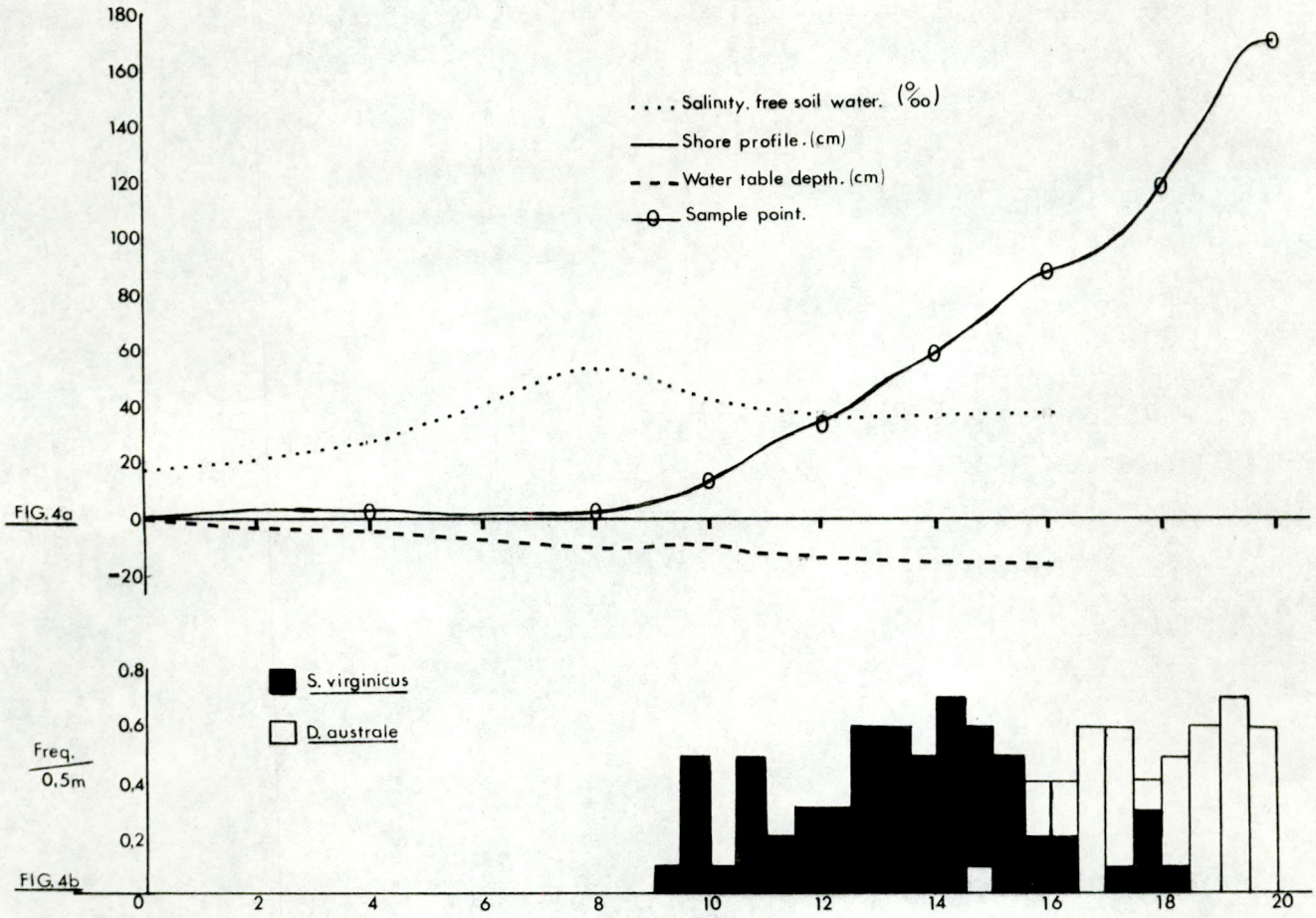


FIG. 4a

FIG. 4b

TRANSECT 4

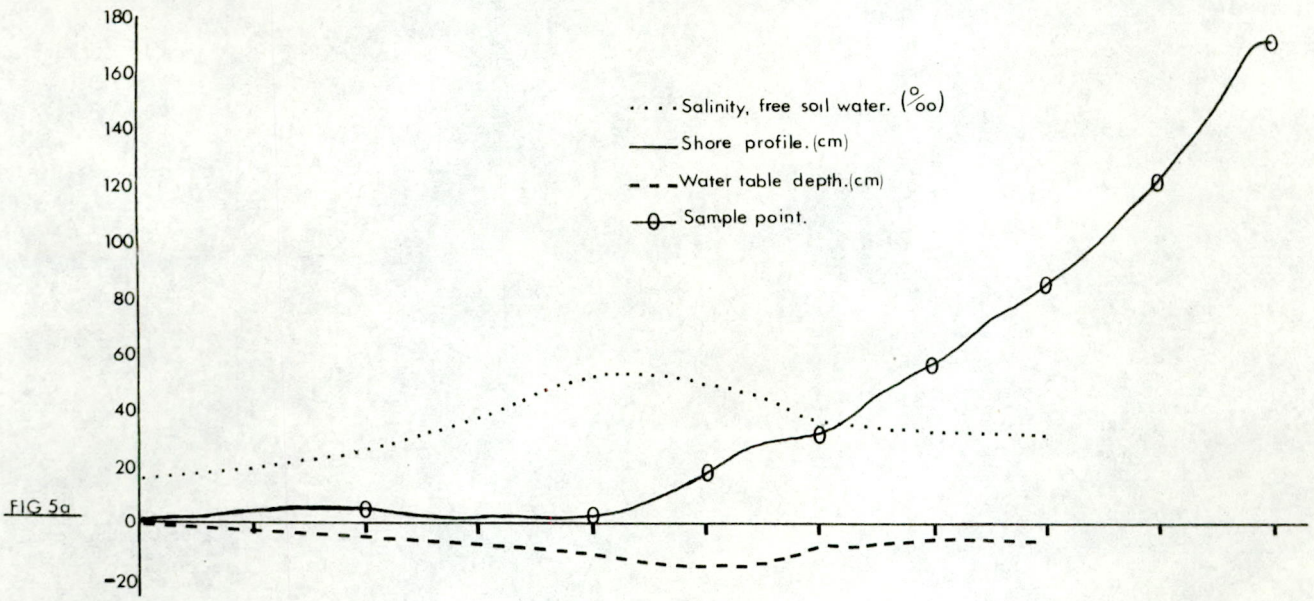


FIG. 5a

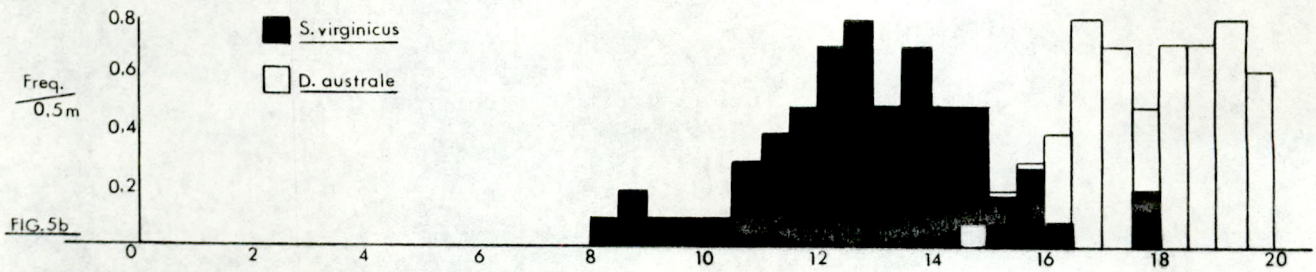


FIG. 5b

Distance from shore line (m)

the sole factor influencing the zonation of Sporobolus. Later in the investigation seedlings of the salt-tolerant Arthrocnemum natalense (Fam. Chenopodiaceae) appeared in this depression.

An important factor, not shown by the frequence data, is that the Sporobolus plants on both edges of this depression were highly stoloniferous. Short, 20 - 30 cm stolons, with low aerial shoots were growing towards the depression, along the surface of the soil.

In both transects 1 and 2 Dactyloctenium first occurred between 15,5 and 16 m from the water. This corresponded with a height above lake level of 70 cm (transect 1) and 67 cm (transect 2) respectively.

The change from pure stands of Sporobolus to those of Dactylocternium occurred over a very short distance and can probably be related to altitude. In transect 1 the distance was 1,5 m and the change in altitude from 70 cm to 88 cm while in transect 2 it was 2 m and from 67 cm to 88 cm respectively. It would appear therefore that height above lake level exerts a profound effect, either directly or indirectly on the zonation.

At Site 2 (Figs. 4a/b and 5a/b) the mud flat was completely bare of vegetation. A sandy "beach" which occurred between 8 m and 10,5 m and was colonised by criss-crossing stolons of Sporobolus that arose from erect growing plants established further up the transect (Plate 2a). Dactyloctenium first occurred between 14,5 m and 15 m in both transects 3 and 4. The corresponding altitudes were 73 cm and 75 cm respectively. When comparing the data of Sites 1 and 2 it is clear that it is altitude and not distance from the shore that is significant in the zonation.

The distribution of Sporobolus in these transects is discontinuous. The significance of the disappearance of Sporobolus at 80 cm above lake level and reappearance later is difficult to assess. It seems unlikely that this is related directly to height and its significance is therefore discussed later.

(iii) Water table depth, free soil water salinity and maximum root depth

Figures 2a and 3a illustrate the water table depth and free soil water salinity along transects 1 and 2 respectively.

