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The Production of Organic Detritus in a South Florida Estuary

Eric J. Heald

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PREFACE

The Sea Grant Colleges Program was created in 1966 to stimulate research, instruction, and extension of knowledge of marine resources of the United States. In 1969 the Sea Grant Program was established at the University of Miami.

The outstanding success of the Land Grant Colleges Program, which in 100 years has brought the United States to its current superior position in agricultural production, was the basis for the Sea Grant concept. This concept has three objectives: to promote excellence in education and training, research, and information services in the University's disciplines that relate to the sea. The successful accomplishment of these objectives will result in material contributions to marine oriented industries and will, in addition, protect and preserve the environment for the enjoyment of all people.

With these objectives, this series of Sea Grant Technical Bulletins is intended to convey useful research information to the marine communities interested in resource development quickly, without the delay involved in formal publication.

While the responsibility for administration of the Sea Grant Program rests with the Department of Commerce, the responsibility for financing the program is shared equally by federal, industrial, and University of Miami contributions. This study, The Production of Organic Detritus in a South Florida Estuary, is published as part of the Sea Grant Program. Graduate research support was provided by grants from the National Park Service and the National Institutes of Health.

A complementary investigation of the estuarine food web was performed concurrently by Dr. William E. Odum whose research report, Pathways of Energy Flow in a South Florida Estuary, is available as Sea Grant Technical Bulletin #7.

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INTRODUCTION

Growing realization of the highly fertile nature of estuaries and coastal marshes has been accompanied by more active consideration of the mechanisms by which this high productivity is maintained. It has become evident that in many instances plant detritus, often of allochthonous origin, is at least in part responsible. Since the estuarine regions of Everglades National Park are dominated by dense mangrove forests, it is important to investigate the role played by mangroves in the productivity of the area. This study, conducted on the North River from 1967 to 1969, is an attempt to delineate and quantify the mechanisms and pathways by which dead plant material, particularly that of red mangroves, becomes incorporated into the aquatic system and thereby constitutes an important energy source.

Odum (1961, 1963), Tabb (1966a), Duke and Rice (1967), and Ketchum (1967) are among the many who have commented that estuaries are among the most fertile natural areas in the world. The gross primary productivity of estuarine marshes has been compared favorably with that of intensive agriculture, such as sugar cane or rice (Odum, 1961). Schelske and Odum (1962) have demonstrated that the high productivity of the Georgia salt marshes is based primarily upon _Spartina alterniflora_ which forms the basis of a detrital food chain. Because only a small portion of the net production of the marsh grass is grazed while it is alive, the major energy flow between autotrophic and heterotrophic levels is by way of the detritus food chain (Odum, 1962, 1963; Odum and de la Cruz, 1963, 1967; Teal, 1962).

Detritus is considered important as an energy source by Hickling (1961) in the inland fisheries of the Far East, by Darnell (1958, 1961, 1967a) in Louisiana estuarine communities, by Krey (1961) in the North Sea, by Riley (1959) in Long Island Sound, and by Parsons and Strickland (1962) in oceanic waters. Likewise, Nelson and Scott (1962), Hynes (1963), Chapman (1966), Egglishaw (1964), and Maciolek (1966) have all emphasized the importance of allochthonous detritus in the productivity of streams.

The undoubted importance of the mangrove-dominated estuaries of South Florida has often been emphasized. Idyll (1965) points out that the pink shrimp, Penaeus duorarum, is dependent upon these areas as a nursery ground. Similarly, Idyll et al. (1968) list several commercially valuable marine species, such as mullet, gray snapper, red drum, and blue crab, which use the estuaries as a nursery area and feeding ground. Tabb (1966b) has shown that at least one species of economic and recreational value (the spotted sea trout, Cynoscion nebulosus) appears to be dependent on the estuary during the greater part of its life cycle.

The principal aims of this study were: to estimate the annual production of dead material by the three main producers--red mangrove, sawgrass, and black-rush; to investigate the mechanisms by which such material enters the detrital 'pool', and the rate at which this proceeds; to determine, as far as possible, fluctuations in the quantity, nature, and origin of the detrital load of the river; to ascertain the potential nutrient value of dead material if consumed at any specific stage of decomposition.

DEFINITIONS

Odum and de la Cruz (1963) have proposed the term "organic detritus" to designate particulate organic material originating from the dead bodies, nonliving fragments, and excretions of living organisms; or, in the words of Darnell (1967b), "all types of biogenetic material in various stages of microbial decomposition. . . ."

Implicit in such a scheme (and recognized by both authors) is a range of particle size from, for instance, dead trees to amino acids and methane molecules. I feel that for present purposes some limitation on size range is necessary to simplify description and avoid needless repetition.

Since the major concerns of this study are the fate of vascular plant tissues and the quantitative investigation of particulate material in the river, it is desirable that definitions relate directly to these topics. Consequently, the term <u>debris</u> has been retained to designate dead plant material such as mangrove leaves and twigs in various stages of decomposition. Thus, debris is roughly equivalent to the term "litter" commonly used to describe decaying plant material in more fully terrestrial communities. It is not, however, the equivalent of "debris" as used by Allen (1939) to describe particulate suspended "detritus", nor is it synonymous with the "organic debris" of Newell (1965).

During the processes of decomposition and disintegration the component parts of plant debris are subjected to autolysis, hydrolysis, oxidation, mechanical fragmentation, and grazing, which result in a gradual reduction of particle size. Eventually the debris is fragmented to the point where individual particle size does not exceed 2 or 3 mm in smallest dimension. Material of this size is referred to as <u>detritus</u> in the present report. It should be pointed out that this division is less arbitrary than it appears since, in practice, suspended organic particles exceeding 3 mm were rarely encountered.

A detrital particle is the product of continuous degradation processes which cause a progressive reduction in the size of a fragment of debris until its component parts can no longer be considered particulate. At this point it enters the ill-defined realm of "colloidal" or "dissolved organic" material which Birge and Juday (1934), Fox et al. (1952, 1953), Baylor and Sutcliffe (1963), and Riley (1963) consider so important in detrital food chains. Diminution in size does not necessarily result in a decline in energy content; and as Odum and de la Cruz (1963) demonstrated, reduction in particle size is accompanied by protein enrichment and increased metabolic activity as a result of adsorbed microbiota.

Thus, the term <u>detritus</u> refers here to particulate material less than 3 mm in size, plus its associated microflora and fauna. Appropriate adjectives describe the nature or origin of specific particles; for instance, suspended detritus, mangrove detritus, sawgrass detritus, algal detritus, allochthonous detritus, inorganic detritus. Included in the last category are shell fragments, fish scales and otoliths, sand grains, and precipitated carbonate particles. The origin of fecal material commonly found in samples of suspended detritus could not be determined.

<u>Detritus</u>, of varied organic and inorganic origin, thus corresponds to the term "tripton" used widely in limnological studies (Welch, 1952; Reid, 1961). The term "seston", frequently used in reference to all living organisms (plankton) and nonliving particles suspended in water, will be similarly employed where appropriate.

DESCRIPTION OF THE AREA

The drainage system of the North River, Everglades National Park, was chosen for study because it exemplifies the prevalent ecosystem of the entire area and it has a relatively simple drainage pattern and a reasonably well-defined basin.

The North River arises as a poorly organized stream system near the edge of the sawgrass prairie and flows southwest into Whitewater Bay, about 14 km from its farthest traceable source (Figure 1). An estimated 21.7 square km (4,100 acres) are drained by the North River system. The predominant drainage pattern is best described as a series of shallow ponds connected by meandering streams which eventually coalesce and enter the main river at various points.

The shallow ponds occupy a total area of approximately 3.5 square km (670 acres), individual ponds being up to 110,000 square meters (20.5 acres) in area. The total length of interconnecting streams is estimated to be about 14.5 km. Although a soft mud layer up to one meter in thickness covers the bottom of the ponds, the streams and the main river flow over exposed bedrock and their banks are undercut. In consideration of this, Spackman et al. (1966) have suggested that many of the mangrove islets are the result of fragmentation and erosion of a once more continuous mangrove cover rather than products of rapid sediment deposition. Evidently the small-scale tidal oscillations and sluggish stream flow are sufficient to prevent permanent deposition of sediments on the stream beds.

Figure 1. Map of the North River, showing sampling locations.

The dominant cover vegetation is red mangrove, Rhizophora mangle, which borders all water areas and covers most of the land between them. The mangroves, which range from low scrub-mangrove to mature stands perhaps eight meters tall, grow on a varied thickness of peat of their own making. Davis (1940) provides a detailed description of the south Florida mangrove community, and he subsequently (1946) considers in detail the peat deposits of the area. An excellent account of the past and present plant communities of the region is presented by Craighead (MS.). In the upper reaches of the river, the mangroves become progressively more restricted to its banks. Initial inland penetration by mangroves is apparently accomplished via river channels such as the Shark River and the North River, as suggested by Scholl (1964). Craighead and Gilbert (1962) also suggest that periodic hurricanes aid the spread of mangroves by inland transportation of seedlings and by solonization of the soils.

White mangroves, Laguncularia racemosa, are mixed with reds. They are nowhere abundant, but single trees are generally found amid thickets of red mangroves at considerable distances from the river. Only rarely do they occur close to open water.

The black mangrove, Avicennia nitida, is absent, and the buttonwood, Conocarpus erectus, is rarely encountered. Consequently, the classical zonation pattern described by Davis (1940) from other areas of south Florida, Golley et al. (1962) in Puerto Rico, and Tabb (pers. comm.) from St. Thomas, is not evident in this area.

Toward the upper reaches of the river, and forming a transitional zone between the estuarine mangrove community and the sawgrass prairie, lie numerous scattered marsh areas dominated by black-rush, Juncus roemerianus. Individual black-rush marshes are usually small in extent and are invariably isolated from the main river by natural levees built up to a height of about 30 cm by mangroves bordering the river. These marshes may be the remnants of shallow ponds. However, Craighead (pers. comm.) has suggested that they are the result of replacement of sawgrass by *Juncus* in response to increased penetration of saline water. The *Juncus* marshes are obviously a well-established feature since they are found growing on one to two meters of their own peat.

Sawgrass, *Mariscus jamaicensis*, occurs abundantly only in the headwaters of the river. Elsewhere it can be found sparsely scattered on elevated tussocks of peat along the river banks beneath dense mangrove cover.

Small, isolated stands of hardwoods occur amid the mangrove forest, usually at some distance from open water.

The estuarine fauna of the Park has been well documented by Tabb et al. (1961, 1962); and the fish fauna of the North River has been extensively investigated by Tabb (MS.).

The hydrography of the system is characterized by marked fluctuations of water level and salinity in response to the seasonal rainfall pattern of south Florida. In general, the months of low rainfall are November to May. During this period, runoff decreases and the water table sinks steadily. Saline water penetrates far up the river until the salinity of the estuarine waters approaches 25 parts per thousand and the headwaters 10 or 12 parts per thousand. Figure 2 shows monthly salinities at three locations depicted on the general map (Figure 1).

The heavy summer rains normally begin in June, and almost immediately the water table rises and salinities fall rapidly. Freshwater conditions were recorded at all three stations from July through November, 1968.

The effect of seasonal fluctuations in water level and salinity on fish stocks in the North River has been described by Tabb (MS.); the

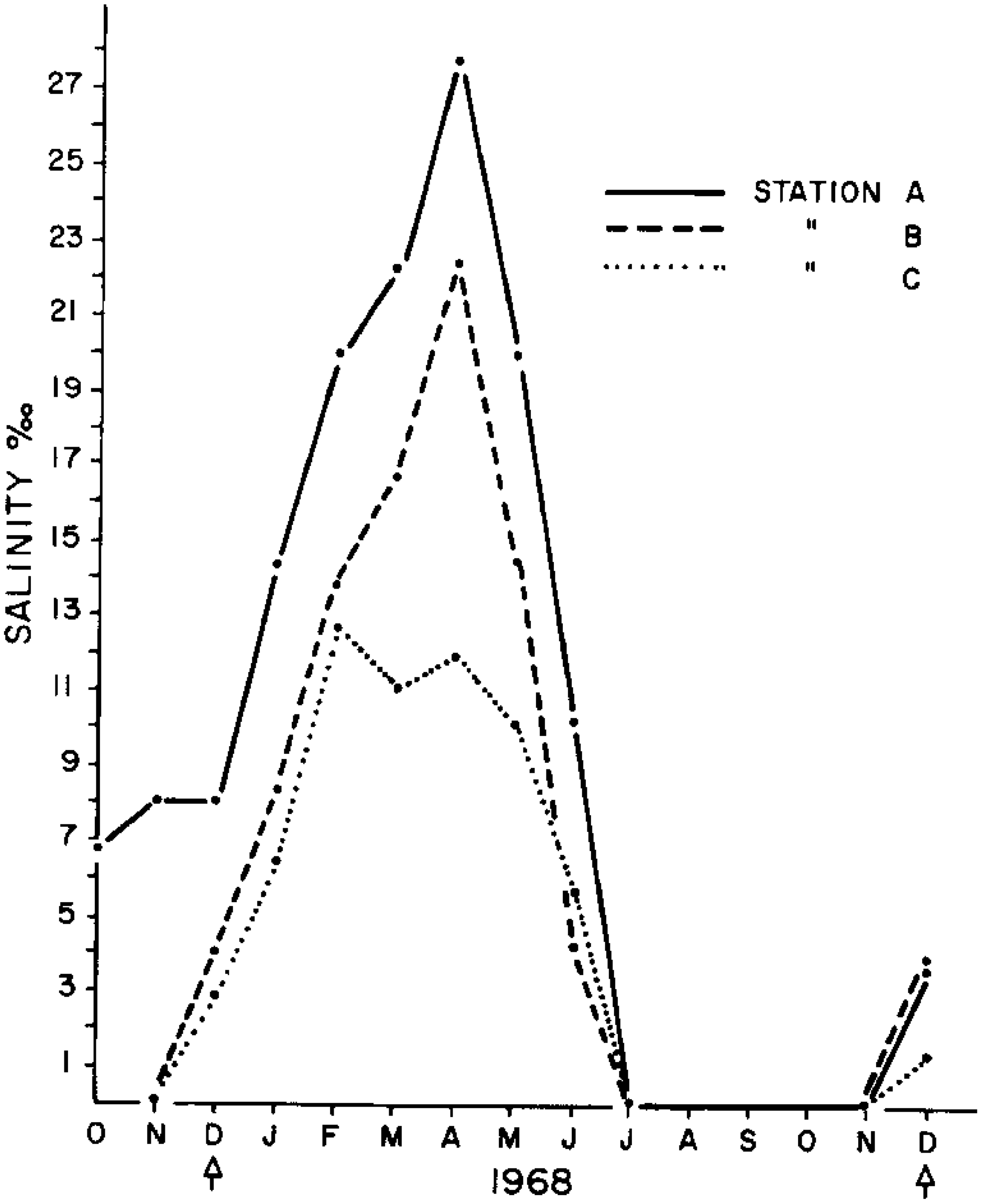

Figure 2. Ambient salinities during the sampling period.

influence of these parameters on patterns of decomposition and degradation of organic debris will be examined in this report.

PRODUCTION OF PLANT DEBRIS

Since the fragmentation of dead leaves, stalks, twigs, and roots constitutes an important source of allochthonous detritus, it was important to determine, as far as possible, the quantity of these materials produced annually by the dominant plant species. Interest was focused primarily upon the quantity of dead leaves shed by red mangroves and on the standing crop of dead material produced in the *Juncus* marshes.

Red Mangrove Debris

Mangroves usually grow in dense thickets in which there is considerable overlap of individuals. Solitary trees are rarely encountered. Under these circumstances it was not possible to collect all the leaves shed by a single tree. Consequently, a "Limb Count" technique, developed by the Florida Crop and Livestock Reporting Service (Anon., 1967) for prediction of the citrus crop, was adapted to present needs.

Methods. The "Limb Count" method of estimating the productivity of a tree involves determination of the productivity of a ten percent sample limb on a large sample of trees (Appendix I). It has been established that bearing surface and limb size of orange trees, as determined by cross-sectional measurement, are highly correlated. The sample limb is thus one in which the cross-secional area (C.S.A.) is approximately ten percent of the trunk C.S.A. Details of the theory of the estimate are described in Appendix Ia.

For estimates of debris production nine trees, representative of the size range of the population, were chosen from a single thicket. On each tree a plastic insect screening of 1 mm mesh was used to cradle a terminal branch of appropriate C.S.A. The C.S.A. of the main trunk and all pertinent branches was obtained from each tree. Trunk cross-sectional areas, ranging from 4.6 cm^2 to 185 cm^2, were measured at the point at which distortion resulting from the emergence of the highest placed prop root was no longer evident.

Fallen leaves, leaf scales, fruits, and twigs were collected from each mesh cradle at monthly intervals, and oven-dried at 104° C. to constant weight. The monthly leaf fall of each tree was then obtained by application of the probability expansion (Appendix Ia).

The relationship between C.S.A. and leaf fall in trees of small and medium size is described by Figure 3. Although this relationship was approximately linear at all times of the year, reference to Figure 4 reveals that this was not true of very large trees during the months of peak production. The line of best fit in June is described by the power function $y = 27.2x^{1.06}$. Thus, very large trees shed proportionally more leaves than do small and medium sized trees. The existence of a similar relationship in the case of total debris produced annually will be seen later.

To provide a check on the validity of the statistical method, a similar mesh screen was erected around a small, isolated tree of 21.5 cm^2 trunk C.S.A. and 2.5 meters high. In this case it was possible to collect, dry, and weigh all leaves shed by the tree each month. As will be seen from Figure 3, actual leaf fall from this tree was always slightly higher than the estimated leaf fall from a tree of identical C.S.A. This might be expected since the tree, standing alone, is free from the effects of

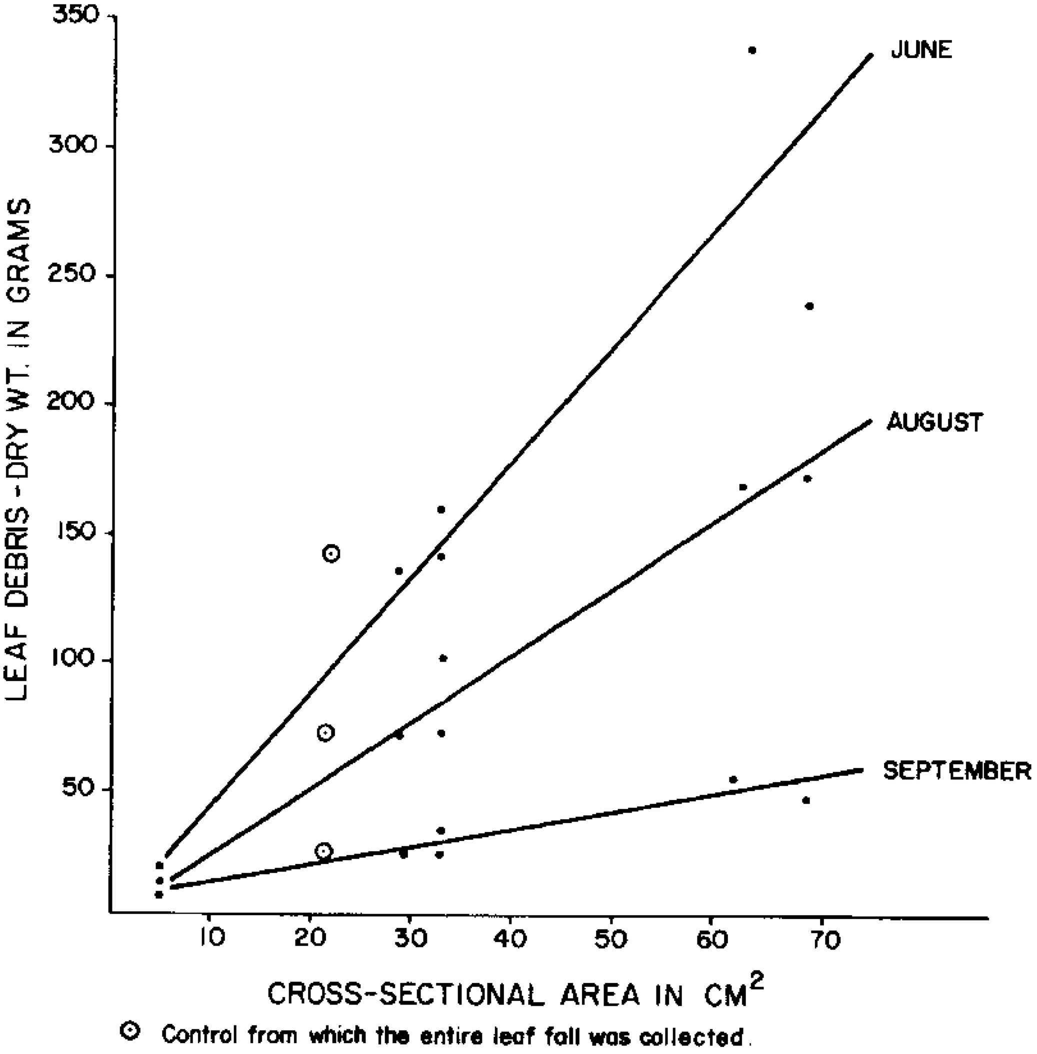

Figure 3. Relationship between cross-sectional area and monthly leaf fall in small and medium-sized red mangrove trees.

