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PRODUCTION AND RELEASE OF PLANT MATERIAL IN BRACKISH AND FRESHWATER WETLANDS

by

Paul L. Wolf and Donald Kinsey
The University of Georgia Marine Institute
Sapelo Island, Georgia 31327

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Project Officer

Harold V. Kibby
Corvallis Environmental Research Laboratory
Environmental Protection Agency
Corvallis, Oregon 97330

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16. ABSTRACT

Production, decomposition, and transport of detritus were investigated in the freshwater and brackish water wetlands of the Altamaha River Delta, Georgia from April 17 1978 to 13 April 1979. Maximum live standing crop biomass of Spartina cynosuroides, a brackish water marsh plant, was observed in July (769 ± 118 g dry wt m^2). Live material was absent in January. Standing dead material ranged from a high of 1800 ± 275 g dry wt m^2 in November to a low of 158 ± 57 in March. The quantity of fallen dead (litter) material was more constant throughout the year averaging 244 ± 21 g dry wt m^2. Net aerial primary productivity (NAPP) of S. cynosuroides was 2029 g m^2 yr^1 with no differences in productivities of plots relative to the distance from the riverbank because of minimal tidal activity in the entire area. Maximum live standing crop biomass of Zizaniopsis miliacea, a freshwater marsh plant, was observed in October (673 ± 122 g dry wt m^2). Live material dropped to a low of 81 ± 12 g dry wt m^2 in March. Standing dead material ranged from a high of 870 ± 222 g dry wt m^2 in April 1978 to a low of 308 ± 101 in August. Aquatic respiration rates of standing and fallen dead material showed a pattern of swamp litter > Z. miliacea > S. cynosuroides. Rates for marsh grasses were generally higher in the spring dropping to a low in fall and winter. Rates in swamp litter were much more variable without distinct seasonal patterns.

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EXECUTIVE SUMMARY

Production, decomposition, and transport of detritus were investigated in the freshwater and brackish water wetlands of the Altamaha River Delta, GA, from 17 April 1978 to 13 April 1979. Maximum live standing crop biomass of Spartina cynosuroides, a brackish water marsh plant, was observed in July (769 ± 118 g dry wt m^{-2}). Live material was absent in January. Standing dead material ranged from a high of 1800 ± 275 g dry wt m^{-2} in November to a low of 158 ± 57 in March. The quantity of fallen dead (litter) material was more constant throughout the year averaging 244 ± 21 g dry wt m^{-2}. Net aerial primary productivity (NAPP) of S. cynosuroides was 2029 g m^{-2} yr^{-1} with no differences in productivities of plots relative to the distance from the riverbank because of minimal tidal activity in the entire area.

Maximum live standing crop biomass of Zizaniopsis miliacea, a freshwater marsh plant, was observed in October (673 ± 122 g dry wt m^{-2}). Live material dropped to a low of 81 ± 12 g dry wt m^{-2} in March. Standing dead material ranged from a high of 870 ± 222 g dry wt m^{-2} in April, 1978, to a low of 308 ± 101 in August. Fallen dead material had an annual average of 159 ± 71 g dry wt m^{-2}. NAPP for Z. miliacea was 1478 g m^{-2} yr^{-1}. Productivities were higher in creekbank plots than in more inland plots (1824 and 1237 g m^{-2} yr^{-1}, respectively) presumably because of longer tidal inundation times in the creekbank zone. In both areas NAPP peaked between April and May and was lowest between November and January. Leaf litter accumulation (primarily Nyssa aquatica, Liquidambar styraciflua, and Taxodium distichum) was highest in November (253 ± 19 g dry wt m^{-2}) and lowest in spring and summer (18 ± 2g dry wt m^{-2}).

Aquatic respiration rates of standing and fallen dead material showed a pattern of swamp litter > Z. miliacea > S. cynosuroides. Rates for marsh grasses were generally higher in the spring dropping to a low in fall and winter. Rates in swamp litter were much more variable without distinct seasonal patterns. Aerial respiration rates of dead plant material ranked Z. miliacea > swamp litter > S. cynosuroides. Fallen dead marsh grass material had a higher respiration rate than standing dead material, with the highest rates occurring during the summer. DOC leaching rates for dead plant material ranked swamp litter > Z. miliacea > S. cynosuroides. Seasonal patterns of leaching were not evident in the marsh grasses, nor were there differences between fallen dead and standing dead materials. Swamp litter had high leaching rates in summer and fall with low rates during the winter months.

Weight losses in marsh grass litter bags ranked submerged > surface > suspended with decomposition rates being higher in Z. miliacea than S. cynosuroides. Z. miliacea surface litter at 11 months decreased to 14% of the original weight while S. cynosuroides showed a decrease of only 40%. Z. miliacea submerged litter at 6 months had only 6% of the original biomass, while S. cynosuroides had 52% remaining. Decomposition rates for swamp litter were similar in both submerged and surface bags with the greatest weight losses occurring between 1 and 6 months.

Aquatic respiration rates of dead material from litter bags were higher in more aquatic situations and were generally higher in the earlier stages of decomposition with the highest rates observed in swamp litter. Although more variable, aerial respiration rates exhibited a pattern similar to that of aquatic respiration. DOC leaching rates for litter bag material ranked S. cynosuroides > Z. miliacea > swamp litter. Swamp litter had a negative leaching rate indicating a possible uptake of carbon. Submerged litter leaching rates were higher in submerged and surface bags for S. cynosuroides while Z. miliacea suspended litter had the highest rate of leaching.

Analyses of mineral composition data for litter bag material indicated an accumulation of Ba, Fe, Na, N, Zn and P over an 11-month period while Al, B, K, and Mg levels decreased. Concentrations of Ca, Cu, Mn, and Sr remained the same. For most of the elements analyzed, levels were generally higher in submerged and surface litter as compared to suspended material, and litter bag material was highest in elemental concentration than plant debris removed from the marsh surface. Species differences in levels of some elements were also demonstrated.

Estimates of the quantity of carbon lost to the estuary as particulate detritus were 372 and 147 g C m^{-2} y^{-1} from S. cynosuroides and Z. miliacea marshes, respectively. However, the results for the swamp forest indicated a possible import of carbon.

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CONTENTS

FIGURES

TABLES

TABLES (Continued)

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Finally, we wish to acknowledge the efforts of Dr. John Gallagher who first initiated the Altamaha River Study in October, 1976; and Dr. Harold Kibby, who served as the project officer.

SECTION 1

INTRODUCTION

The Altamaha River Delta, approximately 7 km south of Sapelo Island, Georgia, is characterized by extensive brackish water marshes, freshwater marshes, and river swamp hardwood forests. Although there have been a few studies of this freshwater to brackish water wetland system, processes within these wetlands and their relationship to the more intensively studied saline zones are poorly understood. The food webs in this system like those of saltwater marshes are predominantly based on detritus produced by the trees and grasses (Wharton and Brinson, 1978). Detrital productivity contributes to invertebrate and vertebrate production and is potential food for export to other components of the coastal system. The rivers associated with the marshes and forests may be point sources of inorganic nutrients and organic compounds for the salt marshes along the coast. Windom, Dunstan and Gardner (1975) have shown that river flow could contribute 20% of the inorganic nitrogen needed by marsh plants. Organic nitrogen compounds are also present in river flow (Dunstan and Atkinson, 1976). Brinson (1977) however, reported that, in some cases, swamp forest areas may act as nutrient sinks. It appears that any alterations in this system which cause a change in the amount, quality, and timing of detrital productivity, and a modification in nutrient transport patterns could have an effect on productivity at the primary and secondary levels within the system. Wharton (1970) reported that channelization and damming projects in freshwater areas have resulted in severe damage with little or no recovery even after a relatively long period of time. Furthermore, large quantities of detritus and nutrients are probably processed in the saline portion of the coast since there is a net flow of water from fresh to saline areas. Without information on detrital productivity and the associated nutrient flux in the freshwater and brackish water wetlands, it would be impossible to predict the impact of alterations of these wetlands on the adjacent estuarine.

In October, 1976, investigators from the University of Georgia Marine Institute, Sapelo Island, Georgia, initiated studies which focused on the detrital and microbial processes in three types of wetlands (swamp, freshwater marshes, and brackish water marshes) in the Altamaha River system. These studies provided some information on potential detritus production, detrital decay rates, and movement of detritus between freshwater wetlands and the adjacent estuary. A preliminary evaluation of the data indicated a need for further work in this area before conclusions could be made concerning the interaction of freshwater, brackish water and saline systems. Even if research would show that the dynamics in the freshwater areas do not result in a significant input into the already-rich coastal area, the timing and placement of the input, the composition of the material, or the pulsing action during high water flow may be critical to the organic nutrition of coastal areas. For example, the river system seems ideally designed to release materials into the adjacent ecosystems in pulses, whereas flow from the salt marshes dominated by semi-diurnal tides would be more uniform and rhythmic.

The main objective of the proposed research was to continue the work on the Altamaha River system. Specifically, we attempted to answer the following questions:

1. How much detritus is produced in the wetland types?

2. How fast does the detritus decay and what is the leaching rate of organic compounds into the water from the dead and dying leaves?

3. What is the quantity of detritus released into the river and transported to the estuary?

4. What are the chemical characteristics of the detritus from the river wetlands?

Although the results of our research should enable the various agencies concerned with ecosystem management to assess the advantages and disadvantages of any alterations in coastal freshwater and brackish water ecosystems, it is apparent that further studies are necessary for a more complete understanding of these systems and their relation to the more saline coastal areas.

SECTION 2

CONCLUSIONS AND RECOMMENDATIONS

The results of this study indicate that the brackish water marshes and freshwater marshes are areas of relatively high productivity which make significant contributions of particulate detritus, organic compounds, and inorganic nutrients to the coastal estuarine system. The role of the freshwater swamp forest has not been as clearly defined. There are indications that these swamp forest areas may be "importers" rather than "exporters" of carbon and other nutrients. Clearly, there is a need for further work in these sensitive wetlands - particularly in the freshwater marshes and swamps. Specifically, the following projects and/or studies are recommended:

1) Underground biomass should be determined in the *Zizaniopsis miliacea* marsh to give a more accurate assessment of net primary productivity and potential detritus production.

2) Studies on *Z. miliacea* should be expanded to include stands in what were formerly areas of rice culture. These old rice fields occupy approximately 2544 ha in the Altamaha River Delta. The present study included only stands of *Z. miliacea* in a relatively narrow zone (182 ha) along river and creekbanks.

3) A more intensive litter bag study should be initiated whereby more bags are utilized and samples are collected much more frequently. The results of this study would provide more accurate information on decomposition rates and nutrient exchanges.

4) The quantities of plant materials (live and dead) consumed by marsh and swamp fauna should be determined.

5) Finally, and perhaps most importantly, elevational data and information on tidal amplitude and frequency of inundation are needed for these areas. These data are needed to quantify more accurately the transport of detritus and nutrients to and from these areas, and will enable us to establish more clearly the relationships between the various type of coastal wetlands.

SECTION 3

MATERIALS AND METHODS

STUDY AREA

The general study area was situated in the Altamaha River Delta approximately 16 km north of Brunswick, GA. Sampling sites (Figure 1) were located in Spartina cynosuroides, a brackish water (0-15 0/00) marsh on the south side of Broughten Island; in Zizaniopsis miliacea, a predominantly freshwater marsh bordering the north side of Hammersmith Creek, a tributary of the Altamaha River; and in two forested areas dominated by Nyssa aquatica, Taxodium distichum, and Liquidambar styraciflua. The forested area was located approximately 26 m from the creekbank on the north side of Hammersmith Creek adjacent to the Z. miliacea productivity plots. This area, designated Riverbend, is subject to flooding only on extremely high tidal conditions. The other area, designated freshwater swamp, was situated on the south side of Hammersmith Creek approximately 0.5 km west of Riverbend. This area was flooded much more frequently than the Riverbend site. Nine collections were made at approximately 6-week intervals between 17 April 1978 and 13 April 1979.

DETRITUS PRODUCTION AND AERIAL PRODUCTIVITY

The question of how much detritus is produced was approached by measuring the calculating net aerial primary productivity (NAPP) and the production of dead plant material. Changes in dead marsh plant biomass during each sampling interval were measured utilizing the paired plots method of Wiegert and Evans (1964) as modified by Lomnicki et al. (1968). In the S. cynosuroides marsh, six plots were placed at 6 m intervals on a transect from riverbank to the higher marsh dominated by Iva frutescens. Similarly, eight plots were placed at 3 m intervals in the Z. miliacea marsh on a transect from creekbank to the hardwood forest. At both sites, plant material in each 0.5 m^2 plot was clear cut (Clear Cut Plots), and bagged, after which fallen dead material (litter) was removed from the marsh surface and bagged. In an 0.5 m^2 area adjacent to each of the clear cut plots, all of the dead material was removed and discarded. These plots were designated as previous cut plots. At the next sampling interval, approximately six weeks later, the previous cut plots were clear cut and the plant material was bagged. Following the collection at each sampling period, the plots were advanced approximately 1 m, and the process of establishing paired plots was repeated. Marsh grass was returned to the laboratory where it was sorted into live and dead material, oven dried at 60° C and massed to the nearest gram. Litter was washed over a No. 18 brass sieve, oven dried at 60° C, and

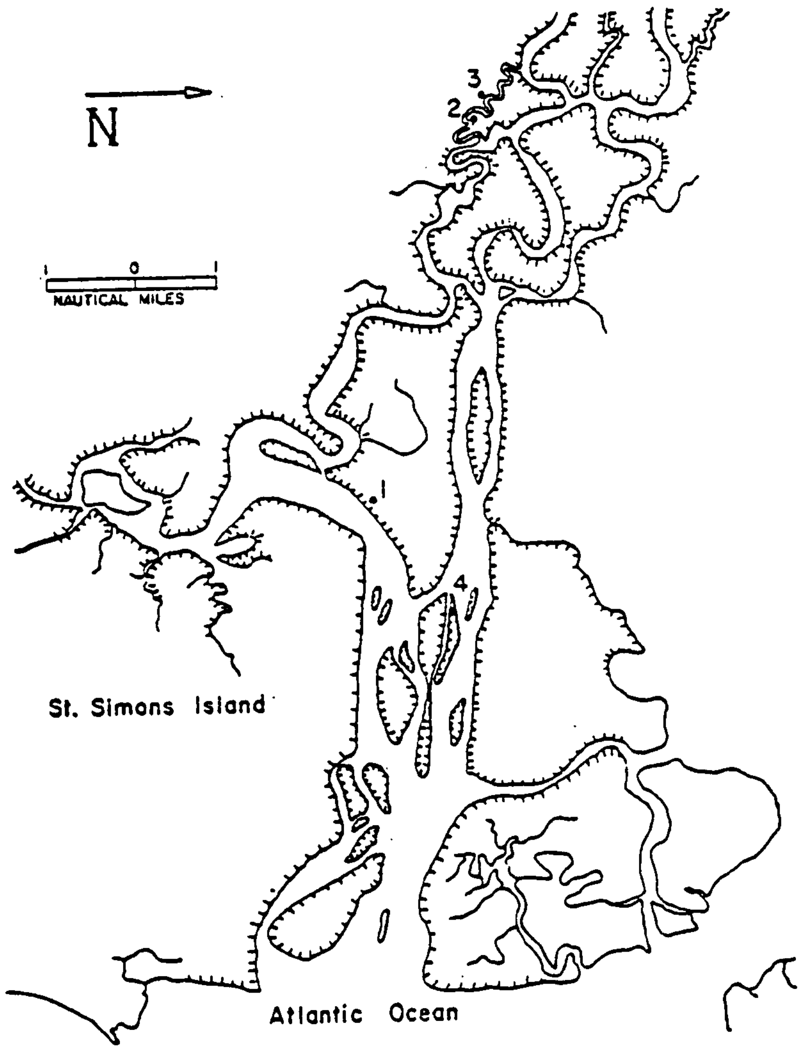


Figure 1. The Lower Altamaha River Delta, Georgia, showing sampling sites. Broughton Island, 1; Riverbend, 2; Freshwater Swamp, 3; and Reese Island, 4.

massed to the nearest gram.

Net aerial primary productivity was calculated with the formula NAPP = ΔG + M, where ΔG = change in live plant biomass during the time interval (Lomnicki et al., 1968). In summing the marsh grass productivities during each time interval to arrive at annual NAPP, negative values were treated as zero productivities.

In each of the two forested areas 12 plastic trash containers (0.1 m in surface area) were mounted on poles to catch material falling from the trees. At each collection the material was harvested, bagged, and returned to the laboratory where it was oven dried at 60° C and massed to the nearest 0.1 gram.

DETRITUS DECAY AND LEACHING STUDIES

At each collection, samples of standing dead marsh plant material, fallen dead marsh plant material, and fallen leaves from the swamp forest were returned to the laboratory for respiration (aerial and aquatic) and leaching studies. Aquatic and aerial respiration rates of the attached dead plant community from each of the plant types were determined as described by Gallagher and Pfeiffer (1977); release of dissolved organic carbon (DOC) from the dead plant parts was measured according to Gallagher, Pfeiffer and Pomeroy (1976).