The high salinity of the free soil water below the littoral pool is undoubtedly a result of accumulation of salt from repeated flooding and later, evaporation of water from this depression.

A fall in water table depth with respect to lake level can be expected with increasing distance from the shore. However, the results indicate that water table depth is also related to the salinity of the free soil water.

Figures 4a and 5a illustrate similar, but less marked, variations of these two parameters along transects 3 and 4 (Site 2) respectively. The less marked variations along these transects can be ascribed to the fact that the mud flat was more recently exposed and would be more frequently flooded. The maximum depths at which roots were found along all four transects are presented in Table I. This part of the investigation was considerably hampered by isolated rock patches in all transects and by the presence of tree roots in transects 3 and 4.

When this data is compared with water table depth along all transects (Figs. 2a, 3a, 4a and 5a) it is evident that the distribution and root penetration of Sporobolus is unaffected by this level. High free soil water salinities such as was found in the depression at Site 1 would however appear to prevent colonisation by Sporobolus (Figs. 2a/b and 3a/b).

At no point did the roots of Dactyloctenium reach the water table. Data for Site 2 are unreliable but at Site 1 a maximum depth of 45 cm was recorded at 14 m from the shore where both species were present. Assuming that Dactyloctenium roots reached this depth, the height above lake level of the lowest roots was 38 cm and 41 cm for transects 1 and 2 respectively. This again indicates the importance of altitude when assessing the factors influencing the zonation of these two grasses.

TABLE I Maximum depth (cm) at which roots were found in soil samples taken along transects 1 and 2 (Site 1) and 3 and 4 (Site 2)

Distance from shore (m)	SITE 1		SITE 2		Species present
	Trans. 1	Trans. 2	Trans. 3	Trans. 4	
0	50	-	-	-	S.v.
1	-	60†	-	-	S.v.
2	53†	-	-	-	S.v.
3	-	54†	-	-	S.v.
4	45†	-	-	-	S.v.
10	-	-	8	10	S.v.
12	30	44	50†	56	S.v.
14	33	40	65	78†*	S.v.
16	45	45	90*	90*	S.v. D.a.
18	42†	43†	97*	50*	D.a.
20	-		60*	50*	D.a.

KEY: † Indicates rock struck at this level but roots were still present.

* Tree roots also present in core samples therefore estimates highly unreliable.

S.v. Sporobolus virginicus

D.a. Dactyloctenium australe

One month after these first results were recorded the water level in the lake had dropped by 13 cm. On this occasion it was found that the water table depth for the first 12 m of transect 2 had dropped by a similar amount but that no change had occurred at 14 m from the shore line.

This confirms that the water table depth is directly related to the water level of the lake and that at least seasonal fluctuations of the latter are expressed in the former. Further the change in salinity of the free soil water ranged from an increase of 5 ppt at 0 m to one of 10 ppt at 12 m. This indicates that there is very little exchange between the lake and the free soil water.

(iv) Hours of shade and sunlight

Earlier in this report it was mentioned that Ward (1972) suggested that Sporobolus was intolerant of shade and also that Chippendall (in Meridith, 1955) refers to Dactyloctenium as a grass which "likes" shade.

It was found that the shadow thrown by the forest vegetation at transect 3 (Site 2) reached the point 16 m from the shore line (i.e. the approximate centre of the area occupied by both species) at about 13.00 hrs on the 14/7/74, and that by 13.45 hrs it had reached 8 m, which marks the start of the Sporobolus community.

This means that the latter community received between 6 and 7 hours' full sunlight out of a total of approximately 11 hrs for that day.

While no significance can be attached to this observation it is interesting to note that the Sporobolus plants representing the uppermost distribution of the species receive only half a day's full sunlight.

Clearly then, the effects of shading on Sporobolus and Dactyloctenium require investigation.

B. SOILS

(i) Mechanical properties and salinity

The mechanical properties and salinity of the soils from transect 1 (Site 1) and transect 3 (Site 2) are illustrated in Figures 5-9 and Figs. 10-12 respectively.

Those figures entitled "Untreated" (Figs. 6, 8, 10 and 11) present the silt and clay content of the respective soils as obtained by Method I (see section 2.1.2 (a)). That is the soils were not treated to facilitate maximum dispersion of particles during analysis.

Figure 7 illustrates the percentage silt and clay of the same samples illustrated in Figure 6 but after analysis by Method II during which the organic carbon, calcium carbonate and floculating ions were removed to determine their effect on dispersion.

When comparing these two figures it is evident that there was little change in the amounts of either silt or clay in the soils from the two extremes of transect 1 when analysed by Method II. There was, however, an almost complete reversal of silt and clay content of those samples taken from between 4 m and 12 m from the shore. Since these samples all had a relatively high salinity (Fig. 9) it would appear that floculating ions were the most important agents affecting dispersal in Method I.

The sudden rise in silt content of the soil at 14 m after complete dispersal (Fig. 7) should be attributed to experimental error since it is unlikely that more efficient dispersal would increase the amount of the heavier particles.

The silt and clay content of those soils taken from maximum root depth would undoubtedly show the same reversal as described above, when completely dispersed during analysis.

On the whole the mechanical properties of the soil do not appear to influence the zonation of Sporobolus and Dactyloctenium at Site 1.

The change in soil salinity along transect 1 (Fig. 9) does however show considerable correlation with the species distribution (Fig. 3b); firstly from a point of view of the high soil salinities found in the shallow depression between 4,5 and 10,5 m which is not colonised by either species and secondly, from the very low salinities recorded at 16 m and 18 m from the shore line which represents the distribution of the Dactyloctenium community.