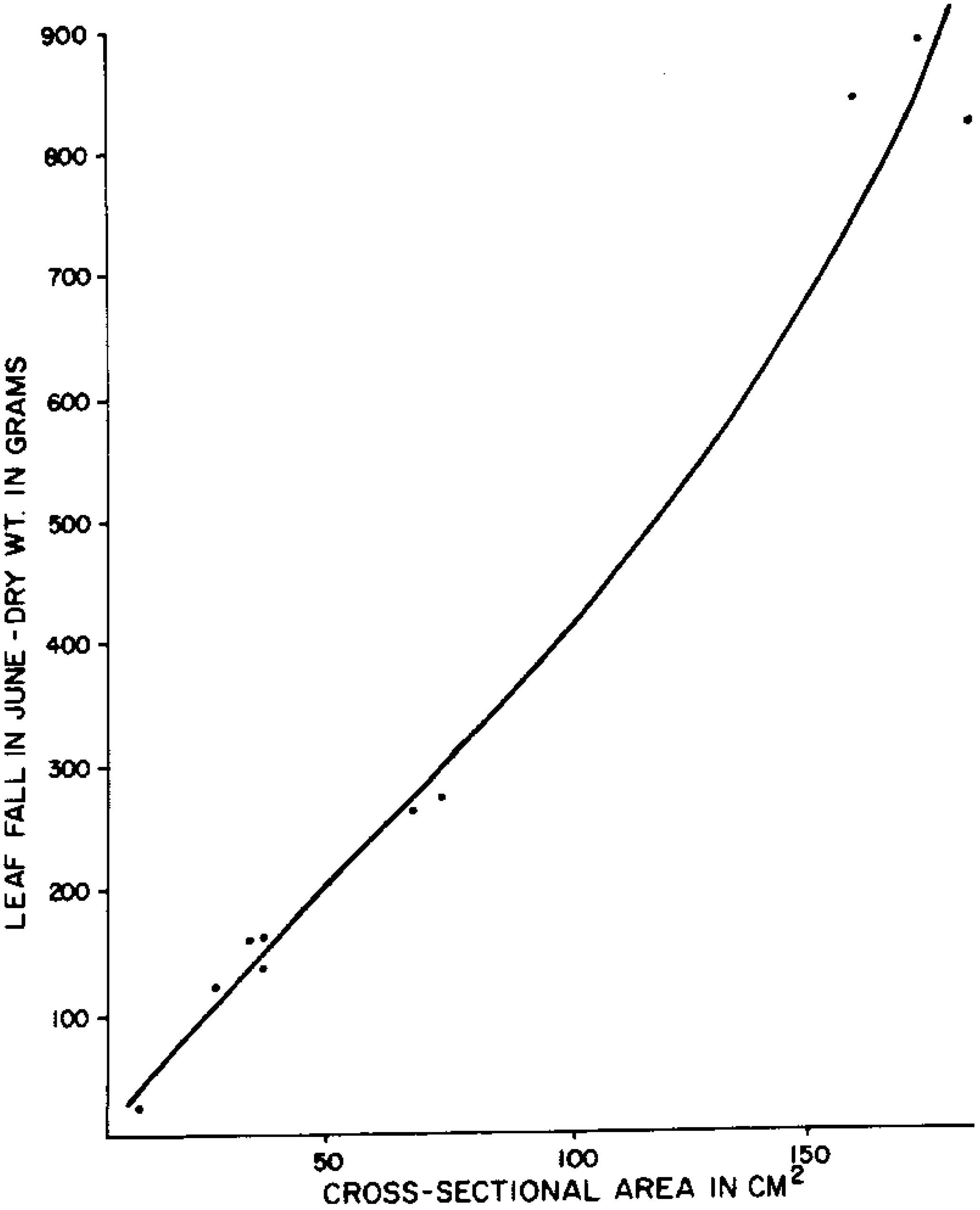

Figure 4. Relationship between cross-sectional area and monthly leaf fall from all trees measured--June, 1968.

competition and shading which influence the growth of individuals in dense thickets. Furthermore, most of its roots are permanently submerged, whereas those of the other trees measured are only wetted at high tide or during the rainy season.

Results. As can be seen from Figure 5, the monthly leaf fall from each tree was greatest in June and July. Leaf fall in June varied from 15.7 g, dry weight, from the smallest tree to 922 g from the largest (see Appendix I). Since maximum monthly weights of leaf scales were also noted from June to October, it appears that the operative mechanism is simply a replacement of old leaves by new ones. In June the solitary tree selected for study shed 411 leaves from an estimated total standing crop of 1,200, and during a twelve-month period it shed 1,080 leaves. Thus, annual leaf fall is approximately equal to standing crop, and there is a complete turnover of leaf material each year.

Figure 6 shows the dry weight of debris of all types produced annually by each tree measured. This varied from 89 g to 3,500 g, dry weight. The relationship of C.S.A. to total debris produced proved to be a power function, $y = 21.6x^{0.96}$. Sources of debris were, in order of importance, leaves, leaf scales, twigs, and flowers. Leaf material accounted for about 83 percent of the total production.

An attempt has been made to estimate the total weight of debris produced annually within the confines of the river drainage system. The estimate is essentially a multiplication involving the total number of mangroves in the area and the annual production of debris by a tree which is representative of the population. Required for this calculation are: (1) the relationship of C.S.A. to debris production; (2) the mean C.S.A. of the mangrove population; (3) the average number of trees per unit area; (4) the total land area occupied by mangroves. The accuracy of the

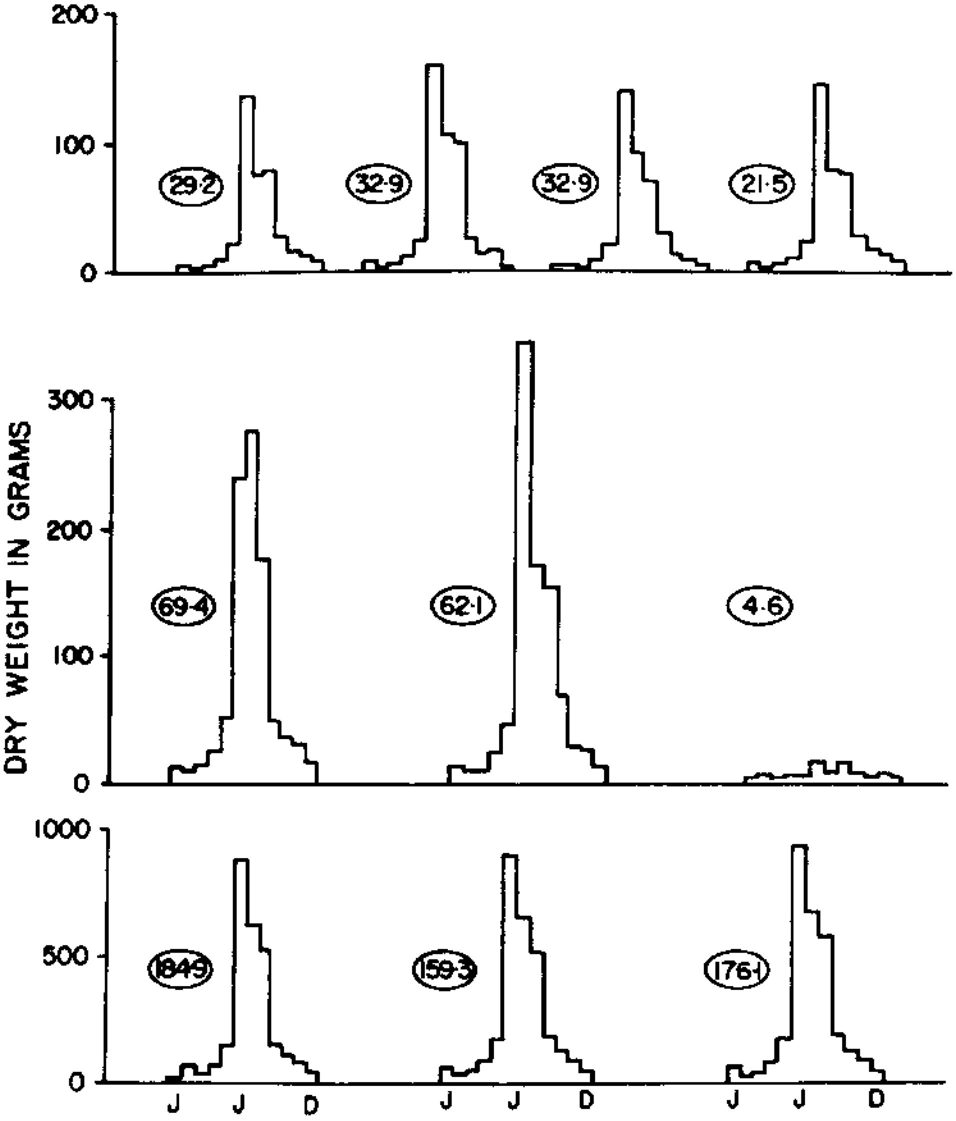

Figure 5. Monthly leaf fall of red mangroves. Circled numbers indicate cross-sectional areas in cm^2.

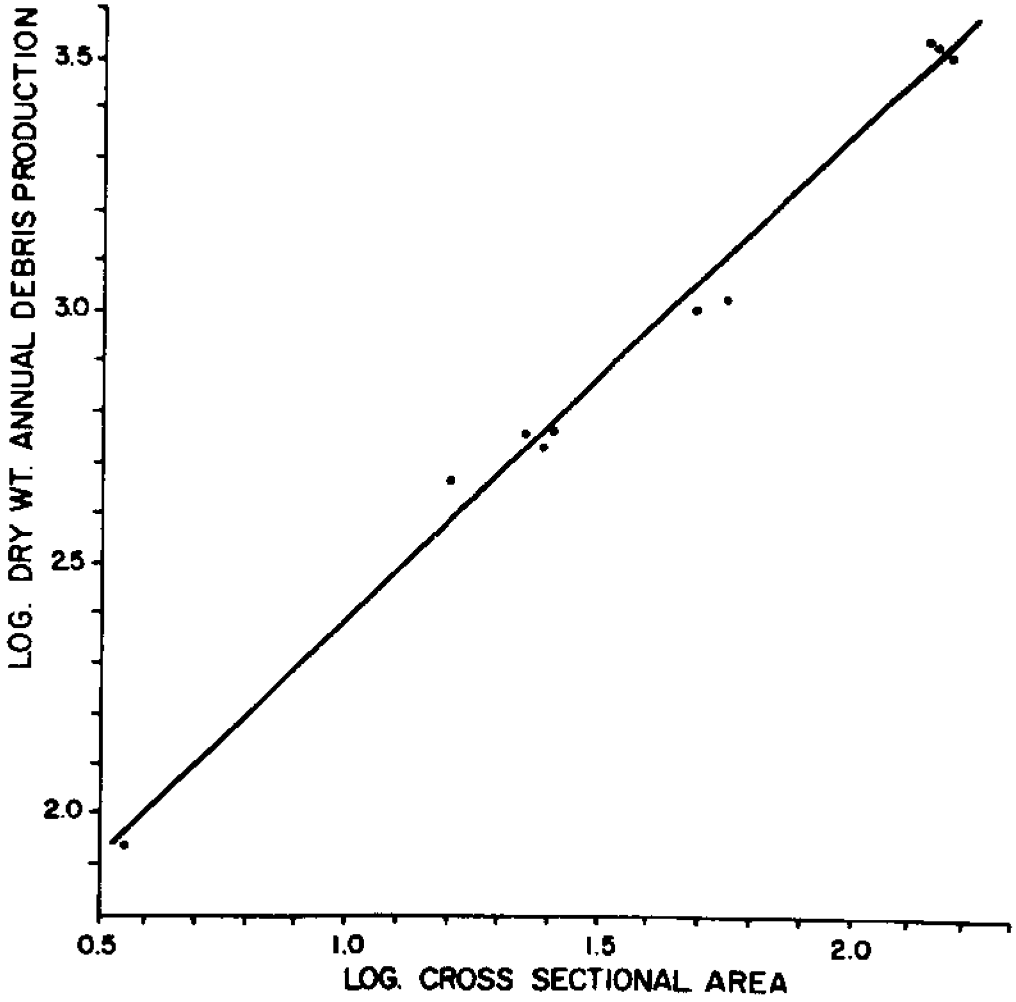

Figure 6. Relationship between cross-sectional area and annual production of debris by red mangroves.

estimate is dependent upon the validity of several assumptions which will be discussed in the following paragraphs.

(1) Although based on only ten datum points, the described relationship (Figure 6) is probably accurate with respect to leaves and scales. The method to be detailed here produces an estimated average daily leaf fall of 1.3 g/m^2 in May, identical with the findings of Golley et al. (1962) in Puerto Rico. However, the comparison may be fortuitous since the red mangrove thickets which they described are very different in character from those found in the North River. The Limb Count method apparently underestimates the production of twig debris since the control tree yielded considerably greater weights of fallen twigs than a tree of similar size would have been expected to produce.

If one accepts the validity of the relationship as established by the Limb Count method, it can be used to predict annual production of debris by a tree of any specified size. Thus, the production from a tree which represents the mean size of all trees in the drainage system can be calculated.

(2) The mean C.S.A. was determined from measurements of 173 randomly selected trees in four easily accessible locations. The C.S.A. of the smallest tree measured was 4.4 cm^2 (2.4 cm diameter), and the largest was 199.3 cm^2 (15.9 cm diameter), the calculated mean being 48.6 cm^2 (7.9 cm diameter). As such, the calculated mean probably adequately describes trees growing in the proximity of permanent waterways. However, the accuracy with which it represents trees growing elsewhere is not known. Many of these trees are virtually inaccessible, and one is forced to assume that they do not differ appreciably from the trees measured Visual observations of tree heights from available vantage points did not reveal any discernible differences in height with increasing distance between tree and waterway.

(3) An estimate of the total number of red mangroves in the area was obtained by determining the mean density of trees and then extrapolating to the total mangrove area, which was determined by examination of aerial photographs. Tree density was measured on 25 m^2 quadrats in four locations believed to be representative of the area. Tree densities of 21, 25, 26, and 32 per 25 meter square were obtained. The high count represents stands dominated by small, but mature, trees growing in shallow soil, while the low count is of large trees growing on the inside banks of bends in the river. As no reliable estimate could be made of the total area occupied by each facies, a mean density of 26 trees per 25 meter square was used for further calculations.

(4) Aerial photographs supplied by the United States Geological Survey, Branch of Water Quality, in Miami were used in conjunction with a polar planimeter to determine that a total land area of approximately 14 million square meters (2,644 acres) is occupied by mangroves. Enlargement of the photographs to a scale of 1:6900 provided sufficient detail without loss of resolution. It proved possible for a person familiar with the region to distinguish mangrove forests from hardwood stands, Juncus marshes, and sawgrass marshes. White mangroves could not be distinguished from reds, so the final estimate includes these also. Since field observations indicated that white mangroves account for no more than one tree in 200, small differences in average size of yearly production of debris by this species can be neglected.

Total Production. Assuming the validity of the information detailed above, the yearly production of leaf, scale, and twig debris within the area can be estimated. If the mean density of mangroves is 0.96 per square meter, 14 million square meters of land will accommodate about 13.5 million trees. The mean C.S.A. of these trees has been estimated at 48.65 cm^2, and (from the equation expressing total debris production) a tree of this size could be expected to have produced 914.7 g dry weight of debris in 1968. Thus, the total weight of debris produced by the red mangrove consocies in 1968 is estimated to be approximately 12,400 metric tons (12.42 million kg). Alternatively, this may be expressed as 0.88 kg/m^2/year, 2.41 g/m^2/day, or 8.8 tons/ha/year. If the total area of the drainage system, including water bodies, is considered, values of 0.57 kg/m^2/year and 1.57 g/m^2/day are obtained. By way of comparison, Stark (1967) estimated the daily production of litter in the Amazon rain forest to be between 7 and 16 g/m^2. Bray and Gorham (1964) state that litter production in the forests of the world generally ranges from 2.5 to 6.8 metric tons/ha/year.

The above are estimates only, and are based on relatively little data. If any of the assumptions are not valid, or if any of the component calculations do not accurately represent the true situation, then the final estimate will be greatly affected. However, it is likely that the values given are reasonable estimates and are adequate for present purposes.

Black-Rush Debris

The black-rush, or *Juncus*, marshes are unimportant producers of debris compared to mangroves. Measurements from aerial photographs reveal that marshes dominated by *Juncus* total approximately 1.5 million square meters (290 acres). This estimate may be conservative since small clumps of *Juncus* often grow beneath mangroves. However, any error is probably compensated for because small mangroves are commonly found growing in *Juncus* marshes.

Production of debris was measured by harvesting four 1/10m^2 marked quadrats in May. Dead and living material was separated and oven-dried for four days at 104° C. The standing crop of each quadrat is given in Table 1.

Table 1. Standing Crop of Juncus roemerianus in May, 1968.

Quadrat #	Dry Weight in Grams Living Tissue	Dead Tissue
1	10.9	89.6
2	20.9	105.0
3	30.4	72.0
4	30.4	73.2
Mean Weight	23.2	84.9

The mean standing crop of dead material was thus 84.9 g/m^2 dry weight. On this basis the total quantity of debris produced annually would be approximately 1,300 metric tons.

The degradation rate of Juncus within the marshes (Figure 12) suggests that 38 percent of the debris produced would be reduced to detritus in twelve months. If this were so, approximately 490 metric tons of debris will be fragmented to the small particulate level in 12 months.

Williams and Murdoch (1968) determined the rates of annual net production and decay of Juncus roemerianus near Beaufort, North Carolina by fitting field data into a compartmental model. They recorded a standing crop of 1,600 g/m^2 and an annual turnover rate of 0.53 for dead material. The productivity of the marshes in North Carolina appears to be much greater than that of the North River.

Sawgrass Debris

Since the North River does not penetrate far into the freshwater sawgrass regions of the Everglades, this species is not considered an important contributor to the detrital 'pool'. No attempt was made to measure the quantity of debris produced by sawgrass, but an approximation can be derived from the findings of Porter (1967). Working in sawgrass areas far to the northeast of the North River, he reported standing crop measurements between 107 and 161 g/m^2 throughout the year. However, two associated species, Muhlenbergia capillaris and Andropogon rhizomatus were together four or five times more important than sawgrass. The standing crop of sawgrass alone varied seasonally from 5 2 to 26 7 g/m^2 dry weight

If it can be assumed that the sawgrass prairie from which the North River rises is similar to the area which Porter (op. cit.) examined, then an estimate of total debris production can be made. The sawgrass area drained by the river system is estimated from aerial photographs to be approximately 411,000 square meters (77.6 acres). Thus, the dry weight of dead sawgrass which might be expected to find its way into the river each year is between 44 and 66 metric tons. This figure is undoubtedly too high since sawgrass in the North River region grows less densely than in the area examined by Porter. Furthermore, little reliance can be placed upon this estimate since it proved impossible to delineate accurately the size of that area of sawgrass savannah which would contribute to the North River as opposed to adjacent watersheds. Consequently, the boundaries used in calculation of the area involved are somewhat arbitrary.

Debris from Other Plants

Stands of hardwoods such as marlberry, Icacorea paniculata, and pigeon plum, Coccoloba diversifola, occupy an estimated 400,000 square meters (75.6 acres), and the potential production from these is unknown. White mangrove is included in the estimates of red mangrove as described earlier.

Fully aquatic plants are apparently of little importance. The bladderwort, Utricularia lutea, grows rapidly in shallow pools during the summer freshwater period, and it certainly provides an additonal source of detrital food for local consumers when it dies. However, its relative contribution to the whole river system must be very small. Production by benthic algae was not measured, and its importance is unknown.

The above account indicates the overwhelming importance of red mangrove as a producer of debris in this area. This species accounts for perhaps 85 percent of all debris produced.

The fate of debris, and the speed with which it enters the detrital 'pool', is largely controlled by local environmental conditions in the area in which it falls or the locality to which it is transported. This will be discussed in the following sections.

DEGRADATION OF DEBRIS

Plant debris can become degraded and enter the detrital 'pool' through the action of several agencies acting singly or in concert. Degradation, as used here, encompasses the terms "decomposition", "decay", and "breakdown" frequently encountered in studies of forest litter. Important mechanisms of degradation include chemical dissolution, autolysis, hydrolysis, oxidation, mechanical attrition and fragmentation, enzymatic lysis by bacteria and fungi, and the activities of scavenging organisms. The roles played by one or several of these in the breakdown of woodland litter has been stressed by many investigators, including Romell (1932), Marten and Pohlman (1942), Shanks and Olson (1961), Witkamp (1963, 1966), Bocock (1964), and Ovington (1965).

The time required for debris to become sufficiently fragmented to be available to deposit feeders and suspension feeders depends largely on the rates at which the above agencies act. The relative importance of these agencies is in turn greatly influenced by the nature and age of the material, and by the environment in which the processes are occurring. To determine the effect of environmental conditions on the mechanisms and rates of degradation of debris, a series of litter bag experiments were conducted. Known weights of red mangrove leaves, red mangrove twigs, white mangrove leaves, Juncus leaves, and sawgrass leaves were subjected to different naturally occurring environmental conditions for over twelve months. The results of these experiments are discussed below.

Red Mangrove Leaves

The degradation rate of leaves is highly variable, and depends not only upon where the leaf falls initially, but also on where it may be transported later. Newly shed leaves may fall directly into the water, in which case they will float for a maximum of six days. During this time they may be carried away and deposited in a different environment. Alternatively, they may fall onto dry ground and remain there for considerable time before rising water levels possibly transport them elsewhere. Attempts were made in this study to investigate breakdown rates in several environments in which magrove leaves might undergo degradation.

Methods. Collections were made of dead, yellowed leaves in which the abscission process was virtually complete. If a leaf detached easily when touched, it was adjudged ready to fall and was included in the sample. Samples, each of approximately 100 grams fresh weight, were then weighed and placed in color-coded nylon mesh bags of 2.5 mm square mesh. The color code of each bag and the weight of its contents was recorded, and all bags were placed in strategic positions in the study area such that their contents would be subjected to a brackish water, a fresh water, or a terrestrial environment.

Additional replicate samples were oven dried at 104° C. until a constant weight was obtained. The relationship between fresh weight and dry weight thus obtained (Appendix II, Table 2) provided a conversion factor (0.316) which was applied to the previously recorded fresh weights of leaves used in the field experiment. To determine the extent of grazing by terrestrial organisms on the leaf before abscission, tracings were made of 100 leaves selected at random. The extent of grazed portions was then measured and expressed as a percentage of total leaf area.

