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COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA. VOLUME I. PR--ETC(U)
DEC 77 J G GOSSELINK, R T PARRONDO

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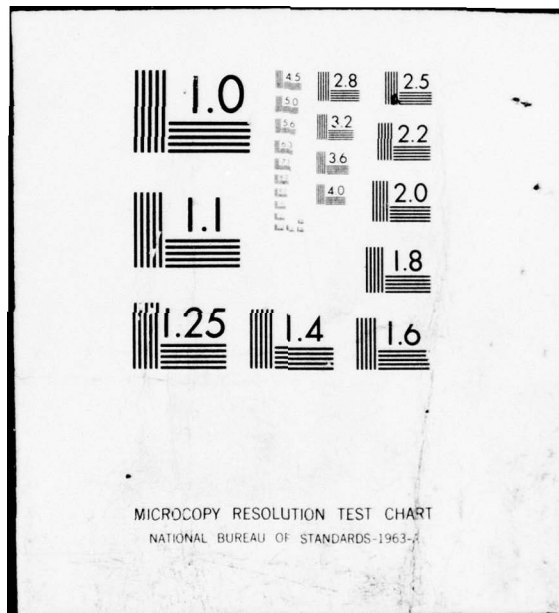
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DREDGED MATERIAL RESEARCH PROGRAM



TECHNICAL REPORT D-77-44

COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA VOLUME I: PRODUCTIVITY

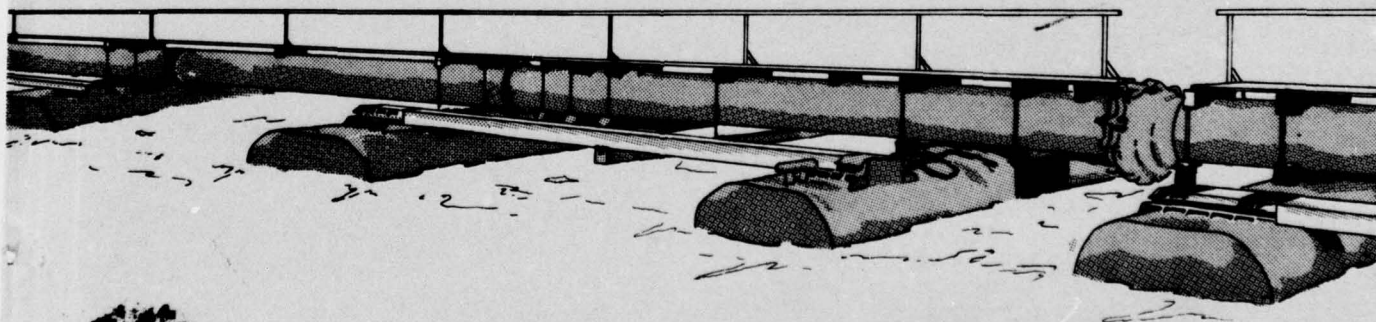
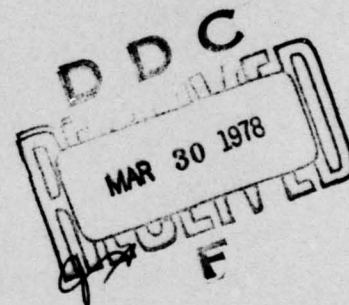
by

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December 1977

Final Report

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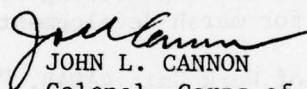
1. The technical report transmitted herewith represents the results of one of the research efforts (Work Units) under Task 4A (Marsh Development) of the Corps of Engineers' Dredged Material Research Program (DMRP). Task 4A is a part of the Habitat Development Project (HDP) of the DMRP and is concerned with developing, testing, and evaluating the environmental, economic, and engineering feasibility of using dredged material as a substrate for marsh development.
2. The report of Work Unit 4A04B, "Common Marsh Plant Species of the Gulf Coast Area," has been separated into two parts, "Volume I: Productivity" and "Volume II: Growth Dynamics." As indicated by their titles and discussed briefly below, each volume addresses a separate but essential aspect of our knowledge of salt marshes.
3. Net annual aerial primary productivity is a commonly used descriptor of the value of salt marshes and is the subject of Volume I. Primary productivity here is considered the rate at which the sun's energy is stored as plant tissue available to the ecosystem. This work unit deals with several aspects that influence the primary productivity of seven marsh species along the coast of Louisiana. Specifically, the influence of growth habit, turnover rate, climate, salinity, nutrients, and water quality is assessed and comparisons of techniques for measuring productivity are discussed. The information derived in this study should be of direct value in evaluating the relative ecological importance of potential dredged material disposal sites. The information provided will also be exceptionally useful in the design of new marsh habitats on dredged material.
4. Volume II deals with the growth dynamics or physiological ecology of salt marsh species under conditions of stress. Although several species were examined, major emphasis was placed on the substrate selective qualities and adaptation mechanism of *Spartina alterniflora*. The results of this study have been integrated into a general conceptual model that has application to the development of marshes on dredged material.

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5. Work Unit 4A04B is one of several research efforts designed by the DMRP to accurately document marsh productivity and the factors that influence the productivity. Closely related work units are 4A04A1, which addresses the productivity of selected marsh species in Louisiana; 4A04A2, which deals with marsh plant substrate selectivity and underground biomass production; and 4A05, in which a simulation model to predict salt marsh productivity was developed. In a less intensive study, Work Unit 4A20 will provide a general evaluation of salt marsh productivity of the Pacific coast of the United States. Additional supportive and comparative data will be forthcoming with the final analysis of the results of field studies at Windmill Point, Virginia, (4A11); Buttermilk Sound, Georgia, (4A12); Apalachicola, Florida, (4A19); and Miller Sands, Oregon, (4B05). Together, these research products provide the Corps with a comprehensive basis for sound management decisions regarding dredged material disposal in salt marsh habitats.



JOHN L. CANNON

Colonel, Corps of Engineers
Commander and Director

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20. ABSTRACT (Continued).

measure productivity over a two-year period of the following species: Distichlis spicata (salt grass), Juncus roemerianus (black rush), Phragmites communis (common reed), Spartina alterniflora (saltmarsh cordgrass), Spartina patens (saltmeadow cordgrass), and Sagittaria falcata (bulltongue).

Productivity was found to be related to the growth habit and turnover rate. S. patens, J. roemerianus, and D. spicata were found to be more productive than S. alterniflora, a species that was known to be highly productive. Productivity was higher in the fresh and brackish marsh species than in the salt marsh species and was higher for species that grow throughout the winter than those that die to the ground in late fall.

An evaluation was also made of several techniques for measuring productivity, including harvest, phenometric, and gasometric methods. The study showed that peak standing crop seriously underestimates production in Gulf Coast marshes and that the Wiegert-Evans harvest technique is the most realistic method presently available. This technique includes an estimate of mortality in addition to live biomass changes and so gives the closest estimate of true net aboveground production. The study also showed that phenometric methods have potential as a nondestructive technique that could be developed into a reliable method.

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SUMMARY

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 must 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 availability 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.

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.

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.

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 Weigert and Evans (1964) is the most realistic presently available, although phenometric analysis holds promise for an excellent, nondestructive method of productivity analysis.

Aside from variation in reported productivity due to differences in techniques, wide geographic variability occurs. High biomass was associated with high silt loads, low organic matter in the sediments, and decreasing salinity.

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.

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.

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.

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.

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.

The relationships discussed in the model are important because they can be used to evaluate how existing data on marsh productivity are interpreted, where dredging and dredged material disposal should occur, and what species and edaphic conditions are optimum for vegetation of newly created marshes.

PREFACE

The work described in this report was performed under contracts DACW39-73-C-0105 entitled "Productivity of Minor Grass Species" and DACW39-73-C-0108 entitled "Physiological Response of Marsh Plants to Environmental Stress," both dated 30 May 1973, between the U.S. Army Engineer Waterways Experiment Station (WES), Environmental Effects Laboratory (EEL), Vicksburg, Miss., and Louisiana State University, Baton Rouge, LA. The research was sponsored by the Dredged Material Research Program (DMRP) under Task 4A, "Marsh Development." The studies included in this report were performed during the period from June 1973 to June 1976.

The research was conducted by Dr. James G. Gosselink, Professor of Marine Sciences; Dr. Roland T. Parrondo, Assistant Professor Botany; and Mr. Charles S. Hopkinson, Research Associate. The main text was written by Dr. Gosselink; Appendix A and B by Mr. Hopkinson, Dr. Gosselink, Dr. Parrondo, and Mr. L. Gulick; and Appendix C by Dr. Parrondo, Mr. E. Bishop, and Mr. Hopkinson. Mr. Pat Cavell, Mr. Lee Grush, Ms. Jean Gosselink, and Ms. Karenlee Kneller were employed to assist with this work. In addition, support from a number of other individuals is acknowledged. Mr. Edwin Bishop, in particular, was responsible for all the technical electronics involved in the photosynthesis studies. Mr. Rodney Adams and Mr. Ralph Cunningham provided reliable field support. Personal communication with Drs. R. J. Reimold and J. L. Gallagher of the University of Georgia was valuable for this report.

The contract was monitored by Dr. C. R. Lee, Ecosystem Processes Research Branch, and Dr. Luther Holloway and Dr. Terry Huffman, Habitat Development Project (HDP), EEL. The study was under the supervision of Dr. Hanley K. Smith, Manager, HDP, and the general supervision of Dr. John Harrison, Chief, EEL.

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

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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:

<u>Multiply</u>	<u>By</u>	<u>To Obtain</u>
miles (U. S. statute)	1.609344	kilometers
acres	4046.856	square meters
cubic yards	0.7645549	cubic meters

COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA

VOLUME I: PRODUCTIVITY

INTRODUCTION

Dredging Activities

1. Each year the U.S. Army Corps of Engineers (CE) dredges 300 million cubic yards* of material from the 22,000 miles of navigable waters of the continental U.S.A. (Boyd et al. 1972). Costs for moving this material vary from about twenty cents to several dollars per cubic yard. The distance to the disposal site is a significant factor in the cost, a fact that is critically important for the present study. Dredging to maintain navigation channels is more extensive than any other single dredging activity throughout U.S. estuaries. Even for the highly industrialized and densely populated eastern coast, from 1955 to 1964 disposal of dredged material was the major reason for filling wetlands (Clark 1967). Here, if anywhere, one would expect wetland filling for industrial and residential needs to predominate. Clark indicates that a total of 45,000 acres was filled from 1955 to 1964, of which 34 percent was filled to dispose of dredged material. These areas, used first for dredged material disposal, are often later used for other development projects.

2. The importance of dredging in estuaries to the Nation's economy is indicated by the fact that 132 of the 170 ocean ports in the United States are located in estuaries. These ports handle about 90 percent of the total U.S. foreign trade. In recent years approximately one half of

* A table of factors for converting U. S. customary units of measurement to metric (SI) can be found on page 9.

the Army Corps of Engineers' budget for maintenance of the Nation's channels and harbors has been for use in coastal areas (Sweet 1971).

3. Thus the use of marshlands as dredged material disposal sites has been a common CE practice for many years. One major reason for this is the cost-benefit ratio that must be applied to federally sponsored engineering projects. The removal of large volumes of dredged material to a disposal site is a significant economic consideration. Marsh areas are fairly accessible to many coastal dredging projects and for many years easements were easily obtainable and relatively inexpensive. In addition these marsh areas have been considered of marginal value (Boyd et al. 1972). Indeed, local interests were often anxious to have marshlands filled because it offered opportunity for future development.

4. In recent years however there has been a sharp increase in awareness of the value of coastal wetlands as natural systems. Because of natural tidal subsidies and the naturally high nutrient levels of most estuaries, wetland productivity is higher than productivity in any terrestrial system. Turner (1976) documented the dependence of coastal fisheries on tidal wetlands. Other studies (Gosselink et al. 1974; Valiella et al. 1975; and Grant and Patrick 1970) have documented the importance of wetlands in tertiary treatment of polluted waters and in the overall global balance of such critical nutrients as nitrogen, phosphorus, and sulfur. As an awareness of the value of natural wetlands has become greater, the availability of these areas for disposal of dredged material has naturally decreased so that coastal wetlands are no longer readily available as disposal grounds. Indeed, the Corps of Engineers itself is readily cognizant of the detrimental effects of disposal on

marshes and is earnestly seeking economically feasible disposal alternatives. At the same time it is realized that because of the magnitude of the dredging necessary to maintain navigable waters in coastal areas, some disposal of dredged material on marshes will continue to be necessary.

5. Through the Dredged Material Research Program (DMRP), the Corps is attacking the problems of disposal of dredged material in coastal zones from a number of different directions. Efforts are being made to identify the tidal wetlands that are of least value in their natural state for possible routes of navigation channels and as disposal sites. Concurrent efforts are identifying methods of minimizing the impact of disposal of dredged material. One of the most viable alternatives to marsh disposal is the positive use of dredged material to create new marshes.

6. For both types of disposal--on existing marshes and by creating new marshes--the question of productivity of marsh vegetation, either existing or to be created, is critical in the response of the ecosystem. Production by marsh plants is the base of the marsh food web. In addition, good evidence from a number of sources (Heald 1969; Teal 1962; and Odum and de la Cruz 1967) indicates that the export of organic matter from tidal marshes is an important food source to consumers (fisheries, shell fisheries, etc.) in estuarine waters. In addition, the extensive root systems of marsh plants are undoubtedly an important factor in stability of sediments. These rooted plants act as traps for fine silt and clay particles in the water column and thus serve to clarify the water and remove materials which otherwise might require

subsequent dredging. For instance, Ambrose, in an article published in 1888 (Coates 1972), described how all of the early harbors on the southeastern coast of England were silted up when the great marshes were first diked and filled. Constant dredging and a vast expenditure of national funds then became necessary to keep harbors operational. These functions and a number of other natural services of the marsh all depend to some extent on the level of primary production of the marsh macrophytes, which are the dominant organisms on the marsh.

7. This study reports the productivity of seven marsh plant species in coastal marshes of Louisiana: Distichlis spicata (salt grass), Juncus roemerianus (black rush), Phragmites communis* (common reed), Spartina alterniflora (saltmarsh cordgrass), Spartina cynosuroides (big cordgrass), Spartina patens (saltmeadow cordgrass), and Sagittaria falcata (bulltongue). The study was conducted between August 1973 and July 1976. It was designed to satisfy one portion of the overall DMRP research and development effort under Task 4A, Marsh Development.

Problems of Measurement of Primary Production

8. Traditional techniques for measurement of primary production involve harvesting plant material, usually at the end of the growing season when aboveground biomass is maximum. This aboveground biomass, in many studies, has been taken to be equivalent to net aboveground production. Parenthetically, until recently the importance of the root biomass has generally been ignored. Aboveground biomass, it was recognized, contributed to the secondary consumers in the food web but the contribution

* 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, D. C.

of the roots was not considered. Figure 1 summarizes in diagrammatic form the dynamics of plant growth. In this figure gross production is represented by the flow of materials into the live biomass compartment. Net production, the growth dynamic of most interest in productivity studies, is gross production less plant respiration. The material which accumulates in the live compartment is dissipated by translocation to the roots, by mortality of the plant, and by leaching losses from plant parts. The dead compartment is important in the wetland food web because, as in most grassland systems, nearly all the plant production is processed by the microbial detritus system before it becomes available to higher consumers. Thus in this diagram (Figure 1), the dying grass is shown to accumulate in a compartment in which bacteria and other organisms act as food processors. The dead grass is thus dissipated by respiration and also by loss from the system, either through incorporation into the sediments or by tidal flushing from the marsh surface into adjacent water bodies. There is also a small input of production from the aufwuchs community, which is epiphytic on the lower parts of the culms of the marsh plants.

9. As Figure 1 shows, measurement of production is not as straightforward as measurement of peak shoot biomass would indicate. In order for biomass to be equivalent to production, it is necessary that no live vegetation be present at the beginning of the growing season and that no mortality, translocation to roots, or leaching occurs during the growing season. Under these circumstances all aboveground production accumulates in the live shoot compartment and the peak biomass in that compartment accurately measures net shoot production. It has been

recognized from the work of Wiegert and Evans (1964), and more recently in marshes from Kirby and Gosselink (1976) and Hopkinson and Day (in press), that this is seldom true, especially in southern marshes.

Wiegert and Evans showed that significant mortality occurs during the summer in old field systems in Michigan, and Kirby and Gosselink's data indicate that the production of S. alterniflora in Louisiana marshes is at least three times the value of the peak standing crop, because many plants die before the end of the growing season.

10. In this study the Wiegert-Evans (1964) technique was used to measure the production of seven marsh plant species because the method includes an estimate of mortality in addition to live biomass changes. Wiegert and Evans measured the loss rate from the dead compartment. During any time period then, the loss rate plus the change in dead biomass estimates mortality, and mortality plus the change in live shoot biomass sums to true net production.

11. This technique yields much higher production estimates than the majority of those found in the literature, so results by this technique are not directly comparable with other work. In the study reported in the following pages, after one year of field work, the estimated values of net production were so high as to be questionable in the minds of many individuals who have used more traditional techniques. Therefore, to be useful, the technique had to be validated against other techniques. As a result, considerable effort was expended in the development of independent measures of production. Harvest technique results were compared with calculations based on stem density and life histories of individual tagged stems and with measurements of direct

carbon dioxide incorporation in plant tissue. These results are presented in the following pages. Best estimates of production and implications for the DMRP are discussed.

TECHNIQUES*

12. The five basic techniques used to measure marsh plant production fall into three categories: harvest techniques that involve clear-cutting of quadrats of vegetation at regular intervals; phenometric techniques that involve the nondestructive measurement of growth parameters of individual plant stems at intervals; and a gasometric analysis involving the measurement of direct carbon dioxide incorporation and evolution by the plants under study.

Harvest Techniques

13. A summary of harvest techniques follows.

- a. Peak live biomass was estimated from the harvest of 0.1- to 1-m² quadrats when live biomass was at a maximum. In practice, this time was determined from the bimonthly harvest samples obtained for the following technique.
- b. Wiegert-Evans Technique (1964): 0.1- to 1-m² quadrats were harvested at eight-week intervals over the two-year period of the study (August 1973 to September 1975). All samples were replicated five times. Vegetation from these plots was separated into live and dead stems, and the dead material on the live shoots was also treated separately. Vegetation was dried at 80°C to constant weight and weighed. Loss rates of dead vegetation were estimated from paired plots; the live vegetation was removed from each plot; the dead vegetation was harvested immediately in one plot and after eight weeks in the second. The loss rate (r) was calculated from the change in the amount of dead vegetation during the interval. The instantaneous loss rate (r = g lost per g dead material per day) was

$$r = \frac{\ln (D_{t_0}/DR_{t_1})}{t_1 - t_0}$$

*Techniques are summarized below; details are given in the Appendixes.

where

D_{t_0} = amount of dead material in the 1st quadrat(s) at time t_0
 DR_{t_1} = amount of dead material remaining in the 2nd quadrat(s)
at time t_1

From this loss rate the disappearance of dead material (X) during a time interval (Δt) is

$$X = r \times \Delta t \times \frac{D_{t_0} + D_{t_1}}{2}$$

where subscripts indicate the sampling time. Mortality (M) for a sampling interval is

$$M = X + \Delta D$$

where

ΔD = change in dead biomass during the sampling interval

Finally, net production (G) for the sampling interval is

$$G = M + \Delta L$$

where

ΔL = change in live biomass during the sampling interval.

Phenometric Analysis

14. At bimonthly intervals the rate of growth and longevity of culms was determined by following at least 119 individual stems of each species throughout most of their life history. Initially plastic tags were placed around 65 different randomly chosen culms of each species. Every eight weeks 15 additional small young culms were tagged and the height and survival of the previously tagged culms ascertained. Density of stems in height class 0-24 cm, 25-49 cm, 50-99 cm, 100-149 cm, and 150 cm was also determined. In addition, randomly selected samples of each species were cut at ground level, measured to the nearest centimeter for height, dried, and weighed to the nearest 0.01 g. A summary of the phenometric techniques used in this study follows.

- a. Williams-Murdoch Technique (1972): This method requires estimates of the ratio of growth to average standing crop (maximum biomass to average biomass) and the mean life span of live culms. The relationship of weight to height was also required. The ratio of growth to average standing crop was

$$(\Sigma B_{\max}/n)/(\Sigma \bar{B}/n)$$

where

$B_{\max}$ = the maximum weight attained by each stem during its life span

n = number of plants

B = the mean weight of a stem during its life span

$\bar{B} = \Sigma(\bar{b} \times \Delta t)/\Sigma \Delta t$ = the mean weight of a stem during its life span

where

$\bar{b}$ = average weight of a stem between successive measurements

Δt = interval between successive measurements

Annual growth (G) was calculated as follows:

$$G = \bar{L} \times (\Sigma B_{\max}/n)/(\Sigma \bar{B}/n) \times \Sigma(\bar{b} \times \Sigma \Delta t)/\Sigma \bar{B}$$

That is, growth ($g \times m^{-2} \times yr^{-1}$) = avg standing crop ($g \times m^{-2}$) $\times$ growth/average biomass $\times$ frequency/year

where

$\bar{L}$ = annual average standing crop of live vegetation.

- b. Mortality Method: This technique used determinations of mortality rates and maximum dry weights of individual culms to estimate annual mortality, which, in a steady-state system, should equal annual production. The generalized equation is:

$$\text{Mortality} = \text{stems dying} \times \text{mass per stem} \times \text{stem density}$$

for each time interval and for each size class at time of death. Weight per culm was calculated from height/weight regressions. Mortality was calculated from data from individual tagged culms. Plant death during each eight-week interval was summed for a one-year period to estimate annual mortality.

Gasometric Analysis--Carbon Dioxide Flux

15. An infrared gas analyzer was used to measure the change in carbon dioxide (CO_2) in air flowing through a clear acrylic plastic cuvette that enclosed a 0.075-m^2 area of the salt marsh. Air temperature in the cuvette was controlled as described in Appendix C, and light was controlled over the cuvette by taking advantage of natural variations in cloud cover and by use of black plastic or layers of cheese cloth. The analysis of CO_2 flux is described in detail in Appendix C and in Mooney et al. (1971). Production comparisons reported in this work are for a single species, S. alterniflora.

16. Figure 2 shows the sampling sites for the seven species. They are more or less along Bayou Lafourche in either the Barataria or the Terrebonne intertributary basins in southeast Louisiana; details are reported in Appendix A.

RESULTS: PRODUCTION OF SEVEN MARSH PLANT SPECIES
COMPARED BY DIFFERENT TECHNIQUES

Comparison of Techniques

Variation in estimates
of net primary production

17. Figure 3 shows annual production estimates from the harvest and phenometric production techniques. The most striking observation about the graph, aside from the very high production levels, is that all the techniques show that peak standing biomass seriously underestimates production. Table 1 shows the relationship of net production to peak live biomass as calculated from different production techniques. With two exceptions values vary from 1.4 to over 4, indicating that peak live biomass always significantly underestimates production. One of the first techniques developed to try to estimate the mortality loss was Smalley's (1959). He was able to correct for an unspecified fraction of mortality. The investigators of this study were able to calculate production by Smalley's technique from harvest data. The comparisons show that on the average Smalley's method was 27 percent lower than the mortality method, 53 percent lower than the Williams-Murdoch method, and 57 percent lower than the Wiegert-Evans paired plot harvesting technique.

18. Only one of the two phenometric techniques, the Williams-Murdoch method, generally agreed well with the Wiegert-Evans technique. On the average the estimates from the Wiegert-Evans technique were only 1.3 times higher than the estimates from the Williams-Murdoch technique. For two of the six species, production estimates by the Williams-Murdoch method were higher than when calculated from the Wiegert-Evans

paired plot harvesting technique. In some instances a qualitative judgment allows evaluation of the two methods for a single species. For instance, for S. falcata it was recognized that the sampling interval was too long to measure accurately the loss rate for the Wiegert-Evans technique. The Williams-Murdoch method is probably more realistic for these data. It may be more realistic than Wiegert-Evans for S. patens also. With this species it was extremely difficult to measure loss rates because of the density of the stands and almost recumbent growth habit of the species. The underlined numbers in Table 1 are considered the most reliable estimates of production.

19. Production estimates based on gasometric analysis (that is, CO₂ flux) are difficult to integrate over periods of time that are compatible with harvest techniques. However, for the single species studied by the gasometric technique (S. alterniflora), the rates of CO₂ fixation are compatible with the highest estimates of net aboveground production from other techniques. On an hourly basis, and in terms of milligrams of carbon fixed per square meter per hour (making allowances for root production), the Wiegert-Evans technique gives average production rates of about $215 \text{ mg C} \times \text{m}^{-2} \times \text{hr}^{-2}$ compared to rough estimates of net production from CO₂ flux of $250 \text{ mg C} \times \text{m}^{-2} \times \text{hr}^{-1}$ (see Appendix C). Thus all the methods used appear to have values that compare very closely to the values derived from the Wiegert-Evans and Williams-Murdoch techniques.

Turnover rates

20. These results all point to an index of production that should

receive more attention in production studies. This index is the "turnover rate," the relationship of net production to mean live biomass. Used with mean biomass the turnover rate allows one to estimate production. If it can be estimated for a number of species and found to be fairly invariable, it could simplify the field work involved in estimating production. This ratio is probably temperature dependent (see Turner 1976), increasing with decreasing latitude. Thus in the United States it is probably highest in Louisiana marshes and lowest along the New England coast. Data from a concurrent study by Reimold and Gallagher (personal communication 1976) should further clarify the relationship of turnover rate to latitude.

Advantages and Disadvantages of the Different Production Techniques

21. A serious consideration in field tests is the cost of the technique used. Peak live biomass requires a single field sampling trip only, requires no elaborate equipment, and is without doubt the simplest measurement to make. On the other hand, it gives no information about seasonal dynamics and as indicated above seriously underestimates true net production. At the other extreme, the harvest technique of Wiegert and Evans combined with the measurement of loss rates, requires intensive field sampling over at least an annual cycle of growth, and it is costly and time-consuming in terms of manpower. It does not, however, require sophisticated equipment aside from a balance and a drying oven. The technique is valuable far beyond the simple figure of annual production that it produces. If the sampling interval is suitable, it also yields data on the seasonal changes in live and dead biomass and on loss

rates, mortality, and production. The phenometric technique of Williams-Murdoch uses valuable averaging methods that tend to minimize errors and also to minimize the number of individual measurements necessary. However, it does not express any seasonal growth dynamics. The mortality technique does show seasonal dynamics of mortality and this can be important in evaluating the effects of disturbances in marsh ecosystems. As with the Wiegert-Evans method, phenometric techniques also require considerable field sampling and are labor intensive, but equipment needs are again minimal. These techniques, in addition, are nondestructive. It is likely that, with appropriate measurements of growth of individual stems, phenometrics can be developed into a good index of seasonal dynamics of growth as well as mortality.

Annual Production of Seven Marsh Plant Species

22. Table 2 summarizes the best estimates of annual production of the seven species. The "best" estimate is either the Wiegert-Evans or the Williams-Murdoch value, depending on a somewhat subjective evaluation of which method was most appropriate for each species. The most striking feature of this table is the extremely high values for above-ground net production for all species compared with, for instance, S. alterniflora, which for many years has been considered to be one of the most productive phanerogams known to man. In comparison with other marsh species for which production has been estimated, however, S. alterniflora turns out to be no more productive than J. roemerianus or D. spicata and far less productive than S. patens.

23. The productivity is related to the growth habit of the species in question. The most productive three species—S. patens, J. roemerianus, and D. spicata—are species that have considerable green vegetation year-round and for which the annual curve of live biomass does not show any strong peaks. At the other extreme the least productive species, P. communis and S. cynosuroides, show a clear seasonal growth curve with no live shoot biomass during the winter and a smooth increase during the spring and summer to a fall peak. The other two species fall between these extremes. S. falcata appears to have a single growth cycle, but in reality its turnover and decomposition rates are much more rapid than any other species studied. It was the only broad-leaved plant analyzed. It usually dies back to the ground with any freeze but regrows rapidly from roots so that it undergoes several flushes of growth during the winter season. S. alterniflora shows a clear seasonal increase in live biomass followed by a high death rate after flowering in the fall, but it also maintains considerable live biomass throughout the winter.

