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DREDGED MATERIAL RESEARCH PROGRAM

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COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA

VOLUME II: GROWTH DYNAMICS

by

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December 1977

Final Report

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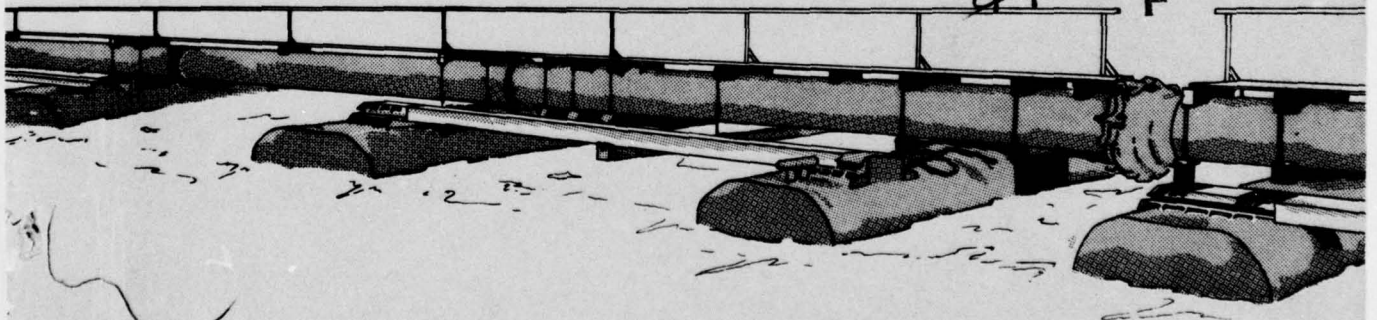| REPORT DOCUMENTATION PAGE	READ INSTRUCTIONS BEFORE COMPLETING FORM

1. REPORT NUMBER	2. GOVT ACCESSION NO.	3. RECIPIENT'S CATALOG NUMBER
Technical Report D-77-44		

4. TITLE (and Subtitle)	5. TYPE OF REPORT & PERIOD COVERED
COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA VOLUME II: GROWTH DYNAMICS	Final report. (In 2 volumes)
	6. PERFORMING ORG. REPORT NUMBER

7. AUTHOR(s)	8. CONTRACT OR GRANT NUMBER(s)
J. G. Gosselink, C. S. Hopkinson, Jr., R. T. Parrondo	Contract No. DACW39-73-C-0108

9. PERFORMING ORGANIZATION NAME AND ADDRESS	10. PROGRAM ELEMENT, PROJECT, TASK AREA & WORK UNIT NUMBERS
Louisiana State University Baton Rouge, La. 70803	DMRP Work Unit No. 4A04B

11. CONTROLLING OFFICE NAME AND ADDRESS	12. REPORT DATE
Office, Chief of Engineers, U. S. Army Washington, D. C. 20314	December 1977
	13. NUMBER OF PAGES
	202

14. MONITORING AGENCY NAME & ADDRESS(if different from Controlling Office)	15. SECURITY CLASS. (of this report)
U. S. Army Engineer Waterways Experiment Station Environmental Effects Laboratory P. O. Box 631, Vicksburg, Miss. 39180	Unclassified
	15a. DECLASSIFICATION/DOWNGRADING SCHEDULE

16. DISTRIBUTION STATEMENT (of this Report)

Approved for public release; distribution unlimited.

17. DISTRIBUTION STATEMENT (of the abstract entered in Block 20, if different from Report)

18. SUPPLEMENTARY NOTES

Appendixes A-G were reproduced on microfiche and are enclosed in an envelope attached to the inside of the back cover.

19. KEY WORDS (Continue on reverse side if necessary and identify by block number)

Coastal marshes	Physiological ecology
Gulf Coast	Plant growth
Marsh plants	Salt marshes

20. ABSTRACT (Continue on reverse side if necessary and identify by block number)

As part of the U. S. Army Corps of Engineers Dredged Material Research Program, administered by the Environmental Effects Laboratory of the U. S. Army Engineer Waterways Experiment Station, Vicksburg, Mississippi, a study of the growth physiology of marsh plants common to the Gulf Coast area was conducted.

The growth physiology study, concerned with the physiological ecology of stress, reports on several experiments on the ability of marsh plants to

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20. ABSTRACT (Continued).

survive, particularly under stresses of salinity and inundation. Although several species are investigated, including Distichlis spicata, Juncus roemerianus, Phragmites communis, Saggitaria falcata, Spartina cynosuroides, and Spartina patens, major emphasis is given to the adaptability and edaphic requirements of Spartina alterniflora: the response of this species is contrasted with that of the other species. Emphasis is given to the substrate qualities to which Spartina alterniflora can adapt and to the adaptation mechanisms.

     Techniques used in the investigation include: field studies of the spatial variation in the peak biomass of salt marsh vegetation; mineral analyses of soil and tissue nutrients in coastal Louisiana and the relationship of spatial distribution of these nutrients to peak live biomass (yield) of Spartina alterniflora; greenhouse and laboratory studies of salinity and sediment drainage effects on growth and carbon dioxide exchange of salt marsh plants; the effect of salinity on ion adsorption rates; and the role of light and temperature in marsh plant photosynthesis.

     Results of the studies are integrated in a general conceptual model that has application to the development of marshes on dredged material.

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SUMMARY

    1. During the 1955-1964 period disposal of dredged material was
a major reason for filling wetlands in the United States. Marsh areas
are fairly accessible to many coastal dredging projects and for many
years easements were easily obtained and relatively inexpensive; hence,
marsh disposal of dredged material improved the cost:benefit ratio that
mush be applied to federally sponsored engineering projects over other
disposal techniques. With the sharp increase in awareness of the
value of coastal wetlands as natural systems in recent years, the avail-
ability of these areas for disposal of dredged material has decreased
and alternatives are being sought. One alternative is to identify tidal
wetlands that are of least value in their natural state and thus could
serve as possible routes of navigation channels and disposal sites.
Perhaps a more viable alternative is the use of dredged material to
create new marshes. For both types of disposal the productivity of
marsh vegetation and the physiological ecology of stress are important
questions.

    2. This study examines the productivity of seven marsh plant
species common in coastal marshes of Louisiana (Vol. I) and reports on
a number of experiments that concern the ability of marsh plants to
survive under the dual stresses of salinity and inundation (Vol. II).
The study was conducted between August 1973 and July 1976 as a portion
of the overall DMRP research and development effort under Task 4A,
Marsh Development.

    3. Productivity of seven marsh plant species was evaluated over
a two-year period. Using a harvesting technique that corrects for

mortality between sampling periods, it was determined that Spartina patens, Juncus roemerianus, and Distichlis spicata were even more productive than Spartina alterniflora, a species that is known to be highly productive. Measured annual net production ($g\ m^{-2}$) was: S. patens, 4200; J. roemerianus, 3300; D. spicata, 2900; Phragmites communis, 2400; Sagittaria falcata, 2300; Spartina cynosuroides, 1100. The fresh and brackish marsh species supported high levels of productivity even though they did not receive as much tidal subsidy as salt marshes. Productivity was higher for species that grow throughout the winter than for those such as S. cynosuroides and P. communis, which die to the ground in late fall. The broad-leaved fresh marsh species, S. falcata, produced only a moderate level of organic matter, but its high nutrient content (up to 3 percent nitrogen) and rapid decomposition rate made it unique among the species investigated.

4. Considerable effort was expended evaluating techniques for measurement of production. Peak standing crop was compared with harvest methods that correct for mortality between sampling periods and with nondestructive phenometric techniques based on recruitment, growth, longevity, and density of individual stems. From the evidence it was concluded that peak standing crop seriously underestimates production in gulf coast marshes, and that the harvest technique of Wiegert and Evans (1964) is the most realistic presently available, although phenometric analysis holds promise for an excellent, nondestructive method of productivity analysis.

5. Aside from variation in reported productivity due to differences in techniques, wide geographic variability occurs. In an

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end-of-the-season study of $\underline{S}$. alterniflora biomass over a wide area of southeastern Louisiana, standing biomass was found to vary from zero to 2244 grams per square meter. Biomass was higher in Barataria Bay than in Terrebonne Bay and also higher on the east side of each bay than on the west side. The higher biomass in Barataria than Terrebonne Bay could be related to the proximity of Barataria Bay to the Mississippi River, which is a large source of both fresh water and nutrients. It is not clear why the east side of these two bays was more productive than the west side, but it is speculated that circulation patterns and dominant winds may control the distribution of nutrients and silt within the bay.

6. Growth was also more vigorous along stream edges compared to 50 to 175 m from the stream. This phenomenon has been reported before and is thought to be related to more vigorous tidal flushing action along the edges of streams.

7. The standing stock of $\underline{S}$. alterniflora did not increase with distance inland from the gulf although the total biomass on the marsh, including species other than $\underline{S}$. alterniflora, did increase.

8. Biomass gradients were paralleled by physical gradients. Flooding frequency decreased with distance from the gulf inland and from the edge of streams into the marsh. With this decrease there was also a decrease in sediment deposition and in the proportion of coarse materials to fine in the sediment; a decrease in salinity; and an increase in organic deposition in the sediments. These physical gradients were poorly correlated with $\underline{S}$. alterniflora biomass, although, in general, high

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biomass was associated with high silt loads, low organic matter in the sediments, and decreasing salinity.

9. Soil and tissue nutrient concentrations were also poorly correlated with S. alterniflora biomass. The highest correlation (negative) was between S. alterniflora biomass and boron (B) $(r = -0.32)$. Nitrogen (N) was also negatively correlated with biomass $(r = -0.19)$. Other significant correlations failed individually to account for as much as 5 percent of the biomass variability. Multiple step-wise regressions were conducted between the dependent variables, S. alterniflora live biomass and total live plus dead biomass, and the independent variables, 14 tissue elements or 8 substrate parameters. The best seven-variable model of tissue nutrients accounted for only 36 to 38 percent of biomass variability. Boron and manganese (Mn) were significant variables in all models. Phosphorus (P), potassium (K), and N also entered the relationship with live biomass, K, and barium (Ba) with total biomass.

10. No soil parameter accounted for more than 11 percent of biomass variability. The only significant relationship was between salinity and total biomass. Thus, it appears in the complex environment of the salt marsh that many factors contribute to yield.

11. These field studies were supplemented by controlled tests in the greenhouse and laboratory. In these tests it was documented that S. alterniflora, S. cynosuroides, and D. spicata are all inhibited by salt in the concentration range of their normal habitat. Kinetic studies with the labelled isotope rubidium (Rb) indicated that a mechanism of action of salt was the inhibition of nutrient absorption since Rb absorption was strongly inhibited in the presence of salt.

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12. In situ studies of photosynthesis of whole salt marsh communities showed that the macrophytes (S. alterniflora) accounted for 90-96 percent of the total photosynthesis of the community. The micro-algae found growing on the lower parts of the S. alterniflora culms and on the surface of the sediments accounted for as much as 10 percent of gross production in the winter, but less in the summertime. However, 64-76 percent of the total community respiration was benthic and attributed to the micro-components of the community. The photosynthetic rate increased from shade to full sunlight, a characteristic of C_4 plants (which are particularly efficient photosynthesizers). The rate of photosynthesis per unit leaf area was higher in December and March than during late spring and summer. The decrease in efficiency in late spring was perhaps related to the N supply to the roots. The rate of photosynthesis was not affected by the diurnal flooding pattern of the marsh, apparently because the marsh substrate was efficiently buffered from rapid daily redox potential (Eh) and salinity changes.

13. These results are discussed in a model of marsh success which identifies several feedback loops that stabilize natural marshes, allowing them to counteract the effects of natural subsidence rates and remain at an elevation just below mean high water level. The inundation regime of the marsh is critical in controlling all of these loops through control of the nutrient and silt supply to the marsh, the salinity of the flooding waters and sediments, and the soil Eh. However, much more needs to be known about the relationship of these factors to the flooding regime.

14. The relationships discussed in the model are important because they can be used to evaluate how existing data on marsh productivity

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are interpreted, where dredging and dredged material disposal should

occur, and what species and edaphic conditions are optimum for vegeta-

tion of newly created marshes.

CONTENTS

Note: Appendixes A-G were reproduced on microfiche and are enclosed in an envelope attached to the inside of the back cover.

CONTENTS

CONTENTS

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

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

Multiply	By	To Obtain
inches	0.0254	meters
feet	0.3048	meters
miles (U. S. statute)	1.609344	kilometers
cubic yards	0.7645549	cubic meters
quarts (U.S. liquid)	0.0009464	cubic meters
gallons (U.S. liquid)	3.785412	cubic decimeters

COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA

VOLUME II: GROWTH DYNAMICS

INTRODUCTION

1. In recent years the U.S. Army Corps of Engineers (CE) has spent
about one half of its budget for maintenance of channels and harbors in
coastal areas. Since the Corps dredges 300 million cu yds* of material
in the continental United States each year (Boyd et al. 1972),** the
volume of dredged sediments to be disposed of in the coastal zone
provides the Corps with a serious dilemma. In former years "useless"
marshes provided a natural disposal area for dredged material, but
recent gains in the public appreciation of the value of coastal wetlands
have led to serious restriction of disposal sites. The Corps is cogni-
zant of the detrimental effects of disposal on marshes and is looking
for economically feasible disposal alternatives. One possibility under
consideration is the placement of a thin layer of dredged material over
existing marshes--a layer thin enough to allow the vegetation to grow
through and to function as a normal marsh. This alternative might be
particularly attractive in areas of rapid subsidence where the dredged
sediments could be used to nourish the marshes. A second alternative is
the creation of new marsh by building islands or adding dredged material
adjacent to existing marshes.

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  * A table of factors for converting U.S. customary units of measure-
     ment to metric (SI) units can be found on page 11.
 ** References at end of this section.

2. In order to accomplish either of these alternatives, the ability of the indigenous plants to respond to the changed circumstances must be known. This raises many technical questions about the ability of a plant to survive and grow in the intertidal zone. Can the habitat of a marsh plant species be defined in physical and chemical terms? What are the critical parameters of this habitat and over what range of these parameters is growth possible? What parameters are not critical? That is, what parameters can be allowed to fluctuate over a wide range without significantly affecting the ability of the plant to grow? What chemical or other environmental relationships exist that might not be important to a plant species per se but might be important in the function of the whole marsh ecosystem? For instance, the ability of marsh plants to take up toxic heavy metals that they do not themselves use could put these metals into the food web and pose danger to higher consumers or to man himself, or the relative development of the roots of the plant system as opposed to the shoots may not affect the plant's survival but may be critical in stabilization of the sediment surface.

3. In this volume studies concerned with answering some of the above questions are reported. Emphasis is on adaptability and edaphic requirements of saltmarsh cordgreas, Spartina alterniflora, since this is a plant of worldwide distribution, found in a wide range of environments, all of which are characterized by saline sediments. Response of S. alterniflora to a number of edaphic conditions is contrasted with that of other species and from this some generalities concerning response of the plant are derived. Emphasis is placed on the substrate qualities to which it can adapt and the mechanism of adaptation. The

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study is not definitive, rather it supplements other studies under way

by the Dredged Material Research Program (DMRP) of the U.S. Army

Engineer Waterways Experiment Station (WES), Vicksburg, Miss.

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TECHNIQUES

Field Study

4. Peak biomass was sampled along four transects extending from the
Gulf of Mexico across the east and west sides of two large interdistribu-
tary basins (Figure 1). The locations of these transects enabled the eval-
uation of the effect of the Mississippi River (Mississippi River effect),
the variation occurring on a gradient from the Gulf of Mexico inland
toward fresh water (gulf-inland gradient), and the micro effect of stream
edges as opposed to inland marshes (streamside effect). Samples were
collected during September 1974. Vegetation was harvested at ground
level; separated into live tissue, dead tissue stripped from live culms,
dead culms, and species other than S. alterniflora; dried; and weighed.
Density and average height of live culms were also recorded. Statis-
tical treatment of the data employed the Statistical Analysis System
software program developed by Barr and Goodnight (Service 1972). In
addition, samples over a 2-year period were taken from seven species of
marsh plants, each at a single location on the coast (Gosselink et al.
1976). The two studies combined show both the geographical and the
temporal fluctuation in biomass and nutrient parameters. (See Appendix
A for details.)

Mineral Analyses

5. Live plant tissue from the field study was dried, ground, and
sent to the Plant Analysis Laboratory of the University of Georgia to be
spectrographically analyzed for 15 nutrients. Nitrogen (N) was determined

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by the micro-Kjeldahl technique (Bremmer 1965), also by the University of
Georgia Laboratory. Soil samples collected at the harvest sites were
analyzed for cations and physical structure by the Louisiana State
University Soils Laboratory. (See Appendix B for details.)

Greenhouse and Laboratory Tests

6. Plant material for use in controlled tests was grown from seed
collected in the Barataria Bay area of south Louisiana. For salinity
studies the seedlings were transferred to solution culture containers
and grown without aeration in a growth chamber under a 16-hour photo-
period at 19000 lux in a temperature of 20°C during the dark, 30°C
during the light. Salinity was controlled by the addition of sodium
chloride (NaCl). For the evaluation of the effect of flooding, seedlings
were transplanted to half-gallon plastic pots containing a mixture of
50-percent river sand and 50-percent fine organic-rich silt from Bara-
taria Bay, La. The pots were maintained in a flooded or drained condi-
tion, depending on the treatment. Platinum (Pt) electrodes inserted
into the sediment monitored the redox potential (Eh). Nutrients were
recycled in the drained pots in order to maintain the same total nutrient
availability to both drained and flooded plants. Dry weight accumulation
was the measure of the plant's response. (See Appendix E for details.)

7. To study the kinetics of ion absorption by excised roots,
seedlings were pretreated in appropriate nutrient solutions before the
roots were excised. These roots were used for short-term tests in which
the absorption of radioactive rubidium (Rb) was measured as it was
affected by manipulation of the other components of the substrate. The

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technique was described by Epstein et al. (1963). In addition, ion
uptake by intact seedlings was measured, using similar techniques, except
that whole seedlings were used and adsorption of radioactive Rb into the
roots and shoot determined. (See Appendix F for details.)

Photosynthesis

8. Carbon dioxide (CO_2) flux was monitored in a cuvette, either in
the field or in pot-grown plants in the greenhouse under controlled
light and temperature regimes. The change in CO_2 concentration of the
air stream flowing through the cuvette was measured with an infrared gas
analyzer, as described by Mooney et al. (1971). (See Appendix G for
details.)

VARIATIONS IN S. ALTERNIFLORA YIELD

Geographic as Related to Edaphic Parameters

Biomass gradients

9. Large variations in growth of S. alterniflora are shown by results of the transect study. The range of biomass from 200 quarter-meter plots harvested at the end of September 1974 was 0 to 2244 g m^{-2}, with a mean of 660 g and a standard deviation of 349 g. These figures emphasize the natural variability of the marsh. The mean biomass was higher in Barataria Basin than in the Terrebonne Basin and also higher on the west side of each basin than on the east side (Figure 2). Nutrient and silt inputs from the Mississippi River are thought to explain some of the differences between the basins, but the reason for the higher productivity of the west side over the east side is unclear. Factors that could be implicated are the geomorphology of the basins and the predominantly southeast winds that blow into the west sides of the basins. An analysis of the individual stations in Barataria and Terre-bonne basins showed that the main differences between basins occurred at the stations near the gulf where the Barataria marshes had much higher biomasses than the Terrebonne marshes. These productive stations were those that would be expected to experience the strongest influence of the Mississippi River. In addition they were more sheltered by the barrier islands of the Barataria Basin than were the more exposed Terre-bonne marshes.

10. The total biomass increased with distance from the gulf; that is, along a gradient of decreasing salinity. Most of this change,

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however, was related to an increase in the biomass of species other than S. alterniflora. In contrast to other reports (Nixon and Oviatt 1973; Broome et al. 1975), no convincing evidence was found to indicate that either the live or the litter biomass of the latter species varied in any consistent manner along this salinity gradient (Figure 3).

11. The so-called streamside effect showed up strongly in the study (Figure 4). As expected from previous work (Kirby and Gosselink 1976; Smalley 1959), the streamside plots contained more live and dead vegetation than the plots 50, 100, or 175 m inland. The effect was strongest in the stations that were farthest from the gulf. The marsh was much more broken up near the coast than it was upstream; that is, small tidal channels penetrated the marsh in a fine network. It is likely, therefore, that close to the coast some of the sample plots 100 or 175 m from the main water body on which the transect originated were influenced by other minor channels.

Edaphic and salinity gradients

12. The biomass gradients were paralled by edaphic and salinity gradients. Salinity decreases with distance from the Gulf of Mexico and tidal energy also attenuates inland. This attentuation is associated with a decrease in the frequency of inundation of the marsh, although the total time inundated per year is not greatly affected (Byrne et al. 1976). The frequency of inundation affects edaphic conditions on the marsh, particularly sediment grain size and organic content. The inter-distributary basins of this study contain almost no sands inshore of the barrier islands. The coarsest sediment particles are fine silt. As

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tidal energy decreases the coarser particles drop out of the water column resulting in an increase in the proportion of fine particles in the sediments with distance from the gulf (Figure 5).

Organic content gradients

13. Organic content is a result of complex processes. Among these are the magnitude of primary production and the tidal energy available to move organic detritus off the marsh. The processes result (Figure 6) in a clear-cut gulf-inland gradient of increasing sediment organic content with distance from the gulf and, also, increasing organic content with distance from the edge of a bayou (streamside effect).

Relationship between biomass and physical gradients

14. The relationship between the biomass gradients and the physical gradients is not clear. There is no significant correlation between salinity and S. alterniflora biomass parameters. On the other hand the presence of species other than S. alterniflora does increase as salinity decreases. As a consequence, the total biomass is strongly negatively correlated with salinity. The implications for S. alterniflora seem to be that this species, itself, is not strongly influenced by salinities in the range (11 to 27 ppt) encountered, but that at low salinities other plants are able to compete successfully with it. The data also indicate that S. alterniflora is dependent on tidal action per se as distinct from salinity. This is shown by the streamside effect, where salinity differences are minimal.

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15. No clear-cut relationship appears to exist between the biomass of $\underline{S}$. alterniflora and the organic content of the sediment (Appendix A), and in general few soil or tissue nutrients were found to be related to biomass. In some cases positive correlations may have been due to luxury consumption. Negative correlations were found between tissue N concentration and yield although the coefficient of correlation (r) was low (-0.19). The best predictor of yield was tissue boron (B), which was also negatively correlated with peak live biomass ($r = -0.32$). Other tissue elements were individually significantly correlated with live $\underline{S}$. alterniflora biomass, but individually each element accounted for 5 percent or less of the observed biomass variation.

16. Stepwise, multiple regression procedures were followed to relate two yield parameters (live $\underline{S}$. alterniflora biomass and total biomass) to 14 tissue and 8 substrate parameters by a maximum r^2 improvement technique (Service 1972). For tissue nutrients the best seven-variable model only accounted for 36 to 38 percent of the biomass variation. Tissue B was a significant variable for all models, as was manganese (Mn). Phosphorus (P), potassium (K), and N also enter the relationship with live biomass, K and barium (Ba) with total biomass.

17. No soil parameter accounted for more than 11 percent of the biomass variability. The only significant relationship was between salinity and total biomass. Thus it appears that in the complex environment of the salt marsh many factors contribute to yield.

18. It should be noted that iron (Fe), which was specifically implicated in $\underline{S}$. alterniflora growth by Adams (1963), did not appear in the field to be significantly related to yield. Extraction procedures

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strongly influence the quantitative measurement of Fe, but growth chamber studies where the species of Fe available to S. alterniflora were controlled (Appendix C) confirmed that high Fe levels were not required for optimum growth. In fact, in this study some growth inhibition seemed to occur as substrate Fe concentrations increased.

19. On a broader scale, encompassing seven species of marsh plants sampled at bimonthly intervals over a year, tissue nutrient content was again poorly related to biomass (Appendix D). This is not surprising since tissue nutrient concentrations tend to correlate with yield only in the concentration range at which deficiencies are rather severe. Above this range the plant responds to increased nutrient availability with increased growth, without appreciable change in tissue concentration (Gerloff 1969).

Salinity and Flooding

20. Controlled environmental studies confirmed previous work by Adams (1963), Seneca (1972), Phleger (1971), and Gosselink (1970) that most salt marsh species are not obligate halophytes but rather tolerate high salt levels although growth is restricted. Spartina alterniflora and S. cynosuroides were both inhibited by salinities greater than about 8 ppt, but Distichlis spicata appeared to tolerate salinities up to at least 16 ppt without adverse effects. The presence of salt in the substrate increased the amount of root relative to shoot production by the salt-stressed plants (Table 1). Analysis of kinetics of Rb uptake showed that the presence of NaCl markedly inhibited the absorption of radioactive Rb by the root tissue (Figure 7). This may be the primary

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mechanism of growth inhibition by salt (Appendix F). The requirement

for calcium (Ca) for ion uptake, found in most glycophytes, is intensi-

fied in S. alterniflora, which requires about five times higher Ca

levels than glycophytes do. Since seawater has a high Mg:Ca ratio and

the ions are similar, the role of Mg in ion uptake was also examined.

It did not competitively inhibit the action of Ca. In fact, it substi-

tuted for it. In tests with intact plants as opposed to seedlings,

NaCl, whether given before or during the period of Rb absorption,

reduced Rb uptake to less than 40 percent of controlled plants. Pre-

loading the plants with salt was more inhibiting than when given at the

same time (Figure 8). In spite of this inhibition of absorption, the

presence of 10 g ℓ^{-1} of salt in the substrate did not affect the growth

of seedlings. Plants are known to accumulate some salts far in excess

of their physiological needs. Presumably these salts are accumulated

in the cell vacuoles where they are thought to be involved in main-

taining an osmotic gradient between the plant and its environment.

21. The results presented in this study indicate that mechanisms

of ion uptake in S. alterniflora are not significantly different from

those of salt-sensitive plants, at least in terms of the sodium-rubidium

relationship. The difference lies in the ability of S. alterniflora to

tolerate high cytoplasmic salt concentrations, which lower the plant's

osmotic potential in relation to the medium in which it is growing.

22. A comparison of S. alterniflora with S. cynosuroides grown

under drained and flooded conditions sheds light on the adaptation of

these two species. The dry weight accumulation by S. alterniflora was

not influenced by flooding, although the root-to-shoot ratio doubled

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from 44 to 87 percent. In contrast, flooding reduced both root and shoot growth by S. cynosuroides without changing the root-to-shoot ratio (Figure 9). These differences in the two species are clearly related to their habitats since S. alterniflora is normally found in the highly reduced intertidal zone, whereas S. cynosuroides grows in areas that are nearly always above high tide level. Measurement of photosynthesis of the same two species under drained and flooded conditions supports the dry weight results reported above, although variability among plants precluded statistical treatment. Spartina alterniflora photosynthesis was higher in flooded sediments than in drained sediments, whereas the S. cynosuroides performed better in drained sediment.

23. These greenhouse tests, combined with field observation of the distribution of marsh plant species in relation to elevation and salinity (see for instance, Chabreck 1972), begin to show a consistent pattern that can be used to characterize the ideal environment of a particular plant species. Distichlis spicata, for instance, appears to have a higher salt tolerance than S. alterniflora or S. cynosuroides. Although the latter two both will tolerate apparently about the same salt levels, S. cynosuroides is strongly inhibited by reducing conditions whereas S. alterniflora is able to tolerate them. It is pertinent that the effect of salt stress and of reduced conditions in S. alterniflora both lead to an increase in root growth at the expense of shoot growth. This is no doubt an adaptive mechanism for the plant, but it has implications for the substrate also, since the root mat stabilizes the marsh against erosion.

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Role of Light and Temperature in Marsh Plant Photosynthesis

24.   Studies of community metabolism in a S. alterniflora salt
marsh show that the contribution of the microbial community to photo-
synthesis is maximal in the winter when it may be as much as 10 percent
of gross photosynthesis. The macrophyte becomes more and more dominant
during the spring and summer, however, so that in May it is responsible
for more than 95 percent of total photosynthesis (Table 2). In contrast,
respiration of the sediment component of the system was 64 percent of
the total community respiration in December and March and about 76
percent in May. Thus the microbial component of the system (which
includes algae, bacteria, fungi, invertebrates, and metazoans) growing
on the marsh sediment surface and the lower parts of the culms of the
dominant grass, is an active consuming community and seldom, if ever,
net productive.

25.   The gross production rate of S. alterniflora was signifi-
cantly higher during December and March than in May and July (Figure
10). At the same time the respiration rate also decreased from about
0.4 to less than 0.2 mg carbon (g dry wt hr)$^{-1}$. Thus during the winter
months the respiration and the photosynthetic rates per unit of tissue
were both high. The high respiration rate during the winter may be due
to the high proportion of old shoots at that time. Since there is
little live tissue present during the winter, total organic production
on a unit of marsh surface is low.

26.   The photosynthetic rate of S. alterniflora as a function of
light intensity is shown in Figure 11. The photosynthetic mechanism is
such that the plant does not achieve light-limited rates, even at full

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light intensity. This explains, in part, its extremely efficient and productive growth habit.

27. In the field, photosynthetic rates did not appear to be changed to any extent over a period of a single day by changes in the salinity or the depth of the flooding waters. Thermocouples in the sediments showed that the root temperature was stable, seldom varying as much as a degree centigrade during the course of 24 hours. The Eh of the soil at a depth of 2 to 3 in. was also rather stable and changed very little during the tidal cycle, even though the marsh could be exposed to air for several consecutive hours. At times when the marsh was exposed for several days in a row, however, the Eh did increase and the sediments became more aerated. The marsh sediments themselves then acted as a buffer to rapid changes in salinity and Eh, and the plant was insulated from wild fluctuations in its root environment.

Discussion

28. On the east coast of the United States, studies by Broome et al. (1975) using similar analytical techniques showed that up to 90 percent of the variability in S. alterniflora yield could be predicted by a combination of soil and tissue nutrients. In this study's survey, very poor predictability was found in Louisiana. At the end of the growing season when the survey was conducted, the plant may no longer have been responding to the environment as it did at times when it was actively growing. The indications were that in the highly organic sediments of the Louisiana coast with its low energy tides, S. alterniflora can grow and flourish in a broad range of environments and that

the growth response is not clearly linked to any easily measured parameter. Overall, considering the other research reports that have appeared concerning this species, salinity over a broad range and Eh of the soil appear to be the most critical factors. The role of salt has been known for some time. The role of Eh has not been as clear; however, the differences in response of S. alterniflora and S. cynosuroides in the greenhouse studies, the relation of tissue sulfur to yield in the North Carolina studies (Broome et al. 1975), and preliminary results of Patrick* all argue to its importance in marsh environment.

29. Photosynthetic rates on the marsh are controlled closely by light intensity. Although microorganisms are the major consumers in the community, the grass is not only the major source of organic production but it also provides a surface for colonization by the microorganisms; thus, mud flats are not a substitute for salt marshes. They are not as productive of organic matter, nor does the flat surface of the mud provide as large a surface for colonization by microorganisms.

30. The marsh sediment appears to provide a relatively stable environment for the roots since both salinity and Eh changes are buffered. As a result the roots of the plant are not subjected to as rapid fluctuations in their environment as, for instance, the surface of the marsh, which is daily flooded and drained by waters that vary widely in salt content. The plants respond slowly to slow shifts in a number of parameters related to Eh, with response times of weeks or months rather than days.

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* Personal communication, W. H. Patrick, Jr., Center for Wetland Resources, Louisiana State University, Baton Rouge, La. 1977.

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31.   In addition to the long-term importance of salt and Eh, it is
possible to pinpoint the importance of the single nutrient N in the
saline estuarine system. This appears to be a limiting factor in salt
marshes from New England to the gulf coast (Patrick and Delaune 1975;
Broome et al. 1975; Valiela and Teal 1975). There is some suggestion
that the availability of this nutrient is highest in the early spring
and that growth is restricted by the rate at which inorganic N becomes
available during most of the summer months. Circumstantial evidence to
support this hypothesis is found in the correlation between growth
rates that are highest in the months of April and May (Kirby 1971) or
earlier (Appendix G) and the availability of inorganic N during the
winter, followed by its rapid disappearance during the early spring (Ho
1971; Brannon 1973).

32. From the foregoing discussion, and from research carried out by many individuals who are gradually clarifying functional relationships in coastal marshes, a general model emerges that should be of some utility in creation of new marshes with dredged material. This model is formulated in terms of three key growth parameters and two control loops that normally stabilize a marsh and determine its success. The critical parameters are salinity, limiting nutrients (usually N), and the degree of chemical reduction (Eh) of the soil. The latter is controlled by the inundation regime (tide range and marsh elevation), organic content of the soil, and soil porosity (sediment grain size). The two control loops, which interact through marsh vegetation growth, can be called the marsh elevation loop and the sediment Eh loop. Although the relationships are complex and quantitative documentation incomplete, the following conceptual scheme is set forth.

Growth Parameters

33. The marsh plant "sees" what its roots contact--levels of salt, nutrients, and the conditions associated with a particular Eh of the soil (low oxygen, low pH, high sulfides, high levels of soluble micronutrients, etc.). These are shown diagrammatically in Figure 12 as soil salinity, turbidity (nutrient supply), and Eh, which directly control the rate of photosynthesis of the marsh plant species. These are primary controllers, but they in turn are controlled by other parameters.

34. The water budget, that is, the balance between rainfall and

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evapotranspiration on the marsh, influences the soil salinity. The source of salt is tidal waters, which reach the marsh through a tidal regime controlled by tide frequency and amplitude, with the actual inundation dependent on the elevation of the marsh. The inundation regime also determines how much silt and nutrients reach the marsh surface. Soil Eh is also influenced by the inundation regime, which through flooding limits the oxygen (O_2) supply to the sediments. In Figure 12 the sign of the growth response is shown in the interaction arrow: increased salinity decreases plant growth (sign is negative); increase in a limiting nutrient increases plant growth; and increased reduction level decreases plant growth (although this is not so clearly established).

Marsh Elevation Loop

35. For a particular site the elevation of the marsh controls the inundation regime and thus indirectly plant success. Normally in areas where tides are strong relative to fresh stream input, the marsh cannot reach an elevation above mean high tide (mht) because the mechanism of deposition depends on flooding waters (Hinde 1954; Johnson and York 1915). Most marshes, especially with highly organic, fine-grained sediments, are subsiding slowly as the sediments compact. In order for the marsh to survive, the deposition rate must equal this subsidence rate. The fact that this normally occurs is testified by the relative stability of a marsh. The processes controlling this marsh elevation loop are shown in Figure 13, which for simplicity isolates the pertinent portion of Figure 12.

36. As the marsh increases in elevation and approaches mht, the frequency and vigor of inundation decrease. Consequently. the silt load available to the marsh decreases and the marsh no longer increases in elevation. This aspect of the process is self-limiting. At the same time, deposition of organic matter occurs as plants die and dead tissues drop onto the sediment surface. When inundation is vigorous, much of this organic matter is swept out of the marsh into adjacent waters, but as the marsh becomes more elevated, hydraulic energy decreases and more of the organic matter remains for incorporation into the sediments. In this process high inundation energy decreases organic deposition and marsh elevation. Thus the organic and the inorganic deposition processes complement each other.

37. When marsh elevation is low and inundation energy high, inorganic deposition increases in importance and organic matter is exported. When the marsh elevation is high relative to mht, organic deposition predominates and inorganic input decreases. Normally neither process can raise the elevation of the marsh above mht, since inorganic deposition requires flooding waters, and organic deposits above mht are oxidized by respiratory processes.

38. Where freshwater inputs of silt are high and floods elevate waters for extended periods, permanently exposed bars can be deposited above mht. This is merely an unusual example of the general process. The important point is that the processes that control marsh elevation tend to be self-stabilizing so that a marsh functioning within normal ranges of elevation tends to maintain itself at that elevation.

Sediment Eh Loop

39. The second control loop mentioned earlier involves the soil Eh. Figure 14 outlines this loop. The degree of reduction of the sediment depends on the flooding regime, porosity of the sediment, and organic content. Response to inundation depends on at least two components of flooding that do not always vary together.

40. First, the longer the period of inundation the lower the oxygen and sulfate ($SO_4^=$) supply for biological oxidation, and therefore, the more reduced the substrate will become. (Oxygen and $SO_4^=$ are probably the primary electron acceptors in saline water. Carbon (C) can become important if these two are exhausted.) With frequent flushing, even if the total inundation is unchanged, more oxygen is available and the degree of reduction is not as great. If the sediment is porous, O_2 penetrates deeper when periodic drainage occurs. The inorganic grain size is a function of the energy of the flooding waters and tends to increase with increasing energy.

41. The other major influence on Eh is the supply of organic compounds available for oxidation. Highly organic flooded soils are usually very anaerobic (highly reduced). Once again the processes tend to be self-stabilizing. If inundation energy decreases, the proportion of plant production deposited on the marsh increases. This results in an increase in the degree of reduction of the soil, which in turn probably inhibits plant growth, reducing the supply of organics to the sediment. As a result, elevation tends to decline and the inundation energy to increase and reverse the process.

32

Loop Interactions

42. Figure 15 combines both control loops with the marsh growth model discussed above, showing how they interact. The point of stability of a particular marsh depends on the magnitude of the major inputs--silt and nutrients, tidal energy, salt, and the water budget. In addition, the mean temperature and the solar input determine the magnitude of potential photosynthesis.

43. In the nearly subtropical Louisiana marshes, the organic content of the soil is a good index of the balance of these processes. As shown in Appendix A, those $\underline{S}$. alterniflora marshes with highest tidal energy have the lowest organic content. Sediments in the brackish and fresh marshes that are very poorly flushed are highly organic (up to 80 percent), depending almost entirely on organic deposition to counteract the normal subsidence rate. On the middle Atlantic coast, the relatively high tidal energy results in much coarser sediments, but the sediment grain size decreases and organic content increases with marsh elevation, as predicted from the model.

44. For establishment of new marsh, the model suggests that the characteristics of the sediment (excluding obviously toxic materials) are not as important as initial elevation. After a sward of grass is established, natural processes should act to change the marsh toward the dynamic equilibrium conditions dictated by the natural driving forces.

45. The elevation range seems to be critical. At elevations low with respect to mht and the tidal range, it may be difficult to establish a marsh, and erosional processes may override natural deposition.

33

Above mht in saline areas, evapotranspiration and rare flushing can often result in large accumulations of salt in the upper soil crust, preventing growth of even the most salt-tolerant species (Gosselink et al. 1971).

46. At elevations in the upper range of the intertidal zone, however, there are plant species that flourish in almost any regime. This is illustrated in Table 3, which identifies from these studies and the excellent reference of Chabreck (1972) the preferred salinity and Eh of several marsh plant species in Louisiana marshes.

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Table 1

Response of Three Marsh Plant Species to Salinity

Nutrient Solution NaCl Conc. g ℓ^{-1}	S. alterniflora		S. cynosuroides		D. spicata	
	Total* Plant g dry wt	Root-to-Shoot Ratio	Total* Plant g dry wt	Root-to-Shoot Ratio	Total* Plant g dry wt	Root-to-Shoot Ratio
0	0.98 ± 0.27	0.36	1.89 ± 0.65	0.25	0.16 ± 0.03	0.25
1	1.04 ± 0.30	0.49	2.35 ± 1.16	0.28	0.16 ± 0.05	0.20
2	0.75 ± 0.16	0.48	2.15 ± 0.43	0.26	0.18 ± 0.05	0.20
4	0.85 ± 0.28	0.48	1.57 ± 0.63	0.25	0.17 ± 0.05	0.27
8	0.84 ± 0.18	0.49	1.41 ± 0.62	0.30	0.16 ± 0.07	0.28
16	0.54 ± 0.16	0.51	0.89 ± 0.34	0.29	0.17 ± 0.04	0.30
32	0.20 ± 0.07	0.49	0.36 ± 0.11	0.64	0.10 ± 0.02	0.33

* Means are shown with standard deviation (n = 10).

Table 2

S. alterniflora Metabolism at 25°C

	Percent of Marsh Community Metabolism*		
	December 1975	March 1976	May 1976
Gross Photosynthesis	89 ± 6	92 ± 6	96 ± 3
Respiration	36 ± 11	36 ± 5	24 ± 9

* Means are shown with standard deviation.