Several bags were retrieved from each locality at monthly intervals. Their contents were carefully washed, excess moisture was removed with blotting paper, and an examination was made to determine the amount of grazing which had occurred since the leaves were placed in the environment. The sample was then dried at 104° C. and weighed. The recorded dry weight of each sample was then compared with its calculated dry weight at the start of the experiment. Selected samples were stored for further analysis to determine caloric content and chemical composition.

Several factors had to be considered in the choice of mesh size to be used. The primary objective was to determine the time required for a population of leaves to break down and enter the detrital system in the form of particles sufficiently small to remain almost permanently in suspension. Observations indicated that a maximum mesh size of 1 mm would approximate the desired conditions; however, the apertures of a small mesh would rapidly become blocked by detrital particles, the flow of water would be restricted, and local anaerobic conditions would develop. The exit of fragmented particles of the leaves would also be prevented. A large mesh (for instance, 1 cm would allow loss of large fragments of leaves, an equally undesirable factor. The compromise of 2.5 mm mesh size finally selected proved adequate in all respects, save that it excluded the larger potential grazing organisms. It proved feasible, by duplicating the experiments with 1.5 cm mesh bags, to investigate the effect of mesh size on the amount of grazing occurring for three or four months until the leaves began to fragment.

Proximate analysis of selected samples was conducted by Law and Co. of Atlanta, Georgia to determine the protein, fat, carbohydrate, crude fiber, and ash content of debris at various stages of degradation. Protein determinations were made by first determining total nitrogen by the Kjeldahl method as specified in the Handbook of The Association of Official Agricultural Chemists. Protein content was then derived by multiplying total nitrogen by 6.25. Additional measurements of total nitrogen were made by the Department of Ecology of the University of Georgia, using a Coleman Nitrogen Analyzer in addition to the Kjeldahl method.

Fat content was determined by the direct 'anhydrous ether' method. Included in this crude fat value are fat, glycerol esters of fatty acids, sterols, chlorophylls, and fatty acids.

Crude fiber included that portion of the leaves which resisted solution when boiled in dilute sulphuric acid followed by dilute sodium hydroxide. It includes cellulose and other relatively insoluble carbohydrates. Ash and moisture content were determined as specified by A.O.A.C.

Nitrogen-free extract (NFE) was derived by subtracting the accumulated percentages of all other components from 100 percent. NFE reputedly includes sugars, starches, soluble portions of complex carbohydrates, and some lignin.

Determinations of caloric content were made by the Department of Ecology of the University of Georgia, using the Paar Adiabatic Bomb Calorimeter.

Results. No accessible regions of the river remained brackish or completely fresh during the entire period of the study; hence, Stations A, B, and C (see Figure 1) were used to exemplify environments as widely divergent as possible. As will be seen from Figure 2, Station A experienced higher salinities for longer periods than Stations B and C, although freshwater conditions actually existed in the estuary (Station A) for a five-month period. Water at Stations B and C reached maximum salinities of 22.6 and 12.9 parts per thousand respectively.

Station B was originally chosen as a "freshwater" location, and Station C as a test site for degradation under "dry" conditions. However, as the salinity at B rose steadily through March and April litter bags were transferred from this site to the river adjacent to Station C where salt water penetration was less.

As Figure 7 shows, a rapid loss in weight occurred during the first month at all three locations. Most of this is probably accounted for by the leaching of water-soluble organics, simple sugars, starches, and organic acids, many of which are liberated during autolysis. Nykvist (1959) found that 22 percent of the original dry weight of leaves of the ash (Fraxinus excelsior) was leached out during the first few days in water. Broadfoot and Pierre (1939) similarly comment that the content of water soluble material in woodland litter correlates well with decomposition rates during early breakdown, but becomes less important as decomposition proceeds. Initial weight loss from mangrove leaves in the terrestrial environment was less than that from submerged leaves; but periodic tidal submergence during October when the general water level was high was evidently sufficient to remove many water soluble materials.

From this point, weight loss proceeded steadily but at different rates in all three locations. The reasons for this divergence of degradation rates must now be examined.

The temperature of the environment might be expected to affect degradation rates through its influence on the rates of chemical reactions, the activity of enzymes, and the metabolism of organisms. Kormondy (1968) found that the highest losses from plates of pure alpha-cellulose occurred when temperatures were between 25 and 26° C., which is the optimal range of mesophilic cellulolytic bacteria. The effect of an 8-10° C. temperature difference on submerged leaf debris is noticeable when weight loss in

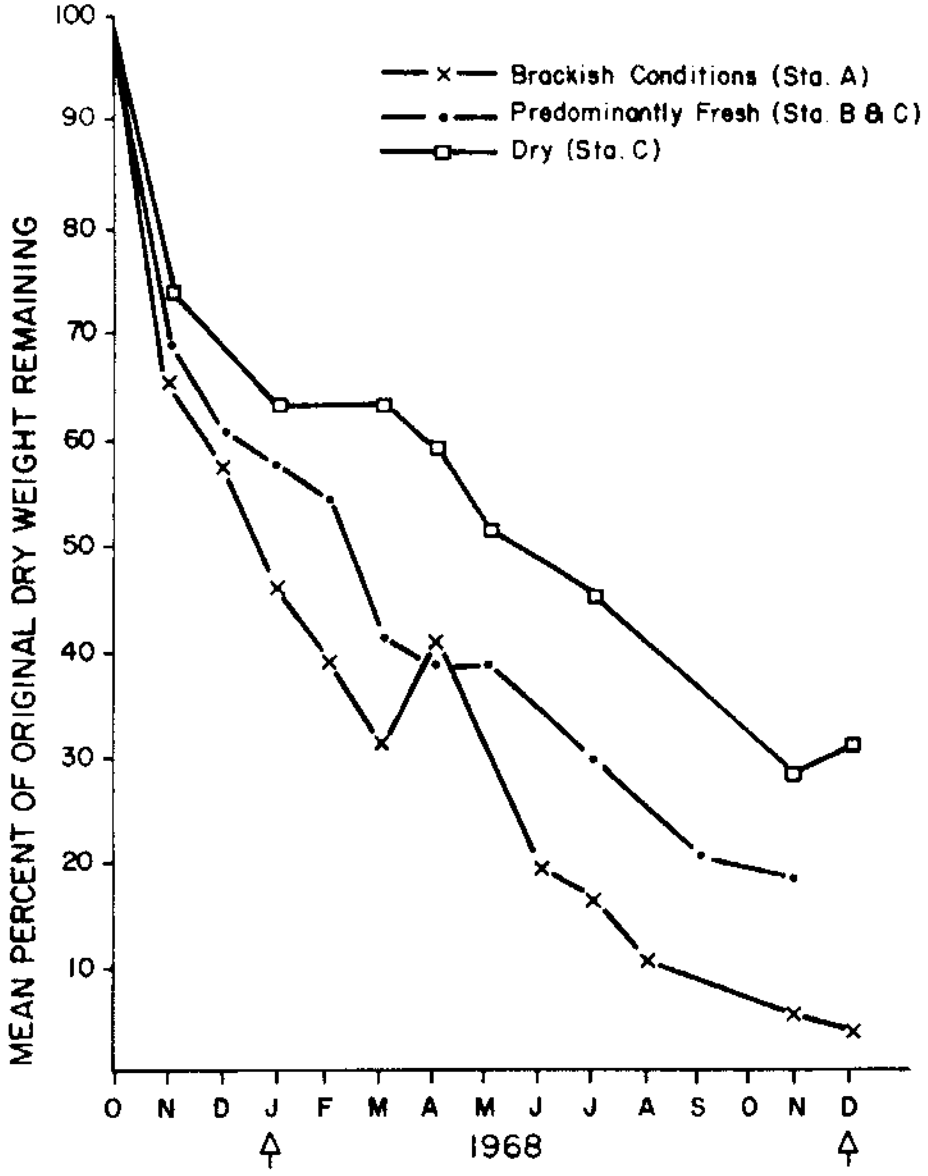

Figure 7. Degradation rates of red mangrove leaves under different environmental conditions. Relevant data are given in Appendix II, Table 4.

"fresh" water during the first six months of breakdown in winter is compared with a similar situation in summer (Figure 8). After three months the difference in weight loss in the two situations was almost 18 percent. After five months, however, there was no longer an obvious difference in weight loss.

The decreased "summer" degradation rate observed between September and November, and the increased "winter" rate between February and April, could possibly have been caused by temperature changes recorded in these months. However, the increased "winter" degradation rate occurred during a time when salinity was rising from 12 to 18 parts per thousand. Consequently, the effect of temperature could not be dissociated from the concomitant influence of salinity. Reference to Figure 7 shows that when samples of leaves were subjected to different salinities at almost identical temperatures (at Stations A and B), the greater long-term degradation rate was associated with the higher salinity environment.

To investigate the effect of increased salinity, several samples of leaves were placed in normal seawater. Weight loss was very rapid; only nine percent of the original dry weight remained after four months (Figure 9). By comparison, 39 and 54 percent remained at the end of a similar period in brackish and freshwater conditions respectively.

The rapid weight loss in normal seawater was a result of heavy "grazing", mainly by amphipods. Numerous specimens of Melita nitida (Melitidae) were found living between individual leaves. The same species was also present, though less commonly, on leaf samples retrieved from brackish water. A second, smaller species, Corophium lacustre (Corophidae), occurred in large numbers on leaves in fresh and slightly brackish water, and may have been responsible for considerable weight loss from these leaves. Thus, it is apparent that the observed effect of salinity on

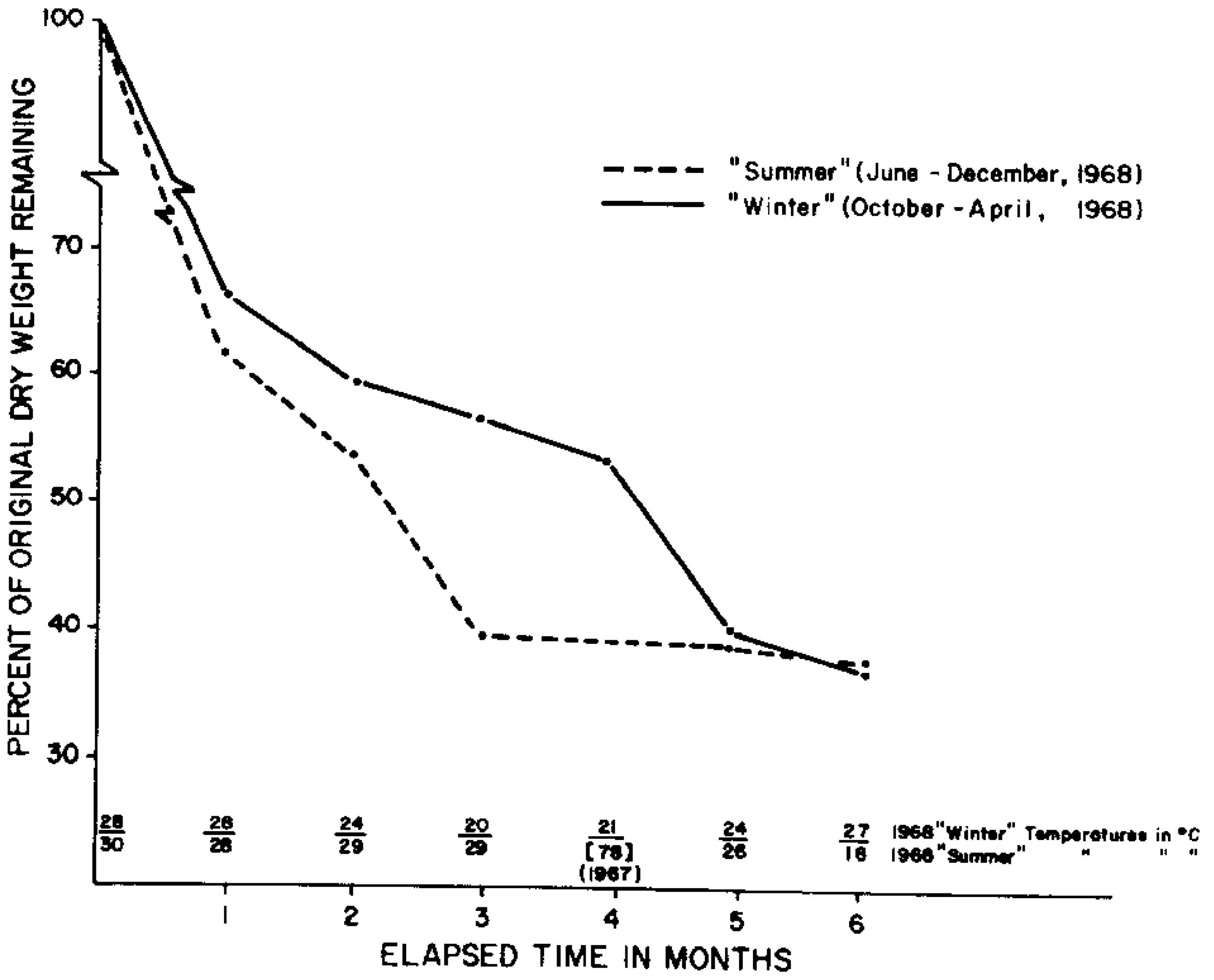

Figure 8. Effect of temperature on the degradation rate of red mangrove leaves.

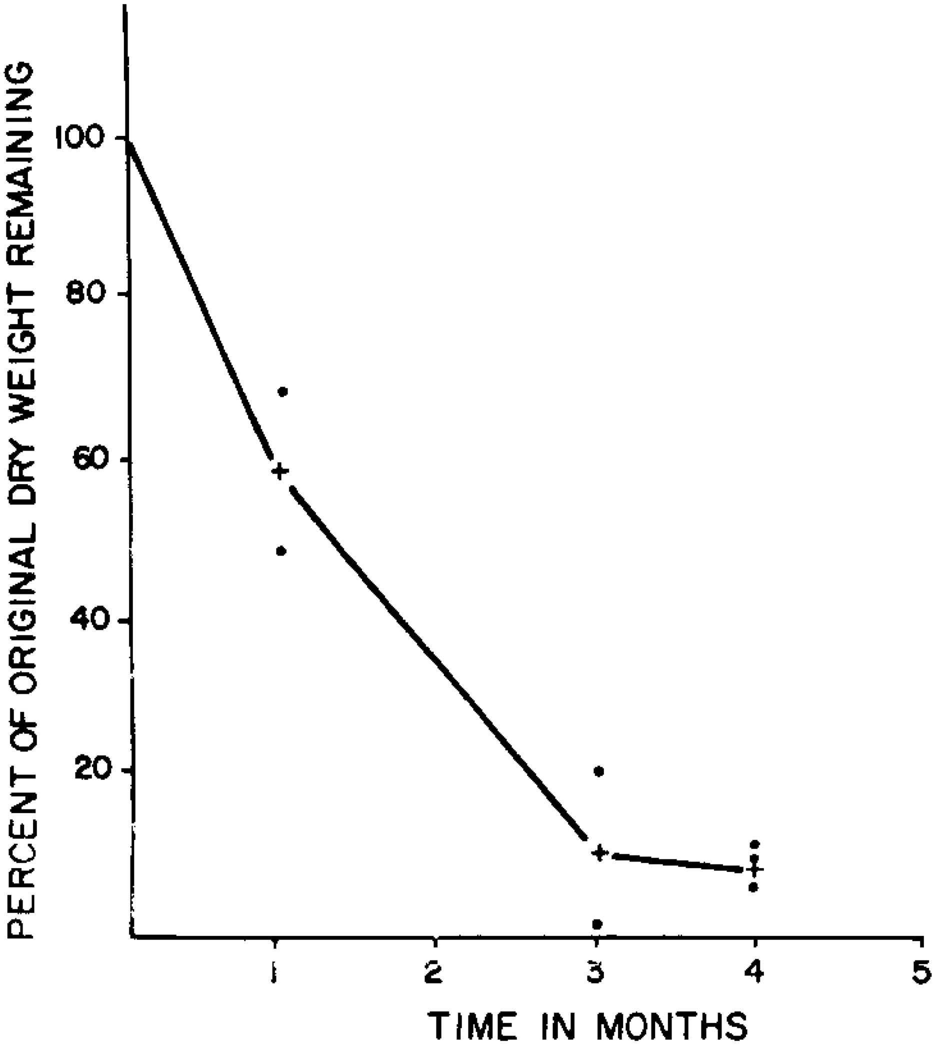

Figure 9. Degradation rate of red mangrove leaves in normal seawater.

degradation rates is in part a reflection of its influence on the abundance and species composition of amphipod populations. The xanthid crab, *Rithropanopeus harrisii*, and the polychaetes, *Eunice rubra* and *Haploscoloplos fragilis*, frequently found in association with leaf debris in brackish water, probably play relatively minor roles as consumers of leaf material. The mangrove coffee snail, *Melampus coffeus*, was never observed during the course of the study.

Red mangrove leaves are not heavily grazed while alive. Careful examination revealed that an average of only 5.1 percent of the leaf was consumed by terrestrial organisms (see Appendix II, Table 2). Several species of aphids appeared to be the major feeders on green leaves.

As Figure 10 shows, leaves lying in brackish water are "grazed" far more heavily than leaves in freshwater or dry conditions. To determine the amount of grazing which had occurred since the start of the experiment, the "mean grazing value" (5.1 percent) of newly-shed leaves was subtracted from the "grazing value" obtained from each monthly sample. After eight months the individual leaves had become so fragmented that accurate determination of losses due to grazing was no longer possible.

Leaves placed in brackish water in 1.5 cm mesh bags revealed no significant increase in grazing rate over a five month period. Evidently the 2.5 mm mesh used in most of the experiments did not exclude many large potential consumers.

In subaerial conditions the amount of grazing increased steadily to 8.8 percent after seven months. This is low when compared with the findings of Bocock (1964), who reported that earthworms and millipedes removed 40 percent of the dry weight of *Fraxinus* litter in the first five months. As earthworms apparently do not occur in the peat soils of the North River, a much lower rate of litter removal is to be expected. Small

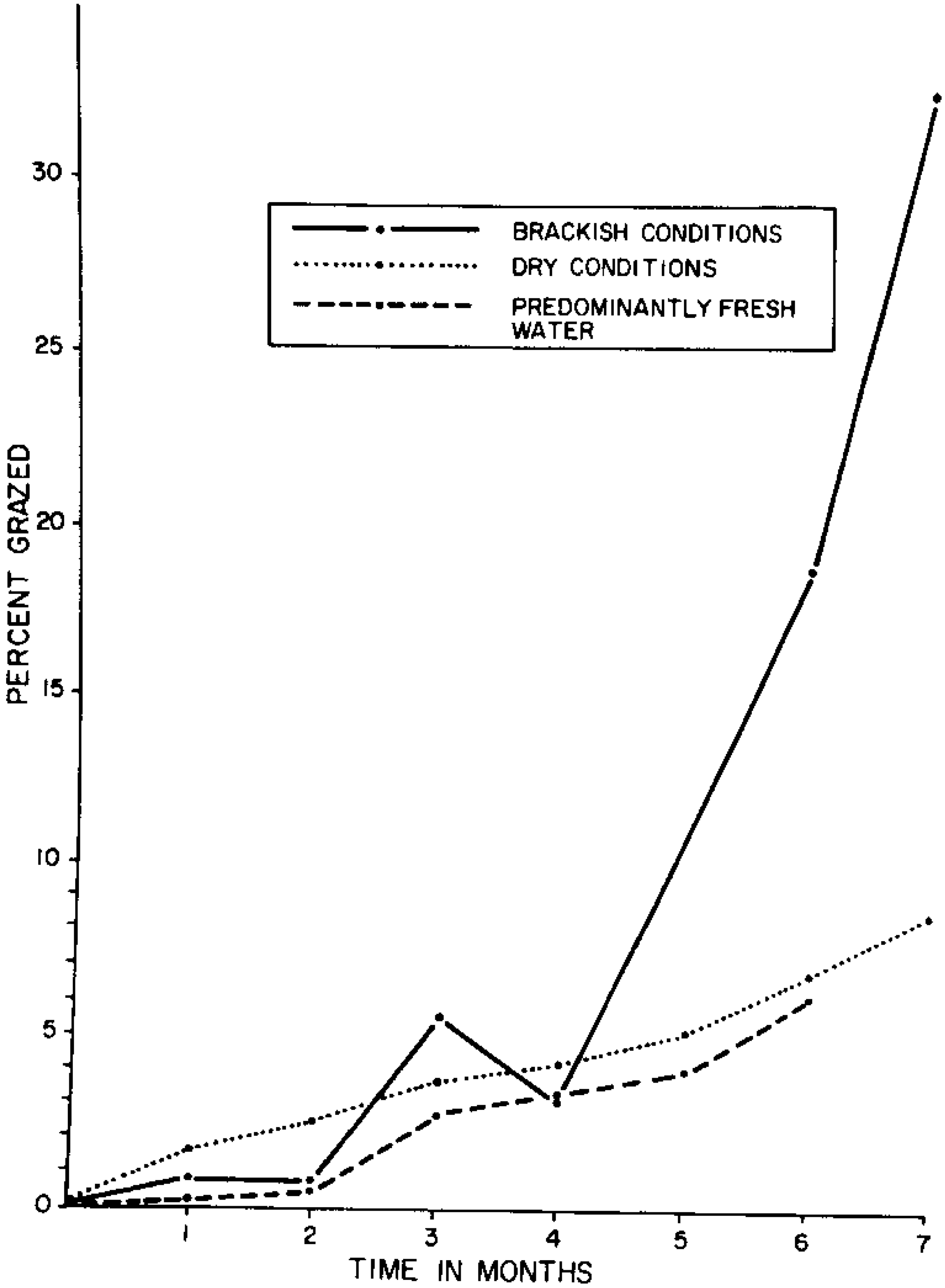

Figure 10. Grazing of red mangrove leaves during degradation in three environments.

millipedes, however, were found beneath fallen branches and were probably responsible for much of the observed grazing.