24. Productivity is related to turnover rate, as indicated by the ratio of production to peak biomass ($P/B_{\max}$). S. cynosuroides and P. communis have low ratios; those species which grow throughout the winter have high ratios. S. falcata has an extremely high ratio. The productivity of S. patens was a major surprise in this study. It has been known to have a large standing biomass of live and dead vegetation year-round, but there has been no previous analysis of its productivity. It is highly productive in spite of the fact that it receives no strong tidal subsidy and apparently depends primarily on recycling for

nutrients. S. patens is not only very productive, but it is the dominant species in Louisiana wetlands, covering an area of 1,565,743 acres (Chabreck 1972).

IMPLICATIONS FOR DMRP

Role of Primary Production in Marsh Ecosystems

25. This study demonstrates that the primary productivity of all the wetland species investigated is very high compared to published reports of productivity of upland plant species. Thus, although there are differences among species, as a general rule wetland productivity is extremely high. Therefore the decision for location of navigable channels for the placement of dredged material on marshes or for the creation of new marshes should not be based primarily on the net productivity of the species concerned. This is true even though it is understood that primary production describes the energetic potential for the whole ecosystem, so that the magnitude of the energy flows through the rest of the food web is limited by the magnitude of primary production.

26. In addition, however, there are other important considerations:

- a. The seasonal dynamics of live and dead vegetation, mortality rates, and disappearance rates are important considerations for developments that impact the marsh ecosystem. For instance, the production of live S. alterniflora occurs at its fastest rate during spring and early summer. As Figure 4 shows, a great deal of this organic matter does not die until October and November and is not released or carried into the surrounding waters until the following spring. Thus, any disruption of primary production on a marsh is not felt through the food chain in any significant fashion until the next year. In contrast to this one-year delay in energy flow, the short life spans and rapid decay of S. falcata leaves suggests that any impact on this plant species is felt immediately by higher links in the food chain (Figure 5). This should be a consideration in planning and timing of impacts on marsh systems and in assessing the effects of these impacts.

- b. The growth habit of the plant is another feature of interest in marsh impact analysis. The contrasting life-style of a plant like S. cynosuroides with a single seasonal growth cycle with that of, for instance, S. patens, which has active growth and mortality throughout the year, dictates different uses for these two species and different approaches to their management (Figure 6). In general, the plant with the year-round growth habit appears to have a higher primary productivity, but also it may be more effective as a stabilizing agent for marsh creation since it maintains an active plant cover all year to help control erosion. All the species studied, however, have perennial root systems that undoubtedly help stabilize the substrate.
- c. Not only is the magnitude of primary production a characteristic of interest, but the quality of the vegetation is also of concern in the food web. Unfortunately there is no simple criterion for determining food quality. A rough index of quality might be the nitrogen concentration of the tissue since as this rises the concentration of proteins tends to increase. The comparison of the quality of grasses such as S. patens with a broad-leaved monocot such as S. falcata emphasizes the concept of quality. S. patens tissues have very low nitrogen concentration of about 0.7 percent as compared with values up to 3 percent in S. falcata. The former decays slowly in comparison to the broad-leaved monocot, which disappears nearly as fast as it dies.
- d. Nutrient cycling strategies are also important in marsh impact analysis. Seasonally the nitrogen concentration in S. patens is fairly constant at about 0.8 percent, while it varies from 1.7 to 3 percent in S. falcata. These differences in concentration when coupled with very different seasonal variations in biomass yield quite different strategies of nutrient cycling (Figure 7). On the one hand S. patens maintains a large constant standing stock of nitrogen in its aboveground biomass although the concentration of nitrogen is low and the palatability of the biomass as a food source is probably also low. In contrast, although S. falcata has a low aboveground biomass, its total aboveground nitrogen content is about equal to S. patens because of the high tissue concentration. The amount of nutrient per unit area varies seasonally by an order of magnitude. S. falcata disappears very rapidly as it dies so that there is a rapid cycling of nutrients. Observations of S. falcata distribution suggest that it is a pioneer species that thrives in disturbed areas or newly formed freshwater marshes, while S. patens is found in much more stable marshes. This may be related to the difference in its strategy of nutrient cycling.

- e. A consideration of importance in coastal marshes is the relative amount of production available to higher consumers in the food web. The primary value of tidal marshes to commercial fisheries is thought to be the organic matter exported from these marshes to surrounding waters which becomes available in the nursery grounds of the fishes. The portion of total primary production exported, then, is an important consideration in the value of the marsh. This may be completely independent of the productivity of the marsh species and may depend almost entirely on the frequency and depth of inundation of the marsh. The export of organic matter from S. alterniflora marshes, for instance, is thought to be one third to one half of its total net production (Teal 1962; Hopkinson 1973). On the other hand, as one moves inland in Louisiana and tidal energy is reduced, marsh sediments become increasingly organic, and it is apparent that a large portion of the primary production is being deposited in the sediment rather than being exported. Thus, in terms of their value as a food source for aquatic consumers, inland marshes might be less valuable than marshes that receive high tidal energies.

Recommendations

27. Since a large part of this study was devoted to techniques for the measurement of primary production, suggestions for optimum techniques for measurement of primary production are set forth below. The convergence of several different techniques on a single methodology of measurement to give reliable estimates of net primary aboveground production led to recommending the Wiegert-Evans technique for routine studies of plant productivity. This technique gives estimates of production which are closest to true net aboveground production and, in addition, documents seasonal variation in standing stocks, loss rates, and mortality. The phenometric methods also give hope as a nondestructive technique that could be developed into a reliable method, and it is recommended that some effort be put into development of a reliable phenometric technique that would be less time-consuming than the

Wiegert-Evans method. The cost of carrying out the Wiegert-Evans technique will be too great, in many cases, for that technique to be used. As an alternative it is suggested that as data accumulate (especially from this study and work presently being conducted in Georgia), average turnover rates can be calculated for different latitudes and different growth habits. Knowing this, production can be estimated from mean biomass. The latter can already be estimated fairly accurately from average stand height for S. alterniflora (Turner and Gosselink 1975).

28. Two additional factors should be considered in field analyses of this kind. One is attention to seasonal changes in root biomass. Evidence is accumulating that the bulk of the total plant biomass is below ground and there is some indication that production as well is greater below ground than above (Reimold and Gallagher, Georgia study in progress). This is extremely important in considerations involving stability and modification of substrates and cannot be ignored in dredged material research studies. A second factor is quality of productivity. The value of production estimates would be increased by judicious use of some index of quality. It is suggested that routine nitrogen analysis of live and dead tissue could usefully supplement information derived from productivity measurements and allow calculation of turnover rates and dynamics of nutrient cycling.

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Table 1
Annual Shoot Production of Seven Marsh Species Estimated by Different Techniques,
With Relationship to Peak Live Biomass

Species	Peak Live Biomass $\text{g} \times \text{m}^{-2}$	Technique				Mortality Production $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$	P/B _{max} *
		Wiegert-Evans Production $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$	P/B _{max} *	Williams-Murdoch Production $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$	P/B _{max} *		
<u>D. spicata</u>	991	2881**	2.9	1967	2.0	1010	1.0
<u>J. roemerianus</u>	1240	3257	2.6	3295	2.7	1850	1.5
<u>P. communis</u>	990	2364	2.3	--	--	--	--
<u>S. falcata</u>	648	1402	2.2	2310	3.6	1113	1.7
<u>S. alterniflora</u>	754	2178	2.9	1381	1.8	1673	2.2
<u>S. cynosuroides</u>	808	1767	2.2	1134	1.4	398	0.5
<u>S. patens</u>	1376	5812	4.2	4159	3.0	2500	1.8
Mean			2.8±0.7		2.4±0.8		1.5±0.6

*Ratio of production to peak live biomass.

**Underlined numbers are considered the most reliable for a species.

Table 2

Summary of Annual Net Shoot Production
by Seven Marsh Plant Species Grouped by Growth Habit

Single seasonal growth cycle:	Production* <u>g^m-2^{yr}-1</u>	<u>P/B_{max}</u>
<u>S. cynosuroides</u>	1100	1.4
<u>P. communis</u>	2400**	2.3
Live biomass all year; growth continues throughout winter:		
<u>D. spicata</u>	2900	2.9
<u>J. roemerianus</u>	3300	2.7
<u>S. alterniflora</u>	2200	2.9
<u>S. patens</u>	4200	3.0
Broad leaved; rapid turnover and decomposition rates:		
<u>S. falcata</u>	2300	3.6

*Best estimate from several methods, rounded to nearest 100 g.

**Probably overestimated because of severe sampling problems.

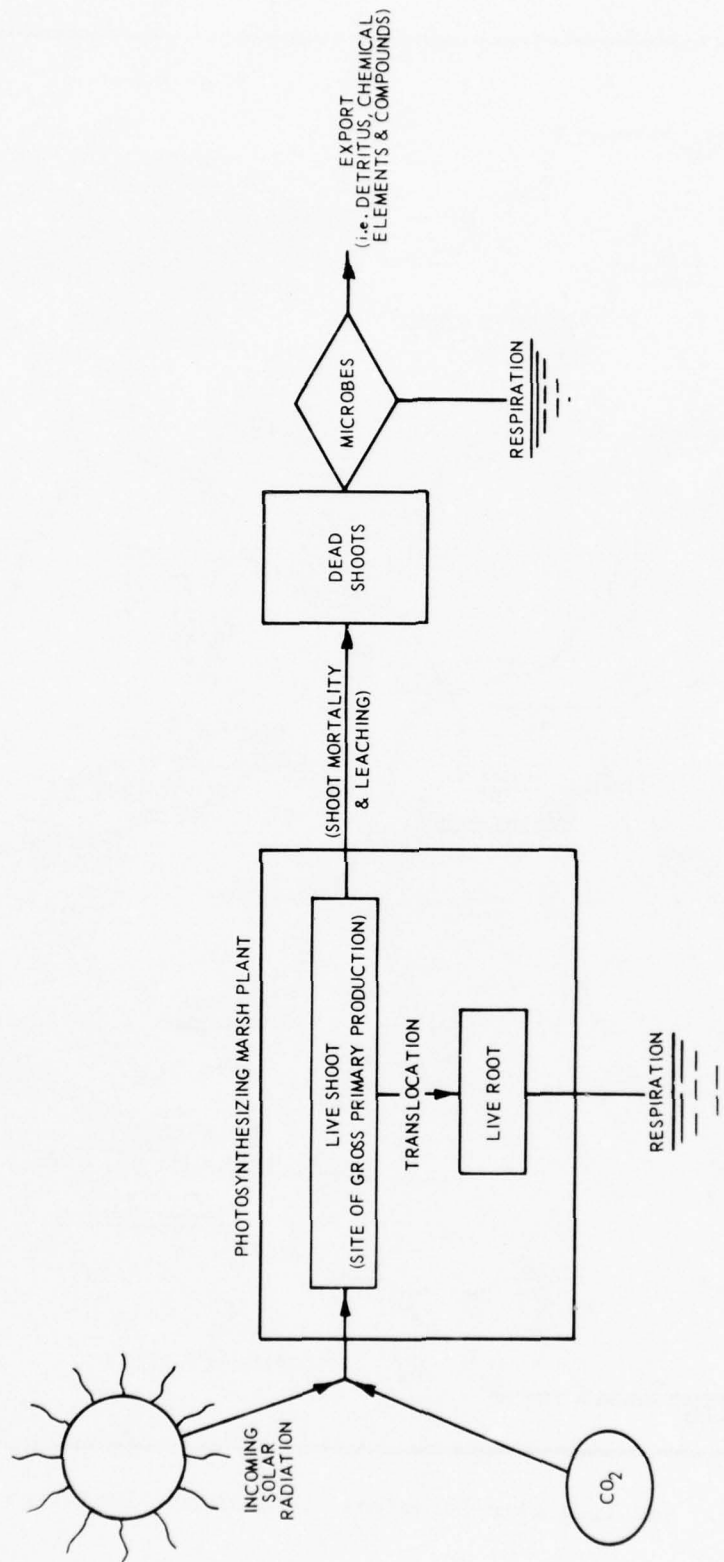


Figure 1. Conceptual model of marsh plant production as it occurs throughout the growing season

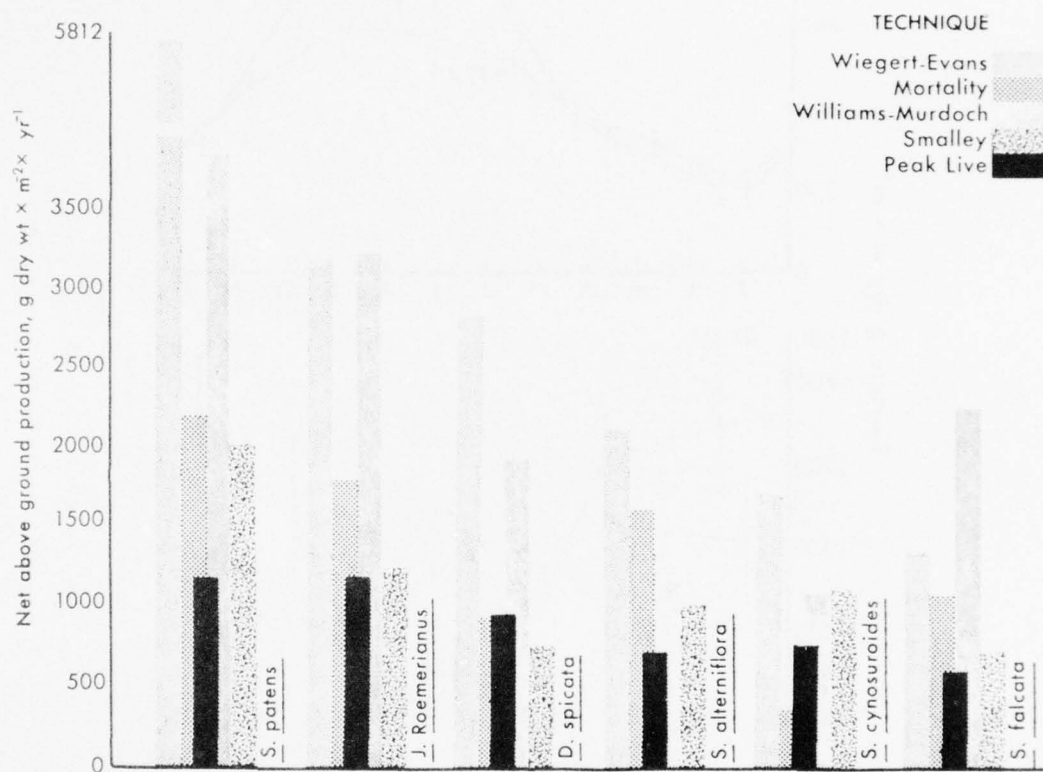


Figure 3. A comparison of production methodologies.

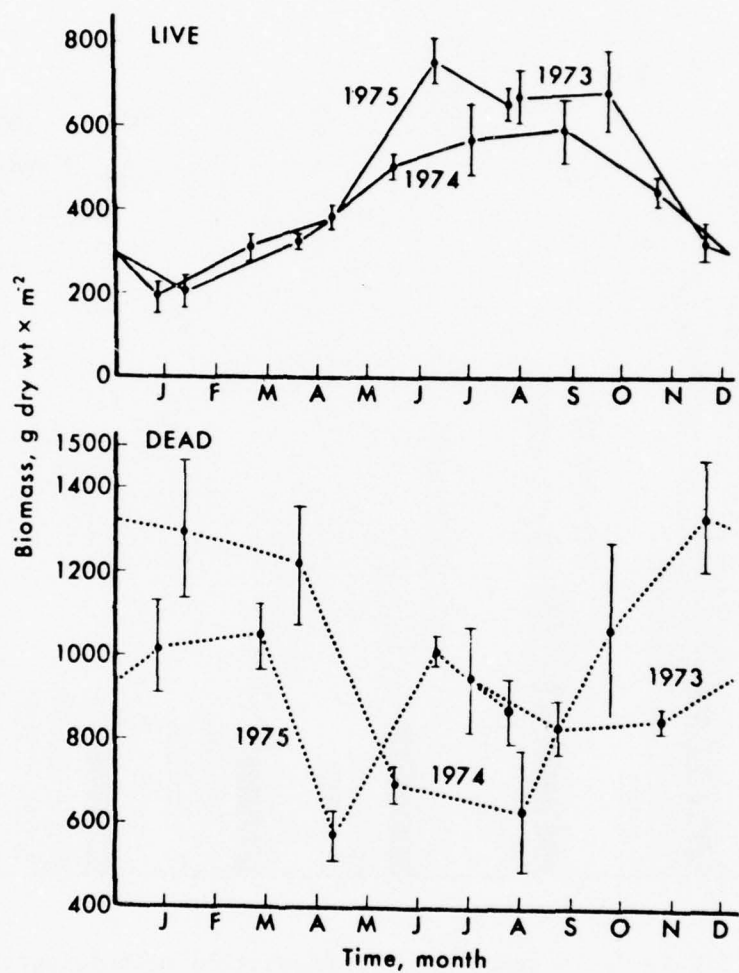


Figure 4. Seasonal changes in live and dead biomass of S. alterniflora.

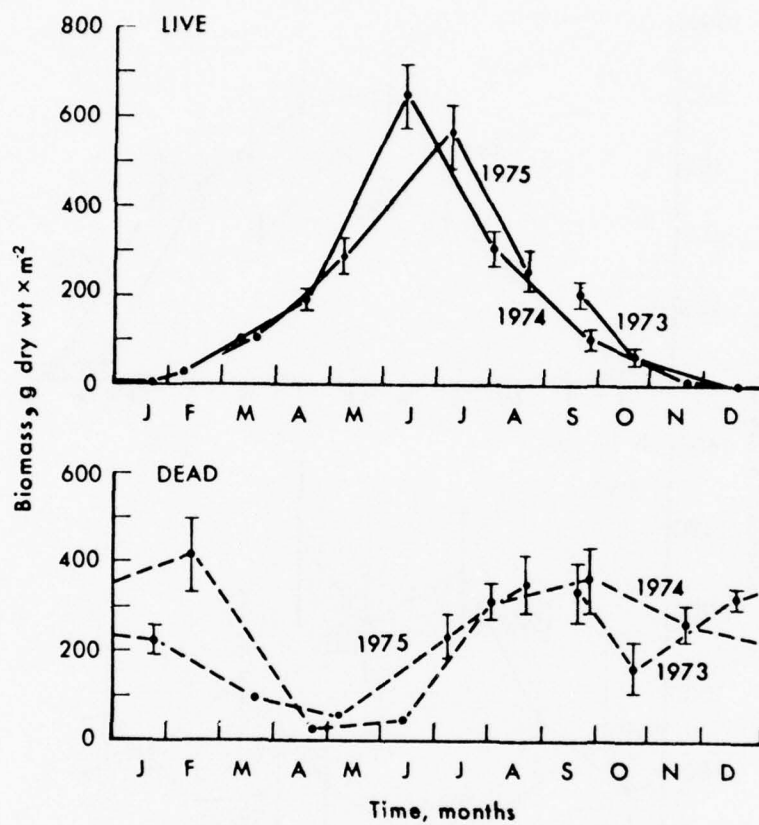


Figure 5. Seasonal changes in live and dead biomass of S. falcata.

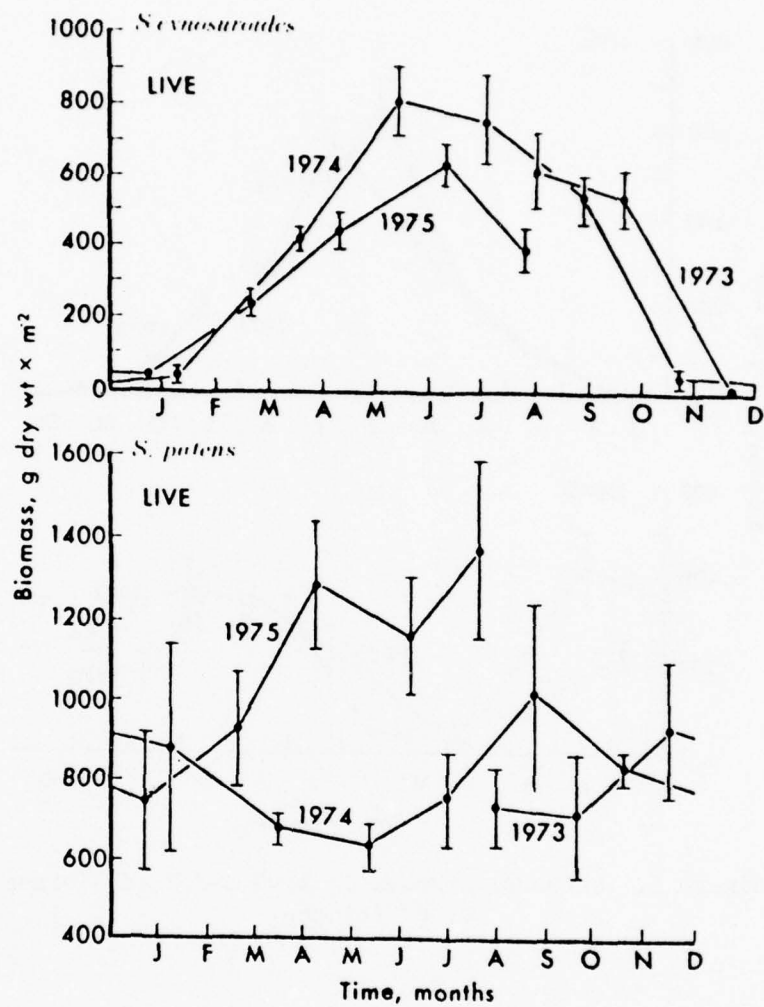


Figure 6. Comparison of the seasonal pattern of live shoot biomass of *S. patens* and *S. cynosuroides*.

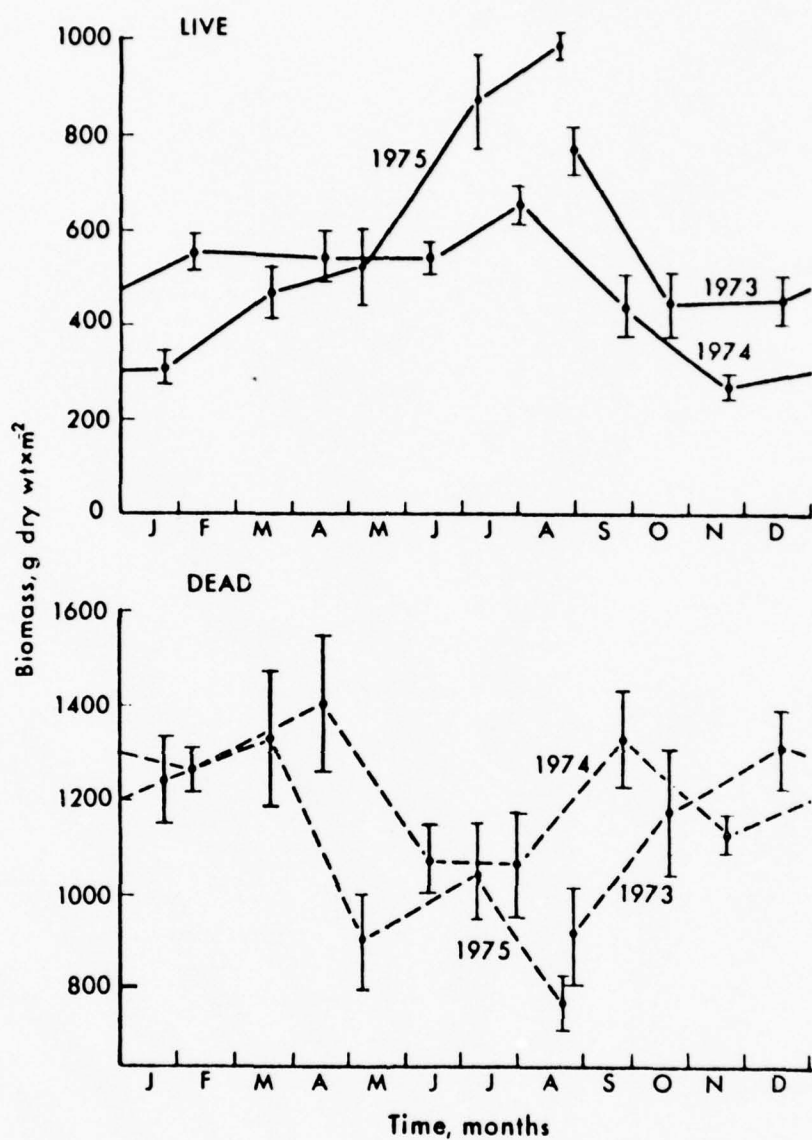


Figure 7. Comparison of seasonal nitrogen dynamics of S. falcata and S. patens.

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Gosselink, James G

Common marsh plant species of the Gulf Coast area; v.1: Productivity / by J. G. Gosselink, C. S. Hopkinson, Jr., and R. T. Parrondo, Louisiana State University, Baton Rouge, La. Vicksburg, Miss. : U. S. Waterways Experiment Station ; Springfield, Va. : available from National Technical Information Service, 1977.

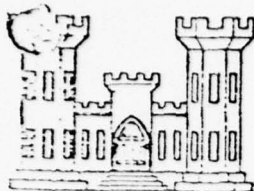
31, p102 p. : ill. ; 27 cm. (Technical report - U. S. Army Engineer Waterways Experiment Station ; D-77-44, v.1)

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Appendixes A-C on microfiche in pocket.

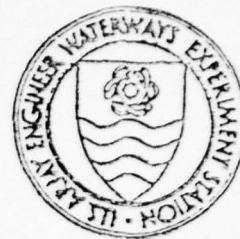
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1. Coastal marshes. 2. Gulf Coast. 3. Marsh plants. 4. Productivity. I. Hopkinson, C. S., joint author. II. Parrondo, R. T., joint author. III. Louisiana State University and Agricultural and Mechanical College. IV. United States Army Corps of Engineers. V. Series: United States Waterways Experiment Station, Vicksburg, Miss. Technical report ; D-77-44, v.1)
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COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA

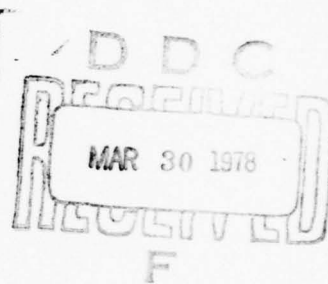
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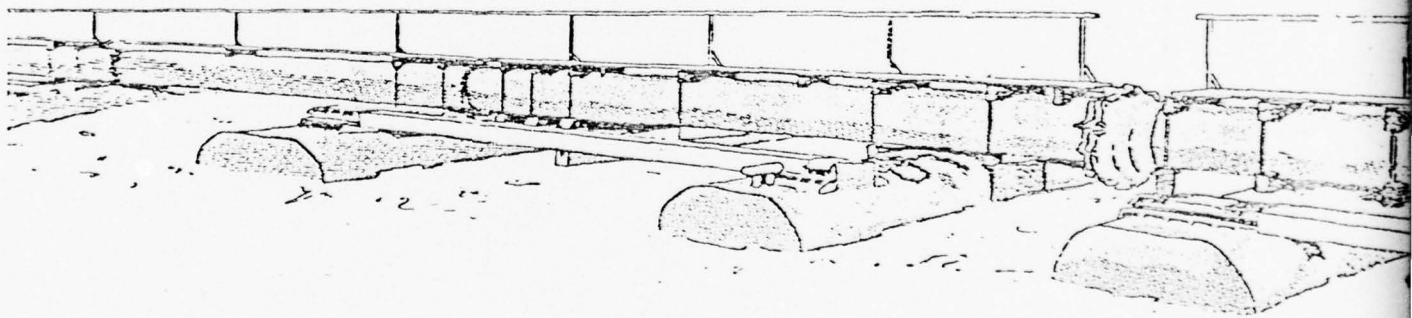
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Final Report



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APPENDIX A: DETERMINATION OF THE PRODUCTIVITY OF SEVEN COMMON MARSH
PLANT SPECIES FOUND IN COASTAL LOUISIANA USING HARVEST TECHNIQUES

Introduction

1. Detrital-based food webs predominate in salt marsh estuarine systems (Heald 1969; Teal 1962; Day et al. 1972; references listed at end of the appendix) with considerable organic matter derived from emergent marsh macrophytes. In Louisiana it has been shown that the contribution of organic matter from Spartina alterniflora marshes to adjacent bays equals the amount produced by aquatic flora within the bays (Hopkinson and Day in press). Much less is known about the importance of brackish and freshwater macrophytes in the overall productivity of marsh ecosystems. Few studies have considered the productivity of even the macrophytes themselves, and in these few the techniques used were often inadequate in that turnover rates were underestimated.

