THE CONTRIBUTION OF *SPARTINA MARITIMA* (CURTIS) FERNALD TO THE PRIMARY PRODUCTION OF THE SWARTKOPS ESTUARY

SHIRLEY MAY PIERCE

DISSERTATION
SUBMITTED IN PARTIAL FULFILMENT OF THE
REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
OF RHODES UNIVERSITY
JANUARY 1979

ACKNOWLEDGEMENTS

I thank Professor T. Erasmus for his unfailing enthusiasm and encouragement in spite of the odds. Through his interest and help this project was made possible. The advice and inspiration of Dr. Clive Howard-Williams provided the motivation essential to the project and I am very grateful for his concern. Thanks are extended to Dr. Roy Lubke for his advice and encouragement in supervising this study. The kindness and trouble taken by Professor S.C. Seagrief is greatly appreciated.

Throughout this study, the help and encouragement of Richard Cowling enabled me to persevere. I am grateful to him for his help on the river. Nic Hanekom was a continual source of help and I thank him and the other students and staff of U.P.E. who toiled with me in the mud. Lynnath Beckley was kind in helping with the design of the export nets.

Data-processing on the computer would not have been possible without the guidance of Gerry Dieckmann, whose interest and advice was invaluable.

The nutrient data on the Swartkops estuary and aerial photographs were made available by the Port Elizabeth City Engineer, Mr. D.M. McCallum. Dr. R.D. Beaumont was kind in assisting with photographs and maps.

I thank Lyndsay Scott-Campbell for her illuatration of *Spartina* and Richard Cowling for his help with the diagrams.

The fortitude of Lindy Boehmke for typing the manuscript is gratefully appreciated.

The financial aid of the Department of Planning and the assistance of a C.S.I.R. bursary are acknowledged.

CONTENTS

ABSTRACT

CHAPTER 1

GENERAL INTRODUCTION 1

1.1 Introduction 1
1.2 Objectives 4

CHAPTER 2

DESCRIPTION AND DISTRIBUTION OF *S. MARITIMA* 5

2.1 Description of *S. maritima* 5
2.2 Nomenclature 7
2.3 World distribution of *S. maritima* 8
2.4 Origin of *Spartina maritima* 8

CHAPTER 3

ENVIRONMENT OF THE SWARTKOPS ESTUARY 11

3.1 Climate 11
3.2 The estuarine features 14

CHAPTER 4

ZONATION OF THE SWARTKOPS SALT MARSH 21
4.1 Introduction 21
4.2 Methods 22
  4.2.1 Production of the vegetation map 22
  4.2.2 Relating zonation to mean sea level 23
  4.2.3 Measurement of substrate characteristics 23
    4.2.3.1 Particle size analysis 23
    4.2.3.2 Substrate content 24
  4.2.4 Measurement of biomass 24

4.3 Results 24
4.3.1 Vegetation map of the Swartkops estuary 24
4.3.2 Zonation of the salt marsh vegetation relative to mean sea level 25
4.3.3 Substrate characteristics of the vegetation zones 28
4.3.3.1 Particle size characteristics 28
4.3.3.2 Contents of substrate of vegetation zones 29
4.3.4 Biomass of the plant species of the salt marsh zones 31
4.4 Discussion and Conclusions 34

CHAPTER 5

BIOMASS, COMMUNITY STRUCTURE AND GROWTH OF S. MARITIMA 37

5.1 Introduction 37
5.2 Methods 38
5.2.1 Area determination 38
5.2.2 Monitoring seasonal changes in Spartina biomass 38
5.2.2.1 Site selection 38
5.2.2.2 Sampling by harvesting 38
5.2.3 Analysis of seasonal composition of Spartina 40
5.2.4 Measurement of seasonal changes in community structure 40
5.2.4.1 Measurement of shoot density and mean shoot mass 41
5.2.5 Determination of fresh height : dry mass relation of Spartina shoots 41
5.2.6 Growth of S. maritima 41
5.3 Results 43
5.3.1 Area covered by S. maritima on the Swartkops marshes 43
5.3.2 Seasonal changes in Spartina biomass 44
5.3.3 Seasonal composition of Spartina 44
5.3.4 Seasonal changes in community structure 47
5.3.4.1 Density and mean shoot mass 47
5.3.5 Fresh height : dry mass regression 47
5.3.6 Shoot growth 47
5.3.7 Leaf development 56
5.4 Discussion and conclusions 56

CHAPTER 6

MEASUREMENT OF NET PRODUCTION OF S. MARITIMA 68

6.1 Introduction 68
6.2 Methods 69
6.3 Results 75
6.4 Discussion and conclusions 75
  6.4.1 Comparison of different methods 75
  6.4.2 Comparison of production of other species of Spartina 85

CHAPTER 7

DECOMPOSITION RATE AND DETRITUS PRODUCTION 88

7.1 Introduction 88
7.2 Methods 88
  7.2.1 Seasonal loss of dead material 88
  7.2.2 Determination of decomposition rate 89
  7.2.3 Determination of detritus production 91
7.3 Results 91
  7.3.1 Seasonal decomposition 91
  7.3.2 Decomposition rate 95
  7.3.3 Detritus production 97
7.4 Discussion and conclusions 97
  7.4.1 Seasonal breakdown of S. maritima 97
  7.4.2 Daily instantaneous rates of decomposition 105
  7.4.3 Monthly and annual detritus production 105

CHAPTER 8

EXPORT OF S. MARITIMA MATERIAL 107

8.1 Introduction 107
8.2 Methods 107
8.3 Results 109
8.4 Discussion and Conclusions 109

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSIONS 114

9.1 S. maritima as a primary producer 114

9.2 Estuarine ecosystem stability 118

9.3 The importance of S. maritima to the Swartkops estuarine ecosystem 119

9.4 Evaluation of production approach to ecosystem studies 120

REFERENCES 121

ADDENDUM

There is a new distribution record of *S.maritima* on the marshes of the Kaferkuils River estuary, Riversdale District (Personal observation,1979).

It is noteworthy that there is no mention of *S.maritima* in the survey which included the Kaferkuils estuary by Muir (1929). Furthermore, Phillips (1931) did not record *S.maritima* in the Knysna and Keurbooms estuaries. This additional information supports the theory of the spread of the distribution of *S.maritima* along the South African coast (Chapter 2.4).

MUIR,J. 1929. The vegetation of the Riversdale area. Mem. Bot. Surv. S.Afr. 13 : 1-82.

PHILLIPS,J.F.V. 1931. Forest-succession and ecology in the Knysna region. Mem. Bot. Surv. S.Afr. 14 : 1-327.

ABSTRACT

The primary production of Spartina maritima, the dominant macrophyte of the intertidal salt marshes of the Swartkops estuary, was determined for inclusion into the proposed ecosystem model,

Several methods for measuring net production devised for North temperate Spartina species were used, as no single method was considered reliable for the local species. In addition, a new method was devised to take into account the aseasonal growth behaviour of S. maritima. Most energy for growth appears to be directed into leaf production, rather than shoot growth. Live net production values were 523-680 g $m^{-2}yr^{-1}$, which are generally lower than estimate of N. American Spartina species. Total Live production of S. maritima for the whole Swartkops estuary was 495,6 x 10^3kg yr^{-1}, which is an estimation of potential food resources.

Formation of S. maritima detritus by decomposition was significantly related to air and water temperatures. Thus detritus production showed a wide seasonal variation about a mean of 374 g $m^{-2}yr^{-1}$. The total S. maritima detritus production of 307,5 x 10^3kg for the whole Swartkops estuary was determined as an estimate of available food resources.

Export of detrital material from Spartina marshes to estuarine waters was negligible. Even during a maximal Equinoctial tide, only 6,26 dry g m^{-2} detritus was exported from the creek catchment area of Spartina stands.

This study has shown that concepts evolved for North temperate estuaries should be carefully considered before being applied to local situations, particularly in view of the relatively low, aseasonal production of S. maritima and the negligible contribution of its detritus to estuarine waters. Furthermore, it is essential that utilisation of primary production by secondary producers be determined before the function of the estuarine ecosystem may be understood.

CHAPTER 1

GENERAL INTRODUCTION

1.1 INTRODUCTION

Estuarine ecosystems have been called the most productive in the world (Odum, 1971), and they have been recognised as key conservation areas for their ecological, economical and aesthetic value. Research towards a management plan for the conservation of the Swartkops estuary (Fig.1.1), has been undertaken by the Zoology Department of the University of Port Elizabeth. The management plan will be based on an ecosystem model which will trace the flow of energy through the primary and secondary producers. Information on the nature of the energy flow within the different components is collected separately for inclusion into the model.

Earlier studies of the Swartkops estuary include an account of the general ecology (Macnae, 1957), the estuarine seaweeds (Pocock, 1955) and a comprehensive environmental study of the Swartkops basin (McCallum, 1972 a-g). More recent work of the University of Port Elizabeth ecosystem project has been done on estuarine fish (Marais, 1976.; Van der Horst, 1976), meiofauna (Dye and Furstenberg, 1978) and macrobenthos (McLachlan, 1972). Studies on other secondary producers are in progress.

There is little information on the link between primary and secondary producers in local estuaries. In North temperate regions, estuaries are said to function on a detritus-based foodweb (Darnell, 1967; Odum and de la Cruz, 1967; Odum, Zieman and Heald, 1972). There the utilisation of living plant material is minimal and the major link between primary and secondary production is via the detritus chain. On the Kowie River marshes, Alexander and Ewer (1969) found negligible grazing on live plants by crabs. Personal observations on the Swartkops marshes tend to support the idea of minimal utilisation of live marsh plants by grazers. The paucity of information on

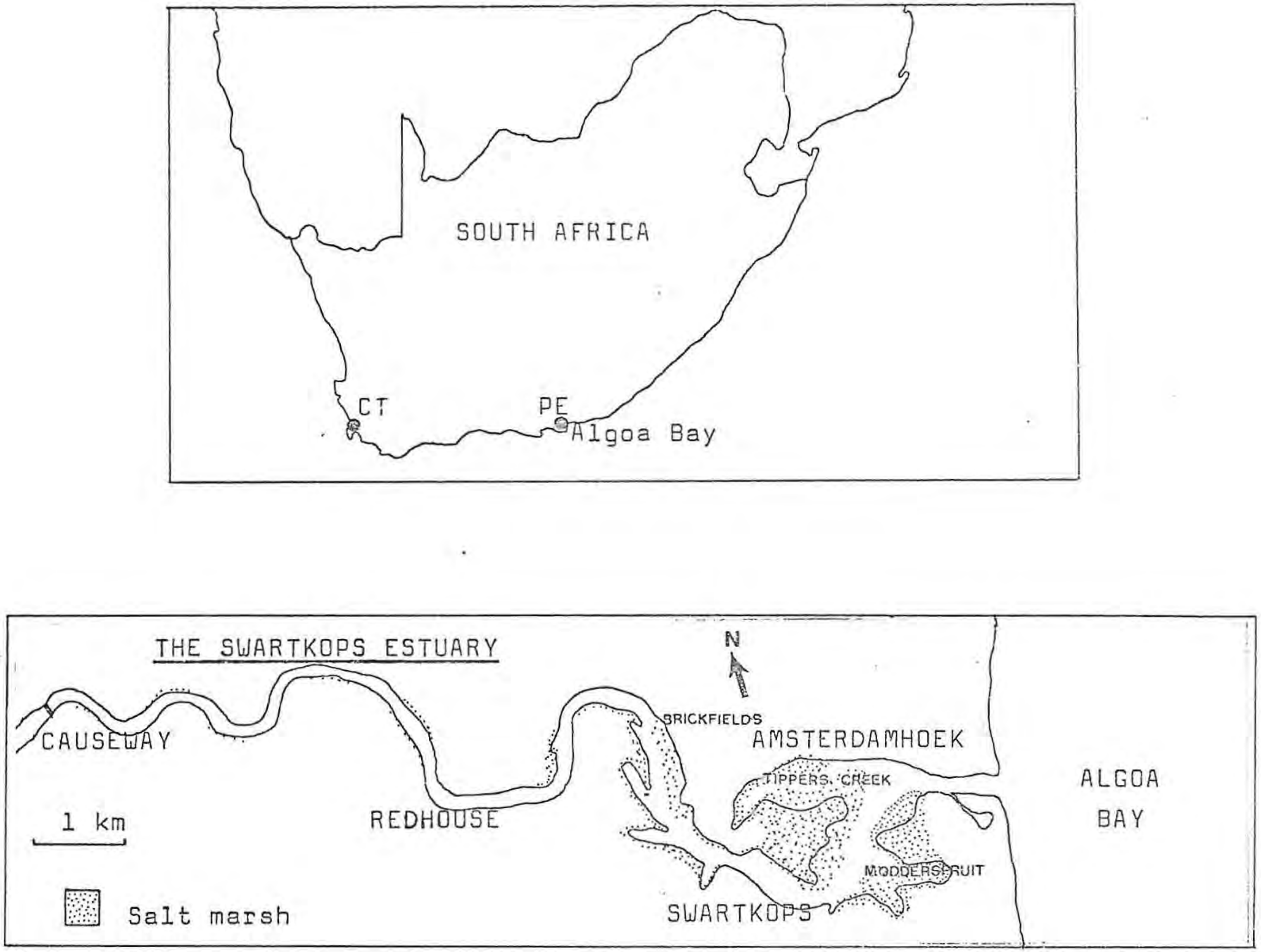


Fig. 1.1 Map of the Swartkops River estuary showing the intertidal salt marshes. Outline by kind permission of the Zwartkops Trust.

local utilisation necessitated a broad approach to the primary production studies including both live and detritus production.

Macrophytes are considered to be the major contributors to primary production in estuaries, supplemented by epibenthic micro-algae and to a lesser extent in shallow estuaries, phytoplankton (Teal and Kanwisher, 1961; Teal, 1962; Odum *et al.*, 1972; Turner and Gosselink, 1975).

The most dominant macrophyte on the salt marshes of the Swartkops estuary is *Spartina maritima*. The genus *Spartina* has been widely studied (see Keefe, 1972; Turner, 1976 for reviews) and found to be one of the most productive higher plants in the world (Keefe, 1972). Its success in the stressed conditions of the estuarine intertidal has been attributed partly to its C_4 photosynthetic pathway, high leaf area index and exploitation of the nutrient-rich tidal waters (Keefe, 1972; Odum and Fanning, 1973).

Spartina is not only an important producer, but plays a vital role in erosion control, sediment trapping, breaking-down of pollutants by oxidation, and flood buffering (Lagna, 1975). Furthermore, by stabilising substrate and ameliorating climatic conditions, *Spartina* communities provide a suitable habitat and refuge from predators for animal populations (Kraeuter and Wolf, 1974).

It is important that the above-mentioned roles as well as the role of primary producer be evaluated when including *Spartina maritima* as a component of the ecosystem.

1.2 OBJECTIVES

The basic aim of the study was to provide information about the role of *S. maritima* as a primary producer in the Swartkops estuarine ecosystem.

The importance of macrophyte production in an estuarine ecosystem and its contribution of particulate organic detritus to coastal waters may be understood by studying four main processes: plant production, decomposition, export of detritus and utilisation of the detritus by consumers (Odum *et al.*, 1972).

Thus in terms of the requirements of the ecosystem project, the aims of this study were:

1. to provide a background description of the Swartkops salt marshes. This was considered necessary for understanding the *S. maritima* community and function;

2. to estimate the magnitude and nature of the source of net production by *S. maritima*, as a potential food resource;

3. to investigate the rate of decay of *S. maritima* and detritus formation and to estimate its availability as a food source;

4. to determine tidal transport of detritus from its source of production on the marsh to aquatic consumers in the estuarine and coastal waters.

CHAPTER 2

DESCRIPTION AND DISTRIBUTION OF S. MARITIMA

2.1 DESCRIPTION OF S. MARITIMA

Spartina maritima is the smallest European species, usually 15-50 cm tall (Marchant, 1967), but in the Swartkops estuary this plant achieves heights of 60cm and even 80 cm. Fig. 2.1 shows the typical growth form of the local plant. It grows in tufts of rigid shoots with strong roots and short, wiry rhizomes. Secondary tufts grow close to the parent stock due to the shortness of the rhizomes. This emphasises the tufted appearance and makes it impossible to distinguish between individual plants. The implications of this are dealt with later. Aerial shoots normally grow until flowering heads form (Marchant and Goodman, 1969). The tallest shoots bear the inflorescenses. The shoots are erect with tight, short sheaths. The leaves are stiff and inrolled, making a very acute angle with the stem. Very characteristic is the shedding of leaf blades, leaving only sheaths behind. Only about the three newest leaves are present on the majority of shoots at any one time (Fig. 2.1).

As a halophyte, Spartina maritima, is restricted to the intertidal mudflats of perennially open estuaries. It occurs as extensive swards at Swartkops, growing from about midway between the High Spring Tide level and High Neap Tide levels down to about Mean Tide level.

A conspicuous feature of S. maritima in the field and characteristic of other species of Spartina is the difference between the tallest, most robust plants bordering the water courses; the shorter, more spindly ones covering the major part of the marsh further inland of the water; and sometimes an extremely short stunted form growing at the highest distribution limits (Smalley, 1959; Teal, 1962; Stroud and Cooper, 1969; Keefe and Boynton, 1973; Nixon and Oviatt, 1973b). Initially all three of these height forms, "Tall", "Medium" and "Short" were sampled, but with further observation of the Spartina stands, it

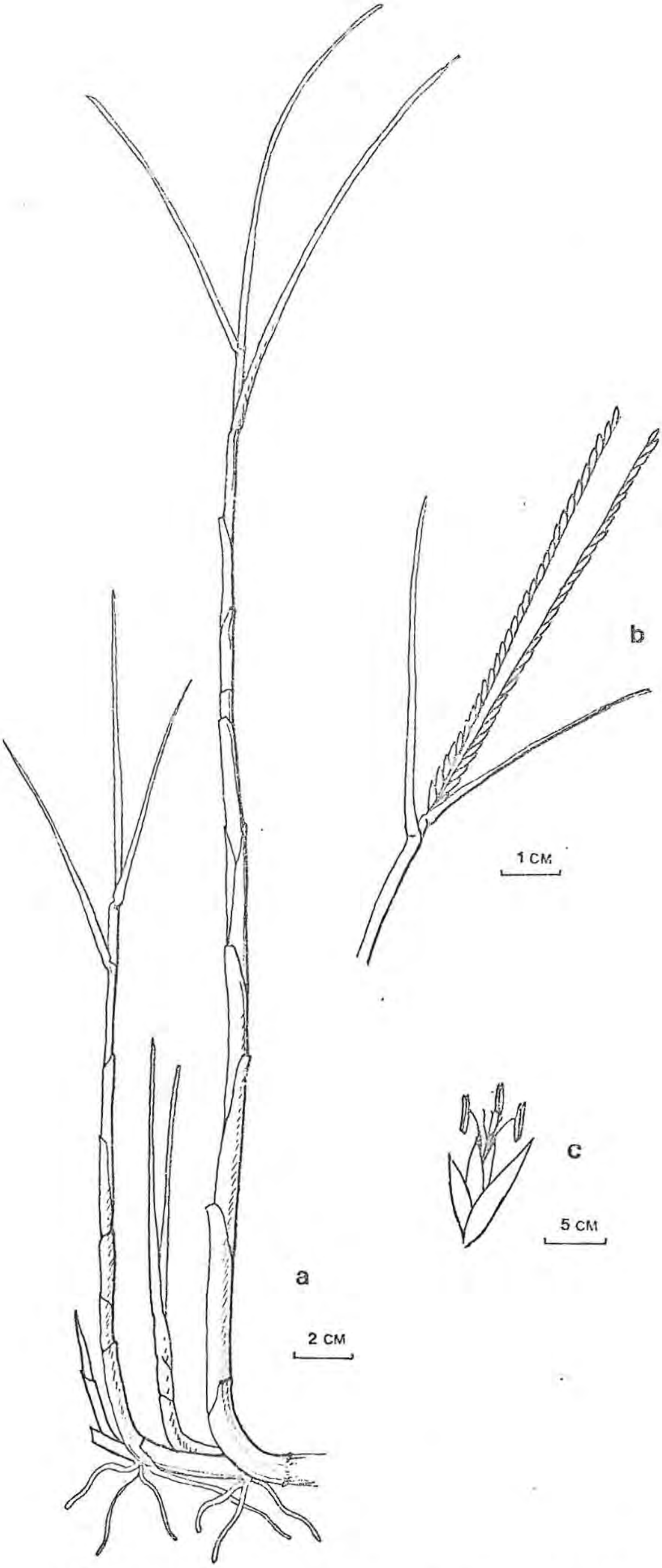


Fig. 2.1 Diagram of S.maritima showing : (a) general growth habit; (b) inflorescence; (c) floret.

was decided that the Short form occurred in such small patches as to be considered negligible. Thus Short form sampling was discontinued and greater effort concentrated on the separate treatment of the Tall, streamside shoots and the Medium height inland forms.

2.2 NOMENCLATURE

There has been confusion in the nomenclature used to describe the species. S. maritima (Curtis) Fernald is conspecific with S. capensis Nees (Mobberley, 1956; Marchant, 1969; Dyer, 1976). The latter epithet has been used in South African literature in more recent years (Meredith, 1955; Day, 1969; McCallum, 1972d) in preference to its earliest name of S. stricta (Ait.) Roth used by Thiselton-Dyer (1900) and Macnae (1957). According to Marchant (1967), the name S. stricta was until recently used in the literature more widely than the correct name, S. maritima. Briefly, he explains that the reason for this was that for more than a century the name Spartina stricta (Ait.) Roth had been used to describe the coastal mudflat grass of Western Europe. Aiton, in describing Dactylis stricta, included references to Dactylis cynosuroides, recognising that the European species described by the authors was distinct from the North American Dactylis cynosuroides. Curtis, however, had come to the same conclusion two years earlier. In 1787 he gave the name Dactylis maritima to Dactylis cynosuroides and Spartum essexianum. Fernald noticed this earlier epithet and made the new combination Spartina maritima in 1916. This name, Marchant (1967) states, only came into common use during the past 20 years.

The confusion surrounding the synonomy led to further literature survey and speculation about the origins of the species.

2.3 WORLD DISTRIBUTION OF S. MARITIMA

Fig. 2.2a shows the distribution of S. maritima from the East coast of England, around the Mediterranean Sea and scattered down the coast of Africa. The distribution pattern of the majority of other species of Spartina is mainly confined to North America (see Fernald, 1929).

2.4 ORIGIN OF SPARTINA MARITIMA

Chevalier (1923 in Marchant, 1967) theorised that S. maritima is indigenous to South Africa and North West Africa and was introduced to higher latitudes (Britain, Holland, Northern Europe) by shipping. Evidence for the formulation of this idea was the more robust nature of the Spanish, Northern Mediterranean and African specimens. In support, Marchant (1967) states that the wide African distribution suggests a tropical African origin for the species. He proposes that the Northern limits of distribution in England are set by July temperatures of 16°C, suggesting warm summer requirements for the species. Furthermore, the retrogression of large stands of S. maritima in the past 100 years is the result of intolerance to recent climatic fluctuations in Britain.

In contrast, the possibility of a Northern origin for S. maritima exists. Bews (1929) states that this plant was introduced to South Africa but unfortunately quotes no supporting evidence.

An examination of the records in the herbarium of the Albany Museum (GRA) and the Bolus Herbarium (BOL) provide some evidence for a Northern origin. The earliest collection of the plant was made by Ecklon and Zeyher (No. 662 in GRA) between 1823-1834 "along the strand of Algoa Bay by Port Elizabeth and Cape Receife". The plant could have been introduced to the Port Elizabeth area by early settlers in the form of fodder for which it is still used today in Britain (Ranwell, 1961). Subsequent collections were made from the Swartkops River mouth and salt marshes by MacOwen and Bolus (No. 791 in GRA) in 1887; Port Alfred west by Galpin (No. 7721 in GRA)

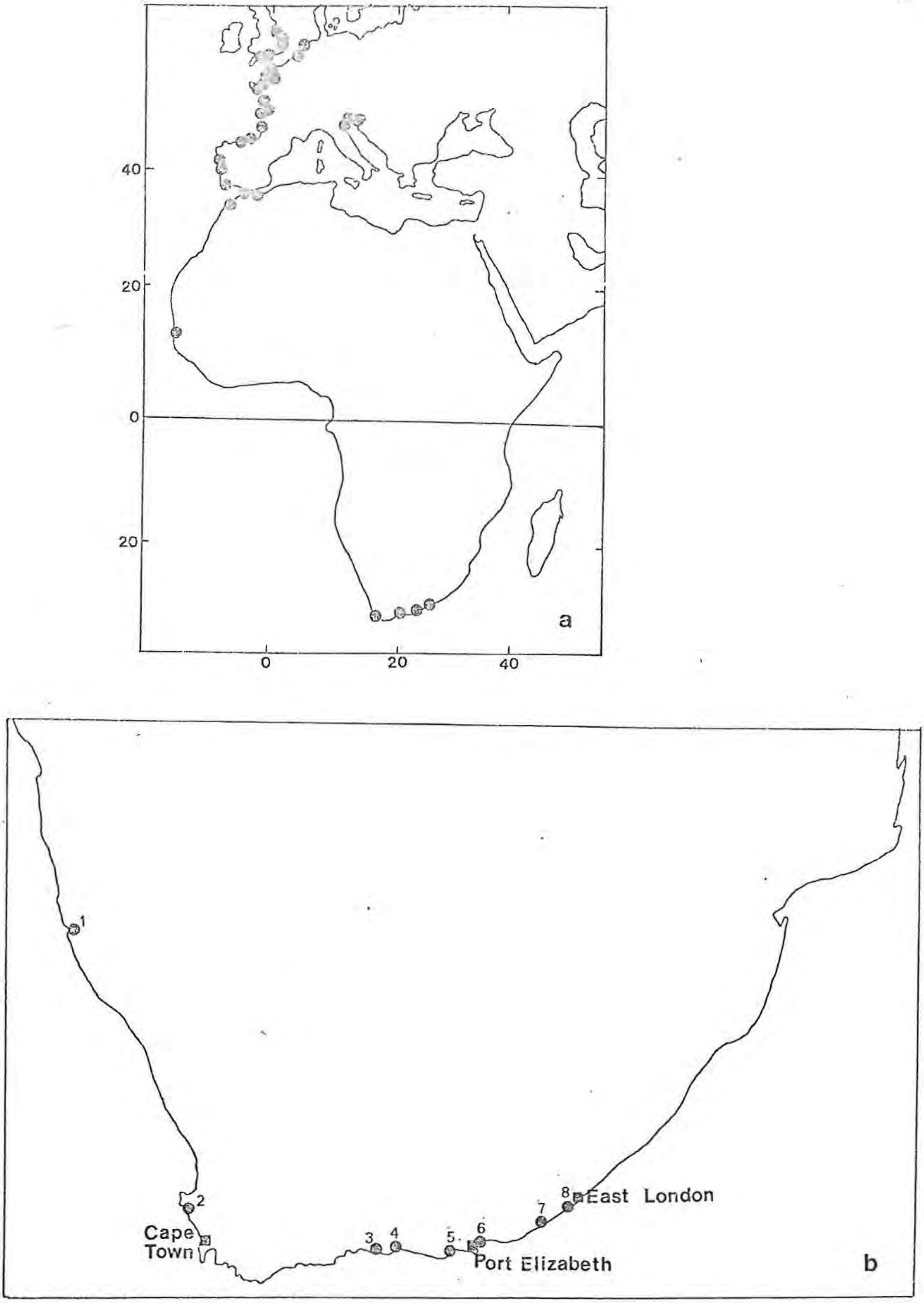


Fig. 2.2 World distribution of S.maritima (a) from Mobberley(1956).
Southern African distribution of S.maritima (b).

1. Luderitz Bay
2. Langebaan Lagoon
3. Knysna Lagoon
4. Keurbooms River
5. Kromme River
6. Swartkops River
7. Kowie River
8. Keiskamma River

in 1906 and Luderitz Bay by Pearson (No. 8043 in BOL) in 1912. This apparent spread in distribution (sec map, Fig. 2.2b) could have been the result of a successful, exotic coloniser.

The Southern origin theory can be disputed on several points. There is strong evidence for a Northern Temperate origin for the whole genus of Spartina (Fernald, 1929). There are no records of other species of Spartina indigenous to the Southern Hemisphere. Spartina was deliberately introduced into New Zealand for stabilisation purposes (Bews, 1929).

Tropical origins for the genus and warm summer requirements proposed by Marchant (1967) are not supported by the findings of Waisel (1972) that Spartina species are cold-requiring and growth is successful only in regions with cold winter temperatures.

The use of apparent vigour of Tropical specimens as the basis for Chevalier's theory could be opposed by the fact of greater success of exotics in an alien environment (Harper, 1977).

Recession of abundant stands in Britain is the result of unsuccessful competition against the aggressive and highly vigorous hybrid, S. townsendii (Hubbard, 1954; Hinde, 1954; Mobberley, 1956). This theory is more acceptable than the idea of cold intolerance and recession from climatic changes.

Literature describing the Northern European and British plants stress the lack of vigour, poor seed production and ineffective vegetative propagation, which have led to its rare and patchy distribution (Hubbard, 1965; Marchant and Goodman, 1969).

By comparision, the abundant meadows of S. maritima on the Swartkops estuary suggest the highly successful colonisation of an alien environment by an exotic.

The significance of S. maritima as an exotic in the estuarine ecosystem will be discussed.

CHAPTER 3

ENVIRONMENT OF THE SWARTKOPS ESTUARY

A résume follows of environmental influences considered to be relevant to this study. The nature of the Swartkops River and its environment has been treated comprehensively in the study edited by McCallum (1972a-g) in which the geology, meteorology, hydrology, hydraulics and ecology are described.

3.1 CLIMATE

The river valley is situated in the Southern temperate zone (Lat. 33°58'S Long. 25°42'E). The area is transitional between summer, winter and year-round rainfall regimes. On an average, rain is distributed throughout most seasons, with slight peaks in spring and autumn. During the year of this study (1977), however, this general pattern was masked by an exceptionally high winter rainfall, resulting in floods (Fig. 3.1). The river is perennial and complete inundation of the flood plains occurs about every 25 years (McCallum, 1972f). Temperatures are generally mild and frost is uncommon (Zwartkops Trust, 1971). Seasonal variation in air temperatures are shown in Fig. 3.2. The hottest month is February which experienced an absolute maximum temperature of 36,3°C in 1977. Relative humidity corresponds to temperature fluctuations with the average monthly reading at 82% in February of the same year. A large rise in temperature was experienced between November and December of 1976. Rapid decreases were apparent in March, April and June, with July being the coldest month. The absolute minimum temperature of 2°C was measured in June of 1977. The lowest monthly relative humidity recorded was 68% in June and August, reflecting the maritimal nature of the area. Typical rapid rise in temperature was recorded in August and September, revealing the very short duration and mildness of winter.