Grazing of submerged leaves was negligible for the first two months, during which time few amphipods were observed in the litter bags. Wundsch (1922) similarly observed that Gammarus pulex will feed on dead leaves in preference to fresh ones. The cause of this apparent avoidance of fresh debris has not been determined; however, several possibilities should be considered.

As mangroves were formerly an important commercial source of tannin, used as a fiber preservative because of its effective antibiotic qualities, the most obvious explanation is one of direct inhibition. According to Bocock (1964), tannins and other free phenolics may influence the palatability of leaf litter to scavenging organisms. The inhibitory nature of Sargassum tannin was demonstrated by Sieburth and Conover (1965). They found that Pseudomonas was inhibited by Sargassum extracts in concentrations in excess of 1 in 500, and nematodes, pycnogonids, and copepods were inhibited or repelled by concentrations greater than 1 in 125.

Eventually much of the tannin found in mangroves will leach out or become diluted, and it may be postulated that consumer organisms such as amphipods then begin to utilize the leaf material. Coulson et al. (1960) reported that phenolics are present in negligible quantities in older litter. An attempt was made in the present study to measure the tannin content of shed leaves at different ages, but the colorimetric method adopted was unsuccessful.

Red mangrove leaves possess a heavy epicuticular wax layer which may protect the leaf from attack for a considerable period after abscission. Eglinton and Hamilton (1967) comment that such waxes may confer resistance to fungal, bacterial, and insect attack. It is possible that grazers such as amphipods are unable to bite or tear off fragments of the leaf until the epicuticle begins to disintegrate.

Perhaps the most likely explanation, however, is that the newly-shed leaves do not constitute a favorable nutrient source for amphipods and other grazers. The epicuticular waxes mentioned earlier may not prevent colonization of the leaf surfaces by micro-organisms, but they could hinder actual penetration of the epidermal layers by fungal spores, as suggested by Siu and Reese (1953). In addition, high initial concentrations of tannins may inhibit rapid growth of bacteria and fungi As will be seen later, surficial and intercellular fungi became increasingly numerous as the leaf aged.

Thus, it is possible that potential consumers, presented with an abundance of available food in the form of "aged" leaves rich in bacterial and fungal protein, select these in preference to newly-shed leaves less rich in protein.

Whatever the reason for the two month delay in the onset of heavy grazing, the amphipods, Melita nitida and Corophium lacustre, which seem to be restricted to salinities above seven or eight parts per thousand, were responsible for most of the heavy grazing observed in brackish conditions. Since almost 33 percent of the leaf sample was removed by grazing in the first eight months, and the total weight loss from the sample in this period was approximately 82 percent, the "scavenger" grazing pathway is obviously an important mechanism by which mangrove debris is incorporated into the food chain.

Debris ingested by amphipods is rapidly reduced to particulate detritus in the form of fecal material which contains fragments of the original plant tissue Alternatively, if the amphipod is eaten by a predator, contribution is made to the energy budget of the next higher trophic level. Thus, by way of the amphipod and xanthid crab populations, debris is either converted directly to animal protein or is reduced to particulate detritus. Detrital material so produced is then available to suspension and deposit feeders. This dual role of amphipods as key converters in the ecosystem will be discussed in greater detail later.

It is obvious that the speed with which mangrove leaf debris is reduced to the size at which suspension feeders are able to utilize it, or is converted to animal protein by the grazing activities of macroconsumers, is influenced by its environment. A leaf may not remain in the same place for long periods. A newly-shed leaf floats for four or five days, during which it could be transported far. It then sinks, and transport is much slower. There are many quiet water areas where leaves accumulate, but these are usually flushed out as the summer rains begin to influence the system.

Although it could not have been discerned at the start of the study, the closest approximation of natural degradation rates would have been obtained by initiating the experiments in June or July when leaf fall was greatest. Initial autolysis, hydrolysis, and microbial activity could then have proceeded under summer temperatures instead of the lower autumn and winter temperatures. The leaves would perhaps then be more susceptible to attack by marine grazing organisms entering the estuary as the isohalines proceeded inland from October onward. Under these circumstances it could be postulated that virtually all leaf debris formed in June and July would have disappeared within twelve months. Only that small portion which fell on dry ground and was not subsequently swept into the water would remain in quantity after one year.

White Mangrove Leaves

The breakdown rate of white mangrove leaves under subaerial conditions was determined in the same manner as described for red mangrove Experiments were not conducted on submerged leaves since they do not occur commonly in this flooded environment

Figure 11 compares weight loss from samples of white and red mangrove leaves under similar conditions. Little difference was observed in the decomposition rates of the two species although red mangrove leaves appeared to break down slightly more rapidly. Approximately 42 percent of the original dry weight of white mangrove leaves remained after twelve months Grazing rates were not measured.

Black-Rush Debris

After reaching mature height, Juncus culms, which grow from perennial rhizomes, persist green and alive for about two months, then slowly die The pulmonate snail, Cecithridea costata, is one of the few grazers of live Juncus culms Consequently, large quantities of plant material remain available for degradation. For some time after death the dry material remains standing, during which time the action of micro-organisms on the almost continuously damp bases of the stems causes a weakening of these regions Eventually the leaf falls to the ground and further breakdown occurs

Initial breakdown takes place mainly in the Juncus marsh areas themselves since there is little or no communication between the marshes and the main stream system during the long dry season. The marshes become flooded during the summer, and accumulated dead Juncus culms in various stages of breakdown are carried into the river system in the autumn months when water levels begin to recede.

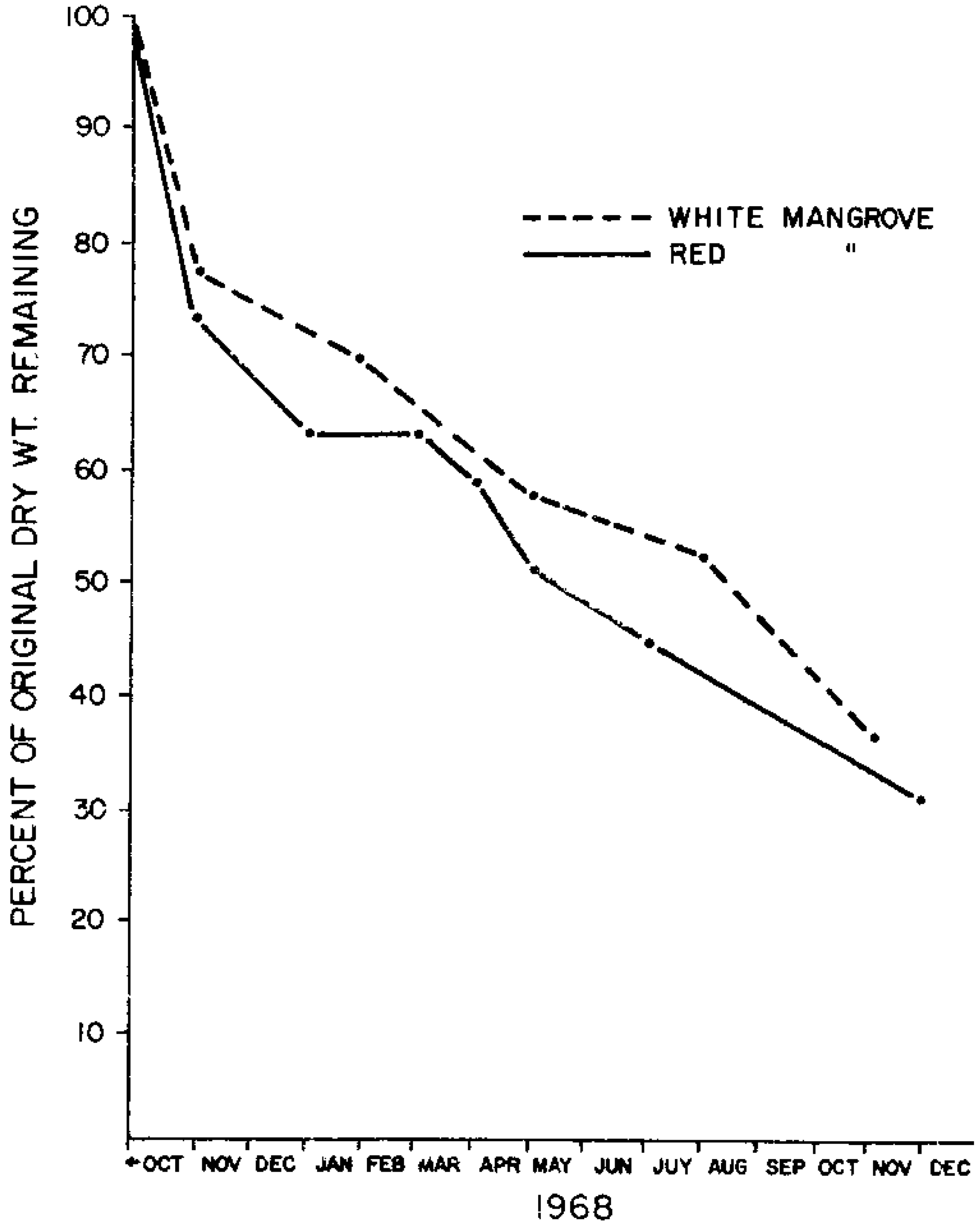

Figure 11. Comparison of the degradation rates of red mangrove and white mangrove leaves under dry conditions.

To determine the degradation rate in situ, known weights of Juncus were placed in mesh bags in the marsh adjacent to Station B. The procedure was identical to that described for red mangrove leaves except that 1 5 mm mesh was used to contain the thin Juncus leaves. The bags were tied to stakes so that they lay on the mud surface.

Breakdown is slow; only 35 to 45 percent of the original weight was lost in 13 months (Figure 12). As will be seen later, dead material about to fall contained 42 percent by weight of crude fiber (Appendix II, Table 3) and had low amounts of soluble carbohydrates. Consequently, little initial leaching occurred. Anaerobic (or at least low oxygen) conditions evidently prevailed at the mud surface at some time during the study period since the action of hydrogen sulfide was discernable on the paint used for color-coding Decomposition rates are usually slower under anaerobic conditions than when oxygen levels are high.

The curve of weight loss steepens after July or August, suggesting that degradation was more rapid from this point. But the change of slope was probably much less rapid than indicated in Figure 12 since a single sample only was retrieved in August, and the two samples representing September show much divergence. The line depicting observed relative water level indicates that the more rapid breakdown rate occurred toward the end of the summer hydroperiod and thereafter. Continual submergence of the material during the summer months perhaps removed less soluble celluloses and hemicelluloses, or rendered such compounds more vulnerable to microbial attack. Forty-eight percent of the original weight of a sample placed in open water at Station B was lost in thirteen months. This suggests that degradation rates under conditions of continuous submergence would be slightly more rapid than in the marsh itself.

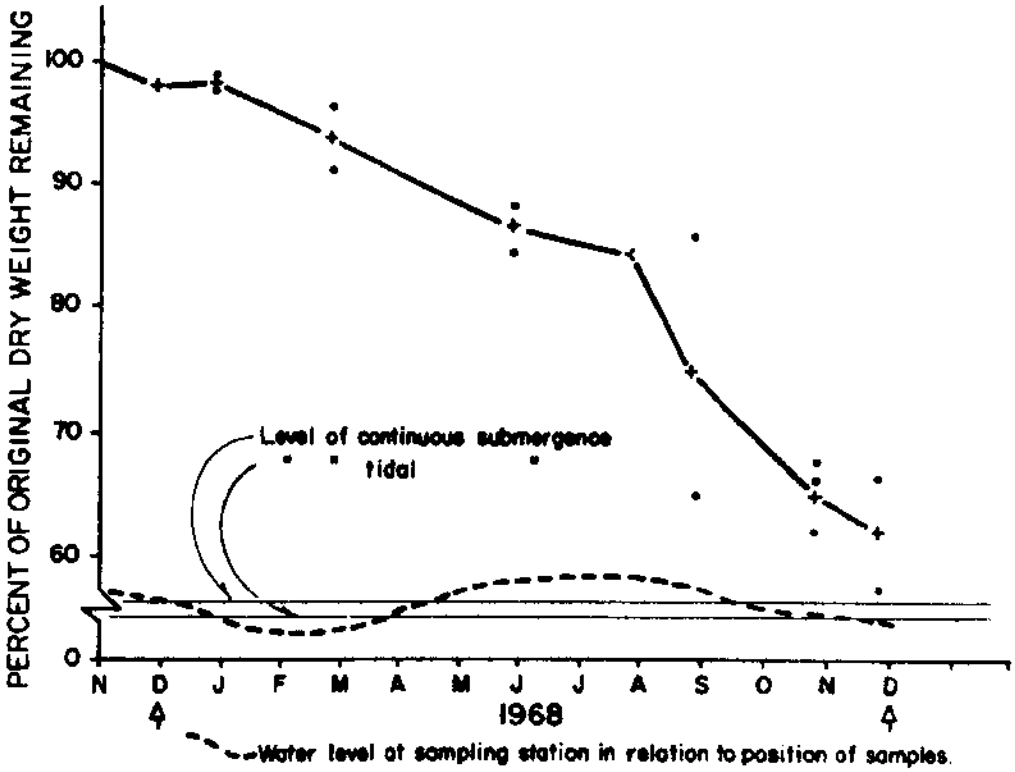

Figure 12. Degradation rate of Juncus.

No evidence of grazing during breakdown was apparent. However, the small mesh used may have excluded many potential grazing organisms. Latter and Cragg (1967) found nematodes and Enchytraidae in association with decaying Juncus squarrosus. They recorded weight losses of 20 to 25 percent in twelve months in an English moorland environment

The slow degradation rate found in the present study will result in considerable carry-over of material from one year to the next This supports the statement of Craighead (MS.) that there is a gradual build-up of sediments (peats) in these areas.

Comparison of Sawgrass, Juncus, and Red Mangrove Debris

Sawgrass leaves, like those of Juncus, remain affixed to the plant for some time after death They eventually fall and begin to degrade in a predominantly damp, subaerial environment. The degradation rate of sawgrass leaves under these conditions was measured using 2 5 mm mesh bags.

The degradation curve of sawgrass leaves indicated little initial leaching effect and was intermediate between those of Juncus and red mangrove under similar conditions (Figure 13). Weight losses from samples of Juncus, sawgrass, and red mangrove in a twelve month period were approximately 35 percent, 45 percent, and 60 percent respectively The degradation rates of sawgrass and mangrove leaves are actually very similar if differences in the first month's weight loss are discounted

The relatively high (42 percent) crude fiber content of fresh Juncus debris in comparison with that of sawgrass (32 percent) and red mangrove (22 percent) is reflected in the slower decomposition rate of Juncus. Burkholder and Bornside (1957) also commented that the crude fiber fraction of Spartina alterniflora is utilized only slowly by heterotrophic bacteria. Alexander (1961) points out that lignins (which account for 5 to 30 percent

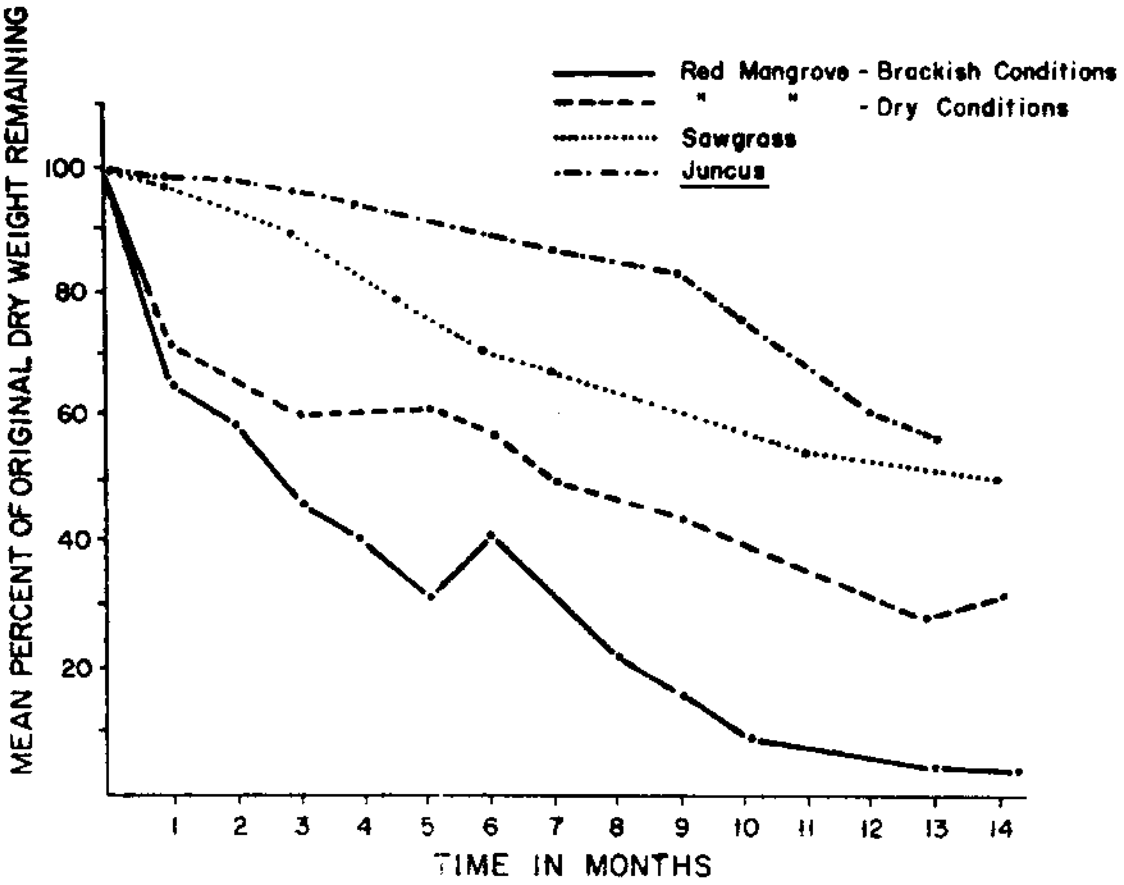

Figure 13. Comparison of the degradation rates of red mangrove, sawgrass, and *Juncus* debris.

of plant constituents) probably have more influence on the decomposition rate of litter than does nitrogen content.

Red Mangrove Twigs

Easily detached twigs were placed in 2.5 mm mesh bags and submerged at Station C.

Weight loss was very slow and seemed to be attributable mainly to the fragmentation and subsequent loss of bark. Weight loss after six months was only seven percent, and only thirteen percent was lost after thirteen months. Small burrowing isopods (Limnora sp.) were found occasionally beneath the bark, but little evidence of utilization was apparent. However, other large pieces of mangrove were often found to be almost hollowed out by boring isopods, suggesting that as dead wood ages it presents a more favorable habitat. Schafer and Lane (1957) found that wood is largely ignored by the boring isopod, Limnoria tripunctata, until it acquires an associated fungal flora. This isopod could not survive on sterile wood but thrived on pure cultures of the fungi normally associated with wood in the marine environment.

The Nutritive Role of Debris

Dead mangrove leaves were heavily grazed by estuarine organisms even during the first eight months of the transition period from debris to particulate detritus. Sawgrass and Juncus debris appeared to be little utilized, possibly because these materials are less easily accessible to estuarine benthos.

The proximate analyses detailed in Appendix II, Table 3 illustrate changes in the constituency of debris as it degrades, and furnish an indication of its relative nutrient value at successive stages. Changes in the chemical composition of red mangrove leaves during breakdown are discussed below. All percentages mentioned are on a dry weight basis. The reader is referred to the appendix for comparative percentages in terms of ash-free dry weight.

An actively photosynthesizing leaf was found to consist of 6.1 percent protein, 1.2 percent fat, 15.7 percent crude fiber, 9.2 percent ash, and 67.8 percent "carbohydrate". Mobilization and withdrawal of proteins and some soluble carbohydrates during the processes leading to abscission resulted in decreased protein (3.1 percent) and carbohydrate (59.6 percent) immediately before leaf fall. Fats were apparently not mobilized since the fat content of a yellowed leaf increased to 6.3 percent. A relatively greater percentage of crude fiber also remained as a consequence of the withdrawal of protein and carbohydrates.

Changes in the relative chemical composition of mangrove leaves undergoing breakdown in brackish water for a period of twelve months are depicted in Figure 14. The large apparent increase in protein content during the first month is obviously a reflection of a concomitant ten percent loss in carbohydrates during the initial leaching process. The small decrease in fat content may not be meaningful, or it may represent the beginnings of disintegration of the wax cuticle. However, the slow but steady decline in fat content from an initial 6.3 percent to 1.5 percent after twelve months is probably a result of fragmentation of the cuticle and microbial utilization of cellular fats.