LITTER BAG STUDIES

Further information on detritus decay rates was obtained through litter bag studies utilizing a modification of Brinson (1977). Standing dead material from two marsh sites and fallen leaves from the river swamp forest were obtained and air dried in a greenhouse. Dried marsh plant material (100 g each) was placed in 120 x 30 cm fiberglass litter bags (1.5 mm mesh size) and returned to Altamaha River Delta. Bags containing Z. miliacea standing dead were located at the productivity collection site. Because the S. cynosuroides collection site had a history of frequent burnings each spring, bags containing that material were located in a S. cynosuroides marsh 1 km NE of the productivity collection site. At the two sites, 18 bags each were suspended on wooden stakes above the marsh surface to simulate decay of standing dead, secured on the marsh surface to simulate decay of fallen dead, and submerged in the water adjacent to the marsh site to simulate decay of dead plant material after it is washed into the river and creek. Air dried swamp leaf litter (20 g each) was placed in 36 x 18 cm fiberglass litter bags (1.5 mm mesh size), returned to the swamp forest where 18 bags each were placed on the forest floor which was free of standing surface water at the time of placement, and submerged in the water of a narrow canal connecting the creek with the swamp forest area. To simulate decay rates in more saline water after material from the marshes and swamp forests had been transported to the estuary, 18 litter bags each with dead plant material from the two marsh sites (100 g each) and the swamp forest (20 g each) were submerged in a tidal creek adjacent to the University of Georgia Marine Institute facilities on Sapelo Island. Six bags were retrieved from each of the treatment areas (suspended, surface, submerged) at each location at one, six, and eleven-month intervals. Following retrieval, plant material was air dried and massed to the nearest gram (marsh grass) and 0.1 gram (swamp leaf litter). Leaching and respiration measurements were made on representative litter samples from each of the treatments at each location. Samples of litter bag plant material and litter collected from the marsh and swamp surfaces at each retrieval were oven dried at 60° C and ground in a Wiley mill (40 mesh screen). Spectographic analyses of P, K, Ca, Mg, Mn, Fe, B, Cu, Zn, Al, Sr, Ba, and Na; and determinations of total N were conducted by the Soil Testing and Plant Analysis Laboratory, Athens, GA.

Statistical analyses were accomplished using the Statistical Analysis Computer Systems Program (SAS) (Barr et al., 1976). Duncan's Multiple Range test was used to evaluate statistical differences in decomposition, respiration, leaching and mineral composition of litter bag materials.

SECTION 4

RESULTS AND DISCUSSION

DETRITUS PRODUCTION AND AERIAL PRODUCTIVITY

S. cynosuroides living biomass for clear cut plots ranged from a high of 769 ± 98 g dry wt m^{-2} in July to a low of zero in January (Figure 2). Standing dead biomass peaked in November (1800 ± 275 g dry wt m^{-2}) and reached a low in March (158 ± 57 g dry wt m^{-2}). However, the latter figure does not represent the amount of standing dead material usually present in early spring because fire swept through the area destroying much of the dead material prior to the March, 1979 collection. In March, 1978, a year in which the marsh was not burned, standing dead biomass averaged 1087 ± 104 g dry wt m^{-2}, and in April, 1978 the amount was 970 ± 94 compared to 215 g dry wt m^{-2} for April, 1979. Fire caused a decrease in litter biomass (88 ± 21 g m^{-2}) in March, 1979 compared to 427 ± 33 in March, 1978. With the exception of the unusually low amount of litter present at the March collection, litter biomass was relatively constant throughout the year.

Z. miliacea living biomass for clear cut plots reached a maximum in October and a low in March (Figure 3). Unlike *S. cynosuroides*, *Z. miliacea* apparently does not experience a complete "die-back" each growing season. Live material was collected at each sampling throughout this study during a two-year period preceding the present study. Standing dead biomass was highest in April, 1978 and lowest in August. Variations in litter biomass were not as pronounced as in live and standing dead material.

Leaf litter accumulations at the forest sites were highest in November with the lowest accumulation occurring in April and July at Riverbend and the freshwater swamp site, respectively (Figure 4).

Net aerial primary productivity for *S. cynosuroides* was 2029 g dry weight m^{-2} yr^{-1} with a turnover time of 2.64. Turnover time is equal to productivity divided by the maximum live biomass. NAPP reached a maximum between 17 April and 30 May 1978 (472 g m^{-2}) and was lowest between 9 January and 5 March 1979 (9 g m^{-2}). Odum and Fanning (1973) reported an NAPP of 2092 g dry wt m^{-2} yr^{-1} for *S. cynosuroides* on the south shore of Rabbit Island in the Altamaha River. However, they did not use the Lomnicki method for calculating productivity and therefore comparisons between the two figures may not be feasible. Linthurst and Reimold (1978) reported NAPP for *S. cynosuroides* in the

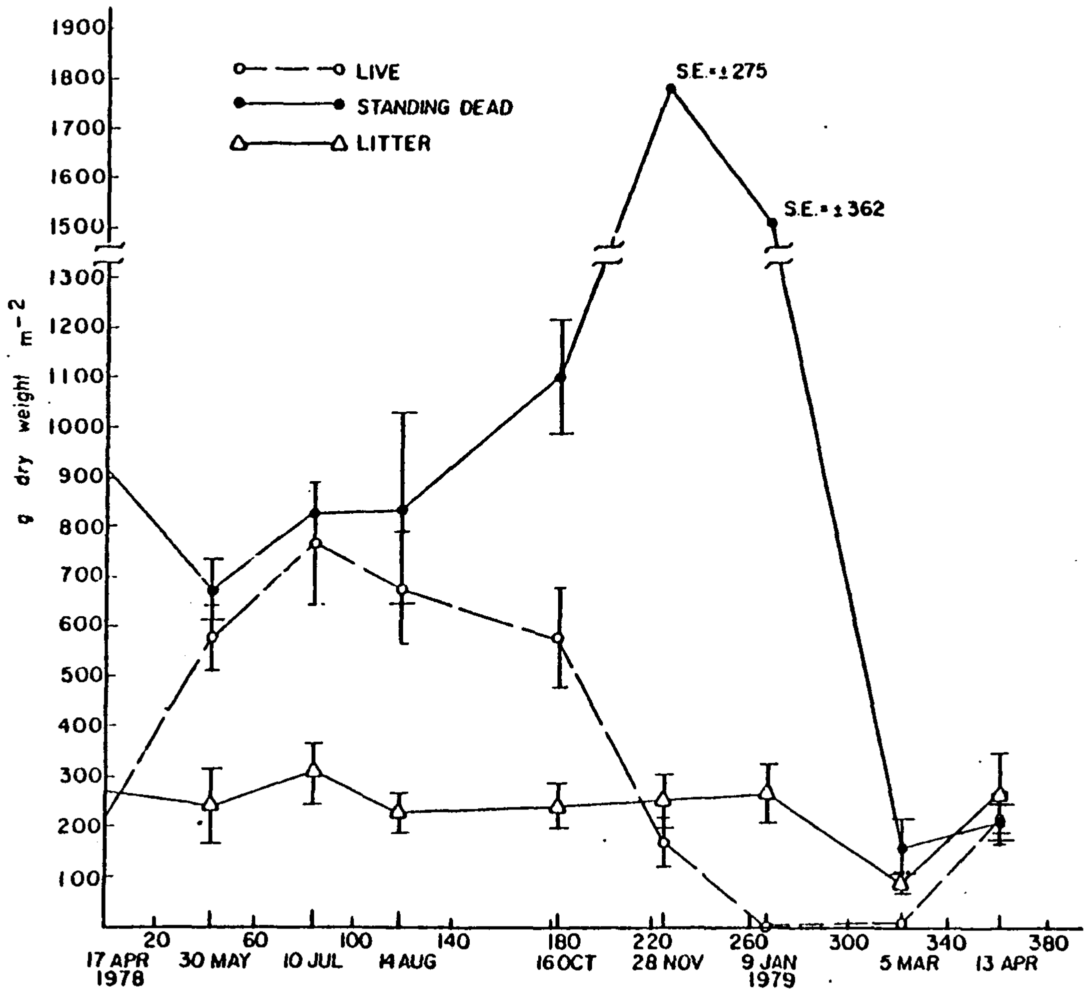


Figure 2. Mean dry weight (g m^{-2} ± S.E.) of <u>Spartina cynosuroides</u> from clear cut plots in the Altamaha River Delta.

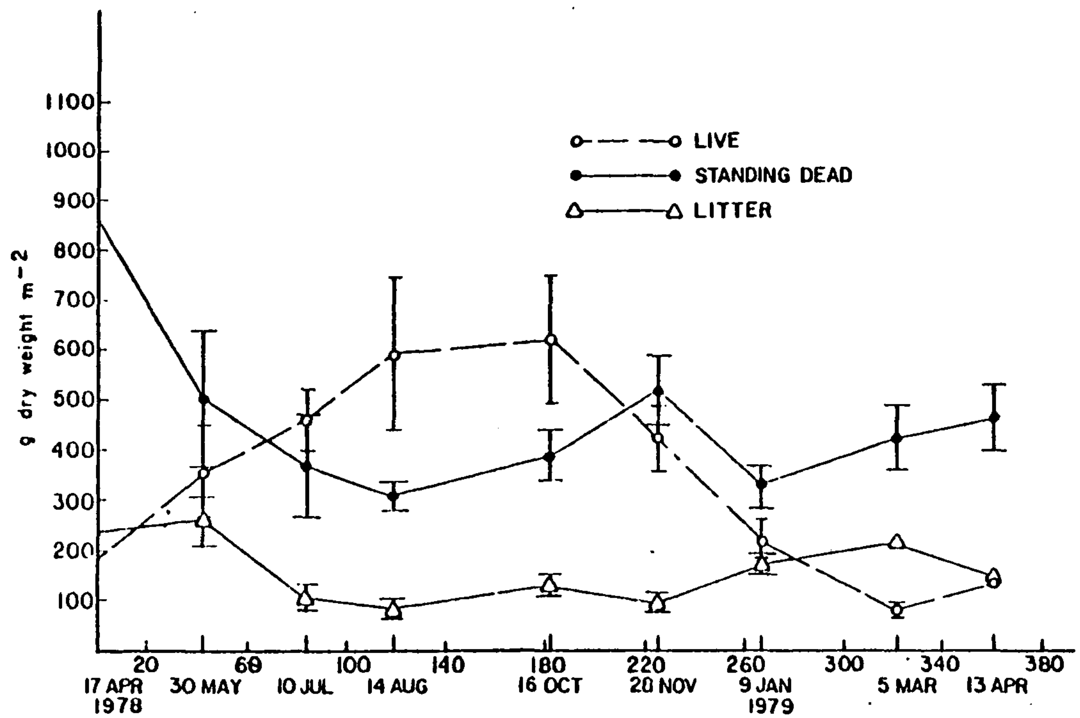


Figure 3. Mean dry weight (g m^{-2} ± S.E.) of <u>Zizaniopsis</u> <u>miliacea</u> from clear cut plots in the Altamaha River Delta.

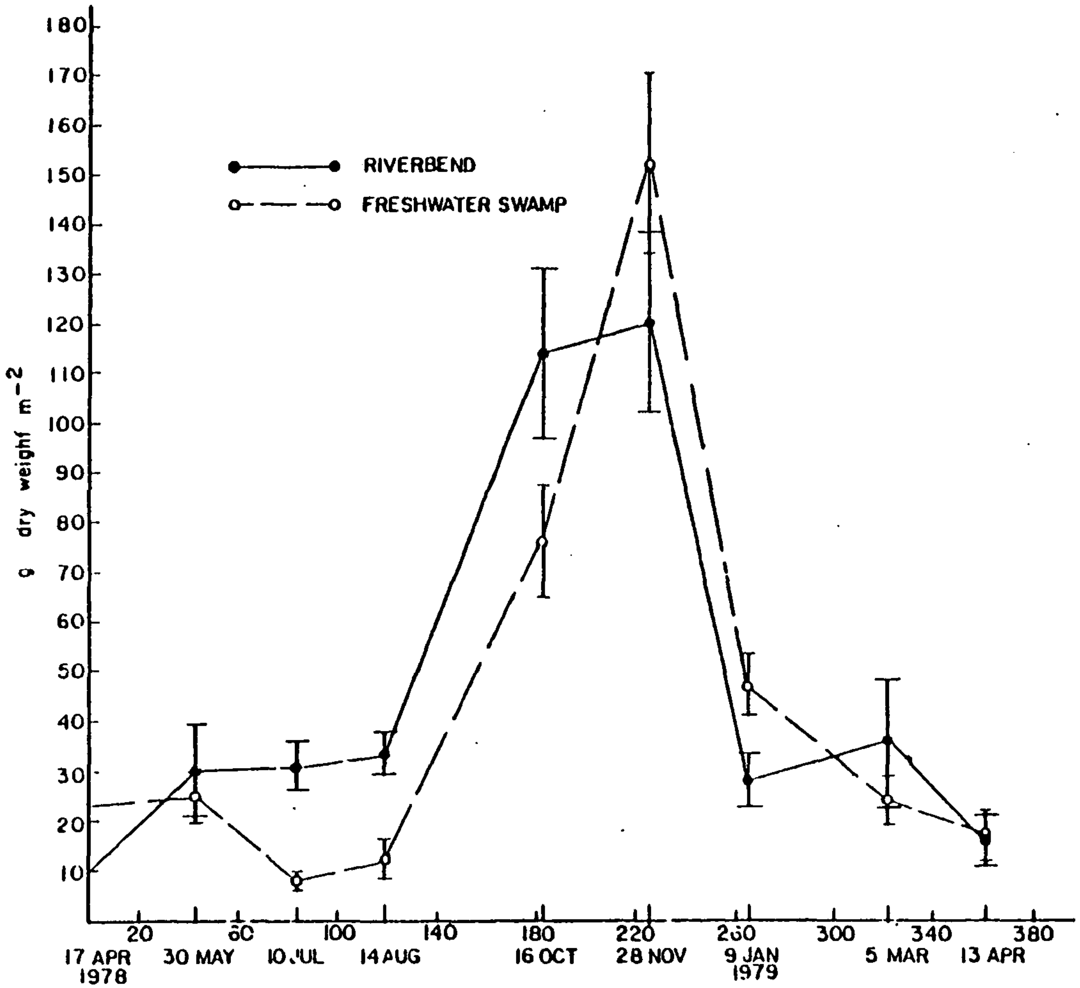


Figure 4. Mean dry weight (g m^{-2} ± S.E.) of leaf litter at two forest locations in the Altamaha River Delta.

ltamaha River Delta ranging from 1742 to 6039 g dry wt m^{-2} yr^{-1} depending on he technique used for calculating NAPP. The Lomnicki method was not used or calculating NAPP in their study. However, Linthurst and Reimold, using he method of Smalley (1958) reported an NAPP of 2789 with a turnover time of ..3. When we calculated NAPP by the Smalley method we obtained an NAPP of '33 g dry wt m^{-2} with a turnover time of 2.3. The possible explanation for :he rather sizable difference in NAPP between the two areas is that the Broughton Island collection site was higher in elevation than the Linthurst-Reimold site. Although elevations were not measured in the present study, it was readily apparent that our area was higher and drier than the Linthurst-Reimold area. Comparing the maximum living biomass between the two areas, Linthurst and Reimold reported a maximum of 2177 g m^{-2} whereas we found a maximum of only 769 g m^{-2}. As a further check on living biomass, in July, 1978, we collected 5, 0.5 m^2 samples of S. cynosuroides from the site where the litter bags had been placed. For that area we obtained a mean of 1395 ± 228 g m^{-2}, a figure almost twice as high as the value for Broughton Island. Again, elevation was not measured, but it was obvious that the Reese Island area was lower and subject to more frequent tidal inundation. Odum and Fanning (1973), and others, have shown that creekbank S. cynosuroides is much more productive than more inland areas, presumably because of more tidal influence in the lower areas. For comparison, we arbitrarily divided the collection site into two zones - a lower zone consisting of 3 pairs of plots within 18 m of the riverbank, and a higher zone of 3 pairs of plots between 19 and 30 m from the creekbank. NAPP in the lower and higher zones were 2048 and 1896 g dry weight m^{-2} yr^{-1}, respectively. Thus our area appears to be more homogeneous than the areas studied by Odum and Fanning. It should be noted that in the collection site, Spartina alterniflora was the dominant plant on the riverbank, occupying a zone approximately 3 m wide.

Productivity in the Broughton Island area may have been adversely affected by fire which swept through the collection site in February, 1979. Although, standing live material is normally absent in late winter and early spring, dead material biomass is usually very high at that time of the year. As a result of the fire, a significant reduction in biomass of dead material was observed in the March collection. This reduction effectively lowered the NAPP value for that time period. The Linthurst-Reimold and Odum-Fanning NAPP values for S. cynosuroides cited previously represent data for stands which had not been burned during the course of the study period.

NAPP for Z. miliacea was 1478 g dry weight m^{-2} yr^{-1} with a turnover time of 2.37. Maximum NAPP was observed between 17 April and 30 May 1978 (351 g m^{-2}) and dropped to zero for the period between 28 November 1978 and 9 January 1979. To determine differences between creekbank NAPP and NAPP farther inland we divided the collection site into two zones - one zone consisting of a series of 4 paired plots within 12 m of the creekbank; the other zone a series of 4 paired plots between 13 and 24 m from the creekbank. NAPP values were 1824 and 1237 g dry weight m^{-2} yr^{-1} for creekbank and inland zones, respectively. Presumably the higher NAPP in the creekbank zone is a result of more tidal activity in this area (Odum and Fanning, 1973). To properly assess the potential contribution of the marshes to the detritus food web, data on elevation and tidal inundation are needed for both areas.

RESPIRATION AND LEACHING STUDIES

In S. cynosuroides the attached dead community on the fallen dead had a higher respiration rate than that of standing dead (Figures 5 and 6). Generally, respiration rates were higher in the spring, somewhat reduced during the summer reaching a low in October, and maintained a low rate until early spring when a significant increase occurred.