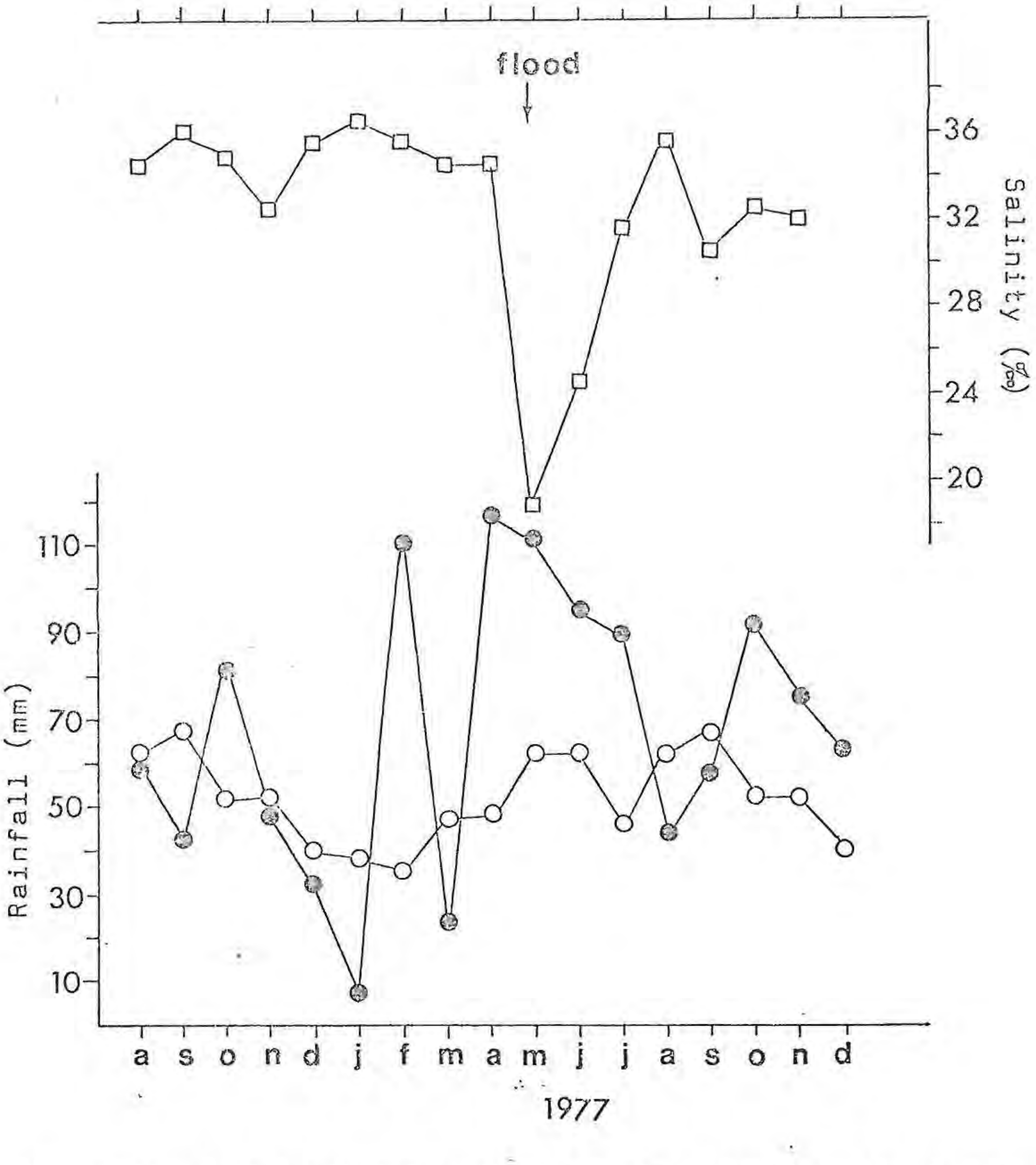
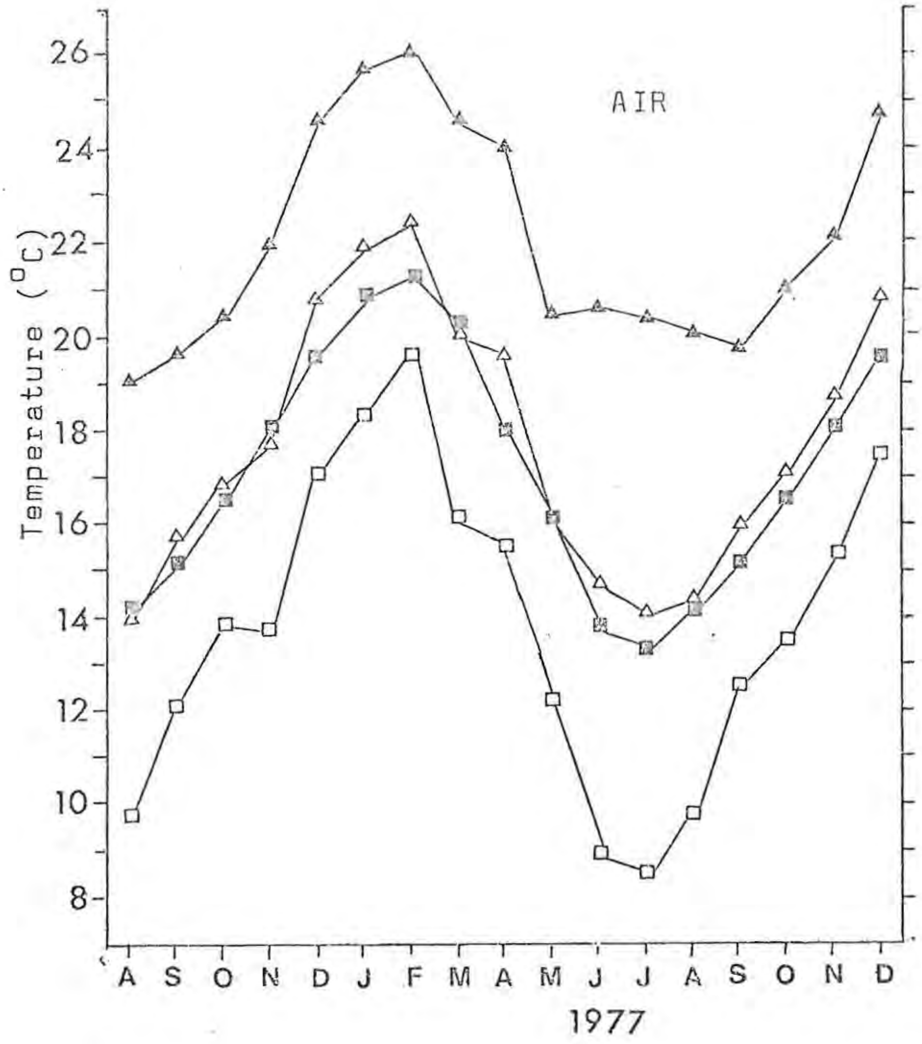


Fig. 3.1 Total monthly rainfall for 1976/77 (●–●) and average monthly rainfall for 1937-1950 (○–○) for the Port Elizabeth region (P.E.Airport).
Average monthly salinity of the Swartkops estuary in the vicinity of the *Spartina* stands (□–□) for 1976/1977 collected by Zoology Dept., U.P.E.



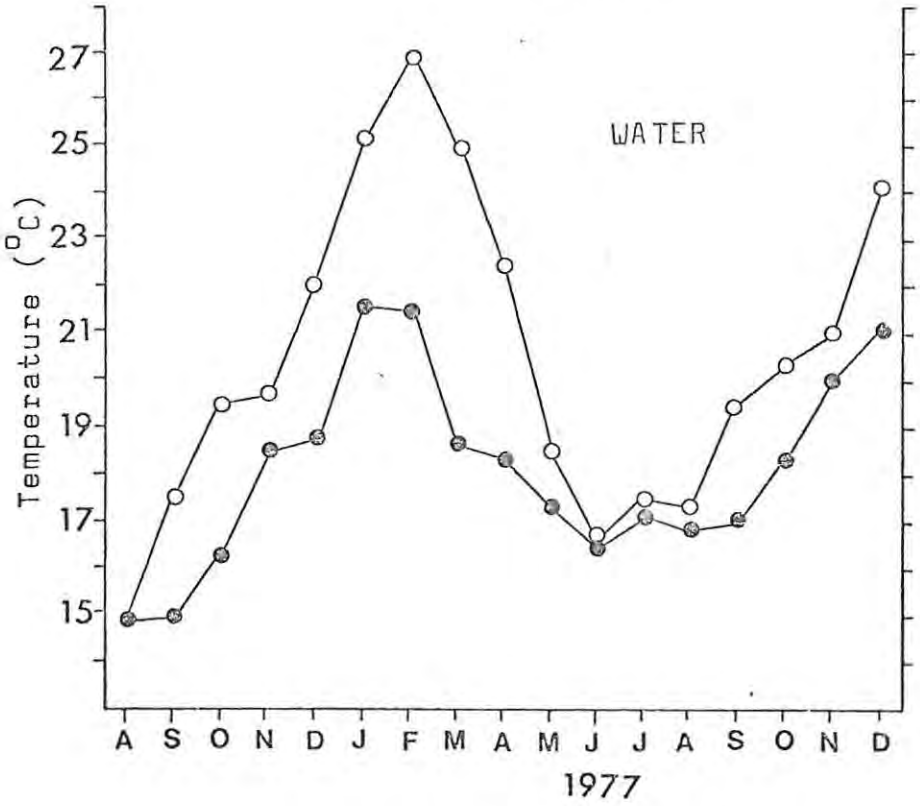


Fig. 3.2 Air and water temperature data for the study area. Air temperatures (P.E.Airport) : average maximum for 1978(▲); monthly average for 1978(△); monthly average for 1937-1950(■); average minimum for 1978(□). Water temperatures for 1978 : mean monthly sea temperatures (●) from Humewood Beach; mean monthly estuarine water temperatures (○) in the vicinity of the *Spartina* stands for 1976/1977 collected by Zoology Dept., U.P.E.

Highest solar radiation is generally experienced in November, and decreases after March (Table 3.1). Total radiation received at the earth's surface is inversely proportional to the cloud cover whereas diffuse radiation varies directly with cloud cover. Irregular variations of cloud cover on successive days indicate the variability of the weather, and large changes in cloud cover are more likely in the SE Cape than anywhere else in RSA (McCallum, 1972g).

Evaporation readings for the Port Elizabeth Area are given in Table 3.1. The data collected from American class "A" evaporation pans are effective in determining the effects of temperature, humidity, wind and solar radiation on evaporation. The results thus tend to correspond to the seasonal variation shown by temperature and radiation.

Fig. 3.3 shows the annual and monthly percentage frequency of winds classed into different velocity categories. This clearly shows the prevalence of strong winds in the spring months and the relatively light winds during winter. The phenomenon of diurnal variation in wind velocity with relative calm in the morning and maximum wind velocity in the afternoon is typical of coastal regions.

3.2 THE ESTUARINE FEATURES

Estuarine conditions extend from the river mouth to about 17 km upstream, where a rise in terrain delimits the tidal influence. The estuarine channel is well-defined down to Swartkops Village. The river then widens, the bed material becomes progressively sandier towards the mouth and the salt marshes reach their fullest development on either side of the main channel flowing between Swartkops Village and Amsterdamhoek.(Figs.1.1 and 3.4) Two large creeks, Tippers Creek and Modderspruit serve as major drainage channels to each of the salt marshes. Fine material precipitates in the creeks and the N content of substrate samples from the estuary increases up the creeks and upriver. See Table 3.2.

TABLE 3.1 MONTHLY EVAPORATION AND RADIATION OF THE PORT ELIZABETH REGION

	J	F	M	A	M	J	J	A	S	O	N	D
Mean monthly evaporation (mm)	249	224	183	130	94	86	78	102	132	180	231	259
Mean monthly radiation ($J\ m^{-2}\ day^{-1}$) All units X 10^8												
Earth's surface	0,248	0,255	0,194	0,141	0,111	0,094	0,105	0,131	0,168	0,214	0,258	0,253
Diffuse radiation	0,094	0,068	0,059	0,046	0,030	0,030	0,030	0,042	0,067	0,073	0,089	0,097

SOLAR RADIATION DATA 1957 -1958 (McCALLUM, 1972g)

EVAPORATION DATA FROM AMERICAN CLASS "A" EVAPORATION PANS 1957-1961 (McCALLUM, 1972g)

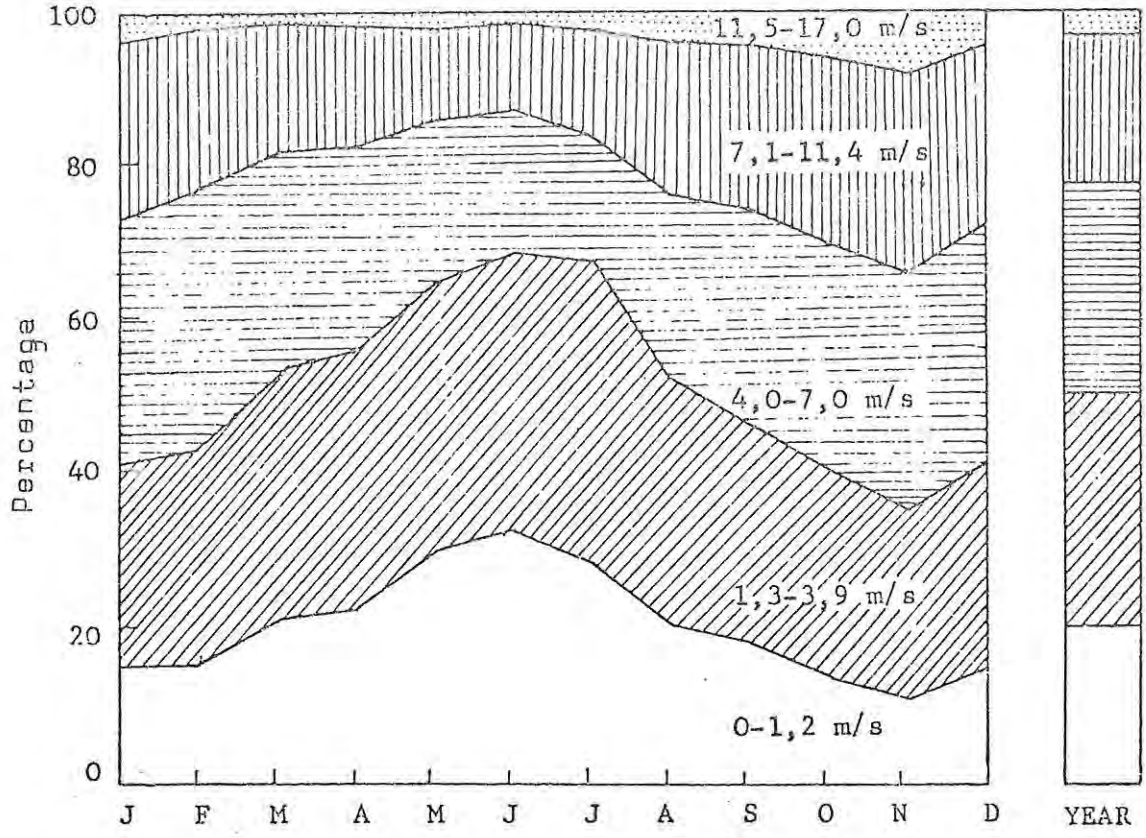


Fig. 3.3 Percentage frequency of wind velocities within given limits for each month and the year (P.E.Airport).

TABLE 3.2

NITROGEN CONTENT OF SUBSTRATE FROM SWARTKOPS ESTUARY

STATIONS	SWARTKOPS MOUTH	AMSTERDAMHOEK	UP TIPPERS CREEK
($mgNg^{-1}$ dry substrate)	0,08	0,29	0,54 0,86 0,90

MODDERSPRUIT	SWARTKOPS	REDHOUSE	CAUSEWAY
1,36	0,54	0,36	0,16

(McLachlan, 1972)

Incoming tides are able to overcome the impedance offered by the sand bar in the estuary mouth, but the frictional resistance of the estuary mouth retards the ebb flow. The result is an elevation of mean water level throughout the estuary. Full tidal effects are felt near the estuary mouth and it is only at the brickfields (See Fig. 1.1) where attenuation of the tidal wave appears significant. Tidal range at the study sites measured at neap tide is about 0,6m and 1,4 m at spring tide (McCallum, 1972f).

Estuarine temperatures are generally warmer than the warm temperate waters of Algoa Bay, but follow a similar regular seasonal variation (Fig. 3.2). Shallow waters tend to exhibit higher temperatures due to diminished tidal exchange.

The salinity of the lower estuary is fairly stable (about 35%) due to the buffering action of the tides. Sporadic floods have the effect of lowering the salinity throughout the estuary appreciably for a few days. This is evident in Fig. 3.1 following the floods in May, 1977.

Measurements of nutrients such as total N, organic N, nitrate and total P in water samples taken at different stations along the length of the estuary vary greatly. Drastic fluctuations occur between monthly readings

Fig. 3.4 The salt marshes of the Swartkops estuary. Sample sites shown are : the River Station (R); the Creek Station (C); Moddersspruit Zonation Station (M) Litterbag Site (L); Export Site on Tippers Creek (E).

which show no seasonal pattern. Table 3.3 gives monthly results of the nutrient status of estuarine water sampled near the study areas. These values are far higher than levels of N and P compounds in Swartvlei, a relatively undisturbed Southern Cape estuary (Liptrot, 1978). The differences in N and P levels between samples from Swartkops and Tippers Creek is clear but the aseasonal fluctuations are difficult to explain. The apparently random peaks in N and P levels may reflect sewage and industrial effluent being discharged into the river above or being carried up the estuary by tidal waters from Algoa Bay.

TABLE 3.3 NUTRIENT CONCENTRATION (N AND P COMPOUNDS) IN SWARTKOPS ESTUARINE WATERS
DATA FROM PORT ELIZABETH MUNICIPALITY

TIPPERS CREEK

Total N	416	520	826	837	794	3201	648	438	460	656	757	1006
Organic N	355	453	598	807	460	2380	394	10	70	467	395	631
NO_3-N	56	36	198	13	37	778	207	223	295	181	252	290
Total P	130	206	107	236	185	416	232	95,7	129	112	169	16

SWARTKOPS VILLAGE CHANNEL

Total N	446	349	740	628	470	1943	769	537	423	669	473	364
Organic N	401	271	676	544	7	784	281	6	106	413	344	310
NO_3-N	42	26	36	6	38	894	409	234	219	182	125	43
Total P	129	143	165	2470	109	150	158	42,7	105	118	148	177

ALL UNITS IN $\mu g\ l^{-1}$

CHAPTER 4

ZONATION OF THE SWARTKOPS SALT MARSHES

4.1 INTRODUCTION

In order to provide quantitative background information to the production study, a vegetation map of the Swartkops salt marshes was plotted and certain zonation characteristics were investigated.

The main function of the vegetation map was to provide a means of measuring the extent of the Swartkops salt marshes and the proportion covered by halophyte communities for production studies. Stroud and Cooper (1969), Gallagher (1974) and Hatcher and Man (1975) have used remote-sensing techniques for area determinations in marsh production studies.

Boucher and Jarman (1977) used aerial photographs to map marsh vegetation around Langebaan Lagoon. Vegetation maps provide a useful tool for showing distribution of communities in relation to each other and to topographical features, such as water courses. Changes in plant communities and water courses may be monitored by means of these maps. They are particularly useful for assessing potential effects of human impact on salt marshes and river banks. Distribution of some invertebrate populations appear to coincide with certain plant communities (D. Baird, pers. comm), thus the vegetation map may prove to be a means of determining animal distributions and abundance as well. For these reasons, a vegetation map provides essential basic information to an ecosystem study.

It is stressed that the investigation of intertidal halophyte zones was primarily for descriptive purposes although speculation was made about factors causing zonation. Major controlling agents of zonation of salt marshes, which show similarity in taxonomic and phanerogamic structure in widely separated geographic regions, have been extensively studied (Chapman, 1974). From the literature surveyed (Clarke and Hannon, 1967, 1969, 1970; Mahall and Park, 1976a, 1976b, 1976c), it appeared that a study of zonation substrate characteristics and tidal inundation, as a function of height above mean sea level, would provide the relevant background information for a better understanding of zonation. Knowledge of factors affecting zonation and the distribution of plant species is necessary information for the ecosystem project and the management plan.

The cover-abundance and dry above- and belowground biomass of the plant species comprising the distinct vegetation zones were measured. These provided quantitative data for the studies on faunal distribution related to plant zonation at Modderspruit (Fig. 3.4). It is possible for the relative importance of the different plant species to be assessed in terms of biomass units.

4.2 METHODS

4.2.1 Production of the vegetation map

Infra-red colour photographs were recommended for wetland ecological studies by Shima, Anderson and Carter (1976). A series of stereoscopic pairs of colour and colour infra-red aerial photograph transparencies scanning the Swartkops basin (scale 1 : 7500) were used for photo-interpretation. The colour infra-red photographs proved to be better in terms of ease of interpretation and information gained. The distinct shades of red allowed the boundaries of individual plant communities to be distinguished rapidly and accurately.

Photo-interpretation involved comparisons between communities observed in the field and communities distinguished in the photographs. Systematic field confirmation was necessary at indistinct boundaries of mixed species associations but the pure-stand nature of halophytic vegetation made most identification simple.

4.2.2 Relating zonation to mean sea level

A site for floral and faunal zonation studies was established on the marsh bank of Modderspruit (Fig. 3.4). Distribution and height of plant species relative to Spring Low Tide levels were measured and drawn onto a contour map. A surveyor's level was set up in the Limonietum Zone. Water level was marked with stakes at the lowest limit reached by Spring Low Tide. Distance and angle measurements of transects were made at 10 cm height intervals for mapping the area with contour lines. The boundaries of the plant zones were surveyed similarly and drawn on the contour map. Tidal level measurements in the Swartkops Estuary (McCallum, 1972f) showed Spring Low Tide levels at 0,25 m below Mean Sea Level. Water level and contours were corrected accordingly to give heights relative to Mean Sea Level. The mean sea level used in the study is that adopted by the Trigonometrical Survey Office and based on the average of mean sea levels measured from 1897-1926 (McCallum, 1972f).

4.2.3 Measurement of substrate characteristics

4.2.3.1 Particle size analysis

Substrate samples were taken from each plant zone at Modderspruit. Duplicate soil cores (25 cm deep) were collected and the soil thoroughly mixed for representative sampling.

The procedure of mechanical analysis by wet sieving was followed (Morgans, 1956). Data were processed according to the methods of Folk and Ward (1957) on the recommendation of Field (1971).
Subsamples of the different size fractions (Wentworth scale, see Morgans, 1956), sorted by wet sieving were ovendried at 80°C for 24h, then ashed in a muffle furnace at 450°C for 5h to determine organic content.

4.2.3.2 Substrate content

Subsamples of mixed soil cores were treated as above for organic content. Nitrogen content was analysed according to the standard micro-Kjeldahl method (Hesse, 1971). All samples were duplicated and repeated until the error was within 1% of the mean.

Salinity measurement was carried out on samples collected at the same time at Low Spring Tide in winter when evaporation was minimal. Mud samples were collected in plastic bags from depths of 1-5 cm and 25-30 cm within the plant zones. Centrifuging at 4000 rpm for 5 min yielded a drop of water, the salinity of which was measured by means of a refractometer.

4.2.4 Measurement of biomass

In December, duplicate quadrats (0,25 m^2) were laid in a rough transect up to the Limonietum to sample pure stands of the emergent intertidal halophytes. Cover-abundance was estimated. All aerial shoots rooted within the quadrat were clipped with hand shears at ground level. Samples were washed and oven dried (80°C for 72h). *S. maritima* material was sorted into Live and Dead Material. Duplicate soil cores of 25 x 25 cm x (root depth) were dug within the areas cleared by harvesting. Mud samples were washed over a 1 mm^2 mesh sieve to separate out the root material and oven-dried (80°C for 72h) before weighing.

4.3 RESULTS

4.3.1 Vegetation map of the Swartkops estuary

In Fig. 4.1 the distinguishable plant communities are mapped. Four major zones or associations were recognisable : the Zosteretum (pure *Zostera* stand); the Spartinetum (pure *Spartina* stand); the Arthrocnemetum-Limonietum (mixed stand); (*sensu* Macnae, 1957) as well as pure stands of *Triglochin bulbosum* L. The conspicuous bright red colour reflected by *Zostera* and *Triglochin* could be due to the health and vigour of the plants or simply indicate the waterlogged nature of the mud surface.

Although the areas covered by the Tall streamside Spartina shoots contrasted as a darker red against the paler colour of the Medium height shoots occurring further inland, the scale of this detail was too small for mapping purposes. Thus both height forms of Spartina were classed as the Spartinetum.

A comparison of the vegetation map (Fig. 4.1) with a map drawn 20 years ago (Macnae, 1957) shows that, apart from the loss of part of the salt marsh by the building of the National road, there has been very little change to the general structure of the salt marshes. The courses of minor drainage creeks have altered but this appears to be a manifestation of the naturally dynamic state of the marshes which are subject to variable tides, sedimentation and floods. From observations in the field the gradual silting up of drainage creeks and the development of new canals following different courses, was noted.

The effect of bait-digging along the edge of S. maritima stands is apparent from the bare ground between the Spartina and Zostera beds. Macnae (1957) warned about the effects of this practice 20 years ago but to no avail. Unfortunately his map is not detailed enough for a comparison of fringing communities then and now. Field studies have shown that bait-digging in this area weakens the fringing belt of Spartina.

4.3.2 Zonation of the salt marsh vegetation relative to mean sea level

Fig. 4.2 shows a clear relation between plant species distribution and height above mean sea level. Species found along the transect from the water's edge in order of appearance were:
Zostera capensis Setchell; S. maritima; Triglochin bulbosum L.; Arthrocnemum perenne (Mill.) Moss ex Fourcade; Chenolea diffusa Thunb.; and Limonium linifolium (Linn.f.) O. Kuntze.

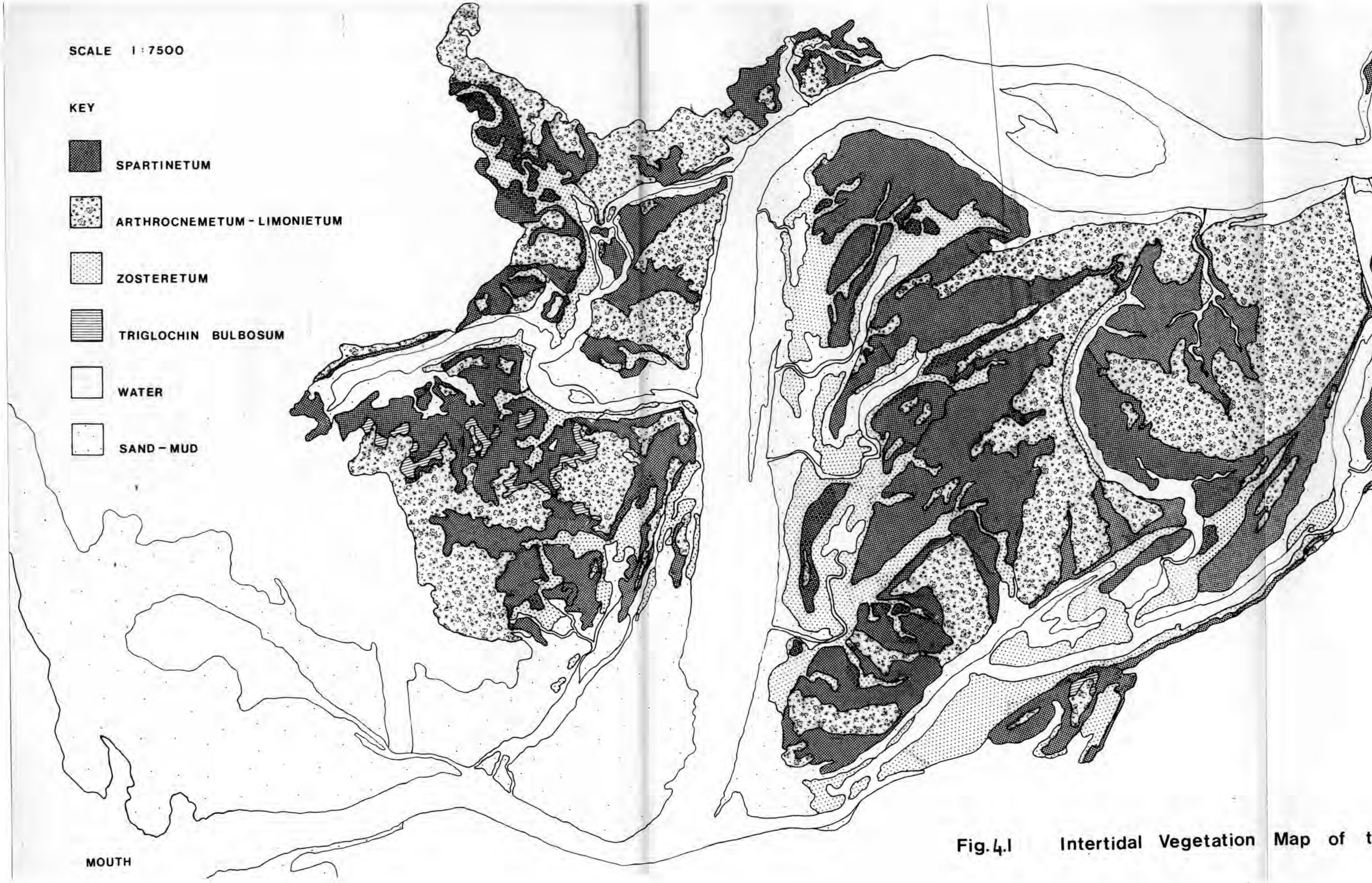


Fig. 4.1 Intertidal Vegetation Map of t

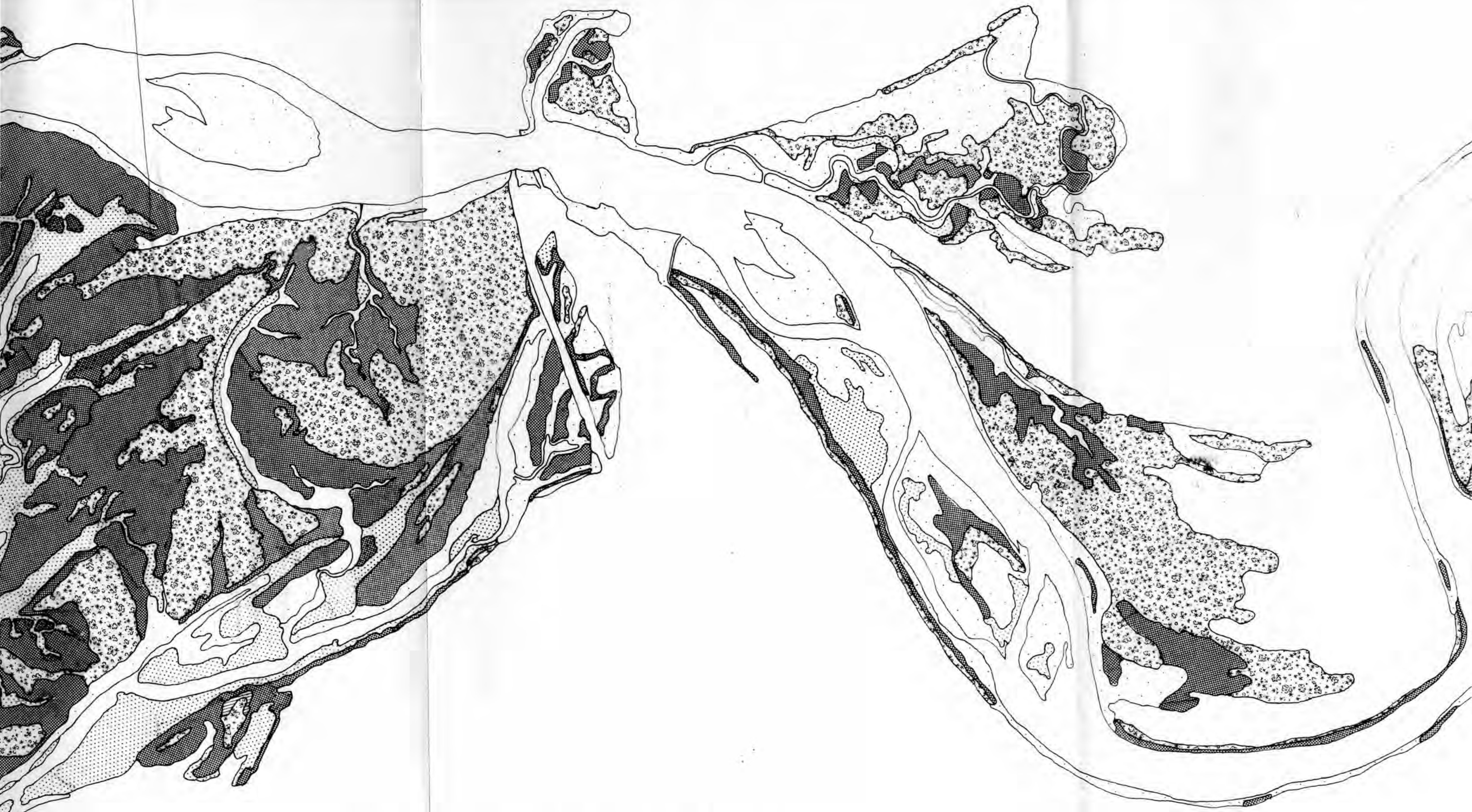


Fig. 4.1 Intertidal Vegetation Map of the Swartkops estuary

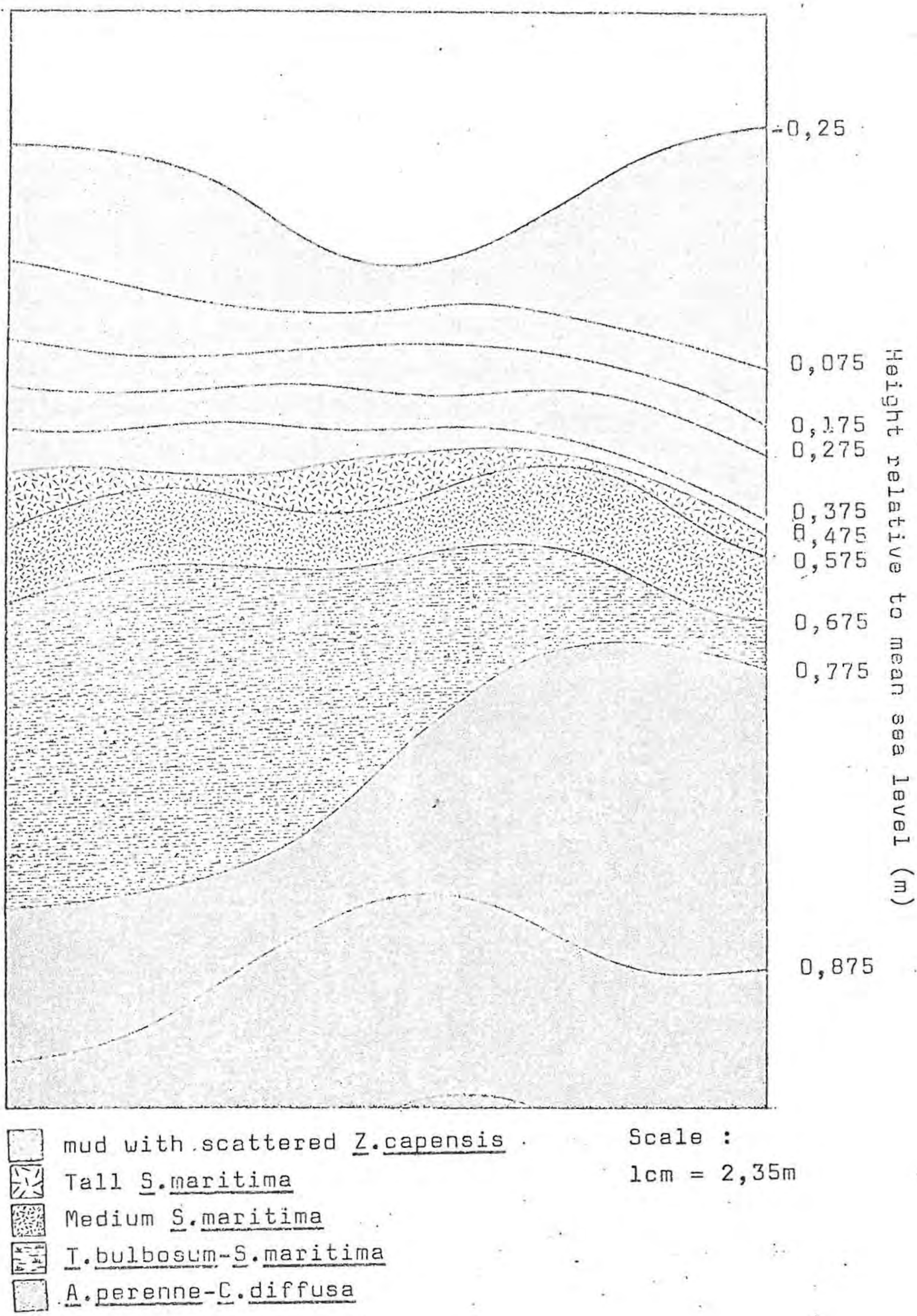


Fig. 4.2 Zonation of marsh vegetation relative to mean sea level at the Moddersspruit Station. (M.S.L. from Trig.Survey)

There is a clear relationship between zone height at Modderspruit and mean sea level, with each zone delimited by elevations as small as 10 cm. The extremely narrow nature of the elevational distribution of salt marsh species and distinct vegetational changes occurring within 30 cm and even about 2,5 cm have been found by Hinde (1954), Adams (1963) and Vogl (1966). A change in ground level of only 7 cm occurred between pure stands of two salt marsh plants Spartina foliosa and Salicornia virginica (Mahall and Park, 1976a). Similarly a distinct relation between zone heights and mean sea level was found by MacDonald (1970) at the Kowie estuary salt marshes.