A steady increase in protein content was recorded over the twelve month period. Eventually almost 22 percent of the debris remaining was composed of protein. Carbohydrate content fell to 36 percent during the first six months as microbial action produced further water-solubles, and increased slightly thereafter. This increase is probably a reflection

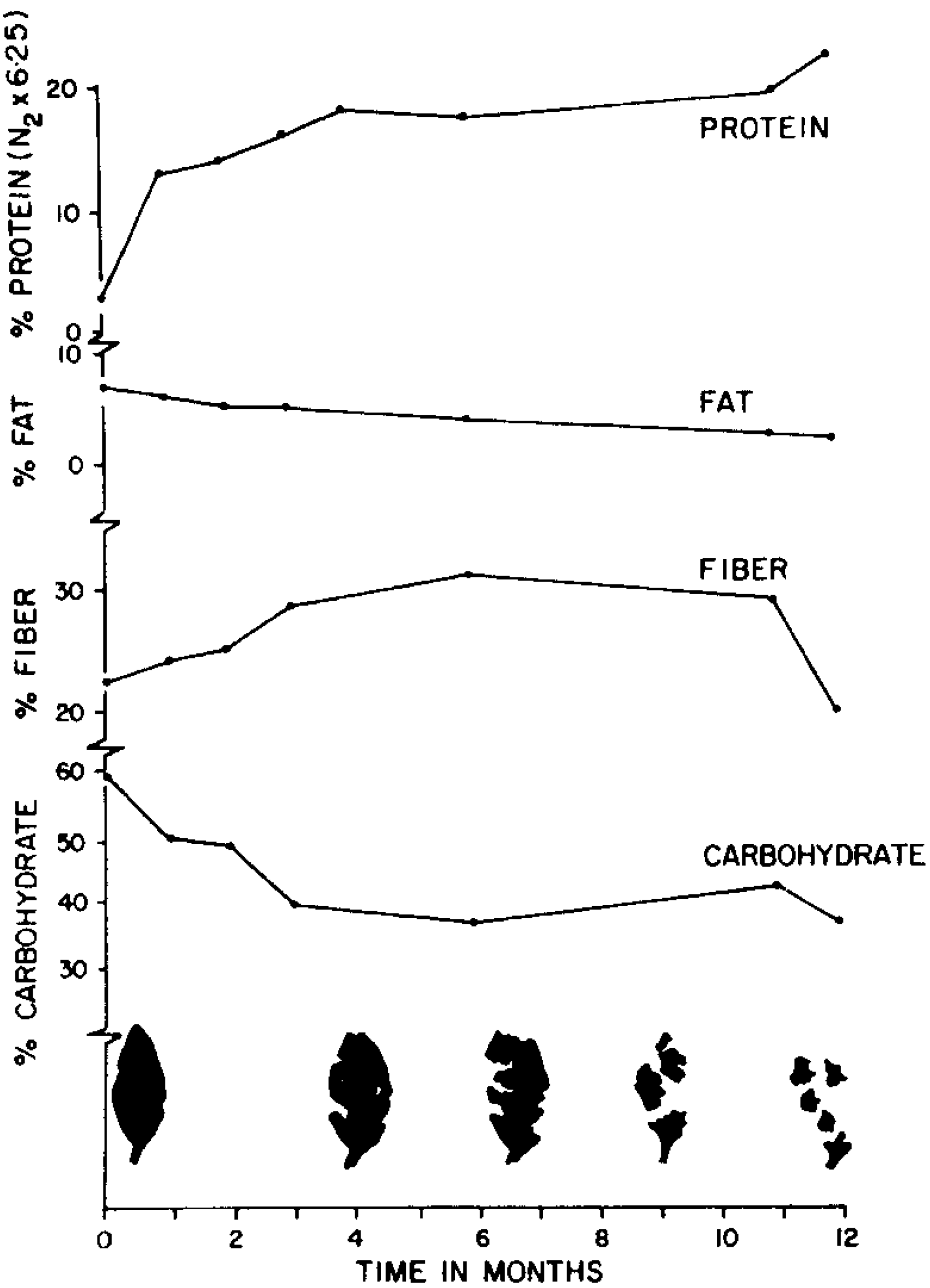

Figure 14. Chemical composition of red mangrove leaves during degradation in brackish conditions.

of the loss of crude fiber when the leaves began to fragment during the latter half of the experiment.

Examination of the caloric content (see Appendix) reveals that after an initial increase from 4.8 Cal/g dry weight in yellowed leaves to 5.1 Cal/g after two months in the water, total energy content decreased to 4.4 Cal/g after six months. This is probably largely due to the 50 percent decline in fat content over the same period since extracted fats were shown to contain approximately 9.7 Cal/g. Bocock (1964) similarly found that the caloric content of *Fraxinus excelsior* increased from 4.5 to 4.9 Cal/g in five months and then fell to 4.25 Cal/g in twelve months. Caloric content, however, does not necessarily indicate energy actually available to consumers. An unknown proportion is in the form of compounds such as waxes and celluloses which are not easily assimilated by most organisms.

If it can be assumed that the experimentally determined nitrogen value is an accurate indication of easily available protein, and if protein content is accepted as an indicator of the nutrient value of a food source, then the value of mangrove leaf debris increases as the material "ages". The original plant protein will be lost gradually during the process of degradation, but it is conceivable that this loss will be more than compensated by increases in the amount of fungal and bacterial protein as microbial colonization proceeds. The concept is depicted in Figure 15.

It was not possible to demonstrate an actual increase in protein with the information available. The data show, however, that a consumer organism will obtain relatively more protein from leaf remains which are twelve months old than from those which have been in the water for only one or two months. Kaushik and Hynes (1968) demonstrated an increase in the percentage of protein during breakdown of elm leaves but could not determine whether or not this indicated a 'real increase in nitrogen'.

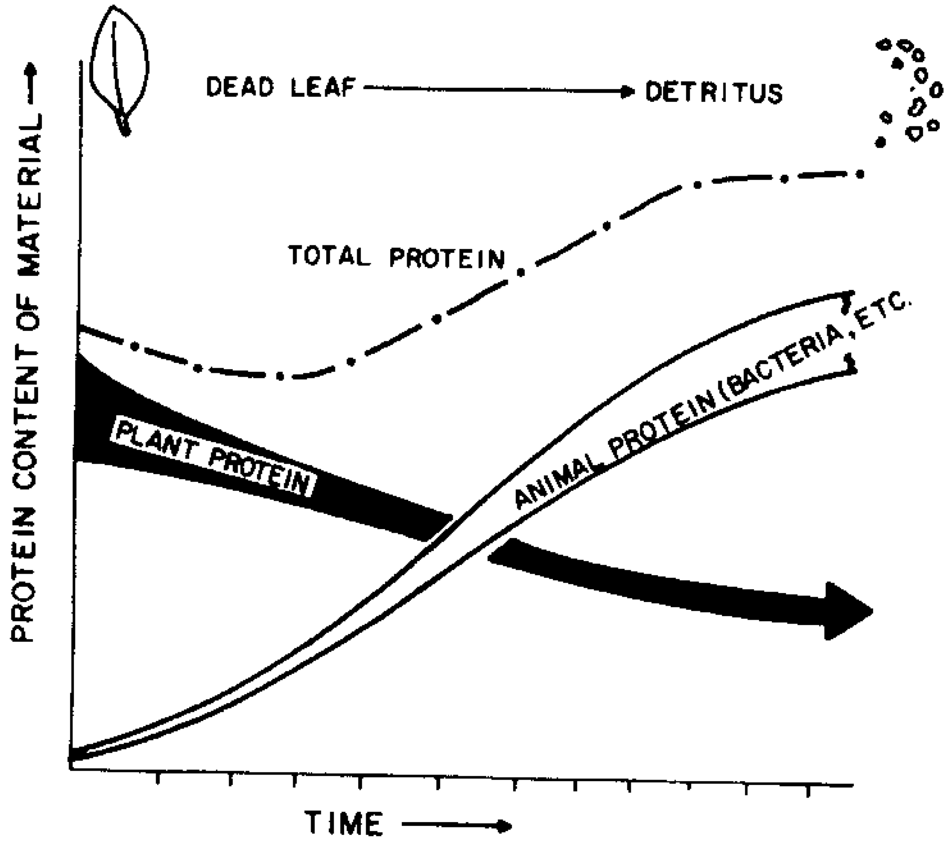

Figure 15. Diagrammatic representation of the principle of protein enrichment of red mangrove debris during degradation.

They also found that the increased percentage of protein was not related to increases in the bacterial population but was associated with increased growth of fungi.

Examination of mangrove leaves during decomposition in brackish water revealed that several species of fungi occur on the leaf surfaces during the first two months. *Fusarium* sp., *Nigrospora* sp., *Dendryphaiella* spp., *Cladosporium* spp., *Alternaria* sp., *Phomopsis* sp., and *Mucor* sp. all occurred commonly. After four or five months fungal colonization was extensive, and hyphae were observed within the leaf. Surface sterilization and plate culture techniques performed by Mr. M. Masters, Institute of Marine Sciences, demonstrated that all the above species were still present and were now growing within the leaf itself. In addition, *Pestalotia* sp. and *Stemphylium* sp. were isolated from leaves after surface sterilization.

The bacteria were regularly represented by several recognizable bacilli and diplococci. No attempt was made to isolate and culture these.

As its populations of fungi and bacteria increase, the leaf debris acquires a faunal complex of Protozoa, nematodes, and rotifers. Large numbers of *Uronema marina*, *Euplotes moebiusi*, and *Holosticha* sp. (Hypotrichida and *Vorticella* sp. (Peritrichida) were observed in five month old leaves. *Uronema*, *Euplotes*, and *Holosticha* all enter the cells of leaves to feed on bacteria once the cell wall becomes ruptured. Small rhabditid nematodes which are known to feed on fungi (Cefalu, pers. comm.) were also found in quantity.

The role played by micro-organisms in the breakdown of leaves and the re-cycling of nutrients from litter in terrestrial environments has been studied in detail by many workers. Marten and Pohlman (1942) investigated the relationship between bacterial and fungal growth and the decay rate of litter, and Witkamp (1963) was able to correlate the decay rate to several types of litter with abundance of bacteria and fungi. Effective correlation between breakdown rate and microbial activity is difficult to demonstrate. As Witkamp (1966) suggests, for prediction of decay rates a model for carbon dioxide evolution is desirable. Such a model cannot be accurately quantified at present.

Birch and Clark (1953) point out that a succession of micro-organisms obtain nutrition from, or are associated with, plant litter. Only a portion of these are able to utilize the litter at any specific stage during its breakdown, and the activities of each successional type make colonization possible by later arrivals.

There is much speculation as to the nature of the relationship between micro-organisms and debris or detritus. To what extent do micro-organisms depend on these materials as a nutrient source? As Johannes (1968) comments, bacteria may often derive much nutrient from an organic substrate, supplementing this by assimilation of dissolved inorganic nutrients, such as nitrogen and phosphorus, from the environment. Bacteria are rather specific in their substrate-reducing capabilities. Rodina (1964) points out that the processes of 'decay, oxidation, and reduction' are caused by different physiological groups of bacteria, and very few materials exist which cannot be utilized by some species or strain of bacterium. The fungi appear to be equally diverse in their activities and, unlike most bacteria, are often able to utilize ligneous matter. The microbial populations of leaf litter thus undoubtedly use their substrate as a nutrient source. On the other hand, particulate, suspended detritus, presumably having lost most of its original nutritional value, probably serves mainly as a physical substrate. Labile organics in the surrounding water provide the required nutrients in this case.

The decomposing leaf with its associated microbiota constitutes an important energy source for consumer organisms such as the amphipods already mentioned. Hynes (1954) found that Gammarus duebeni and G. pulex consume large amounts of vegetable matter. Between 40 and 75 percent of their food was vegetable material, mostly plant vascular tissue. Kaushik and Hynes (1968) consider that in view of the relatively high protein content of newly-fallen leaves consumers may be obtaining mainly plant protein at this stage. However, as fungi and bacteria increase in numbers they will inevitably assume an increasingly important nutritional role.

Several species of amphipods have been reared in the laboratory using leaf material as a food source. Sexton (1928) reared Gammarus on dead elm leaves, and Kaushik and Hynes (1968) successfully maintained Hyalella azteca on elm leaves. The adequacy of oak leaf litter as a food source was demonstrated by McConnell (1968), who kept the freshwater snail, Helisoma, on extracts of litter.

It is not known if a consumer, such as an amphipod, gains nutrients from plant debris itself or from associated microbiota. Experiments by Seki et al. (1968) showed that Artemia was unable to survive on detritus until an inoculum of Pseudomonas had converted the detrital biomass into bacterial biomass. Rodina (1964) demonstrated that Daphnia magna could be sustained on artificially sterile detritus, but would not develop and reproduce. He concluded that bacteria probably provide essential amino acids and vitamins. In this context, Starr (1956) found that vitamin B_{12}, produced as a result of the activities of micro-organisms, occurs in significantly greater concentrations at the heads of streams in the Spartina marshes of Sapelo Island, Georgia, than in the open sounds. It would seem then that micro-organisms associated with leaf litter contribute to the diet of scavengers, which may ingest them accidentally or intentionally.

The above discussion has been based primarily upon the potential nutrient value of red mangrove leaves. The same arguments can be applied to Juncus and sawgrass leaves as they degrade. However, increase in protein content with age was not as noticeable in either species as in red mangrove (see Appendix II).

During eleven months the protein content of sawgrass debris increased from 5.3 to 10.3 percent. Fat content remained at approximately one percent, carbohydrate content at approximately 59 percent, and the percentage of crude fiber fell from 32 to 25 percent. Caloric content in the first six months declined by 100 calories from an initial 4.615 Cal/g.

The percentage of protein in Juncus debris rose from 3.7 to 7.4 in ten months, during which time a slight decline in fat (1.5 to 1.1 percent) and a relative gain of carbohydrate (from 51 to 55 percent) was recorded. The caloric content of dead Juncus was not determined. However, comparison of the energy value of live Juncus (4.723 Cal/g) with that of debris after five months (4.039 Cal/g) indicates considerable loss of high caloric material.

The high fiber content and the comparatively low rate of protein enrichment during at least the first year of degradation may largely explain the observed lack of grazing. If the debris does not provide a favorable substrate for micro-organisms, potential consumers may tend to ignore it. Detailed investigations of the microbial populations of Juncus and sawgrass debris were not attempted in the present study. It is probable that careful investigation would have revealed larger numbers of micro-organisms. Latter and Cragg (1967) reported a fungal succession on debris of Juncus squarrosus in England. They observed that Sphaeropsidales and Ascomycetes were followed by Hyphomycetes such as Penicillium and Trichoderma. These were in turn succeeded by Mortierella and Mucor

(Phycomycetes). Considering the biomass associated with the litter, they recorded, in order of importance, bacteria, small scavengers, Protozoa, and fungi.

SUSPENDED DETRITUS

The quantity and the nature of suspended detritus in the North River could be expected to vary in response to seasonal changes in water levels, and should reflect the availability of allochthonous plant debris of several origins. A sampling program was designed to determine secular variations in the quantity, composition, and size distribution of suspended detritus, and to provide an estimate of the total export of detritus from the river system. The samples also provided material for proximate analysis, caloric determinations, and the measurement of metabolic activity.

Methods

Field Sampling Methods. Single monthly samples were taken at two locations (A and C) as shown in Figure 1. Station A was chosen as a representative estuarine location, while Station C, near the headwaters of the river, was selected in the expectation that any increase in the contribution of sawgrass to the detrital load would be more easily detected at a point close to its origin.

Suspended detritus was collected by pumping a known volume of water, usually about 1,000 liters, through a sieve of 50 microns mesh. The residue was then resuspended in a small volume of pre-filtered river water and transported to the laboratory for further analysis. The sample was taken on an ebb tide at a depth of 0.5 meter in the same location each month. Preliminary sampling revealed no quantitative or qualitative differences between samples taken at 0.5 meter and those taken just above the bottom in 1.75 meters depth. Tidal currents and turbulence were apparently sufficiently strong to produce thorough mixing of particulate material of low specific gravity. To test the variability of samples from a single location, six replicates were made in December, 1967. The results are given in Table 2.

Table 2

Replication of Samples of Suspended Material

Station A - December, 1967

Replicate	Dry weight of sample (mg/l)
1	118.6
2	116.8
3	109.1
4	115.4
5	119.3
6	115.7

Mean = 115.8

C.I. ($p = 0.05$) = 115.8 ± 6.27
= 109.5 to 122.1 mg/l

Serial samples taken at seven meter intervals along a transect across the river channel produced closely similar quantities of detritus. For instance, in September, 1968, identical volumes of water yielded 9.1 mg, 8.3 mg, 7.8 mg, 7.3 mg, and 6.4 mg respectively. The regular sampling point, also on the transect, yielded 7.1 mg on the same occasion. As repetition of this experiment on other occasions produced similar results, it was concluded that a single sample would adequately represent the suspended detrital load at any particular time.

Methods of Analysis. Resuspended samples were filtered through plankton-net screens of 350 microns and 50 microns to provide two arbitrarily selected size fractions. Originally, a screen of 150 microns was interposed, but this was abandoned in final analysis. Collected material was washed onto an S & S filter paper and thus concentrated for drying and weighing.

A subsample of each size category was temporarily removed from the filter paper and was examined under the microscope to determine its composition. By reference to photomicrographs and permanent mounts of artifically produced detritus of known origins, it was possible to identify the origin of specific detrital particles. Photomicrographs of detritus are included in Appendix III. It proved possible to assign most particles to a definite category; for instance, mangrove peat, mangrove leaf epidermis, Juncus root parenchyma, mangrove root conductive tissue. However, a certain percentage was always unidentifiable, particularly in the smaller size category. Unidentifiable particles were usually either fragments of plant tissues not represented in the reference collection or structureless aggregates of fine particulate material.

The relative importance of each contributory source was ascertained by determining the total area covered by particles of a specific origin on a hemacytometer microscope slide with a grid of 40 micron squares. The percentage composition of each size fraction was thus obtained, and the total weight of material of a given origin in the sample was calculated. The assumption inherent in this procedure is that the weight of a particle is directly proportional to the area it covers. For present purposes it must be assumed that this is so.

After microscopic analysis the samples were oven-dried for four days at 104° C. and weighed.

Total organic content was determined on three samples as follows. After the oven-dried sample plus filter paper was weighed, it was placed in a crucible of known weight, and the filter paper was destroyed by adding a few drops of concentrated nitric acid and evaporating under an extraction hood. The sample was then ashed in a muffle furnace at 550° C. for one hour. Following the method detailed by the American Public Health Association (1955), the ash residue, after cooling, was wetted thoroughly with a 5% solution of ammonium bicarbonate to reconvert oxides formed in ashing back to carbonates. The sample was then dried at 104° C. and weighed. The S & S filter paper on which samples were incinerated had an ash residue of less than 0.07 mg.

A sample of unfractionated suspended detritus was forwarded to Law & Co., Atlanta, Georgia, for proximate analysis to determine its content of protein, fat, crude fiber, ash, and nitrogen-free extract.

The metabolism of suspended particulate material was determined by light and dark bottle experiments. Samples of suspended detritus were fractionated in the field, and each fraction was resuspended in filtered water in 250 ml BOD bottles. A blank was taken at the same time. The sample bottles were submerged for two hours in the river at a depth of approximately 15 cm. Oxygen content was determined by the Winkler Method.

Although the light and dark bottle method has been widely criticized (Pratt and Berkson, 1959; Vaccaro and Ryther, 1954), it was considered adequate for present purposes.

Results

Organic and Inorganic Content. Weight loss after ignition is often used as a measure of total organic content. However, it should be remembered that this is not always a true measure. The ashing procedure also causes halides to volatilize, and drives off biologically and chemically bound water which is too tightly bound to escape during oven drying at low temperatures. Treatment with ammonium bicarbonate restores some of this by reconverting oxides to carbonates, but the net loss is probably still considerable.

In the present study, the percentage weight losses from three samples (those of February, April, and May, 1968) were 63, 57, and 67 respectively. The mean loss was 62.3 percent. Despite the inadequacies of the method, a high organic content is indicated.

The inorganic fraction, which averaged 37.7 percent, is high when compared to that of mangrove leaves from which much of the suspended detritus is derived. As shown in Appendix II, the ash content of mangrove leaves at various stages of degradation was never more than 16 percent. The high ash content of suspended detritus is largely due to carbonates in suspension, since the bedrock over which the river flows is a bryozoan limestone (Hoffmeister et al., 1967). The main river channels are eroded to bedrock, and active erosion by solution is presumably still operative.

Size Composition. Table 3 compares the quantity of seston greater than 350 microns with that of particles between 50 and 350 microns. Material from 50 to 350 microns was found to constitute the greater portion of the seston. Fine colloidal particles, which Fox et al. (1952, 1953) reported present in large quantities off the coast of California, which Riley (1963) found to be the largest size category in Long Island Sound, and which Haven and Morales-Alamo (1968) found to be important in the James River, Virginia, were not observed in quantity in the present study. A 15 liter water sample was taken with a Niskin bottle, passed through sieves of 350 and 50 microns, and filtered through a Millipore HA filter of minimum aperture 5 microns. It contained only four percent by weight of particles smaller than 50 microns.

Table 3

The Size Composition of Suspended Particulate Material

Station A (Estuary)

	Coarse (over 350 microns) % of total	Fine (50-350 microns) % of total	Nanno (less than 50 microns) % of total
Dec, 1967	34	66	*
Jan, 1968	11	85	4
Nov, 1968	12	88	*

Station C (Headwaters)

	Coarse (over 350 microns) % of total	Fine (50-350 microns) % of total	Nanno (less than 50 microns) % of total
Dec, 1967	17	83	*
Jan, 1968	15	85	*
Feb, 1968	2	98	*
Mar, 1968	11	89	*
May, 1968	19	32	*

*-Not determined

Quantity of Detritus. Greatest amounts of seston at Station A were found from November through February as shown in Figure 16. The least amount occurred in July (1.9 mg/l), and the maximum (93.0 mg/l) was recorded in January, 1968 (see Appendix III). At Station C, near the headwaters, generally high amounts were taken from November through April. The maximum quantity (126 mg/l), however, was recorded in May (Figure 16). This sample was taken about three hours after the end of a prolonged (8 - 10 hours) rainstorm which had flooded the surrounding marshes. Water could be seen pouring over the mangrove levees into the river channels. The influence of this export of detrital material from the marshes to the river was also discernable in the estuary (Station A), although the detrital load had either become diluted in passage downstream or most of it had perhaps not arrived in the estuary by the time the sample was taken.