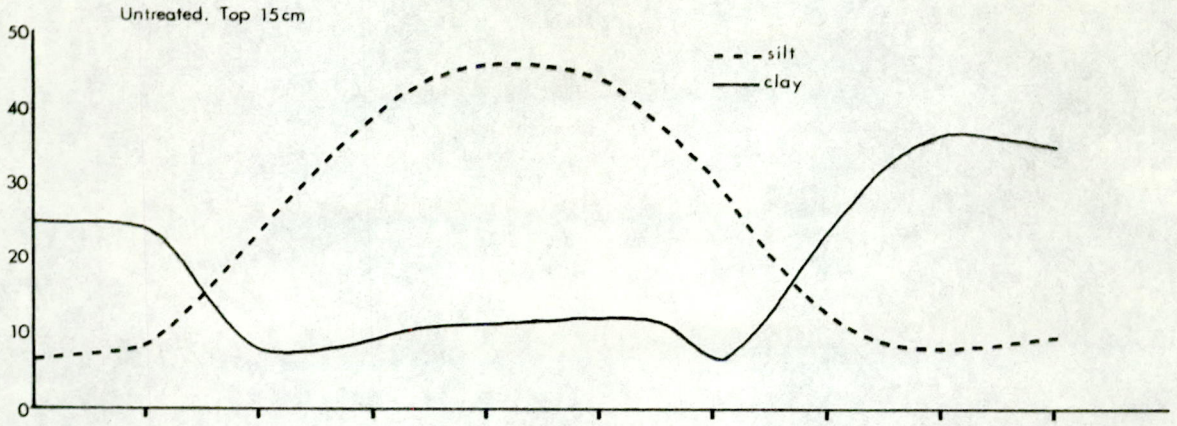


FIG. 6

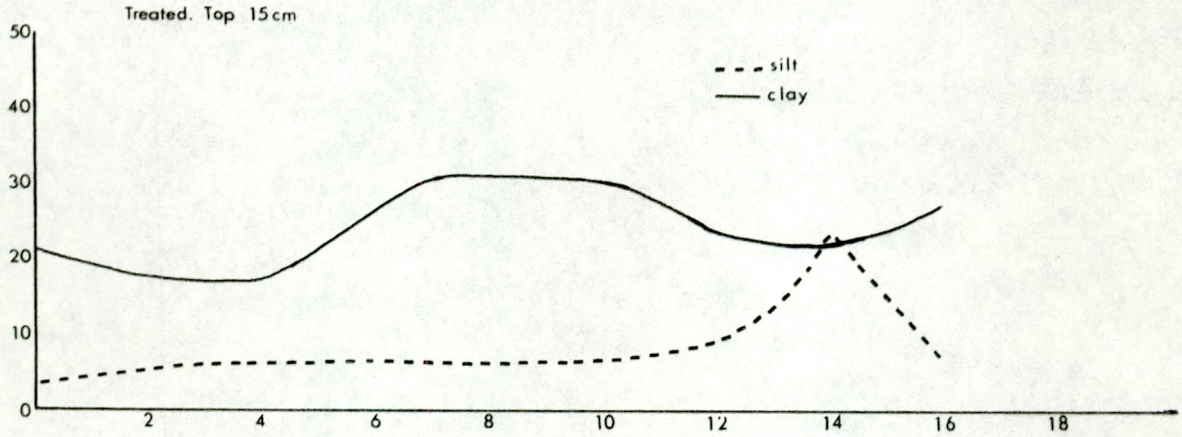


FIG. 7

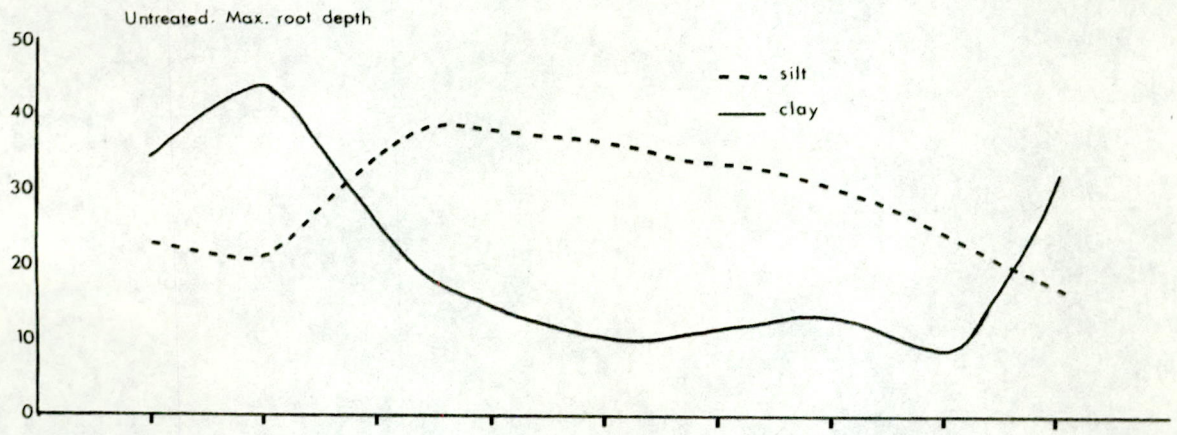


FIG. 8

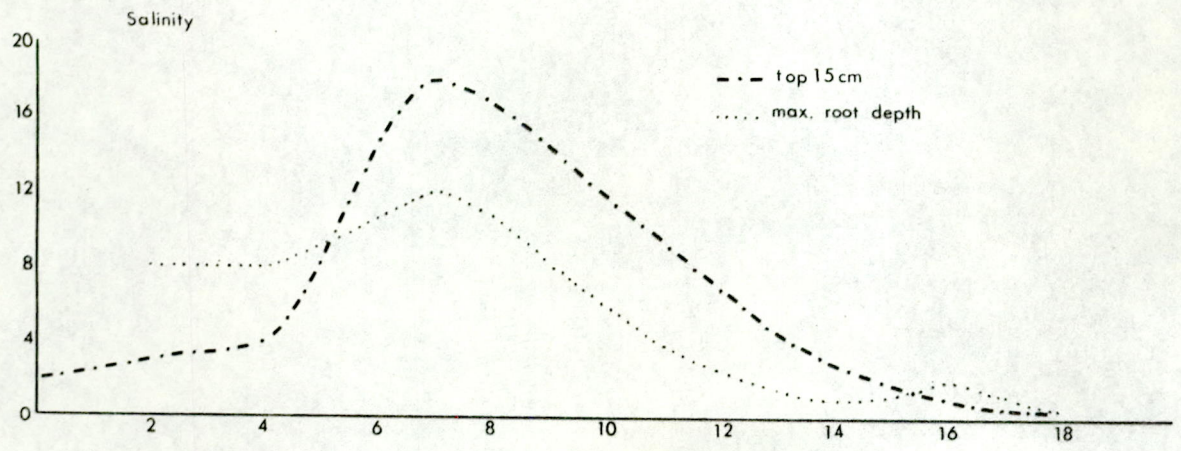


FIG. 9

Untreated. Top 15cm

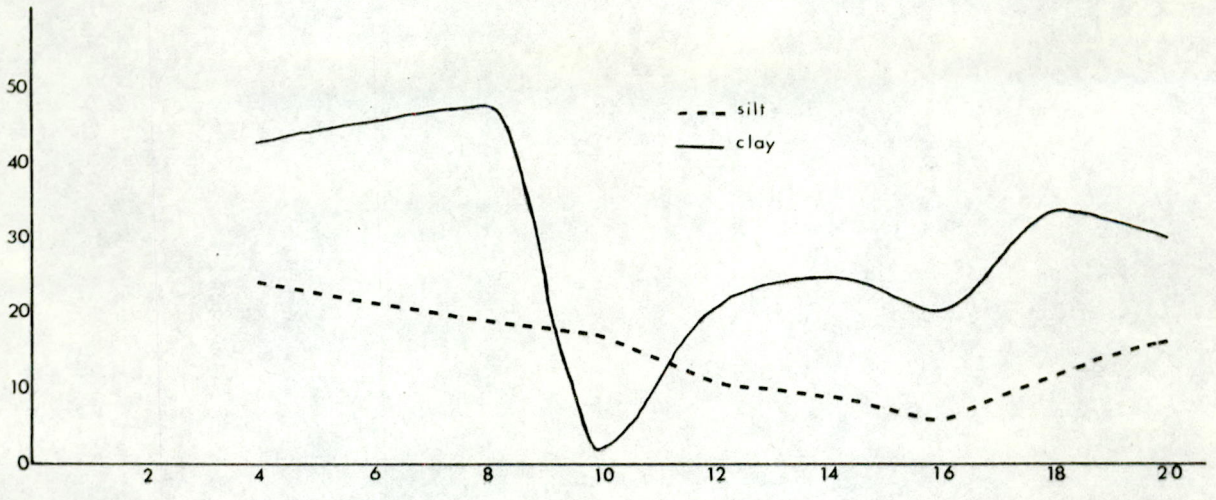


FIG.10

Untreated. Max root depth.

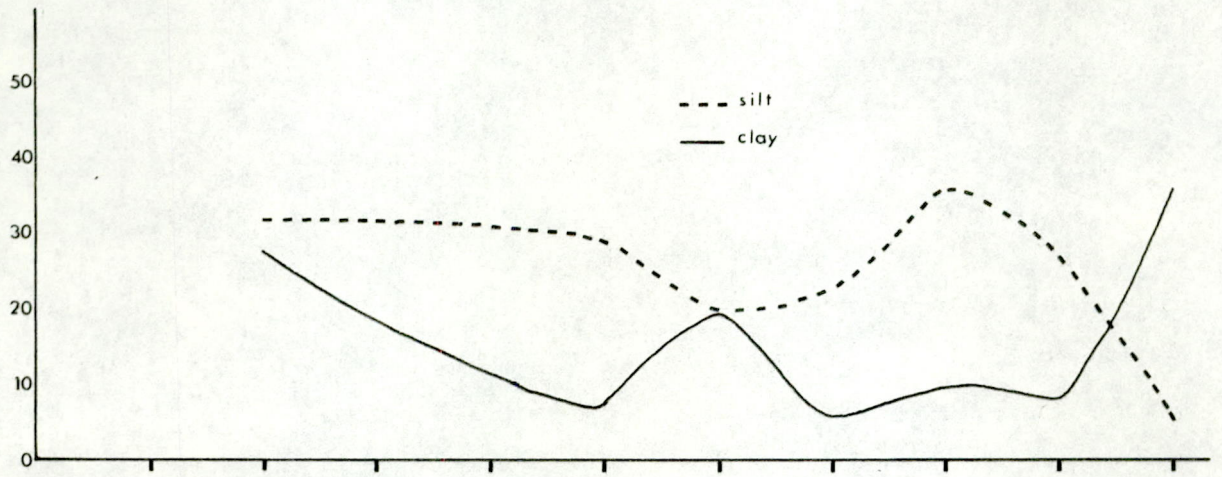


FIG.11

Salinity

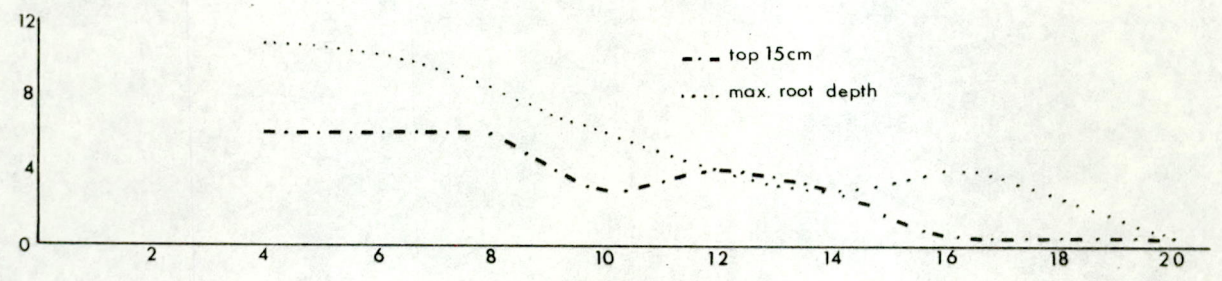


FIG.12

Distance from shore line (m)

The low salinities recorded for the top 15 cm of soil along transect 3 (Fig. 12) and the results obtained by Method I for the silt and clay content of these soils (Fig. 10) (i.e. high clay, low silt) make it unlikely that the treatment by Method II would alter these results to any great extent.

The low clay content of the soil at 10 m (Fig. 10) is to be expected since this point represents the sandy "beach" discussed in section A (ii).

The results for those samples taken at maximum root depth (Fig. 11) on the other hand are likely to show a similar reversal to that for transect 1 when analysed by Method II.

At 16 m from the shore line in transect 3 there is a marked drop in silt and clay content of the top 15 cm of soil (Fig. 10) and a corresponding increase at maximum root depth (Fig. 11). There is also an increase in soil salinity at maximum root depth (Fig. 12). This may relate in some way to the first disappearance of Sporobolus at 16,5 m from the shore line at Site 1.

The very low soil salinity between 16 m and 20 m (Fig. 11) from the shore line again suggests that salinity has a marked influence on the distribution of Dactyloctenium.

(ii) Calcium carbonate and organic carbon

The calcium carbonate contents of the soils from Site 1 are presented in Table II (i.e. wt $CaCO_3$/5 g and calcium carbonate %).

