

# DREDGED MATERIAL RESEARCH PROGRAM



TECHNICAL REPORT D-77-35

## MODELING OF ECOLOGICAL SUCCESSION AND PRODUCTION IN ESTUARINE MARSHES

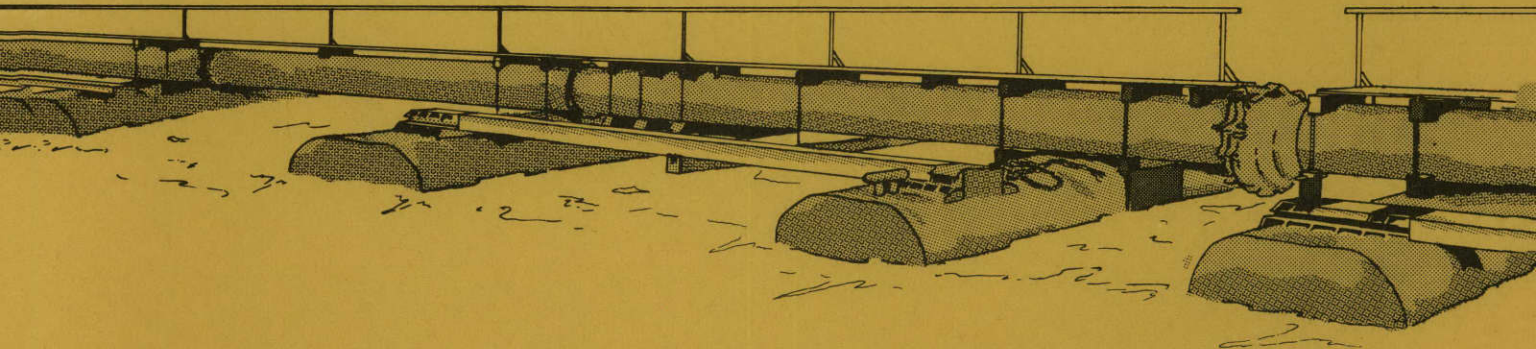
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1. The technical report transmitted herewith represents the result of Work Unit 4A05 regarding the development and testing of a predictive model for marsh productivity and succession. This work unit was conducted as part of Task 4A (Marsh Development) of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 4A is a part of the Habitat Development Project of the DMRP and is concerned with developing, testing, and evaluating the environmental, economic, and engineering feasibility of using dredged material as a substrate for marsh development.
2. The purpose of this work unit was to develop a simulation model of plant growth and succession on salt marshes. The model was created by identification of the biotic and physical factors that control plant growth and the measurement of these factors under field conditions. The model appears to have great potential for use in establishing criteria and specifications for salt marsh development; however, additional parameterization and verification will be required before the system becomes fully operational.
3. Work Unit 4A05 is one of several research efforts designed by the DMRP to accurately document marsh productivity and the factors which influence that productivity. Closely related work units are 4A04A1 and 4A04B, which address the productivity of minor marsh species along the Atlantic and Gulf coasts, respectively; 4A04A2, which deals with marsh plant substrate selectivity and underground biomass production; and 4A20, a less intensive effort that will provide a general evaluation of salt marsh productivity on the Pacific coast of the United States. Additional supportive and comparative data will be forthcoming with the final analysis of the results of field studies at Windmill Point, Virginia, (4A11); Buttermilk Sound, Georgia, (4A12); Apalachicola, Florida, (4A19); Bolivar Peninsula, Texas, (4A13); Pond No. 3, California, (4A18); and Miller Sands, Oregon, (4B05). Together these

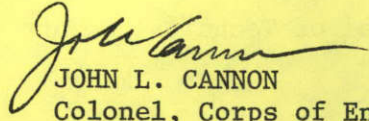


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research products provide the Corps with a comprehensive basis for sound management decisions regarding habitat development on dredged material and disposal in natural marsh habitats.



JOHN L. CANNON

Colonel, Corps of Engineers  
Commander and Director

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20. ABSTRACT (Continued).

positive correlation with the elevation and tidal inundations at the two major study sites, Taskinas Creek and Bennett's Creek, in Virginia. S. alterniflora showed a negative correlation with soil salinity and significant positive correlation with available iron. Responses of S. patens and Distichlis spicata were more variable, but where regular flooding occurred there was a strong positive correlation with S. patens abundance and negative correlation with D. spicata.

Records from the continuous monitoring study reinforce the concept of tidal inundation acting as a master variable. Power spectrum analysis of continuous research of temperature and pH in the sediments revealed that in the S. alterniflora zone the sediment surface temperature showed the major power peak to be 0.089 cycle/hour, which is the tidal frequency for this area. In the higher S. patens - D. spicata zone the frequency with the largest power component is that of nearly 1 cycle/day corresponding to the input of solar radiation. The analysis of pH data showed a large influence in the low S. alterniflora at the tidal frequency but not in the high marsh.

A model was developed which depicted plant growth and succession across a transect. The model was driven by solar radiation, temperature, soil salinity, and tidal inundation. The model showed plant growth controlled primarily by tidal inundation, with influences felt from radiation and temperature, but little influence due to salinity. The model appears to have great utility for future use but presently is limited in application by incomplete parameterizations.

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## EXECUTIVE SUMMARY

Rapid disappearance and deterioration of wetlands as a consequence of increasing human utilization coupled with growing recognition by the scientific community of the ecological importance of these areas indicate the need to investigate ecologically sound alternatives for using dredged material. Attempts to recolonize disposal areas after deposition have thus far met with mixed success. In attempting to establish a desired community, two options are available: (1) create environmental conditions favorable for the colonization of the desired species, or (2) introduce a species that is compatible with the present environmental conditions and allow natural succession to produce the desired species or community. In order to achieve the desired ecosystem by either of the two above approaches, the dominant controlling forces on the communities must be known and described.

Three parallel studies were conducted with the development of a simulation model of plant growth and succession on a salt marsh being the ultimate objective. The first component was concerned with determining the biotic and chemical parameters present at a series of marshes. The second component was concerned with obtaining continuous records of several physical and chemical parameters within several vegetation zones. The third component of the project was the development of the simulation model.

Field studies showed that Spartina alterniflora exhibited a strong positive correlation with elevation and tidal inundations at the two major study sites, Taskinas Creek and Bennett's Creek, in Virginia.

S. alterniflora showed a negative correlation with soil salinity and significant positive correlation with available iron. Responses of S. patens and Distichlis spicata were more variable, but where regular flooding occurred there was a strong positive correlation with S. patens abundance and negative correlation with D. spicata.

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## PREFACE

This report presents the results of an investigation of factors influencing plant zonation and succession on salt marshes. The study was supported by the U. S. Army Engineer Waterways Experiment Station (WES), Habitat Development Project, Dredged Material Research Program, Vicksburg, Mississippi, under contract No. DACW39-73-C-0121 to the University of Virginia, Charlottesville, Virginia.

The project was directed by Joseph C. Zieman and William E. Odum of the Department of Environmental Sciences of the University of Virginia. Field Sampling and laboratory analysis were performed by Mark L. Gleason, Thomas G. Wolaver, Jeffrey E. Drifmeyer, and Michael B. Robblee.

The study was conducted under Dr. Kent Thornton, Contract Manager, and Dr. Hanley K. Smith, Habitat Development Project Manager, WES. The study was under the general supervision of Dr. John Harrison, Chief, Environmental Effects Laboratory, WES.

The Directors of WES during the study and the preparation of this report were COL G. H. Hilt, CE, and COL J. L. Cannon, CE. Technical Director was Mr. F. R. Brown.

## CONTENTS

	Page
EXECUTIVE SUMMARY . . . . .	1
PREFACE . . . . .	3
LIST OF FIGURES . . . . .	6
LIST OF TABLES . . . . .	11
CONVERSION FACTORS, U. S. CUSTOMARY TO METRIC (SI) UNITS OF MEASUREMENT . . . . .	12
PART I: INTRODUCTION . . . . .	13
PART II: PROJECT CONCEPT AND DEVELOPMENT . . . . .	15
PART III: STUDY SITES . . . . .	20
General Description . . . . .	20
Marsh Development History . . . . .	22
PART IV: METHODS . . . . .	29
Field Procedures . . . . .	29
Laboratory Procedures . . . . .	31
Plant samples . . . . .	31
Sediment cores . . . . .	32
Nutrient analysis . . . . .	32
PART V: FIELD STUDY RESULTS AT INTENSIVE SITES . . . . .	34
Habitat Factors . . . . .	34
Vegetation . . . . .	34
Elevation . . . . .	39
Number of inundations . . . . .	47
Salinity. . . . .	49
Organic matter . . . . .	49
Plant-Available Nutrients. . . . .	52
Ammonia-N . . . . .	52
Phosphate . . . . .	55
Iron . . . . .	55
Manganese . . . . .	58
Calcium . . . . .	58
Magnesium . . . . .	61
Correlation Analyses . . . . .	61
Competition Analyses . . . . .	72
Gradient Analysis. . . . .	73

	Page
PART VI: MONITORING RESULTS . . . . .	89
PART VII: MARSH SUCCESSION MODEL . . . . .	113
Model Concept . . . . .	115
Model Structure . . . . .	120
PART VIII: SUMMARY AND CONCLUSIONS . . . . .	152
REFERENCES . . . . .	155
APPENDIX A: CONTINUOUS MONITORING SYSTEM . . . . .	A-1
Concept . . . . .	A-1
Configuration. . . . .	A-2
Field Sensors . . . . .	A-2
pH . . . . .	A-5
Eh . . . . .	A-6
Salinity . . . . .	A-6
Solar radiation . . . . .	A-7
Tide height . . . . .	A-7
Signal Amplifiers and Housings . . . . .	A-7
Junction Box . . . . .	A-8
Recorder . . . . .	A-9
Data Processing . . . . .	A-10
APPENDIX B: MODEL USER INFORMATION* . . . . .	B-1
General . . . . .	B-1
Data Input . . . . .	B-1
Data Card Preparation . . . . .	B-4
Sample Data Set . . . . .	B-11
Program Listing . . . . .	B-11
APPENDIX C: SURVEY SITES. . . . .	C-1

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\* Appendix B is reproduced on microfiche and is enclosed in an envelope attached to the inside of the back cover.



## LIST OF FIGURES

Figure		Page
1	Location map indicating intensive study sites on the James and York Rivers.	21
2	Cross section of sediment at Taskinas Creek and Bennett's Creek.	24
3	Experimental plot design at intensive study sites.	30
4	Ranges of plant species across transects at Taskinas Marsh and Bennett's Marsh	35
5	Maximum values for live standing crop at Taskinas Marsh and Bennett's Marsh.	36
6	Maximum values for standing dead crop at Taskinas Marsh and Bennett's Marsh.	38
7	Maximum values for stem density of <u>Spartina alterniflora</u> at Taskinas and Bennett's Marsh.	40
8	Maximum values for stem density of <u>Spartina patens</u> and <u>Distichlis spicata</u> at Taskinas Marsh and Bennett's Marsh.	42
9	Maximum values for stem height of <u>Spartina patens</u> and <u>Distichlis spicata</u> at Taskinas Marsh and Bennett's Marsh.	44
10	Elevation of the sample stations above mean low water.	46
11	Number of inundations per year at sample stations.	48
12	Salinity of interstitial water.	50
13	Percent organic matter of marsh sediments.	51
14	Concentration (ppm) of plant-available ammonia-N in marsh sediments at sample stations.	54
15	Concentrations (ppm) of plant-available phosphate-P in marsh sediments at sample stations	56

## List of Figures

<u>Figure</u>		<u>Page</u>
16	Concentration (ppm) of plant-available iron in marsh sediments at sample stations.	57
17	Concentration (ppm) of plant-available manganese in marsh sediments at sample stations.	59
18	Concentration (ppm) of plant-available calcium in marsh sediments at sample stations.	60
19	Concentration (ppm) of plant-available magnesium in marsh sediments at sample stations.	62
20	Community gradient plots of live standing crop vs. elevation at Taskinas Marsh and Bennett's Marsh.	74
21	Community gradient plots of live standing crop vs. salinity at Taskinas Marsh and Bennett's Marsh.	76
22	Complex gradient plots of live standing crop vs. organic matter and elevation at Taskinas Marsh and Bennett's Marsh.	80
23	Complex gradient plots of live standing crop vs. manganese and phosphate at Taskinas Marsh .	82
24	Complex gradient plots of live standing crop vs. manganese and calcium at Bennett's Marsh.	83
25.	Solar radiation at Taskinas Marsh from 25 to 28 November 1975.	91
26	Tidal height at Taskinas Marsh from 25 to 28 November 1975.	93
27	Temperature at the sediment surface at Taskinas Marsh from 25 to 28 November 1975.	95
28	Temperature at 10 cm in the sediment at Taskinas Marsh from 25 to 28 November 1975.	97
29	pH at the sediment surface at Taskinas Marsh from 25 to 28 November 1975.	99

## List of Figures

<u>Figure</u>		<u>Page</u>
30	pH at 10 cm in the sediment at Taskinas Marsh from 25 to 28 November 1975.	101
31	Power spectrum of tide at Taskinas Marsh.	105
32	Power spectrum of solar radiation at Taskinas Marsh.	107
33	Power spectrum of pH at the surface in the <u>Spartina alterniflora</u> zone at Taskinas Marsh.	108
34	Power spectrum of temperature at the surface in the <u>Spartina alterniflora</u> zone at Taskinas Marsh.	109
35	Power spectrum of pH at the surface in the <u>Spartina patens</u> - <u>Distichlis spicata</u> zone at Taskinas Marsh.	110
36	Power spectrum of temperature at the surface in <u>Spartina patens</u> - <u>Distichlis spicata</u> zone at Taskinas Marsh.	111
37	Conceptual diagram of a single species module.	116
38	Conceptual diagram of the linking of several species modules with environmental forcing functions to form a model of a single point in the marsh.	118
39.	Conceptual diagram showing the coupling of several point models to produce a coupled model of transect with several stations.	119
40	General flow diagram of the model, MARSH1.	121
41	Flow diagram of the main subroutine, SSPECIE.	123
42	Seasonal solar radiation values for the eastern coast of the United States.	125
43	Seasonal temperature values for the eastern coast of the United States.	127
44	Inundation curves at various stations on the Atlantic and Gulf coasts.	129



## List of Figures

<u>Figure</u>		<u>Page</u>
45	Relationship between peak tidal height (maximum predicted spring tide) and the projected point where the main body of the curve would intercept the vertical axis.	130
46	Normalized curve for tidal inundation as a function of height of maximum spring tide.	132
47	Marsh salinity as a function of tidal height.	133
48	Normalized growth response of <u>Spartina alterniflora</u> to environmental driving parameters.	135
49	Normalized growth response of <u>Spartina patens</u> and <u>Distichlis spicata</u> to environmental driving parameters.	136
50	Results of a simulation at latitude 30°N, with a creek salinity of 20 o/oo, a mean tide range of 4 ft (1.22 m), a maximum range of 6 ft (1.83 m), and a time period of 48 months. This first figure depicts the simulation at the 1-ft (0.31-m) elevation above mlw on the marsh.	140
51	Depicts the simulation at the 2-ft (0.61-m) elevation above mlw on the marsh.	141
52	Depicts the simulation at the 3-ft (0.91-m) elevation above mlw on the marsh.	142
53	Depicts the simulation at the 4-ft (1.22-m) elevation above mlw on the marsh.	143
54	Depicts the simulation at the 5-ft (1.52-m) elevation above mlw on the marsh.	144
55	Depicts the simulation at the 6-ft (1.83-m) elevation above mlw on the marsh.	145
56	Results of a simulation at latitude 35°N, with a creek salinity of 20 o/oo, a mean tide range of 4 ft (1.22 m), and a maximum range of 6 ft (1.83 m) for 48 months. This figure depicts the simulation at the 2-ft (0.61-m) elevation above mlw on the marsh.	146

## List of Figures

<u>Figure</u>		<u>Page</u>
57	Depicts the simulation at the 3-ft (0.91-m) elevation above mlw on the marsh.	147
58	Depicts the simulation at the 4-ft (1.22-m) elevation above mlw on the marsh.	148
59	Depicts the simulation at the 5-ft (1.52-m) elevation above mlw on the marsh.	149
60	Depicts the simulation at the 6-ft (1.83-m) elevation above mlw on the marsh.	150
A-1	General configuration of the data monitoring system.	A-3
A-2	Typical configuration of one submersible housing unit	A-4
C-1	Location of survey sites along the central eastern coast of the U. S.	C-3

## LIST OF TABLES

<u>Table</u>		<u>Page</u>
1	Means and standard errors of habitat parameters from the study sites	53
2	Correlation coefficients between plant variables and habitat variables at Taskinas Marsh	63
3	Correlation coefficients between plant variables and habitat variables at Bennett's Marsh	64
4	Correlation coefficients between habitat variables at Taskinas Marsh	68
5	Correlation coefficients between habitat variables at Bennett's Marsh	69
6	Limits of tolerance to tidal inundation for three species of marsh grasses at Taskinas Marsh and Bennett's Marsh	86
C-1	List of sites	C-5
C-2	Plant identification codes	C-6



CONVERSION FACTORS, U. S. CUSTOMARY TO METRIC (SI)  
UNITS OF MEASUREMENT

The U. S. customary units of measurement used in this report can be converted to metric units as follows:

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
microns	0.000001	meters
inches	2.54	centimeters
feet	0.3048	meters
acres	4046.856	square meters
pounds (force) per square inch	6894.757	pascals
miles (U. S. statute)	1.609344	kilometers

## PART I: INTRODUCTION

1. In recent years the value of tidal wetland as nursery areas, as buffers against shoreline erosion, and as sources of energy for shellfish and commercial and sport fisheries has become widely recognized (Schelske and Odum, 1971; Teal, 1962; Odum and de la Cruz, 1967; Cooper, 1969; Williams and Murdoch, 1969; Keefe, 1972; Odum, Zieman and Heald, 1972). Estuaries are among the most productive natural ecosystems on earth, and serve as vital recreational, transportation, industrial, commercial, and population sites (Allen, 1964).

2. With accelerating human uses of estuaries have come alterations and modifications of the natural ecosystem. Chief among these is dredging and dredged material disposal. Dredging and filling has altered over 7 percent of the total estuarine habitat in the United States; 570,000 out of 8 million acres<sup>\*</sup> have been lost (Marshall, D. E., 1970). Along the northeastern Atlantic coast, dredging is the predominant means of wetland alteration (Marshall, D. E., 1970; Schmidt, 1966). For example, of the 45,000 acres of wetlands between Maine and Delaware destroyed from 1955 to 1964, fully one-third was lost to dredged material disposal (Schmidt, 1966). During this same period, South Carolina lost 10 percent of its total wetland acreage to dredged material disposal, while Florida filled 60,000 acres, or 7.5 percent, of its most important estuarine areas (Teal and Teal, 1969; Marshall, D. E., 1970). Along the Gulf Coast dredging and fill operations have also impacted

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\* A table of factors for converting U.S. customary units of measurement to metric (SI) units can be found on page 12.

estuaries; Texas lost 55,000 acres of shallow marine bay habitat and 23,000 acres of brackish marsh (Chapman, 1967).

3. The biological effects of dredging and disposal are often deleterious, as has been discussed by Thompson, 1961; Chapman, 1967; and Odum, 1970. Excessive sedimentation, increased turbidity and alteration of circulation patterns may adversely affect benthic populations, photosynthetic activity, and energy flow. For example in Boca Ciega Bay, Florida, 3,500 acres of dredged material deposition severely reduced annual production of seagrasses (by 25,851 metric tons), infauna (by 1,091 metric tons), and fisheries (by 73 metric tons) (Marshall, D. E., 1970). While not an exhaustive list, the above show that dredging operations have the potential to alter significant portions of existing wetlands.

4. Rapid disappearance and deterioration of wetlands as a consequence of burgeoning human utilization, coupled with growing recognition by the scientific community of the ecological importance of these areas, indicate the need to investigate ecologically sound alternatives for using dredged material. In particular, the possibility of using dredged material to build new marshes has been suggested repeatedly (Smith, 1942; Larimer, 1968; Teal and Teal, 1969; Woodhouse et al., 1972; Connecticut State Board of Fisheries and Game, undated).



## PART II: PROJECT CONCEPT AND DEVELOPMENT

5. Understanding of marsh plant physiology and ecology is presently insufficient to offer design criteria for dredged material disposal that would facilitate rapid recolonization of marshes. Attempts to recolonize disposal areas after deposition have met with mixed success (Windom, 1972; Woodhouse et al., 1972; Vittor, 1971; Larimer, 1968). Ecological succession is an orderly process of community development that involves changes in species composition and community processes over time. In marsh areas, the sequence of plant species is well documented, but the processes and driving forces behind these changes are poorly understood. As one community (an assemblage of populations within a given area) grows, it modifies its environment, creating conditions favorable for a subsequent community. The environment of a mature community may resemble that of its early successional predecessors only slightly--a fact that is often overlooked by those who attempt to establish particular communities artificially.

6. In attempting to establish a desired community, two options are available: (1) create the environmental conditions favorable for the colonization of a desired species, or (2) introduce a species that is compatible with the present environmental conditions and allow natural succession to produce the desired species or community. In order to achieve the desired ecosystem by either of the above approaches, the dominant controlling forces on the communities must be known and described. In addition, the second procedure requires knowledge of the direction in which succession will proceed.

7. A comprehensive understanding of the development of estuarine marshes requires knowledge of the physical and chemical parameters affecting marsh plants. The ways in which sediment characteristics such as organic content, sediment texture, and mineralogy condition the habitat of marsh plants have been elucidated by previous workers (Richards, 1954; Fleming and Alexander, 1961; Windom, 1972).

8. According to the classification of Sanders (1969), marsh ecosystems are controlled primarily by physical factors. The ecological stresses imposed by the broad variability of physical factors reduce the relative influence of biotic competition as a control of species distribution. Since relatively few plants and animals can withstand rapid tidal, salinity, and temperature fluctuations, species diversity in tidal marshes tends to be low. In a study of saline and brackish marshes in Louisiana, Chabreck (1972) found that in the low marsh zone, dominated by Spartina alterniflora and strongly influenced by tides, three species accounted for over 70 percent of the higher plants encountered.

9. The tools of simulation modeling which are beginning to come into use in environmental studies offer great potential for the future (Patten, 1971, 1972). However, most attempts to apply modeling techniques to ecological problems have suffered from several crucial deficiencies. First, to be a useful decision tool, a model must be designed to answer specific questions. Thus far, few ecological models have been so structured; rather, most attempt to describe the "normal behavior" of a particular system, and have thus been largely

descriptive. Second, to properly develop a simulation model of an ecosystem it is necessary to understand component interactions and the biological theory behind these interactions. Third, for proper implementation the best conceived model still requires reliable dynamic information, such as flux rates. This information has seldom been measured in the past and generally is not available in the literature. For best results, the input parameters should be measured simultaneously and continuously.

10. At present the difficulty of collecting accurate dynamic field data and ignorance of the biological functioning of the marsh ecosystem are more serious hindrances to ecological modeling than misapplications of systems analysis and modeling techniques. One of the toughest problems faced by ecological modelers today is in the gathering of accurate environmental data at closely spaced intervals of time. For years, physical scientists have recorded data at exceptionally high acquisition rates; biologists, however, have been restricted to sampling field sites on a weekly or monthly basis, distorting interpretation of environmental parameters that vary widely and rapidly.

11. Simulation modeling is essentially a cyclical process centered around the design and conceptualization of the model, the formulation process, the parameterization of this model, and field studies to verify the model. Following the completion of one cycle, the information gained is used to modify the original concept and resulting model. The process can be repeated until satisfactory results are produced.

12. The ultimate objective of this project was to produce an

ecological simulation model capable of predicting vegetation succession on marshes and dredged material islands. Three parallel studies were pursued. The first component was concerned with determining the biotic and chemical parameters in a series of marshes. The objectives were to determine the range of selected environmental parameters that dominant species of marsh plants tolerate, and second to determine the seasonal variation of selected physicochemical parameters and the response of certain biotic compounds. A series of marshes from New Jersey to Georgia were visited and surveyed, but intensive effort was concentrated at two sites in Virginia. The results of this study are discussed in Part V.

13. The second study was concerned with obtaining continuous records of several physical and chemical parameters within several vegetative zones. The objective of this study was to characterize the magnitude of variation of edaphic factors in the major marsh communities. This involved the development of a continuous recording data-monitoring system described in Appendix A and the data and results are discussed in Part VI.

14. The third study of the project was the development of a simulation model of plant growth and succession on the marsh. The initial models were developed based on information available in the literature on the functioning of estuarine salt marshes. As the project progressed, information was added from field studies and contact with other scientists in the field. The latter input was aided by several meetings on marsh growth and reclamation at the Waterways

Experiment Station, Vicksburg, Mississippi. Part VII contains the development of the marsh succession model.

### PART III: STUDY SITES

#### General Description

15. Field research was conducted intensively at two sites in Virginia as described below. In addition, surveys were conducted at a variety of marshes from New Jersey to Georgia. The data from the marsh surveys are presented in Appendix C.

16. Taskinas Creek Marsh is situated adjacent to the York River (lat.  $37^{\circ}25'$ , long.  $76^{\circ}43'$ ), 16 km southeast of the city of West Point. The marsh and much of its watershed are included within York River State Park (Figure 1 ). The second marsh site is located on the east bank of Bennett's Creek, a tributary of the Nansemond River, about 300 m south of U.S. Route 17 (lat.  $36^{\circ}51'$ , long.  $76^{\circ}28'30''$ ), 8 km west of Portsmouth. The marsh and adjacent uplands are privately owned.

17. Although they are approximately 60 km apart, Taskinas Creek Marsh and Bennett's Creek Marsh are alike in several respects. Both are small (less than 37 ha) pocket marshes adjoining the tidal tributaries of Chesapeake Bay. Their average tidal range (approximately 1 m) differs by less than 5 cm. Salinity of the creek water ranges from zero to approximately 15 percent at both sites. The distribution of vegetational communities is also similar. Spartina alterniflora dominates the lower margin of each marsh along the creek banks while a Spartina patens - Distichlis spicata association occupies the adjacent high marsh zone. Scirpus olney, and Scirpus robustus predominate where the marsh borders the uplands. The average width of each marsh



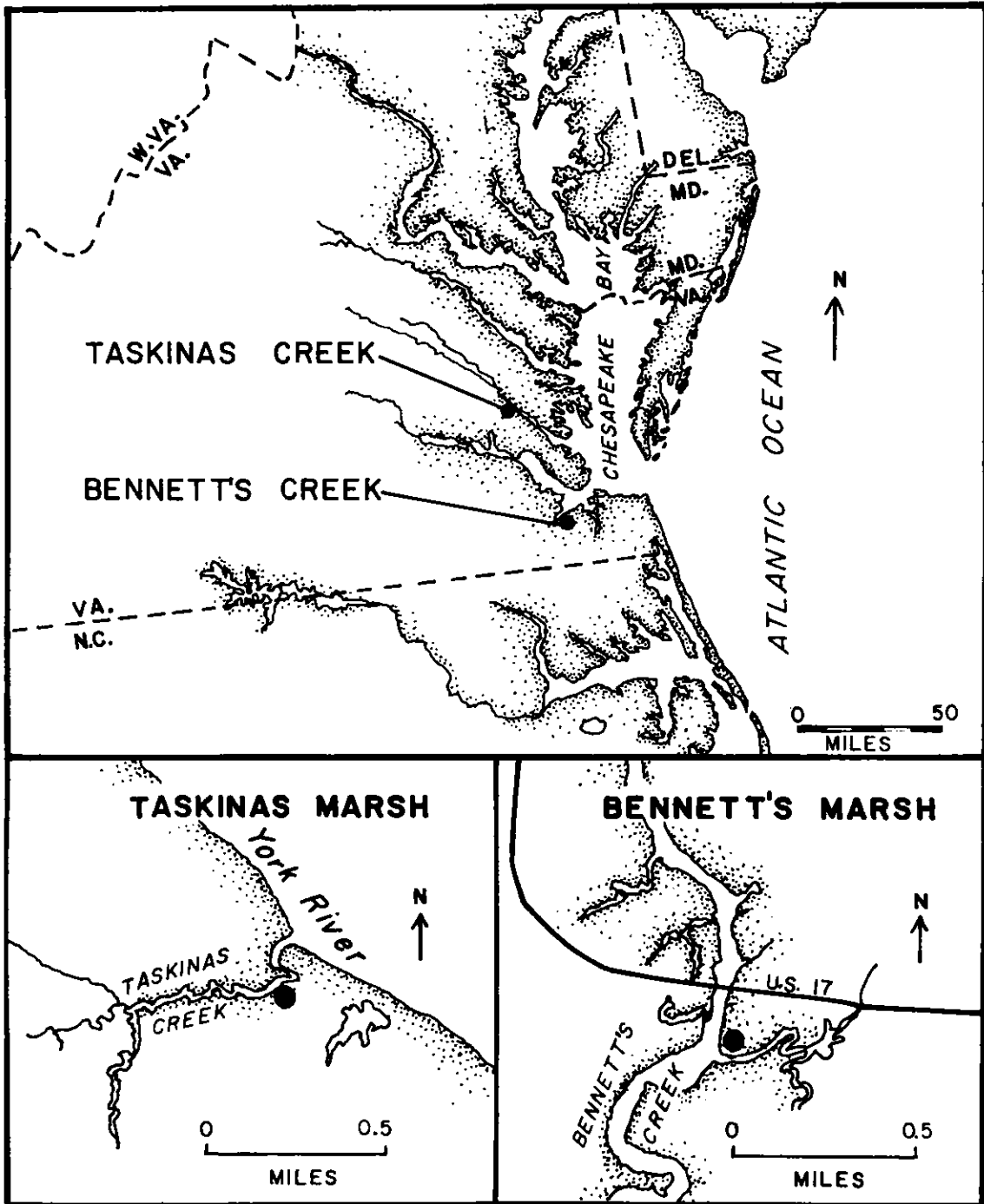


Figure 1. Location map indicating intensive study sites on the James and York Rivers.

from creek bank to upland is approximately 100 meters.

### Marsh Development History

18. Abundant evidence suggested that vegetation distribution can change extensively as a marsh develops (Redfield and Rubin, 1962; Redfield, 1967; Redfield, 1972; Newman and Rusnak, 1965; Bloom, 1964; Knight, 1934). The frequently stated hypothesis that plant species distribution was somehow intimately influenced by elevation of the marsh surface relative to tidal changes in water level (Redfield, 1972; Johnson and York, 1915; Adams, 1963) implied that a change in elevation will alter the species distribution. Consequently, the history of plant distribution in a tidal marsh reflected a dynamic balance among factors that influence elevation: accretion of sediment on the marsh surface, compaction of sediments after burial, eustatic changes in sea level, and subsidence of uplifting of the land mass (Bloom, 1964; Newman and Rusnak, 1965; Redfield, 1972; Redfield and Rubin, 1962). Reconstructing the evolution of a marsh can furnish a useful context for understanding present patterns of plant distribution; accordingly a brief study was undertaken to outline the developmental histories of Taskinas Creek Marsh and Bennett's Creek Marsh.

19. The peaty sediments underlying the marsh surface retain vestiges of the environment that prevailed when the sediments were deposited (Redfield, 1967). In order to gain a general picture of environmental change over time, peat cores were sampled from high and low marsh stations at each marsh, using an Oakfield Apparatus Company

sectioned peat corer, to a maximum depth of 8.5 m. Sixteen-centimeter core sections were retained at 1.25-m depth intervals for the following laboratory analyses: percent moisture, percent organic matter, and plant species identification.

20. Core sections were analyzed for moisture and organic matter as outlined under "Laboratory Procedures" in Part IV. Subsamples of each section were washed through three sediment screens, of mesh sizes 2 mm, 250  $\mu$ m, and 63  $\mu$ m, respectively. The fraction retained on each screen was examined under a dissecting microscope; when possible, root and stem remains were identified by species. Each fraction was also described qualitatively, noting abundance of organic matter, presence of foraminiferan tests, type of inorganic sediment, and other observable features.

21. Approximate stratigraphic sequences in each marsh have been reconstructed from the data. Figure 2 depicts cross sections on low marsh to high marsh transects at Taskinas Creek Marsh and Bennett's Creek Marsh, respectively. Solid-line borders between adjacent strata connect points for which data exist; dashed lines represent more speculative extrapolations.

22. The deepest stratum sampled at Taskinas Marsh (Figure 2) appeared to be sedge peat, characterized by sparsely scattered sedge stems. Overlying the sedge peat was a relatively thick wedge of fine-textured clay silt, nearly devoid of identifiable detritus particles. Above the mud layer was a thick wedge of dense, fibrous high marsh peat composed predominantly of S. patens and D. spicata rhizome remains,

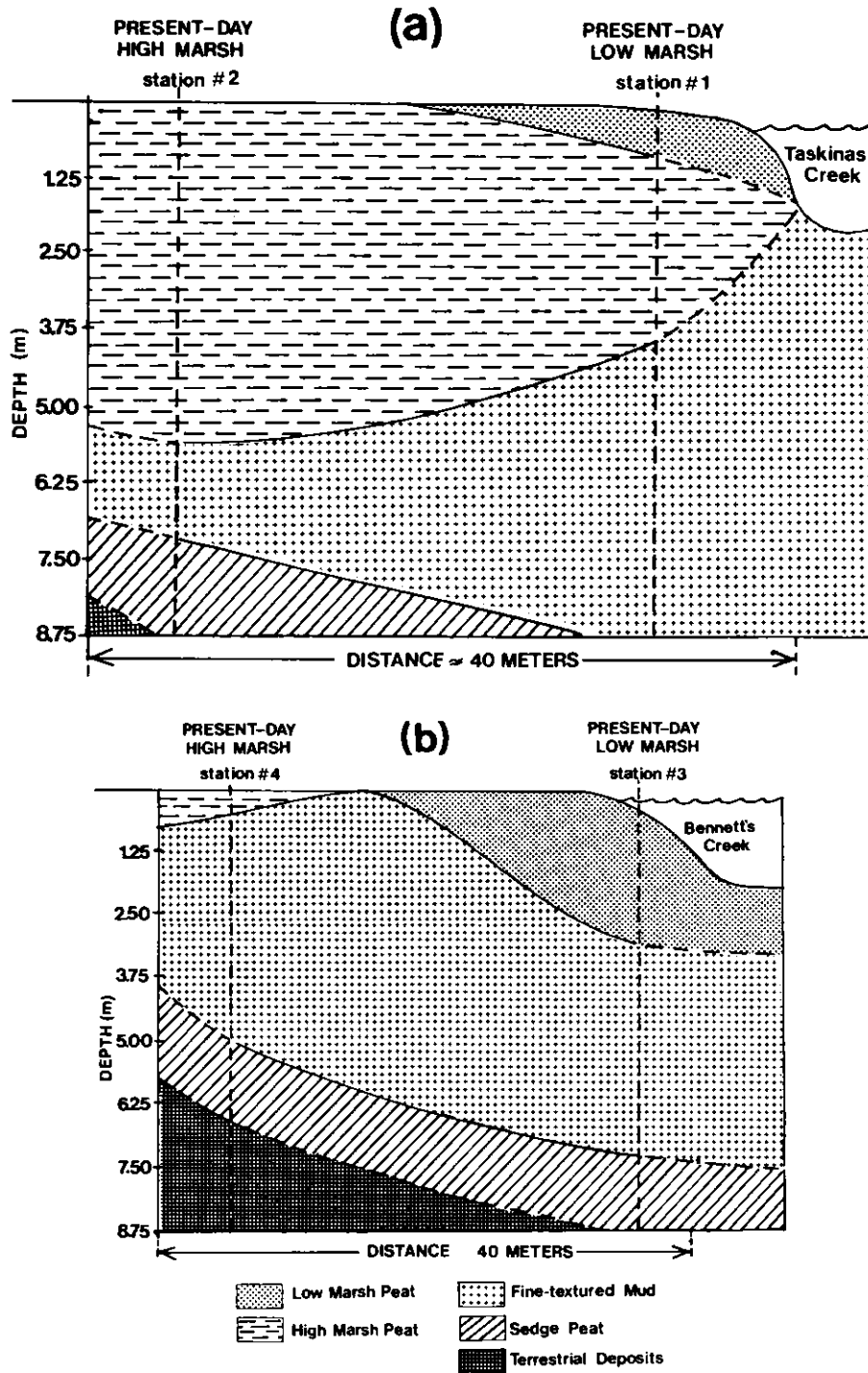


Figure 2. Cross section of sediment at Taskinas Creek (a) and Bennett's Creek (b).

which extended uninterrupted to the marsh surface in the present-day high marsh. The most recent deposit was a relatively shallow (.7-1.0 m) lens of low marsh (S. alterniflora) peat covering the modern intertidal zone.

23. The stratigraphic sequence at Bennett's Marsh (Figure 2 ) was similar to the Taskinas profile, but with several important distinctions. Terrestrial sediments found at a depth of 6.8 m at station #4 indicated that the total thickness of marsh sediments may be considerably less than at Taskinas Creek--at least 1.9 m less. As at Taskinas Marsh, a layer of sedge remains was covered by a thick deposit of silty clay. However, low marsh deposits originated considerably deeper at Bennett's than at Taskinas, while high marsh peat at Bennett's that underlaid the modern high marsh surface was comparatively shallow (less than 0.6 m).

24. Lacking radiocarbon analyses of the peat samples, it was difficult to accurately establish the age of each stratum. Nevertheless, a general sequence of events was deduced by the principle of superposition (Leet and Judson, 1965).

25. Scattered studies of marshes bordering the East Coast of the United States suggested that contemporary marshes were of relatively recent origin. Bloom (1964) estimated a maximum age of approximately 7000 years before present (B.P.) for peat at the basement of a Connecticut salt marsh. Redfield's (1967, 1972) Cape Cod marsh dates back to 4000 years B.P., while the Wachapreague Marshes of Virginia's eastern shore appeared about 5000 years ago (Newman and Rusnak, 1965). It seemed reasonable, then, to infer that Taskinas Creek Marsh and Bennett's Creek Marsh originated within the last 4000 to 7000 years.

26. Based on core samples, the earliest macrophyte community at both marshes was apparently a brackish-water association characterized by sedges such as Scirpus. Bloom (1964) found a similar association in Connecticut marsh deposits. These early sedge marshes may have formed as narrow fringes separating the uplands from adjacent shallow bays. As sea level rose relative to the land, the fringing marshes continued to colonize the borders of the drowning uplands, while their seaward edges were reclaimed by the bays. Even today, the most abundant stands of Scirpus in Virginia salt marshes congregate along the upland margins. The association of a sedge zone fringing shallow bays has also been identified in Connecticut (Bloom, 1964), and elsewhere in Virginia (Newman and Rusnak, 1965).

27. The histories of Taskinas Marsh and Bennett's Marsh appeared to diverge with the initiation of a high marsh (S. patens and D. spicata) community at Taskinas, at a maximum depth of about 5.5 m below the present marsh surface. The data suggested that the transition from shallow bay mud to fibrous high marsh peat occurred relatively rapidly, perhaps even without an intervening low marsh stage (Redfield, 1972). Expansion of the high marsh may have coincided with the slow-down in rate of relative sea level rise that occurred along the East Coast around 2000-3000 years B.P., facilitating uplift of the marsh surface by sediment accretion (Redfield and Rubin, 1962; Newman and Rusnak, 1965; Bloom, 1964). The high marsh community spread across Taskinas Marsh, until the relatively recent appearance of S. alterniflora along the creek banks. Organic remains in the upper 0.9 m of



sediment indicated progressive expansion of this low marsh species rearward across previous high marsh. Furthermore, Taskinas high marsh was dotted with Iva frutescens, a shrub generally associated with a more elevated habitat (Kurz and Wagner, 1957). Almost all of the I. frutescens were dead. Coupled with the invasion of S. alterniflora over the high marsh, these observations suggested that Taskinas Marsh is presently undergoing a drowning phase; that is, the rise in relative sea level is outstripping the vertical accretion of sediment, and retrogressive succession (Kurz and Wagner, 1957) appears to be occurring.

28. The mud stratum at Bennett's Marsh extended upward considerably closer to the surface than at Taskinas Marsh. Although relative ages of similar strata in each marsh could not be determined without radio-carbon techniques, it seemed plausible that an open-water environment persisted until more recently at Bennett's Marsh, particularly in the zones now occupied by high marsh species.

29. It appeared that a S. alterniflora community occupied the intertidal zone at Bennett's long before a S. patens - D. spicata association became established, since the high marsh peat layer is much shallower than the low marsh peat (Figure 2). The presence of low marsh and high marsh associations above the mud stratum suggested that Bennett's Marsh has recently been undergoing an accreting phase; that is, the vertical accumulation of sediment is surpassing the rise in relative sea level. However, the data were insufficient to indicate whether high marsh is now succeeding low marsh, or vice versa, or whether the balance is stable.

30. In summary, the marsh stratigraphy investigation afforded the following perceptions:

(a) The development of Taskinas Marsh and Bennett's Marsh paralleled the general patterns outlined for other East Coast salt marshes (Redfield, 1967, 1972; Newman and Rusnak, 1965; Bloom, 1964; Hill and Shearin, 1970).

(b) Taskinas Marsh is presently undergoing a drowning phase, as sea level has risen relative to the surface of the marsh.

(c) Bennett's Marsh has recently been experiencing an accreting episode; i.e., the marsh surface has been elevated relative to sea level.

## PART IV: METHODS

### Field Procedures

31. After the results of preliminary studies were evaluated, a final transect design was adopted at the two intensive study sites, Taskinas Creek and Bennett's Creek. Three parallel belt transects were established in each marsh, extending across the ecotone from low marsh to high marsh. The transects (Figure 3) were 8 m longer at Bennett's Marsh than at Taskinas Marsh, and thereby encompassed two more sample zones in order to accommodate Bennett's broader distribution of vegetative zones.

32. Within each transect were equidistant "sample zones", 4-m x 1-m areas from which all plant and sediment samples were taken (Figure 3). Samples were gathered randomly within each zone by means of randomized assignment of numbers of the four adjacent 1-m<sup>2</sup> quadrats in each sampling zone.

33. Plant samples and sediment cores were taken at four times during the spring and summer of 1975: 5-7 April, 29-30 May, 21 July, and 13 September. On each occasion, a single plant sample (shoots only) and three sediment cores were taken from each sample zone. Quadrats harvested were 0.1 m<sup>2</sup> in zones where S. alterniflora appeared to be prevalent, and 0.04 m<sup>2</sup> where S. patens and D. spicata predominated. Cores were taken with a brass coring apparatus (6.35 cm i.d.) and were extruded and frozen immediately.

34. Plant growth indices (stem biomass, height, density per m<sup>2</sup>) and plant-available nutrient concentrations in sediments (NH<sub>3</sub>, PO<sub>4</sub>, Mn,

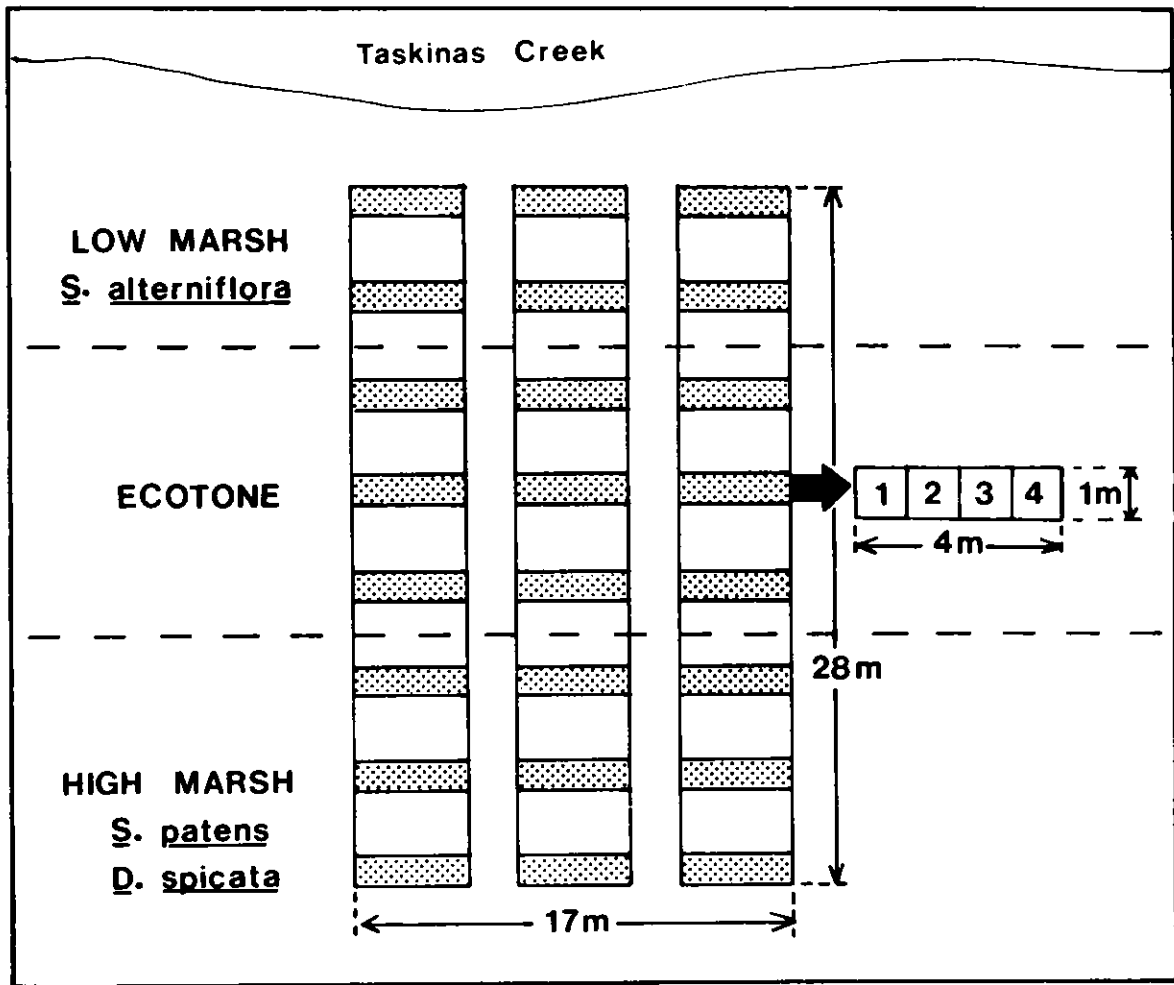


Figure 3. Experimental plot design at intensive study sites.

Ca, and Mg) were measured at all four sampling periods mentioned above. Two environmental factors were determined for a single sampling period only--organic matter content of sediments (21 July) and interstitial salinity (13 September).

35. Relative elevations of all sample sites were determined with a transit, plane table, and stadia rod on 2 July 1975. Elevations of Taskinas Marsh were rechecked on 9 September. Because no U.S.G.S. elevation bench marks were available for reference, a Mean Low Water datum for both creeks was established from tide height estimates published by the National Ocean Survey (U.S. Dept. of Commerce, 1974). The elevation of the creek surface at slack low water was measured relative to the sample zones, then corrected for departure from true mean low water as gauged at nearby NOAA tide stations. Slack low water level was surveyed at both creeks on 14 November 1975, a day of minimal wind activity, and rechecked during similar wind conditions at Taskinas Creek on 28 February 1976.

### Laboratory Procedures

#### Plant samples

36. All live stems were separated by species and all dead stems were also grouped together. The number of live stems of each species was counted, and stem height was measured to the nearest centimeter for subsamples of ten stems per species. Live standing crop data for each species and total standing dead were obtained by drying grass samples in a drying oven for 48 hours at 105<sup>o</sup>C. Dried samples were weighed to  $\pm$  0.1 gram on a Mettler model P1200N top-loading balance.

### Sediment cores

37. Analyses at the intensive sites were confined to the upper 20 cm of the sediment since none of the major plant species present extends its roots significantly below that level. (Valiela and Teal, 1973; Broome et al., 1973). Soil subsamples were combined with a weak acid extractant solution (Nelson et al., 1953), homogenized in a blender, and filtered to obtain samples for nutrient analyses. Additional subsamples were ashed in a muffle furnace to determine organic content of soils (see Appendix A for details of procedures).