2. This appendix reports the study of aboveground production of seven species of marsh plants, each from different salinity, soil, and tidal regimes. The production measured is helpful in understanding the trophic energetics of various marsh species in Louisiana and its comparative importance to the whole system.

Description of Area

3. The areas under study are in the southeastern Louisiana coastal plain, which comprises several overlapping Mississippi River delta lobes formed during the last 7,000 years. The seven marsh plant study sites (Figure A1) lie along lower Bayou Lafourche with some sites in the Barataria drainage basin and the others in the Terrebonne drainage basin

(Chabreck 1972). These two adjacent hydrologic units are separated by the natural levee of Bayou Lafourche, a recently abandoned distributary of the Mississippi River. The interdistributary plain is comprised of water bodies (lakes, bays, and bayous), natural swamps, marshes devoid of topographic relief except along low natural levees, man-made levees, and spoil banks. The region has been fully described geologically by Frazier (1967) and Gagliano and van Beek (1970).

4. Along a line running inland from the coast, several gradients are apparent. The normal coastal tides that inundate the coastal marshes decrease and disappear as one approaches the upper reaches of the basin. Salinity also decreases with decreasing tidal influence. These physical gradients result in fairly distinct zones of vegetation running roughly parallel to the coast. The zones have been characterized as fresh marsh (0-5 ppt salinity), brackish marsh (5-20 ppt salinity), saline marsh (20 ppt salinity and up), and levee bank vegetation (Chabreck 1972). The marsh soils are generally described as peats, muds, and clays. Organic and clay content is highest in the fresh and brackish areas. The saline marshes tend to be predominantly fine silts (Gosselink et al. 1975).

5. The Mississippi River discharge and high levels of rainfall, insolation, and temperature contribute to the high productivity of the coastal marshes. The Mississippi River discharge into the shallow coastal waters of the Gulf of Mexico modifies the salinity and increases the nutrient and suspended load of the inshore saline marshes. Rainfall ($150 \text{ cm} \times \text{yr}^{-2}$) and insolation ($200\text{-}500 \text{ g-cal} \times \text{cm}^{-2} \times \text{day}^{-1}$) are fairly evenly distributed throughout the year. The climate is nearly

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subtropical with annual temperatures averaging 20°C. Freezes occur on the average once every seven years in the saline area and at least once a year in the fresh area. The coastal area has been described physically, chemically, biologically, and ecologically by Day et al. (1972), Chabreck (1972), Penfound and Hathaway (1938), and Gosselink et al. (1975).

6. Sampling sites were established for the following seven marsh plant species as shown in Figure A1: Distichlis spicata (salt grass), Juncus roemerianus (black rush), Phragmites communis (common reed), Sagittaria falcata (bulltongue), Spartina alterniflora (saltmarsh cordgrass), Spartina cynosuroides (big cordgrass), and Spartina patens (saltmeadow cordgrass).

7. The P. communis site was a relatively homogeneous stand in a freshwater marsh along Bayou des Allemands. Water levels here were controlled entirely by rainfall and wind and fluctuated at least 18 cm seasonally. Shoreline wave energy created by strong northwest winds was at times high as evidenced by a shoreline erosion of 2-6 m between August 1972 and August 1975. Dead plant material was often rafted up to 10 m into the cane stand. Because of a changing water level regime during the investigation, the importance of Phragmites declined while Panicum hemitomon and Leersia sp. became dominant, making up over 75 percent of the biomass by August 1975.

8. S. falcata was studied in a fresh marsh along Little Bayou Blue, west of Bayou Lafouche. A high levee of dredged material separated the site from the bayou, but occasional breaks in the levee allowed water to circulate through the site. Tidal influence was small,

but water depths up to 20 cm over the marsh were associated with prolonged southeasterly winds, and the marshes were drained when winds were out of the north. A relatively pure stand was selected in August 1973, but it became increasingly mixed with Eleocharis sp. and Eichhornia crassipes during the course of the study.

9. The S. patens site was located along Little Bayou Blue about 20 km south of the S. falcata site. This was part of a large area of brackish marsh dominated by S. patens with small amounts of D. spicata mixed with it. The study area was about 15 m inland from the bayou and almost always covered with water. Rain, winds, and tides controlled water level fluctuations. Salinity varied between 5 and 10 ppt.

10. The area selected for the study of J. roemerianus was on the northern edge of the salt marsh zone, along the natural levee of Bay Vasier in the northwest portion of Caminada Bay. Although this was a relatively homogeneous stand, S. alterniflora and D. spicata were also present in lesser amounts. The surrounding marsh vegetation was dominated by S. alterniflora and Avicennia nitida (black mangrove). The typical Louisiana gulf coast diurnal tidal cycle (15- to 60-cm amplitude) occurred in this area. The site is exposed to a 1.5-km fetch from the east and southeast across Bay Vasier, and occasional high energy storms have exposed roots and bare areas along the shore. Salinity in this area ranged between 8 and 20 ppt.

11. Sites were selected along the coast, inland from Bay Champagne and between Bayou Moreau and Bayou Lafourche, for the study of S. alterniflora and D. spicata. Salinity was generally over 20 ppt and tidal amplitudes were typically 15-60 cm. The S. alterniflora site was

a homogeneous stand situated inland (8 m) from a natural levee crest surrounding a small marsh lake. The D. spicata site was also a homogeneous stand on the back slope of the natural levee of Bayou Moreau (an old abandoned Mississippi River distributary). Wave energy was low in both areas.

12. The stand of S. cynosuroides selected for study was situated on the edge of the natural levee along which Louisiana Highway 1 was constructed, about 8 km west of the Caminada Bay bridge. The vegetation community changed with elevation on the levee. As elevation dropped the dominant species changed in zones from Quercus virginiana (live oak) to P. communis, Iva frutescens (marsh elder), and Panicum virgatum (switch grass); to S. cynosuroides and D. spicata; to pure D. spicata; and finally to S. alterniflora. D. spicata was mixed with the S. cynosuroides in the study site as a subcanopy vegetation. The elevation of the site generally precluded any tidal influence. Flooding was quite infrequent and was controlled predominantly by winds.

Methods

13. Net aboveground production was measured by the method of Wiegert and Evans (1964). This technique does not account for grazing losses, which for S. alterniflora have been estimated to be less than 5 percent of maximum live standing crop (Teal 1962).

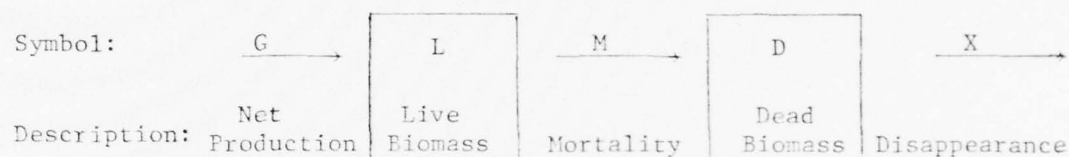
14. Sampling of all seven species commenced in August or September 1973 and continued for two years at roughly eight-week intervals. Quadrat size and shape were dictated by uniformity of growth, density of shoots, and time limitations. Square 1.0-m² quadrats were used to

sample P. communis, S. cynosuroides, and S. falcata. Square 0.25-m² quadrats were used for S. alterniflora and J. roemerianus, and 0.1-m² circles were used for D. spicata and S. patens. Five paired plots (A:B) were randomly chosen each period at each site, with precautions that no quadrat was sampled more than once, no quadrat was sampled that had been trampled during previous cuttings, and paired plots were visually similar in species composition and density. From the first quadrat (A of the A:B pair), all aboveground material was cut at ground level, placed in plastic bags, and taken to the laboratory where it was sorted into four categories: live, dead, dead parts removed from live plants, and other species. Samples were then dried at 80°C to constant weight. From the second quadrat (B of the A:B pair), all live material was removed. Care was taken to avoid damaging fragile dead-standing plant material. Normally, the B quadrat was resampled approximately eight weeks later when all dead material remaining was removed, bagged, and carried back to the laboratory for drying and weighing, but for S. falcata it was necessary to reduce this interval to three weeks because of the rapid decomposition rate of this species. All results are reported as dry weight per square meter.

15. In S. alterniflora, D. spicata, and J. roemerianus plots, secondary species contributed negligibly to biomass. In S. falcata and S. cynosuroides plots, secondary species were occasionally important but were sufficiently different to make separation of both live and dead material possible. Therefore, results for these sites are for single species. The S. patens plots contained considerable D. spicata, which could not realistically be distinguished from S. patens when dead.

Therefore, data from these plots are for the whole community in which S. patens was dominant. Sampling of dead vegetation in the P. communis plots was so unreliable that it was discontinued the second year. In addition, secondary species became an important component of the community during the second year. Therefore, data from only one year are included and represent production of a nearly pure stand of that species.

16. The calculation of net production by the method of Wiegert and Evans (1964) fits the following schematic:



where fluxes (G, M, X) are in units of grams dry weight (g) per unit area (m^2) per unit time (t), and standing stocks (L, D) are in grams dry weight (g) per unit area (m^2).

17. Live and dead biomass determinations were based on weights in the A plots of the A:B pair. The disappearance rate of dead vegetation was determined from the difference between the dead biomass in A and the dead biomass remaining in B eight weeks later.

18. To begin the calculation an instantaneous loss rate (r) was calculated as follows:

$$r = \frac{\ln (D_{t_0}/D_{Rt_1})}{t_1 - t_0}$$

where

r = instantaneous loss rate (g lost per g dead material per day)
 D_{t_0} = amount of dead material in A quadrat(s) at time t_0
 DR_{t_1} = amount of dead material remaining in B quadrat(s) at time t_1

From this loss rate the disappearance of dead material (X) during a time interval (Δt) is

$$X = r \times \Delta t \times \frac{D_{t_0} + D_{t_1}}{2}$$

where subscripts indicate the sampling time. Mortality for a sampling interval is:

$$M = X + (\Delta D)$$

Finally net production for the sampling interval is:

$$G = M + (\Delta L)$$

Results and Discussion

Aboveground biomass

19. Reliability. Figures A2 through A8 show the bimonthly biomass of live and dead vegetation of the seven species for the period of study. Three criteria were used to judge the reliability of these data: (a) the sequential nature of the biomass changes from sample to sample; (b) the degree of repetition of the annual cycle; and (c) the confidence limits or variance around each data point.

- a. Seasonal changes: Five of the species investigated showed clear seasonal increases in live biomass, from a low value in winter to a summer maximum. Peak biomass occurred in June for S. falcata and S. cynosuroides but later in the summer for P. communis, S. alterniflora, and D. spicata. Neither J. roemerianus nor S. patens showed any clear seasonal trends, as their live biomasses did not change appreciably over the year. This relative constancy of biomass has been reported previously for J. roemerianus (Williams and Murdoch 1969). Dead biomass trends were also clear for P. communis, S. alterniflora, and S. falcata but not for the other species. For the first two

species the seasonal curve of dead material was inverse to live biomass, with a peak in midwinter and a minimum in late summer. Kirby's (1972) data also show this clearly for S. alterniflora. Biomass of dead S. falcata increased during the summer from a low value in spring. The lack of clear trends in the other species can be attributed to several factors. The large weight of dead biomass year-round tends to mask relatively small seasonal changes. The fact that growth, mortality, and disappearance of dead vegetation occur continuously with some species (S. patens, J. roemerianus, D. spicata) means that clear seasonal peaks do not occur. The disappearance rate of dead S. falcata was extraordinarily high, keeping the dead biomass low at all times.

- b. Annual cycle. For five species the annual cycle was repeated closely in the second year. Both live and dead biomass of J. roemerianus increased steadily throughout the study, indicating that this site is in a transitional state. The dead biomass of S. patens also appeared to increase throughout the study.
- c. Confidence limits. Table A1 shows the range and average ratios of the standard error expressed as a percentage of the mean for live and dead biomass. Wiegert and McGinnis (1975), in a study of productivity of an old field in South Carolina, used this ratio as an index of reliability of field data. Their ratios averaged 15 to 24 percent for live material and 10 to 21 percent for dead material. Values in this study averaged 9 to 18 percent for live vegetation and 8 to 16 percent for dead. Thus, sample variance is within limits found acceptable by Wiegert and McGinnis.

20. Gauged by these three criteria, the reliability of the biomass data is acceptable for a field study of this kind.

21. Comparative results. Table A2 shows a wide range in magnitude of peak live biomass, from a low of $648 \text{ g} \times \text{m}^{-2}$ for S. falcata to a high of $1376 \text{ g} \times \text{m}^{-2}$ for S. patens. The range of live biomass encountered was roughly comparable to other reports, except that biomasses of D. spicata and S. patens were substantially higher than reported in any other studies (see Tables A3 and A4).

22. Perhaps the most significant difference in biomass between the sites of this study and others is the low ratio of live to dead vegetation. The ratios for all species on an annual average basis were less than one, ranging from 0.21 to 0.91. A ratio of 0.49 for S. alterniflora from this study compares with a ratio range of 0.64 - 1.9 for the same species in Georgia (Smalley 1959). The difference in ratios for this species is even more dramatic when end-of-season biomass maximums are used. The live-to-dead ratio from 0.7 to 1.0 in this study compared to 5.3 in Georgia (Smalley 1959) and 2.1 in Maryland (Keefe and Boynton 1973) may be a reflection of the high turnover rate of live vegetation and low tidal energy (responsible for flushing dead vegetation from the marsh) of the Louisiana gulf coast.

Instantaneous loss rates of dead material

23. Figures A9 to A11 and Table A5 show the results obtained from the paired plot measurements of the loss of dead vegetation for each of the species. The instantaneous loss rates (r) can be calculated on individual paired plots and then averaged, or the replications can be pooled before calculation to give a single $\bar{r}$ value. The two methods of calculating $\bar{r}$ give different mean rates because of the logarithmic nature of the calculations. The means are similar for some species and considerably dissimilar for others, with no consistent pattern of difference between the two methods of calculation. For any species, however, the rate calculated from pooled means is within the limits of the standard error calculated using the individual paired plots.

24. During each sampling interval there was a great deal of

variation among instantaneous loss rates calculated from individual paired plots. Apparently five pairs of plots are too few for consistent estimations. On occasion negative mean instantaneous loss rates (an increase of dead vegetation in the plot during a sampling interval) were observed. There are several possible explanations for this anomaly. There could have been unequal amounts of dead material in any paired plot; that is, sampling variation could account for a negative value. When negative mean values occurred, however, all five individual $\bar{r}$ values were usually negative or very low; sampling variation is probably not the major reason for these negative values. If the sampling interval is too long, live material can grow up and die in the B quadrat during the interval. More importantly for marshes, high water associated with strong wind or tidal action can cause the redistribution of plant debris into the B plots. Ideally, in order to measure the true disappearance rate from individual plots, there should be no additions of dead material to the B plots during the sampling interval. In the dynamic environment of the marsh, however, rafting is a common occurrence. Tides or high water pick up dead material and move it from one area to another. Consequently, some areas experience very high loss rates of dead material while others have very low or even negative loss rates. For an integrated picture of instantaneous loss rates for the whole marsh, these aberrant values must be included. (For this study it has been assumed that manipulation of the B plot does not make it any more or less likely to trap debris carried by flooding waters.)

25. The fluctuation of observed instantaneous loss rates from month to month is a function of the dynamic nature of marsh environments

and was expected. The general lack of any annual repetition of seasonal cycles was also expected as many parameters that strongly influence loss rates, such as storms (including hurricanes) and periods of rapid water level change, do not themselves follow precise year to year cycles. Also expected was the wide variation in loss rates among species. Inherent variation in the susceptibility of different species to decomposition has been reported (Odum and de la Cruz 1967). In addition some species have most of their dead biomass standing while others have it lying on the marsh where it is constantly or intermittently flooded, thus affecting both decomposition and flushing rates. In this respect it is interesting to note that S. cynosuroides and P. communis, which have most of their dead biomass standing and, consequently, above the influence of changing water levels, had the lowest instantaneous loss rates of dead material.

26. For comparative purposes the bimonthly loss rates were combined to give an annual mean (Table A5). On a yearly basis S. falcata had the highest instantaneous loss rate ($25.2 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$), followed by J. roemerianus ($11.5 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$), S. patens ($10.5 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$), D. spicata ($7.7 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$), S. alterniflora ($6.7 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$), S. cynosuroides ($4.9 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$), and P. communis ($4.7 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$). Seasonal rates were calculated for a seven-month (April-October) summer period and a five-month (November-March) winter period. When values for both years are combined, all of the species had higher rates of disappearance in the summer than in the winter. However, for only three species, D. spicata, J. roemerianus, and S. cynosuroides, were both summer rates of disappearance higher than both winter rates. As an

example, the disappearance rate of S. patens during the 1974 summer was higher than during the 1974-75 winter but lower than during the 1973-74 winter. The fact that S. falcata data indicate a higher r during both winters than during the 1974 summer is possibly an artifact of the sampling interval during the first year. During the summer the S. falcata leaves grow and die so rapidly that considerable regrowth and death in the B quadrats occurred between samples. Shortening the sampling interval for the B quadrats from eight to three weeks in 1975 mitigated this sampling problem, as is evident by the substantially higher rates encountered thereafter.

27. The lack of clear seasonal differences in instantaneous loss rates (Figures A9 to A11) indicates two noteworthy attributes of these marshes. First, because of the nearly subtropical temperatures, decomposition occurs at a measurable rate year-round. Second, wind and tide-driven waters inundate the marshes periodically and cause large changes in dead biomass during the course of a single storm. As a result, high and low r values occur independently of season.

28. It is appropriate to compare the loss rates recorded during this study with those calculated in other studies. Wiegert and Evans (1964) and Wiegert and McGinnis (1975) measured paired-plot and litterbag loss rates in old fields in Michigan and South Carolina. In these fields their summer paired-plot loss rates were comparable with this study's rates. However, their litterbag loss rates were considerably lower (summer rates were $12 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$ for paired-plots vs. $2.3 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$ for litterbags). Kirby (1972), who measured loss rates of S. alterniflora from litterbags in a Louisiana marsh, suggested that

litterbag loss rates were more realistic for tidal marshes than for old fields because of regular tidal flushing. This study supports his observation. For streamside S. alterniflora, Kirby's maximum summer rate was $8.5 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$; his annual mean rate was $6 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$. For the same species this study's maximum summer loss rate was $16.6 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$, with an annual average of $6.7 \text{ mg} \times \text{g}^{-1} \text{ day}^{-1}$. Whereas paired-plot rates were 5.2 times greater than litterbag rates in the old field studies, they were only 1.9 times greater in a S. alterniflora marsh during summer and on an annual basis only 1.1 times greater. Although annual disappearance rates are similar for the two techniques in an S. alterniflora marsh, the litterbag method does not show the degree to which loss rates fluctuate from month to month as measured with the paired-plot method. Litterbags prevent the possibility that strong tidal action will remove great amounts of dead material and do not measure the input of dead material by rafting.

Net aboveground production

29. Table A2 summarizes annual production for the seven species studied and Figures A12-A13 show results seasonally. The reliability of these data can be assessed in a number of ways. The calculations of net production involve the rates of disappearance of dead vegetation and the seasonal changes in live and dead vegetation. Statistical reliability of these parameters is indicated in previous figures and tables. As mentioned, the variability in live and dead standing crop measurements, as indicated by the ratio of standard error to mean, is well within acceptable limits for field data of this kind. Variability in the

disappearance rates during a single two-month period, however, was high. This is the largest source of uncertainty in the production estimates.

30. Although bimonthly measured production rates show large oscillations because of the large fluctuations in both $\underline{r}$ values and dead biomass, in general they show that production is highest during the summer months, and that for four of the species (S. alterniflora, S. patens, D. spicata, and J. roemerianus) considerable growth occurs during the winter. S. falcata, P. communis, and S. cynosuroides plants die to the ground in late fall and exhibit little or no new growth during the winter.

31. To get the estimates of annual net aboveground production shown in Table A2, bimonthly production calculations were made by the Wiegert-Evans method, using lumped mean $\underline{r}$ values for each two-month interval. The table shows also the annual values for the first year of the study compared to the second.

32. An additional estimate reported is the annual disappearance of dead organic matter from the marsh. This was calculated from mean annual instantaneous loss rate and mean annual dead biomass. Production and disappearance should be equal where the average annual biomass is not changing (Wiegert and Evans 1964). The two values are therefore comparable but somewhat independently derived. The disappearance rate is one component of the production calculation, but the latter includes the additional parameters of live and dead biomass change. In addition, the production calculations were based on bimonthly data whereas the annual disappearance rate was based on annual averages. The magnitude of production for any single two-month period depends heavily on the

magnitude of the instantaneous loss rate and of the dead biomass during that period. For instance, a high production estimate results from coincidence of high instantaneous loss rate and high dead biomass. This "fine structure" was lost in calculating the annual disappearance rate, so this estimate can be used as a check on production. The two values agree closely, except in sites that appear to be in some kind of transition. These are the S. patens and J. roemerianus sites, in which the annual biomass of vegetation increased dramatically during the study. The production and disappearance rates for P. communis are considered tentative since measurement of loss rates and dead biomass at this site entailed very large variability, and some of the measured dead biomass increases were not realistic in view of the available live vegetation.

33. The last column of Table A2 shows the annual turnover rates of live and dead vegetation. For the first six species listed the high live turnover rates indicate the dynamic character of production in these southern marshes. Four of these six species have no single annual growth cycle. Young shoots emerge continuously and mature and die in all seasons. Although S. falcata and P. communis are killed to the ground in winter, green shoots emerge following each killing frost and several overlapping cycles of growth occur during the year. S. cynosuroides is an exception in that it does have a single annual flush of growth in spring. Production for this species was only 1.6 times peak live standing crop.

34. The turnover rates for dead material are also very high. Differences among species are attributed to differences in ease of decomposition, in the growth habit of the species, and in the hydrologic

regime that keeps the vegetation wet and flushes it out of the marsh. The high rate of loss of S. falcata is probably related to the fact that upon dying the vegetation immediately falls onto a constantly flooded marsh surface and to the high nitrogen content of the leaf tissue, which averages about 3 percent compared to about 1 percent for the other species (unpublished data, this study).

Summary

35. These estimates of aboveground net productivity represent the first detailed comparative study of a number of marsh phanerogams in the same geographical area of the gulf coast. Note the magnitude of production in all these species as compared to S. alterniflora, for which the high productivity has been well documented. The production figures for S. alterniflora are comparable with those of Kirby (1972) for the same area and therefore are not unusual. Its high production has been related to tidal subsidies by Schleske and Odum (1961). Odum and Fanning (1973) suggested that higher production by S. alterniflora than S. cynosuroides in Georgia was evidence in support of the tidal energy subsidy. This study shows S. patens, J. roemerianus, and D. spicata to have considerably higher production than S. alterniflora, although of these three only J. roemerianus received comparable tidal energy. S. patens marshes are peat-forming and brackish with sluggish water exchange characteristics. Consequently, the relationship of tidal energy subsidy to production of different species apparently does not hold in Louisiana marshes. It might be valid to compare the subsidy-production relationship for one species at a time as done by Warren et al. (in

press). The original tidal energy subsidy theory of Schleske and Odum (1961) should not be extended to interspecies comparisons but restricted to explain the high production of coastal marsh systems in general.

36. The differences in productivity are closely related to the growth habits of these species. Those with relatively low productivity rates are the species (P. communis, S. falcata, and S. cynosuroides) that die to the ground each winter. They have strong seasonal patterns of growth. In contrast, S. patens, J. roemerianus, and D. spicata all grow significantly throughout the winter. S. alterniflora is intermediate in its habit; distinct summer peaks in biomass (Figure A8) and growth rate occur, and most culms die after flowering in late fall. However, new shoots do emerge continuously and mature and die throughout the year.

37. This study points out the need for standardization of productivity techniques. Peak standing biomass measurements are simple to carry out, but in this study in some cases underestimated true net production by a factor of >5. This factor probably decreases with latitude, so that even for comparative purposes peak live biomass is misleading. Therefore a second parameter that should be a component of any productivity study is the turnover rate, which relates biomass to true net productivity.

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Table A1
Sampling Variability for Seven Marsh Plant Species
at Individual Sampling Times*

<u>Species</u>	<u>Live Vegetation</u>		<u>Dead Vegetation</u>	
	<u>Range</u>	<u>Mean</u>	<u>Range</u>	<u>Mean</u>
<u>S. alterniflora</u>	6-19	11	3-28	11
<u>D. spicata</u>	2-15	9	3-12	8
<u>J. roemerianus</u>	10-25	18	7-30	15
<u>S. patens</u>	5-29	15	5-30	14
<u>S. falcata</u>	0-24	11	6-37	16
<u>S. cynosuroides</u>	0-41	13	6-30	15
<u>P. communis</u>	8-33	17	4-19	10

*Expressed as the ratio of the standard error to the mean $\times 100$.

NOTE: $n = 5$.

Table A2

Annual Biomass and Production Parameters of Seven Species of Marsh Grass

Species	Live Biomass Annual Mean $g \times m^{-2}$	Dead Biomass* Annual Mean $g \times m^{-2}$	Peak Live Biomass $g \times m^{-2}$	Production** Mean & Range $g \times m^{-2} \times yr^{-1}$	Disappearance† $g \times m^{-2} \times yr^{-1}$	Turnover Rates	
						Prod: Mean Live Biomass	Loss: Mean Dead Biomass
<u>S. patens</u>	900	1530 (0.58)	1376	6043 (5924-6163)	5138	6.7	3.4
<u>J. roemerianus</u>	827	905 (0.91)	1240	3416 (3039-3794)	3105	4.1	3.4
<u>L. spicata</u>	560	1143 (0.49)	991	3237 (3108-3366)	3171	5.7	2.8
<u>S. alterniflora</u>	469	958 (0.49)	754	2658 (2523- 794)	2412	4.6	2.5
<u>L. communis</u>	478	2222 (0.21)	990	2318 (1825-2811)	3244	4.9	1.5
<u>S. falcata</u>	199	228 (0.87)	648	1501 (1389-1613)	1572	7.5	6.9
<u>S. cynosuroides</u>	394	951 (0.41)	808	1355 (1052-1659)	1631	3.4	1.7

* Number in parentheses shows the ratio of the live to dead biomass.

** Calculated from bimonthly data using pooled mean r values. Range shown indicates variation found using two different 12-month periods for calculation.

† Disappearance = $\bar{D} \times \bar{r} \times 365$ days where $\bar{D}$ = annual mean dead biomass, and $\bar{r}$ = annual mean disappearance rate calculated from pooled means.

Table A3

Summary of Data on Standing Crop ($g \times m^{-2}$) and Annual Production ($g \text{ dry wt} \times m^{-2} \times yr^{-1}$)of *S. alterniflora*

Geographical Location and Reference	Marsh Location	Peak Standing Crop		Net Production Per Year Method			
		Live	Dead Total	Peak Live Standing Crop	Smalley's Other	Wiegert and Evans	
Texas Turner and Gosselink 1975	Average	756					
Louisiana Kirby 1972	Streamside	1018	942	1960	1410	2857	2645
	Inland	787	757	1544	1006	1960	1323
	Average	845	784	1629	1140	2180	
This study	Tall-Medium	754	1015	1769	754	1063	2658
Florida Reimold et al. 1975	Average	798	445	1243	798		
Young (per. comm.)	Average	580					
Georgia Odum and Fanning 1973 (included est. of material flushed by tides)	Tall Medium Average	3018 2018 2335	297 164 2335	3315 2182 2335		3990 2362 2883	
Reimold et al. 1972	Infrared: red light red blue red blue	1618 480 416 291	247 243 187 67	1865 723 603 358			

(continued)

*Different marsh areas identified by color signature from aerial color infrared imagery. Red corresponds with streamside areas, other colors with higher, less productive marshes.

Table A3. Continued.