The overall pattern in 1968 seems to have been as follows. Detrital load was high at the beginning of the year, and decreased steadily through

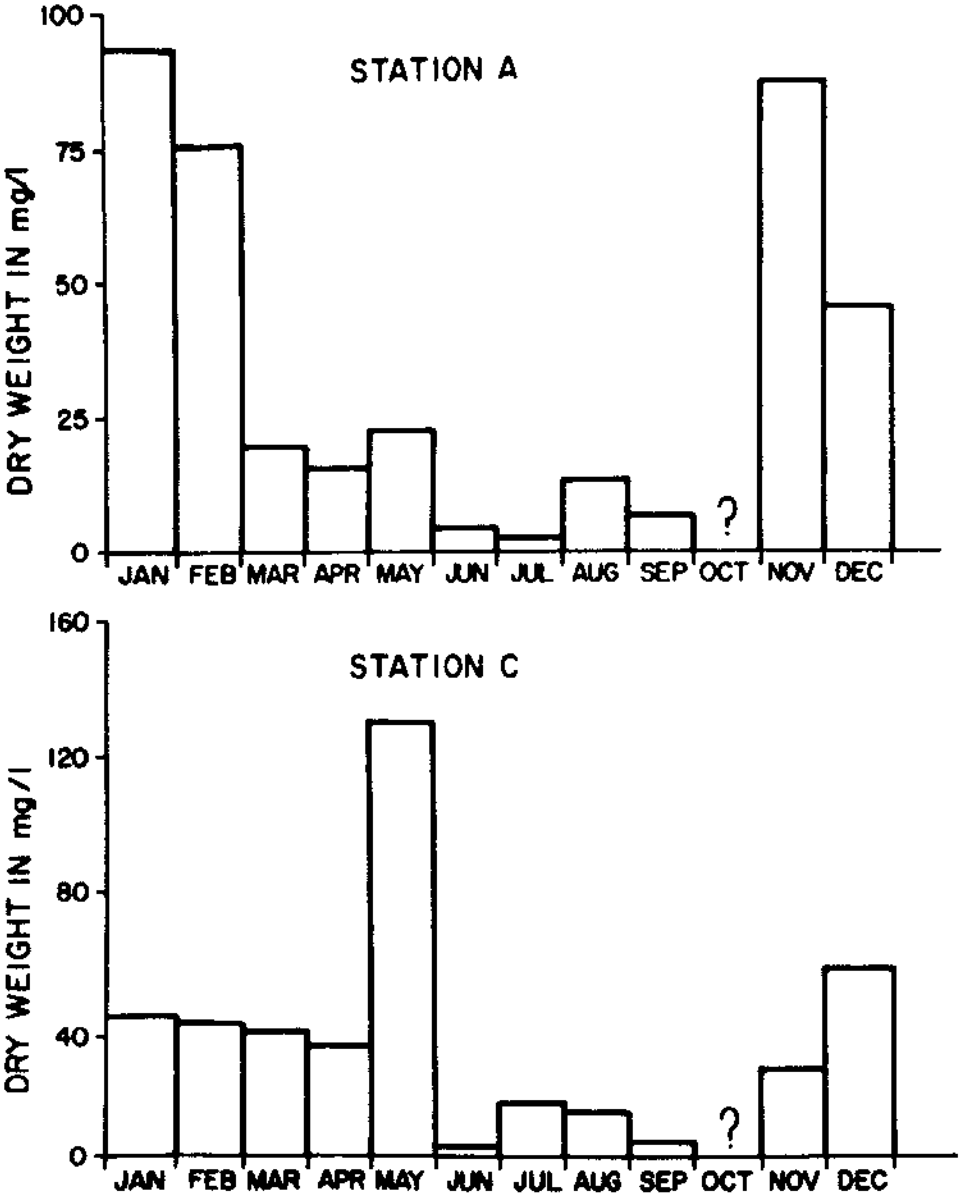

Figure 16. Monthly variation in weight of suspended material--1968.

April as water levels fell and contact between marshes and river became progressively smaller. The lowest concentrations of detritus were recorded from July to September, when summer rains caused water levels to rise until the marshes were flooded (Appendix III, Figure b). It will be seen later that the total export of detritus from the river system was also lowest in these months in spite of the increased water volumes. It is believed that, although widespread contact existed between mangrove swamps, _Juncus_ marshes, and the main drainage channels, water levels were uniformly high, and there was consequently little exchange of water between marshes and river. Under these conditions of tranquil flow patterns, much of the suspended detritus will settle on the bottom and remain in the marshes. During the autumn, however, a change of prevailing winds from southeast to northeast blows the coastal waters offshore, resulting in a strong river flow. The differential in water levels thus created between marsh and river results in large-scale draining of the marshes. Water pouring into the river channels carries with it detritus which has accumulated during the previous seven or eight months.

Hurricane "Gladys" and other unforeseen factors prevented the taking of samples in October, 1968. It is believed that the pattern in October would have been similar to that of preceding months, because the offshore winds did not begin to blow until November. As Table 5 indicates, the quantity of detritus taken in October, 1967 compared closely with values obtained in August and September of 1968. Large amounts of suspended detritus were taken in November and December of 1967 and 1968, and in January, 1968. Draining of the high-marsh areas from November through January is also reflected in the increased amount of _Juncus_ and sawgrass detritus found in the samples during these months.

Composition. The percentage composition of suspended detrital samples from both stations is given in Appendix III. Monthly variation at each station and comparisons between stations are discussed below.

The estuarine samples (Station A) were dominated by mangrove detritus, which constituted between 36 and 60 percent of the total (Figure 17). Figure 18, however, shows that maximum quantities of mangrove detritus were recorded in January (50 mg/l) and February (45 mg/l). In July, when mangrove detritus accounted for 59 percent of the total, concentrations of less than 1 mg/l were found.

The contribution of sawgrass detritus was consistently low (Figure 17), the maximum being 13 percent in May. As Figure 19 shows, the greatest quantities were recorded from December through January when the total detrital load of the river was also greatest. The Juncus marshes contributed only small amounts of detritus to the estuarine regions except during November when 11.8 mg/l were recorded (Figure 19). The percentage contribution of Juncus was very low during the early months of the year and began to increase from April onwards as shown in Figures 17 and 19. As mentioned earlier, this seasonal pattern is believed to be the result of export of accumulated material during the late autumn. The November samples accounted for over 50 percent of all Juncus detritus taken during the year (Figure 20). The flushing effect of the heavy rainstorm already referred to is noticeable in Figure 19.

Filamentous green and blue-green algae, although represented in the samples for most of the year, were abundant only in January, 1968, when they accounted for 8 percent of the sample weight. Diatoms were recorded on several occasions, and various species were probably present for much of the year. Small numbers occurred in February, and a bloom in April accounted for 17 percent of the total suspended load. In general, however,

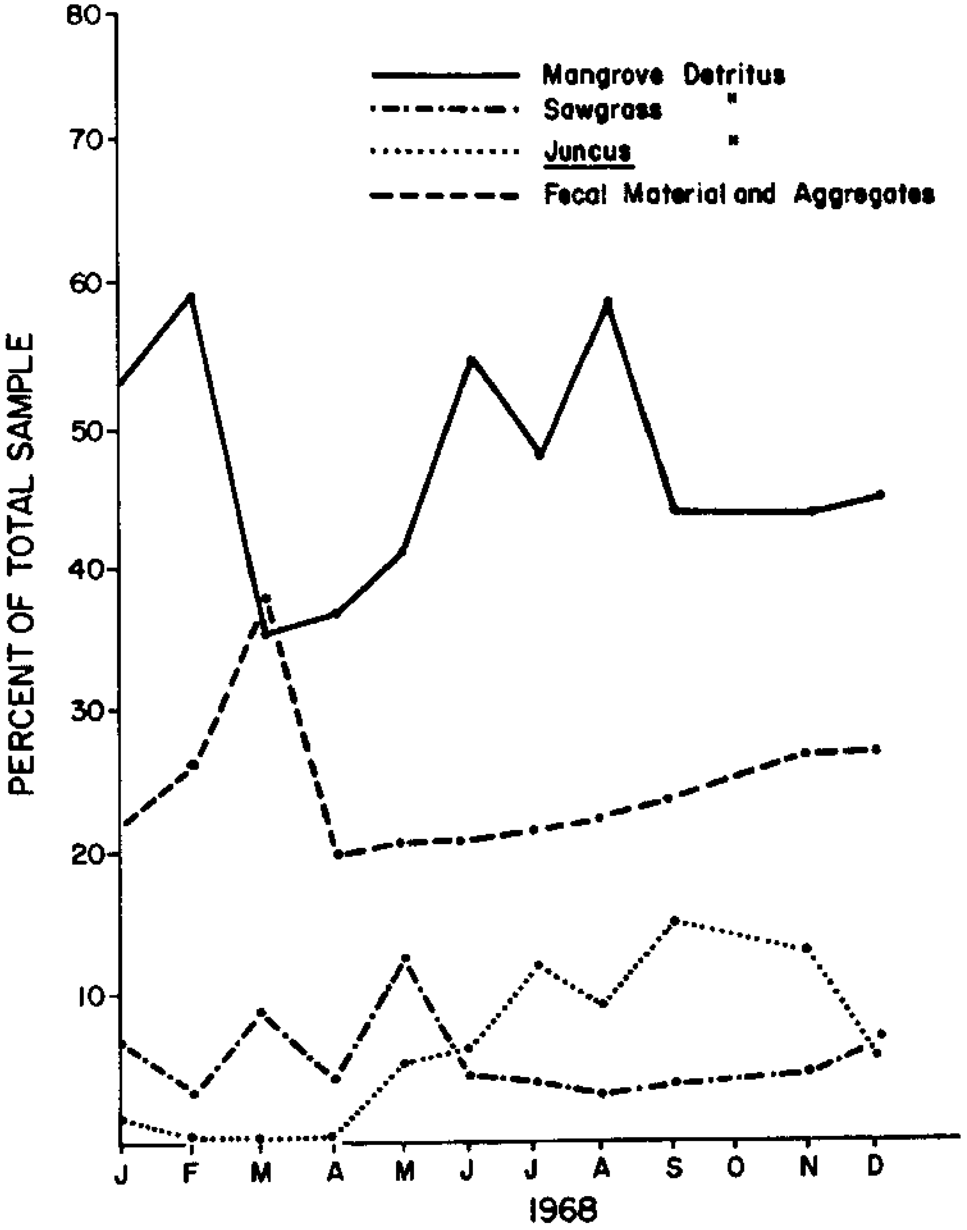

Figure 17. Percentage contribution of four major sources of detritus in estuarine samples.

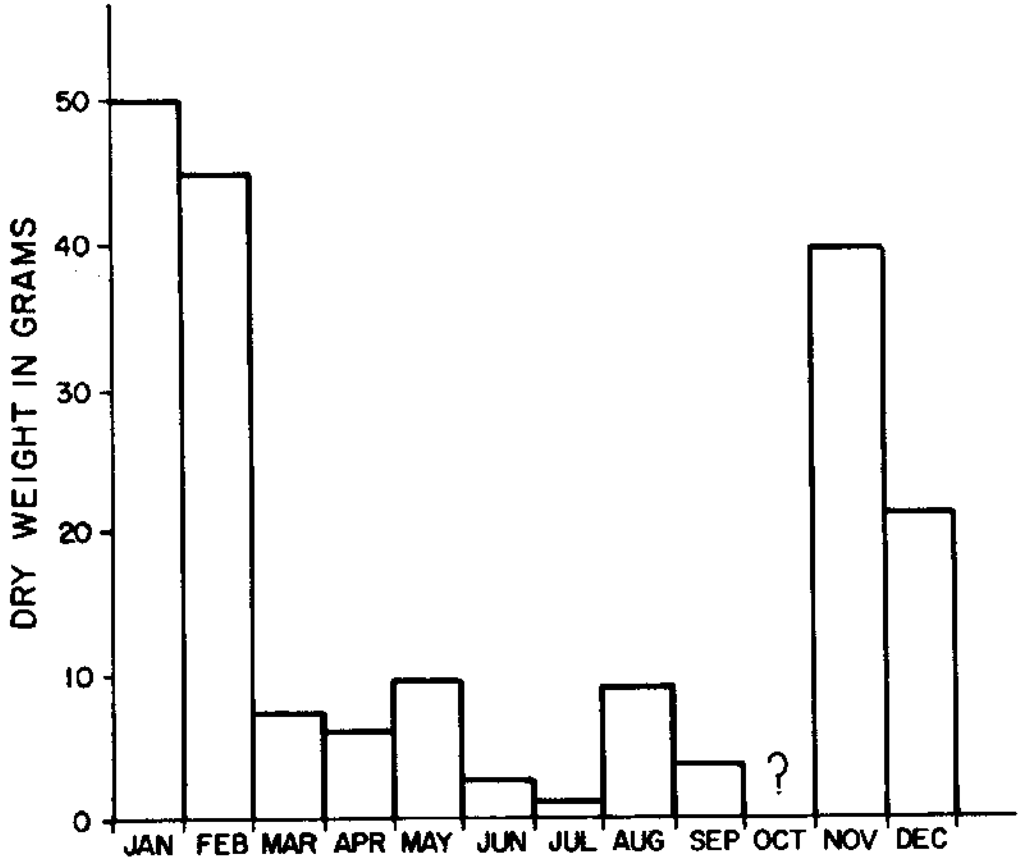

Figure 18. Monthly variation in the weight of red mangrove detritus in estuarine samples--1968.

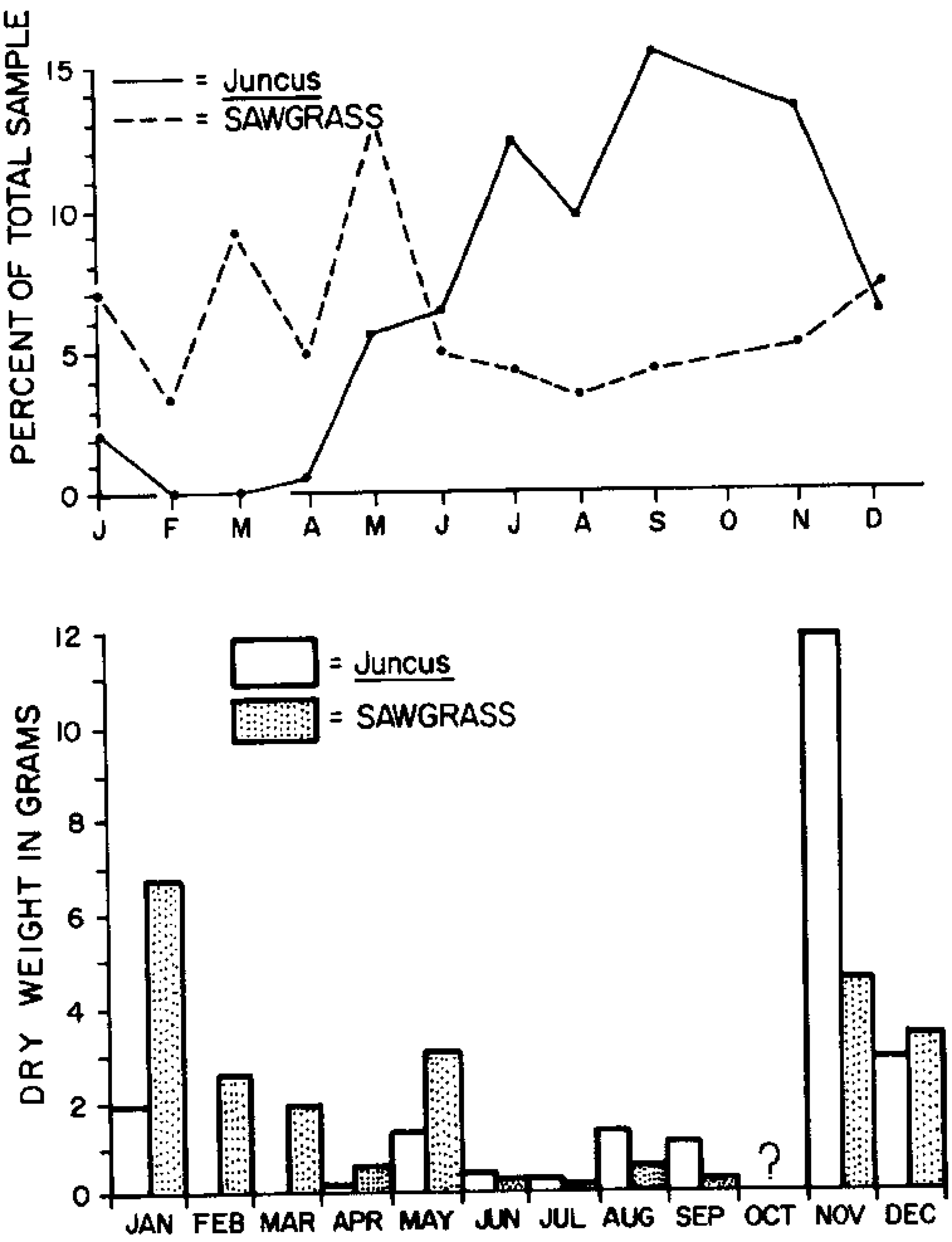

Figure 19. The contribution of *Juncus* and sawgrass to the detrital load in the estuary--1968.

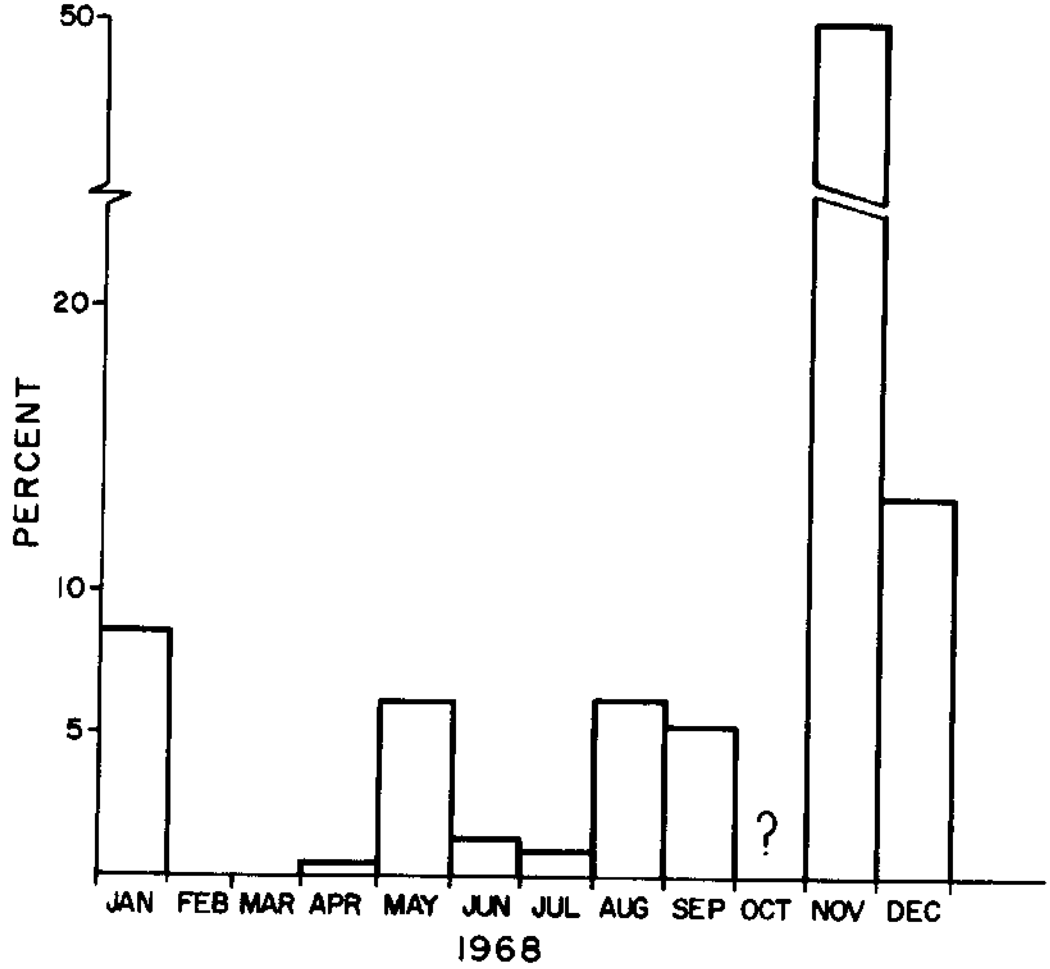

Figure 20. The proportion of the annual total of Juncus detritus taken each month.

phytoplankton appeared to be relatively unimportant members of the system. Patten et al. (1966) similarly reported that in the lower York River, Virginia, phytoplankton 'comprise only a small fraction of the suspensoid load at any given time'.

Copepods and cladocerans occurred regularly at different times of the year, but never accounted for more than five percent of the total particulate material during the daylight hours when sampling was conducted. Crustacean remains are evidently a contributory source of detritus since fragments of chitin were found occasionally. The low ratio of phytoplankton to zooplankton indicates that the latter rely heavily on detritus as a food source.

Fragments of peat, the nature of which was not determined, were always present in the samples. Reference to Tables 2a and 2b in Appendix III reveals that the highest percentages (13.4 and 14.7) were found in March and April, while the greatest quantities occurred from December through April. The presence of measurable quantities of peat lends support to the erosion theory of Spackman et al. (1966).

The percentage of fecal material varied throughout the year (Figure 17), and no seasonal pattern was apparent. Greatest weights were found in January, February, and November, although the highest percentage occurred in September. Recognizable fecal pellets thus accounted for between 3.5 and 13 percent of the total suspended material at this station. Moore (1931) found that up to 40 percent of the Clyde muds were composed of fecal material, and Haven and Morales-Alamo (1968) reported that fecal pellets accounted for between 2 and 56 percent of suspended solids recovered on fine mesh sieves in the James River, Virginia.