### Nutrient analysis

38. Concentrations of iron, manganese, calcium, and magnesium in filtered samples were measured in a Varian Atomic Absorption Spectrophotometer (model AA-5R). Sample intake was regulated by a Technicon Sampler II automatic sampling apparatus, and data were recorded as peak heights on a Varian model A-25 strip chart recorder. Calcium and magnesium were run at 60 samples per hour using the Technicon proportioning pump to add and mix one ml of  $\text{SrCl}_2$  (5,000 ppm) to each ml of magnesium and calcium sample.

39. Phosphate analyses were conducted on a Technicon Auto-Analyzer; a combined reagent (0.18 M ammonium molybdate + .011 M ammonium metavanadate) was used (adapted from Steckel and Flannery, 1966). The Sampler was set at 40 samples per hour, and peak heights recorded on a Technicon "Recording System" strip chart. Duplicate determinations were performed on all the foregoing automated analyses of each sample.

40. Ammonia concentrations were measured with an Orion model 95-10 ammonia electrode and an Orion model 401 specific ion meter. Two ml of 10 M NaOH were added to 20 ml of constantly stirred sample solution to obtain a pH of approximately 11.00; after equilibration, ammonia concentration was measured to  $\pm 0.1$  ppm.



## PART V: FIELD STUDY RESULTS AT INTENSIVE SITES

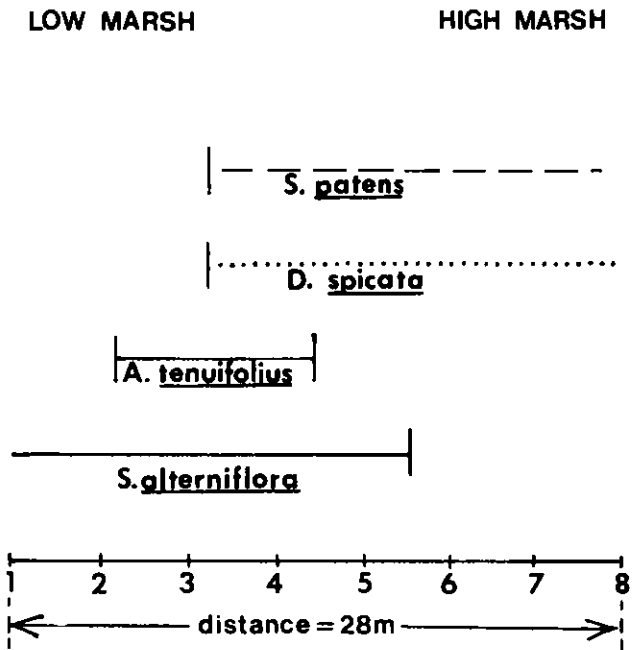
### Habitat Factors

#### Vegetation

41. Four species of macrophytic phanerogams were encountered at both study sites: S. alterniflora, S. patens, D. spicata, and Aster tenuifolius (Figure 4). S. alterniflora predominated in the low marsh zone fringing the tidal creeks, and S. patens and D. spicata occupied adjacent high marsh areas. All three species inhabited the ecotone separating the zones, in varying proportions. A. tenuifolius, a minor constituent throughout, occurred most frequently in the low marsh and ecotone.

42. Seasonal data for live standing crop, standing dead, stem density, and stem height of all species were condensed into annual summary values (Figures 5-9). Because of its relative scarcity, A. tenuifolius was omitted from the summaries. Maximum live standing crop of the three major species was graphed for Taskinas Marsh (Figure 5a) and Bennett's Marsh (Figure 5b). At both sites, standing crop of S. alterniflora generally declined from the low marsh toward the high marsh (left to right on the graphs). Maximum values occurred in the sample zones closest to the creeks. S. patens live standing crop exceeded D. spicata over most of their common range at both sites, although S. patens decreased both landward and seaward from peak values. Miller and Egler (1950) identified the S. patens - D. spicata association in Connecticut tidal marshes; they termed the species "ecological

(a) TASKINAS MARSH



(b) BENNETT'S MARSH

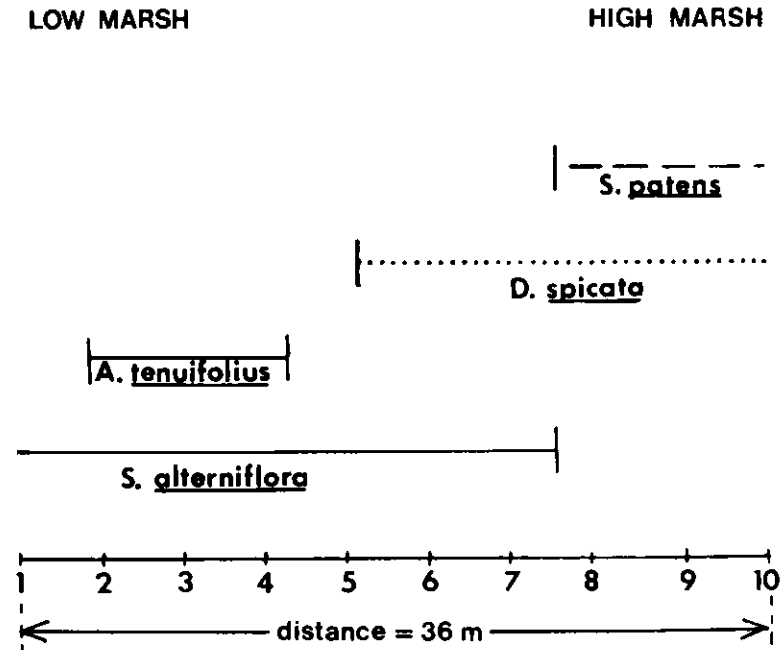


Figure 4. Ranges of plant species across transects at Taskinas Marsh and Bennett's Marsh.

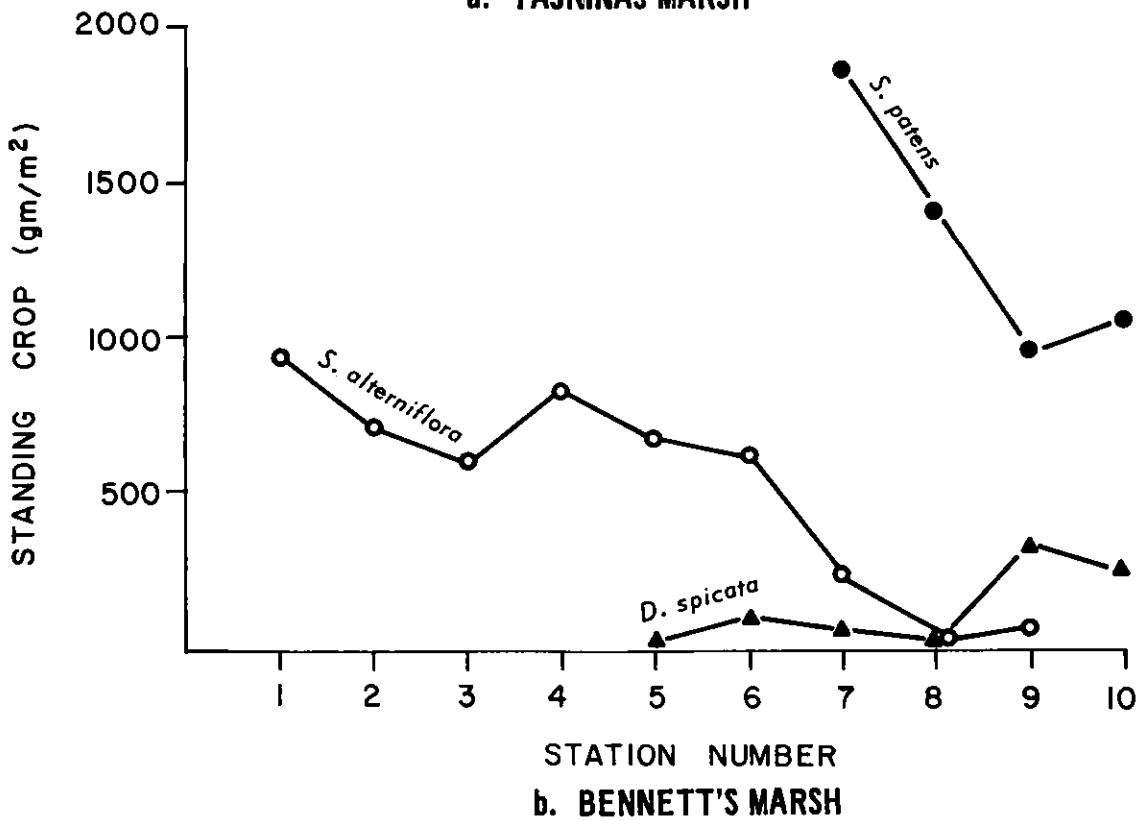
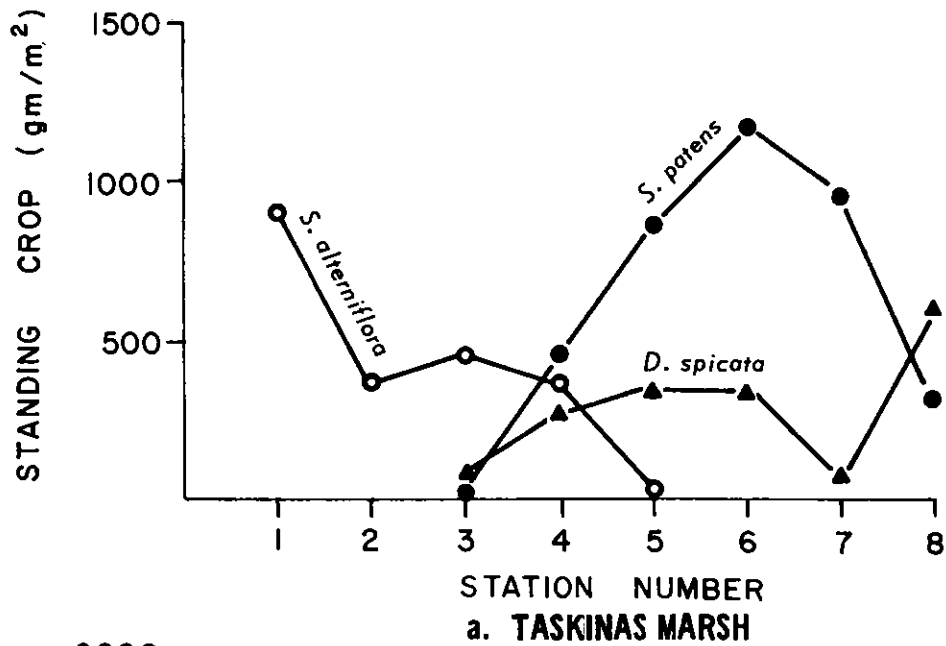


Figure 5. Maximum values for live standing crop at Taskinas Marsh (upper) and Bennett's Marsh (lower).

equivalents", while affirming that S. patens is usually dominant where they occur together. However, D. spicata surpassed S. patens along the seaward margin of their common range at Taskinas; indeed, at Bennett's Marsh, S. patens was entirely absent from sample zone 5, the seaward limit of D. spicata growth (Figure 5).

43. It is noteworthy that the largest standing crop values of S. patens exceeded those of S. alterniflora at both marshes--a reversal of the pattern reported from many other Virginia marshes (Keefe, 1972).

44. The spatial distribution of total standing dead material (Figure 6) is interesting for several reasons:

a) Accumulation of standing dead is considerably greater in the high marsh zone (S. patens, D. spicata) than in the low marsh (S. alterniflora).

b) The landward edge of the ecotone, adjoining the high marsh community, is marked by an abrupt change in the amount of standing dead.

c) The ratio of live standing crop to dead standing crop (L/D) in both low marsh and high marsh zones was considerably higher at Bennett's than at Taskinas. Since L/D ratios are considered to vary directly with the amount of tidal inundation that a marsh receives (Keefe and Boynton, 1973; Mendelssohn, 1973), Bennett's Marsh evidently has experienced more inundation than Taskinas Marsh. Predicted inundation values (discussed below) bolster this contention.

45. Data from July and September sampling periods (around the end of the growing season in Virginia marshes) were combined to yield

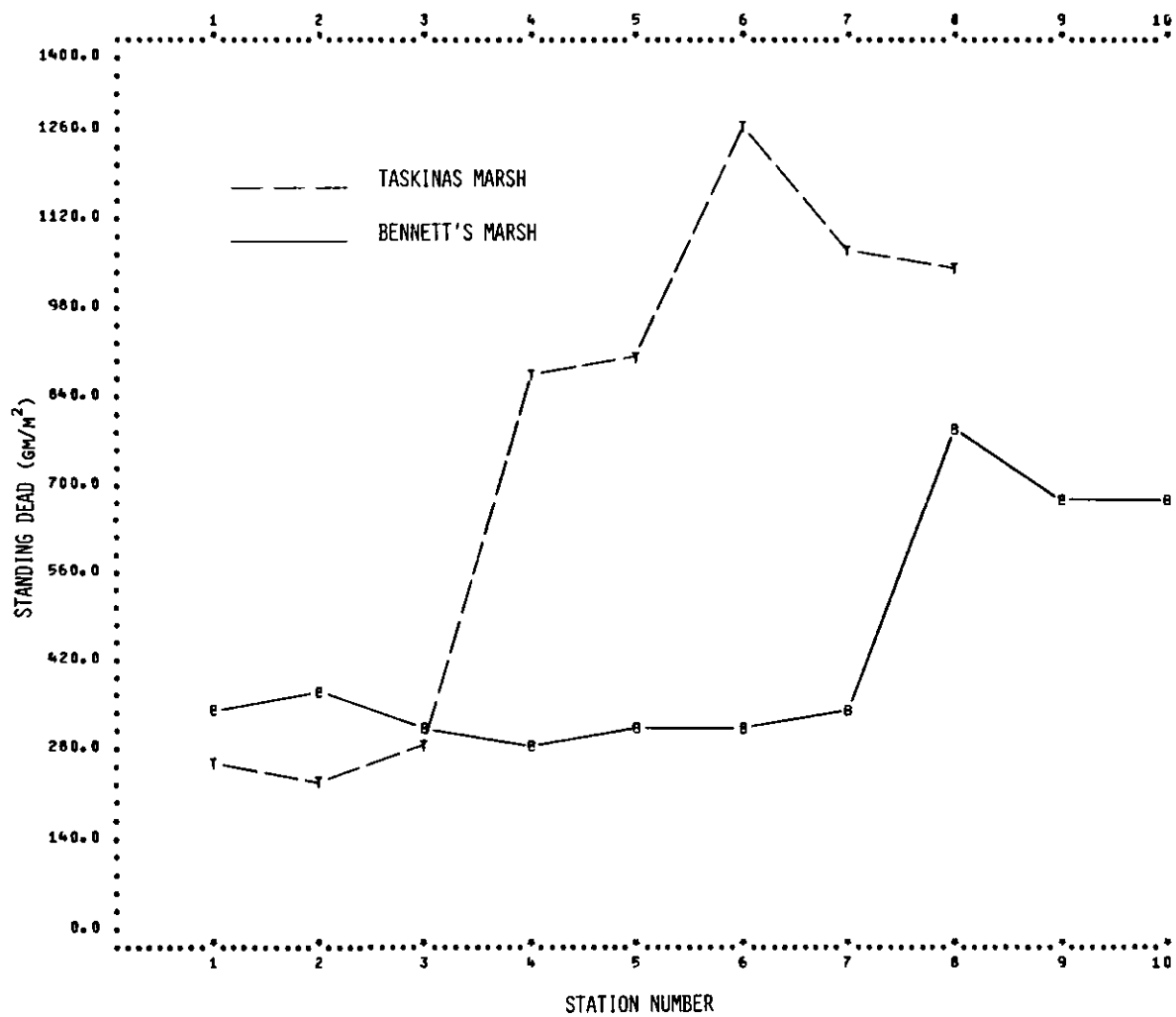


Figure 6. Maximum values for standing dead crop at Taskinas Marsh and Bennett's Marsh.

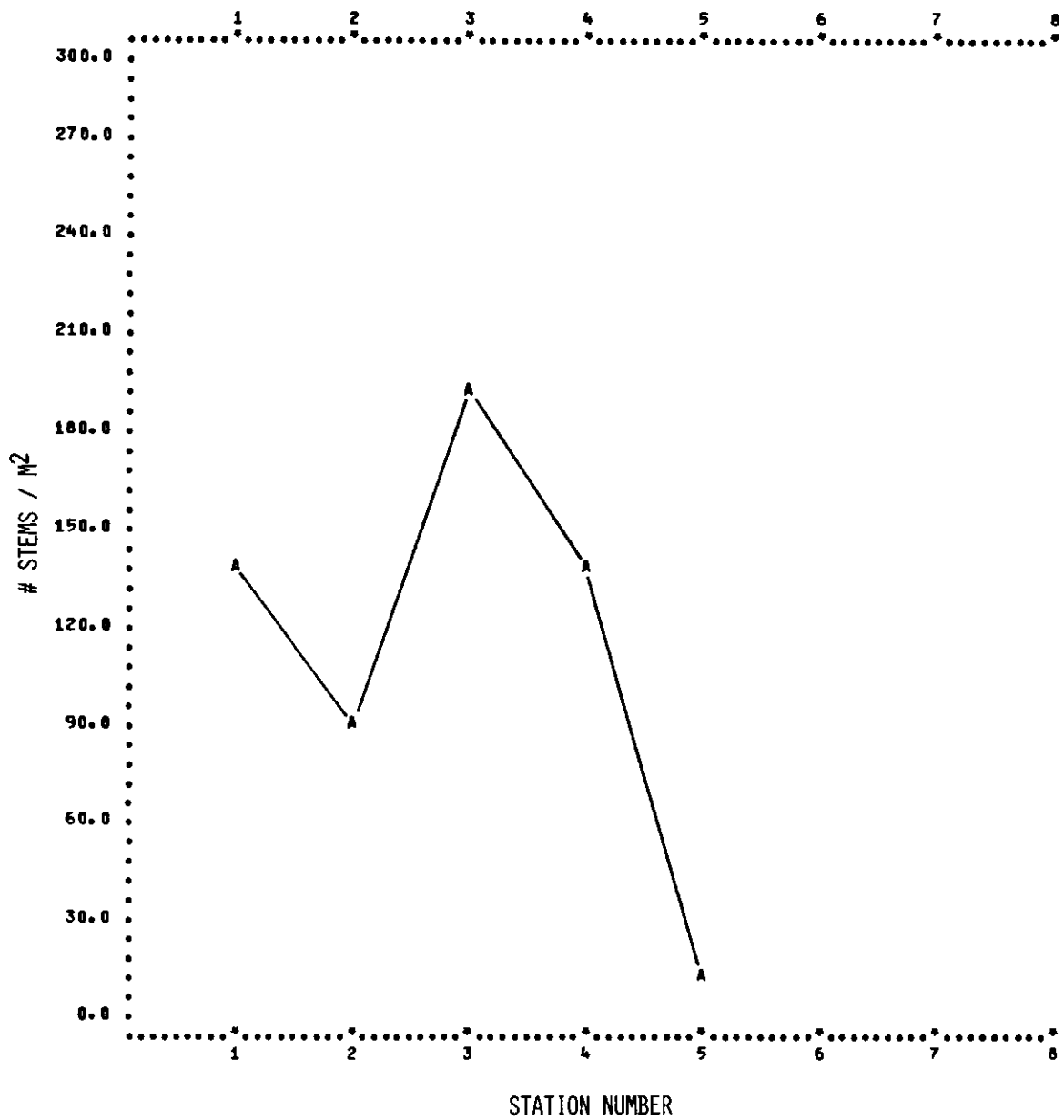
average maximum values for stem density and stem height. These averages were adopted to approximate the maximum standing crop of the plants and to reduce the amount of variability in the data.

46. The trend of spatial variation in stem density was similar in both marshes (Figures 7 and 8); stem density reached a maximum in the middle of the S. alterniflora range, followed by a precipitous decrease at the ecotone. Comparison with Figure 5 indicated that maximum standing crop was not strictly coincident with maximum stem density, although their patterns of fluctuation were qualitatively similar. Stem densities for the S. patens - D. spicata association (Figure 8) also resembled the respective standing crop trends (Figure 5). In both marshes, D. spicata exhibited its highest standing crop and stem density values at the landward extremes of the transects.

47. Stem heights (Figure 9), like stem densities, represented averages of July and September data. S. alterniflora steadily declined in height rearward; the zone closest to the creek possessed both the tallest stems and the largest standing crop values. While S. patens and D. spicata were similar in stem height, S. patens was slightly taller over most of their common range. Following the trend for standing crop and stem density, D. spicata was taller than S. patens at the seaward margin of the ecotone at Taskinas Marsh.

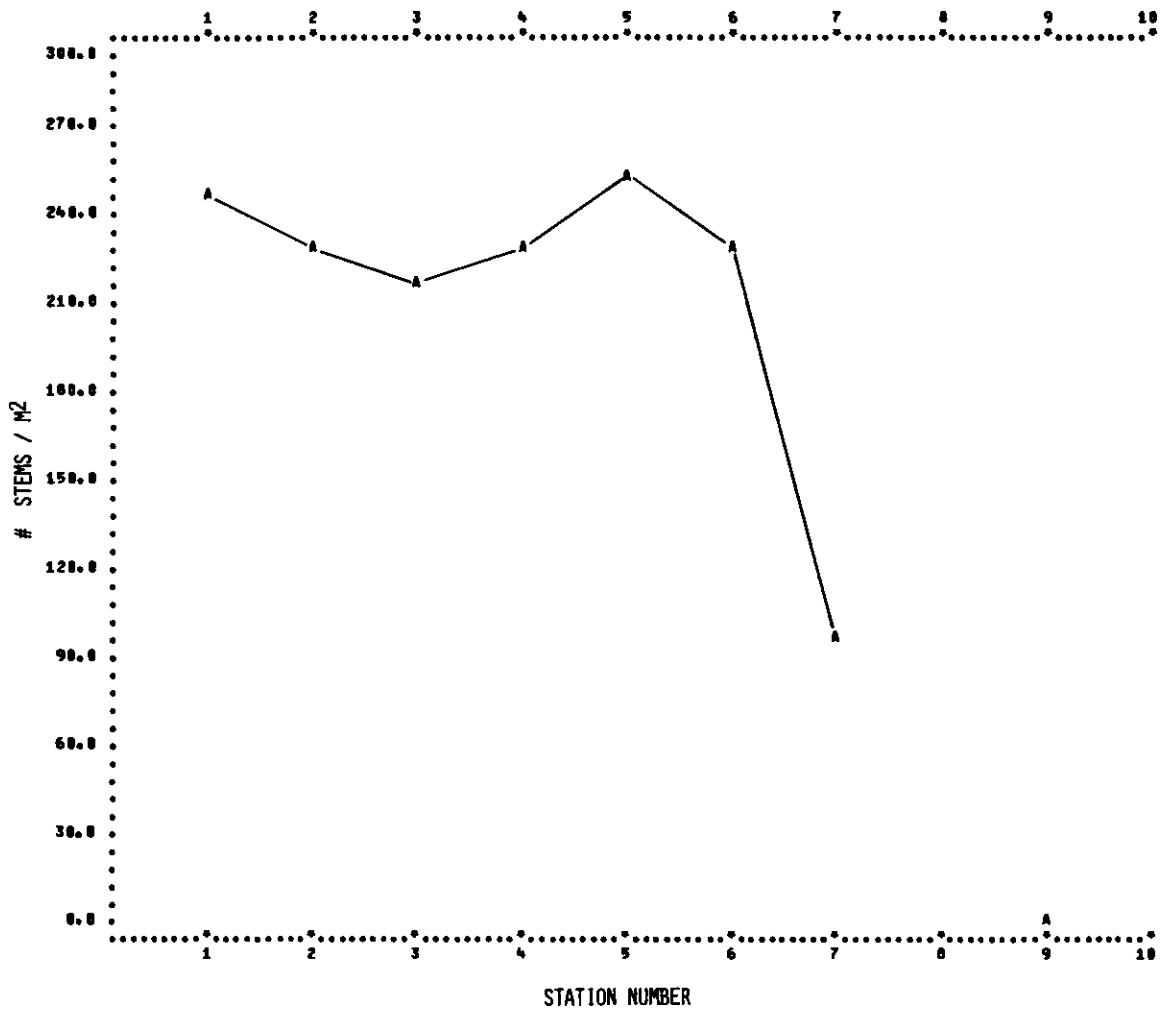
#### Elevation

48. Profiles of average elevation at Taskinas Marsh and Bennett's Marsh (Figure 10), following the transects from low marsh (on the left) to high marsh (on the right), offer several contrasts:



a. Taskinas Marsh

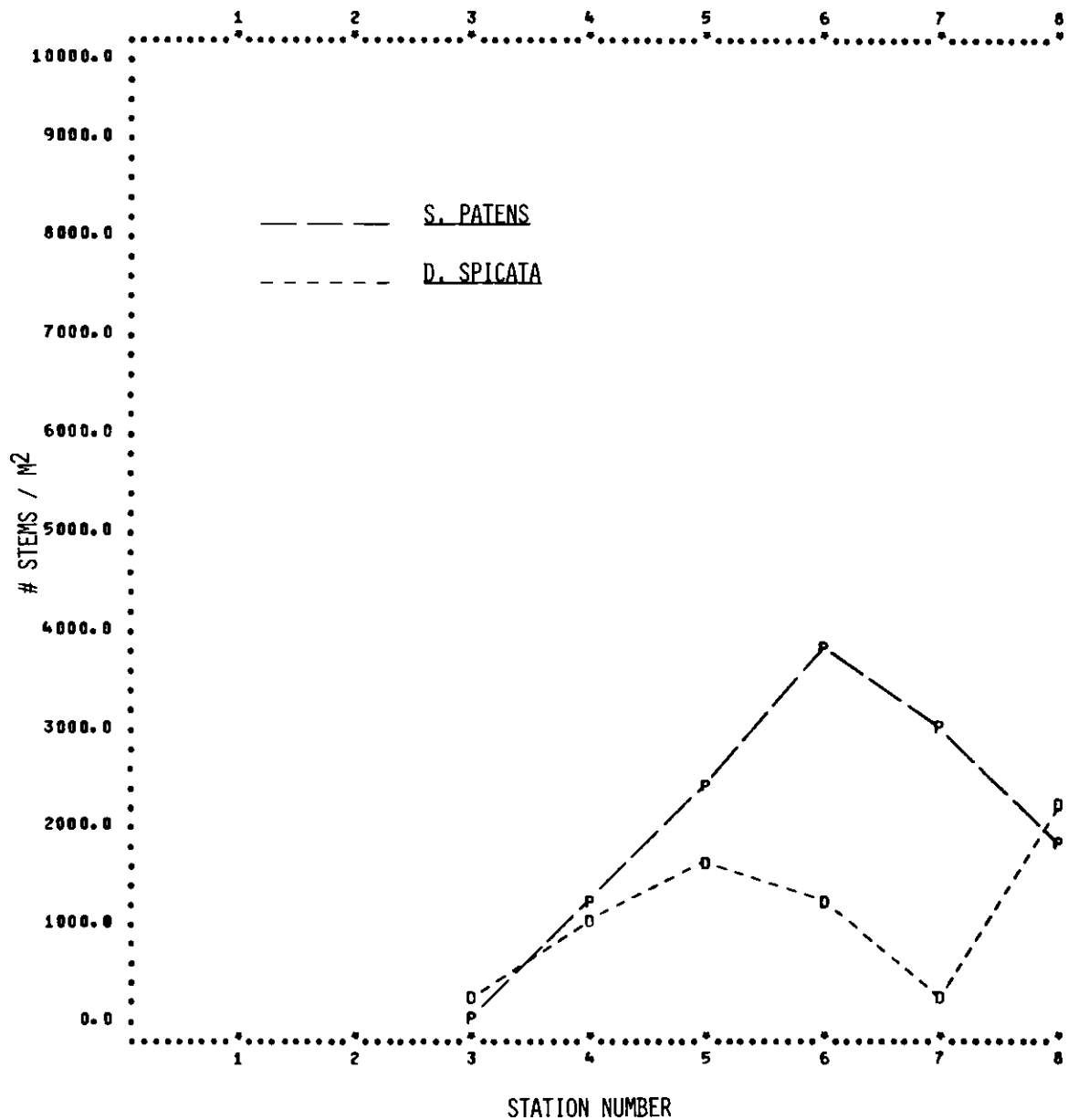
Figure 7. Maximum values for stem density of Spartina alterniflora at Taskinas and Bennett's Marsh (sheet 1 of 2).



b. Bennett's Marsh

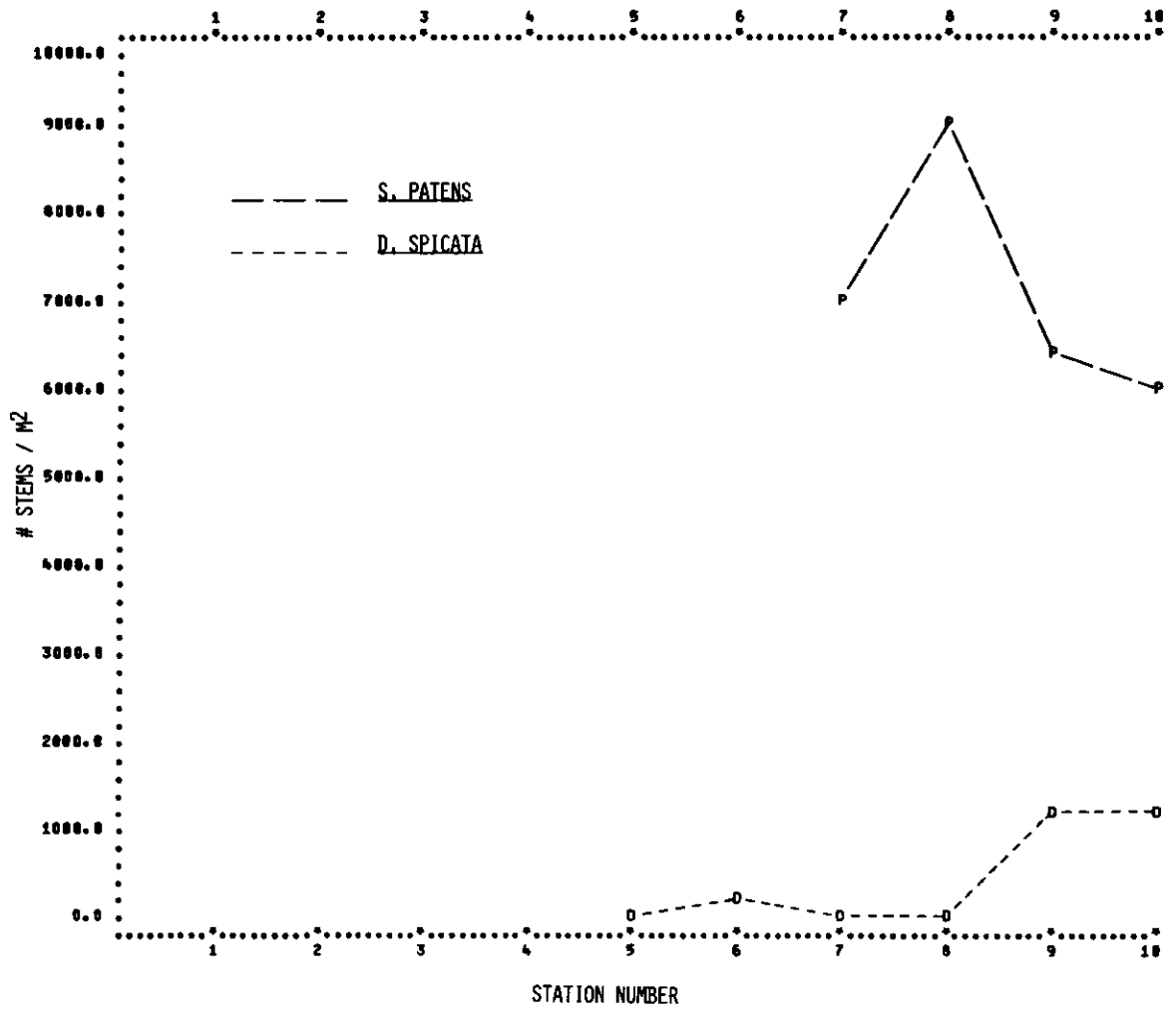
Figure 7 (sheet 2 of 2).





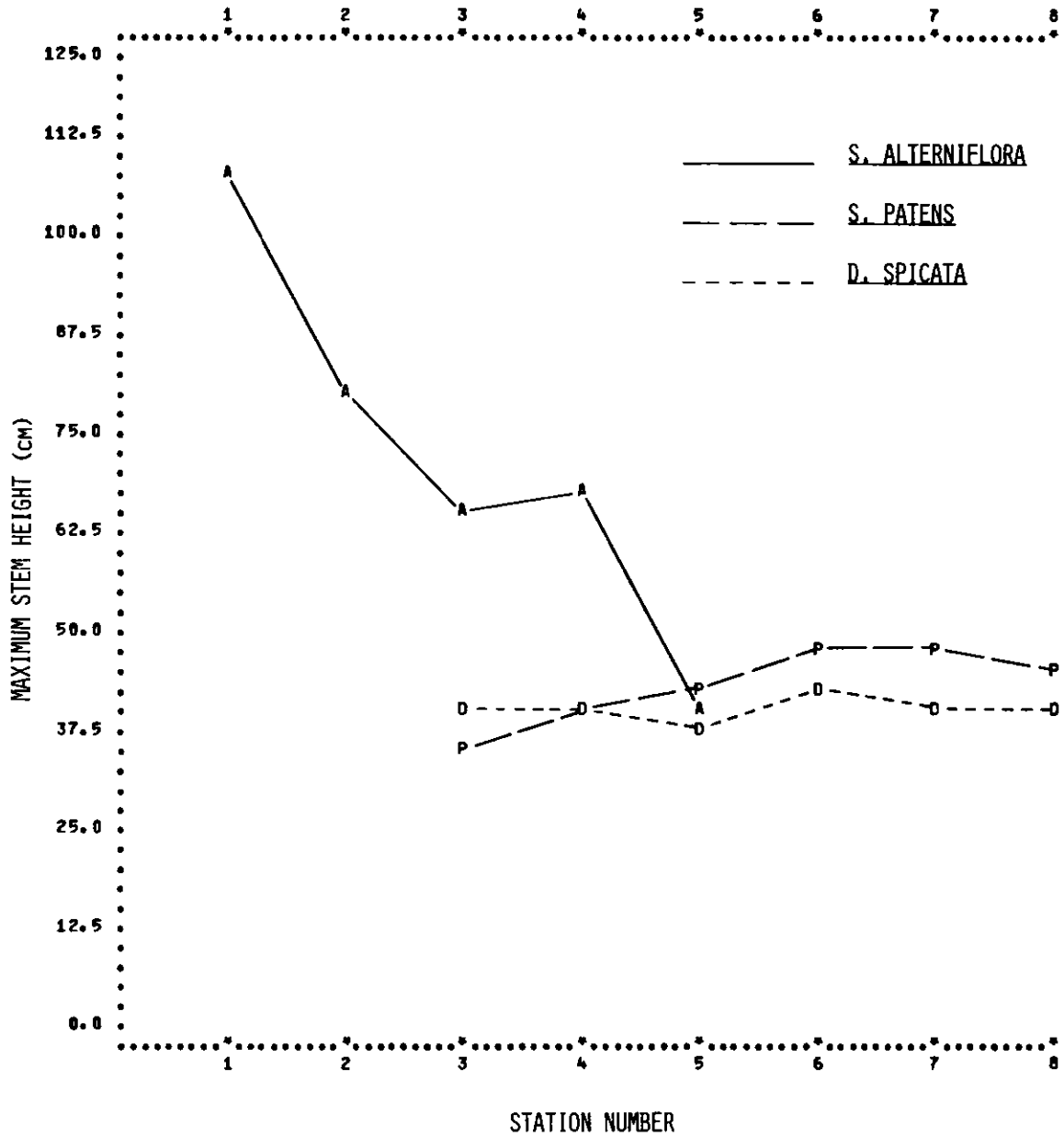
a. Taskinas Marsh

Figure 8. Maximum values for stem density of *Spartina patens* and *Distichlis spicata* at Taskinas Marsh and Bennett's Marsh (sheet 1 of 2).



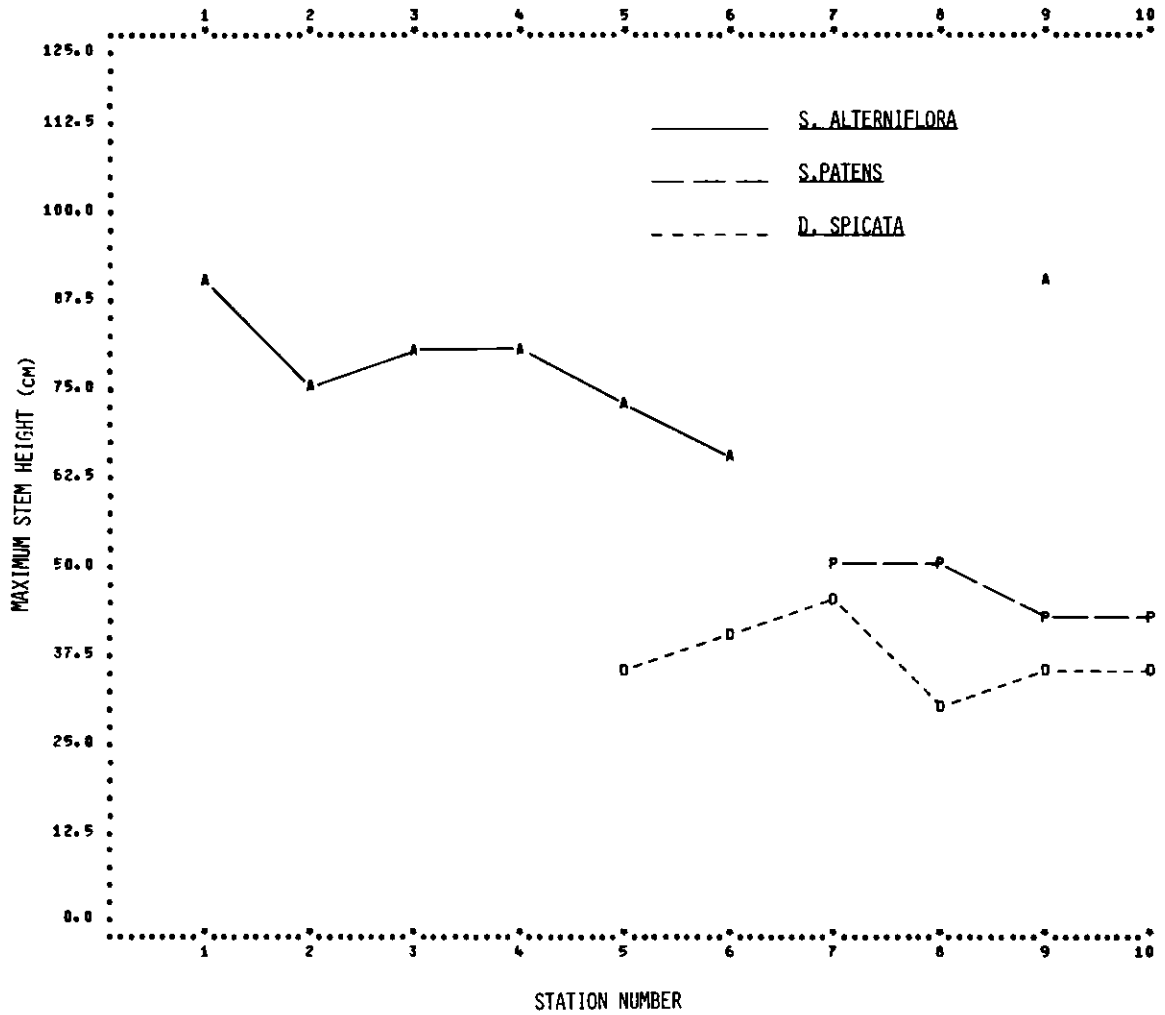
b. Bennett's Marsh

Figure 8 (sheet 2 of 2).



a. Taskinas Marsh

Figure 9. Maximum values for stem height of *Spartina patens* and *Distichlis spicata* at Taskinas Marsh and Bennett's Marsh (sheet 1 of 2).



b. Bennett's Marsh

Figure 9 (sheet 2 of 2).

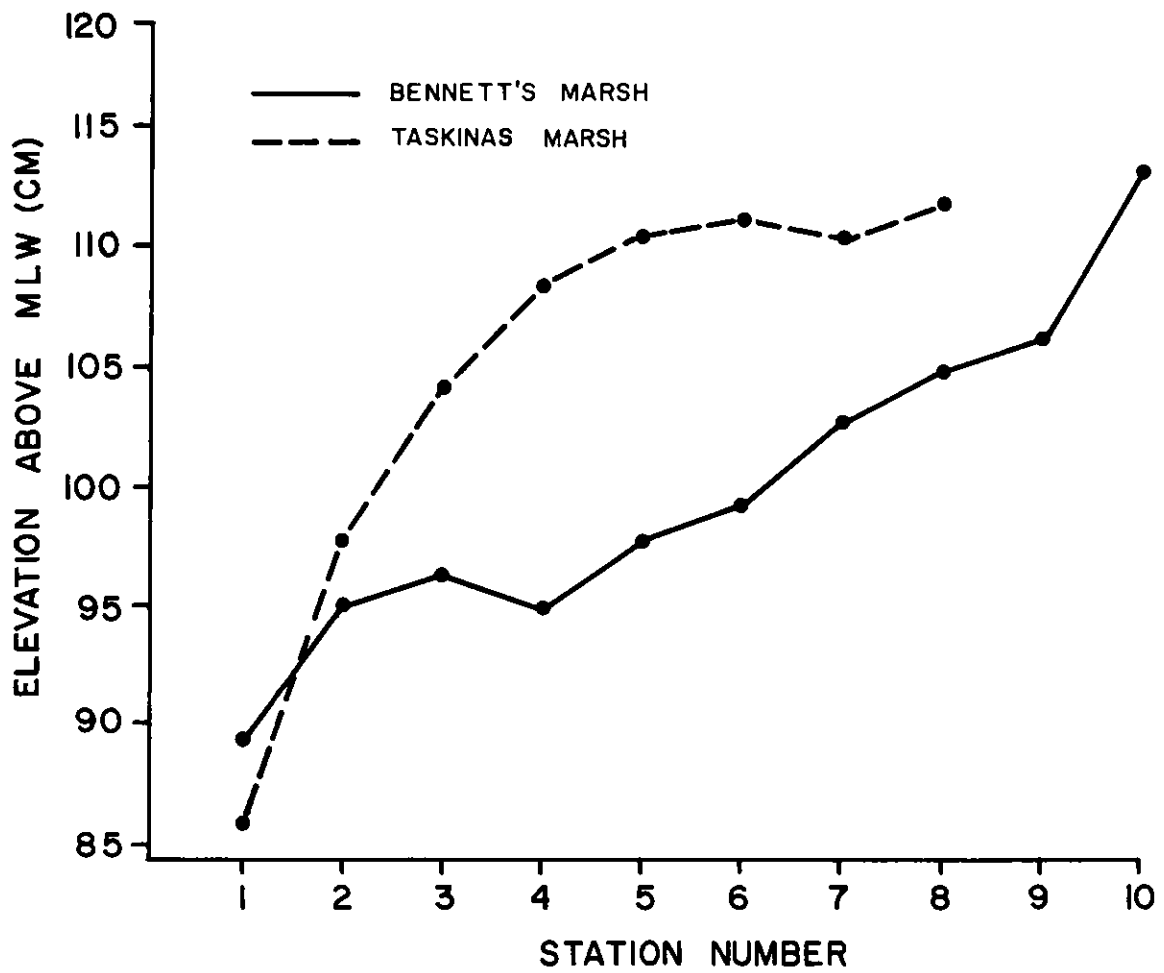


Figure 10. Elevation of the sample stations above mean low water.

a) Elevation at Taskinas Marsh increased sharply rearward from the low marsh (zones 1-4), then leveled off in the high marsh (zones 5-8). Bennett's Marsh also rose toward the rear, but with a more gradual, constant slope than Taskinas Marsh.

b) The slightly mounded profile of Bennett's low marsh, centered on zone 3, was a natural levee. Levees are common features of sloping marsh foreshores (Kurz and Wagner, 1957). No such structure existed in the Taskinas low marsh.

c) Most of the Taskinas site was considerably higher above mean low water than the Bennett's Creek site.

#### Number of inundations

49. A FORTRAN computer program (Program TIDE) translated elevation data into estimates of the number of inundation events per year at each sample zone. An inundation event was defined as any instance in which tidal water covered the sediment surface. The results can be summarized as follows (Figure 11):

a) The sharpest decline in number of inundations occurred between zones 1 and 2 (the zones closest to the tidal creek) in each marsh.

b) Inundation events declined rapidly away from the creek at Taskinas low marsh; in fact, no inundation at all is predicted landward of zone 3. At Bennett's Marsh, inundation dropped more gradually toward the rear, and only the two highest zones (9 and 10) were above the reach of predicted tides.

50. Thus, predicted tidal inundation was considerably more

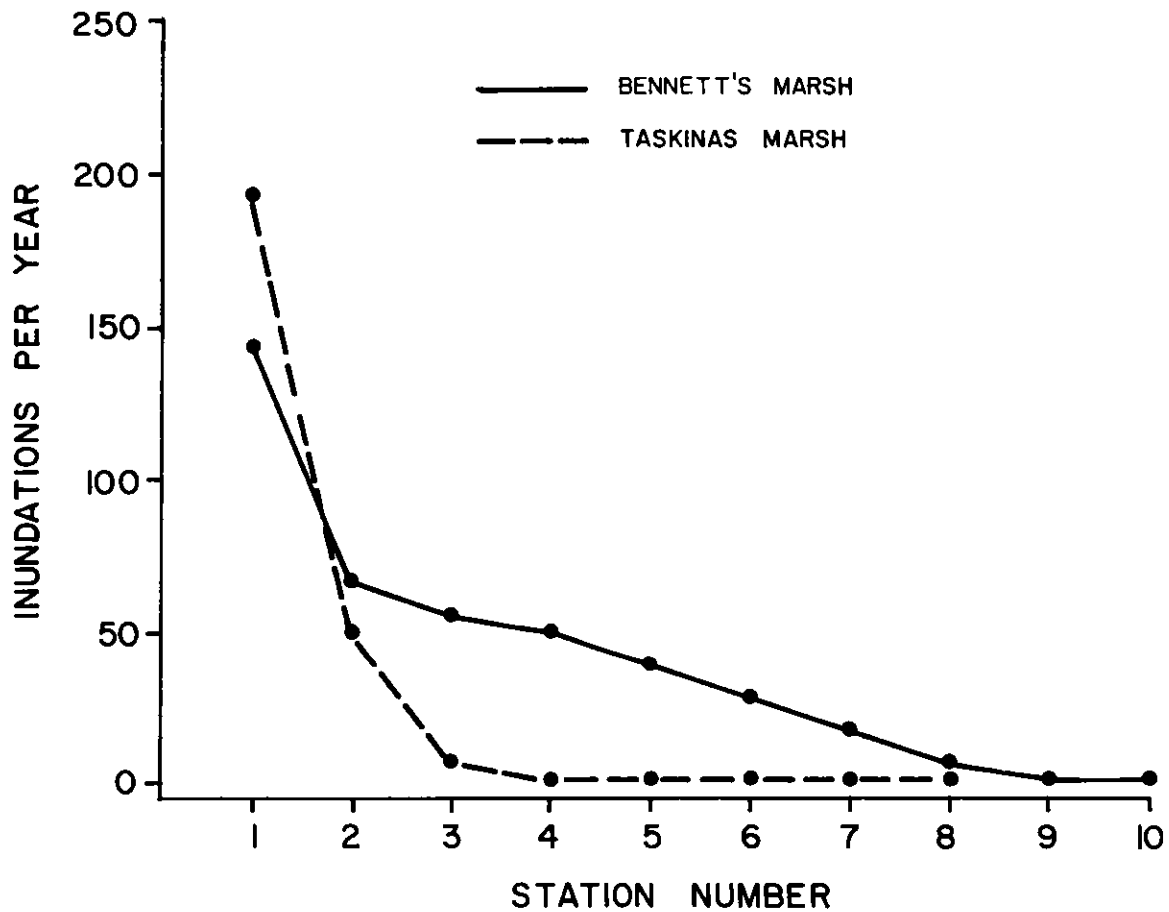


Figure 11. Number of inundations per year at sample stations.

extensive at Bennett's Marsh than at Taskinas Marsh. As previously stated, the fact that L/D ratios (living:dead standing crop) at Bennett's exceeded those at Taskinas in both low marsh and high marsh corroborates the prediction of greater flooding at the Bennett's Creek site (Mendelssohn, 1973).