Table 3

Habitat Preference of Common Marsh plant Species

Salinity, °/oo	Eh		
	Very Reduced*	Somewhat Reduced	Usually Oxidized**
Greater than 10	Spartina alterniflora	Distichlis spicata Juncus roemerianus	Iva frutescens
2 to 10	Spartina patens Scirpus olneyi		Spartina cynosuroides
1 to 2	Sagittaria falcata Scirpus validus	Phragmites communis†	
Less than 1	Panicum hemitomom		

*Low marshes, very organic.
**Above mht, low organic content.
†Phragmites communis is a commonly accepted name for the common reed and appears throughout many current literary works; however, the U. S. National Herbarium has recently accepted P. australis as the proper name for this grass (Personal Communication, 2 August 1977, Dr. Thomas R. Soderstrom, Agrostologist, Dept. of Botany, Smithsonian Institute, Washington, DC.
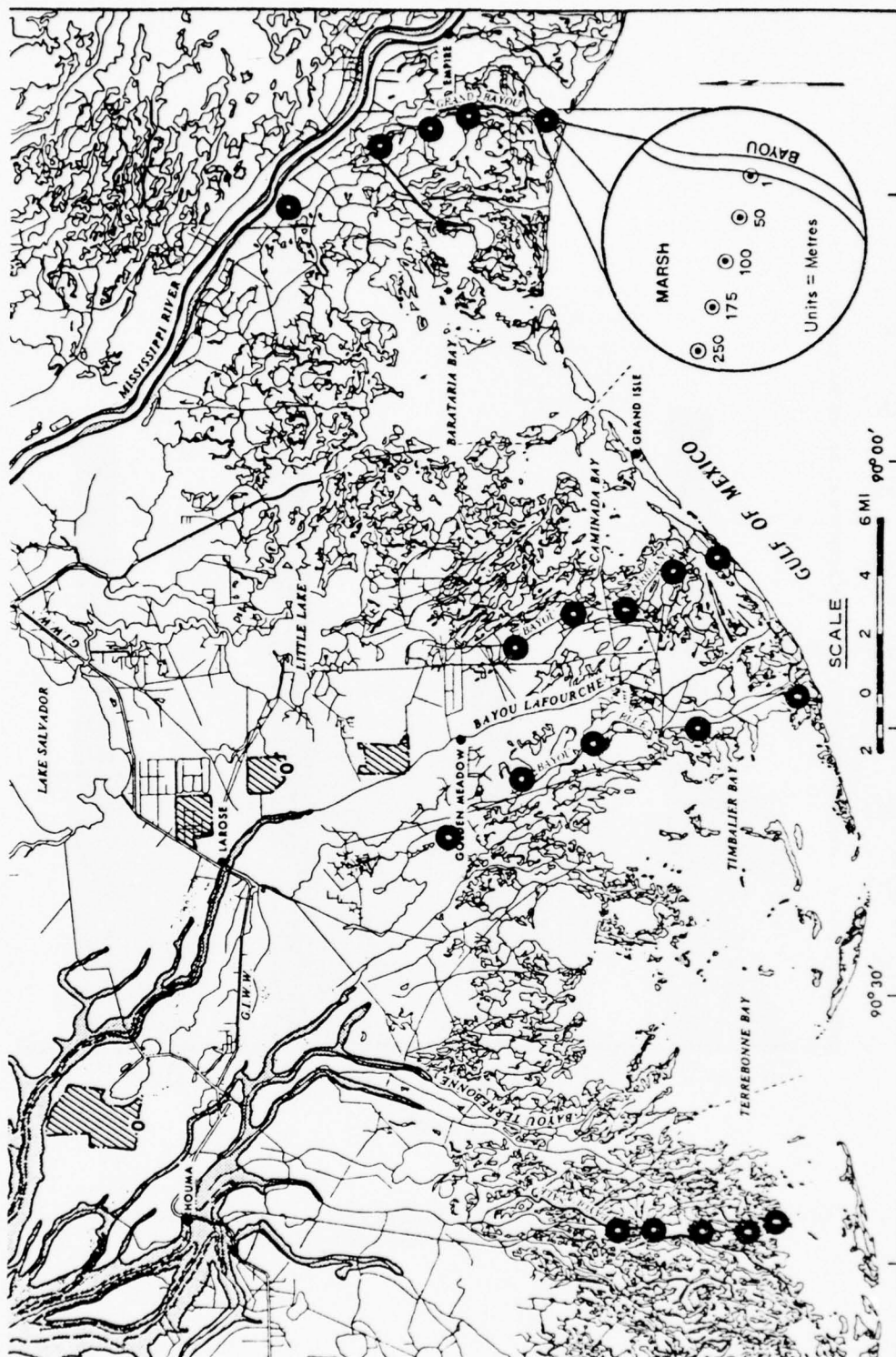
Figure 1. Location of field sampling sites on the Louisiana coast.
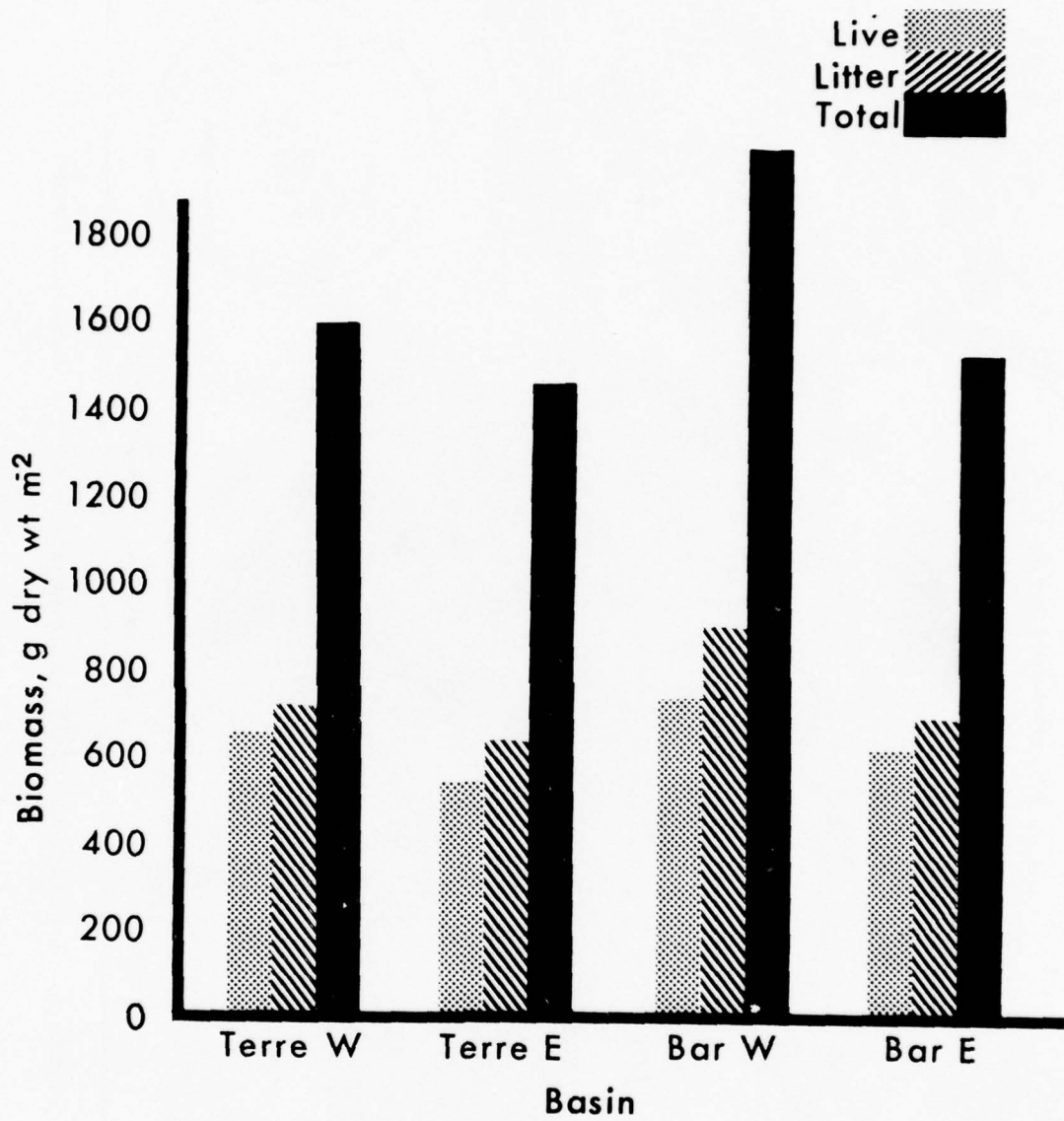
Figure 2. Variation in <u>S. alterniflora</u> biomass related to distance from Mississippi River.
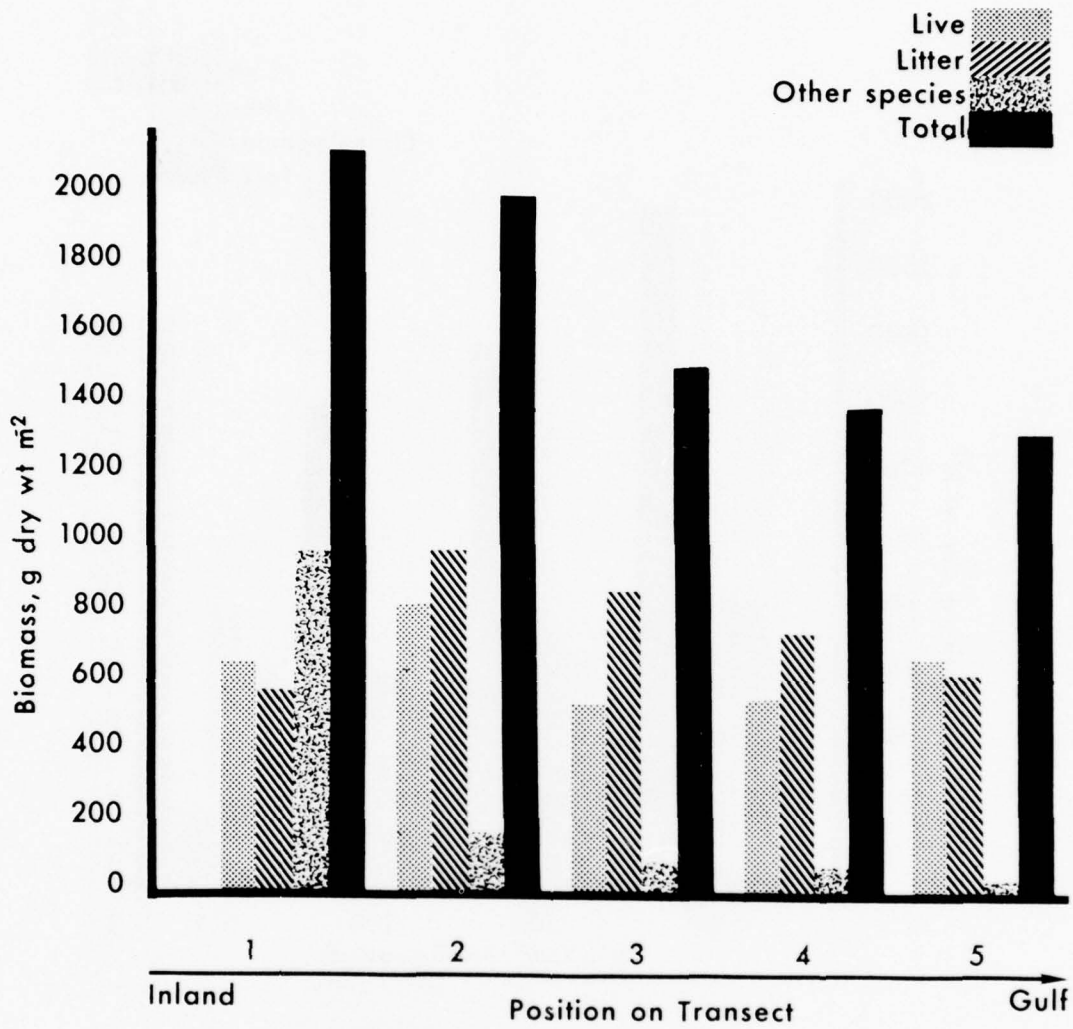
Figure 3. Gulf-inland variations in biomass parameters in S. alterniflora marshes.
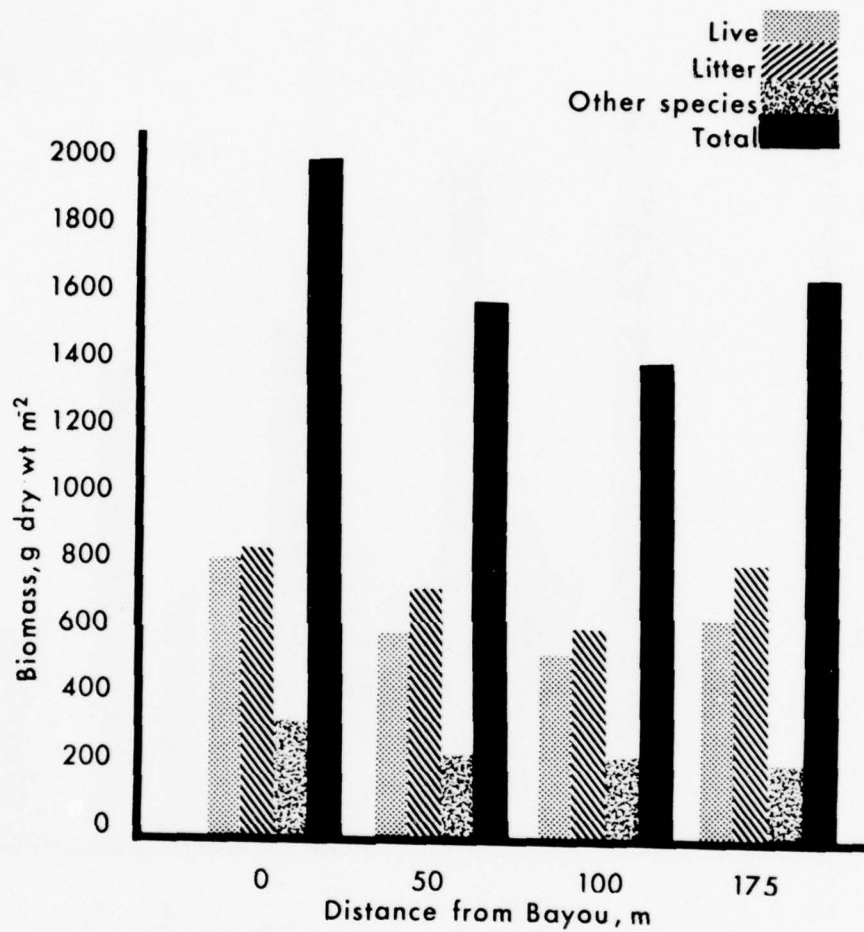
Figure 4. Streamside influence on biomass parameters in S. alterniflora marshes.
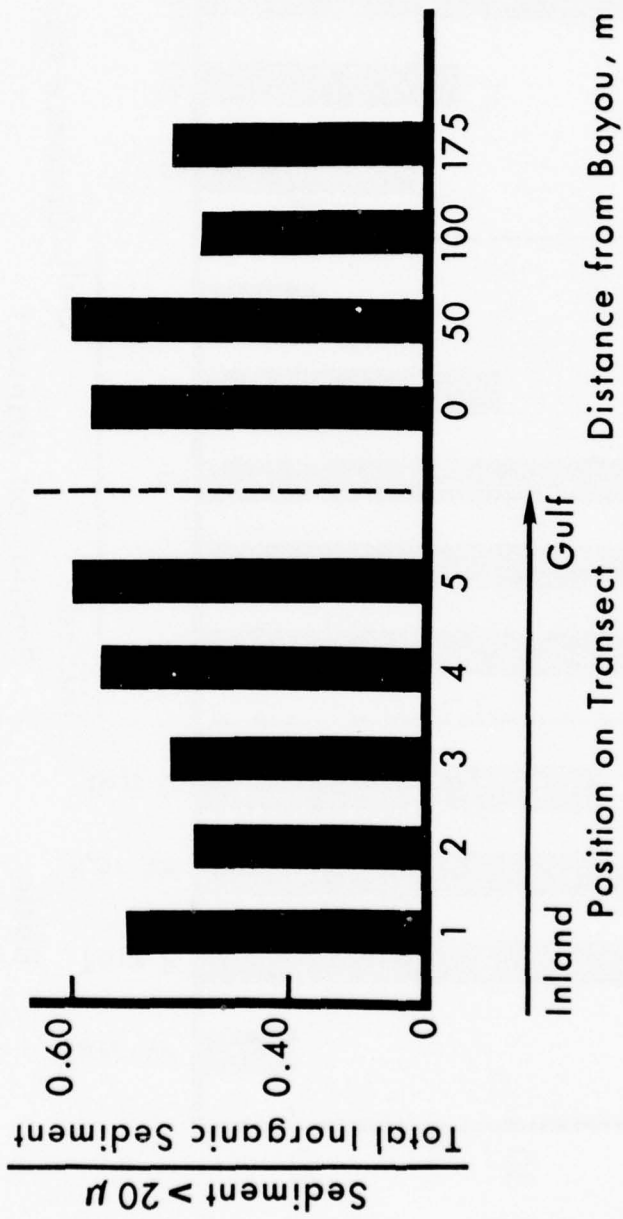
Figure 5. Change in the proportion of the coarse sediment fraction to total inorganic sediments with distance from the gulf and from local bayous.
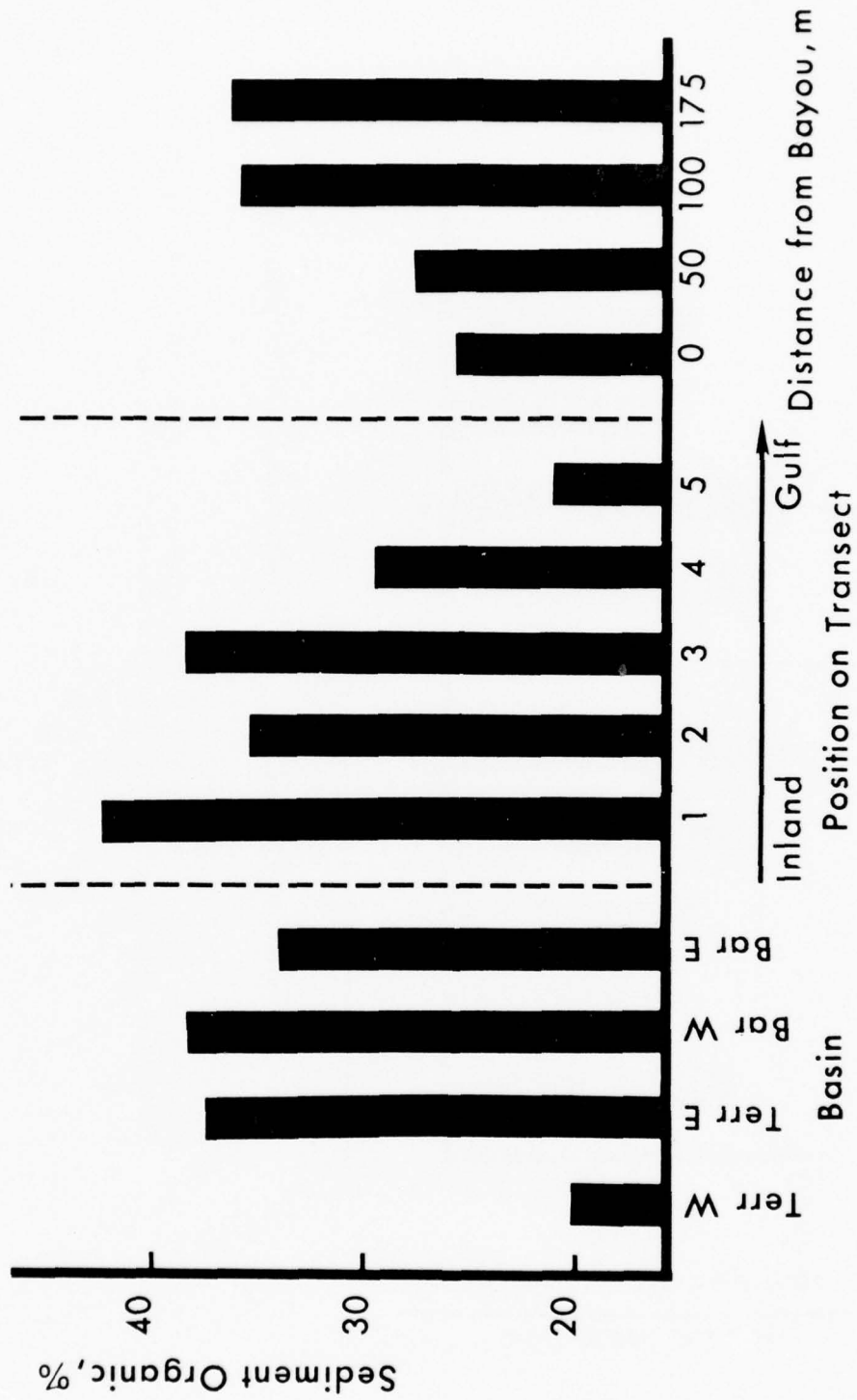
Figure 6. Organic concentration in salt marsh sediments. Mississippi River, gulf-inland, and streamside effects are all highly significant (P <0.01).
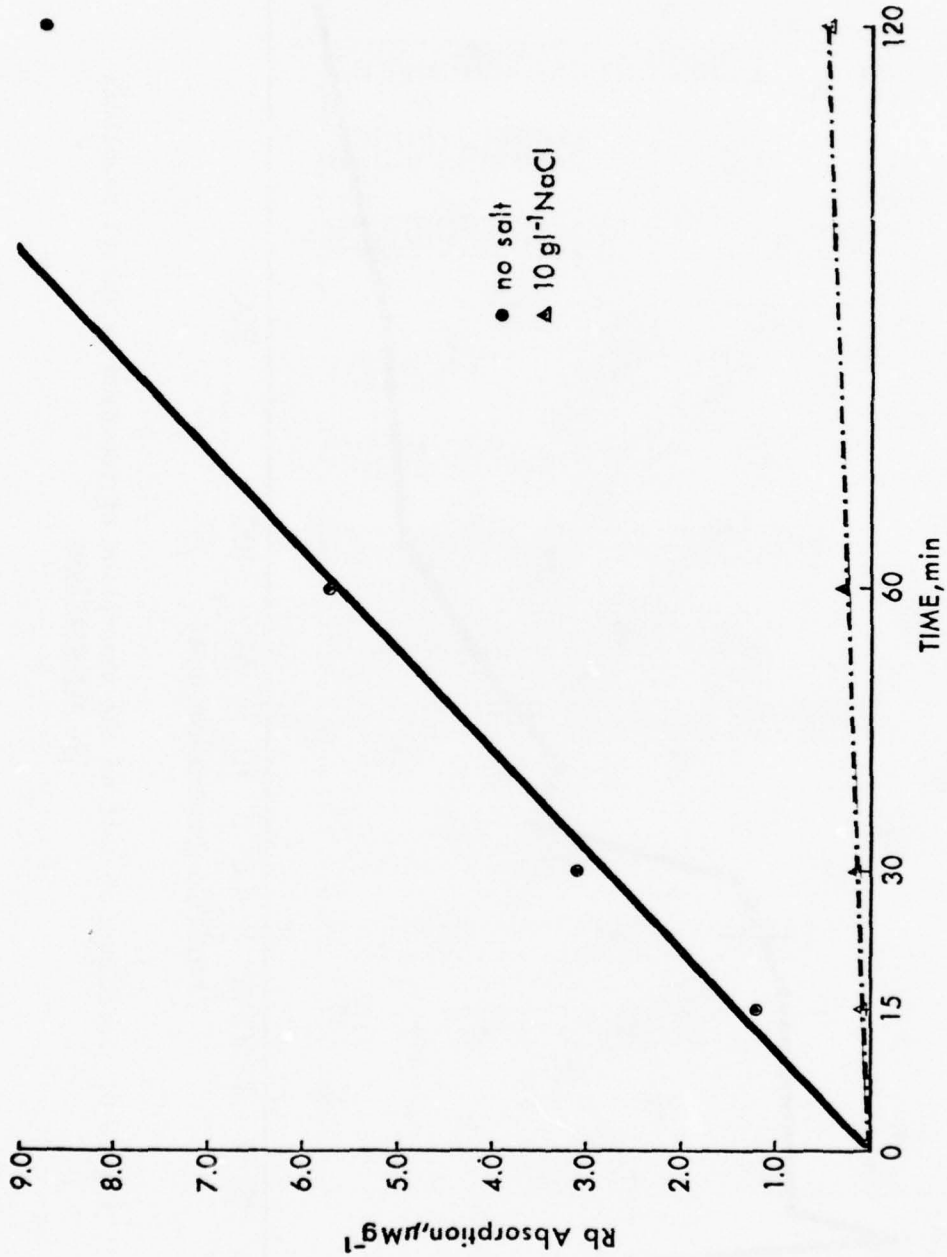
Figure 7. Time course of rubidium uptake by S. alterniflora roots in the presence and absence of NaCl.
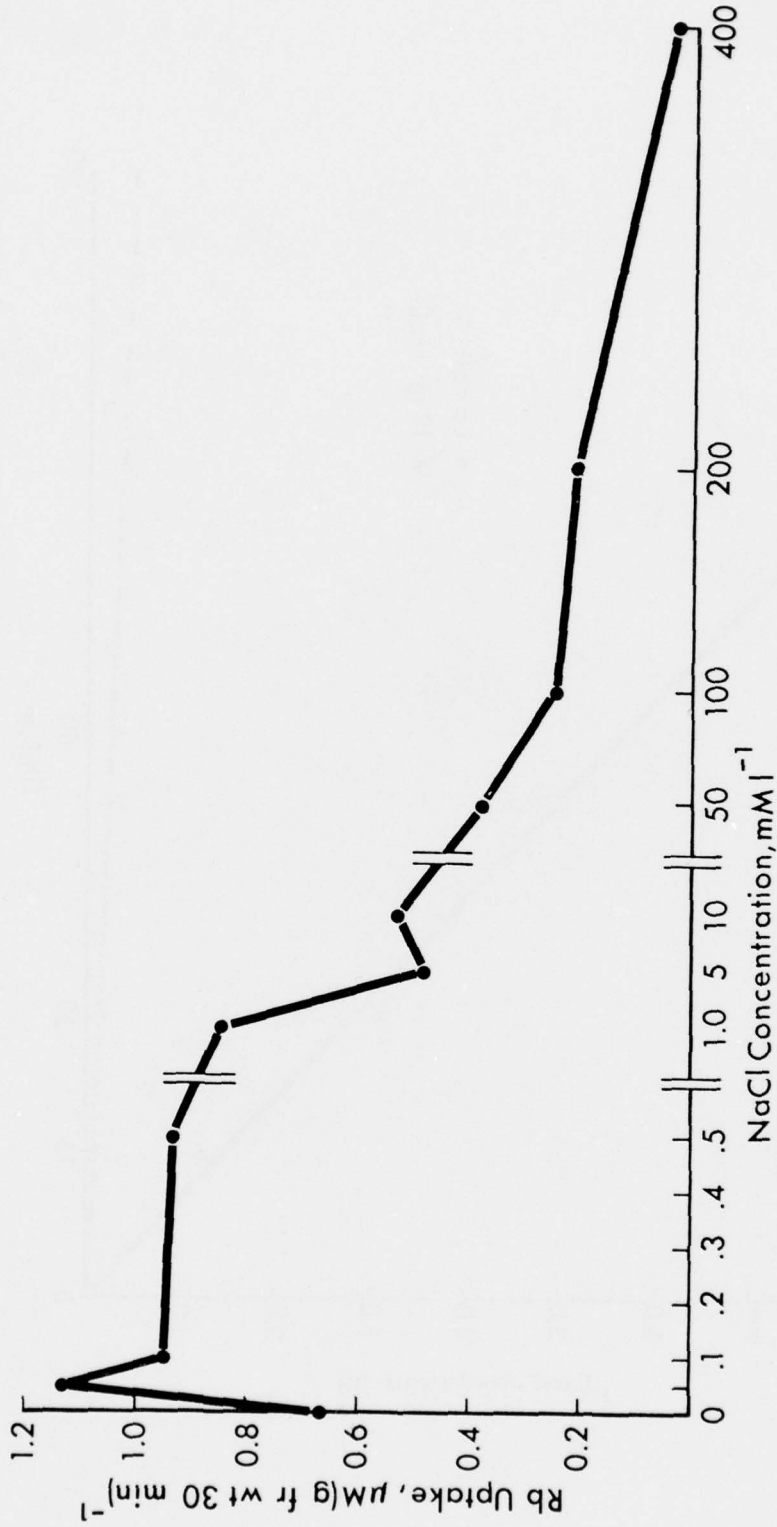
Figure 8. Influence of salt on the absorption of rubidium by intact seedlings
S. alterniflora.
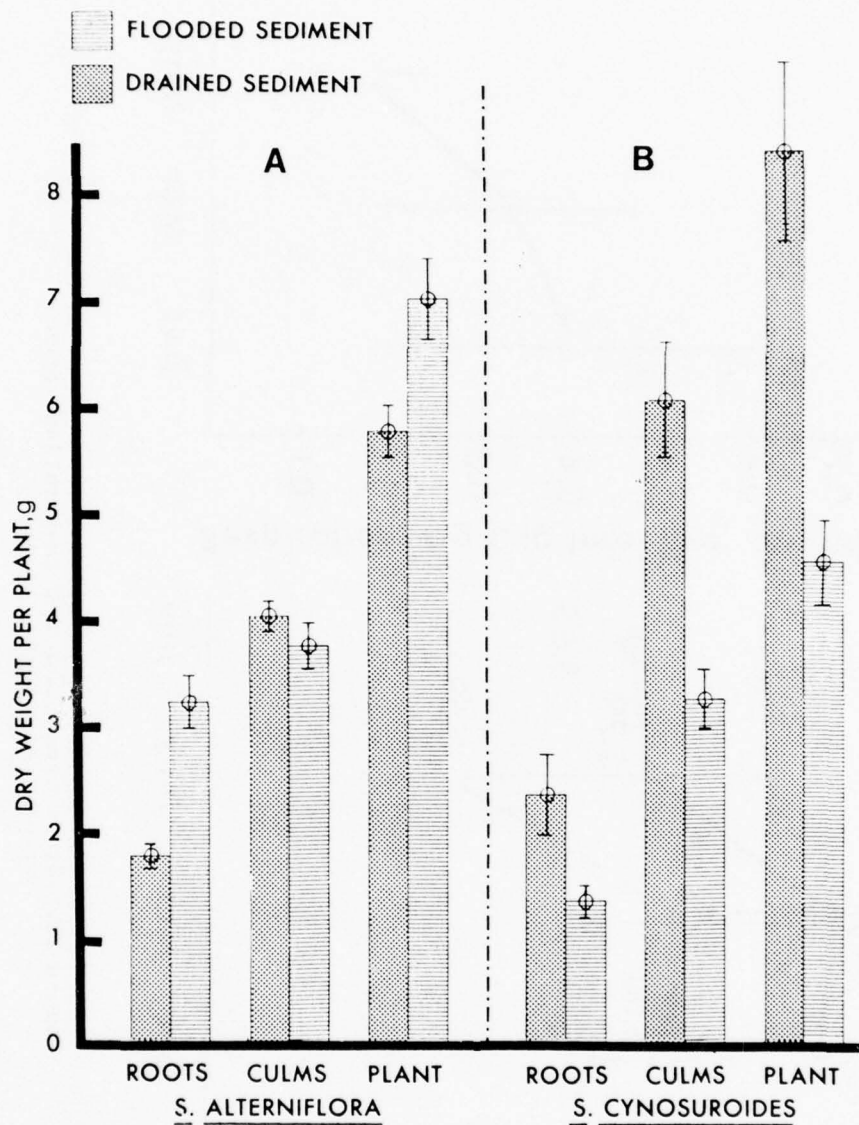
Figure 9. Relative growth of S. alterniflora and S. cynosuroides in drained and flooded sediments.
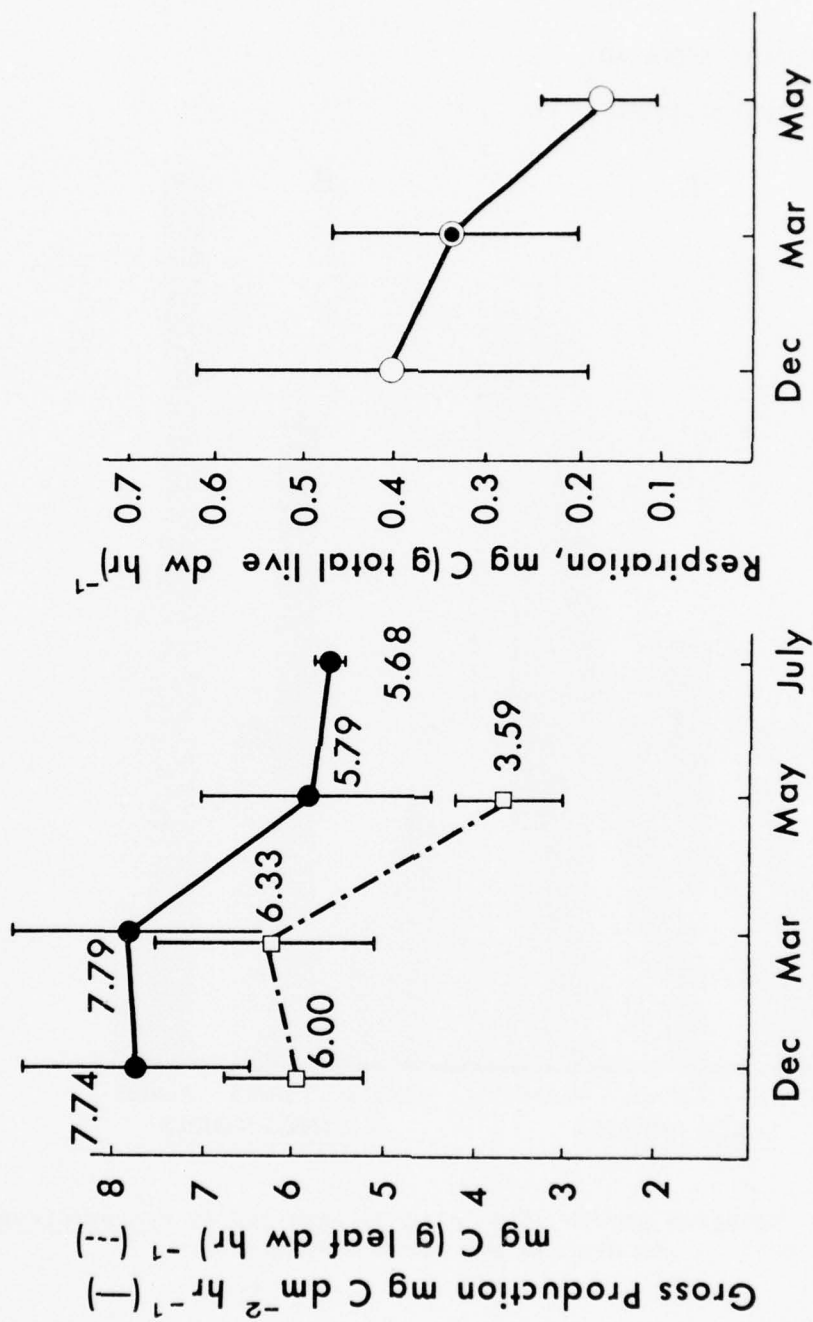
Figure 10. Gross production and respiration rates of S. alterniflora at 25°C.
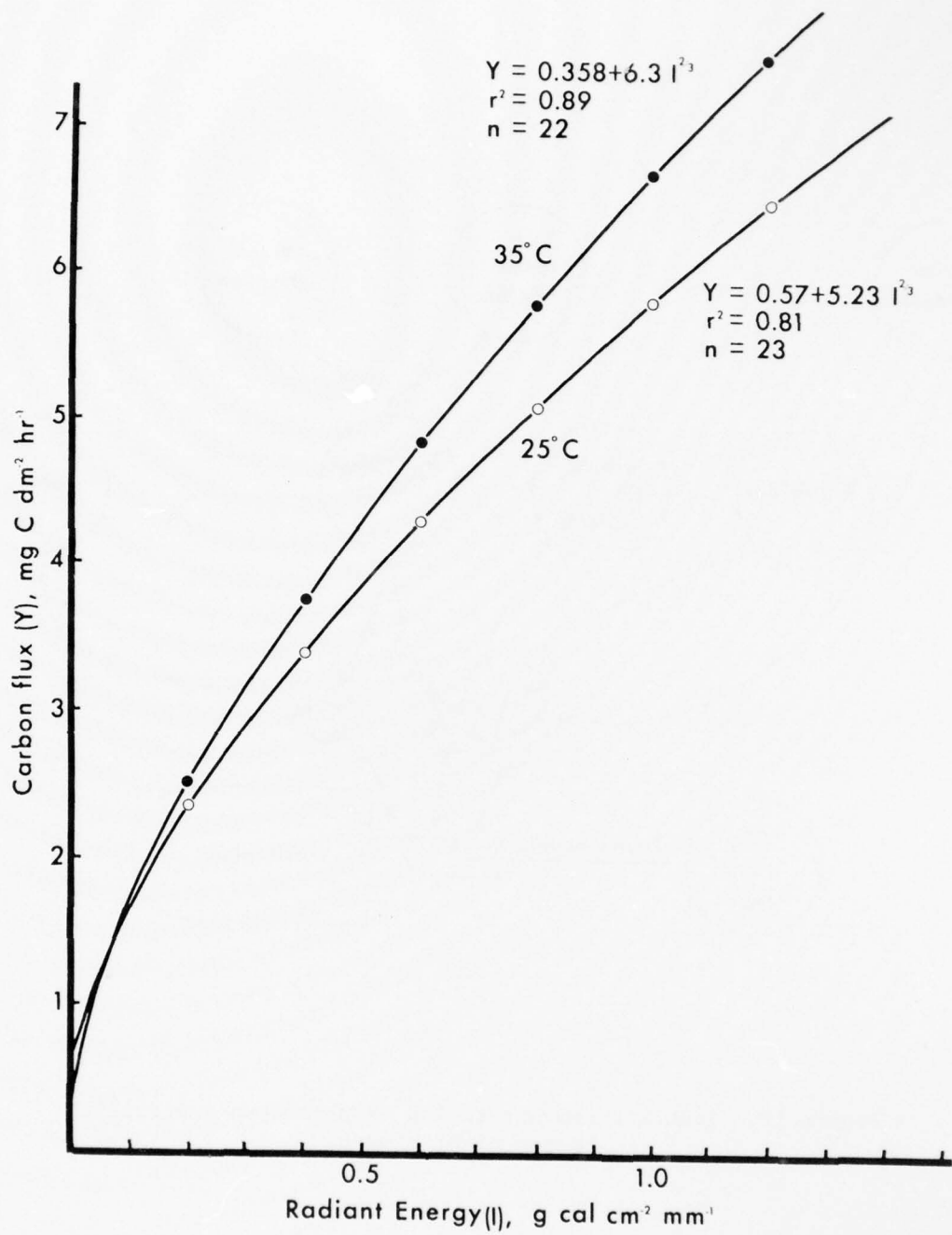
Figure 11. Photosynthesis light response curve for S. alterniflora. (See Appendix G for details.)
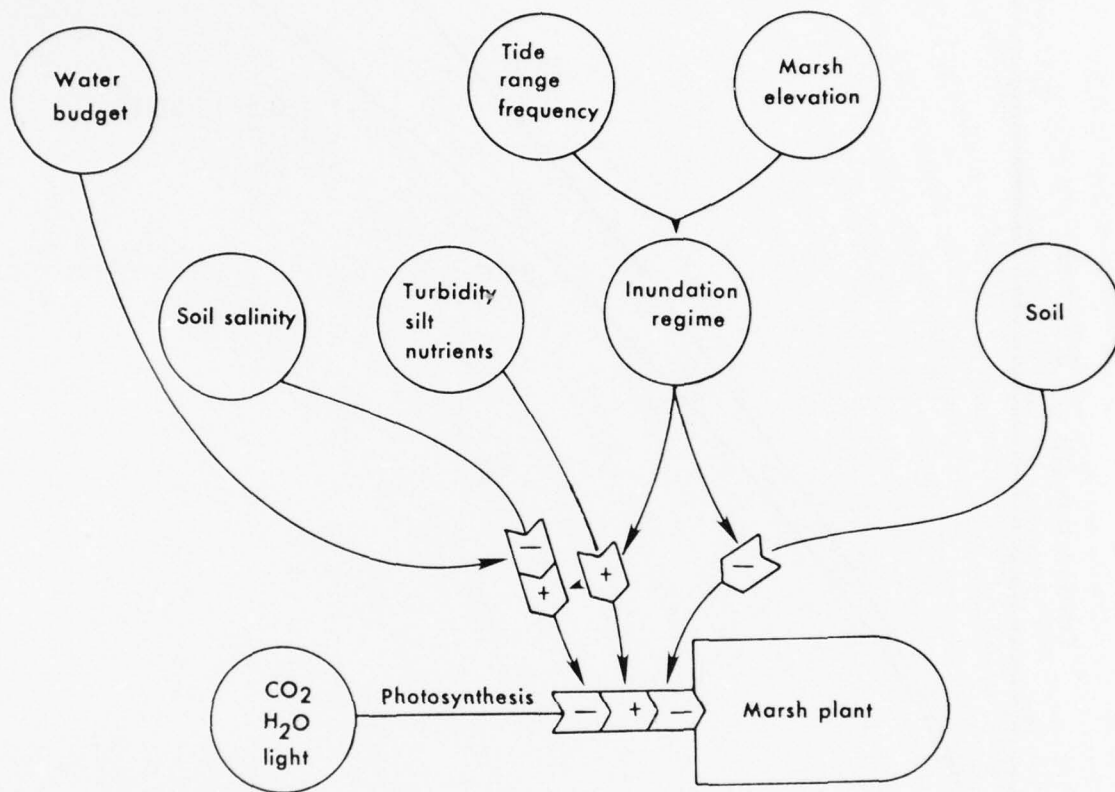
Figure 12.   Symbolic representation of processes controlling
marsh plant growth.
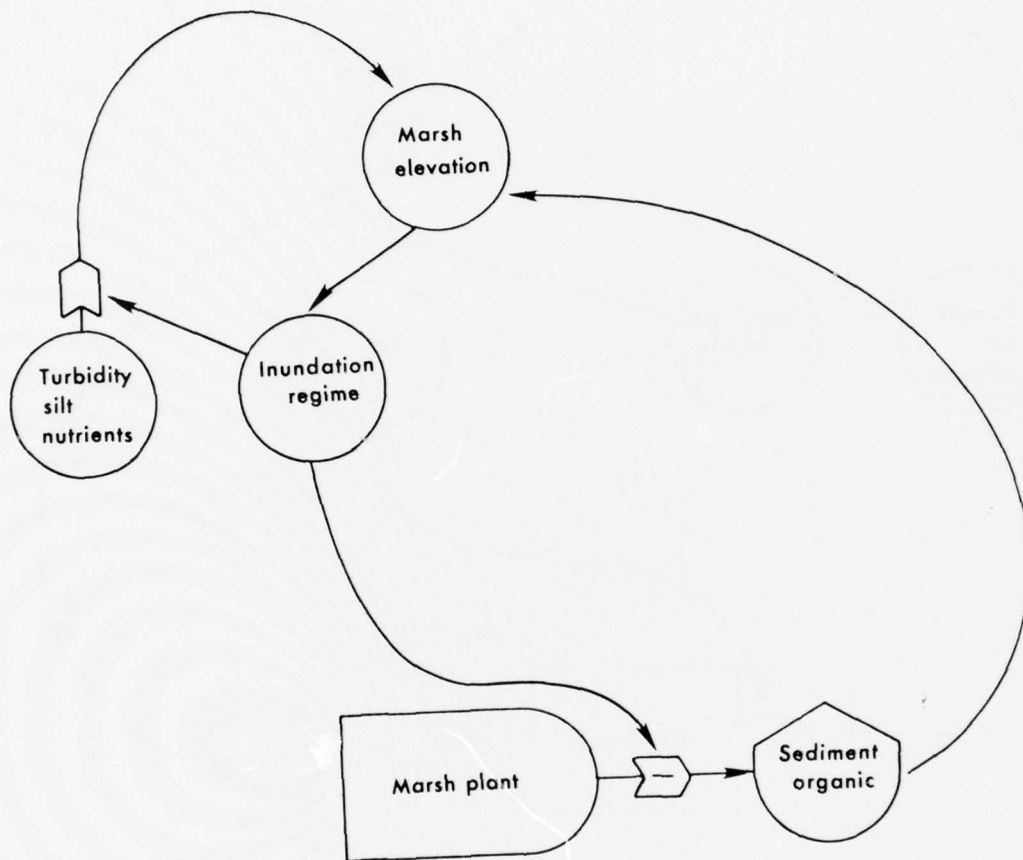
Figure 13.   Symbolic representation of processes controlling
marsh elevation.
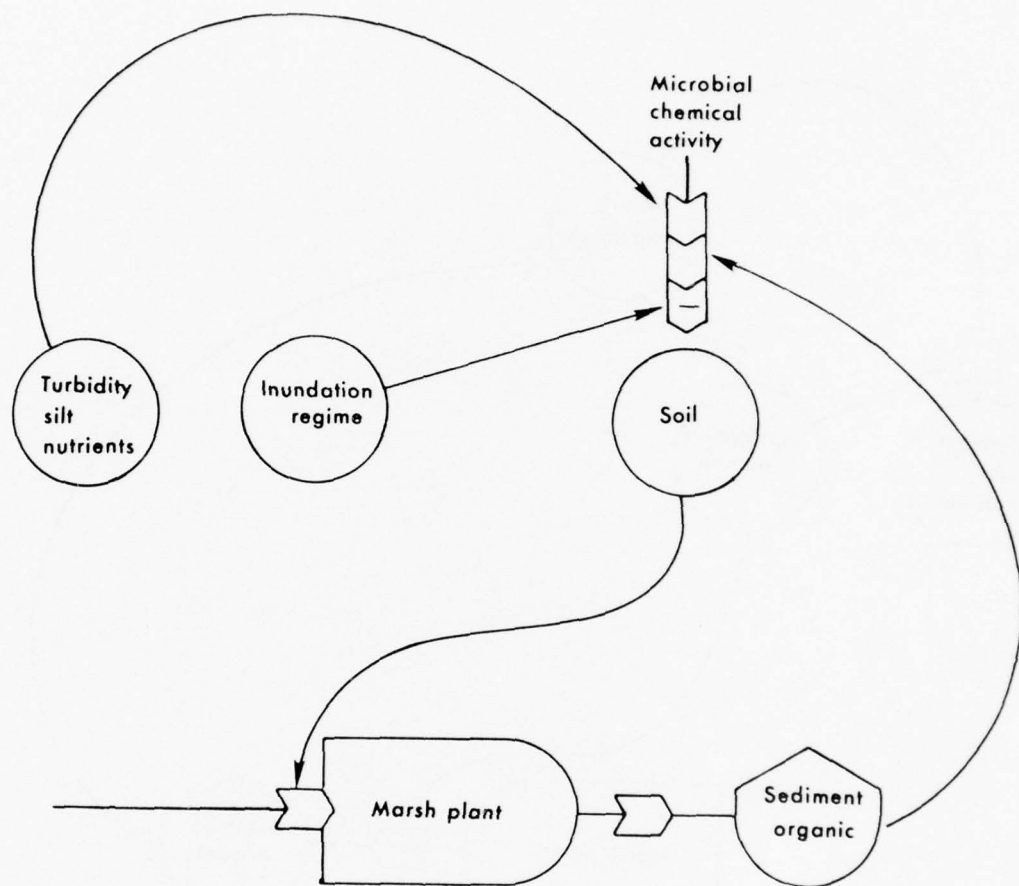
Figure 14. Symbolic representation of processes controlling sediment reducing potential (Eh).
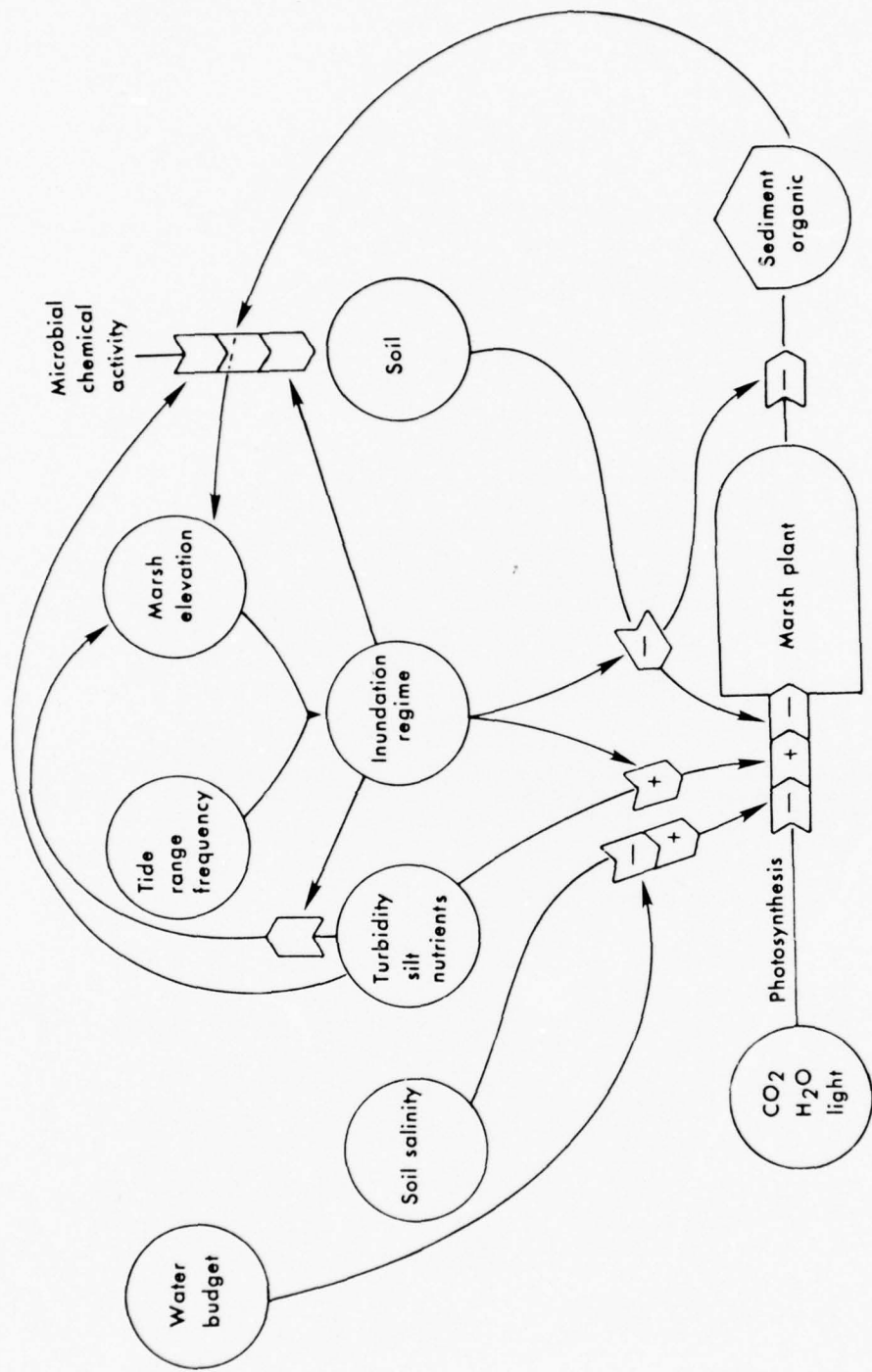
Figure 15. Figure 12-14 combined to show interaction among processes controlling marsh success.