The data illustrate a very marked decrease in $CaCO_3$ at 16 m and 18 m from the shore line. This distance corresponds with the distribution of Dactyloctenium at this site (Figs. 2a/b and 3a/b).

While the total calcium carbonate content of the soil may influence zonation, it should be pointed out that most of the $CaCO_3$ at a distance of 14 m or less consists of particles of molusc shell which are easily visible with the naked eye. The amount of $CaCO_3$ available to the plants over this distance is therefore considerably less than shown by the results and might well be similar over the whole length of the site.

TABLE II Data used for the computation of organic carbon content of soil samples taken from Site 1. 5 g of soil was used for each determination. The wt. CO_2 lost = $\frac{44}{100}$ of the $CaCO_3$ present in 5 g of soil sample, i.e. in wt. $CaCO_3$/ 5 g

Distance from shore (m)	Wt. loss @ 550°C (g)	Wt. loss @ 950°C (g)	Total wt. loss (g)	Wt. $CaCO_3$/5g (g)	Wt. CO_2 lost (g)	Organic carbon (g)	Organic carbon (%)	Calcium carbonate (%)
0	0,385	0,050	0,435	0,186	0,082	0,354	7,07	3,72
2	0,295	0,054	0,349	0,262	0,115	0,337	6,74	5,24
4	0,385	0,074	0,459	0,281	0,123	0,447	8,94	5,61
7	0,560	0,121	0,681	0,253	0,111	0,570	11,40	5,06
10	0,405	0,071	0,476	0,320	0,141	0,463	9,25	6,40
12	0,370	0,126	0,496	0,369	0,162	0,480	9,59	7,38
14	0,264	0,104	0,368	0,293	0,129	0,355	7,09	5,86
16	0,357	0,038	0,385	0,170	0,008	0,388	7,75	0,32
18	0,373	0,052	0,425	0,031	0,014	0,412	8,23	0,63

The percentage organic carbon of the soils, also presented in Table II, would not appear to influence the zonation of the grasses.

The validity of these results, is however questionable.

Replicate samples ignited at 950°C produced no gas (CO_2) when tested in the Collins calcimeter. This indicates that all $CaCO_3$ had been combusted. However, those replicate samples ignited at 550°C evolved gas when tested, but, the volume of this gas was insufficient to account for the second loss of weight after ignition at 950°C.

This indicates that: (1) certainly not all carbonate was combusted at 550°C; (2) possibly not all organic carbon was combusted at 550°C; or (3) combustion of other compounds, not accounted for, occurred at 950°C.

The technique used to determine organic carbon should therefore be revised. It is suggested that the time allowed for combustion at 550°C be extended to possibly as long as 36 hrs as opposed to 4 hrs, and that no combustion at 950°C be used.

C. PLANT SAMPLES

(i) Metal cation content

The results of the analysis of plant samples for sodium (Na^+), potassium (K^+), calcium (Ca^{++}) and magnesium (Mg^{++}) are presented in Table III.

The prime objective of this experiment was to determine the sodium content of the grasses at intervals along both sites and to compare this with the salinity of the soil.

In general the salinity of the soils, where plants of one or other grass species were established decreased with increasing distance from the shore. While the sodium content of both Sporobolus and Dactyloctenium also show such a decrease, the values for the latter are in general higher than those for Sporobolus. This is particularly evident where both species are represented at the same point.

TABLE III The sodium (Na^+), potassium (K^+), calcium (Ca^{++}) and magnesium (Mg^{++}) content of plant samples collected at Sites 1 and 2. Results expressed in parts per million

Distance from shore (m)	Species	Sodium	Potassium	Calcium	Magnesium
S I T E 1					
2	S.v.	9 320	8 120	3 840	2 440
4	S.v.	8 080	7 880	4 136	2 520
14	S.v.	7 880	7 880	4 464	2 200
16	S.v.	6 920	7 000	2 480	3 680
16	D.a.	11 760	14 400	4 040	3 952
18	D.a.	9 720	11 600	3 920	3 480
S I T E 2					
10	S.v.	15 150	74 000	4 400	5 800
12	S.v.	12 120	67 200	3 824	3 280
14	S.v.	11 840	9 800	3 264	2 120
16	S.v.	13 520	12 600	5 040	1 720
18	S.v.	8 400	7 600	3 780	2 960
16	D.a.	12 000	36 000	3 720	3 208
18	D.a.	13 040	33 600	5 280	3 728
20	D.a.	11 400	32 800	4 600	3 240

KEY: S.v. *Sporobolus virginicus*
D.a. *Dactyloctenium australe*

At 16 m in Site 2 however, Sporobolus shows an increase in sodium content. This corresponds with an increase in soil salinity at maximum root depth at this point (Fig. 12). The value for sodium in Dactyloctenium at this point is lower than that for Sporobolus. This is further evidence that the discontinuous distribution of Sporobolus at Site 2 is not directly related to altitude.

The results also show that the potassium content of both species is closely related to that of sodium, while the calcium and magnesium contents are more variable.

These results indicate that Sporobolus has some mechanicm, which is at least more efficient than any in Dactyloctenium, whereby the sodium concentration within the aerial parts of the plant is maintained at a relatively low level.

This is also further evidence that salinity has considerable influence on the zonation of these two grasses.

(ii) Dry weight/fresh weight percentages

While fresh weight represents the whole system of a living plant, dry weight provides a measure of the amount of reduced carbon units which have been used in building up this total structure. Variations in these reduced carbon units for a given fresh weight can therefore yield information on the conditions of growth (Evans, 1972).

The dry weight of plant samples collected at Lister Point was therefore expressed as a percentage of the fresh weight to obtain an index which could be related to conditions found at Sites 1 and 2. This data is presented in Table IV along with the average salinity of the soil at the surface and at maximum root depth, and the average altitude of the points between which the samples were collected - (e.g. at Site 2 the average altitude for 16 m on transects 3 and 4 was calculated).

From the above discussion it can be seen that plants with a low percentage value contain relatively less reduced carbon units and more water than those with a high percentage value. However as nothing is known of the water relations of

TABLE IV The relationships between the dry weight/fresh weight percentage ($^{Dw}/_{Fw}$ %) of plant samples collected at Sites 1 and 2, and the average soil salinity and altitude of the respective sample points

Distance from shore (m)	Species	$^{Dw}/_{Fw}$ %	Soil salinity (ppt)	Altitude (cm)
S I T E 1				
2	S.v.	38,4	5,50	6,5
4	S.v.	44,1	6,00	4,0
14	S.v.	38,4	2,00	53,5
16	S.v.	37,3	1,50	77,5
16	D.a.	25,6	1,50	77,5
18	D.a.	24,9	0,50	107,0
S I T E 2				
10	S.v.	20,4	4,50	15,5
12	S.v.	25,7	4,00	33,0
14	S.v.	39,5	3,00	59,5
16	S.v.	37,1	2,25	86,0
18	S.v.	44,5	1,15	121,0
16	D.a.	29,0	2,25	86,0
18	D.a.	32,0	1,50	121,0
20	D.a.	34,8	0,50	170,0

KEY: S.v. = Sporobolus virginicus
D.a. = Dactyloctenium australe

either grass species it is impossible to say what percentage level signifies good, or on the other hand adverse, conditions for growth.

From Table IV it will be seen that there is little correlation between the data presented for Site 1, while at Site 2 an increase in dry weight/fresh weight percentage was associated with both a decrease in salinity and an increase in altitude.

On the date of collection of plant samples from Site 1, light rain had fallen for about 3 hrs before harvesting. Since the dry weight/fresh weight percentage is intimately related to the water status of the plant at the time of harvest, it is possible that this affected the results.

The data from Site 2 however, add further evidence to the fact that salinity and altitude are important factors affecting the zonation of Sporobolus and Dactyloctenium.

A further point of interest is the slightly lower percentage value for Sporobolus at 16 m in Site 2. This indicates that there is indeed some factor or group of factors causing the first disappearance of Sporobolus and that these are related to growth in some way.

D. GERMINATION

The percent germination of Dactyloctenium under all conditions described in section 3.1 (p. 13) was extremely low.

Germination of 3,3% was obtained in soil under greenhouse conditions. Under all other conditions germination was approximately 1%.

No germination occurred when a 2 cm^3 piece of fresh apple was introduced into the petri dish in an attempt to increase the ethylene concentration of the atmosphere.

An attempt at scarification of the seeds was made by shaking them mechanically, at high speed, in a specimen tube containing acid-washed sand for periods of 1, 2, 4 and 8 minutes. Whether or not scarification was successful was not determined; however no increase in germination above the 1% level was obtained.

Further, it was necessary to store the seed in a frozen state to prevent total loss of viability.

It would appear therefore that while Dactyloctenium flowers prolifically and produces abundant seed, (field observations) the seed has an extremely low viability.

Sporobolus seeds had a high percentage germination in soil under greenhouse conditions (86%) and on the laboratory bench (83,5% in tap water). No germination took place under all other conditions. It would appear therefore that Sporobolus seeds require alternating dark and light conditions for germination.

Since evaporation of water from the seed containers was extremely rapid in the greenhouse, the effects of salinity on germination were tested on the laboratory bench. These results are presented in Table V.

While the germination of Dactyloctenium seeds was still very low the data indicate that they show tolerance of only very low salt concentrations and that concentrations above 10 ppt cause total loss of viability.

Sporobolus seeds however still exhibit some germination (0,5%) at a salt concentration of 20 ppt and the viability of the seeds is not appreciably affected by exposure to concentrations of up to 40 ppt. The seeds were exposed to these concentrations for 7 days before transference to tap water.