#### Salinity

51. Interstitial salinity (Figure 12) increased relatively sharply across the low marsh at Taskinas (zones 1-4), then peaked in the ecotone (zones 4-5) and declined in the high marsh. Salinity at Bennett's Marsh rose initially to a small peak at zone 2, then declined slightly before increasing again in the high marsh.

52. Although they are not shown by the averaged values in Figure 12, maximum soil salinities exceeded 20 o/oo at both sites, a concentration exceeding the highest values measured in the creek water (about 15 o/oo). Soil salinities exceeding the maximum salinity of tidal water have also been noted in other brackish estuarine marshes (Lindberg and Harriss, 1973).

#### Organic matter

53. Samples from both marshes showed a nearly linear increase in percent organic matter from the low marsh through the high marsh (Figure 13). Taskinas Marsh had the greater range, possessing both the lowest value (zone 1) and the highest value (zone 8). The rearward increase in organic matter at Bennett's Marsh was more gradual and somewhat less linear than at Taskinas Marsh. Buttery et al. (1965) noted a similar rise in organic matter content from low marsh to high marsh.

54. The organic content of tidal marsh sediments is largely a



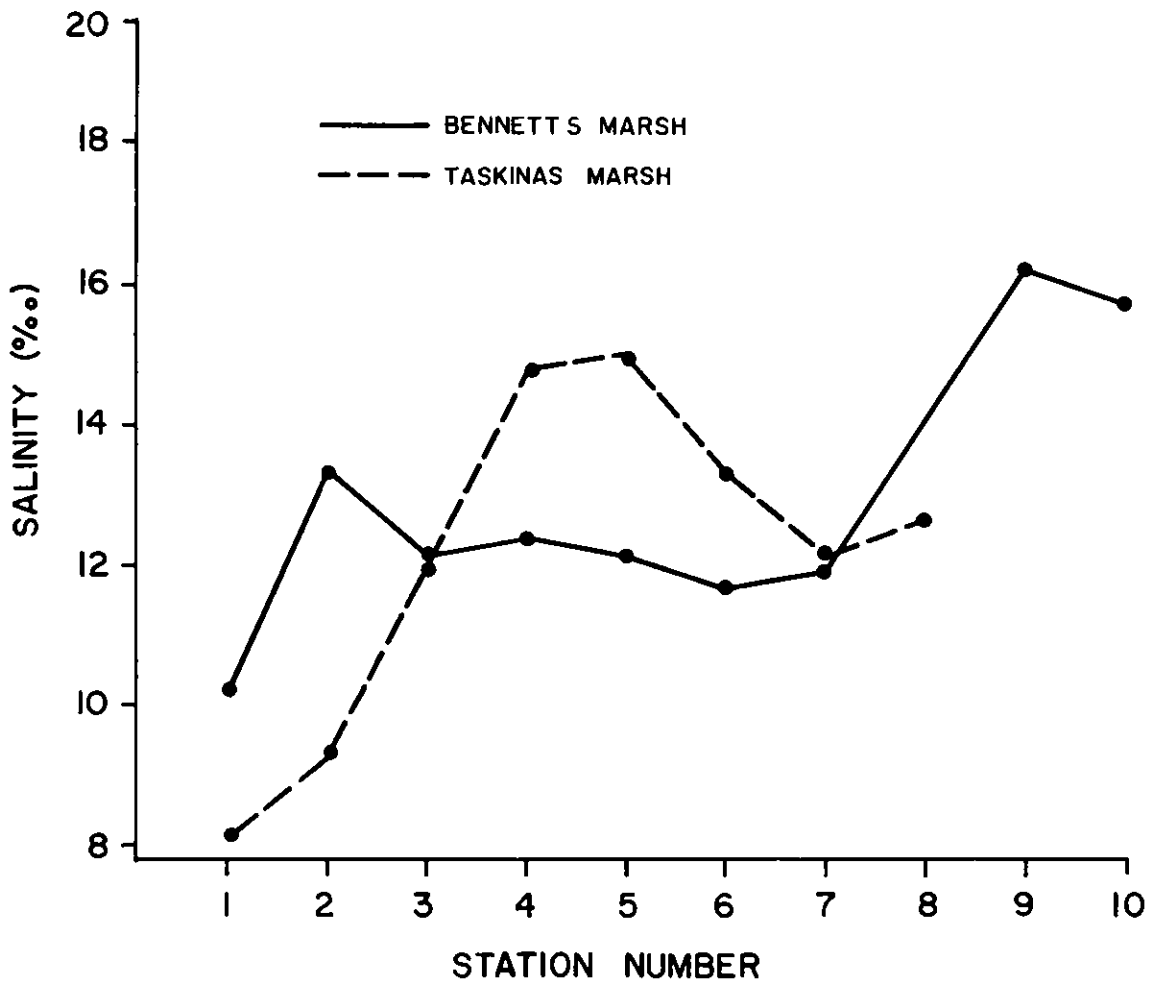


Figure 12. Salinity of interstitial water.

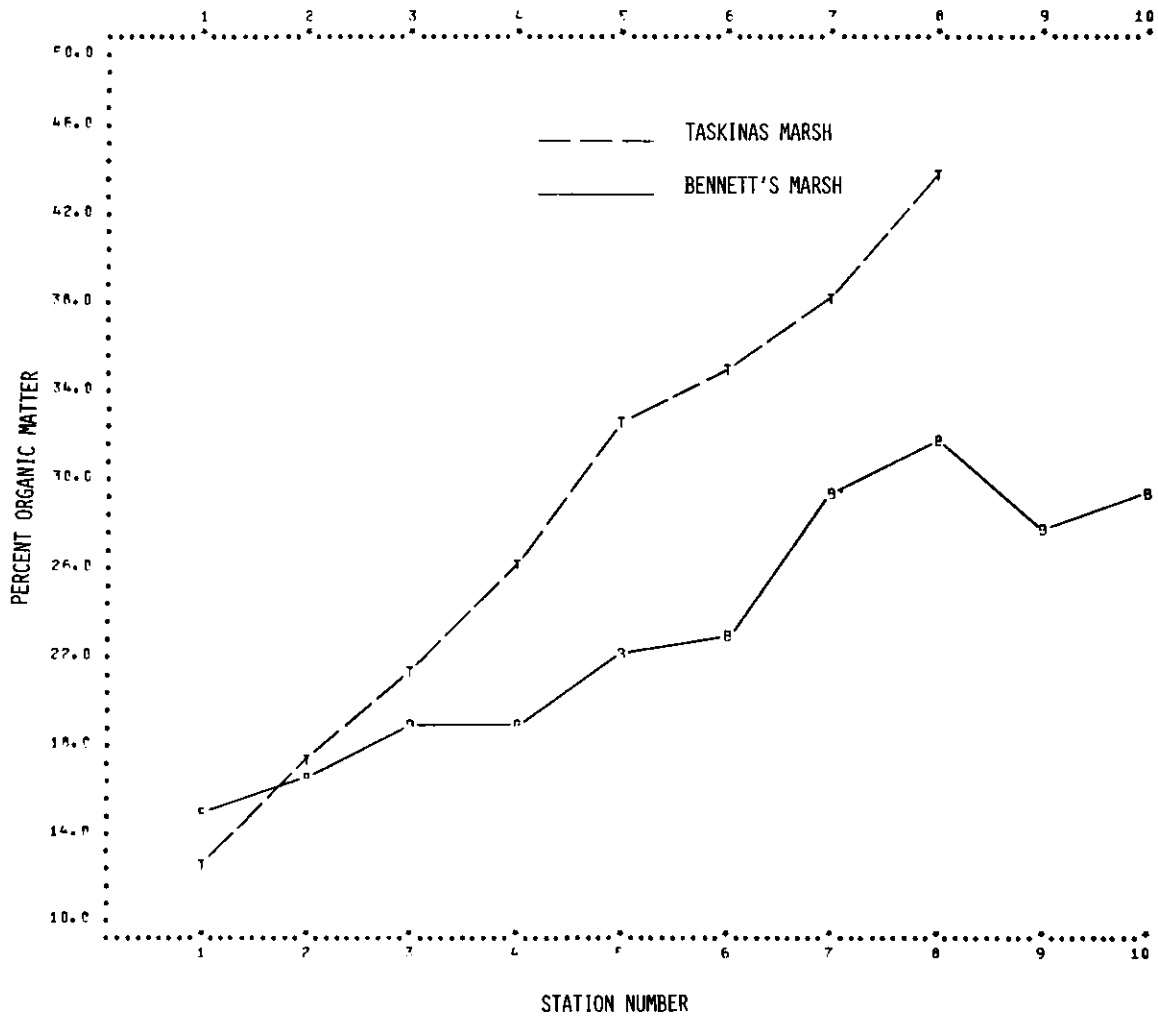


Figure 13. Percent organic matter of marsh sediments.

function of the amount of plant material produced in situ, together with the effects of consumption, decay, sedimentation, and tidal flushing. Assuming that consumption and decay rates were roughly comparable at Taskinas Marsh and Bennett's Marsh, the differences in organic content may be ascribed to variations in productivity, sedimentation, and tidal influences. Shoot biomass in the high marsh community considerably exceeded that of the low marsh (Figures 5a and 5b). The frequency of tidal incursions (Figure 11) and, concomitantly, the rate of sediment deposition (Broome et al., 1973) were reduced toward the rear marsh. Both these factors may help account for the landward rise in organic content. The fact that Taskinas high marsh produced more plant tissue than Bennett's high marsh and received less tidal flooding relative to its low marsh may explain the steeper front-to-rear rise in organic matter content at Taskinas.

#### Plant-Available Nutrients

55. Summary graphs presented and discussed in the following paragraphs represent averages of three transects, all four sampling times, and both depth ranges (0-10 cm and 10-20 cm); that is, each data point on the figures encompasses 24 individual values obtained by sediment analysis. The means and standard errors for the habitat variables are given in Table 1.

#### Ammonia-N

56. Summary values for estimated plant-available ammonia-N (Figure 14) indicated that, at both marshes, slightly higher values tended to characterize the high marsh sediments. However, the range of

Table 1  
Means ( $\bar{X}$ ) and Standard Errors (S.E.M.) of Habitat Parameters from the Study Sites

Sample Zone	Elevation (n=3)		Inundation (n=3)		Organic Matter (n=6)		Salinity (n=3)		NH <sub>3</sub> -N (n=24)		PO <sub>4</sub> -P (n=24)		Ca (n=24)		Mg (n=24)		Mn (n=24)		Fe (n=24)		
	$\bar{X}$ (cm)	S.E.M.	$\bar{X}$ (#/yr)	S.E.M.	$\bar{X}$ (%)	S.E.M.	$\bar{X}$ (%)	S.E.M.	$\bar{X}$ (ppm)	S.E.M.	$\bar{X}$ (ppm)	S.E.M.	$\bar{X}$ (ppm)	S.E.M.	$\bar{X}$ (ppm)	S.E.M.	$\bar{X}$ (ppm)	S.E.M.	$\bar{X}$ (ppm)	S.E.M.	
<u>Taskinas Marsh</u>																					
1	86.0	2.1	192.7	38.5	13.1	0.2	8.0	--	7.5	1.0	16.1	4.6	406.5	17.7	677.5	27.4	94.0	11.3	1104.8	80.0	
2	97.7	--	52.0	34.2	17.3	0.6	9.3	6.6	7.2	1.1	62.5	8.9	426.5	13.0	762.3	22.3	33.7	3.9	797.5	69.7	
3	104.3	2.2	7.7	5.7	21.6	1.3	12.0	--	6.4	0.9	82.5	8.0	470.3	17.9	887.8	33.3	18.8	2.1	634.6	67.8	
4	108.3	1.2	1.7	0.7	26.5	1.4	14.8	1.8	8.1	1.3	85.0	9.4	467.0	18.6	894.7	43.9	15.5	2.9	722.3	93.3	
5	110.3	0.3	0.0	--	32.7	2.1	15.0	1.0	6.9	1.1	95.3	7.4	449.6	19.5	829.6	49.7	13.9	2.6	665.2	99.2	
6	111.0	0.3	0.0	--	34.9	0.8	13.4	1.2	6.8	0.9	117.3	9.0	438.8	17.0	815.8	45.0	6.7	1.1	590.7	104.9	
7	110.7	1.2	0.0	--	38.4	1.8	12.1	1.1	8.5	1.5	104.7	5.6	430.4	16.0	775.0	34.2	5.7	1.2	319.9	53.6	
8	112.0	0.6	0.0	--	43.6	1.8	12.8	0.7	8.1	1.1	105.1	7.2	439.1	16.0	749.8	27.9	5.0	1.0	374.0	62.2	
<u>Bennett's Marsh</u>																					
1	89.3	0.9	147.3	14.2	15.1	0.4	10.4	--	6.0	0.7	105.7	11.7	422.0	28.7	731.3	29.1	12.7	1.0	600.8	46.1	
2	95.3	0.3	69.7	3.3	16.9	0.7	13.3	--	6.9	1.2	151.7	7.8	433.6	28.4	802.1	32.3	5.6	0.5	532.7	46.0	
3	96.3	0.7	58.8	7.3	18.9	0.6	12.1	0.7	6.6	0.8	155.0	4.7	428.3	10.7	850.0	23.5	4.4	0.4	477.0	40.5	
4	95.0	1.0	54.3	8.7	19.2	0.4	12.5	0.7	8.1	1.0	154.6	4.9	444.2	9.9	896.6	16.4	3.6	0.2	351.6	26.3	
5	98.0	0.6	41.3	5.2	22.5	1.1	12.3	0.6	7.7	0.9	140.6	3.9	419.1	11.4	829.1	25.3	3.2	0.3	339.0	28.8	
6	99.7	0.9	30.7	5.0	23.3	0.6	11.6	--	7.8	0.8	129.9	3.2	383.0	6.7	754.9	21.3	2.3	0.2	291.6	41.3	
7	103.0	0.6	17.0	1.7	29.7	2.1	11.9	0.9	8.5	0.8	133.4	4.5	360.6	14.2	729.8	43.9	3.9	0.6	259.8	41.9	
8	105.0	0.6	10.0	2.3	31.7	2.3	14.0	1.9	6.8	1.1	144.8	7.2	388.7	12.2	786.9	38.1	2.7	0.3	215.9	40.0	
9	106.7	0.3	4.0	1.0	28.0	2.0	16.2	1.4	8.7	1.2	136.7	13.0	499.6	10.9	991.8	34.4	3.3	0.3	963.2	83.6	
10	113.3	2.2	1.3	0.3	29.5	2.5	15.7	1.7	8.5	1.7	113.5	15.4	500.6	14.1	981.6	42.2	5.5	0.9	1045.2	96.4	

Note: Nutrient data include 4 sampling periods (4-5 April, 29-30 May, 21 July, and 13 September) and 2 depth ranges in sediment (0-10 cm and 10-20 cm). Sample zones are numbered consecutively along transects from low marsh to high marsh; transect length = 28 m (Taskinas Marsh) and 36 m (Bennett's Marsh).

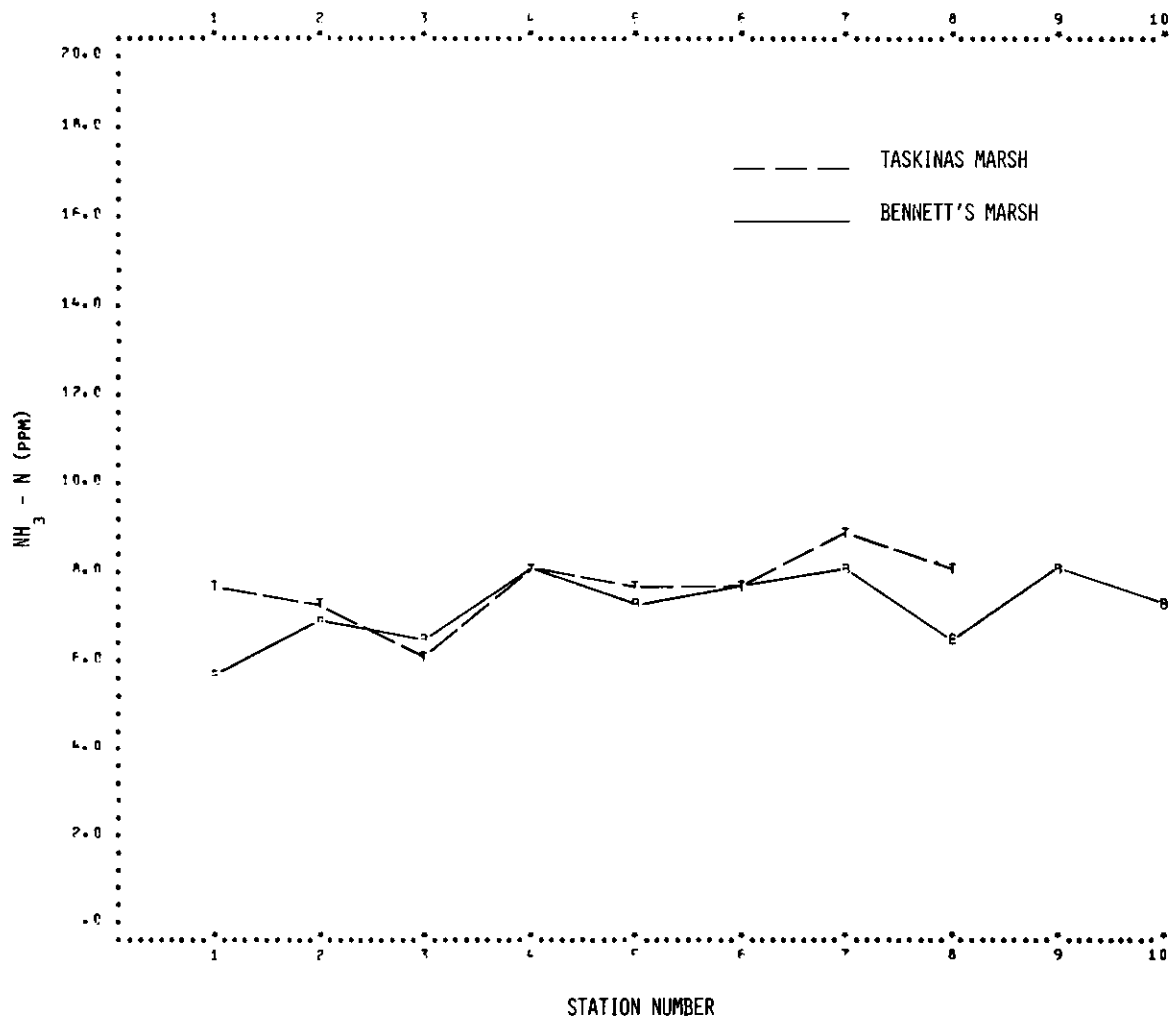


Figure 14. Concentration (ppm) of plant-available ammonia-N in marsh sediments at sample stations.

variation was small (5.5-9.0 ppm) and clear patterns of spatial change were not evident.

57. Jeffrey (in Piggott, 1969) also found that concentrations of ammonia exhibited little pattern across a marsh. However, since inorganic nitrogen can change quite rapidly in form and amount in soils (by microbial uptake and release, plant absorption, volatilization, immobilization in humus, absorption within crystal lattices, and mineralization of organic matter) concentrations of ammonia-N at a few instants of time may not accurately represent the soil's capacity to supply inorganic nitrogen to plants over an entire growing season (Tusneem and Patrick, 1971).

#### Phosphate

58. Both marshes displayed a relatively rapid increase in available phosphate concentration from zone 1 to zone 2 (Figure 15). Piggott (1969) also reported a landward increase in phosphorus content of marsh soils. At Taskinas, the values continued to increase rearward but at a slower rate, leveling off in the high marsh. The Bennett's Creek transect showed two small peaks, one each in the high marsh and low marsh, with a slight trough toward the rear of the ecotone (zone 6). Concentrations at Taskinas were generally somewhat lower than at Bennett's Creek.

#### Iron

59. Concentrations of plant-available iron declined gradually from the low marsh toward the rear zones at both study sites (Figure 16). At Taskinas, the concentrations were somewhat higher and the rearward decline was less linear than at Bennett's. However, zones 9 and 10 mark a major departure: a sudden steep increase in concentration,

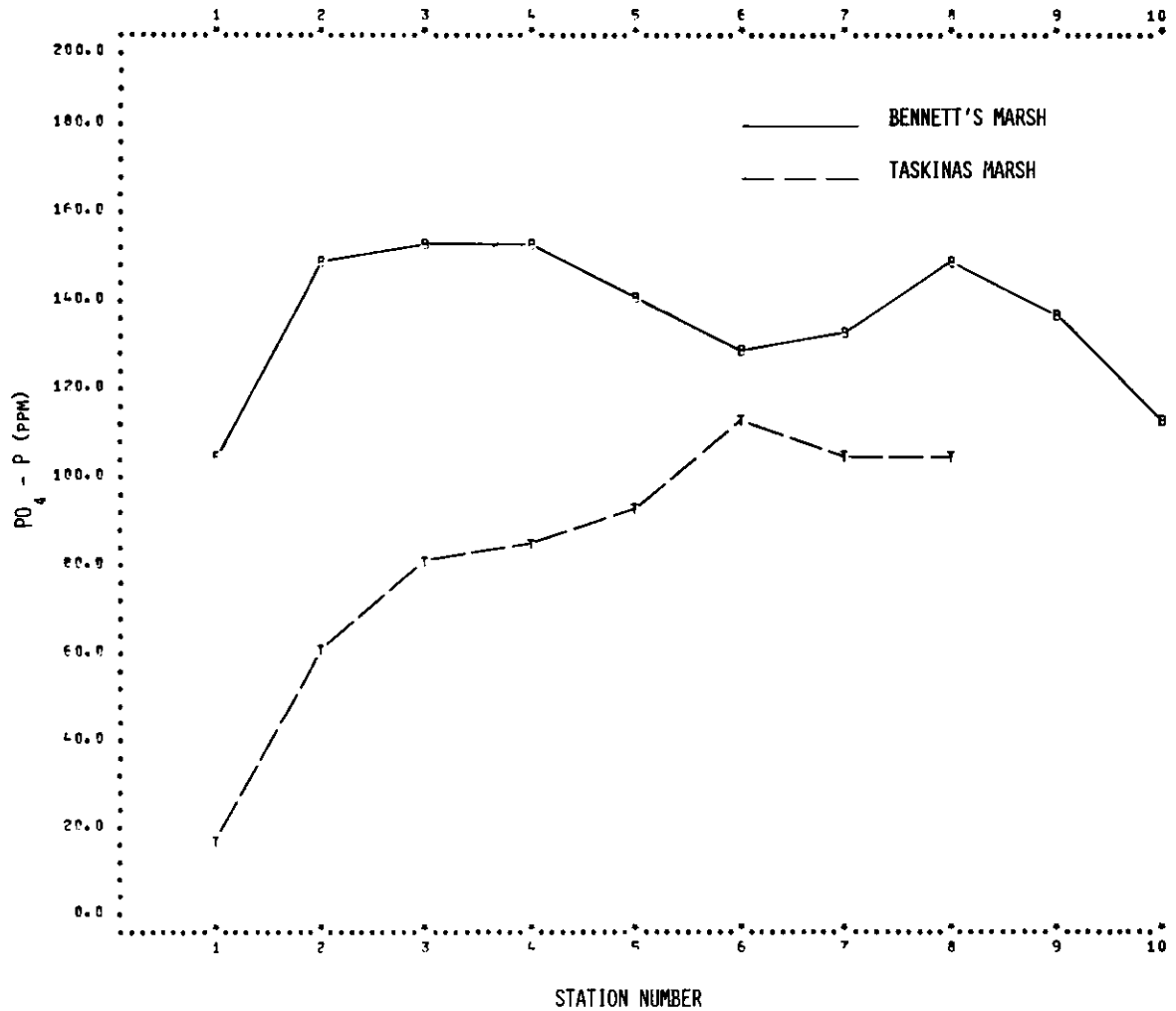


Figure 15. Concentrations (ppm) of plant-available phosphate-P in marsh sediments at sample stations.

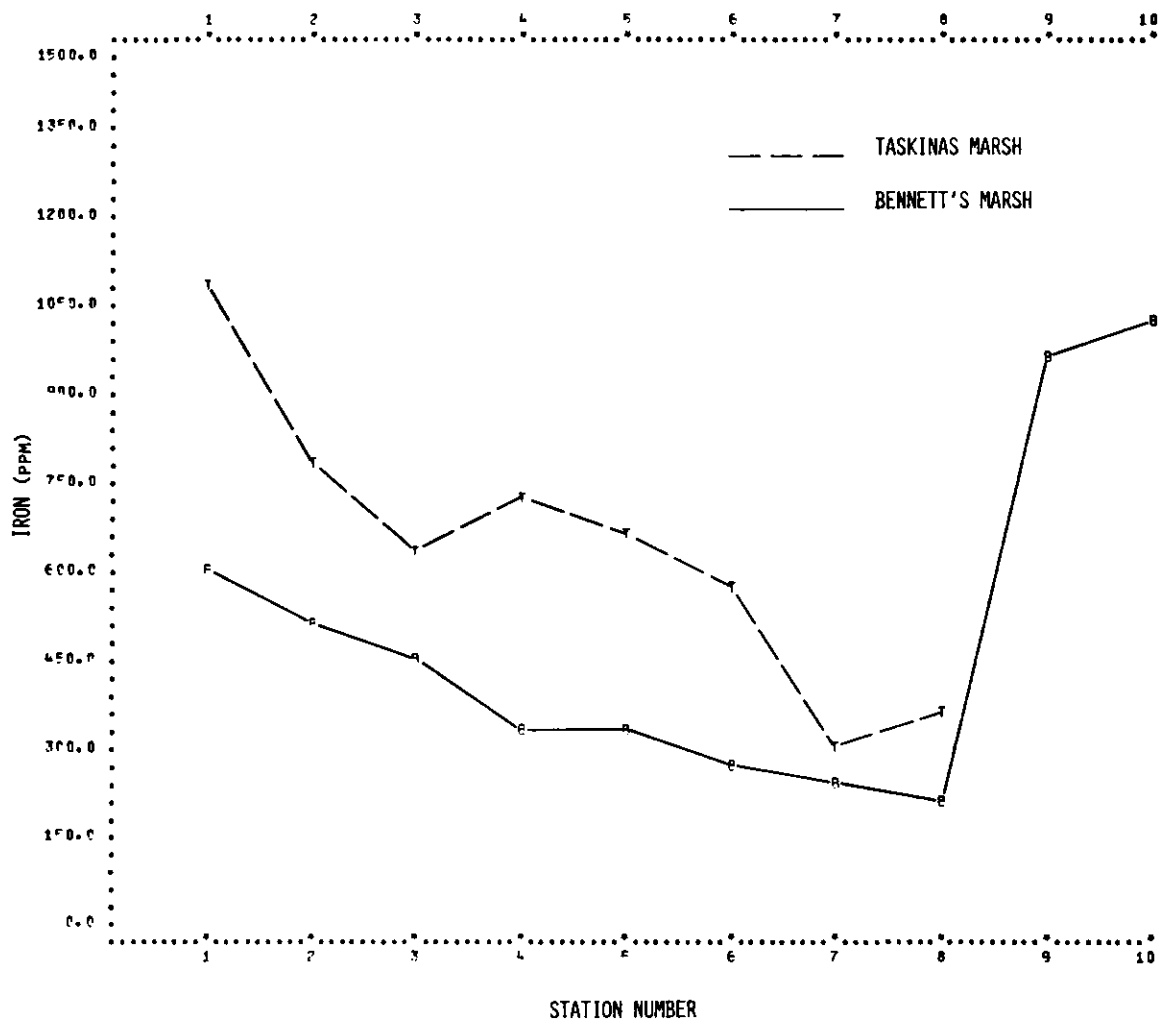


Figure 16. Concentration (ppm) of plant-available iron in marsh sediments at sample stations.



attaining the highest values recorded for Bennett's Marsh.

60. The results varied with regard to Adams' (1963) contention that tall S. alterniflora tended to be associated with higher iron concentrations than the S. patens - D. spicata association. The data from Taskinas Marsh agreed with Adams' findings, but Bennett's Marsh data indicated exactly the opposite pattern: higher iron concentrations in the high marsh. Direct comparisons with Adams may be tenuous, however; he did not specify the extraction procedures he used, and the iron concentrations recorded from his North Carolina marshes were more than an order of magnitude lower than those from the present study.

#### Manganese

61. Both sites displayed a rapid decrease in available manganese concentration from the low marsh toward the high marsh, with nearly all the reduction confined to the first few zones (Figure 17). At Taskinas Marsh, however, the highest value (zone 1) was more than six times greater than the maximum at Bennett's Marsh, and the initial decline was much more precipitous. Concentrations from the ecotone landward were low and variability was minimal; averages at Bennett's Marsh fluctuated within only 0 to 4 ppm between zone 4 and zone 9.

#### Calcium

62. Calcium concentrations at the two marshes varied in a very similar manner (Figure 18). Both exhibited a peak value in the low marsh adjacent to the ecotone, a decline rearward through the ecotone, and some upward recovery in the high marsh (the latter trend was more evident at Bennett's Creek Marsh).

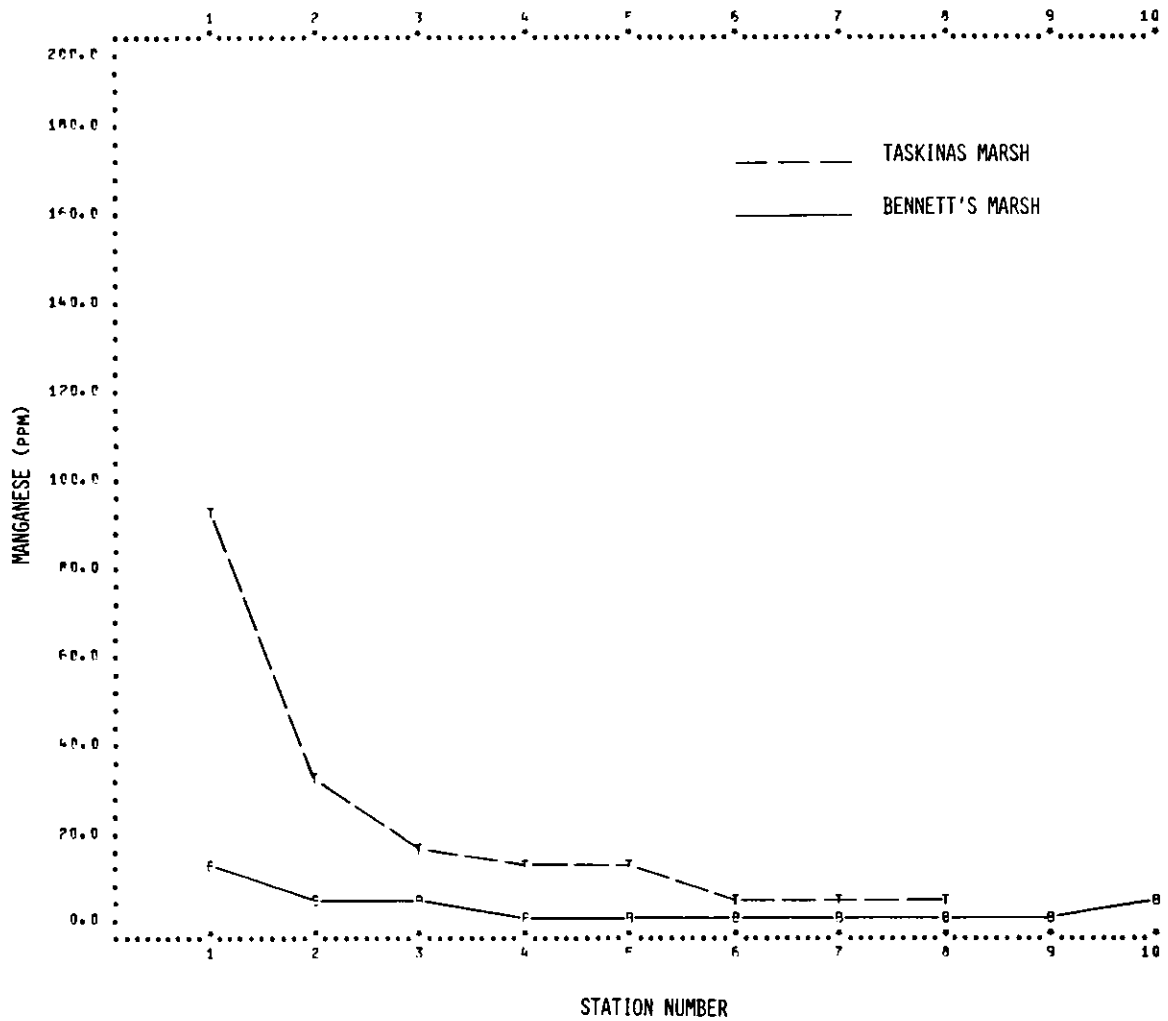


Figure 17. Concentration (ppm) of plant-available manganese in marsh sediments at sample stations.

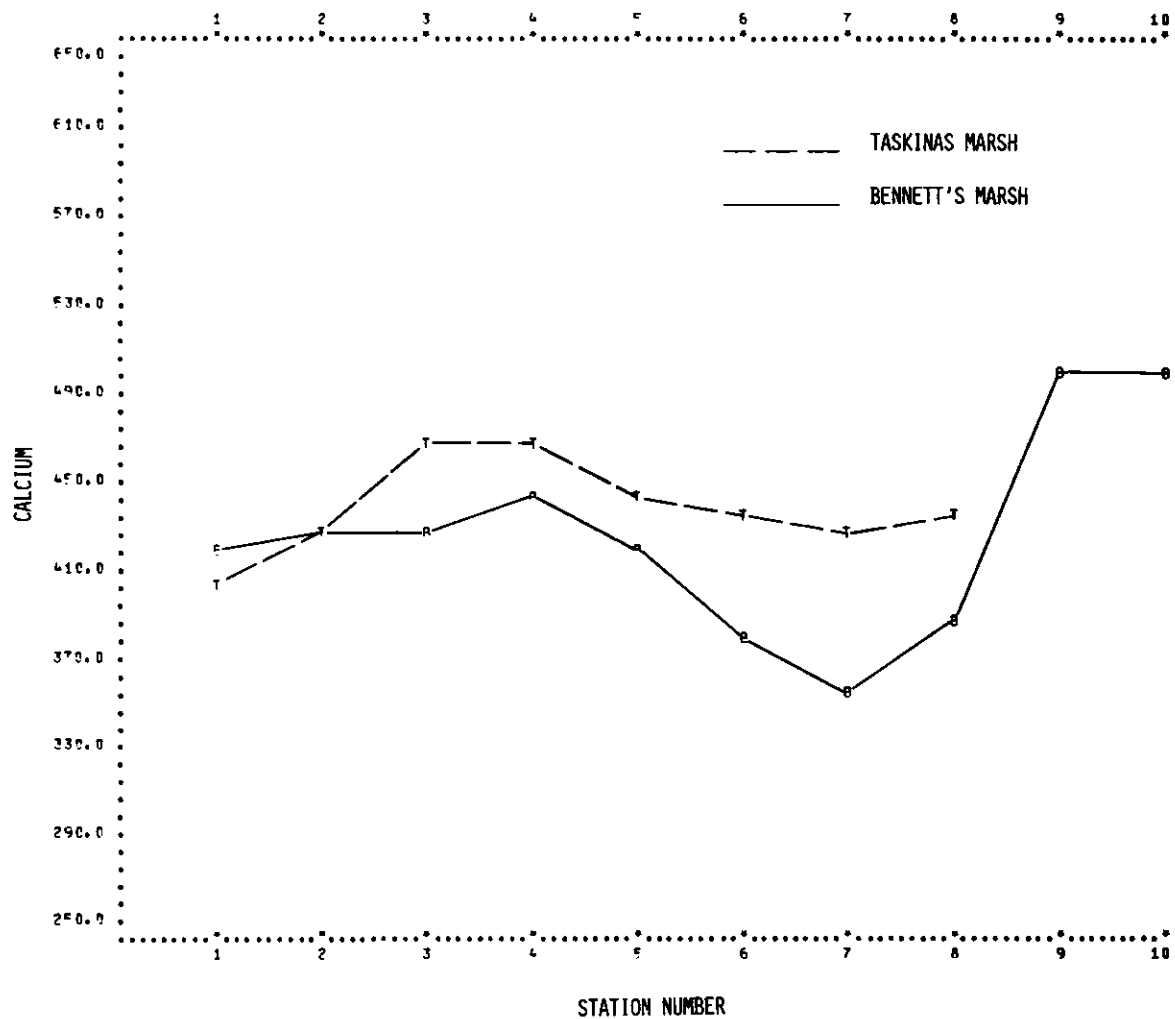


Figure 18. Concentration (ppm) of plant-available calcium in marsh sediments at sample stations.

### Magnesium

63. The graphs of available magnesium (Figure 19) showed a striking resemblance to the pattern for calcium (Figure 18). As with calcium, both marshes varied in nearly identical fashion: high values occurred at the seaward edge of the ecotone, and Bennett's Marsh attained its highest concentrations in zones 9 and 10.

### Correlation Analyses

64. Statistical correlation is a useful first step toward identifying the habitat factors most closely related to plant growth and distribution. Bivariate correlation is a statistical technique for measuring the intensity of relationship between co-occurring variables. The correlation statistic employed here is the Pearson product-moment correlation coefficient, "r".

65. The test used assumes that the data are randomly sampled, normally distributed, and there is a linear relation between the variables. The data set was sufficient to generally satisfy the latter two correlations. The data were sampled by a form of stratified random method, whereby samples were collected randomly from within specified sample areas. Values of "r" and their associated statistical significance were calculated with the "Scattergram" subprogram of Statistical Package for the Social Sciences (SPSS) (Nie et al., 1975).

66. Tables 2 and 3 display correlation coefficients relating plant growth variables to habitat variables at Taskinas Marsh and Bennett's Marsh, respectively. The three growth variables measured--

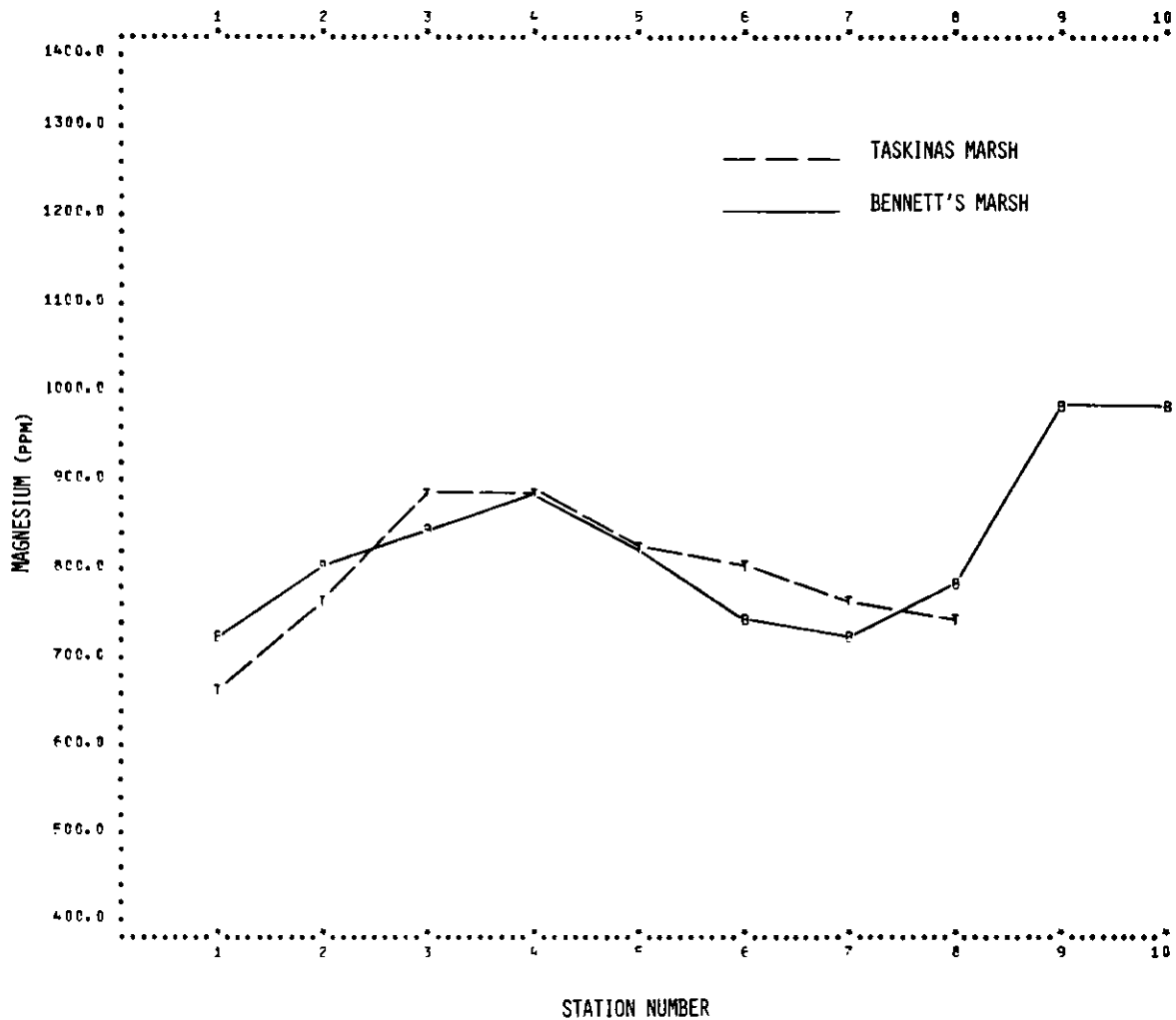


Figure 19. Concentration (ppm) of plant-available magnesium in marsh sediments at sample stations.

Table 2  
Correlation Coefficients Between Plant Variables and Habitat  
Variables at Taskinas Marsh

Species	Plant Variable	Habitat Variable									
		Elevation cm*	No. of inundations per year	Organic Matter %	Salinity ppm	NH <sub>3</sub> ppm	PO <sub>4</sub> ppm	Ca ppm	Mg ppm	Mn ppm	Fe ppm
<u>S. alterniflora</u>	Standing Crop	-0.76**	0.73**	-0.82**	-0.50	-0.46	-0.73**	-0.22	-0.38	0.77**	0.61
(df = 22)	Stem Height	-0.85**	0.84**	-0.67*	-0.79**	0.05	-0.52	-0.75**	-0.88**	0.72**	0.31
	Stem Density	0.35	-0.28	0.07	0.68	-0.18	-0.07	0.41	0.53	-0.09	0.12
<u>S. patens</u>	Standing Crop	0.53*	-0.36	0.32	0.27	-0.05	0.04	-0.14	0.02	-0.19	0.21
(df = 34)	Stem Height	0.26	0.04	0.18	-0.46	0.45	-0.40	-0.01	-0.21	-0.31	-0.21
	Stem Density	0.39	-0.07	0.05	0.30	-0.49	-0.18	-0.22	-0.02	-0.08	-0.12
<u>D. spicata</u>	Standing Crop	0.45	0.22	0.57*	-0.16	0.34	0.47	-0.18	-0.50*	-0.47*	-0.33
(df = 34)	Stem Height	0.12	0.43	0.14	-0.47	0.11	0.33	0.14	-0.31	-0.35	-0.11
	Stem Density	0.41	-0.13	-0.49	-0.02	0.19	0.41	-0.26	-0.44	-0.37	-0.33

NOTE: Standing crop represents maximum live standing crop; stem height and density are average values of July and September data.

\* Significant at 5% level

\*\* Significant at 1% level

Table 3  
Correlation Coefficients Between Plant Variables and Habitat  
Variables at Bennett's Marsh

<u>Species</u>	<u>Plant Variable</u>	<u>Habitat Variable</u>									
		<u>Elevation cm</u>	<u>No. of inundations per year</u>	<u>Organic Matter %</u>	<u>Salinity ppm</u>	<u>NH<sub>3</sub> ppm</u>	<u>PO<sub>4</sub> ppm</u>	<u>Ca ppm</u>	<u>Mg ppm</u>	<u>Mn ppm</u>	<u>Fe ppm</u>
<u>S. alterniflora</u>	Standing Crop	-0.73**	0.58**	0.77**	-0.55**	-0.06	-0.10	0.54*	0.19	0.44*	0.54*
(df = 40)	Stem Height	-0.80**	0.69**	0.71**	-0.38	0.20	-0.30	0.34	-0.03	0.66**	0.49
	Stem Density	-0.04	0.05	-0.15	-0.31	-0.31	-0.25	0.03	-0.14	0.01	-0.09
<u>S. patens</u>	Standing Crop	-0.44	0.72**	0.14	-0.56	0.25	0.22	-0.83**	-0.79**	-0.12	-0.71**
(df = 34)	Stem Height	-0.40	0.53	0.14	-0.17	0.30	0.37	-0.55	-0.57	-0.21	-0.65*
	Stem Density	0.39	-0.32	0.63*	0.27	-0.53	0.34	0.17	-0.16	-0.38	-0.05
<u>D. spicata</u>	Standing Crop	0.68**	-0.65**	0.27	0.59**	-0.07	-0.12	0.71**	0.62**	0.15	0.76**
(df = 34)	Stem Height	-0.17	-0.05	0.34	-0.11	0.15	0.11	-0.43	-0.25	-0.25	-0.26
	Stem Density	0.81**	-0.75**	0.31	0.79**	-0.14	-0.04	0.75**	0.70**	0.21	0.79**

NOTE: Standing crop represents maximum live standing crop; stem height and density are average values of July and September data.

\* Significant at 5% level

\*\* Significant at 1% level

standing crop, stem height, and stem density--are listed for each of the three predominant plant species: S. alterniflora, S. patens, and D. spicata.

67. Several of the plant-habitat correlations deserved special emphasis. It was evident from comparing spatial patterns of standing crop (Figure 5) and stem height (Figure 8 ) with elevation and inundation (Figures 10 and 11) that growth of S. alterniflora exhibited a highly significant positive correlation with tide factors. This relationship had been observed repeatedly (Johnson and York, 1915; Adams, 1963; Kurz and Wagner, 1957); but since the sampling sites in the present study did not extend to the seaward extreme of S. alterniflora distribution, the contention that tidal inundation restricted the species along the lower margin of its range within the marsh (Johnson and York, 1915; Teal and Kanwisher, 1961) could not be tested. For S. patens and D. spicata, the measured responses to tides differed conspicuously between the two marshes. At Taskinas, where tidal water very seldom reached the high marsh (Figure 10) growth of neither species was closely related to inundation or elevation; Bennett's high marsh, which received some regular flooding during spring tides, showed close correlations of tide with S. patens (positive) and D. spicata (negative).

68. As indicated by previous investigators (Gosselink, 1970; Palmisano, 1970; Phleger, 1971), growth of certain species tends to be inhibited by increasing soil salinity. Negative correlations were significant for S. alterniflora at both marshes and less pronounced for S. patens. D. spicata, the most salt-tolerant of the three species



(Adams, 1963), showed positive correlations with salinity at Bennett's Marsh.

69. The absence of significant correlations between ammonia-N concentration and growth of any species appears to support Tusneem and Patrick's (1971) contention that sampling only at isolated instances (as was done in this study) may misrepresent the plant response to soil nitrogen over a growing season. The fact that nitrogen availability clearly limits growth of marsh grasses (Valiela and Teal, 1973; D.E. Marshall, 1970; Broome et al., 1973), coupled with the low concentrations found in the soil (Figure 14), suggested that rapid depletion by plant uptake may engender considerable fluctuation of ammonia-N levels. Analysis of available nitrogen in both soil and plant tissue at frequent intervals over the growing season might provide a better measure of plant response to soil nitrogen. Working with aquatic species, Gerloff and Krombholz (1966) noted a critical level of nitrogen concentration in plant tissues of 1.3 percent below which growth was inhibited; similar data for salt marsh species would help elucidate the relationship between plant growth and nitrogen availability in soils.