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DREDGED MATERIAL RESEARCH PROGRAM

COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA
VOLUME II: GROWTH DYNAMICS

by

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December 1977

Final Report

APPLNDIX A: SPATIAL VARIATION IN THE PEAK BIOMASS OF SELECTED MARSH
PLANT SPECIES FOUND IN COASTAL LOUISIANA

Introduction

1. Productivity of the salt marsh grass S. alterniflora has been
studied intensively by a number of individuals in a number of locations
on the east and gulf coasts of the United States (Hopkinson et al.
1976).* As accurate productivity assessment requires sequential measure-
ments of plant biomass over at least 1 year in a single location, these
studies have been intensive rather than extensive and have yielded
little information about geographic variation in productivity of this
species. In Louisiana, Chabreck et al. (1968) described the areal
extent of the salt marsh dominated by S. alterniflora, but they did not
attempt to show areal variation in the vigor or biomass of this species.
In fact only two studies of S. alterniflora productivity (Kirby and
Gosselink 1976, Hopkinson et al. 1976) have been completed in Louisiana,
so that little is known about the variation in S. alterniflora production
in these extensive (255,083 ha) marshes. Turner (1976) analyzed the data
from a number of studies in the United States and showed that in general
the productivity of this species increases with decreasing latitude, a
relationship apparently closely related to mean air temperatures.

2. A wide local variation in production (Nixon and Oviatt 1973) is
presumably superimposed on this latitudinal gradient. Differences
between streamside and inland production have been widely reported in

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* References listed at the end of the appendix.

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both the east and gulf coasts (Kirby and Gosselink 1976; Smalley 1959; Williams and Murdoch 1969; Morgan 1961). In addition, production can be expected to vary as nutrients, substrate, elevation, and other factors change.

3. As indicated previously, accurate measurement of primary production requires detailed sampling through time. For this study, however, peak biomass has been used as an index of production. The limitations of this index have been reported elsewhere (Hopkinson et al. 1976), but its use enables broad coverage of an area with a reasonable field effort. The variation in end-of-the-season peak biomass is described in this study as related to the distance from three primary influences along the Louisiana coast: the Mississippi River on the east (Mississippi River effects), the Gulf of Mexico on the south (gulf-inland gradient), and local bayous within the wetlands (streamside effects).

4. The Mississippi River pours immense quantities of nutrients and sediments into the coastal Gulf of Mexico waters. These fresh waters are carried generally westward, their influence on the coastal marshes attenuating as they move. This study evaluated the effect, if any, of the Mississippi River discharge on the biomass of S. alterniflora at different locations westward along the Gulf coast.

5. Louisiana marsh vegetation associations occur in fairly clear-cut zones parallel to the gulf coast (Chabreck et al. 1968). The southernmost zone, the salt marsh, is dominated by S. alterniflora, which lies on a gradient of decreasing mean salinity and decreasing tidal energy with distance inland from the coast. At the landward extreme of the salt marsh zone, S. patens and other characteristic brackish species become

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dominant instead of S. alterniflora. The field sampling design in this study permitted evaluation of changes that occur in S. alterniflora growth parameters across this gradient inland from the coast.

6. Finally, the study also evaluated the relationship of growth parameters to the distance from tidal bayous and lakes. In Louisiana marshes the natural levee of tidal water bodies is slightly elevated (about 7 cm above the mean marsh elevation), and this streamside location stimulates vigorous growth. The width of the levee depends on stream flow; in this study it was always less than 50 m. Elevation decreases on the back slope of the natural levee. Locations in the marsh away from the bayou sustain lower yields of S. alterniflora (Kirby and Gosselink 1976).

Methods

7. Sampling locations were chosen along four transects extending inland from the Gulf of Mexico across the east and west sides of two large interdistributary basins (Figure A1). The locations of these transects enabled evaluation of the Mississippi River effects. The Barataria Basin, lying just west of the Mississippi River, is more influenced by the river than the Terrebonne Basin, west of Barataria. Each transect extended from the gulf to the landward limit of the salt marsh, as identified by Chabreck et al. (1968). The transects generally followed major bayous: Bayou Sale and Oak Bayou in Terrebonne-W; Bayou Blue in Terrebonne-E; Bayou Ferblanc in Barataria-W; and Grand Bayou in Barataria-E. The five sampling locations on each transect allowed evaluation of the gulf-inland salinity gradient. At each of the five sampling locations on each transect, subtransects extended into the marsh

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from the edge of the bayou with sample stations at 1 to 3, 50, 100, and 175 m. These stations were used to evaluate the streamside effect. At each station duplicate $0.25\text{-}m^2$ quadrats were harvested. One of these was chosen at random. The second had one edge in common with the first in order to avoid bias in the sample selection because of the clumpy habit of S. alterniflora.

8. Samples were collected during September 1974, the time of peak live biomass in Louisiana marshes (Hopkinson et al. 1976; Kirby and Gosselink 1976). All vegetation in the plot was harvested at ground level; separated into live tissue, dead tissue stripped from live culms, dead culms, and species other than S. alterniflora; and then dried at 80°C and weighed. Density and average height of live culms were also recorded.

9. Statistical treatment of the data employed the Statistical Analysis System software program (Service 1972).

Results and Discussion

Variability

10. The end-of-season biomass of S. alterniflora varied widely over the marshes sampled. Ignoring causes of this variability, live biomass ranged from 0 to 2244 $g\ m^{-2}$ with a mean of 660 $g\ m^{-2}$ and a standard deviation of 349 $g\ m^{-2}$. These figures emphasize the natural variability of the marsh and point up the need for care in selection of sampling locations and in interpretation of results from field tests at restricted locations.

11. Table A1 summarizes analyses of variance for selected growth parameters. Not only are the main sources of variance highly significant,

A4

but the interactions are also highly significant. For instance, for all measured growth parameters, the gulf-inland gradient along each transect had a different slope. The following sections discuss the major components of the variation found in S. alterniflora growth parameters.

Distance from Mississippi River

12. Figure A2 shows live and litter biomass of S. alterniflora and the total biomass of all species, averaged for each transect. The live, litter, and total biomass all vary in the same manner. Orthogonal comparisons show that mean biomass is higher in Barataria than in Terrebonne marshes, and that values from the west side of each basin are higher than those on the east side. The reasons for these differences are not obvious, and the significant interactions complicate the picture, as will be discussed below.

13. The Barataria Basin is undoubtedly more strongly influenced by the Mississippi River than the Terrebonne Basin, and this may relate to the higher biomass of Barataria Bay, but causes of the east-west differences within basins are obscure. Marshes on the west side of each basin are more extensive as well as more vigorous. Factors that could be implicated in these differences are the geomorphology of the basins and the predominant southeast winds blowing into the west sides of the basins. It is pertinent to note that the sampling sites for two recent studies of S. alterniflora productivity (Hopkinson et al. 1976; Kirby and Gosselink 1976) were both along the Barataria-west transect line and thus may have been in marshes of above-average productivity.

A5

Gulf-inland salinity gradient

14. An analysis of the biomass change along each transect sheds some light on the average transect values of Figure A2. Figures A3 and A4 show live and total biomass values at five locations on each transect. These locations lie on a gradient from the least saline inland limit of the S. alterniflora marshes (Station 1) to the Gulf of Mexico (Station 5).

15. Except for the Barataria-E transect, biomass very generally decreased from north to south, as salinity and tidal energy increased. The inland stations along the Barataria-E transect appeared to be highly impacted by petrochemical activity. The figures show that the main difference between the Barataria and Terrebonne values occurs at the stations near the gulf, where biomass at stations 4 and 5 are much higher in Barataria than in Terrebonne marshes. These productive stations are those that would be expected to experience the strongest influence of the Mississippi River. In addition they are more sheltered by the barrier islands of the Barataria Basin than are the more exposed Terrebonne marshes.

16. The increase in total biomass with increasing distance from the gulf, is shown more clearly in Figure A5. More than 90 percent of the gulf-inland variation in total biomass can be accounted for in linear regression (Table A2). Clearly most of this change in total biomass is related to changes in the biomass of species other than S. alterniflora. In contrast there is no convincing evidence that either the live or the litter biomass of S. alterniflora varies in any consistent manner from north to south. Linear regressions of live and litter S. alterniflora

A6

biomass on distance from the gulf accounted for less than 10 percent of the variation. When individual transects were analyzed, as in Figure A3, live $\underline{S}$. $\underline{alterniflora}$ biomass in Terrebonne marshes decreased from north to south. However, in Barataria marshes this trend was reversed at the two stations closest to the coast. This was explained as an influence of the Mississippi River and of the degree of protection afforded by the barrier islands.

Streamside influence

17. Figure A6 shows the influence of distance of the sample plot from a local bayou on biomass parameters. As expected from previous work, the streamside plots contained more live vegetation than the plots 50, 100, or 175 m inland. It is interesting to note, however, that statistically this effect did not hold true for other species in the plots, although the tendency was the same. It is also interesting that the streamside effect on live $\underline{S}$. $\underline{alterniflora}$ biomass was most pronounced at the stations farthest from the gulf (Figure A7).

18. Two observations may help to explain these results. First, tidal energy decreased with distance from the coast. The stations farthest from the gulf therefore received less tidal energy and this energy was dissipated closer to the edges of the bayous, compared to stations closer to the coast where tides more frequently inundated the whole marsh. In addition the marsh was much more broken up near the coast than it was upstream; that is, small tidal channels penetrated the marsh in a fine network. It is likely, therefore, that although an effort was made to select uniform gradients for each subtransect, some of

A7

the sample plots 100 and 175 m from the main water body on which the subtransect originated were actually closer to another minor channel. The streamside effect shows clearly when comparing the streamside to the 50-m inland samples. Values at 100 and 175 m should be interpreted with caution.

Tillers

19. _Spartina alterniflora_ flowers and matures fruit during September in Louisiana. Figure A8 shows that the distribution of flowering tillers was far from random. Flowering was concentrated on the Barataria-east transect at the upper (fresher) ends of the transects and away from the stream edge. Analyses of the interactions suggest a patchy occurrence of flowering rather than any systematic gradients (the coefficient of variation was a high 49 percent), although the effects are all highly significant statistically.

Environmental factors related to biomass

20. The physical gradients of major concern in this study were those associated with distance from the Gulf of Mexico, especially salinity and tidal energy. Both have been implicated in many studies of the productivity and distribution of _S. alterniflora_ (Odum and Fanning 1973). Figure A9 shows how salinity in the bayou adjacent to each subtransect decreased with distance inland from the gulf. It is more difficult to document the attenuation of tidal energy away from the coast, but Figure A10 shows the decrease in tidal amplitude on a gulf-inland gradient in Barataria Bay. This is associated with a decrease in the frequency of

inundation of the marsh, although the total period of inundation per year is not greatly affected (Byrne et al. 1976).

21. Marsh sediment characteristics are controlled to a large extent by the tidal regime. Two parameters related to marsh productivity are sediment grain size and organic content. The interdistributary basins of this study contain almost no sands inshore of the barrier islands. The coarsest sediment particles are fine silts. As tidal energy decreases, the coarser particles drop out of the water column. This is shown in Table A3 as a negative correlation between the percentage of sediment grains greater than 20 μ in diameter and distance from the gulf and also in Figure A11 as a decrease in the coarse mineral component of the sediment with distance from the gulf and 100 m or more from the edge of bayous.

22. Organic content of the sediment is a result of complex processes. Among these are the magnitude of primary production and the tidal energy available to move organic detritus off the marsh. These processes result (Figure A12) in a clear statistically significant gulf-inland gradient of increasing sediment organic content with distance from the gulf and an increasing organic content with distance from the edge of a bayou (streamside effect).

Relationship of biomass parameters to edaphic parameters

23. The gradients of salinity and tidal energy described in Figures A9 and A10 have no sharp effect on either the live or the dead S. alterniflora biomass. There is no significant correlation between these biomass parameters and salinity (Table A3); although they do correlate weakly

A9

with distance from the gulf, Figure A5 and Table A2 show that the gradient is not convincing. On the other hand the presence of other species does increase as salinity decreases (Table A2 and A3, Figure A5). As a consequence, total biomass (live and dead of all species) is strongly negatively correlated with salinity and positively correlated with distance from the gulf. The implication for S. alterniflora seems to be that this species itself is not strongly influenced by salinities in the range encountered, but that at low salinities other plants are able to compete successfully with it.

24. The data also indicate that S. alterniflora is dependent on tidal action per se, as distinct from salinity. This is shown by the increased streamside effect seen on the subtransects farthest from the gulf (Figure A7), where the frequency of tidal flushing is diminished and its effect confined more to the edges of waterways. As Figure A6 shows, other species in this study showed no streamside stimulation, although such stimulation has been documented for fresh marsh species by Buttery and Lambert (1965).

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A11

Table A1

Analyses of Variance of S. alterniflora Biomass Parameters

Sources of Variance	Live Biomass	Dead Biomass	Other Species	Total Biomass	Avg. Height	Live:Dead	Stem Density
Mississippi River	**	**	**	**	**	*	**
Gulf-inland	**	**	**	**	**	**	**
Streamside	**	**	ns	**	**	ns	**
Mississippi River x Gulf-inland	**	**	**	**	**	**	**
Mississippi River x Streamside	**	**	**	**	**	**	**
Gulf-inland x Streamside	**	**	**	**	**	**	**
Mississippi River x Gulf-inland x Streamside	**	**	**	**	**	**	**
Coefficient of Variation $\left(\frac{s}{\bar{x}} \times 100\right)$	27	18	97	23	16	29	16

* denotes $P < 0.05$.
** denotes $P < 0.01$.

Table A2

Analysis of Regression of the Gulf-Inland Variation in Biomass ($g\ m^{-2}$)

| Source of Variation | Degrees of Freedom | Percent of Total Variation* | | | |
		S. alterniflora Live	Dead	Other Species Live + Dead	Total Biomass Live + Dead
Transect (total)	4	100	100	100	100
Regression	1	9	2	66	91
Deviation from Regression	3	91	98	34	9

* The percentage of the total variation (sum of squares for the dependent variable) that can be accounted for by the distance from the Gulf of Mexico.

Table A3

Simple Correlation Matrix for Growth Parameters, Salinity, and Substrate

	Biological					Physical				
	1	2	3	4	5	6	7	8	9	10
Live S. alterniflora		0.53	ns	0.72	0.59	ns	ns	ns	ns	0.49*
Dead S. alterniflora			ns	0.59	0.23	ns	ns	0.27	ns	0.42*
Other Species Biomass				0.64	-0.30	-0.46*	0.32	ns	-0.26	0.46*
Total Biomass					0.16*	-0.55	ns	ns	ns	0.64
Stem Density						ns	-0.30	ns	0.25*	ns
Salinity							ns	ns	ns	-0.80
Sediment Organic (%)								-0.24*	-0.81	0.53*
Sediment Clay (<20 µ)									-0.33	ns
Sediment Fraction (>20 µ)										-0.47
Distance from Gulf										

Note: Numbers in matrix are correlation coefficients when $P < 0.01$, except where denoted by *, in which case $P < 0.05$.
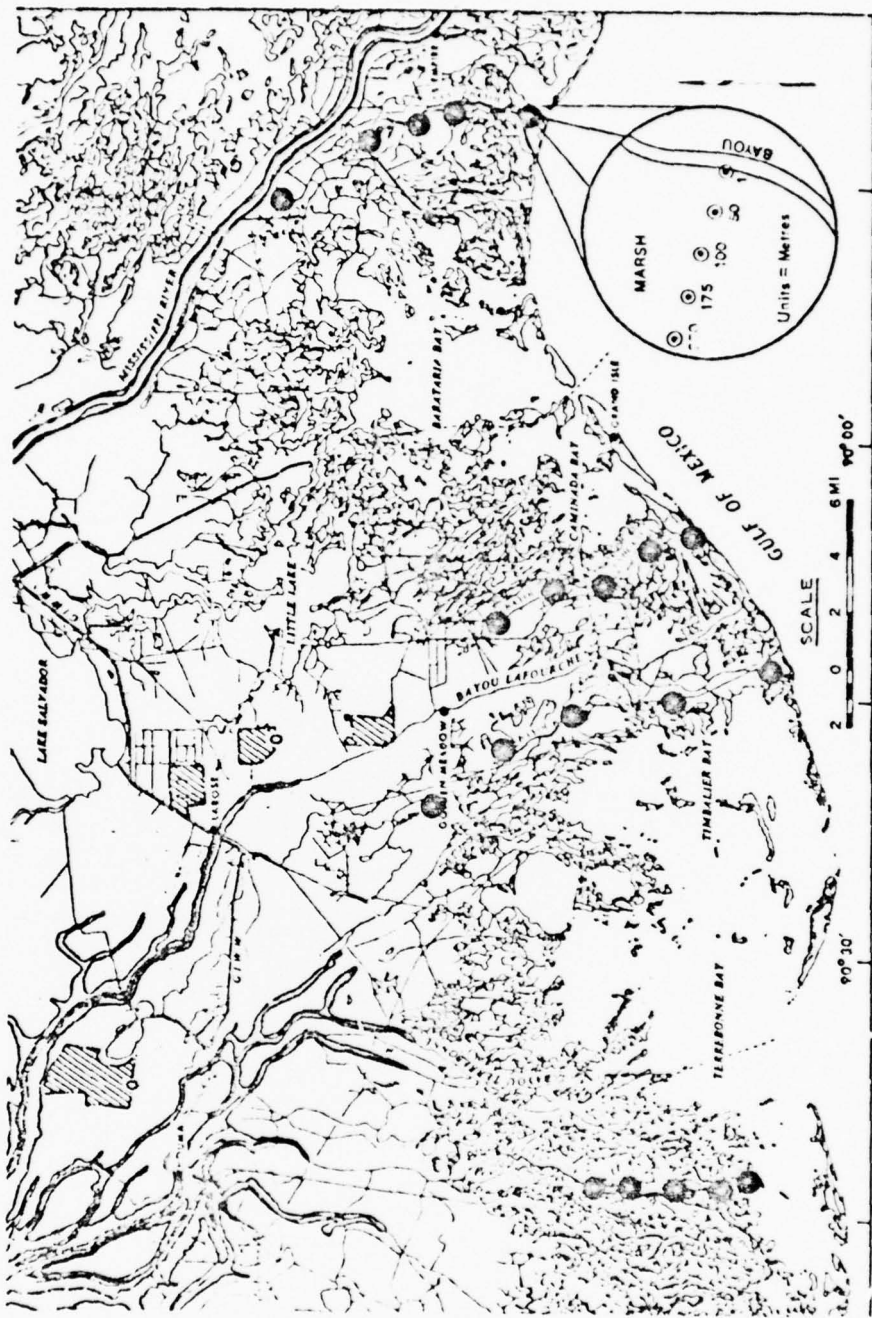
Figure A1. Location of field sampling sites on the Louisiana coast.
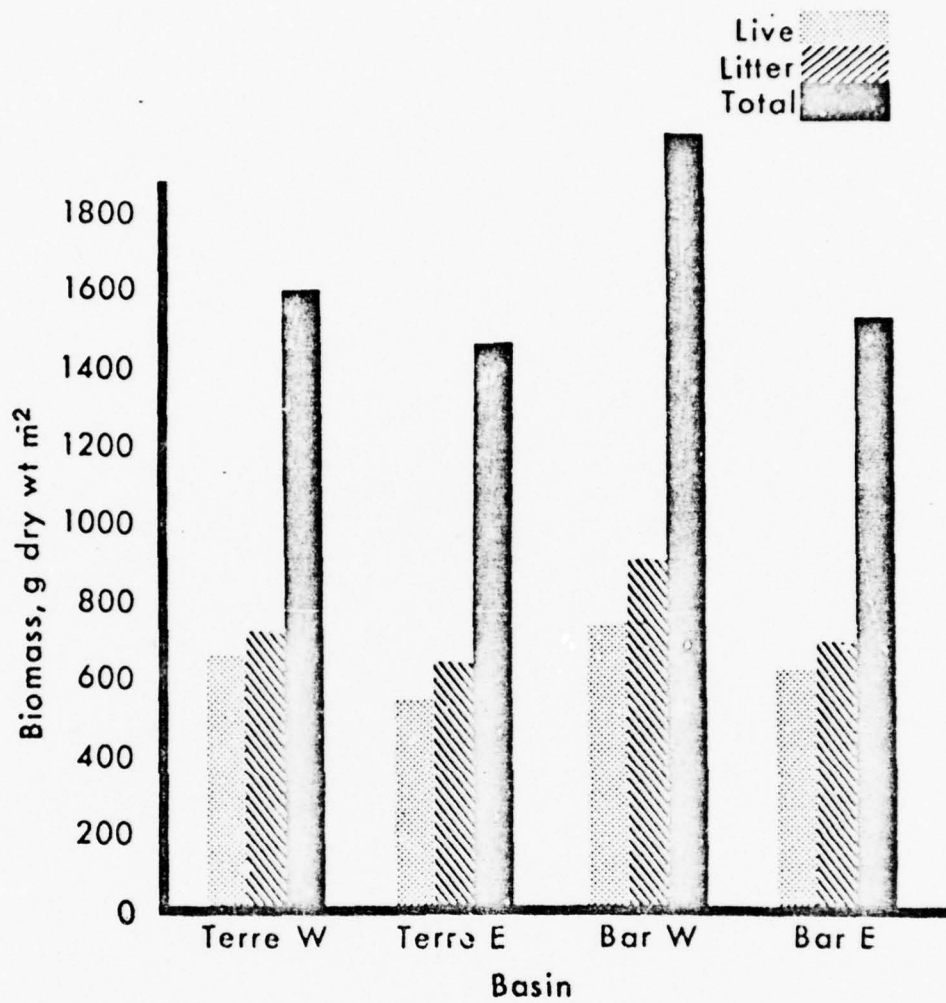
Note: Each value is a mean of 40 quadrats. Live and dead vegetation
are S. alterniflora only. Total vegetation includes other
species. All differences are statistically significant at the
P <0.01 level.

Figure A2. Live, litter, and total biomass of vegetation
on four transects.
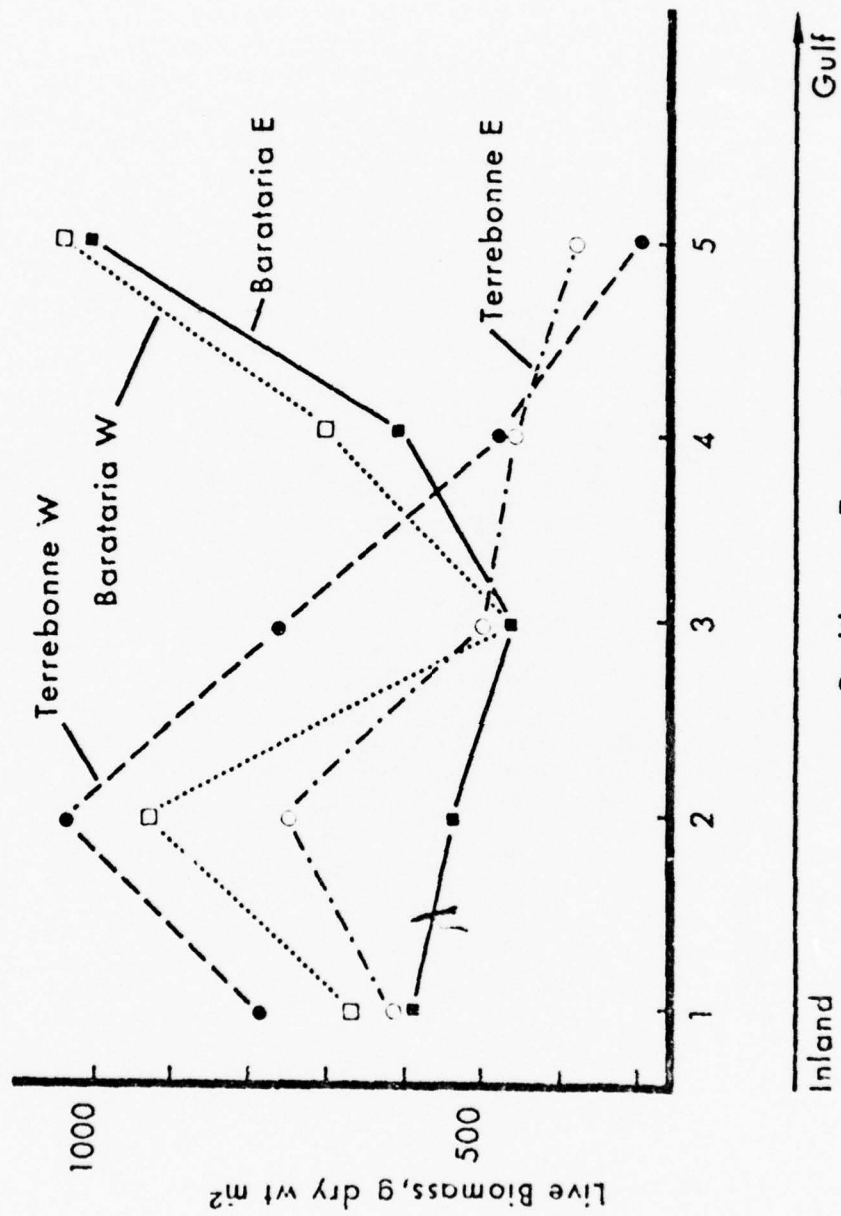
Figure A3. Variation in live biomass of $\underline{S.}$ $\underline{alterniflora}$ along four gulf-inland transects. Each point is a mean of eight quadrats.
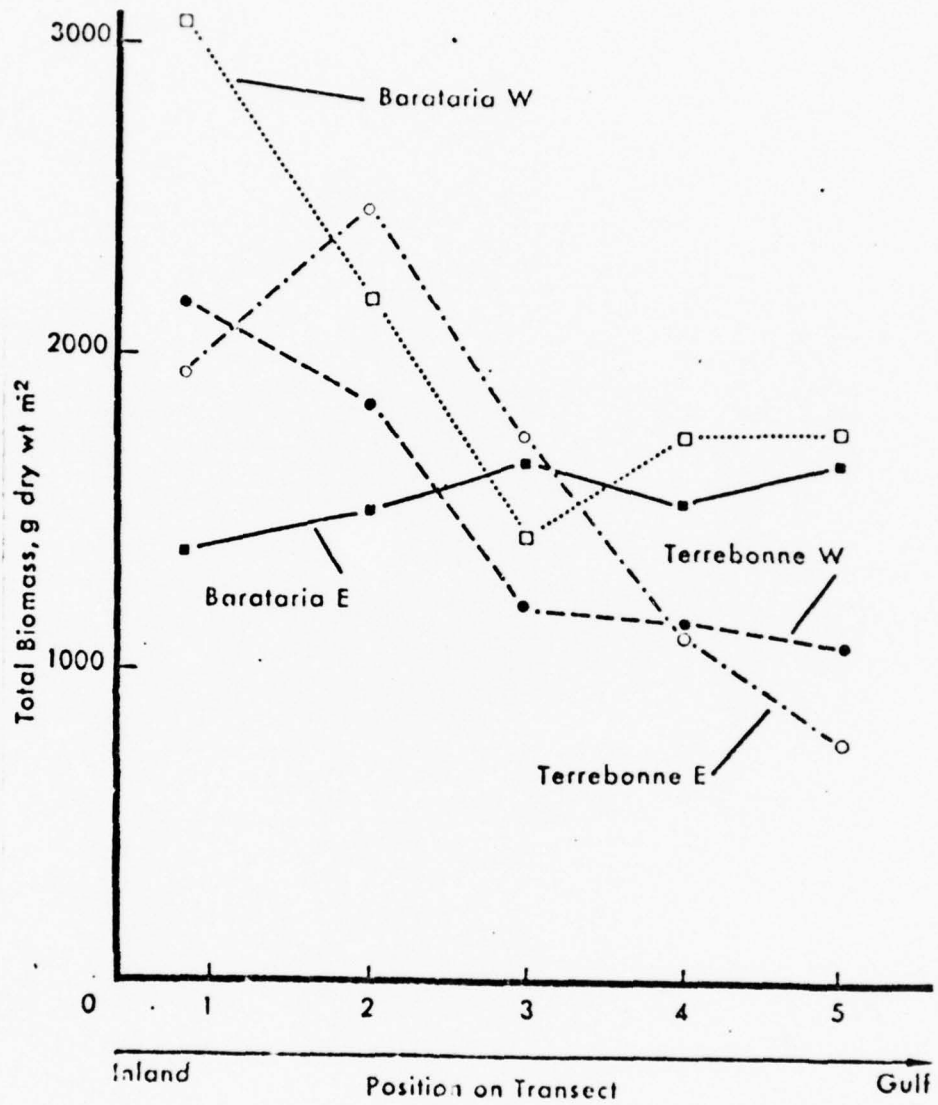
Figure A4. Variation in total biomass of all vegetation along four gulf-inland transects. Each point is a mean of eight quadrats.
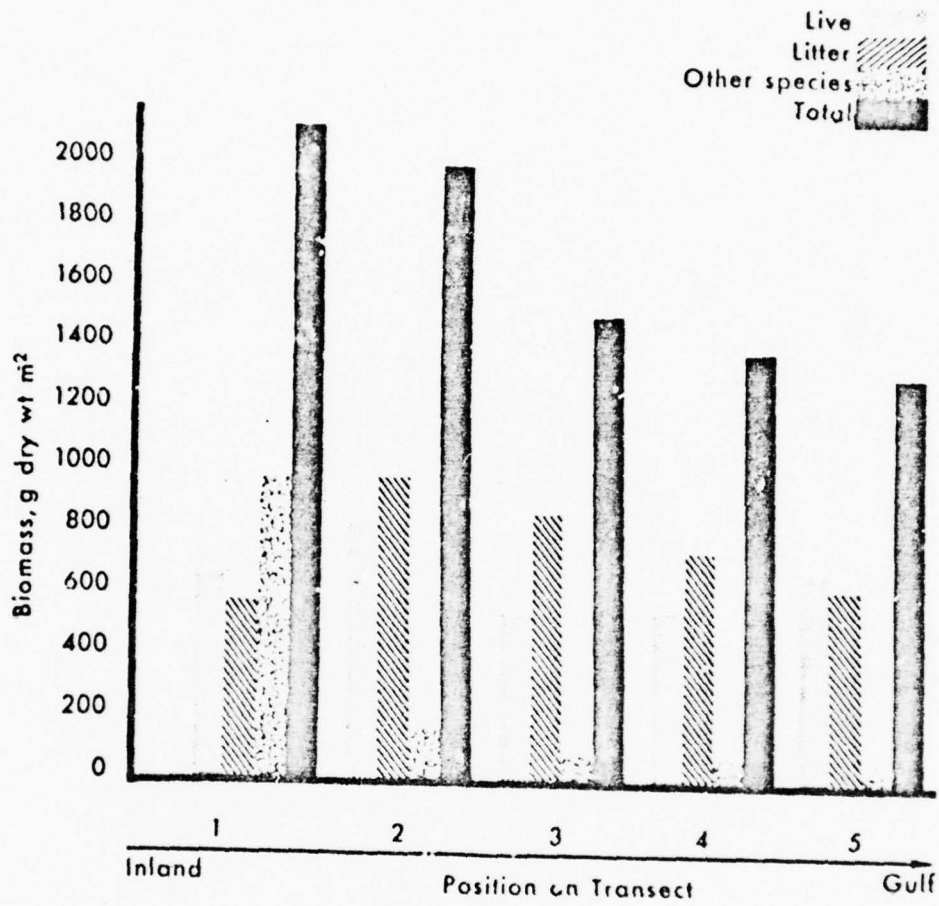
Note: Each value is a mean of 32 quadrats. See Table A2 for statistical analysis.

Figure A5. Variation in S. alterniflora biomass parameters with distance from the Gulf of Mexico.