Even exposure to a salinity of 110 ppt, the highest salinity known to have been attained at Lister Point in recent years (Hutchenson, 1974), did not cause total loss of viability.

During the course of this experiment it was observed that the outer covering surrounding those seeds which germinated in tap and distilled water became extended and a clear gelatinous substance formed between this covering and the seed. Although no definite count was made, the number of seeds which exhibited this phenomenon were observed to decrease along with the germination in the salt treatments. Furthermore, no seeds which were treated with salt solutions of 30 ppt or higher exhibited this, until they were transferred to tap water, whereupon formation of this gelatinous substance again occurred only around those

TABLE V Germination of Sporobolus and Dactyloctenium seeds in solutions of varying salt concentrations, and after transfer to tap water of those seeds which did not germinate in the initial treatment. All results expressed as a percentage of the total number of seeds used per initial treatment

Initial treatment	% GERMINATION					
	Sporobolus			Dactyloctenium		
	Initial	Tap water	Total	Initial	Tap water	Total
Distilled water	78,5	//	78,5	1,0	//	1,0
Tap water	83,5	//	83,5	1,0	//	1,0
Salt 5 ppt	59,5	12,5	72,5	0,5	-	0,5
10	46,0	42,0	88,0	-	0,5	0,5
15	14,5	58,5	73,0	-	-	-
20	0,5	89,5	90,0	-	-	-
30	-	87,0	87,0	-	-	-
40	-	75,0	75,0	-	-	-
60	-	49,0	49,0	-	-	-
80	-	36,0	36,0	-	-	-
110	-	29,0	29,0	-	-	-

KEY: // Not transferred

seeds which eventually germinated.

It is suggested that this outer covering acts as a semipermeable membrane, so protecting the seed from the high salinities surrounding it and also preventing germination under conditions which would be adverse to seedling growth.

E. INUNDATION OF SEEDLINGS

Since water levels in False Bay show considerable fluctuations on both short- and long-term bases, inundation of plants, particularly seedlings, with saline water is an important factor to consider in relation to colonisation of exposed shores such as the mud flat found at Site 2.

This experiment was carried out with the aim of determining the resistance of Sporobolus and Dactyloctenium seedlings to permanent, but not periodic, inundation with saline solutions of various concentrations.

The inundation of the seedlings began at 10.00 hrs on the first day. By the afternoon of the second day large salt crystals had formed on the leaves of the majority of seedlings in the 30, 40, 60 and 80 ppt salt solutions. These are illustrated in Plate 3. Droplets of saline water (to the taste) were present on the leaves of those seedlings in 10 and 20 ppt solutions, while there was no evidence of either water or salt on the leaves of the seedlings in distilled water or any Dactyloctenium seedlings.

The result of inundation was that from the third day on, the leaves of those Sporobolus seedlings in 30 - 80 ppt and those Dactyloctenium seedlings in 20 and 30 ppt salt solutions became progressively more necrotic, until on the 7th day all plants in these solutions were dead.

At this stage two of the three seedlings of Dactyloctenium in the 10 ppt solution were dead and the third exhibited considerable anthrocyanin formation.

The Sporobolus seedlings in 10 and 20 ppt salt showed necrosis of the tips of the youngest leaves on the 7th day and water droplets were still forming on the leaves in the afternoons. While these seedlings showed no increase in height, those in the distilled water had grown approximately 1 cm and showed no signs of

PLATE 3 Salt crystals on the leaves of a seedling of Sporobolus virginicus which had been inundated with a solution of 40 ppt salt (x5)

being affected by inundation.

No further change in the amount of necrosis of any seedlings had occurred after a further week of inundation. It was assumed at this stage that the Sporobolus seedlings would survive indefinitely, or at least for a considerable length of time, in solutions of up to 20 ppt salt and they were therefore harvested for fresh and dry weight determinations.

The results of these determinations and the analysis of seedlings for sodium (Na^{+}), potassium (K^{+}), calcium (Ca^{++}) and magnesium (Mg^{++}) content are presented in Table VI.

The state of the plants at the start of the experiment is illustrated by the data obtained from 40 seedlings harvested before inundation began.

The dry weights of each group of 40 seedlings after completion of the experiment, indicate that only those seedlings inundated with distilled water showed significant growth during the experiment. The dry weight/fresh weight percentages of these latter seedlings are similar to that of the seedlings harvested before inundation while that of the seedlings inundated with salt solutions is somewhat higher. This would indicate that increased water uptake is associated with increased salinity of the substrate and not moisture content (of substrate). Further, since seedlings inundated with salt solutions were observed to secrete saline water droplets, the increased turgidity appears to be related to secretion of excess salt. This data should not be compared with that for the plant samples collected in the field however, since not only were the conditions of growth entirely different but there is also a considerable age difference.

The increased sodium content of the plants with increased salinity of the substrate (Table VI) (the distilled water would leach salts from the soil so that the salinity or sodium concentration would be less than before inundation) suggests that there is no barrier, mechanical or physiological, to the absorption of salt by the roots and that absorption is entirely passive.

The potassium content, while greater than both that of calcium and magnesium for all treatments, does not appear to be related to the sodium content as was

TABLE VI Data obtained from Sporobolus seedlings harvested before and after inundation with various concentrations of saline water. The sodium (Na^+), potassium (K^+), calcium (Ca^{++}) and magnesium (Mg^{++}) contents of the respective harvests are expressed in parts per million. $^{Dw}/_{Fw}$ % refers to the dry weight/fresh weight percentage

Treatment	Fresh wt. (g)	Dry wt.)g)	$^{Dw}/_{Fw}$ %	Sodium	Potassium	Calcium	Magnesium
Before inundation	0,088	0,023	25,7	7 610	22 666	3716	3362
Distilled water	0,253	0,086	24,0	3 446	17 757	1397	1368
10 ppt salt	0,127	0,037	29,2	17 520	17 520	5889	1994
20 ppt salt	0,114	0,032	28,2	34 567	10 802	1666	1944

the case with the plant samples collected in the field. The fact that Sporobolus seedlings did not survive in salt concentrations of higher than 20 ppt enhances the credibility of the suggestion (p. 34) that the outer covering of the seed of this species prevents germination under unfavourable conditions for seed growth.

F. SALT GLANDS

Small glandular structures resembling the salt glands described by Liphschitz and Waisel (1974) for Sporobolus arenarius and Dactyloctenium aegyptium were found in both S. virginicus and D. australe.

The small (0,04 mm) glands in D. australe (Plate 4) were not conclusively shown to be salt glands since no plant which had not been treated with salt was available. However, since there was no evidence of salt secretion during inundation of seedlings with saline water, it would appear that if these structures are salt glands, their efficiency is low.

Plate 5 illustrates the general structure of the leaf of a Sporobolus plant which had received no salt treatment. The leaf is strongly ridged on the adaxial surface and numerous papillae are located on the sides and apices of these ridges. One of these papillae (arrowed) is considerably longer than the rest and is flanked by two others which are also large. These are shown at a higher magnification in Plate 6 and it can be seen that the longest papilla is only lightly cuticularised.

All papillae, but particularly the longer ones described above, appear swollen and apparently fully turgid in sections from plants which were watered with a strong saline solution. Plate 7 illustrates one ridge of a leaf on which these swollen papillae are evident.

In the previous section (p. 36) it was suggested that the increased water content (turgidity) of seedlings inundated with saline solutions was associated with secretion of excess salt. Furthermore, salt crystals were observed to have formed along the furrows between the ridges of other leaves of the same plant used in this investigation.

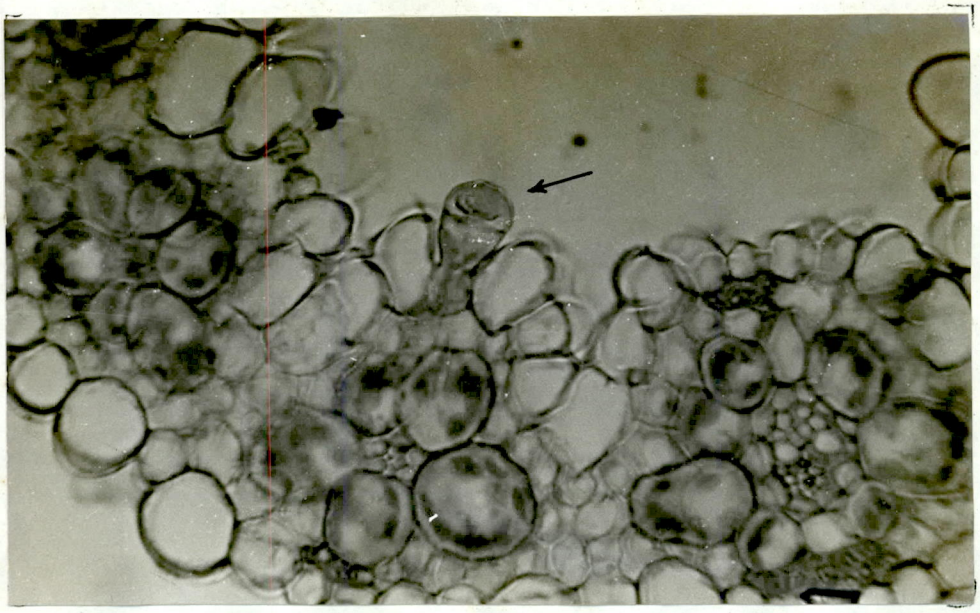


PLATE 4 A small two-celled gland (arrowed) probably a salt gland, in the adaxial epidermis of a leaf of Dactyloctenium australe (x350)