Aquatic respiration rates in the Z. miliacea marsh followed the same pattern as that in S. cynosuroides (Figures 5 and 6). However, the rates in Z. miliacea were somewhat higher, with the highest rates being observed in the standing dead community. Because of the frequent flooding at the Riverbend site, the standing dead community was subjected to inundation for a larger period of time than the similar community at Broughton Island, which conceivably could have resulted in higher respiration rates. Incubation temperatures, which ranged from a low of 8° C in January to a high of 27° C in July, did not appear to have an effect on the pattern of respiration rates. It is more likely that the previous history of the dead material was the most important factor in the development of the microbial community and concomitant respiratory rates. Aquatic respiration rates for the swamp forest leaf community were, generally, significantly higher than the rates observed for the two marsh communities (Figure 7). Among the three species of tree leaves studied, Taxodium distichum showed the highest mean respiratory rate for the entire year (238 ± 90 µg C g^{-1} dry wt hr^{-1}) while Liquidambar styraciflua showed the lowest rate (121 ± 27). The highest rate recorded for Taxodium was almost an order of magnitude higher than that recorded for marsh grass. The reasons for these differences are not clear, although it may be related to nutrient mediated events in the two environments.

In S. cynosuroides, aerial respiration of the standing dead microbial community was fairly constant during the entire year with the exception of a peak in October (Figure 8). The fallen dead community generally had a higher respiration rate showing a relatively low rate in the spring and early summer, a fairly constant higher rate during late summer, fall, and winter, and a return to a lower rate in early spring. The differences in respiration rates between the fallen dead and standing dead communities may be related to a larger microbial biomass on the fallen dead material and/or differences in nutrient content. Likewise, at Riverbend in Z. miliacea, the standing dead community had a relatively low, constant respiration rate (Figure 9), while the fallen dead community had a much higher rate at each sampling period and was much more variable. However, the annual cycle was different in that the lower rates were observed in November and January, rather then early spring.

Aerial respiration data for the microbial community on swamp forest leaves are difficult to interpret. Over the entire year, Nyssa aquatica and Taxodium distichum communities had similar respiration rates, which were considerably higher than the L. styraciflua community (Figure 10). T. distichum microbial aerial respiration exhibited a pattern of higher rates for late spring and summer, a reduction in fall and winter with the lowest rate occurring in April. The N. aquatica community showed an increase in respiration rates from early spring through July with a peak in August, a drop in October to early summer levels, and a series of high and low values

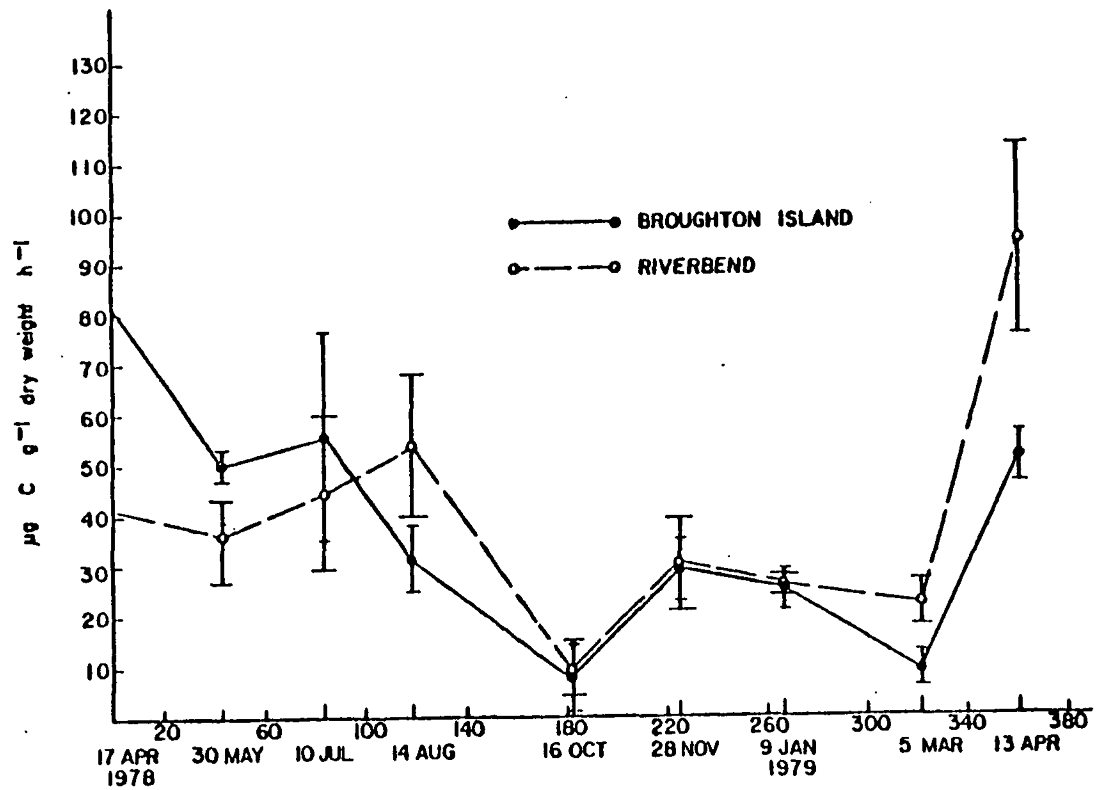


Figure 5. Aquatic respiration (µg C g^{-1} dry wt h^{-1} ± S.E.) of attached dead plant community in fallen dead material from Broughton Island (*Spartina cynosuroides*) and Riverbend (*Zizaniopsis miliacea*). Incubation time, 3.5 h.

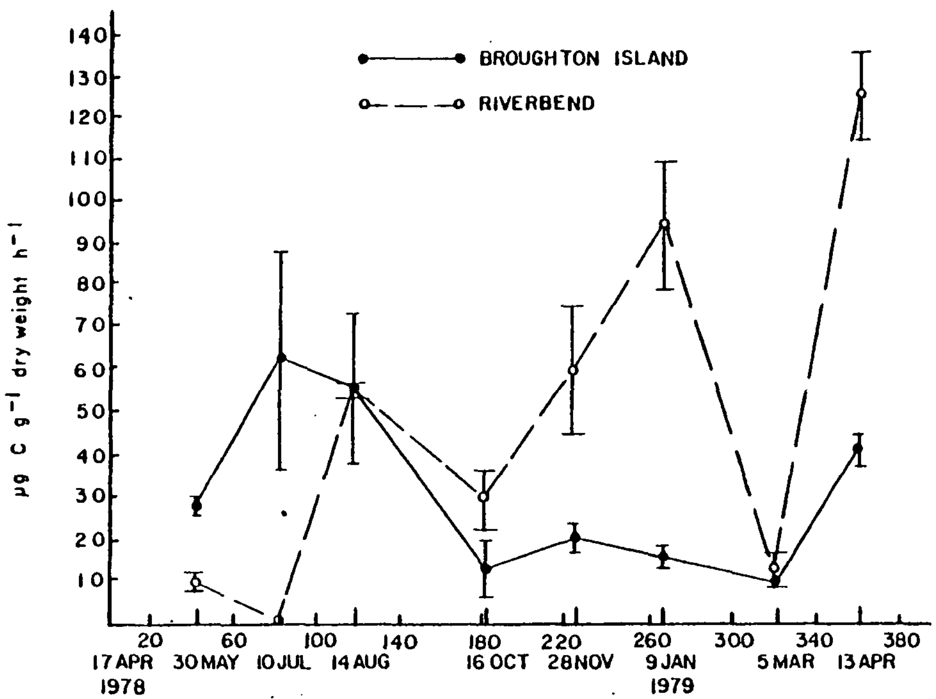


Figure 6. Aquatic respiration (μg C g^{-1} dry wt h^{-1} ± S.E.) of attached dead plant community in standing dead material from Broughton Island (*Spartina cynosuroides*) and Riverbend (*Zizaniopsis miliacea*). Incubation time, 3.5 h.

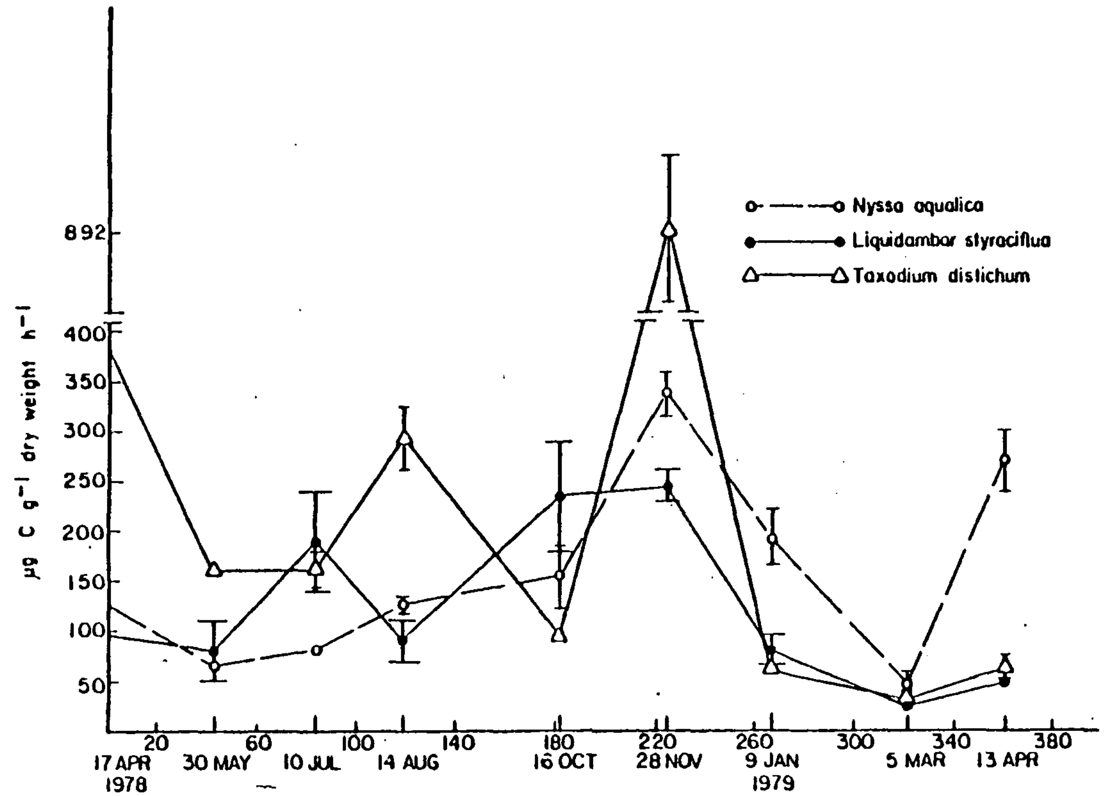


Figure 7. Aquatic respiration (μg C g^{-1} dry wt h^{-1} ± S.E.) of the attached dead plant community for three species of swamp forest leaves. Incubation time, 3.5 h.

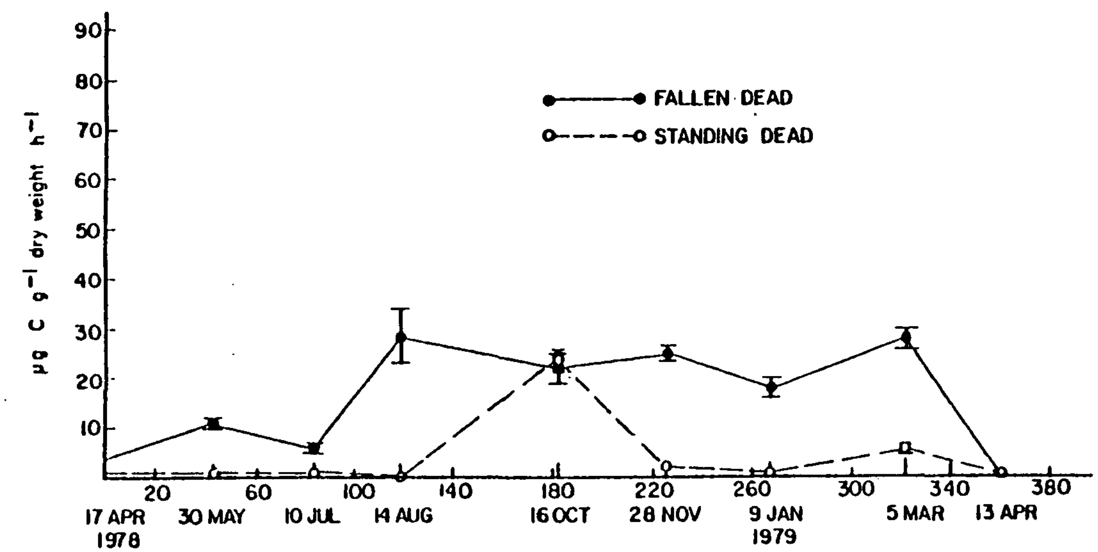


Figure 8. Aerial respiration (µg C g^{-1} dry wt h^{-1} ± S.E.) of the attached dead plant community in fallen and standing dead Spartina cynosuroides. Incubation time, 3 h.

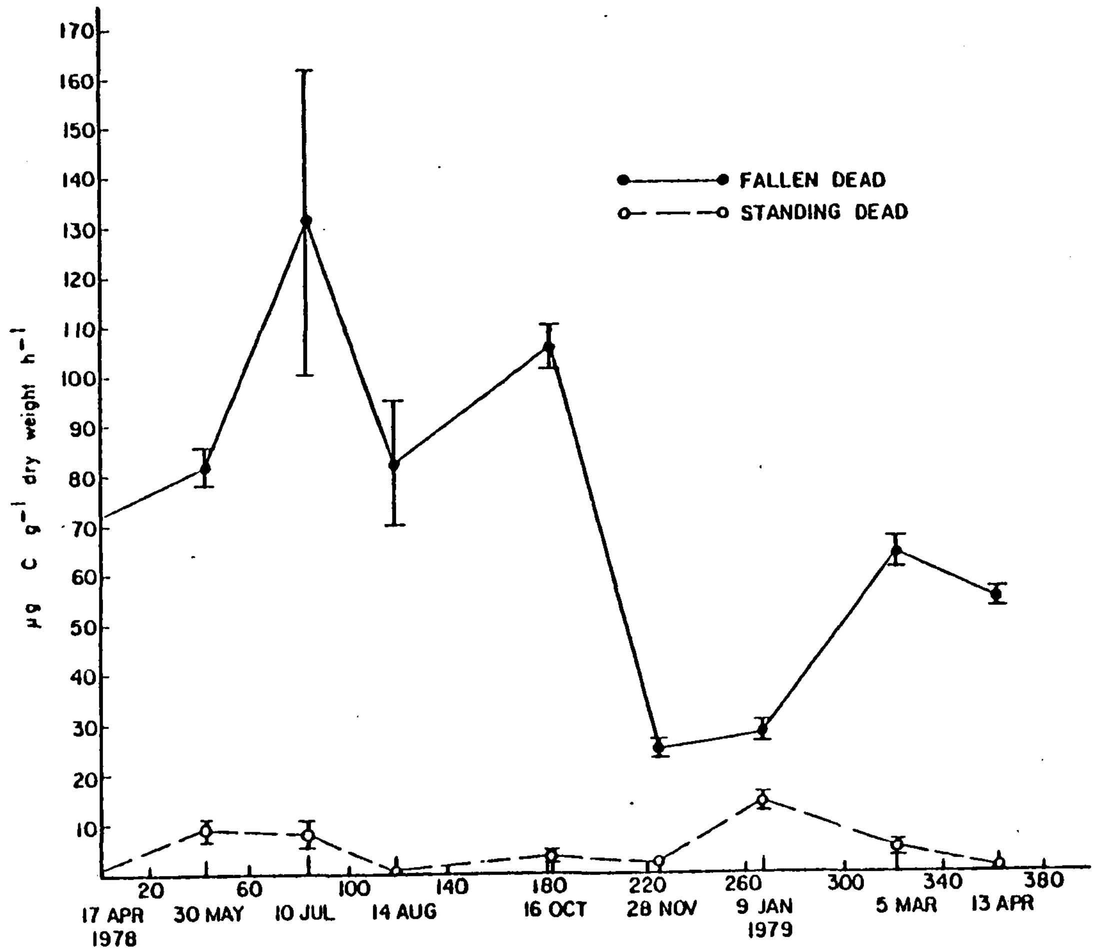


Figure 9. Aerial respiration (μg C g^{-1} dry wt h^{-1} ± S.E.) of the attached dead plant community in fallen and standing dead *Zizaniopsis miliacea*. Incubation time, 3 h.