70. Phosphate concentrations were not closely correlated with plant growth, either. Since fine-textured, highly reduced sediments, such as typify Taskinas Marsh and Bennett's Marsh, usually possess abundant available phosphorus (Broome et al., 1973), the absence of a close relationship with plant growth was not surprising.

71. S. alterniflora standing crop correlated significantly with iron availability at both marshes, supporting the theory that this

species thrives where iron is plentiful (Adams, 1963; Mooring et al., 1971; Nixon and Oviatt, 1973). S. patens and D. spicata showed opposite patterns of correlation at Bennett's Marsh: S. patens was negatively correlated to iron, while D. spicata had a highly significant positive correlation.

72. A contrast is discernible between Table 2 and Table 3 in the arrangement of significant correlations. Significant plant-habitat correlations were almost entirely restricted to S. alterniflora at Taskinas Marsh, while all three species exhibited significant correlations at Bennett's Marsh. This difference suggests that more of the habitat factors measured were closely related to growth of high marsh species (S. patens and D. spicata) at Bennett's Marsh than at Taskinas Marsh.

73. Figure 10 and Figure 11 indicate that while Taskinas Marsh received no regular tidal influence, Bennett's high marsh was inundated to some extent. This pattern of correlations appeared to support the hypothesis (Hinde, 1954; Gray and Bunce, 1972) that tidal changes in water level may exert a controlling influence upon plant growth by modification of other habitat conditions.

74. Tables 4 and 5 are matrices of correlation coefficients that indicate the intensity of relationships among habitat factors. Values of "r" and their significance were calculated for the distinct communities in each marsh. Low marsh correlations included only the range of S. alterniflora, while high marsh correlations were restricted to the S. patens - D. spicata community.

Table 4  
Correlation Coefficients between Habitat Variables at Taskinas Marsh

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) Elevation	--	--	0.23	0.64**	-0.12	0.08	-0.21	-0.25	-0.29	-0.03
(2) # of Inundations	--	--	-0.23	-0.30	-0.23	0.12	0.11	0.18	-0.04	-0.18
(3) Salinity	0.87*	-0.70	--	-0.43	-0.64*	-0.71**	0.33	0.63**	0.70**	0.61*
(4) Organic Matter	0.77**	-0.72**	0.67	--	0.34	0.57*	-0.53*	-0.69**	-0.81**	0.59*
(5) Ammonia-N	0.67*	-0.03	0.98*	0.23	--	0.55	-0.47	-0.38	-0.32	-0.53
(6) Phosphate-P	0.58	-0.62*	0.20	0.84**	-0.03	--	-0.53*	-0.80**	-0.88**	-0.80**
(7) Calcium	0.67*	-0.65*	0.69	0.52	-0.21	0.27	--	0.73**	0.58*	0.82**
(8) Magnesium	0.71	-0.65*	0.84*	0.57*	-0.02	0.32	0.91*	--	0.79**	0.84**
(9) Manganese	-0.79**	0.87**	-0.52	-0.78**	0.18	-0.82**	-0.63**	-0.59*	--	0.60*
(10) Iron	0.37	0.41	-0.04	-0.68*	-0.10	0.92**	0.00	-0.11	0.53**	--

\* = significant at 5% level; \*\* - significant at 1% level.

Note: Values above the main diagonal are for the high marsh; values below the main diagonal are for the low marsh.

Table 5  
Correlation Coefficients between Habitat Variables at Bennett's Marsh

	(1)	(2)	(3)	(4)	(5)	(6)	(7)	(8)	(9)	(10)
(1) Elevation	--	--	0.43	0.42	0.65**	-0.10	0.59**	0.58*	0.50*	0.65**
(2) # of Inundations	--	--	-0.52**	-0.61**	0.45	0.03	-0.49**	-0.58*	-0.27	-0.65**
(3) Salinity	-0.05	-0.28	--	0.11	0.38	-0.25	0.65*	0.49	0.47	0.69**
(4) Organic Matter	0.83**	-0.73**	0.18	--	0.29	0.18	0.04	0.08	-0.15	0.02
(5) Ammonia-N	-0.79**	-0.23	0.78**	0.38	--	-0.01	0.08	-0.05	0.46	0.16
(6) Phosphate-P	0.26	-0.45**	0.57*	-0.02	0.11	--	-0.12	-0.05	-0.71**	0.65*
(7) Calcium	-0.50	0.40	-0.16	-0.60**	0.24	0.14	--	0.96**	0.32	0.84**
(8) Magnesium	0.04	-0.23	0.14	-0.18	-0.11	0.72**	0.61**	--	0.31	0.81**
(9) Manganese	-0.78**	0.92**	-0.35	-0.58**	-0.23	-0.66**	0.16	-9.41	--	0.60*
(10) Iron	-0.79**	0.79**	0.00	-0.78**	-0.46	-0.12	0.39	-0.05	0.78**	--

\* = significant at 5% level; \*\* - significant at 1% level.

Note: Values above the main diagonal are for the high marsh; values below the main diagonal are for the low marsh.

75. As a source of inorganic nutrients, a provider of abundant sites for cation sorption, and a fuel for microbially mediated reactions, organic matter is a vital constituent of the soil environment (Buckman and Brady, 1969). Because reduction of manganese and iron to plant-available forms is facilitated by anaerobic bacteria (Turner and Patrick, 1968), strong positive correlations between organic content and these cations might be expected. In fact, most of the correlations were highly negative (Tables 4 and 5). Nixon and Oviatt (1973) noted a close positive correspondence between iron concentration and percent organic matter, but the organic content of their Connecticut marshes averaged less than half that found in the present research. Conceivably, available cations in the highly organic soils of Taskinas Marsh and Bennett's Marsh were rapidly incorporated into microbial biomass, and thus became unavailable to plants. Organic matter was not the sole influence on iron and manganese availability; however, long periods of waterlogging tended to liberate large amounts of available  $Mn^{2+}$  and  $Fe^{2+}$  (Leeper, 1947); indeed, a strong positive correlation existed between tidal inundation and levels of these cations, particularly in the low marsh zone (Tables 4 and 5).

76. Many species of cations are influenced by the behavior of iron in marsh soils. When surface sediments become aerated during tidal emergence, a number of trace elements, including manganese, co-precipitate with iron in the presence of organic matter (Bloomfield, 1963). Like manganese, iron is readily reduced by microbes. The consistently high positive correlations between iron and manganese

(Tables 4 and 5) further indicate that the behavior of iron and manganese in marsh soils was closely allied. Iron is also directly involved in the absorption of phosphorus by marsh soils (Jitts, 1959). Hydrated iron oxides provide binding sites for phosphorus ions; ferrous phosphate is believed to be an important mobile compound in reduced soils (Patrick and Khalid, 1974). Iron and phosphate concentrations showed close positive correlation at Taskinas low marsh and Bennett's high marsh, but elsewhere the relationship was either weak or strongly negative. Calcium phosphates are also said to be an important phosphorus source in marsh soils (Broome et al., 1973), but calcium and phosphate correlations were inconsistent.

77. Calcium and magnesium concentrations were highly correlated at both marshes, reflecting the very close resemblance of their spatial profiles (Figures 18 and 19). Laboratory studies indicated that both cations increase in concentration during prolonged submergence, and that their availability is similarly influenced by the decay of organic matter (Robinson, 1930).

78. The foregoing discussion of edaphic interactions raises more questions than it answers. However, it demonstrates that the interactions among sediment variables possess a high degree of complexity and variability--a variability that contributes heavily to the heterogeneity of marsh soils and of their associated vegetation (Gray and Bunce, 1972).

79. Further examination of the habitat intercorrelations (Tables 4 and 5) reveals that the tidal factors (elevation, inundations per year, and hours of inundation) displayed numerous significant

correlations throughout Bennett's Marsh and at Taskinas low marsh, but lacked significant correlations at Taskinas high marsh--the same pattern that typified the plant-habitat correlations (Tables 2 and 3). Of all the habitat factors considered, only the tide variables possessed similar patterns of correlation with both plant factors and other habitat factors.

80. In regularly inundated areas, both tide vs. habitat and plant growth vs. habitat correlations were strong; above the reach of the tides plant growth is no longer closely related to the habitat conditions measured. This contrast lends circumstantial support to the theory that tides act to influence plant growth by controlling other aspects of the marsh habitat. However, it does not diminish the likelihood that inundation also influences plant growth directly (Hinde, 1954) by imposing restrictions upon root respiration, nutrient uptake, seed germination, or other biotic processes. It seems likely that direct and indirect tidal influences are both important controls on plant growth.

#### Competition Analyses

81. The present data indicate that plant growth is not closely related to edaphic conditions in the absence of tidal inundation. Several investigators (Johnson and York, 1915; Chapman, 1938; Reed, 1947) have suggested that competition may affect zonation of marsh plants above the tide line. Johnson and York (1915) theorized that the landward limit of occurrence of S. alterniflora is determined primarily by competition with species, such as S. patens and D. spicata, whose inability to tolerate prolonged submergence precludes their seaward expansion. Reed

(1947) amplified the competition hypothesis by suggesting that the accretion of sediments on top of S. alterniflora at the ecotone might confer an advantage upon high marsh species in competing for growing space. Additional mechanisms of competition may be physical, such as inhibition of photosynthesis by shading of leaf surfaces (Ranwell, 1964; Buttery, 1965), or chemical, such as allelopathic interactions. Examination of Figures 5 and 9 reveals that S. patens usually enjoys an advantage in the competition for sunlight.

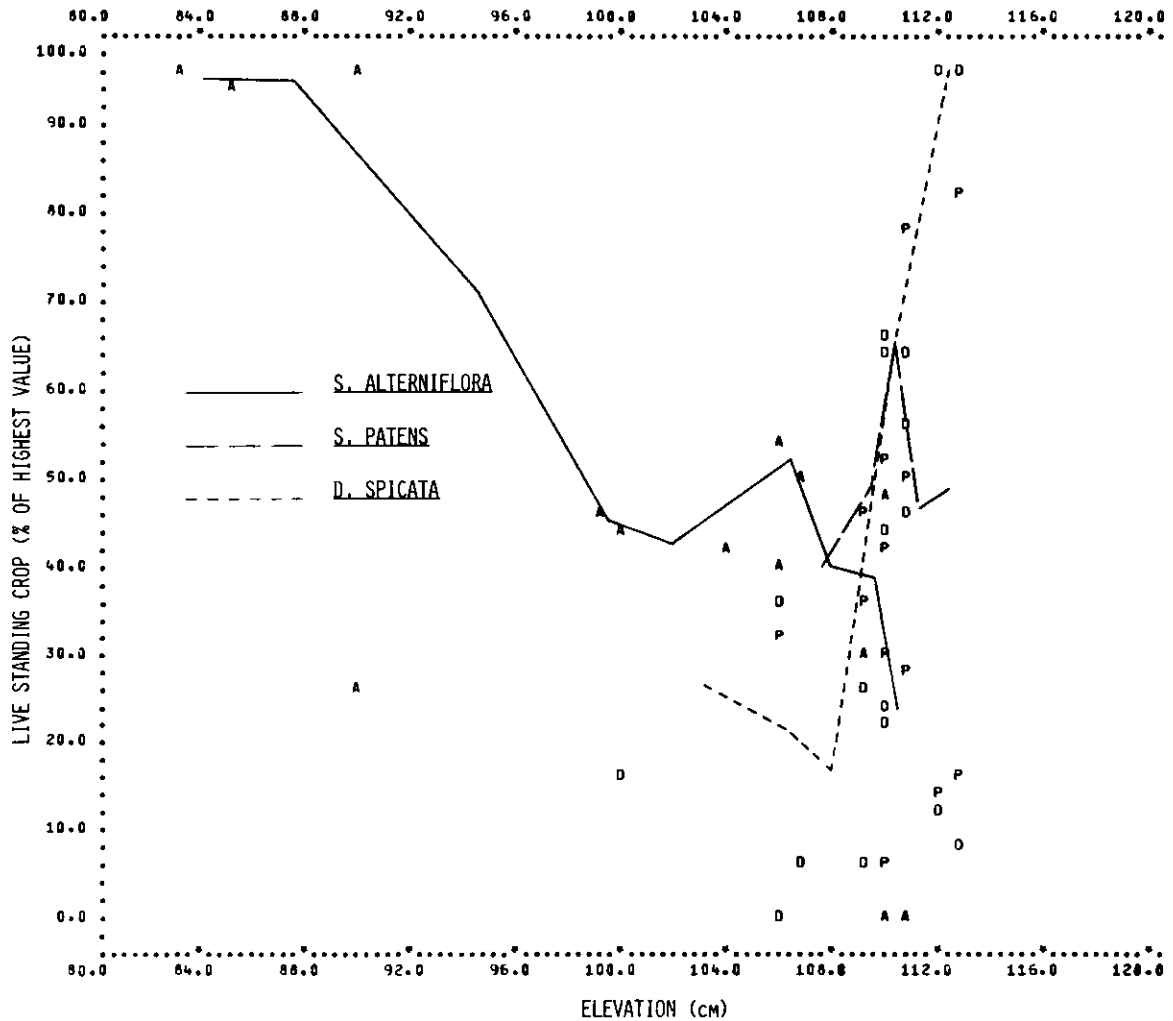
82. Competitive success or failure is closely tied to habitat phenomena, yet even less is known about plant interactions than about the nature of the marsh habitat. In fact, a thorough quantitative study of plant competition in marshes has never been accomplished.

#### Gradient Analysis

83. Figures 20 and 21 are examples of community gradient graphs of the study sites. On each figure, values of a single habitat factor were matched with corresponding values of maximum live standing crop data for each species; the standing crop data were expressed as percentages of the largest value. Lines were drawn to indicate patterns of change in standing crop (y-axis) over the range of the particular habitat factor (x-axis). Each line represents a two-point running mean of the data points.

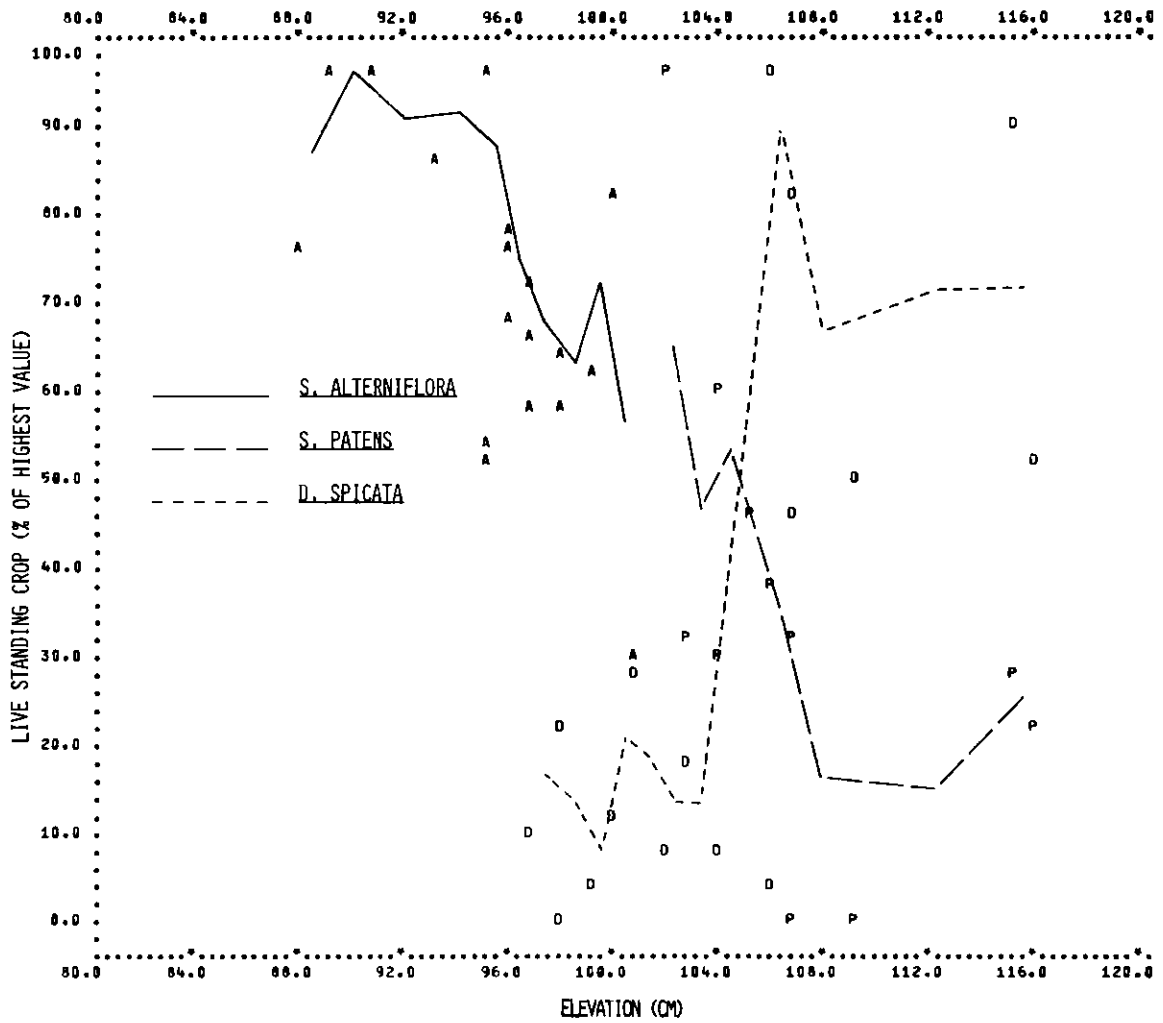
84. The extent to which a given habitat factor influences the segregation of the two communities can be estimated by the degree of isolation of the growth maximum of S. alterniflora (low marsh) from the growth maxima of S. patens and D. spicata along the habitat axis.



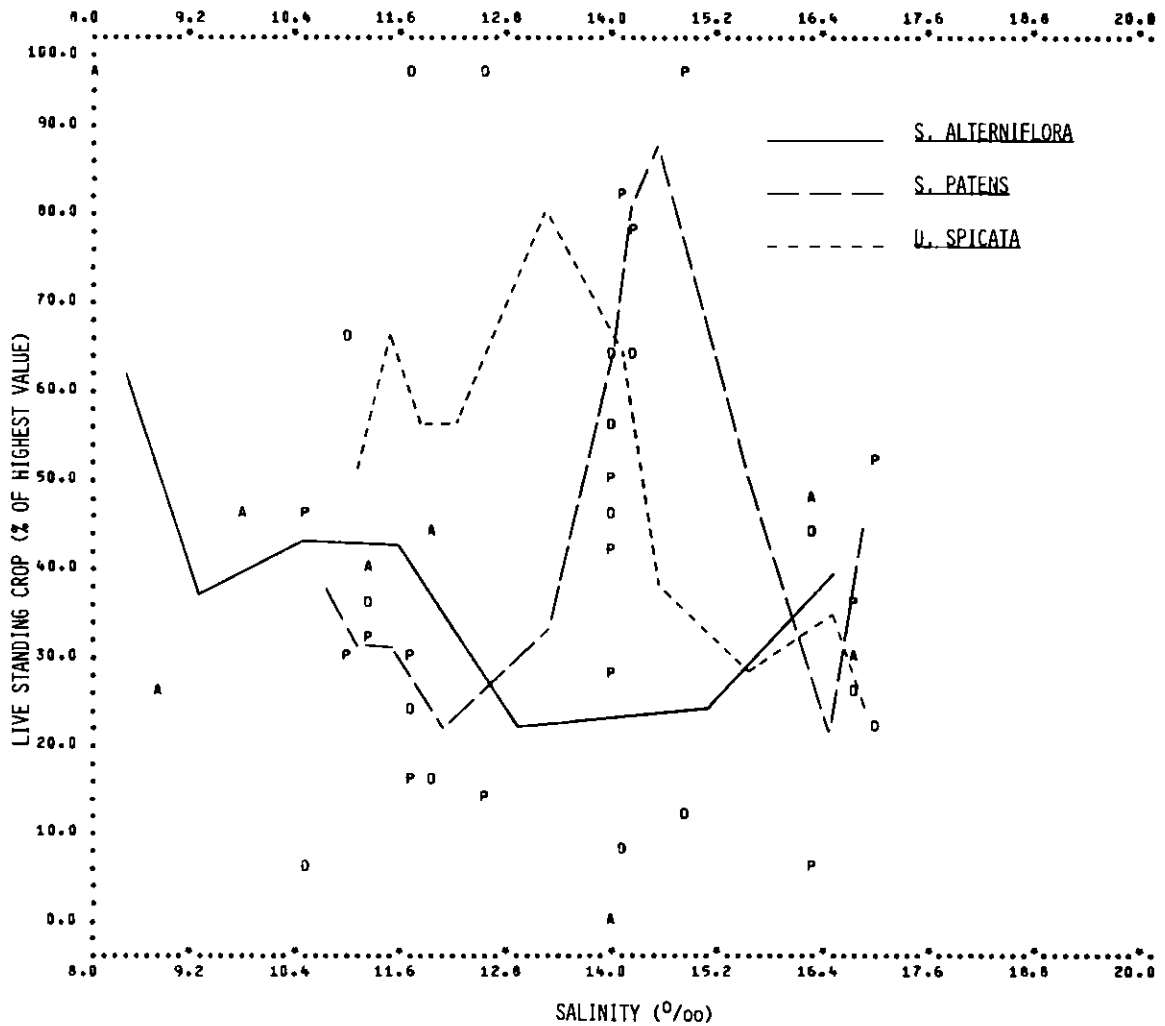


a. Taskinas Marsh

Figure 20. Community gradient plots of live standing crop vs. elevation at (a) Taskinas Marsh and (b) Bennett's Marsh (sheet 1 of 2).

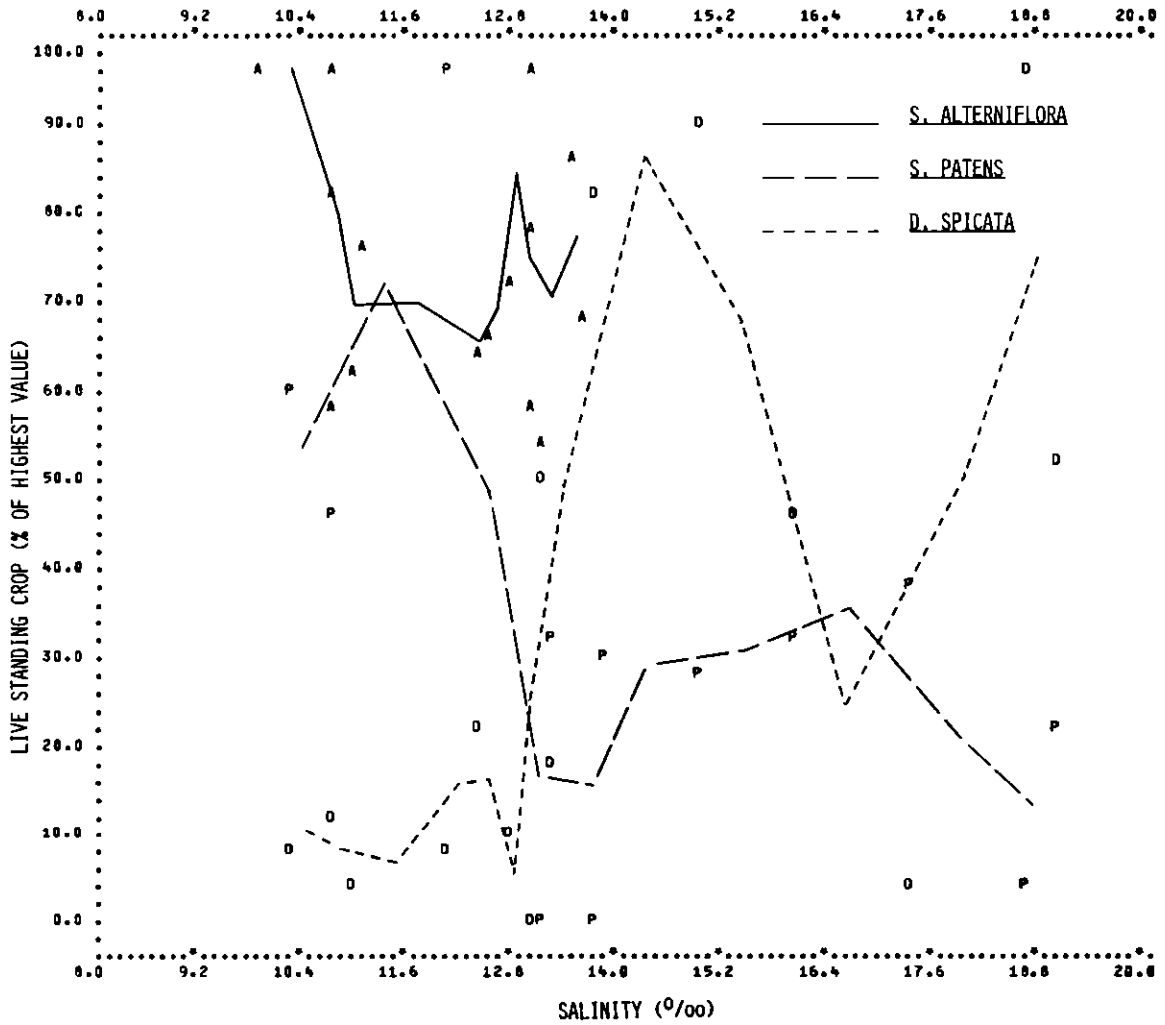


b. Bennett's Marsh  
 Figure 20 (sheet 2 of 2).



a. Taskinas Marsh

Figure 21. Community gradient plots of live standing crop vs. salinity at (a) Taskinas Marsh and (b) Bennett's Marsh (sheet 1 of 2).



b. Bennett's Marsh

Figure 21 (sheet 2 of 2).

Because the scales of the habitat factors have not been normalized, this evaluation is somewhat arbitrary; nevertheless, the patterns represented can be compared qualitatively. For example, Figure 20 shows clearcut separation of the S. alterniflora response peak from the peaks of S. patens and D. spicata. In contrast, Figure 21 displays multiple response peaks for each species, with poorly defined separation of the S. alterniflora peak from the peaks of the high marsh species. Comparing these results yields the conclusion that, in both marshes, elevation is a relatively more active agent than ammonia concentration (not shown) in separating high marsh from low marsh communities. While only Figures 20 (elevation) and 21 (salinity) are presented here for purposes of illustration, community gradient graphs were prepared for each habitat variable (tidal factors were represented by the elevation variable only).

85. The following variables manifested the clearest separation of S. alterniflora peaks from S. patens and D. spicata peaks:

TASKINAS MARSH

elevation  
 organic matter  
 phosphate  
 manganese

BENNETT'S MARSH

elevation  
 organic matter  
 calcium  
 magnesium  
 manganese  
 iron

The community gradient technique thus singled out the above factors as the most influential in dividing the vegetational zones.

86. A second phase of gradient analysis, the complex gradient approach (Whittaker, 1967), arrayed pairs of these selected habitat factors on opposing axes and plots corresponding standing crop data in habitat spaces. Standing crop data were plotted on a two-level rating scale:

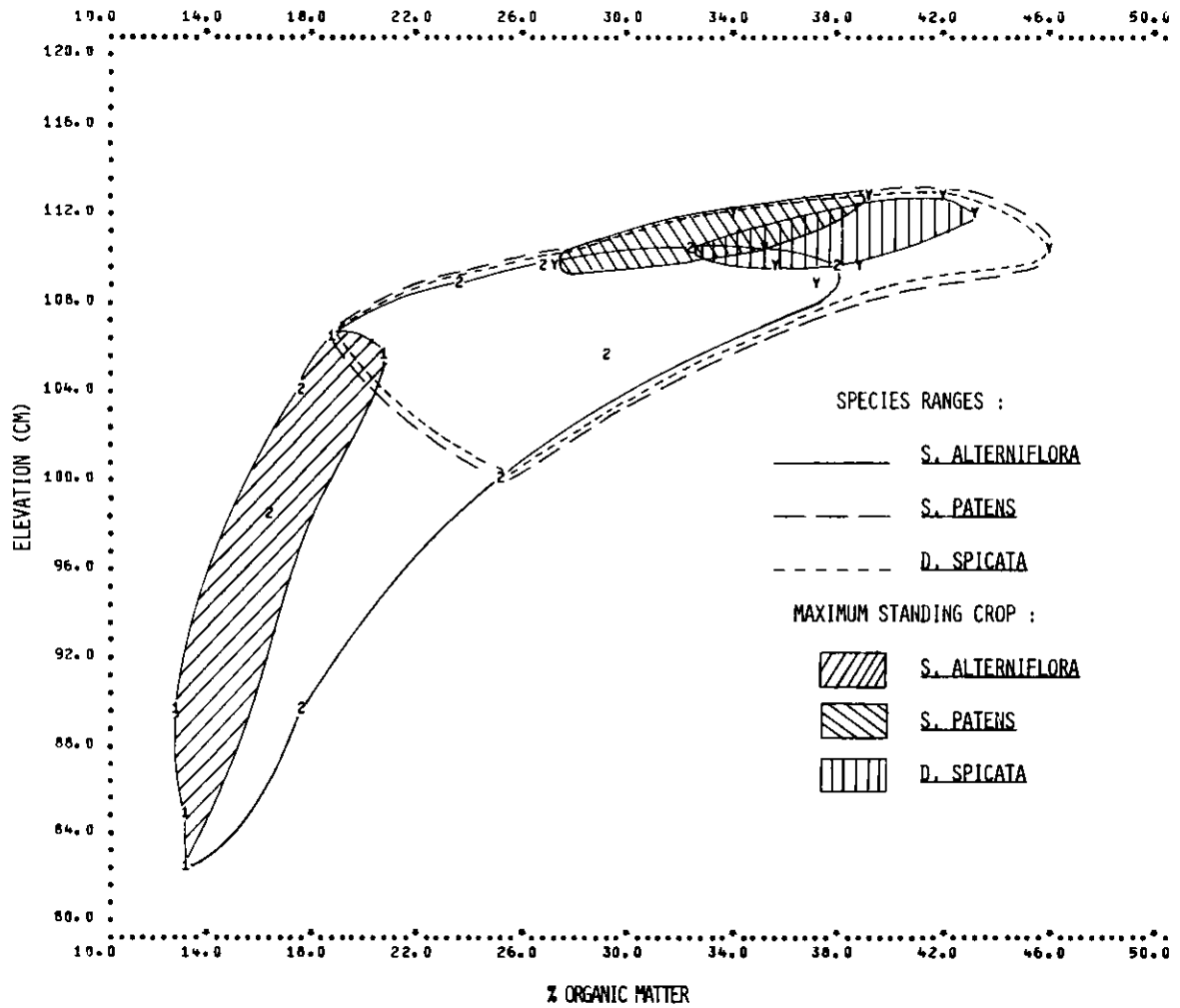
optimal - 50 percent or more of maximum live standing crop  
sub-optimal - less than 50 percent of maximum live standing  
crop

This two-part scale superseded the "percent" scale used on community gradient graphics.

87. The object of the complex gradient analysis was to pinpoint pairings of habitat factors that most clearly separate the optimal ranges of S. patens and D. spicata from that of S. alterniflora.

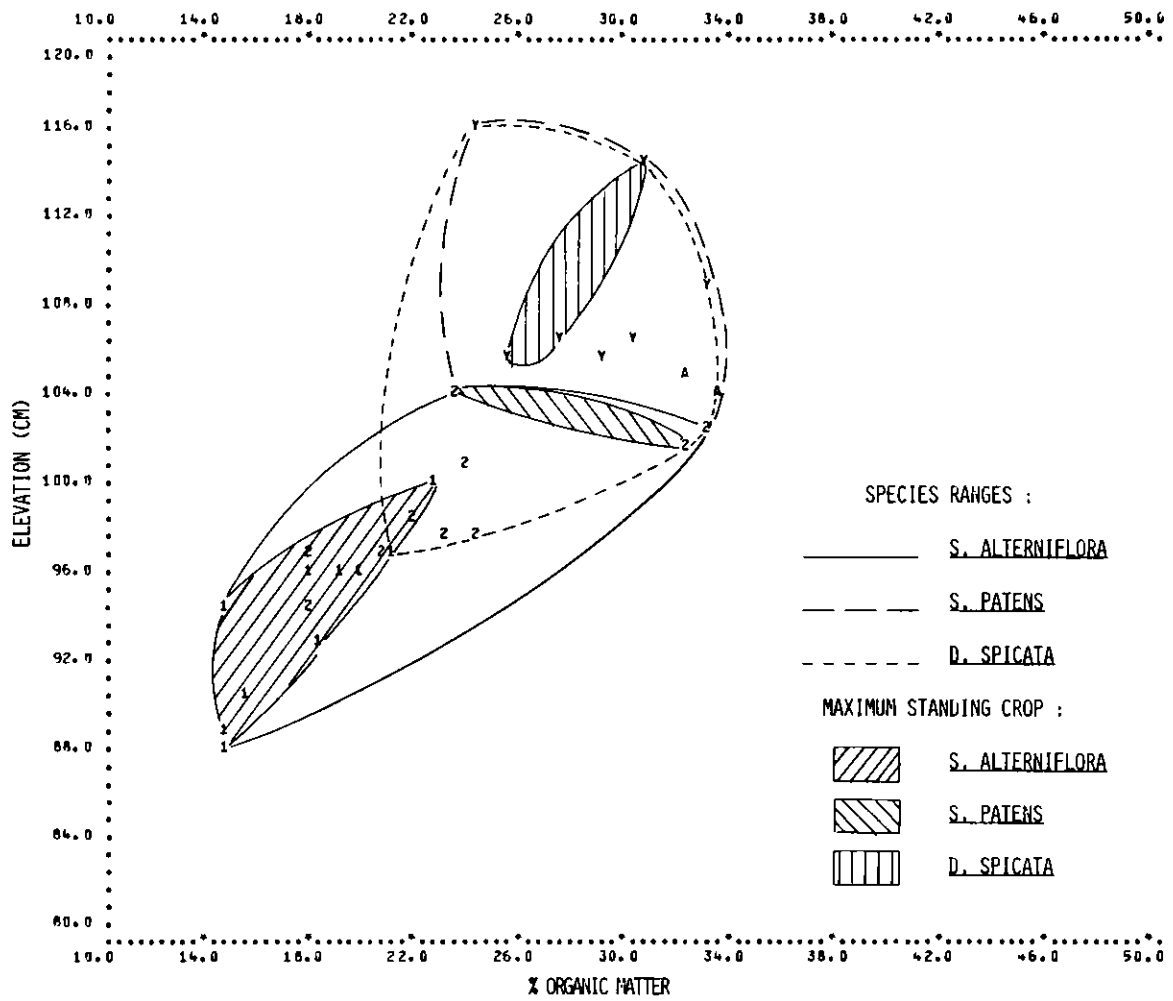
88. Illustrative examples of complex gradient plots are presented for Taskinas Marsh (Figures 22 and 23) and Bennett's Marsh (Figures 22 and 24). In each plot, the optimal portion of a species' range is shaded by parallel lines, while the sub-optimal range is merely outlined.

89. At Taskinas Marsh, the combination of elevation and organic matter (Figure 22) appeared to produce the clearest separation of high marsh and low marsh optima along both axes. Other combinations of selected factors, such as manganese and phosphate (Figure 23), show a greater degree of overlapping of optima. Similarly, only the graph of elevation and organic matter at Bennett's Marsh (Figure 22) clearly separated the S. alterniflora optimum from the optima of the high



a. Taskinas Marsh

Figure 22. Complex gradient plots of live standing crop vs. organic matter and elevation at (a) Taskinas Marsh and (b) Bennett's Marsh (sheet 1 of 2).



b. Bennett's Marsh  
 Figure 22 (sheet 2 of 2).



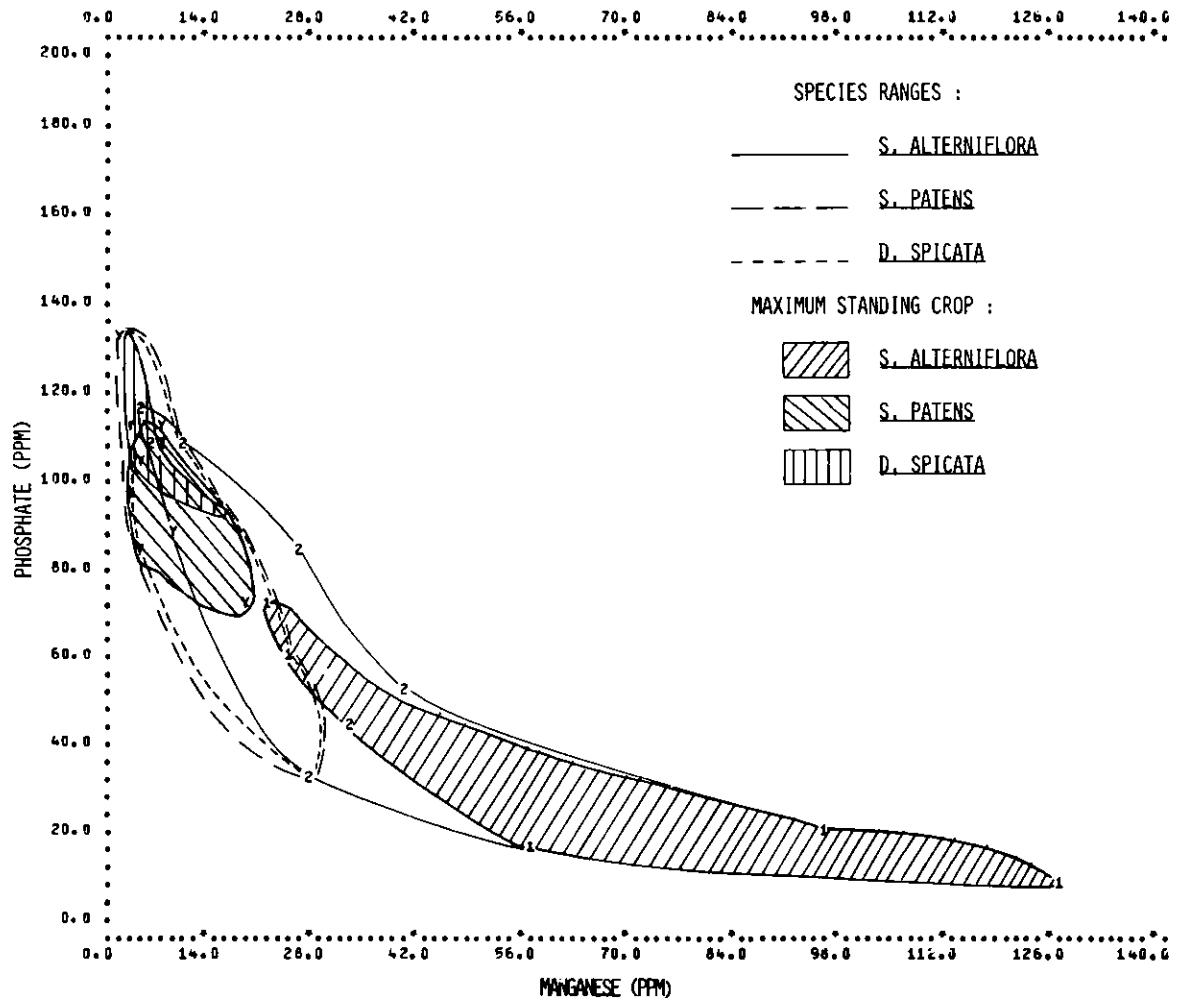


Figure 23. Complex gradient plots of live standing crop vs. manganese and phosphate at Taskinas Marsh.

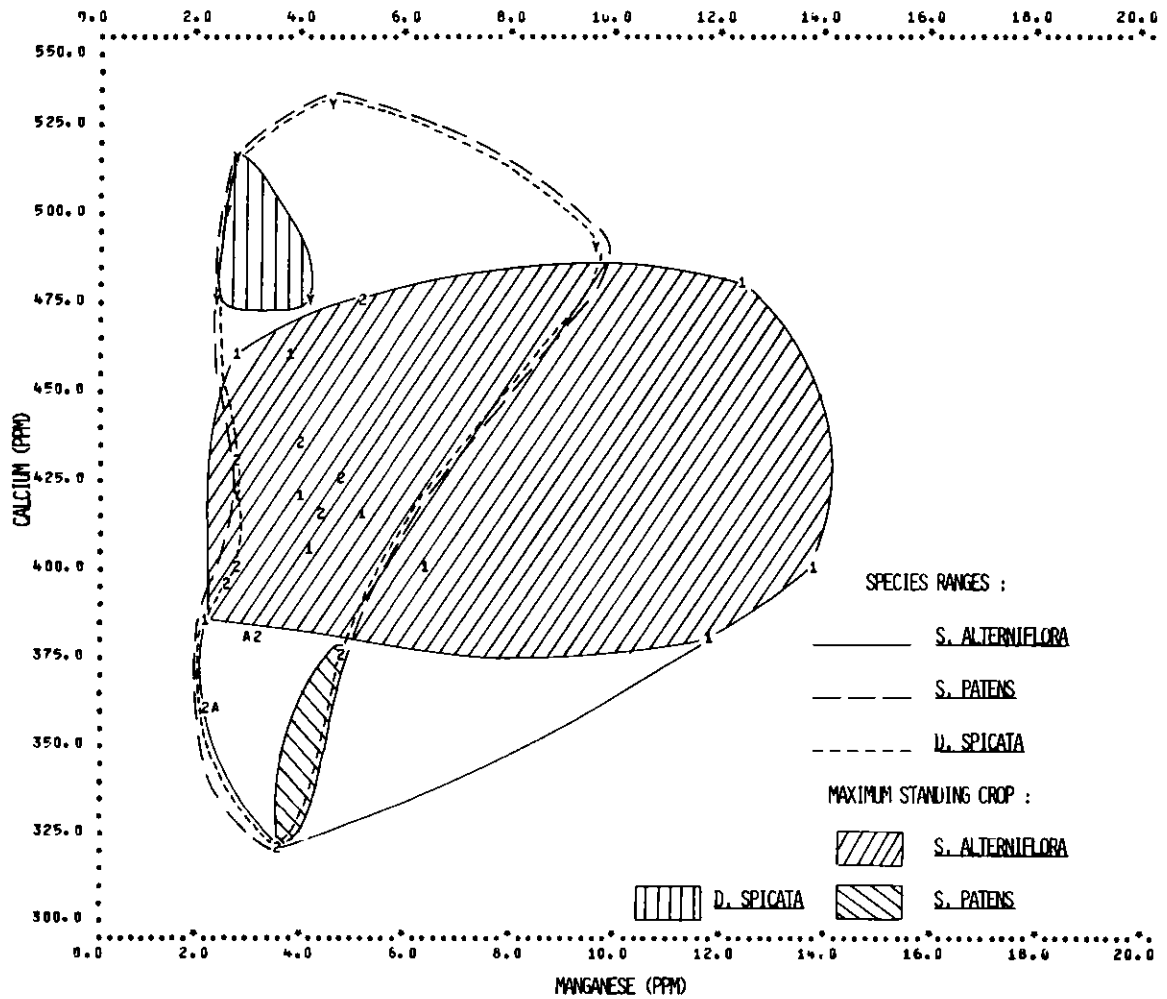


Figure 24. Complex gradient plots of live standing crop vs. manganese and calcium at Bennett's Marsh.

marsh species along both axes. The consistency of the results between the plot of manganese and calcium at Bennett's Marsh (Figure 24) exemplified factor combinations with overlapping low marsh and high marsh optima and led to the conclusion that, among the habitat factors considered in this study, elevation and organic matter were most closely associated with community zonation.

90. Both organic matter content and tidal variables were closely associated with plant growth and distribution at the study sites; however, their influences were dissimilar in nature. Highly organic soils often support very productive flora because detrital decay releases inorganic nutrients and abundant colloidal particles bind exchangeable cations (Albrecht, 1941; Buckman and Brady, 1969). In addition, decay of organic matter tends to lower soil pH, altering the availability of many plant nutrients. Thus, organic matter seems most likely to affect plant growth through its influence on the availability of inorganic plant nutrients (Bloomfield, 1963).

91. Where plant growth is correlated to some extent with available nutrient levels, one might expect to find a similar degree of correlation between organic matter content and these nutrient concentrations. Tables 2 and 3, together with Tables 4 and 5, indicate that this correspondence was found in the low marsh zones, but not in the high marsh zones. Considering all three major plant species together, then, the influence exerted by organic matter upon plant growth appears to be somewhat inconsistent. As noted previously, tide-habitat correlation patterns are paralleled by tide-plant growth correlation

patterns. Comparing tide and organic matter correlation patterns in this manner suggests that tidal influences may be the more pervasive. Furthermore, since sedimentation rate, a determinant of the organic matter content of marsh soils, is itself largely a function of the degree of tidal inundation (Broome et al., 1973), it seems apparent that tides exert some control over organic matter content. The sum of the evidence in this project, therefore, appears to point toward tidal inundation as the major controlling influence upon plant growth and zonation.

92. Prevalence of the close relationship between tide factors and vegetation tends to obscure major differences between the marshes. Certain habitat factors were significantly correlated with plant growth at only one marsh (Tables 2 and 3); interrelationships among habitat factors (Tables 4 and 5) also varied between Taskinas Marsh and Bennett's Marsh.

93. Even the zonations of species with regard to tidal inundation were somewhat dissimilar. Table 6 contrasts the two marshes in terms of species tolerance to tidal inundation. The two inundation parameters were calculated only for the extremes of species distribution that fell within the sample zone; that is, the landward limit of S. alterniflora and the seaward limits of S. patens and D. spicata.

94. Inundation tolerances were uniformly greater at Bennett's Marsh than at Taskinas Marsh. S. alterniflora tolerated a minimum of six inundations per year at Bennett's, but survived with no inundation at Taskinas. Both S. patens and D. spicata survived considerably more inundation at the lower limits of their range at Bennett's than

Table 6  
Limits of Tolerance to Tidal Inundation for Three Species of  
Marsh Grasses at Taskinas Marsh and Bennett's Marsh

Species	Inundation Events per Yr.				Hrs. of Inundation per Yr.			
	<u>Taskinas</u>		<u>Bennett's</u>		<u>Taskinas</u>		<u>Bennett's</u>	
	<u>Max.</u>	<u>Min.</u>	<u>Max.</u>	<u>Min.</u>	<u>Max.</u>	<u>Min.</u>	<u>Max.</u>	<u>Min.</u>
<u>S. alterniflora</u>	--	0	--	6	--	0	--	3.5
<u>S. patens</u>	8	0	17	--	6.5	--	22	--
<u>D. spicata</u>	8	--	41	--	6.5	--	65	--

Note: Max. = maximum number of events recorded  
 Min. = minimum number of events recorded  
 -- = not measured within sampling sites

at Taskinas. While D. spicata tolerated several times more inundation than S. patens at Bennett's, the two species showed the same tolerance limits at Taskinas.

95. It should be noted, however, that annual estimates of tidal inundation are subject to inaccuracy from several environmental sources, including alteration of the tidal prism by wind, hindrance of tidal waters by physical resistance of the vegetation, and variability of sediment drainage rates (Kurz and Wagner, 1957). Inundation of Taskinas high marsh, though not predicted, has been observed when high tides coincide with strong northwest winds (J. Pickral, 1976, personal communication<sup>\*</sup>).

96. Despite estimation errors, tidal tolerances of each plant species appeared to differ markedly between the two marshes. Assuming that a given species has the genetic potential for response to tidal inundation in both marshes (Mooring et al., 1971), differences in response might be explained by the divergent past histories of the marshes. As discussed previously, Taskinas Marsh is presently undergoing a "drowning" phase, while Bennett's Marsh appears to be building upward by sediment accretion. A gradually sloping foreshore, such as at Bennett's Marsh, is frequently associated with a young, expanding marsh (Redfield, 1972), while the steeper foreshore at Taskinas is more typical of a mature marsh (Stevenson and Emery, 1958). The difference profoundly affects the extent of tidal inundation (Figure 11). The

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\* J. Pickral, 1976, Dept of Environmental Sciences, University of Virginia, Charlottesville, VA 22903.

absence of predicted inundation in Taskinas high marsh may result from a relatively recent high stand of the marsh, as evidenced by the presence of scattered dead I. frutescens among the high marsh grass. In other words, the contemporary tidal regime of the high marsh was conditioned by this past episode as well as by the current drowning phase.