Live
Litter
Other species
Total

2000
1800
1600
1400
1200
1000
800
600
400
200
0

Biomass, g dry wt m²

0   50   100   175

Distance from Bayou, m
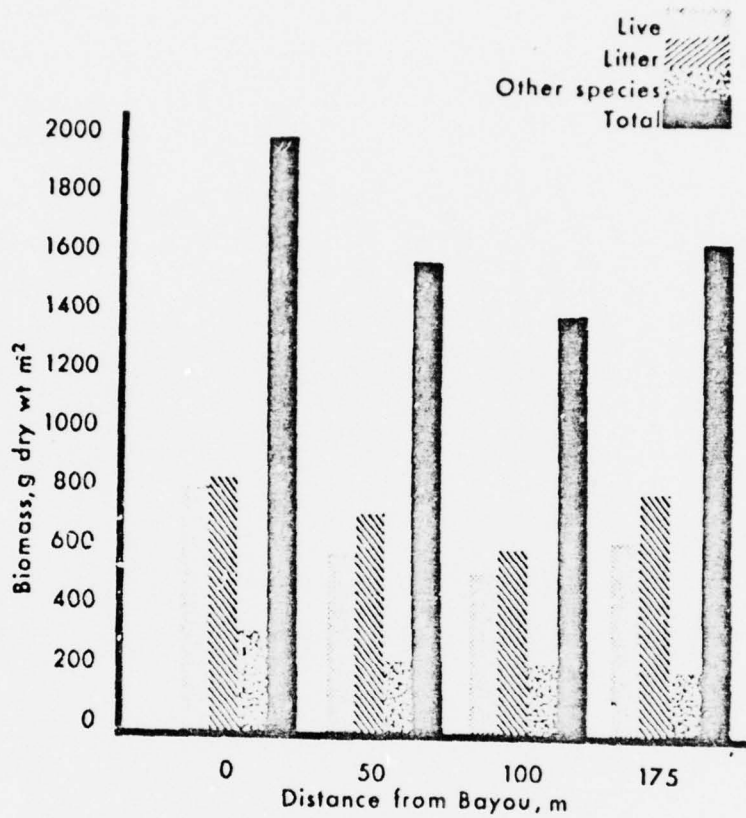
Note: Each value is a mean of 40 quadrats.

Figure A6. Variation in S. alterniflora biomass parameters
with distance from local bayous (streamside effect).
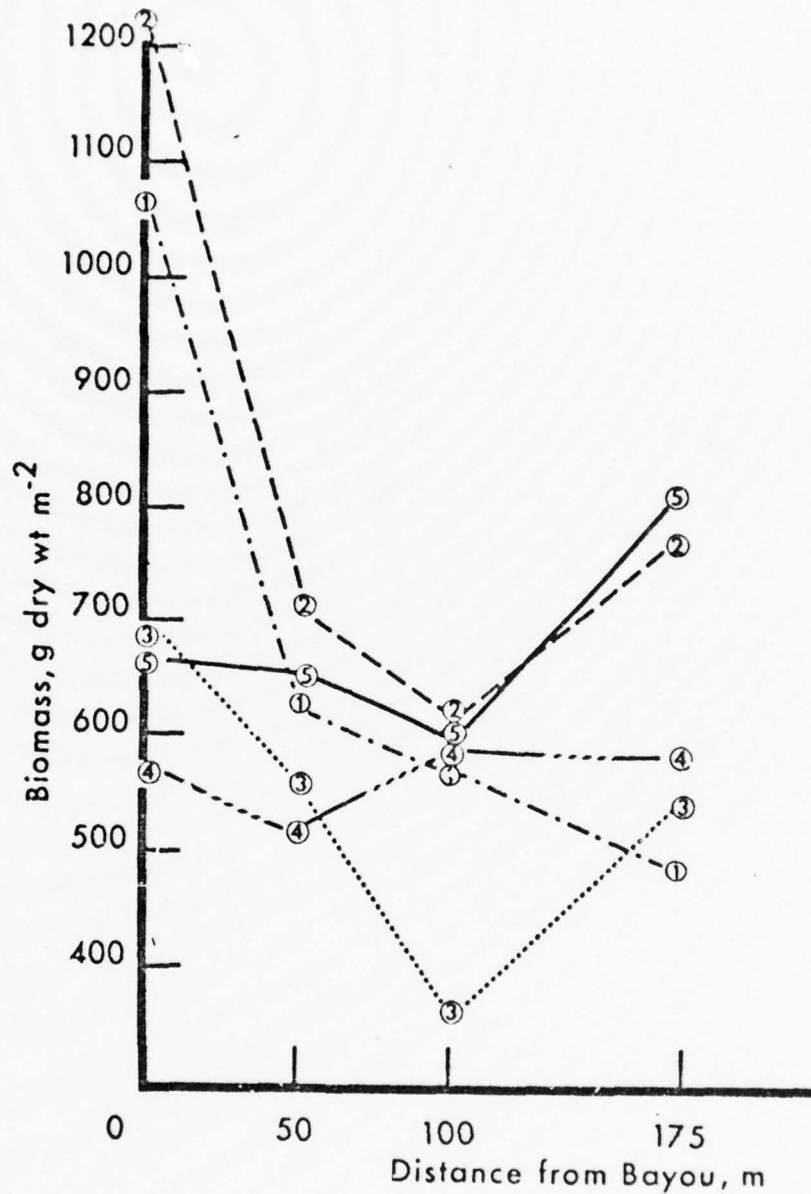
Note: Curve ① is farthest inland; curve ⑤ is adjacent to the gulf. Each point is a mean of eight quadrats.

Figure A7. Differences in the streamside effect on live biomass of S. alterniflora with distance from the Gulf of Mexico.
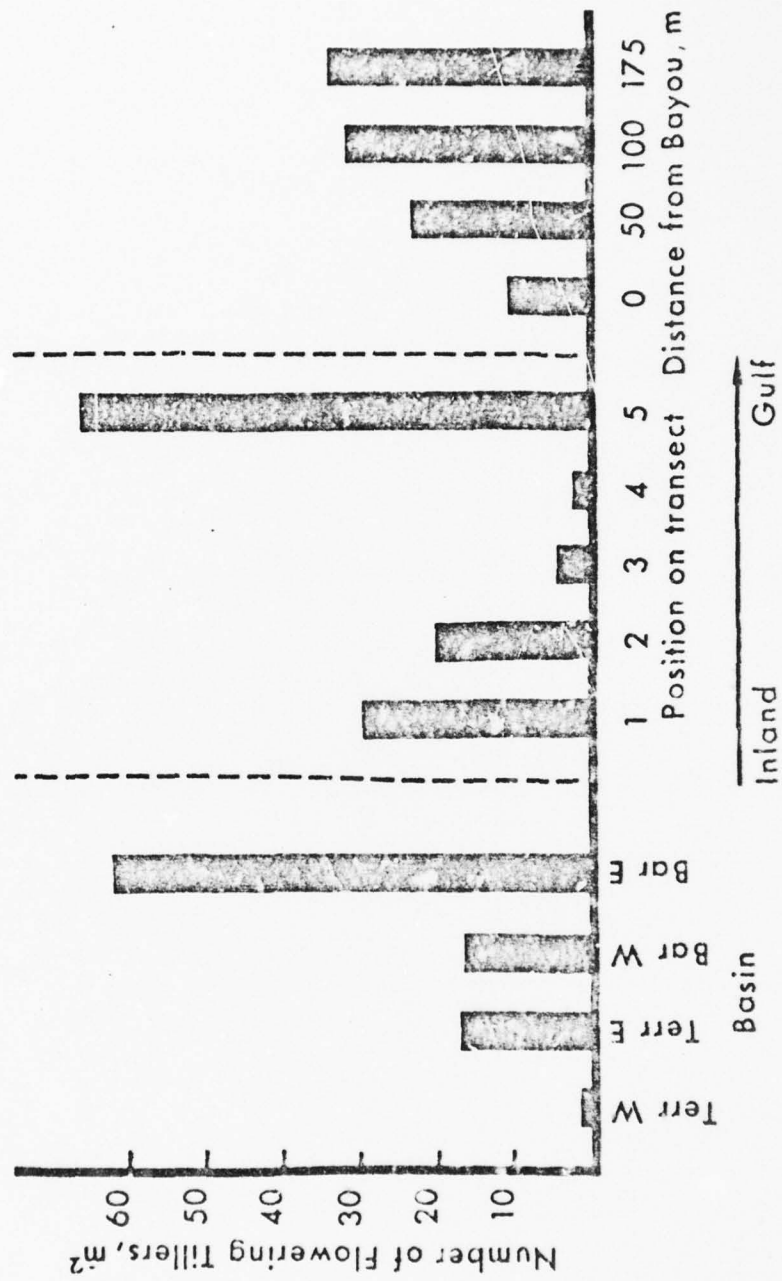
Figure A8. Distribution (average numbers) of flowering tillers of S. alterniflora in louisiana coastal marshes.
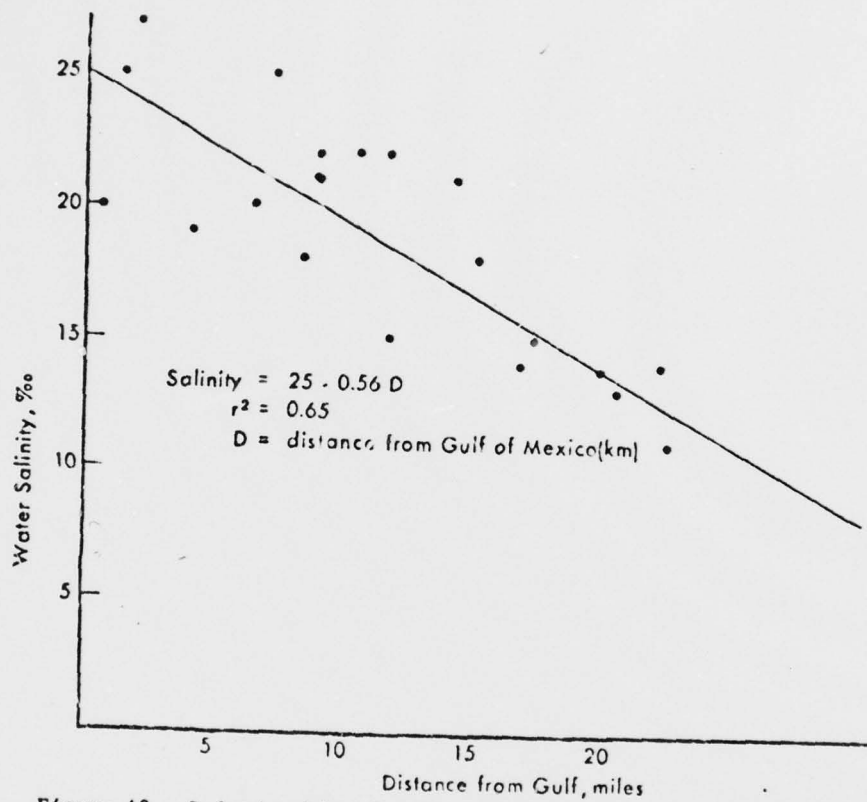
Figure A9. Relationship of salinity to distance inland from the Gulf of Mexico in September 1974.
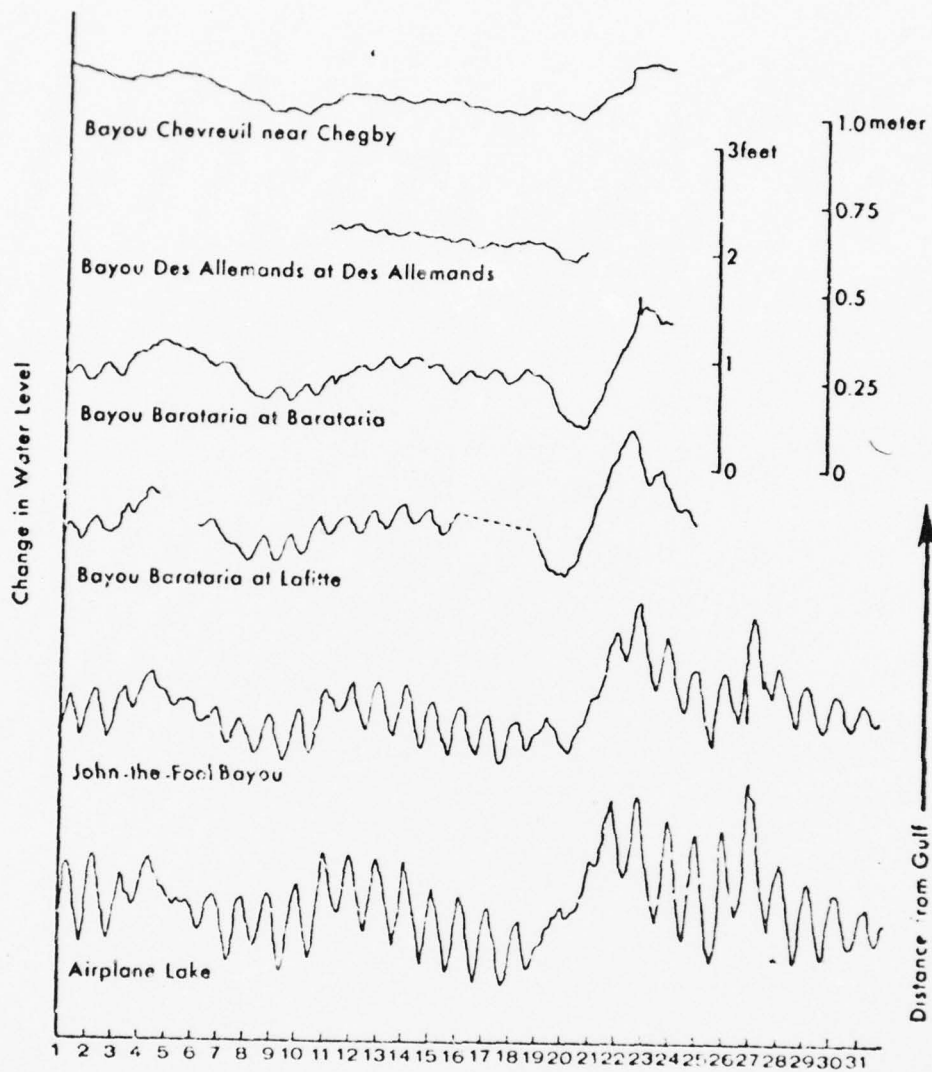
Note: Airplane Lake is near the gulf; John-the-Fool Bayou is just above the salt marsh/brackish marsh interface. Other stations are in increasingly fresher waters (Gosselink et al. 1976).

Figure A10. Simultaneous tide guage readings at various stations along a gulf-inland gradient in Barataria Bay, showing attentuation of the tidal record with distance from the gulf.
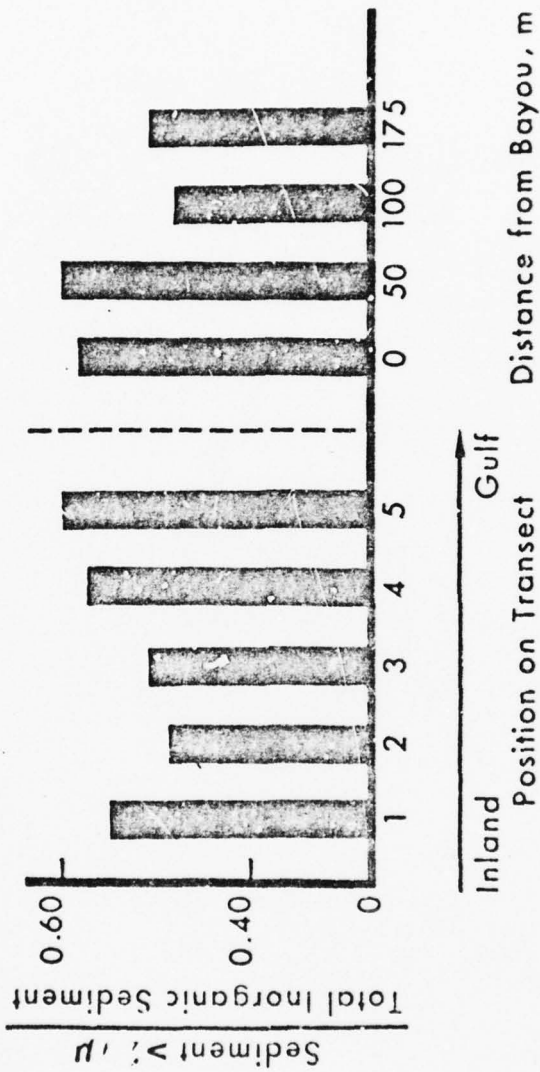
Note: Each value is a mean of 16 samples (gulf-inland transect) or 20 samples (streamside effect).

Figure A11. Change in the proportion of the coarse sediment fraction to total inorganic sediments with distance from the gulf and from local bayous.
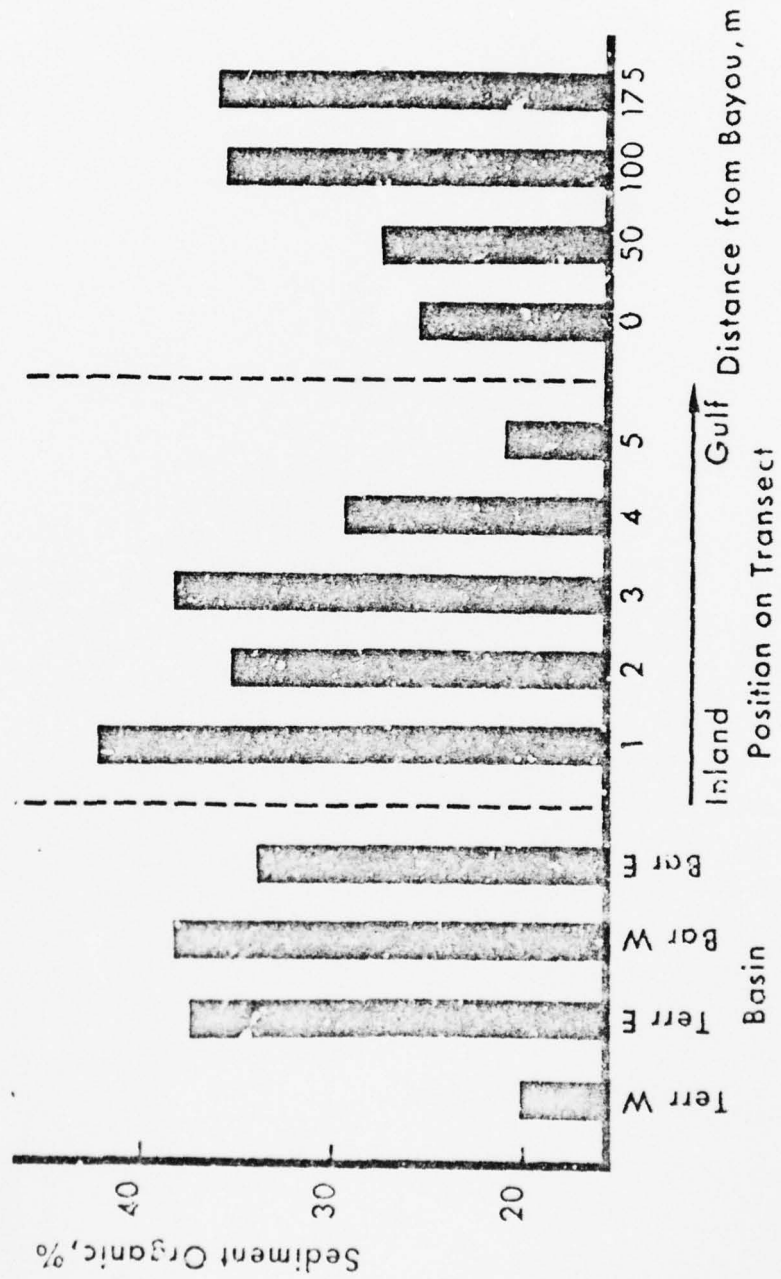
Figure A12. Variation in sediment organic concentration in Louisiana S. alterniflora marshes.

APPENDIX B: SOIL AND TISSUE NUTRIENTS IN LOUISIANA MARSHES AND THEIR
RELATIONSHIP TO THE YIELD OF SPARTINA ALTERNIFLORA

Introduction

1. The salt marsh grass Spartina alterniflora has been shown to be
a highly productive grass (Hopkinson et al. 1976; Turner 1976).* In a
number of different studies, this productivity has been shown to be
related to latitude (Turner 1976), to elevation (high vs. low marsh,
Smalley 1959), to tidal energy (Schleske and Odum 1971) to salinity
(Nixon and Oviatt 1973; Broome et al. 1975a), to available nitrogen
(Broome et al. 1975b; Valiela and Teal 1974; Patrick and DeLaune 1975),
and to soil redox potential (Eh) and pH (Gambrell et al. 1977).

2. Under natural conditions in Louisiana marshes, variability in
yield is high. In a recent study (Appendix A), Gosselink, Hopkinson,
and Parrondo have related this variability to salinity, tidal energy,
and marsh elevation gradients. This appendix examines the same data in
order to determine to what extent nutrient differences resulting from
the natural hydrologic and geologic processes at work in the marsh can
be related to the yield of marsh vegetation.

3. Broome et al. (1975a) conducted a similar study in North
Carolina and were able to account for about 90 percent of the yield
variation through stepwise multiple-regression techniques. Salinity of
the soil solution and tissue sulfur (S) and manganese (Mn) were impor-
tant factors in yield. Nixon and Oviatt (1973) found salinity in New

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* References at end of this appendix.

B1

England salt marshes to be negatively correlated with yield. Both of these studies showed S. alterniflora yield to be negatively correlated with salinity of the surface water, although the relationship was not as strong as laboratory and greenhouse studies suggest it should be (Adams 1963; Gosselink 1970; Mooring et al. 1971; Phleger 1971). In recent pot culture tests, Gambrell et al. (1977) have shown that reduced soils, in combination with low pH, reduce yield. Since reduced soils increase the level of toxic sulfides, this is also one explanation for the negative correlation between tissue sulfur and yield in the study of Broome et al. (1975a).

4. Louisiana's salt marshes are different in many ways from the east coast marshes in which previous studies have been localized. The extent of these marshes (41 percent of the total U.S. wetlands), the extremely low relief, the 0.3-m average diurnal tide range, the highly organic soils, and the strong influence of the Mississippi River on the salinity and nutrient budgets of the estuaries, all combine to make these marshes unique. This study examined the spatial distribution of nutrients in two interdistributary basins in coastal Louisiana and related this distribution to the yield (peak live biomass) of S. alterniflora.

Methods

5. Some 196 quadrats, each 0.25 m^2, were harvested in the salt marshes of the Barataria and Terrebonne watersheds of coastal Louisiana during September 1974. Details of the sampling plan are described in Appendix A. Summarizing these details, four transects were established

running from the Gulf of Mexico to the inland extent of the salt marsh in two watersheds west of the Mississippi River. On each transect five subtransects were established perpendicular to the banks of a bayou and quadrats were harvested in pairs at 1, 50, 100, 175, and 250 m from the bayou (Figure B1). Live vegetation was dried, ground in a Wiley mill, and analyzed for 13 elements by spectrographic methods. Analyses were completed by the Plant Analysis Laboratory, University of Georgia, Athens, Ga. Nitrogen (N) content was determined by the micro-Kjeldanl method (Bremner 1965) by the same laboratory. Soil samples (3-in.-deep cores) from the paired quadrats were combined into single samples for analysis. These were air dried, ground, then analyzed for fractions greater than and less than 20 μ, organic content (OM), and the 0.1 N HCl extractable elements sodium (Na), potassium (K), calcium (Ca), and magnesium (Mg) as described by Brupbacher et al. (1968). Salinity of surface water was determined in situ with a refractometer.

6. The data were subjected to analyses of variance. Simple correlation techniques and multiple stepwise regressions were used to elucidate the relationships among variables.

Results and Discussion

Distribution of soil and tissue nutrients

7. Soil parameters. Table B1 records the results of statistical analyses of variance of soil and tissue parameters. Of all soil parameters, organic concentration varied the most predictably. It was also closely related to changes in soil cations. Figure B2 shows the spatial main gradients all statistically highly significant (P <0.01): organic

B3

percentage was lower on the Terrebonne-West transect than on the other three; it increased from the gulf-inland toward fresher water, and was higher away from the edges of bayous (100 and 175 m) than on the stream banks. The latter two gradients were inversely associated with a reduction in tidal energy with distance from the edges of streams and from the Gulf of Mexico.

8. Table B2 shows that the concentration of major soil cations was positively correlated with soil organic concentration. This is to some extent a result of the reporting convention for agricultural soils (used in this study), which reports nutrients on a soil dry weight basis. Where organic concentration was high, soil dry weight per unit volume was low and other soil parameters were inflated by this relationship. On this dry weight basis, soil cation concentrations increased with distance inland from the gulf and were higher on the backslopes of natural stream levees than on the levee itself.

9. Tissue nutrients. Tissue nutrient concentration presents a different and far more complex picture of salt marsh nutrient relationships. The concentrations reported represent samples of live S. alterniflora culms during September when live biomass was at its peak and when flowering and fruiting were occurring. How this sample is related to the seasonal pattern of tissue nutrient concentration is shown in Figure B3, which reports bimonthly samples from a single location. The tissue concentration at any time results from a complex interaction of a number of factors including: nutrient availability (concentration and renewal rate) in the substrate; growth rate of the plant; interactions with other nutrients, external and internal to the plant; and physiological

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control mechanisms within the plant itself. It is hardly surprising, therefore, that the resulting picture is far from clear. The following tabulation summarizes the behavior of tissue nutrients as related to the spatial gradients of the marsh:

TRANSECT GRADIENT - From Gulf to 20 miles Inland

Increasing Concentration

Barium (Ba)

Decreasing Concentration

Ca, Mg, Iron (Fe), Boron (B), Zinc (Zn), Aluminum (Al), Molybenum (Mo),

Strontium (Sr)

No Clear Gradient

N, Phosphorus (P), K, Mn, Copper (Cu)

SUBTRANSECT GRADIENT - Streamside (compared with 50 to 175 m away from

stream)

Streamside Lower

Mg, Fe, B, Sr, Al

Streamside Higher

P, K, Mn, Zn

No Clear Difference

N, Ca, Cu, Mo, Ba

Most of the elements are highest in concentration near the gulf, decreasing with increasing distance from the coast. This is in sharp contrast to the concentration of most of the same elements in the sediment. As reported in the previous section, the major soil cations increase in concentration with distance from the coast. Ho and Schneider (1976) have also reported that soil micronutrients increase in concentration on

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the same gradient. As indicated, the soil parameters are reported on a dry weight basis. The tissue concentrations suggest that regardless of the soil concentrations reported, the availability of nearly all of these nutrients per unit volume of sediment is highest near the coast and decreases inland. Barium was the only tissue element reported that clearly increased at inland locations. These results indicate that in coastal embayments such as the Barataria Basin, tidal waters as opposed to freshwater drainage from upstream are the primary source of nutrients for the marsh vegetation. The nutrients appear to be introduced primarily in suspended particulate form rather than in the dissolved state. This is certainly true for N (Ho and Barrett 1975; Patrick and Delaune 1975).

10. The pattern of distribution of nutrient elements in vegetation along stream banks as compared with 50 to 175 m back from the stream edge is puzzling (see above tabulation). The backslope of natural streamside levees tends to be at a lower elevation than the levee itself and sediments are usually more reduced. It is possible to speculate that Fe is found in higher tissue concentrations on backslopes because its availability increases with increased soil reduction. However, the elements Sr and Mn behaved the same way although they are only slightly influenced by Eh; Mn, like Fe, becomes increasingly available with decreasing Eh and was found to be more concentrated on the streamside levee.

Relation of tissue and soil nutrients
to yield of S. alterniflora

11. Despite the complications in interpretation of the relation-ship of tissue nutrient concentration to yield, tissue nutrient analysis

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has been a valuable tool in diagnosis and treatment of nutrient problems in horticultural and agronomic crops. At deficiency tissue nutrient levels within a fairly narrow concentration range, the growth rate of a species is quite well correlated with the tissue concentration of a limiting nutrient. Above the limiting range, luxury uptake can occur, which is not reflected in a yield increase (that is, tissue nutrient concentrations increase without concomitant dry weight gains). Between these extremes, over mo' of the limiting range, growth proceeds as fast as the limiting nutrient or nutrients become available so that tissue concentration remains unchanged (Gerloff 1969). To illustrate this, N has been cited as a limiting factor in S. alterniflora growth by several individuals (Broome et al. 1975b; Patrick and DeLaune 1975). Broome et al. (1975a), however, found N tissue concentration to be independent of yield in North Carolina salt marshes.

12. This study found (Table B3) a significant negative correlation between tissue N concentration and yield (live biomass) although the coefficient of correlation was low ($r = -0.19$). The best predictor of yield was B, which was also negatively correlated with peak live biomass ($r = -0.32$). Other tissue elements individually significantly correlated with live S. alterniflora biomass were P ($r = 0.24$), K ($r = +0.23$), Mn ($r = ^+0.29$), and Ba ($r = 0.20$).

13. The following tissue parameters were implicated in the total biomass (live plus litter): B, Mn, P, and K were all individually very highly significantly correlated with total yield ($r = >0.30$; $P <0.001$); Cu, Zn, Ba, Al, and Mg were significantly ($P <0.05$) correlated with yield.

B7

14. Of the substrate parameters measured, the only one that was significantly related with yield was the salinity of flooding water, which was negatively correlated with total biomass ($r = -0.55$; $P < 0.01$), but not with live S. alterniflora biomass alone.

15. Since many of these variables were intercorrelated, a stepwise multiple-regression procedure was followed that related the two yield parameters (live S. alterniflora biomass and total biomass) to 14 tissue and 8 substrate parameters by a maximum r^2 improvement technique (Service 1972). Tables B4 and B5 show the best-fit one to seven variable models relating the dependent variables live S. alterniflora biomass and total biomass, to tissue and soil parameters. For tissue nutrients the best seven-variable model only accounted for 36 to 38 percent of the biomass variation. Not much improvement occurred above a four-variable model. Boron was a significant variable in all models, as was Mn. Phosphorus, K, and N also entered the relationship with live biomass, K and Ba with total biomass.

16. No soil parameter vs biomass-regression model was able to account for more than 11 percent of the variability. The only significant relationship was between salinity and total biomass.

Summary

17. In the complex environment of the salt marsh, many factors appear to contribute to yield (peak biomass) of S. alterniflora In this study, with the analytical techniques used, the spatial variations of edaphic parameters in two Louisiana interdistributary basins were poorly related to S. alterniflora yield differences. Salinity of the

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flooding water was the single exception; it was significantly negatively correlated with total live plus dead biomass of all species, although it was poorly correlated with live S. alterniflora biomass alone.

18. Tissue B, K, and Mn appeared in the best four-variable regression models for live S. alterniflora biomass and total yield. However, even the best seven-variable model failed to account for over 38 percent of the variability in yield.

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1.0

1.1

1.25

4.5
5.0
5.5

2.8
3.2
3.6
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2.5
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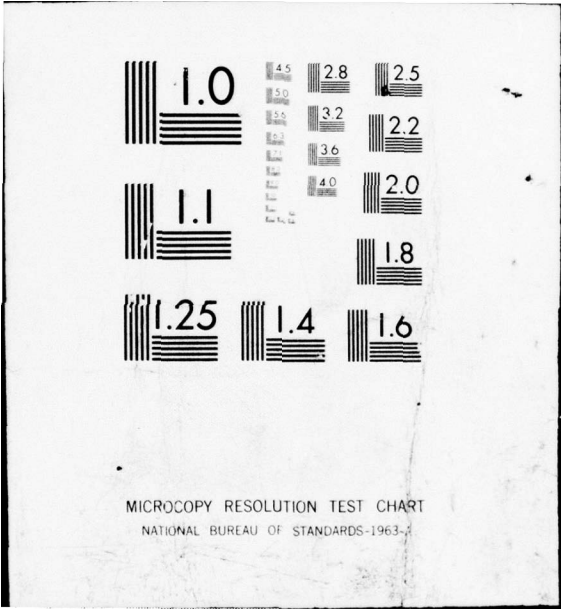
MICROCOPY RESOLUTION TEST CHART
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Table B1

Analysis of Variance of S. alterniflora Tissue Elements and Soil Parameters

	Degrees of Freedom	Tissue														Soil						
		N	P	K	Ca	Mg	Mn	Fe	B	Cu	Zn	Al	Mo	Sr	Ba	K	Ca	Mg	Na	OM	Clay <20u	>20u
		%					ppm									%						
Mississippi River	3	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	**	ns	**
Gulf-inland	4	ns	**	**	**	**	**	**	**	**	**	**	**	**	**	ns	**	**	ns	**	ns	**
Streamside	3	ns	**	**	**	**	**	*	ns	*	**	ns	ns	ns	ns	**	*	**	**	**	**	**
Mississippi River x Gulf-inland	12	**	**	**	**	**	**	**	*	**	**	**	**	**	**	**	*	**	**	**	ns	**
Mississippi River x Streamside	9	**	**	**	*	ns	**	ns	ns	ns	ns	ns	ns	*	ns	ns	ns	ns	ns	ns	*	
Gulf-inland x Streamside	12	ns	**	*	**	**	**	ns	*	**	ns	us	**	ns	**	ns	ns	ns	ns	ns	ns	
Mississippi River x Gulf-inland x Streamside	36	**	**	**	**	**	**	**	**	**	**	**	**	**	*	ns						
Coefficient of variation $\left(\frac{s}{\bar{x}} \times 100\right)$		8	28	18	41	14	18	34	31	30	18	44	33	17	38	21	24	17	14	26	31	27

* Significant at 95 percent confidence level ($P < 0.05$).
** Significant at 99 percent confidence level ($P < 0.01$).

Table B2

Simple Correlation Matrix for Soil and Tissue Nutrients

Parameters →	Soil					Tissue														Water Salinity
	K	Ca	Mg	Na	Organic	N	P	K	Ca	Mg	Mn	Fe	Cu	Zn	Al	Mo	B	Sr	Ba	
live S. alterniflora biomass	ns	ns	ns	ns	ns	-	+	+	ns	ns	+	ns	-	-	-	-	-	-	ns	ns
Soil K		+	+	+	+	ns	-	ns	ns	ns	-	-	-	-	ns	ns	ns	ns	-	ns
Ca			+	+	+	ns	ns	ns	ns	ns	-	ns	-	-	ns	-	ns	ns	ns	ns
Mg				+	+	ns	-	ns	ns	ns	-	-	-	-	ns	-	ns	ns	ns	ns
Na					+	ns	-	ns	ns	ns	-	-	-	-	ns	-	ns	ns	ns	ns
Organic						ns	ns	ns	ns	ns	-	-	-	-	-	-	ns	ns	ns	ns
Tissue N							+	+	ns	ns	+	+	+	+	+	+	+	ns	ns	ns
P								+	+	ns	+	+	+	+	+	+	+	+	+	ns
K									-	ns	+	ns	ns	ns	ns	ns	-	ns	ns	ns
Ca										+	+	ns	ns	ns	ns	ns	+	+	+	+
Mg											ns	ns	ns	ns	ns	ns	+	+	+	-
Mn												+	ns	ns	ns	+	ns	+	+	+
Fe													+	+	+	+	+	ns	+	ns
Cu														+	+	+	+	ns	+	ns
Zn															+	+	+	ns	ns	ns
Al																+	+	ns	+	+
Mo																	+	ns	+	+
B																		+	+	ns
Sr																			+	ns
Ba																				ns

Table B3

Correlation of Leaf and Soil Nutrient Concentration with Live
S. alterniflora Biomass and with Total Biomass
(Live and Dead of All Species)

	Correlation Coefficient (r)		Mean		
	Live				
Tissue	S. alterniflora	Total			±Standard
Nutrient	Biomass	Biomass	Concentration %		Deviation
N	-0.19**	-0.03	1.02	±	0.16
P	+0.24**	+0.31***	0.07	±	0.04
K	+0.23**	+0.32***	0.90	±	0.32
Ca	+0.008	+0.06	0.11	±	0.07
Mg	-0.14	-0.26**	0.36	±	0.09
			ppm		
Mn	+0.29**	+0.30***	61.0	±	29.0
Fe	-0.16*	-0.12	436.0	±	262.0
B	-0.32***	-0.34***	5.9	±	3.3
Cu	+0.25**	+0.19*	3.2	±	1.4
Zn	+0.25**	+0.20*	9.4	±	3.9
Al	-0.23**	-0.26**	294.0	±	200.0
Mo	-0.06	-0.05	2.2	±	1.2
Sr	-0.08	-0.11	29.0	±	7.0
Ba	+0.20**	+0.22**	12.0	±	10.0
Soil Nutrient			dry wt, %		
K	-0.18	-0.07	0.18	±	0.07
Ca	-0.15	-0.02	0.26	±	0.09
Mg	-0.15	+0.09	0.45	±	0.14
Na	-0.14	-0.01	1.11	±	0.22
Organic	-0.20	+0.16	0.33	±	0.16
			weight/volume, %		
Water Salinity	-0.30	-0.55**	1.9	±	0.5

* Significant at the 95 percent confidence level (P <0.05).
** Highly significant (P <0.01).
*** Very highly significant (P <0.001).

Table B4

**Selected Linear Regression Models for Predicting Yield (Peak Biomass)
of Live S. alterniflora from Tissue Nutrient Content**

Live S. alterniflora Biomass

No. Variables	Variable	r^2	CV, %
1	B	0.10	51
2	P, B	0.20	48
3	N, P, Mn	0.28	46
4	N, K, Mn, B	0.32	45
7	N, K, Mn, Fe, B, Cu, Ba	0.36	43

Total Biomass

No. Variables	Variable	r^2	CV, %
1	B	0.10	43
2	K, B	0.21	40
3	K, Mn, B	0.30	38
4	K, Mn, B, Ba	0.33	37
7	K, Mg, Mn, B, Al, Sr, Ba	0.38	36

Note: All probabilities significant at 0.0001 level.