Although mean particle size of substrate samples from different plant zones did not vary and described all samples as fine sand, there appeared a slight gradation from very little silt and clay in the lower Spartina zone to higher proportions of fine material in the upper zones.

The slight increase in organic content in the 63 µm particle size may indicate the level at which microbial activity in the soil functions. In fact, Hanson and Wiehe (1977) found that 70% of microbial activity in detritus is associated with size particles of 14-180 µm.

4.3.3 Substrate characteristics of the vegetation zones

4.3.3.1 Particle size characteristics

Particle-size cumulative curves used for determining statistical parameters were similar for all samples (Fig. 4.3) The nature of the substrate in terms of mean particle size, sorting and frequency distribution, were determined graphicall from reading selected percentiles off the cumulative curves (Table 4.1).

The graphic mean size characterises the general nature of the substrate. Values for the different zones range between phi-values of 2,22 and 2,63 indicating a generally fine sand structure. The standard deviation is a measure of sorting indicating the poorly sorted nature of substrate in all the zones except for both S. maritima forms, where there is moderate sorting.

Characterisation of a substrate sample by the mean and standard deviation is unlikely to have any biological meaning (Field, 1971). Frequency distribution of particle size was subjected to more vigorous measures. Inclusive Graphic Skewness, Sk_1, (sensu Folk and Ward, 1957) is a measure of overall skewness i.e. it determines asymmetry at the central part of the distribution and at the extremes, and is independent of the spread of the curve. The positive value of substrate sampled in the Tall *S. maritima* belt indicates only a "tail" of fine grains. The distribution is nearly symmetrical about the mean according to the value $Sk_1 = +0{,}0517$, which is close to zero. Medium *S. maritima* substrate is similarly almost symmetrical, with $Sk_1 = -0{,}0213$. The negative value, however, indicates a "tail" of coarse grains. Substrates from the other zones also have a "tail" of coarse grains and show negative skewness, particularly *A. perenne* zone samples. These are very negatively skewed, with $Sk_1 = -0{,}3878$. Graphic kurtosis, K_G, is a measure of the ratio of the sorting in the extremes of the distribution, compared with that in the central part. It is a more vigorous test of the normality of the distribution than Sk_1 (Folk and Ward, 1957). Substrates from both *S. maritima* zones are classified as mesokurtic or having normal distribution. All other zones are platykurtic (=deficiently peaked) indicating that particle size is better sorted at the tails than in the central area.

4.3.3.2 Contents of substrate of vegetation zones

Differences in total organic content exist between substrates of the different plant species, with *S. maritima* zone having the lowest value of 4,22%. There is a tendency for the substrate of higher-occurring species to contain higher percentages of organic matter. The highest value of 8,19% measured in *A. perenne* soil is comparable to organics in the *S. alterniflora* stands at Rhode Island Sound, U.S.A., which are in the order of 9,2-11,5% (Nixon and Oviatt, 1973b).

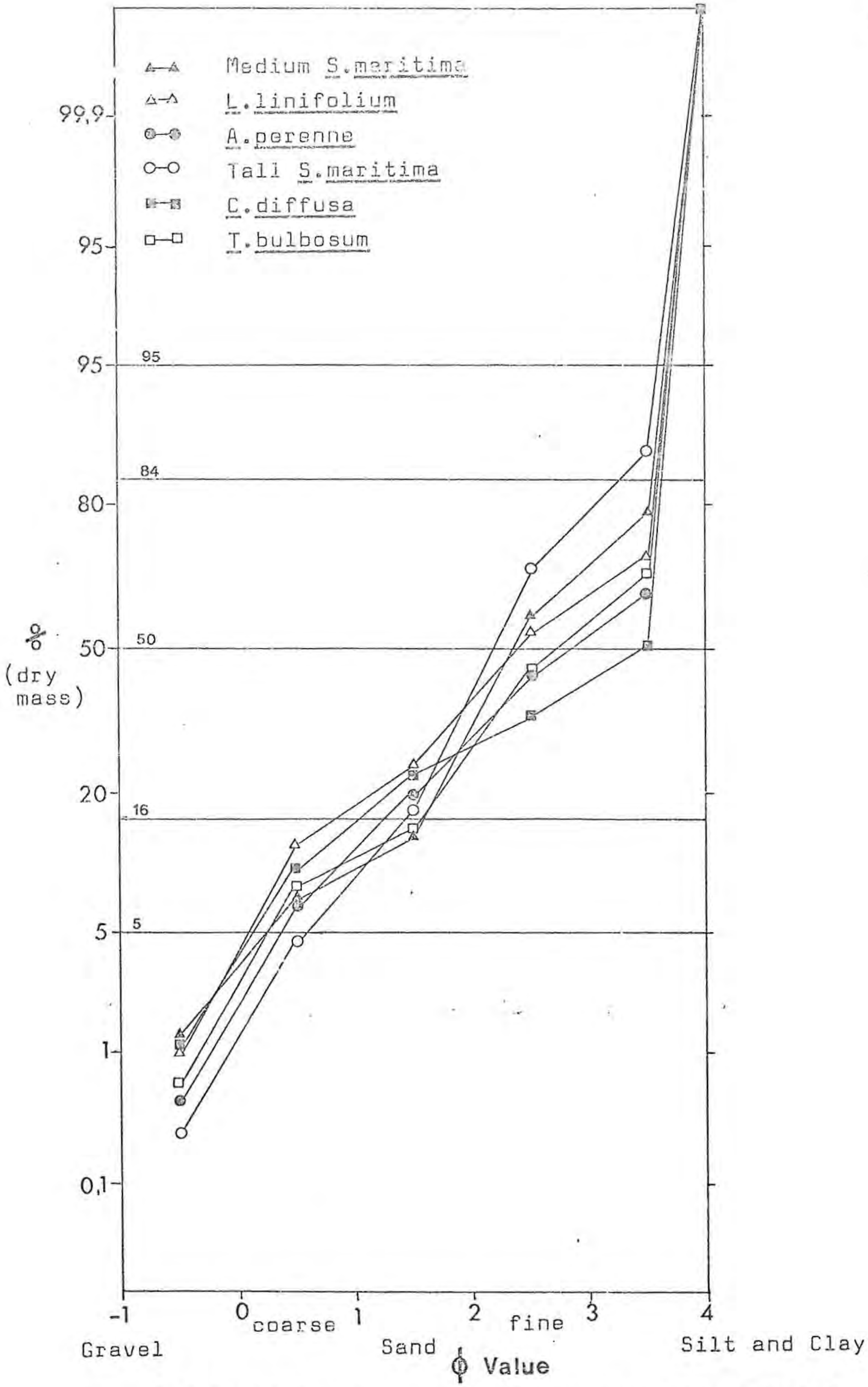


Fig. 4.3 Particle-size cumulative curves for sediment samples taken in the vegetation zones at Modderspruit. Symbols denote mean of two samples.

Ashing of different size fractions of soil (Wentworth Scale, Morgans, 1956) showed similar patterns for all zones (Table 4.1). Organic content decreased with particle size, but showed a slight increase at the 63 µm grade. It appears that the larger particles of substrate from each zone has the highest organic content.

The discrepancy between total organic content and the sum of organics of the particle fractions may be explained by inefficient mixing and subsampling in the analysis of total organic content.

Soil nitrogen levels did not correlate with organic content as would be expected. Nixon and Oviatt (1973b) found a significant correlation between sediment organic content and nitrogen in salt marshes of Rhode Island. Their values ranged from 0,49% to 0,36% organic content of sediment which are much lower than the Swartkops figures. Higher estimates in the order of 1,54%-0,928% were obtained in *S. alterniflora* marshes in New Jersey (Squiers and Good, 1974)

4.3.4 Biomass of the plant species of the salt marsh zones

Samples taken across the intertidal zone included: *Z. capensis*; Tall and Medium *S. maritima*; *T. bulbosum*; *A. perenne*; *C. diffusa* and *L. linifolium* (Table 4.2). Percentage errors of duplicate samples were less than 20%. Results for *Z. capensis* are expressed for whole plants. Aerial and below-surface dry biomasses were given separately for the other species.

Dry biomass of *A. perenne*, *C. diffusa* and *L. linifolium* were higher than for *S. maritima*, which implies that these plants may be more important that *S. maritima* in terms of potential production. Their role as producers has not been considered by other authors, making comparisons in terms of contribution to estuarine ecosystems difficult. The greater part of the biomass of these other plants lies in woody stems and lignified tissue, which may imply slow growth and turnover.

TABLE 4.1 CHARACTERISTICS OF SUBSTRATE IN INTERTIDAL ZONES AT MODDERSPRUIT

SUBSTRATE CHARACTERISTICS		SPECIES IN VEGETATION ZONES					
		Tall *S. maritima*	Medium *S. maritima*	*T. bulbosum*	*A. perenne*	*C. diffusa*	*L. linifolium*
Mean particle size (Ø value)		2,22	2,46	2,63	2,56	2,66	2,24
Standard deviation		± 0,92	± 0,97	± 1,04	± 1,09	± 1,22	± 1,24
Inclusive graphic skewness (Sk_1)		0,0517	-0,0213	-0,2634	-0,3878	-0,1881	-0,2003
Graphic kurtosis (K_G)		1,0691	0,9423	0,8522	0,7377	0,7455	0,7108
Organic content(%) of different particle size fractions (µm)	1000	42,96	39,52	36,21	27,47	47,42	41,11
	500	12,61	15,09	9,99	8,88	10,13	10,02
	250	7,11	10,34	7,37	8,02	12,97	7,32
	125	2,13	2,86	2,76	4,15	7,03	3,07
	63	5,04	4,66	4,99	5,27	8,15	7,04
Total organic content (%)		4,22	5,04	4,37	8,19	7,57	7,45
Nitrogen content (mgN g^{-1} dry soil)		2,2691	0,8865	0,8882	-	0,8237	-
Salinity at Depths (‰)	1 - 5 cm	35,5	38,0	-	46,5	70	-
	25 - 30 cm	34	36	-	46,5	62	-

TABLE 4.2 ABOVE AND BELOW SURFACE BIOMASS OF INTERTIDAL VEGETATION AT MODDERSPRUIT

PLANT SPECIES	AERIAL BIOMASS	BELOW SURFACE BIOMASS	COVER
	(dry g m^{-2})	(dry g m^{-2})	(%)
Tall *S. maritima* Live	592,32 (2%)[1]	5826 (4%)	75
Dead	97,70 (1%)		
Medium *S. maritima* Live	500,80 (10%)	6303 (20%)	65
Dead	92,14 (20%)		
T. bulbosum	210,0 (6%)	1761 (11%)	80
A. perenne	1290,2 (19%)	229 (4%)	90
C. diffusa	889,0 (9%)	579 (2%)	70
L. linifolium	563,28 (8%)	38 (3%)	50
Z. capensis	[2]139,44 (13%)		

[1] Values in brackets indicate percentage error

[2] Whole plant

Lubke and Curtis (1977) measured below surface biomass of different aged stands of local *Spartina* species on the banks of the Kowie River. Young, intermediate and mature stands showed similar aerial : below surface ratios to the Swartkops stands. Below surface biomass of *S. maritima* was much higher than for the other species. This finding may explain the extremely high numbers of nematodes found by Furstenberg (pers. comm.) in *Spartina* substrate compared to soil samples from the other zones.

There are few studies on below surface biomass of salt marsh species (Mahall and Park, 1976a), probably because of the laborious and tedious nature of the work required. Valiela, Teal and Persson (1976) found seasonal variation in below surface biomass related to the growing season of the aerial parts. Maximum biomass of *S. alterniflora* and *S. patens* were 8450 g m^2 and 8750 g m^2 for depths of 20 cm respectively. Comparisons are difficult in view of the difference in units used, as local species were sampled to depths of 40 cm. In addition, aerial biomass borne by the different species varies, and *S. maritima* in Swartkops does not show the marked seasonality of the other species. (see Chapter 5).

4.4 DISCUSSION AND CONCLUSIONS

Field observation during photo-interpretation led to speculation on the role of interspecific competition at higher levels. The clear differentiation between zones of pure stands near water courses becomes less marked at higher levels where zones are broadly classified according to their mixed nature : the Arthrocnemetum and the Limonietum. On a large scale, the vegetation map describes the findings of Pielou and Routledge (1976) that overlapping of upslope zones is the result of interspecific competition, whereas distinct downslope zone limits are set by the physiological tolerance for submersion in salt water.

The highest soil nitrogen levels were measured in the Tall *Spartina* zone. There is some controversy over the theory of nitrogen as a limiting factor in salt marsh production studies, with Gosselink (1970), Valiela and Teal (1974) and Steever, Warren and Niering (1976) as proponents of the theory. Ranwell (1964) and Mendelssohn and Marcellus (1976) discount the influence of soil nitrogen on salt marsh plants.

An important fact which is ignored in the literature dealing with soil characteristics as primary factors governing zonation, is that the presence of the plants themselves is as much a controlling factor of substrate character as vice versa. Transplant and colonisation studies of S. capensis on the banks of the Kowie River indicated that sandy, dense soil in newly colonised areas developed into less dense, silty soil in mature stands of Spartina. These changes were accompanied by changes in other soil properties such as chloride, water soluble salts, pH and water-holding capacity (Lubke and Curtis, 1977).

A review of the literature shows that there is disagreement over the influence of different factors on controlling zonation patterns.

Tide-elevation-salinity interactions are proposed as the major governing factors by Hinde (1954), Adams (1963) and Clarke and Hannon (1967, 1969, 1970), Chapman (1974), Mahall and Park (1976b, 1976c), MacDonald (1970). In contrast, Lagna (1975) reviewed the literature and stated that factors other than tide-elevation are important, eg. aeration, salinity, drainage and soil factors. Clarke and Hannon's (1967) zonation studies showed that soil characters were unimportant and Mahall and Park (1976c) concluded that soil aeration is not a determining factor in zonation. Salinity was not found to be a major factor by Parrondo, Gosselink and Hopkinson (1978). These disagreements are unreasonable in view of what Zedler (1977) so obviously states. He states that change in elevation brings about change in the environmental factors such as salinity, soil etc. Possibly the best attitude is shown by Chapman (1938), who states that few environmental factors act wholly independently of the others and that interpretation of studies of one or two factors must be done with caution. Judging by the disagreement, his advice has been largely ignored.

MacDonald (1970) made detailed studies of causal factors of zonation at Kowie River and concluded that tide-elevation-salinity play a major role, although complex interactions of soil characters are to be considered.

The proximity of the Kowie estuary to the Swartkops, the similarities in zonation and the distinct relationship between zone heights and mean sea level on both marshes, allow conclusions to be extrapolated from the Kowie for the Swartkops marsh. Ignoring soil properties as causal factors on tautological grounds, the major controlling agents of zonation are proposed as tide-elevation-salinity factors at lower elevations, and competition between species at higher levels where stress caused by varying lengths of inundation is less.

CHAPTER 5

BIOMASS, COMMUNITY STRUCTURE AND GROWTH OF S. MARITIMA

5.1 INTRODUCTION

The dependence of the ecosystem on the primary producer has been re-emphasised by Squiers and Good (1974). For the purposes of the Swartkops ecosystem project it was necessary to know the amount of potentially available food resources. Thus an estimate of the area of Swartkops salt marsh covered by, and the biomass of *S. maritima* was required.

Primary production measures are generally based on temporal increases in biomass (see Chapter 6). Thus seasonal sampling of biomass through the year was necessary. In addition to seasonal biomass and production, seasonal changes in composition are essential for understanding the physiological ecology of the species and the nutritional ecology of the system (Squiers and Good, 1974).

Because of the lack of any information on the growth of *S. maritima*, more detailed studies on the seasonal behaviour of the Swartkops community were made. The community structure in terms of the numbers of different aged shoots was monitored for any seasonal changes. It was hoped that this would provide a new means of measuring seasonal production (see Chapter 6).

Shoot mortality and leaf turnover may contribute significantly to estimates of primary production, making growth monitoring of shoots essential for understanding the contribution of individuals to overall biomass and structure of the plant community (Hardisky and Reimold, 1977).

5.2 METHODS

5.2.1 Area determination

The vegetation map traced off infra-red aerial photographs was used for area determinations (see Fig. 4.1). The use of remote sensing as a means of estimating cover has been reviewed and investigated by Stroud and Cooper (1969) and found to be successful for relatively pure stands of salt marsh vegetation, particularly S. alterniflora. The same method on the same species yielded cover estimates of about 0,5% error in Nova Scotia (Hatcher and Mann, 1975).

All areas covered by S. maritima on the map were defined and measured by planimetry. The method of a dot-grid overlay was used to measure the total intertidal salt marsh area outlined on ortho-photographs (McCallum, 1972d). The area occupied by the S. maritima community was expressed as a percentage of total salt marsh area.

5.2.2 Monitoring seasonal changes in Spartina biomass

5.2.2.1 Site selection

Representative sites for biomass sampling and growth measurements of S. maritima were selected in the best developed salt marshes between Swartkops Village and Amsterdamhoek (see Fig. 1.1 and Macnae, 1957). Within the extensive S. maritima stands, two areas were chosen to represent local variation (see Fig. 3.4). The River Station was established next to the main channel for average river conditions while the Creek Station was chosen to include any local variation as a result of differences in hydrology and substrate between the river and creek environments (see Chapter 3.2).

5.2.2.2 Sampling by harvesting

Sampling was carried out every month from September 1976 to January 1978 except when only one sampling collection was made for the November /December periods. An effort was made to coincide sampling time with Low Spring Tide so that tidal removal effects on dead biomass were consistent.

Quadrat size of 0,25 m^2 was chosen as the largest size possible for efficient harvesting. This size is accepted as standard for grassland studies (Milner and Hughes, 1970).

The minimum number of samples required for statistically acceptable results was determined from initial harvesting trials. Three samples of each height-form yielded dry Live biomass estimates of less than 10% error, which is within the limits allowed for clip-plot studies by IBP standards (Milner and Hughes, 1970). After February, however, the number of samples was increased to narrow the margin of error as far as was practicable. Logistic limitations were imposed by the sheer bulk of the 20 harvested samples which required almost 3 weeks of each month to collect and process.

At both Stations, the quadrats were placed about 2 m apart in a transect across the Spartina zone, starting at its lowest limit. The first five quadrats were laid in the fringing belt of Tall Spartina and the last five plots in the more elevated Medium height form.

Samples included all shoots rooted within the quadrat which were cut at ground level, as well as dead shoot material. In the laboratory, shoots were washed clean of mud and sorted into Live and Dead components on the basis of green tissue. Dry biomass was determined after the sorted material had been dried in a forced-air drying oven at 80°C for 48 h. Higher temperatures resulted in ignition of early samples. Thus 80°C was considered safer, and judged sufficient to stop all metabolic activity (Squiers and Good, 1974).

The number of Live and Dead flowering culms was noted each month.

Subsamples of dried Live and Dead material were ground in a mill for analysis of composition.

Biomass results were expressed per square meter. Differences in biomass amongst Tall and Medium S. maritima at each

Station, and variation amongst monthly samples during the year were tested for sigificance by means of two-way analysis of variance (Bishop, 1966).

5.2.3 Analysis of seasonal composition of Spartina

Nitrogen content of dried, ground sub-samples of Live and Dead *S. maritima* was determined by the standard micro-Kjeldahl method (Hesse, 1971). Results were expressed as a percentage of one gram dry mass.

Carbon content was analysed on a Carbon Nitrogen Hydrogen Analyser by the South African Wool and Textile Research Institute. Results were expressed as a percentage of one gram dry mass.

Organic content (=ash-free content) were determined by ashing dry, ground material in a muffle furnace at 450°C for 5h. Samples were removed from the cooled furnace, dried in an oven at 80°C for 4h, then cooled in a desiccator, before weighing. This figure was then expressed as a percentage of the original dry mass.

Potential energy content was measured on dry, ground samples by means of an adiabatic bomb calorimeter. Results were expressed as joules per one gram dry mass.

All analyses were done in duplicate or repeated until the error was within 1% of the mean for energy values and 5% for nitrogen and organic contents. Consecutive monthly values were averaged for seasonal estimates.

5.2.4 Measurement of seasonal changes in community structure

From December 1976 to November 1977, three out of the five dried, harvested samples of each of the Tall and Medium shoots collected at the River Station were processed. All individual shoots within each sample were weighed and the dry mass sorted into class sizes of 0,1 g intervals. Results for the three samples were averaged and expressed as percentage frequency for the whole sample. These percentage frequencies for each size class were expressed as histograms.

5.2.4.1 Measurement of shoot density and mean shoot mass

Additional data obtained by this method were density and mean individual shoot mass. Average number of shoots in $0{,}25\ m^{-2}$ was determined each month from three quadrats and expressed as density per square meter. Average monthly density divided into corresponding biomass value gave mean individual shoot mass. Thus seasonal changes in density and mean individual shoot mass were monitored.

5.2.5 Determination of Fresh height : Dry mass relation of S. maritima shoots

The height of fresh, washed shoots was measured. Each shoot was then labelled and dried in a forced-air oven at 80°C for 24h. The dried shoots were cooled in a desiccator and then weighed. The data were fitted to a power curve by the method of least squares regression.

5.2.6 Growth of S. maritima

At both River and Creek Stations, 50 Tall and 50 Medium *S. maritima* shoots were labelled with numbered insulating tape and a plastic tag tied to the base of the shoot. Shoots were selected as the nearest to a nylon thread stretched between two stakes, so that a range in size was obtained. From March 1976 to January 1978, monthly readings of shoot heights from tagged base level to growing tip were taken. Numbers of new and old leaves present each month were counted and development and loss by abscission were monitored by numbering leaves with a felt-tipped pen.

Leaf mass of a range of sizes was weighed as dry weight. These data were grouped into size classes : small; medium; large, according to the size of shoot from which they were taken; 0-0,19 g; 0,2-1,09 g; 1,1 g respectively. Mean dry mass for each size class was calculated. These masses were multiplied by the appropriate frequency of shoots per square meter (data from Fig. 5.4 corrected for m^2) for estimation of leaf production.

Loss of labels, temporary covering of tags by a fine layer of silt and loss of marker stakes by human interference were some of the problems encountered. Gaps in data on the 200 marked shoots necessitated the combination of River and Creek Station results for an average growth curve for Tall shoots and an average in growth curve for Medium shoots. Initial development was monitored from young shoots which grew in close proximity to marked shoots, thus giving height for shoots of known age.

A curve of height against months of the year was plotted for the plants of known age. This curve was extrapolated by plotting heights recorded for the other shoots against the appropriate months of the year. In this way age in terms of years was estimated for older shoots. These plotted points of height recorded in different months accounted for seasonality.

Three possible types of growth curve : exponential; symmetrical; and unsymmetrical sigmoid curves, were fitted by the method of least squares regression to the above plotted data. The BMDP 3R computer program for non-linear regression was used (Dieckman, 1978). Maximum heights of Tall and Medium shoots were used for the asymptotic heights respectively. Coefficients of determination were calculated for the curves.

The three types of growth curve are described by the equations below.

1. The Von Bertalanffy growth equation:

$$L_t = L_\infty \ (1-e^{-k(t-t_o)})$$

where L_t is the length (=height) at time t ;
L_∞ is the asymptotic length (=height) ;
k is the growth rate and t_o is the time of initiation of growth (Jones, 1976).

2. The logistic equation:

$$N_t = \frac{N_{max}}{1 + e^{-a(t-t_o)}}$$

where N_t is length (=height) at time t ;
N_{max} is the asymptotic length (=height) ;
t_o is equal to $\frac{N_{max}}{2}$ or age at half the asymptotic length ;
a is the growth rate (Dieckman, 1978).

3. The Gompertz equation:

$$y = ab^{c^t}$$

where a is the asymptotic length (=height) when $t = \infty$;
b and c are obtained by linear estimation ;
estimates of c lie at $0<c<1$ and of b at $0<b<1$
(Riffenbergh, 1959; Newman, 1969).

There is no a priori reason for preferring any one of these equations and their use is best assessed on their "goodness of fit" to the data (Jones, 1976).

5.3 RESULTS

5.3.1 Area covered by S. maritima on the Swartkops marshes

Possible error incurred from aeroplane tilt was minimal according to the tilt indication on the aerial photographs. Topographic variation on the marsh was not greater than 1,4 m by definition (spring tide range = 1,4 m) so that any inaccuracy as a result of the method of remote sensing is negligible, apart from possible edge distortion on the photographs.

Total area covered by *S. maritima* = 82,3275 ha
Total area of intertidal salt marsh = 363,217 ha
Thus *S. maritima* covers 22,7% of the total intertidal marsh.

5.3.2 Seasonal changes in Spartina biomass

Percentage error of dry biomasses for all sites rarely exceeded 10%, and none exceeded 16%. Thus sampling yielded representative results according to IBP standards (Milner and Hughes, 1970).

Tall shoots sampled at the River Station showed marked fluctuations in Live matter but less variation in Dead material (Fig. 5.1). A more consistent seasonal pattern was shown by the samples from the other three sites (Fig. 5.1 and Fig. 5.2).

Two-way analysis of variance showed a significant difference in biomass between River samples of Tall and Medium forms, probability = 0,02, but insignificant differences during the year. The marked biomass fluctuations of the Tall shoots at the River Station appear to be at random. This may have masked any significant seasonality of the Medium shoots in the two-way analysis of variance test. A one-way analysis of variance was performed on the Medium form biomass data and seasonal variation was found to be significant, with probability = 0,05.
Two-way analysis of variance on Creek Station biomass data showed a highly significant difference between Tall and Medium shoots, probability = 0,01. Variation due to seasonal effects was significant for both forms at the Creek, probability = 0,05.

Peak flowering season of S. maritima extended from November to March for both Tall and Medium shoots (Fig. 5.3).

5.3.3 Seasonal composition of Spartina

The composition of Live and Dead S. maritima in terms of potential energy, nitrogen content and carbon was almost constant through the year. Tendencies towards a spring maximum become clear with the averaging of monthly results into seasonal values (Table 5.1).

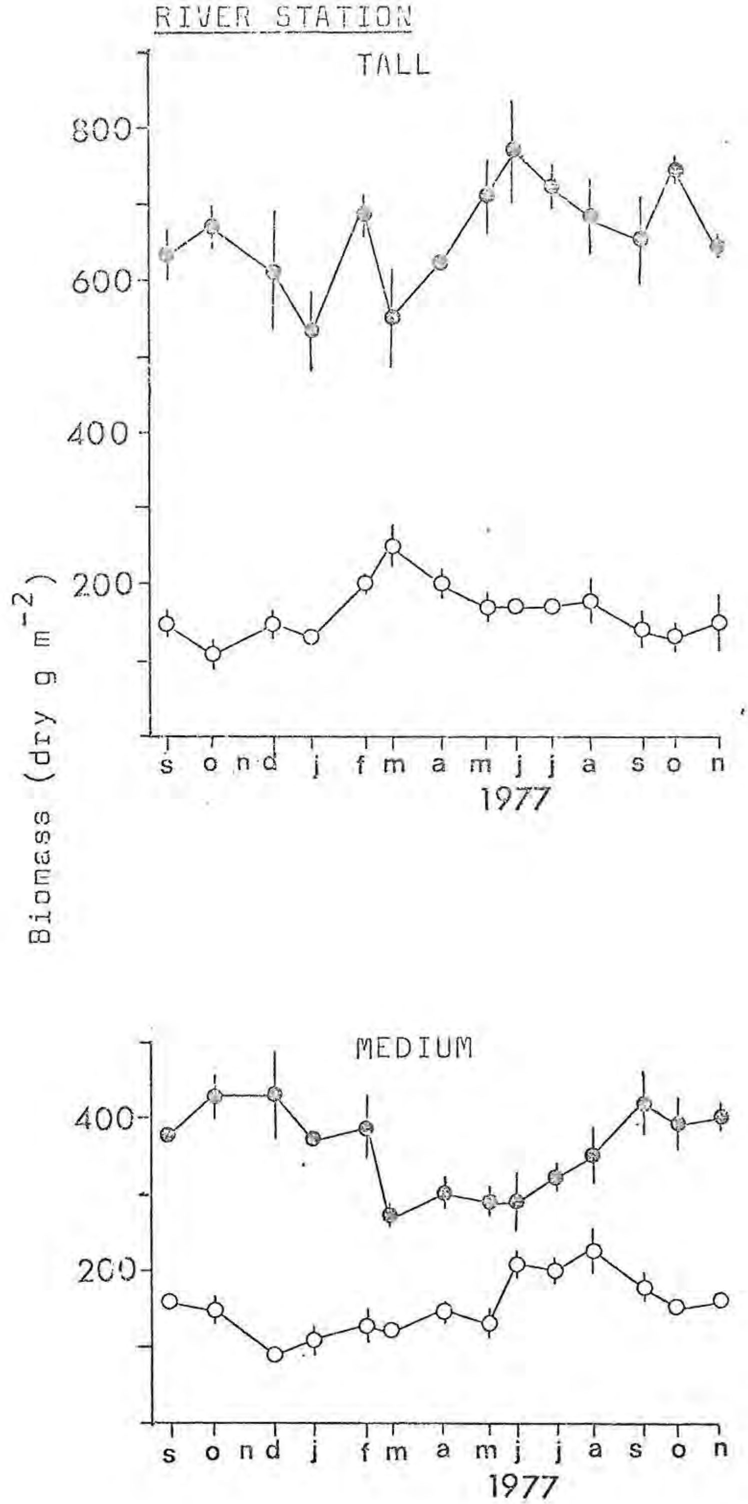


Fig. 5.1 Live (●) and Dead (○) biomass of Tall and Medium *S. maritima* shoots at the River Station. From September, 1976-February, 1977, points indicate the mean of 3 samples, and from March onwards, the mean of 5 samples. Vertical lines indicate two standard error units.

Live biomass of Tall and Medium shoots significantly different, $p = 0{,}02$. Seasonal variation in Tall Live biomass not significant. Seasonal variation in Medium Live biomass significant, $p = 0{,}05$.