Geographical Location and Reference	Marsh Location	Peak Standing Crop		Net Production Per Year Method			
		Live	Dead	Total	Peak Live Standing Crop	Smalley's	Wiegert and Evans
Georgia Smalley 1959	Levee	1230	830	2060			2240
	High marsh	472	297	769		643	
	Average	762			762		1364
North Carolina Williams and Murdoch 1969	Tall	1550	650	2200			
	Medium	750	750	1500			
	Short	400	700	1100			
	Average	545			545		650
Stroud and Cooper 1968	Tall	1320	433	1753		1296	1563
	Medium	477	409	886		461	471
	Short	259	196	455		329	280
	Average	382			382	492	646
Virginia Wass and Wright 1969	Tall			1570			
	Short			695			
	Average			1140			
Maryland-Virginia Keefe and Boynton 1973	Tall + Short	558	497	1055			
	Short	427	242	669			
	Average	484			484		
Delaware Morgan 1961	Streamside	441					
	Inland	249			249-441		455
New Jersey Squiers and Good 1974	Tall	1592	110	1702			
	Short	592	90	682			

(continued)

Table A3. Concluded.

Geographical Location and Reference	Marsh Location	Peak Standing Crop		Net Production Per Year Method		
		Live	Dead	Total	Peak Live Standing Crop	Smalley's Other Wiegert and Evans
New Jersey Good 1965	Tall Average	532 300			300	
New York Udell et al. 1969	Tall Short Average			827 505 548		
Connecticut Steever 1972	Tall Stunted	717 313	187 211	904 524		
Rhode Island Nixon and Oviatt 1973a,b	Tall + Medium Short Average			446-946 432 466		
Massachusetts Valiela and Teal 1974	Low High	320 385				
Nova Scotia Mann 1972	Average					757

Table A4

Summary of Data on Standing Crop ($g \times m^{-2}$) and Annual Production ($g \text{ dry wt} \times m^{-2} \times yr^{-1}$)

of *D. spicata*, *S. patens*, *S. cynosuroides*, *P. communis*, and *J. roemerianus*

Species	Geographical Location and Reference	Peak Standing Crop		Net Production
		Live	Dead Total	
<i>D. spicata</i>	Georgia			
	Gallagher et al. 1973	246	357	603
	Virginia			360
	Wass and Wright 1969			1320*
	Delaware			
	Morgan 1961	453		
	New York			
	Udell et al. 1969			648
	Connecticut			
	Steever 1972	359	526	885
<i>S. patens</i>	Rhode Island			
	Nixon and Oviatt 1973b*			680
	Louisiana			
	This study	991	757	1748
				3237
	North Carolina			
	Waits 1967	641	655	1296
	Virginia			
	Wass and Wright 1969			805
	New Jersey			
<i>S. patens</i> and <i>D. spicata</i> mixture.	Nadeau 1972	463	160	623
	New York			
	Udell et al. 1969			503
	Harper 1918			991
	(continued)			

**S. patens* and *D. spicata* mixture.

Table A4. Continued.

<u>Species</u>	<u>Geographical Location and Reference</u>	<u>Peak Standing Crop</u>		<u>Net Production</u>
		<u>Live</u>	<u>Dead</u> <u>Total</u>	
<u>S. p. tens</u> <u>continued</u>	Connecticut			
	Steever 1972	285	478	763
	Louisiana			
	This study*	1376	2484	3860
				6043
<u>S. cynosuroides</u>	Georgia			
	Odum and	724	305	1029
	Fanning 1973**	Avg: 515-2142	110-850	
	Virginia			
	Wass and Wright 1969	512	913	1425
	Mendellsohn 1973 [†]	546	442	988
	Louisiana			546
	This study	808	1336	2144
				1225
<u>P. communis</u>	New York			
	Harper 1918			2688
	Rhode Island			
	Nixon and Oviatt 1973b			800-1000
	England			
	Pearsall and Gorham 1956			750-1300
	Buttery and Lambert 1965			497
	Sweden			
	Stake 1967			3687
	Louisiana			
	This study	990	1468	2298
				2318
<u>J. roemerianus</u>	Florida			
	Heald 1969	232	849	1081
				849

(continued)

**Production calculated by adding dead increment from April-August.

[†]S. cynosuroides is dominant species.

Table A4. Concluded.

<u>Species</u>	<u>Geographical Location and Reference</u>	<u>Peak Standing Crop</u>		<u>Net Production</u>
		<u>Live</u>	<u>Dead</u> <u>Total</u>	
<u>J. roemerianus</u> continued	North Carolina			
	Foster 1968	828		560-1028
	Waits 1967	612	1270	895-1360
	Stroud and Cooper 1968	804	952	796-1215
	Williams and Murdoch 1972	743	1709	754
	Virginia			
	Wass and Wright 1969	656		
	Louisiana			
	This study	1240	1456	3416
			2696	

Table A5

Annual Mean and Seasonal Mean Instantaneous Loss Rates ($\text{mg} \times \text{g}^{-1} \times \text{day}^{-1}$)
of Seven Marsh Plant Species, Calculated by Two Different Methods

Species	Annual			
	Calculated from Pooled Replications*		Calculated from Individual Replications*	
	Average	Range	Average	Range
<u>S. alterniflora</u>	6.9	6.2 - 7.7	6.7	5.9 - 7.6
<u>D. spicata</u>	7.5	7.5 - 7.6	7.7	7.6 - 7.8
<u>J. roemerianus</u>	9.4	6.8 - 12.1	11.5	8.0 - 15.0
<u>S. patens</u>	9.2	8.4 - 10.0	10.5	7.1 - 13.9
<u>S. falcata</u>	18.9	17.7 - 20.1	25.1	19.5 - 30.8
<u>S. cynosuroides</u>	4.7	3.7 - 5.7	4.9	4.7 - 5.1
<u>P. communis</u>	4.0	2.3 - 4.9	4.7	3.2 - 5.4

Species	Seasonal**					
	Summer			Winter		
	1974	1975	Mean†	1974	1975	Mean
<u>S. alterniflora</u>	8.5	5.4	7.0	7.8	4.0	4.0
<u>D. spicata</u>	8.8	9.1	9.0	5.6	5.7	5.7
<u>J. roemerianus</u>	16.9	11.8	14.4	11.1	0.75	5.9
<u>S. patens</u>	10.1	13.7	11.9	12.6	5.7	9.1
<u>S. falcata</u>	19.4	40.0	25.7	21.9	26.2	24.1
<u>S. cynosuroides</u>	4.7	8.2	6.4	3.0	2.4	2.7
<u>P. communis</u>	6.2	†	6.2	1.3	†	1.3

*See text (beginning on page 45) for explanation. Range shown indicates variation found using two different 12-month periods for calculation.

**Calculated for individual replications.

†Sampling discontinued due to technical difficulty which made the data unreliable.

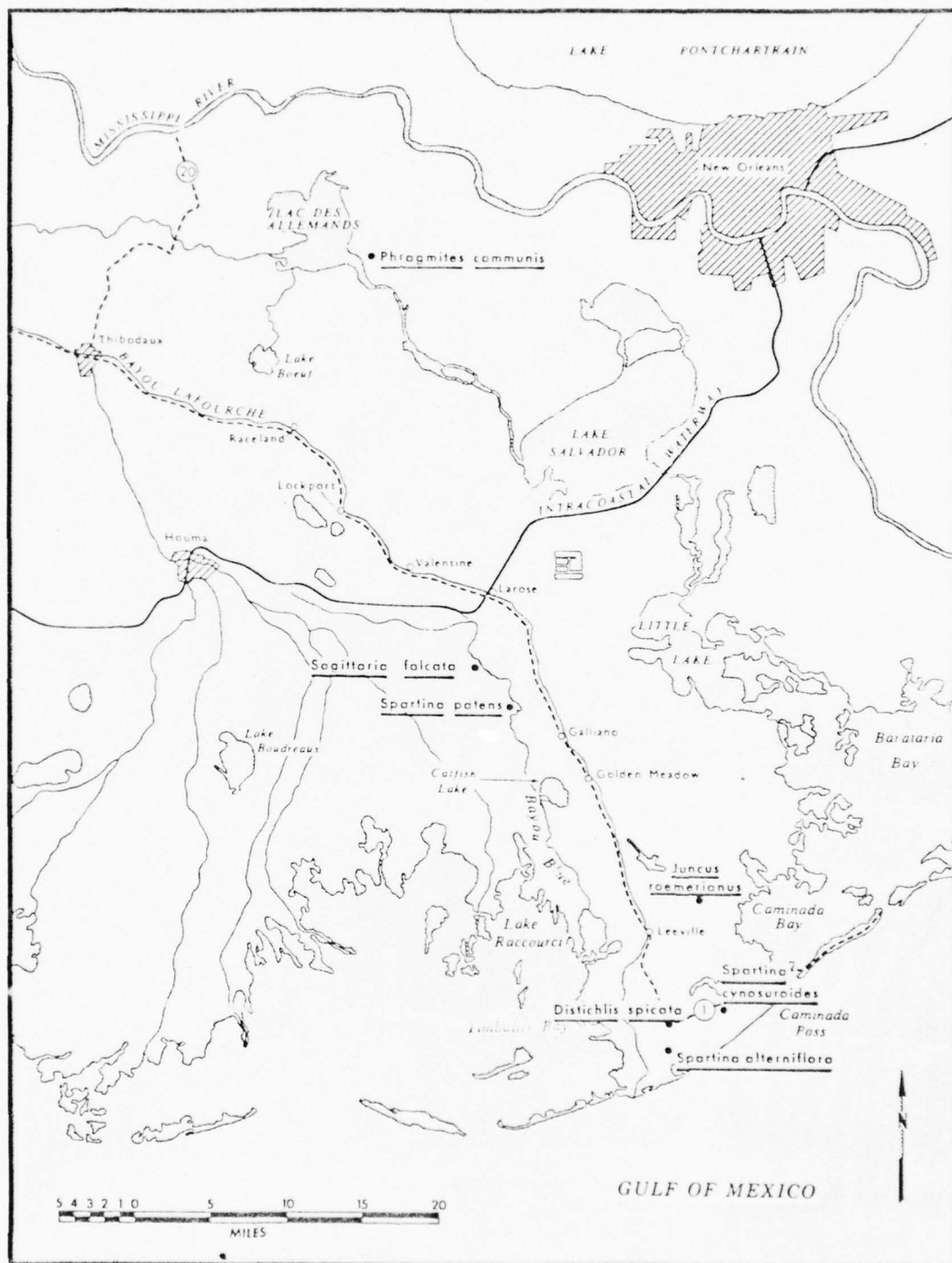


Figure A1. Sampling site locations.

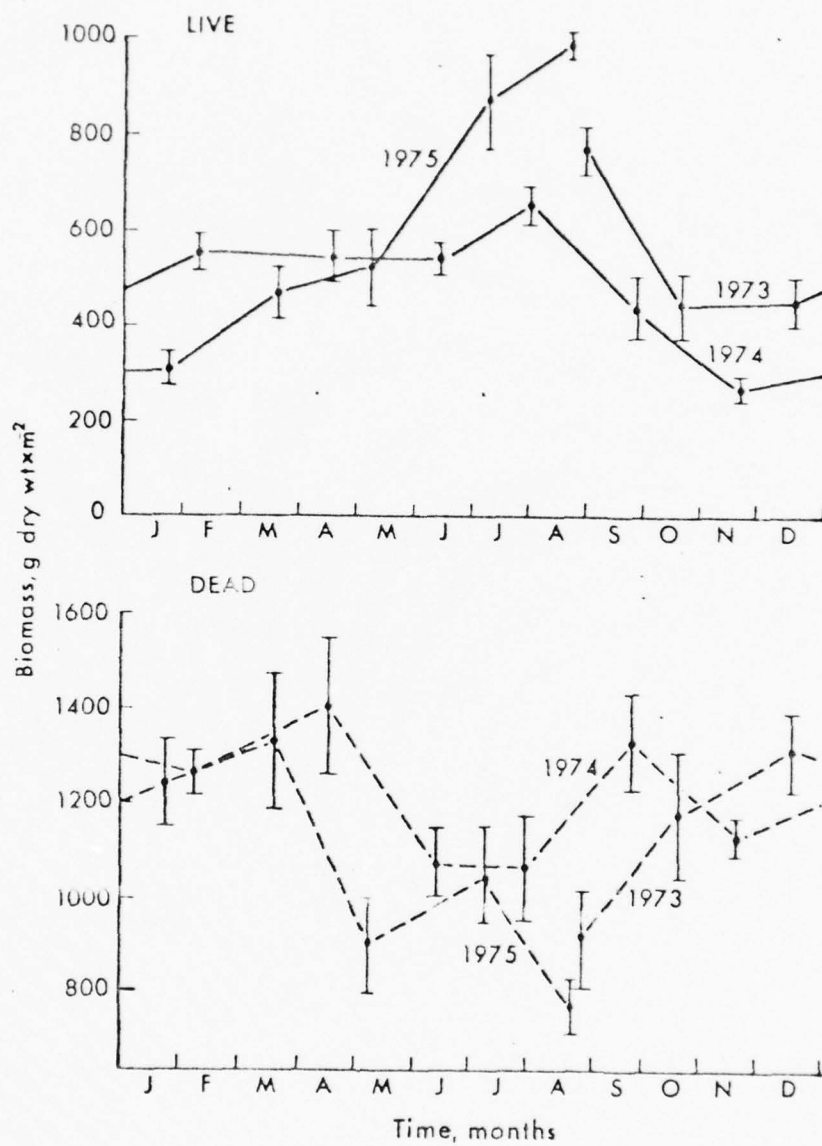


Figure A2. Seasonal changes in live and dead biomass of D. spicata.

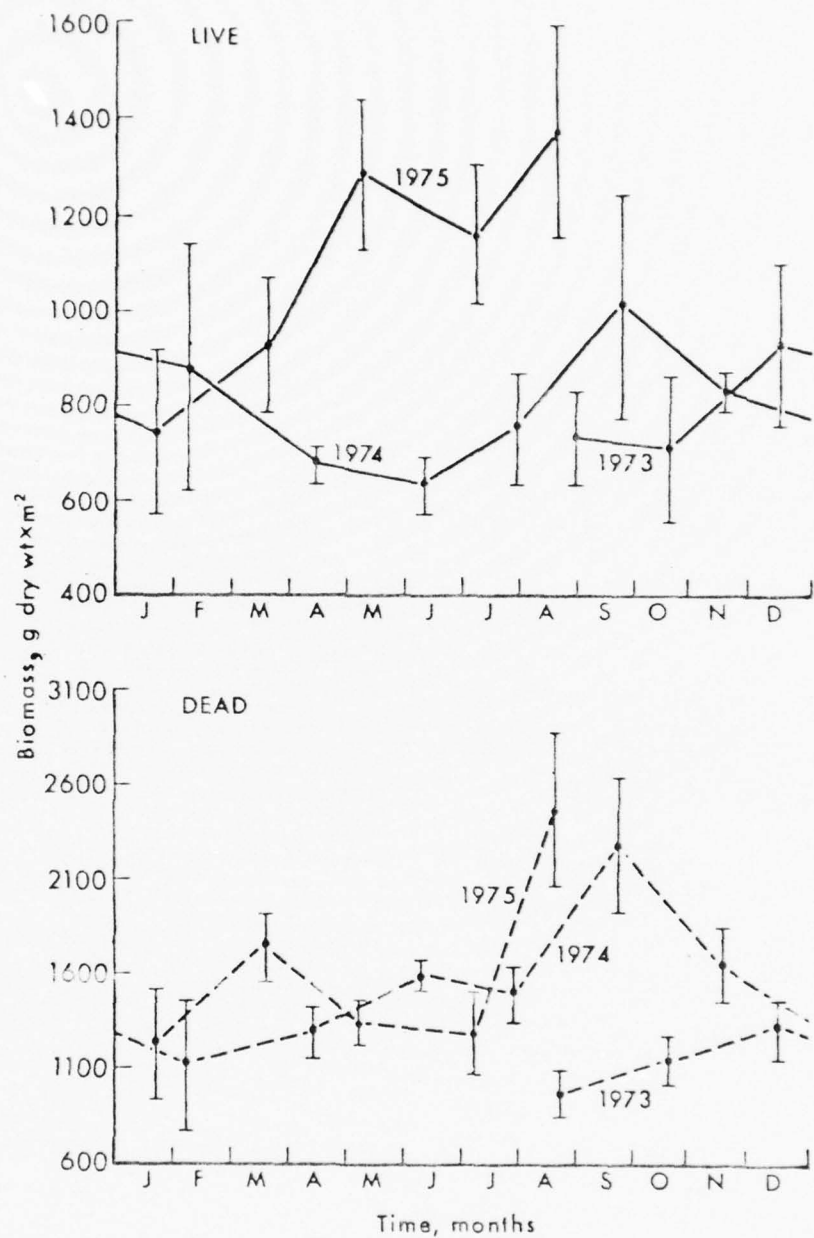


Figure A3. Seasonal changes in live and dead biomass of *S. patens*.

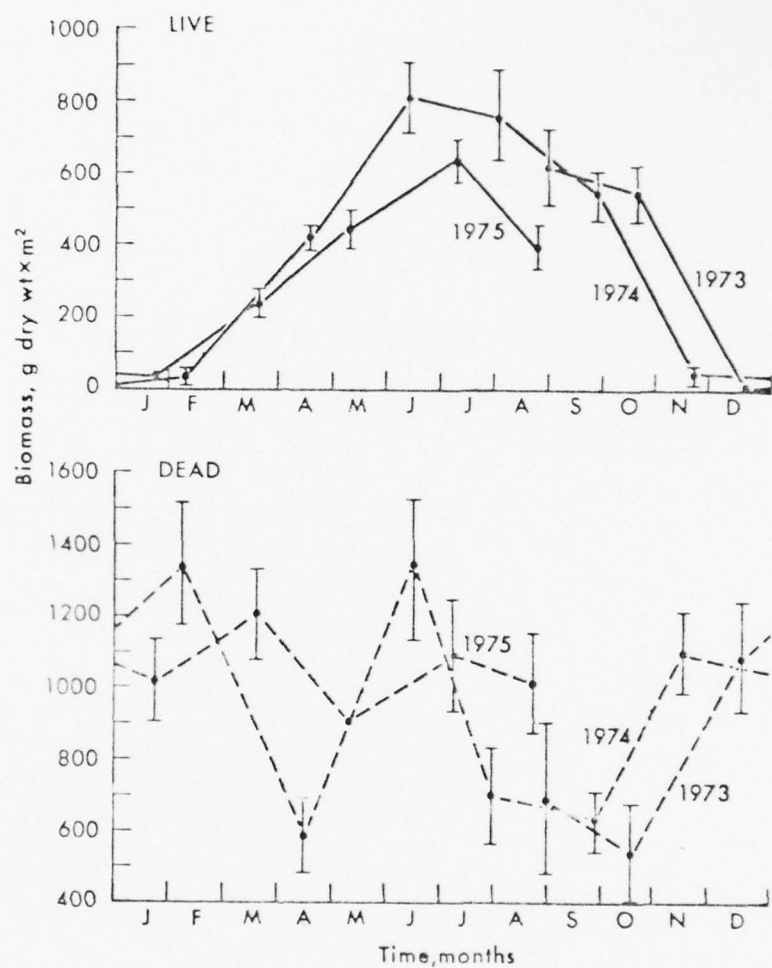


Figure A4. Seasonal changes in live and dead biomass of S. cynosuroides.

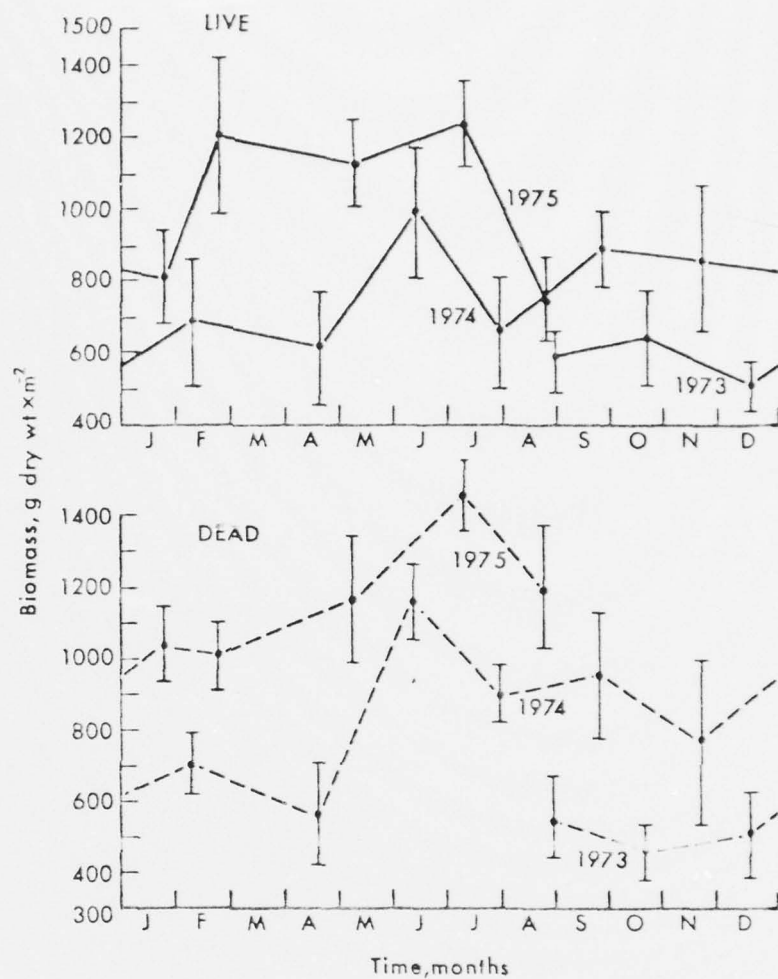


Figure A5. Seasonal changes in live and dead biomass of *J. roemerianus*.

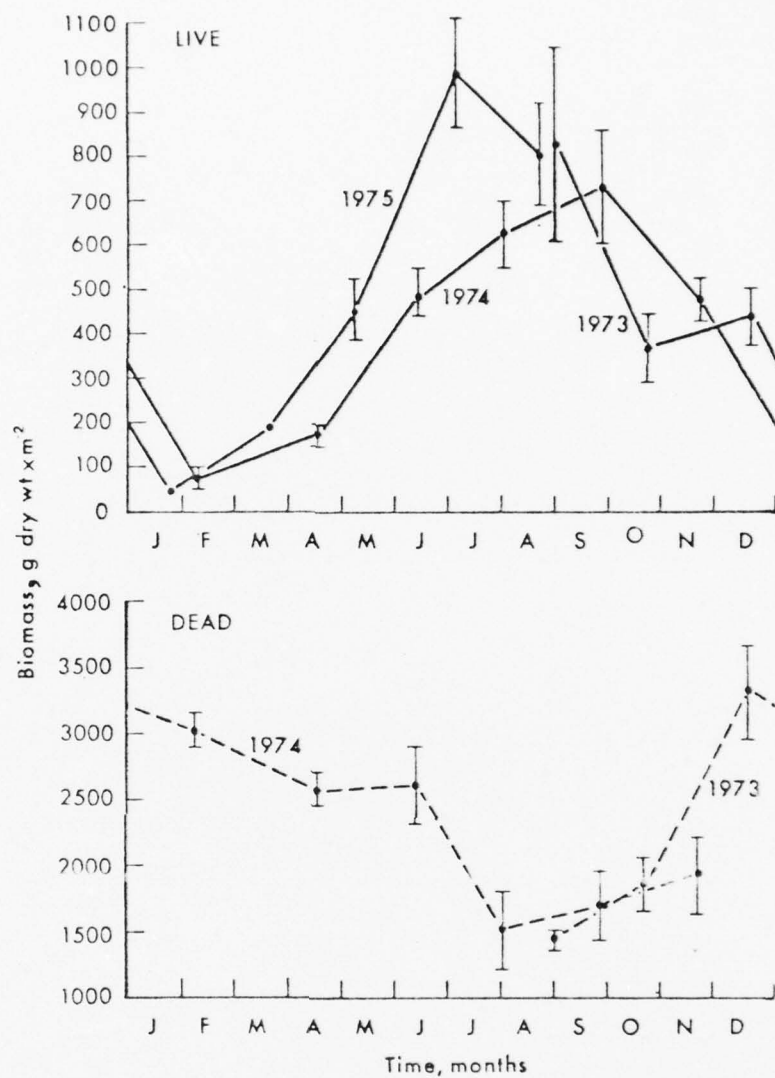


Figure A6. Seasonal change in live and dead biomass of *P. communis*.

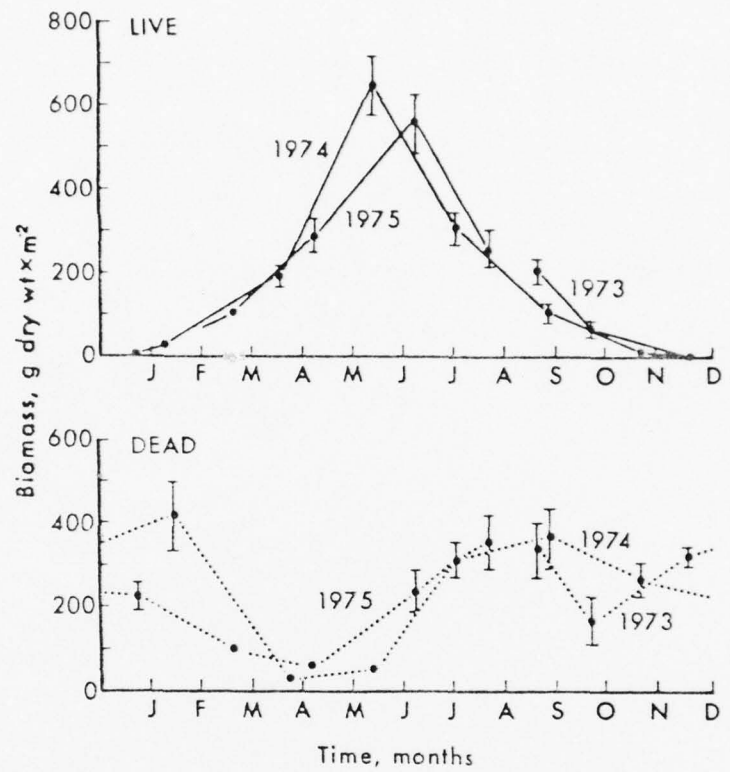


Figure A7. Seasonal change in live and dead biomass of *S. falcata*.

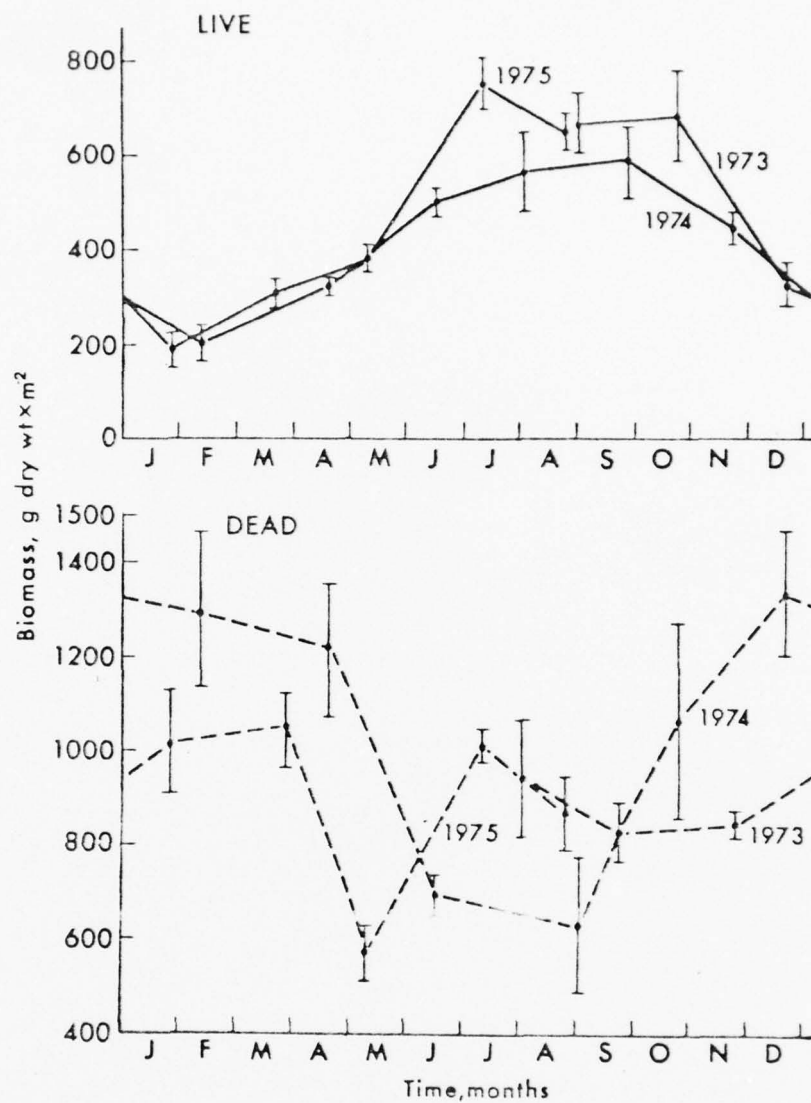


Figure A8. Seasonal change in live and dead biomass of *S. alterniflora*.