Table 15

Selected Linear Regression Models for Predicting Yield of Live
S. alterniflora and Total Biomass from Soil Parameters

No. Variables	Variable	r^2	Significance Level*	CV %
	Live S. alterniflora Biomass			
1	Clay >20 μ	0.03	0.11	45
2	Na, Clay >20 μ	0.04	0.25	45
3	K, Na, Clay >20 μ	0.04	0.35	46
7	Ca, Mg, Na, OM, Clay <20 μ, Clay >20 μ, Salinity	0.06	0.73	47
	Total Biomass			
1	Salinity	0.07	0.01**	41
2	OM, Salinity	0.08	0.04	41
3	K, Na, Salinity	0.09	0.09	41
7	Ca, Mg, Na, OM, Clay <20 μ, Clay >20 μ, Salinity	0.11	0.33	42

* Probability (P) that the relationship between indicated soil
parameters and biomass occurs by chance. Significant relationship
is taken by convention to occur when P ≤0.05.
** Highly significant.
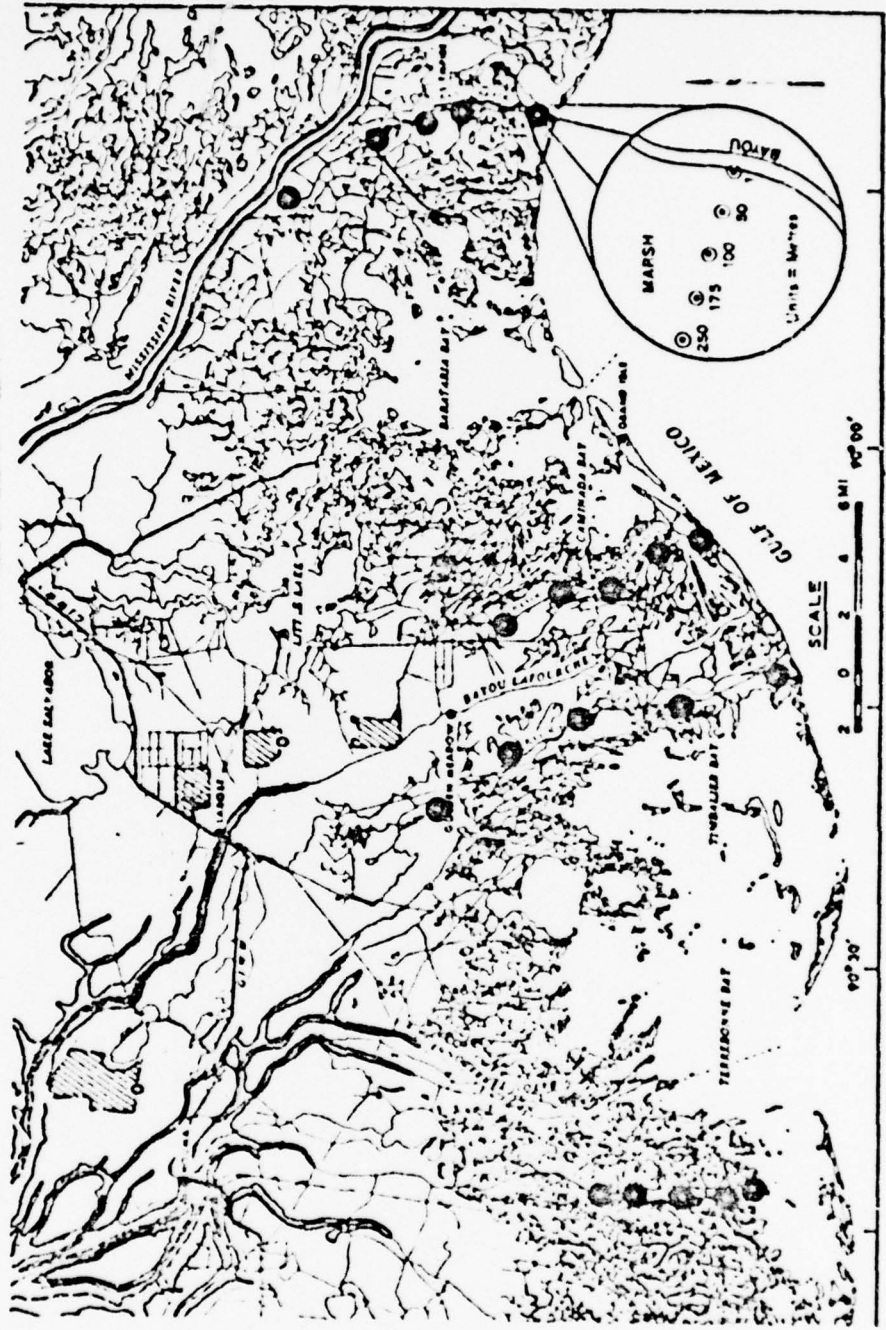
Figure B1. Location of field sampling sites on the Louisiana coast.
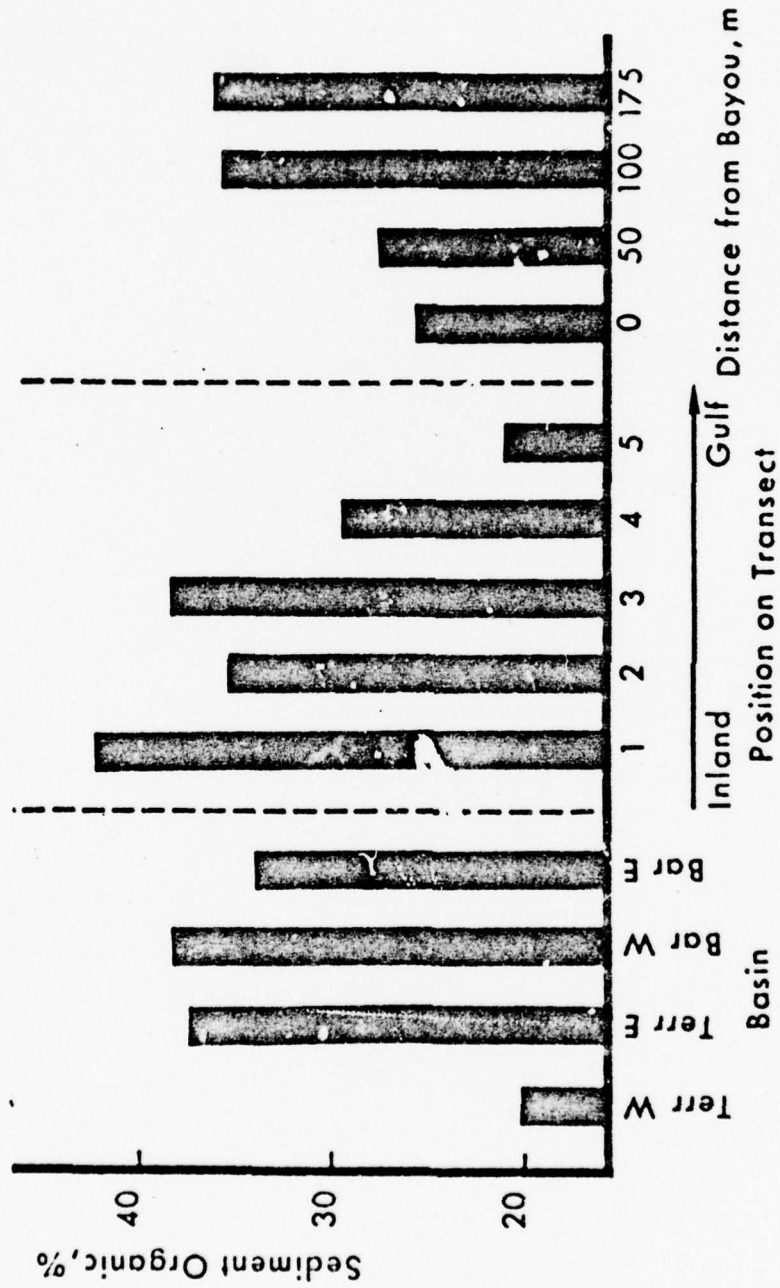
Figure B2. Variation in sediment organic concentration in Louisiana's salt marshes.
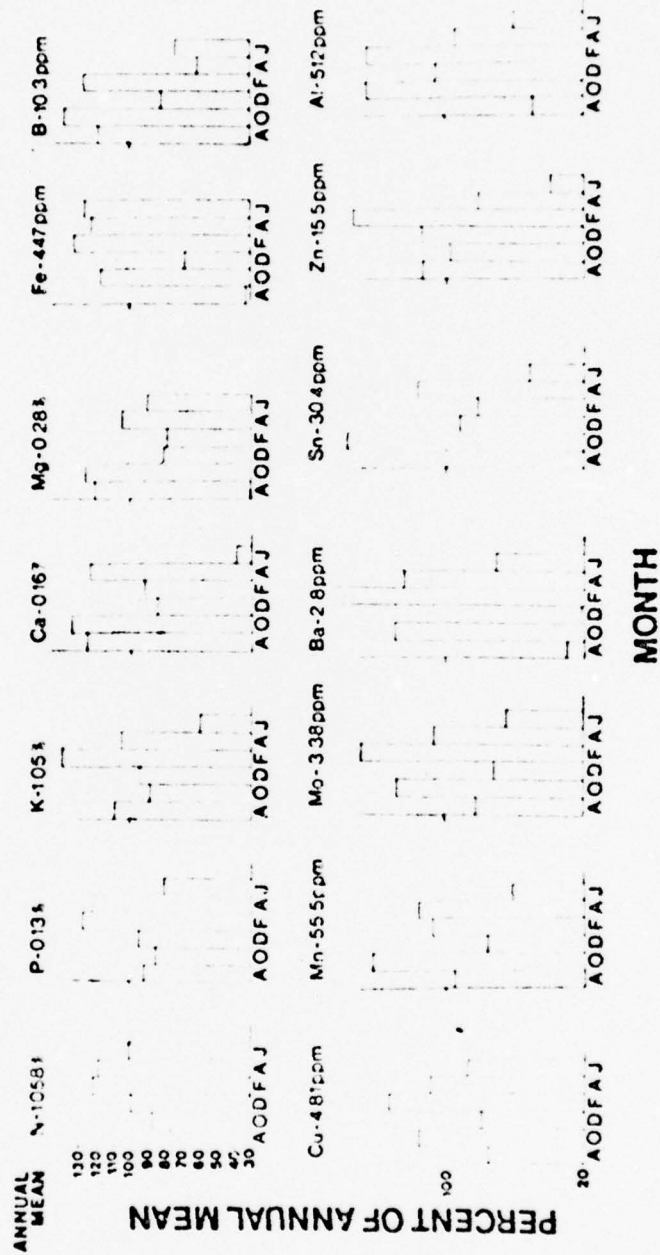
Figure B3. Seasonal changes in concentration of nutrients in live _S. alterniflora_ shoots.

APPENDIX C: INFLUENCE OF IRON SOURCE AND CONCENTRATION ON
GROWTH OF SPARTINA ALTERNIFLORA

Introduction

1. Spartina alterniflora requires high concentrations of available iron (Fe) to avoid chlorosis and attain optimum growth (Adams 1963).* The flooded marsh sediments in which S. alterniflora grows are highly reduced through the metabolic activities of facultative anaerobic soil microorganisms. This reduced environment is conducive to successional Fe transformations from the ferric to the ferrous Fe species (Gotoh and Patrick 1974). Christ (1974a) found that monocotyledonous plant species are inefficient in the utilization of the ferric ion forms, whether the ferric ion is chelated or not. He also noted that to avoid chlorosis and attain optimum growth, monocotyledonous plants generally require higher Fe concentrations (regardless of Fe species) than dicotyledonous plants. Iron concentrations in S. alterniflora tissue in Appendix B ranged from 154 to 632 ppm depending upon the season of collection. These values are similar to the 590-ppm average found by Williams and Murdoch (1967).

2. Spartina alterniflora is one of the dominant species inhabiting the highly reduced salt marshes of Louisiana. These marsh sediments have high Fe content, and, since they are reduced, they have high ferrous concentrations. In common with many hydrophytes, the air lacunae in S. alterniflora allow passage of atmospheric oxygen (O_2) from the leaves to

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* See references at end of this appendix.

the roots (Teal and Kanwisher 1966). This oxygen diffuses out of the roots, creating an oxygenated rhizosphere within which the ferrous ion species may be oxidized to the ferric form. Thus, although the reducing condition of the sediment favors the ferrous ion equilibrium, the immediate microenvironment of the root may be favoring the oxidized ferric equilibrium. As a hydrophytic monocotyledonous plant, is S. alterniflora using the ferrous Fe species abundant in the sediment or is it utilizing the ferric Fe species produced in the rhizosphere?

3. The following experiment was designed to determine the ionic Fe species and the ferrous concentration necessary for optimum growth. Christ (1974b) outlines the experimental difficulties of maintaining soluble Fe in nutrient solutions and developed a procedure that overcomes this solubility difficulty. This study follows his technique with some modification.

Methods

4. Seeds were germinated and grown in a saline marsh sediment collected from the Fourchon area of coastal Louisiana until two to three leaves developed, i.e., to the approximate height of 10 cm. The seedlings were then transferred into nutrient solutions in 2-quart polyethylene freezer containers painted black. The plants were supported through holes in the lids with Permagum strips (Virginia Chemicals Inc.). There were ten plants per container and one container per treatment.

5. After transplanting, the seedlings were allowed to acclimate for 1 week in a modified Hewitt's (1966) nutrient solution minus

C2

Fe.* All solutions used throughout this experiment were adjusted to pH 4.

6. The following growth conditions were maintained for the duration of the experiment: a light intensity of 19,000 lux and a photoperiod of 16 hours of light at 32°C and 8 hours of dark at 20°C.

7. After the acclimation period the plants were subjected to an Fe treatment of 0.5, 1, 2, 10, or 20 ppm ferrous sulfate; or 1 ppm ferric sulfate; or 1 ppm Fe as Sequestrene NaFe iron chelate (ferric ethylene-diamine-tetraacetate; 17% Fe_2O_3). All Fe treatments contained 4 millimole per liter (mM ℓ^{-1}) $Ca(NO_3)_2$ as a nitrogen source, and all Fe treatments with the exception of a control contained 10 mM ℓ^{-1} hydroquinone as a reducing agent. The control received 1 ppm chelated Fe. In a preliminary experiment using the same Fe concentrations, but with the omission of hydroquinone, an iron oxide precipitate was observed. Since the amount of precipitated Fe was not known the results of this first test are not reported here. However, the general trends coincide with those reported below.

8. The experiment consisted of a 3-day growth period in the indicated treatment alternating with a 4-day growth period in modified Hewitt's nutrient solution minus Fe (Hewitt 1966). This alternation of solutions was continued for 4 weeks. At the end of the fourth week the plants were harvested; the length of the longest root and shoot were measured. The plants were dried at room temperature to constant weight;

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*This nutrient solution contained KNO_3 (4mM ℓ^{-1}); $Ca(NO_3)_2$ (4mM ℓ^{-1}); $MgSO_4$ (1.5 mM ℓ^{-1}); NaH_2PO_4 (1.33 mM ℓ^{-1}); Mn (0.55 ppm); Cu (0.05 ppm), Zn (0.05 ppm as sulfates); B (0.5 ppm as H_3BO_3); and Mo (0.05 ppm as Na_2MoO_4).

the root, shoot, and total weight were determined as well as the root to shoot weight ratio. The results were then analyzed statistically.

Results

9. Table C1 gives the treatment means for the portion of this study concerned with determining the optimum Fe concentration for growth. Of the six parameters analyzed, only three showed any statistically significant differences. There is a highly significant difference in growth as measured by root length, shoot length, and the root to shoot dry weight ratio of S. alterniflora plants subjected to different concentrations of ferrous sulfate. However, the six concentrations of ferrous Fe tested do not differ in their effects on root weight, shoot weight, or total weight of S. alterniflora.

10. A least-squares regression was performed to determine if the relationship between tissue length or dry weight and Fe concentration is linear. Figure C1 is the graphical representation of the regression analyses. Of the six parameters measured, only root weight did not exhibit a significant linear relationship with Fe concentration. The low coefficient of correlation (r^2) values indicate, however, that within each treatment the individual plant's response to the treatment was highly variable.

11. Table C2 gives the treatment means for the portion of this study dealing with the preferred Fe species for optimum growth. Of the six parameters measured, only root weight differences showed any statistical significance, i.e., there is a significant difference in the root weight of S. alterniflora   ated to the type of Fe in solution.

4

From the table it can be seen that the 1-ppm chelated treatment with hydroquinone consistently gave the highest averages of the six parameters measured.

Discussion

12. Maximum growth occurred at the lowest ferrous concentrations; however, the optimum concentration of ferrous ion cannot be directly established from the data obtained as concentrations lower than 0.5 ppm were not tested. Apparently Fe in the natural ecosystem is not limiting. This has also been suggested by Broome et al. (1975a), who noted that in the field Fe fertilizers did not stimulate growth. The negative slope of the regression of root length, shoot length, shoot weight, and total weight to increasing ferrous concentrations indicates toxicity at concentrations greater than 5 ppm, which is much lower than concentrations found in the field. However, in the field no clear evidence of toxicity appeared (Broome et al. 1975b). The high tissue levels of Fe in natural stands may be an indication that Fe, although abundantly available in the environment, somehow becomes unavailable once it is within the tissue (through precipitation, sequestration, or oxidation). The addition of hydroquinone may maintain Fe in an available form so that much lower ferrous concentrations are effective.

C5

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Table C1

Mean Growth Response of S. alterniflora Seedlings to Different
Ferrous Concentrations

Concentration ppm	Fe^{+2} N	Length, cm		Weight, g dr wt			Dry Wt Ratio Root:Shoot
		Root	Shoot	Root	Shoot	Total	
0.5	10	25.8	38.6	0.0833	0.1981	0.2814	0.4277
1.0	10	22.1	36.7	0.0891	0.1845	0.2736	0.4788
2.0	10	19.9	40.4	0.0739	0.1720	0.2459	0.4352
5.0	10	22.1	37.3	0.0877	0.1722	0.2619	0.5123
10.0	10	20.9	36.3	0.0743	0.1565	0.2527	0.5832
20.0	10	19.1	28.6	0.0707	0.1221	0.1927	0.5832
Overall Means		21.6	36.3	0.0801	0.1676	0.2513	0.4898
F value		5.1*	4.4*	0.93^{ns}	2.18^{ns}	1.47^{ns}	4.07*

* $P < 0.01$.

Table C2

Mean Growth Response of S. alterniflora Seedlings to Different Iron Species at 1-ppm Concentration

Treatment			Means					
Reducing Agent	Iron Species at 1 ppm	N	Length, cm Root	Shoot	Weight, g dr wt Root	Shoot	Total	Dry Wt Ratio Root:Shoot
Hydroquinone	Ferrous	10	22.1	36.7	0.089	0.185	0.274	0.479
"	Ferric	10	22.3	36.7	0.082	0.174	0.256	0.471
"	Chelated	10	23.1	39.3	0.138	0.241	0.379	0.577
Control, no hydroquinone	Chelated	10	19.9	37.8	0.111	0.179	0.290	0.617
Overall Means			21.8	37.6	0.105	0.194	0.300	0.536
F Value			1.66^{ns}	0.53^{ns}	3.90^{ns}	2.26^{ns}	2.8^{ns}	$6.45*$

* $P < 0.05$.
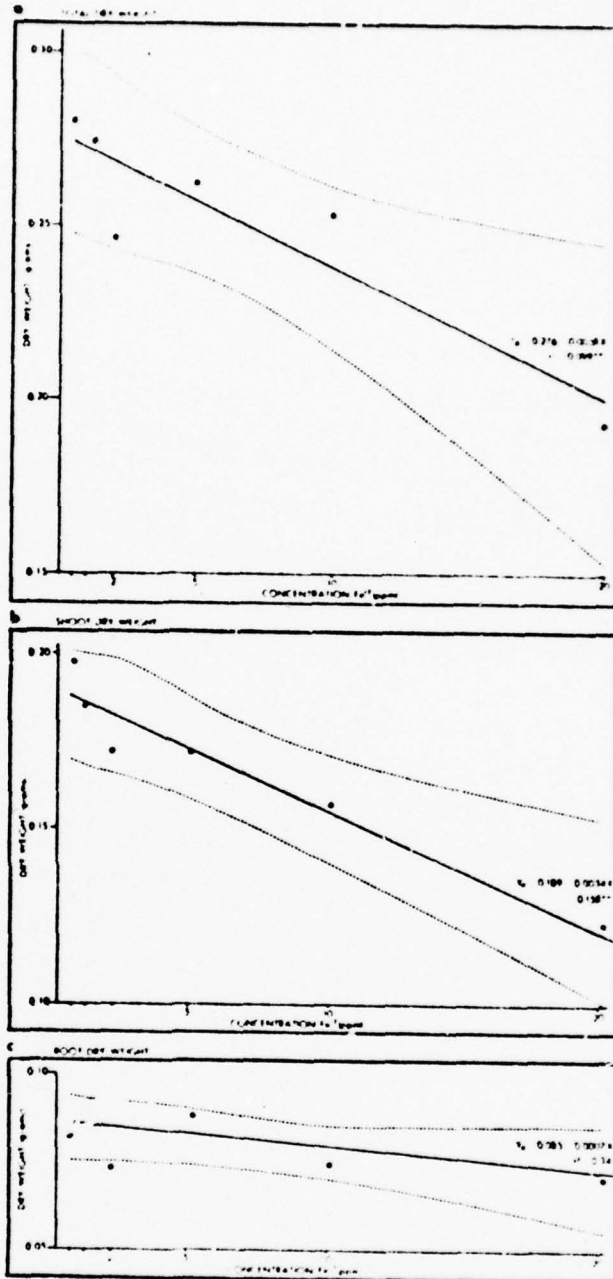
Figure C1. Relationship of growth parameters to substrate ferrous
ion concentrate for S. alterniflora seedlings (each
point represents a mean of 10 plants).
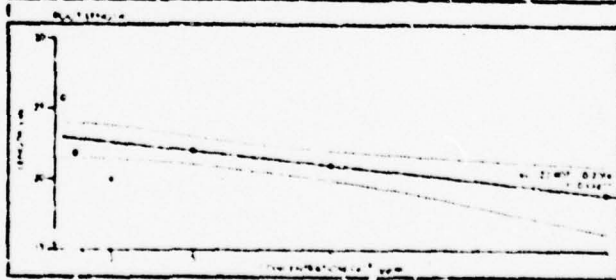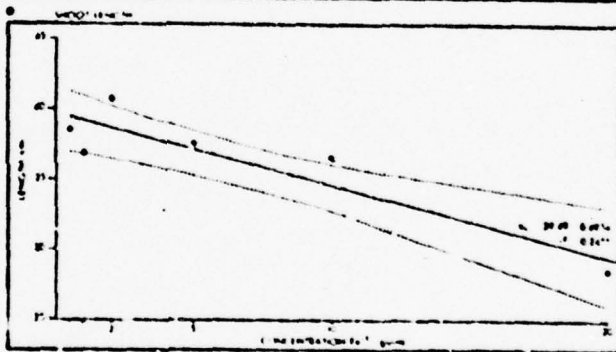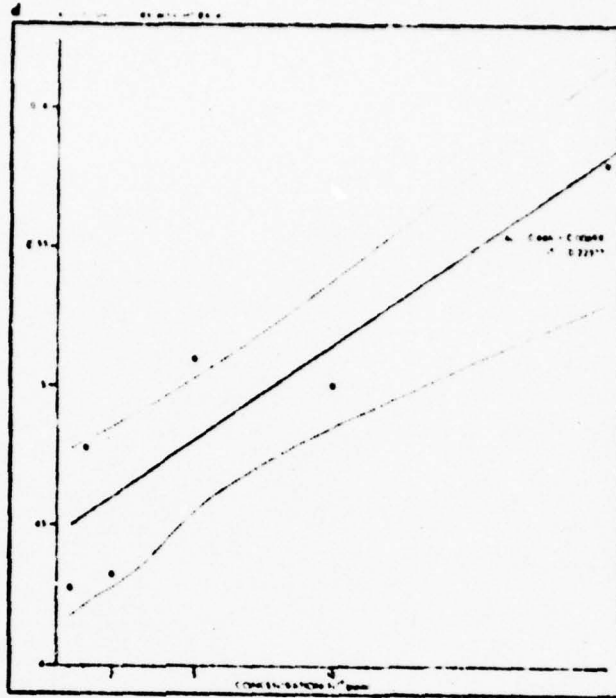
Figure C1. (Continued)

APPENDIX D: TISSUE, MINERAL ANALYSIS FOR SEVEN COMMON
MARSH PLANT SPECIES FOUND IN COASTAL LOUISIANA

Introduction

1. Tissue analyses are a useful adjunct in ecosystem investigations.
Taken alone, they are not a sufficient diagnostic tool; instead they are
but one of many, all of which taken together can elucidate the physiological
processes of an ecosystem.

2. The following does not constitute an in-depth analysis of the
nutrient requirements of the seven species studied, as it does not
contain coincident measurements of the soil availability of these nu-
trients nor of the nutrient composition of decomposing plant material.
Nevertheless, the results as presented in tabular form provide a base of
information useful for further research.

Materials and Methods

3. At approximately 8-week intervals beginning in August 1973 for
48 weeks, five plots each of Distichlis spicata, Juncus roemerianus,
Phragmites communis, Saggitaria falcata, Spartina alterniflora, Spartina
cynosuroides, and Spartina patens were harvested at sites in the Bara-
taria and Terrebonne basins of the Louisiana coast. Details of site
location and harvest techniques are described in Hopkinson et al. (1976).*
From each sample the live material was separated from the dead. The

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* Hopkinson, C. S., J. G. Gosselink, and R. J. Parrondo. 1976. Appen-
  dix A, Vol. 1, Spatial variation in the peak biomass of salt marsh
  vegetation in coastal Louisiana. Final rept., Corps of Engrs., WES,
  Vicksburg, Miss.

D1

live tissue was dried at 80°C and ground in a Wiley mill. Aliquots were analyzed spectroscopically for 13 elements by the Plant Analysis Laboratory at the University of Georgia, at Athens, Ga. Nitrogen (N) was determined by the micro-Kjeldahl technique at the same laboratory. The resulting data were analyzed statistically using analysis of variance and simple regression methods.

Results

4. Tables D1-D14 present the mean nutrient concentration and mean total nutrient content of the tissues from the studied marsh species by sampling period. Annual mean values are included.

5. The next seven tables (Tables D15-D21) present the analysis of variance statistics obtained when testing for seasonal differences in either tissue concentration, total tissue content, or biomass. This gives some indication of seasonal trends existing in the tissue nutrients of each species and a measure of the natural variability in tissue nutrient content.

6. Tables D22-28 show the relationship between aboveground live biomass and total standing crop of mineral nutrients for the seven species studied. With few exceptions tissue nutrient concentration was independent of biomass as determined by linear regressions of nutrient concentration on biomass.

Discussion

7. The outstanding feature of the data presented in this report is the variability in tissue concentration among species and among nutrients. Any generalizations must necessarily be so broad as to be nearly meaningless

D2

when individual elements or individual species are analyzed in detail. Therefore, in this discussion, rather than generalize the results, the availability of a large data set is emphasized and the utility of the statistical displays provided for interpretation of the behavior of individual nutrients is discussed.

Nutrient concentrations

P   The annual mean values for each nutrient by species are displayed in Tables D15-D22. A quick comparison shows that concentrations of nutrients in tissues of S. falcata are high compared to the other species. This was the only broad-leafed monocot examined. The grasses, S. alterniflora, S. patens, S. cynosuroides, D. spicata, and P. communis, all tend to have fairly low nutrient concentrations, roughly comparable in range with the rush, J. roemerianus.

9.   The second column of these same tables shows whether seasonal (bimonthly) concentration changes were statistically significant. The coefficient of variability (CV) in the third column is an index of the variation in concentration among plots sampled at one time. Used together the two values show the natural variability of the tissue nutrient and its variation through time. There is a wide range of values in both columns. Coefficients of variability in field collections of biological data typically are 20 to 30 percent even in well-controlled tests. These are also typical values in these tables, although some of the micronutrient concentrations were extremely variable. Examples are barium (Ba), with a CV range from 48 to 132 percent, and zinc (Zn), which had a CV of 147 percent in S. falcata.

D3

10. Variation through time was most pronounced in those species that have the strongest seasonal growth patterns. These are S. falcata, P. communis, and S. cynosuroides. For these three species the seasonal variation in concentration of nearly every nutrient was highly significant. On the other hand those species that vary little in live biomass through the year (J. roemerianus and S. patens) had relatively constant nutrient concentrations also. Patterns for specific nutrients and species are displayed in Tables D1-D14. These two basic patterns suggest that seasonal changes in nutrient concentrations are probably a function of tissue age. Spartina patens and J. roemerianus grow actively throughout the year and all vegetation samples had a mixture of young, mature, and senescing tissues. In contrast the species in the other group die to the ground during the winter and tend to have a single growth cycle during the spring-summer-fall period. A spring sample was nearly all young tissue, which tended to have higher nutrient concentrations than mature summer tissues or senescing fall tissues.

Nutrient standing crop

11. The last three columns of Tables D15-D21 show the annual mean standing stock of individual nutrients, the statistical probability that bimonthly changes are significant, and the CV. The standing stock is the product of concentration and live biomass. When biomass varies seasonally the standing stock nearly always does also; so that for most species and nutrients, there is a statistically strong seasonal fluctuation in standing stock. This is not true for J. roemerianus and S. patens, however, which are relatively constant nutrient reservoirs

D4

throughout the year. Figure D1 illustrates two extreme cases, S. patens, which shows little second variation in N concentration and standing stock compared to S. falcata, which varies widely in both.

12. If biomass and nutrient concentration are not closely related, the variability of total nutrient standing stock should be greater than the variability of either component alone. This is true, in general, as a comparison of the third column with the last column in Tables D15-D21 shows. If variability in total nutrient standing stock is reduced compared to nutrient concentration, it means that the nutrient is diluted (concentration is reduced) as biomass increases, suggesting that the nutrient supply to the roots is limited. This occurred most conspicuously with S. cynosuroides. In this species, the CV's for total standing stock of N, phosphorus (P), potassium (K), manganese (Mn), copper (Cu), and molybdenum (Mo) were all reduced compared to the variability of the nutrient concentration. This is probably a reflection of high initial concentrations of these elements in the spring followed by dilution as biomass increased and tissues matured.

Predictability of aboveground nutrient stocks

13. Tables D22-D28 show the predictability of aboveground nutrient stocks based on standing biomass, without regard to season. These linear regressions are based on 30 nutrient-biomass pairs for each nutrient and species. The r^2 value is the percentage of the variability in nutrient stock that can be attributed to biomass differences. For some species, notably S. falcata, the fit is quite good: r^2 values nearly all are above 80 percent. For others it is poor: D. spicata r^2

D5

values are 0 to 51 percent. In the linear regression analysis, values associated with extremes of biomass receive more weight than values in the middle of the range. Consequently those species with strong seasonal biomass changes tend to show higher r^2 values than those with small biomass ranges.

14. The nutrients Ba and aluminum (Al)--neither of which is currently considered essential for all plants--vary unpredictably with high CV values and low r^2 values.

15. The nutrients with the highest predictability were N and P. Comparing the five nutrients with the best regression fits for each species, N appeared in all species except P. communis, and P appeared in all species but P. communis and S. falcata. Extrapolating, it is tempting to suggest that marsh plant growth is most likely to be limited by these two nutrients since biomass closely follows the total amount of N and P absorbed by the plants.

Conclusions

16. The data presented in this report vary widely from plot to plot and month to month. Means and statistical treatment provide information about expected tissue concentrations and variability of mineral elements in Louisiana coastal marshes.

Table 1

Mean Nitrogen Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. %	August Total g m⁻²	October Conc. %	October Total g m⁻²	December Conc. %	December Total g m⁻²	February Conc. %	February Total g m⁻²	April Conc. %	April Total g m⁻²	June Conc. %	June Total g m⁻²	Annual Conc. %	Annual Total g m⁻²
S. alterniflora	0.800	5.24	0.920	6.30	1.040	1.41	1.280	3.55	1.240	4.07	1.040	5.30	1.02	4.26
D. spicata	0.820	6.10	1.100	6.78	1.020	4.55	1.180	6.56	1.150	9.29	1.200	6.49	1.04	5.62
J. roemerianus	1.020	6.00	1.180	7.48	1.000	5.02	1.140	7.71	0.800	5.60	1.100	11.97	0.98	6.69
S. cynosuroides	0.640	3.99	0.660	1.61	—	—	1.500	0.60	1.300	5.09	0.660	6.35	0.73	3.37
S. falcata	1.960	4.14	2.220	1.42	—	—	1.100	0.41	2.550	4.88	1.720	11.13	1.64	3.57
P. communis	1.160	9.67	1.160	6.26	1.160	7.42	1.980	1.53	2.175	15.32	1.575	7.95	1.53	6.89
S. patens	0.660	2.60	0.660	5.21	0.660	5.91	0.660	5.97	0.600	5.61	0.920	5.46	0.70	4.62

Table 2

Mean Phosphorus Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. %	August Total g m⁻²	October Conc. %	October Total g m⁻²	December Conc. %	December Total g m⁻²	February Conc. %	February Total g m⁻²	April Conc. %	April Total g m⁻²	June Conc. %	June Total g m⁻²	Annual Conc. %	Annual Total g m⁻²
S. alterniflora	0.120	0.79	0.110	0.74	0.124	0.40	0.166	0.33	0.160	0.52	0.104	0.51	0.13	0.52
D. spicata	0.120	0.92	0.118	0.52	0.126	0.56	0.150	0.66	0.145	0.76	0.120	0.64	0.12	0.69
J. roemerianus	0.118	0.68	0.122	0.78	0.122	0.52	0.132	0.68	0.170	0.80	0.125	1.29	0.12	0.79
S. cynosuroides	0.092	0.56	0.094	0.51	—	—	0.275	0.12	0.152	0.59	0.062	0.48	0.10	0.36
S. falcata	0.366	0.77	0.318	0.19	—	—	0.498	0.12	0.492	0.92	0.314	2.01	0.32	0.66
P. communis	0.150	1.24	0.170	0.64	0.174	0.75	0.342	0.22	0.307	2.47	0.215	1.10	0.22	0.96
S. patens	0.106	0.40	0.102	0.61	0.090	0.82	0.106	0.76	0.077	0.45	0.054	0.36	0.08	0.55

Table 3

Mean Potassium Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. %	August Total g m⁻²	October Conc. %	October Total g m⁻²	December Conc. %	December Total g m⁻²	February Conc. %	February Total g m⁻²	April Conc. %	April Total g m⁻²	June Conc. %	June Total g m⁻²	Annual Conc. %	Annual Total g m⁻²
S. alterniflora	1.146	7.59	0.922	5.87	0.990	3.26	1.508	2.97	1.200	3.61	0.620	3.22	1.01	4.14
D. spicata	0.606	4.60	0.446	2.77	0.506	2.62	2.064	10.15	0.602	3.63	0.716	3.87	0.86	4.49
J. roemerianus	1.044	6.05	0.686	4.42	0.878	4.42	1.048	6.60	0.860	6.26	1.037	11.06	0.86	5.59
S. cynosuroides	0.372	2.26	0.016	0.22	—	—	2.460	1.09	1.030	4.06	0.508	4.16	0.62	1.79
S. falcata	5.992	12.71	4.476	4.62	—	—	4.660	1.26	4.185	7.94	3.700	23.33	4.10	8.05
P. communis	1.426	11.06	1.370	5.19	1.384	6.04	4.608	2.84	2.910	18.64	1.233	6.32	1.98	7.52
S. patens	0.712	2.78	0.462	3.19	0.460	4.25	0.598	4.56	0.650	3.90	0.544	3.28	0.55	3.53

Table D4

Mean Calcium Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August		October		December		February		April		June		Annual	
	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}
S. alterniflora	0.198	1.29	0.214	1.49	0.132	0.44	0.144	0.29	0.195	0.83	0.060	0.29	0.15	0.70
D. spicata	0.104	0.78	0.109	0.46	0.078	0.34	0.070	0.34	0.057	0.32	0.028	0.14	0.07	0.40
J. roemerianus	0.082	0.48	0.072	0.46	0.068	0.34	0.090	0.61	0.057	0.42	0.025	0.24	0.06	0.41
S. cynosuroides	0.174	1.08	0.152	0.85	-	-	0.095	0.04	0.155	0.60	0.104	0.60	0.11	0.54
S. falcata	0.434	0.92	0.632	0.29	-	-	0.596	0.15	0.657	1.27	0.524	3.47	0.63	0.97
P. communis	0.208	1.82	0.078	0.29	0.054	0.24	0.094	0.06	0.115	0.74	0.107	0.56	0.10	0.58
S. patens	0.108	0.42	0.082	0.55	0.084	0.77	0.088	0.62	0.07	0.43	0.028	0.16	0.07	0.46

Table D5

Mean Magnesium Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August		October		December		February		April		June		Annual	
	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}	Conc. %	Total g m^{-2}
S. alterniflora	0.336	2.21	0.352	2.39	0.226	0.77	0.218	0.46	0.290	0.95	0.250	1.24	0.27	1.24
D. spicata	0.134	1.02	0.208	0.90	0.126	0.56	0.078	0.42	0.140	0.74	0.164	0.88	0.14	0.73
J. roemerianus	0.070	0.39	0.116	0.73	0.096	0.47	0.098	0.68	0.145	1.00	0.167	1.79	0.11	0.77
S. cynosuroides	0.136	0.83	0.154	0.86	-	-	0.087	0.04	0.232	0.91	0.192	1.53	0.12	0.67
S. falcata	0.282	0.59	0.272	0.18	-	-	0.404	0.10	0.375	0.70	0.324	2.11	0.26	0.58
P. communis	0.214	1.55	0.030	0.11	0.022	0.09	0.058	0.03	0.160	0.89	0.160	0.70	0.09	0.51
S. patens	0.070	0.30	0.072	0.45	0.056	0.49	0.074	0.51	0.123	0.76	0.118	0.71	0.08	0.52

Table D6

Mean Manganese Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August		October		December		February		April		June		Annual	
	Conc. ppm	Total g m^{-2}	Conc. ppm	Total g m^{-2}	Conc. ppm	Total g m^{-2}	Conc. ppm	Total g m^{-2}	Conc. ppm	Total g m^{-2}	Conc. ppm	Total g m^{-2}	Conc. ppm	Total g m^{-2}
S. alterniflora	52.6	33.83	79.6	54.29	42.6	13.89	60.2	12.10	64.25	21.16	54.0	16.96	53.4	23.8
D. spicata	348.8	283.37	299.0	126.76	270.2	116.09	304.0	144.99	340.50	184.72	304.8	165.09	303.2	167.0
J. roemerianus	86.0	51.27	74.8	48.79	56.6	29.05	66.6	47.11	50.50	44.68	79.25	81.13	65.7	46.3
S. cynosuroides	84.2	50.10	131.6	66.6?	-	-	106.7	4.72	210.50	81.05	92.2	67.01	92.0	43.5
S. falcata	318.0	72.72	401.8	26.16	-	-	415.0	11.25	363.25	69.48	265.6	157.77	285.1	53.0
P. communis	98.8	91.36	67.2	16.04	16.8	16.64	70.8	4.93	61.50	38.21	94.5	18.63	55.3	29.1
S. patens	67.0	18.62	76.0	52.79	51.8	51.94	62.0	51.01	58.75	35.87	52.6	52.10	56.3	39.2

Table 37

Mean Iron Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	Total g m⁻²	October Conc. ppm	Total g m⁻²	December Conc. ppm	Total g m⁻²	February Conc. ppm	Total g m⁻²	April Conc. ppm	Total g m⁻²	June Conc. ppm	Total g m⁻²	Annual Conc. ppm	Total g m⁻²
S. alterniflora	154.2	100.91	558.0	370.17	325.6	101.79	632.0	118.56	566.0	190.92	667.60	172.48	485.0	144.0
D. spicata	193.0	167.04	484.8	209.98	418.8	192.35	621.4	228.05	608.25	306.12	862.00	447.75	676.2	268.0
J. roemerianus	70.8	45.10	179.0	122.83	163.0	76.57	150.0	101.29	206.50	160.66	273.50	266.12	151.0	123.0
S. cynosuroides	84.2	54.41	115.2	66.88	—	—	214.0	9.96	158.50	60.12	180.00	133.49	113.0	51.0
S. falcata	970.6	208.35	1731.6	101.02	—	—	1196.6	37.59	929.25	181.68	607.60	367.99	651.0	163.7
P. communis	73.8	61.13	141.2	56.80	68.6	29.17	590.6	12.26	369.25	215.73	171.75	198.54	242.0	84.6
S. patens	70.6	25.91	136.7	63.60	97.8	93.60	109.6	89.41	245.25	144.67	164.60	104.30	123.0	61.9

Table 38

Mean Boron Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	Total g m⁻²	October Conc. ppm	Total g m⁻²	December Conc. ppm	Total g m⁻²	February Conc. ppm	Total g m⁻²	April Conc. ppm	Total g m⁻²	June Conc. ppm	Total g m⁻²	Annual Conc. ppm	Total g m⁻²
S. alterniflora	12.2	8.02	14.2	9.29	8.4	2.71	13.0	2.44	6.25	2.06	7.6	3.82	10.1	4.54
D. spicata	16.4	10.92	20.8	9.31	16.6	7.49	12.6	6.06	12.5	6.44	15.6	8.41	15.0	8.02
J. roemerianus	18.2	10.99	16.8	11.31	14.0	7.16	19.0	13.00	17.75	13.60	15.5	17.00	15.8	11.1
S. cynosuroides	4.8	2.71	8.0	6.25	—	—	10.5	0.46	3.75	1.45	6.4	3.41	6.77	1.99
S. falcata	31.6	6.95	31.6	2.07	—	—	48.4	1.28	11.75	6.02	28.4	10.12	27.5	5.54
P. communis	7.8	6.55	6.6	1.60	6.6	2.06	11.2	0.76	7.0	6.50	6.3	2.16	6.17	2.76
S. patens	10.2	5.79	7.2	6.00	8.2	7.56	8.0	6.16	7.0	6.29	8.2	6.90	8.03	6.97

Table 39

Mean Copper Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	Total g m⁻²	October Conc. ppm	Total g m⁻²	December Conc. ppm	Total g m⁻²	February Conc. ppm	Total g m⁻²	April Conc. ppm	Total g m⁻²	June Conc. ppm	Total g m⁻²	Annual Conc. ppm	Total g m⁻²
S. alterniflora	3.6	2.45	5.6	3.07	3.0	1.16	6.4	1.23	5.2	1.72	4.2	2.10	4.63	1.97
D. spicata	5.2	4.00	6.6	2.85	5.0	2.49	8.0	4.63	9.3	6.02	7.2	3.99	6.6	3.42
J. roemerianus	7.0	6.04	4.8	3.13	6.6	3.41	12.0	6.97	9.25	6.04	8.0	8.08	7.17	6.92
S. cynosuroides	7.2	6.25	3.8	2.06	—	—	11.0	0.58	10.25	1.09	7.6	5.95	6.20	2.44
S. falcata	16.2	3.54	17.6	1.16	—	—	20.2	0.51	19.25	3.05	11.0	6.72	13.6	2.48
P. communis	10.2	8.81	10.5	3.86	10.6	6.54	13.6	0.95	11.0	7.03	6.5	1.17	9.7	4.39
S. patens	5.8	2.23	7.0	6.64	16.2	13.09	7.6	5.13	11.75	6.00	5.6	1.62	8.57	5.26

Table D10

Mean Zinc Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	August Total g·m⁻²	October Conc. ppm	October Total g·m⁻²	December Conc. ppm	December Total g·m⁻²	February Conc. ppm	February Total g·m⁻²	April Conc. ppm	April Total g·m⁻²	June Conc. ppm	June Total g·m⁻²	Annual Conc. ppm	Annual Total g·m⁻²
S. alterniflora	17.6	11.26	15.0	9.96	17.6	5.60	23.8	6.37	12.75	5.11	6.0	4.13	25.0	5.91
D. spicata	17.6	13.33	14.6	7.31	20.0	8.81	19.6	10.95	12.75	6.58	11.6	6.24	15.6	8.6
J. roemerianus	17.6	10.06	16.6	10.58	16.0	8.96	20.0	12.63	13.5	9.72	11.0	10.62	15.3	9.76
S. cynosuroides	20.6	12.74	17.0	9.57	–	–	21.5	1.22	14.0	5.45	15.2	12.03	16.6	6.58
S. falcata	26.2	5.28	87.0	6.14	–	–	51.0	1.36	26.0	4.80	16.8	10.44	33.3	6.55
P. communis	33.2	16.5	32.2	12.41	34.2	16.99	45.0	3.06	47.25	10.57	22.75	12.09	39.6	15.1
S. patens	25.2	9.32	12.5	7.39	14.0	12.73	14.6	10.63	9.5	5.61	7.0	4.27	13.5	8.20