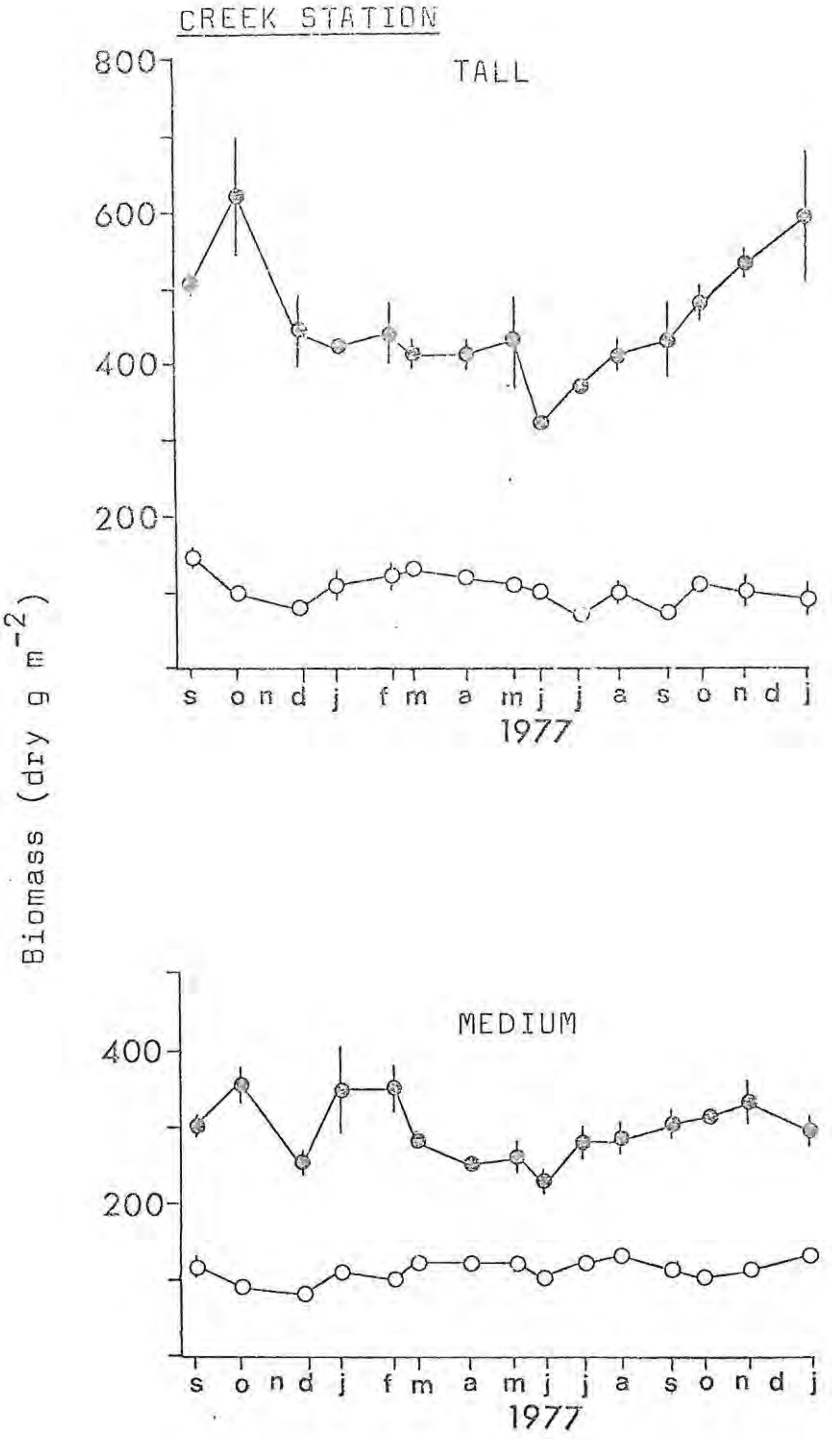


Fig.5.2 Live (●) and (○) Dead biomass of Tall and Medium *S.maritima* shoots at the Creek Station. From September,1976-February,1977, points indicate the mean of 3 samples, and from March onwards, the mean of 5 samples. Vertical lines indicate two standard error units.

Live biomass of Tall and Medium shoots significantly different, $p = 0,01$. Seasonal difference in both Tall and Medium shoots significant, $p=0,05$.

5.3.4 Seasonal changes in community structure

The community structure in terms of size and number of Tall and Medium shoots were similar and stayed almost constant throughout the year (Fig. 5.4). Disturbance of the Tall community did not appear to affect structure. The populations were strongly skewed with about 50% of the shoots less than 0,2 g (= 17,5 cm in height). The other half of the populations were spread in decreasing frequency from size classes 0,2 g up to 2,7 g. Tall *S. maritima* samples included larger shoots than the Medium samples.

5.3.4.1 Density and mean shoot mass

The variable nature of Tall data does not allow for easy interpretation of density data (Fig. 5.5), possibly because of the random effects of human interference. The Medium shoots show a marked drop in density in March, but increase gradually towards spring (Fig. 5.5). Mean shoot mass decreases after March (Fig. 5.6).

5.3.5 Fresh height : dry mass regression

Power curves fitted to data on fresh height to dry mass of individual shoots gave high values for the coefficient of determination, r^2=0,95 for Tall shoots and r^2=0,91 for Medium shoots (Fig. 5.7).

5.3.6 Shoot growth

Fig. 5.8 and Fig. 5.9 show the curves of best fit, determined by least squares regression, for growth data on Tall and Medium shoots respectively. They were the Von Bertalanffy and Gompertz growth curves respectively. The coefficient of determination, r^2, was high for both growth curves : r^2=0,90 for Tall shoot growth and r^2=0,97 for Medium shoot growth.

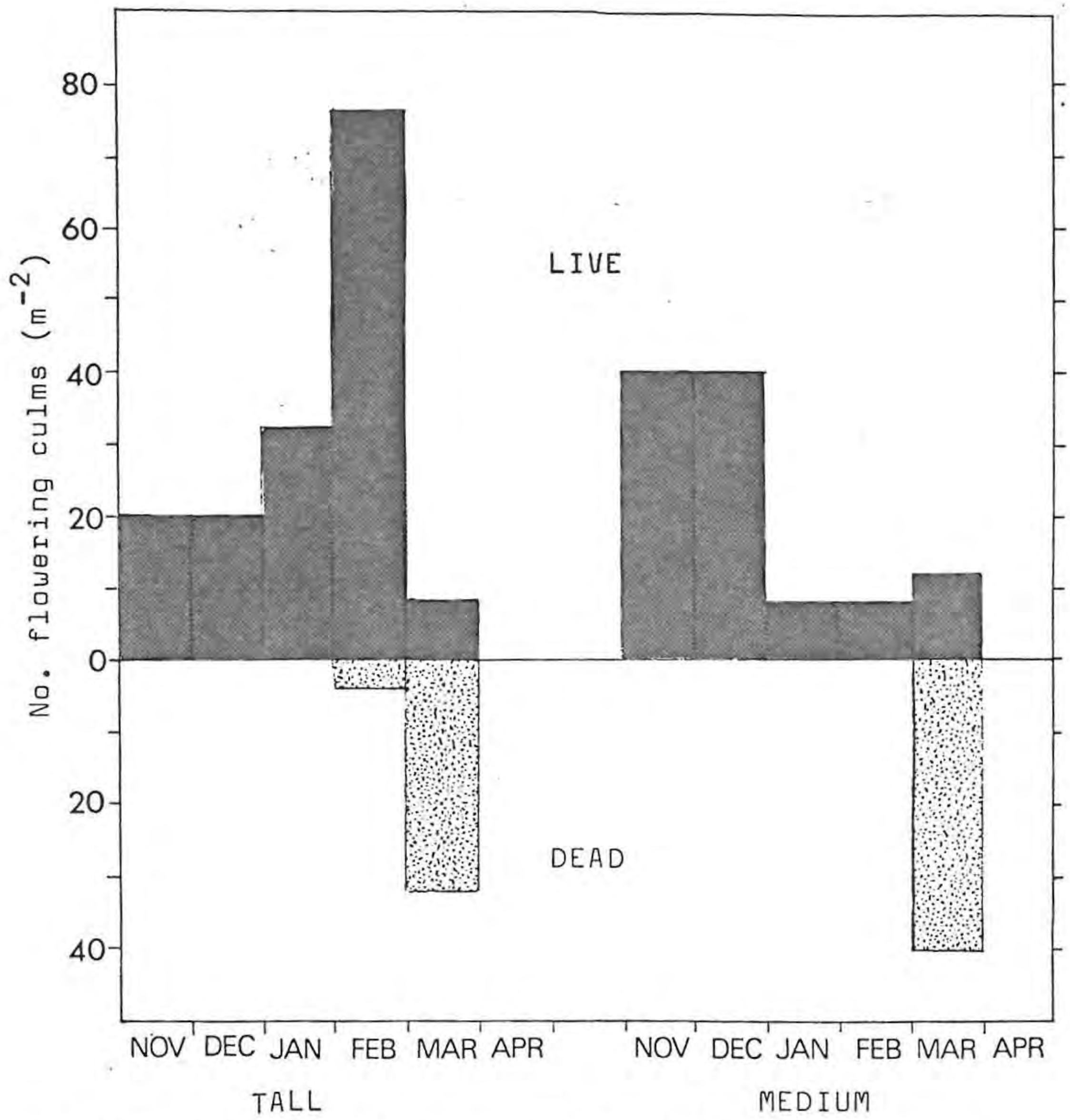


Fig. 5.3 Number of live and dead flowering culms of Tall and Medium S.maritima per square meter.

TABLE 5.1 SEASONAL COMPOSITION OF LIVE AND DEAD S. MARITIMA

	SEASONS				
LIVE	J F M	A M J	J A S	O N D	MEAN
Potential energy content ($J\ g^{-1}$ dry mass)	16662	16912	17760	17685	17255 ± 275,26
Organic content (% dry mass)	90,34	90,30	89,66	90,90	90,3
Nitrogen content (% dry mass)	1,2451	1,3675	1,3822	1,2022	1,2993
Carbon content (% dry mass)	42,30	43,13	44,60	42,70	43,18
DEAD					
Potential energy content ($J\ g^{-1}$ dry mass)	15642	15263	17113	16387	16101 ± 410
Organic content (% dry mass)	87,24	85,97	87,54	85,22	86,5
Nitrogen content (% dry mass)	0,8777	0,9592	1,0139	0,8897	0,9351
Carbon content (% dry mass)	39,85	40,93	43,10	39,00	40,72

± precedes standard error

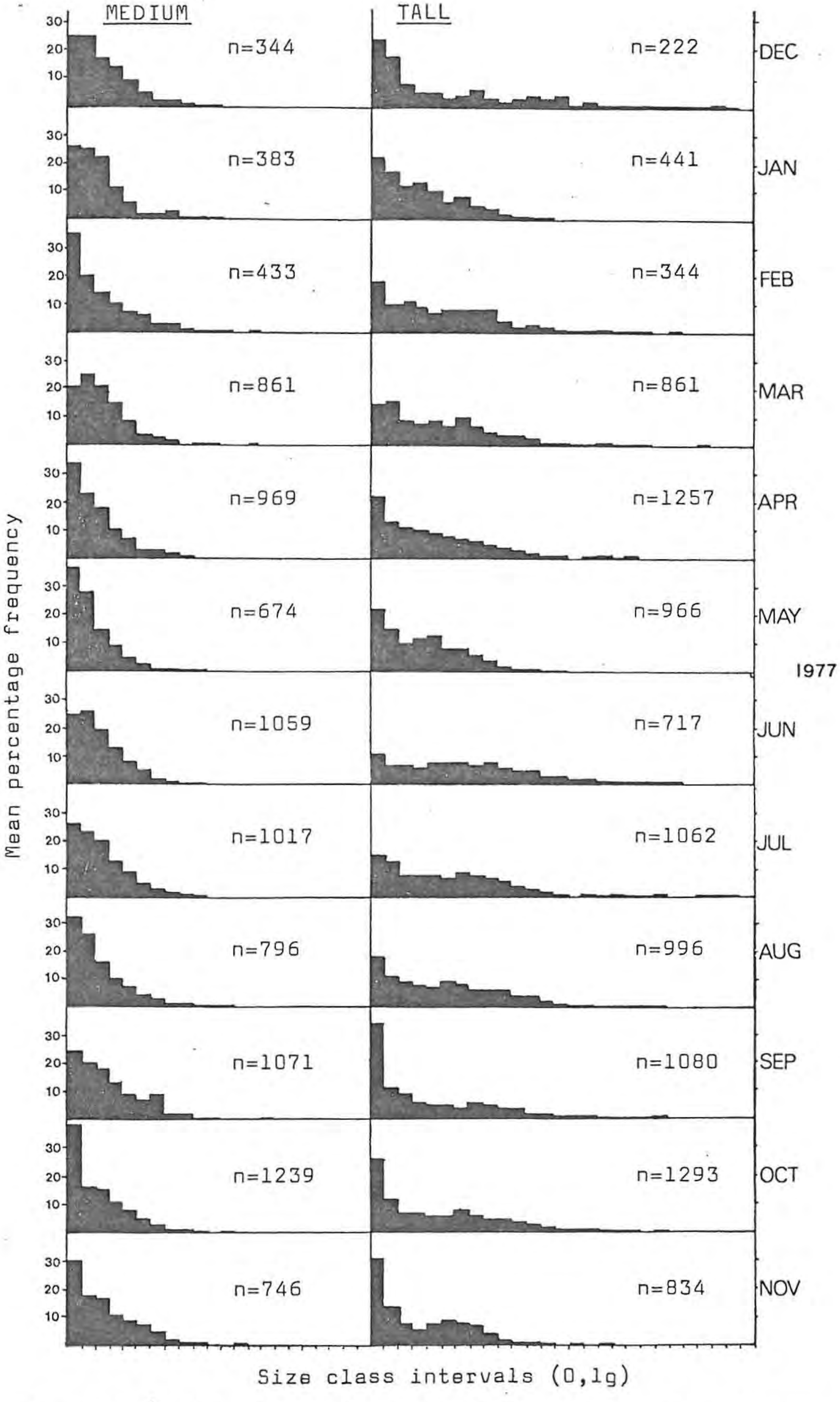


Fig. 5.4 Monthly frequency histograms of 0,1g size classes of Tall and Medium S.maritima at the River Station. n = no. individuals.

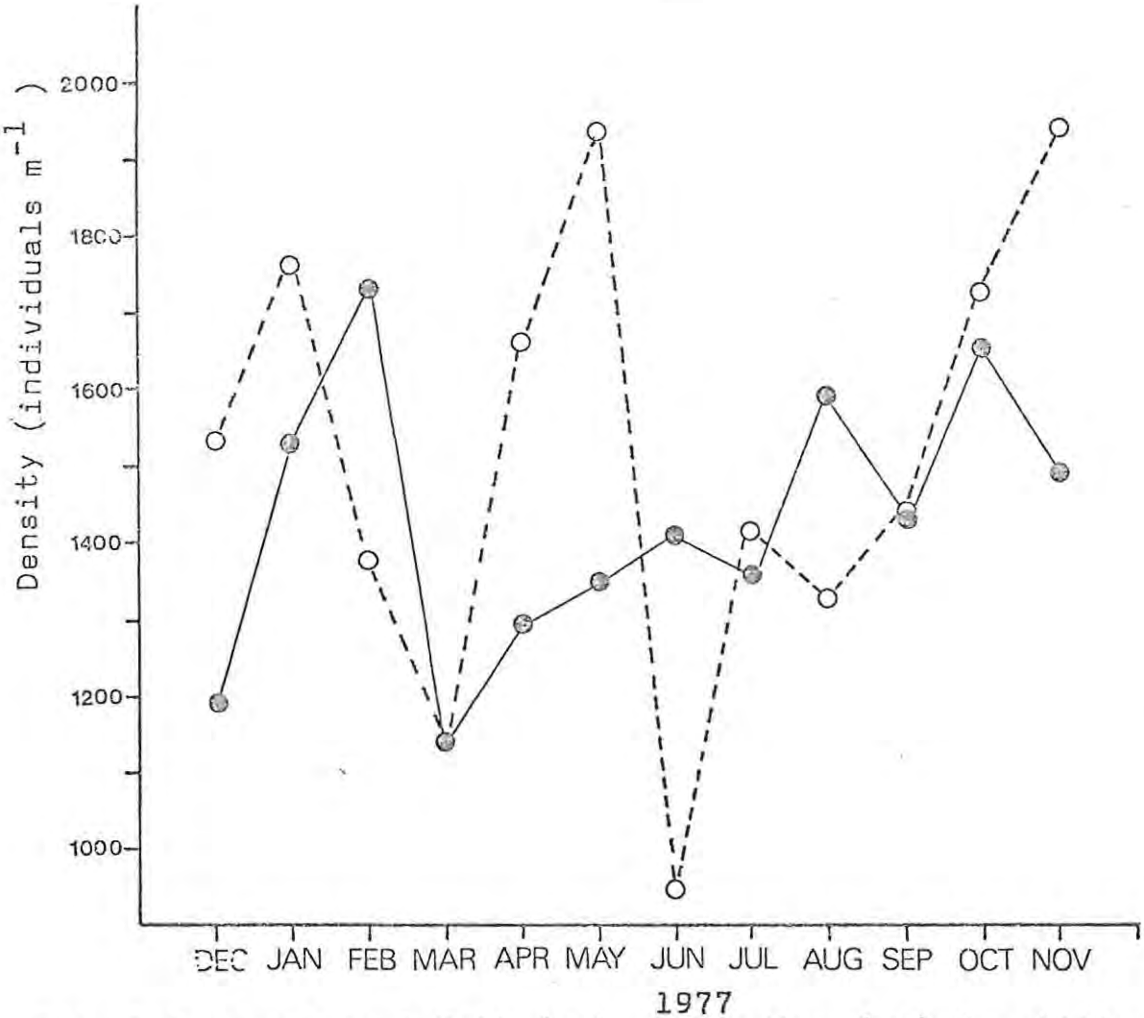


Fig. 5.5 Density of Tall (○) and Medium (●) S. maritima shoots each month at the River Station.

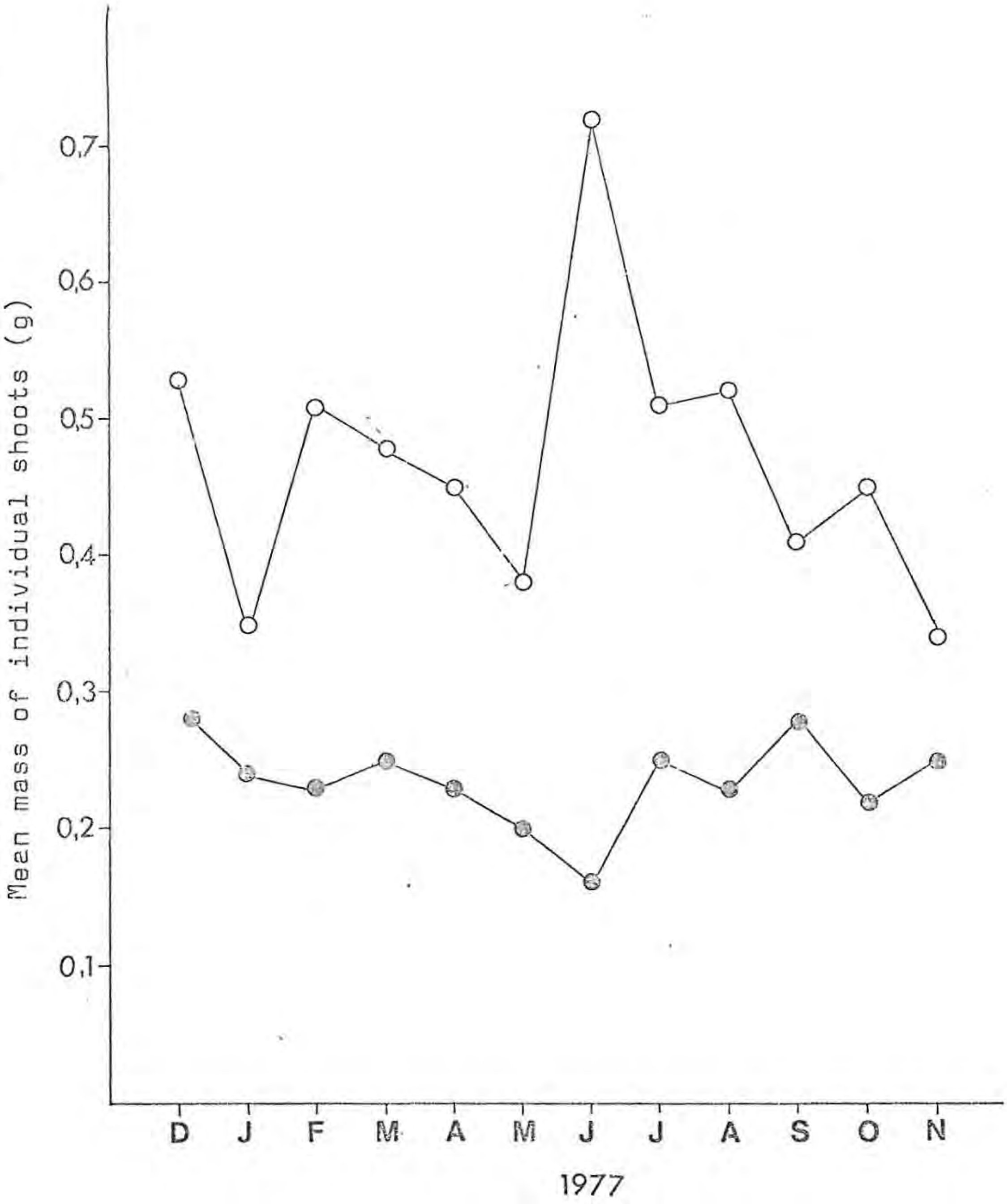


Fig. 5.6 Mean monthly mass of individual shoots of Tall (○) and Medium (●) S. *maritima* at the River Station.

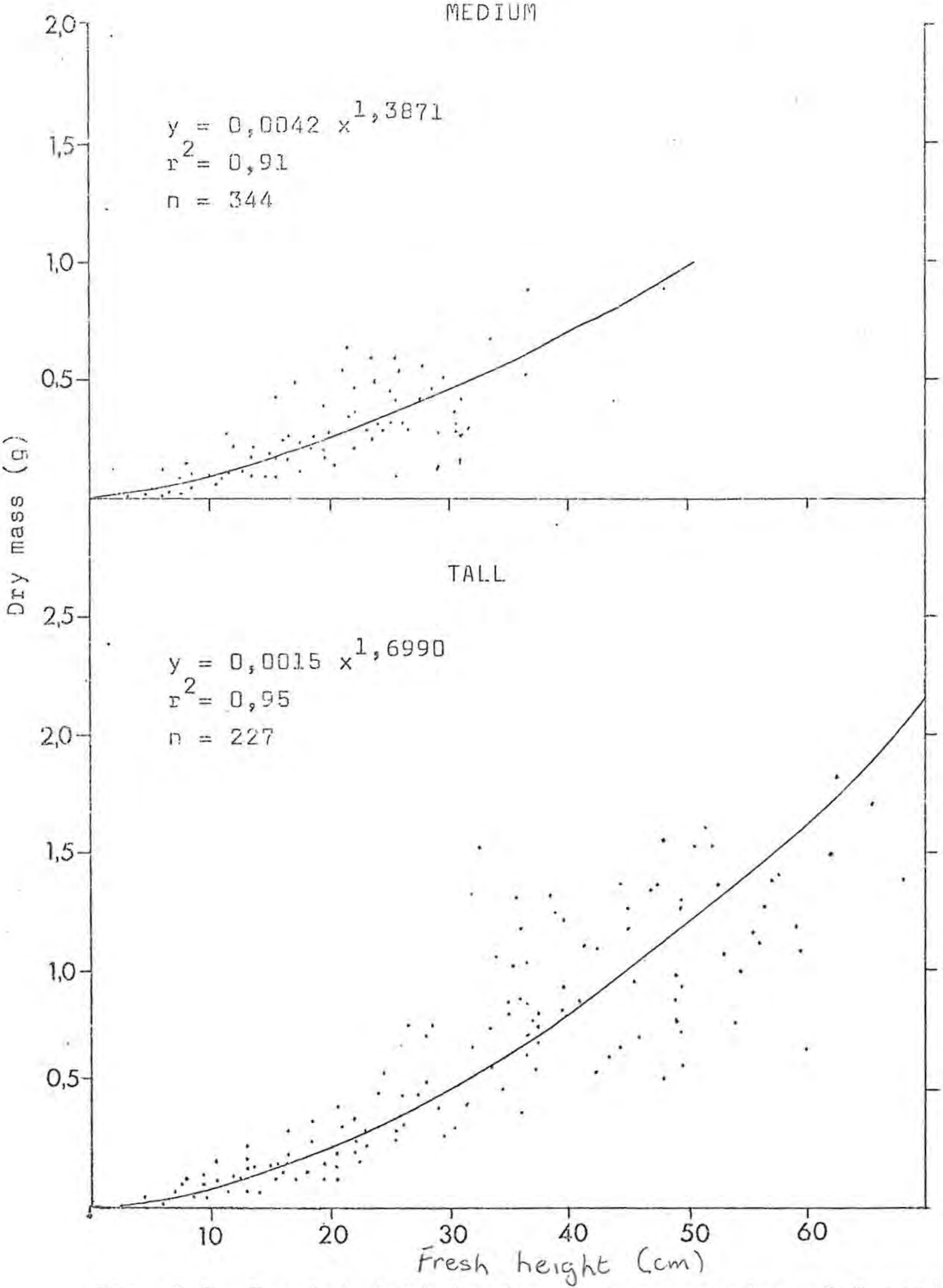


Fig. 5.7 Fresh height to dry mass regression of S.maritima shoots fitted by least squares method.

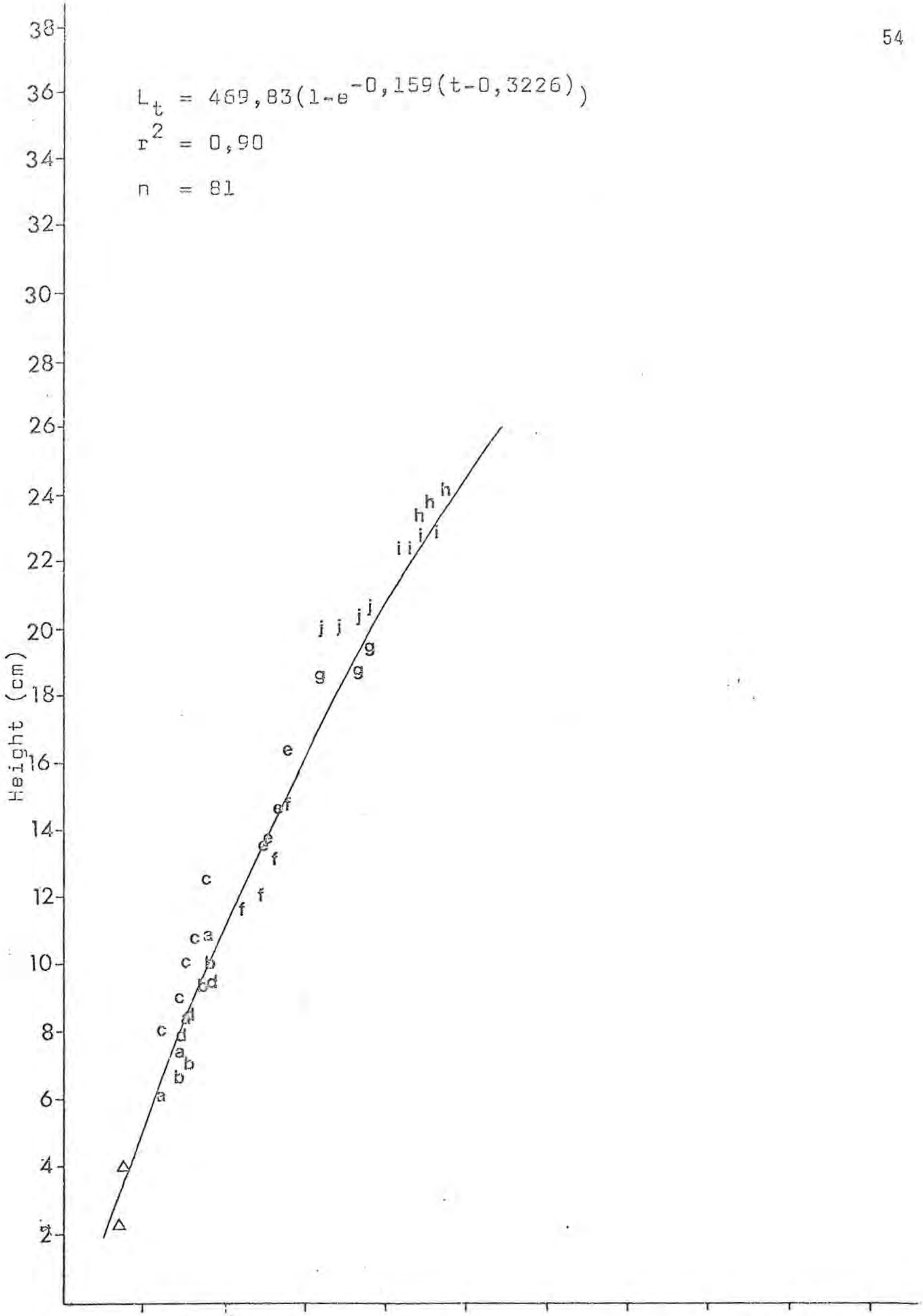


Fig. 5.8 Von Bertalanffy growth curve fitted to height data on Tall S.maritima shoots of known age (symbols) and of unknown age (letters). Data collected from River and Creek Stations. Each symbol and letter denotes a single shoot. Successive measures on individual shoots are denoted by the appropriate letter or symbol

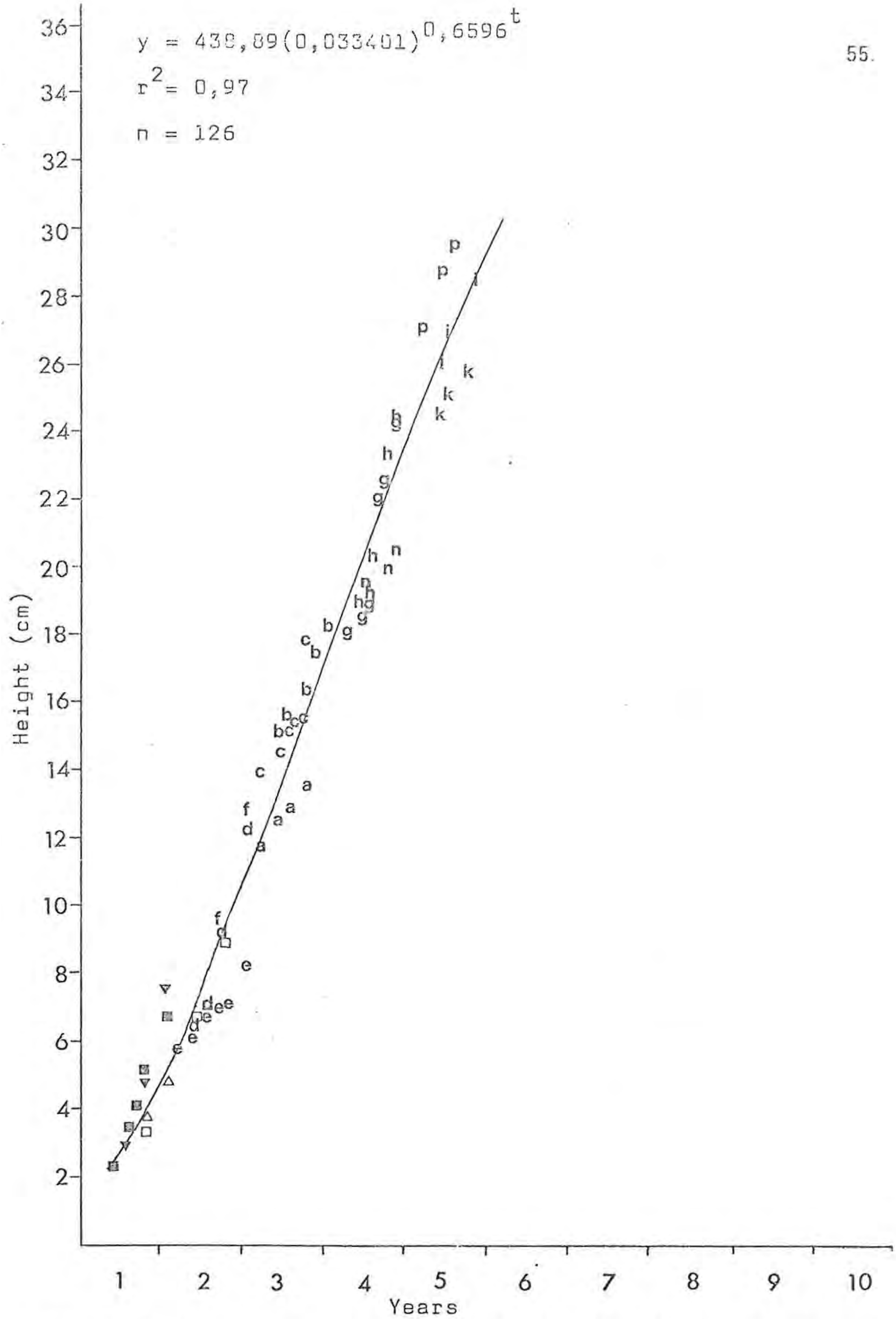


Fig. 5.9 Gompertz growth curve fitted to height data on Medium *S.maritima* shoots of known age (symbols) and of unknown age (letters). Data collected from River and Creek Stations. Each symbol and letter denotes a single shoot. Successive measures on individual shoots are denoted by the appropriate letter or symbol

5.3.7 Leaf development

An average of one new leaf was produced, and one dead leaf was lost by abscission per shoot each month during the year. Table 5.2 gives the mean leaf mass for shoots of different sized shoots. The low percentage error of the means of each shoot class is about 10%, which indicates the uniform grading. The classes are thus assumed to be equally representative.