97. In mature marshes, particularly, vegetational succession in response to changing relative sea level experiences time lags. Reed (1947) suggested that, in an aggrading marsh, S. alterniflora stems buried by accumulating sediments may remain alive for some time, since their roots continue to exist under relatively unchanged conditions. Eventually, the high marsh species encroaching on the new sediments smother the S. alterniflora beneath them, and the transition is completed. Similarly, the retrogressive succession accompanying rising relative sea level (Kurz and Wagner, 1957) often requires that an invading species (e.g., S. alterniflora at Taskinas Marsh) establish itself among a dense, fibrous mat of high marsh vegetation. Ranwell (1964) observed that competition from Spartina townsendii appeared to retard the advance of invading species, even when habitat conditions would have permitted the invaders to expand more rapidly. Pre-existing vegetation thus may possess a competitive advantage by virtue of its physical occupation of the growing space, enabling it to persist for some time despite an increasingly unfavorable habitat. The equilibration time of marsh vegetation during periods of change in relative sea level may significantly modify the relationship between vegetational distribution and tidal inundation.

## PART VI: MONITORING RESULTS

98. As the monitoring equipment was built, it was tested successfully in the laboratory; in the harsher environment of the salt marsh, however, unforeseen problems arose. Throughout the field monitoring phase, the equipment was plagued by component failure of varying severity. The initial difficulties were most serious; failure of one or more components would induce problems in others, and the system's performance would totally deteriorate. Chief among these early problems were loss of amplifiers due to electronic failure, and disappearance of a transmitted signal or shorting out due to water leakage around the submersible connectors.

99. When the amplifiers malfunction, the unit frequently sets up an overvoltage. The recorder normally receives an input of 0.0 to 1.0 v-d.c.; any higher voltage produces erroneous records on the channel in which the overvoltage occurs and in adjacent channels as well. A sufficiently high overvoltage damages the recorder itself. Ultimately, voltage regulators were installed on the outputs of all amplifiers to prevent overvoltages, but many records were lost before this problem was alleviated.

100. The other major problem, which was not fully resolved, involved the shorting out of signals between the amplifiers and the junction boxes. The major cause of this problem proved to be leakage in the submersible cable connectors. Since it was frequently necessary to carry the equipment several hundred meters to the study site, the units were designed in a modular fashion to facilitate handling assembly



on the marsh. Despite careful handling, bits of sediment and droplets of salt water frequently became attached to exposed connectors and were not completely removed by a final cleaning prior to assembly of the connectors. Any trace of water or salt on the connectors allowed the voltage to leak, either to ground or to another connector. This leakage periodically caused erroneous behavior which was often perplexing and difficult to trace. Despite the host of electronic problems in the system and the consequent lack of complete records, the results from the monitoring system were quite encouraging. The main value of this part of the project was the demonstration of the feasibility of recording small time interval variations in sedimentary parameters and relating these variations to plant distribution.

101. The most complete set of data collected with the system was collected between 25 and 28 November, 1975 at Taskinas Creek; portions of this are shown in Figures 25 to 30. The figures depict incoming solar radiation in Taskinas Creek, tidal fluctuation, and pH and temperature at the surface and 10 cm below the sediment surface in several marsh zones. These figures readily show the high degree of variability present in the marsh, and also the difficulty in analyzing this type of continuous data. The curves of solar radiation (Figure 25) and tidal height (Figure 26) were relatively smooth and easy to interpret, since the diurnal periodicity of radiation and semidiurnal nature of the tides were readily apparent. However, graphical analyses of temperature and pH curves is a formidable task, since patterns of behavior are masked by wide variation and signal noise (Figures 27 to 30).

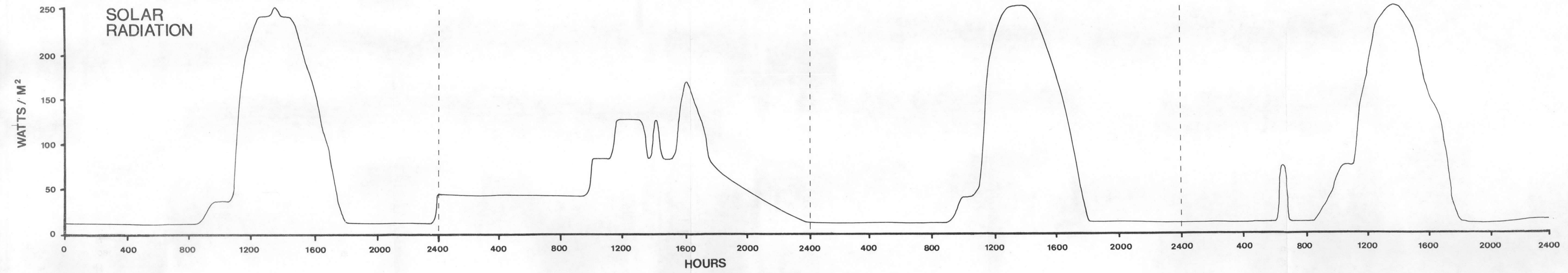


Figure 25. Solar radiation at Taskinas Marsh from 25 to 28 November 1975.



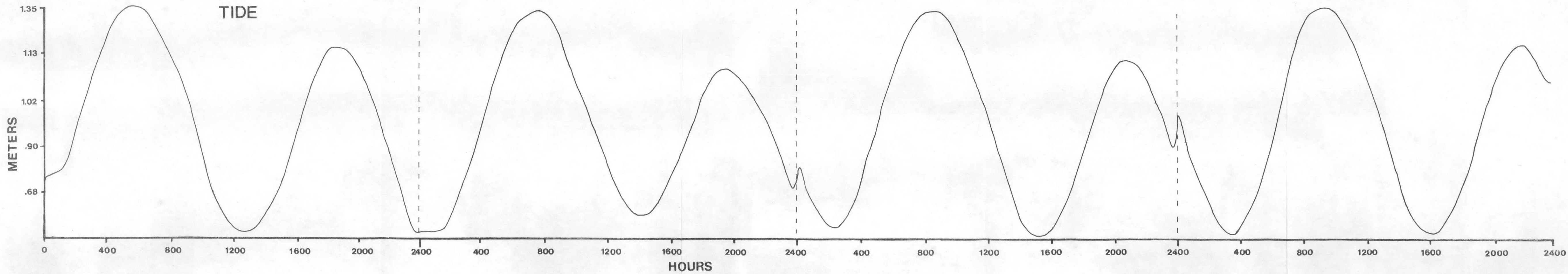


Figure 26. Tidal height at Taskinas Marsh from 25 to 28 November 1975.





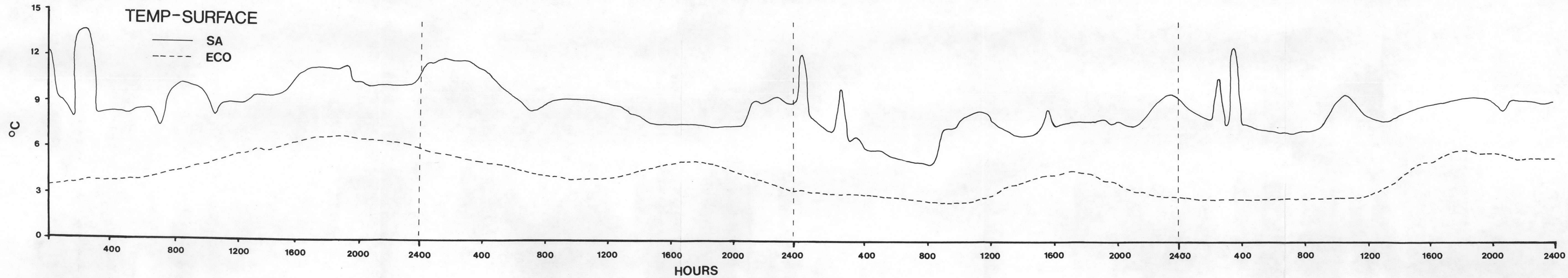


Figure 27. Temperature at the sediment surface at Taskinas Marsh from 25 to 28 November 1975.





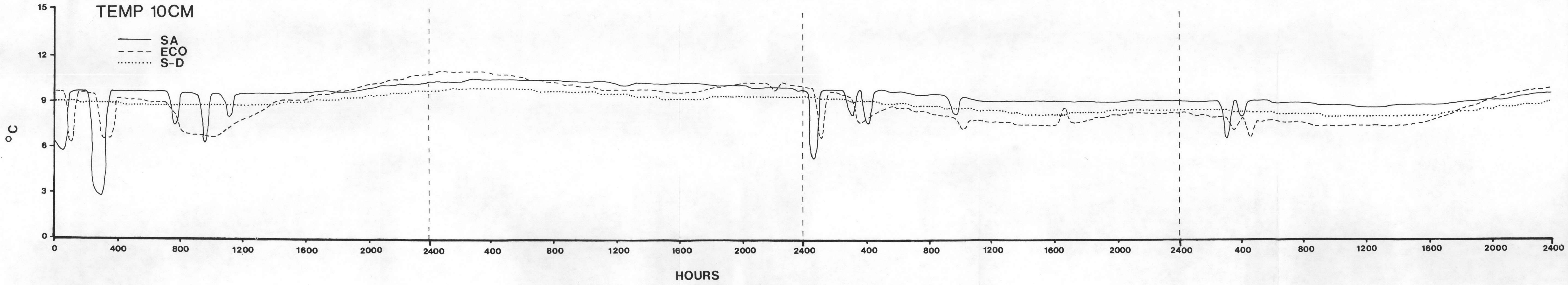


Figure 28. Temperature at 10 cm in the sediment at Taskinas Marsh from 25 to 28 November 1975.





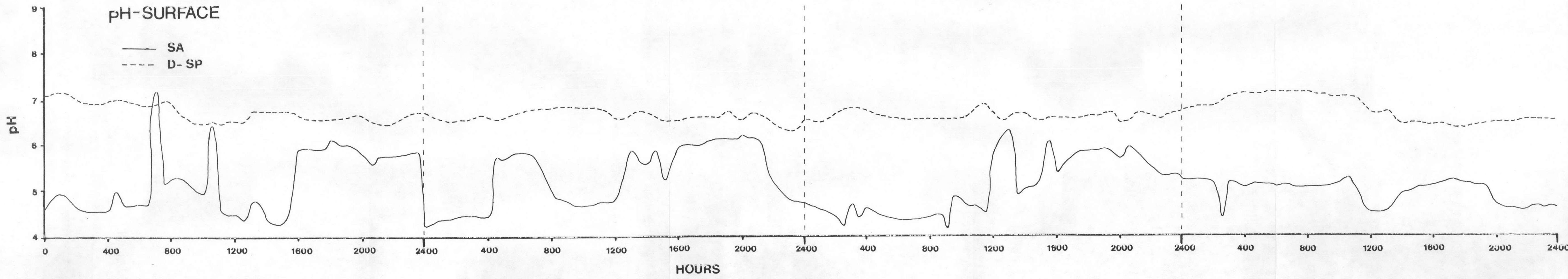


Figure 29. pH at the sediment surface at Taskinas Marsh from 25 to 28 November 1975.





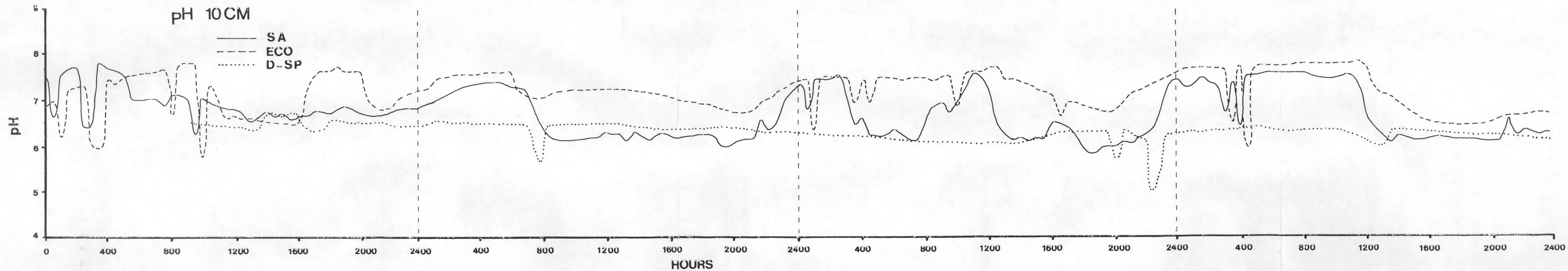


Figure 30. pH at 10 cm in the sediment at Taskinas Marsh from 25 to 28 November 1975.



102. Because the data were continuous and spanned several cycles of the driving function, they could be analyzed by rigorous mathematical techniques, including Fourier series analysis (Rayner, 1971; Platt and Denman, 1975). This technique is utilized to determine if an environmental forcing function such as tide or radiation exerts an effect on another parameter. Alternatively, it can be used to reduce large amounts of data, such as the voluminous time series records collected here. A Fourier series is a composite of sines and cosines that represent the decomposition of a time series. In this sense it is a form of curve fitting, because the sum of a set of sines and cosines results in the replication of the original curve  $\tilde{S}(t)$ , where:

$$\tilde{S}(t) = a_0 + \sum_{i=1}^{j-1} a_i \sin(2\pi f_i \Delta t) + b_i \cos(2\pi f_i \Delta t)$$

$\tilde{S}(t)$  = approximation of original time series

$a_0, a_i, b_i$  = Fourier coefficients

$f_i$  =  $i^{\text{th}}$  harmonic of fundamental frequency

$\Delta t$  = data sample time interval

The coefficients  $a_0, a_i,$  and  $b_i$  are Fourier coefficients and reflect the influence of each sine and cosine component in the reconstitution of the original information.

103. For example, if the original time series  $\tilde{S}(t)$  is a tidal record with zero amplitude at time zero ( $t_0$ ), the Fourier series representation of this curve would be

$$\tilde{S}(t) = a_i \sin(2\pi f_i \Delta t)$$

where  $\sin(2\pi t/T)$  represents a frequency of 2 cycles/day. All of the other frequencies would have very small coefficients associated with them since tides in the Virginia area are nearly sinusoidal, with a primary frequency of 2 cycles/day (U.S. Dept. of Commerce, 1974). The above information is often displayed in graphical format resulting in what is called a power spectrum. This graph depicts the relationship between frequency and power. The term power signifies the importance of a particular frequency in reconstituting the original data and is a function of the Fourier coefficients. Thus, for a tidal curve, a power spectrum would be composed of a single spike at a frequency of 2 cycles/day (Figure 31), all other frequencies having very little power.

104. In many cases the power spectrum for a time series is dwarfed by a spike at zero frequency. When this occurs it is often difficult to determine if any other frequencies occur as a significant component of the original data. The zero frequency represents the mean of the data series, and a filtering procedure is often utilized to eliminate such low frequencies. Following this filtering, it can be ascertained whether the ecologically important frequencies such as 1 and 2 cycles/day are present in the time series under study. For example, consider a pH time series for surficial sediment in a salt marsh. The pH may vary around a mean of approximately 5 to 7 pH. To analyze this time series for frequencies in the range of 1 to 2 cycles/24 hours, the mean must be removed from the data. This is often accomplished by utilizing a differencing filter, or simply by subtracting the mean of the data set from each individual data point. In the case of the differencing filter the data point of a time series at time  $t$  is subtracted

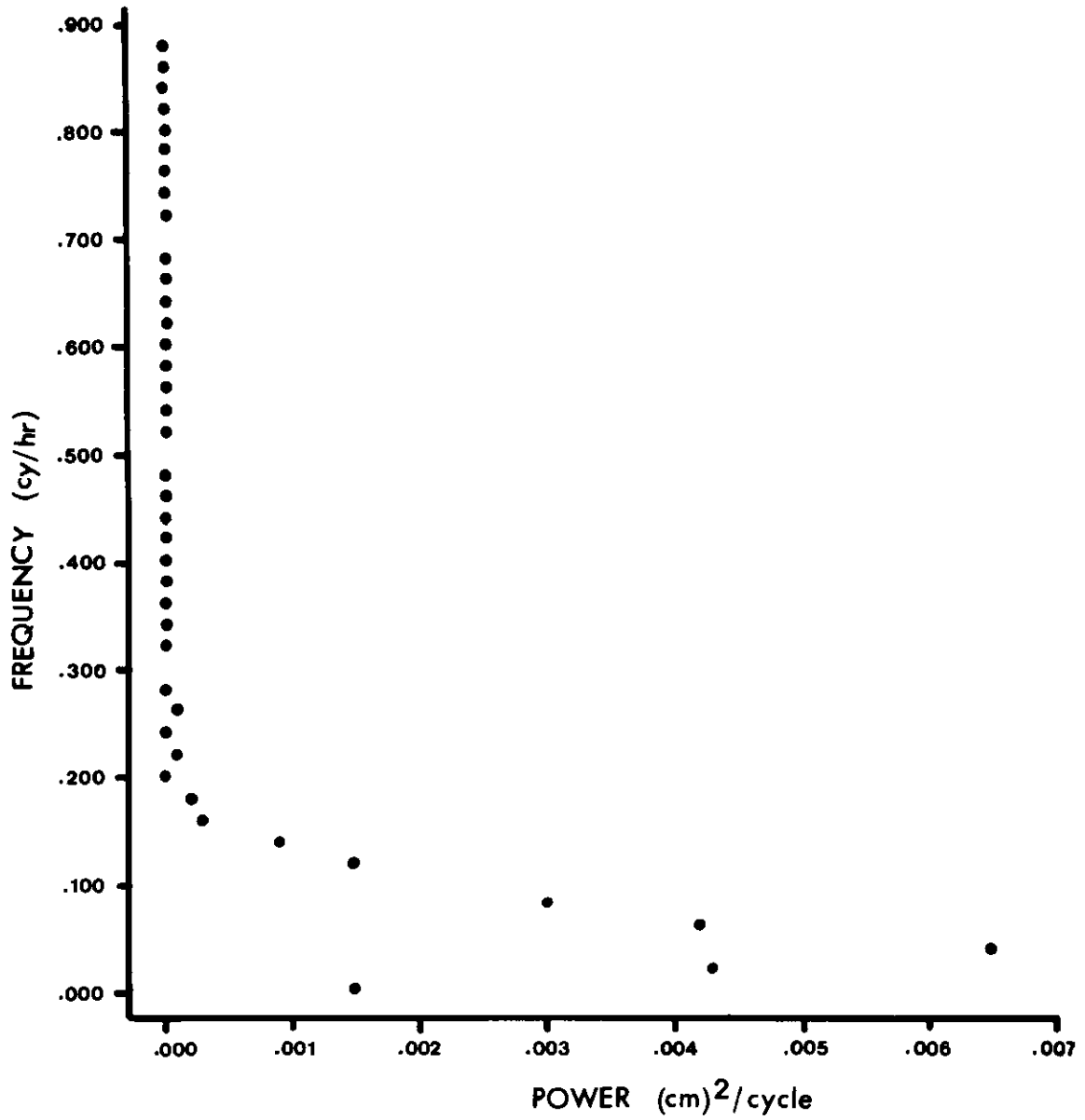


Figure 31. Power spectrum of tide at Taskinas Marsh.



from the data point at time  $t+1$ , thus constituting a new value at time  $t$ . The process is continued for the entire time series. The result of this mathematical manipulation is the loss of low frequencies from the original time series.

105. The power spectrum analyses were conducted on continuous monitoring data for which a sufficient number of data points existed. Power spectra for tide, radiation, pH, and temperature at the surface of the salt marsh are displayed in Figures 31-36. These data were collected at low marsh and high marsh sites at Taskinas Creek for the period of 25 to 28 November, 1975. The tide and radiation data were unfiltered, while the temperature and pH data were manipulated by the use of a differencing filter. As might be expected, the power spectra for the tide and radiation data have spikes at 0.089 and 0.044 cycle/hour, respectively (two cycles and one cycle, respectively, per 24 hours). There is little power at any other frequency except zero since the mean was not subtracted from these time series. The power is primarily at one frequency since tide and radiation are both predominantly single-frequency forcing functions.

106. If the pH and temperature time series data were analyzed to determine the effect of the tide and radiation forcing functions, the resultant power spectra for pH (Figure 33) indicate this parameter in the low marsh appeared to have a significant frequency component around 0.089 cycle/hour (tidal frequency), while this frequency was absent in the high marsh pH data. The surficial temperature data also reflect the tidal influence elucidated above. As is seen in Figure 34, the temperature power spectrum for low marsh had a large spike at the tidal frequency of 0.089 cycle/hour. The temperature time-series data

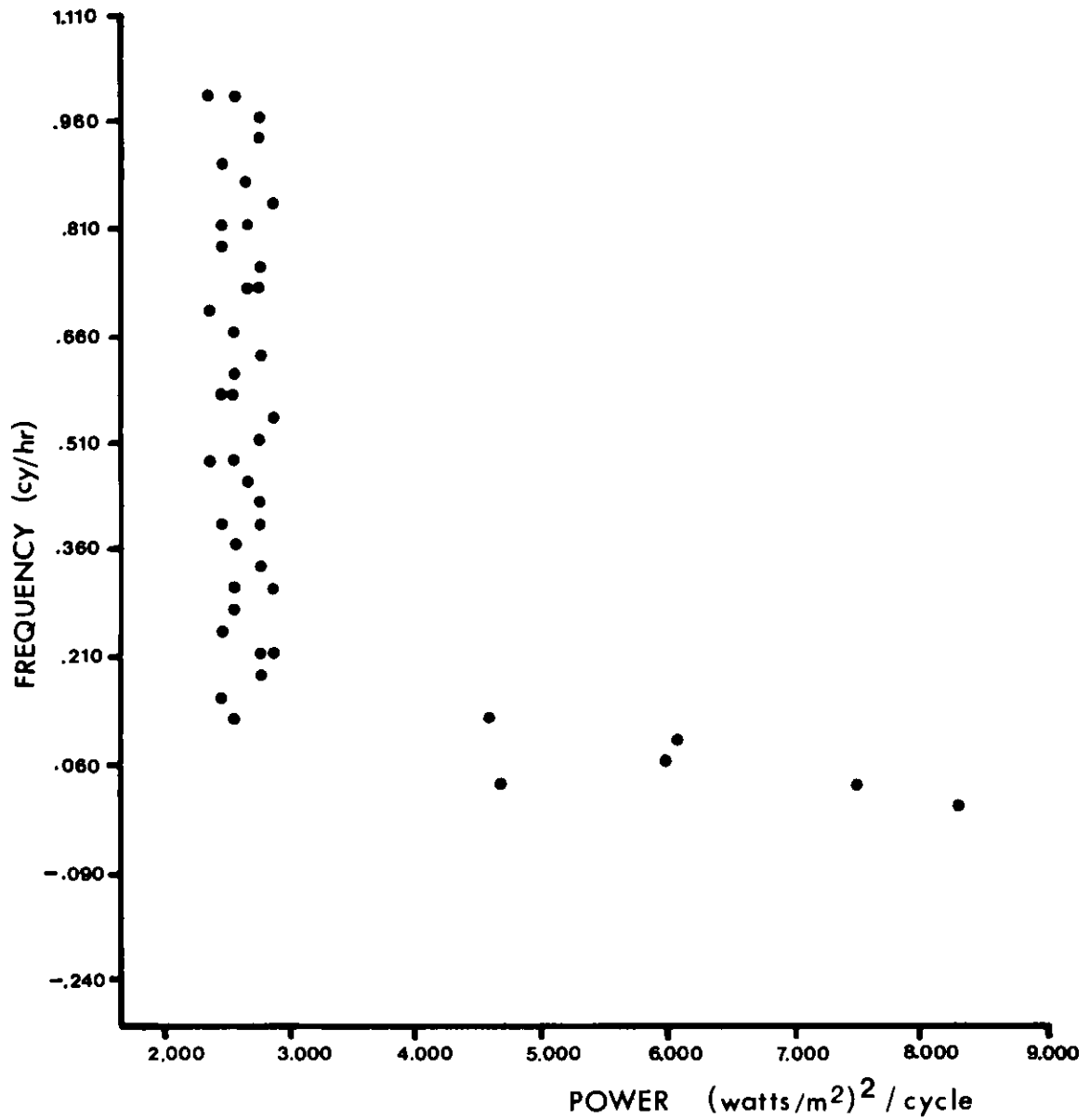


Figure 32. Power spectrum of solar radiation at Taskinas Marsh.

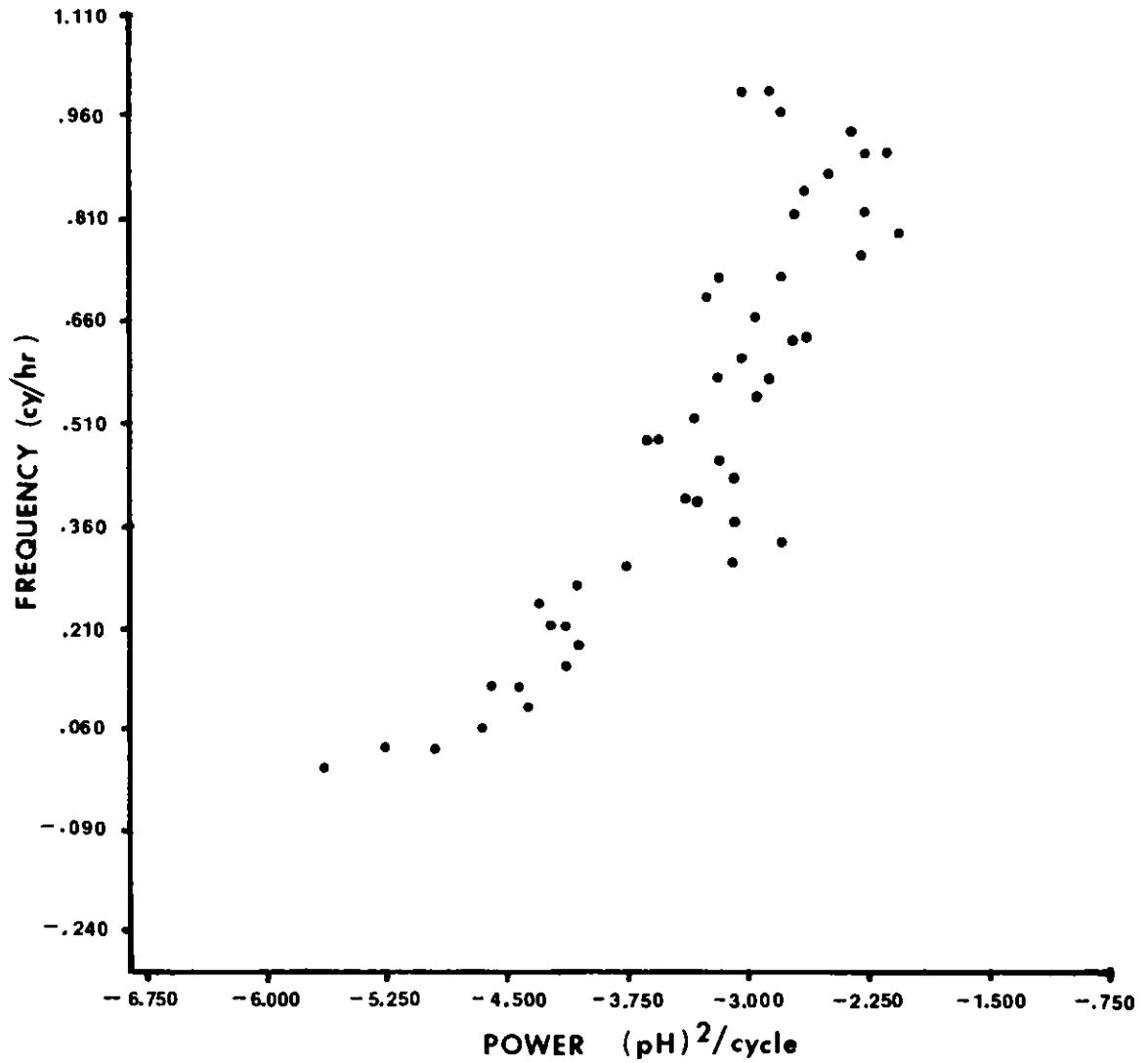


Figure 33. Power spectrum of pH at the surface in the Spartina alterniflora zone at Taskinas Marsh.

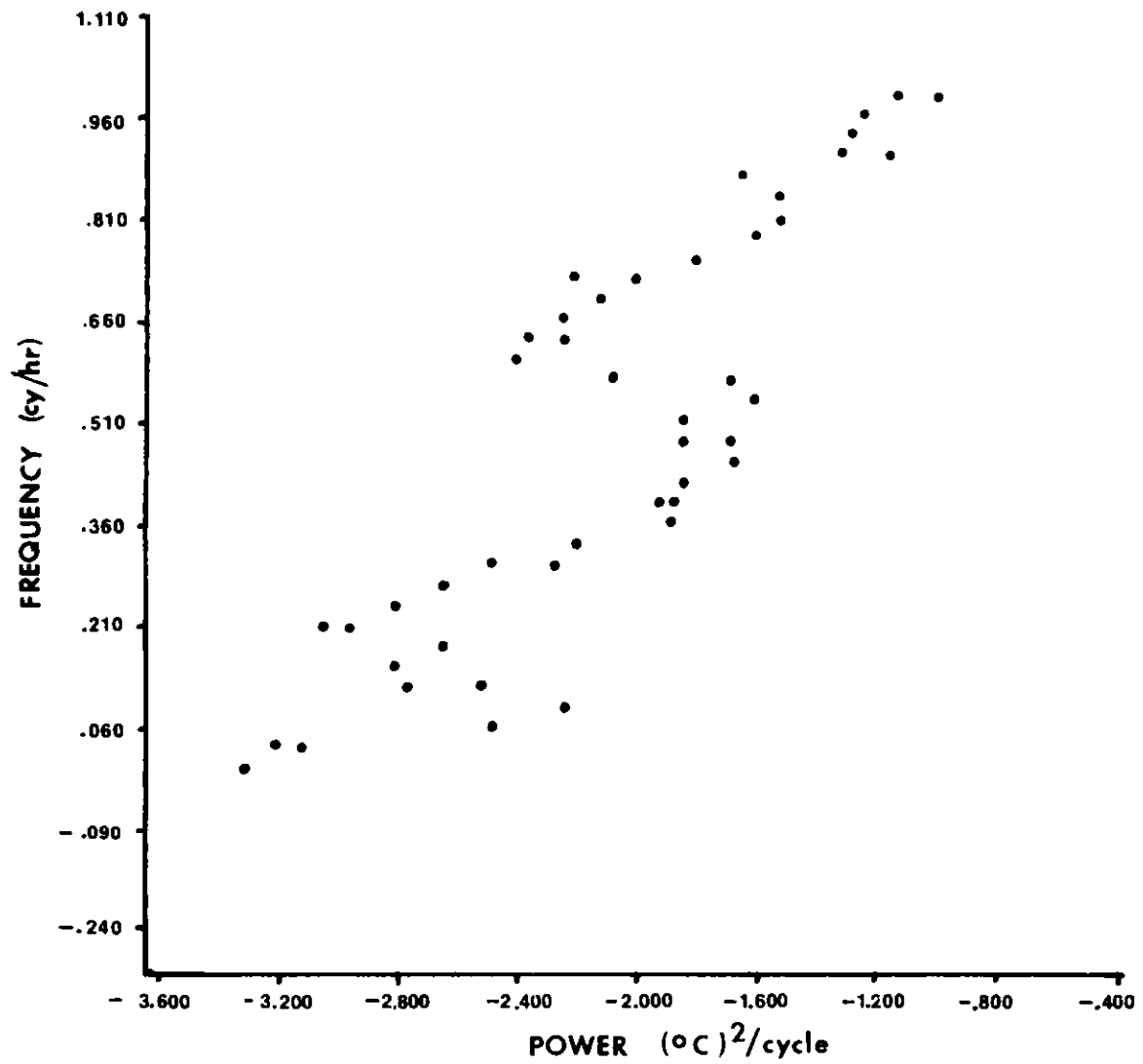


Figure 34. Power spectrum of temperature at the surface in the Spartina alterniflora zone at Taskinas Marsh.

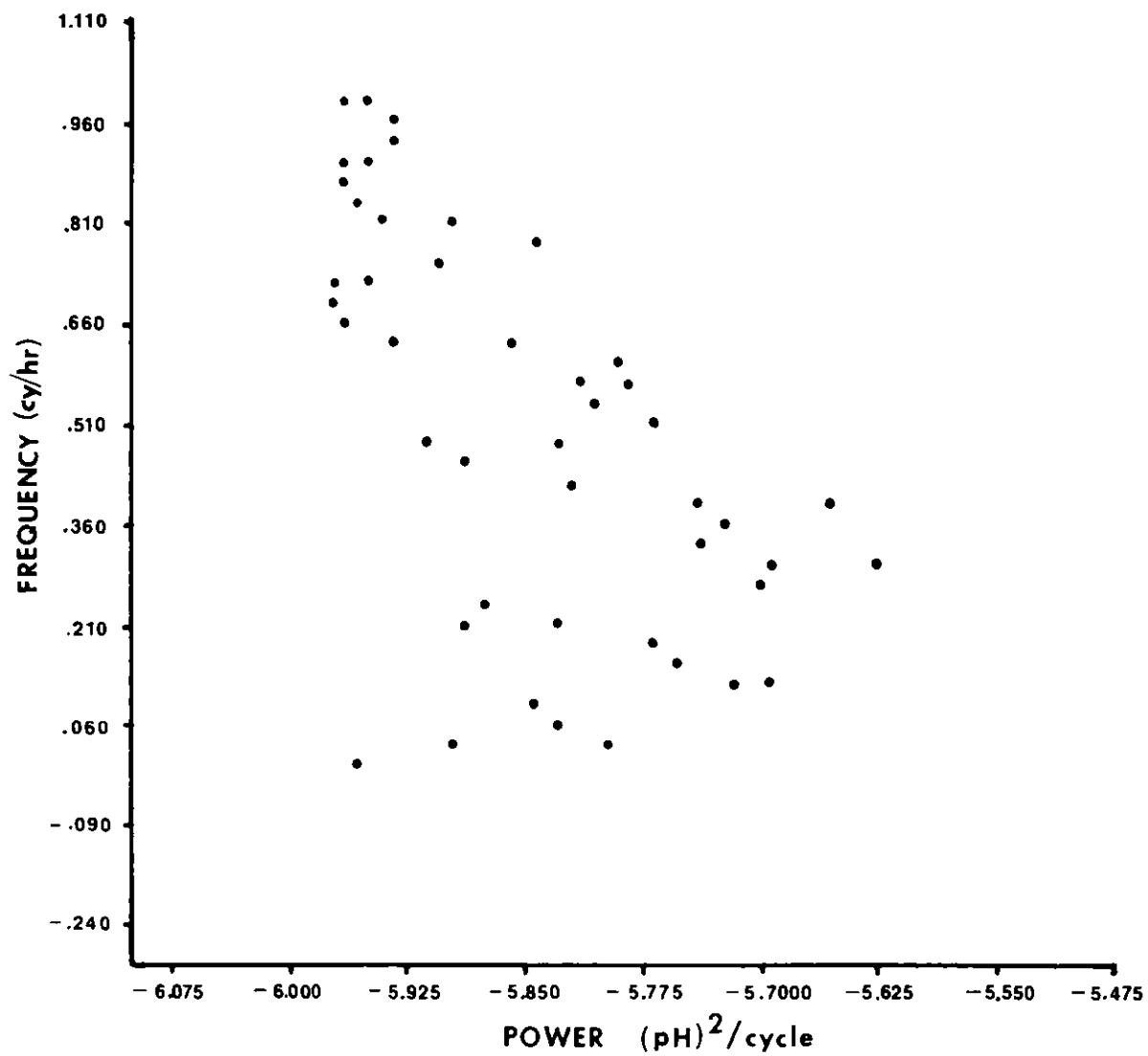


Figure 35. Power spectrum of pH at the surface in the Spartina patens - Distichlis spicata zone at Taskinas Marsh.

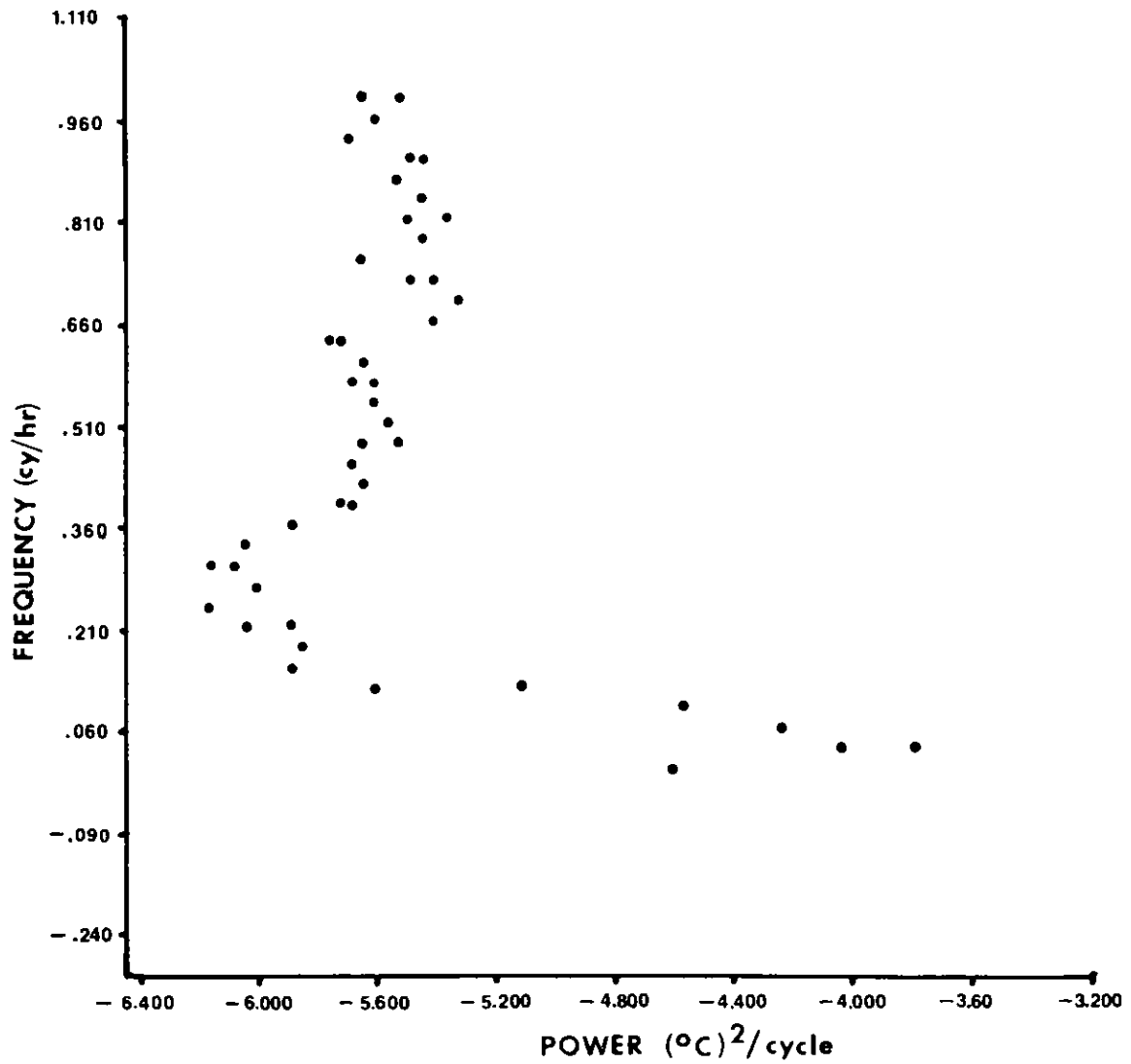


Figure 36. Power spectrum of temperature at the surface in Spartina patens- Distichlis spicata zone at Taskinas Marsh.

for the high marsh lacked the tidal frequency but had a large frequency component near 1 cycle/day, which was the primary radiation frequency.

107. This analysis supplements, and to a degree substantiates, some of the earlier conclusions derived from the nutrient analysis of marsh sediments. It indicates that the low marsh was being affected to a greater extent by tidal forces than the high marsh.

## PART VII: MARSH SUCCESSION MODEL

108. One of the major objectives of this project was to develop a model to simulate the growth and succession of major plant species on natural marshes and on dredged material disposal sites. Accordingly, model development paralleled the field phase of the project. To produce a simulation model of plant growth and succession on salt marshes, several modeling approaches may be taken. The ideal approach is to work from a complete understanding of the underlying ecological principles that cause the growth and death of plants. This yields a model that can accurately depict the response of a plant to the environmental factors--physical, chemical, and biological--that influence the study species. However, the biology of most organisms is insufficiently understood to develop models at this level of resolution. The other extreme in model design is a model whose linkages are totally empirical. Such a device is usually developed to test the accuracy of predicting outputs from a series of chosen inputs, with little attention given to the realism of the model's internal processes. Superficially, this type of model seems ideal for many purposes. However, as any type of model is produced, it is inevitably necessary to make some simplifying assumptions ; and in the case of the highly empirical model, the assumptions may severely limit the usefulness of the final product.

109. Early experimental models produced for this study were highly realistic growth models based primarily on studies involving Spartina alterniflora. However, their extreme complexity made them



difficult to use. One of the major concerns in this project was that the final model should be easily manipulable for individuals with only a basic understanding of the use of computers; it was therefore judged that the highly realistic models, which demand thorough acquaintance with both computer science and salt marsh ecology, were unsuitable.

110. The inherent complexity of the initial models also emphasized another problem that aided in the development of the present model. Like any complex mechanical device, a model is limited by its weakest components (consequently constructing a model that is complex in some of its functions but crude in others can often be futile exercise). The marsh literature, though extensive, is largely descriptive in nature, and little information is sufficiently quantitative to be applied toward development of a simulation model. Spartina alterniflora has been studied extensively, yet there are sufficiently large uncertainties about the physiological ecology of this plant that constructing a realistic growth model is difficult. Knowledge of the physiology and ecology of S. patens and D. spicata is even more limited. Thus, in constructing a realistic model using these three species, one must make a choice: either be constrained by the species for which the least information is available, or make assumptions about this species' responses based on the behavior of closely related species.

111. Since assumptions must always be made in building a model, constraints must be imposed on the model's use. For instance, if a growth model is developed to simulate the response of a species to several factors within an assumed salinity range of 10 to 35 percent, a

salinity input of 5 percent may produce a response that is seriously misleading.

### Model Concept

112. The central units of the succession simulation were sub-models of the growth dynamics of each species, called species modules. The original species module developed was for Spartina alterniflora, because there was more information available for this species than for other salt marsh plants. A frequent drawback of simulation models developed with scarce data was their inability to evolve as the data base increased. The species modules were developed to be open-ended; that is, as more information became available documenting the response of the plants to environmental factors, it could be used to increase the realism of the module.

113. The same basic species module structure, considered to be representative of a generalized salt marsh plant, was used for all species (Figure 37). The differing responses of the individual species were incorporated by imbedding response curves within each module to characterize the response of given species to selected environmental variables.

114. The model described here utilized three species modules, representing S. alterniflora, S. patens, and D. spicata, but possessed the capability of utilizing up to 10 species modules whether they were used to represent individual species or functional groups of species.

115. The species modules were combined into a point model that

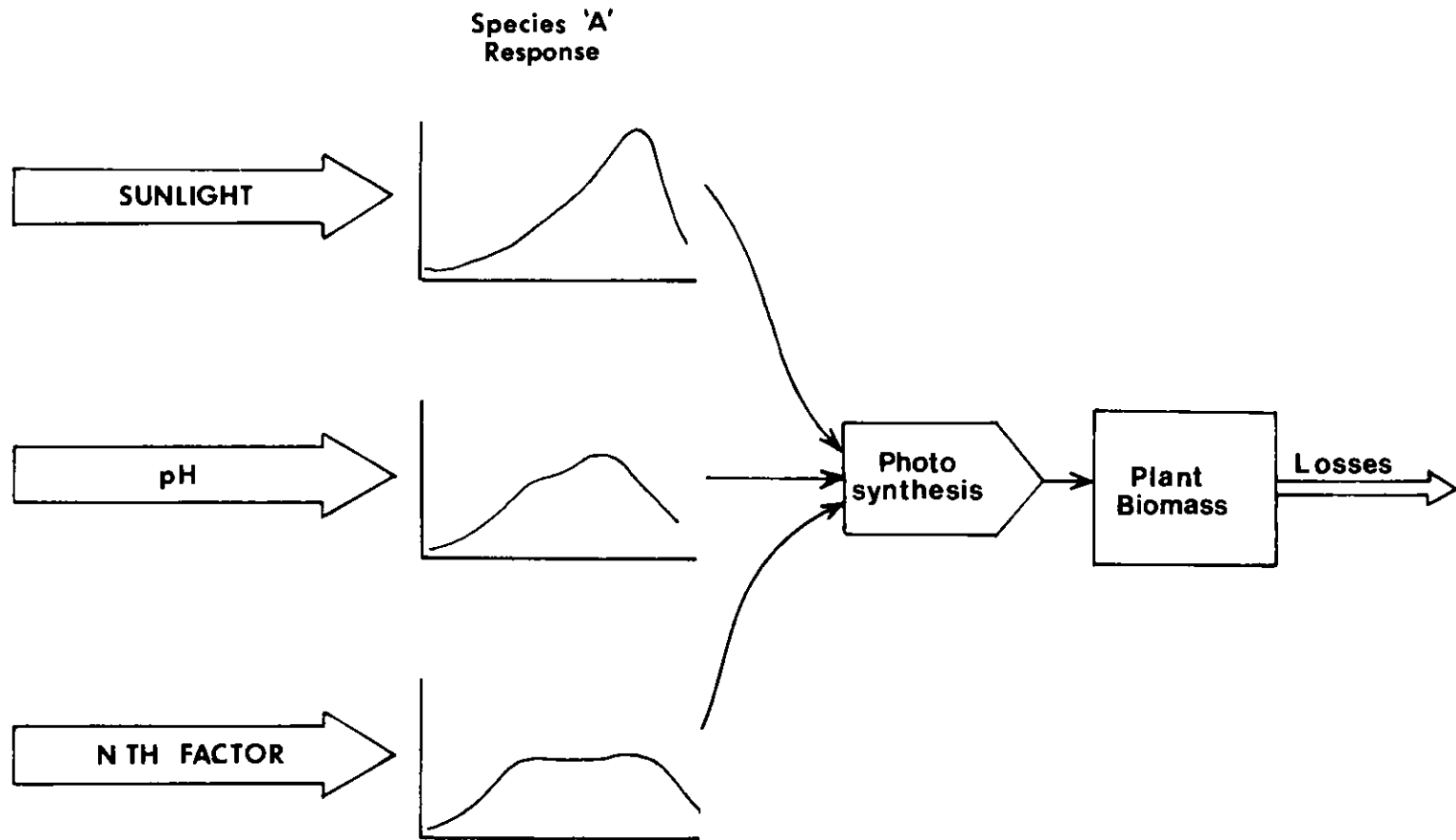


Figure 37. Conceptual diagram of a single species module. The curves represent a generalized response of the plant (y-axis) and the level of the driving variable (x-axis).

simulates the growth of each species on a particular square meter of marsh surface (Figure 38). Because each point model contains all species modules, it can simulate the growth of co-occurring species at a particular point in the marsh through time. The current model can depict plant growth and succession on a transect across a salt marsh by using physical variables to link series of point models. Coupling of the point models, each of which represents a discrete point on the marsh surface, enables simulation of plant growth both temporally and spatially (Figure 39) on the marsh from the tidal creek to the high marsh.

116. The current version of the model, MARSH1, contains the three species modules previously described, and is driven by four environmental factors: solar radiation, temperature, soil salinity, and tidal inundation. A wide variety of mathematical formulations are available to describe the growth of the plant using such a set of driving variables. Probably the most common method utilizes a multiplication technique where growth is a result of some factor "A" times a factor "B" times a factor "C" and so on so that the result is a product of a series of driving variables. This is often a very unrealistic way to simulate a response to a series of variables as it assumes interactions among the variables that may be ill-understood or nonexistent.