Table D11

Mean Aluminum Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	August Total g·m⁻²	October Conc. ppm	October Total g·m⁻²	December Conc. ppm	December Total g·m⁻²	February Conc. ppm	February Total g·m⁻²	April Conc. ppm	April Total g·m⁻²	June Conc. ppm	June Total g·m⁻²	Annual Conc. ppm	Annual Total g·m⁻²
S. alterniflora	353.0	165.62	745.6	556.29	535.6	171.51	741.6	166.62	480.5	157.73	312.6	154.49	494.0	217.0
D. spicata	170.3	136.95	373.2	138.00	342.0	160.16	447.2	246.24	285.0	142.76	290.6	156.41	310.0	162.0
J. roemerianus	90.6	60.43	305.2	207.28	230.0	121.67	193.0	153.10	101.0	79.60	163.3	166.29	170.0	121.0
S. cynosuroides	27.6	16.92	31.0	17.00	–	–	87.7	6.01	8.0	2.78	34.4	24.84	28.3	10.7
S. falcata	648.0	165.06	1226.0	68.35	–	–	1080.0	52.53	689.7	140.71	264.0	169.56	783.0	91.5
P. communis	52.2	28.10	113.0	46.21	39.0	16.37	190.2	15.11	102.5	59.94	66.5	39.12	85.2	30.0
S. patens	81.0	28.07	140.2	82.03	112.0	109.56	127.2	107.05	77.0	65.53	69.6	44.41	96.6	68.0

Table D12

Mean Molybdenum Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	August Total g·m⁻²	October Conc. ppm	October Total g·m⁻²	December Conc. ppm	December Total g·m⁻²	February Conc. ppm	February Total g·m⁻²	April Conc. ppm	April Total g·m⁻²	June Conc. ppm	June Total g·m⁻²	Annual Conc. ppm	Annual Total g·m⁻²
S. alterniflora	2.8	1.62	4.3	2.85	2.6	0.79	5.0	0.95	3.6	1.17	2.2	1.08	3.3	1.35
D. spicata	1.9	1.39	2.6	1.13	2.5	1.15	2.9	1.57	2.2	1.31	2.0	1.09	2.3	1.29
J. roemerianus	1.6	0.85	1.1	0.69	1.7	0.89	2.2	1.50	1.9	1.35	1.5	1.63	1.5	1.06
S. cynosuroides	1.8	0.79	1.6	0.70	–	–	1.7	0.07	1.6	0.63	0.7	0.54	1.0	0.44
S. falcata	2.5	0.52	4.5	0.27	–	–	15.3	0.43	5.0	0.40	2.5	1.53	4.8	0.59
P. communis	1.1	0.88	1.0	0.44	0.7	0.30	2.9	0.19	1.9	1.19	0.7	0.35	1.3	0.50
S. patens	1.7	0.68	1.6	0.68	1.3	1.19	1.6	1.36	1.4	0.84	0.9	0.60	1.4	0.89

Table 313

Mean Strontium Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	August Total g m⁻²	October Conc. ppm	October Total g m⁻²	December Conc. ppm	December Total g m⁻²	February Conc. ppm	February Total g m⁻²	April Conc. ppm	April Total g m⁻²	June Conc. ppm	June Total g m⁻²	Annual Conc. ppm	Annual Total g m⁻²
S. alterniflora	30.6	20.25	47.6	33.35	20.0	9.11	23.0	5.17	35.5	11.65	15.0	7.22	29.2	13.0
D. spicata	17.0	8.00	19.8	4.71	8.4	1.64	8.0	4.49	12.1	6.66	7.6	6.15	10.9	5.86
J. roemerianus	9.0	5.32	6.8	6.25	5.2	2.66	7.6	5.00	9.8	7.31	6.3	9.05	7.11	6.92
S. cynosuroides	11.0	7.29	9.8	5.45	-	-	9.0	0.61	15.3	5.93	6.8	5.28	7.97	3.84
S. falcata	65.0	13.04	61.4	6.16	-	-	50.2	1.55	71.1	13.29	46.6	31.77	46.5	10.9
P. communis	16.8	14.88	5.6	2.01	3.6	1.61	6.6	0.66	11.5	7.19	6.1	3.15	7.83	6.60
S. patens	10.8	6.13	11.2	7.70	5.6	5.32	7.2	5.05	11.0	7.16	8.0	6.72	8.70	5.65

Table 314

Mean Barium Values for Live Tissue of Seven Marsh Plant Species in Louisiana

Species	August Conc. ppm	August Total g m⁻²	October Conc. ppm	October Total g m⁻²	December Conc. ppm	December Total g m⁻²	February Conc. ppm	February Total g m⁻²	April Conc. ppm	April Total g m⁻²	June Conc. ppm	June Total g m⁻²	Annual Conc. ppm	Annual Total g m⁻²
S. alterniflora	6.8	3.51	5.6	2.67	0.8	0.22	6.6	1.57	3.5	1.14	2.0	3.99	2.7	1.07
D. spicata	0.4	0.34	4.0	2.05	1.2	0.53	1.6	0.73	6.3	3.36	3.6	1.94	2.6	1.37
J. roemerianus	0.4	0.29	0.6	0.68	0.4	0.20	0.6	0.33	1.3	0.78	0.5	0.39	0.60	0.37
S. cynosuroides	0.0	0.00	0.4	0.28	-	-	0.5	0.03	3.5	1.37	0.6	0.39	0.70	0.30
S. falcata	24.8	5.78	38.8	2.51	-	-	61.2	1.62	50.0	9.46	81.2	48.45	41.0	10.9
P. communis	7.6	6.94	2.4	0.94	2.6	1.07	5.0	0.34	13.1	8.59	9.0	4.62	5.8	3.33
S. patens	3.6	1.22	6.6	3.76	6.8	6.84	5.4	4.31	12.3	7.10	9.0	6.21	7.0	6.70

Table D15

Analysis of Variance Statistics of Tissue Nutrients in S. alterniflora

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[*]	F Value[**]	CV, %	Ann. Mean[‡]	F Value[**]	CV, %
N	1.02	2.08	24.4	4.24	3.43*	40.3
P	0.13	2.5	24.6	0.516	2.91*	42.0
K	1.01	2.82*	38.8	4.14	1.95	63.6
Ca	0.15	7.65**	29.3	0.696	7.99**	56.9
Mg	0.27	4.78**	22.7	1.24	9.72**	43.9
Mn	53.4	3.81*	33.7	23.8	7.73**	54.0
Fe	458.0	4.88**	41.1	188.0	7.74**	51.2
B	10.1	6.53**	31.3	4.54	7.48**	55.5
Cu	4.63	2.48	34.1	1.94	4.84*	53.4
Zn	15.0	10.04**	29.2	5.92	6.76**	43.6
Al	496.0	2.24	64.6	217.0	3.95**	86.2
Mo	3.26	3.86	39.6	1.35	5.92**	53.1
Sr	29.2	9.64**	25.6	13.8	10.14**	53.4
Ba	2.70	2.08	123.0	1.07	2.93**	96.1
Live Biomass				437.0	5.92**	38.5

* Units are percentage for N, P, K, Ca, and Mg and are $\mu g\ g^{-1}$ (ppm) for other nutrients.

** F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:

    * — $P < 0.05$

    ** — $P < 0.01$.

‡ Units are $g\ m^{-2}$ for N, P, K, Ca, and Mg and are $mg\ m^{-2}$ for other nutrients.

Table D16

Analysis of Variance Statistics of Tissue Nutrients in D. spicata

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[*]	F Value[**]	CV, %	Ann. Mean[‡]	F Value[**]	CV, %
N	1.04	2.18	22	5.62	1.47	31
P	0.126	1.54	23	0.689	3.64*	29
K	0.860	1.53	124	4.49	2.01	101
Ca	0.072	15.5**	25	0.401	14.86**	32
Mg	0.136	7.62**	25	0.732	4.13**	35
Mn	303.2	0.62	34	167.0	5.46**	35
Fe	478.2	6.58**	40	248.0	5.98**	41
B	15.0	4.44**	26	8.02	2.75*	34
Cu	6.63	0.74	40	3.61	1.04	46
Zn	15.9	5.24**	26	8.65	6.20**	32
Al	310.0	4.43**	34	162.0	2.81*	36
Mo	2.26	0.89	45	1.23	0.50	52
Sr	10.9	9.39**	31	5.84	5.27**	39
Ba	2.60	4.31**	76	1.37	2.74*	97
Live Biomass				550.6	5.21**	21

[*] Units are percentage for N, P, K, Ca, and Mg and are $\mu g\ g^{-1}$ (ppm) for other nutrients.

[**] F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:
   * - P <0.05
   ** - P <0.01.

[‡] Units are g m^{-2} for N, P, K, Ca, and Mg and are mg m^{-2} for other nutrients.

Table D17

Analysis of Variance Statistics of Tissue Nutrients in J. roemerianus

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[+]	F Value[++]	CV, %	Ann. Mean[‡]	F Value[++]	CV, %
N	0.977	1.85	33	6.69	1.13	61
P	0.115	0.87	29	0.736	0.65	53
K	0.860	1.81	32	5.59	1.42	54
Ca	0.063	11.5**	27	0.408	1.88	58
Mg	0.105	1.28	41	0.766	2.54	68
Mn	65.7	1.53	38	46.3	0.90	63
Fe	151.0	1.86	54	115.0	2.21	77
B	15.8	1.42	31	11.1	0.	65
Cu	7.37	2.36	48	4.91	1.65	57
Zn	15.3	4.86**	29	9.78	0.72	49
Al	170.0	9.28**	39	121.0	2.00	76
Mo	1.52	2.11	41	1.06	0.90	74
Sr	7.13	0.85	43	4.92	0.99	61
Ba	0.600	0.48	118	0.37	0.53	126
Live Biomass				671.0	1.35	48

[+] Units are percentage for N, P, K, Ca, and Mg and are $\mu g\ g^{-1}$ (ppm) for other nutrients.

[++] F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:
  * - P < 0.05
  ** - P < 0.01.

[‡] Units are $g\ m^{-2}$ for N, P, K, Ca, and Mg and are $mg\ m^{-2}$ for other nutrients.

Table D18

Analysis of Variance Statistics of Tissue Nutrients in S. cynosuroides

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[+]	F Value[++]	CV, %	Ann. Mean[‡]	F Value[++]	CV, %
N	0.733	6.31**	51	3.17	16.9**	43
P	0.098	7.59**	60	0.357	10.9**	46
K	0.618	10.8**	80	1.79	12.2**	61
Ca	0.105	8.57**	45	0.544	9.52**	60
Mg	0.123	10.32**	42	0.667	16.3**	48
Mn	92.0	4.97**	62	42.5	9.22**	56
Fe	113.0	2.62*	81	51.8	10.1**	65
B	4.77	6.88**	56	1.99	10.1**	61
Cu	6.20	5.05**	60	2.64	14.4**	51
Zn	14.4	8.78**	42	6.58	16.5**	47
Al	28.3	1.75	149	10.7	0.98	216
Mo	1.00	4.83**	57	0.44	12.2**	49
Sr	7.97	7.75**	45	3.85	12.2**	50
Ba	0.700	6.56**	132	0.297	5.86**	132
Live Biomass				404.0	21.8**	39

[+] Units are percentage for N, P, K, Ca, and Mg and are $\mu g\ g^{-1}$ (ppm) for other nutrients.

[++] F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:
  * - $P < 0.05$
  ** - $P < 0.01$.

[‡] Units are $g\ m^{-2}$ for N, P, K, Ca, and Mg and are $mg\ m^{-2}$ for other nutrients.

Table D19

Analysis of Variance Statistics of Tissue Nutrients in S. falcata

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[†]	F Value[††]	CV, %	Ann. Mean[‡]	F Value[††]	CV, %
N	1.84	22.31**	26	3.57	29.6**	47
P	0.315	10.01**	38	0.642	25.0**	52
K	4.10	13.84**	35	8.05	34.3**	41
Ca	0.419	11.05**	34	0.97	16.9**	72
Mg	0.264	12.52**	33	0.59	29.2**	55
Mn	285.1	14.8**	32	53.9	17.4**	57
Fe	907.0	11.86**	44	143.0	18.0**	49
B	27.5	17.2**	31	5.54	36.4**	45
Cu	13.4	7.41**	44	2.48	26.5**	44
Zn	33.3	2.00	147	4.55	3.78*	96
Al	783.0	26.2**	40	91.5	3.96**	77
Mo	4.75	11.79**	73	0.59	10.0**	64
Sr	48.5	11.8**	33	10.3	19.0**	58
Ba	41.0	10.3**	48	10.9	64.5**	47
Live Biomass				191.0	48.5**	41

[†] Units are percentage for N, P, K, Ca, and Mg and are $\mu g\ g^{-1}$ (ppm) for other nutrients.

[††] F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:
* – $P < 0.05$
** – $P < 0.01$.

[‡] Units are $g\ m^{-2}$ for N, P, K, Ca, and Mg and are $mg\ m^{-2}$ for other nutrients.

Table D20

Analysis of Variance Statistics of Tissue Nutrients
in P. communis

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[+]	F Value[++]	CV, %	Ann. Mean[‡]	F Value[++]	CV, %
N	1.53	2.15	39	6.89	3.60*	66
P	0.220	4.50**	40	0.955	4.20**	69
K	1.98	13.0**	40	7.52	4.28**	65
Ca	0.102	9.51**	38	0.580	5.74**	102
Mg	0.091	2.63*	108	0.513	5.26**	110
Mn	55.3	4.67**	48	29.1	3.23**	133
Fe	242.0	1.67	141	84.8	3.44*	91
B	6.17	7.53**	38	2.74	4.13**	84
Cu	9.7	4.05**	31	4.39	3.77*	71
Zn	33.4	3.30*	32	15.1	4.32**	63
Al	85.2	6.64**	61	30.8	1.22ns	93
Mo	1.30	4.19**	71	0.50	2.64*	91
Sr	7.83	12.18**	39	4.60	6.35**	104
Ba	5.83	4.22**	60	3.31	4.11**	100
Live Biomass				440.0	3.76*	64

[+] Units are percentage for N, P, K, Ca, and Mg and are $\mu g \ g^{-1}$ (ppm) for other nutrients.

[++] F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:
   * – $P < 0.05$
   ** – $P < 0.01$.

[‡] Units are $g \ m^{-2}$ for N, P, K, Ca, and Mg and are $mg \ m^{-2}$ for other nutrients.

Table D21

Analysis of Variance Statistics of Tissue Nutrients
in S. patens

Nutrient	Concentration			Total Nutrient per m^2		
	Ann. Mean[†]	F Value[††]	CV, %	Ann. Mean[††]	F Value[‡]	CV, %
N	0.783	1.72	24	4.92	1.50	48
P	0.086	7.67**	21	0.551	2.33	56
K	0.551	1.25	34	3.53	0.43	68
Ca	0.074	6.10**	34	0.483	2.17	67
Mg	0.082	3.47*	32	0.513	1.46	50
Mn	56.3	1.58	35	39.2	1.25	75
Fe	123.0	2.98*	50	81.9	1.53	72
B	8.63	2.12	30	4.97	2.05	50
Cu	8.57	0.71	124	5.76	1.24	144
Zn	13.5	2.91	64	8.20	2.34	61
Al	98.6	2.15	50	68.0	1.85	88
Mo	1.35	1.37	40	0.893	1.10	74
Sr	8.70	2.42	36	5.43	0.68	62
Ba	6.97	2.42	51	4.70	1.81	73
Live Biomass				642.0	1.51	48

[†] Units are percentage for N, P, K, Ca, and Mg and are $\mu g\ g^{-1}$ (ppm) for other nutrients.

[††] F = statistical probability that bimonthly changes are significant and is included for comparisons among times of sampling. Notations following numerical entries are as follows:
    * – $P < 0.05$
    ** – $P < 0.01$.

[‡] Units are $g\ m^{-2}$ for N, P, K, Ca, and Mg and are $mg\ m^{-2}$ for other nutrients.

Table D22

<u>Regression Equations for Standing Crop of Mineral Nutrients in the Live Shoots of S. alternitlora</u>

Nutrient	Regression Equation [+]	r^{2} [++]
N	$Y = 0.79 + 0.0079\ W$	0.79
P	$Y = 0.083 + 0.00099\ W$	0.83
K	$Y = 0.68 + 0.0079\ W$	0.41
Ca	$Y = -0.24 + 0.0021\ W$	0.70
Mg	$Y = -0.30 + 0.0035\ W$	0.88
Mn	$Y = -4.5 + 0.065\ W$	0.62
Fe	$Y = 49 + 0.32\ W$	0.27
B	$Y = 1.3 + 0.013\ W$	0.69
Cu	$Y = -0.00014 + 0.0044\ W$	0.58
Zn	$Y = 0.35 + 0.013\ W$	0.64
Al	$Y = -18 + 0.54\ W$	0.29
Mo	$Y = 0.014 + 0.0031\ W$	0.51
Sr	$Y = -5.3 + 0.044\ W$	0.72
Ba	$Y = 0.31 + 0.0018\ W$	0.11^{ns}

[+] Y = standing crop of nutrients in live shoots (g m^{-2} for nutrients 1-5, mg m^{-2} for nutrients 6-14). W = dry wt of live shoots in g m^{-2}.

[++] All regressions are highly significant (P <0.01) unless otherwise indicated.

Table D23

Regression Equations for Standing Crop of Mineral Nutrients in the Live Shoots of D. spicata

Nutrient	Regression Equation[+]	$r^{2[++]}$
N	$Y = 1.66 + 0.72\ W$	0.36
P	$Y = 0.072 + 0.11\ W$	0.50
K	$Y = 3.78 + 0.13\ W$	0.00^{ns}
Ca	$Y = -0.13 + 0.096\ W$	0.37
Mg	$Y = 0.16 + 0.10\ W$	0.23
Mn	$Y = -33.4 + 0.36\ W$	0.51
Fe	$Y = 251 - 0.00046\ W$	0.00^{ns}
B	$Y = 2.7 + 0.00007\ W$	0.22
Cu	$Y = 0.78 + 0.00051\ W$	0.22
Zn	$Y = 0.053 + 0.0016\ W$	0.39
Al	$Y = 126 + 0.0067\ W$	0.02^{ns}
Mo	$Y = 0.40 + 0.00015\ W$	0.14^{*}
Sr	$Y = 1.02 + 0.00087\ W$	0.19^{*}
Ba	$Y = 0.96 + 0.000074\ W$	0.01^{ns}

[+] Y = standing crop of nutrients in live shoots ($g\ m^{-2}$ for nutrients 1-5, $mg\ m^{-2}$ for nutrients 6-14). W = dry wt of live shoots in $g\ m^{-2}$.

[++] All regressions are highly significant ($P < 0.01$) unless otherwise indicated.

Table D24

Regression Equations for Standing Crop of Mineral
Nutrients in the Live Shoots of J. roemerianus

Nutrient	Regression Equation[+]	r^{2} [++]
N	$Y = -0.35 + 0.010\ W$	0.71
P	$Y = 0.047 + 0.0011\ W$	0.81
K	$Y = 0.038 + 0.0087\ W$	0.77
Ca	$Y = 0.15 + 0.00039\ W$	0.26
Mg	$Y = -0.26 + 0.0015\ W$	0.75
Mn	$Y = 2.6 + 0.073\ W$	0.70
Fe	$Y = -38.8 + 0.23\ W$	0.61
B	$Y = -1.71 + 0.019\ W$	0.83
Cu	$Y = 1.1 + 0.0057\ W$	0.41
Zn	$Y = 4.1 + 0.0085\ W$	0.36
Al	$Y = -11.5 + 0.20\ W$	0.42
Mo	$Y = -0.16 + 0.0018\ W$	0.59
Sr	$Y = 0.44 + 0.0067\ W$	0.54
Ba	$Y = 0.34 + 0.000038\ W$	0.00[ns]

[+]Y = standing crop of nutrients in live shoots ($g\ m^{-2}$ for nutrients 1-5, $mg\ m^{-2}$ for nutrients 6-14). Dry wt of live shoots in $g\ m^{-2}$.

[++]All regressions are highly significant ($P < 0.01$) unless otherwise indicated.

Table D25

Regression Equations for Standing Crop of Mineral
Nutrients in the Live Shoots of S. cynosuroides

Nutrient	Regression Equation	r^{2++}
N	$Y = 0.32 + 0.007\ W$	0.79
P	$Y = 0.09 + 0.00066\ W$	0.67
K	$Y = 0.39 + 0.0035\ W$	0.39
Ca	$Y = 0.038 + 0.0013\ W$	0.66
Mg	$Y = -0.0087 + 0.0017\ W$	0.83
Mn	$Y = 9.4 + 0.0082\ W$	0.55
Fe	$Y = 3.8 + 0.012\ W$	0.54
B	$Y = 0.34 + 0.00041\ W$	0.49
Cu	$Y = 0.22 + 0.00060\ W$	0.68
Zn	$Y = 0.10 + 0.0016\ W$	0.83
Al	$Y = 1.5 + 0.0023\ W$	0.11[ns]
Mo	$Y = 0.080 + 0.000089\ W$	0.66
Sr	$Y = 0.57 + 0.00081\ W$	0.69
Ba	$Y = 0.19 + 0.000027\ W$	0.03[ns]

[+] Y = standing crop of nutrients in live shoots ($g\ m^{-2}$ for nutrients
1-5, $mg\ m^{-2}$ for nutrients 6-14). W = dry wt of live shoots in
$g\ m^{-2}$.

[++] All regressions are highly significant ($P < 0.01$) unless otherwise
indicated.

Table D26

Regression Equations for Standing Crop of Mineral Nutrients in the Live Shoots of S. falcata

Nutrient	Regression Equation[+]	r^2 [++]
N	$Y = 0.34 + 0.017\ W$	0.95
P	$Y = 0.067 + 0.0030\ W$	0.87
K	$Y = 1.57 + 0.034\ W$	0.84
Ca	$Y = -0.088 + 0.0055\ W$	0.91
Mg	$Y = -0.030 + 0.0033\ W$	0.95
Mn	$Y = 7.8 + 0.24\ W$	0.87
Fe	$Y = 47.9 + 0.500\ W$	0.71
B	$Y = 0.33 + 0.027\ W$	0.95
Cu	$Y = 0.68 + 0.0094\ W$	0.77
Zn	$Y = 1.85 + 0.014\ W$	0.93
Al	$Y = 50.8 + 0.213\ W$	0.33
Mo	$Y = 0.20 + 0.002\ W$	0.62
Sr	$Y = 0.80 + 0.050\ W$	0.91
Ba	$Y = -1.89 + 0.067\ W$	0.77

[+] Y = standing crop of nutrients in live shoots (g m^{-2} for nutrients 1-5, mg m^{-2} for nutrients 6-14); W = dry wt of live shoots in g m^{-2}.

[++] All regressions are highly significant ($P < 0.01$) unless otherwise indicated.

Table D27

Regression Equations for Standing Crop of Mineral Nutrients in the Live Shoots of P. communis

Nutrient	Regression Equation	r^{2++}
N	$Y = 0.75 + 0.014\ W$	0.75
P	$Y = 0.12 + 0.0019\ W$	0.64
K	$Y = 1.38 + 0.014\ W$	0.61
Ca	$Y = -0.35 + 0.0021\ W$	0.81
Mg	$Y = -0.093 + 0.0014\ W$	0.40
Mn	$Y = -20.9 + 0.11\ W$	0.72
Fe	$Y = 27.3 + 0.13\ W$	0.24
B	$Y = -0.71 + 0.0078\ W$	0.87
Cu	$Y = -0.25 + 0.011\ W$	0.90
Zn	$Y = 0.73 + 0.033\ W$	0.87
Al	$Y = 10.8 + 0.046\ W$	0.29
Mo	$Y = -0.017 + 0.0012\ W$	0.61
Sr	$Y = -2.9 + 0.017\ W$	0.78
Ba	$Y = -1.32 + 0.011\ W$	0.77

[+] Y = standing crop of nutrients in live shoots ($g\ m^{-2}$ for nutrients 1-5, $mg\ m^{-2}$ for nutrients 6-14). W = dry wt of live shoots in $g\ m^{-2}$.

[++] All regressions are highly significant ($P < 0.01$) unless otherwise indicated.

Table D28

Regression Equations for Standing Crop of Mineral
Nutrients in the Live Shoots of S. patens

Nutrient	Regression Equation[+]	r^2[++]
N	$Y = 0.58 + 0.68\ W$	0.79
P	$Y = -0.069 + 0.097\ W$	0.82
K	$Y = -0.43 + 0.62\ W$	0.75
Ca	$Y = -0.10 + 0.091\ W$	0.68
Mg	$Y = 0.17 + 0.053\ W$	0.40
Mn	$Y = -14.8 + 0.084\ W$	0.82
Fe	$Y = -4.91 + 0.14\ W$	0.50
B	$Y = 0.22 + 0.0074\ W$	0.77
Cu	$Y = 0.35 + 0.0084\ W$	0.10[ns]
Zn	$Y = 0.33 + 0.012\ W$	0.51
Al	$Y = -37.3 + 0.16\ W$	0.68
Mo	$Y = -0.25 + 0.0018\ W$	0.74
Sr	$Y = 0.92 + 0.0070\ W$	0.47
Ba	$Y = -0.45 + 0.0080\ W$	0.49

[+] Y = standing crop of nutrients in live shoots ($g\ m^{-2}$ for nutrients
1-5, $mg\ m^{-2}$ for nutrients 6-14). W = dry wt of live shoots in
$g\ m^{-2}$.

[++] All regressions are highly significant ($P < 0.01$) unless otherwise
indicated.
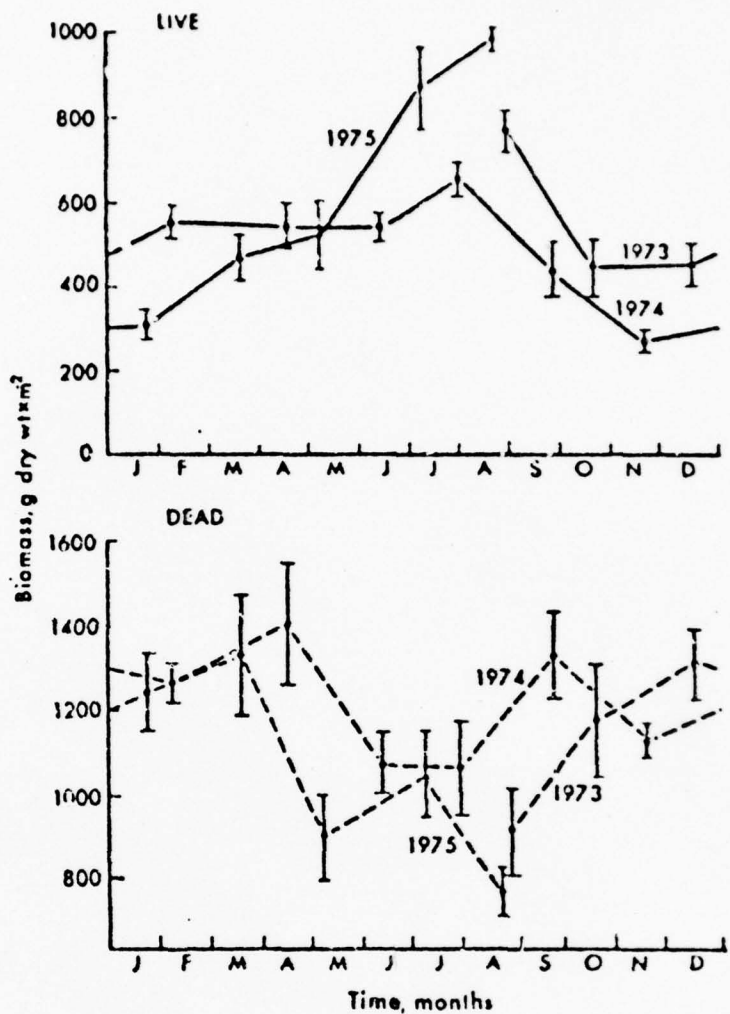
Figure D1. Comparison of seasonal nitrogen dynamics of S. falcata and S. patens.

APPENDIX E: SALINITY AND SEDIMENT DRAINAGE EFFECTS ON THE GROWTH
AND CARBON DIOXIDE EXCHANGE OF SELECTED SALT MARSH PLANT SPECIES

Introduction

1. The vegetation of the salt marshes is composed of a relatively
few species of grasses and sedges that occupy fairly distinct zones
(Nichols 1920; Wells 1928; Penfound and Hathaway 1938; Hinde 1954; and
Kurtz and Wagner 1957).* The low species diversity and high productivity
of this habitat are indicative of a stressed ecosystem (Odum 1971).
Most research on this subject indicates that the stress factors are
edaphic and hydrologic rather than biotic. There is less agreement as
to what these factors are. Penfound (1952) has summarized those he
considered to affect plant community distribution in southern swamps and
marshes. However, literature pertaining to specific stress factors in
the salt marsh is scanty. Those stress factors most commonly thought to
determine plant distribution in salt marshes are salinity and flooding
conditions. The effects of high salinity on plant growth are osmotic,
toxic, and competitive with nutrients.

2. Early studies of the effects of salinity on the growth and
distribution of salt marsh species were based on field studies (Johnson
and York 1915; Taylor 1939; Reed 1947; Jackson 1952). In general these
reports indicated that, of the major grass species inhabiting the salt
marsh, Spartina alterniflora was the most tolerant to salinity. Mooring
et al. (1971) showed that seedlings of S. alterniflora grew taller in

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* References at end of this appendix.

E1

0.5 to 1.0 percent NaCl than in 0 percent. Best growth as measured by
increase in dry weight occurred in concentrations of 0.5 percent NaCl.
Greenhouse studies by Adams (1963) indicated that Distichlis spicata
could tolerate higher NaCl concentration than S. alterniflora or Juncus
roemerianus. Seneca (1972) showed that Spartina patens had the highest
tolerance to salt although best growth took place in fresh water; however,
neither S. alterniflora nor D. spicata were included in this study.
Phleger (1971) has shown that Spartina foliosa grew best in fresh water.
In contrast, Webb (1966) showed that Salicornia bigelovii seedlings
showed best growth at 10 g ℓ NaCl, while plants grown in fresh water
died. Gale et al. (1970) showed that the effect of salinity on the
growth of Atriplex halimus depended on humidity. With high humidity,
increasing the salinity of the medium brought about a reduction in
growth; however, at low humidity, growth was optimum at 120 mM ℓ^{-1} NaCl.
Black (1960) showed a reduction in dry matter yields of roots and shoots
of Atriplex vinian with increasing salinity. Greenway (1968) showed
that optimum growth of Atriplex numularia occurred at 100 mM ℓ^{-1} NaCl.
Ashby and Beadle (1957) grew Atriplex inflata and A. numularia in differ-
ent salts and showed increased growth in both species to added salt, the
greatest response being to NaCl, then to KCl, and lastly to Na_2SO_4.
Similar results were obtained by Mozafar et al. (1970) for A. halimus.

Salinity

3. Salinity affects not only the overall growth of the whole
plant but also the differential growth rate of its organs. Here again,
the effect depends on the species. According to Troughton (1960) and

E2

Stocker (1960), water stress favors an increase in the root:shoot ratio. However, in a later study Troughton (1967) showed that high salinity reduced root growth somewhat more than it did shoot growth, concluding that the effects of high salinity are different from the effects of water stress per se. High salinity reduced growth of roots and shoots to the same degree in _Limonium vulgare_ (Boorman 1968). Repp (1939), as cited in Waisel (1972), has given values of shoot:root ratios for various halophytes indicative of high ratios. However, many salt marsh species were not included.

4. The literature on the effect of salinity on the growth of agriculturally economic species, particularly of forage crops, is more abundant (Greenway 1962; Greenway and Rogers 1963; Troughton 1967; Elzam and Epstein 1969). Waisel (1972) has given schematic representations of the effects of salinity on the growth curve of glycophytes and halophytes. The growth of a typical halophyte increased with salinity, reached a maximum at some concentration, and declined with further increases in salinity. The growth of glycophytes decreased linearly with increasing salinity in the medium. Waisel included a third category, semihalophytes, which showed a growth response intermediate to halophytes and glycophytes.

Flooding

5. Literature dealing with the effect of flooding on plant growth is scarce. Flooding conditions create an anaerobic environment around the root system that few species can tolerate. Plants adapted to live under flooded sediment must develop some mechanism to provide for metabolism of roots growing in an oxygen-depleted environment. Daubenmire (1974)

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mentioned that these adaptions are morphologic or physiologic. Alberda (1953) mentioned three forms of adaption to a reduced medium around the roots of plants: (1) ability to transport oxygen (O_2) from shoots to roots, (2) root tolerance to low O_2 concentration, and (3) development of specialized roots or organs to obtain O_2 from the surface and transport it to roots below. Laing (1940) reported that rhizomes of several aquatic species survived under anaerobic conditions without any signs of injury, concluding that these species respire anaerobically under natural conditions, at least part of the time.

6. Under anaerobic reduced conditions, the availability and chemical form of many elements are affected (Turner and Patrick 1968), making some elements limiting, while others may reach toxic concentrations.

7. Despite the fact that salinity and flooding have been recognized for a long time as factors affecting the growth of plants in the salt marsh, little is known about the mechanism of adaption by the plants. This study concerns the effect of salinity and flooding conditions on several growth parameters of salt marsh plant species.

Materials and Methods

Plant material

8. Plants were grown from seeds collected in the Barataria Bay area in south Louisiana. Seeds were spread in trays on a mixture of sand and peat or on sediment brought from the field, and the trays were covered and placed in a dark growth chamber at 30°C. After 5 to 7 days, the trays were taken out of the dark and placed in a growth chamber under a 16-hour photoperiod at 19000 lux and a thermoperiod of 20°C dark,

30°C light. When the seedlings reached the 2- to 3-leaf state, they were transferred to the different treatments as described below.

Salinity studies

9. The seedlings were washed free of sand or sediment and transferred to half-gallon polyethylene buckets containing a modified Hoaglands solution (Johnson et al. 1957). Ten seedlings were inserted through perforated holes on the top of the containers and supported with a strip of Permagum (Virginia Chemicals Inc.). The containers were placed in a growth chamber under the same light and temperature conditions as described above, and the seedlings were allowed to grow for 1 week before the salt treatment was applied. No attempt was made to aerate the nutrient solution since these species grow under anaerobic conditions in the marsh, and earlier tests (Gosselink 1970) showed no response to aeration. Sodium chloride was added to the nutrient solution, starting with 1 g ℓ^{-1} and doubling the concentration every 3 or 4 days until the final concentration was attained. The nutrient solution was changed every time salt was added, and the plants were rinsed with tap water to remove salt accumulated on the leaves. The plants were allowed to grow for a period of 21 days after the final salt increment to the medium, during which time the solution was changed twice a week. On the twenty-first day, the plants were harvested and washed with tap water; the length of the culm measured; and the fresh weight determined. The tissue was dried at 70°C in a forced draft oven for 2 weeks before dry weight determinations were made.

E5

Drainage condition study

10. Seedlings were transplanted to half-gallon plastic pots containing a mixture of 50 percent river sand and 50 percent sediment (very fine organic-rich silt from the Barataria Bay area). One seedling was transplanted to each container, ten drained and ten flooded. The salinity of the sand-sediment mixture ranged from 2 to 5 g ℓ^{-1}. A platinum (Pt) electrode was inserted to a depth of 3 in. in the sediment in each of three drained and flooded pots to monitor the redox potential (Eh) of the substrate. The pots were watered daily with deionized water and once a week with Hoagland's solution in which NH_4NO_3 was the source of nitrogen (N). In order to prevent loss of nutrients from drained pots, a cup was placed under the pots and this water recycled. The seedlings were grown in the greenhouse under natural light intensity from 16 February to 23 April 1976, when all the plants were harvested and washed with tap water, and fresh weight and culm length determined. The plants were dried and weighed as described earlier.

Carbon dioxide exchange determinations

11. Potted plants were enclosed in a cylindrical Plexiglas cuvette, 30 cm in diameter by 77 cm high and carbon dioxide (CO_2) exchange measured as described in Appendix G. The cuvette was placed under a metal halide lamp located in a darkened room such that the light intensity at the top of the plant was about 44000 lux. The CO_2 content of air entering and exiting the cuvette was recorded, switching from one to the other until three consecutive readings had reached a steady state. After CO_2 exchange in the light had been determined, CO_2 evolution in the dark was

E6

measured. (The system usually took about 30 minutes to reach a new steady state.) After completion of CO_2 exchange determinations, the culms were harvested and the leaf blade area determined with an electronic leaf-area meter.

Results

Effect of NaCl on growth parameters

12. The effects of salt on the dry weight accumulation of S. alterniflora are summarized in Table E1. The NaCl in the nutrient medium reduced the dry weight at concentrations of 16 g ℓ^{-1} or higher. However, at lower salt concentrations NaCl did not appear to affect dry weight. Sixteen g ℓ^{-1} of NaCl reduced the dry weight to about 55 percent of that of plants grown without salt. Doubling the salt concentration to 32 g ℓ^{-1} further reduced the dry weight to about 24 percent of that of plants grown in fresh water. High salinity had a differential effect on the growth of shoots and roots. At 16 g ℓ^{-1} NaCl reduced the mean dry weight of roots to about 71 percent, while the mean dry weight of shoots was 50 percent of that of plants grown in fresh water. Similar results were obtained with plants grown at 32 g ℓ^{-1} NaCl. The differential effect of salinity on root and shoot growth is shown in the root:shoot ratio. Plants lacking NaCl in the root medium showed a low root to shoot ratio compared to plants grown in the presence of NaCl. The dry weight to fresh weight ratio was not influenced by salt concentrations up to 16 g ℓ^{-1} but increased at 32 g ℓ^{-1}.

13. The effect of salinity on the length of the culm is shown in Figure E1. High NaCl reduced culm length significantly. At 16 g ℓ^{-1}

E7

the culm length was about 58 percent of that of plants grown in nutrient solution without salt. At 32 g l^{-1}, it was about 45 percent of the control. Salinity between 2 and 8 g l^{-1} reduced the culm length slightly.

14. The effect of substrate NaCl on the accumulation of dry weight in Spartina cynosuroides is summarized in Table E2. Low salinities (1 to 4 g l^{-1}) appear to have very little effect on the dry weight of this species. However, salinities of 16 g l^{-1} or above reduced the dry weight significantly. The mean dry weight of plants grown with 16 and 32 g l^{-1} of NaCl in the medium was about 47 and 19 percent, respectively, of that of plants grown in fresh water. There is an indication of growth inhibition at 4 and 8 g l^{-1} also. Shoot dry weight was affected to a greater degree than root dry weight. At 16 g l^{-1} NaCl the mean root dry weight was 54 percent of roots of freshwater plants, while mean shoot dry weight was 45 percent. The differential inhibition of roots and shoots is even greater at 32 g l^{-1} NaCl, where the mean dry weight of roots was 49 percent of freshwater roots, while the mean shoot dry weight was 18 percent of freshwater shoots. As a result the root: shoot ratio for plants grown in fresh water was lower than for plants grown in the presence of NaCl in the medium. There is also a trend toward an increased dry weight to fresh weight ration.

15. The effect of salinity on culm length in S. cynosuroides is shown in Figure E2. Low salinities had little effect on the length of the culm; however, salinities of 16 and 32 g l^{-1} significantly reduced the culm length.

E8

16. A summary of the effect of substrate NaCl concentration on the dry weight accumulation in $\underline{D. \text{ spicata}}$ is presented in Table E3. The NaCl at all concentrations, except 32 g ℓ^{-1}, failed to affect the accumulation of dry weight compared to control plants grown in fresh nutrient media. Indeed, plants grown in NaCl at 1 to 16 g ℓ^{-1} are slightly stimulated. The mean dry weight of plants grown in 32 g ℓ^{-1} NaCl was 66 percent of that of plants grown in freshwater nutrient medium. The dry weight of roots increased with increased salinity up to 16 g ℓ^{-1}. At 32 g ℓ^{-1} NaCl the root dry weight was less, 81 percent of the roots of control plants, while the dry weight of shoots was considerably lower, 62 percent of the dry weight of shoots of plants grown in fresh water. The differential effect of salinity on the growth of roots and shoots is indicated by the root:shoot ratio as salinity in the root medium was increased. It appears that salt concentrations above 2 g ℓ^{-1} favored root growth over shoot growth. No trend was evident in succulence as indicated by the dry weight to fresh weight ratio.

Effect of sediment drainage conditions
on growth parameters

17. Drained vs. flooded sediment conditions had little effect on the accumulation of dry weight in $\underline{S. \text{ alterniflora}}$ plants (Figure E3). However, under drained conditions the dry weight accumulation by roots (roots and rhizomes) was significantly lower than under flooded conditions. Shoot dry weight accumulation was not significantly different between drained and flooded plants. Drainage conditions did not have any significance in the length of the culm (Figure E4). The root:shoot ratio was

E9

different between drained and flooded plants: 0.44 and 0.87 percent, respectively.

18. Figures E5 and E6 show that drainage conditions of the substrate affected the growth of S. cynosuroides. Under flooded conditions all parameters of growth were reduced although the root:shoot ratio was unaffected (0.41 for flooded plants, 0.39 for drained plants).

Carbon dioxide exchange

19. Figure E7 shows the rate of CO_2 uptake as a function of cuvette CO_2 concentration by S. alterniflora under full sunlight ($\sim$ 96000 lux). The net photosynthetic rate falls off sharply below about 180 ppm CO_2 in the cuvette. Above 200 ppm it is relatively constant. Measurements of photosynthesis reported below were always made with cuvette CO_2 concentrations greater than 250 ppm.

20. The contribution of the leaf sheath to the total CO_2 uptake rate was monitored and found to be insignificant (see Appendix G).

21. Table E4 summarizes the patterns of CO_2 exchange by S. alterniflora as affected by substrate drainage conditions. There was wide variation among replicate plants in both drained and flooded sediments. The values given for respiration were based on the dry weight of the whole plant, although it was not possible to separate the contribution to respiration by the sediment. The mean value of Eh over a 2-week period is also included. The drained soils showed an oxidized environment around the root system, while the flooded sediments showed a reduced environment around the root system (around -100 mV).