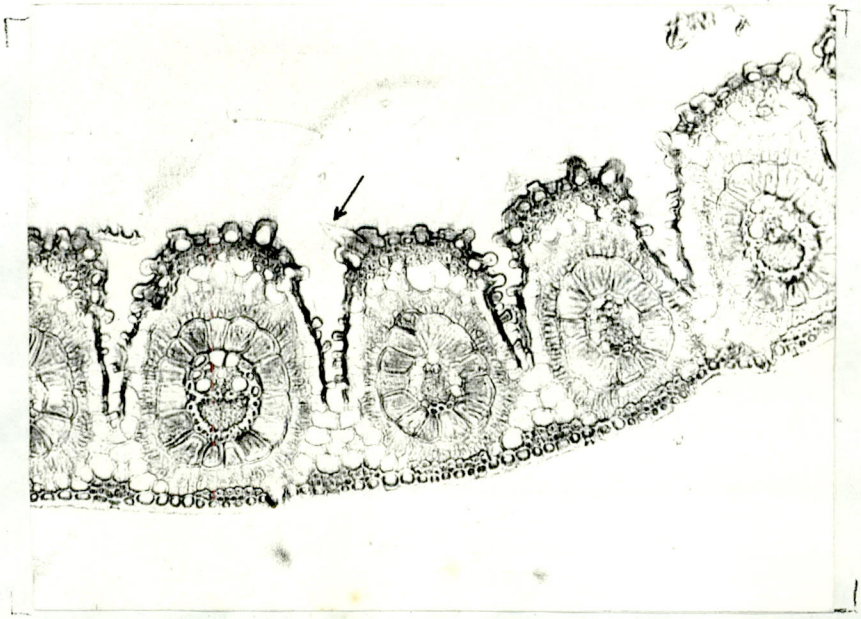


PLATE 5 A section of a leaf of Sporobolus virginicus showing the ridged adaxial surface, the numerous epidermal papillae and one much larger, lightly cuticularised papilla (arrowed) (x100)

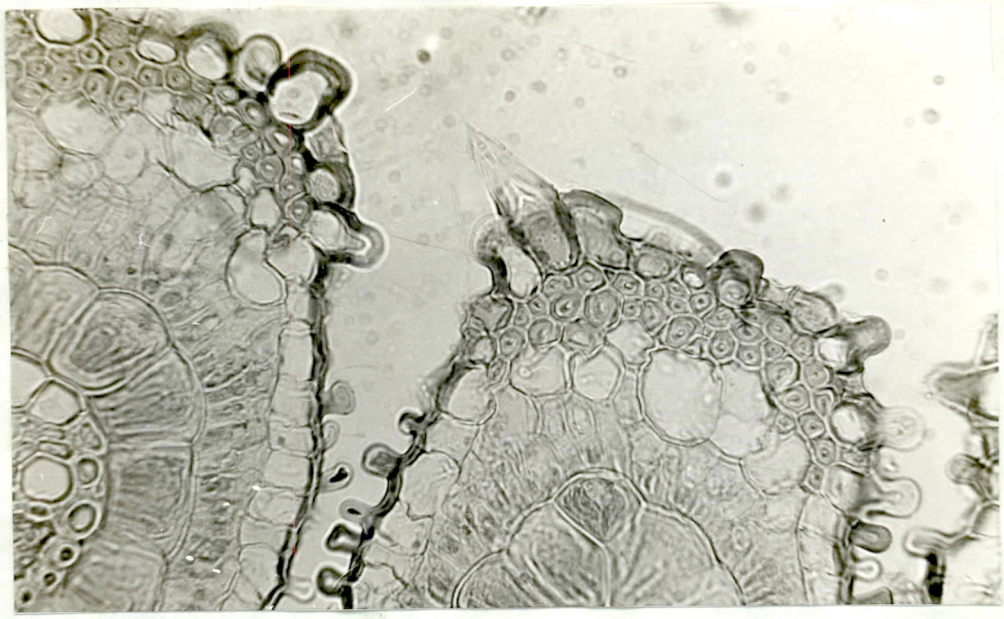


PLATE 6 The large papilla shown in Plate 5 at a greater magnification (x350). Note the two papillae flanking it. The plant from which this section was obtained had been watered with tap water only

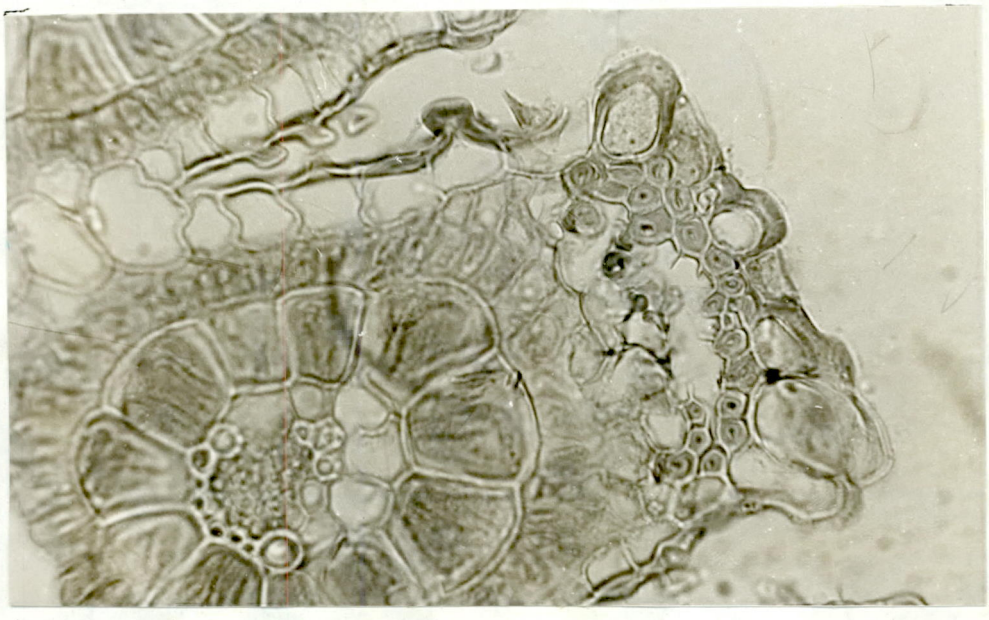


PLATE 7 Three papillae in the adaxial epidermis of a leaf Sporobolus virginicus taken from a plant which had been watered with a strong salt solution. Note how much more turgid are these papillae than those shown in Plate 6 (x350)

It can therefore be safely concluded that these large papillae do in fact act as salt secreting organs.

GENERAL DISCUSSION

The information presented thus far clearly indicates that, of those aspects of the environment studied, height above lake level (altitude) and soil salinity are the most important factors influencing the zonation of Sporobolus and Dactyloctenium on the northern shores of Lister Point. Not only did the species distribution, along the four transects studied, show remarkable correlation with these two factors but the dry weight/fresh weight percentages of plant samples collected at Site 2, clearly indicate that the salinity and altitude relate to both the water status and growth of the plants.

As mentioned in the introduction to this report both the level and salinity of the water in False Bay fluctuate considerably. The fluctuations in level over the past 12 years are presented in Table VII. All water levels relate to a datum, the mean estuary level (MEL) established by the South African Department of Water Affairs for a point in the St Lucia estuary 500 m from the sea (Hutchenson, 1974).

The water level at the time field studies took place was 7 cm above MEL (Bloc, 1974; pers. comm.). From Table VII it can be seen that while the water level may remain well below this for periods of up to 2 years it does show sudden increases of variable magnitude. As recently as February 1972 the level rose to 76 cm above MEL, in other words, 69 cm above the level at the time of field studies. This shows a very close correlation with the first appearance of Dactyloctenium plants along the transects at both study sites. The altitude of these occurrences ranged between 67 cm (transect 2) and 75 cm (transect 4).

It will be recalled that the salinity of the surface soil colonised by Dactyloctenium (i.e. altitude above 67 cm) was 0,5 ppt in all cases, while at lower altitudes, where Sporobolus was present, it was at all times higher and showed a general increase towards the shoreline. Since the salinity of the soil at altitudes above that reached in February 1972 was uniform, the general increase at lower altitudes can be attributed, at least partly, to this period of

TABLE VII Water levels at Lister Point. Figures for 1963-72 are the water level at the end of the month after Hutcheneon (1974). Figures for 1973-74 are the average level for the month (except for July '74 - see below) after Bloe (1974). All figures are relevant to the mean estuary level (MEL) and are given in cm

YEAR	JAN	FEB	MAR	APR	MAY	JUN	JULY	AUG	SEP	OCT	NOV	DEC
1963	†	†	†	†	†	†	†	58	25	†	-3	-3
1964	18	9	0	15	31	20	18	9	†	0	-12	-17
1965	-23	-27	-35	-33	-33	-23	-21	-17	†	-4	-9	-18
1966	-6	15	-3	-4	-7	-11	-15	-17	-26	-33	-39	-44
1967	-43	-33	-20	-1	3	2	3	-7	-7	-7	-15	†
1968	-36	-33	†	-23	-21	-15	-17	-18	-20	-23	-21	-35
1969	-38	-44	11	†	12	12	17	†	-17	-3	†	-17
1970	-30	-36	-36	†	†	-36	-39	†	†	-33	-23	-36
1971	-26	-18	-15	-17	-1	-7	-9	-11	-17	†	-21	-12
1972	-1	76	61	28	34	†	15	6	-18	†	†	†
1973	†	†	†	†	†	†	-16	-9	-12	31	19	21
1974	17	16	11	11	12	12	7*	†	†	†	†	†

KEY: † Indicates missing data

* Level at time of field studies, i.e. 7 July 1974

inundation when the salinity of the lake water was 23 ppt.