117. Plant physiologists have clearly established the interaction of temperature and solar radiation in controlling photosynthetic rate. The curves of Gates (1968) depict photosynthesis as a function of various light levels and differing temperatures. However, detailed information is not available for most marsh plants; thus it was felt

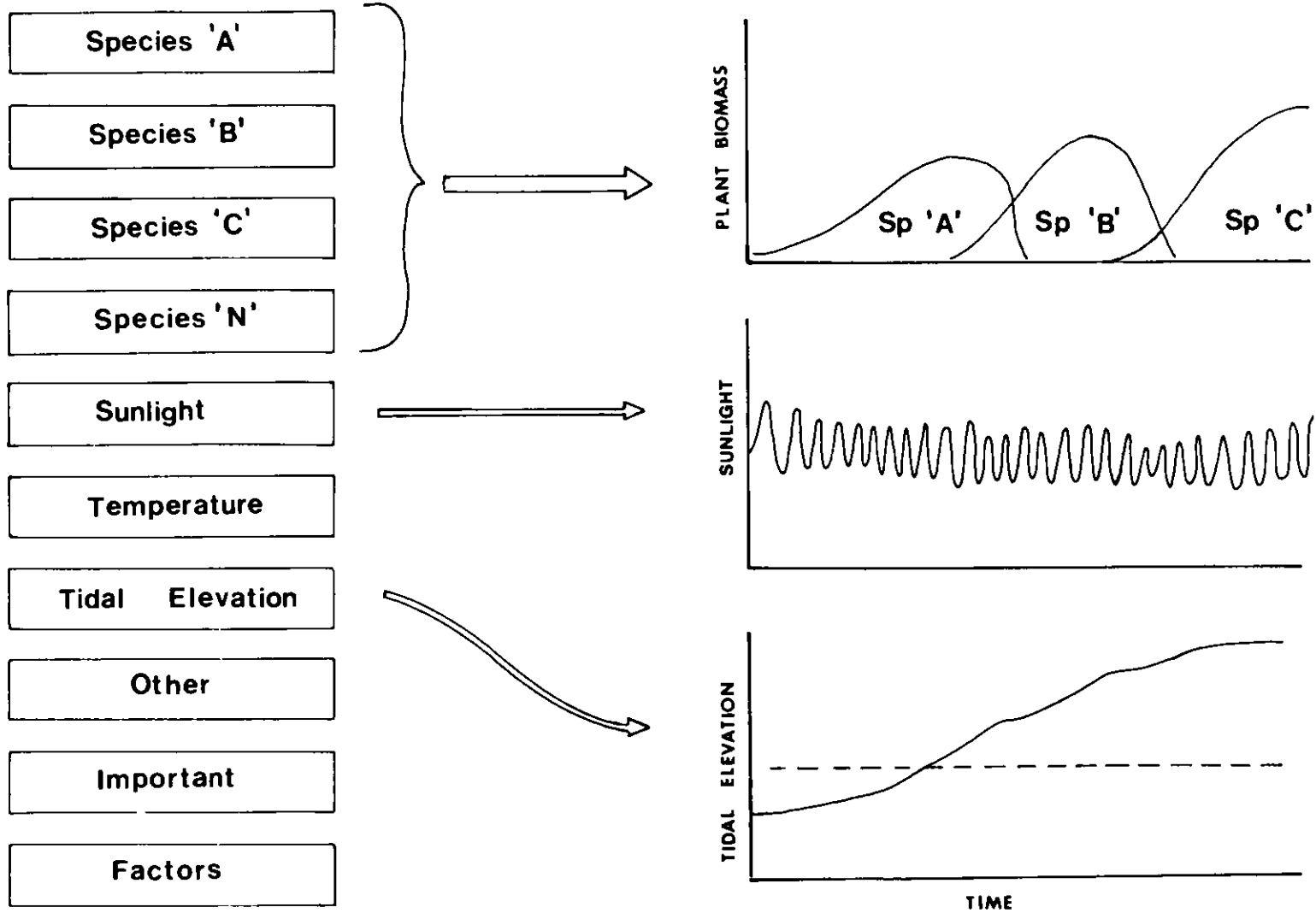


Figure 38. Conceptual diagram of the linking of several species modules with environmental forcing functions to form a model of a single point in the marsh.

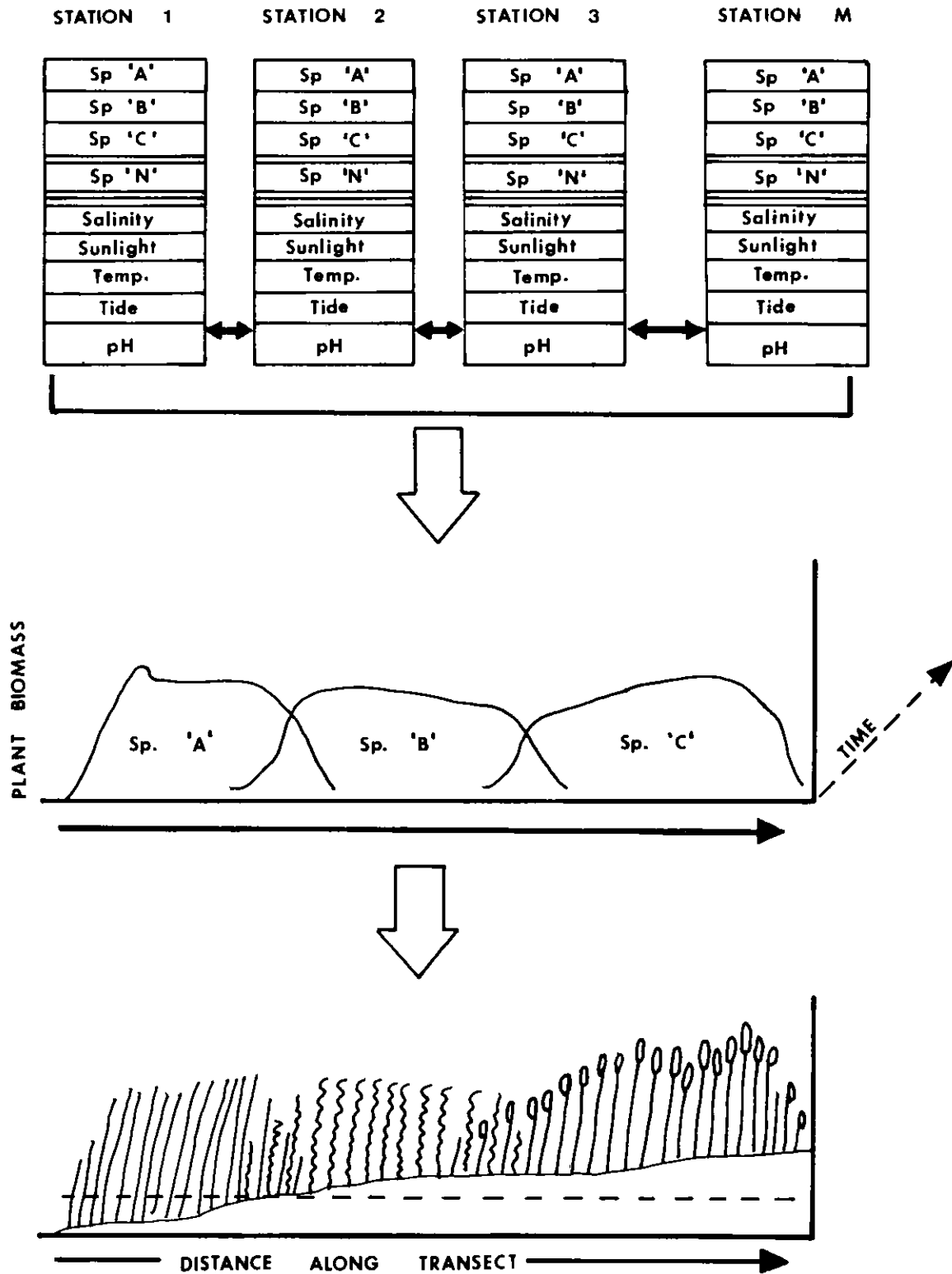


Figure 39. Conceptual diagram showing the coupling of several point models to produce a coupled model of transect with several stations. The middle and lower sections represent generalized plant species distributions on the marsh. The dashed line in the lower section represents mean high water.

that a better approach would be to devise a series of independent limiting functions formulated according to Liebig's concept that implies that of the variety of factors which control the growth of organisms, there is one element in least supply at any given time, termed the "limiting factor."

118. At each time step the model calculates the amount of growth that is possible due to each of the independent driving parameters. The model then checks to determine which of these calculated functions is the most limiting, or conversely, which permits the least growth. The incremental growth function is then determined according to the value of this limiting parameter. It should also be noted that the model's driving variables, which will be described in detail below, are primarily physical in nature. This is due in part to the paucity of information currently available on direct effects of biological factors, such as competition, upon marsh plant growth. The model has been designed so that other factors that influence plant growth, such as soil nutrients, may be added as sufficient information becomes available. Interactions between factors, both positive and negative, may also be added when these are sufficiently understood.

#### Model Structure

119. Using these concepts, the model MARSH1 was formulated, and its general structure is shown in Figure 40. When a set of data is read into the program, it is immediately printed out with appropriate descriptions and formatting. The inputting data fully fall into three

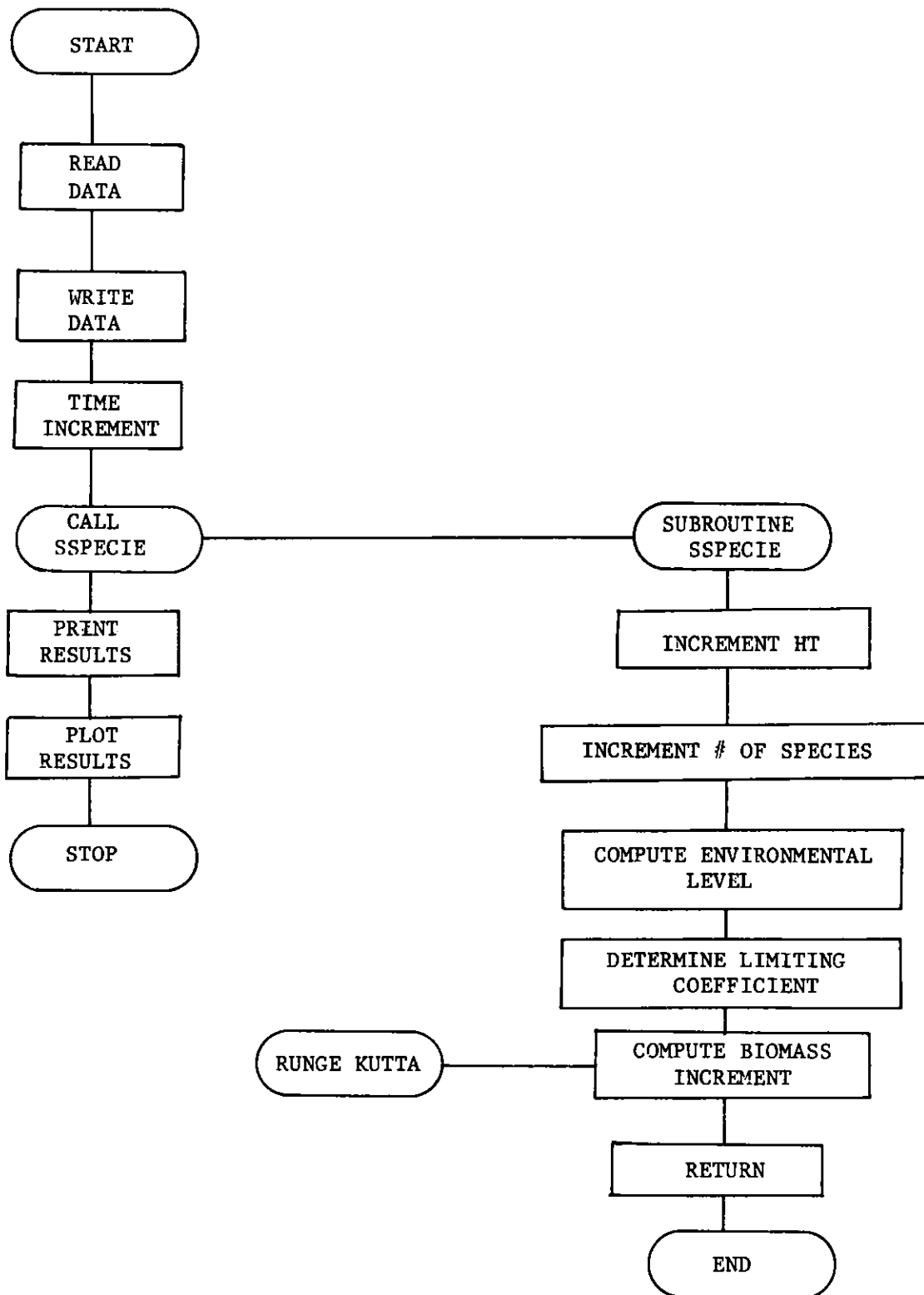


Figure 40. General flow diagram of the model, MARSH1.



general categories: site-specific data, model parameterization data, and plant parameterization data. The site-specific data include the numbers of stations along the transect, the number and species of plants to be included in the parameterization, and the latitude of the site. The model parameterization values include such information as the type of growth algorithm, the time step for the numerical integration, and intervals for printing and plotting. The plant parameterization section includes plant-specific intrinsic growth rates and the curves of species' response to the driving variables. The most frequently changed cards, the site-specific data, are placed first in the data deck, in order to facilitate manipulation.

120. Next, the time increment is set and the subroutine SSPECIE is called. A simplified flow chart of SSPECIE is included in Figure 40 but will be explained in more detail in the following paragraphs. When all plant growth values for a particular computer run are calculated the program returns to the main flow and the results of the simulation are printed or plotted with an internal plot routine, or both.

121. The bulk of the computation is performed within the subroutine SSPECIE. The flow diagram for this subroutine is shown in Figure 41.

122. Upon entering the subroutine, the initial procedures set the counters of two loops to proper initial values. The general flow is through the two DO loops--the inner loop (KO) controls the particular species of plant being dealt with at the moment, and the outer loop (NN) determines the particular station on the marsh for which

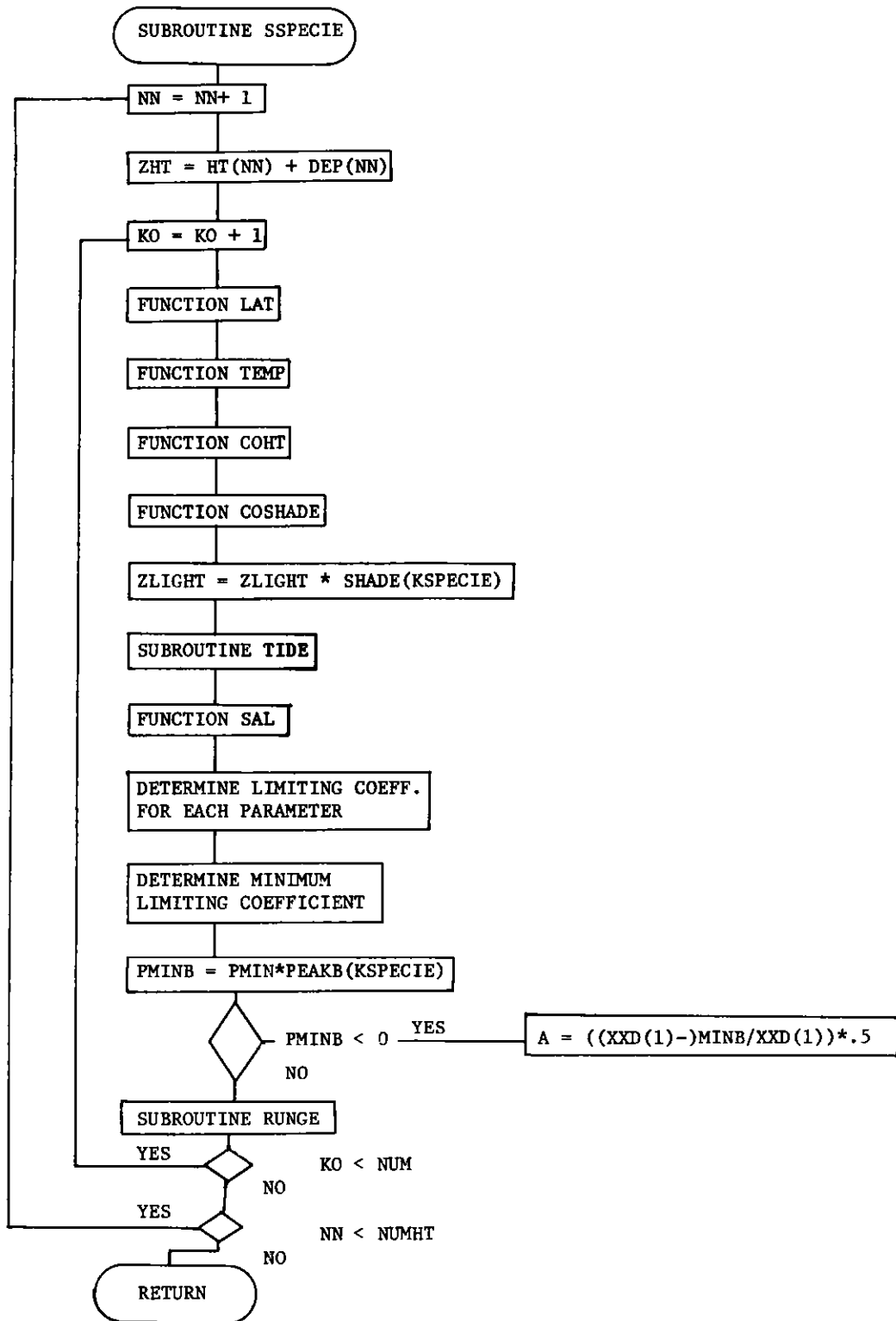


Figure 41. Flow diagram of the main subroutine, SSPECIE.

plant biomass is being calculated. The routine begins at station 1 (NN=1) and at this station calculates the biomass of each species (K)=L to NUM (where NUM = the n<sup>th</sup> species under consideration), based on the minimum limiting coefficient.

123. The first function in the subroutine SSPECIE, determines the level of solar radiation incident upon the plant species under consideration. The basis for the driving curves (Figure 42) were seasonal values calculated from twenty-year means given in the Climatological Atlas (U.S. Dept. of Commerce, 1973). These averaged seasonal values for light along the the eastern seaboard between 25° to 45°N show graphically how light may act as a control in plant growth along a latitudinal gradient. The maximum values reached during the summer are quite consistent throughout the entire range shown, suggesting that light would not be any more limiting in the higher latitudes in the summer than in the lower latitudes. However, the minimum winter light levels are dramatically different. At 30°N, roughly the latitude of Jacksonville, Florida, the light levels in December are as high as the level at 40°N, near Delaware Bay and the New Jersey marshes, in early October (Figure 42).

124. The curves shown are incorporated in the model as a set of third-order polynomial equations. The output values represent sunlight intensity at the top of the plant canopy. If a selected latitude is intermediate between any two of the five curves, a routine calculates an interpolated value.

125. Competition between plant species at a site is determined

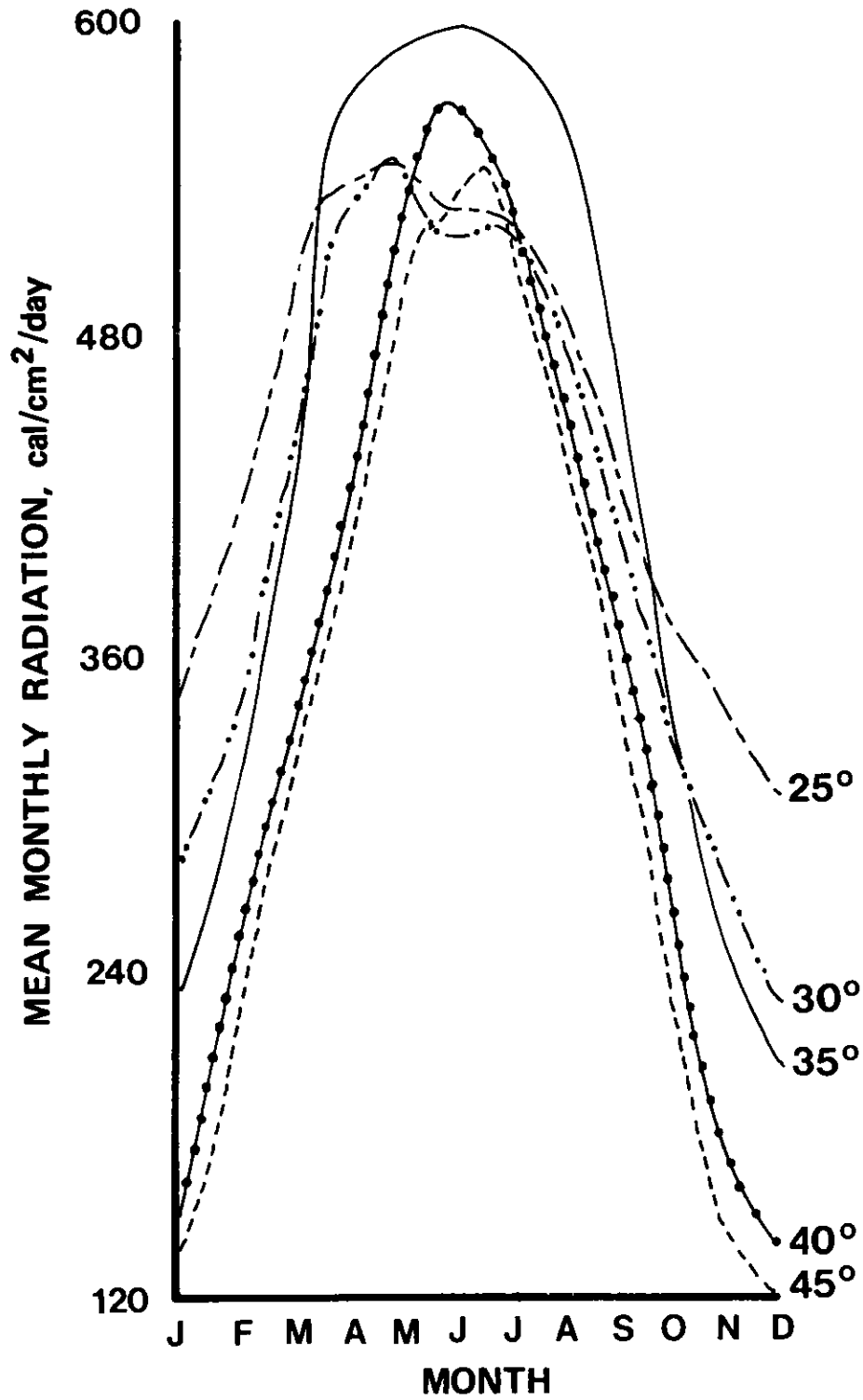


Figure 42. Seasonal solar radiation values for the eastern coast of the United States.

by FUNCTION COHT, which assumes that all individuals of a particular species at a site are equal in height. The height differentials among species are utilized to calculate the ambient light level among the plants by simulating attenuation of sunlight from the canopy to the sediment surface. The amount of radiation as a function of height within the stand is calculated in Function COSHADE (see Figure 41). It is important to note that due to differences in the density of foliage, different plant zones in the marsh have varying degrees of radiation attenuation with depth of canopy (Gates, 1968).

126. The next environmental factor considered is temperature. Again the Climatological Atlas (U.S. Dept. of Commerce, 1973) was used to obtain data on the seasonal variation of temperature as a function of latitude. At the lower latitudes, temperatures show little seasonal change up to 27°N, varying from 15-20°C. In contrast, seasonal temperatures indicate that vegetation in the high latitudes experiences a wide seasonal range of temperature with a lower mean yearly maximum (16-22°C) (see Figure 43). As with the radiation data, this information is incorporated into the model with third-order polynomial equations. These formulations are embedded in Function TEMP (see Figure 41). When latitude data are entered, the monthly variation of temperature at the location specified will be determined.

127. One of the most important environmental parameters affecting plant zonation is tidal inundation. This has been recognized by numerous investigators and was further substantiated in other sections of this report. It was shown herein that tidal inundation is the most

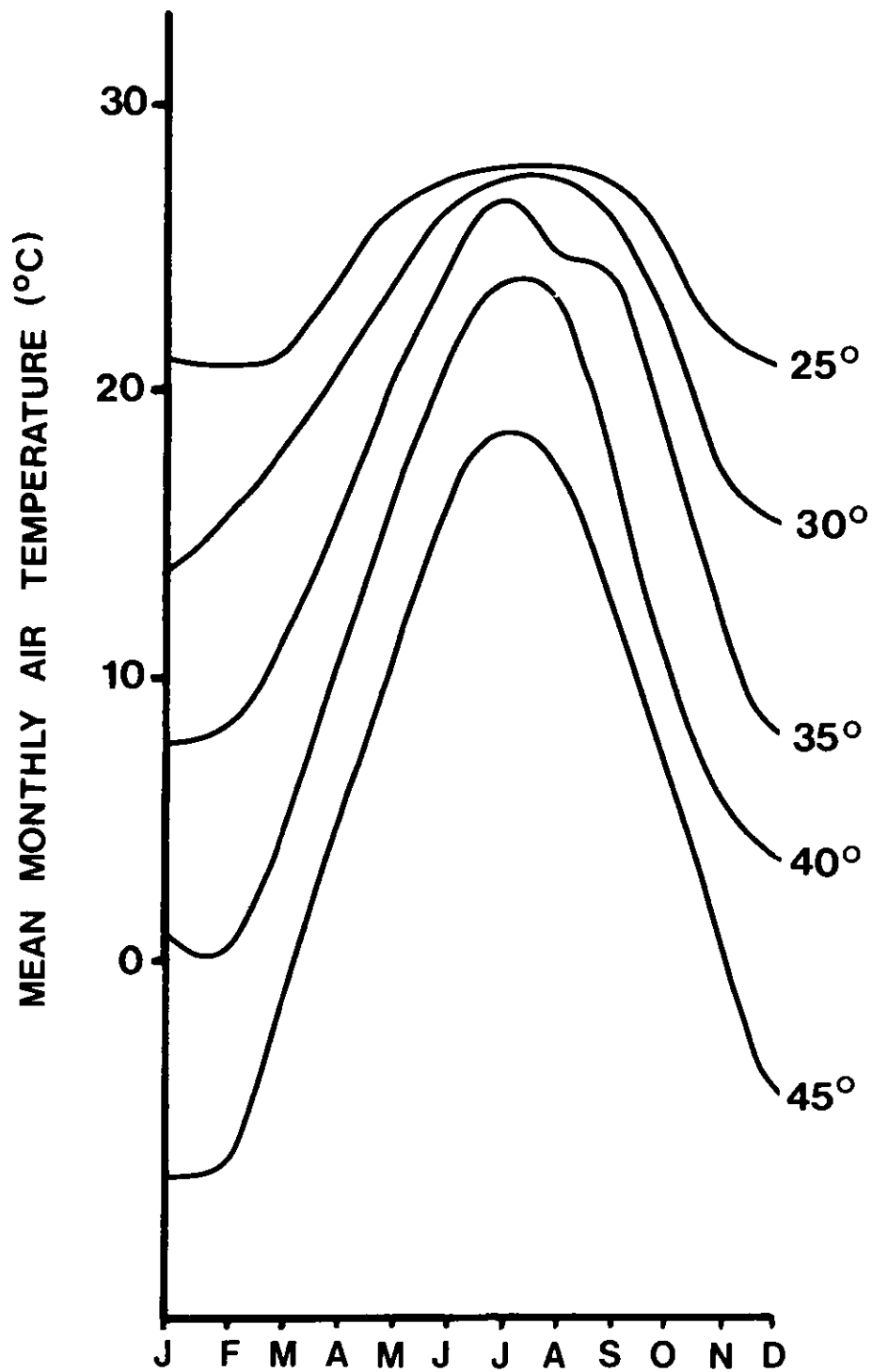


Figure 43. Seasonal temperature values for the eastern coast of the United States.

significant factor affecting the levels of marsh soil nutrients and the resultant marsh plant productivity.

128. A computer program, Program TIDE, was developed at the University of Virginia to calculate the time of tidal inundation and the number of tidal inundations per year at any height within a marsh. The data base for this program includes times and heights of each daily high and low tide at a series of stations along the East Coast from Key West to Maine. The results of this analysis (Figure 44) indicate that, with minor variations, each of the curves can be resolved into two nearly linear slopes. The lowest curve on Figure 44, the inundation curve for the Patuxent River, serves for illustration. The highest point inundated by maximal spring tides is about 1.01 m above mlw. The area from mean high tide, approximately 0.76 m, to this point receives minimal inundation, as shown by the slope of the curve at this point. However, the inundation time between mlw and mhw is an essentially linear function from 0 to 0.76 m. Thus, while the total tidal range from mlw to spring high water is 1.01 m, the upper 25 percent of the tidal range receives less than 5 percent of maximum inundation.

129. While all of the inundation curves depicted show a similar form, the pattern is extended in regions of extremely large tidal ranges, such as Maine and parts of Georgia. The relationship between the maximum tide and the inflection point is shown in Figure 45 and indicates the consistency of the relationship. Because of the high correlation between the inflection point and the maximum tidal height, the series of curves for tidal inundation can be condensed into a normalized

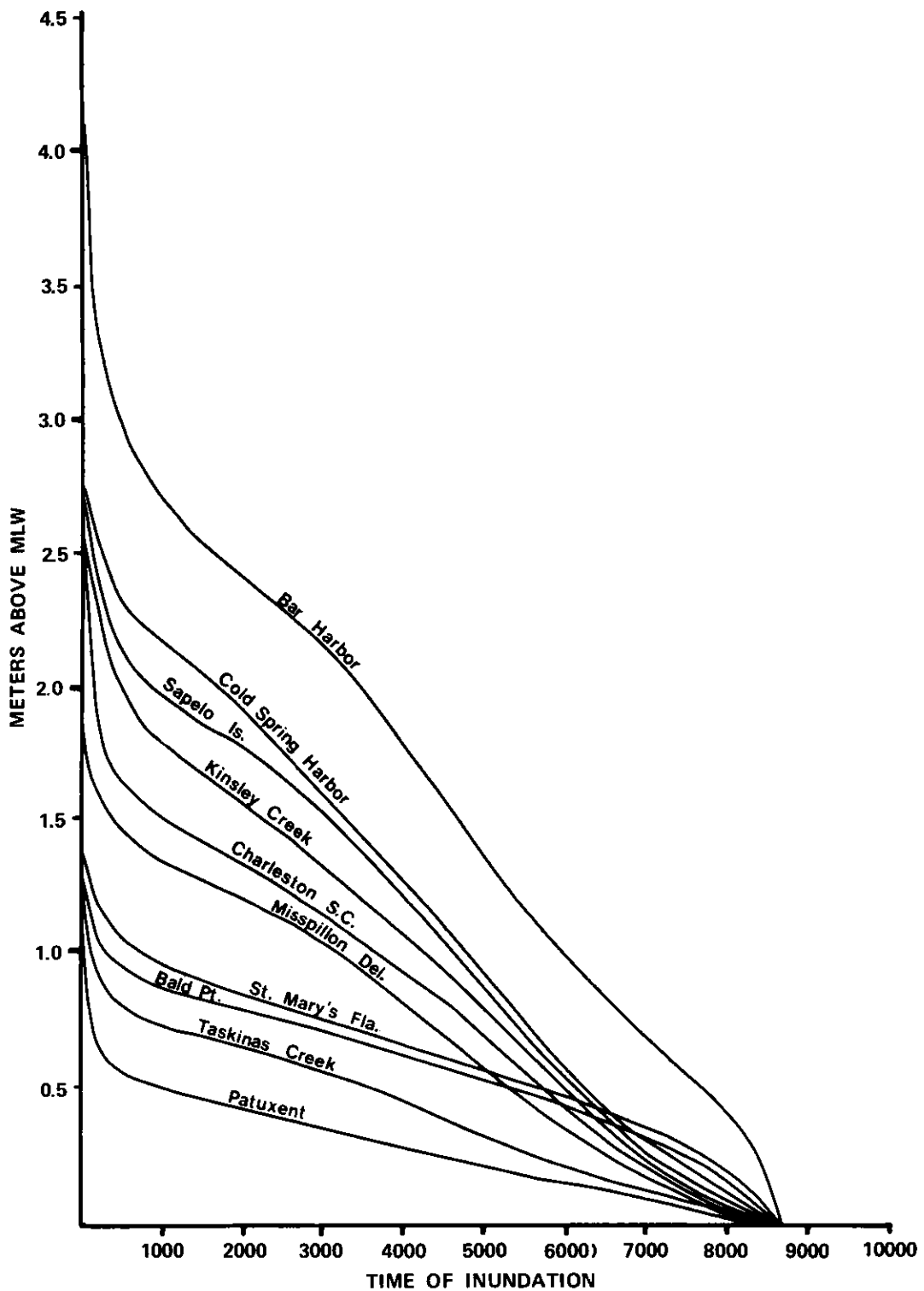


Figure 44. Inundation curves at various stations on the Atlantic and Gulf coasts.



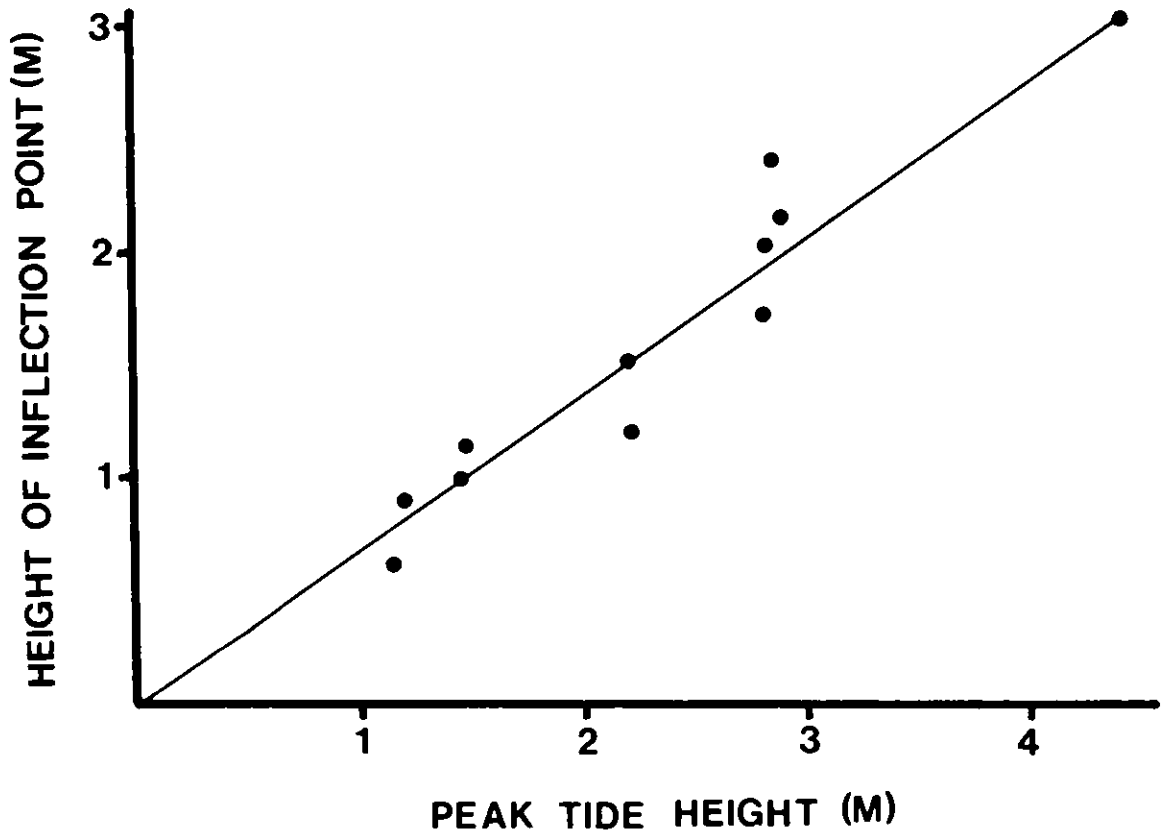


Figure 45. Relationship between peak tidal height (maximum predicted spring tide) and the projected point where the main body of the curve would intercept the vertical axis.

relationship (Figure 46) by taking each curve from Figure 44 separately and dividing the value on each axis by the maximum value for that site relating both the height and inundation values of percent of minimum. The normalized curve (Figure 46) permits calculation of the time of inundation given the height of the station of interest and height of the spring tides above mlw. The inflection point in the normalized curve occurs at 75 percent of the maximum tidal height and corresponds to mhw. This is also the level on a marsh where the interface between the S. alterniflora zone and S. patens - D. spicata zone usually occurs. The region above mhw is inundated less than 4 percent of the year.

130. Within the succession model, the relationship between relative height and percent inundation is represented by a piecewise linear formulation embedded in subroutine TIDE.

131. The final environmental parameter considered is soil salinity. Figure 12 shows changes in soil salinity along a series of transects in Bennett's and Taskinas marshes. Salinity in the hydrologically active low marsh is comparable to that found in the contiguous marsh creek. Higher salinity is found at higher elevations above mlw. This trend is simulated in the model by a piecewise linear formulation (Figure 47), which is represented by graphing relative height in a marsh (station height/mean tidal range) versus salinity. This graph shows that an increase in elevations on the marsh surface results in a soil salinity nearly double that found in the nearby marsh creek; the difference may be caused by evaporation and possibly by water loss due to transpiration. Where the marsh borders the upland, freshwater runoff dilutes soil salinity to almost 0 ppt.

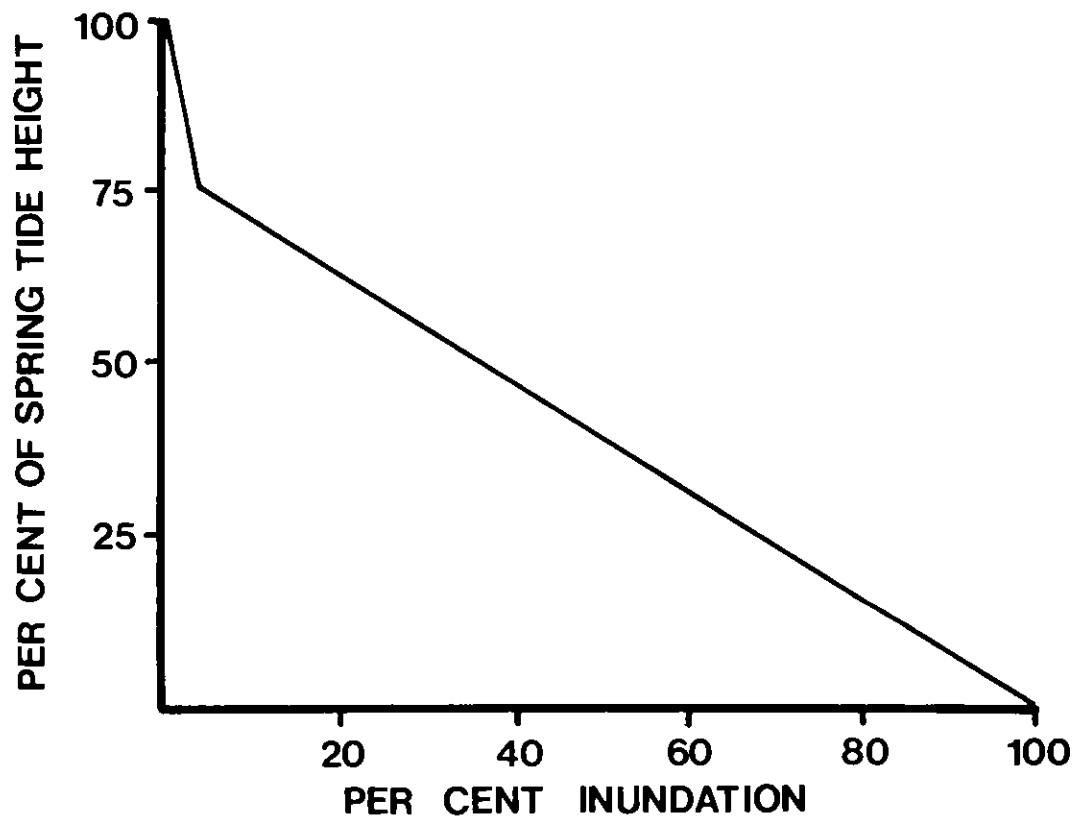


Figure 46. Normalized curve for tidal inundation as a function of height of maximum spring tide.

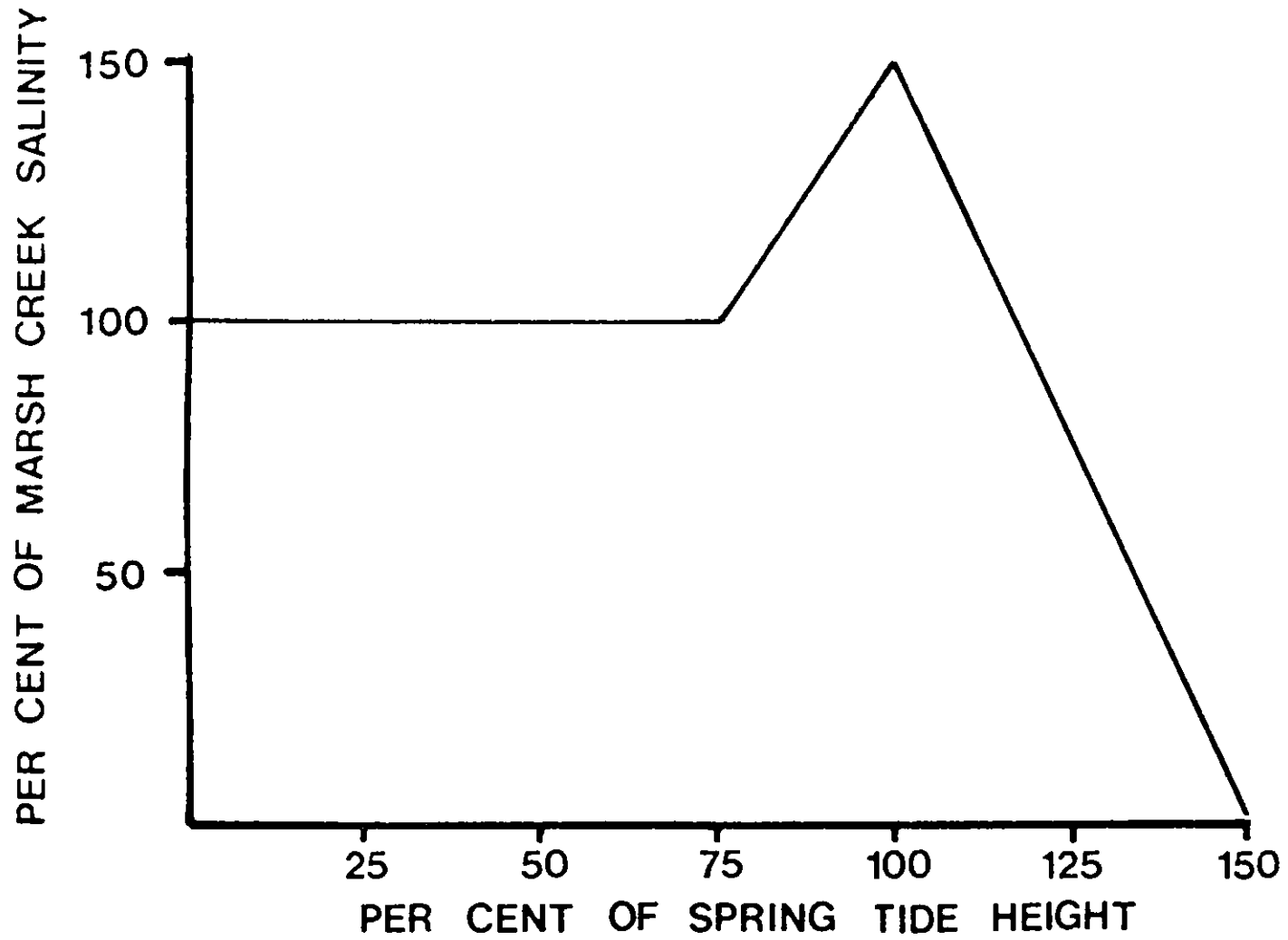


Figure 47. Marsh salinity as a function of tidal height.

132. In order to determine how much each species is curtailed by environmental interaction, a series of parameterization curves were developed. These curves, mathematically embedded within the model, represent plant response to solar radiation, temperature, tidal inundation, and soil salinity. The x-axis of the parameterization curve reflects the level of the chosen forcing function, while the y-axis represents a normalized growth response. The response of a plant to a specific level of an environmental forcing function ranges between 0 and 1; if the plant response is 0, the environmental factor has inhibited growth; a response of 1 indicates the level of the factor is optimum for growth.

133. Figure 48 depicts the responses of S. alterniflora to temperature, radiation, percent inundation, and salinity. The radiation and temperature parameterization curves are similar to those presented by Gates (1968). These curves represent generalized plant responses to the above parameters, since they were generated from data collected on many phylogenetically divergent species. The response of S. alterniflora to salinity reflects the fact that this plant is considered a facultative halophyte. Therefore, an increase in salinity results in a decreased biomass response. The percent inundation parameterization curve indicates the tolerance of this plant to submergence since this plant is found only in the low marsh.

134. The response of S. patens and D. spicata to each of the environmental parameters is depicted in Figure 49. Competition between the species is not modeled explicitly; however, the data do reflect natural situations. Lacking data to the contrary, the parameterization

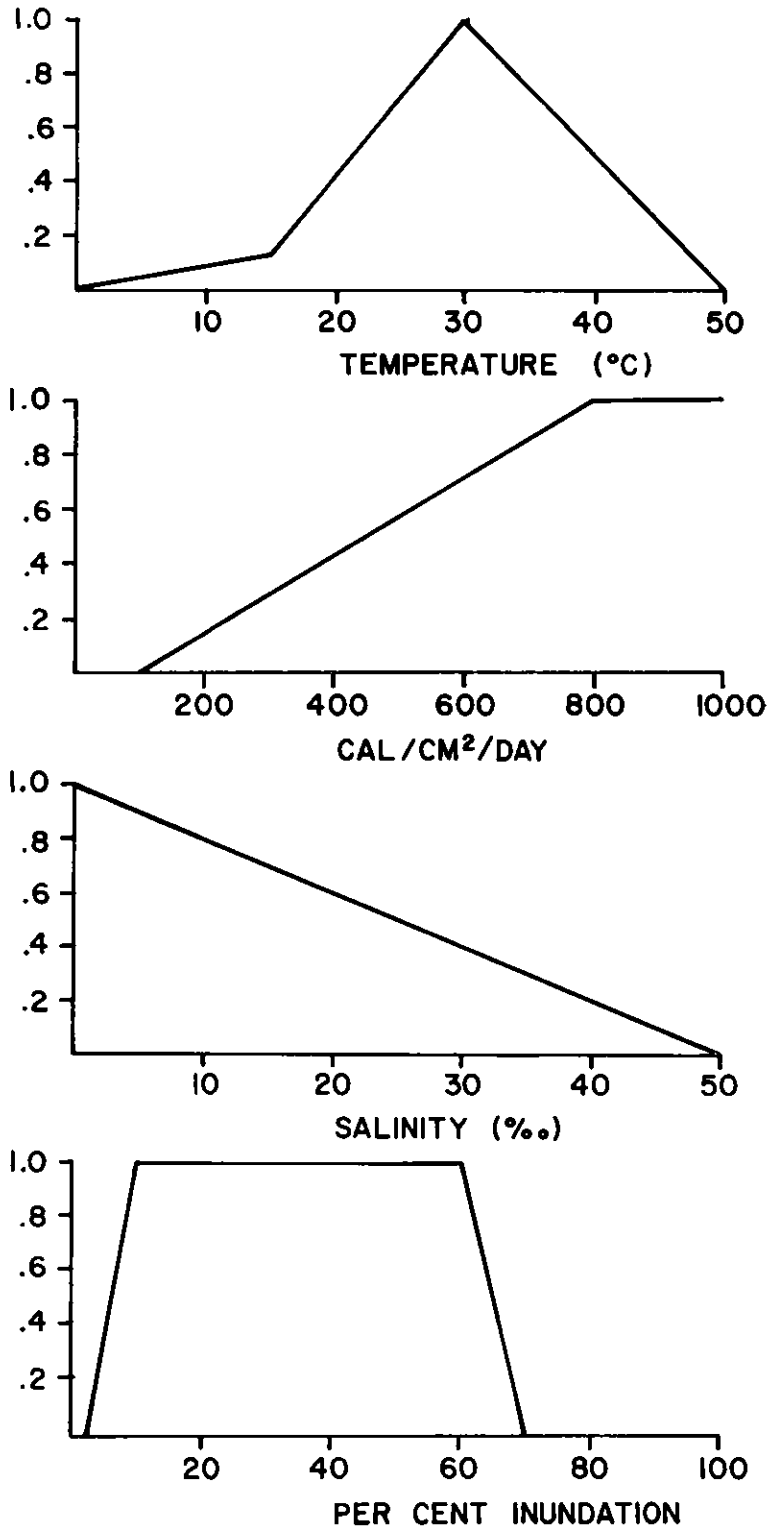


Figure 48. Normalized growth response of *Spartina alterniflora* to environmental driving parameters.