22. The patterns of CO_2 exchange by S. cynosuroides are summarized

E10

in Table E5. The rate of CO_2 absorption by plants in drained sediments was slightly higher than in flooded soils although, again, there was wide variation among replicate samples, particularly among plants grown under drained conditions. For both species the respiration of the whole community (plant and sediment) was higher under drained conditions than under flooded conditions.

Discussion

23. The salt concentration tests indicated that D. spicata was the most salt tolerant of the three species tested, followed by S. alterniflora and S. cynosuroides. Distichlis spicata showed a slight increase in dry weight over control plants at all salt concentrations, except 32 g l^{-1}. Spartina alterniflora and S. cynosuroides showed very little change in dry weight at low salinities (1 and 2 g l^{-1}). At medium salinities (4 to 8 g l^{-1}), a definite decrease in dry weight was shown by S. alterniflora and S. cynosuroides but not by D. spicata. At 16 and 32 g l^{-1} the dry weight of S. alterniflora was 55 and 20 percent of control plants, respectively, while the dry weight of S. cynosuroides was slightly less, 47 and 19 percent of control plants. However, the dry weight of D. spicata grown in a solution with 16 g l^{-1} NaCl was greater than control plants, and at 32 g l^{-1} NaCl, it was 66 percent of control plants. These results support the findings published by Adams (1963) showing D. spicata to be more salt tolerant than S. alterniflora.

24. The effects of salinity on the growth of roots and shoots showed similar trends. The species arranged themselves in the same order of tolerance to salinity by roots and shoots. However, the

E11

inhibitory effect of salinity on the accumulation of dry weight in S. alterniflora and S. cynosuroides was greater in shoots than it was in roots. In D. spicata, although salinity did not inhibit growth except at 32 g ℓ^{-1}, the shoot growth was less than root growth on a percent of control basis. The differential effect of salinity on the growth of roots and shoots is indicated in the root:shoot ratio in Tables E1-E3. In all three species the root:shoot ratio increased, particularly at salinities of 16 and 32 g ℓ^{-1}.

25. There was no evidence of increased succulence brought about by increasing salinity in the medium. The increase in the dry weight:fresh weight ratio with increasing salinity in S. alterniflora and S. cynosuroides was probably due to salt accumulation in the tissue.

26. The effect of salinity on the length of the culm of S. alterniflora and S. cynosuroides shown in Figures E1 and E2 further supports the relative tolerance to salt in these two species. The reduction in culm length was greater in S. cynosuroides than in S. alterniflora. Culm length values for D. spicata were not included because it was not possible to distinguish the culm of the original plant from the culm of tillers.

27. While salinity reduced the growth of S. alterniflora, flooding the sediment did not affect the shoot dry weight (Figure E3) nor the length of the culm. On the contrary, root growth under drained substrate conditions was significantly less than under flooded conditions. The total dry weight of the plants grown in drained sediments was slightly less than that of plants grown in flooded soil. It appeared that S. alterniflora growing on high ground may have a lower root mass than

E12

plants growing under at least some flooding. In contrast to S. alterniflora, both dry weight and culm length of S. cynosuroides in flooded sediments was reduced. This indicates that S. cynosuroides is less tolerant to continuous flooding than S. alterniflora. However, these plants were grown under drained and flooded conditions for a period of 2 months only, and perhaps this experiment should be carried out in larger containers with longer growth periods. These results tend to explain partially the distribution of these two species in the marsh. While S. alterniflora occupies the low marsh, S. cynosuroides is usually found growing on the high marsh and along levees and road banks.

28. While accumulation of dry weight is a good indicator of the growth of a plant, it yields data in which the plant response to a given factor is integrated over a relatively long time period. The response of a plant to a given imposed factor may vary with the age of the plant. Moreover, plants, like any other organism, have the ability to adjust to changes in the environment. For example, plants increase their osmotic potential in response to an increase in the osmotic potential of the medium (Bernstein 1961). Any adjustment of a plant to a particular environmental factor does not become apparent in dry weight accumulation studies. Waisel (1972) has indicated that dry matter production is reduced under conditions of low water potential due to reduced photosynthesis and increased respiration. While this may be true in general, different species may respond differently. Gas exchange techniques yield data in which the response of a plant to manipulation of environmental factors can be determined almost immediately. Carbon dioxide exchange by S. alterniflora and S. cynosuroides under flooded and

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drained substrate conditions is summarized in Tables E4 and E5. Total CO_2 fixation by S. alterniflora was not significantly different in drained and flooded plants; however, it was slightly higher in S. cynosuroides grown under drained sediment conditions. The photosynthetic rates are calculated on a leaf area basis since the contribution of the algal community on the soil surface could not be detected upon removal of the culms. The contribution of the leaf sheath to the total photosynthesis was also negligible. Since it was not possible to separate the respiration of the plant from that of soil microorganisms, the values given include microbial respiration. The respiration rate under drained sediment conditions was greater in both species. The difference might have been due to increased O_2 supply to both roots and soil microorganisms under drained conditions.

29. The Eh of the flooded sediment in S. cynosuroides was slightly lower than in S. alterniflora. This may be an indication that S. alterniflora has a more efficient mechanism of O_2 transport to the roots. Teal and Kanwisher (1966) have reported an O_2 diffusion capacity in S. alterniflora from one third to twice the amount needed by the roots, and this O_2 may be available to the sediment.

30. In summary, D. spicata tolerates high salinity better than S. alterniflora. Based on these results and the results of Adams (1963) and Mooring et al. (1971), it can be concluded that salinity is not the factor preventing D. spicata from inhabiting the low marsh along with S. alterniflora. Spartina alterniflora on the other hand, is slightly more salt tolerant than S. cynosuroides. This slight difference in salinity tolerance may not be the principal factor restricting the latter species

E14

to the high marsh. Flooding conditions of the substrate appear to be more significant as a determining factor, as indicated by growth data and gas exchange under flooded and drained conditions. The data obtained in this study were consistent with field observations on the distribution of _S_. _cynosuroides_ in the marsh.

31. The results and conclusions presented in this appendix are incomplete and point to the need for continued research in order to clarify the factors involved in the distribution of plant communities in the salt marsh.

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Table E1

Effects of NaCl on the Growth of *S. alterniflora*

NaCl Conc. g l⁻¹	Total Plant g dry wt	g fresh wt	Dry Wt to Fresh Wt Ratio	Root g dry wt	Shoot g dry wt	Root-to-Shoot Ratio
0	0.98 ± 0.27	5.41 ± 1.61	0.18	0.26 ± 0.06	0.72 ± 0.21	0.36
1	1.04 ± 0.30	5.84 ± 1.82	0.18	0.34 ± 0.11	0.70 ± 0.19	0.49
2	0.75 ± 0.16	3.52 ± 0.91	0.21	0.24 ± 0.07	0.51 ± 0.11	0.48
4	0.85 ± 0.28	4.05 ± 1.44	0.21	0.27 ± 0.11	0.57 ± 0.18	0.48
8	0.84 ± 0.18	3.85 ± 0.97	0.22	0.28 ± 0.07	0.56 ± 0.12	0.49
16	0.54 ± 0.16	2.84 ± 0.86	0.19	0.18 ± 0.04	3.36 ± 0.12	0.51
32	0.20 ± 0.07	0.77 ± 0.29	0.26	0.07 ± 0.03	0.14 ± 0.05	0.49

Note: The mean ± standard deviation is for 10 replicate plants per treatment.

Table E2

Effects of NaCl on the Growth of S. cynosuroides

| NaCl Conc. g l-1 | Total Plant | | Dry Wt to Fresh Wt Ratio | Root | Shoot | Root-to-Shoot Ratio |
	g dry wt	g fresh wt		g dry wt	g dry wt	
0	1.89 ± 0.65	10.59 ± 3.70	0.18	0.37 ± 0.12	1.52 ± 0.54	0.25
1	2.35 ± 1.16	12.87 ± 6.11	0.18	0.51 ± 0.26	1.84 ± 0.93	0.28
2	2.15 ± 0.43	11.74 ± 2.09	0.18	0.45 ± 0.10	1.71 ± 0.33	0.26
4	1.57 ± 0.63	8.82 ± 3.31	0.18	0.32 ± 0.14	1.26 ± 0.49	0.25
8	1.41 ± 0.62	7.31 ± 2.87	0.19	0.33 ± 0.17	1.09 ± 0.45	0.30
16	0.89 ± 0.34	4.30 ± 1.59	0.21	0.20 ± 0.08	0.69 ± 0.26	0.29
32	0.36 ± 0.11	1.46 ± 0.45	0.25	0.18 ± 0.12	0.28 ± 0.09	0.64

Note: The mean ± standard deviation is for 10 replicate plants per treatment.

Table E3

Effects of NaCl on the Growth of D. spicata

NaCl Conc. g l^{-1}	Total Plant		Dry Wt to Fresh Wt Ratio	Root	Shoot	Root-to-Shoot Ratio
	g dry wt	g fresh wt		g dry wt	g dry wt	
0	0.16 ± 0.03	0.72 ± 0.16	0.22	0.031 ± 0.012	0.125 ± 0.022	0.25
1	0.16 ± 0.05	0.83 ± 0.40	0.19	0.027 ± 0.008	0.132 ± 0.047	0.20
2	0.18 ± 0.05	0.85 ± 0.38	0.21	0.029 ± 0.009	0.149 ± 0.038	0.20
4	0.17 ± 0.05	0.84 ± 0.36	0.20	0.036 ± 0.016	0.133 ± 0.039	0.27
8	0.16 ± 0.07	0.70 ± 0.33	0.23	0.035 ± 0.014	0.127 ± 0.058	0.28
16	0.17 ± 0.04	0.73 ± 0.28	0.24	0.040 ± 0.009	0.133 ± 0.034	0.30
32	0.10 ± 0.02	0.64 ± 0.29	0.16	0.025 ± 0.004	0.077 ± 0.014	0.33

Note: The mean ± standard deviation is for 10 replicate plants per treatment.

Table 24

Carbon Dioxide Exchange by S. alterniflora Grown in Flooded or Drained Sediments

Plant No.	Flooded Sediment				Drained Sediment			
	Eh Sediment (mV)	Gross Photosynthesis µl(cm² min)⁻¹	Respiration µl(g dr wt min)⁻¹	Net Photosynthesis µl(cm² min)⁻¹	Mean Sediment (mV)	Gross Photosynthesis µl(cm² min)⁻¹	Respiration µl(g dr wt min)⁻¹	Net Photosynthesis µl(cm² min)⁻¹
1	-110 ± 31	0.79	10.55	0.53	+568 ± 110	0.64	29.11	0.37
2	-145 ± 38	1.64	11.12	1.18	+481 ± 167	0.92	20.50	0.70
3	-125 ± 25	1.09	7.58	0.92	+574 ± 113	1.07	38.51	0.63
Mean		1.10 ± 0.32	9.75 ± 1.90	0.87 ± 0.32		0.83 ± 0.19	29.37 ± 9.00	0.56 ± 0.17

Note: Cuvette air temperature was maintained at 30°C ± 1°C. Sediment temperature was monitored during CO_2 exchange determinations and ranged from 25°C at the beginning of gas exchange measurements to 30°C at the end. Means are shown with standard deviations.

Table 25

Carbon Dioxide Exchange by S. cynosuroides Grown in Flooded or Drained Sediments

Plant No.	Flooded Sediment				Drained Sediment			
	Sediment (mV)	Gross Photosynthesis µl(cm² min)⁻¹	Respiration µl(g dr wt min)⁻¹	Net Photosynthesis µl(cm² min)⁻¹	Mean Sediment (mV)	Gross Photosynthesis µl(cm² min)⁻¹	Respiration µl(g dr wt min)⁻¹	Net Photosynthesis µl(cm² min)⁻¹
1	-170 ± 28	1.25	19.36	0.84	+525 ± 99	1.64	21.92	1.20
2	-209 ± 25	1.38	15.62	0.99	+535 ± 76	2.00	32.95	1.07
3	-129 ± 56	1.35	11.73	0.96	+546 ± 80	1.36	19.32	0.99
Mean		1.32 ± 0.06	15.58 ± 3.81	0.93 ± 0.07		1.66 ± 0.12	24.73 ± 7.23	1.08 ± 0.10

Note: Cuvette air temperature was maintained at 30°C ± 1°C. Sediment temperature was monitored during CO_2 exchange determinations and ranged from 25°C at the beginning of gas exchange measurements to 30°C at the end. Means are shown with standard deviations.

Figure E1. Effects of salt concentration in the root medium on S. alterniflora culm length.
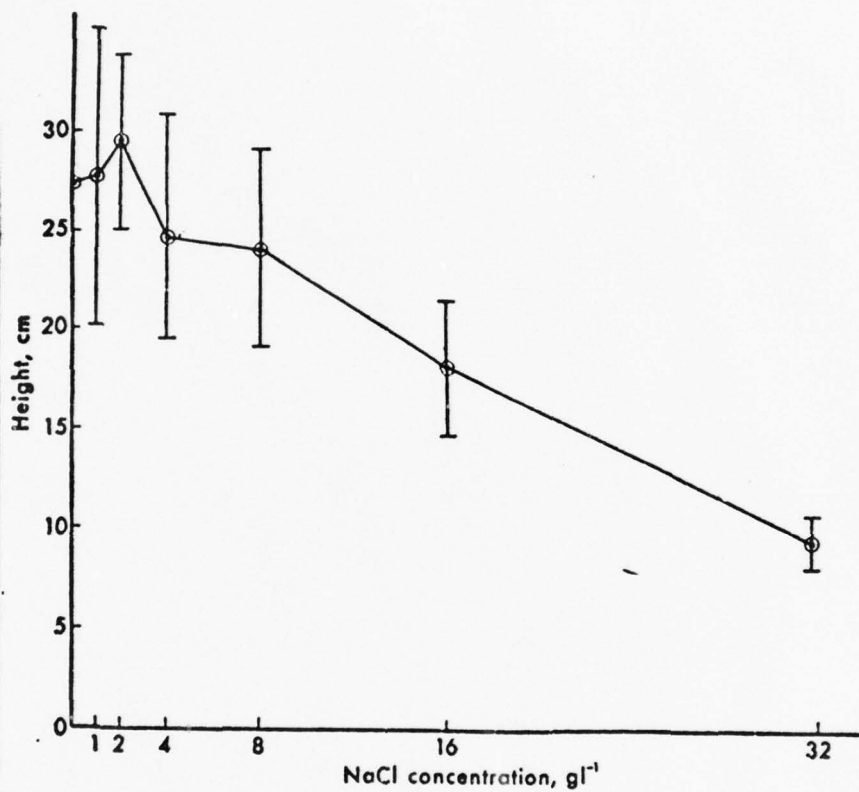
Figure E2.   Effect of salinity on culm length in S. cynosuroides.
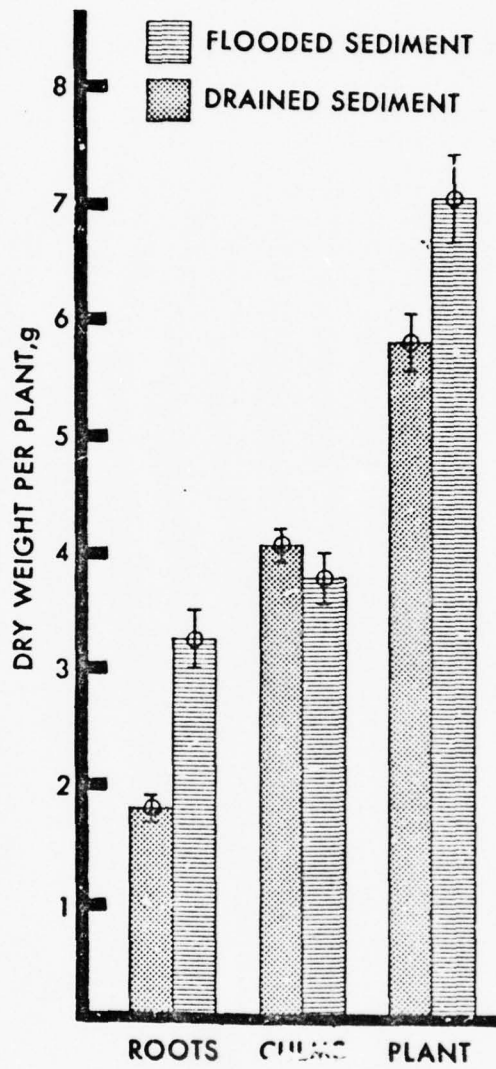
Figure E3. Effects of drained vs. flooded sediment conditions on dry weight in S. alterniflora.
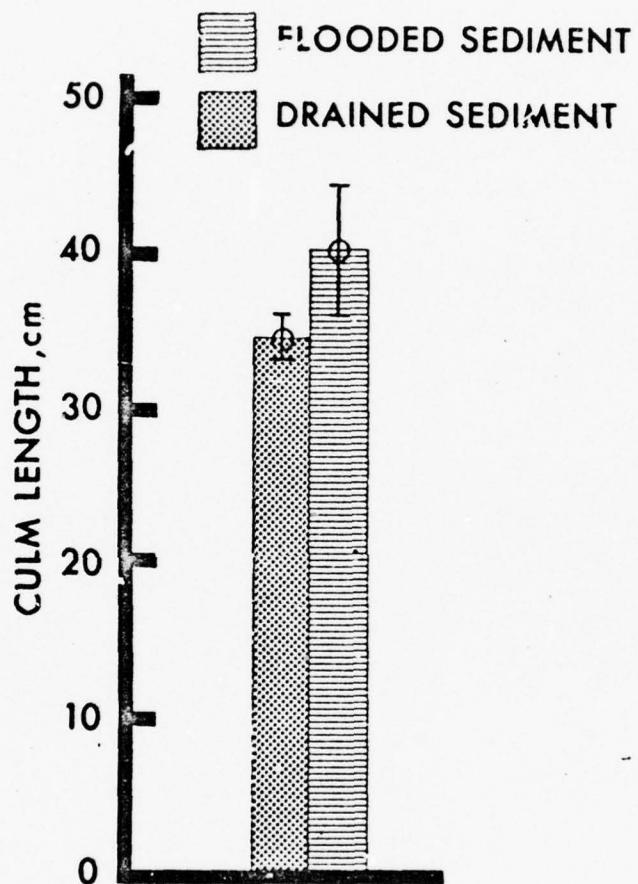
Figure E4. Effects of drainage conditions on culm lengths of S. alterniflora.
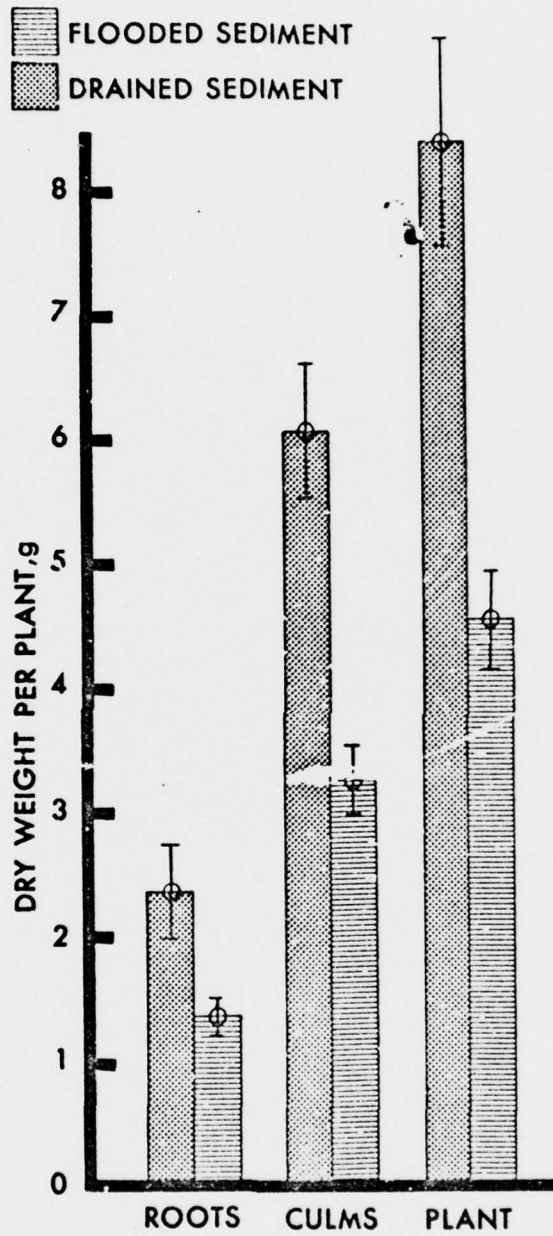
Figure E5. Effects of drained vs. flooded sediment conditions
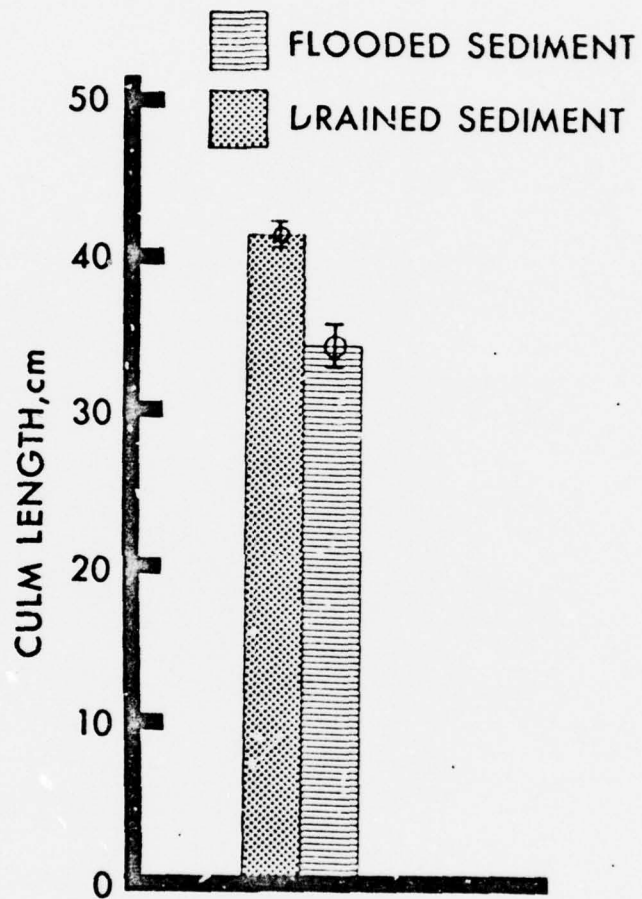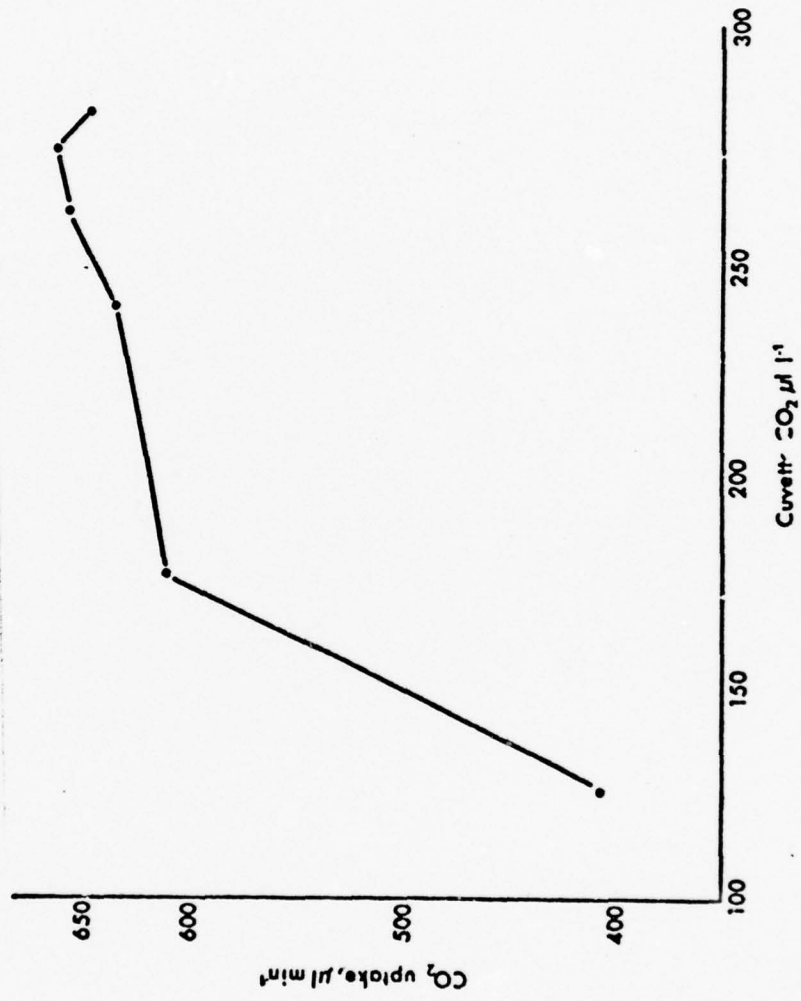on dry weight in S. cynosuroides.

Figure E6. Effects of drainage conditions on culm lengths of S. cynosuroides.

Figure E7. Net photosynthesis by *S. alterniflora* as a function of cuvette CO_2 concentration.

APPENDIX F: EFFECT OF SALINITY ON THE RATE OF RUBIDIUM ABSORPTION
BY SPARTINA ALTERNIFLORA

Introduction

1. As indicated by the volume of recent literature, much attention has been focused lately on the ecological value of the salt marsh (Reimold and Queen 1974).* This habitat is characterized by a low species diversity and high productivity (Odum 1971). The relatively few species of vascular plants that inhabit the salt marsh do so because they are capable of tolerating the high prevailing salinity levels. Salinity has been shown to reduce the growth of many of the species of vascular plants found in the salt marsh (Appendix E; Phleger 1971); yet the mechanism that enables them to survive is not known. It is apparent, however, that salt is not required for growth and survival of many of these species since they grow just as well in fresh water (Appendix E; Adams 1963; Taylor 1939). The mechanism developed by mangroves to withstand an identical stress is better known and involves either the exclusion of sodium (Na) from the root or excretion of salt from leaves by salt glands (Scholander et al. 1962). Avicennia nitida, a species that does not exclude salt, absorbs potassium (K) preferentially over Na (Rains and Epstein 1967).

2. In normal salt-sensitive crop plants, the presence of high solute concentrations in the root medium has been shown to reduce the absorption of nutrients (Greenway et al. 1968; Smith et al. 1973; Rains

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* References listed at end of this appendix.

F1

1972). Calcium (Ca) plays a major role in protecting such plants by increasing their salt tolerance. LaHaye and Epstein (1969), for instance, reported that in the presence of Ca, bean seedlings could tolerate higher concentrations of salt in the root medium, and Elzam and Epstein (1969) found the same relationship was true for two species of Agropyron differing in salt sensitivity. This may occur because Ca reduces the Na influx. For instance, Osmund (1968) showed a reduced Na influx and K efflux by leaf slices of Atriplex spongiosa in the presence of calcium chloride ($CaCl_2$). Certainly the importance of Ca in membrane integrity, especially as related to mineral ion absorption, is well documented (Epstein 1961).

3. In another study (Appendix E), the effects of salinity on the growth of several salt marsh grasses were examined. However, in this type of study the response of the plant to salinity is integrated over a period of weeks and not much is revealed concerning the mechanisms responsible for the observed patterns of growth. In order to elucidate the adaptive mechanisms to high salinity developed by species inhabiting the salt marsh, short-term studies of ion absorption may give an insight into the dynamic response to salinity stress. The advantages and techniques of short-term tests of ion absorption in plant tissue have been discussed by Epstein et al. (1963). Spartina alterniflora was chosen as the experimental material because it is the most abundant species along the gulf and east coasts of the United States and because more is known about its ecology than that of other salt marsh species.

F2

Materials and Methods

Seed germination

4. Plants were grown from seed as follows: Seeds were spread on the surface of sand or sediment brought from the field and allowed to germinate in the dark at 30°C. After a week, the trays were moved to a growth chamber with a photoperiod of 16 hours at an intensity of 17000 lux, and a temperature of 30°C, and an 8-hour dark period at 20°C. After the plants were about 2 in. tall (approximately 3 weeks from germination), they were washed free of sand or sediment and transferred to 2-ℓ black polyethyelene containers with half strength Hoagland's solution as modified by Johnson et al. (1957). Iron (Fe) was supplied at a concentration of 5 mg Fe ℓ^{-1}. Plants (ten per container) inserted through holes in the top of the containers were supported by a strip of Permagum (Virginia Chemicals Inc.) pressed gently around the stem. After a week of acclimation, the different treatments were started as described below.

Ion uptake studies with excised roots

5. After being transferred to a nutrient solution, the seedlings were grown with or without salt (as determined by the subsequent test treatment) for a period of 2 weeks, at which time root growth was abundant. The solution was then changed to 2 mM ℓ^{-1} CaCl$_2$ (again with or without salt as the treatment dictated) and grown with frequent changes to lower the nutrient level in the root tissue. After 1 week in this solution, 2-cm apical segments of roots were cut and used immediately to determine short-term absorption rates. The technique used was

F3

that of Epstein et al. (1963), except that a fine-mesh nylon material was used to hold the tissue during the experimental procedure. The basic procedure consisted of allowing the tissue to absorb rubidium (Rb) from 400 ml of a solution of rubidium chloride (RbCl) labelled with ^{86}Rb and $CaCl_2$ of known concentration for 30 minutes at 30°C, after which time absorption was discontinued by three 1-minute rinses with a cold (3°C) solution consisting of 2 mM ℓ^{-1} $CaCl_2$ and 5 mM ℓ^{-1} potassium chloride (KCl). Each sample was allowed to desorb for a further 30-minute period in a solution of identical composition and temperature as the rinse; after which the samples were rinsed with distilled water, placed in aluminum (Al) planchets, and ashed at 500°C. The activity of each sample was determined with a Beckman windowless gas flow counting system. Superimposed on this general method were various modifications that are described below.

Ion uptake by intact seedlings

6. The seedlings were grown in nutrient solution in polyethelene containers as described before. They were divided into two groups. To one group, 10 g ℓ^{-1} NaCl was added regularly every time the solution was changed. The other group was grown in nutrient solution only. The seedlings were allowed to grow 2 weeks before the solution was changed to 2 mM ℓ^{-1} $CaCl_2$ plus 10 g ℓ^{-1} NaCl. After 3 days in this solution the experiment was carried out. At this time individual seedlings were rinsed with distilled water and suspended on a glass rod over a 2-mM ℓ^{-1} $CaCl_2$ solution with the roots submerged to within 1 cm of the base of the stem until five seedlings were mounted. The seedlings were

F4

transferred to an absorption solution consisting of 1 mM l^{-1} RbCl labelled with ^{86}Rb and 2 mM l^{-1} CaCl$_2$. To this basic absorption solution, 10 g l^{-1} NaCl was added as needed, according to experimental design. The temperature of the absorption solution was maintained at 30°C by a water bath and the seedlings allowed to absorb Rb for 4 hours under room illumination. After absorption, the plants were given three 1-minute rinses in a cold (3°C) solution consisting of 2 mM l^{-1} CaCl$_2$ plus 5 mM l^{-1} KCl to remove Rb adsorbed to the root surface. The plants were separated into roots and shoots, and the fresh weight of the roots determined. The roots and shoots were packed lightly in separate test tubes, and the radioactivity determined by a sodium iodide (NaI) crystal gamma scintillation system.

7. The results represent values obtained from single experiments. Each experiment was performed two or more times, and all data obtained are consistent with the following results.

Results and Discussion

8. The effect of increasing Rb concentration on the rate of Rb absorption, shown in Figure F1, indicates a dual isotherm of ion uptake similar to that established for other species (Epstein 1972). The range of the first plateau is somewhat shorter than in mangroves (Rains and Epstein 1967). The high concentration isotherm (>0.35 mM l^{-1} Rb) does not saturate as rapidly as the first isotherm. In succeeding experiments two concentrations of Rb were used (0.1 and 1 mM Rb), one on each of the plateaus of Figure F1. These test the two absorption mechanisms identified in the literature (Welch and Epstein 1968).

F5

9. In view of the role of Ca in ameliorating the effects of salt in plants, it appeared important to determine the optimum Ca concentration for the absorption of Rb. Figure F2 shows the rate of Rb absorption as a function of the substrate Ca concentration by both mechanisms of ion uptake. The Ca concentration for optimum Rb at both Rb concentrations is 2 mM l^{-1}. The optimum Ca concentrations range appears to be wider for mechanism 1 than when both mechanisms are in operation. In the presence of 10 g l^{-1} of NaCl in the absorption medium the rate of Rb uptake from 1 mM l^{-1} Rb was drastically lower (Figure F2) and Ca concentration appeared to be of little significance.

10. Magnesium (Mg) is present in seawater in concentrations much higher than Ca. Since high Mg concentrations interfere with seed germination of some plants (Palmisano and Newsom 1967), the possible interference of Mg in the range of concentration present in the marsh with the absorption of Rb was tested. Figure F3 indicates that Mg does not significantly affect the absorption of Rb at either 0.1 or 1 mM l^{-1} Rb. Moreover, Rb absorption was not significantly different from that when Ca was present.

11. The time course of Rb uptake was investigated over a 2-hour period in the presence as well as in the absence of salt. Figure F4 shows that 10 g l^{-1} (171 mM l^{-1}) of NaCl inhibited the accumulation of Rb by more than 90 percent. However, the linearity of the Rb accumulation with time indicated that although the rate of absorption was greatly reduced, the integrity of the absorption mechanism was retained. The linearity of experimental and control groups also indicated that the

F6

rate of accumulation was constant, suggesting the absence of the washing effect that has appeared in the literature recently (Leonard and Hanson 1972; Parrondo and Smith 1976). Since Na and Rb are both monovalent cations, inhibition of Rb absorption by Na could be competitive.

12. Figure F5 shows that salt does not compete with Rb for uptake by mechanism 1 until the Na:Rb ratio is higher than 10 to 1. On the contrary, the presence of Na at low concentrations appeared to have a synergistic effect on the absorption of Rb. This synergistic effect has been shown previously in other halophytes (Rains and Epstein 1967; Jefferies 1973).

13. The effect of root pretreatment with NaCl on the Rb uptake by intact seedlings is shown in Figure F6. Roots from plants grown in salt solutions were compared to treatments that received salt only during the Rb uptake period. Sodium chloride, whether given before or during Rb absorption, reduced the Rb uptake to less than 40 percent of control plants. However, preloading the plants with NaCl was more effective in reducing the uptake of Rb than when given at the same time. In spite of the inhibition of absorption of NaCl in the nutrient medium, NaCl did not appear to affect the growth of the seedlings (Appendix E).

14. Plants are known to accumulate ions far in excess of their physiological needs (Epstein 1972). Presumably, this luxury consumption is accumulated in the vacuoles where it is thought to be involved in maintaining an osmotic gradient between the plant and the medium. The results presented in this study indicate that, unlike mangroves (Rains and Epstein 1967), the mechanisms of ion uptake in S. alterniflora are not significantly different from those of salt-sensitive plants in terms

of the Na-K relationship. This species has been shown to grow very well in a freshwater medium (Appendix E; Taylor 1939). The difference lies in the ability of S. alterniflora to tolerate high cytoplasmic salt concentrations, which lower the plants osmotic potential in relation to the medium in which it is growing.