Table 5.3 shows the almost constant monthly leaf production of Tall and Medium shoots through the year. Higher frequencies in the largest size classes explain the higher leaf production for Tall shoots in comparison with Medium shoots.

5.4 DISCUSSION AND CONCLUSIONS

The results show that *S. maritima* covers nearly a quarter of the Swartkops intertidal region. The Swartkops estuarine salt marshes are considerably smaller than those at Langebaan, which cover an area of 2172 ha of which 241 ha are *S. maritima* stands (Christie, 1976 pers comm.). The size of these major South African estuaries is very small in comparison with those in North America (see Turner and Gosselink, 1975). For example, the area of St. Louis Bay salt marshes in Mississippi is 2300 ha (Gabriel and de la Cruz, 1974); Chincoteague Bay marshes are about 9500 ha (Keefe and Boynton, 1973) and in North Carolina, Oak Island marshes extend 28550 ha.

Dead Biomass for all sites showed no seasonal pattern, and very little variation. The effects of tidal removal were consistent as sampling was carried out at the same phase of the tidal cycle each month. Values did not drop even after the floods in May. This suggests that most dead material remains on the marsh and that the amount of Dead material present does not reflect the changes in Live Biomass. The significance of these phenomena will be discussed below.

TABLE 5.2 MEAN DRY MASS OF LEAVES FROM DIFFERENT SIZE SHOOTS

	SHOOT SIZE CLASSES		
	Small (0-0,19 g)	Medium (0,2-1,09 g)	Large (1,10 g)
Mean leaf mass (dry g)	0,0102	0,0317	0,0564
Standard deviation	± 0,0024	±0,0141	±0,0190
Standard error	0,0008	0,0036	0,0055
Percentage error	8%	11%	10%

The significant seasonal variation in biomass throughout the year shows maximal summer biomass except for the data on Tall shoots at the River Station (Fig. 5.1).

TABLE 5.3 MONTHLY AND ANNUAL LEAF PRODUCTION* FROM TALL AND MEDIUM S. MARITIMA SHOOTS AT THE RIVER STATIO

	SIZE CLASS	D	J	F	M	A	M	J	J	A	S	O	N	ANNUAL
	Small	2,20	3,88	2,49	1,71	3,67	4,24	1,06	2,24	2,41	5,06	4,73	6,24	
TALL	Medium	8,88	23,24	12,68	11,79	17,75	22,95	6,21	12,93	12,05	11,41	14,71	17,50	
	Large	22,11	36,32	41,28	34,29	42,64	44,67	36,10	44,44	40,16	32,94	44,89	43,99	
	TOTAL	33,19	63,66	56,45	47,79	64,06	71,86	43,37	59,61	54,62	49,41	64,33	67,73	676,08
	Small	3,47	4,12	6,16	2,41	4,53	5,10	3,55	3,51	5,26	3,59	6,49	4,57	
MEDIUM	Medium	24,6	28,4	24,22	22,44	21,05	22,44	25,99	23,97	26,25	22,82	22,19	22,57	
	Large	14,66	13,08	20,53	11,51	10,38	7,90	13,76	14,44	13,99	20,08	17,82	18,72	
	TOTAL	42,73	45,6	50,91	36,36	35,96	35,44	43,30	41,92	45,50	46,49	46,50	45,86	516,5

* Values obtained by multiplying mean mass of each size class by relative frequency of appropriate size class of shoots m^{-2}. Units expressed as dry g m^{-2}.

The discontinuous nature of the river-fringing community, but more probably the disturbance of adjacent substrate by repeated bait-digging caused the aseasonal fluctuations. Trends from the other three samples suggest that biomass decreases are related to winter temperatures of the air and water, and lower radiation (Fig. 3.2 and Table 3.1). The influence of dissolved nutrients, particularly nitrogen and phosphorus, as limiting factors to biomass is impossible to assess due to the apparently aseasonal fluctuations through the year (Table 3.3). Higher nitrogen content in the substrate of Tall _S. maritima_ (see Table 4.1) may be a contributing factor to high biomass. Taking this further, the very high values of nitrogen reported for the substrate in Tippers Creek (Table 3.2 and McLachlan, 1972) should result in appreciably higher biomass values for Creek Station samples compared to River samples. This is not so, necessitating a factor other than nitrogen levels in the substrate to explain the difference in biomass.

Factors determining significant differences in biomass between Taller, greener streamside communities and the shorter, less robust stands, inland of the water courses at higher elevations have been investigated for other species of _Spartina_. Because most production estimates in the literature are a function of biomass values (see Chapter 6.1), it follows that production values also differ between the height forms.

S. alterniflora shoots of heights greater that 2 m near streamsides and only 20 cm tall further inland are recognised by Stalter and Batson (1969) as varieties, var. _glabra_ and var. _pilosa_. Mooring, Cooper and Seneca (1971) found evidence that environmental rather than genetical effects govern the height forms.

Primary environmental factors governing the ecophenes (_sensu_ Mooring, Cooper and Seneca 1971), have been proposed as salinity and tidal height (Adams, 1963). Phleger (1971) found growth and survival of _S. foliosa_ better in fresh water. However, the studies of Parrando, Gosselink and Hopkinson (1978) indicate wide salinity tolerances for S. alterniflora and S. cynosuroides. They also found that drainage is not a limiting factor to plant growth. Their findings are in contrast to the speculation by Chapman (1974) that better drainage immediately adjacent to creeks and water courses affords a more favourable substrate environment to plant communities. The question of salinity affecting growth is further complicated by the facultative C4 photosynthetic pathway in S. foliosa which operates according to changes in salinity. The C4 strategy and higher photosynthetic rates were observed at high salinities, suggesting that the plant can facultatively adapt to the stress of high salinities (Mallot, Davy, Jefferies and Hutton, 1975).

When nutrients, particularly nitrogen, were applied topically to salt marshes, an increase in production was observed (Sullivan and Daiber, 1974; Valiela and Teal, 1974). Thus Valiela and Teal relate variation in height, colour and standing crop of S. alterniflora to nitrogen supplies, but not to phosphorus. Nutrient concentration of waters was high near marshes of high biomass, and sediment nitrogen and phosphorous and surface NH_3 concentrations were significantly related to local variation in streamside plant communities of S. alterniflora (Nixon and Oviatt, 1973a).

Steever, Warren and Niering (1976) determined a very good statistically significant relationship between tidal amplitudes and streamside biomass in different sites at Long Island Sound, with a correlation coefficient of 0,96. All other factors, salinity, climate, edaphic, soluble nitrate, NH_3 and phosphate were similar. Obviously a point is reached where physical stress of higher tidal flux outweighs the benefits. Odum and Fanning (1973) also found streamside biomass proportional to tidal amplitude. Maximal biomass occurred at an optimal tidal range with ranges too high or too low providing too great a stress. The two studies support Odum's (1969, 1971, 1975) theory that salt marshes are systems subsidised by the energy of the tides, and show that tidal energy is a significant factor affecting

Spartina standing crop. This more than compensates for the other prevailing stresses of salinity and temperature fluctuations and inundation.

The variable nutrient content of the Swartkops estuary and the lack of overall correlation between high biomass and substrate nitrogen, suggest that tidal subsidy may account for differences in *S. maritima* height forms, with the Tall streamside-form subject to longer periods of tidal inundation. Tidal attenuation in the narrow Creek may result in lower tidal subsidy and hence explain the lower overall biomass at the Creek Station.

A comparison of biomasses of *S. maritima* in different localities and with other species of *Spartina* is shown in Table 5.4. It appears that Swartkops plants have greater biomass than at Kowie, where the stands occur only as fringes 1,5 m wide. *S. maritima* biomass data from Langebaan Lagoon is higher that for Swartkops, suggesting a more favourable environment, perhaps in terms of the nutrient supplies from the nutrient-rich Atlantic Ocean waters in the vicinity.

Other species of *Spartina* are listed for academic interest only, as different growth forms render direct comparisons meaningless. For example, *S. alterniflora* grows to 2 m tall with densities of only 100-200 m^{-2} compared to the local species (Fig. 5.5). Generally, *S. alterniflora* appears to have higher dry biomass than *S. maritima* in South Africa. *S. patens* and *S. townsendii* estimates are closer to those of the local species.

Geographic and local variation in North American species have been discussed critically (Keefe, 1972; Nixon and Oviatt, 1973a, 1973b; Hatcher and Mann, 1975; Turner and Gosselink, 1975; Turner, 1976). The general consensus is that biomass decreases with increasing latitude, and local variation is due to environmental parameters, such as nutrients and tidal range which are not yet fully understood.

In view of their inconclusive deductions, and the putative role of tidal subsidy in this study, the differences

TABLE 5.4 BIOMASS OF SPECIES OF SPARTINA IN DIFFERENT LOCALITIES

SPECIES	BIOMASS (dry g m^{-2})	LOCALITY	SOURCE
S. maritima	293-656	Swartkops estuary	This study
	285-429	Kowie estuary	Lubke and Curtis (1977)
	402-1002	Langebaan Lagoon	Christie (pers. comm.)
S. alterniflora	259-1320	N. Carolina	Stroud and Cooper (1969)
	250-2100	N. Carolina	Williams and Murdoch (1966)*
	493	Maryland-Virginia	Keefe and Boynton (1973)
	1332	Virginia	Wass and Wright (1969)*
	1290	Georgia	Teal (1962)
	413	Delaware	Morgan (1961)*
	300	New Jersey	Good (1965)*
	840	Rhode Island	Nixon and Oviatt (1973a)
	580	Nova Scotia	Mann (1972 in Nixon and Oviatt, 1973a)
S. patens	640-1296	N. Carolina	Waits (1967 in Keefe and Boynton, 1973)
	805	Virginia	Wass and Wright (1969)*
S. cynosuroides	1456	Virginia	Wass and Wright (1969)*
S. townsendii	700-1060	S. England	Ranwell (1961)

* in Turner (1976)

between Tall and Medium ecophenes and between Creek and River Stations, are treated here simply as local variations. Thus averaging of all sample biomasses gives a representative estimate of S. maritima of Swartkops estuarine marshes.

The number of flowering culms appears low in terms of square meters, but the growth habit of the grass (Fig. 2.1) makes it impossible to distinguish the number of individual plants in a unit area without tracing all the interlinking rhizomes. Thus the number of flowers per plant is not known. The summer flowering period reported here agrees with the flowering season in the Northern Hemisphere, from June to November (Mobberley, 1956).

Seasonal variation in potential energy, organic, nitrogen and carbon content of both Live and Dead material was minimal, though there was a slight increase in energy and nitrogen content in both samples towards spring, when biomass begins to show an increase. This may be related to the growth strategy of the plant in translocating nutrients from roots to the stem.

The accumulation of nitrogen in aerial parts of S. alterniflor early in the growing season has been observed by Squiers and Good (1974) and Mendelssohn and Marcellus (1976). High values of 2,01% nitrogen per g dry mass dropped to 0,64% by mid growing season, indicating that early growth of S. alterniflora is accompanied by a much higher nitrogen content compared to S. maritima (see Table 5.1).

Slight increases in caloric content in Live and Dead material are evident in early spring, perhaps related to higher percentages of cellulose and hemicellulose, coinciding with biomass increases. No seasonal variation in calorific content, based on ash-free values, was observed in S. alterniflora by Squiers and Good (1974). Ash-free values of S. maritima did not vary seasonally, but were similar to S. alterniflora estimates of 11% of dry mass (Udell, Zarudsky, Doheny and Burkholder, 1969; Squiers and Good, 1974).

It is noteworthy that Live material appears to be of slightly higher nutritional status than Dead material in terms of nitrogen, and potential energy content. This suggests that microbial enrichment of Dead material is not yet important. The slight seasonal change in composition in both Live and Dead material is probably of little significance. Thus mean figures were used in determining the quality of nutritional resources available to consumers.

Although a high proportion of young shoots was noted in December 1976 in both Tall and Medium ecophenes, the "peak" of young shoots did not appear to increase in size over a time period of 12 months. The constant structure of the S. maritima population may be explained by the extremely slow growth of the shoots (see Chapter 5.3.6). The growth rate of 0,00133 g month^{-1} of Medium shoots and 0,00045 g month^{-1} of Tall shoots is insufficient for the limits of the smallest size class (0-0,1 g) to be exceeded. Thus data on the structure remained constant as the "cohort" was being measured each time.

Half the population is smaller than 0,2 g per shoot. A possible explanation is that average size at death is $\pm$ 0,2 g (=17,5 cm) according to the height : mass regression (see Chapter 5.3.5). This interpretation is supported by marked shoot data. The average height of 40 monitored shoots which died during the measuring period was 17,82 cm.

Mortality of larger plants ($>$1,0 g) is apparent from the Medium plant data (Fig. 5.4). The absence of a similar pattern in Tall shoot histograms may be due to disturbance effects (see Chapter 5.3.2). Though percentage frequency of size classes remains nearly constant, the lowest frequency in terms of actual numbers, of the smallest size class ($<$ 0,1 g) was recorded in April. The lowest number of developing shoots thus follows the end of the flowering season (Fig. 5.3).

Mortality of older shoots in Medium stands from April to June (Fig. 5.5) is compensated for by increase in density as a result of young shoot growth. Changes in density coincide with seasonal biomass.

The increase in individual shoot mass towards spring may indicate the rise in numbers of young shoots. Alternatively, the results may be interpreted simply as a direct function of biomass and density trends.

The high coefficients of determination for the regressions allow reliable conversion of growth data in cm to dry mass in grams. The difference in structure between the more robust Tall shoots and the Medium shoots only becomes noticeable at heights of 15 cm. After this height, Tall shoots have greater mass per unit height in cm.

The curves for the two height forms were based on data from marked shoots growing at the River and Creek Stations giving an average measure which takes local variation into account.

The faint trend in seasonal fluctuation in growth rate apparent in the raw plotted data is not shown by the growth curves. The seasonal tendency was too slight to be shown statistically. Also the growth curves are simply an approximation since it is usual to find seasonal variations in growth rate superimposed on the annual growth pattern (Jones, 1976).

The curves may be criticised as being theoretical, but increment calculations, using raw data of height measurements indicated the same order of magnitude of growth rate. It must be stressed that shoot growth is not the same as plant growth. Individual plants may develop a number of shoots which all grow slowly. Thus whole plant growth is in fact far greater than culm growth rates given here, being the sum of its component culm growth. Unfortunately it is almost impossible to distinguish individual plants.

Growth curves of Tall and Medium shoots are expressed in terms of height. Tall shoots have greater mass per unit height than Medium shoots at heights greater than 15 cm (see Fig. 5.7). Thus growth rate in terms of height and in terms of mass increment, is slower in Tall shoots. However, Tall shoots have higher leaf production than Medium shoots. The discrepancy in shoot growth may be explained by this difference in growth stategy. Alternatively, Medium plants may give rise to fewer shoots and thus are able to concentrate more energy into fewer shoots. Lack of data on actual plant numbers does not allow this to be confirmed.

From the growth curves in Fig. 5.8 and Fig. 5.9, a maximum age of 14 years is predicted for the tallest plants in the community (up to 60 cm for Tall and 40 cm for Medium shoots). This estimate seems extremely high but unfortunately no similar growth measures have been done on S. maritima, or for that matter, on any other grass (Tainton, 1978 pers. comm.). Further evidence that S. maritima is extremely slow growing is given by the absence of any regrowth in the harvested plots, even a year after clearing and in spite of potential vegetative propagation from surrounding stocks.

Leaf loss for S. maritima was independent of shoot age and season. Other studies have found that S. alterniflora produced only 4,5 leaves per shoot in a year, while S. cynosuroides and S. patens produced 13,7 and 9,5 leaves respectively. Obviously the leaves of S. alterniflora are considerably larger than the local species leaves.

There are certain similarities between S. patens and S. maritima including similar leaf production, independence of leaf number from shoot size, and lack of seasonality. The significance of these similarities will be discussed later in terms of production and seasonal behaviour.

Interpretation of growth behaviour is made difficult by the fact that shoot rather than individual plant characteristics have been measured. Considering the growth habit (Fig. 2.1), plant numbers must be considerably lower that shoot densities. On this basis, the following interpretation of energy partitioning in S. maritima is made.

The extremely slow growth rates measured for shoots of this plant are supported by the absence of regrowth in cleared plots even after a year. Furthermore, the order of magnitude of monthly growth rate was too small to be detected in 12 months monitoring of the 0,1 g size class (see Fig. 5.4). The extremely slow growth of shoots may be the result of divided growth resources of the parent plant which develops many shoots. In addition, most energy is directed into leaf production, rather than into shoot growth. In Spring, nitrogen, potential energy and carbon composition of shoots are maximal. Causal factors may be translocation of reserves from roots to shoots, and full exploitation of spring resources such as warmer temperatures and higher radiation, allowing better use of available nutrients. This build-up in plant protein and carbohydrates coincides with the beginning of culm elongation and development of inflorescences. Flowering extends through midsummer (Fig. 5.3) till March, when the parent plant stock is depleted of energy resources. The actual number of young developing shoots (<0,1 g) is at its lowest at this time and shoot densities are minimal. During winter, young shoot numbers increase slowly. Towards Spring the plant begins to recover from the drain on its resources. Biomass increases in spring to reach a peak in summer, when high light intensities and warm temperatures are exploited. Resources are restored for flowering requirements again. Variation in energy resources through the year are slight, and detected by sensitive-measures only. The changes with season are so small as to be indetectible by the gross scale measures used in the production studies.

CHAPTER 6

MEASUREMENT OF NET PRODUCTION OF S. MARITIMA

6.1 INTRODUCTION

Net production of higher plants is generally estimated by measurement of changes in biomass or determined from photosynthetic and respiration rates. The accuracy of the latter approach is limited by technical difficulties, particularly in dealing with regularly inundated halophytes. Gas methods are unrealistic for vascular plants subject to submergence due to the presence of air lacunae (Hartman and Brown, 1967). Further problems arise in converting Gross Production to Net production over long periods, correcting for effects of photorespiration and conversion of data into production in terms of organic matter (Mathews and Westlake, 1969).

Great difficulties are encountered in simulating intertidal environments. Also it is totally unrealistic to attempt to extrapolate hourly rates into monthly and even yearly rates, unless continuous radiation data-collecting equipment is available. Annual estimates in terms of dry matter and energy content are essential for incorporation of primary production data into the energy flow model.

In view of the above-mentioned difficulties, changes in biomass were selected as the means of measuring production of S. maritima.

There is much literature describing the production of Spartina species in North America (see Keefe, 1972 and Turner, 1976 for reviews), but none on the local species.

The reasons for the great interest shown in the American species are the dominance of this plant in the extensive wetlands of the continent, its major role as a primary producer in the rich estuarine ecosystems, and its extremely high productivity, as high as that of subsidised cultivars, in the stressed intertidal environment (Teal, 1962; Odum and de la Cruz, 1967; Odum 1969, 1971, 1975; Keefe and Boynton, 1973;

Provost, 1976; Turner, 1976; Wetzel, 1977).

Production methods have been reviewed and criticised by Keefe (1972), Turner and Gosselink (1975) and Turner (1976). No standard procedure has been established for halophytes, though certain methods have been recommended above others. Essentially, all the methods measure increase in biomass, in accordance with the definition of production. This proves to be suitable for the marked spring and summer growth and winter die-back of North American species of Spartina. Only one production study has been initiated on S. maritima, growing at Langebaan Lagoon (Christie, 1976). The absence of any marked seasonal growth and winter die-back was noted in the Swartkops plants. Thus the lack of a single reliable method which accounts for continuous growth through the year necessitated the use of several methods in this study.

Aerial biomass data required for production measurement were collected as described in Chapter 5.3.2 and corrected for monthly periods.

6.2 METHODS

Method 1

Allen's graphical method of production measurement was attempted here because of the high proportion of young shoots observed in December, 1976, which suggested the emergence of a spring cohort. This method is widely used in animal production studies but was considered feasible for plant studies after the preliminary work of Mathews and Westlake (1969). The rationale behind the method is described by Edmondson and Winberg (1971). The principle behind the method is the same for Method 5. (see Mathews and Westlake, 1969). Briefly, the frequency (N) of a size/class of individuals of size w, followed over a time course t, will give an estimate of production from Net Production = $N\Delta\bar{w}_t$ where $\Delta\bar{w}_t$ is the growth in mean mass of the population in the time interval. It is assumed that each cohort (group of individuals of the same generation) follows the same time course. Thus a sequential arrangement of the size classes gives the time course of a single cohort. Production is determined graphically from the curve.

Method 2

Milner and Hughes (1970) and Gabriel and de la Cruz (1974) used the change in biomass between sampling periods to determine production (after Penfound, 1956). By this method:

$$\text{Monthly net production} = \frac{B_n - B_{n-1}}{t_n - t_{n-1}}$$

where B_n is aerial Live biomass at n^{th} sample period
t_n is time at the n^{th} sample collection
Annual net production $= \sum$ monthly production

Method 3

Net annual production is measured as the difference between maximum and minimum Live biomass measured during the year. This method has been used by Smalley (1958), Stroud and Cooper (1969) and Williams and Murdoch (1969).

$$\text{Annual net production} = \text{Live biomass}_{\text{max}} - \text{Live biomass}_{\text{min}}$$

during period of one year

Method 4

Edmondson and Winberg (1971) describe this method for estimating production of invertebrate populations

$$\text{Net production} = \frac{\text{mean biomass of population X time interval}}{\text{turnover time of individuals}}$$

The average height of Tall and Medium shoots which died during growth monitoring of marked shoots was calculated as 17,82 cm (see Chapter 5.4). The corresponding age was determined from the appropriate growth curves (Fig. 5.8 and Fig. 5.9). The average age of mortality of Tall shoots was 1169 days and 1153 days for Medium shoots. These ages indicate turnover time of individuals.

$$\text{Average Live biomass} = \frac{\text{biomass}_1 + \text{biomass}_2}{2}$$

for time $= t_2 - t_1$

Method 5

This method was formulated on the same basis as Method 1 and gives the same results with idealised data (Mathews and Westlake, 1969).

A form of Ricker's equation is used to derive production.

$$\text{Net production} = (\ln(Wt/Wo))\,\frac{Bo + Bt}{2}$$

where Bo and Bt are Live biomass at start and end of time period respectively

Wo and Wt are mean dry mass of individual (see Fig.5.8) at start and end of time interval

Annual production $= \sum$ monthly net production

Method 6

Smalley's (1958) method measures increases in Live biomass during each sampling period and accounts for losses by death, grazing and removal from the area between samples.

Net production is calculated as follows:

1. if there was both an increase in the Live biomass and an increase in Dead biomass, then Net Production = the sum of the increases;

2. if both Live and Dead biomass decreased, then production was zero. Since production is defined as synthesis of organic matter, it cannot be negative, and decreases must be accounted for in terms of consumption, sedimentation or loss from the system;

3. if the Live biomass increases and Dead biomass decreased, production was equal to the increase in Live matter. Any decrease in Dead biomass is assumed to be due to loss to the tidal waters, but an increase in Live biomass can only be due to net production;

4. if the Dead biomass increased and Live biomass decreased, they were added algebraically; if the result was negative, production was zero; if the result was positive, the resulting figure was equal to production.

This method has been widely accepted (Teal, 1962; Williams and Murdoch, 1969; Stroud and Cooper, 1969; Odum *et al*, 1972; Turner and Gosselink, 1975; Gallagher, Pfeiffer and Pomeroy, 1976; Kirby and Gosselink, 1976). Although it is difficult to determine how accurate the method is, and though leaf loss is disregarded, resulting in underestimation, it is a preferable method to annual estimates based on end-of-season Live biomass (Turner, 1976).

Method 7

Wiegert and Evans (1964) formulated their method specifically for ungrazed grasslands. Production is calculated from change in Live biomass plus mortality losses, where mortality includes amount of dead material produced and loss by decomposition. This method has been used with success by Kirby and Gosselink (1976) on *S. alterniflora* and is highly recommended by Turner (1976).

The following parameters are measured:

t_i = time interval (days)
a_{i-1} = standing crop Dead material at start
a_i = standing crop Dead material at end
b_{i-1} = standing crop Live material at start
b_i = standing crop Live material at end
r_i = instantaneous daily rate of disappearance of dead material during interval

Amount of dead material disappearing during an interval $= x_i = \frac{(a_i + a_{i-1})}{2} \times r_i t_i$

Changes in standing crop of Live $= \Delta b_i = b_i - b_{i-1}$

Changes in standing crop of Dead $= \Delta a_i = a_i - a_{i-1}$

The change in dead standing crop during an interval is equal to mortality (ie. the dead material added) and the disappearing material (ie. decomposition)

$$\therefore \quad \text{mortality} = d_i = \overset{\text{amount of}}{\text{disappearing material}} + \Delta \overset{\text{dead}}{\text{standing crop}}$$

$$d_i = x_i + \Delta a_i$$

Growth and mortality result in a change in Live standing crop ie. live standing crop = growth − mortality

$\therefore$ total growth = Δ Live standing crop + mortality

$\therefore$ Net Production $= \Delta b_i + d_i$

The decomposition rates are expressed as instantaneous daily rates (g : g : day) for use in the production measurements.

$$\text{Instantaneous rate of disappearance of dead material} = r_i = \frac{\ln (W_o/W_1)}{t_1 - t_o}$$

where $t_i - t_o$ = number of days
W_o and W_1 are litter weights at start and end of time interval

(Wiegert and Evans, 1964)

Method 8

This method was especially devised to account for S. maritima shoot growth and leaf loss during monthly time intervals. The growth curves of Tall (Fig. 5.8) and Medium (Fig. 5.9) S. maritima shoots were divided into sections according to constant slope of curve. The sections correspond to different size classes. Height increments were converted to mass increments by means of the height : mass regressions (Fig. 5.7). The growth rate for these different size classes was multiplied by the biomass proportional to the frequency of the appropriate size classes. The sum of shoot growth of all classes of the population equals monthly production. Leaf production measurement was described in Chapter 5.2.6 and the results given (Chapter 5.3.7) and discussed (Chapter 5.4).

Monthly net production = shoot growth m^{-2} + leaf production m^{-2}

Annual net production = sum of monthly production

All methods are summarised in Table 6.0 for easy reference

TABLE 6.0 SUMMARY OF METHODS USED TO MEASURE NET PRODUCTION OF S. MARITIMA

NUMBER	METHOD	REFERENCE
1	NP = size frequency X △mean mass of population in time interval	(Allen curve) Mathews & Westlake (1969)
2	NP = △Live biomass during time interval	Milner & Hughes (1970)
3	Annual NP = max biomass − min biomass	Stroud & Cooper (1969)
4	$\text{NP} = \dfrac{\text{mean biomass x time interval}}{\text{turnover time of individuals}}$	Edmondson & Winberg (1971)
5	NP = growth rate X mean biomass	Mathews & Westlake (1969)
6	If △Live and △Dead biomass both +ve, NP = △Live + △Dead biomass If △Live and △Dead biomass both −ve, NP = 0 If △Live biomass is −ve, and △Dead +ve NP = △Live + △Dead biomass if 0, otherwise NP = 0 If △Live biomass +ve and △Dead −ve, NP = △Live biomass	Smalley (1958)
7	$\lambda_1 \downarrow$ = NP $\boxed{L_I = \text{Live Biomass}}$ $\lambda_2 \downarrow$ = Production of Dead $\boxed{L_2 = \text{Dead biomass}}$ $\lambda_3 \downarrow$ = Decomposition X mean Dead biomass $\text{NP} = \lambda_2 + \lambda_3$	Wiegert & Evans (1964)
8	NP = shoot growth + leaf production	This study

6.3 RESULTS

Incomplete data on community structure did not permit the application of all methods of production measurement to Tall and Medium shoots (Table 6.3 and Table 6.4 respectively) at the Creek Station. Data on shoot production required for Method 8 on Tall and Medium Spartina at the River Station is given in Tables 6.1 and 6.2 respectively. A comparison of production estimates from all seven methods was possible for Tall and Medium shoots (Table. 6.5 and Table 6.6 respectively) growing at the River Station. Negative results were expressed as zero production because negative production is a contradiction in terms. Results from the most reliable method and representative of typical S. maritima shoots were averaged. The mean production estimate, accounting for local variation, was converted into units of energy and crude protein (Table 5.1) and expressed for the whole estuary (Table 6.7).

6.4 DISCUSSION AND CONCLUSIONS

6.4.1 Comparison of different methods

Refer to Table 6.0 for summary of methods used, and Table 6.5 and Table 6.6 for results.

Method 1 is better-suited to non-ideal data than Method 4 and detects changes in population behaviour, even though both methods are derived from the same principle (Chapter 6.2). Because of the slow growth of the shoots, the size class structure remained constant through the year (Fig. 5.4). The youngest shoots grew so slowly in the year that their mass did not increase beyond the first size class (0-0,9 g) during the 12 month monitoring period. The method may have been successful if smaller size classes were used and the monitoring period extended. In terms of effort and time involved, this would have been unfeasible.

Method 2 concurs exactly with the theoretical definition of production in measuring the increase in biomass for a given time interval. Practically, however, this method ignores mortality and leaf losses, and relies on a marked seasonal peak in production. Monthly fluctuations in biomass result in negative values where low biomass is

TABLE 6.1 MONTHLY AND ANNUAL SHOOT PRODUCTION* OF TALL *S. MARITIMA* AT THE RIVER STATION

(Dry g m^{-2})

CLASS SIZE (g)	GROWTH RATE (g $month^{-1}$)	1977 D	J	F	M	A	M	J	J	A	S	O	N	ANNUAL TOTAL
0-0,09	0,00045	0,066	0,053	0,056	0,037	0,061	0,07	0,038	0,048	0,055	0,099	0,087	0,089	
01,029	0,00032	0,053	0,049	0,046	0,044	0,048	0,057	0,034	0,048	0,043	0,042	0,045	0,045	
0,30-0,39	0,00019	0,006	0,013	0,012	0,008	0,012	0,016	0,009	0,011	0,01	0,007	0,01	0,007	
0,4-0,69	0,00042	0,031	0,054	0,066	0,06	0,063	0,086	0,077	0,072	0,068	0,038	0,063	0,067	
0,7-2,69	0,00042	0,082	0,027	0,084	0,06	0,052	0,036	0,143	0,096	0,085	0,071	0,087	0,043	
Monthly Totals		0,238	0,196	0,264	0,209	0,236	0,265	0,303	0,275	0,261	0,257	0,292	0,251	3,047

* Value obtained by multiplying growth rate by appropriate biomass m^{-2}, proportional to frequency of size class in sample.

TABLE 6.2 MONTHLY AND ANNUAL SHOOT PRODUCTION* OF MEDIUM S. MARITIMA AT THE RIVER STATION

(Dry g m^{-2})

		1977												
CLASS SIZE (g)	GROWTH RATE (g month^{-1})	D	J	F	M	A	M	J	J	A	S	O	N	ANNUAL TOTAL
0-0,09	0,00133	0,144	0,126	0,181	0,076	0,14	0,144	0,097	0,11	0,15	0,134	0,197	0,158	
0,1-0,49	0,00177	0,497	0,414	0,349	0,333	0,308	0,296	0,340	0,366	0,37	0,444	0,345	0,386	
0,5	0,00128	0,055	0,047	0,069	0,031	0,027	0,023	0,033	0,037	0,041	0,086	0,06	0,076	
Monthly Totals		0,696	0,587	0,599	0,44	0,475	0,463	0,470	0,513	0,561	0,664	0,602	0,620	6,69

* Values obtained by multiplying growth rate by appropriate biomass m^{-2}, proportional to frequency of size class in sample.