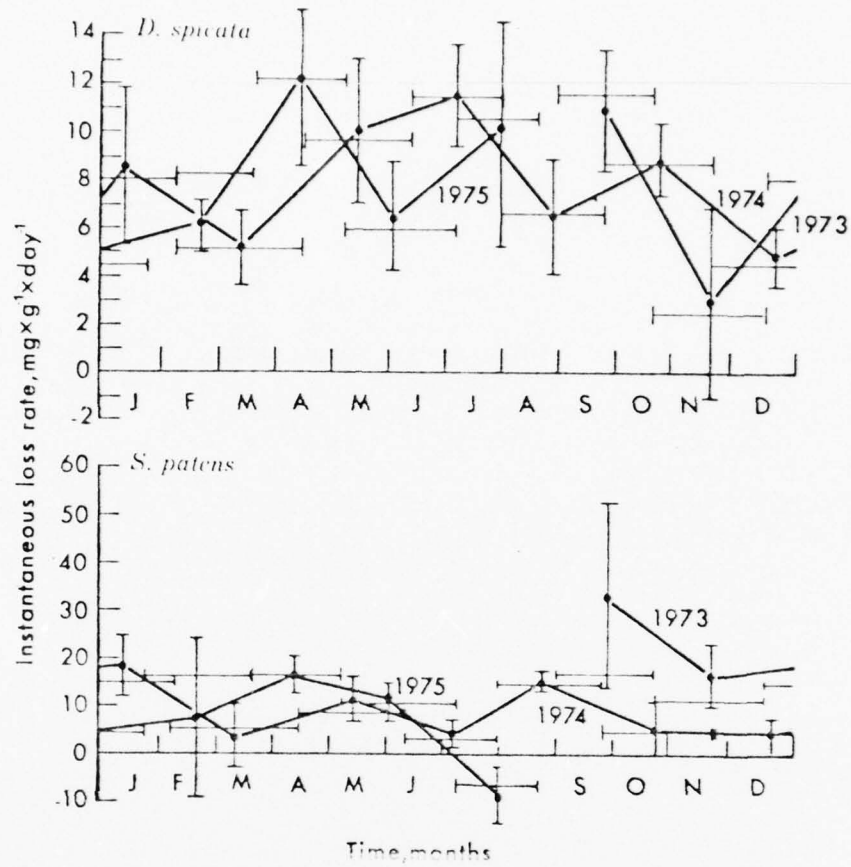


Figure A9. Comparison of instantaneous loss rate for *D. spicata* and *S. patens*.

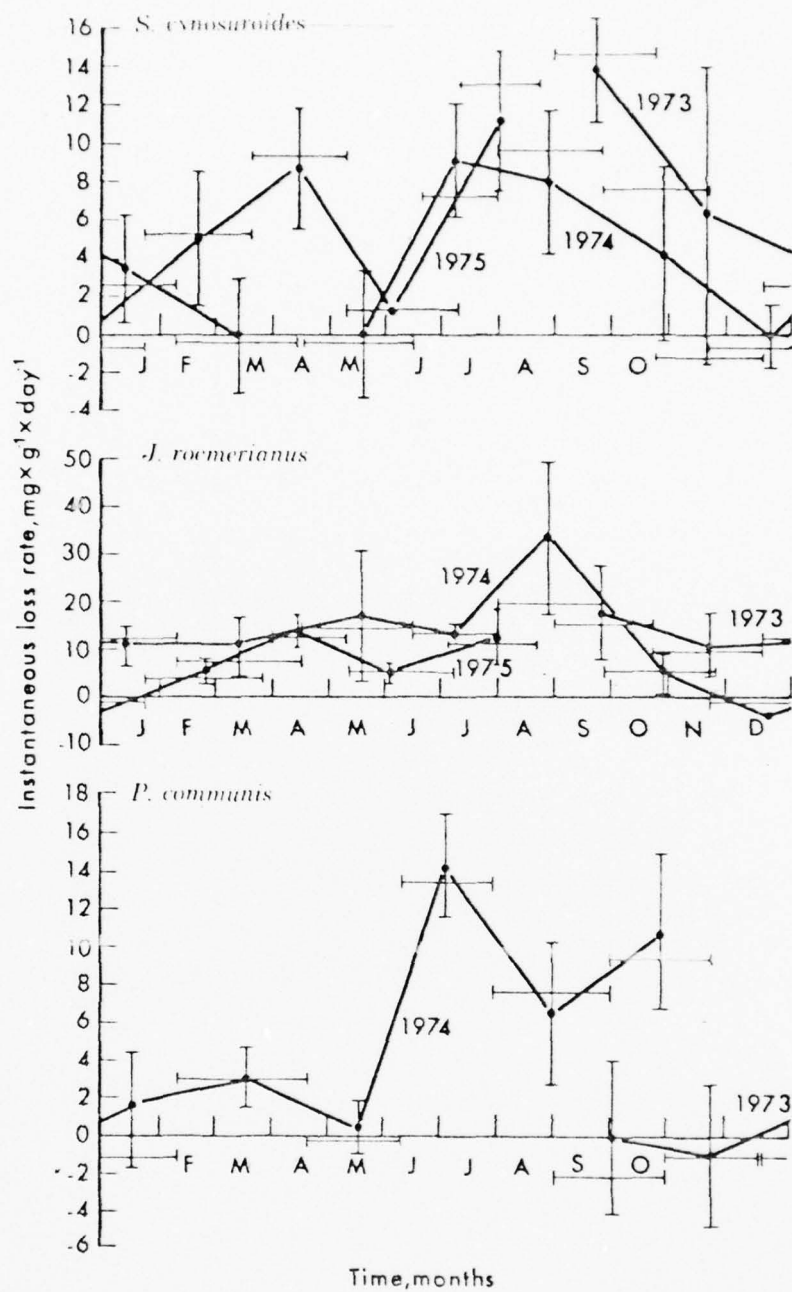


Figure A10. Comparison of instantaneous loss rate for *S. cynosuroides*, *J. roemerianus*, and *P. communis*.

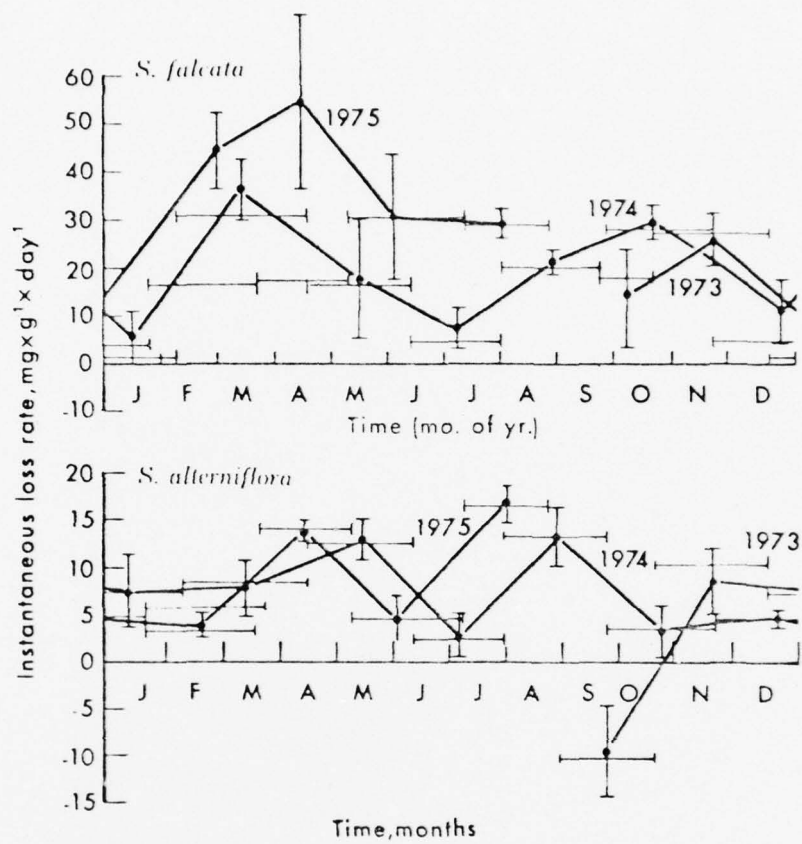


Figure A11. Comparison of instantaneous loss rate for S. falcata and S. alterniflora.

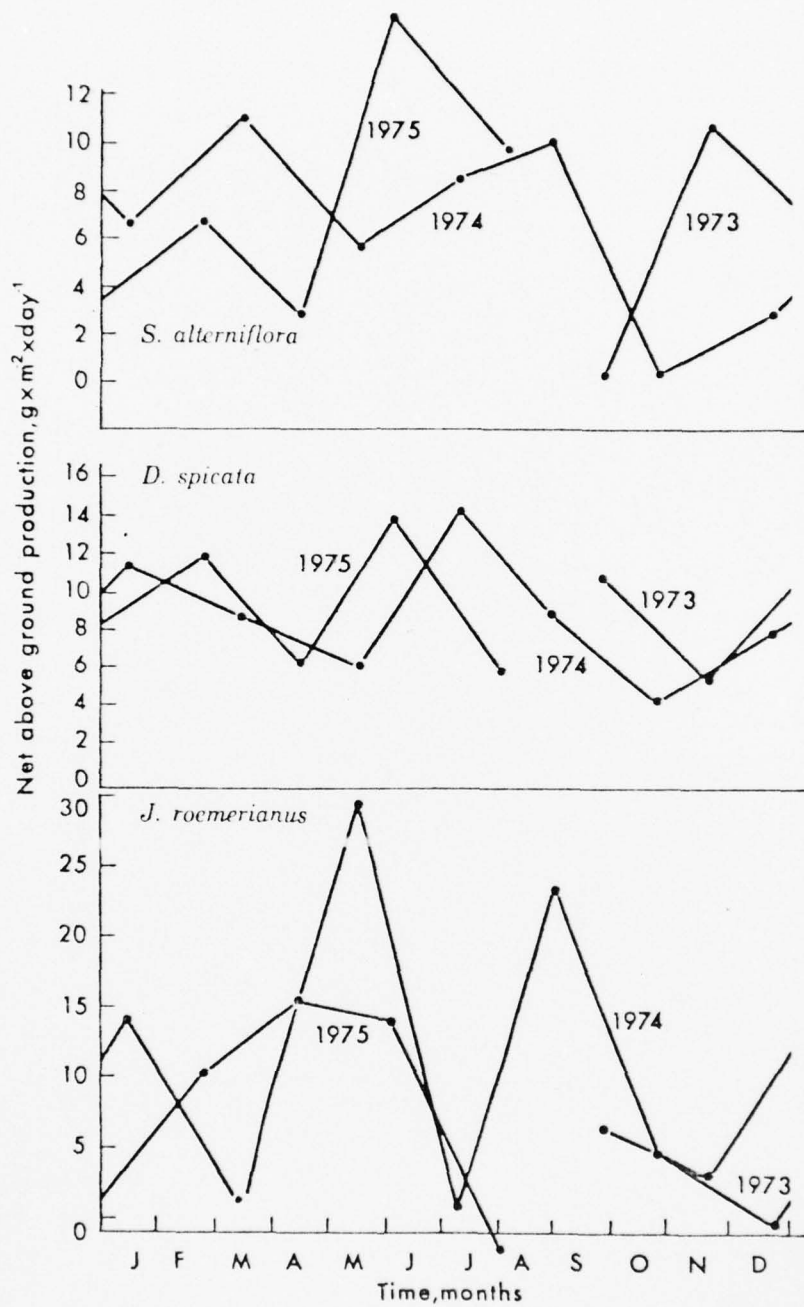


Figure A12. Net aboveground production for *S. alterniflora*, *D. spicata*, and *J. roemerianus*.

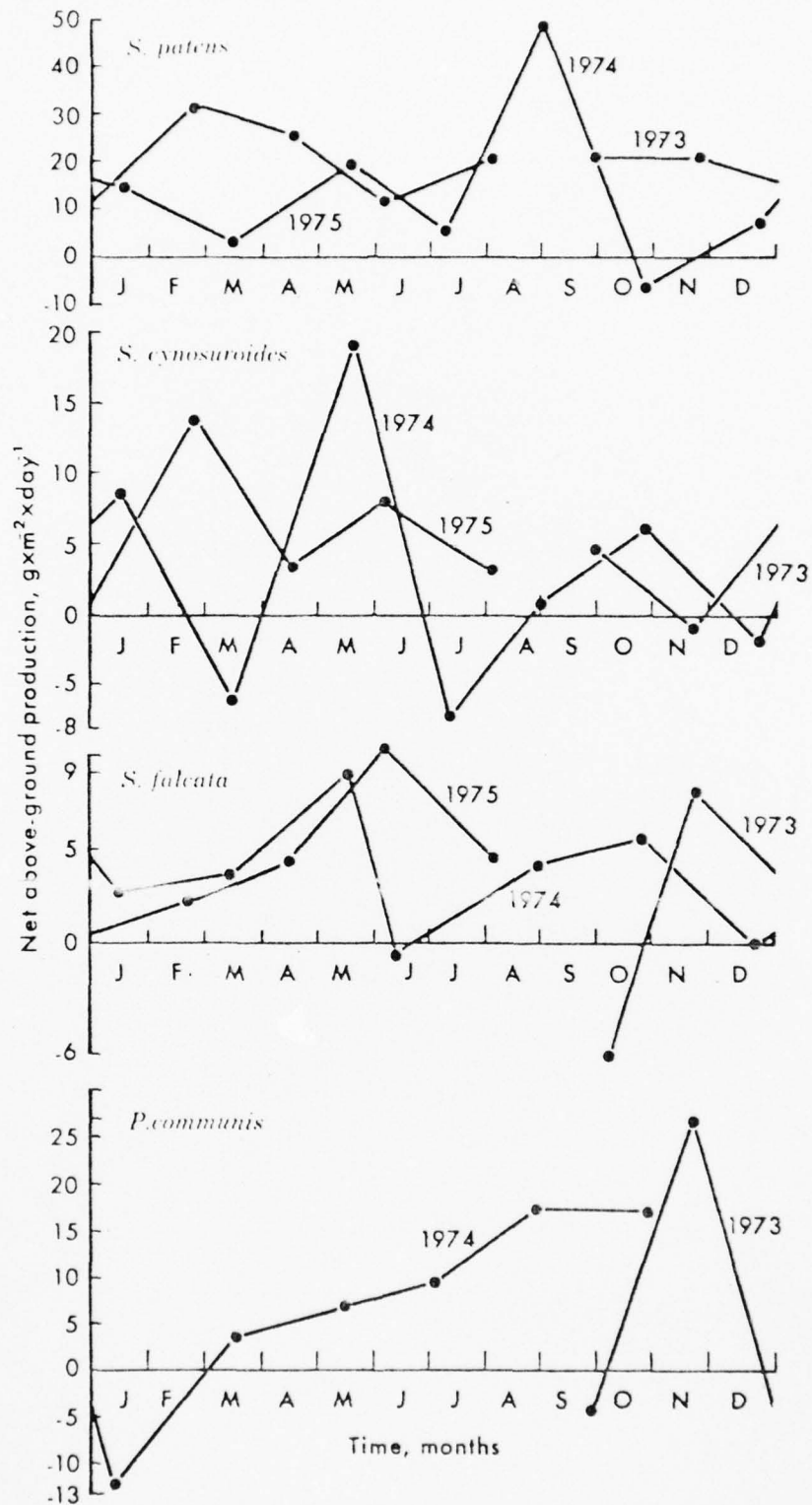


Figure A13. Net aboveground production for *S. patens*, *S. cynosuroides*, *S. falcata*, and *P. communis*.

APPENDIX B: PRODUCTION OF SIX COMMON COASTAL LOUISIANA MARSH
PLANT SPECIES AS DETERMINED BY PHENOMETRIC ANALYSIS

Introduction

1. The importance of organic matter derived from marsh macrophytes to support the trophic structure of coastal estuaries has been well documented (Teal 1962; Heald 1969; references listed at end of the appendix). Of paramount importance in systems studies is the quantification of the aboveground production by the marsh plants. The variety of techniques used to measure plant production give growth estimates that vary by a factor of up to 20 (see Appendix A). Methods based on peak standing biomass or on biomass changes (Milner and Hughes 1968), and even the method developed by Smalley (1959) that accounts for some mortality during the growing season, fail to show any production during the winter months even though fresh green vegetation is present. This paradox led the investigators in this study to try the paired-plot technique of Wiegert-Evans (1964), which corrects harvest data for mortality between sampling times. Preliminary results based on nine-month data from this technique yielded production estimates that were up to 3.6 times higher than estimates derived by the Smalley method. It was felt that another method based on growth or longevity of individual culms could be used as a check on the values reached with the Wiegert-Evans technique.

2. The initial production study used the Wiegert-Evans technique on seven species of marsh macrophytes in Louisiana coastal marshes along Bayou Lafourche, an abandoned Mississippi River distributary. For each

species, Distichlis spicata, Juncus roemerianus, Sagittaria falcata, Spartina alterniflora, Spartina cynosuroides, and Spartina patens, a 200-m² study area was selected where that species occurred in a nearly pure stand (Figure B1). The site of the seventh species, Phragmites communis was transitional and sampling difficulties resulted in its discontinuance the second year. The species is not included in this appendix. The results of this initial production study and descriptions of the deltaic area and each study site are given in Appendix A.

Methods

3. Measurements of dry weights of aboveground live and dead plant material and of disappearance rates of dead vegetation were made at roughly eight-week intervals beginning August 1973 and continuing for two years (Appendix A). Additionally, stem densities in each of the following height classes were concurrently determined: 0-25 cm, 26-50 cm, 51-100 cm, 101-105 cm, and greater than 150 cm.

4. Commencing in May 1974, the rate of growth and longevity of leaves or culms was determined by following at least 119 individual stems of each species throughout most of their life histories. Initially, numbered plastic tags were placed around 65 randomly chosen culms of each species. Every eight weeks 15 additional small, young plants were tagged and the height and survival of the previously tagged plants ascertained. This procedure was carried out for 468 days until the termination of the concurrent harvesting study. In addition randomly selected samples of each species were cut at ground level, measured to the nearest centimeter for height, dried, and weighed to the nearest 0.01 g.

Methods of Calculating Production

5. From the randomly selected samples of plants cut in the field, the relationship of weight to length was obtained. Height was regressed against weight with and without logarithmic transformations to find the relationship that best described the data.

Mortality method

6. In a steady-state system annual mortality should equal annual production. This technique used determination of mortality rates, stem densities, and dry weights at time of death to estimate annual mortality (M). The generalized equation is

$$M = \text{percent culms dying} \times \text{mass culm}^{-1} \times \text{stem density} \quad (1)$$

for each time interval and for each size class at time of death. Weight per culm was calculated from the height-weight regression. Mortality was calculated from data from individual tagged culms. At each time interval the number of live plants tagged in each size class (0-25 cm, 25-50 cm, etc.) was determined. At the following sampling date, the same plants were reexamined. A percent mortality matrix ($P_{i,j}$) was constructed from these observations for each size class of origin (t_1) and size class at death (t_2) according to the following equation:

$$P_{i,j} = D_{i,j}/N_i \quad (2)$$

where

$D_{i,j}$ = the number of plants that were alive and in size class i at time t_1 but were dead and in size class j at time t_2 .
 $D_{i,j} = 0$ if $j < i$

N_i = the number of live plants in size class i at time t_1 .

7. To calculate mortality for the interval each percent mortality measure was multiplied by the stem density and by the average weight per stem at death in each size class. Thus:

$$M_i = \sum_{j=1}^5 S_i \times P_{i,j} \times W_j \quad (3)$$

where

M_i = mortality for size class i

S_i = the number of stems per m^2 in size class i at the beginning of the period (t_1).

W_j = the weight per stem of stems in size class j for the period

Total mortality for one time interval was the sum of mortalities in each size class, or:

$$M = \sum_{i=1}^5 M_i = \sum_{i=1}^5 \sum_{j=1}^5 S_i \times P_{i,j} \times W_j \quad (4)$$

8. Annual mortality was calculated by summing interval mortalities for a one-year period. As the study lasted 468 days, mean yearly production was estimated by taking the average of two overlapping 365-day intervals.

Williams-Murdoch method

9. Production was also estimated by the technique developed by Williams and Murdoch (1972) for J. roemerianus in North Carolina. The advantages of this method were that it had been published, that accurate production estimates did not depend on a great deal of individual stem data, and that it afforded valid comparisons between their study and this one, especially with respect to J. roemerianus. The method requires estimates of the ratio of growth to average standing crop and to the

mean life span of live culms. The relationship of weight to height was also required.

10. The ratio of growth to average standing crop (R) was defined:

$$R = \left[(\Sigma B_{\max}/n) \right] / (\Sigma \bar{B})/n \quad (5)$$

where

$B_{\max}$ = the maximum weight attained by each stem during its life span

n = number of plants

$\bar{B} = \Sigma(\bar{b} \times \Delta t) / \Sigma \Delta t$ = the mean weight of a stem during its life span

where

$\bar{b}$ = average weight of a stem between successive measurements
 Δt = interval between successive measurements

Annual growth was calculated as follows:

$$G = \bar{L} \times R \times \Sigma(\bar{B} \times \Sigma \Delta t) / \Sigma \bar{B} \quad (6)$$

That is,

Growth ($\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$) = average standing crop ($\text{g} \times \text{m}^{-2}$) $\times$ growth/
 average biomass $\times$ frequency/year

where

$\bar{L}$ = average live standing crop.

Results

Standing crop

11. Table B1 shows the magnitude and range of peak and average biomass for the six species observed during the two years. Peak live biomass ranged from a low of $648 \text{ g} \times \text{m}^{-2}$ for S. falcata to a high of $1376 \text{ g} \times \text{m}^{-2}$ for S. patens. The annual mean biomass of live material ranged from $199 \text{ g} \times \text{m}^{-2}$ for S. falcata to $900 \text{ g} \times \text{m}^{-2}$ for S. patens.

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LOUISIANA STATE UNIV BATON ROUGE
COMMON MARSH PLANT SPECIES OF THE GULF COAST AREA. VOLUME I. PR--ETC(U)
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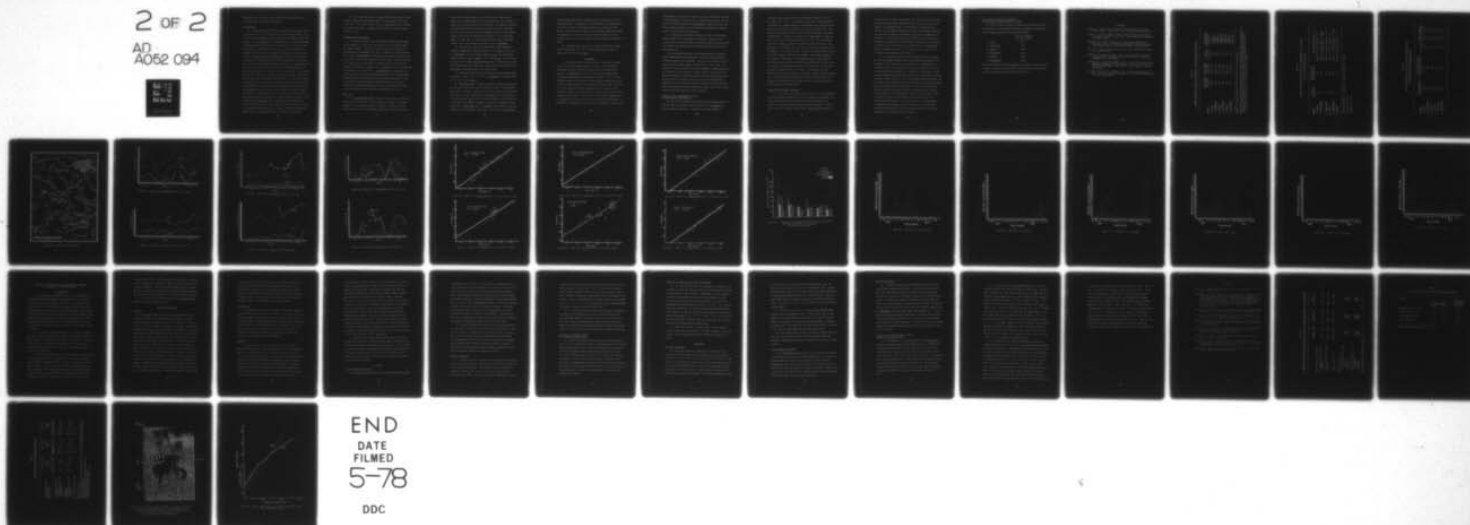
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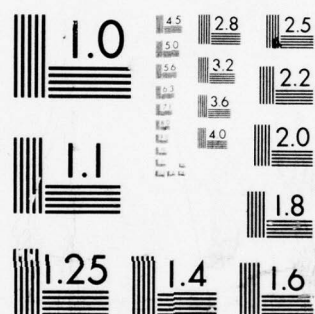
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Seasonal changes in biomass and an evaluation of the reliability of these data have been reported in Appendix A.

Stem densities

12. Figures B2 through B7 show the bimonthly culm densities of the six species in each of the size classes for the period of study. Four of the species investigated showed clear seasonal changes in total culm density. S. cynosuroides and S. falcata died back to the ground during the winter months and showed rapid increases in the densities of stems in the spring. Both show a single wave of culms that appears in the smallest size class in the spring and grows with time into larger size classes. D. spicata and S. alterniflora also exhibited clear seasonal patterns, but as these plants do not die back during winter in Louisiana, the patterns were quite different from those of S. cynosuroides and S. falcata. For both species there were two periods during the year when the recruitment rate of small plants was quite high. The densities of stems under 25 cm were highest in midsummer and again in midwinter. Whereas there were two periods of maximum density of small stems, there was only one for large stems and for both species this occurred in late summer/early fall. Williams and Murdoch (1969) reported that most new S. alterniflora culms appeared in the late summer and remained small over winter. In Louisiana many of these summer recruits die before the following spring but are followed by a second flush in the winter. Stem densities of J. roemerianus and S. patens increased throughout the study, indicating that these sites were in a transitional state. Small J. roemerianus plants (less than 25 cm high) seemed most dense during winter, while the tallest plants were most dense in late summer.

13. On a comparative basis, S. patens exhibited the greatest stem density, ranging from 1400-3600 stems $\times$ m⁻² and averaging about 2500 stems $\times$ m⁻². The tallest plant studied, S. cynosuroides, also exhibited the lowest stem density, ranging from 0-105 stems $\times$ m⁻² and averaging 60 stems $\times$ m⁻².

Length-weight relationships

14. Highly significant correlations were obtained between length or log length of a culm and the log weight for all six species (Table B2, Figures B8-B13). Each figure shows the regression equation, the observations, the regression line, and the coefficient of determination (R^2). For S. alterniflora two regression equations were determined, one for plants up to 75 cm and another for taller plants. With the exception of D. spicata, all coefficients of determination were above 0.80 and ranged up to 0.94 for S. falcata. For D. spicata the best fit coefficient of determination was only 0.58. J. roemerianus and S. falcata do not shed any leaf parts before reaching maximum height so the length-weight relationship accurately reflects total dry weight production by a stem. The other four species, however, slough off old leaves or parts of leaves before reaching maximum height. For these species the length-weight relationships underestimate total production of a stem.