Between 7 and 27 percent of the sample each month consisted of aggregates of amorphous material. Individual aggregates rarely exceeded

150 microns and appeared to be composed mainly of very small (less than 10 microns) loosely adherent particles of indeterminate origin (see photograph, Appendix III). It was observed that artificial fragmentation of a fecal pellet produced an aggregation indistinguishable from those encountered in the samples. The break-up of fecal pellets during fractionation of the sample may thus account for all or part of the observed aggregates. An equally possible explanation is provided by the work of Riley (1963), who described aggregates as amorphous matrices from 5 microns to 2 mm in diameter. These contain both organic and inorganic materials and can be formed by adsorption of dissolved organic matter on bubbles and other naturally occurring surfaces (Baylor and Sutcliffe, 1963; Wangersky and Gordon, 1965). Rodina (1964) points out that bacteria are capable of cementing together small detrital particles to make 'conglomerates'. The aggregates observed in this study may thus be the otherwise poorly represented colloidal material referred to earlier. Even if this is so, the amount of colloidal detritus observed in the system was still relatively small.

At Station C, situated close to the landward margin of the mangrove belt, mangrove detritus was less markedly dominant. Between 19 and 50 percent of suspended detritus was of mangrove origin. Greatest amounts were recorded from December through May. The maximum weight occurred in May after the rainstorm although mangrove detritus accounted for only about 26 percent of this sample. Suspended detritus samples taken in March and June were not completely analyzed. Consequently, the composition of detritus during these months in unknown, as is that occurring in October, for reasons already stated.

The percentage of sawgrass detritus in the samples from Station C was fairly consistent throughout the year and was usually higher than at

Station A. Detailed information is presented in Appendix III, Table 3. Similarly, total weights were usually greater at Station C except during the winter months when both higher percentage contributions and greater total weights were recorded at Station A. The highest percentage and largest weight from either station occurred in May at Station C after heavy rain.

The status of Juncus detritus at Station C followed approximately the same seasonal pattern as at Station A. Juncus detritus was, however, less important, and its increased contribution during the autumn was less marked (see Appendix III, Table 3). Since aerial photographs indicate that Station C lies upstream from the majority of the Juncus marshes, the effect of seasonal flushing of these marshes would be less apparent.

During the early summer months (April through July) the percentage composition and the standing crop of aggregates was greater at Station C than at Station A. The situation was reversed from August to March. Maximum amounts were observed at Station C in May, indicating that local runoff from the surrounding marshes contributed large quantities. Recognizable fecal material was invariably more abundant at Station C than at Station A. Fecal pellets accounted for between 17 and 32 percent of all suspended detritus at Station C and were the largest single component on three occasions.

As might be expected, peat was a less important contributory source of detritus at Station C, never exceeding 4.5 percent of the detrital load. Calcereous shell fragments, many of which were probably derived from the freshwater gastropods Helisoma and Planorbia, occurred more frequently in samples from Station C, but were never an important constituent.

Filamentous algae also occurred more frequently and more abundantly at Station C, especially during the summer. Large numbers of diatoms were observed in February, and smaller numbers occurred in April and May.

Although the components discussed above constituted over 98 percent of the total seston, a diverse assemblage of additional items were encountered at one or both stations. These include the tests of Foraminifera, animal hair, fragments of leaf waxes, fish scales, unidentified zygospores, and pieces of the bladderwort *Utricularia lutea*. Sand grains and small fragments of limestone were also observed occasionally

Export of Detritus

The following estimate is based on a tenuous chain of assumptions and it should be regarded only as an approximation.

The estimate is achieved by multiplying the observed monthly standing crop of detritus at the estuarine station by the net volume of water calculated to have moved out of the river each month. The calculation is based as follows: (1) The cross-sectional area of the river at the sampling point is measured; (2) The total discharge of water during the ebb tide is determined; (3) Multiplication of (1) and (2) gives the volume of water passing the transect line in a single ebb tide; (4) The number of tides occurring in each month is obtained from Tide Tables; (5) The standing stock of detritus is obtained from the regular monthly samples; (6) The standing stock on an ebb tide times the number of tides that month provides the monthly total standing stock of detritus on ebb tides; (7) The net monthly export of detrital material is then obtained by subtracting total standing crop on flood tides from that of ebb tides. The procedures, techniques, and assumptions inherent in each step are discussed below.

(1) The cross-sectional area of the river at the sampling station was obtained by direct measurement of width, and of depth at one meter intervals. The total cross-sectional area was then calculated.

(2) A mechanical current meter was used to determine tidal flow. The data obtained represented conditions on a single tidal cycle only. The necessary assumption is that the single datum point approximates the mean of all tides during that month. Tidal flow readings were, however, taken only in March, April, May, and July, 1968. Water transport during the remaining months was interpolated on the basis of relative water levels as recorded by the U. S. Geological Survey, Water Resources Division. The water level in Well Number G596 (Everglades) is believed to reflect very closely the volume of water in the North River system (Tabb, pers. comm.). By equating the observed tidal flow data from March, April, May, and July with corresponding water levels in G596 (Appendix III, Figure a), tidal flow values for all other months were derived. This assumes a linear relationship between well height and tidal flow.

(3) The total volume of water involved in an "average" ebb tide each month was obtained by multiplying the tidal flow data (in meters) by the cross-sectional area (in square meters). The quotient was then converted to liters to facilitate application of later steps.

(4) Tide Prediction Tables, published by the U. S. Coast and Geodetic Survey, were used to determine the amplitude of each tide and the number of tides occurring each month. Since these were predictive tables, no allowance could be made for the effect of local wind conditions on the duration of ebb or on tidal amplitude. It must be assumed that the net total transport figures derived above can be expanded by a direct relationship to represent monthly values.

(5) Again, it is necessary to assume that a single sample of total seston, obtained at a single point in time each month, can be used to predict total detrital transport on a single tide and also total monthly transport. The danger in this assumption is demonstrated by the "abnormally" large quantities of detritus taken at Station C in May after the heavy rainstorm. Standing crop of detritus would probably have fallen to a much lower level within two or three days at most. The magnitude of the error thus introduced can be determined only by repetitive or continuous sampling, both of which were impractical in the present study. Three unsuccessful attempts were made to obtain continuous samples through an entire tidal cycle, but this was abandoned because the filters of the collecting device became clogged so rapidly that filtration was no longer effective after 20 or 30 minutes.

(7) To obtain the net weight of seston exported from the system, the standing crop of particulate material on flood tides was subtracted from that of the preceding ebb tide. Collections of suspended detritus from flood tides were made only in February, May, and November, 1968. These results are given in Table 4.

Table 4

Comparison of detrital load on ebb and flood tides.

Dry weights in mg/l.

	Ebb (E)	Flood (F)	Export (E-F)	E-F/E
Feb	75.1	28.8	46.3	0.6165
May	22.9	7.6	15.3	0.6681
Nov	89.5	37.6	51.9	0.5799
				Mean = 0.6215

Net export of detritus was thus estimated to be about 62 percent of the observed standing crop. Correction of the standing crop value by the factor (0.62) produced estimates of the monthly export of suspended material summarized in Table 5. Phytoplankton and zooplankton, which probably represent between 2 and 10 percent of the total seston, are included in this total.

The annual export of suspended particulate material from the system is estimated at 6,000 metric tons. Alternatively, this can be expressed as an annual export of 1.5 metric tons per acre. Once more, it must be emphasized that this is a gross estimate, the accuracy of which is completely dependent upon the validity of every assumption employed in its derivation.

Table 5

The monthly export of suspended material.

1968	Water level in G596	Vol (liters $\times 10^6$) passing transect in 1 tidal cycle		Detritus mg/l. on Ebb tide	Detrital load (metric tons) on Ebb tides	Monthly export (metric tons)**
		Observed	Interpolated			
Jan	4.8	-	548.0	93.0	2140.6	1311.1
Feb	4.4	-	502.4	75.1	1584.5	970.5
Mar	4.0	437.5	-	20.4	419.5	256.9
Apr	3.3	224.4	-	16.1	148.1	90.7
May	2.4	147.3	-	22.9	134.9	82.6
Jun	6.7	-	770.7	4.7	141.3	86.5
Jly	6.8	808.9	-	1.9	63.0	38.6
Aug	5.9	-	673.6	13.7	406.0	248.7
Sept	6.3	-	719.3	7.1	224.7	137.6
Oct	6.4	-	730.7	13.0*	427.5	261.8
Nov	7.2	-	822.0	89.5	3090.0	1892.6
Dec	6.0	-	685.0	46.0	1197.4	773.4
					9977.6	6111.3

*October, 1967

**The mean relationship between detrital load on ebb and flood tides is 0.6215

Total Export = 6,111 metric tons per year from a drainage
area of 4,100 acres

Detritus Particles as a Food Source

Odum and de la Cruz (1967) pointed out that a detritus particle is a highly active micro-ecosystem containing a diverse microbiota. They also demonstrated that the metabolism associated with a particle increases relatively as the particle size diminishes. The operative principle is that smaller particles have a larger surface to volume ratio. A relatively larger area is consequently available for microbial colonization. The light and dark bottle experiments conducted in this study produced similar results (Appendix III, Table 4).

The fine fraction of suspended detritus samples from the North River contained large quantities of aggregates (Figure 17) composed of very small particulate material. Riley (1963) comments that these aggregates provide a substrate and a food source for bacteria and are a supplemental food for plankton. Rodina (1964) describes detritus particles as consisting of an organic core and associated bacteria. Whether or not bacteria use their substrate also as a food source depends largely upon the nature of the particle. Rodina (op. cit.) further points our that detritus, being of heterogeneous origin, provides a number of microscopic biotopes for bacteria; hence, a varied flora of non-antagonistic forms is found. Burges (1965) develops this concept, stating that colonies of bacteria and fungi are related to variations in the microsurface of soil particles.

The organic detritus particle, plus its associated microbiota, constitutes a relatively protein-rich food source for suspension or deposit feeders. Newell (1965) demonstrated that the percentage of nitrogen in detrital samples increases as particle size decreases. Proximate analysis of suspended detritus from the North River revealed that although approximately 40 percent consisted of ash, the protein content (on an ash-free basis) was 21 percent. This can be compared with red mangrove, sawgrass, and Juncus debris which contained 20.5, 10.8, and 7.3 percent protein respectively after 11 months of decomposition. The suspended detritus evidently reflects in part the high percentage of mangrove which it contains.

Fat values were very low (0.5 percent on a dry weight basis; 0 9 percent of ash-free dry weight). Similarly, crude fiber accounted for 12.1 and 20.1 percent, and carbohydrate (NFE) for 35.0 and 58.0 percent.

Diplococci and bacilli were observed in quantity under fluorescence microscopy, and many yeasts were observed in and cultured from samples of detritus. Agar plate-cultures for fungi resulted in the identification of Alternaria, Fusarium, Stachybotrys, and Phoma.

Many investigators have recognized the importance of detritus and its associated microbiota in trophic relationships. Fox (1950, 1957) stated that a filter feeder such as Mytilus californianus cannot filter and digest sufficient phytoplankton for its nutritional needs, and suggested that detritus might serve as a supplemental food source. Darnell (1969) cited mullet, shad, and menhaden as species which consume large quantities of detrital material, but pointed out that some of this may have been ingested accidentally. He found that the food of menhaden consisted of 99 percent organic detritus.

The importance of micro-organisms, principally bacteria, as an energy source was recognized by Zobell and Feltham (1938). They were able to maintain Urechis caupo and Mytilus californianus solely on bacterial foods, but concluded that bacteria were not generally sufficiently abundant in nature to form an important food source unless aggregated on surfaces. Marzolf (1966) has shown that the distribution of the amphipod, Pontoporeia affinis, in Lake Michigan is directly correlated with bacterial counts in the sediments. He points out that the role of bacteria will be increasingly important when primary production is limited and secondary production is high; for instance, in an oligotrophic lake where allochthonous material is abundant. Newell (1965) stated that the deposit feeders, Hydrobia ulvae and Macoma balthica, are able to utilize micro-organisms, which are more abundant in finer deposits. Odum (1968) demonstrated that the striped mullet (Mugil cephalus) ingests large quantities of detritus, and suggested that the mullet is able to utilize bacteria and other small organisms adsorbed on the surface of particles. He subsequently pointed out that ingested particles, whether organic or inorganic, are excreted by mullet apparently unchanged except for removal of their microbiota (Odum, 1969). Excreted particles will probably rapidly acquire a new microflora or fauna.

The picture which emerges is one in which particulate material serves as a substrate, and possibly a food source, for bacteria and fungi. The smaller particles have a large surface to volume ratio and thus sustain relatively more bacteria or fungi. They are therefore richer in protein and constitute an important energy source for potential consumers.

The consumer may obtain a small amount of energy from the organic "nucleus" of the particle, but probably derives the bulk of its energy requirements from adsorbed micro-organisms. In addition to deliberate ingestion, variable quantities of detrital material are ingested accidentally by many organisms, which nevertheless are doubtless able to utilize the nutrient so acquired. The detrital particle, minus its microbiota, is often excreted after passage through the gut of the consumer, and probably once more serves as a substrate for colonization.

ECOLOGICAL CONSIDERATIONS

Energy Relationships at the Lower Trophic Levels

Energy input to the aquatic system is mainly in the form of dead mangrove leaves. These may fall directly into the water, or may reside for a time on the bank before being swept into the streams. Many must fall directly into the water, since the inter-connecting pond and stream system provides at least 176 km (109 miles) of banks lined by mangroves.

Leaching of water soluble organics as well as inorganic compounds from fallen leaves furnishes nutrients for micro-organisms, and probably for other animals also (Stephens, 1967). The leaf debris itself becomes a substrate for bacteria and fungi, many of which obtain all or a part of their energy requirements from the breakdown of plant proteins, fats, hemicelluloses and celluloses. Release of further soluble compounds doubtlessly occurs as a result of these activities.

The extent to which the total microbial population is dependent upon the leaf material as an energy source at any specific time will depend largely upon the micro-environment provided by the leaf at that time. Cellulolytic forms will probably derive a large percentage of their energy requirements from the leaf; other forms will assimilate larger amounts of dissolved nutrients. Many of these nutrients in solution originate, of course, from mangrove leaves during the early states of degradation.

A succession of bacterial and fungal population occurs as each microbial community makes the substrate or microhabitat more suitable for subsequent populations. In general, the density of fungal populations appears to increase as the leaf debris ages, whereas numbers of bacteria do not appear to increase greatly.

The microbiota established on leaf debris provides a food source for primary consumers, such as Protozoa, small nematodes, rotifers, and micro-crustaceans. Upon this form of secondary production much of the detrital food web is fabricated.

Several species of amphipods, two species of polychaetes, and a xanthid crab consume fragments of leaves as they become structurally weakened and acquire an abundant fauna of fungi, bacteria, Protozoa, and nematodes. The amphipods are particularly important in this respect and appear to be a key link between micro-consumers and higher carnivores. In a concurrent study, W. E. Odum has found that amphipods are consumed in large numbers by many of the important forage fish, such as *Fundulus grandis*, *Lophiogobius cyprinoides*, *Harengula pensacolae*, and *Eucinostomus gula*. Two species of catfish, *Galeichthys felis* and *Bagre marinus*, also feed heavily upon amphipods. In this manner, mangrove leaf debris contributes substantially to the nutrition of the higher carnivores even before it becomes fragmented into fine particles.

Fine particulate material (detritus) is derived from mangrove leaves in two ways: Simple fragmentation of the weakened leaf eventually produces detrital material; or the activities of consumer organisms result in detritus. When consumers are excluded in laboratory tests, parenchymatous tissues become fragmented within three months, epidermal tissue takes approximately six months, and lignified structures are still virtually intact after a year. If eaten, fragments of the leaf probably pass through the gut of a consumer physically unchanged except for partial or complete removal of their microbial elements. The leaf material thus becomes incorporated into the detrital "pool" as the fecal pellet disintegrates. It then presumably acquires a new microbiota, and a cyclical process of ingestion and subsequent egestion commences. The particle microbial complex gradually becomes smaller, but relatively richer in protein since its surface to volume ratio increases.

The above process probably ends only if the particle is removed from the system by deposition and burial in the sediments, or when it becomes so reduced in size that it can no longer support an abundant microbiota. Even then, very fine (colloidal) particulate matter often remains available in the form of aggregates loosely bonded by bacteria, fungi, or molecular forces. A particle may not be permanently removed from the system by deposition since erosion and sedimentation patterns are not static. Peat which may have been deposited hundreds of years earlier is occasionally washed out into the river and probably serves as a physical substrate for micro-organisms.

Particulate detritus occurs in the stomach contents of the majority of local species of fish, molluscs, and crustaceans examined by W E. Odum. The pink shrimp, Penaeus duorarum, two species of mysids, Taphromysis bowmani and Mysidopsis almyra, and the molluscs, Brachiodontes exustus, Crassostrea virginica, and Congeria leucophaeata depend heavily on detritus. Among the fishes, Mugil cephalus, Lophiogobius cyprinoides, Cyprinodon variegatus, and Poecilia latipinna are prominent detritivores. From this list, representing only a portion of the species found to be detritus feeders, it becomes obvious that within the mangrove belt a detritus-based trophic structure predominates.

The Problems of Pollution

The dependence of so many estuarine species on detritus as a food source intensifies the problem of pollution in various forms. Particularly serious in this respect are the numerous chlorinated hydrocarbons commonly used as pesticides. Many of these compounds degrade relatively slowly and are often concentrated by specific organisms. Pesticide residues can become adsorbed onto the surfaces of detritus particles or may be concentrated by the adsorbed microbiota. An organism assimilating these particles can thus rapidly acquire lethal or debilitating sub-lethal amounts of pesticides and pesticide residues. As a result, the entire process of biological concentration of pesticides in food chains may be accelerated.

Other forms of pollution may prevent particle enrichment. A film of crude oil around a particle may prohibit microbial colonization of the surface. Detergents and many chemical pollutants in relatively low concentrations are sufficient to eliminate or inhibit the micro-organisms essential to particle enrichment.

Thermal pollution poses a special problem. Since the metabolism of organisms is usually accelerated by moderate increases in temperature, the oxidative breakdown of organic materials will proceed more rapidly in heated waters. This results in a higher biological oxygen demand and could produce undesirably low levels of dissolved oxygen in areas where replenishment by tidal flushing is inadequate.

Phytoplankton, which might aid in replenishment of oxygen, is rarely an important element in the estuarine waters examined here. Thus, the equilibria of those detritus-laden estuaries in which water exchange is poor can be easily upset by artificial increases in temperature which tend to diminish the oxygen supply even more.

The Value of the Mangrove Community to Adjacent Areas

The importance of the mangrove forest as an energy source does not end at the boundary of the forest. Large amounts of mangrove detritus are exported from the system into adjacent bays and coastal areas. This material is consequently available to additional suspension and deposit feeders such as *Tozeuma carolinense*, *Chaetopterus variopedatus*, *Branchiomma nigromaculata*, *Amphitrite affinis*, *Terebella rubra*, and *Tagelus divisus* which are unable to tolerate estuarine conditions. Large populations of mullet are also probably sustained in part by detrital material exported from the mangrove estuaries.

A further energy export from the system occurs in the form of migratory species such as snappers, groupers, menhaden, sea trout, redfish, snook, and shrimp which utilize the estuaries as nursery areas. Feeding at various levels in the detritus food chain, they grow rapidly during the estuarine phase of their lives and eventually move out into coastal or offshore waters. The export of energy in this manner must be considerable but is not easily measured.

Without this contribution to their energy budget, areas such as Biscayne Bay, Florida Bay, and Whitewater Bay would probably be unable to support their present population levels of important sport fishes. The estuarine and coastal mangrove areas are an essential component of the south Florida biotope.

SUMMARY

1. Red mangrove (*Rhizophora mangle*) is the dominant primary producer in the North River drainage system. The mangrove forest within the study area was estimated to cover approximately 2,600 acres. *Juncus* marshes and sawgrass marshes occupied less than 400 acres.

2. Approximately five percent of the total annual leaf production by mangroves is consumed by terrestrial grazers. The remainder eventually enters the aquatic system as debris. This imported material is an important energy source for the detrital food chain.

3. The production of mangrove debris in the form of leaves and twigs was estimated to average 2.4 $g/m^2/day$, oven dry weight. This was equivalent to almost nine tons/ha/year. Most of this was produced during June and July when maximum leaf fall occurred. Other plants accounted for less than 15 percent of the total debris produced annually.

4. The degradation rate of red mangrove leaves was found to be largely dependent upon the environment under which degradation occurred. The most rapid degradation occurred under brackish conditions, and was associated with a high grazing rate. Two species of amphipods, *Melita nitida* and *Corophium lacustre*, and the xanthid crab, *Rithropanopeus harrisii*, were found to be important consumers of leaf debris in brackish waters.

5. Slower degradation rates and lower levels of grazing were observed in leaves placed in fresh water. Under subaerial conditions breakdown was relatively slow and utilization by consumer organisms was low.

6. *Juncus* and sawgrass leaves were found to degrade very slowly. Little evidence of grazing was observed.

7. As plant debris from various sources degraded, it became relatively richer in protein. It is suggested that this is caused by gradual build-up of a microbial population which utilizes the debris as a nutrient source and as a physical substrate.

8. Highest quantities of suspended particulate detritus occurred from November through February. During this period dry weights between 46 and 93 mg/l were obtained. From March to October the dry weight of suspended material ranged from 2 to 23 mg/l.

9. Detritus of mangrove origin accounted for between 35 and 60 percent of the total suspended material each month. Sawgrass and *Juncus* rarely constituted more than ten percent each.

10. It was estimated that approximately half of the total annual production of debris was exported from the estuary to adjacent bays in the form of fine particulate material.

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APPENDIX I

The "Limb Count" Method of Estimating Productivity

The ten percent sample limb is randomly selected with probability proportionate to limb C.S.A. These probabilities are then used to expand the sample limb count to tree total. The principle involved is depicted in Figure 1a, in which the leaf weight of 20 grams on the sample limb expanded to a tree total of 378 grams. The stepwise procedure includes measurement of the trunk to determine that a limb of 1 cm^2 (ten percent of 10 cm^2) is needed to provide the optimum size sample unit of ten percent of the leaf bearing surface.