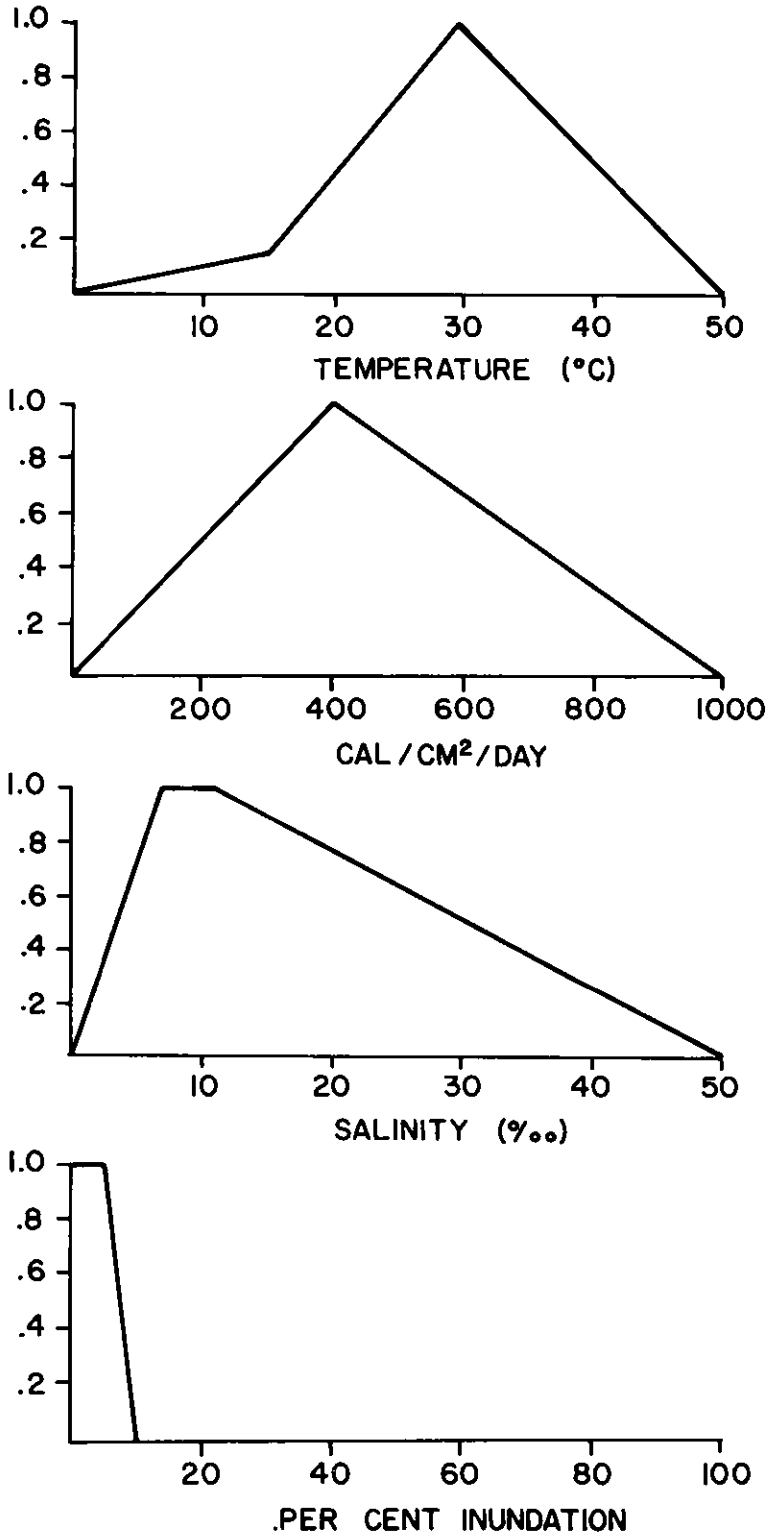


Figure 49. Normalized growth response of *Spartina patens* and *Distichlis spicata* to environmental driving parameters.

curves for radiation and temperature are assumed to be identical to those of S. alterniflora. However, the actual responses of S. alterniflora and S. patens are not identical, since their heights and the resultant shading effects are usually quite different. It was assumed that S. patens is better adapted to higher salinities since it is found in the high marsh. This is reflected in the salinity parameterization curve. Similarly, as a result of its position in the marsh, maximum growth response of S. patens to percent inundation was found at a lower value than that of S. alterniflora.

135. D. spicata and S. patens have similar responses to the four environmental parameters (Figure 49). The difference lies in the fact that the tolerance to salinity and percent inundation of D. spicata is greater than that of S. patens. Parameterization curves for S. alterniflora, S. patens, and D. spicata have been discussed because these three plants dominate the marsh vegetation in many localities, but curves for any other species can be formulated if the necessary field data are available.

136. At this point in the program a plant response value or limiting coefficient is determined for each species and each environmental factor. The assumption that certain environmental parameters are largely responsible for restricting growth (law of the minimum) simplifies the task of determining the relative effect of the limiting factors. At each calculation the limiting factor is stored, so that the operator may recall at any time the parameter that is limiting a particular species. With this information, a Runge-Kutta numerical



integrating subroutine is accessed to calculate plant productivity. Within this subroutine two options for calculating productivity are available: a logistic method and a maximum productivity method. Several assumptions are inherent in using these methods. In the logistic formulations productivity is determined as a function of the intrinsic growth rate, the limiting coefficient, and the contemporaneous biomass. Also included is a negative feedback term associated with environmental inhibition. The maximum productivity algorithm is the product of the limiting coefficient multiplied by maximum productivity per unit time. Within this model alterations are made for relative elevation and all species of interest. The output yields plotted and printed biomass estimates for each species as a function of time and space.

137. As described above, the marsh model is composed of a series of point models that are linked spatially (Figure 40). The real world basis of this linkage is the lateral transport of water-borne sediments. Within the model, relative elevation in the marsh controls, to a great extent, the interaction between plant and environment. At each location in the marsh, allowance is made for a temporal increment of sediment, and the resulting changes in elevation control the spatial distribution of plant species.

138. The above discussion serves to illustrate the logic and assumptions inherent in the succession model. A complete listing of the model, with detailed instructions on assembly of the data cards and use, is contained in Appendix B. Using only the parameterization curves given for the three species utilized, a vast number of simulations are possible. The following discussion will illustrate the

results of one set of simulations.

139. For these experimental simulations, latitude and tidal range were varied to study the effect of elevation on plant growth and species location on the marsh surface. The first simulation (Figures 50-55), the growth of plants on salt marsh at latitude 30°N, with a tidal creek salinity of 20 o/oo, a spring tidal range of 1.83 m, and a mean tidal range of 1.3 m was depicted at stations varying from 0.31 to 1.33 m above mlw. The three letters at the right-hand side of the figure illustrate which of the four environmental variables was limiting for each species (T = temperature, H = tidal height, S = salinity, and L = light). The first letter refers to the environmental variable limiting the first species listed, the second letter refers to the second species, and the third letter refers to the third species.

140. S. alterniflora was found growing in the low marsh as expected with growth beginning at 0.62 m above mlw or near the mean tidal height. With an increase in elevation, the pure stand of S. alterniflora graded into a mixed association including S. patens and D. spicata near the mean high tide mark. On Figures 50-55, the graphs indicate species 1 (S. alterniflora) and 3 (D. spicata) only. S. patens (#2) was present but had the same value as D. spicata. When this occurs, the plotting routine prints the single highest species number encountered. In the high marsh above mlw only S. patens and D. spicata were found. In this simulation, S. patens and D. spicata were excluded from the low marsh due to excessive inundation, while growth on the high marsh for these plants was most limited due to light and temperature.

141. In the second simulation shown here (Figures 56-60), the

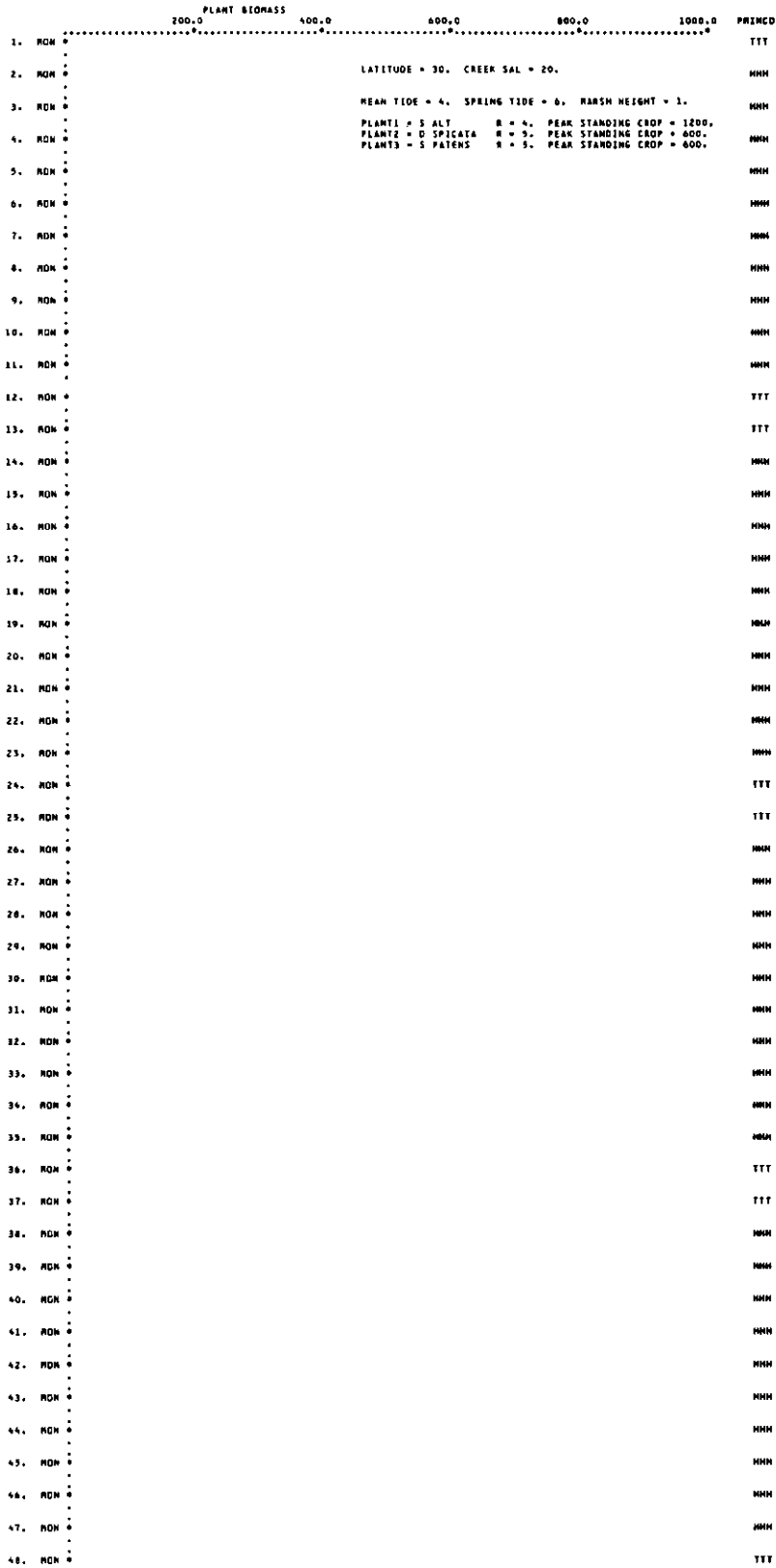


Figure 50. Results of a simulation at latitude 30°N, with a creek salinity of 20 o/oo, a mean tide range of 4 ft (1.22 m), a maximum range of 6 ft (1.83 m), and a time period of 48 months. This first figure depicts the simulation at the 1-ft (0.31-m) elevation above mlw on the marsh.

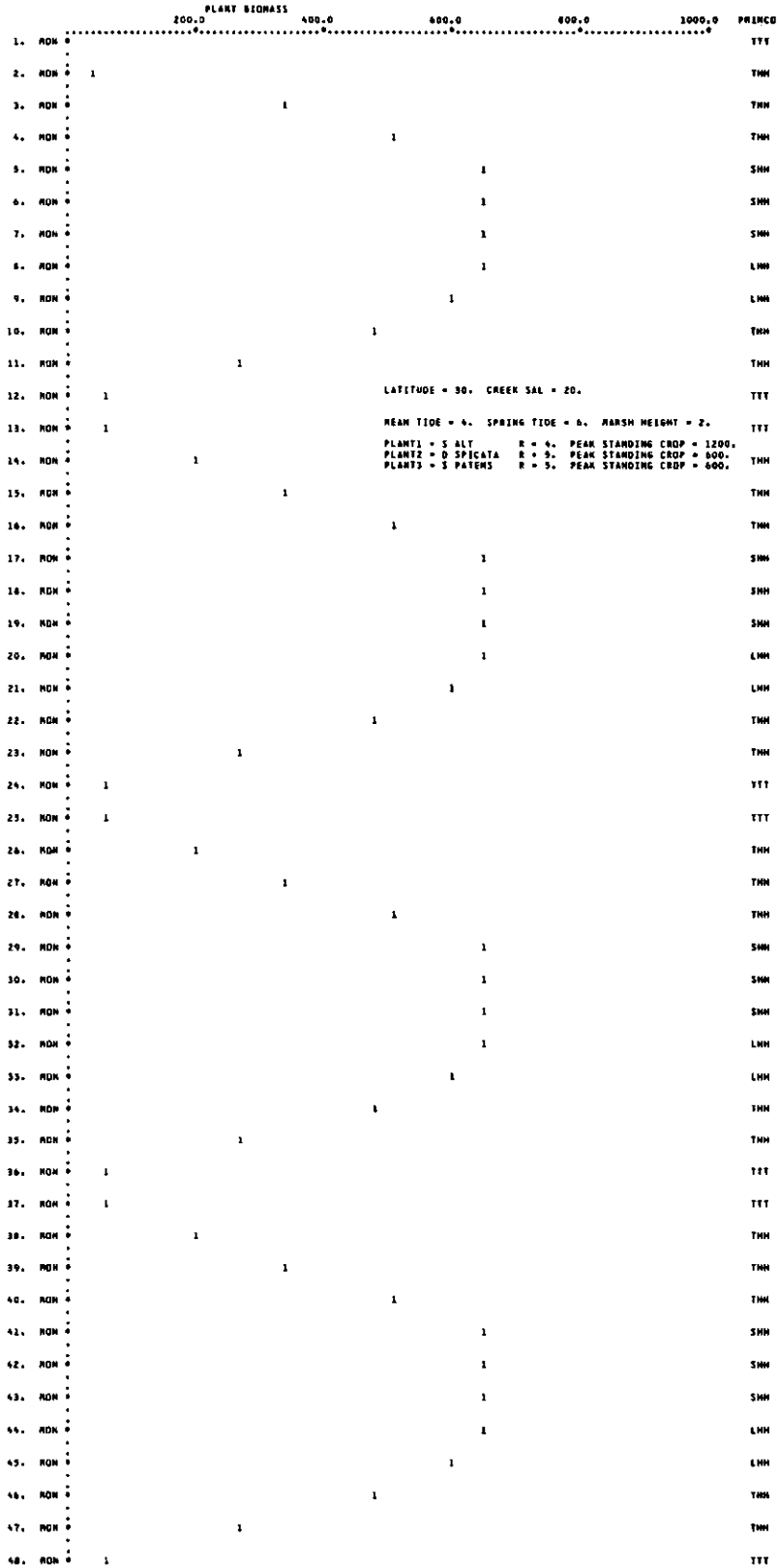


Figure 51. Depicts the simulation at the 2-ft (0.61-m) elevation above mlw on the marsh.

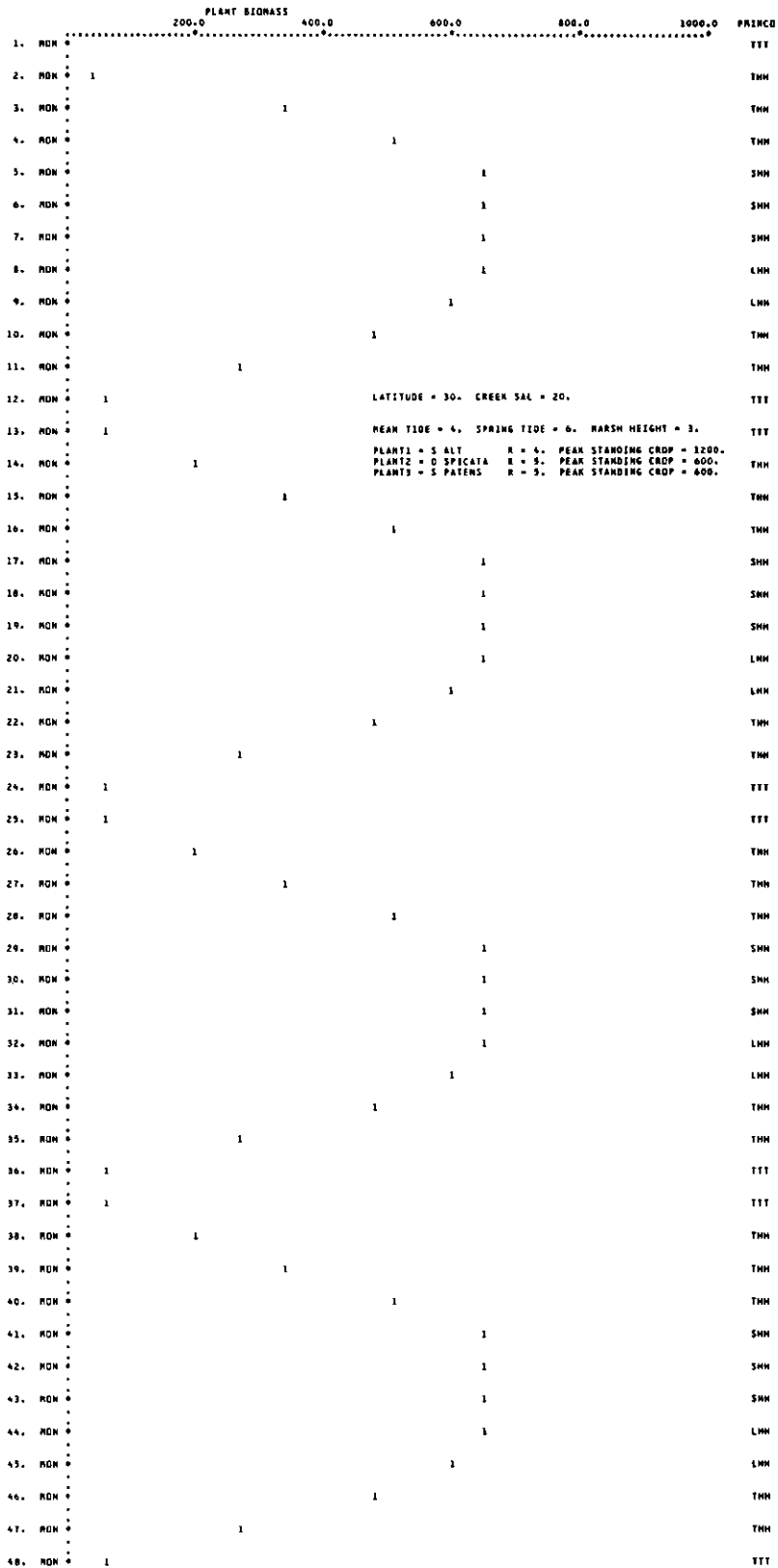


Figure 52. Depicts the simulation at the 3-ft (0.91-m) elevation above mhw on the marsh.

		PLANT BIOMASS							
		200.0	400.0	600.0	800.0	1000.0	PRINCD		
1.	NDM						TTT		
2.	NDM	1 3					TTT		
3.	NDM		3	1			HTT		
4.	NDM			3	1		LTT		
5.	NDM		1		3		LTT		
6.	NDM		1			3	LTT		
7.	NDM		1			3	LTT		
8.	NDM		1			3	LTT		
9.	NDM		1			3	LTT		
10.	NDM		1		3		LTT		
11.	NDM		1 3				LTT		
12.	NDM		31				TTT		
13.	NDM		31				TTT		
14.	NDM		3	1			TTT		
15.	NDM			3	1		HTT		
16.	NDM				3	1	LTT		
17.	NDM			1		3	LTT		
18.	NDM			1		3	LTT		
19.	NDM			1		3	LTT		
20.	NDM			1		3	LTT		
21.	NDM			1		3	LTT		
22.	NDM			1		3	LTT		
23.	NDM			1 3			LTT		
24.	NDM			31			TTT		
25.	NDM			31			TTT		
26.	NDM			3	1		TTT		
27.	NDM				3	1	HTT		
28.	NDM					3	1	LTT	
29.	NDM				1		3	LTT	
30.	NDM				1		3	LTT	
31.	NDM				1		3	LTT	
32.	NDM				1		3	LTT	
33.	NDM				1		3	LTT	
34.	NDM				1		3	LTT	
35.	NDM				1 3		LTT		
36.	NDM				31		TTT		
37.	NDM				31		TTT		
38.	NDM				3	1	TTT		
39.	NDM					3	1	HTT	
40.	NDM						3	1	LTT
41.	NDM				1		3	LTT	
42.	NDM				1		3	LTT	
43.	NDM				1		3	LTT	
44.	NDM				1		3	LTT	
45.	NDM				1		3	LTT	
46.	NDM				1		3	LTT	
47.	NDM				1 3		LTT		
48.	NDM				31		TTT		

LATITUDE = 30. CREEK SAL = 20.  
 NEAN TIDE = 4. SPRING TIDE = 6. MARSH HEIGHT = 4.  
 PLANT1 = 5 ALT R = 5. PEAK STANDING CRUP = 1200.  
 PLANT2 = 0 SPICATA R = 5. PEAK STANDING CRUP = 800.  
 PLANT3 = 5 PATEMS R = 5. PEAK STANDING CRUP = 600.

Figure 53. Depicts the simulation at the 4-ft (1.22-m) elevation above mhw on the marsh.

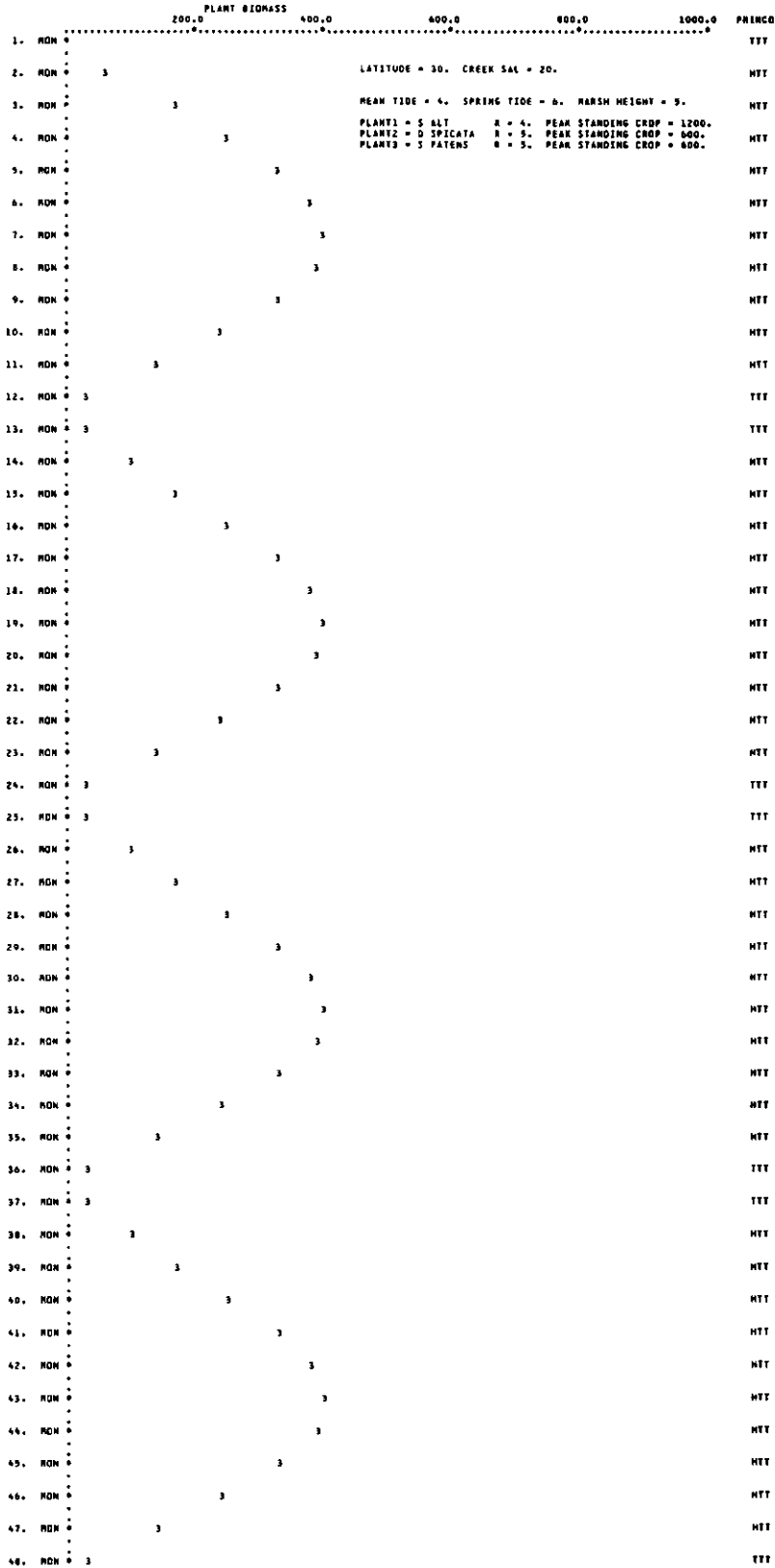


Figure 54. Depicts the simulation at the 5-ft (1.52-m) elevation above mhw on the marsh.

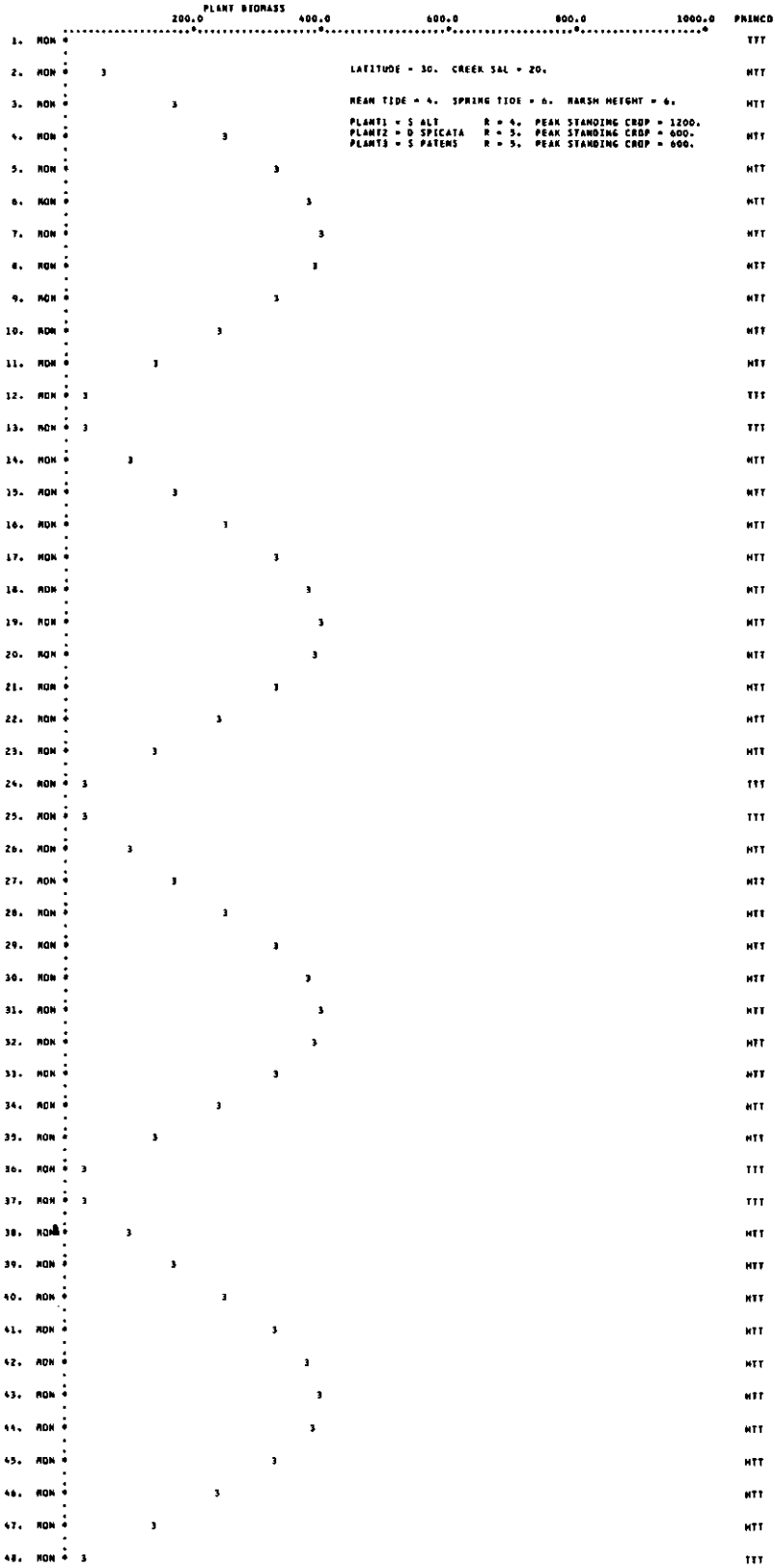


Figure 55. Depicts the simulation at the 6-ft (1.83-m) elevation above mlw on the marsh.



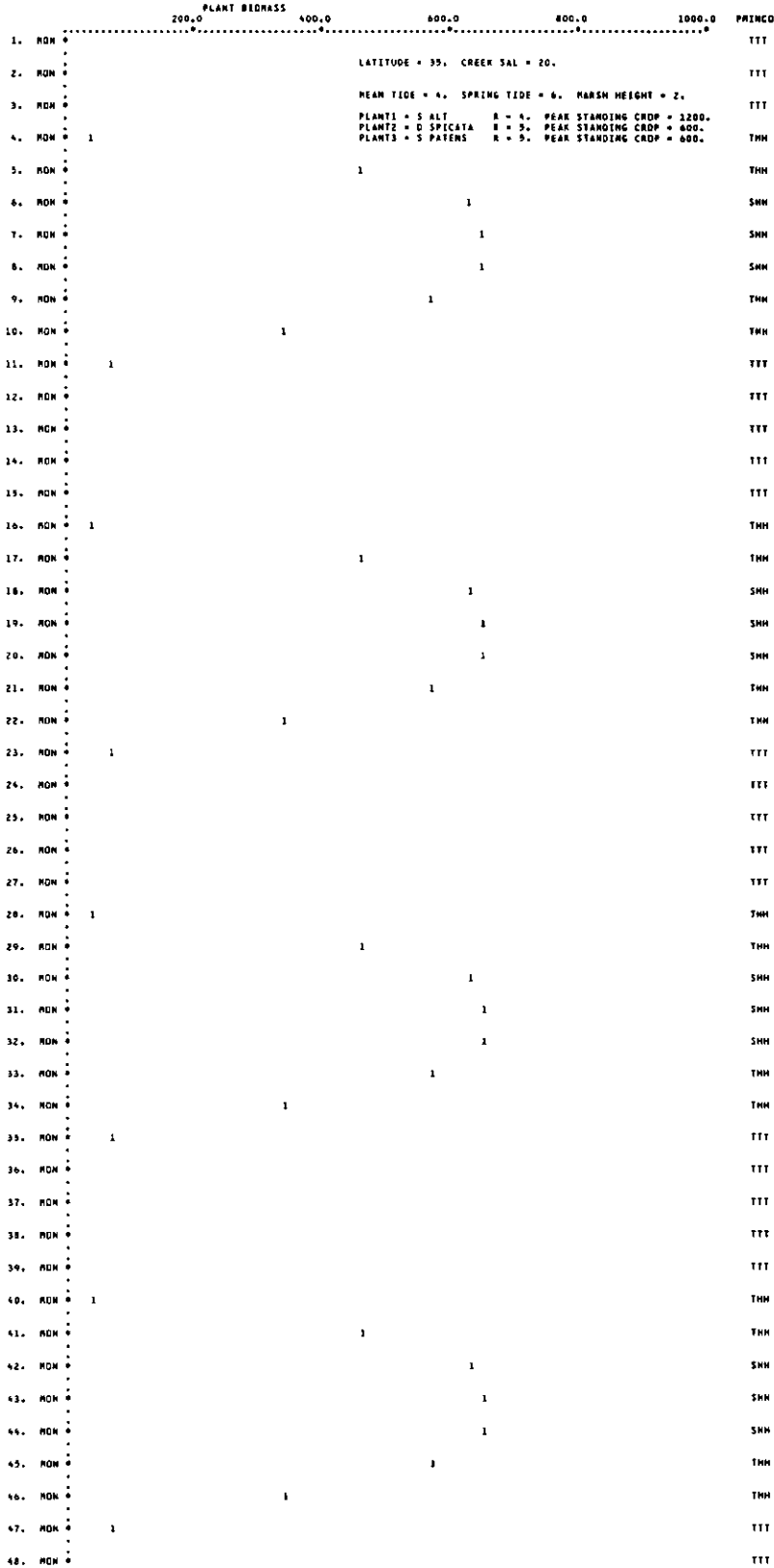


Figure 56. Results of a simulation at latitude 35°N, with a creek salinity of 20 o/oo, a mean tide range of 4 ft (1.22 m), and a maximum range of 6 ft (1.83 m) for 48 months. This figure depicts the simulation at the 2-ft (0.61-m) elevation above mhw on the marsh.

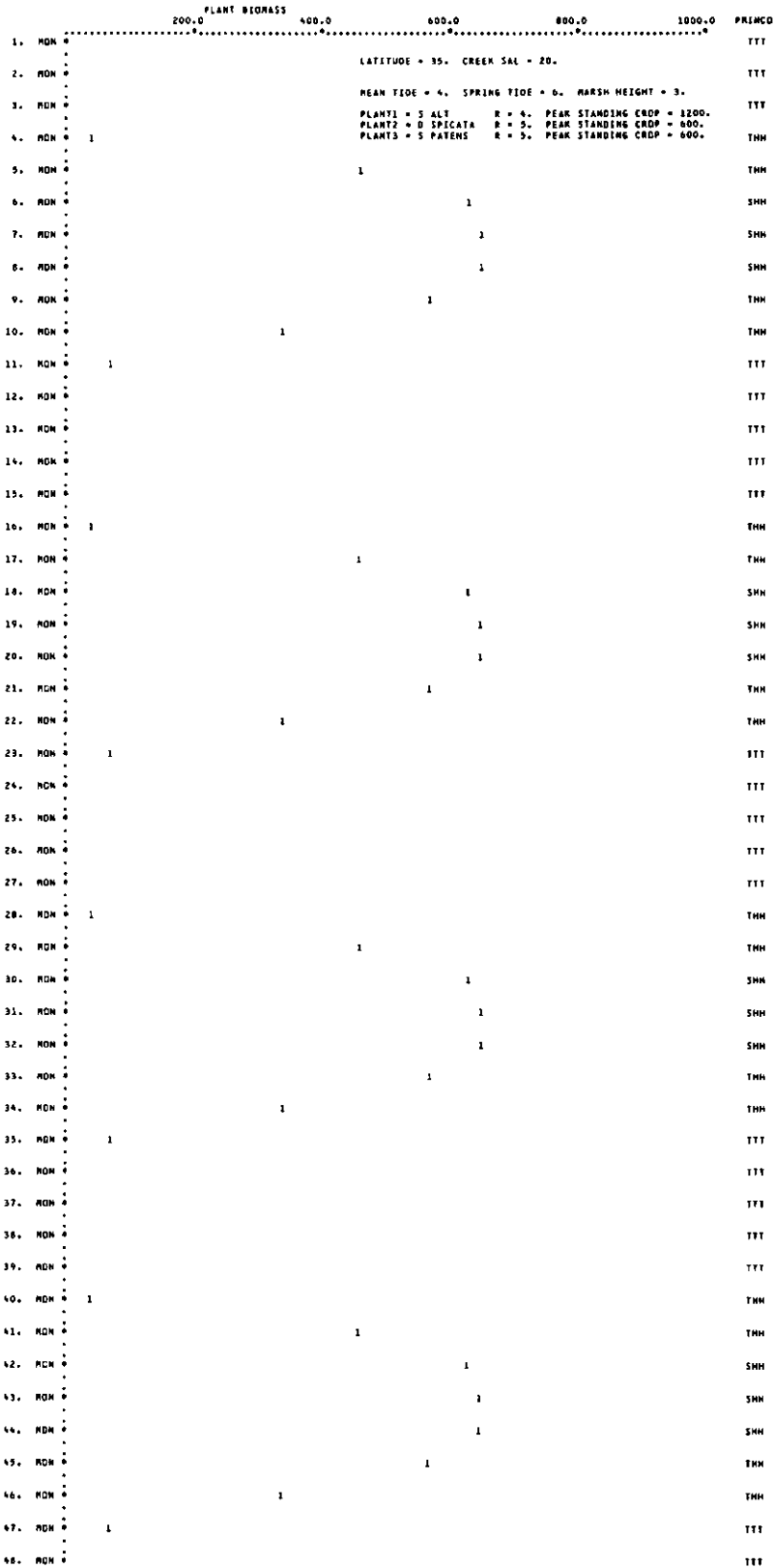


Figure 57. Depicts the simulation at the 3-ft (0.91-m) elevation above mhw on the marsh.

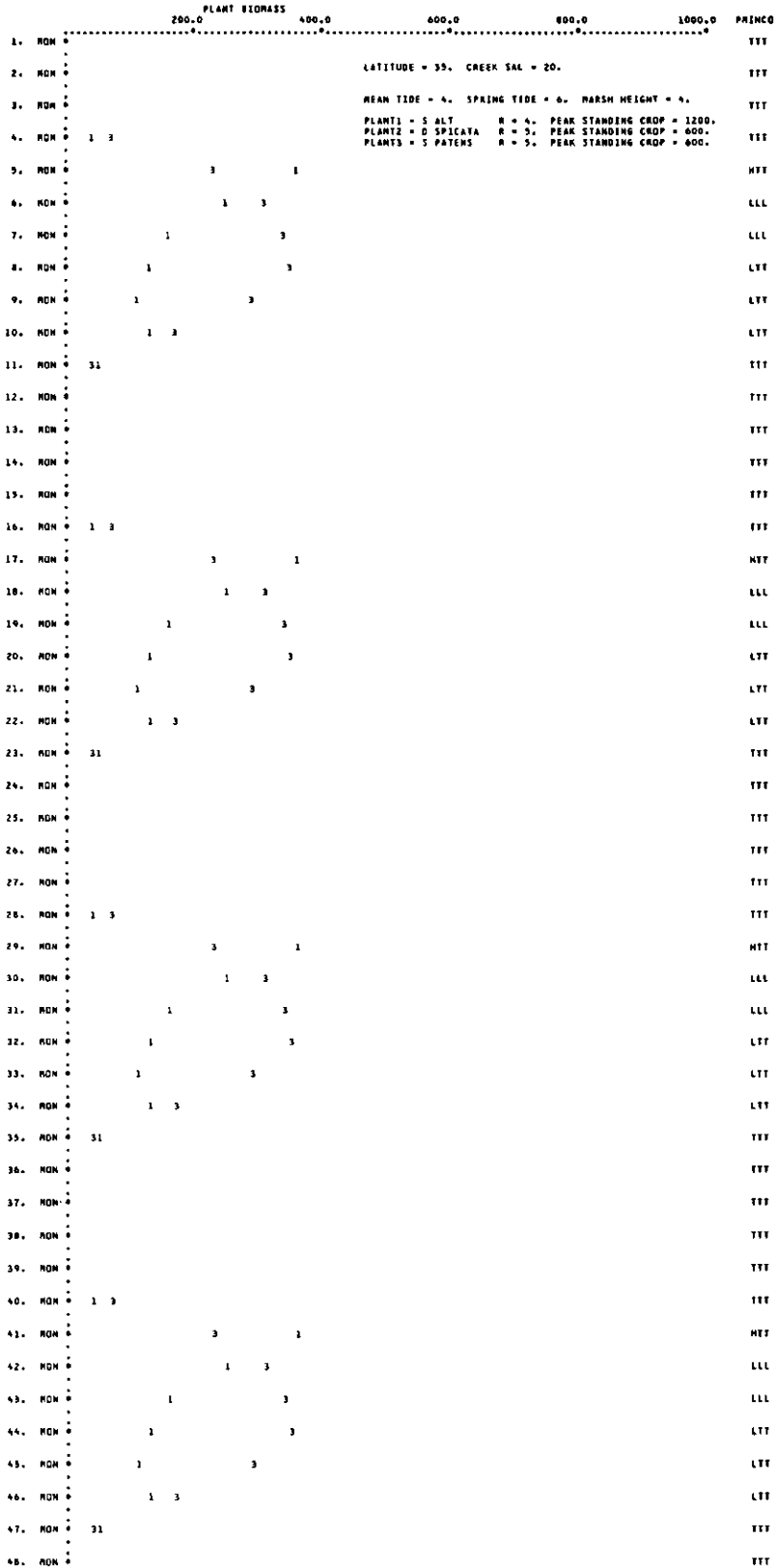


Figure 58. Depicts the simulation at the 4-ft (1.22-m) elevation above mlw on the marsh.

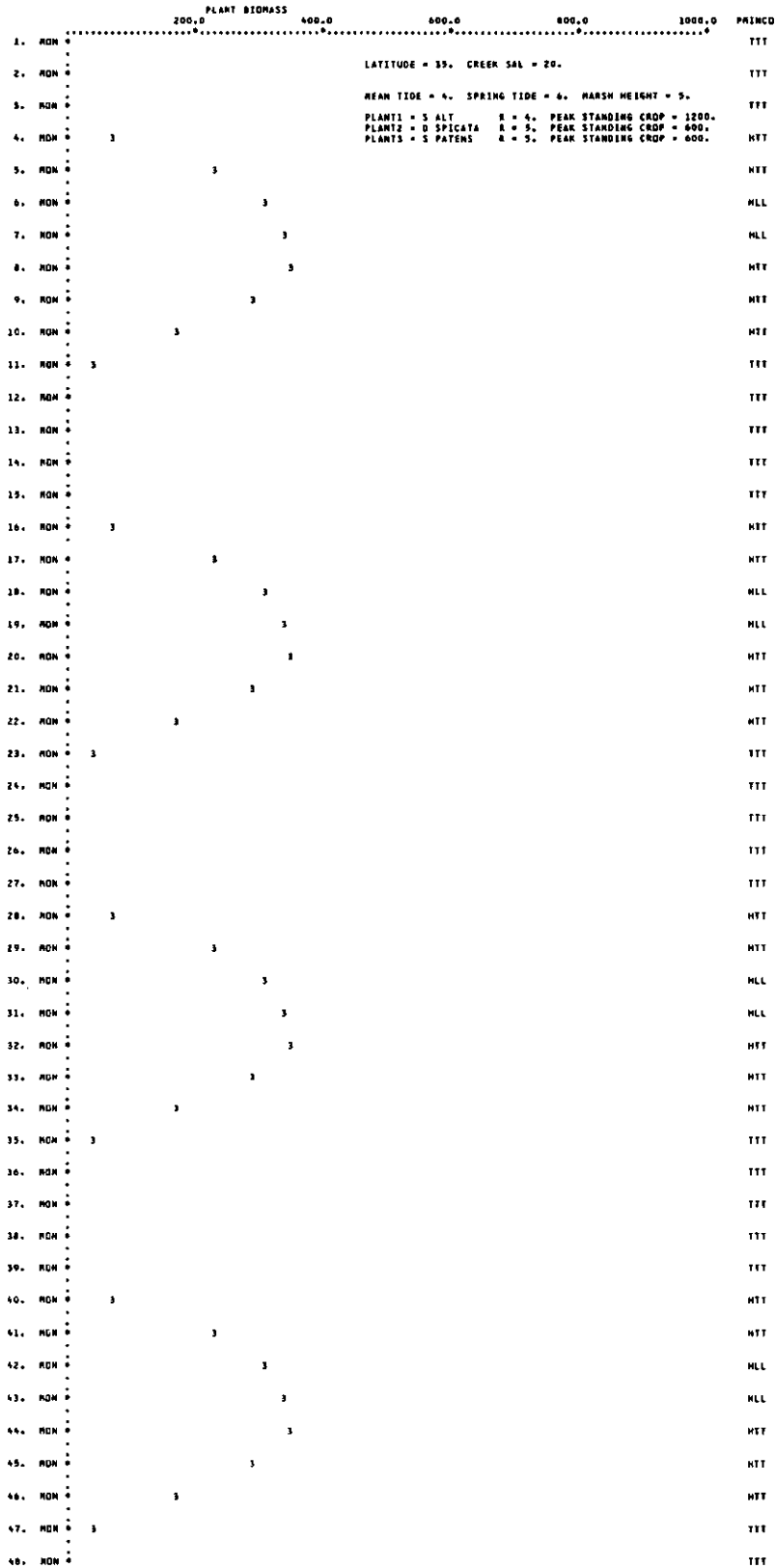


Figure 59. Depicts the simulation at the 5-ft (1.52-m) elevation above mlw on the marsh.