Production

15. Williams-Murdoch method. Table B3 shows production of the six plant species calculated by the Williams-Murdoch method. This method depends on the accurate assessment of longevity of individual stems; consequently, the initial 65 randomly tagged plants could not be used

unless their original heights were less than 25 cm. Additionally, plants that were tagged late in the study and had not yet died when the project was terminated could not be considered. The number of plants of each species on which the results are based are listed in the table. Due to the very rapid turnover of S. falcata, almost all stems tagged could be used in the determination of production: out of 349 plants tagged, 245 were used. In contrast only 20 plants out of 119 tagged could be used in determining the production of S. cynosuroides.

16. The average of the mean weights ($\Sigma \bar{B}/n$) of the samples of individual tagged culms ranged from 0.08 g for S. patens to 0.64 g for S. alterniflora. The mean maximum weight ($\Sigma B_{\max}/n$) for each species ranged from 0.21 g for S. patens to 1.23 for S. falcata. The low ratio of production to biomass ($B_{\max}/\bar{B}$) indicates that a great number of stems die before entering the largest size classes shown in Figures B2-B7 and, consequently, that the turnover rate must be high.

17. Production calculated from the Williams-Murdoch method ranged from a low of $1134 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$ for S. cynosuroides to a high of $4159 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$ for S. patens.

18. Mortality method. Figure B14 summarizes annual production for the six species calculated from the mortality method. Figures B15-B20 show results seasonally. The species showed differing seasonal patterns of mortality. Both S. falcata and S. cynosuroides die back completely in the winter after which time they have no mortality. Whereas the rate of mortality rises rapidly through the spring for S. falcata, it rises slowly for S. cynosuroides and J. roemerianus, which reach peak rates of mortality in late summer and early fall. In contrast, S. alterniflora

and D. spicata exhibit their highest rates of mortality in late fall and early winter. S. patens has a high mortality rate throughout the year, but it appears to be highest during fall, winter, and early spring. The very clear seasonal patterns and their repetition through the second year of the study indicate that the mortality data are reliable; however, it is not possible to attach limits of variability to them.

19. Calculated mortality on a yearly basis (Figure B14) ranged from a low of $398 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$ for S. cynosuroides to a high of $2500 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$ for S. patens.

Discussion

20. In Figure B14 the large discrepancy in production estimates between the two mathematical methods is obvious. Williams-Murdoch production estimates averaged 1.8 times higher than the mortality method. S. alterniflora was the sole exception that showed higher calculated production with the mortality technique. A very real and probable source of error inherent in the mortality method, which would lead to an underestimate of true production, is that weights determined for leaves using the regression equations do not account for plant production (leaves + leaf parts) that has dropped from the culm prior to reaching maximum length. This was not a problem with J. roemerianus or S. falcata as these plants do not drop off dead parts before dying. In sampling S. alterniflora plants for use in determining the length-weight

relationship, every effort was taken to pick green plants that had lost a minimum number of leaves in order to minimize this problem. Williams and Murdoch (1969) found that S. alterniflora production in North Carolina was underestimated by about 15 percent if material that had died prior to harvest was not accounted for.

21. Although the regression equations are used in the Williams-Murdoch method also, they should not constitute a source of error because weights calculated using the regression equations appear in both the numerator and denominator in the equations and the errors cancel (see equation 6).

22. The mortality method of calculating production is based on three independently derived parameters. For two of these parameters, confidence limits can be calculated. These are the estimates of stem density and the average weights per dead stem in a size class. Unfortunately, the data acquisition was not designed to enable analysis of the variation in the percentage of plants that die in each size class during each interval. Because of wide variances in the two measurable parameters and the cumulative property of error terms during data manipulation, the information gained from putting confidence intervals around the production estimates would be of dubious use, as the overall variance would undoubtedly be of large magnitude.

Comparison of J. roemerianus production
in North Carolina and Louisiana

23. Use of the Williams-Murdoch method of calculating production invites a direct comparison between production of J. roemerianus in North Carolina and Louisiana. Production is 4.1 times higher in

Louisiana marshes than in North Carolina marshes ($3295 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$ vs. $792 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$). As mentioned earlier the technique depends on measurements of average standing stock determined from field harvesting, the ratio of production to biomass, and the mean residence time. The parameter responsible for most of the production difference is average standing stock. Average live biomass is 2.4 times higher in Louisiana ($827 \text{ g} \times \text{m}^{-2}$) than in North Carolina ($344 \text{ g} \times \text{m}^{-2}$). On an individual leaf basis, both B_{max} and $\bar{B}$ are considerably lower in Louisiana. The $\Sigma B_{\text{max}}/n$ was 1.1 g (range 0.17 - 2.17 g) in North Carolina and only 0.25 g (range 0.1 - 1.2 g) in Louisiana. Average stem weight ($\Sigma \bar{B}/n$) is 0.719 g in North Carolina and 0.11 g in Louisiana. The ratio of $B_{\text{max}}/\bar{B}$ is 1.5 times higher in Louisiana. The average life span of stems however is only 28 days longer in North Carolina, which means that the above ratios of production to biomass are achieved 1.5 times per year in North Carolina and 1.7 times per year in Louisiana. Consequently, the main differences in black rush marshes in Louisiana compared to North Carolina are: (a) a much greater density and year-round standing stock of live material, (b) a shorter overall height, and (c) a much more rapid turnover of very small subcanopy stems.

Production methodology comparisons

24. It is evident from Figure B14 that there are as many estimates of marsh macrophyte production as there are production techniques. The figure demonstrates that all methodologies show production by all species to be greater than that predicted from live biomass. An exception is that the mortality method shows S. cynosuroides production to

be less than its maximum live standing crop. As this species dies back completely every winter, production must at least equal end-of-season biomass. The probable faults in the mortality technique for this species are the predicted weights derived from the regression equation and the very low number of individually tagged culms available in the analysis. If, in place of the regression-derived weight used in the mortality calculations, the average weight (calculated from harvesting of stems) in each size class is used, production of S. cynosuroides is shown to be about $1214 \text{ g} \times \text{m}^{-2} \times \text{yr}^{-1}$, which is much closer to the estimates derived from the other methods.

25. As an initial purpose of this investigation was to evaluate the harvest methods of Smalley (1959) and Wiegert-Evans (1964), it is important to note that (with the exception of S. cynosuroides) both techniques used in this study give estimates of production much closer to the Wiegert-Evans technique than to Smalley's calculations. On the average, estimates using Smalley's method are 27 percent lower than the mortality method, 53 percent lower than the Williams-Murdoch method, and 57 percent lower than the Wiegert-Evans paired-plot harvesting technique. For two of the six species, production estimates using the Williams-Murdoch technique were higher than that calculated from the Wiegert-Evans technique. On the average the estimates from the Wiegert-Evans technique were only 1.3 times higher than the estimates from the Williams-Murdoch technique. It is concluded that the Wiegert-Evans technique may overestimate production, but not by much. The extraordinarily high estimates of marsh macrophyte production in coastal Louisiana are not artifacts of the technique.

Best possible estimates of production
of six species of marsh plants in Louisiana

26. Without further evidence to support one production estimate over another, a best estimate can be made by averaging the results of the two tagging methods and the paired-plot method.

	Production Estimate $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$
<u>S. patens</u>	4157
<u>J. roemerianus</u>	2797
<u>D. spicata</u>	1952
<u>S. alterniflora</u>	1744
<u>S. falcata</u>	1608
<u>S. cynosuroides</u>	1099

All three techniques showed S. patens to be the most productive species studied in Louisiana, and according to values in the literature, also the most productive grass reported in North America.

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Table B1

Annual Biomass and Production Parameters of Six Species of Marsh Plants

Species	Live Biomass Annual Mean $\text{g} \times \text{m}^{-2}$	Dead Biomass* Annual Mean $\text{g} \times \text{m}^{-2}$	Peak Live Biomass $\text{g} \times \text{m}^{-2}$	Production** Mean and Range $\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$
<u>S. patens</u>	900	1530 (0.58)	1376	6043 (5924-6163)
<u>J. roemerianus</u>	827	905 (0.91)	1240	3416 (2039-3794)
<u>D. spicata</u>	560	1143 (0.49)	991	3237 (3108-3366)
<u>S. alterniflora</u>	469	958 (0.49)	754	2658 (2523-2794)
<u>S. falcata</u>	199	228 (0.87)	648	1501 (1389-1613)
<u>S. cynosuroides</u>	394	951 (0.41)	808	1355 (1052-1659)

*Number in parentheses shows the ratio of the live to dead biomass.

**Calculated by the method of Wiegert and Evans (1964) from bimonthly data using pooled mean $\bar{r}$ values. Range shown indicates variation found using two different 12-month periods for calculation. Disappearance = $\bar{D} \times \bar{r} \times 365$ days where $\bar{D}$ = annual mean dead biomass and $\bar{r}$ = annual mean disappearance rate calculated from pooled means.

Table B2

Regression Equations Describing the Length-Weight Relationships

for Six Species of Marsh Plants

Species	No. of Observations	Coefficient of Determination R ²	Regression Equation*
<u>S. falcata</u>	68	0.94	Log wt = 1.73 log length - 3.12
<u>S. alterniflora</u>	92	0.89	log wt = 0.0218 length** - 0.9128 log wt = 0.0161 length [†] - 0.6014
<u>J. roemerianus</u>	50	0.89	Log wt = 0.0076 log length - 0.7671
<u>S. patens</u>	50	0.85	Log wt = 2.28 log length - 4.22
<u>S. cynosuroides</u>	49	0.80	Log wt = 3.6559 log length - 7.1186
<u>D. spicata</u>	71	0.58	Log wt = 1.079 log length - 2.0

*All regressions are statistically highly significant (P < 0.01).

**Culms under 75 cm.

†Culms over 75 cm.

Table B3

Annual Production of Six Marsh Plants Calculated by the

Method of Williams and Murdoch (1972)

Species	Annual Production ($\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$)	Mean Live Biomass During 468-Day Interval ($\text{g} \times \text{m}^{-2} \times \text{yr}^{-1}$)		No. Plants	Max Wt/ Culm (g)		Mean Wt/ Stem (g)
<u>S. patens</u>	4159	999		72	0.21	0.08	
<u>J. roemerianus</u>	3295	949		49	0.25	0.11	
<u>S. falcata</u>	2310	255		245	1.23	0.58	
<u>D. spicata</u>	1967	505		50	0.29	0.11	
<u>S. alterniflora</u>	1381	475		65	1.13	0.64	
<u>S. cynosuroides</u>	1134	438		20	0.82	0.55	

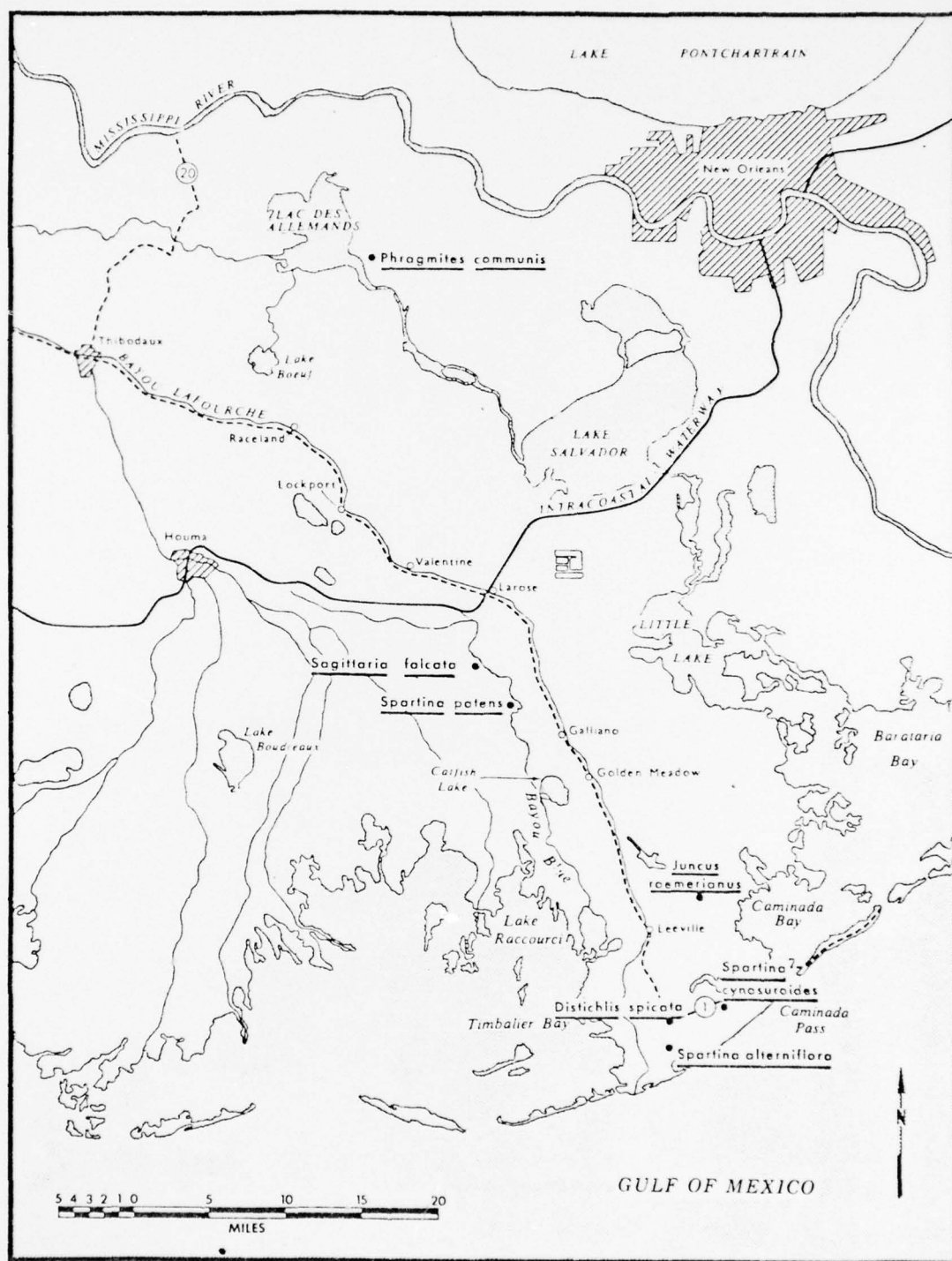


Figure B1. Location of sampling sites.

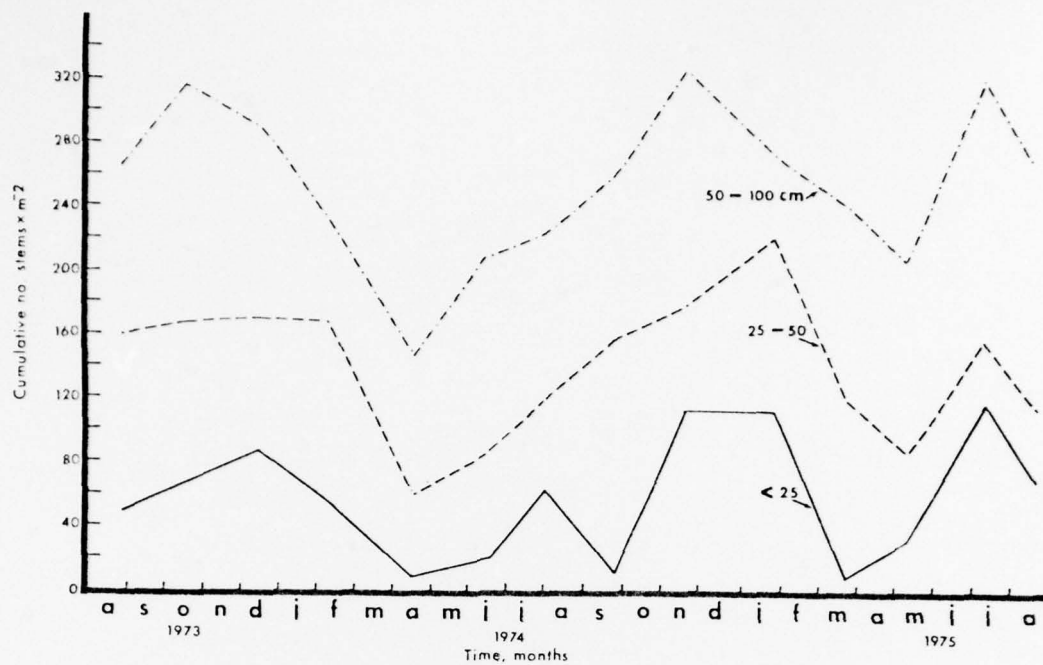


Figure B2. Density of *S. alterniflora* stems by size class.

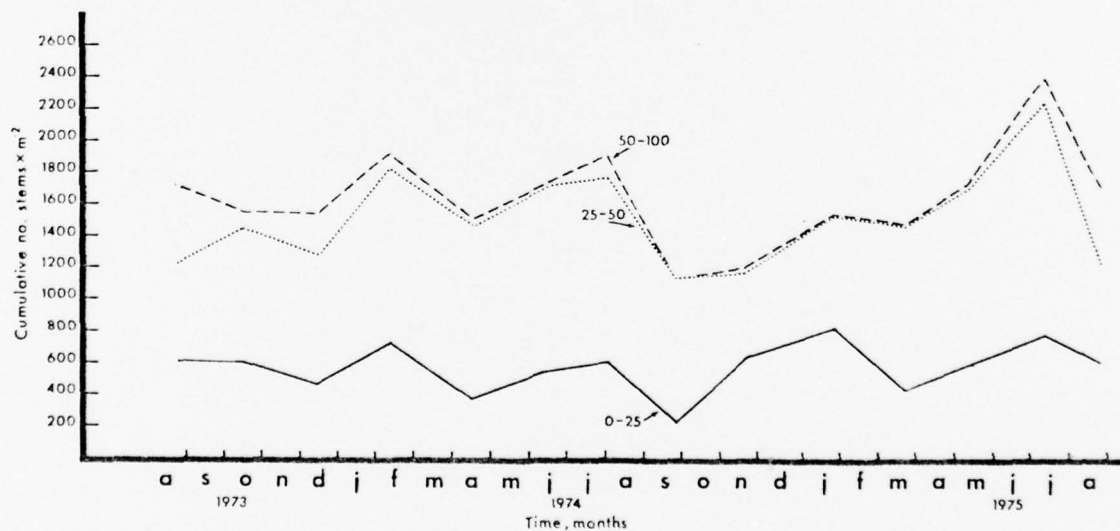


Figure B3. Density of *D. spicata* stems by size class.

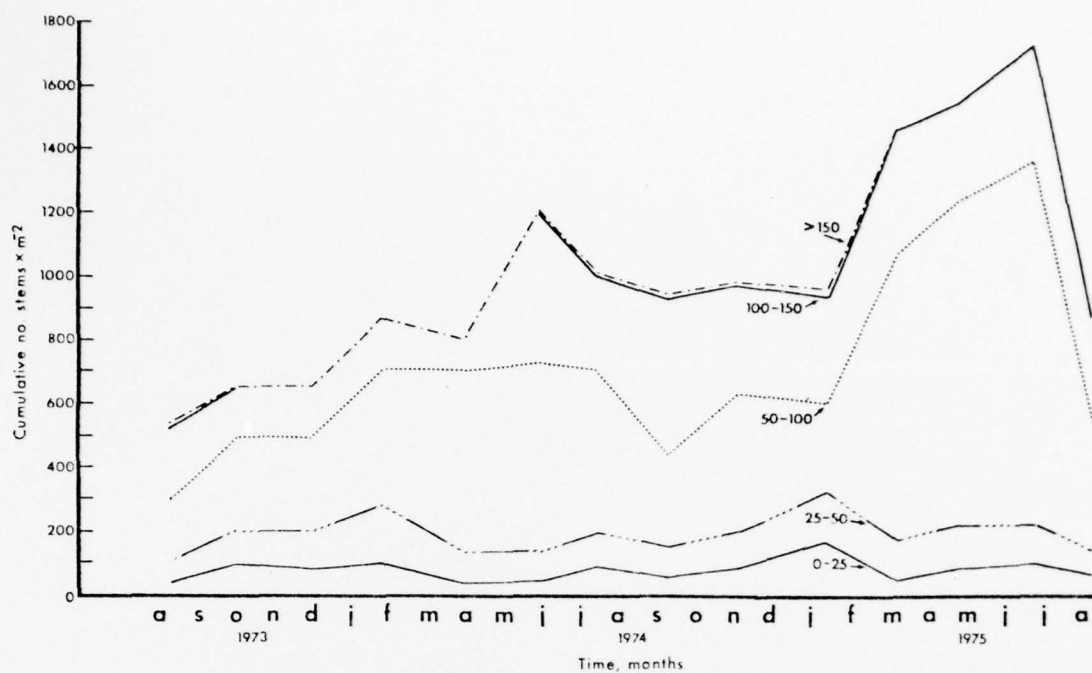


Figure B4. Density of J. roemerianus stems by size class.

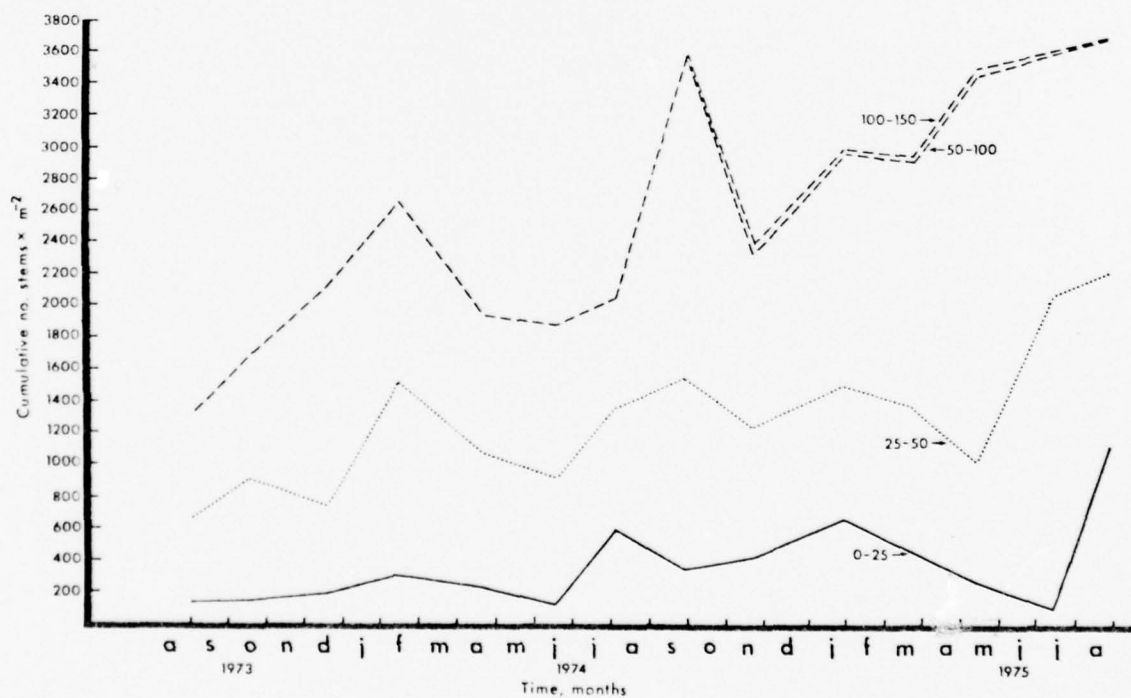


Figure B5. Density of S. patens stems by size class.

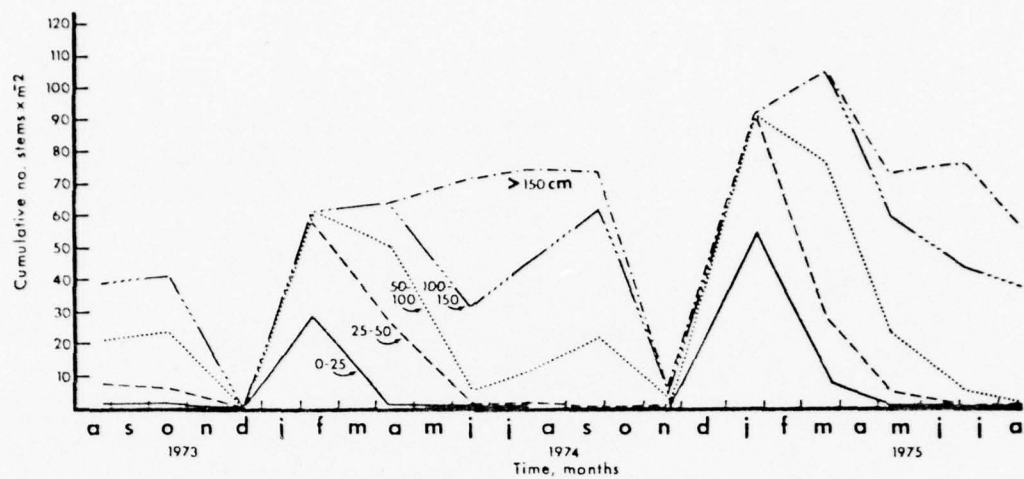


Figure B6. Density of *S. cynosuroides* stems by size class.

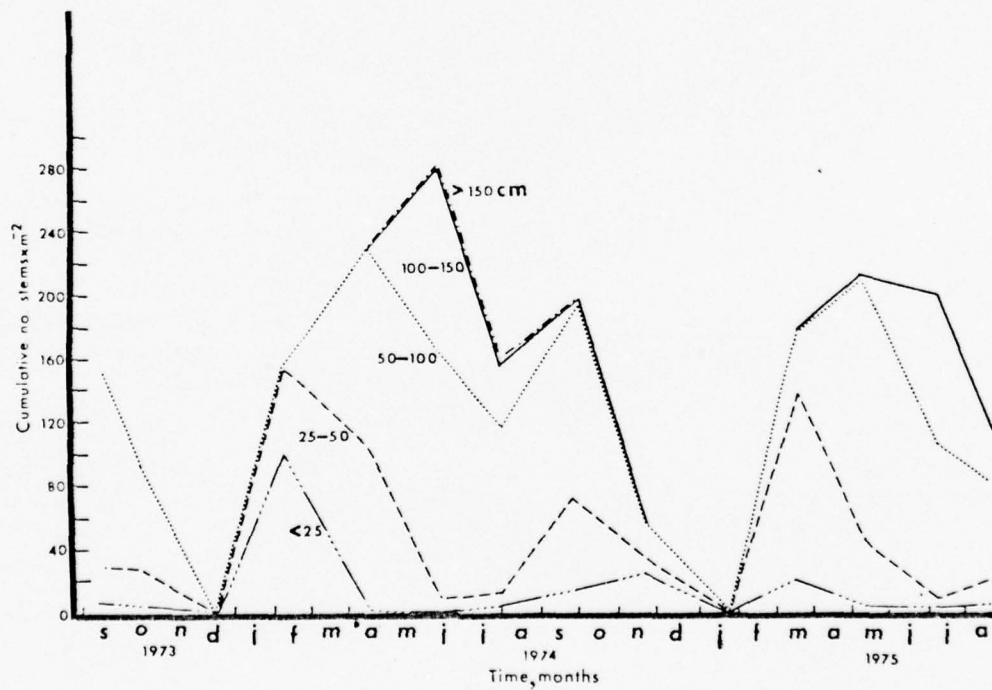


Figure B7. Density of *S. falcata* stems by size class.