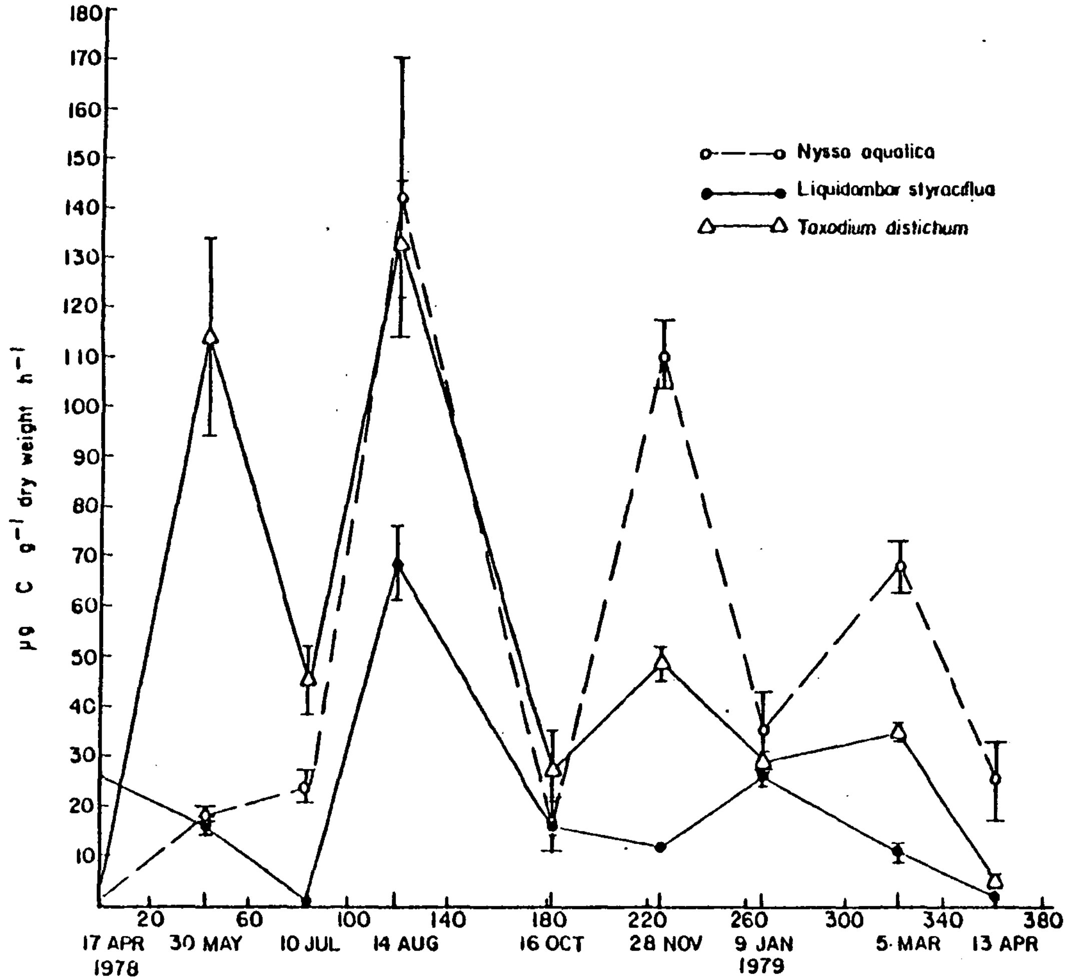


Figure 10. Aerial respiration (μg C g^{-1} dry wt h^{-1} ± S.E.) of the attached dead plant community for three species of swamp forest leaves. Incubation time, 3 h.

for the remainder of the year. The L. styraciflua community, however, had a more constant rate with the exception of a lower and higher rate in July and October, respectively. Without further speculation, we conclude that these variations reflect only species differences.

In S. cynosuroides and Z. miliacea marshes seasonal patterns in DOC leaching rates are not apparent (Figures 11 and 12). For both species of grasses there are no significant differences in the rate of leaching between fallen dead and standing dead averaged over the entire year. However, Z. miliacea had a rate approximately 100 μg C g^{-1} dry weight h^{-1} higher than S. cynosuroides which may have been a result of longer inundation times for the Z. miliacea marshes.

T. distichum showed a definite increase in DOC release from May through August 1978 with a decline to a low in January, 1979 and then an increase through March and April of 1979 (Figure 13). L. styraflua exhibited a similar pattern except that the highest rate was observed in October, 1978, with a subsequent decline to a low in March, 1979, followed by an increase in April. N. aquatica, on the other hand, had levels of DOC significantly lower than the other two species over the entire year. Seasonal trends in leaching rates were not as apparent as the patterns of leaching observed in the other two species. DOC leaching rates for N. aquatica in this study for a 3 hr period were comparable to DOC rates for the same species reported by Brinson (1977). Leaching rates for the 3 species of the leaves were significantly higher than those of the marsh grasses.

As indicated above, respiration and leaching rates were quite variable, and although we have not fully identified the factors causing these variations we might suggest probable causes. Marsh grass and swamp forest leaf litter were removed randomly from the marsh surfaces and forest floor. Consequently, data relative to residence times in these areas and times of tidal inundation were not available. Obviously, the age of the material and length of exposure to tidal inundation would have had significant effects on the rates. In addition, the proportion of leaves and stems in the sample may have affected dead plant microbial community respiration rates and DOC releases (Gallagher et al., 1976). Because no attempts were made to ensure equal masses of stems and leaves at each collection, it is conceivable that the disproportionate representation of these components would have caused the rather wide variations observed in this study. Furthermore, we would expect less variations in rates among newly fallen leaves and standing dead material compared to aged stems. Data for aerial respiration and DOC leaching rates over the entire year showed less variations in standing dead (predominantly leaves) compared to fallen dead (a mixture of leaves and stems). Also, aquatic respiration rates for S. cynosuroides standing dead were less variable than for the fallen dead material. However, in Z. miliacea, standing dead material had a wider variation in aquatic respiration rates than did the fallen dead. Thus, for a more accurate assessment of respiration and leaching rates, more information relative to the age of the material and tidal inundation times should be obtained, and in marsh grasses, measurements should be made separately on stems and leaves.

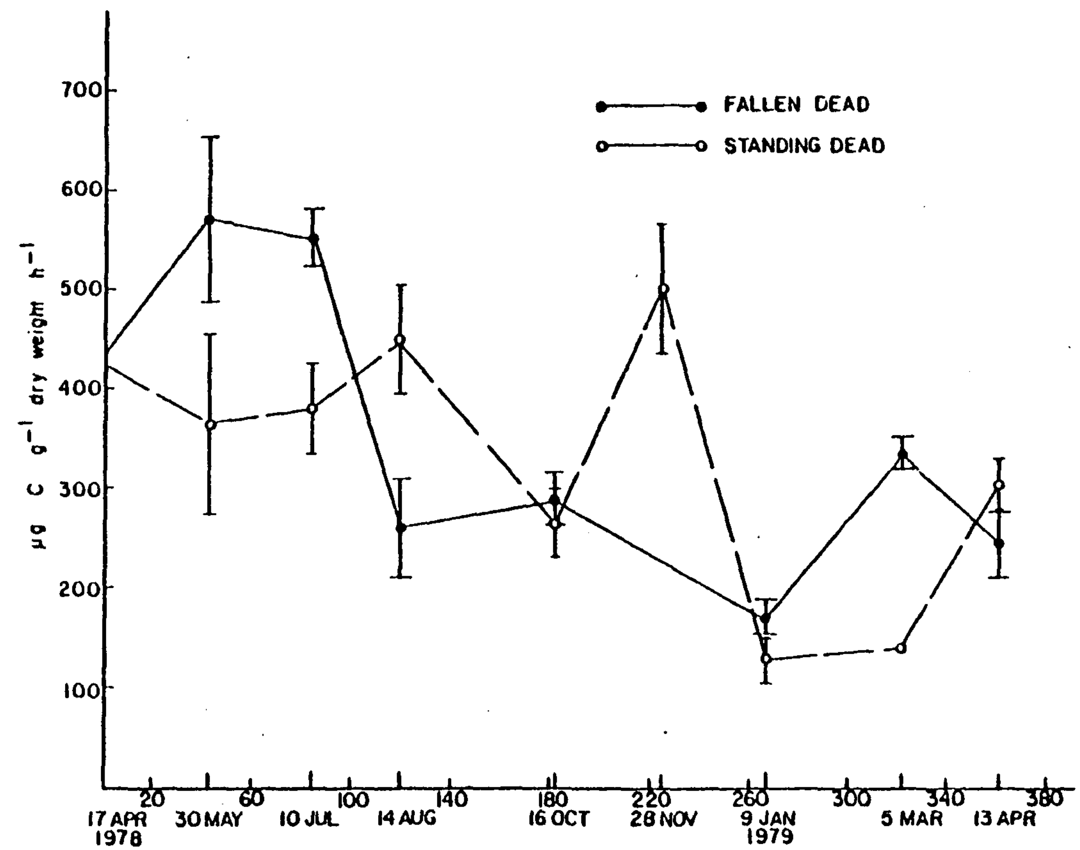


Figure 11. DOC released (μg C g^{-1} dry wt h^{-1} ± S.E.) from fallen and standing dead Spartina cynosuroides. Incubation time, 3 h.

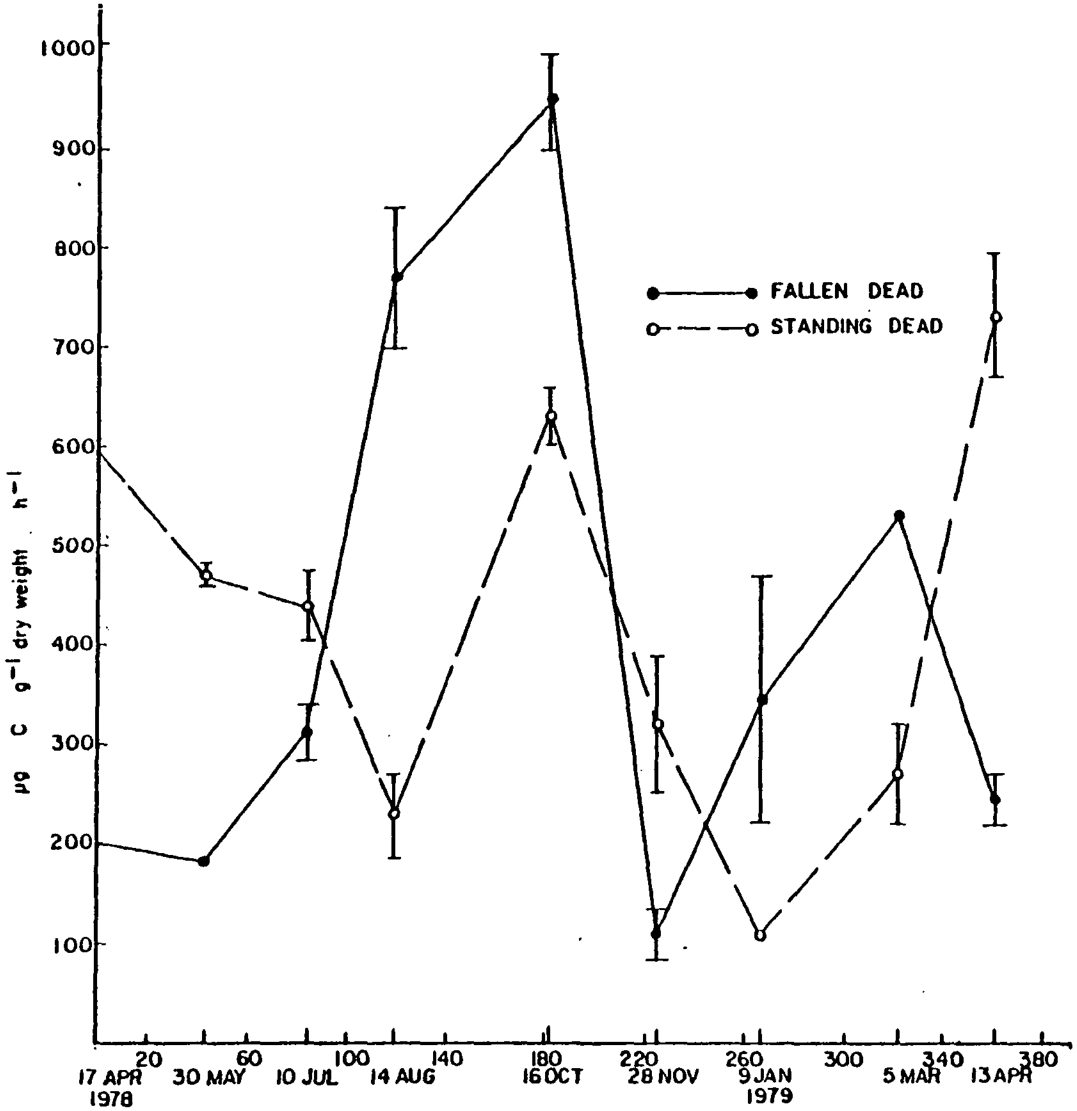


Figure 12. DOC released (µg C g^{-1} dry wt h^{-1} ± S.E.) from fallen and standing dead *Zizaniopsis miliacea*. Incubation time, 3 h.

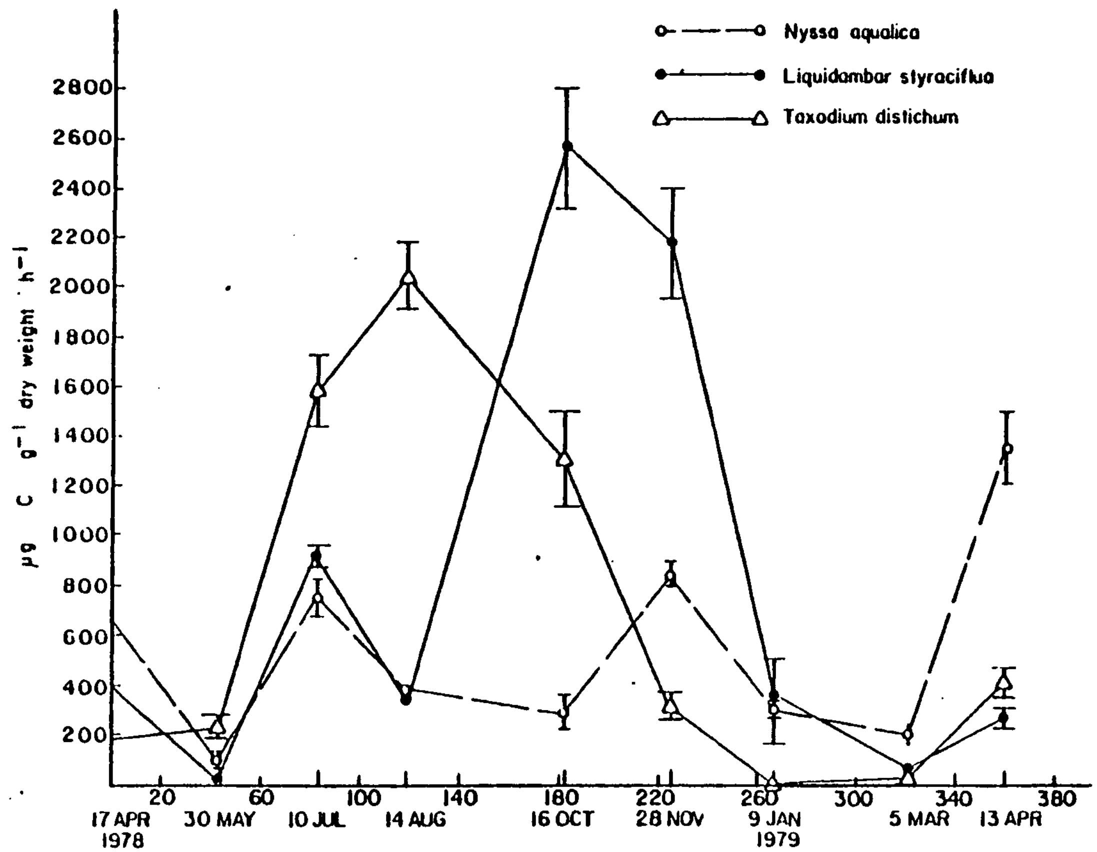


Figure 13. DOC released (g C g^{-1} S.E.) from three species of decomposing swamp forest leaves. Incubation time, 3 h.

LBS - WEIGHT LOSSES

In the S. cynosuroides marshes, suspended litter showed the slowest rate of decomposition (Tables 1 and 2). Significant weight losses did not appear until the 11-month collection. However, surface litter decomposed rather rapidly, showing a 31% weight loss at 6 months and a 60% loss at 11 months. The submerged litter experienced a significant weight loss during the first month (16%) and a subsequent loss of 32% at the 6-month collection. Litter submerged in salt water showed a pattern similar to that of other submerged bags at the 1-month collection. Rates of decay for suspended, surface, and submerged litter are expressed in the following formulae:

suspended (11 months) $\hat{y} = 99.5 - 0.74X$
surface (11 months) $\hat{y} = 100.3 - 0.18X$
submerged (6 months) $\hat{y} = 96.5 - 0.25X$,
where $\hat{y}$ = percent remaining at time X,
and X = time in days.

Decomposition rates for Z. miliacea litter follow the same general trends as those for S. cynosuroides litter - submerged > surface > suspended. However, the rates in Z. miliacea are greater than those in S. cynosuroides. Suspended litter showed a 58% decrease at 6 months without a further significant decrease at 11 months. Surface bags exhibited a 17% decrease at 1 month and a 72% decrease at 6 months with an 86% decrease at 11 months. The greatest magnitude of decomposition was observed in the submerged bags - a 19% decrease in biomass at 1 month with a 94% decrease at 6 months. In fact, only one of six bags contained litter at the 6-months collection period. Thus, the decrease in biomass was indeed dramatic between the 1-month and 6-months collection periods. Linear regression equations depicting decomposition rates for the three types of litter are as follows:

suspended (11 months) $\hat{y} = 94.8 - 0.19X$
surface (11 months) $\hat{y} = 93.5 - 0.27X$
submerged (11 months) $\hat{y} = 98.5 - 0.52X$

Thus, suspended Z. miliacea litter had a decay rate comparable to S. cynosuroides surface litter, while Z. miliacea surface litter had a rate comparable to the S. cynosuroides submerged litter. The submerged Z. miliacea decay rate was approximately twice that of S. cynosuroides submerged litter. The more rapid decay rates observed for Z. miliacea suspended and surface litter are probably related to the longer time of tidal inundation in the freshwater marshes. The rather wide difference in weight losses between the two types of submerged marsh grass litter cannot be fully explained at this time. We suggest that differences in current velocity and composition of the grasses are factors. Z. miliacea has a higher water content than S. cynosuroides (73 and 67% respectively).