TABLE 6.3 MONTHLY AND ANNUAL NET PRODUCTION (dry g m^{-2}) OF TALL S. MARITIMA AT THE CREEK STATION DETERMINED BY DIFFERENT METHODS (see Table 6.0)

									1977						
METHOD	S	O	N/D	J	F	M	A	M	J	J	A	S	O	N/D	ANNUAL NP
2	119	0	0	20	0	0	12	0	56	35	26	43	48	66	306
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	492
4	13	16	21	11	10	11	11	11	8	10	11	11	13	14	133
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	119	0	22	32	12	0	12	0	56	63	26	82	48	66	419
7	0	0	0	79	0	0	31	0	46	76	6	95	56	-	389
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

- (Incomplete data)

TABLE 6.4 MONTHLY AND ANNUAL NET PRODUCTION (dry g m^{-2}) OF MEDIUM S. MARITIMA AT THE CREEK STATION DETERMINED BY DIFFERENT METHODS (see Table 6.0)

		1976							1977						
METHOD	S	O	N/D	J	F	M	A	M	J	J	A	S	O	N/D	ANNUAL NP
2	51	0	102	5	0	0	11	0	56	4	19	6	20	0	223
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	208
4	8	10	6	10	9	7	6	7	6	7	7	8	8	9	91
5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	51	0	115	5	25	0	11	0	73	9	19	6	29	26	318
7	44	0	77	38	0	0	29	0	94	28	15	3	50	-	334
8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-

\- (Incomplete data)

TABLE 6.5 MONTHLY AND ANNUAL NET PRODUCTION (dry g m^{-2}) OF TALL S. MARITIMA GROWING AT RIVER STATION DETERMINED BY DIFFERENT METHODS (see Table 6.0)

	1976			1977										
METHOD	S	O	N/D	J	F	M	A	M	J	J	A	S	O	N/D	ANNUAL NP
2	41	0	0	155	0	72	87	6	0	0	0	92	0	-	412
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	597
4	16	18	16	14	17	14	16	18	20	19	18	17	20	17	205
5	-	-	-	228	0	0	0	471	0	13	0	65	0	-	777
6	41	0	0	223	51	72	87	0	0	15	0	92	19	-	559
7	30	0	0	292	0	99	99	79	0	0	0	99	0	-	668
8	-	-	33	64	57	48	64	72	44	60	55	50	65	68	680

- (Incomplete data)

TABLE 6.6 MONTHLY AND ANNUAL NET PRODUCTION (dry g m^{-2}) OF MEDIUM S. MARITIMA AT THE RIVER STATION DETERMINED BY DIFFERENT METHODS (see Table 6.0)

	1976			1977										
METHOD	S	O	N/D	J	F	M	A	M	J	J	A	S	O	N/D	ANNUAL NP
2	44	0	0	22	0	31	0	0	27	36	65	0	6	0	187
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	308
4	10	11	11	10	10	7	8	8	7	9	10	11	10	10	112
5	-	-	-	0	27	0	0	0	136	0	76	0	50	-	290
6	44	0	20	44	0	59	0	80	27	67	65	0	17	0	379
7	62	0	0	96	0	105	0	0	54	99	76	0	49	-	479
8	-	-	43	46	52	37	36	36	44	42	46	47	47	47	523

- (Incomplete data)

TABLE 6.7 ANNUAL AERIAL NET PRODUCTION OF S. MARITIMA PER SQUARE METER AND FOR THE WHOLE OF THE SWARTKOPS ESTUARY (Results from Method 8)

	DRY MASS (g)	ORGANIC MATERIAL (g)	POTENTIAL ENERGY (J)	CRUDE PROTEIN* (g)	CARBON CONTENT (g)	P/B
Tall *S. maritima* (m^{-2})	680	614	11733400	55,22	293,62	1,04
Medium *S. maritima* (m^{-2})	523	472	9024365	42,47	225,83	1,15
Mean (m^{-2})	602	543	10378883	48,85	259,73	1,10
Total estuarine production	$495{,}6 \times 10^3$ kg	$447{,}1 \times 10^3$ kg	$8{,}5 \times 10^9$ kJ	$40{,}2 \times 10^3$ kg	$213{,}8 \times 10^3$ kg	-

* = crude protein determined by multiplying N content by 6,28 (Squiers and Good, 1974)

P = annual production

B = mean biomass

preceded by a higher biomass. The almost constant nature of the production of S. maritima is accounted for in Method 3, which measures any seasonal annual production as the difference between maximum and minimum biomass during the year. However, leaf and mortality losses are again ignored.

Mortality, as a function of average lifespan is used in Method 4 to modify monthly biomass values. The age of mortality or turnover time is almost constant through the year, (see Capter 5.4), so that it does not appear to affect production seasonally. Again, leaf losses are not accounted for. Growth rate as an exponential function of individual shoot mass increment over time interval, multiplied by average biomass, is used in Method 5. However, individual shoot mass is a direct function of biomass, and monthly changes in mass were sometimes negative (see Fig. 5.6). This method fails, as growth, by definition, may not be negative. These values are not valid and expressed as zero. It is interesting to note that Methods 1 and 5, based on the same theoretical principle (Mathews and Westlake, 1969), failed for different reasons.

Losses by mortality are combined with Live material changes in Method 6. This method has been criticised on the grounds that the magnitude of inaccuracies can not be determined (Turner, 1976). On the whole, though, this method is more representative than either Method 3 or where net production is assumed to equal maximum biomass in the year (Turner, 1976). Method 7 has been recommended as the most accurate means of measuring overseas species of Spartina (see Turner, 1976). Production is corrected for losses by mortality as well as amount of dead material lost by decomposition. This method is again dependent on a continuously increasing biomass followed by a winter die off. The "abberant" behaviour of S. maritima growing continuously, but with variable biomass results in zero production for some months.

A general criticism may be levelled at all the above mentioned overseas methods and which became apparent in this study on grasslands with very slow growth and low production. Production of North American species must be so great as to excede natural variation. In S. maritima, seasonal increases and decreases in production are slight and are masked by variation in the stands. This occurs even though the accuracy of the monthly sampling was low, the percentage error being about 10%, acceptable by IBP standards (Milner and Hughes, 1970). In effect then, the overseas methods, devised for measures on vigorous producers, prove to be too crude for the subtle seasonal changes of S. maritima production in Swartkops.

Tables 6.5 and 6.6, show clearly the conflicting monthly and annual production estimates determined by the different methods. Production measured by Methods 2-7 for a particular site during any one month, show little correlation, which suggests that values are "artefacts" as a result of the methods used, and do not reflect the true nature of S. maritima production. This criticism can not be levelled at Method 8, which is based directly on the growth habit of the shoots.

A point worth raising is apparent in Tables 6.5 and 6.6. If monthly production is ignored and annual production only, is calculated by any one method of Methods 2-7, the result appears to be satisfactory, when if fact, it is a misrepresentation. The closeness in annual production estimates from Methods 2-7 to Method 8 may be related to the fact that leaf production coincides with leaf loss. Thus turnover is higher than is apparent from the almost constant biomass from one sampling period to the next.

The last method, Method 8, was devised to take into consideration the nature of the plant. Leaf monitoring showed that each plant produced, and simultaneously lost, one leaf per month. Leaf production is shown to be relatively high in Table 5.3. Shoot production, however, is almost negligible, even when weighted to account for different age (=size) classes (Tables 6.1 and 6.2). This method is proposed as the most reliable method, giving the most representative results for S. maritima production measurement. Seasonal pattern is not apparent, but the variation, according to raw data on growth of marked shoots, is in the order of 0,0001 g. This small scale seasonal variation is undetectible at the scale of measure used in production measures.

6.4.2 Comparison of production of other species of Spartina

Table 6.8 shows that in general, North American species of Spartina have higher net production than S. maritima production. This is probably the result of production measures based directly on biomass values. Higher biomass values for North American species have been discussed (Chapter 5.4). More valid comparisons are possible by comparing production : biomass (P/B) ratios (see Table 6.8). S. maritima has lower P/B values than the vigorous S. alterniflora, and is similar to the other species, S. cynosuroides and S. patens.

Comments made earlier on the methods of production measures are applicable to overseas data. Method 2 and 3 underestimate production by ignoring leaf and mortality losses. Method 6 also ignores these leaf losses, but accounts for loss of dead material. Turner (1976) has given a critical evaluation of this method when used on overseas species.

S. alterniflora dominated communities produced 1108 g m^{-2} yr^{-1} (Gabriel and de la Crux, 1974). Though these authors found no difference between normal and treated production (regrowth after repeated clipping), Hubbard (1970) reports that regrowth and increased density of S. anglica shoots were stimulated by cutting. The discrepancy in species behaviour renders this method unreliable. Furthermore, observations of harvested plots showed no regrowth of S. maritima shoots even a year after harvesting.

Efficiency of conversion of radiation by S. alterniflora is 0,2-0,35% (Turner, 1976) which is higher than that of S. maritima, which is 0,14-0,17%. (Efficiency = energy fixed by net production (J m^{-2} yr^{-1}) expressed as a percentage of solar radiation (J m^{-2} yr^{-1})).

TABLE 6.8 NET PRODUCTION OF SPECIES OF SPARTINA IN DIFFERENT REGIONS

	PLACE	SPECIES	METHOD 2	METHOD 3	METHOD 6	METHOD 7	METHOD 8		P/B
1.	Swartkops estuary (This study)	*S. maritima*	187-412	208-597	318-559	334-668	523-680		1,19
2.	Louisiana (Kirby and Gosselink, 1976)	*S. alterniflora*	-	700-752	1005-1409	1323-2645	-		1,35
3.	Georgia (Smalley, 1958)	*S. alterniflora*	-	354-1098	643-1098	-	-		1,33
4.	N. Carolina (Stroud and Cooper, 1969)	*S. alterniflora*	-	223-1170	329-1296	-	-		1,75
5.	Mississippi (Gabriel and de la Cruz, 1974)	" mixed	-	-	-	-	-	1108*	
6.	Connecticut (Steever, 1972)	*S. patens*	-	-	360	-	-		1,23
7.	Virginia (Mendelssohn, 1973)	*S. cynosuroides*	-	-	563	-	-		1,03
8.	Massachusetts (de la Cruz, 197[illegible])	*S. cynosuroides*	-	-	2190	-	-		1,18

* denotes Method of regrowth

The difference in growth strategy between *S. maritima* and the overseas species *S. alterniflora*, is clear in the values expressing leaf production as a percentage of net production. Though the values were derived by different methods, the discrepancy is obvious. *S. maritima* leaf production is almost 99,9% of net production, (see Tables 5.3, 6.5 and 6.6), whereas it varies from 15,6% in Georgia (Odum and Fanning, 1973) to 19,3% in N. Carolina (Williams and Murdoch, 1972) to 29% in Nova Scotia (Hatcher and Mann, 1975) for *S. alterniflora*.

Net production of *S. patens* appears comparable to that of *S. maritima* when data is treated by the same method, viz. Method 6 (see Table 6.8). It is noteworthy that *S. patens* is the only North American species which overwinters, with 25% of the population surviving through winter to the next growing season (Hardinsky and Reimold, 1977). Other similarities between this species and *S. maritima* are the independence of leaf production from culm elongation and no seasonal leaf abscission (Chapter 5.3.7, and Hardisky and Reimold, 1977). These authors concede that the "problem of assessing annual primary productivity is complicated by this carry-over of material" and are the only authors to have acknowledged this. They stress that the study of individual culms, is essential for community production studies of all species of *Spartina*.

The statements of Hardisky and Reimold (1977) support the reliability of the method devised in this study for production measurement.

CHAPTER 7

DECOMPOSITION RATE AND DETRITUS PRODUCTION

7.1 INTRODUCTION

Day (1967) states that the main source of basic food in the South African estuary, Knysna Lagoon, is organic detritus. Thus for a complete study of the energy flow through the Swartkops estuarine primary producer, S. maritima, the rate of decomposition and the production of detritus were measured seasonally. The rate of formation, the amount and the nutritional value of Spartina detritus as a food source for detritus feeders on the Swartkops salt marshes was thus determined.

Decomposition rate of S. maritima was estimated from losses of dead material from nylon mesh litterbags placed in situ for given time intervals. Litterbags are widely used in measuring degradation of salt marsh plants (Odum and de la Cruz, 1967; Gessner and Goos, 1973; May, 1974; Gosselink and Kirby, 1974; Odum and Heald, 1975). The alternative method recommended by Reimold et al (1975) and modified by Lominicki, Bandola and Kankowska (1968) is the "paired-plots" method, devised by Wiegert and Evans (1964).

7.2 METHODS

7.2.1 Seasonal loss of dead material

In the winter month of June, 1977 and in the spring month of October, 1977 a series of 192 litterbags were prepared and placed in the field to monitor seasonal breakdown of S. maritima. (A winter series initiated in April of 1977 was destroyed by human interference and was thus repeated in June).

Dead standing plant material was placed in litterbags to simulate the stage when detritus formation begins in nature. The litterbags were made of nylon mesh of three sizes: Fine = 0,4 mm^2; Medium = 0,5 mm^2; Coarse = 1,5 mm^2. Each bag was numbered, filled with a known mass of dried material and sewn closed. The bags were secured to the mud surface by means of nylon threads tied to stakes in a stan of Medium shoots (see Fig. 3.4). The bags lay flat on the marsh surface and were subject to regular tidal inundation The site was selected for minimal chance of human interference, which had proved to be a major problem in the past.

Major errors incurred in litterbag studies are not due to oven drying effects, but due to inaccuracies in mass measurement as a result of spillage during transportation from the laboratory to the field (Suffling and Smith, 1974). On the day of initiation of both summer and winter series, 15 litterbags, (5 of each mesh size) were returned directly to the laboratory, dried at 80°C for 24h, cooled in a desiccator and weighed. Loss by spillage in transit was expressed as a percentage of initial mass in grams.

After time intervals of about 5, 10, 20, 40 ....,etc. days, five bags of each mesh size were collected and washed clean of mud. Animals present in the detritus were removed for later identification. The plant matter was oven dried (80°C for 24h), cooled in a desiccator and weighed. Subsamples from the winter series were analysed for nitrogen content and energy value (see Chapter 5.2.3).

Litter remaining in the bags after given time periods was expressed as a percentage of original mass.

7.2.2 Determination of decomposition rate

Daily instantaneous rates of disappearance of dead material were estimated over monthly periods using the same method of litterbags described above. Five litterbags of each mesh size were placed *in situ* and collected after a month. Contents of the bags were processed as above.

Daily instantaneous rates of disappearance, r_1, were calculated as follows:

$$r_1 = \frac{\ln (W_o/W_1)}{t_1 - t_o}$$

where W_o and W_1 are dry dead litter mass at start and end of time interval respectively
$t_1 - t_o$ = time interval in days
(Wiegert and Evans, 1964)

The relationship between r_1 and ambient and estuarine water temperature was tested statistically for linear regression by the method of least squares (Hewlett Packard 65, Stat Pac 1-22). The nature of the data allowed the goodness of fit to be expressed as the correlation coefficient, r, and for the significance of the relationship to be tested (Bishop, 1966).

The method of "paired-plots" for decomposition measurement was attempted here. Unfortunately, repeated theft of the plot frames forced this approach to be abandoned. Briefly, the method involved enclosing a fixed area of Spartina with netting. At time t_o, (refer to decomposition equation above), dead material was removed from one half of the plot, washed and weighed ($=W_o$). At a later time t_1, dead material from the other half of the plot was collected and weighed ($=W_1$). From the above decomposition equation, r_1 is calculated. The method gives a more representative estimate by allowing effects of grazers to be measured.

7.2.3 Determination of detritus production

Rate of detritus production was determined from Wiegert and Evans' method (1964) of determining amount of material disappearing during a given time interval (Reimold *et al.*, 1975). Mean dry mass of Dead biomass during a time interval was multiplied by the disappearance rate of dead material per day.

$$\text{Detritus production} = x_i = \frac{(a_i + a_{i-1})}{2} \times r_1 t_1$$

where a_{i-1} and a_i are Dead biomass at start and end of time interval t_1

r_1 = instantaneous daily rate of disappearance of dead material during time interval (see Chapter 6.2)

(Wiegert and Evans, 1964)

Annual detritus production = sum of monthly values

7.3 RESULTS

7.3.1 Seasonal decomposition

Errors incurred by spillage losses were considered to be negligible in litterbag studies here (Table 7.1).

TABLE 7.1 Percentage litter lost from litterbags by spillage during transportation

	Mesh size of litterbag		
	FINE	MEDIUM	COURSE
	(0,4 mm^2)	(0,5 mm^2)	(1,5 mm^2)
Winter series	2,0	9,92	5,61
Summer series	0,45	3,02	1,31

Decomposition curves for winter (Fig. 7.1) and summer (Fig. 7.2) indicate the rate of release into the water of soluble material and particles small enough to pass through the mesh of the bags.

Linear regressions were fitted to the percentage values only from Day 6 onwards, owing to the initial, rapid leaching losses during the first five days (Hewlett Packard 65, Stat Pac 1-22).

During the first six days, loss of material was rapid (almost 10%), but evened out to a constant loss rate indicated by the straight slopes in Figs. 7.1 and 7.2. Rate of loss of different particle sizes was not significantly different (see standard error units) in the first 40 days of exposure in winter, and 110 days in summer. Overall, summer loss rate of mean particle size was slightly faster (0,0018 g g^{-1} d^{-1}) than in winter (0,0016 g g^{-1} d^{-1}). The half-life, $t_{0,5}$ of S. maritima litter in summer months was predicted at 216 d and in winter months, about 245 d.

Nitrogen and energy content of litter monitored during the winter months showed an initial drop, then gradually increased to a value higher that the original (Table 7.2).

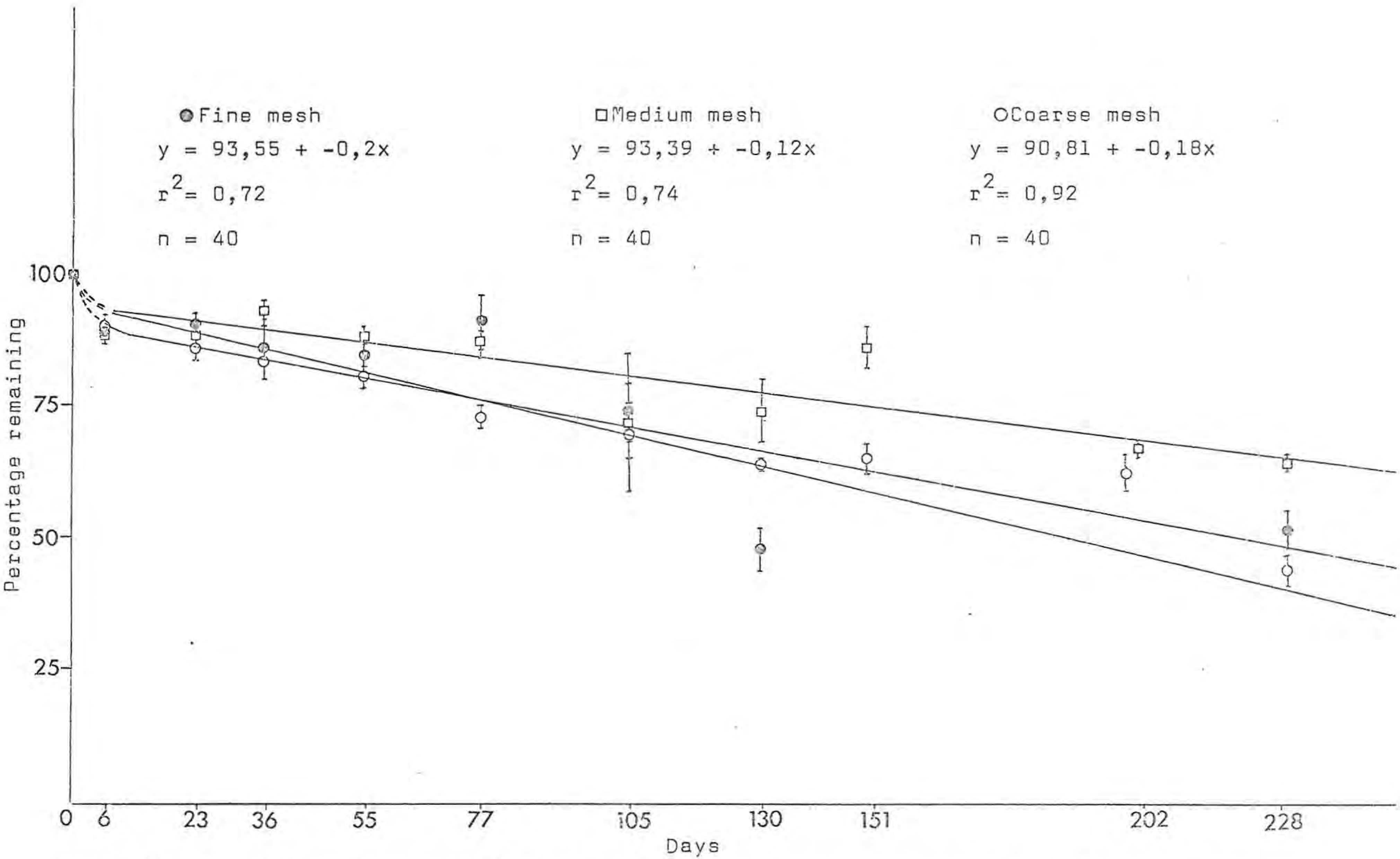


Fig. 7.1 Loss of S.maritima litter from litterbags during winter months. Initial date 22-6-77. Linear regression fitted by least squares method.

Points indicate means of 4 samples. Vertical lines indicate two standard error units.

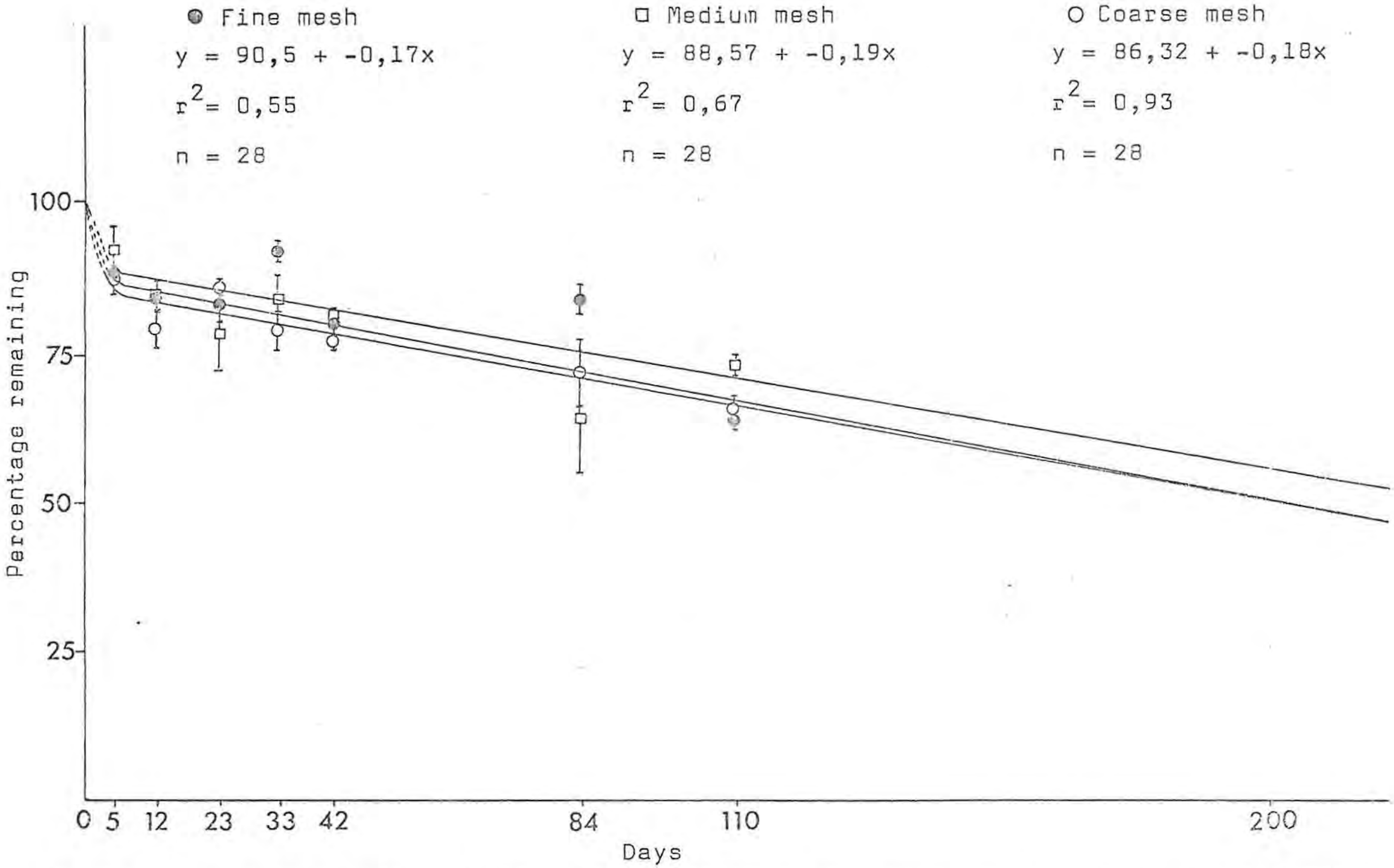


Fig. 7.2 Loss of S.maritima litter from litterbags during summer months. Initial date 19-10-77. Linear regression fitted by least squares method.
Points indicate means of 4 samples. Vertical lines indicate two standard error units.

TABLE 7.2 COMPOSITION OF LITTER MONITORED DURING WINTER BREAKDOWN

Period of exposure (days)	Nitrogen content (% dry mass)	Potential Energy (J)
0	1,0865	15263
36	0,6076	-
55	0,7989	14598
77	0,7174	13190
105	0,9337	15167
151	0,9007	14929
228	1,1726	16014

\- Denotes no data

All samples repeated until percentage error less than 3% for nitrogen analysis and 1% for energy determination.

The pattern of animal succession of S. maritima litter could only be tentatively suggested due to insufficient data (Table 7.3). No fauna such as amphipods, gastropods, decapods or insects were found in the Fine mesh bags.

7.3.2 Decomposition rate

Instantaneous daily rates of decomposition based on monthly periods of litterbag exposure showed a significant linear relationship with mean monthly ambient temperature, with the correlation coefficient, $r = 0,86$, probability = 0,01, and with mean monthly estuarine water temperature, with $r = 0,80$, probability = 0,01 (Fig. 7.3). The strong correlation allowed missing decomposition rates for the months January, February, and March (as a result of human interference with the litterbags) to be predicted from temperature data. Fig. 7.4 shows daily instantaneous decomposition rates, r_1, measured over monthly periods as means of data from all three mesh size litterbags. Averages were used because loss rates from the meshes during the first 30 days are not significantly different (Fig. 7.1 and 7.2).

TABLE 7.3 MACROFAUNA FOUND IN DIFFERENT MESH SIZE LITTERBAGS PLACED *IN SITU* FOR GIVEN TIME INTERVALS

SERIES	MESH SIZE	INITIAL DATE	LATER DATE	NO DAYS	NO ANIMALS PER LITTERBAG	SPECIES
	Medium	30.3.77	6.4.77	7	8	*Anurida maritima*
	Coarse	"	6.4.77	7	10	" "
April Series	"	"	2.6.77	63	4	*Assiminea cf. ponsonbyi*
	"	"	11.11.77	225	85	*Assiminea globulus*
	"	"	"	225	2	*Cleistostoma edwardsii*
	"	"	"	225	1	*Ochaetostoma sp.*
	Coarse	22.6.77	8.9.77	77	1	*As. globulus*
Winter Series	"	"	6.10.77	105	1	*C. edwardsii*
	"	"	"	105	4	*Assiminea bifasciata*
	"	"	21.11.77	151	5	*As. bifasciata*
	Medium	19.10.77	11.11.77	23	17	*An. maritima*
Summer Series	"	"	11.1.78	84	5	*As. globulus*
	Coarse	"	6.2.78	110	12	*As. bifasciata*

7.3.3 Detritus production

Fig. 7.5 shows appreciable seasonal fluctuation in detritus production measured for Tall and Medium S. maritima stands at both the River and Creek Stations. This is a direct result of decomposition rate rather than an expression of Dead biomass, which shows little seasonal variation (Figs. 5.1 and 5.2). More specifically, detritus production is an estimate of the amount of dead S. maritima breaking down into particles smaller than 1,5 mm^2.

Annual detritus production of particles $>1,5$ mm^2 was calculated from the sum of monthly data and expressed as an average for all sites. Thus local variation afforded by the different Stations and ecophenes was accounted for. S. maritima detritus production on the Swartkops marshes is given in Table 7.4.

7.4 DISCUSSION AND CONCLUSIONS

7.4.1 Seasonal breakdown of S. maritima

The term decompostion is used here to encompass decay, degradation and breakdown of formerly living plant material into detritus. Important mechanisms involved in decay are chemical dissolution, autolysis, hydrolysis, oxidation, mechanical fragmentation by waves and mastication by fauna and enzymatic lysis by bacteria and fungi (Fenchel, 1972). Litterbag studies have been criticised as being unrealistic in excluding mastication effects of large macrofauna (Odum, Zieman and Heald, 1972). Confirmation of this possible error by comparison with results of the "paired-plots method (Wiegert and Evans, 1964) was not possible in this study due to repeated interference with the plot frames. Litterbag studies and laboratory incubation studies of S. alterniflora have been done in other studies and similarities allow certain assumptions to be made concerning S. maritima decay.

Generally, the process of breakdown may be treated as three phases (Odum et al., 1972). Each phase is represented by a change in slope of the decomposition curve, though this study terminated before development of phase III

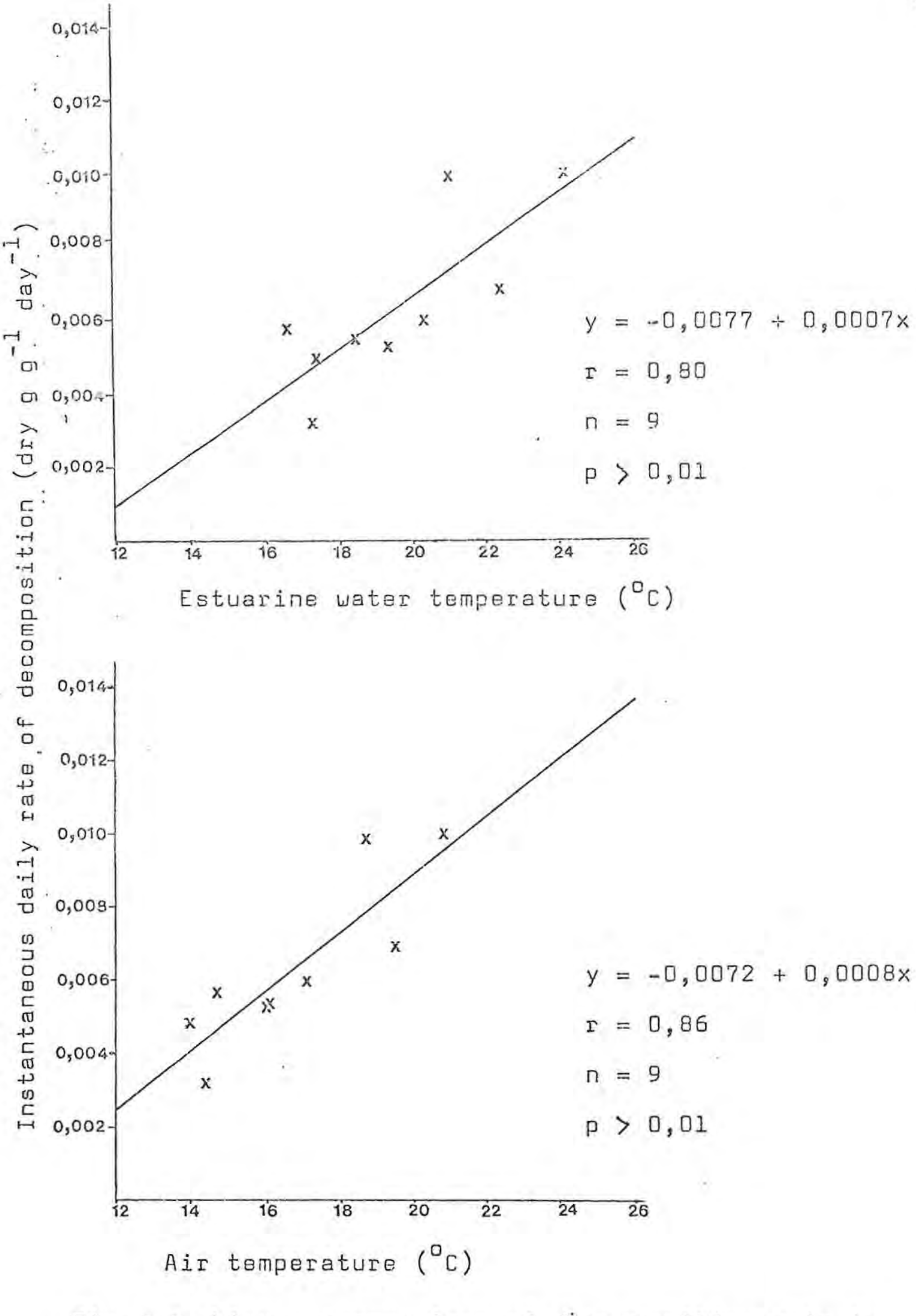


Fig. 7.3 Linear regressions of decomposition rate to temperature fitted by the method of least squares.