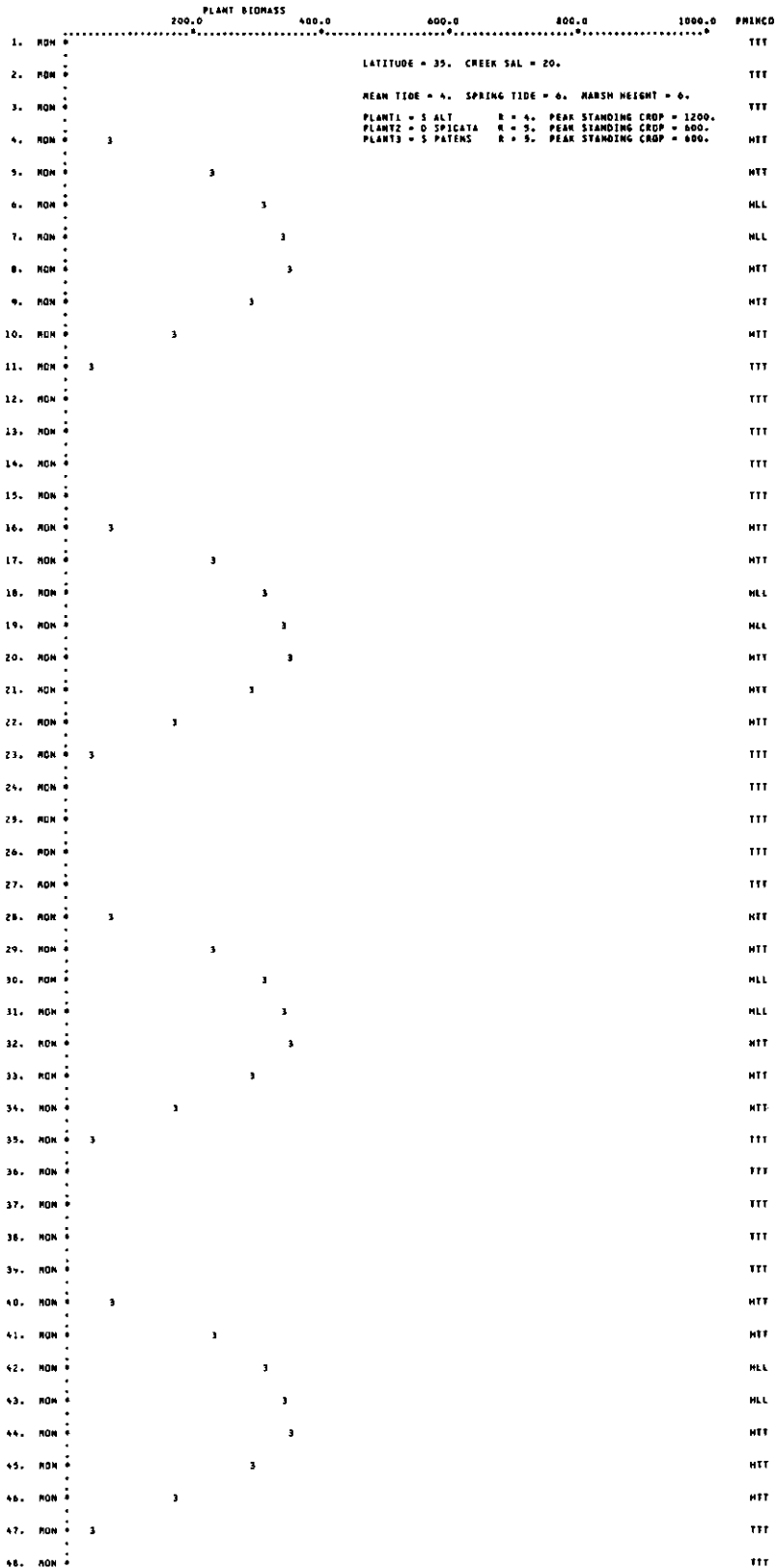


Figure 60. Depicts the simulation at the 6-ft (1.83-m) elevation above mlw on the marsh.

marsh was located at a latitude of  $35^{\circ}\text{N}$ , and all other parameters were held constant. The location of species within the marsh with respect to tidal height was similar to that for the marsh at  $30^{\circ}\text{N}$ , but the temporal change of biomass and peak biomass varied considerably. In this more northerly area, the growing season would be shorter. This was reflected in a more rapid increase in biomass after growth is initiated. A slightly lower peak biomass level was found at this higher latitude, but because the growing season is shorter, the total area under the curve is considerably less than at  $30^{\circ}\text{N}$ . This relationship was found for all locations within the marsh.

142. The simulations used for illustration showed that radiation, temperature, and, particularly, tidal inundation controlled plant growth and plant location on the marsh surface. Salinity was seldom seen to be the limiting factor which generated the above results (Figures 50-60). This, however, may be largely due to an artifact of the parameterization of the model.

143. No model is any better than the data and constructional information used to generate the model. The model presented is of more utility than the results presented here. The results are limited by the parameterizations that were available when this model was originally constructed. However, the model was not so structured, and is limited only by the knowledge available when it is utilized. Therefore, all new data and theory generated that affects growth, distribution, and succession on a marsh may be incorporated in future simulations.

## PART VIII: SUMMARY AND CONCLUSIONS

144. At the outset of this project three parallel studies were designed to gain insight into the processes that determine plant growth and succession on estuarine salt marshes. The first was concerned with both the daily and seasonal ranges of marsh physicochemical parameters and the subsequent biotic responses within different vegetative zones. A series of marshes were visited and surveyed, but effort was concentrated on two intensive sites in Virginia.

145. The second study involved obtaining continuous records of several selected physical and chemical parameters from within the vegetation zone. This required the development of a continuous recording data monitoring system suitable for use in the estuarine system.

146. The third study of the project was the development of a simulation model of plant growth and succession on the marsh. The initial models were developed using information available in the literature on the functions of estuarine salt marshes. As the project progressed, information was added from field studies and contact with other scientists in the field.

147. Data from the first study were analyzed with correlation analysis of plant growth related to habitat condition and showed clearly that the growth of S. alterniflora exhibited a strong positive correspondence with elevation and tidal inundation at both major study sites. In addition, this plant demonstrated a negative correlation with soil salinity, while the standing crop was significantly correlated with iron availability.

148. For S. patens and D. spicata, the measured responses to tides differed conspicuously. At one site where the high marsh was rarely flooded, the growth of neither species was closely related to inundation or elevation. At the other intensively studied site, which receives flooding during spring tides, there was a strong correlation of tide with S. patens (positive) and D. spicata (negative) growth. Wherever regular flooding takes place the growth of S. alterniflora and S. patens demonstrated a negative correlation with soil salinity while the more salt-tolerant D. spicata was positively correlated with salinity.

149. The fact that habitat factors are closely associated with both tide and plant growth wherever fairly regular inundation occurs suggests that inundation acts as a master variable influencing plant growth both directly and by controlling other features of the marsh habitat.

150. Conclusions drawn from the second study and the records of continuous field monitors tend to reinforce the concept of tidal inundation as the master variable for explaining plant distribution, especially in the region between the low tide marsh and the upper extent of spring high tides. The power spectrum analysis of continuous monitoring data from the marsh with an infrequently flooded high marsh provides a good example. The surface temperatures from the S. alterniflora zones showed the major power peak to be at 0.089 cycle/hour, which is the tidal frequency for this area, while in the higher S. patens - D. spicata zone, the frequency with the largest power



component is that of nearly 1 cycle/day, corresponding to the input of solar radiation. The analyses of pH data further showed a large spike of the tidal frequency in the low S. alterniflora marsh, but not in the high marsh.

151. The third objective of this project, the development of a marsh successional model, was designed around the concept of species modules that depict the growth dynamics of S. alterniflora, S. patens, and D. spicata.

152. The species modules were combined into a point model that simulates the growth of each species on a particular square meter of marsh surface. Coupling of a series of point models enables simulation of plant growth both temporally and spatially across the marsh. The total marsh model is driven by four environmental variables: solar radiation, temperature, soil salinity, and tidal inundation. A special subprogram was developed to calculate the time of tidal inundation and number of tidal inundations per year at any height within a marsh.

153. Experimental simulations demonstrated that radiation, temperature, and, particularly, tidal inundation were responsible for controlling plant location and growth on the marsh surface. Salinity, at least in these preliminary runs, seldom appeared to be a limiting factor. In the final analysis, the model appears to have great utility for future research, but is limited at the moment by incomplete parameterizations.

## REFERENCES

- Adams, D. A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. *J. Ecology*. 44: 445-456.
- Albrecht, W. A. 1941. Soil organic matter and ion availability for plants. *Soil Sci.* 51: 487-494.
- Allen, G. W. 1964. Estuarine destruction--a monument to progress. 29th N. Amer. Wildlife Conf. pp. 324-331.
- Bloom, A. L. 1964. Peat accumulation and compaction in a Connecticut coastal marsh. *J. Sed. Petrol.* 34(3): 599-603.
- Bloomfield, C. 1963. Mobilization phenomena in soils. Rothamsted Exp. Sta. Rep., pp. 226-239.
- Broome, S. W., W. W. Woodhouse, and E. D. Seneca. 1973. An investigation of propagation and the mineral nutrition of Spartina alterniflora. Sea Grant Publication UNC-SG-73-14.
- Buckman, H. O. and N. C. Brady. 1969. The Nature and Properties of Soils. 7th edition. Macmillan Co., New York.
- Buttery, B. R. and J. M. Lambert. 1965. Competition between Glyceria maxima and Phragmites communis in the region of Surlingham Broad. I. The competition mechanism. *J. Ecol.* 53: 163-181.
- Buttery, B. R., W. T. Williams, and J. M. Lambert. 1965. Competition between Glyceria maxima and Phragmites communis in the region of Surlingham Broad. II. The fen gradient. *J. Ecol.* 53: 183-195.
- Chabreck, R. H. 1972. Vegetation, water and soil characteristics of the Louisiana Coastal Region. *Agric. Exp. Stat. La. St. Univ. Bull.* #644.
- Chapman, S. B. 1967. Nutrient budgets for a clay heath ecosystem in the South of England. *J. Ecology*. 55: 677-689.
- Chapman, V. J. 1938. Studies in salt marsh ecology. Section I-III. *J. Ecol.* 26: 144-179.
- Connecticut State Board Fisheries and Game. (undated) The tidal marsh and spoil disposal. 2pp.
- Cooper, A. W. 1969. Salt marshes. H. T. Odum, et al. (ed's.) Coastal ecological systems of the United States. *Instit. Mar. Sci. Univ. of N. C. Chapel Hill.* I: 567-611.

- Fleming, J. F. and L. T. Alexander. 1961. Sulfur acidity in South Carolina tidal marsh soils. Proc. Soil Sci. Soc. Am. 25: 94-95.
- Gates, D. M. 1968. Toward understanding ecosystems. Advances in Ecological Research. Vol. #5, Academic Press.
- Gerloff, G. L. and P. H. Krombholz. 1966. Tissue analysis as a measure of nutrient availability for the growth of angiosperm aquatic plants. Limnol. and Oceanogr. 11: 529-537.
- Gosselink, J. G. 1970. Growth of Spartina patens and Spartina alterniflora as influenced by salinity and source of nitrogen. Coastal Studies Bulletin No. 5.
- Gray, A. J. and R. R. Bunce. 1972. The ecology of Morecambe Bay. VI. Soils and vegetation of the salt marshes: a multivariate approach. J. Appl. Ecol. 9(1): 221-234.
- Hill, D. E. and A. E. Shearin. 1970. Tidal marshes of Connecticut and Rhode Island. Connecticut Exp. Sta. Bull. No. 709. 33 pp.
- Hinde, H. P. 1954. The vertical distribution of salt marsh phanerogams in relation to tide level. Ecol. Mongr. 24: 209-225.
- Jitts, H. R. 1959. The absorption of phosphate by estuarine bottom sediments. J. of Mar. and Freshwater Res. 10: 7-21.
- Johnson, D. S. and H. H. York. 1915. The relation of plants to tide levels. Publication no. 206, Carnegie Institute, Washington, D. C.
- Keefe, C. 1972. Marsh production: a summary of the literature. Cont. Mar. Sci., Univ. of Texas. 16: 165-181.
- Keefe, C. W. and W. R. Boynton. 1973. Standing crop of salt marshes surrounding Chincoteague Bay, Maryland-Virginia. Ches. Sci. 14: 117-123.
- Kelly, M. G., G. M. Hornberger, and B. J. Cosby. 1975. A method for monitoring eutrophication in rivers.
- Knight, J. B. 1934. A salt marsh study. Am. J. Sci. 28: 161-181.
- Kurz, H. and K. Wagner. 1957. Tidal marshes of the Gulf and Atlantic Coasts of northern Florida and Charleston, South Carolina. Florida State Univ. Studies, Tallahassee, Fla., no. 24.

- Larimer, E. J. 1968. An investigation of possibilities for creating salt marsh in the estuaries of the Atlantic and Gulf Coasts. In: J. W. Webb (ed.) Proc. of the 22nd Conference of Southeastern Assoc. of Game and Fish Commissioners. pp. 82-88.
- Leeper, G. W. 1947. Forms and reactions of manganese in the soil. Soil Sci. 63: 79-94.
- Leet, L. S. and S. Judson. 1965. Physical Geology. 3rd edition. Prentice-Hall Inc., New Jersey.
- Lindberg, S. E. and R. C. Harriss. 1973. Mechanisms controlling pore water salinities in a salt marsh. Limnol. and Oceanogr. 18: 788-791.
- Marshall, D. E. 1970. Characteristics of Spartina marsh which is receiving treated municipal sewage wastes. In: Studies of marine estuarine ecosystems developing with treated sewage wastes, H. T. Odum and A. G. Chestnut (eds.). Univ. of N. C., Chapel Hill, N. C.
- Marshall, N. 1970. Food transfers through the lower trophic levels of the benthic environment. In: J. H. Steele, (ed.) Marine Food Chains, pp. 52-66. Oliver and Boyd, Edinburgh.
- Mendelssohn, I. A. 1973. Angiosperm production of three Virginia marshes in various salinity and soil nutrient regimes. MS thesis, College of William and Mary.
- Miller, W. R. and F. E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal marshes, Connecticut. Ecol. Mongr. 20: 143-172.
- Mooring, M., A. W. Cooper, and E. D. Seneca. 1971. Seed germination response and evidence for height ecophenes in Spartina alterniflora from North Carolina. Am. J. Bot. 58(L): 48-53.
- Nelson, W. L., A. Mehlich, and E. Winters. 1953. The development, evaluation and use of soil tests for phosphorus availability. Agronomy. 4: 153-158.
- Newman, W. A. and G. A. Rusnak. 1965. Holocene submergence of the Eastern Shore of Virginia. Science 148: 1464-1466.
- Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical Package for the Social Sciences. Level 6.0. (2nd edition) McGraw-Hill Inc., New York.
- Nixon, S. W. and C. A. Oviatt. 1973. Analysis of local variation in the standing crop of Spartina alterniflora. Botanica Marina 16: 103-109.

- Odum, E. P. and A. A. de la Cruz. 1967. Particulate organic detritus in a Georgia salt marsh-estuarine ecosystem. pp. 383-388. In: Estuaries, G. H. Lauff (ed.) AAAS Pub. #83, Washington, D.C.
- Odum, W. E. 1970. Insidious alteration of the estuarine environment. *Trans. Amer. Fisheries Soc.* 99: 4: 836-847.
- Odum, W. E., J. C. Zieman, and E. J. Heald. 1972. The importance of vascular plant detritus to estuaries. *Proc. 2nd Marsh Estuary Management Conf., L.S.U.* pp. 91-114.
- Palmisano, A. W. 1970. Plant community-soil relationships on Louisiana coastal marshes. Ph.D. dissertation, Louisiana State Univ., Baton Rouge, La.
- Patrick, W. H. and R. A. Khalid. 1974. Phosphate release and sorption by soils and sediments: effect of aerobic and anaerobic conditions. *Science.* 186: 53-55.
- Patten, B. C. 1971. *Systems Analysis and Simulation in Ecology*, Vol. 1, Academic Press.
- Patten, B. C. 1972. *Systems Analysis and Simulation in Ecology*, Vol. 2, Academic Press.
- Phleger, C. G. 1971. Effect of salinity on growth of a salt marsh grass. *Ecology.* 52: 908-911.
- Piggott, C. D. 1969. Influence of mineral nutrition on the zonation of flowering plants in coastal salt-marshes. In: I. H. Rorison (ed.) Ecological Aspects of the Mineral Nutrition of Plants, *British Ecol. Soc. Symp. #9*, Blackwell Scientific Pub., Oxford, England.
- Platt, T. and K. L. Denman. 1975. *Spectral Analysis in Ecology.*
- Ranwell, D. S. 1964. *Spartina* salt marshes in southern England. III. Rates of establishment, succession, and nutrient supply at Bridgewater Bay, Somerset, *J. Ecol.* 52: 95-105.
- Rayner, J. N. 1971. *An Introduction to Spectral Analysis.* Pion Limited, London.
- Redfield, A. C. 1967. The ontogeny of a salt marsh estuary. In: G. H. Lauff (ed.) Estuaries, AAAS Pub., #83, Washington, D. C.
- Redfield, A. C. 1972. Development of a New England salt marsh. *Ecol. Mongr.* 42: 201-237.

- Redfield, A. C. and M. Rubin. 1962. The age of salt marsh peat and its relation to recent changes in sea level at Barnstable, Massachusetts. *Proc. Nat. Acad. Sci.* 48: 1728-1735.
- Reed, J. G. 1947. The relation of the Spartinetum glabrae near Beaufort, N. C. to certain edaphic factors. *Am. Midl. Natur.* 38: 605-614.
- Richards, L. A., ed. 1954. Diagnosis and improvement of saline and alkali soils. U.S.D.A. Handbk. 60, U. S. Govt. Printing Office, Washington, D.C. 160 pp.
- Robinson, W. O. 1930. Some chemical phases of submerged soil conditions. *Soil Sci.* 30: 197-217.
- Sanders, H. L. 1969. Benthic marine diversity and the stability-time hypothesis. *Brookhaven Symposium in Biology.* #22: 71-81.
- Schelske, C. L. and E. P. Odum. 1961. Mechanisms maintaining high productivity in Georgia estuaries. *Proc. Gulf and Carib. Fish Instit.* 14: 75-80.
- Schmidt, R. A. 1966. Needed--a coastwise comprehensive program for development of estuaries. American Fisheries Society Special Pub. #3. pp. 102-109.
- Smith, R. H. 1942. Management of Salt Marshes on the Atlantic Coast of the U. S., *North Amer. Wildlife Conf.* 7: 272-277.
- Steckel, J. E. and R. L. Flannery. 1966. Automated determination of phosphorus, potassium, calcium, and magnesium in wet digestion solutions of plant tissue. In: L. T. Sleggs (ed.) Automation in Analytical Chemistry, Mediad, New York.
- Stevenson, R. E. and K. O. Emery. 1958. Marshlands at Newport Bay, California. U.S.C. Occasional Papers, no. 20.
- Teal, J. M. 1962. Energy flow in the salt marsh ecosystem of Georgia. *Ecology.* 43: 614-624.
- Teal, J. N. and M. Teal. 1969. Life and death of the salt marsh. Audubon/Ballantine Books, New York. 274 pp.
- Teal, S. M. and J. Kanwisher. 1961. Gas exchange in a Georgia salt marsh. *Limnol. Oceanogr.* 6: 388-399.
- Thompson, S. H. 1961. What is happening to our estuaries? *Trans. 26th N. Amer. Wildlife and Natural Resources Conf.* pp. 318-322.

- Turner, F. T. and W. H. Patrick. 1968. Chemical changes in waterlogged soils as a result of oxygen depletion. Int. Congr. Soil Sci. Trans. 9th, Adelaide, Australia, IV.
- Tusneem, M. E. and W. H. Patrick. 1971. Nitrogen transformations in waterlogged soil. LSU Dept. Agric., Agric. Exp. Stn.
- United States Dept. of Commerce. 1973. Climatological Atlas of the States. National Ocean and Atmospheric Administration.
- United States Dept. of Commerce. 1974. Tide tables. High and low water predictions. East Coast of North and South America. National Ocean Survey.
- Valiela, I. and J. M. Teal. 1973. Nutrient limitation in salt marsh vegetation. In: Ecology of Halophytes. R. J. Reimold and W. H. Queen (ed.), Academic Press, New York.
- Vittor, B. A. 1971. Use of dredging spoil for the construction of salt marsh islands. World Dredging and Marine Const. pp. 38-40.
- Whittaker, R. H. 1967. Gradient analysis of vegetation. Biol. Rev. 42: 207-264.
- Williams, R. B. and M. B. Murdoch. 1969. The potential importance of Spartina alterniflora in conveying Zn, Mn, and Fe into estuarine food chains. 2nd. Natl. symp. Radioecology, Ann Arbor, Michigan, pp. 431-439.
- Windom, H. L. 1972. Environmental response of salt marshes to deposition of dredged materials. ASCE National Water Resources Eng. Meet. pp. 1-25.
- Woodhouse, W. W., E. D. Seneca, and S. W. Broome. 1972. Marsh building with dredge spoil in North Carolina. Bull. 445, Agric. Exper. Station, N. C. State Univ. at Raleigh, pp 1-27.

## APPENDIX A: CONTINUOUS MONITORING SYSTEM

### Concept

1. One severe limitation on the application of modern analytical techniques in estuarine ecology has been the inability to measure environmental variability in the field at a rapid rate. Most ecological measurements are made at infrequent intervals, and the time period between samples is relatively long. The experimental field data system described here was designed to monitor various physical and chemical parameters at a rapid rate and to monitor these parameters at several sites on the marsh simultaneously.

2. Because there was no commercially available system that would perform all of the functions desired, a unit was designed in a modularized fashion, combining commercially available components with sections whose designs were tailored to the project's needs. The objective of this segment of the study was to develop the capability to compare both long-term and short-term variations among different zones on the marsh. For this reason a system was designed and built that was able to monitor stations spread across several hundred meters of marsh surface. A similar data recording system was constructed by several other members of the University of Virginia Department of Environmental Sciences for monitoring eutrophication in rivers. The final report of this study (Kelly et al., 1975) describes the theory and circuitry in great detail



### Configuration

3. Figure A-1 illustrates the overall configuration of the system as deployed in the field, and Figure A-2 depicts the contents of one submersible amplifier unit with sensors and power supply. The system consisted of the following major components:

- a. Sensors to measure the magnitude of the described parameter.
- b. Cable leads to connect the sensors to the electronic amplifiers.
- c. Signal amplifiers with power sources to amplify the measured signal and connect it to voltage compatible with the data recorders.
- d. Waterproof housing to shield the amplifiers and batteries.
- e. Connecting cables to transmit the amplified signal to the data recorders.
- f. Junction or distribution boxes to allow the selection of the various parameters that are to be recorded at a particular time.
- g. Digital data recorders to record the signals.
- h. Waterproof housing to shield the recorders.

### Field Sensors

4. Temperature was measured electronically by a twin bead thermistor and an accompanying amplifier. A Fenwal GB 34PMG2 Iso-curve glass head thermistor was used. The variable resistance of the thermistor is measured by the amplifier and the signal converted to a 0.0 to 1.0 v-d.c. output. The amplifier may be adjusted so that the one valid output range corresponds to a variety of temperature ranges. For

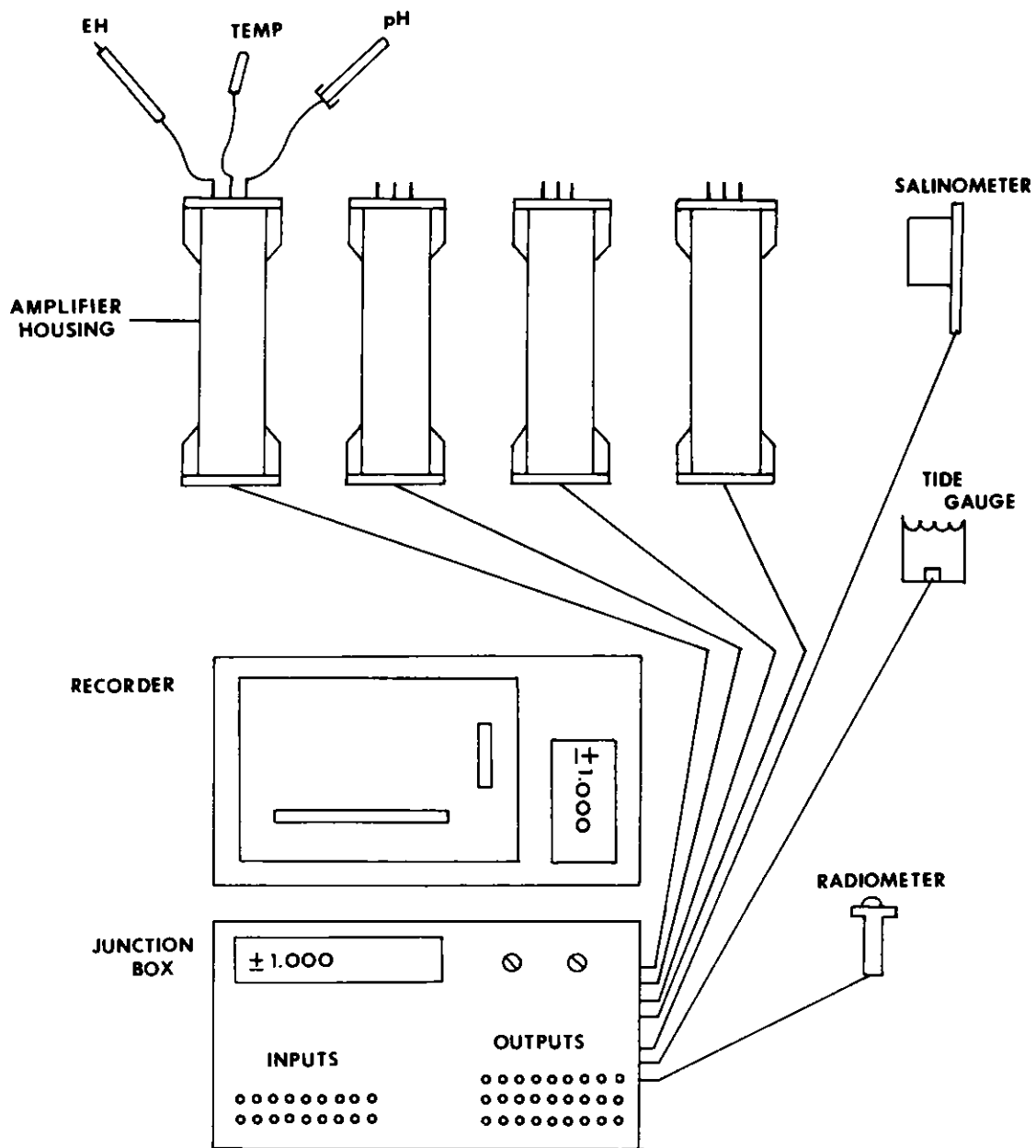


Figure A-1. General configuration of the data monitoring system.

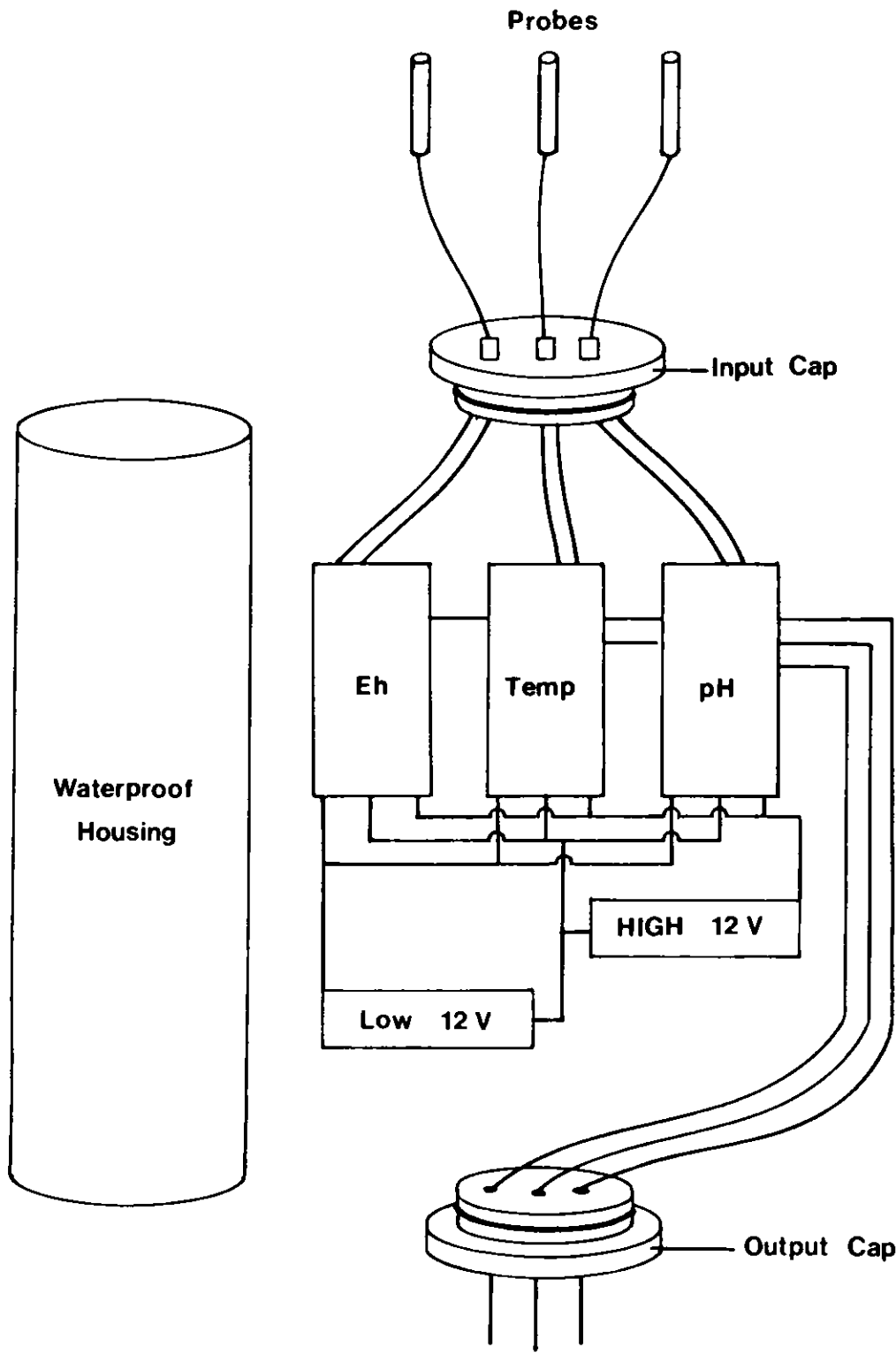


Figure A-2. Typical configuration of one submersible housing unit.

the uses of this project the range selected was 0-40°C. The thermistor is soldered to a lead wire, and the thermistor and solder joint are molded into a 10-cm length of clear polymer plastic using Scotchcast electrical potting compound to provide electrical insulation and structural strength. The resulting unit is exceptionally rugged and resists damage from general field use. Accuracy is approximately  $\pm 0.1^{\circ}\text{C}$ .

#### pH

5. Combination pH/reference electrodes have been found to give satisfactory performance under the extreme conditions of use they would experience in this project. Electrodes must withstand submergence for extended periods of time in seawater, and must be able to function in sediments that are abrasive and frequently anaerobic.

6. Initially the Thomas 4094-510 sheathed-in-glass combination probe was used. This gave satisfactory performance, but was vulnerable to breakage. Because it is not sealed, it required modification for this field use. Furthermore, it has to be refilled periodically.

7. The electrode generally used was the Sensorex Model S300C, which is a combination electrode with a completely sealed construction. This is permanently filled with a saturated gell KCl, and is contained in a high impact polymer case. These electrodes may be used as purchased for short times, if great care is taken. For heavy or prolonged use it proved necessary to further protect the cable lead and the joint where the cable lead enters the probe. This was done by threading the lead wire through a length of 1/8-in. Tygon tubing and sealing the tubing to the head of the probe with household caulking compound. The joint was then securely wrapped with electrical tape.

8. The pH amplifier was a solid state, expanded scale pH meter with an Analog Devices model 173J Isolation Amplifier to reduce current leakage problems from the electrodes and errors due to ground loops in the highly conductive medium where the system must function. The pH amplifier gives an output of 0.0 to 1.0 v-d.c., which is normally equivalent to pH 4.0 to 10.0  $\pm$  0.1, although this range is adjustable.

#### Eh

9. The oxidation-reduction potential or Eh system utilizes the same expanded scale pH amplifier as the pH sensor, but as the signal is several orders of magnitude greater than across a pH sensor pair, the isolation amplifier is omitted at present. The platinum electrode is made by soldering a 22 gauge platinum wire about 405 cm long into a 12-cm brazing rod. This unit is sealed into a 20-cm pyrex tube with polyester resin. For a reference, this unit utilizes a Sensorex reference electrode or shares the reference half of the combination pH electrode. The amplifier gives 0.0 to 1.0 v-d.c. output for Eh values in the range of  $\pm$  400 millivolts. This unit, however, has been the source of major problems: current leakages that cause erratic Eh recordings and also interfere with the pH readings. Another problem is that there are few standards with which to calibrate the units. The most commonly used is Zobell's solution with an Eh of +430 millivolts at 25<sup>o</sup>C.

#### Salinity

10. Salinity of the water in tidal creeks was measured by an Instro Company model 300 inductance salinometer. Salinity was determined by an inductive-conductive measurement that was internally compensated for temperature effects and linearized. The unit

required a nominal 9 to 15 v-d.c. input and gave an output of 0.0 to 1.0 v-d.c. which corresponded to 0 to 40 ppt.

#### Solar radiation

11. Incident solar radiation was measured by an LI-200 SR Pyranometer (Lamda Instrument Corporation) that consisted of a silicon solar cell mounted beneath a diffusing surface and designed to give a cosine response. As the relative spectral response is not constant over the full range of the solar spectrum, the sensor should be used only in the open air and not under plant canopies or artificial lights. This instrument measures radiation directly in watts per square meter, giving total energy input. Absolute accuracy is  $\pm 5$  percent when calibrated against an Epply Pyranometer under natural daylight and clear conditions.

#### Tide height

12. The tidal level in the nearby marsh was measured by a Sontec Model FJE pressure transducer, an absolute pressure unit with a reference of 14.3 psi sealed in the reference chamber. It possessed built-in electronics, received  $\pm 12$  v-d.c. inputs, and gave an output of 0.0 to 1.0 v-d.c. corresponding to 0.0 to 6.09 m of water pressure with an accuracy of  $\pm 0.1$  percent of full scale.

#### Signal Amplifiers and Housings

13. The sensors for temperature, pH, Eh, and solar radiation were connected via waterproof cables and connectors to housing which contained signal conditioning amplifiers for the sensors. Because of the extremely low voltages and current across the sensors, especially the

pH probe, there was a limitation in the length of the lead wire between the sensors and amplifiers. In the field unit, this length was kept below 3.5 m.

14. The signal conditioning amplifiers required  $\pm 12$  v-d.c. that was supplied by battery packs. The battery packs and amplifiers were housed in pressureproof housings. These housings were milled from 10.6-cm i.d. PVC tubing, and were closed with O-ring sealed end PVC caps. The battery packs used sixteen 15 v-d.c. transistor batteries (D cells) each; one pack powered a set of three or four amplifiers clustered together in each tube for over two weeks. An alternate method to supply power would be to run power cables from a central battery source to each tube and to the data recorder. This option was tried initially, but was discarded due to problems with current leaks and ground loops between the sensors, recorders, and amplifiers.

15. From the amplifier tubes, the signals were fed back through waterproof cables and connectors to a junction box.

16. Certain instruments, such as the salinometer, current meter, and tide gauge, were protected by their own self-contained housings, and linked directly into the junction box.

#### Junction Box

17. All field sensors were connected to a junction or distribution box. This was currently capable of receiving the input from 40 field sensors. A Fluke model 8000 digital multimeter was utilized as a readout device, and all of the 40 inputs could be monitored on the

digital meter by dialing the appropriate input channel. A patch panel was provided on the front of the junction box, and any of the 40 input channels could be patched into the 16 inputs to the tape recorder for continuous monitoring. Thus, 16 channels could be monitored continuously by the recorder, or 40 channels of data might be monitored intermittently by use of the digital output unit. When using this device manually, however, coding was necessary as the sensor amplifiers read out as 0.0 to 1.0 v-d.c. outputs and not as scaled values. As a result, conversion curves of nomographs were used to determine the actual value of the parameter being measured.

#### Recorder

18. The data were transmitted from the junction box through moistureproof cables and couplings to the recorder unit. The recorder was a Metrodata D1-616 data logger coupled with a DR-99 digital readout. The data logger recorded on a 6.35-mm endless loop tape cartridge in serial format. The analog input was converted to digital format for filing on the tape. Recording times could be varied from continuous (approximately 2.5 full 16 channel scans per second) to one scan each 73 minutes via a switch from a quartz clock. The unit was capable of operating from either a 115 Hz or 12 v-d.c. source.

19. Although these units were rather sophisticated, the field record was quite acceptable. The only consistent stoppages occurred when the temperature dropped below freezing. Modifications were required to decrease the sensitivity of the end-of-tape markers; aluminum



foil markers were placed to keep the recorder from overrunning the end of the tape. A photocell sensed the reflected light from a small light source, but in field use the intense natural light, even when units were shielded, caused premature shut-off.

20. The major problem encountered with the recorder data, as opposed to the actual recording, was with the retrieval of the data. During the recording of field data, especially if 12 v-d.c. was used as the power source, the recorders may occasionally have skipped one or more of the 16 channels that were being recorded. This presented few difficulties if the location of the lost channels were known. In practice, this was one of the several drawbacks of the entire continuous recording system.

21. The format of the data recorded on the field units was filed in a unique way that was not compatible with the normal data processing computer. For this reason, it was transcribed from 6.35-mm data tape to 12.7-mm computer tape in compatible format. This was done by using a metrodata tape transcriber.

#### Data Processing

22. After transcription, the field data were processed to convert the raw millivolt readings from the amplifiers into the absolute values for each of the parameters.

23. The processing of the recorded data proceeded via several steps. The cartridge tape records retrieved from the field were reformatted and transcribed onto industrial standard seven-track magnetic tapes using a Metrodata model 625 tape reader driving a Digi-Data

recorder. A block length of 960 characters was used as optimal for input to the CDC 6400 computer used in this study. This taped information was then used as input into a series of computer programs resulting in diurnal curves of radiation, tide, pH, and temperature.

24. The first program accessed was TRANSCRIBE (see Kelly et al., 1975, for complete description), which converted the recorded input voltages on the seven track tape into decimal equivalents. Simultaneously, it checked for outlier data points and errors in recording. The output from this program was written onto a permanent master tape that could be accessed at some future date.

25. At this stage a program, PROCESS, was utilized to convert the millivolt readings into absolute values (see Kelly et al., 1975, for detailed description). This conversion utilized the output tape produced by TRANSCRIBE in addition to field calibration information. Within the program, the continuously monitored information was averaged for a period of time specified by the operator and then converted to absolute values via a series of mathematical formulations. This information could be either printed, punched onto cards, or written onto another tape or disc file. For purposes of visual display and analysis, the punched card output was used as input to a plot routine, which plotted the radiation, tide, temperature, and pH as a function of time. This information could be displayed in a variety of formats that included fixed and variable scales for the y-axis as well as plotting all environmental parameters at one station and/or comparing parameters between stations.



## APPENDIX C: SURVEY SITES

1. Plant and sediment surveys were conducted at a variety of sites along the eastern seaboard, from New Jersey to Georgia, to attempt to determine if the pattern shown by the zonation of the marsh plants was reflected by certain constituents within the sediments. Most of these sites were visited only once--on extended survey trips--although a subsequent trip was conducted to several of the sites in order to collect a biomass estimate from the end of the growing season. Many of the sites were visited by students and personnel only partially connected with this study, and as a result, the data sets are not uniform.

2. The name and computer abbreviation of the survey sites are listed in Table C-1 and the location of the sites is shown in Figure C-1. The objective at these sites was not the creation of detailed vegetation maps and fine scale resolution of the changes in chemical and biotic parameters, but the general depiction of trends in certain chemical constituents of the sediments, and their relation to changes in the dominant vegetative species.

3. At the survey sites, sampling stations were located on a transect that extended from the lowest elevation colonized by Spartina alterniflora, through the S. alterniflora zone into the high marsh where this pattern existed. The stations with the lowest numbers were the lowest areas colonized by S. alterniflora and the highest numbers

were generally the uppermost region of the high marsh. (Exceptions to this are Taskinas Marsh and Bennett's Marsh, but these are described in detail.) Transect lengths varied greatly but these, unfortunately, were not always recorded. Vegetation samples and sediment cores were attempted at each station. Single or duplicate samples of live standing crop were taken; however, some samples were lost. Quadrat size was varied according to plant type and density; 0.1m<sup>2</sup> quadrat samples were harvested in the S. alterniflora zone and 0.04 m<sup>2</sup> samples were taken where the much denser S. patens or D. spicata predominated. These samples were sealed in plastic bags for transporting to the laboratory for counting and weighing. Table C-2 gives the computer abbreviations for the plant data.

4. Sediment cores were taken with either a 7.6-cm (3-inch) internal diameter P.V.C. corer or a 6.35-cm (3.5-inch i.d.) brass core tube. These were extruded in the field, wrapped securely in plastic bags, and frozen with dry ice for transportation to the laboratory.

5. For certain samples, the pH and oxidation-reduction potential (EH) of the sediment were measured immediately upon extrusion of the core. pH was measured using a Sensorex S 200 c combination pH electrode, and an Orion model 401 portable pH meter. Eh was measured using the reference half of the combination pH electrode and a Thomas 4096-D20 platinum electrode.

6. Cores were stored at -15<sup>o</sup>C prior to lab analysis. After thawing for 12-18 hours at room temperature, each core was divided into 10-cm sections. A subsample weighing 12.5 g (wet weight) was

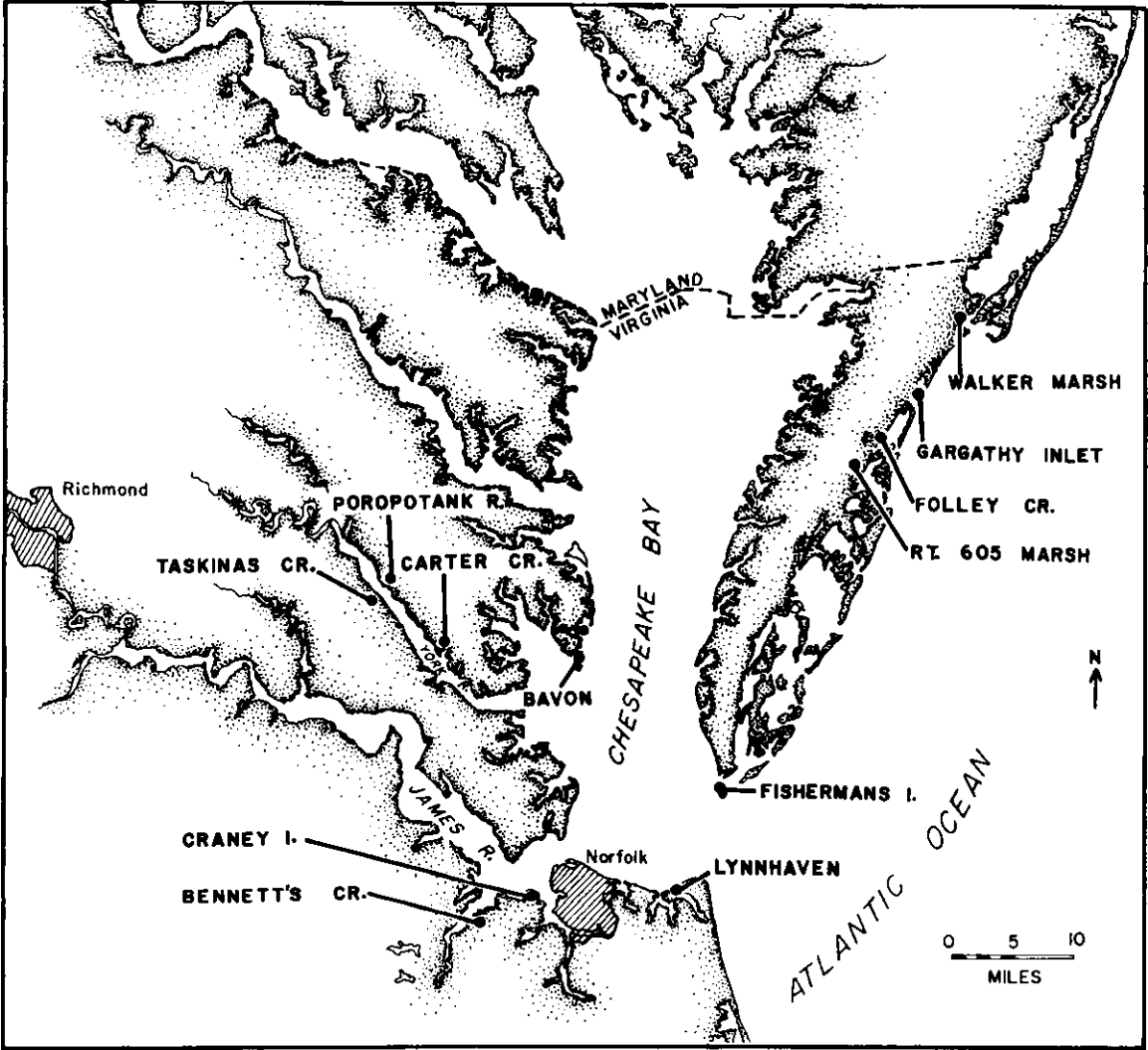


Figure C-1. Location of survey sites along the central eastern coast of the U. S. The two sites not shown on the figure are Avalon, New Jersey, and Sapelo Island, Georgia.

cut from each of these sections on a longitudinal strip. These subsamples, representing the three cores obtained from the same sample zone and depth range (a total of 37.5 g of sediment), were consolidated with 150 ml of extractant solution (0.025 N HCl + 0.01 H<sub>2</sub>SO<sub>4</sub>) (Nelson et al., 1953) and homogenized for 30 seconds at high speed in a stainless Waring blender. The resulting solution was filtered through Whatman #42 filter paper and collected in plastic sample bottles. Several drops of chloroform were added to each sample bottle to inhibit bacterial activity. Filtered samples were frozen until analysis. Cores from the survey sites were treated similarly, but only one core was utilized per analysis.

7. Subsamples from all three cores representing a given sample zone were consolidated, as above. Consolidated subsamples were dried in a warming oven for 48 hours at 100°C. Dried samples were cooled and reweighed, then pulverized with mortar and pestle. Subsamples of approximately one gram were transferred to crucibles and weighed within ± 0.0002 g on a Sartorius analytical balance. The samples were then ashed in a muffle furnace for 12 hours at 550°C and were reweighed after cooling in a desiccator. Percent organic matter was determined by weight loss during ashing.

8. In the data section that follows, the following units are used: biomass (grams dry weight/m<sup>2</sup>), stem height (cm). All chemical values are in parts per million (p.p.m.) and the day in the Julian day of the year.

Table C-1. List of Sites

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1	AVA	Avalon, New Jersey
2	BAV	Bavon, Virginia
3	BEN	Bennett's Creek, Virginia
4	CAR	Carters Creek, Virginia
5	CRA	Craney Island, Virginia
6	FIS	Fishermans Island, Virginia
7	FOL	Folley creek, Virginia
8	GAR	Gargathy Inlet, Virginia
9	LYN	Lynnhaven Inlet, Virginia
10	POR	Poropotank River
11	SAP	Sapelo Island, Georgia
12	605	Route 605 Bridge, Virginia
13	TAS	Taskinas Creek, Virginia
14	WAL	Walker Marsh, Virginia



Table C-2. Plant Identification Codes

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S.ALT	<u>Spartina alterniflora</u>
D.SPI	<u>Distichlis spicata</u>
S.PAT	<u>Spartina patens</u>
PHRAG	<u>Phragmites communis</u>
SCIR	<u>Scirpus</u> sp.
J.ROM	<u>Juncus romerianus</u>
J.GER	<u>Juncus gerardi</u>
TYPHA	<u>Typha</u> sp.
S.EUR	<u>Spartina europea</u>
S.BIG	<u>Spartina Bigelowi</u>
SALIC	<u>Salicornia</u> sp.
S.DEAD	Standing dead
T.DEAD	Total dead
LITT	Litter
UNK	Unknown
SP-DS	<u>S. patens</u> and <u>D. spicata</u> mixed
SA-DS	<u>S. alterniflora</u> and <u>D. spicata</u>
SA-SP	<u>S. alterniflora</u> and <u>S. patens</u>
P-DS	<u>S. alterniflora</u> , <u>S. patens</u> , and <u>D. spicata</u>

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Appendix B on microfiche in pocket.

References: p. 155-160.

1. Dredged material. 2. Ecological models. 3. Ecological succession. 4. Estuarine ecology. 5. Plant growth. 6. Salt marshes. I. Odum, William E., joint author. II. United States. Army. Corps of Engineers. III. Virginia. University. Dept. of Environmental Sciences. IV. Series: United States. Waterways Experiment Station, Vicksburg, Miss. Technical report ; D-77-35.

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APPENDIX B: MODEL USER INFORMATION

**DREDGED MATERIAL RESEARCH PROGRAM**



ENVIRONMENTAL EFFECTS LABORATORY

U. S. ARMY ENGINEER WATERWAYS EXPERIMENT STATION

P. O. Box 631  
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