Swamp forest leaf litter showed significant decreases in weights at each time interval with the greatest losses occurring between one and six months (45%). Following the 6-months collection, only another 10% decrease occurred. A significant difference in the rate of decomposition between surface litter and submerged litter was not observed as is illustrated in the following linear regression equations:

$$\text{surface (11 months) } \hat{y} = 89.1 - 0.25X$$
$$\text{submerged (11 months) } \hat{y} = 93.5 - 0.25X$$

The similarity in decomposition rates is probably related to the fact the surface bags were inundated for long periods of time during the study. At each of the collections, the surface bags were covered with approximately 25 cm of water which indicated that surface and submerged bags were exposed to the same general environmental conditions.

LBS - AQUATIC RESPIRATION

Respiration rates for the three types of saltwater submerged litter were significantly higher than in all other treatments (Figure 14; Tables 1 and 2). This is somewhat surprising in that Gallagher (1977) reported lower rates for similar material suspended in saltwater as compared to freshwater. In the latter work, material had been submerged for a period of only 7 days which may account, in part, for the differences observed. The aquatic respiration rate in suspended litter was significantly lower than in surface and submerged litter in both species of marsh grasses. No significant differences were observed between surface and submerged litter for the three types of litter.

In comparing aquatic respiration rates between species (Table 2), swamp litter showed a significantly higher rate (81 µg C g^{-1} hr^{-1}) than did _S. cynosuroides_ (48 µg C g^{-1} hr^{-1}) and _Z. miliacea_ (42 µg C g^{-1} hr^{-1}) litter. In combining aquatic respiratory data for all types of litter, saltwater submerged litter had the highest rates, suspended litter the lowest rates, with surface and submerged litter having similar, intermediate rates.

For _S. cynosuroides_ and _Z. miliacea_ combined aquatic respiratory rates for all types of litter were significantly higher at 1 month than at 6 months, with no differences between 6 months and 11 months. The combined respiratory rate for swamp litter was significantly higher at 1 and 6 months than at 11 months with no significant differences between 1 month and 6 months. Briefly summarizing the above material, aquatic respiratory rates were higher in more aquatic situations (excluding the saltwater treatment) and were generally higher in the earlier stages of decomposition.

LBS - AERIAL RESPIRATION

Generally, aerial respiration rates were higher in the earlier stages of decomposition as is indicated when comparing the combined rates of all litter types, or when comparing the rates of each type to time (Tables 1 and 2 and Figure 15). Rates were significantly higher at 1 month with no significant differences between 6 and 11 months.

Unlike the situation for aquatic respiration, swamp litter exhibited the lowest aerial respiratory rate with _Z. miliacea_ showing the highest rate. However, in comparing types of litter (all species) saltwater litter had the highest rate followed in decreasing order (all significant differences) by submerged, surface and suspended litter.

In comparing respiratory rates for litter representing each species, the trend observed above is not as pronounced. For S. cynosuroides both saltwater and on-site submerged litter had higher aquatic respiration rates than suspended and surface litter but did not differ from each other. However, surface litter had a significantly higher rate than suspended litter. For Z. miliacea, saltwater litter exhibited a significantly higher rate than the other three types, submerged was higher than surface and suspended, but no differences occurred between the latter two types. In swamp litter, saltwater submerged aerial respiratory rates were significantly higher than surface submerged rates while surface rates were higher than submerged rates. Thus, while the pattern for aerial respiration generally resembles that of aquatic respiration, more variation occurred within the individual species.

LBS - DISSOLVED ORGANIC CARBON (DOC)

When comparing the combined DOC leaching rates for all litter types, the following trends were noted (Tables 1 and 2, and Figure 16). As was observed for respiration rates (aquatic and aerial), leaching rates were generally higher in the earlier stages of decomposition. S. cynosuroides litter had significantly higher leaching rates than Z. miliacea and swamp litter, while Z. miliacea was significantly higher than swamp litter. Surprisingly, swamp litter showed a net negative leaching rate which indicates an uptake of carbon. At this point, we cannot explain these results. When comparing types of litter for all species involved, suspended material had a higher rate than all other types with no significant differences in rates between the other types. This is also somewhat surprising, since we would have expected higher leaching rates in the submerged and surface litter. In terms of individual species, however, S. cynosuroides on-site submerged litter showed a significantly higher leaching rate than the other types. Suspended, surface, and saltwater submerged litter did not differ in DOC leaching. In Z. miliacea, DOC leaching rates were significantly higher for suspended litter with no differences occurring between the other types. DOC leaching rates of swamp forest leaf litter in surface and submerged bags did not differ significantly. Many negative values were recorded which may indicate an uptake of DOC by the material.

Comparisons of mean aquatic respiration, aerial respiration, and DOC leaching rates of litter bag material for the three collection periods to rates for material (standing dead and fallen dead) from "natural areas" averaged over the entire year show the following patterns. For both species of marsh grasses, aquatic respiration rates were similar for litter bag material, fallen dead, and standing dead. Aerial respiration rates for S. cynosuroides litter were higher than those of fallen dead and standing dead. In Z. miliacea, litter bag material and fallen dead aerial respiration rates were similar and significantly higher than standing dead rates. DOC leaching rates were similar in all S. cynosuroides material, but Z. miliacea litter bag material had a rate approximately 2 1/2 times lower than that of fallen dead and standing dead grass.

TABLE 1. RESULTS OF DUNCAN'S MULTIPLE RANGE TEST* FOR TIME AND TYPE DIFFERENCES IN MEAN BIOMASS (WT), AQUATIC RESPIRATION (AQUA), AERIAL RESPIRATION (AER), AND DOC LEACHING (DOC) FOR TWO SPECIES OF MARSH GRASSES AND SWAMP FOREST LEAVES ENCLOSED IN LITTER BAGS SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB) AND SALTWATER TREATED (SALT)†

TIME	WT	AER	AQUA	DOC	TYPE	WT	AER	AQUA	DOC
				Spartina cynosuroides					
0					SUS	90a	11c	13c	261b
1 month	89b	61a	70a	527a	SUR	77c	44b	37b	288b
6 months	74c	31b	19b	109b	SUB	84b	74a	44b	692a
11 months	55d	26b	20b	-177c	SALT	93a	63a	143a	118b
				Zizaniopsis miliacea					
0	100a				SUS	70b	47c	7c	322a
1 month	86b	84a	71a	181a	SUR	62c	51c	46b	92b
6 months	30c	43c	34b	131a	SUB	62c	85b	65b	75b
11 months	25c	60b	21b	296a	SALT	94a	124a	141a	153b
				Swamp Litter					
0	20a				SUR	11c	34b	83b	11a
1 month	16b	56a	114a	- 1a	SUB	12b	29c	53b	5ab
6 months	6c	22b	90a	-32a	SALT	18c	58a	163a	-58b
11 months	4d	19b	24b	-49a					

* Means with the same letters are not significantly different

† Wt in grams dry weight; AER, AQUA and DOC in μg C g^{-1} dry weight h^{-1}

TABLE 2. RESULTS OF DUNCAN'S MULTIPLE RANGE TEST* FOR TIME, SPECIES, AND TYPE DIFFERENCES IN MEAN BIOMASS (WT), AERIAL RESPIRATION (AER), AQUATIC RESPIRATION (AQUA), AND DOC LEACHING (DOC) FOR SPARTINA CYNOSUROIDES (SCYN), ZIZANIOPSIS MILIACEA (SMILI), AND SWAMP FOREST LITTER BAG MATERIAL - POOLED DATA†

	WT	AER	AQUA	DOC
TIME				
0	77a			
1 month	67b	67a	82a	250a
6 months	37c	33b	43b	81b
11 months	29d	35b	22c	-60c
SPEC				
SCYN	85a	43b	42b	330a
ZMILI	70b	65a	48b	165b
SWAMP	13c	35c	81a	-18c
TYPE				
SUS	80a	32d	10c	290a
SUR	49c	43c	55b	135b
SUB	47c	55b	54b	158b
SALT	65b	81a	149a	87b

* Means with the same letter are not significantly different

† WT in grams dry weight; AER, AQUA, and DOC in μg C g^{-1} dry weight h^{-1}

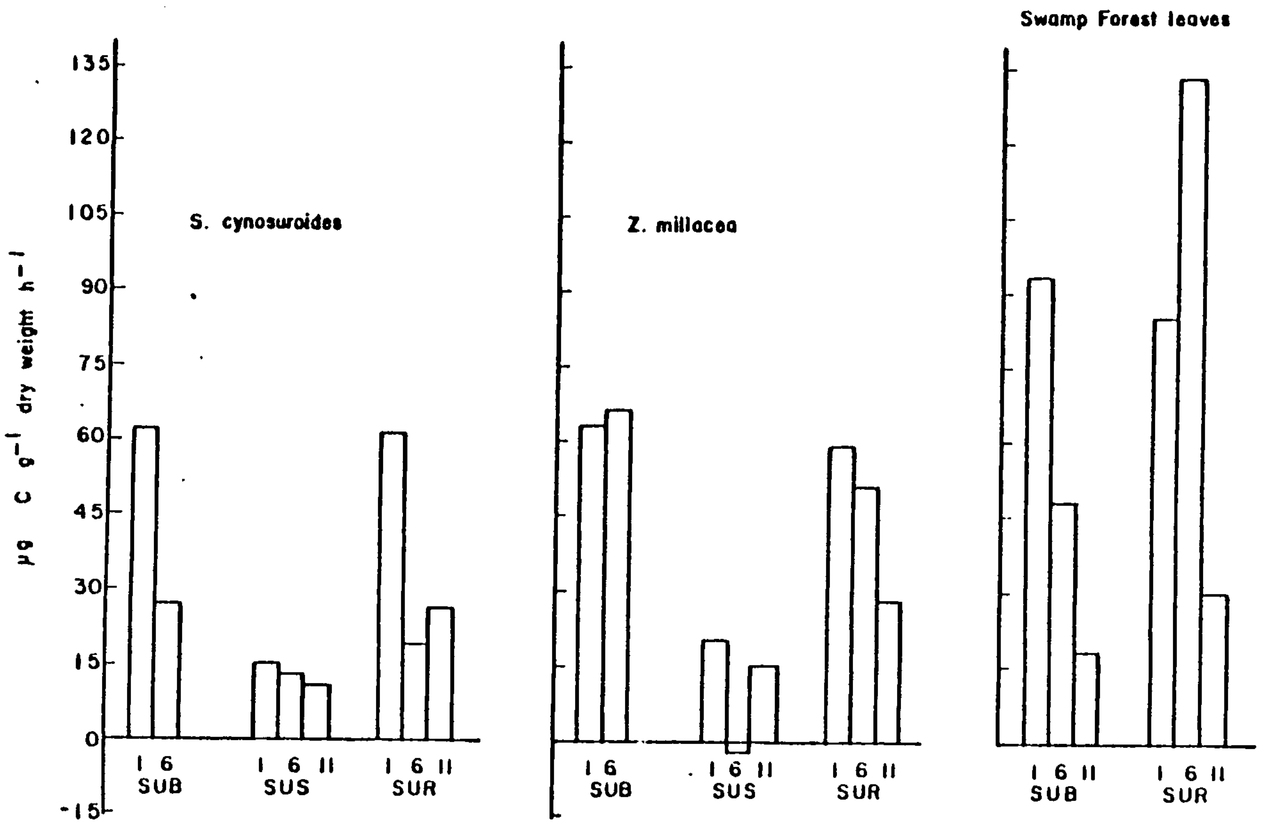


Figure 14. Aquatic respiration (μg C g^{-1} dry wt h^{-1} ± S.E.) of the attached dead plant community from dead plant material enclosed in suspended (SUS), surface (SUR), on-site submerged (SUB), and saltwater submerged (SAL) litter bags. Incubation time, 3 h.

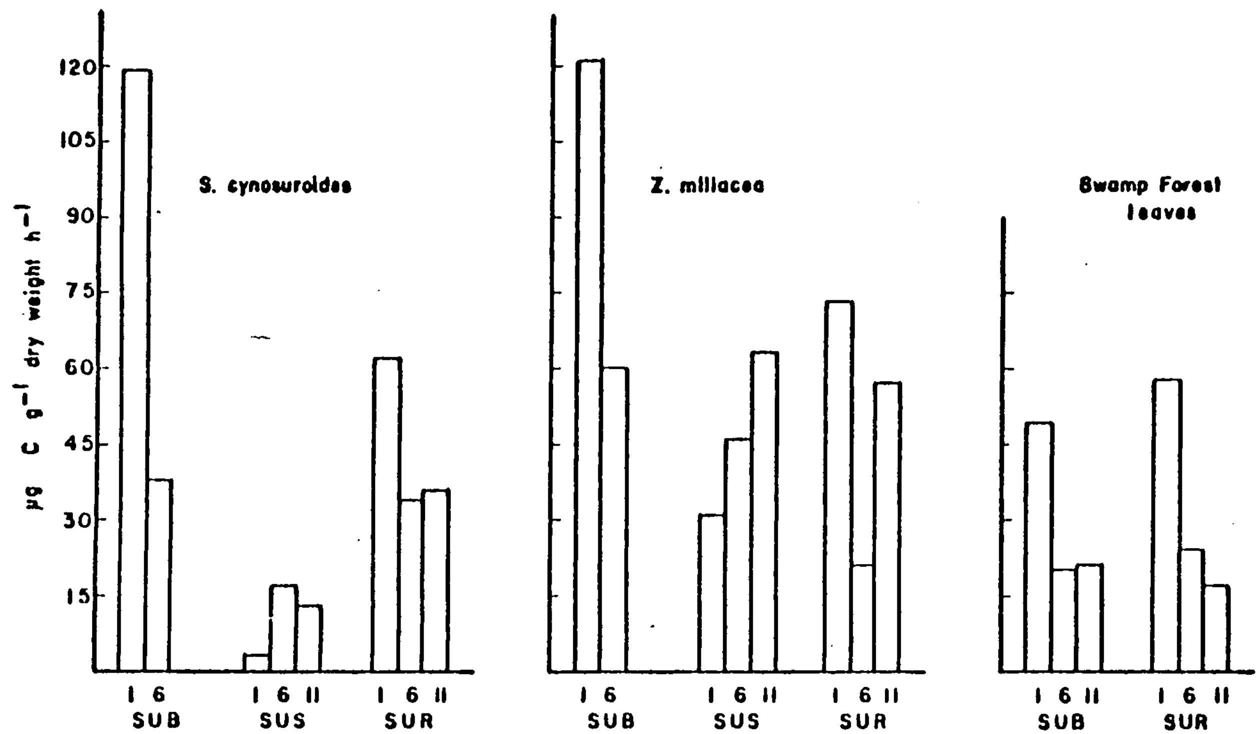


Figure 15. Aerial respiration (µg C g^{-1} dry wt h^{-1} ± S.E.) of the attached dead plant community from dead plant material enclosed in suspended (SUS), surface (SUR), on-site submerged (SUB), and saltwater submerged (SAL) litter bags. Incubation time, 3 h.

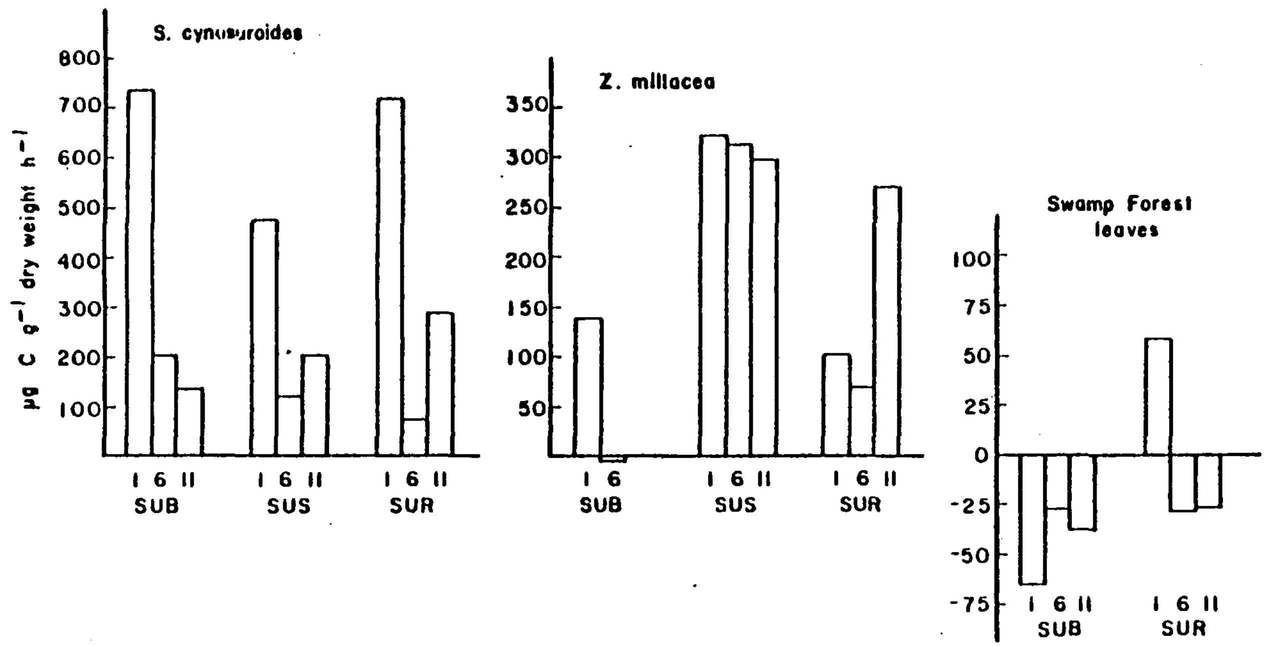


Figure 16. DOC released (μg C g^{-1} dry wt h^{-1} ± S.E.) from dead plant parts enclosed in suspended (SUS), surface (SUR), on-site submerged (SUB) and saltwater submerged (SAL) litter bags. Incubation time, 3 h.