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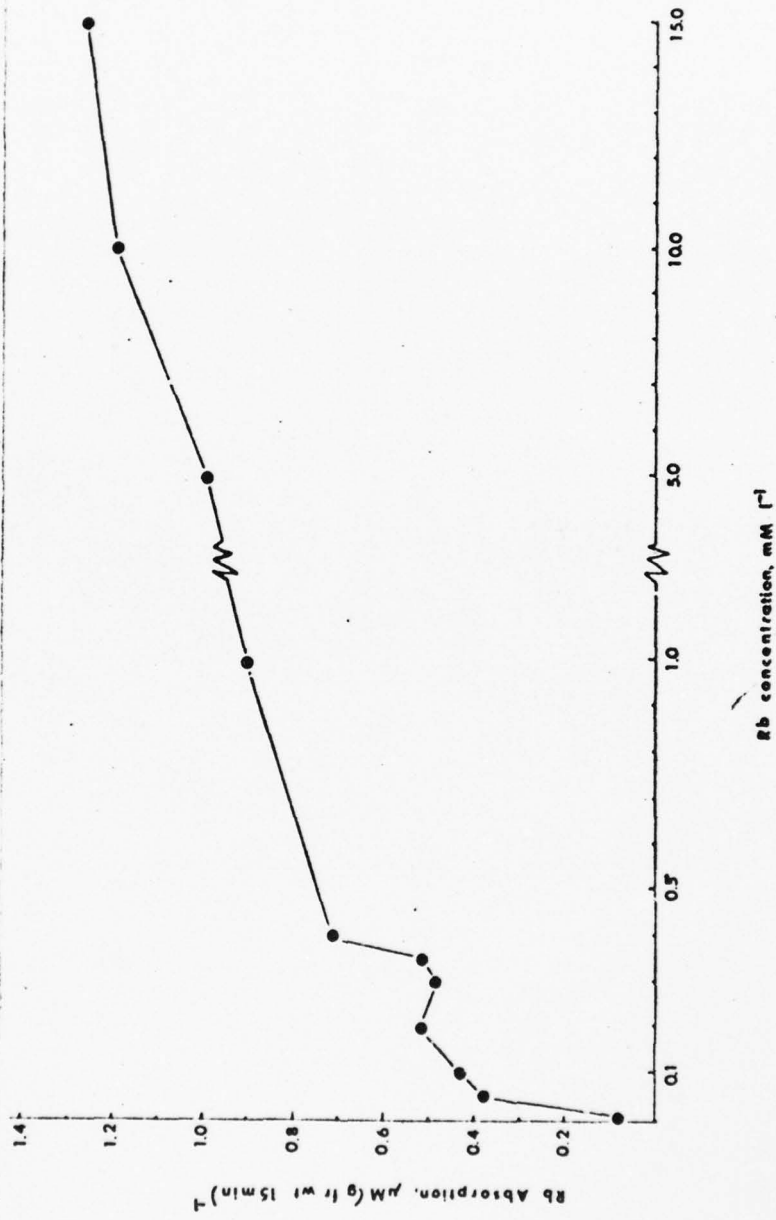
Figure F1. Effect of increasing Rb concentration on the rate of Rb absorption, showing dual isotherm.
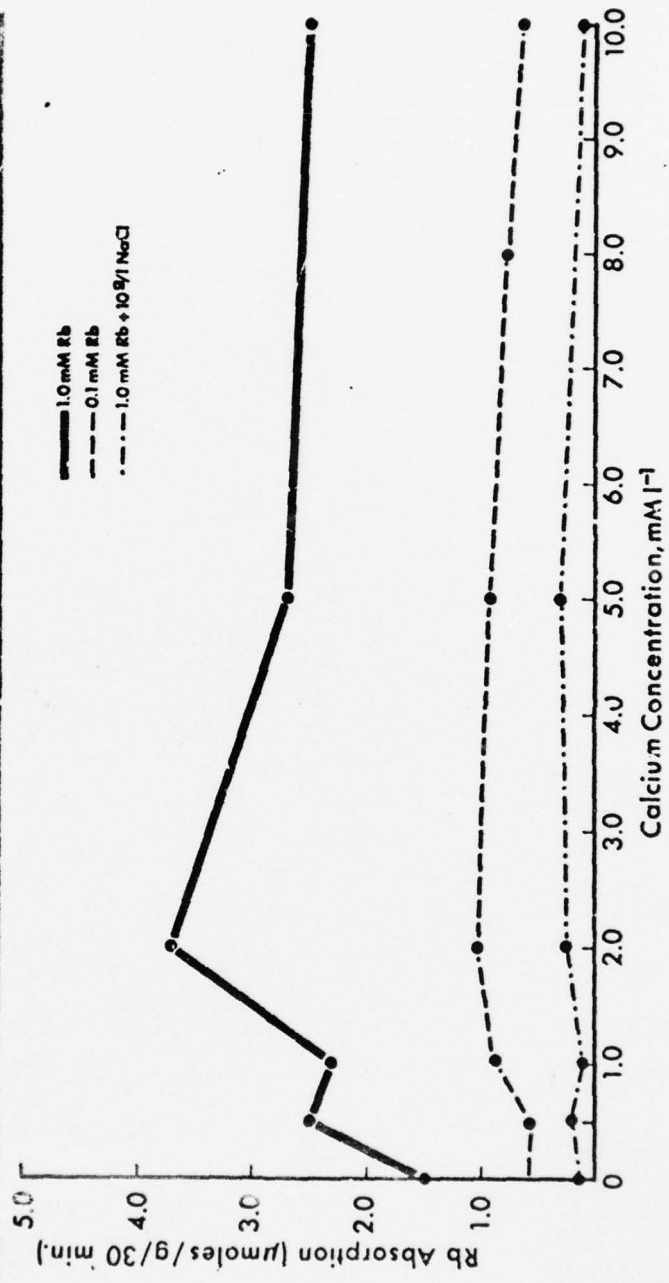
Figure F2. Effect of substrate Ca concentration on the rate of Rb absorption.
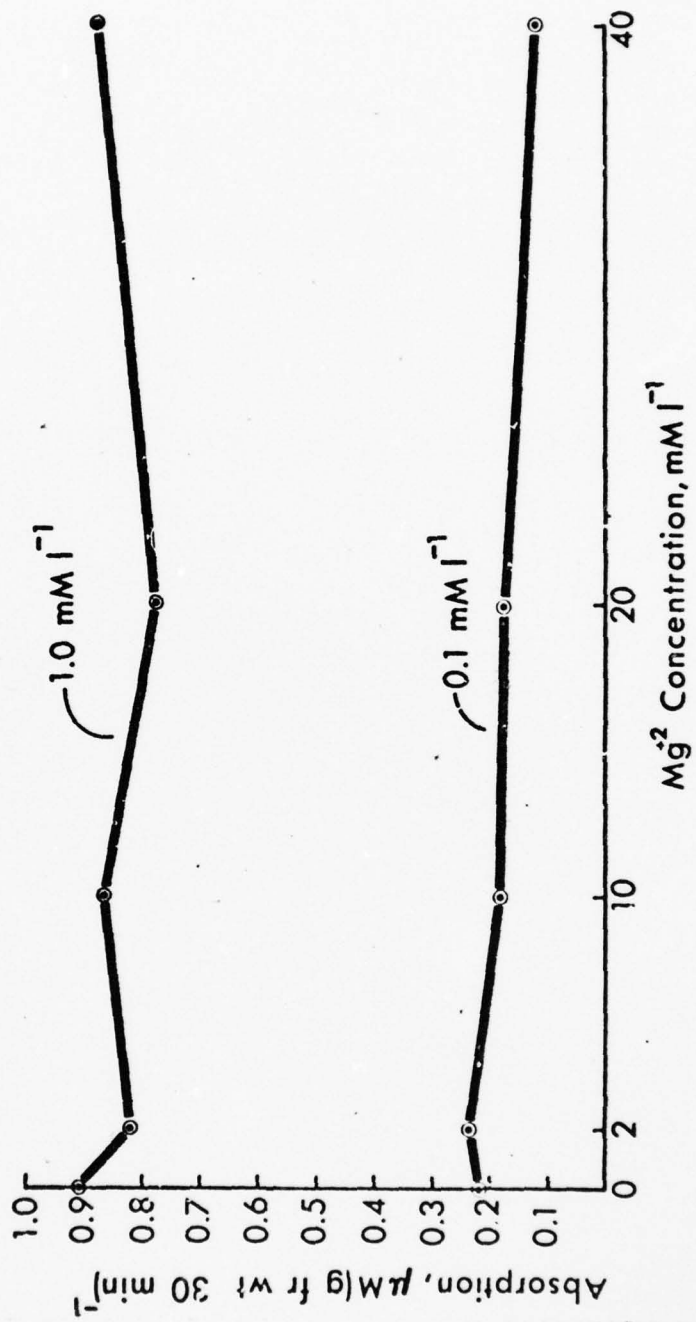
Figure F3. Effect of substrate magnesium concentration on the rubidium absorption rate.
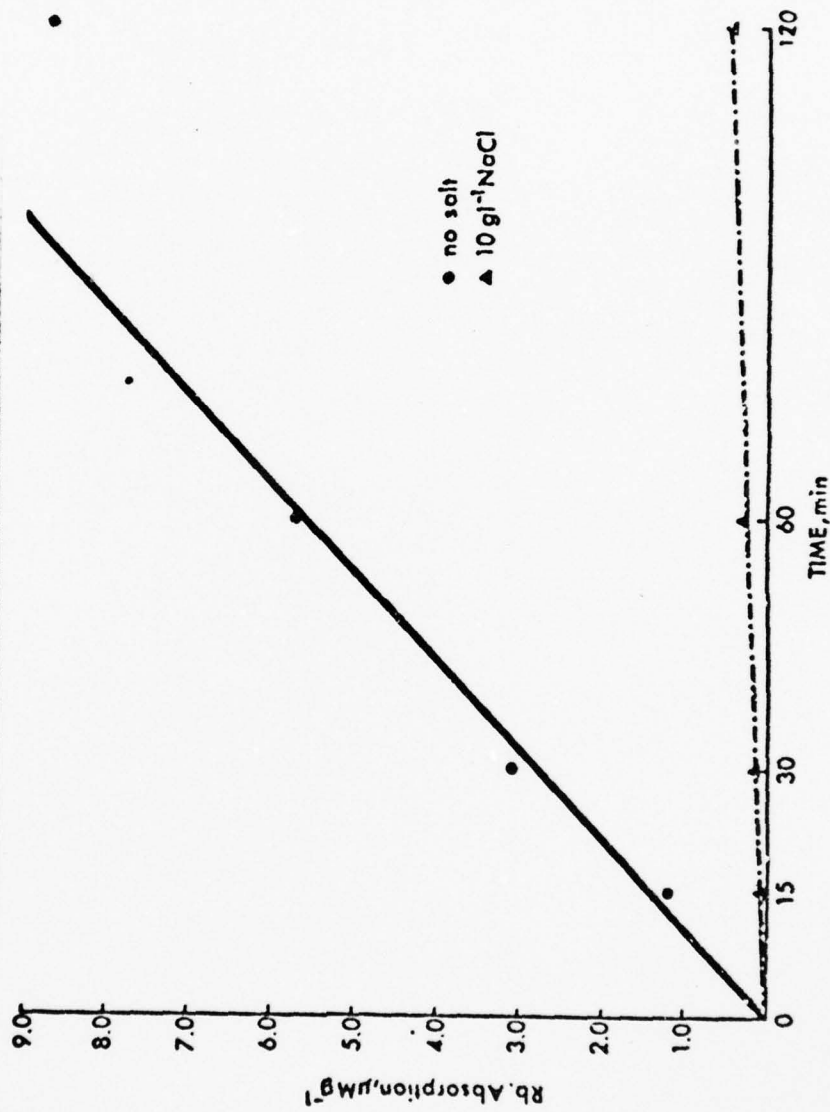
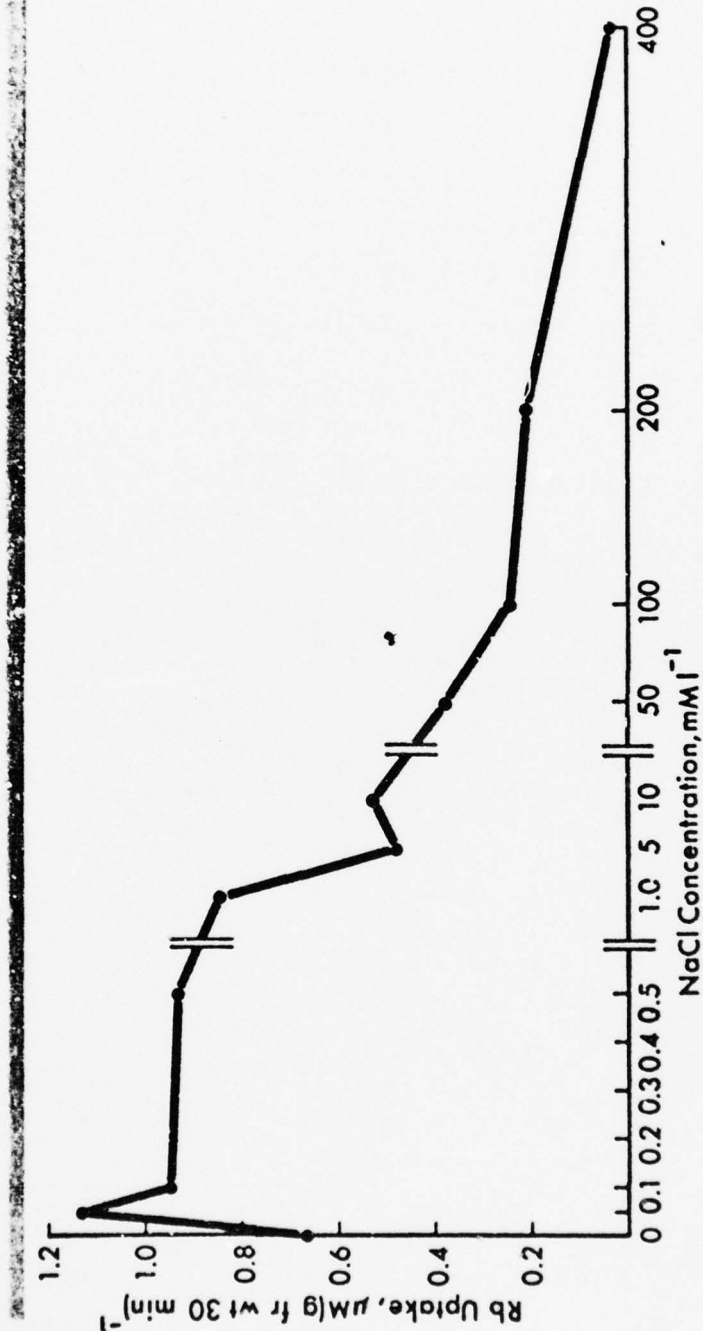Figure F4. Time course of Rb uptake by *S. alterniflora* roots in the presence and absence of NaCl.

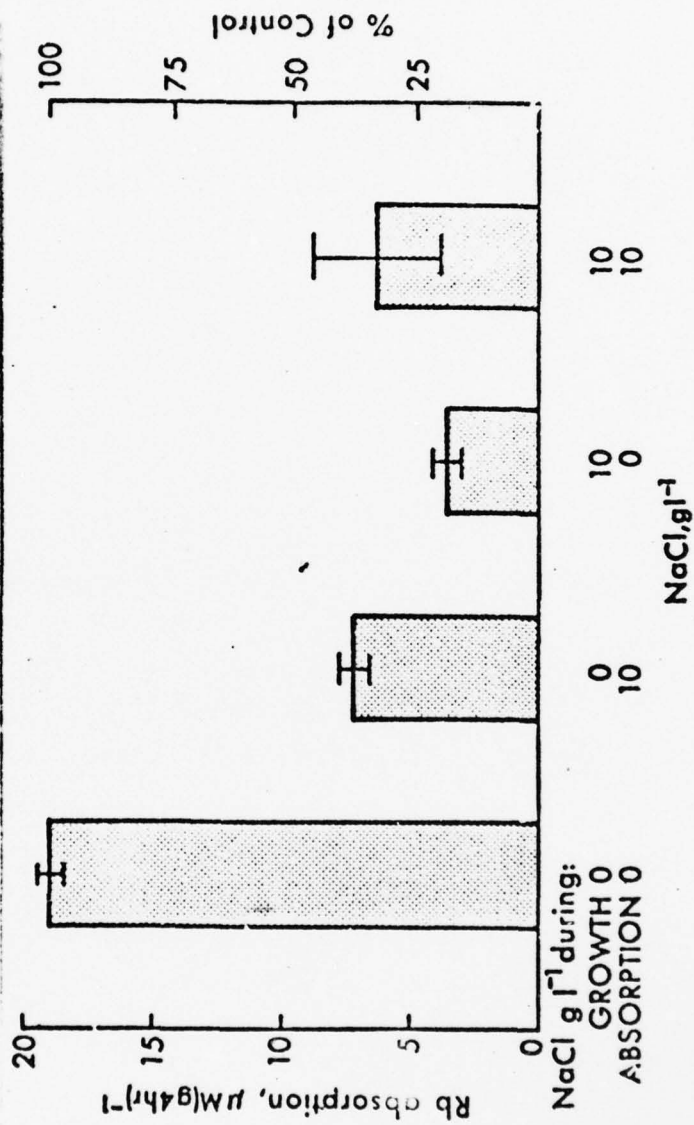Figure F5. Effect of substrate salt concentration on the rate of rubidium absorption.

Figure F6. Effect of root pretreatment with NaCl on Rb uptake by intack seedlings.

APPENDIX G: LIGHT AND TEMPERATURE RESPONSES IN PHOTOSYNTHESIS
OF SPARTINA ALTERNIFLORA

Introduction

1. The salt marsh grass Spartina alterniflora grows in a periodi-
cally flooded wetland zone that provides a unique laboratory for the
study of stress. The overwhelming influence of two factors in the
physical environment, salt and periodic flooding, make biotic inter-
actions minimal for this emergent plant. Just how salt and inundation
interact and how plants adapt to them are the object of intensive
scrutiny. Photosynthesis and respiration are fundamental metabolic
processes that reflect the ability of a plant to trap light energy and
to use it efficiently in the presence of these stresses, yet almost
nothing is known about either process in S. alterniflora.

2. This appendix describes, in a preliminary way, the processes of
photosynthesis and respiration which interact with the stress factors of
the whole salt marsh community.

Methods

General design

3. Metabolic carbon dioxide (CO_2) exchange was measured in a plant
chamber, or cuvette, in which temperature was controlled and through
which air flowed at a controlled rate. Carbon dioxide flux was deter-
mined from the flow rate through the cuvette and the difference between
ingoing and outflowing CO_2 concentration in the air stream. The system

G1

was the open cuvette type, modified from Mooney et al. (1971)* and described in Figure G1.

4. The cuvette was a 31-cm-diam. cylinder of three parts. A 20-cm-high aluminum (Al) base with sharpened bottom edge was attached to a 15-cm-high Plexiglas collar to which all the lines and sensors were attached. This in turn was attached through an O-ring to a 45-cm-high closed Plexiglas top (Figure G2). In use, the base of the cuvette with the collar and control lines attached to it was placed over a stand of S. alterniflora and pushed into the sediment to a depth of 10 to 15 cm. Care was taken to avoid disturbing the community. A thermocouple was inserted into the sediment to a depth of 10 cm; another thermocouple was attached to a leaf; and a third was suspended in the shade inside the cuvette. Following the positioning of the thermocouples, the Plexiglas top was attached to the cuvette collar and the air flow to the cuvette turned on. Cuvette air temperature was controlled by recirculating air through a radiator maintained at the desired temperature by chillers, heaters, and controllers in a houseboat.

5. This 21-ft houseboat served as a floating laboratory, housing all instrumentation for the CO_2 analysis and for the control circuits. In this study it was operated from land adjacent to a salt marsh, for access to line power, but generators are available to make the operation entirely self-contained.

6. The marsh investigated was located at Leeville, La. It was a small marsh, bounded by La. Highway 1 on one side and a shell road on

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* References listed at end of this appendix.

G2

two other sides. It received tidal waters through a dredged canal that connects to Bayou Lafourche. The marsh received raw sewage from a number of mobile homes and small houses along the shell road.

7. For each plot, at constant air temperature, CO_2 flux was measured in light, and it was measured in the dark by covering the cuvette with black plastic. Flux rates under different light intensities were obtained by taking advantage of intermittent cloud cover or by shading the cuvette with cheese cloth. Following measurements on the intact community, the top of the cuvette was removed and the green tissue removed by cutting each live culm below its lowest green leaf. The top of the cuvette was replaced and CO_2 exchange was determined again in light and dark. Carbon dioxide exchange under these conditions was considered to be due to the microbial community.

Measurements

8. Measurements were made over a period of about 10 days each in December 1975, and March, May, and July 1976. During this period all tide stages were encountered, and measurements were made at all times of day and night. Neither tide stage nor time of day appeared to influence the CO_2 flux rates as effects separable from responses to light intensity and temperature.

9. Table G1 shows the surface water salinity, sediment temperature, and ambient daytime air temperature during the measurement periods. Chamber temperature was maintained at 15°, 25°, or 35°C (± 1°C) as desired.

G3

Results

Independence of CO_2 flux and CO_2 concentration

10. Figure G3 shows the relationship between cuvette CO_2 concentration and the uptake of CO_2 by greenhouse-grown S. alterniflora. The figure indicates that CO_2 uptake is relatively independent of cuvette CO_2 concentration above about 200 $\mu\ell$ CO_2 ℓ^{-1}. In the field the independence of CO_2 flux and cuvette CO_2 concentration was periodically checked by changing the flow rate. As long as the cuvette concentration was maintained above 250 $\mu\ell$ CO_2 ℓ^{-1}, CO_2 flux was unaffected.

Relationship of leaf area to leaf dimensions and dry weight

11. Since a leaf area meter was not available during all field trips, leaf areas recorded in this report are all determined from leaf dimensions. Figure G4 shows the relationship between blade area determined with an electronic leaf area meter and blade area determined from blade dimensions. The regression equation indicates that 86 percent of the variability in the former is accounted for in the calculated area.

Relationship of S. alterniflora to total community metabolism

13. Table G2 shows that S. alterniflora shoots, between December and May, were responsible for over 90 percent of the community photosynthesis, but only 24 to 36 percent of its dark respiration (see also Gosselink et al. 1976). Respiration reported is the difference between community respiration and CO_2 evolution by the community after S. alterniflora shoots were removed. Under the circumstances, any root CO_2

G4

exchange would be recorded as part of community respiration, not S. alterniflora shoot respiration. The percentages recorded in Table G2 are for CO_2 exchange at 25°C. The proportion between S. alterniflora and the rest of the community varied little at 15° or 35°C. Algal photosynthesizers on the sediment surface and on the lower leaf sheaths of S. alterniflora (Stowe 1972) appeared to be more important during the winter when more light penetrates the grass canopy, than later on in the spring. Spartina alterniflora live shoot respiration appeared to decline during May, as a proportion of total community respiration. At this time much of live tissue is young, and the dead standing biomass is large (Kirby and Gosselink 1976). Earlier in the year most of the live shoots are mature and often appear to be senescing (tips yellowing, necrotic spots).

Seasonal rates of gross production and respiration

14. Gross photosynthesis and dark respiration rates of S. alterniflora are shown in Figure G5. The two graphs are not directly comparable since respiration rates are recorded for total live shoot dry weight, whereas photosynthetic rates are based on leaf blade tissue only. Nevertheless, both respiration and photosynthesis show a sharp drop during May, and in terms of photosynthesis per unit leaf area, the May level continued into July. Light saturation curves were used to adjust all photosynthesis values in this figure to a standard light intensity of $1 \text{ g cal cm}^{-2} \text{ min}^{-1}$.

Temperature

15. The seasonal rates of photosynthesis and respiration are

G5

temperature dependent (Figure G6). In March respiration increased with temperature, and gross photosynthesis peaked at 25°C. The resulting net production optimum was 25°C. In May gross photosynthesis and net production both were higher at 35°C. The magnitude of the apparent upward shift in optimal temperature response in May was not enough to account for the drop in efficiency (at 25°C) shown in Figure G6, that is, the plants did not simply shift to a higher temperature optimum at the same rates of photosynthesis. There were, in addition, overall drops in both photosynthesis and respiration rates in May.

16. In March different plots were analyzed at different temperatures. As a result the variance is high, especially for gross photosynthesis. In May three plots were examined first at 25°C, then at 35°C, so that the interplot variation could be separated from the temperature affect. As a result, although the differences in photosynthetic rates were not large, they were consistent and statistically highly significant. Respiration rates in May were not significantly different. Net production, calculated from gross production and respiration, was not statistically analyzed.

Light

17. The light response was much more dramatic than the temperature response. Figure G7 shows light response curves at two temperatures during May. The shape of the curve is the same for March also. These curves are for gross photosynthesis of the whole community. Therefore they are about 5 percent higher than rates for S. alterniflora alone (see Table G2). Preliminary evidence indicates that the microbial component

G6

MICROCOPY RESOLUTION TEST CHART

NATIONAL BUREAU OF STANDARDS-1963-A
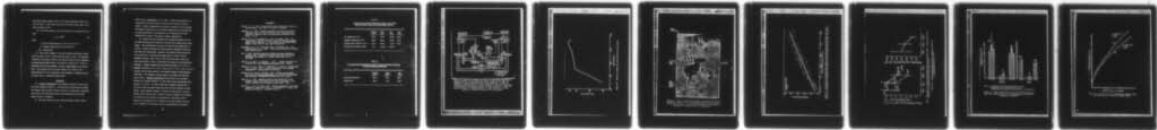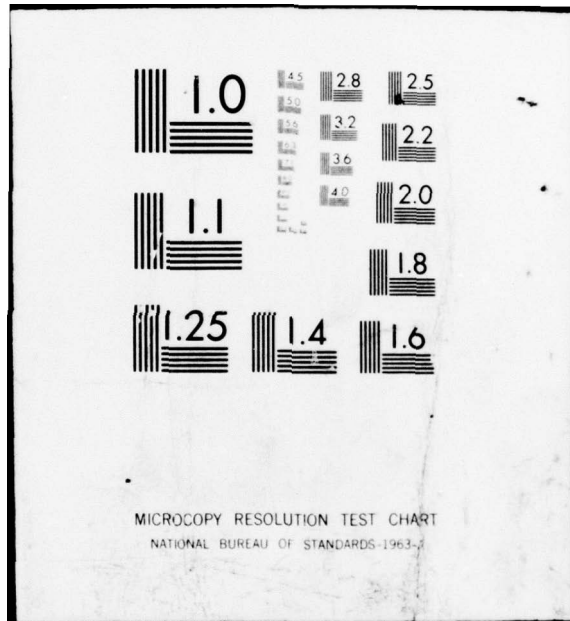
saturates (reaches maximal rates) at low light intensities (below 0.2 g cal cm^{-2} min^{-1}). This would account for the initial steep slope of the light saturation curve.

18. The light response curves were found to fit an equation of the form

$$Y = a + bI^{2/3} \tag{1}$$

where

        Y = gross photosynthesis in g Carbon (C) cm^{-2} hr^{-1}

        I = radiant energy flux in g cal cm^{-2} min^{-1}

     a,b = coefficients

19. The curves in Figure C7 are each fitted by pooling all values from four plots at 25°C and the same four plots at 35°C. The equations indicated in the figure account for 81 and 89 percent of the variability in gross photosynthesis (GP) at 25° and 35°C, respectively. Rates for individual plots varied somewhat but were always higher at 35° than at 25°C. The response curve is clearly steeper at 35° than at 25°C. Photosynthesis is still increasing at full sunlight, a response typical of plants with C_4 metabolism (Black 1973).

Discussion

20. Spartina alterniflora is the dominant carbon (C) fixer in the salt marsh community (Table 2). The 10-percent contribution by aufwuchs and sediment algae during the winter, however, is significant, especially since algal cells generally provide a more palatable and nutritious organic source to consumers.

21. The light saturation curve confirms previous reports (Black

C7

1973) that $\underline{S}$. $\underline{alterniflora}$ is a C_4 plant. Unlike most glycophytes its photosynthetic apparatus does not saturate well below full light intensity. Rather, photosynthesis continues to increase to full sunlight. The apparent upward shift in the optimal temperature for photosynthesis as spring progressed is interesting but not surprising since plant communities are known to acclimate to ambient temperatures.

22. Perhaps the most unexpected and intriguing disclosure is the decreased photosynthetic efficiency in May and July compared with winter months. The photosynthetic rate per unit leaf area decreased about 25 percent. During the spring live tissue density increased so there may have been some leaf-shading. However, leaf density within the cuvette was low and did not increase much (mean values 4.4 and 5.6 cm^2 in December and March and 8.4 and 6.7 cm^2 in May and July), since thin plots were chosen in order to stay within the capacity of the analytical equipment. Sediment temperatures increased from about 18° to $20^o C$ in December and March to 21° to $23^o C$ in May and 24° to $27^o C$ in July, and this increase may have been related to the observed change in photosynthetic efficiency. The inorganic nutrient supply to the plant may also have been a factor. $\underline{Spartina}$ $\underline{alterniflora}$ has been shown to be nitrogen-limited in its growth (Valiela and Teal 1975; Patrick and Delaune 1975; Broome et al. 1975). Ho (1971) showed that inorganic nitrogen (N) in the water column increased during the winter and fell abruptly in early spring. Marsh sediment inorganic N follows the same pattern, although Brannon (1973) reported that it peaked as early as November and December. It follows that the decrease in photosynthetic efficiency could be related to the availability of inorganic N for tissue growth, and that as N is depleted in the spring, rates of photosynthesis also decline.

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Table G1

Daily Air and Sediment Temperature Range   and Surface
Water Salinity During Field Measurement Periods

	December 1975	March 1976	May 1976	June 1976
Air Temperature (°C)	20-25	25-27	24-28	30-32
Sediment Temperature (°C)	18-20	19-20	21-23	24-27
Surface Water Salinity (°/..)	15-17	12-16	8-14	17-19
Leaf Area Per Cuvette (dm^2)	4.4±	5.6±2.6	8.4±2.0	

Table G2

S. alterniflora Metabolism at 25°C as Percent ±Standard Deviation
of Marsh Community Metabolism

	December 1975	March 1976	May 1976
Gross Photosynthesis	89± 6	92±6	96±3
Respiration	36±11	36±5	24±9
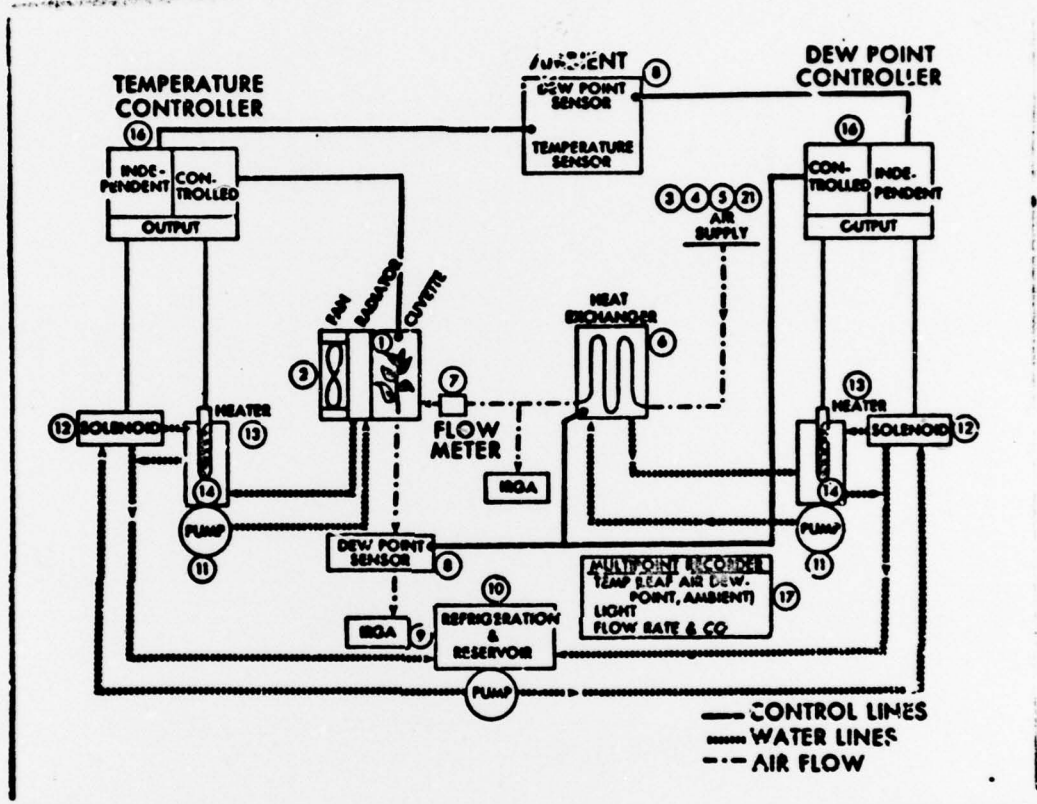
Figure G1. System for measuring CO_2 flux. 1, Plexiglas cuvette with 2, fan and radiator to recirculate air through cuvette; 3, air pump and reservoir; 4, gas pressure regulator; 5, air humidifier; 6, heat exchanger for humidity control; 7, mass flowmeter; 8, dew point hygrometer; 9, differential infrared gas analyzer; 10, water chiller; 11, pumps, 12, solenoid valves; 13, immersion heater; 14, water reservoir; 16, controller; 17, multipoint recorder; 21, gas cylinder.
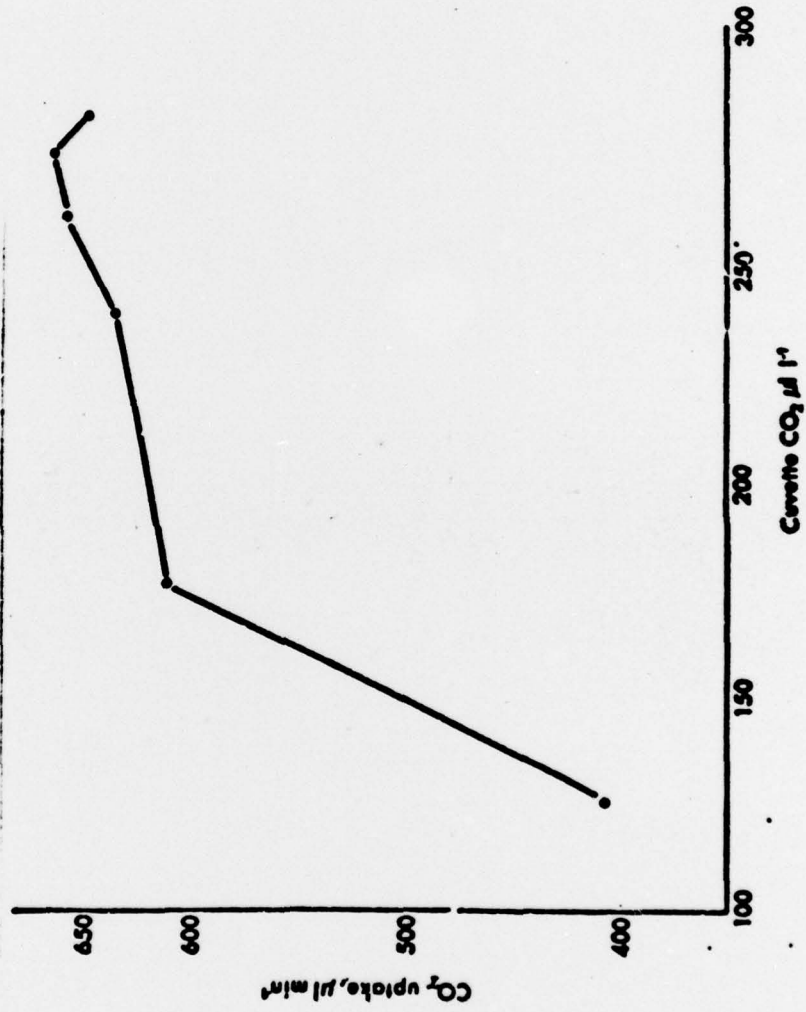
Figure 63. Effect of cuvette CO_2 concentration on CO_2 uptake.

Figure G2. Cuvette in place on the marsh. The white box contains a radiator to control cuvette air temperature and a fan to circulate air through the cuvette. Air circulates through the black hose in foreground. Pyroheliometer is in background.
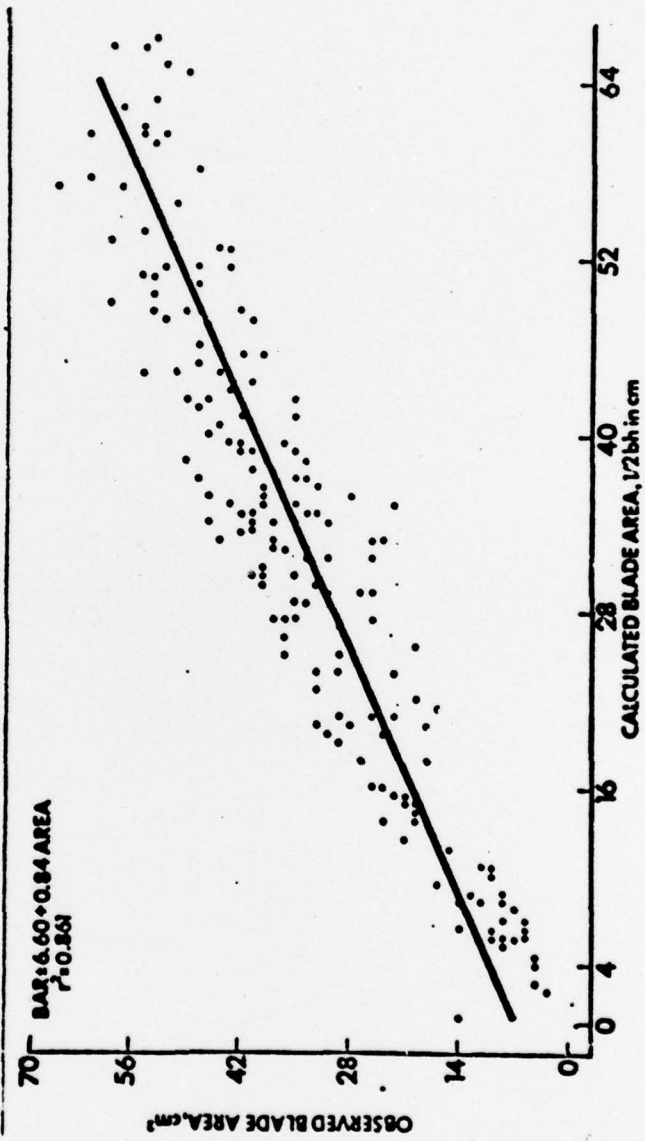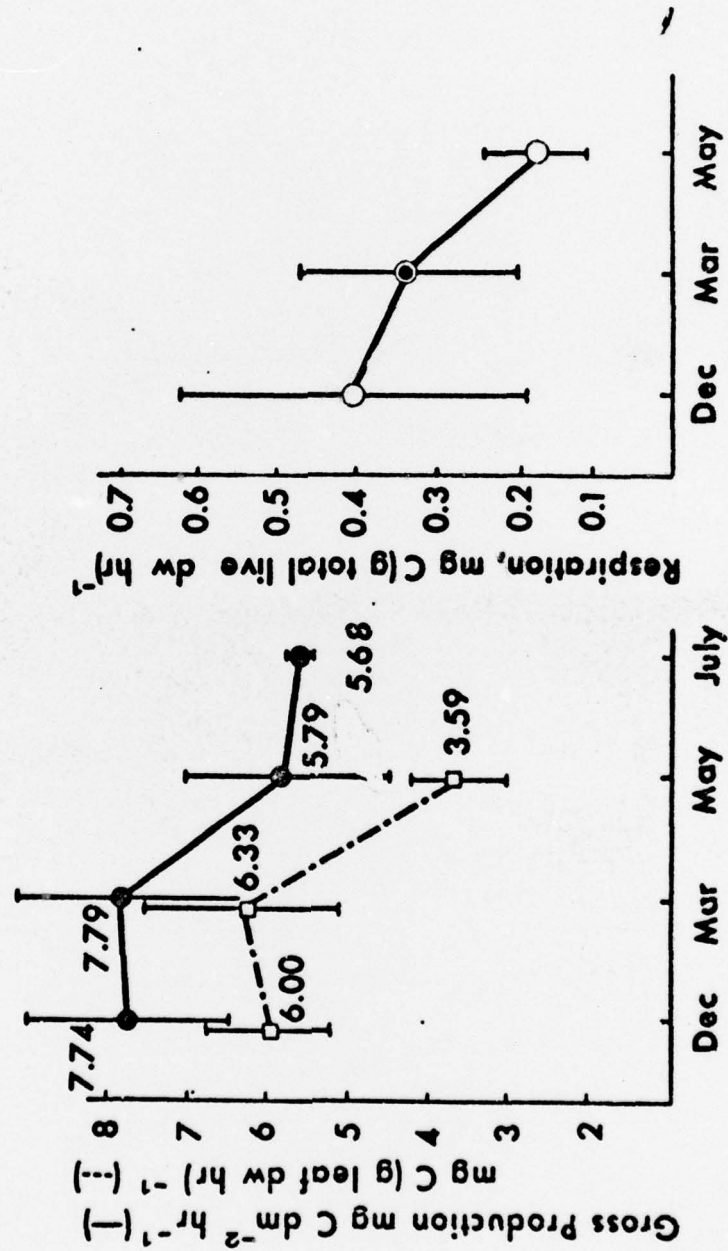
Figure C4. Regression of observed blade area as determined with an electronic leaf area meter on leaf blade area calculated from basal width and length—BAR and AREA, respectively.

Figure C5. Gross photosynthesis and dark respiration rates of _S. alterniflora_ shoots at 25°C.

Note: Each point is a mean of measurements on 3 to 6 separate plots. Gross production is adjusted to a radiant flux of 1 g cal cm^{-2} hr^{-1}.
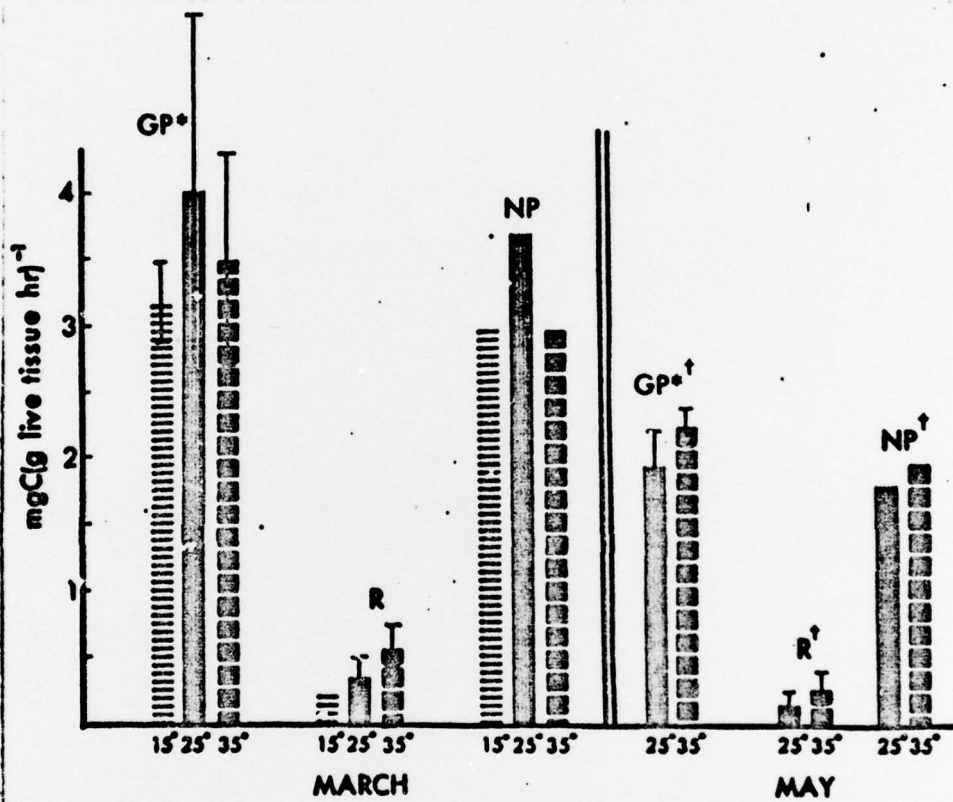
Note: * Difference in GP is highly significant (P <0.01).
  † Difference in R is not significant (P >0.05).
  Gross production adjusted to a radiant flux of 1 g cal cm^{-2} hr^{-1}.

Figure G6. Rates of gross (GP) and net (NP) daytime production and of dark respiration (R) of S. alterniflora as influenced by temperature and season.
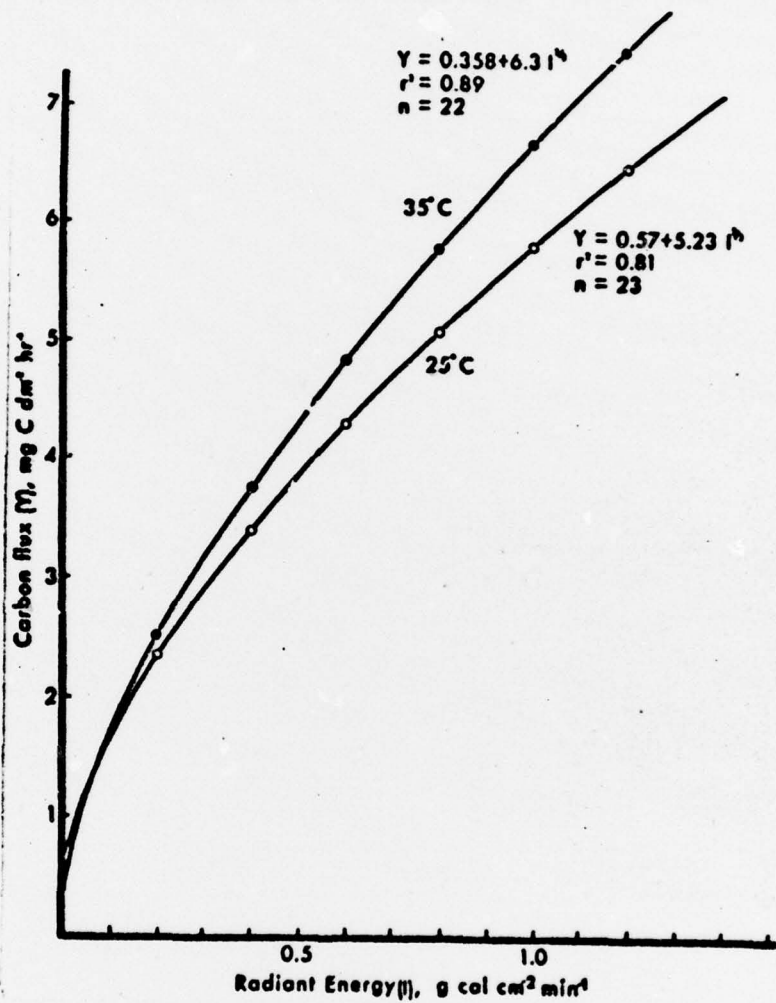
Figure G7. Fitted curves of S. alterniflora community gross photosynthesis as a function of radiant energy.

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