The rise in water level in 1972 would appear therefore to have greatly influenced the observed zonation of Sporobolus and Dactyloctenium.

Investigations performed during this study have clearly illustrated that Sporobolus is tolerant of far higher salinities than is Dactyloctenium. This applies not only to adult plants, but also to seedlings and the germination of seeds. Further, since there is apparently no mechanical or physiological barrier to sodium uptake by the roots, this higher salinity tolerance can be attributed to the greater number and probably greater efficiency of salt glands in the leaves.

This tolerance enables Sporobolus to colonise muddy saline shores, such as at Site 2, which are exposed at low lake levels. Once colonisation has begun the plants would act as silt traps, with the result that a low bank, enclosing an impermanent littoral pool or depression such as is seen at Site 1, would develop.

The presence of Arthrocnemum natalense in this particular depression (i.e. at Site 1) might indicate that this species acts as the primary coloniser of exposed shores ahead of Sporobolus. However, no A. natalense plants were observed growing in any area exposed to wave action, and further, Ward (1971) reports that, at the Isipingo estuary, Natal, this species becomes dominant where the substrate is muddy and experiences long periods of dryness, but it is not tolerant of prolonged periods of inundation, particularly if the water is saline. It is therefore unlikely that A. natalense plays a major role in the colonisation of exposed shores which would be frequently inundated by saline lake waters.

Sporobolus can without a doubt be classified as a halophyte, but it would not necessarily appear to be an obligate halophyte since; adult plants were grown successfully in Umgeni sand and only watered with tap water (section F); seedlings inundated with distilled water exhibited more growth than those inundated with salt solutions; and a greater percentage germination of seeds occurred in tap water than in a 5 ppt salt solution.

The disappearance of Sporobolus at higher altitudes should therefore not be attributed to a decrease in soil salinity or to less frequent inundation, but to some other factor; probably the inability of this species to compete with Dactyloctenium under conditions apparently favourable for both species. It will be recalled that Ward (1971) described Sporobolus as being unable to compete with other sand-dune pioneers at Isipingo.

The relatively short distance over which competition between the two species occurred and the fact that conditions in the areas where Dactyloctenium formed pure stands were not shown to be in any way adverse with regard to Sporobolus, indicate that some factor such as competition or shade, prevents the establishment of Sporobolus plants at higher altitudes.

However, that there may be an, or a group of, environmental factors associated with the disappearance of Sporobolus is indicated by the apparent reappearance of this species at Site 2, although the reasons for this cannot be pinpointed.

While Dactyloctenium extends well into the forest vegetation the factor preventing establishment at lower altitudes than those observed, is undoubtedly its inability to survive under saline conditions.

CONCLUSION

Sporobolus virginicus was found to be confined to the immediate shore line (i.e. low altitudes) of the northern shores of Lister Point, while the distribution of Dactyloctenium australe which occurred inland (i.e. at higher altitudes) of the Sporobolus communities, extended into the forest vegetation. Both grass species occurred in pure stands and the distance over which competition between them took place was very short (± 2 m).

The most important environmental factors affecting the zonation of Sporobolus and Dactyloctenium are altitude and soil salinity. These two factors are most probably related to the high lake water level attained in February 1972.

Sporobolus has a higher tolerance of salinity than does Dactyloctenium and acts as the primary coloniser of exposed shores. Very high salinities such as are found in the impermanent littoral pool at Site 1, do however, appear to prevent colonisation by Sporobolus.

While the restriction of Dactyloctenium to the higher altitudes can undoubtedly be attributed to lack of tolerance of both saline soils and inundation with saline water, no definite conclusions could be made as to the factor(s) restricting Sporobolus to the lower altitudes.

REFERENCES

BAVER, L. D. 1956. Soil Physics. Wiley and Sons Inc., New York.

BAYER, A. W. & TINLEY, K. L. 1966. The Vegetation of the St Lucia Lake area, in, Report of the Commission of Inquiry into the alleged threat to Animal and Plant Life in St Lucia Lake, 1964 - 1966.

EVANS, G. C. 1972. The Quantitative Analysis of Plant Growth. Blackwell Sci. Pub., Oxford.

HUTCHENSON, I. P. G. 1974. St Lucia Lake Research Report. Vol. 2; St Lucia Lake and Estuary Hydrographic Data. Hydrological Research Unit, Univ. of Witwatersrand, South Africa.

JACKSON, M. L. 1965. Soil Chemical Analysis. Prentice Hall Inc., N.J., U.S.A.

KRIEL, J. P. 1966. Report on the Hydrology of the St Lucia Lake System, in, Report of the Commission of Inquiry into the alleged threat to Animal and Plant Life in St Lucia Lake, 1964 - 1966.

LIPHSCHITZ, N. & WAISEL, Y. 1974. Existence of Salt Glands in various Genera of the Graminae. New Phytol. 73, 507 - 513.

MERIDITH, D. 1955. (Ed.). The Grasses and Pastures of South Africa. CNA, South Africa.

TRUSWELL, J. F. 1970. An Introduction to the Historical Geology of South Africa. Purnell, Cape Town.

WARD, C. J. 1971. The Plant Ecology of the Isipingo Beach area, Natal, South Africa. M.Sc. Thesis, Dept. of Botany, Univ. of Natal, South Africa.

WHITE, W. S. & WETZEL, R. G. 1973. A modified Sedimentation Trap. J. of Limnol. and Ocean. 18, 986 - 988.

APPENDIX I

MECHANICAL ANALYSIS OF SOIL SAMPLES: METHOD I
PROCEDURE FOR THE BOUYOUCOS HYDROMETER METHOD FOR SILT AND CLAY

50 g of oven-dried (105°C), sieved soil were transferred to a high speed mixer containing 200 ml of distilled water and 15 ml of 0.5 N sodium oxalate, and mixed for 20 mins to disperse the soil.

The suspension was then washed into a Bouyoucos sedimentation cylinder and diluted to the lower mark, with the hydrometer in the liquid. The hydrometer was removed and the suspension mixed by closing the mouth of the cylinder and shaking well for a few seconds. The cylinder was then placed on the bench and the time of commencement of sedimentation noted.

The percentage of silt plus clay in suspension was determined by noting the hydrometer reading after 5 mins of sedimentation had taken place. The percentage of clay in suspension was determined by noting the hydrometer reading after 5 hours' sedimentation. To make these readings the hydrometer was carefully introduced into the suspension 20 - 30 seconds before the pre-determined time. When frothing at the surface of the suspension made it difficult to read the scale, two drops of teepol were added to break the froth.

The temperature of the suspension was taken at both 5 mins and 5 hrs. Since the hydrometer is adjusted for a temperature of 19.4°C a correction was made by adding 0.3 units to the scale reading for every degree above 19.4°C or subtracting the same amount for every degree below. The values so obtained correspond directly to the percentage of silt plus clay and clay alone in the oven-dried soil, if 100 g of soil was used. However, since only 50 g of oven-dried soil was used the corrected scale readings were multiplied by 2.

APPENDIX II

MECHANICAL ANALYSIS OF SOIL SAMPLES: METHOD II
SILT AND CLAY DETERMINATIONS
BY THE BOUYOUCOS HYDROMETER METHOD AFTER
REMOVAL OF CALCIUM CARBONATE, ORGANIC MATTER
AND FLOCULATING SALTS

0,5 N HCl was added to 50 g of oven-dried, sieved soil in a 250 ml Erlinmeyer flask in 10 ml aliquots until no further reaction took place. This removed the carbonates from the sample.

Organic material was removed by oxidation with H_2O_2 (30 vols) to CO_2.

A 10 ml aliquot of H_2O_2 was added to the above acid medium. This addition was made with caution since the reaction was apt to be very vigorous. The flask was then transferred to a waterbath at 90°C until the reaction was complete. Further 10 ml aliquots of H_2O_2 were added until no further reaction took place. The solution was then made up to 250 ml with distilled water and placed on one side to cool and allow the soil particles to settle.

To remove the majority of dissolved (floculating) salts, the supernate was pipetted off and centrifuged at 2000 g for 5 mins. The resulting supernate was discarded and the centrifugate washed back into the flask with distilled water. The solution was again made up to 250 ml with distilled water, shaken vigorously and left to stand until the soil had settled. The supernate was again removed and centrifuged.

This was repeated until the supernate (after centrifugation) appeared faintly hazy (i.e. fine clay particles remained in suspension). The solution was then considered to be free of all dissolved salts which would interfere with dispersal of the soil particles. Both the supernate and centrifugate were then washed back into the flask. The contents of the flask were in turn washed into a high speed mixer and 15 mls of 0,5 N sodium oxalate added.

The experiment was then continued as for Method I (Appendix I).

The above method, except for a few minor modifications, was suggested by Dr Le Roux of the Soil Science Department, Faculty of Agriculture, University of Natal, Pietermaritzburg.

APPENDIX III

PROCEDURE USED FOR THE ANALYSIS OF PLANT SAMPLES SODIUM (Na^+), POTASSIUM (K^+), CALCIUM (Ca^{++}) AND MAGNESIUM (Mg^{++})

The plant samples were dried in a forced-draught oven at 60°C for 5 days. They were then rapidly washed in distilled water to remove any salt (NaCl) which may have accumulated on the leaves from salt spray or active secretion, and returned to the oven to dry.