Aerial respiration rates of swamp litter bags material was similar to the rates of fallen leaves. Aquatic respiration rates of litter bag material were much lower than rates for the three species of the leaves utilized in this study. Mean DOC leaching rates for litter bag material, a composite of fallen leaves representing several species of trees, was -18 $\mu g\ C\ g^{-1}\ hr^{-1}$. Rates for fallen leaves representing N. aquatica, L. styraciflua, and T. distichum, were 541, 794, and 675 $\mu g\ C\ g^{-1}\ hr^{-1}$, respectively, Obviously, confining the swamp litter in bags served to reduce the leaching rates. The causes of these reductions are not known, and a repeat of the experiment would be helpful to determine whether the reduction was real or simply a result of experimental error.

LBS - MINERAL COMPOSITION

Swamp litter had significantly higher concentrations of P, Ca, Mg, N, Mn, Fe, Al, B, Cu, Sr, and Ba (Table 3). For the above elements, S. cynosuroides and Z. miliacea were similar in concentrations with the exception of P, N, and Ba which were significantly higher in S. cynosuroides than Z. miliacea. Z. miliacea had significantly higher concentrations of Zn than did S. cynosuroides with no differences in levels between Z. miliacea and swamp litter, and no difference between swamp litter and S. cynosuroides. S. cynosuroides had a significantly higher level of Na than the other two types with no differences occurring between swamp litter and Z. miliacea. Marsh grasses and swamp litter did not differ significantly in K levels.

When pooled data (Table 3, all treatments, all species) were compared to time, the following five trends were noted:

1) significant increases in P concentrations at 6 months; no significant decreases at 11 months; 11-month levels somewhat higher than 1-month level

2) significant increases of Ca, Cu, Mn, and Sr at 6 months; further significant decreases at 11 months to 1-month levels

3) significant increases of Ba, Fe, Na, and N at 6 months; no further changes at 11 months; 6 and 11-month levels significantly higher than 1-month level

4) no changes in Zn between 1 month and 6 months; increases at 11 months to a level significantly higher than at 1 month

5) significant decreases of K, Mg, Al, and B at 11 months; 6 and 11-month levels significantly lower than 1-month levels

Thus, at the end of the 11-month period, levels of Ba, Fe, Na, N, Zn and P represent elemental accumulations while K, Mg, Al and B levels indicate losses. No significant changes appeared to have occurred in concentrations of Ca, Cu, Mn, and Sr.

TABLE 3. RESULTS OF DUNCAN'S MULTIPLE RANGE TEST* FOR TIME, SPECIES AND TYPE DIFFERENCES (POOLED DATA) FOR MEAN ELEMENTAL COMPOSITION OF SPARTINA CYNOSUROIDES (SCYN), ZIZANIOPSIS MILIACEA (ZMILI), AND SWAMP FOREST LEAF (SWAMP) LITTER BAG MATERIAL - SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB) AND SALTWATER TREATED (SALT)†

	P	K	Ca	Mg	N	Mn	Fe	Al
TIME								
1 month	.0959b	.0899a	.5330b	.1936a	.82b	1110b	3980b	6304a
6 months	.1189a	.0329b	.8363a	.1523b	1.29a	1758a	5257a	5077b
11 months	.1078ab	.0183b	.6086b	.1180b	1.27a	994b	6405a	4383b
SPEC								
SCYN	.0676c	.0516a	.2974b	.1438b	.76c	576b	2602b	4377b
ZMILI	.0966b	.0604a	.3943b	.1537b	1.13b	941b	3827b	4962b
SWAMP	.1659a	.0558a	1.3952a	.2007a	1.39a	2597a	9365a	7566a
TYPE								
SUS	.0622c	.0276b	.3051d	.1015b	.8867b	383d	1655c	2583c
SUR	.1087b	.0364b	.7480b	.1237b	1.1967a	1052c	5922ab	5531b
SUB	.1296a	.0463b	.8878a	.1253b	1.1429a	1839b	6925a	6352b
SALT	.1372a	.1887a	.5239c	.4775a	.8978b	2652a	4801b	9484a

(Continued)

TABLE 3. (Continued)

	B	Cu	Zn	Sr	Ba	Na
<u>TIME</u>						
1 month	20.82a	4.215b	49.4b	38.92b	46.92b	194b
6 months	9.91b	5.400a	294.1b	53.93a	97.09a	1393a
11 months	7.04b	4.684b	690.2a	41.36b	75.50a	413a
<u>SPEC</u>						
SCYN	8.32b	3.001b	39.3b	25.42b	13.72c	1099a
ZMILI	7.01b	3.177b	449.2a	29.90b	43.79b	376b
SWAMP	31.06a	8.734a	317.2ab	85.56a	170.94a	269b
<u>TYPE</u>						
SUS	4.97c	2.500c	579a	18.51d	26.92b	958a
SUR	8.75b	4.973b	192a	45.12c	90.16a	748ab
SUB	9.06b	6.461a	157a	55.35b	107.89a	268b
SALT	59.23a	4.785b	37a	69.74a	13.03b	116b

* Means with the same letter are not significantly different

† P, K, Ca, Mg, N, in %; others in PPM

Comparison of mineral content among suspended, surface, on-site submerged, and saltwater litter showed that K, Mg, Mn, Sr, Al and B levels were significantly higher in saltwater submerged litter than in other types. When saltwater submerged litter is excluded from the comparisons, the following trends were noted. No differences in levels of K, Mg, and Zn were noted. For P, Ca, Mn, Cu, and Sr concentrations in on-site submerged > surface > suspended. N, Fe, Al, B, and Ba levels were equally higher in submerged and surface litter than in suspended litter. Generally, surface litter was intermediate in elemental concentrations, with suspended material usually having the lowest concentrations with the exception of Na which was significantly higher in suspended material.

The patterns of elemental composition for S. cynosuroides, Z. miliacea, and swamp litter vary somewhat from those observed above. When comparing S. cynosuroides litter concentrations at the collection periods, three general patterns were noted (Table 4). P, K, Al, and Cu showed steady decreases through time until 11-month levels were significantly lower than 1-month levels. Ca, Mn, Sr, Ba, Na, and Fe concentrations increased between 1 and 6 months followed by a decrease between 6 and 11 months to levels characteristic of the 1-month collection. N levels followed the latter pattern with the exception that although the 11-month value was lower than the 6-month value, it was significantly higher than the 1-month concentration. B, Mg, and Zn concentrations did not differ significantly with time.

In S. cynosuroides, elemental concentrations were highest in saltwater and/or on-site submerged litter. K, Mg, Mn, Al, and B concentrations were highest in saltwater treated litter. In comparing only suspended, surface, and on-site submerged litter the following relationships were noted. K, B, Zn, Mg, and Mn did not differ significantly. For P and N, on-site submerged > surface > suspended; on-site submerged litter levels of Ca, Cu, Ba, and Sr were higher than surface and suspended; and Al and Fe levels for surface and submerged were higher than suspended. Only in Na levels were higher levels seen for surface and suspended litter as compared to submerged litter. It appears that elemental accumulation was accelerated in the more aquatic conditions.

No significant changes in P, Mn, Al, Ba, and Na concentrations in Z. miliacea occurred during the 11-month study period (Table 5). Although Ca and Sr levels were significantly higher at 6 months, further decreases occurred so that 11-month levels were similar to 1-month levels. B, K, and Mg concentrations at the 11-month collection were significantly lower than at the 1-month collection. Cu, Fe, N, and Zn showed significant increases at 11 months with Cu and N accumulating more rapidly than Fe and Zn. As in S. cynosuroides, Z. miliacea saltwater submerged litter was higher in K, Mg, Mn and B levels. In addition, Sr was significantly higher in the saltwater treatment. Comparing only suspended, surface, and on-site submerged litter showed again that suspended material was generally lower in elemental concentrations than the other two types. No significant differences in concentrations of B, Ba, Ca, Mn, Na, and Zn were observed between the three types of litter. Al, Cu, Fe, and P levels were similar in submerged and surface bags with both being higher in concentration then suspended litter. Submerged

TABLE 4. RESULTS OF DUNCAN'S MULTIPLE RANGE TEST* FOR TIME AND TYPE DIFFERENCES IN MEAN ELEMENTAL COMPOSITION OF SPARTINA CYNOSUROIDES LITTER BAG MATERIAL - SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB), AND SALTWATER TREATED (SALT)†

	P	K	Ca	Mg	N	Mn	Fe	Al
TIME								
1 month	.0661b	.0806a	.2217b	.1508a	.57c	473.8b	2604ab	5033a
6 months	.8777a	.383b	.4686a	.1525a	1.01a	1093.1a	3475a	4431ab
11 months	.0441c	.0114c	.2207b	.1181a	.82b	90.9b	1435b	2995b
		B	Cu	Zn	Sr	Ba	Na	
1 month		8.26a	3.35a	30.45a	20.14b	10.23b	277.6b	
6 months		10.23a	3.64a	46.27a	38.87a	25.13a	2396.6a	
11 months		5.90a	1.45b	47.84a	18.07b	5.51b	996.5ab	
	P	K	Ca	Mg	N	Mn	Fe	Al
TYPE								
SUS	.0388c	.0313b	.2121b	.1166b	.65c	114b	607b	1322c
SUR	.0593b	.0359b	.2749b	.1218b	.77b	202b	2717a	4056b
SUB	.1058a	.0500b	.4584a	.1326b	.95a	-	4220a	5398b
SALT	.0933a	.1566a	.2705b	.3048a	.64c	1110a	4343a	11449a
		B	Cu	Zn	Sr	Ba	Na	
SUS		6.29b	2.23b	40.99a	14.11c	4.87b	1253ab	
SUR		7.91b	2.72b	36.87a	23.05bc	11.64b	1856a	
SUB		5.31a	4.35a	46.87a	38.42a	31.28a	398b	
SALT		21.00a	3.21b	27.23a	36.71ab	8.46b	77b	

* Means with the same letter are not significantly different

† P, K, Ca, Mg, N, in %; others in PPM

TABLE 5. RESULTS OF DUNCAN'S MULTIPLE RANGE TEST* FOR TIME AND TYPE DIFFERENCES IN MEAN ELEMENTAL COMPOSITION OF ZIZANIOPSIS MILIACEA LITTER BAG MATERIAL - SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB), AND SALTWATER TREATED (SALT)†

	P	K	Ca	Mg	N	Mn	Fe	Al
TIME								
1 month	.0874a	.1053a	.3474b	.1943a	.81b	1043a	3260b	5309a
6 months	.1025a	.0217b	.4832a	.1325b	1.36a	951a	3909ab	4551a
11 months	.0874a	.0156b	.3847ab	.0971c	1.51a	758a	4864a	4748a
		B	Cu	Zn	Sr	Ba	Na	
1 month		9.98a	2.61b	29.1b	25.92b	37.28a	105a	
6 months		5.20b	3.97a	105.9b	35.55a	47.94a	1052a	
11 months		3.18c	3.38a	1690.0a	31.25ab	51.97a	130a	
	P	K	Ca	Mg	N	Mn	Fe	Al
TYPE								
SUS	.089b	.0247c	.3795a	.0894b	1.08b	598b	2494c	3592b
SUR	.1095a	.0281c	.4400a	.1053b	1.37a	931b	5349a	5911a
SUB	.0860ab	.0414b	.2742a	.0579c	0.82b	612b	4918ab	5801a
SALT	.1210a	0.2950a	.4391a	.6089a	0.91b	2449a	2611bc	5840a
		B	Cu	Zn	Sr	Ba	Na	
SUS		3.92b	2.72b	1099a	22.02c	44.56a	721a	
SUR		3.68b	3.77a	109a	32.52b	53.29a	180a	
SUB		2.58b	3.01ab	34a	14.26c	46.05a	164a	
SALT		31.71a	3.10ab	18a	63.90a	10.50b	28a	

* Means with the same letter are not significantly different

† P, K, Ca, Mg, N, in %; others in PPM

litter was clearly higher in K concentration, while surface litter was significantly higher than both suspended and submerged litter. Significantly lower concentrations of Mg were recorded for submerged material.

Patterns of elemental accumulation and loss in swamp litter appeared to be more clearly established than those of the marsh grasses (Table 6). Fe, P, and Cu showed significantly higher levels at 11 months than at 1 month with accumulation being most rapid for P and Cu. Al, B, K, and Mg levels were significantly lower at 11 months than at 1 month with losses occurring more rapidly for B, K, and Mg. Initial accumulation at 6 months followed by losses at 11 months to 1-month levels were observed for Ba, Ca, Mn, N, Na, Sr, and Zn. Brinson (1977) reported accumulations of Ca and Fe in swamp forest leaves with losses of K and Mg. He, however, showed also an accumulation of N and a strong accumulation of P followed by a loss. We also showed accumulation of N and P, however, the P levels remained higher than the 1 month level and N accumulation was followed by a loss.

Forest leaf litter showed no significant differences in nutrient levels between surface and submerged litter. This is not surprising, since, as stated earlier, the environmental conditions, at least time of inundation, were similar. In comparing the three treatments, saltwater submerged litter showed accumulation of Al, B, K, Mn, P, and Sr, with losses of Ba, Ca, Mg, N, and Zn. No differences were observed between Cu, Fe, and Ba levels.

Specific comparisons of mineral content of litter bag material to natural litter removed from the marsh surfaces at each collection are difficult to make. The material collected from the marsh surface was more heterogeneous in composition because it consisted of stem and leaves in various stages of decomposition. Presumably, litter bag material was more homogeneous because standing dead marsh grass material at the same stage of decomposition was used for the litter bags. In addition, only one sample of marsh litter material was analyzed for mineral composition, making statistical comparisons virtually impossible. Nevertheless, some generalizations can be made in comparing suspended, surface, and on-site submerged litter to natural litter for the two species of marsh grasses. Comparisons were not made for swamp forest leaf litter.

Al, Cu, Fe, Mg, Mn, N, Na, Sr, and Zn levels were lower in natural litter than in litter bag material. Qualitatively, the differences ranged from somewhat lower to much lower. Al and Fe were particularly outstanding in that concentrations of these elements were, in some cases, two orders of magnitude lower in natural litter. Ca and B levels were more variable but generally similar in concentration in the four types of litter. K levels were lower in S. cynosuroides litter but higher in Z. miliacea litter. P concentrations showed definite similarities to suspended litter levels in S. cynosuroides while being lower in concentration than surface and submerged material. In Z. miliacea, however, K levels in natural litter were more similar to surface litter levels at 1 month with no differences at 6 and 11 months. Thus, it appears that, for many of the elements analyzed, enclosure in litter bags resulted in an accumulation of minerals leading to an elevation of concentrations over natural levels. The causes of these increases are not clear. The

TABLE 6. RESULTS OF DUNCAN'S MULTIPLE RANGE TEST* FOR TIME AND TYPE DIFFERENCES IN MEAN ELEMENTAL COMPOSITION OF SWAMP FOREST LEAF LITTER BAG MATERIAL - SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB), SALTWATER TREATED (SALT)†

	P	K	Ca	Mg	N	Mn	Fe	Al
TIME								
1 month	.1469b	.0818a	1.195b	.2498a	1.18b	2045b	6775b	9327a
6 months	.1800a	.0387b	1.739a	.1751b	1.58a	3812a	9207b	6553ab
11 months	.1836a	.0298b	1.343b	.1431b	1.53b	2131b	14217a	5612b
		B	Cu	Zn	Sr	Ba	Na	
1 month		52.03a	7.51b	101.6b	81.26b	108.7b	201.4b	
6 months		14.62b	9.41a	686.7a	95.45a	250.4a	453.7a	
11 months		13.06b	10.13a	261.7b	81.42ab	187.8ab	169.0b	
	P	K	Ca	Mg	N	Mn	Fe	Al
TYPE								
SUR	.1574b	.0454b	1.533a	.1442b	1.45a	2025b	9700a	6627b
SUB	.1637b	.0456b	1.440a	.1451b	1.41a	2564b	9707a	7273ab
SALT	.1974a	.1146a	.862b	.5187a	1.14b	4398a	7447a	11164a
		B	Cu	Zn	Sr	Ba	Na	
SUR		14.65b	8.42a	431.4a	79.75b	205.6a	330.8a	
SUB		14.31b	9.34a	286.0ab	83.45b	188.5a	209.0a	
SALT		125.00a	8.05a	57.7b	108.61a	20.1b	243.7a	

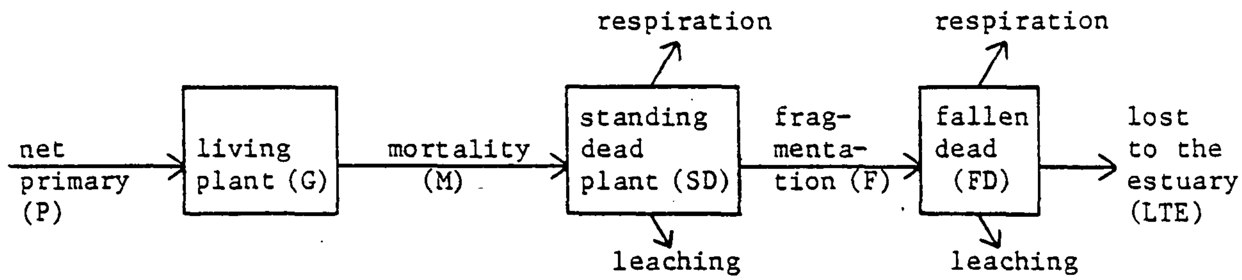
* Means with the same letter are not significantly different

† P, K, Ca, Mg, N, in %; others in PPM

litter enclosed in bags may act to remove suspended sediments from water flowing through the bags and thus, through adsorption on the smaller particles of marsh grass, increase nutrient levels. On the other hand, the increases may be a reflection of a more rapid loss of organic matter than minerals from the litter. This, however, would not explain why natural litter levels are usually lower than the litter bag material unless one assumes that natural litter is continually "recruiting" material from the standing dead material and thus significant accumulations of elements do not occur.