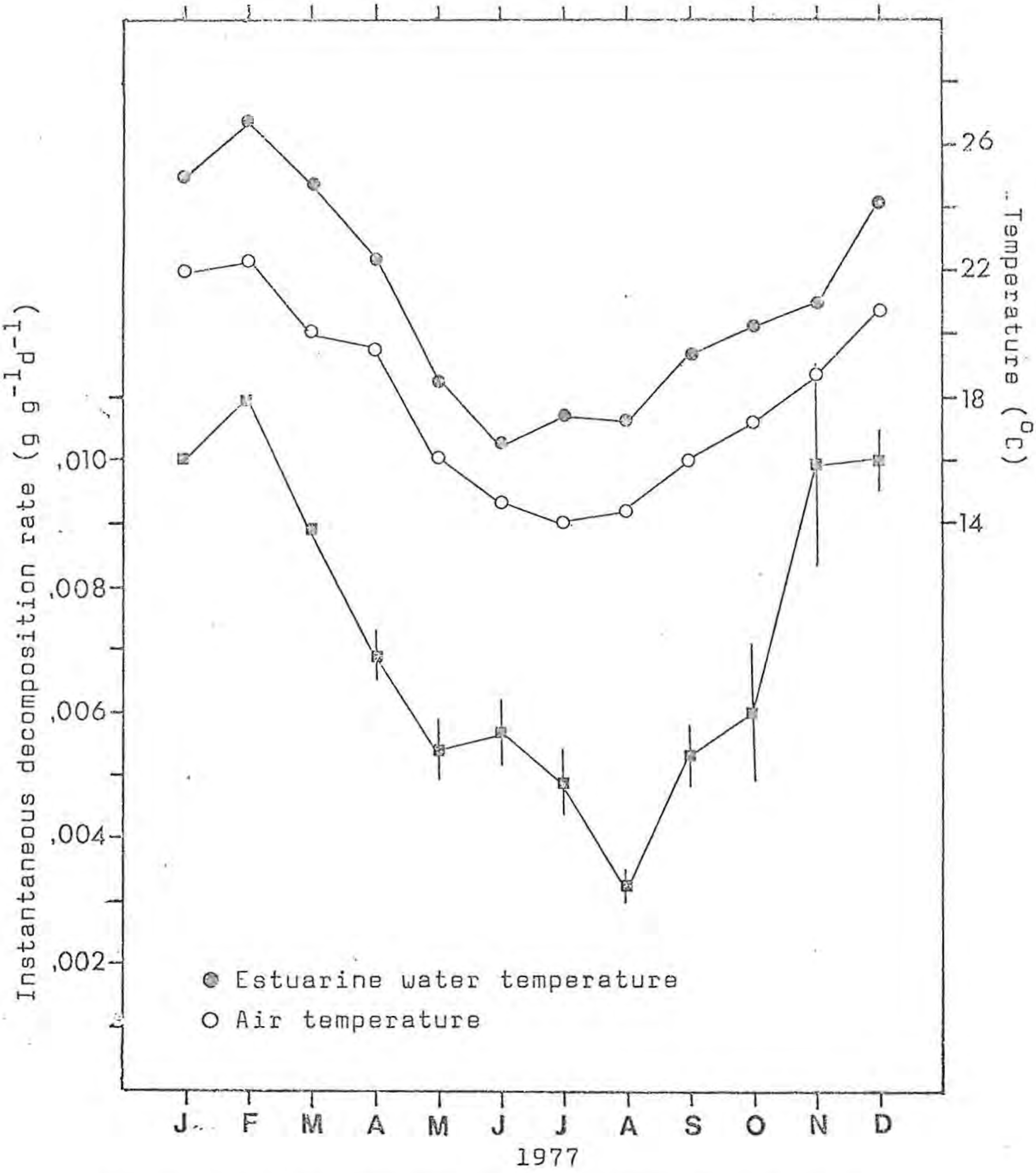


Fig. 7.4 Instantaneous rate of decomposition of S.maritima for different months of the year. (▨). Points indicate average of three mesh-size litterbags, with mean size of 0,8mm^2. Vertical lines indicate two standard error units.

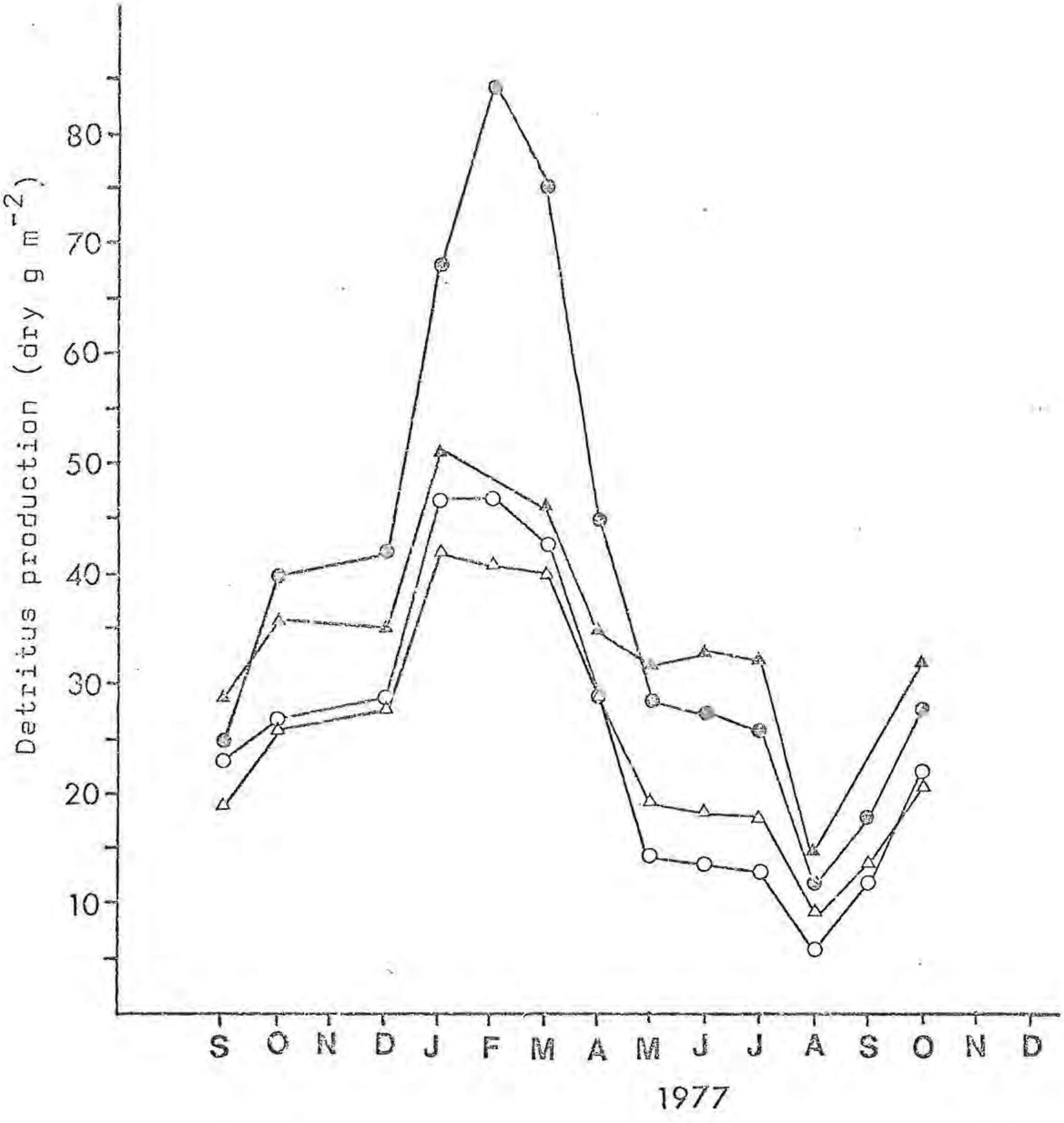


Fig.7.5 Monthly detritus production of Tall and Medium *S.maritima* at the River and Creek Stations.

● Tall shoots at the River Station

▲ Medium shoots at the River Station

○ Tall shoots at the Creek Station

△ Medium shoots at the Creek Station

TABLE 7.4 ANNUAL DETRITUS PRODUCTION OF S. MARITIMA PER SQUARE METER AND FOR THE WHOLE OF THE SWARTKOPS ESTUARY

	DRY MATTER (g)	ORGANIC MATERIAL (dry g)	POTENTIAL ENERGY (J)	CRUDE PROTEIN (dry g)	CARBON (dry g)
Mean production ($m^{-2}yr^{-1}$)	373,5	6013723,5	323,08	21,83	152,09
Total estuarine production (yr^{-1})	307,5x10^{3}kg	265,9x10^{3}kg	4,9509482 x 10^{12}kg	17,9x10^{3}kg	125,2x10^{3}kg

(Figs. 7.1 and 7.2). Briefly, each phase, indicated by a change in rate of loss, is the cumulative effect of the different mechanisms of decay, acting at varying intensities on the decomposing substrate.

Phase I

The initial steep slope is caused by rapid leaching of soluble organic compounds. Varying losses expressed as percentages of original mass have been reported for *S. alterflora*, ranging from 25% (Fenchel, 1970; Odum *et al.*, 1972) to 40% (Witkamp, 1966). In *S. maritima*, leaching during the first six days appears to account for about 10% of material lost. The dissolved organic compounds are important as they are converted directly and efficiently into bacterial biomass which acts as a food source to filter and deposit feeders (Gallagher, Pfeiffer and Pomeroy, 1976). After this initial period of rapid loss, leaching becomes less important in the degradation process (Odum *et al.*, 1972).

Phase II

The more gradual slope usually represents microbial breakdown by bacteria and fungi of moderately labile compounds and initial mechanical reduction by larger fauna, such as amphipods and gastropods.

The insignificant difference in losses between the Medium and Coarse mesh litterbags, which contained animals, and the fauna-free Fine mesh bags suggests that the role of insects, gastropods and amphipods in mechanical fragmentation is not of major importance during the first seven months of decomposition. The rate of loss during the second phase can thus be attributed primarily to microbial breakdown. Rate of decomposition may be underestimated as a result of litterbag exclusion of larger macerating agents eg. crabs which have the effect of increasing microbial numbers and thus increasing breakdown (Heinle, Harris, Ustach and Fremer, 1977).

The activities of microbial colonisers are limited by temperature, surface area of particles, O_2 diffusion and availability of nutrients (Fenchel, 1972). In this study, long-term temperature effects are clearly apparent in the faster summer decomposition rate. The small seasonal variation between summer and winter rates, 0,0018 $g\ g^{-1}d^{-1}$ and 0,0016 $g\ g^{-1}d^{-1}$ respectively, is probably a reflection of the mild climate of the Swartkops region (Chapter 3.1). In July, (mid-winter) mud surface temperatures as high as 19,9°C have been recorded.

Bacterial and protozoan action results in maceration and breakdown of cellulose and lignin (Gosselink and Kirby, 1974). The micro-organisms mineralise some of the S. alterniflora photosynthate and release another portion into the estuarine waters as dissolved organic compounds (Gessner and Goos, 1973; Gallagher et al., 1976). Energy is derived from detritus, and nitrogen and phosphorus are assimilated from estuarine waters (Newell, 1965; Fenchel, 1972). The conversion of cellulose into bacterial and protozoan protoplasm, the incorporation of nitrogen and phosphorus, the concentration of trace elements such as Mg, Mn, Zn, Mo by coprophagy effects and microbial activities (Kraeuter, 1976) all have the effect of raising the nutritional value of detritus to a much higher status than that of the original plant material. Increases in nitrogen content of S. alterniflora detritus with time have been reported (Burkholder and Bornside, 1957; Teal, 1962; Darnell, 1967; Odum and de la Cruz, 1972; Squiers and Good, 1974). In this study, decomposing S. maritima litter showed an initial drop in nitrogen content (Table 7.2). The loss of amino acids during leaching may account for this, as suggested by Hall, Weimer and Lee (1970) for S. alterniflora. With time, S. maritima detritus increased in nitrogen content. After about eight months, the nitrogen value exceeded that of recently dead material (Table 7.2).

Nitrogen levels in Live material were not attained by detrital particles, as expected from other studies (Teal, 1962; Odum and de la Cruz, 1967). It is probable that the series was not monitored for long enough. Alternatively, the fraction of particles associated with 70% of bacterial activity ranges from 14-180 µm (Hanson and Wiehe, 1977). This putative nitrogen-rich fraction is lost through the litterbag mesh and is not accounted for.

Studies requiring this level of detail must therefore involve laboratory incubation methods of microbial study (Harrison and Mann, 1976).

Detailed studies have shown that attached microflora and micro-organisms on detritus particles are the actual food source for detritus consumers (Newell, 1965; Darnell, 1967; Fenchel, 1970, 1972; Odum, 1971). It is generally concluded that microfauna such as amphipods play an insignificant role in chemical breakdown as detritus passes out undigested and "cleaned" of all attached micro-organisms. Mechanical breakdown, however, by mastication into smaller particles increases available surface area, resulting in greater recolonisation (Heinle et al., 1977).

Phase III

This phase, characterised by the most gradual slope, and thus the slowest rate of loss, is a manifestation of a continuation of the earlier mentioned processes acting on the residual, resistant materials. Presumably, this study was not continued long enough for this slower phase to be represented in the decomposition curves.

Litterbag studies allow comparisons of break-down rates to be made in terms of decomposition half-life ($t_{0,5}$) which is the time taken for 50% of litter to be degraded (Louisier and Parkinson, 1976). Decomposition rates are difficult to compare where climate and mesh size vary. Here, *S. maritima* $t_{0,5} = \pm$ 7 months for mesh size 1,5 mm^2. Similar studies on *S. alterniflora* in Georgia, gave $t_{0,5}$ = 6 months for mesh size of 2,5 mm^2 (Odum and de la Cruz, 1967). The loss rate for the first month of the Georgia study was 25%, which was very much greater than the value of 8% for 1 mm^2 mesh size measures by Gessner and Goos (1973). However, $t_{0,5}$ for both studies was 6 months. A standardisation of mesh sizes is essential before meaningful comparisons can be made.

Only a faint trend was seen in animal succession in the litterbags (Table 7.3). Earliest colonisers appear to be *Anurida maritima*, followed by species of *Assiminea*.

It is clear that a considerably higher number of litterbag samples are required before assumptions can be made about faunal succession associated with detrital formation.

7.4.2 Daily instantaneous rates of decomposition

From the discussion and interpretation of the growth curves, it is apparent that decomposition in the first 30 days is the result of leaching and microbial breakdown. Thus instantaneous daily rates of decomposition, r_1, calculated from monthly measures are a manifestation of Phase I and II mechanisms. The significantly high correlation between decomposition, and estuarine and ambient temperatures indicate the direct relationship of microbial activity to temperature (Fig. 7.3). The finding is important as a predictive means of estimating decomposition rate from temperature data.

7.4.3 Monthly and annual detritus production

The full importance of the temperature-dependent nature of *S. maritima* decomposition is shown when monthly detritus production is monitored (Fig. 7,5). This agrees with Turner's (1976) review on North American studies that dead material turnover increases with increasing temperature. The seasonal variation is mostly a function of the instantaneous rate of decomposition, as Dead biomass is almost constant through the year (Figs, 5.1 and 5.2). Overall differences in detritus production at the different sites are attributable to the varying amounts of Dead biomass produced by the Live biomass present. Average production is highest for Tall *S. maritima* at the River Station, by virtue of its highest amount of Dead biomass. Although decomposition rates are higher, the average monthly production of detritus here is considerably smaller than Georgian salt marshes with values of 198-113 g $m^{-2}month^{-1}$. The difference is probably attributable to the appreciably higher source of Live production of *S. alterniflora* (Table 6.8).

At this point, it is stressed that the detritus particle with its attached "load" of interacting micro-organisms, adsorbed compounds and trace elements, and the effects of mastication, coprophagy, and recycling on the particle forms an ecosystem of its own. The complexities and processes are described by Darnell (1967), Odum (1971), Fenchel (1972), Odum and Heald (1975), Odum _et_ _al_. (1972). For simplicity, the detritus particle has been considered here as a single unit.

Production of detritus represents the potential input of food resources to the estuarine ecosystem. The instantaneous decomposition rate from the marsh is a measure of the rate at which grams of dead material are entering the detritus food web.

There is a discrepancy between Live Production and Detritus Production (Tables 6.7 and 7.4, respectively). Detritus production is about 62% of Live production. Turner and Gosselink (1975) estimate that 25-50% of organic mass of _S. alterniflora_ is lost just before culm death by translocation into the roots and leaching.

Values of detritus production may be underestimates, resulting from the use of litterbags for rate measurements. Smalley (1959) estimated that 90% of aerial primary production of salt marsh plants enters the detritus food web when the plants die.

The time-lag between Live production and Dead production accounts for the discrepancy. The two processes obviously function at different rates during a monthly period. The significance of this time-lag will be discussed later. It is sufficient to say, that the instantaneous decomposition rate is a measure of the rate at which grams of dead material are entering the detritus food web either through microbial growth, tidal harvest or incorporation into the soil system (Reimold _et_ _al_., 1975). This rate term was used in determining the potential detritus input to the estuarine system by _S. maritima_.

CHAPTER 8

EXPORT OF S. MARITIMA MATERIAL

8.1 INTRODUCTION

The importance of salt marshes to estuarine and coastal waters in North temperate regions is undisputed and well-documented (Lagna, 1975). Assumptions on the effect of salt marsh production on South African estuarine and coastal waters has been based largely on overseas findings. The only export study on a South African estuary is that of Liptrot's (1978) on the Swartvlei estuary, which showed a minimal export of organic particulate matter.

Thus in order to assess the contribution of organic material from the *S. maritima* salt marsh stands to the estuarine and hence coastal waters, tidal import and export was measured. This fulfils the requirements for understanding the importance of primary production to the estuarine ecosystem (see Chapter 1.1 and Odum *et al.*, 1972).

8.2 METHODS

Measurements were made on 2 separate occasions, one as an estimate of maximum, irregular tidal flushing at Equinoctial Spring Tide, and the other to assess regular Spring Tide Waters. Tidal transport by the waters of Tippers Creek was selected for logistic reasons. The sampling site was established near the confluence of the Creek and the main Swartkops channel (Fig. 3.4). The catchment area of the Creek covered by *S. maritima* was determined by planimetry from the vegetation map (See Fig. 4.1).
At mean Neap tide, the morphometry of a transect across the Creek channel (See Fig. 8.1) was surveyed and drawn to scale with the water level relative to the jetty.
A system of nets was designed to trap particles floating and submerged in the tidal waters. A pole projected from the jetty, and suspended vertically by a weighted rope were three nets held at adjustable depths in the

channel (Fig. 8.2). The nets were secured at different depths by means of brass bolts to ensure representative sampling in the water column, which varied in height during the tidal cycle. A fourth net was suspended at water level to sample floating particles. Nets of mesh size of 1,5 mm^2 were selected to trap particles corresponding to the largest litter bag mesh. The nets were in operation for 15 minutes out of every hour for 6 hours of ebb and 6 hours of flow. Water levels relative to the jetty were recorded for calculation of the water transect width and area for the appropriate stage in tidal cycle. Debris collected was washed off the nets and sorted into : Live and Dead fractions of S. maritima; other plant species; animal matter and unidentifiable detritus. Samples were dried, and potential energy, nitrogen composition and organic content determined (Chapter 5,2,3). The mass of imported and exported materials was calculated from the sum of three samples collected hourly during tidal ebb and flow respectively.

Material (g) transported past study site per hour

$$= \text{Floating material} + \text{Submerged material}$$

$$= (W \times (4 \times \text{net width}) \times M_f \times 4) + (A \times (1,33) \times M_s \times 4)$$

Where W = width of Creek in meters, corrected for tidal height

(4 x net width) = correction for net width into meters

M_f = dry mass of surface sample

4 = conversion of 15 min sample to 1 h

A = area of Creek in square metres, corrected for tidal height

1,33 = correction for area of 3 nets into meters

M_s = dry mass of submerged sample

(modified from Liptrot, 1978)

Net Import and Export were calculated as the difference between total import and export values. Total Export values divided by the catchment area gave an estimate of contribution of S. maritima to estuarine waters.

8.3 RESULTS

The S. maritima catchment area of Tippers Creek was calculated as 201993,75 m^2. Debris carried by tidal waters included: Live and Dead fractions of S. maritima; leaves of Zostera capensis; Arthrocnemum perenne; Triglochin bulbosum; and some Enteromorpha sp.. The plant detritus was too mixed and decayed for more detailed sorting. Animal detritus consisted mainly of decaying crab and prawn exo-skeletons.

The equinoctial spring cycle resulted in a Net Export of all materials while the regular Spring Tide cycle resulted in some Net import and some Net export (Table 8.1). Contribution of S. maritima in terms of quality and quantity to Equinoctial Tidal waters and hence estuarine waters is given in Table 8.2.

According to catchment area measures, total export of S. maritima per Equinoctial cycle is 6,26 dry g m^{-2}. The earlier floods in May, and the resultant loss of debris from the marshes may have resulted in an underestimation of "average" equinoctial export. The figure thus can not be expressed as a half yearly estimate.

8.4 DISCUSSION AND CONCLUSIONS

Regular Spring Tides appear unimportant for transport of detritus $>1,5$ mm^2 from the source of production on the marsh to aquatic consumers (Table 8.1). Even measurements on Equinoctial Spring Tidal waters showed that transport of particulate matter $>1,5$ mm^2 from the salt marshes was negligible : only 6,26 dry g m^{-2} in comparison to Live and Detritus production of S. maritima (see Tables 6.7 and 7.4 respectively).

Marsh grasses probably contribute the lowest percentage of their net production to nearby bodies of water. Irregular flooding results in long periods for microbial respiration on the marsh (Odum et al., 1972). Only 45% of aerial production of S. alterniflora was transported by estuarine

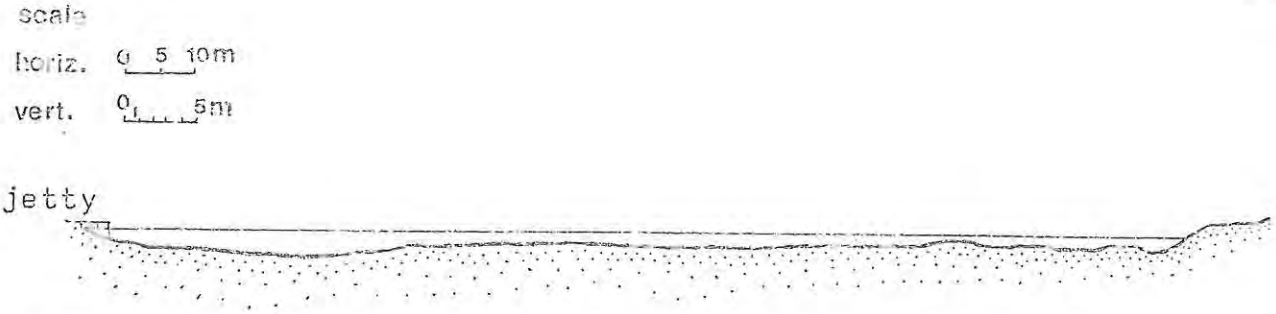


Fig. 8.1 Profile of Tippers Creek at site of Export study.

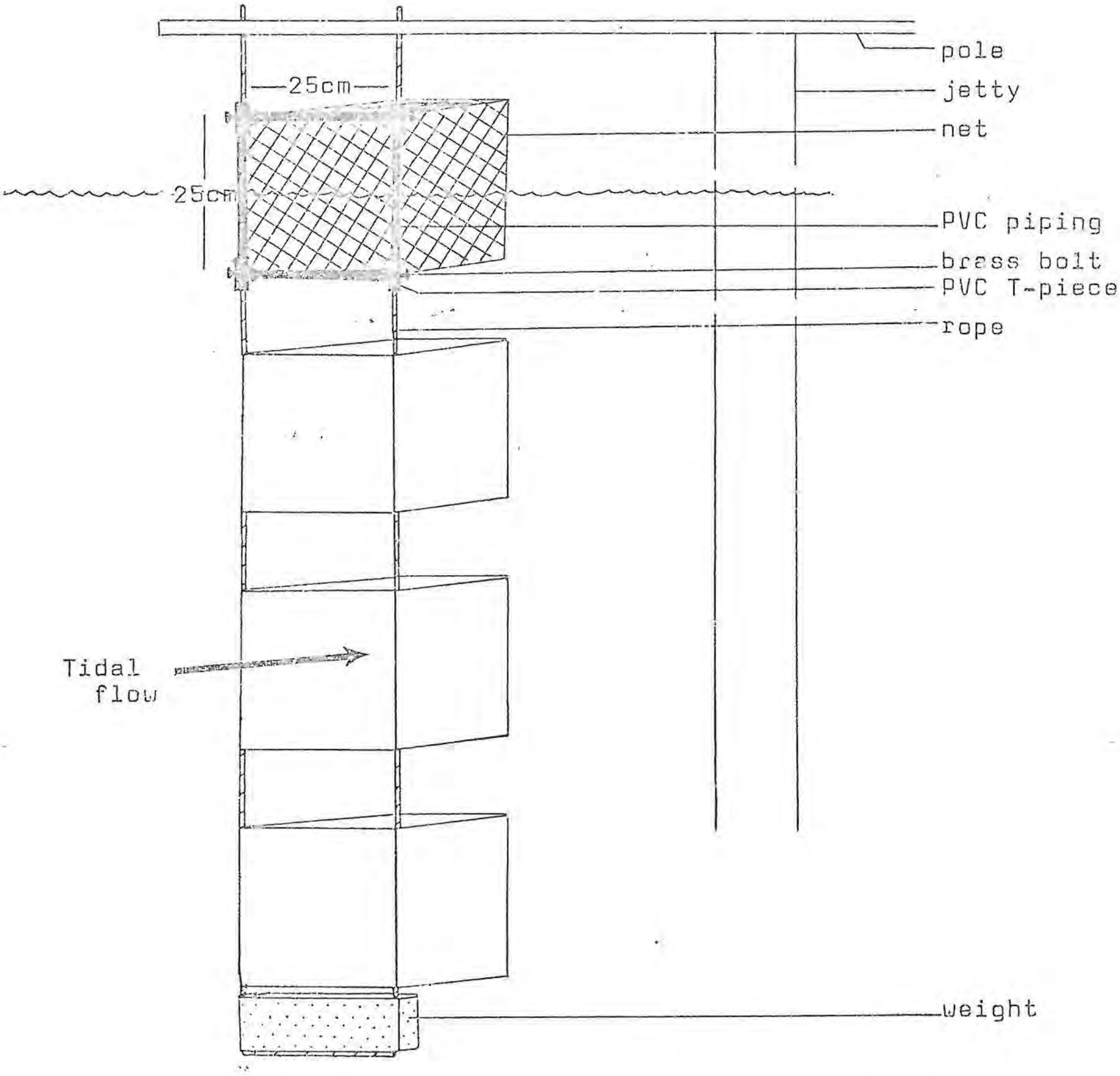


Fig. 8.2 Diagram of equipment used to measure import and export by tidal waters.

waters in Georgia (Teal, 1962) and 51% in a Louisiana marsh (Odum *et al.*, 1972). Spring Tide *import* in Tippers Creek, 9,5 kg, contrasts with transport in similar sized *S. alterniflora* Georgian salt marshes. Odum and de la Cruz (1967) measured Spring Tidal *exports* of 140 kg organic matter and 25 kg in a Neap Tide cycle from a 10-25 ha marsh area. Also, comparisons are not strictly valid considering the gross difference in growth form of the two species of *Spartina*. *S. alterniflora* plants of up to 2 m in height must give rise to higher litter production.

The low detrital particle losses indicate that spring tide removal of litter does not affect the accuracy of Dead biomass estimates greatly.

Entire marsh "flushing" by estuarine waters occurs at least twice a year as a result of Equinoctial tides and irregular flooding. Floating masses of *S. maritima* litter have been observed out in Algoa Bay as a result of high seas combined with Spring Tides and strong off-shore winds. The small amount of tidal transport and the irregular nature of salt marsh contribution to estuarine and coastal waters are suggested here to have important consequences. Theories have been proposed elsewhere as stabilising strategies but are modified here to explain the findings of this study (Darnell, 1967; Odum, 1969).

A strategy for stabilising the irregular supply of energy and nutrients lies in the nature of plant litter transported to coastal waters. The slow and highly involved recycling of decomposing organic material ensures a steady supply of food resources between the irregular supplies to the aquatic consumers in the sea.

It is obvious that dissolved organic compounds are lost to tidal waters. Also subparticulate matter is more readily transported by water currents to other areas than particulate matter. It is hypothesised that particulate organic detritus stays on the marsh and is an important storage place for energy and nutrients which may be used locally (Darnell,1967). In this way the marsh is a self-perpetuating system, retaining nutrients for use by primary producers.

TABLE 8.1 IMPORT AND EXPORT IN TIPPERS CREEK BY EQUINOX AND SPRING TIDAL CYCLES
(Expressed as dry mass in kg)

		S. MARITIMA		*Z. CAPENSIS*	*A. PERENNE*	*T. BULBOSUM*	*ENTEROMORPHA SP.*	PLANT DETRITUS	ANIMAL DETRITUS
		LIVE	DEAD						
EQUINOX TIDE	EXPORT	742,031	527,436	24,637	3,329	1,306	0,063	20,551	4,958
	IMPORT	3,561	0,673	0,095	0,119	0,001	0	0,805	0,006
	NET EXPORT	738,470	526,762	25,542	3,209	1,305	0,063	19,745	4,951
SPRING TIDE	EXPORT	0	5,108	5,310	0,006	0	0	0,049	0
	IMPORT	0	14,607	5,006	5,005	0	0	0,260	0,430
	NET IMPORT	0	9,495	0	0	0	0	0,211	0,430
	NET EXPORT	0	0	0,303	0,001	0	0	0	0

TABLE 8.2 NET EXPORT OF S. MARITIMA FROM TIPPERS CREEK BY EQUINOCTIAL SPRING TIDES

	DRY MASS (kg)	ORGANIC MATERIAL (kg)	CRUDE PROTEIN (kg)	POTENTIAL ENERGY CONTENT (J)
Live *S. maritima*	738,47	666,83	59,96	$1,2742303 \times 10^{10}$
Dead *S. maritima*	526,76	455,65	30,15	$0,9035034860 \times 10^{10}$
Total *S. maritima*	1265,23	1122,48	90,12	$2,1777337 \times 10^{10}$

CHAPTER 9

GENERAL DISCUSSION AND CONCLUSIONS

9.1 S. MARITIMA AS A PRIMARY PRODUCER

Primary productivity is related to the plant's ability to transform available nutrients and solar energy into organic biomass (Odum, 1971) and is perhaps the most fundamental dimension of an ecosystem (Whittaker, 1970).

Production of S. maritima, as a function of biomass, showed local variation at Swartkops between Tall streamside and Medium height inland shoots. The variation is definitely related to factors associated with tidal inundation (Fig. 4.2). Substrate nitrogen cannot be assumed as a limiting factor here (Chapter 4.4). The higher production of streamside shoots, and the overall higher biomass of River shoots compared to Creek shoots is possibly determined by variable "energy subsidies" afforded by tidal waters (Steever et al., 1976 and Chapter 4.4). In addition, the general distribution of S. maritima is clearly associated with water levels (Fig. 4.1). This is important in estuarine management as restriction of the tidal prism will adversely affect S. maritima abundance and production (Odum, 1971; Steever et al., 1976).

The continual all year round growth of S. maritima led to considerable difficulty in adapting American methods of production measure to this study. Hardisky and Reimold (1977) are the only authors who have acknowledged this difficulty when measuring the production of S. patens growing in a region of mild seasonal change. The Swartkops study has emphasised the importance of measuring growth characteristics in order to understand the nature of S. maritima production. Almost all energy goes into leaf rather than stem production in contrast to energy partitioning in S. alterniflora (Chapter 5.4).

Live production estimates, 601 g $m^{-2} y^{-1}$ of S. maritima were lower than for other Spartina species (Table 6.8) and less efficient in the conversion of solar radiation (0,16% efficiency). Though the genus Spartina has a reputation for high production (Keefe, 1972), all reports on S. maritima stress its lack of vigour (Mobberley , 1956; Marchant, 1967; Marchant and Goodman, 1969). This casts doubt on the assumption by Ellis (1977), based on anatomical studies only, that S. maritima has a C_4 photosynthetic pathway. Solar efficiencies calculated as energy trapped by net production as a percentage of available radiation energy are under-estimates, as below-ground production is ignored and so are losses by respiration. However, comparison may be possible if similarly calculated efficiencies are used. Solar conversion efficiency of different species is difficult to compare as this property is often influenced more by life-cycles of the plant than the efficiency of its photosynthetic mechanism (Westlake, 1963). The marked growth of S. alterniflora during its short growing season is difficult to compare with the continual growth of S. maritima throughout the year.

Total live production of S. maritima in Swartkops estuary, 495611,6 kg yr^{-1} gives an estimation of the total amount of potential food (Table 6.7), but underestimates whole-plant production by ignoring root and rhizome growth. Below-ground production is extremely tedious to measure, and is considered relatively unimportant from an aquatic trophic standpoint, as much of it seem to go into substrate formation rather than estuarine food webs (Odum, et al., 1972). Live production as a "potential" food source is emphasised particularly in this study as little information exists on direct use of live shoots. From field observations, the only live plant consumer noted was a member of the Miridae. As only eight specimens were seen in the one and a half years of study, their role as grazers was considered negligible. Less than 5% of net production of S. alterniflora was found to be grazed directly (Odum and Smalley, 1959). Detailed studies on local fauna are essential for confirmation of the assumption that direct grazing is negligible.