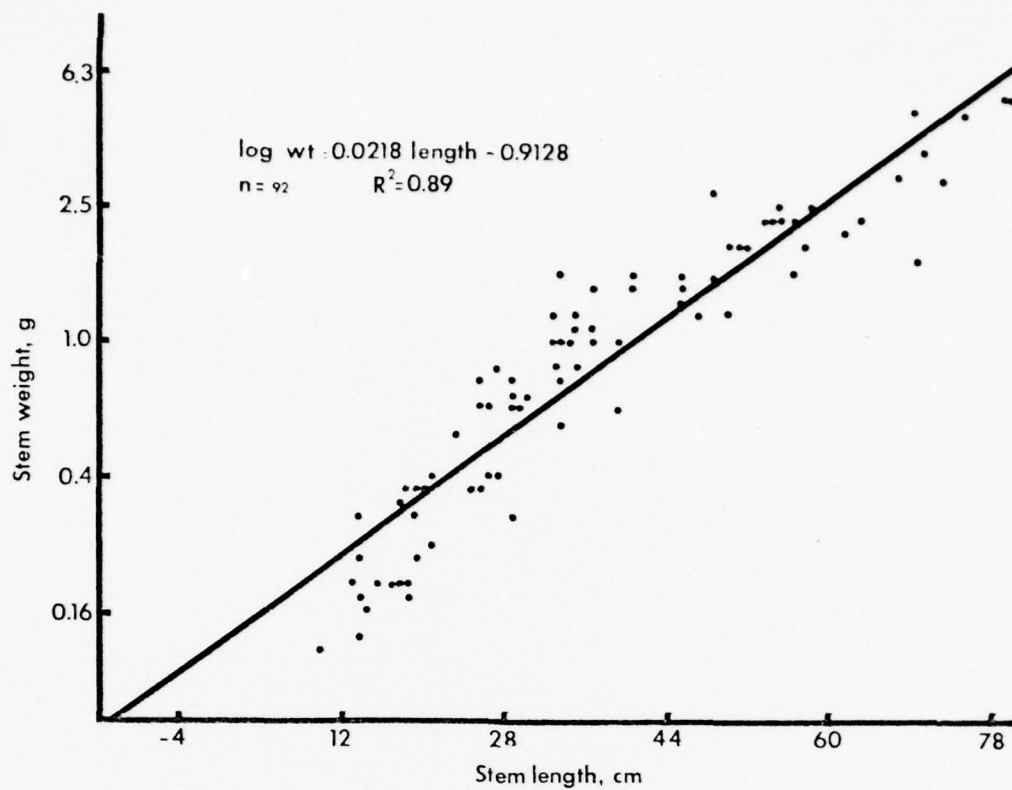


Figure B8. Weight of *S. alterniflora* plants as a function of length.

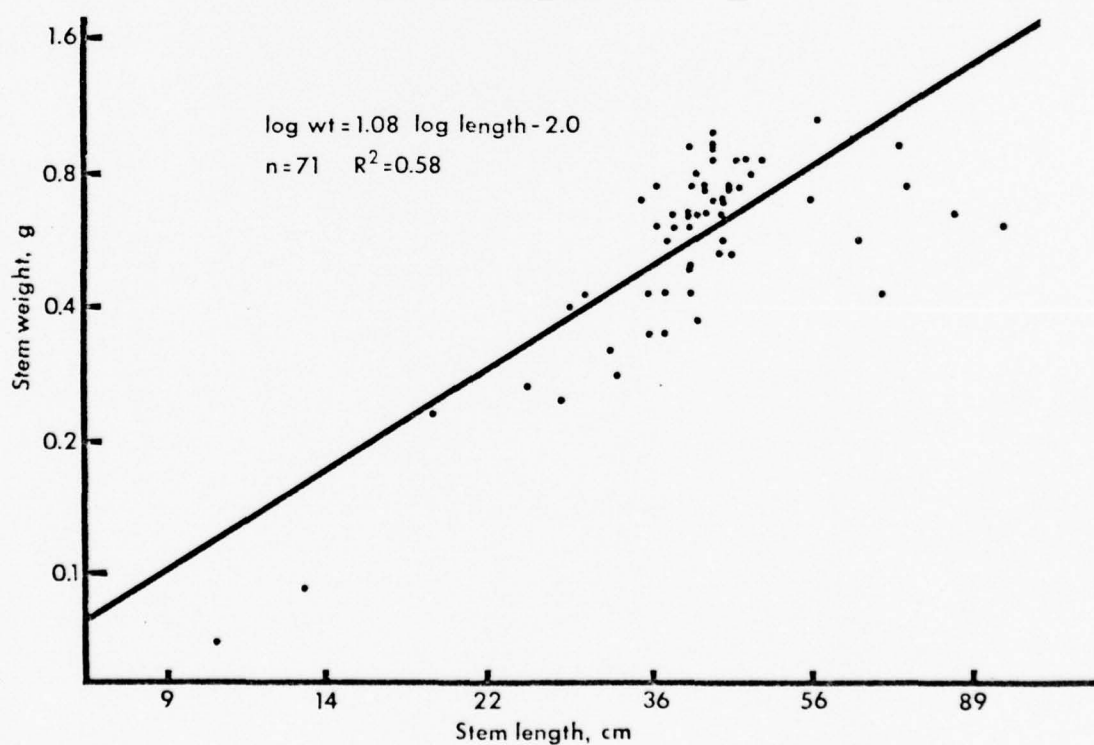


Figure B9. Weight of *D. spicata* plants as a function of length.

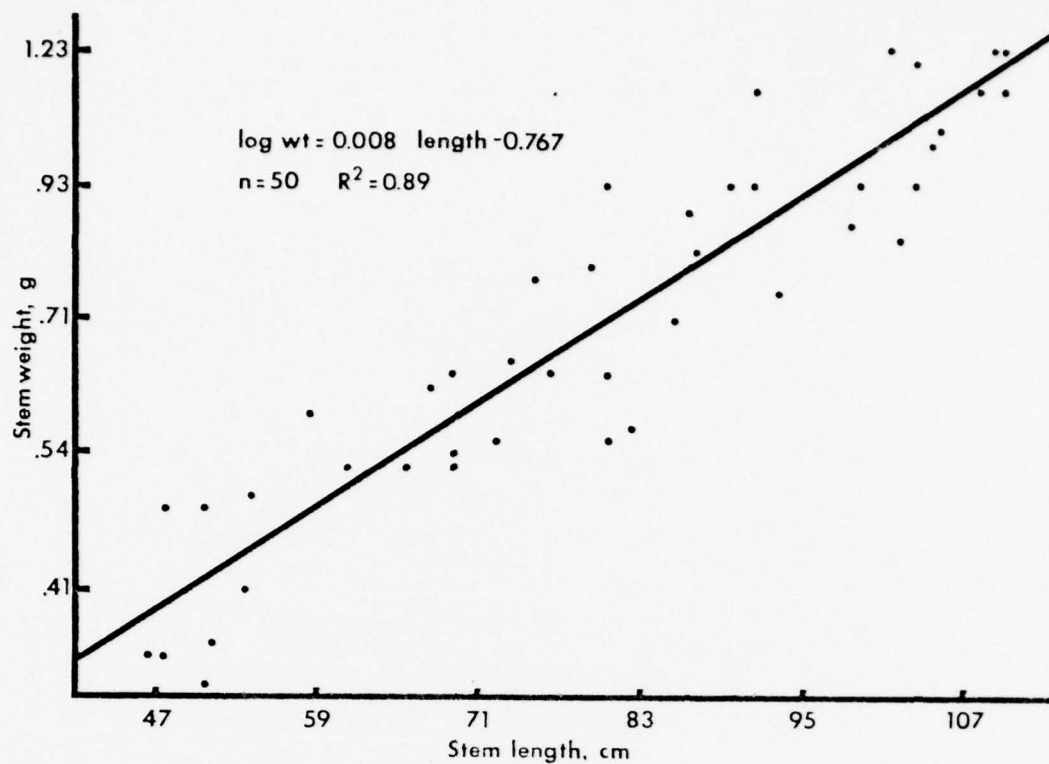


Figure B10. Weight of J. roemerianus plants as a function of length.

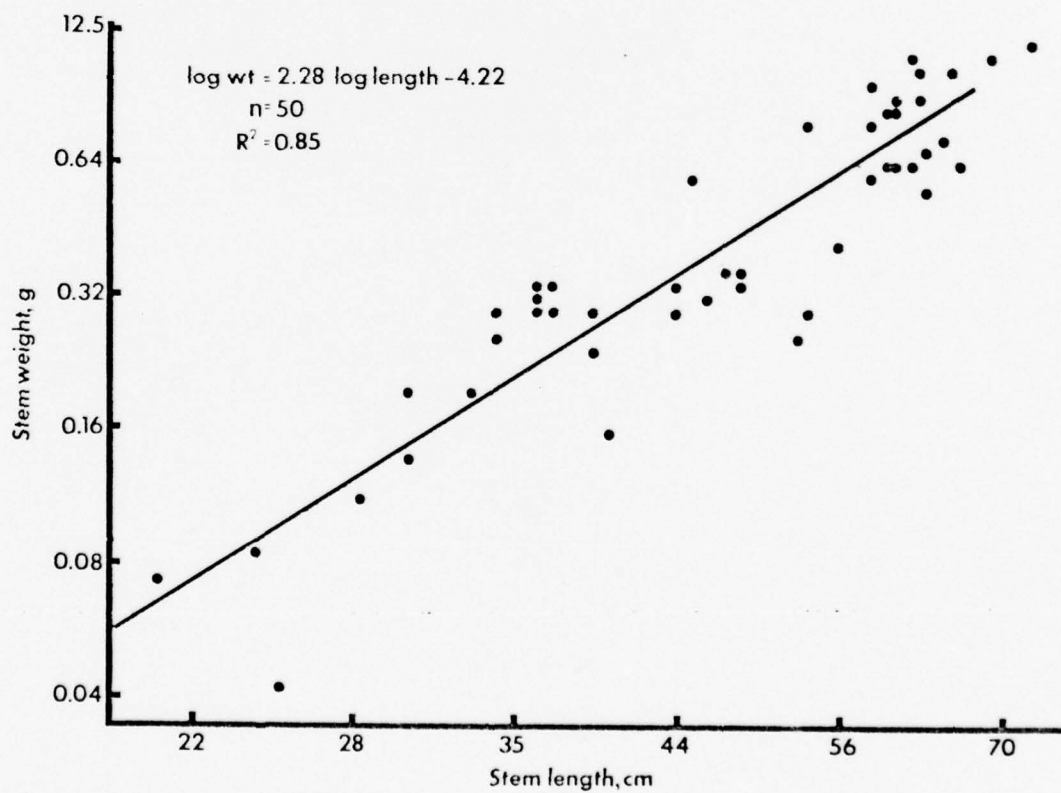


Figure B11. Weight of S. patens plants as a function of length.

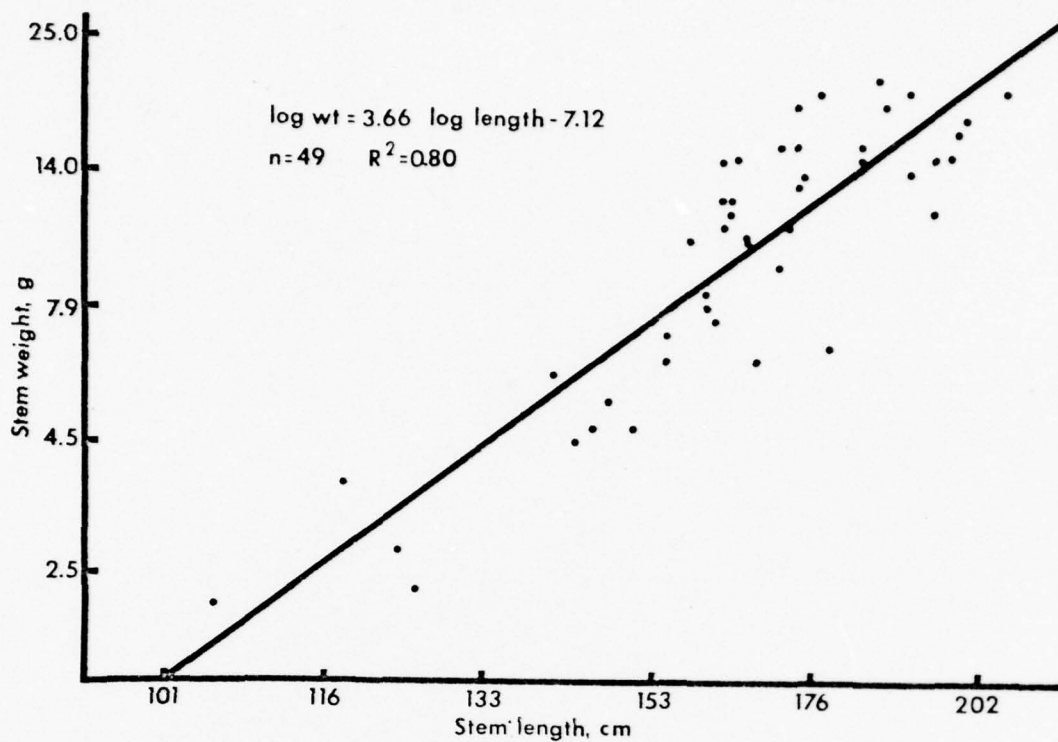


Figure B12. Weight of *S. cynosuroides* plants as a function of length.

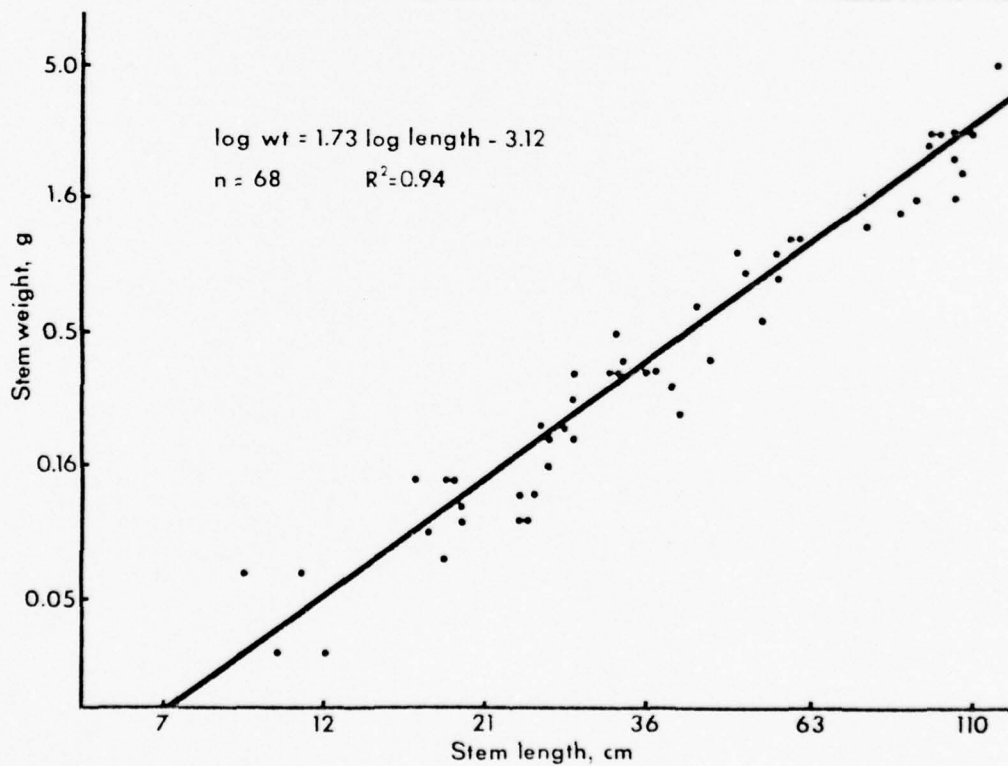


Figure B13. Weight of *S. falcata* plants as a function of length.

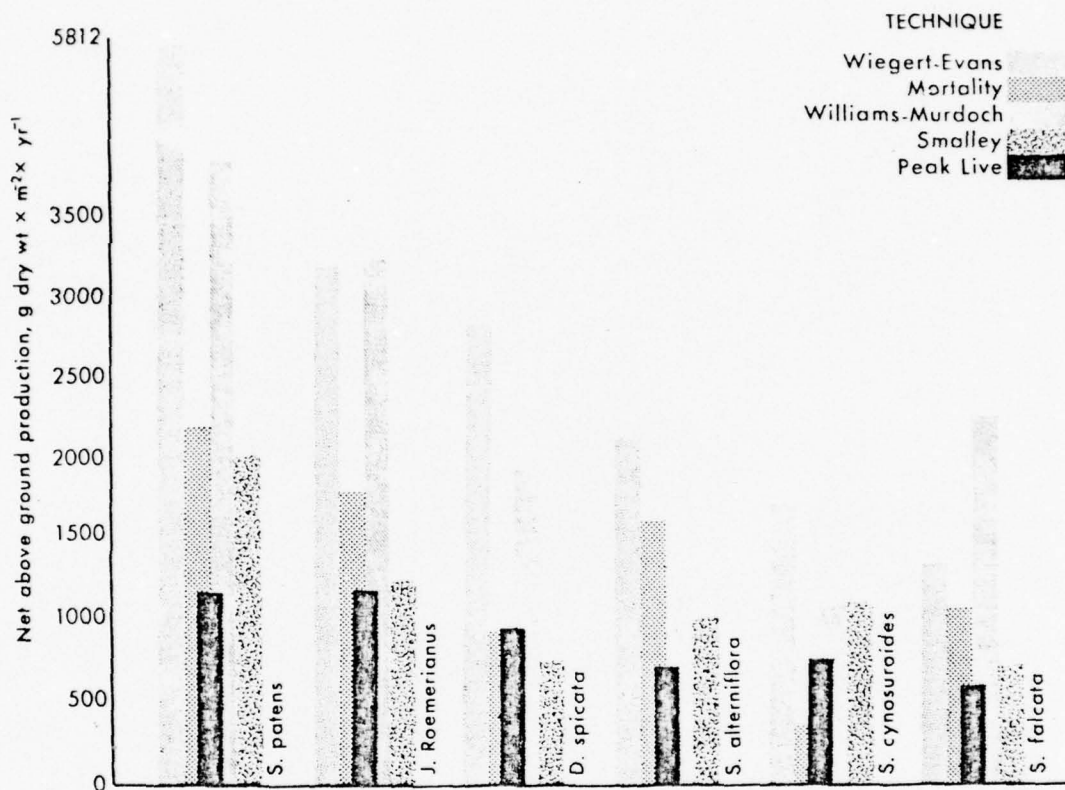


Figure B14. Comparison of production estimates calculated using five different techniques for six species of Louisiana marsh plants.

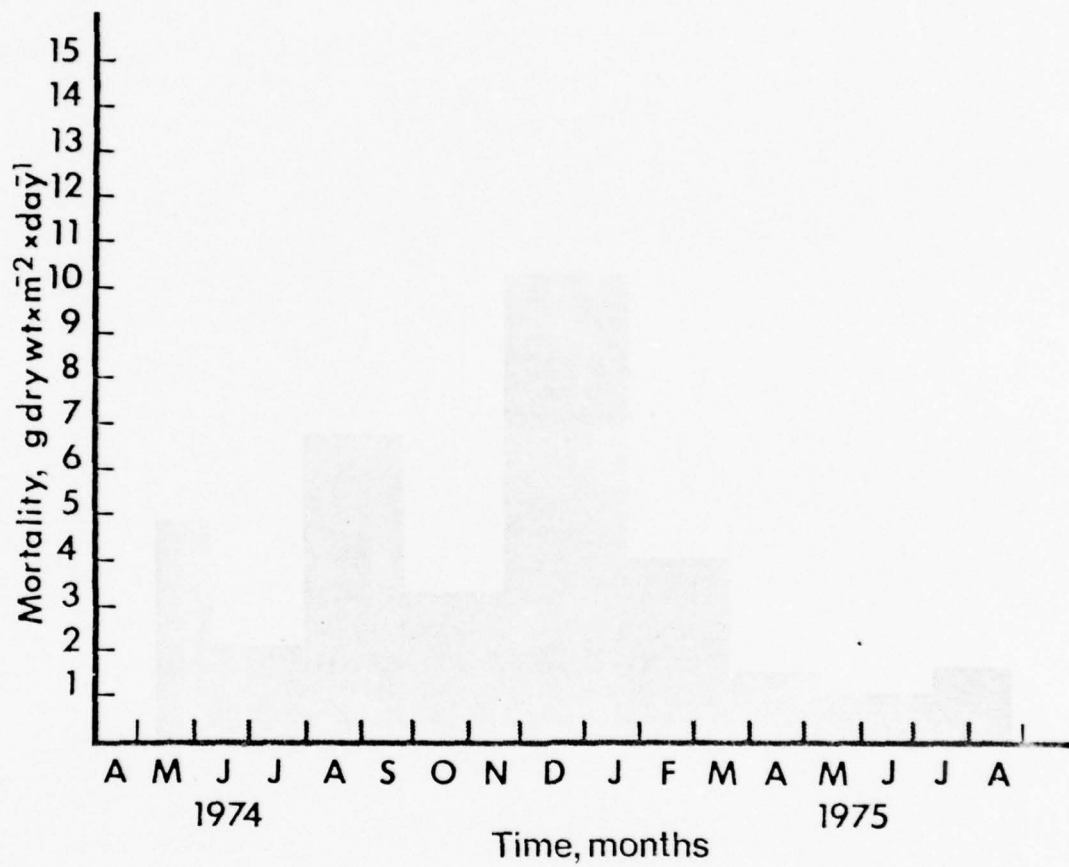


Figure B15. Mortality of *S. alterniflora*.

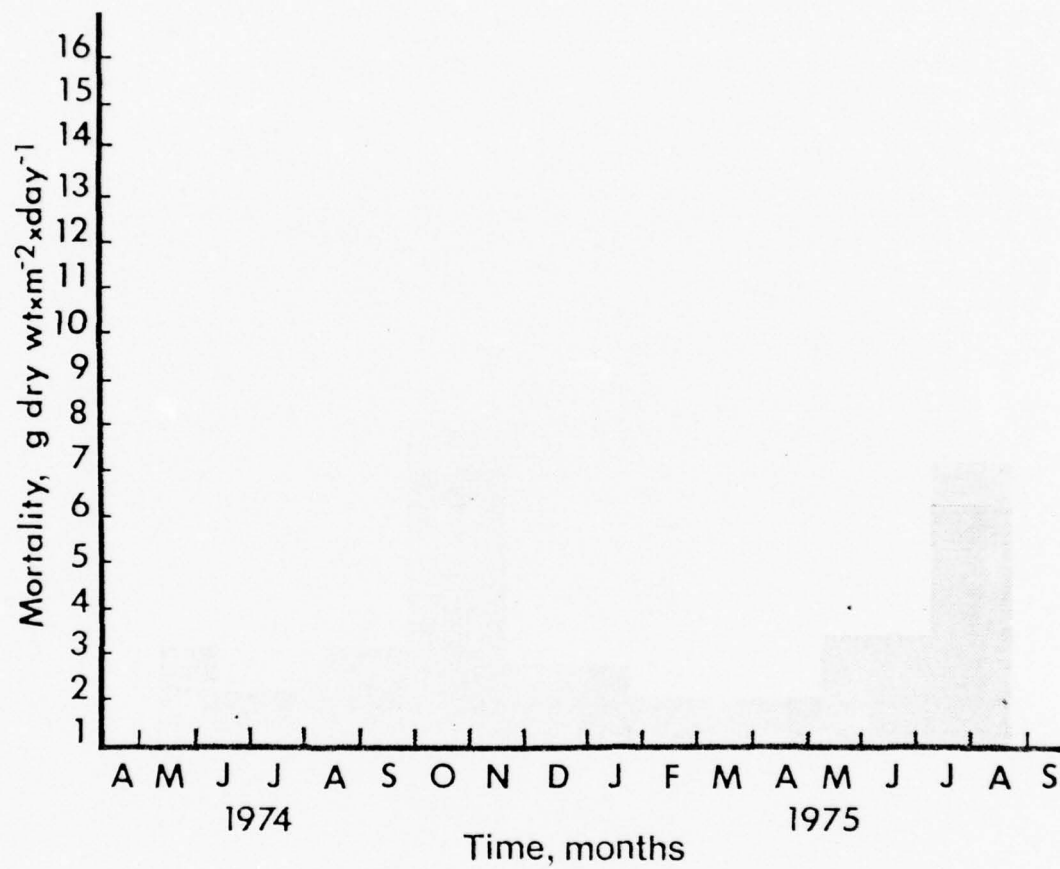


Figure B16. Mortality of D. spicata.

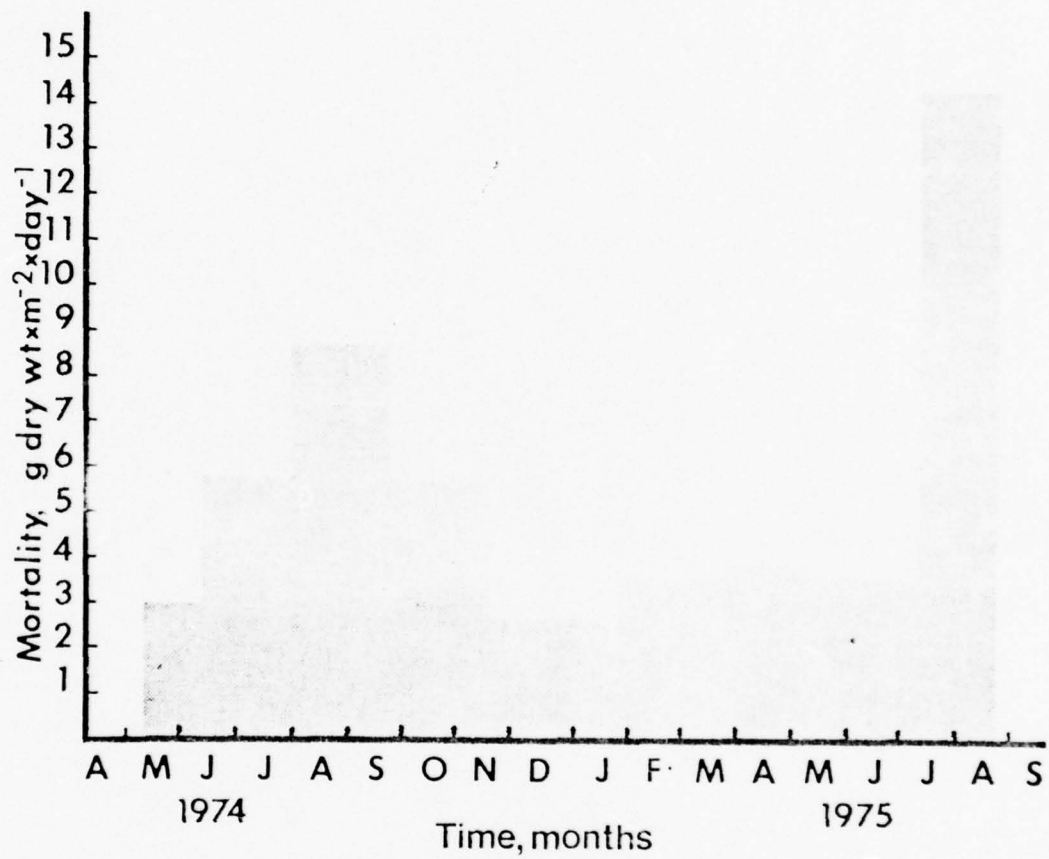


Figure B17. Mortality of J. roemerianus.

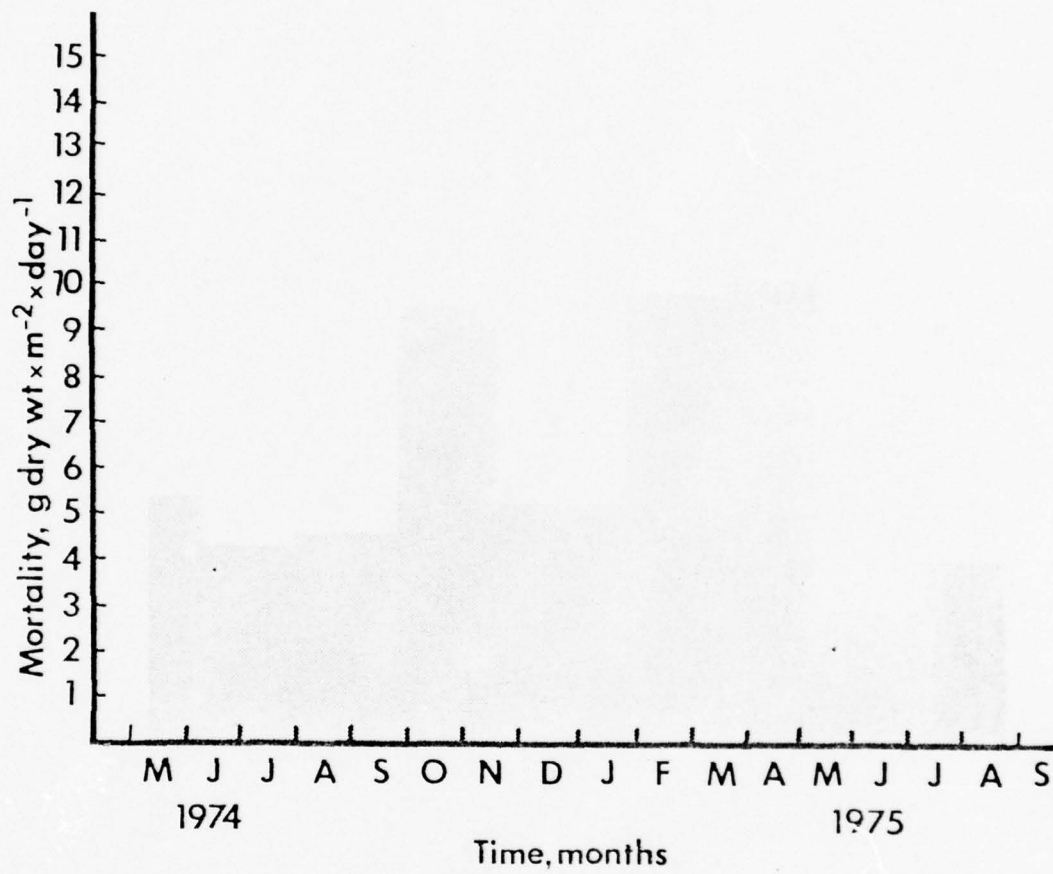


Figure B18. Mortality of S. patens.