EXPORT ESTIMATES

To estimate the quantity of organic material transported to the estuary, we modified a series of equations developed by Gallagher (1977). The equations are based on the model of carbon fixation and subsequent losses as shown in the following diagram:



where $P = \Delta G + M$, $\Delta G = G_{ti-1} - G_i$; $\Delta SD = SD_{ti-1} - SD_{ti}$; $\Delta FD = FD_{ti-1} - T_i$;

and T_{i-1} and T_i = harvest at beginning and end of time interval, respectively. Decomposition of standing dead and fallen dead (litter) marsh plant material was calculated with the following equations:

$$DE_{SD} = \left(\frac{SD_{ti-1}+SD_{ti}}{2}\right)\left\{t_s\left[\left(\frac{SD_{lti-1}+SD_{lti}}{2}\right) + \left(\frac{SD_{sti-1}+SD_{sti}}{2}\right)\right] + t_a\left(\frac{SD_{ati-1}+SD_{ati}}{2}\right)\right\}$$

$$DE_{FD} = \left(\frac{FD_{ti-1}+FD_{ti}}{2}\right)\left\{t_s\left[\left(\frac{FD_{lti-1}+FD_{lti}}{2}\right) + \left(\frac{FD_{sti-1}+FD_{sti}}{2}\right)\right] + t_a\left(\frac{FD_{ati-1}+FD_{ati}}{2}\right)\right\}$$

where,

DE_{SD} = Decomposition (respiration and leaching) of standing dead during time interval,

DE_{FD} = Decomposition (respiration and leaching) of fallen dead during time interval,

t_s = time submerged during time interval,

t_a = time emergent during time interval,

SD_l = rate of leaching of DOC from the standing dead community,

SD_s = submerged or aquatic respiration of the standing dead community,

SD_a = emergent or aerial respiration rate of the standing dead community,

FD_l = rate of leaching of DOC from the fallen dead community,

FD_s = submerged or aquatic respiration rate of the fallen dead community, and

FD_a = emergent or aerial respiration rate of the fallen dead community.

After calculating decomposition, export was estimated with the following equations:

$$F = \Delta SD + M - DE_{SD}, \text{ and}$$

$$LTE = \Delta FD + F - DE_{FD}.$$

Export values were determined for each time interval and then summed to yield total export of organic matter for the entire time period. It was assumed that the dry weight of plant material was about 50% carbon. Using a 2% tidal inundation time for the S. cynosuroides marsh, the equation yielded an export of 372 g C m^{-2} yr^{-1}. In the Z. miliacea marsh, a 5% inundation time for standing dead and a 10% inundation time for fallen dead yielded an annual export rate of 147 g C m^{-2}. These export values account for 37% and 20% of net annual primary productivity for S. cynosuroides and Z. miliacea, respectively. The lower export value for the Z. miliacea marsh can be explained, in part, by the higher respiration and leaching rates in this area and by the greater proportion of time the freshwater marsh is exposed to tidal inundation, Thus, more carbon is lost through respiration and leaching resulting in less being available for export as detritus. Nevertheless, it is apparent that both marsh areas are making significant contributions to the estuarine system. Values for carbon export from S. cynosuroides and Z. miliacea marshes have not been reported. However, Teal (1962) estimated that 45% of tall form Spartina alterniflora net annual primary productivity is removed by tidal action before it can be utilized by marsh consumers. Odum and Fanning (1973) reported export values of 25% and 8% of net annual primary productivity for tall form and short form S. alterniflora, respectively. Thus the values reported in this study are comparable to estimates for tall form S. alterniflora.

Although the equations shown above were formulated to estimate export from marsh areas, we attempted to utilize them in calculating the potential export of carbon from the swamp forest areas. Combining leaf litter fall from the two forest collection sites (Figure 4), and assuming a 50% tidal inundation time, the data show a negative export of carbon (-211 g C m^{-2} yr^{-1}) which may indicate a transport of carbon into these areas. Positive values for carbon export were obtained only for the April-May collection period

($6\ g\ C\ m^{-2}$) and the August-October period ($42\ g\ C\ m^{-2}$). The latter value is associated with relatively large quantities of leaf litter fall during this time period, whereas the former value is probably related to lower rates of respiration and leaching during this time period resulting in more carbon available for transport in plant material. Thus it appears that the forest swamp areas may act as a sink not only in the accumulation of some nutrients as shown in this study and by Brinson (1977), but also as a recipient of carbon. A more accurate account of tidal inundation time will enable us to refine these estimates.

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APPENDIX A - BIOMASS, AQUATIC RESPIRATION, AERIAL RESPIRATION, AND DOC LEACHING FOR STANDING DEAD AND FALLEN DEAD IN TWO SPECIES OF MARSH GRASS, AND FOR SWAMP FOREST LEAVES.

TABLE A-1. MEAN DRY WEIGHT (g m^{-2} ± S.E.) OF TWO SPECIES OF MARSH GRASSES (N=6 AND N=8, RESPECTIVELY) IN CLEAR CUT PLOTS FROM THE ALTAMAHA RIVER DELTA

Date	Live	Standing Dead	Litter	Total Biomass
		Spartina cynosuroides		
17 Apr 1978	216 ± 69	920 ± 94	276 ± 44	1412 ± 126
30 May 1978	582 ± 57	676 ± 53	246 ± 69	1504 ± 87
10 Jul 1978	769 ± 118	828 ± 147	316 ± 63	1913 ± 201
14 Aug 1978	682 ± 107	837 ± 194	228 ± 40	1747 ± 297
16 Oct 1978	584 ± 94	1105 ± 114	244 ± 15	1105 ± 193
28 Nov 1978	173 ± 44	1800 ± 275	256 ± 53	2229 ± 320
9 Jan 1979	0	1530 ± 362	273 ± 57	1803 ± 405
5 Mar 1979	9 ± 2	158 ± 57	88 ± 21	255 ± 42
13 Apr 1979	218 ± 49	215 ± 38	269 ± 84	702 ± 137
		Zizaniopsis miliacea		
17 Apr 1978	179 ± 44	870 ± 222	235 ± 62	1284 ± 321
30 May 1978	357 ± 93	506 ± 138	254 ± 61	1117 ± 276
10 Jul 1978	459 ± 61	368 ± 101	106 ± 27	933 ± 199
14 Aug 1978	593 ± 157	308 ± 24	77 ± 13	978 ± 178
16 Oct 1978	623 ± 122	393 ± 51	129 ± 22	1145 ± 168
28 Nov 1978	426 ± 60	521 ± 76	96 ± 21	1043 ± 117
9 Jan 1979	222 ± 41	332 ± 39	168 ± 15	722 ± 67
5 Mar 1979	81 ± 12	426 ± 61	216 ± 8	723 ± 77
13 Apr 1979	135 ± 13	465 ± 65	147 ± 11	747 ± 73

TABLE A-2. MEAN DRY WEIGHT (g m^{-2} ± S.E.) OF TWO SPECIES OF MARSH GRASSES (N=6, AND N=8, RESPECTIVELY) IN PREVIOUS CUT PLOTS FROM THE ALTAMAHA RIVER DELTA

Date	Live	Total Dead	Total Biomass
	Spartina cynosuroides		
30 May 1978	682 ± 96	106 ± 14	788 ± 98
10 Jul 1978	596 ± 80	209 ± 35	805 ± 96
14 Aug 1978	764 ± 98	305 ± 33	1069 ± 100
16 Oct 1978	593 ± 140	335 ± 73	928 ± 187
28 Nov 1978	287 ± 33	638 ± 51	925 ± 79
9 Jan 1979	0	408 ± 81	408 ± 81
5 Mar 1979	Plots destroyed by fire		
13 Apr 1979	118 ± 23	5 ± 1	123 ± 22
	Zizaniopsis miliacea		
30 May 1978	212 ± 64	172 ± 32	384 ± 80
10 Jul 1978	490 ± 47	193 ± 38	683 ± 67
14 Aug 1978	468 ± 70	98 ± 16	566 ± 80
16 Oct 1978	601 ± 186	209 ± 58	810 ± 243
28 Nov 1978	453 ± 14	252 ± 75	705 ± 89
9 Jan 1979	146 ± 16	178 ± 26	324 ± 37
5 Mar 1979	70 ± 9	300 ± 47	370 ± 57
13 Apr 1979	139 ± 15	66 ± 11	205 ± 22

TABLE A-3. MEAN DRY WEIGHT (g m^{-2} ± S.E.) OF LEAF LITTER AT TWO FOREST LOCATIONS (N=12) IN THE ALTAMAHA RIVER DELTA

Date	Riverbend	Freshwater Swamp
17 Apr 1978	10.1 ± 0.9	23.12 ± 3.1
30 May 1978	29.9 ± 10.6	24.80 ± 3.8
10 Jul 1978	20.8 ± 5.2	8.20 ± 1.2
14 Aug 1978	23.9 ± 3.5	12.30 ± 3.5
16 Oct 1978	114.8 ± 17.3	76.40 ± 11.1
28 Nov 1978	120.1 ± 18.0	152.80 ± 18.8
9 Jan 1979	27.7 ± 5.1	46.90 ± 6.2
5 Mar 1979	35.8 ± 11.6	23.90 ± 3.4
13 Apr 1979	15.8 ± 3.4	17.30 ± 2.6

TABLE A-4. AQUATIC RESPIRATION* (μg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) OF ATTACHED DEAD PLANT COMMUNITY IN TWO SPECIES OF MARSH GRASSES IN THE ALTAMAHA RIVER DELTA

	Spartina cynosuroides		*Zizaniopsis miliacea*	
Date	Fallen Dead	Standing Dead	Fallen Dead	Standing Dead
18 Apr 1978	82 ± 12		41 ± 4	
30 May 1978	50 ± 7	27 ± 3	36 ± 8	10 ± 2
10 Jul 1978	55 ± 20	63 ± 26	44 ± 15	1 ± 3
14 Aug 1978	31 ± 1	55 ± 17	54 ± 14	55 ± 3
16 Oct 1978	8 ± 4	13 ± 7	9 ± 5	29 ± 7
29 Nov 1978	29 ± 6	21 ± 4	30 ± 9	59 ± 14
9 Jan 1979	25 ± 4	15 ± 3	26 ± 2	94 ± 16
5 Mar 1979	9 ± 3	9 ± 1	23 ± 4	12 ± 5
13 Apr 1979	51 ± 4	41 ± 5	94 ± 18	126 ± 11

* Incubation time, 3.5 h; N=3.

TABLE A-5. AQUATIC RESPIRATION* (μg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) OF ATTACHED DEAD PLANT COMMUNITY FOR THREE SPECIES OF SWAMP FOREST LEAVES IN THE ALTAMAHA RIVER DELTA

Date	*Nyssa aquatica*	*Liquidambar styraciflua*	*Taxodium distichum*
18 Apr 1978	125 ± 9	95 ± 16	383 ± 78
30 May 1978	63 ± 2	77 ± 30	160 ± 7
10 Jul 1978	79 ± 4	190 ± 53	161 ± 18
14 Aug 1978	126 ± 6	92 ± 22	296 ± 30
16 Oct 1978	153 ± 30	236 ± 56	97 ± 14
30 Nov 1978	335 ± 21	243 ± 17	892 ± 72
9 Jan 1979	189 ± 26	81 ± 14	59 ± 2
5 Mar 1979	46 ± 9	24 ± 1	31 ± 5
13 Apr 1979	277 ± 28	47 ± 11	62 ± 3

* Incubation time, 3 h; N=3.

TABLE A-6. AERIAL RESPIRATION* (μg C g^{-1} DRY WEIGHT·h^{-1} ± S.E.) OF ATTACHED DEAD PLANT COMMUNITY IN TWO SPECIES OF MARSH GRASSES FROM THE ALTAMAHA RIVER DELTA

	Spartina cynosuroides		*Zizaniopsis miliacea*	
Date	Fallen Dead	Standing Dead	Fallen Dead	Standing Dead
17 Apr 1978	4 ± 1 (6)	1 ± 0.3 (6)	72 ± 5 (6)	1 ± 0.4 (6)
30 May 1978	11 ± 0.6 (6)	1 ± 0.5 (6)	81 ± 3 (6)	9 ± 1 (6)
10 Jul 1978	6 ± 1	0.8 ± 0.2	132 ± 31	8 ± 2
14 Aug 1978	28 ± 5	-4 ± 2	82 ± 12	-4 ± 1
16 Oct 1978	22 ± 3	24 ± 1	106 ± 4	3 ± 2 (8)
30 Nov 1978	25 ± 1	2 ± 0.4	25 ± 1	2 ± 0.4 (7)
9 Jan 1979	18 ± 2	1 ± 0.1	28 ± 2	14 ± 1
5 Mar 1979	28 ± 2	6 ± 1	64 ± 3	5 ± 1 (7)
13 Apr 1979	1 ± 0.1 (6)	1 ± 0.3 (6)	55 ± 1	1 ± 0.2

* Incubation time, 3 h; N=9, unless otherwise indicated.

TABLE A-7. AERIAL RESPIRATION* (µg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) OF ATTACHED DEAD PLANT COMMUNITY FOR THREE SPECIES OF SWAMP FOREST LEAVES IN THE ALTAMAHA RIVER DELTA

Date	*Nyssa aquatica*		*Liquidambar styraciflua*		*Taxodium distichum*	
17 Apr 1978	1 ± 0.4	(6)	26 ± 8	(6)	2 ± 0.5	(6)
30 May 1978	18 ± 1	(6)	16 ± 2	(6)	114 ± 20	(6)
10 Jul 1978	24 ± 4		1 ± 0.3	(8)	45 ± 7	(10)
14 Aug 1978	142 ± 28		68 ± 7		133 ± 11	
16 Oct 1978	16 ± 5	(7)	16 ± 2	(10)	27 ± 7	
30 Nov 1978	110 ± 7		12 ± 0.3	(6)	49 ± 3	
9 Jan 1979	35 ± 7	(8)	26 ± 2		29 ± 1	
5 Mar 1979	68 ± 5	(6)	11 ± 2	(8)	35 ± 2	(8)
13 Apr 1979	26 ± 7		2 ± 0.2	(7)	5 ± 1	(7)

* Incubation time, 3 h; N=9, unless otherwise noted.

TABLE A-8. DOC RELEASED* (µg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) FROM DEAD PLANT PARTS FOR TWO SPECIES OF MARSH GRASSES FROM THE ALTAMAHA RIVER DELTA

	Spartina cynosuroides				*Zizaniopsis miliacea*			
Date	Fallen Dead		Standing Dead		Fallen Dead		Standing Dead	
17 Apr 1978	435 ± 18	(7)	425 ± 33	(6)	201 ± 15	(8)	594 ± 71	(7)
30 May 1978	573 ± 83		364 ± 92		183 ± 3		468 ± 12	
10 Jul 1978	552 ± 31		379 ± 44		313 ± 25		441 ± 36	(8)
14 Aug 1978	262 ± 48		448 ± 54		769 ± 71	(8)	230 ± 41	
16 Oct 1978	290 ± 26	(7)	265 ± 37	(6)	954 ± 49	(5)	628 ± 27	(8)
30 Nov 1978			501 ± 67	(3)	109 ± 24	(4)	322 ± 65	(4)
9 Jan 1979	169 ± 18	(4)	127 ± 21	(7)	346 ± 126	(3)	107	(1)
5 Mar 1979	335 ± 16	(3)	142	(1)	532	(1)	270 ± 52	(3)
13 Apr 1979	247 ± 32	(8)	304 ± 24		246 ± 24		731 ± 62	

* Incubation time, 3 hr; N=9, unless otherwise indicated.

TABLE A-9. DOC RELEASED* (μg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) FROM THREE SPECIES OF SWAMP FOREST LEAVES COLLECTED IN THE ALTAMAHA RIVER DELTA

Date	*Nyssa aquatica*		*Liquidambar styraciflua*		*Taxodium distichum*	
17 Apr 1978	660 ± 104		398 ± 33		179 ± 9	
30 May 1978	94 ± 20	(5)	22 ± 11	(6)	224 ± 37	
10 Jul 1978	746 ± 78	(8)	927 ± 35		1578 ± 135	(8)
14 Aug 1978	390 ± 77		342 ± 40	(6)	2054 ± 113	
16 Oct 1978	289 ± 41	(8)	2570 ± 249	(8)	1308 ± 175	(8)
30 Nov 1978	842 ± 46	(2)	2183 ± 219	(3)	316 ± 41	(2)
9 Jan 1979	299 ± 25	(3)	356 ± 143	(2)	-22	(1)
5 Mar 1979	199 ± 46	(3)	72	(1)	25 ± 5	(3)
13 Apr 1979	1349 ± 143	(6)	272 ± 4	(5)	409 ± 47	(7)

* Incubation time, 3 h; N=9, unless otherwise indicated.

APPENDIX B - BIOMASS, AQUATIC RESPIRATION, AERIAL RESPIRATION, DOC LEACHING AND ELEMENTAL COMPOSITION OF LITTER BAG PLANT MATERIAL FOR TWO SPECIES OF MARSH GRASSES AND SWAMP FOREST LEAVES.