Detritus production from S. maritima in the Swartkops estuary 307493,2 kg y^{-1} takes into account the formation rate of and the amount of available food (Odum and Heald, 1975; Odum et al., 1972; Reimold et al., 1975). Again, the values obtained here (Table 7.4) are considerably lower than in North American studies. Detritus production from a Georgian S. alterniflora salt marsh was 1845,8 g m^{-2} yr^{-1} (Reimold et al., 1975). Obviously detritus production is a direct function of live production, explaining the discrepancies between local and overseas results. The difference between S. maritima live production and detritus production, however is very large. About 90% of aerial production of S. alterniflora was calculated as entering the detritus foodweb (Smalley, 1959). Only 63% of annual net production of S. maritima appears to form detritus, but the discrepancy may be explained by the time-lag between the two processes. If both live production and detritus formation are expressed as rates for the same time interval, the slower process of decomposition will cause the difference in rate between live production and detritus formation to appear greater than in reality. Though utilisation of live material may account for some loss of live production, as well as translocation to roots before death, it is logical to assume that matter produced ultimately becomes detritus or dissolved organic compounds.

The contribution of S. maritima detritus ($>1,5$ mm^2) on the Swartkops salt marshes to estuarine and coastal waters was minimal, being 6,26 g m^{-2} of marsh at equinoctial tides (Chapter 8.4). This low percentage of tidal export of either live or detritus production on the marsh supports the theory that detritus plays a vital role in storing energy and nutrients on the marsh surface (Darnell, 1967; Fenchel, 1972). Furthermore, the retention of nutrients on the marsh by detritus is beneficial to overall marsh production by ensuring that recycled nutrients are available to the primary producers (Mendelssohn and Marcellus 1976).

The formation of detritus is a highly complex process involving several auto- and heterotrophic cycles.

Bacterial and fungal colonisation: exploitation of detrital energy in combination with adsorbed nutrients; predation by protozoans and nematodes on other micro-organisms; and mechanical fragmentation by faunal grazing, resulting in even greater microbial recolonisation, are just a few of the processes involved (Burkholder and Bornside, 1957; Darnell, 1967; Fenchel, 1970; May, 1974; Kraeuter, 1976). The associated microflora and fauna and adsorbed organic compounds are the actual food source of detritus feeders (Newell, 1965; Fenchel, 1970, 1972; Wetzel, 1977). From the above, it is clear that detritus formation should not be regarded simply as a link in energy flow. It is on the detritus particle that nutrients are recycled and the primary product "enriched". A closer study of detritus, as the basis of the estuarine foodweb is warranted. This is essential in order to understand the role of primary production in estuarine ecosystems, and to answer the questions, what part of and where is primary production utilised? This study has shown clearly that production studies would be more efficient in terms of time and labour input, and information gain, if the answers to these two questions are known before the initiation of primary production studies.

However, within the requirements of the production approach to the Swartkops estuarine ecosystem, the essential processes which control primary production and which ultimately dictate the value of each plant species to the ecosystem are the amount of leaf production, continual shoot mortality and the pulses of detritus export which are all species dependent (Hardisky and Reimold, 1977).

9.2 ESTUARINE ECOSYSTEM STABILITY

Salt marshes are cited as classical examples of highly stressed systems with little biological structure and low diversity (Nixon, Oviatt, Garber and Lee, 1976). The low diversity of plant species, the few niches and biomass restricted by tidal removal leads to broad, unrestricted food habits (Teal, 1962). Though the latter phenomenon of tidal removal is not significant in the Swartkops estuary (Chapter 8.4), the similarities in terms of stressed conditions and low diversity are close enough to accept the idea of a wide detritus diet by secondary producers as a strategy for stability.

The time-lag between Live production and Detritus production is considered to be another stabilising strategy. In North America, primary production of Spartina is strongly seasonal. It is theorised that by levelling out the effects of temporal variation in primary production and by reabsorption of dissolved nutrients, detritus is vitally important in stabilising the ecosystem (Odum and de la Cruz, 1967; Odum, 1971; Fenchel, 1972).

The danger of blind extrapolation of overseas concepts to our own estuaries became apparent in this study. The concept of detritus-stabilised production is not applicable here as there is a continuum of plant production as a result of the growth pattern of S. maritima, and the mild climate. It is apparent that in N. America , estuaries are far more important than in South Africa in terms of area alone (Chapter 5.4, Turner,1976;Turner and Gosselink, 1975). In addition, S. maritima is a lower producer compared to the American species, S. alterniflora. Furthermore, little is known about the exploitation of detritus by secondary producers.

Transport of marsh detritus from Swartkops marshes into these waters occurs in discrete supplies during the equinoxes and at the time of floods. Decomposition of the litter carried in these waters probably continues at a slow rate, dampening the discontinuity in supplies of energy and nutrients and prolonging availability of detrital food to consumers.

These detritus-based strategies for stability further emphasise the importance of a specific detritus study in Swartkops.

9.3 THE IMPORTANCE OF S. MARITIMA TO THE SWARTKOPS ESTUARINE ECOSYSTEM

The role of S. maritima as a primary producer in the Swartkops cannot be fully evaluated until utilisation of live and detrital material, by secondary producers has been determined. The necessity for closer studies of detritus exploitation has been stressed above.

The fact that S. maritima may be an exotic further complicates an evaluation of its role in the Swartkops estuary. The plant is apparently a highly successful coloniser and outcompetes Zostera capensis (Macnae, 1956, 1957). In England, a similar situation is reported where S. townsendii outcompetes Z. nana (Oliver, 1925). Primary production of Zostera is highly important in overseas estuaries (Penhale, 1977) and in South Africa Z. capensis has been shown to play an important role in the Sedgefield estuary (Liptrot, 1978). Zostera production may be higher than Spartina production, and the successful establishment of the exotic, in outcompeting Zostera, may have had the effect of reducing primary production in the Swartkops estuary. However, production estimates alone are insufficient for evaluation of roles until nutrient cycling by the two plant and their exploitation by secondary producers is known. Potential roles of S. maritima, determined for S. alterniflora are involvement in nutrient cycling as phosphorus "pumps" (Reimold and Daiber, 1970) and absorption of sewage pollution (Nixon and Oviatt, 1973b). The latter would prove particularly important inview of the urban and industrial surroundings of the Swartkops River. Substrate stabilisation has been found to be a function of Spartina on the Kowie estuary (Lubke and Curtis, 1977). S. maritima appears to be a better buffer of erosion than Zostera in that Spartina stands are unattractive to bait diggers (personal observation). Furthermore, Zostera distribution shows seasonal behaviour at Swartkops, whereas Spartina stands are perennial, providing all-year-round substrate stabilisation.

9.4 EVALUATION OF PRODUCTION APPROACH TO ECOSYSTEM STUDIES

The approach to ecosystem studies, based on primary productivity and the energy flow pathways should be critically evaluated. My criticisms of this approach are that an estimate of production does not lead to greater understanding of the system. The resultant figure may not warrant the effort involved. These thoughts are shared by Orians (1974) who states that the production and energy budget approach to ecosystem study has serious limitations implicit in its goals and methods. Firstly, the direct answer to production studies in one system, cannot be extended to other ecosystems, except by repeating the laborious field work which was invested to obtain the first estimate. Secondly, the effects of selective agents, and more particularly, those of Man, and the resultant changes are not recognised by this approach.

Finally, the point made clear in this study and appropriately stressed, was stated as early as 1961 by Odum - a management system based on utilisation rather than production, is needed in order to avoid serious mistakes in conservation of estuarine ecosystems.

REFERENCES

ADAMS, D.A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44 : 445-456.

ALEXANDER, S.J. and D.W. EWER. 1969. A comparative study of some aspects of the biology and ecology of *Sesarma catenata* Ort. and *Cyclograpsus punctatus* M.Edw., with additional observations on *Sesarma meinerti* de Man. Zoo. Afr. 4 : 1-35.

BEWS, J.W. 1929. The world's grasses. Longmans, Green and Co., London.

BISHOP, O.N. 1966. Statistics for biology. 2nd ed. Longman, London.

BOUCHER, C. and M.L. JARMAN. 1977. The vegetation of the Langebaan area, South Africa. Trans. Royl. Soc. S. Afr. 42 : 241-272.

BURKHOLDER, P.R. 1956. Studies on the nutritive value of *Spartina* grass growing in the marsh areas of coastal Georgia. Bull. Torrey Bot. Club 83 : 327-334.

________________ and G.H. BORNSIDE. 1957. Decomposition of marsh grass by aerobic marine bacteria. Bull. Torrey Bot. Club 84 : 366-383.

CHAPMAN, V.J. 1938. Studies in salt marsh ecology, I-III. J. Ecol. 26 : 144-179.

____________. 1974. Salt marshes and salt deserts of the world. Verlag van J. Cramer, Lehre.

CHRISTIE, N.D. 1976. Primary production in Langebaan Lagoon. Poster paper given at Water Conference, July 1976. Univ. Port Elizabeth.

CLARKE, L.D. and N.J. HANNON. 1967. The mangrove swamp and salt marsh communities of the Sydney district. I. Vegetation, soils and climate. J. Ecol. 55 : 753-771.

______________________________. 1969. The mangrove swamp and salt marsh communities of the Sydney district. II. The holocoenotic complex with particular reference to physiography. J. Ecol. 57 : 213-234.

______________________________. 1970. The mangrove swamp and salt marsh communities of the Sydney district. III. Plant growth in relation to salinity and waterlogging. J. Ecol. 58 : 351-369.

DARNELL, R.M. 1967. Organic detritus in relation to the estuarine ecosystem, p. 376-382. In G.H. Lauff (ed.) Estuaries. Am. Assoc. Adv. Sci., Washington D.C.

DAY, J.H. 1967. The biology of Knysna estuary, South Africa, p. 397-407. In G.H. Lauff (ed.) Estuaries. Am. Assoc. Adv. Sci., Washington D.C.

________ 1969. A guide to marine life on South African shores. A.A. Balkema, Cape Town.

DE LA CRUZ, A.A. 1973. The role of tidal marshes in the productivity of coastal waters. Amer. Soc. Biol. 20 : 147-156.

DIECKMANN, G.S. 1978. Aspects of growth and production of Laminaria pallida (Grev.) J. Ag. off the Cape Peninsula. M.Sc. thesis, Univ. Cape Town.

DYE, A.H. and J.P. FURSTENBERG. 1978. An ecophysical study of the meiofauna of the Swartkops estuary. II The meiofauna : composition, distribution, seasonal fluctuation and biomass. Zoo. Afr. 13 : 19-32.

DYER, R.A. 1976. The Genera of Southern African Flowering Plants. Vol 2. Dept. Agric. Technical Services, Pretoria.

EDMONDSON, W.T. and G.G. WINBERG. 1971. A manual on methods for the assessment of secondary productivity in fresh waters. IBP Handbook No. 17. Blackwell Scientific Publications, Oxford.

ELLIS, R.P. 1977. Distribution of the Kranz syndrome in the Southern African *Eragrostoideae* and *Panicoideae* according to bundle sheath anatomy and cytology. Agroplantae *9* : 73-110.

FENCHEL, T. 1970. Studies on the decomposition of organic detritus dereived from the turtle grass *Thalassia testudinum* Limnol. Oceanogr. *15* : 14-20.

__________. 1972. Aspects of decomposer food chains in marine benthos. Varhandlungen der Deutscher Zoologischen Gesellschaft *65* : 14-22.

__________. 1977. Aspects of the decomposition of seagrasses, p. 123-145. *In* C.P. McRoy and C. Helfferich (ed.) Seagrass ecosystems. A scientific perspective. Marcel Dekker, New York.

FERNALD, M.L. 1929. Some relationships of the floras of the Northern Hemisphere. Proc. Int. Congress of Plant Sciences *2* : 1437-1507.

FIELD, J.G. 1971. A numerical analysis of changes in the soft-bottom fauna along a transect across False Bay, South Africa. J. Exp. Mar. Biol. Ecol. *7* : 215-253.

FOLK, R.L. and W.C. WARD. 1957. Brazos River Bar : A study in the significance of grain size parameters. J. Sed. Petrol. *27* : 3-26.

GABRIEL, B.C. and A.A. DE LA CRUZ. 1974. Species composition, standing stock and net primary production of a salt marsh community in Mississippi. Chesapeake Sci. *15* : 72-77.

GALLAGHER, J.L. 1974. Remote sensing as a tool for studying the ecology of halophytes, p. 511-523. *In* R.J. Reimold and W.H. Queen (ed.) Ecology of halophytes. Academic Press, New York.

GALLAGHER, J.L., PFEIFFER, W.J. and L.R. POMEROY. 1976. Leaching and microbial utilization of dissolved organic carbon from leaves of Spartina alterniflora. Estuarine and Coastal Mar. Sci. 4 : 467-472.

GERLOFF, G.C. and P.H. KROMBHOLZ, 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnol. Oceanogr. 11 : 529-537.

GESSNER, R.V. and R.D. GOOS. 1973. Fungi from decomposing Spartina alterniflora. Can. J. Bot. 51 : 51-55

GOSSELINK, J.G. 1970. Growth of Spartina patens and S. alterniflora as influenced by salinity and source of nitrogen. Coastal Studies Bull. 5 : 97-110.

______________ and C.J. KIRBY. 1974. Decomposition of salt marsh grass, Spartina alterniflora Loisel. Limnol. Oceanogr. 19 : 825-832.

HALL, K.J., WEIMER, W.C. and C.F. LEE. 1970. Amino acids in the estuarine environment. Limnol. Oceanogr. 15 : 162-164.

HANSON, R.B. and W.J. WIEBE. 1977. Heterotrophic activity associated with particulate size fractions in a Spartina alterniflora salt marsh estuary, Sapelo Island, Georgia, USA and the continental shelf waters. Mar. Biol. 42 : 321-330.

HARDISKY, M.A. and R.J. REIMOLD. 1977. Salt marsh plant geratology. Science 198 : 612-614.

HARPER, 1977. Population biology of plants. Academic Press, London.

HARRISON, P.G. and K.H. MANN. 1976. Detritus formation from eelgrass (Zostera marina L.): The relative effects of fragmentation, leaching and decay. Limnol. Oceanogr. 20 : 924-934.

HARTMANN, R.J. and D.L. BROWN. 1967. Changes in internal atmosphere of submerged vascular hydrophytes in relation to photosynthesis. Ecology 48 : 252-258.

HATCHER, B.G. and K.H. MANN. 1975. Above-ground production of marsh cordgrass (*Spartina alterniflora*) near the northern end of its range. J. Fish. Res. Board. *32* : 83-87.

HEINLE, D.R., HARRIS, R.P., USTACH, J.F. and D.A. FLEMER. 1977. Detritus as food for estuarine copepods. Mar. Biol. *40* : 341-354.

HESSE, P.R. 1971. A textbook of soil chemical analysis. J. Murray, London.

HINDE, H.P. 1954. The vertical distribution of salt marsh phanerogams in relation to tide levels. Ecol. Monogr. *24* : 209-225.

HOUGH, R.A. 1974. Photorespiration and productivity in submerged aquatic vascular plants. Limnol. Oceanogr. *19* : 912-927.

HUBBARD, J.C.E. 1954. Grasses. Penguin, Middlesex.

________________. 1965. The earliest record of *Spartina maritima* in Britain. Proc. Bot. Soc. Br. Isl. *6* : 119.

________________. 1970. Effects of cutting and seed production in *Spartina anglica*. J. Ecol. *58* : 329-334.

INMAN, D.L. 1952. Measures for describing the size distribution of sediments. J. Sed. Petrol *22* : 125-145.

JONES, R. 1976. Growth of fishes, p. 251-279. *In* D.H. Cushing and J.J. Walsh. (ed.) The ecology of the seas. Blackwell Scientific Publications, London.

KEEFE, C.W. 1972. Marsh production : a summary of the literature. Contrib. Mar. Sci. *16* : 163-181.

__________ and W.R. Boynton. 1973. Standing crop of salt marshes surrounding Chincoteague Bay, Maryland - Virginia. Chesapeake Sci. *14* : 117-123.

KERSHAW, K.A. 1976. The vegetational zonation of the East Pen. Island salt marshes, Hudson Bay. Can. J. Bot. 54 : 5-13.

KIRBY, C.J. and J.G. GOSSELINK. 1976. Primary production in a Louisiana Gulf Coast Spartina alterniflora marsh. Ecology 57 : 1052-1059.

KRAEUTER, J.N. 1976. Biodeposition by salt marshes inverterbrates. Mar. Biol. 35 : 215-223.

______________ and P.L. WOLF. 1974. The relationship of marine macroinvertebrates to salt marsh plants, p. 449-462. In R.J. Reimold and W.H. Queen (ed.) Ecology of halophytes Academic Press, New York.

LAGNA, L. 1975. The relationship of Spartina alterniflora to mean high water. Marine Sciences Research Centre. New York State University, Stony Brook.

LAUFF, G.H. (ed.) 1967. Estuaries. Am. Assoc. Adv. Sci. Publ. 83., Washington D.C.

LIPTROT, M. 1978. Community metabolism and phosphorus dynamics in a seasonally closed South African estuary. M.Sc. Thesis, Rhodes Univ.

LOMINICKI, A., BANDOLA, E. and K. KANKOWSKA. 1968. Modification of the Wiegert-Evans method for estimation of net primary production. Ecology 49 : 147-149.

LOUSIER, J.D. and D. PARKINSON. 1976. Litter decomposition in a cool temperate deciduous forest. Can. J. Bot. 54 : 419-436.

LUBKE, R.A. and B.A. CURTIS. 1977. The role of Spartina capensis Nees ex Trin. in the reclamation of eroding banks of the Kowie River, Eastern Cape, South Africa. Poster paper presented at the First European Ecological Symposium. Ecological Processes in Coastal Environment. Univ. East Anglia, Norwich.

MACNAE, W. 1956. Aspects of life on muddy shores in South Africa. S. Afr. J. Sci. 53 : 40-43.

MACNAE, W. 1957. The ecology of the plants and animals in the intertidal regions of the Zwartkops estuary near Port Elizabeth, South Africa. J. Ecol. 45 : 113-131.

MAHALL, B.E. and R.B. PARK. 1976a. The ecotone between Spartina foliosa Trin. and Salicornia virginica L. in salt marshes of Northern San Francisco Bay. I. Biomass and production. J. Ecol. 64 : 421-433.

____________________. 1976b. The ecotone between Spartina foliosa Trin. and Salicornia virginica L. in salt marshes of northern San Francisco Bay. II. Soil water and salinity. J. Ecol. 64 : 793-810.

____________________. 1976c. The ecotone between Spartina foliosa Trin. and Salicornia virginica L. in salt marshes of northern San Francisco Bay. III. Soil aeration and tidal immersion. J. Ecol. 64 : 811-821.

MALLOT, P.G., DAVY, A.J., JEFFERIES, R.L. and M.J. HUTTON. 1975. Carbon dioxide exchange in leaves of Spartina anglica Hubbard. Oecologia 20 : 351-358.

MANN, K.H. 1972. Ecological energetics of the sea-weed zone in a marine bay on the Atlantic coast of Canada. II. Productivity of the seaweeds. Mar. Biol. 14 : 199-209.

MARAIS, J.K.F. 1976. Comparative studies on the nutritional ecology of mullet in the Swartkops estuary. Ph.D. thesis, Univ. Port Elizabeth.

MARCHANT, C.J. 1967. Evolution in Spartina (Gramineae). I. The history and morphology of the genus in Britain. Bot. J. Linn. Soc. 60 : 1-24.

____________ and P.J. GOODMAN. 1969. Spartina maritima (Curtis) Fernald, p. 285-313. In P.J. Goodman, E.M. Braybrooks, J.M. Lambert and C.J. Marchant. Spartina Schreb. Biological Flora of the British Isles. J. Ecol. 57 : 235-313.

MATHEWS, C.P. and D.F. WESTLAKE. 1969. Estimation of production by populations of higher plants subject to high mortality. Oikos 20 : 156-160.

MAY, M.S. 1974. Probable agents for the formation of detritus from the halophyte, *Spartina alterniflora*, p. 429-440. In R.J. Reimold and W.H. Queen (ed .) Ecology of halophytes. Academic Press, New York.

McCALLUM, D.M. (ed.) 1972a. Environmental Study, Swartkops River Basin. General evaluation report.1. Hill, Kaplan, Scott and Partners.

__________________ 1972b. Introduction. Ibid. 2(1)

__________________ 1972c. Geology, terrain and materials, groundwater. Ibid. 2(2)

__________________ 1972d. Vegetation. Ibid 2(3)

__________________ 1972e. Estuarine ecology. Ibid 2(4)

__________________ 1972f. Hydrology, Hydraulics. Ibid 2(5)

__________________ 1972g. Meteorology. Ibid 2(6)

McDONALD, E.A. 1970. Some aspects of the ecology of an Eastern Cape salt marsh. Hons. thesis, Rhodes Univ.

McLACHLAN, A. 1972. Studies on burrowing bivalves in the Swartkops estuary. M.Sc. thesis, Univ. Port Elizabeth.

MENDELSSOHN, I.A. 1973. Angiosperm production of three Virginia salt marshes in various salinity and soil nutrient regimes. M.A. thesis, Coll. William and Mary, Virginia.

________________ and K.L. MARCELLUS. 1976. Angiosperm production in three Virginia marshes in various salinity and soil nutrient regimes. Chesapeake Sci. 17 : 15-23.

MEREDITH, D. (ed.) 1955. The grasses and pastures of South Africa. C.N.A., Johannesburg.

MILNER, C. and R.E. HUGHES. 1970. Methods for the measurement of the primary production of grassland. IBP Handbook No. 6. Blackwell Sci. Publishers, Oxford and Edinburgh.

MOBBERLEY, D. 1956. Taxonomy and distribution of the genus Spartina. Iowa St. Col. J. Sci. 30 : 471-574.

MOORING, M.T., COOPER, A.W. and E.D. SENECA. 1971. Seed germination response and evidence for height ecophenes in Spartina alterniflora from North Carolina. Am. J. Bot. 58 : 48-55.

MORGANS, J.F.C. 1956. Notes on the analysis of shallow-water soft substrata. J. Animal Ecology 25 : 367-387.

MORTON, J. and M. MILLER. 1973. The New Zealand Sea Shore. 2nd edn. William Collins Sons and Co. Ltd., Glasgow.

NEWELL, R. 1965. The role of detritus in the nutrition of two marine deposit feeders, the prosobranch Hydrobia ulvae and the bivalve Macoma balthica. Proc. Zool. Soc. Lond. 144 : 25-45.

NEWMAN, G. 1969. A review of mathematical growth models. Sea Fisheries Report. Dept. of Industries, S.A.

NIXON, S.W. and C.A. OVIATT. 1973a. Analysis of local variation in the standing crop of Spartina alterniflora. Bot. Mar. 16 : 103-109.

______________________________. 1973b. Ecology of a New England salt marsh. Ecol. Monogr. 43 : 463-498.

___________________________, GARBER, J. and V. LEE. 1976. Diel metabolism and nutrient dynamics in a salt marsh embayment. Ecology 57 : 740-750.

ODUM, E.P. 1961. The role of tidal marshes in estuarine production N.Y. St. Conserv. 15 : 12-15.

__________. 1969. The strategy of ecosystem development. Science 164 : 262-270.

ODUM, E.P. 1975. Halophytes, energetics and ecosystems, p. 599-602. *In* L.E. Cronin (ed.) Estuarine Research Vol. 1. Academic Press Inc., New York, San Francisco, London.

__________. 1971. Fundamentals of Ecology. 3rd. edn. W.B. Saunders Company, Philadelphia.

__________ and A.E. SMALLEY. 1959. Comparison of population energy flow of a herbivorous and a deposit-feeding invertebrate in a salt marsh ecosystem. Proc. of the Nat. Acad. of Sciences *45* : 617-622.

__________ and A.A. DE LA CRUZ. 1967. Particulate organic detritus in a Georgia salt marsh – estuarine ecosystem, p. 383-388. *In* G.H. Lauff (ed.) Estuaries Am. Assoc. Adv. Sci. Publ. 83, Washington D.C.

__________ and M.E. FANNING. 1973. Comparison of the productivity of *Spartina alterniflora* and *Spartina cynosuroides* in Georgia coastal marshes. Bull. Ga. Acad. Sci. *31* : 1-12

ODUM, W.E., ZIEMAN, J.C. and E.J. HEALD. 1972. The importance of vascular plant detritus to estuaries. Proc. Coastal Marsh and Estuary Management Symposium, Louisiana State University. Louisiana State University Publ., Baton Rouge.

__________ and E.J. HEALD. 1975. The detritus-based food-web of an estuarine mangrove community, p. 265-286. *In* L.E. Cronin (ed.), Estuarine Research Vol. 1. Academic Press Inc., New York, San Francisco, London.

OLIVER, F.W. 1925. *Spartina townsendii*, its mode of establishment, economic uses and taxonomic status. J. Ecol. *13* : 74-91.

ONUF, C.P., TEAL, J.M. and I. VALIELA. 1977. Interactions of nutrients, plant growth and herbivory in a mangrove ecosystem. Ecology *58* : 514-526.

ORIANS, G.H. 1974. An evolutionary approach to the study of ecosystems, p. 198-200. Proceedings of the First International Congress of Ecology. Centre for Agricultural Publishing and Documentation, Wageningen.

PARRONDO, R.T., GOSSELINK, J.G. and C.S. HOPKINSON. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. Bot. Gaz. 139 : 102-107.

PENFOUND, W.T. 1956. Production of vascular aquatic plants. Limnol. Oceanogr. 1 : 92-101.

PENHALE, P.A. 1977. Macrophyte-epiphyte biomass and productivity in an eelgrass (Zostera marina L.) community. J. Expt. Mar. Biol. Ecol. 26 : 211-223

PHLEGER, F. 1971. Effects of salinity on growth of salt marsh grass. Ecology 52 : 908-911.

PIELOU, E.C. and R.D. ROUTLEDGE. 1976. Salt marsh vegetation: Latitudinal gradients in the zonation patterns. Oecologia 24 : 311-321

POCOCK, M.A. 1955. Seaweeds of the Zwartkops estuary. S. Afr. J. Sci. 52 : 73-75.

POMEROY, L.R. 1959. Algal productivity in the salt marshes of Georgia. Limnol Oceanogr. 4 : 367-386.

PROVOST, M.W. 1976. Tidal datum planes circumscribing salt marshes. Bull. Mar. Sci. 26 : 558-563.

RANWELL, D.S. 1961. Spartina salt marshes in Southern England. 1. The effects of sheep grazing at the upper limits of Spartina marsh in Bridgewater Bay. J. Ecol. 49 : 325-340.

____________ 1964. Spartina salt marshes in Southern England. III. Rates of establishment, succession, and nutrient supply at Bridgewater Bay, Somerset. J. Ecol. 52 : 95-105.

REDFIELD, A.C. 1972. Development of a New England salt marsh. Ecol. Monogr. 42 : 201-237.

RIFFENBERGH, R.H. 1959. A new method for estimating parameters for Gompertz growth curve. J. du Conseil. 25 : 285-293.

Reimold, R.J. and F.C. Daiber. 1970. Dissolved phosphorus concentrations in a natural salt marsh of Delaware. Hydrobiologia *36* : 361-371.

______________. and W.H. QUEEN. 1974. Ecology of halophytes. Academic Press Inc., New York and London.

______________, GALLAGHER, J.L., LINTHURST, R.A. and W.J. PFEIFFER. 197 Detritus production in coastal Georgia salt marshes, p. 217-228. *In* L.E. Cronin (ed.) Estuarine Research I. Academic Press Inc., New York.

SHIMA, L.J., ANDERSON, R.R. and V.P. CARTER. 1976. The use of aerial color infrared photography in mapping the vegetation of a fresh-water marsh. Chesapeake Sci. *17* : 74-85.

SMALLEY, A.E. 1958. The role of two invertebrate populations, *Littorina irrorata* and *Orchelimum fidicinium*, in the energy flow of a salt marsh ecosystem. Ph.D. thesis, Univ. Georgia.

______________. 1959. The growth cycle of *Spartina* and its relation to the insect populations in the marsh. Proc. Salt Marsh Conf. Sapelo Island, Georgia.

______________. 1960. Energy flow of a salt marsh grasshopper population. Ecology *41* : 672-677.

SQUIERS, ER and RE GOOD. 1974. see p. 133

STALTER, R. and W.T. BATSON. 1969. Transplantation of salt marsh vegetation, Georgetown, South Carolina. Ecology *50* : 1087-89.

STEEVER, E.Z. 1972. Productivity and vegetation studies of a tidal salt marsh in Stonington, Connecticut; Cotrell marsh. M.A. thesis, Conn. Coll., New London.

______________, WARREN, R.S. and W.A. NIERING. 1976. Tidal energy subsidy and standing crop production of *Spartina alterniflora* Estuarine and Coastal Mar. Sci. *4* : 473-479.

STROUD, L.M. and A.W. COOPER. 1969. Color-infrared aerial photographic interpretation and net primary productivity of a regularly flooded North Carolina. Water Resources Research Institute. Report No. 14. Univ. North Carolina.

SQUIERS, E.R. and R.E. GOOD. 1974. Seasonal changes in the productivity, caloric content and chemical composition of a population of salt marsh cord grass (*Spartina alterniflora*). Chesapeake Sci. 15 : 63-71.

SUFFLING, R. and D.W. SMITH. 1974. Litter decomposition studies using mesh bags : Spillage inaccuracies and the effects of repeated artificial drying. Can. J. Bot. 52 : 2157-2163.

SULLIVAN, M.J. and F.C. DAIBER. 1974. Response in production of cord grass *Spartina alterniflora*, to inorganic nitrogen and phosphorus fertilizer. Chesapeake Sci. 15 : 121-124.

TEAL, J.M. 1962. Energy flow in the salt marsh ecosystem of Georgia. Ecology 43 : 614-624.

_________ and J. KANWISHER. 1961. Gas exchange in a Georgia salt marsh. Limnol. Oceanogr. 6 : 388-399.

THISELTON-DYER, W.T. (ed.) 1900. Flora Capensis. Vol. 7. Lovell Reeve and Company Ltd., London.

TURNER, R.E. 1976. Geographic variations in salt marsh macrophyte production : a review. Contrib. Mar. Sci. 20 : 47-68.

__________ and J.G. GOSSELINK. 1975. A note on standing crops of *Spartina alterniflora* in Texas and Florida. Contrib. Mar. Sci. 19 : 113-118.

UDELL, H.F., ZARUDSKY, J., DOHENY, T.E. and P.R. BURKHOLDER. 1969. Productivity and nutrient values of plants growing in the salt marshes of the town of Hampstead, Long Island. Bull. Torrey Bot. Club. 96 : 42-51.

VALIELA, I., TEAL, J.M. and W. SASS. 1973. Nutrient retention in salt marsh plots experimentally fertilized with sewage sludge. Estuarine and Coastal Mar. Sci. 1 : 262-269.

VALIELA, I. and J.M. TEAL. 1974. Nutrient limitation in salt marsh vegetation, p. 547-563. In R.J. Reimold and W.H. Queen (ed.) Ecology of halophytes. Academic Press, New York.

__________, TEAL, J.M. and W. SASS. 1975. Production and dynamics of salt marsh vegetation and the effects of experimental treatment with sewage sludge : Biomass, production and species composition. J. Appl. Ecol. 12 : 973-982.

__________, TEAL, J.M. and N.Y. PERSSON. 1976. Production and dynamics of experimentally enriched salt marsh vegetation : Belowground biomass. Limnol. Oceanogr. 21 : 245-252.

VAN DER HORST, G. 1976. Aspects of the reproductive biology of Liza dumerili (Steindachner, 1869) (Teleosti, Mugelidae) with special reference to sperm. Ph.D. thesis, Univ. Port Elizabeth.

VOGL, R.J. 1966. Salt marsh vegetation of Newport Bay, California. Ecology 47 : 80-87.

WAISEL, Y. 1972. Biology of halophytes. Academic Press, New York.

WESTLAKE, D.F. 1963. Comparisons of plant productivity. Biol. Rev. 38 : 385-425.

WETZEL, R.L. 1977. Carbon resources of a benthic salt marsh invertebrate Nassarus obsoletus Say (Mollusca : Nassariidae). Estuarine processes. Third International Estuarine Conference. Galveston, Texas.

WHITTAKER, R.H. 1970. Communities and ecosystems. Macmillan, London.

WIEGERT, R.G. and F.C. EVANS. 1964. Primary production and the disappearance of dead vegetation on an old field in South-eastern Michigan. Ecology 45 : 49-63.

WIEHE, P.O. 1935. A quantitative study of the influence of tide upon populations of Salicornia europea. J. Ecol. 23 : 323-333.

WILLIAMS, R.B. and M.B. MURDOCH. 1969. The potential importance of *Spartina alterniflora* in conveying zinc, manganese and iron into estuarine food chains, p. 431-439. *In* D.J. Nelson and F.C. Evans (ed .) Proc. 2nd Nat. Symp. Radioecol. A.S.A.E.C.

________________________________. 1972. Compartmental analysis of the production of *Juncus roemerianus* in a North Carolina salt marsh. Chesapeake Sci. 13 : 69-79.

WITKAMP, M. 1966. Decomposition of leaf litter in relation to environment, microflora and microbial respiration. Ecology 47 : 194-201.

ZEDLER, J.B. 1977. Salt marsh community structure in the Tijuana estuary, California. Estuarine and Coastal Mar. Sci. 5 : 39-53

ZWARTKOPS TRUST, 1971. The Swartkops estuary - an ecological survey. Zwartkops Trust, Port Elizabeth.