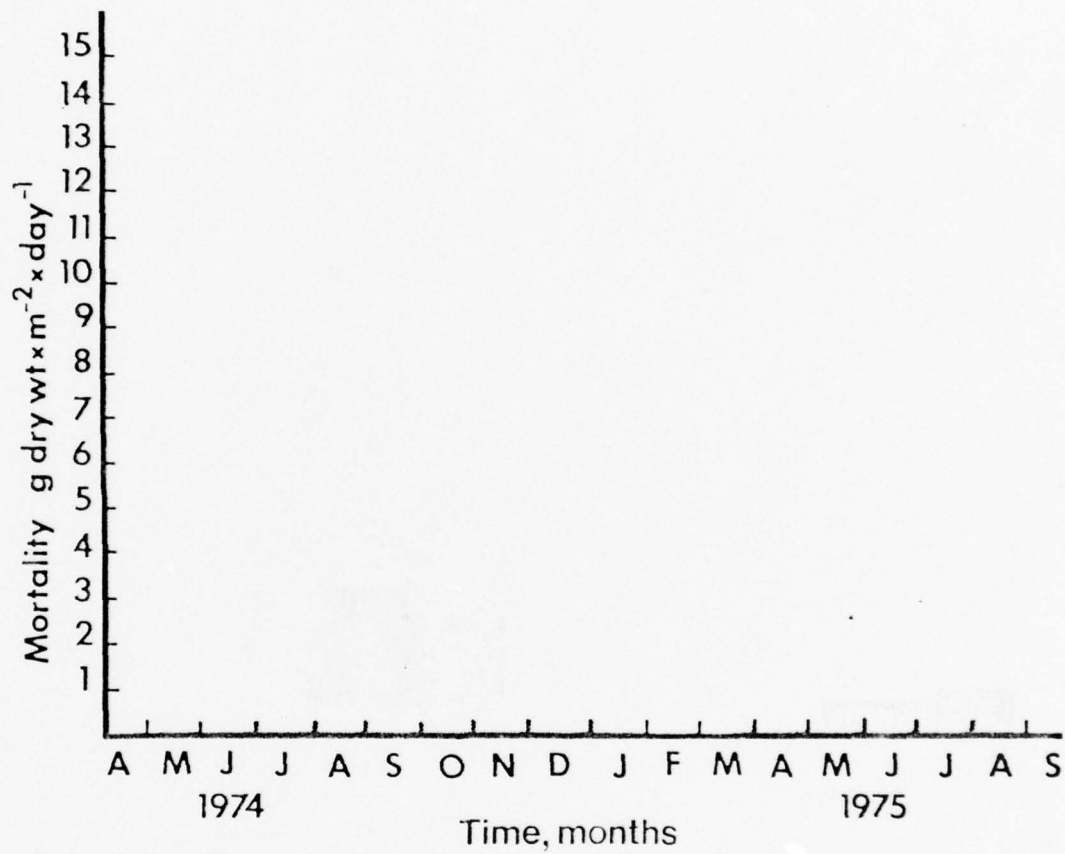


Figure B19. Mortality of S. cynosuroides.

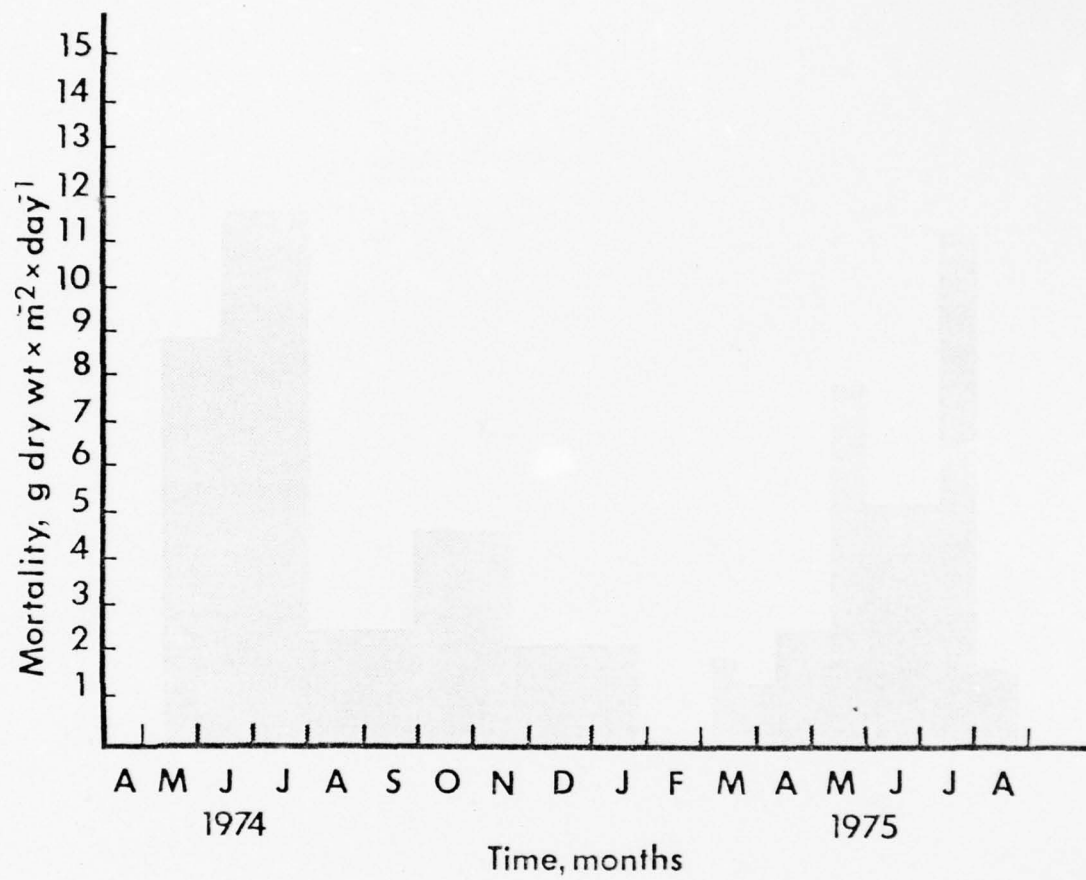


Figure B20. Mortality of *S. falcata*.

APPENDIX C: PRODUCTIVITY OF A SPARTINA MARSH COMMUNITY
AS DETERMINED BY GASOMETRIC ANALYSIS

Introduction

1. Marsh vegetation productivity studies are usually based on aboveground dry weight accumulation, which integrates over time the plant response to its environment. The result is an estimate of net production which lacks accuracy for reasons discussed by Milner and Hughes (1968; references listed at end of the appendix). Major sources of error are mortality between sampling periods, translocation of photosynthate to roots, and leaching of organic compounds from live plants. Harvest techniques also fail to reflect, except indirectly, stresses that affect the relationship of net production to gross production and respiration.

2. In contrast the carbon dioxide (CO_2) flux through a community is a direct and nearly instantaneous index of the metabolic activity of that community. It gives a dynamic picture of plant growth. By monitoring this gas, it is possible to determine the plant response to transient phenomena and thus come closer to establishing critical components of its environment.

3. In addition, field analysis of CO_2 flux allows the partitioning of the major components of the energy flow of the community, using a single measuring technique that can be applied consistently across the whole community. Since previous research has concentrated usually on only one segment of the community (for instance Stowe [1972] and Blum [1968] on aufwuchs; Pomeroy [1959] on sediments microorganisms; Kirby and Gosselink 1976 on macrophytes) and each has used a variety of

techniques which are not easily comparable, direct CO₂ flux measurements offer an opportunity to integrate a number of previous studies through a single methodology. Teal and Kanwisher (1961) previously measured CO₂ flux to estimate the respiration of the whole salt marsh community, but they did not have the equipment to measure photosynthesis as well.

4. Measurements of community metabolism of a Spartina alterniflora salt marsh are reported herein.

Materials and Methods

Apparatus

5. The apparatus used in this study was modeled after that of Mooney et al. (1971). It consisted of a plant chamber or cuvette attached to control and detecting devices in a houseboat. The cuvette was a 30-cm-diameter cylinder consisting of three parts. A 20-cm-high aluminum base with a sharpened bottom edge was attached to a 15-cm-high acrylic plastic collar through which all the lines and sensors entered the cuvette. This in turn was attached through an O-ring with a 45-cm-high closed acrylic plastic top (Figure C1). The base of the cuvette with the collar and control lines attached to it was placed over a stand of marsh plants and pushed into the sediment to a depth of 10 to 15 cm. Care was taken to avoid disturbing the community. One thermocouple was pushed into the sediment to a depth of 10 cm; another was attached to a leaf; and a third was suspended in the shade inside the cuvette. Following the positioning of the thermocouples, the top was attached to the cuvette collar and the air flow to the cuvette turned on. The air-flow rate through the cuvette was adjusted to prevent CO₂

from limiting the rate of photosynthesis. Generally, fluctuations in CO₂ concentration between 250 ppm and ambient (330 ppm) had little effect on CO₂ uptake by the enclosed plants (Gosselink et al. 1976). Cuvette air temperature was controlled within 2°C by recirculating air through a separate radiator maintained at the desired temperature by chillers, heaters, and controllers in a houseboat nearby.

Sampling site

6. Measurements of CO₂ flux were made in a salt marsh bordering Louisiana Highway 1 at Leeville. The highway, and a trailer court from which raw sewage drained, bordered the marsh. Marsh tidal flushing occurred through a navigable dredged canal connected to Bayou Lafourche. The marsh appeared to be subsiding rapidly and changing to open water. Plots varied in amount of vegetation but were generally chosen to contain less biomass than unsampled areas because of limitation in capacity of the analytical equipment (Table C1).

Procedure

7. Measurements were made 4-8 December 1975, 27 February-5 March, and 13-20 May 1976. For each plot, at constant air temperature, CO₂ flux was measured in light and then in the dark by covering the cuvette with a black plastic sheet. The CO₂ 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 cuvette was opened and the green tissue removed by cutting each live culm below its lowest green leaf. The top of the cuvette was replaced and CO₂ exchange was

determined again in light and dark. Since measurements on greenhouse-grown S. alterniflora plants failed to show any significant photosynthesis by the green culms, carbon dioxide exchange under these conditions was considered to be due to the microbial community found on the lower parts of culms and on the sediment surface. The term "microbial" is used for convenience since the community also contains meiofaunal consumers that contributed to respiration. Gas exchange of the dead standing plant tissue was also assumed to be microbial. During December 1975 and March 1976, respiration of all plots was measured after sealing the cut culm ends with petrolatum to prevent diffusion from or into the roots. Results were variable but seldom changed respiration rates as much as 5 percent, so this technique was abandoned. As reported herein, therefore, metabolism of the microbial compartment includes any metabolic contributions of the lower portions of live culms and of roots of S. alterniflora.

8. Measurements on a single plot usually consumed most of the daylight hours of one day, so that different times in the daily cycle of growth and different tidal stages were encountered. It was possible to control the degree of flooding of the cuvette by slight variation in the positive pressure caused by the air stream flowing through it. Except as discussed below, the cuvette was operated with the sediment surface wet but not flooded.

Results

Substrate flooding and drying

9. Community respiration rates were strongly influenced by depth

of flooding of the substrate, since most of the respiratory gas evolution was from the substrate surface or from the lower portions of the culms that support an active flora and fauna (Stowe 1972; Hopkinson 1973). Table C2 shows respiration rates of three plots under flooded and drained conditions: two plots contained no vascular plant material and the third a normal S. alterniflora community. In all cases the gas exchange rate was decreased to low levels by flooding. In the plot containing grass (Plot 3, Table C2), the respiration of the aerial portion of the plants contributed to CO₂ exchange. In the bare sediment plots, significant CO₂ exchange occurred under flooded conditions, indicating a diffusion of CO₂ across the water-air interface.

10. When water levels on the marsh were low, the slight positive pressure of air in the cuvette on occasion caused a penetration of air into the substrate. During the course of about six hours of measurement in one plot redox potentials of implanted platinum electrodes increased gradually about 180 mv, while electrodes in the surrounding marsh remained stable. However, during this period the community respiration rate increased only about 10 percent, indicating that the effect of sediment aeration on respiration was small.

Community metabolism

11. Table C3 summarizes community metabolism during three sampling periods in winter and spring. The absolute magnitude of photosynthesis and respiration varied widely. Photosynthetic rate was strongly dependent on total leaf area in the cuvette and on light intensity (Gosselink et al. 1976). Except for the December 1975 data, the rates

in Table C3 were adjusted from light saturation curves to values for a light intensity of $1 \text{ gcal} \times \text{cm}^{-2} \times \text{min}^{-1}$. Leaf area in individual plots varied considerably (Table C1) and the data in Table C3 reflect this. Community respiration correlated well with total biomass in the cuvette. Most of the respiratory CO_2 exchange occurred on the sediment surface and on the bases of the S. alterniflora culms, so total biomass is probably an index of microbial surface area.

12. As the season progressed from December to May, the magnitude of community gross production (at constant light and temperature) increased while community respiration decreased from a high in December, with a resulting tripling in net daytime community production. During this period microbial respiration always exceeded its photosynthesis, so that this portion of the community was always heterotrophic.

Partition of metabolism between
S. alterniflora and microbiota

13. Despite fairly large variation among plots in absolute metabolic rates, the distribution between S. alterniflora and the microbial community was fairly constant. The vascular plants were responsible for 89 to 96 percent of gross community photosynthesis (at $1 \text{ gcal} \times \text{cm}^{-2} \times \text{min}^{-1}$ radiant energy) but only 24 to 36 percent of community respiration. As leaf area increased during the spring, the contribution of S. alterniflora to photosynthesis increased (with accompanying decrease in the microbial proportion from 11 to 5 percent), but its respiration did not increase, either absolutely or relative to the microbial contribution.

Influence of temperature and light on metabolism

14. The data of Table C3 are for a single air temperature, 25°C. As Figure C2 shows, when the temperature was elevated, both respiratory and photosynthetic rates increased. Consequently, at 35°C community respiration in the dark was greater, but photosynthesis was also greater so the light response curve was steeper. As a result net photosynthesis was decreased at low light intensities and increased at high light intensities. In four plots measured during May 1976 the light intensity at which net photosynthesis was equal at 25°C and 35°C was quite high--above $0.7 \text{ g cal} \times \text{cm}^{-2} \times \text{min}^{-1}$. This is about 50 percent of full sunlight, indicating that as temperatures rise net photosynthesis is only increased on cloudless days.

15. Figure C2 also shows a typical light intensity response curve, showing that photosynthesis is not light saturated, even in full sunlight. This is discussed more fully elsewhere (Gosselink et al. 1976).

Discussion

Community metabolism

16. During the periods of sampling, net community production rates were 24 to 70 percent of gross production. During the winter, because of the small amount of live tissue and the accumulation of dead material, the community was often respiring more carbon dioxide than it fixed even during daylight hours. As the season progressed, however, the amount of live biomass and the live:dead ratio increased, and net production increased correspondingly. It should be emphasized that the

net production rates in Table C3 are for daylight hours only. Net production rates averaged over 24 hours would be much lower. Roughly estimating these rates, a 12-hour light/12-hour dark regime would halve the average gross production rates (on a per hour basis). This calculation shows that the macrophyte portion of the community is net productive over a 24-hr cycle, but the total community is net heterotrophic during December.

17. The absolute photosynthetic rates reported probably underestimate rates on undisturbed marshes. Table C1 shows that the live biomass in the cuvette plots was less than the average live biomass reported in Appendix A and by Kirby and Gosselink (1976), although it was quite close to the biomass in the latter's inland plots. Leaf area in the plots was undoubtedly also less than normal density.

18. Dead biomass (which community respiration follows closely) was also lower than average values of Kirby and Gosselink (1976) and Appendix A, suggesting that community respiration rates are also underestimated.

S. alterniflora metabolism

19. S. alterniflora photosynthetic rates increased from December to May (Table C3) as leaf area increased (Table C3). At the same time absolute shoot respiration rates appeared to decrease, so that S. alterniflora shoot respiration was reduced to only 8 percent of gross production in May from a high of 24 percent in December. Further tests are needed to determine the root contribution before the net production of the entire plant can be accurately determined.

Microbial metabolism

20. As Table C3 indicates, some photosynthetic CO₂ fixation by the microbial community was measured. The levels were low, however, never more than about 10 percent of community gross production and decreasing in importance as macrophyte production increased during the spring. In contrast the sediment and epiphytic flora and fauna are clearly the major organisms responsible for CO₂ evolution. Attempts to partition the respiratory CO₂ flux between the microbial community and S. alterniflora roots were unsuccessful, but together they accounted for about 75 percent of community respiration. Teal and Kanwisher (1961) found that in Georgia salt marshes, on the average, root respiration was 73 percent of shoot respiration. If this is also true in Louisiana marshes, then somewhat more than 50 percent of total community respiration is microbial.

Comparison of harvest production values with net photosynthesis rates

21. The calculated net annual production of S. alterniflora in Louisiana from harvest data is about 2500 g dry wt $\times m^{-2}$ (Kirby and Gosselink 1976; Appendix A). On an hourly basis in carbon units (considering that organic dry weight is about twice organic carbon) this is 143 mg C $\times m^{-2} \times hr^{-1}$ for net shoot production. In laboratory-grown plants (Gosselink et al. 1976) shoot:root ratios indicated that root growth was about one half the aerial growth. This may underestimate root growth in the marsh, but using this figure the harvest estimate for total plant production would be about 215 mg C $\times m^{-2} \times hr^{-1}$.

22. In comparison, net S. alterniflora production rates can be roughly calculated from the CO₂ flux data in several ways. Two estimates were made, the first based on the May rates, assuming that they represent average annual rates. For this estimate, gross S. alterniflora production was 48 mg C × hr⁻¹ (for a 0.075-m² cuvette). The average rate over 24 hours would be about one half of that figure, or 24 mg C × hr⁻¹. Shoot respiration for May was 4 mg C × hr⁻¹. Doubling this figure to accommodate root respiration and subtracting from the gross production rate, net production would be 16 mg C × hr⁻¹. As mentioned previously the cuvettes did not contain as much plant material as the marsh average. Therefore, the net production value should be adjusted by the ratio of average to cuvette live biomass (Table C1). This ratio is (0.5) (35 + 28.5)/22.8 = 1.38. Multiplying 16 × 1.38 = 22 mg C × hr⁻¹ per cuvette. On a square meter basis, this is 294 mg C × m⁻² × hr⁻¹, the calculated net production rate.

23. A second method of calculating production considers the average production rate per unit live S. alterniflora shoot biomass and the average stand density. Considering again only the May data, there is a fairly consistent relationship between CO₂ flux and live biomass, especially for photosynthesis. Gross photosynthetic rates averaged (± standard deviation) 2.17 ± 0.27 mg C (g dry wt × hr)⁻¹ at 1 gcal × cm⁻² × min⁻¹ radiant flux (Gosselink et al. 1976). This is about three fourths full sunlight flux over the period December 1975 to May 1976. The lower part of the light saturation curve is steep (see Figure C2), so an average value for gross photosynthesis during daylight hours is about 1.8 mg C (g dry wt × hr)⁻¹. Over a 24-hour cycle,

the average value would be about $0.9 \text{ mg C (g dry wt} \times \text{hr)}^{-1}$. Respiration of the plant top averaged $0.13 \text{ mg C (g dry wt} \times \text{hr)}^{-1}$. Double this to accomodate root respiration. From these figures for gross photosynthesis and respiration, net photosynthesis, very roughly, averages $0.6 \text{ mg C (g dry wt} \times \text{hr)}^{-1}$. The annual average S. alterniflora live biomass density is about $500 \text{ g dry wt} \times \text{m}^{-2}$ (Kirby and Gosselink 1976). Multiplying this gives a net production rate of $300 \text{ mg C} \times \text{m}^{-2} \times \text{hr}^{-1}$. Considering the crude nature of the estimates, these two values of CO_2 flux, 294 and $300 \text{ mg C} \times \text{m}^{-2} \times \text{hr}^{-1}$, are in reasonable agreement with the Wiegert-Evans technique. Therefore, the latter does not appear to overestimate net production, and comes closest of the different techniques to estimating true net production.

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Table C1

S. alterniflora Density with Standard Deviation in This Study Compared to Previous Work*

	December 1975	March 1976	May 1976
Cuvette Values - This Study:			
<u>S. alterniflora leaf area,</u> <u>dm² × m⁻²</u>	58.0 ± 11.1	74.7 ± 34.3	111.9 ± 26.1
<u>S. alterniflora live biomass,</u> <u>g × m⁻²</u>	237.3 ± 64.0	138.7 ± 66.7	304.0 ± 72.0
Total biomass, g × m ⁻²	1060.0 ± 557.3	602.7 ± 281.3	716.0 ± 230.7
Reference plots:			
Live biomass, g × m ⁻²			
Kirby and Gosselink (1976)			
Streamside	505	330	567
Inland	253	102	362
Appendix A	300	300	380
Total biomass, g × m ⁻²			
Kirby and Gosselink (1976)			
Streamside	1773	1808	1786
Inland	1208	1002	1278
Appendix A	1670	1500	--

* Means are shown with standard deviation.

Table C2

Effect of Water Level on Marsh Community Respiration*

Plot No.	1	2	3
	Bare Sediment		<u>S. alterniflora</u>
	<u>Dec 1975</u>	<u>May 1976</u>	<u>Community</u> <u>March 1976</u>
Flooded (1-5 cm of water)	3.9	2.6	4.6
Drained (surface wet)	8.9	12.0	9.6
Soil temperature, °C	21	21	20
Air temperature, °C	25	25	15

*Units are in $\text{mgC} \times \text{m}^{-2} \times \text{hr}^{-1} \times 0.075 \text{ m}^{-2}$.

Table C3

Summary of Salt Marsh Community Metabolism*

	December 1975**		March 1976		May 1976	
	(mgC×hr ⁻¹)	(%)†	(mgC×hr ⁻¹)	(%)†	(mgC×hr ⁻¹)	(%)†
Soil Temperature, °C	18-22		16-20		22-24	
Salinity, ppt	14-16		12-17		8-14	
No. of Plots	3		4		5	
Gross photosynthesis††						
Community			46 ± 18		50 ± 15	
S. alterniflora shoots	34 ± 11	89 ± 6	43 ± 18	92 ± 6	49 ± 16	96 ± 3
Microbiota	4 ± 2	11 ± 6	3 ± 1	8 ± 6	2 ± 1.6	4 ± 3
Respiration						
Community	29 ± 13		14 ± 6		16 ± 6	
S. alterniflora shoots	8 ± 6	25 ± 9	5 ± 3	36 ± 5	4 ± 2	24 ± 9
Microbiota	21 ± 7	75 ± 9	9 ± 4	64 ± 5	12 ± 5	76 ± 9
Net community production†			32 ± 14		34 ± 14	
Number of plots	3		4		6	

*CO₂ flux in mgC×hr⁻¹ ± standard deviation for a cuvette of 0.075-m² marsh surface; air temperature, 25°C.

**Light intensity varied; values not adjusted.

†Percentage of community rate.

††At 1 gcal×cm⁻²×min⁻¹ radiant flux.

LIGHT
SENSOR

RADIATOR
AND
FAN

AIR
SUPPLY
AND
RETURN
HOSES

CUVETTE



Figure C1. 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. The black hoses in the foreground carry air to and from the sensing and control units in the houseboat.

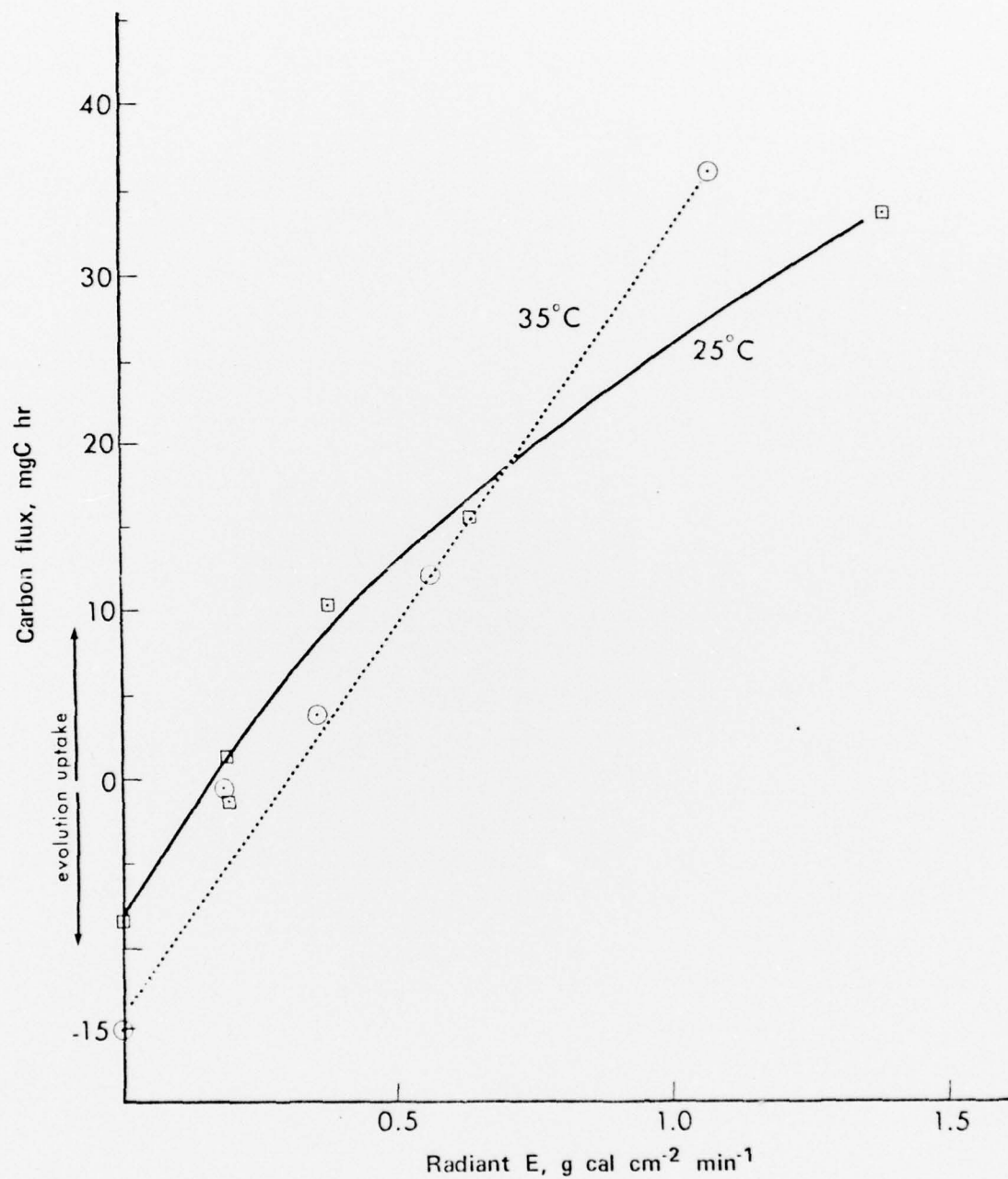


Figure C2. Typical light saturation curves for net carbon flux at 25°C and 35°C, May 1976.

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