TABLE B-1. WEIGHT OF DECOMPOSING MARSH GRASS AND SWAMP FOREST LEAVES* (g DRY WEIGHT ± S.E.) FROM LITTER BAGS AT FOUR LOCATIONS IN THE ALTAMAHA RIVER DELTA AT THREE COLLECTION PERIODS†

	1 month	6 months	11 months
Spartina cynosuroides			
Suspended	96 ± 1.0	92 ± 0.3	61 ± 5.0 (5)
Surface	95 ± 1.0	69 ± 0.2	40 ± 4.0 (5)
Submerged	84 ± 1.0	52 ± 1 (3)	
Saltwater	82 ± 2.0 (4)		
Zizaniopsis miliacea			
Suspended	93 ± 1.0	42 ± 4.0	38 ± 5.0 (5)
Surface	83 ± 0.4 (5)	28 ± 3.0 (4)	14 ± 2.0 (4)
Submerged	81 ± 2.0 (4)	6 ± 6.0	
Saltwater	88 ± 3.0 (6)		
Forest Leaves			
Surface	16 ± 0.4	7 ± 0.6	5 ± 0.8
Submerged	17 ± 1.0	4 ± 0.4	3 ± 0.6 (5)
Saltwater	16 ± 2.0		

* Initial weight of marsh grass = 100g/bag
Initial weight of forest leaves = 20g/bag

† N=6, unless otherwise indicated

TABLE B-2. AQUATIC RESPIRATION* (μg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) OF ATTACHED DEAD PLANT COMMUNITY FROM DEAD PLANT PARTS ENCLOSED IN SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB) LITTER BAGS AT THE COLLECTION SITE AND SUBMERGED BAGS IN SALTWATER (SAL)

	1 month	6 months	11 months
Spartina cynosuroides			
SUB	62 ± 7	27 ± 3	
SUS	15 ± 5	13 ± 13	11 ± 3
SUR	61 ± 25	19 ± 5	26 ± 7
SAL	143 ± 19		
Zizaniopsis miliacea			
SUB	63 ± 3	66 ± 24	
SUS	20 ± 10	-2 ± 10	15 ± 2
SUR	59 ± 10	51 ± 23	28 ± 3
SAL	141 ± 13		
Forest Leaves			
SUB	93 ± 12	47 ± 17	18 ± 4
SUR	85 ± 19	133 ± 56	30 ± 8
SAL	163 ± 21		

* Incubation time, 3.5 h; N=3.

TABLE B-3. AERIAL RESPIRATION (μg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) OF ATTACHED DEAD PLANT COMMUNITY FROM DEAD PLANT PARTS ENCLOSED IN SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB) LITTER BAGS AT THE COLLECTION SITE, AND SUBMERGED BAGS IN SALTWATER (SAL)

	1 month		6 months		11 months	
Spartina cynosuroides						
SUB	119 ± 5		38 ± 3	(8)		
SUS	3 ± .04	(7)	17 ± 2	(6)	13 ± 2	(8)
SUR	62 ± 5		34 ± 2		36 ± 4	
SAL	63 ± 3					
Zizaniopsis miliacea						
SUB	121 ± 6	(6)	60 ± 2			
SUS	31 ± 5		46 ± 3		63 ± 2	
SUR	73 ± 3		21 ± 3		57 ± 3	(8)
SAL	124 ± 3					
Forest Leaves						
SUB	49 ± 3	(8)	20 ± 1	(10)	21 ± 1	
SUR	58 ± 2	(10)	24 ± 1		17 ± 2	
SAL	58 ± 6					

* Incubation time, 3h; N=9, unless otherwise indicated.

TABLE B-4. DOC* RELEASED (μg C g^{-1} DRY WEIGHT h^{-1} ± S.E.) FROM DEAD PLANT PARTS ENCLOSED IN SUSPENDED (SUS), SURFACE (SUR), SUBMERGED (SUB) LITTER BAGS AT THE COLLECTION SITE AND SUBMERGED IN SALTWATER (SAL)

	1 month		6 months		11 months	
Spartina cynosuroides						
SUB	733 ± 37		203 ± 120	(2)	137 ± 27	(2)
SUS	473 ± 205		123 ± 25		203 ± 98	(3)
SUR	718 ± 119	(8)	73 ± 10		287 ± 145	(2)
SAL	78 ± 20					
Zizaniopsis miliacea						
SUB	139 ± 11		-4 ± 28			
SUS	332 ± 9		312 ± 82	(7)	296	(1)
SUR	100 ± 13		70 ± 23		270 ± 52	(3)
SAL	153 ± 26					
Forest Leaves						
SUB	-65 ± 4		-27 ± 29	(8)	-37 ± 85	(4)
SUR	57 ± 14		-28 ± 10	(7)	-27 ± 24	(4)
SAL	-4 ± 14					

* Incubation time, 3 h; N=9, unless otherwise indicated.

TABLE B-5. MINERAL CONTENT* OF SPARTINA CYNOSUROIDES STANDING DEAD ENCLOSED IN SUSPENDED (SUS), SURFACE (SUR) AND SUBMERGED (SUB) LITTER BAGS AT THE COLLECTION SITE; SUBMERGED MATERIAL IN SALTWATER (SAL); AND FALLEN DEAD MATERIAL (LIT) COLLECTED FROM THE MARSH SURFACE AT EACH SAMPLING PERIOD†

	P	K	Ca	Mg	N
1 month					
SUS	.035 ± .007	.048 ± .012	.169 ± .002	.079 ± .003	0.46 ± 0.01
SUR	.050 ± .001	.046 ± .014	.238 ± .015	.089 ± .003	0.47 ± 0.03
SUB	.081 ± .011	.072 ± .006	.209 ± .025	.131 ± .004	0.69 ± 0.06
SAL	.093 ± .008	.157 ± .015	.270 ± .026	.305 ± .031	0.64 ± 0.06
LIT	.038	.058	.086	.0543	0.54
6 months					
SUS	.038 ± .009	.035 ± .006	.181 ± .015	.164 ± .022	0.73 ± 0.03
SUR	.080 ± .001	.047 ± .003	.415 ± .029	.168 ± .042	0.98 ± 0.13
SUB	.125 ± .002	.027 ± .005	.708 ± .133	.134 ± .004	1.21 ± 0.05
LIT	.053	.014	.222	.096	0.68
11 months					
SUS	.041 ± .004	<.008	.270 ± .105	.128 ± .018	0.77 ± 0.01
SUR	.048 ± .006	.014 ± .004	.172 ± .029	.109 ± .003	0.86 ± 0.05

(Continued)

TABLE B-5. (Continued)

	Mn	Fe	Al	B	Cu
1 month					
SUS	157.8 ± 39.3	364 ± 24.4	479 ± 55	3.13 ± 0.38	2.66 ± 0.59
SUR	183.3 ± 11.9	1651 ± 507	2342 ± 863	3.33 ± 0.24	3.13 ± 0.42
SUB	444.0 ± 87.9	4057 ± 521	5862 ± 270	5.58 ± 0.37	4.38 ± 0.33
SAL	1110 ± 351	4343 ± 237	11449 ± 454	21.00 ± 2.07	3.21 ± 0.72
LIT	222.2	73	34	4.31	3.21
6 months					
SUS	87.9 ± 11.7	503 ± 165	2527 ± 490	8.36 ± 5.64	2.43 ± 0.15
SUR	322.2 ± 99.1	4200 ± 1052	5701 ± 209	14.35 ± 5.41	3.75 ± 0.41
SUB	2527 ± 468	4383 ± 758	4935 ± 783	5.04 ± 0.27	4.31 ± 0.08
LIT	251.9	114	73	6.92	1.80
11 months					
SUS	81.1 ± 16.7	570 ± 87	1865 ± 1215	5.75 ± 0.86	1.61 ± 0.13
SUR	100.6 ± 42.1	2299 ± 1430	4125 ± 774	6.04 ± 0.69	1.29 ± 0.12

(Continued)

TABLE B-5. (Concluded)

	Zn	Sr	Ba	Na
1 month				
SUS	24.28 ± 1.82	8.18 ± 0.56	5.46 ± 0.27	343.30 ± 53.80
SUR	33.62 ± 4.46	16.00 ± 1.97	12.48 ± 1.42	273.90 ± 13.90
SUB	36.67 ± 5.60	19.67 ± 3.78	14.51 ± 1.89	416.70 ± 25.00
SAL	27.23 ± 2.23	36.71 ± 1.84	8.46 ± 0.28	76.73 ± 5.40
LIT	37.34	2.19	2.64	92.90
6 months				
SUS	44.85 ± 7.00	16.00 ± 3.41	2.97 ± 0.47	4580 ± 691
SUR	42.91 ± 16.07	35.35 ± 3.99	5.24 ± 0.21	4769 ± 211
SUB	57.07 ± 1.93	57.18 ± 12.14	48.05 ± 3.56	379.00 ± 37.00
LIT	7.56	11.65	2.56	–
11 months				
SUS	61.61 ± 14.45	18.34 ± 8.13	5.42 ± 0.94	385.50 ± 44.60
SUR	34.07 ± 13.44	17.80 ± 4.14	5.61 ± 1.15	1913 ± 82

* P, K, Ca, Mg, N in %±S.E.; Mn, Fe, Al, B, Cu, Zn, Sr, Ba, Na in PPM±S.E.

† N=3 for all values except LIT, where N=1.

TABLE B-6. MINERAL CONTENT[*] OF ZIZANIOPSIS MILIACEA STANDING DEAD ENCLOSED IN SUSPENDED (SUS), SURFACE (SUR), AND SUBMERGED (SUB) LITTER BAGS AT THE COLLECTION SITE; SUBMERGED MATERIAL IN SALTWATER (SAL); AND FALLEN DEAD MATERIAL (LIT) COLLECTED FROM THE MARSH SURFACE AT EACH SAMPLING PERIOD[†]

	P	K	Ca	Mg	N
1 month					
SUS	0.079 ± 0.006	0.046 ± 0.001	0.358 ± 0.022	0.054 ± 0.001	0.78 ± 0.02
SUR	0.064 ± 0.002	0.038 ± 0.002	0.639 ± 0.002	0.056 ± 0.004	0.74 ± 0.02
SUB	0.086 ± 0.007	0.414 ± 0.001	0.086 ± 0.007	0.058 ± 0.003	0.82 ± 0.05
SAL	0.121 ± 0.010	0.295 ± 0.008	0.439 ± 0.046	0.609 ± 0.013	0.91 ± 0.04
LIT	0.063	0.088	0.331	0.038	0.75
6 months					
SUS	0.097 ± 0.014	0.020 ± 0.006	0.481 ± 0.061	0.118 ± 0.015	1.29 ± 0.06
SUR	0.132 ± 0.004	0.021 ± 0.004	0.592 ± 0.119	0.133 ± 0.005	1.65 ± 0.08
SUB	0.140	0.016	0.507	0.073	0.13
LIT	0.047	0.048	0.834	0.059	0.84
11 months					
SUS	0.084 ± 0.013	<.008	0.354 ± 0.032	0.067 ± 0.008	1.29 ± 0.11
SUR	0.132 ± 0.009	0.023 ± 0.002	0.416 ± 0.022	0.127 ± 0.001	1.72 ± 0.04
LIT	0.108	0.080	0.247	0.050	0.88

(Continued)

TABLE B-6. (Continued)

	Mn	Fe	Al	B	Cu
1 month					
SUS	601.9 ± 25.2	2062 ± 583	4047 ± 336	3.04 ± 0.18	2.17 ± 0.11
SUR	512.8 ± 30.1	3448 ± 417	5548 ± 733	2.59 ± 0.12	2.17 ± 0.19
SUB	611.6 ± 44.3	4918 ± 879	5800 ± 771	2.58 ± 0.10	3.01 ± 0.35
SAL	2449 ± 279	2611 ± 202	5840 ± 281	31.71 ± 0.33	3.10 ± 0.22
LIT	299	546	620	2.37	1.72
6 months					
SUS	690.0 ± 82.3	3143 ± 1183	4098 ± 1646	3.83 ± 0.66	3.71 ± 0.55
SUR	1057 ± 329	5754 ± 652	5841 ± 480	4.50 ± 0.39	4.78 ± 0.24
SUB	3875	7165	5558	3.27	5.20
LIT	223	300	61	3.98	1.43
11 months					
SUS	679.8 ± 104.6	2884 ± 1155	3151 ± 1266	2.40 ± 0.43	2.39 ± 0.37
SUR	1222 ± 675	6844 ± 577	6345 ± 144	3.97 ± 0.16	4.37 ± 0.12
LIT	504	548	755	2.45	1.27

(Continued)

TABLE B-6. (Concluded)

	Zn	Sr	Ba	Na
1 month				
SUS	36.4 ± 2.3	12.70 ± 1.87	48.52 ± 4.22	108.7 ± 8.8
SUR	27.6 ± 2.4	12.70 ± 2.56	44.07 ± 0.86	120.1 ± 10.2
SUB	34.3 ± 3.6	14.26 ± 2.16	46.05 ± 5.00	164.3 ± 12.4
SAL	18.1 ± 1.51	63.90 ± 2.15	10.50 ± 0.69	28.83 ± 2.26
LIT	16.5	10.07	30.78	75.4
6 months				
SUS	90.5 ± 3.4	33.68 ± 3.65	46.54 ± 5.20	257.3 ± 33.1
SUR	145.3 ± 23.9	44.39 ± 2.71	64.47 ± 7.20	229.3 ± 24.1
SUB	169	22.66	102.70	209.9
LIT	7.9	15.46	25.91	35.8
11 months				
SUS	3227 ± 1840	22.14 ± 4.27	52.62 ± 10.50	71.4 ± 13.5
SUR	152.7 ± 21.3	40.36 ± 2.22	51.32 ± 7.71	189.3 ± 12.1
LIT	16.8	2.74	23.11	902.1

* P, K, Ca, Mg, N in %±S.E.; Mn, Fe, Al, B, Cu, Zn, Sr, Ba, Na in PPM±S.E.

† N=3 for all values except LIT, where N=1.

TABLE B-7. MINERAL CONTENT* OF DEAD SWAMP FOREST LEAVES ENCLOSED IN SURFACE (SUR), AND SUBMERGED (SUB) LITTER BAGS AT THE COLLECTION STIE; AND DEAD LEAVES SUBMERGED IN SALT WATER (SAL)†

	P	K	Ca	Mg	N
1 month					
SUB	0.128 ± 0.006	0.062 ± 0.005	1.344 ± 0.048	0.114 ± 0.009	1.21 ± 0.01
SUR	0.115 ± 0.010	0.068 ± 0.005	1.380 ± 0.019	0.117 ± 0.005	1.20 ± 0.15
SAL	0.197 ± 0.012	0.115 ± 0.004	0.862 ± 0.037	0.519 ± 0.004	1.14 ± 0.06
6 months					
SUB	0.174 ± 0.002	0.033 ± 0.009	1.594 ± 0.161	0.173 ± 0.009	1.52 ± 0.01
SUR	0.186 ± 0.010	0.045 ± 0.012	1.883 ± 0.361	0.177 ± 0.011	1.63 ± 0.04
11 months					
SUB	0.202 ± 0.024	0.040 ± 0.009	1.352 ± 0.142	0.150 ± 0.002	1.55 ± 0.20
SUR	0.171 ± 0.006	0.023 ± 0.004	1.336 ± 0.075	0.138 ± 0.004	1.51 ± 0.06

(Continued)

TABLE B-7. (Continued)

	Mn	Fe	Al	B	Cu
1 month					
SUB	1010 ± 155	8347 ± 2540	10868 ± 2765	14.61 ± 1.00	7.49 ± 0.65
SUR	727 ± 27	4530 ± 330	5949 ± 318	16.49 ± 1.28	7.00 ± 0.23
SAL	4398 ± 450	7447 ± 416	11164 ± 513	125.00 ± 9.36	8.05 ± 0.43
6 months					
SUB	3733 ± 674	7094 ± 161	4782 ± 365	13.80 ± 0.82	10.02 ± 0.88
SUR	3892 ± 828	11319 ± 1700	8325 ± 1872	15.45 ± 0.98	8.79 ± 0.31
11 months					
SUB	3144 ± 650	15665 ± 1173	5619 ± 151	14.62 ± 0.94	11.10 ± 0.94
SUR	1456 ± 733	13252 ± 1126	5608 ± 37	12.01 ± 0.74	9.48 ± 1.13

(Continued)

TABLE B-7. (Concluded)

	Zn	Sr	Ba	Na
1 month				
SUB	134.1 ± 1.8	69.38 ± 5.21	154.3 ± 7.22	182.9 ± 2.07
SUR	113.0 ± 17.2	65.80 ± 0.88	151.5 ± 2.17	177.7 ± 2.74
SAL	57.7 ± 8.7	108.60 ± 8.50	20.1 ± 1.74	249.7 ± 34.60
6 months				
SUB	455.3 ± 62.2	96.00 ± 11.10	202.6 ± 26.00	282.1 ± 94.00
SUR	918.0 ± 244	94.90 ± 5.80	298.0 ± 101.60	631.9 ± 269.50
11 months				
SUB	259.4 ± 75.2	85.80 ± 2.70	218.7 ± 11.60	148.4 ± 19.30
SUR	263.2	75.50 ± 7.50	167.1 ± 9.70	182.8 ± 8.30

* P, K, Ca, Mg, N in %±S.E.; Mn, Fe, Al, B, Cu, Zn, Sr, Ba, Na in PPM±S.E.

† N=3 for all values.