The samples were then ground to a fine powder, redried at 60°C for 24 hrs and then cooled in a desiccator. Exactly 2,500 g of the powder from each sample was weighed into a vitreosole capsule previously cleaned with phosphoric acid.

The capsules containing the samples were then placed in a furnace, which had been set at 490°C, and the vapours given off by the plant material ignited. When all the flames had finally gone out the door of the furnace was closed and the residue ashed for 4 hrs. After ashing was complete, the samples were removed from the oven and placed on a clean asbestos surface, covered with a glass sheet, and allowed to cool to room temperature.

The ash in each capsule was then treated with 5,0 ml of concentrated HCl. Each capsule was swirled gently to ensure complete wetting of the ash and the resultant solution was evaporated to dryness on a waterbath at 90°C. After dehydration was completed the capsules were heated on the waterbath for a further 60 mins.

5,0 ml of concentrated nitric acid was then added to the crystaline residue in each capsule and the solution stirred with a teflon rod to loosen any material which may have stuck to the capsule. When all the material in each capsule had been loosened, about 10 ml of distilled water was added to each mixture to dilute it slightly. The solutions were then filtered through preleached Whatmans No. 41 filter papers into 50 ml volumetric flasks. The flasks were made up to volume

by successive washings of the capsule and filter paper.

5.0 ml of these original ash solutions were added to a 100 ml volumetric flask containing 5.0 ml of Lanthanum's solution and made up to volume (100 ml) with distilled water. These solutions were now a 1/20 dilution of the original ash solution.

For the determination of the respective elements by atomic absorption spectroscopy it was necessary to make further 1/10 and in some cases 1/100 dilutions of these solutions. This produced 1/200 and 1/2000 dilutions of the original ash solutions respectively.

The amount of each element present in the plant samples was calculated in ppm from the following formula:

$$\text{Conc. of element (ppm)} = \frac{\text{dil. fact. x ml final soln. x ppm in final soln.}}{\text{g plant material}}$$

where dil. fact. = Number of times by which the original ash solution has been diluted (i.e. 200 or 2000);

ml. final soln. = Volume of solution from which the sample was taken for analysis by atomic absorption spectroscopy, (i.e. the volume up to which the last dilution was made);

ppm final soln. = Concentration of the respective element in the above solution. This was calculated from a calibration curve using the reading obtained from the atomic absorption spectroscope;

g-plant material = 2.5 g .

APPENDIX IV

PROCEDURES USED DURING THE INUNDATION OF SEEDLINGS

(1) The cultivation of Sporobolus virginicus and Dactyloctenium australe seedlings.

(2) The inundation with saline water of these seedlings.

(3) The analysis of harvested seedlings for Sodium (Na^{+}), Potassium (K^{+}), Calcium (Ca^{++}) and Magnesium (Mg^{++}).

(1) Cultivation of seedlings

Forty plastic pots 7 cm in diameter and 9 cm deep were filled to within 1,5 cm of the top with a mixture of 1 : 1 Umgeni sand and black earth.

Twenty pots were sown with 30 Sporobolus seeds each and the remaining 20 with the same number of Dactyloctenium seeds.

All the pots were kept in the greenhouse and watered with tap water once a day until the seedlings were about 1 week old. Thereafter they were watered twice a week with a Fe EDTA nutrient solution. On all other days they were watered with distilled water to prevent accumulation of salts on the soil surface.

When the Sporobolus seedlings were 3 months old (± 2 cm high) they were thinned to twenty seeds per pot.

Only 9 Dactyloctenium seedlings were large enough to use in this experiment (the total germination was 3,3%) so no thinning was required.

(2) Inundation with saline water

The sides of the pots containing the seedlings were punctured a number of times and 2 cm wide gaps were cut opposite each other in the top 1,5 cm of the pot rim (i.e. to the soil surface). Each pot was then placed in a 12 x 12 cm wide by 10 cm deep plastic container (Plate 8).

Two of the containers were filled to 0,5 cm above the soil level with distilled water. This was repeated with pairs of the remaining Sporobolus containers using 10, 20, 30, 40, 60 and 80 ppt salt solutions respectively.

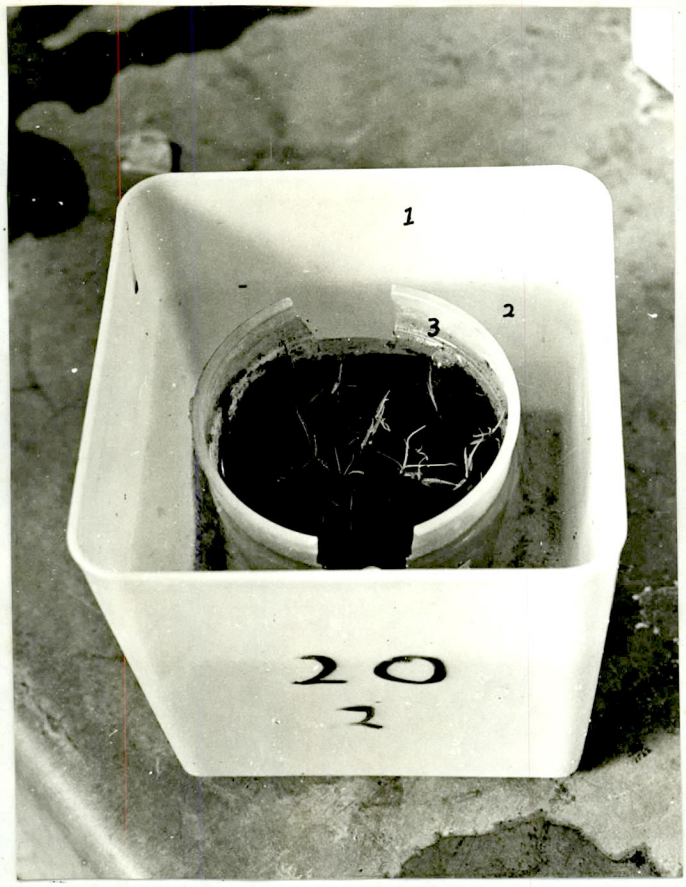


PLATE 8 Apparatus used for inundation of seedlings.

1. Plastic container.
2. Salt solution.
3. Plastic pot containing Sporobolus seedlings; note the gaps cut in the rim to facilitate circulation of the solution

Three pots each containing 3 Dactyloctenium seedlings were treated (as for Sporobolus) with 10, 20 and 30 ppt salt solutions respectively. The level of the solutions within the containers was maintained with distilled water. The gaps cut in the rim of the pots allowed a free circulation of solution thus preventing an increase of salt concentration within the pots.

(3) The analysis of harvested seedlings

Forty Sporobolus seedlings from two pots were harvested before the actual inundation phase of the experiment began.

Those Sporobolus seedlings still surviving after 14 days of inundation were also harvested.

The harvest samples were washed in distilled water to remove any salt on the leaves, dried with paper towels and their fresh weight determined.

The seedlings from the respective treatments were then dried at 60°C in a forced-draught oven, cooled in a desiccator and their dry weight determined for each treatment.

The harvest samples were then ashed in a furnace at 490°C for 4 hrs and the sodium (Na^+), potassium (K^+), calcium (Ca^{++}) and magnesium (Mg^{++}) determined by atomic absorption spectroscopy as for the plant samples collected in the field (Appendix III). The original ash solutions were however only diluted to 1/20. The dilution factor used to calculate the concentration of the respective elements was therefore 20.

APPENDIX V

PROCEDURE USED FOR THE SECTIONING AND STAINING OF GRASS LEAVES

2 cm lengths of leaves were fixed in FAA (formalin/acetic acid/alcohol) under vacuum (-30 atmospheres) for 24 hrs.

Dehydration of the leaves was carried out by leaving them in the following solutions contained in corked specimen tubes for at least 2 hrs.

Composition (ml)	SOLUTION				
	1	2	3	4	5
Distilled water	50	30	15	0	0
95% Ethyl alc.	40	50	50	45	0
3° Butyl alc.	10	20	35	55	75
Abs. alc.	0	0	0	0	25

Solution 5 was replaced by two changes of pure butyl alcohol, the second overnight, and finally a 1 : 1 solution of liquid paraffin/butyl alcohol for 2 hrs.

A specimen tube was then half filled with paraffin wax and left until the top solidified. The leaves in paraffin/butyl were then poured onto the wax and the tube placed in an oven at 60°C. When the leaf portions had been settled at the bottom of the tube for at least an hour the wax mixture was poured off and replaced with pure paraffin wax.

Sections of the leaves, 1 cm long, were then embedded in paraffin wax and 10µ thick serial sections cut on a microtome. The sections were placed in a pool of 10% formaldehyde on a glass slide previously smeared with Haupts' adhesive and left to dry on a warming plate.

Once dry, the wax was removed by two 5 min treatments with xylol and the

sections rehydrated by passing them through absolute alcohol, to 95% alcohol and finally 70% alcohol (5 mins for each treatment). The sections were then stained in Safranin for 6 hours, washed in running water for a few seconds and dehydrated and differentiated in 0,5% picric acid in 95% alcohol for 10 secs. Dehydration was completed in ammoniacal alcohol (2 min) and absolute alcohol (7 min) before counterstaining in fast green/clove oil for 15 secs. The sections were cleaned in clove oil for a few seconds and then passed rapidly through each of the following treatments:

clove oil/xylol/abs. alcohol, xylol (1), xylol (2) and xylol (3). They were then mounted in DPX.