The sample limb is determined by a random selection at each scaffolding of limbs, with a probability proportionate to limb C.S.A. In Figure 1a the probability of selecting the 8 cm limb as a random path is 8/8+3. Thus, the probability of selecting the 1 cm limb is the product of scaffold probabilities. Expanding the leaf weight of 20 g on this limb to the estimated tree total of 378 g is accomplished by multiplying the sample weight of 20 g by the reciprocal probability at the final stage sampling.

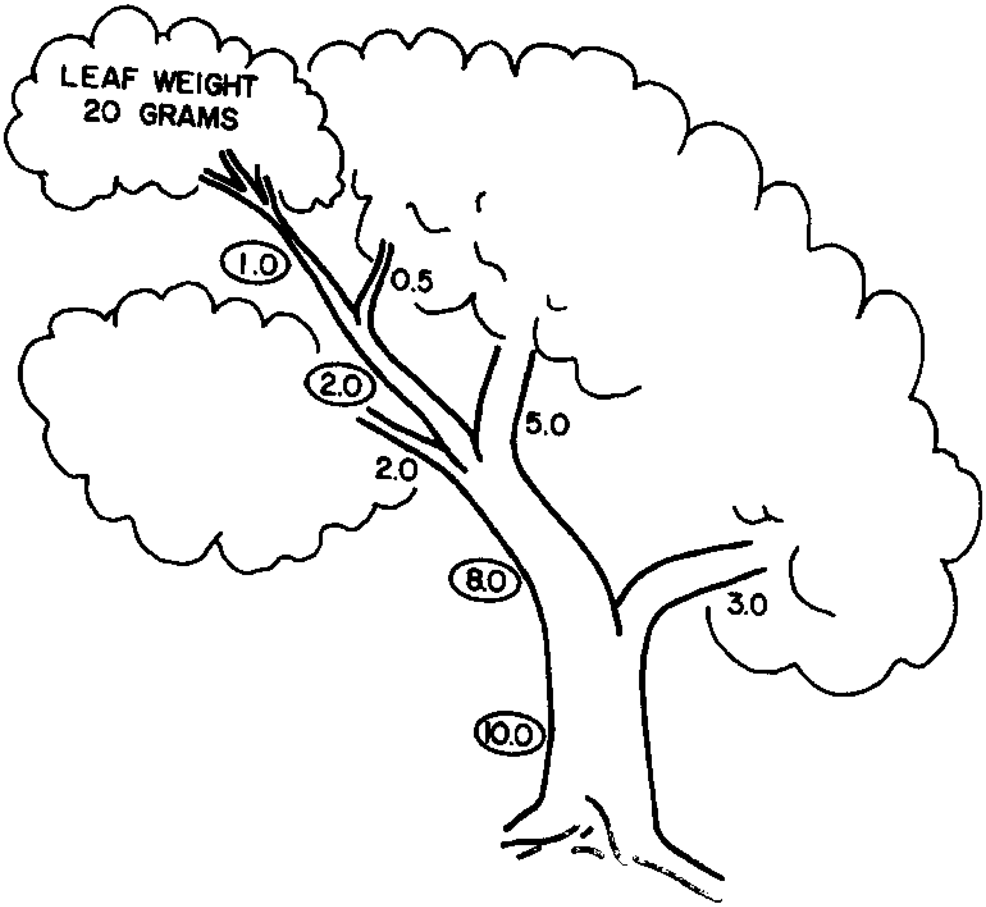

Figure Ia. The theory of the Limb Count Method. Numbers represent cross-sectional areas. Circled numbers are chosen at random.

Estimated foliage weight of tree $= \frac{11.0}{8.0} \times \frac{9.0}{2.0} \times \frac{1.5}{5.0} \times 20g.$

$= 378.0$ grams

APPENDIX I

Table 1

Monthly production of debris by red mangroves. Dry weight in grams by direct determination and as calculated by the Limb Count Method

Cross sectional area of trunk in cm^2		4.57	21.50	29.19	32.94	32.94	62.08	69.38	159.34	176.11	184.89
Dry wt. of debris			*								
Jan	Leaves	1.5	7.5	7.5	5.9	10.1	12.3	11.2	52.2	54.8	22.8
	Scales	0.3	0.6	1.0	0.9	0.8	1.8	1.1	4.2	4.4	4.0
	Twigs	-	3.0	-	17.4	-	14.6	10.0	17.3	6.6	2.7
Feb	Leaves	3.1	3.1	3.9	6.3	3.9	9.6	11.1	20.4	22.7	63.5
	Scales	-	0.6	1.0	1.0	0.7	1.5	1.2	5.1	4.7	4.2
	Twigs	-	-	7.3	11.0	11.1	1.7	-	32.1	-	24.6
Mar	Leaves	0.0	4.7	4.7	4.7	6.7	9.9	11.5	32.6	35.4	33.4
	Scales	0.2	1.3	1.8	1.1	1.4	2.9	2.7	8.0	9.0	5.8
	Twigs	-	-	1.2	-	1.0	1.1	0.4	-	5.3	-
Apr	Leaves	1.8	10.1	10.0	10.9	12.9	23.2	23.2	70.2	73.6	70.3
	Scales	0.8	1.7	1.4	1.6	1.8	3.0	3.5	11.8	16.8	6.8
	Twigs	-	-	1.7	3.1	-	-	-	-	4.9	4.0
May	Leaves	3.4	21.7	22.8	23.9	27.4	46.7	49.9	150.7	154.7	149.7
	Scales	0.6	2.3	2.0	2.5	2.5	4.9	5.1	16.0	12.4	16.0
	Twigs	-	8.2	-	1.1	7.2	2.1	-	-	10.7	4.5
June	Leaves	15.7	142.9	136.3	142.7	160.0	341.5	237.4	885.2	922.1	871.7
	Scales	8.5	14.0	13.8	12.8	14.7	27.6	28.8	77.4	102.2	70.3
	Twigs	-	0.9	1.1	-	1.3	2.4	15.9	5.8	21.8	7.4

Table 1-continued

Cross sectional area of trunk in cm^2		4.57	21.50	29.19	32.94	32.94	62.08	69.38	159.34	176.11	184.89
Dry wt. of debris			*								
July	Leaves	6.1	76.7	74.4	94.3	105.8	168.4	272.5	636.9	658.6	621.3
	Scales	3.6	9.4	9.1	7.6	13.8	17.8	23.4	60.2	54.1	61.1
	Twigs	0.2	0.5	0.5	-	-	1.2	-	-	-	-
Aug	Leaves	12.9	74.1	74.7	72.4	101.3	153.8	172.4	512.1	562.1	518.4
	Scales	4.1	10.2	10.1	11.1	14.1	20.4	22.1	33.2	68.6	70.3
	Twigs	0.6	5.7	-	0.8	0.3	-	2.0	-	12.7	1.8
Sept	Leaves	4.7	23.7	26.0	31.3	26.1	57.1	47.2	168.4	173.2	147.9
	Scales	2.0	9.1	11.7	9.0	13.3	20.3	19.6	62.6	80.3	54.6
	Twigs	-	2.7	4.3	-	1.3	1.9	0.6	-	-	1.9
Oct	Leaves	3.6	14.3	17.1	16.9	16.7	30.0	34.5	117.0	120.7	105.8
	Scales	1.6	11.2	11.4	9.1	11.0	21.3	20.7	77.5	66.4	75.2
	Twigs	-	10.5	1.7	1.1	-	2.8	2.3	18.3	12.4	4.9
Nov	Leaves	6.3	13.0	12.6	13.7	18.0	28.4	29.9	90.4	94.9	91.5
	Scales	1.2	8.0	8.2	8.1	10.3	12.7	23.0	56.4	48.4	56.0
	Twigs	-	3.7	4.8	-	-	3.8	-	-	-	6.0
Dec	Leaves	3.2	6.3	6.3	6.7	7.8	13.9	15.1	44.0	38.8	44.5
	Scales	0.9	1.8	2.0	1.9	2.3	3.8	4.1	9.0	14.1	12.9
	Twigs	1.7	2.8	7.0	-	9.7	6.4	-	21.6	5.8	3.4

*Total debris obtained by direct measurement

APPENDIX I

Table 2

Distance and area measurements made from aerial photographs of the North River.

Length of river from mouth to farthest traceable point = 14.12 km (8.7 miles).

Total distance of banks of ponds and streams which are lined with mangroves - approx. 176 km (109 miles).

Total drainage area = 21.66 km^2 (4,100 acres)

Area occupied by mangroves = approx. 14 km^2 (2,644 acres)
" " " hardwoods = approx. 76 acres
" " " <u>Juncus</u> marshes = approx. 1.5 km^2 (290 acres)
" " " sawgrass = approx. 411,00 m^2 (78 acres)
" " " lakes and ponds = approx. 3.6 km^2 (674 acres)
" " " marl prairie = approx. 342,000 m^2 (65 acres)
" " " river-stream system = approx. 1.1 km^2 (200 acres)

APPENDIX II

APPENDIX II

Table 1

Conversion of fresh weight to dry weight in red mangrove leaves

Fresh weight in grams	Dry weight in grams after drying at 104°C	Conversion Factor
97.3	30.2	0.310
100.9	32.2	0.319
102.4	32.3	0.315
101.7	32.3	0.318
100.6	31.9	0.317
107.1	33.3	0.311
102.5	32.8	0.320
109.3	36.1	0.330
91.2	28.4	0.312
94.8	29.9	0.315
100.0	30.9	0.309
97.4	31.0	0.318
98.5	30.7	0.312
101.6	31.9	0.314
100.3	31.8	0.317
98.3	31.6	0.321
103.1	31.9	0.309
98.1	31.0	0.316
99.9	31.7	0.317
101.5	32.4	0.319

Mean conversion factor = 0.316

C.I. = 0.316 ± 0.003 ($p = 0.05$)

APPENDIX II

Table 2

The percentage of leaf surface removed by grazing organisms before abscission of 50 red mangrove leaves.

% grazed
3.83
0.47
8.57
0.49
6.27
9.15
4.48
2.32
6.10
6.03
0.29
1.15
16.80
14.68
3.53
0.00
3.94
2.58
11.22
8.13
5.71
7.56
1.63
0.39
2.01

% grazed (cont.)
5.84
16.17
4.69
4.85
4.45
2.52
5.22
0.80
14.15
0.38
6.15
5.61
0.45
9.79
0.68
16.34
1.08
0.40
2.27
3.46
0.82
17.95
0.94
0.00
0.00

Mean percentage grazed = 5.05

APPENDIX II

Table 3

Chemical composition and caloric content of debris at successive stages of degradation

	% PROTEIN LAW	Ga	% FAT LAW	% FIBER LAW	% NITROGEN FREE EXTRACT LAW	% ASH LAW	Ga	Cal/g Ga *
RED MANGROVE LEAVES								
Green	6.1(6.7)	8.8(9.2)	1.1(1.2)	15.7(17.3)	67.9(74.8)	9.2	3.7	4.564(4.742)
Dead	3.1(3.4)	5.5(5.8)	6.3(6.9)	21.9(24.1)	59.6(65.6)	9.2	4.5	4.818(5.004)
<u>In Brackish Water</u>								
After 1 Month	13.2(14.2)	12.6(13.0)	5.8(6.2)	24.4(25.9)	50.4(53.6)	6.1	3.4	5.020(5.197)
2 Months	14.1(15.1)	14.0(14.6	4.9(5.3)	25.1(26.9)	49.4(52.8)	6.4	4.1	5.061(5.302)
3 Months	16.0(18.0)	16.1(17.4)	4.7(5.3)	28.4(31.9)	39.9(44.8)	10.9	7.7	4.568(4.945)
4 Months	----	18.1(19.6)	----	----	----	----	7.6	4.602(4.981)
6 Months	----	18.9(20.9)	----	----	----	----	10.1	4.433(4.921)
11 Months	18.9(20.5)	----	1.7(1.8)	28.6(31.1)	42.8(46.6)	8.0	----	----
12 Months	21.6(25.6)	----	1.5(1.7)	19.5(29.2)	36.5(43.4)	15.7	----	----
<u>In Dry Condition</u>								
1 Month	10.7(11.1)	----	5.9(6.2)	24.2(25.1)	55.4(57.6)	3.8	----	----
5 Months	----	16.2(17.4)	----	----	----	----	6.9	4.648(4.992)
12 Months	20.9(23.3)	----	1.4(1.6)	25.2(28.2)	41.9(46.8)	10.5	----	----
SAWGRASS								
Dead	5.3(5.4)	5.9(6.0)	0.8(0.8)	32.1(33.3)	58.2(60.4)	3.6	1.8	4.615(4.698)
After 3 Months	----	5.4(5.4)	----	----	----	----	2.7	4.521(4.648)
6 Months	----	5.0(5.2)	----	----	----	----	2.1	4.514(4.602)
11 Months	10.3(10.8)	----	1.0(1.0)	24.9(26.1)	59.0(62.0)	4.8	----	----
<u>**JUNCUS**</u>								
Live	----	8.2(8.2)	----	----	----	----	1.4	4.723(4.791)
Dead	3.7(3.8)	----	1.5(1.6)	41.7(42.4)	51.2(52.2)	1.8	----	----
After 5 Months	----	7.1(7.4)	----	----	----	----	5.6	4.039(4.279)
10 Months	7.3(7.4)	----	1.1(1.1)	34.5(35.2)	55.1(56.2)	2.0	----	----

Table 3-continued

	% PROTEIN		% FAT	% FIBER	% NITROGEN FREE EXTRACT	% ASH		Cal/g	*
	LAW	Ga.	LAW	LAW	LAW	LAW	Ga.	Ga.	
SUSPENDED DETRITUS	12.7(21.1)	----	0.5(0.9)	12 1(20.1)	35.0(58.0)	39.6	----	----	

***Values are given on dry weight basis**
Values in parentheses are on ash free dry weight basis
LAW = Analyses performed by Law & Co., Atlanta, Georgia
Ga. = Analyses performed by University of Georgia, Department of Ecology

APPENDIX II

Table 4

Degradation rates of red mangrove leaves under three environmental conditions. Mean values are given in parentheses.

Elapsed time	Brackish % remaining	Predominantly Fresh % remaining	Dry % remaining
1 month	59.8 (61.9)	76.8 (66.6)	73.1 (73.2)
	66.7	59.9	73.3
	59.2	63.1	-
2 months	61.3 (57.3)	64.7 (60.0)	-
	55.3	62.4	-
	55.3	54.0	-
3 months	45.4 (45.8)	55.5 (57.5)	60.1 (61.9)
	48.8	59.5	63.6
	43.2	-	-
4 months	39.0 (39.0)	58.9 (54.3)	-
	39.0	49.8	-
5 months	31.2	41.6 (41.0)	62.5
	-	40.4	-
6 months	40.4	37.9 (38.6)	60.1 (59.5)
	-	43.7	58.8
	-	37.0	59.6
	-	35.8	-
7 months	-	38.9	51.2
8 months	20.1 (19.5)	-	-
	19.0	-	-
9 months	16.7	29.6	45.6
10 months	9.4 (7.7)	-	-
	6.0	-	-
11 months	-	19.7	-
13 months	5.9 (4.7)	18.1	28.2
	3.5	-	-
14 months	2.9	-	30.8 (32.6)
	-	-	34.4

APPENDIX III

APPENDIX III

Table 1

Dry weights of suspended detritus in mg/l.

		Station A	Station C
1967	Nov	65.0	32.5
	Dec	86.9	85.2
1968	Jan	93.0	45.8
	Feb	75.1	44.4
	Mar	20.4	42.0
	Apr	16.1	37.2
	May	22.9	126.6
	June	4.7	2.9
	July	1.9	15.6
	Aug	13.7	12.2
	Sept	7.1	3.4
	Oct	--*	--*
	Nov	89.5	25.6
	Dec	46.0	56.5

*No Trip - Hurricane

APPENDIX III

Table 2a

Composition of samples of seston in 1968

STATION A

*	Jan		Feb		Mar		Apr		May		Jun		Jly		Aug		Sept		Oct		Nov		Dec	
	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%
Mangrove leaf material	21.9	23.6	29.1	38.7	3.6	17.6	1.4	8.8	5.1	22.4	1.6	32.9	INSIGNIFICANT AMOUNTS	26.0	5.2	38.2	1.9	26.8	NO SAMPLE		27.9	31.2	11.5	25.2
Mangrove root material	10.5	19.9	15.1	20.1	2.7	13.4	3.9	24.1	4.1	18.1	0.9	20.1		16.2	1.6	12.8	1.0	14.0			9.0	10.1	7.6	16.6
Mangrove bark material	9.6	10.3	0.8	1.1	1.0	4.9	0.7	4.5	0.3	1.4	0.1	2.1		6.1	1.1	8.0	0.3	3.5			2.7	3.0	1.8	3.9
Sawgrass leaf material	6.7	7.2	2.6	3.5	1.3	6.6	0.2	1.4	2.0	8.7	0.2	4.0		1.6	0.3	2.6	0.3	3.7			4.5	5.0	2.1	4.7
Sawgrass root material					0.6	2.7	0.5	3.4	1.0	4.3	0.05	0.9		3.0	0.1	0.7	0.1	0.4					1.1	2.3
Juncus leaf material	1.8	1.9			+		0.1	0.6	0.8	3.6	0.2	4.1		10.9	1.0	7.2	1.1	15.4			10.0	11.2	2.5	5.4
Juncus root material									0.5	2.1	0.1	2.2		1.5	0.3	2.5					1.8	2.0	0.3	0.7
Filamentous algae	7.1	7.7							1.6	7.2				6.6	+						0.3	0.3	+	
Non-filamentous algae	+		1.5	2.0	+		2.9	17.8			0.1	2.3									+		+	
Fecal material	0.8	9.5	7.7	10.3	2.2	10.7	2.0	12.7	0.8	3.6	0.3	5.9		8.6	0.6	4.1	0.9	12.9			6.3	7.1	3.2	6.9
Zooplankton	+		1.6	2.2	0.7	3.5	0.8	4.8	0.8	3.6	0.1	2.6		1.4	0.2	1.9	0.2	3.0			3.6	4.0	1.7	3.8
Peat	6.6	7.0	3.5	4.7	2.7	13.4	2.4	14.7	0.3	3.6	0.2	4.7		4.9	0.2	1.4	0.2	2.7			2.7	3.0	2.4	5.3
Aggregates	12.0	12.9	12.1	16.1	5.5	27.2	1.0	6.4	4.0	17.4	0.7	15.2		13.2	2.5	18.6	0.8	11.1			17.9	20.0	9.4	20.4
Unident. tissues	+		+		+		0.1	0.7	0.3	1.4	0.1	2.1		0.2	0.3	2.0	0.5	6.5			2.7	3.0	0.3	0.7
Miscellaneous			1.0	1.3					0.3	1.4	0.1	0.9	+								+		1.9	4.1

+ present in sample but not on counting grid
* calculated dry weight in mg/l

APPENDIX III

Table 2b

Composition of samples of seston in 1960

STATION C

	Jan		Feb		Mar		Apr		May		June		Jly		Aug		Sept		Oct		Nov		Dec	
	* wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%	wt	%
Mangrove leaf material	17.3	37.8	4.3	10.4	NOT ANALYZED		5.2	13.9	10.5	8.3	NOT ANALYZED		3.1	19.8	2.7	22.2	0.4	12 2	NO SAMPLE		1.9	7.4	11.9	21.0
Mangrove root material	3.5	7.7	2.4	5.4			3.4	9.1	17.9	14.1			0.7	4.6	1.8	14.7	0.3	8.1			1.6	3.6	6.1	10.8
Mangrove bark material	1.3	2.8	1.5	3.4			1.4	3.7	3.8	3.0			0.8	5.4	0.4	3.2					1.3	5.2	3.2	5.7
Sawgrass leaf material	2.0	4.4	1.1	2.5			2.2	5.9	10.1	7.9			0.6	4.2	0.5	4.4	0.1	4.3			1.3	4.9	3.6	6.4
Sawgrass root material							0.1	0.2	2.7	2.2			0.3	1.9	0.2	1.7					0.1	0.5		
Juncus leaf material	2.4	5.3	0.6	1.4			1.4	3.7	4.2	3.3			0.6	3.6	0.4	3.3		2.0			1.8	6.9	3.5	6.2
Juncus root material							0.4	1.1	1.4	1.1			0.1	0.9	0.3	2.7		1.7			0.8	3.3	1.1	2.0
Filamentous algae		0.1	0.3	0.7					0.3	0.3			0.5	3.4							0.2	0.8		
Non-filamentous algae		0.1	7.1	15.6			0.2	0.5	1.9	1.5			0.3	2.1				1.6						
Fecal material	8.4	18.4	14.1	31.5			9.3	24.9	21.2	16.8			3.4	22.0	3.1	25.5	1.1	32.5			2.4	[illegible]	13.3	23.5
Zooplankton	0.2	0.3	5.0	11.2			1.5	3.9	4.9	3.8			0.5	3.2	0.3	2.4	0.1	3.2			0.7	2.9	2.2	3.9
Peat	1.8	3.8	1.6	3.6			1.6	4.4	0.4	0.3			0.4	2.9		0.4	0.1	3.1			0.4	1.7	0.7	1.3
Aggregates	6.6	14.3	4.7	10.6			9.8	26.3	44.4	35.1			2.6	16.7	2.1	17.5	0.7	19.9			4.6	16.6	4.2	7.5
Unidentified tissues			+				0.8	2.2	2.3	1.9			1.1	7.4			0.3	10.4			1.4	5.4	6.6	11.7
Miscellaneous	+		1.8	4.1			+		2.0	1.5			0.3	1.7	0.2	2.0		0.6			1.9	7.3		

+ present in sample but not on counting grid
* calculated dry weight in mg/l

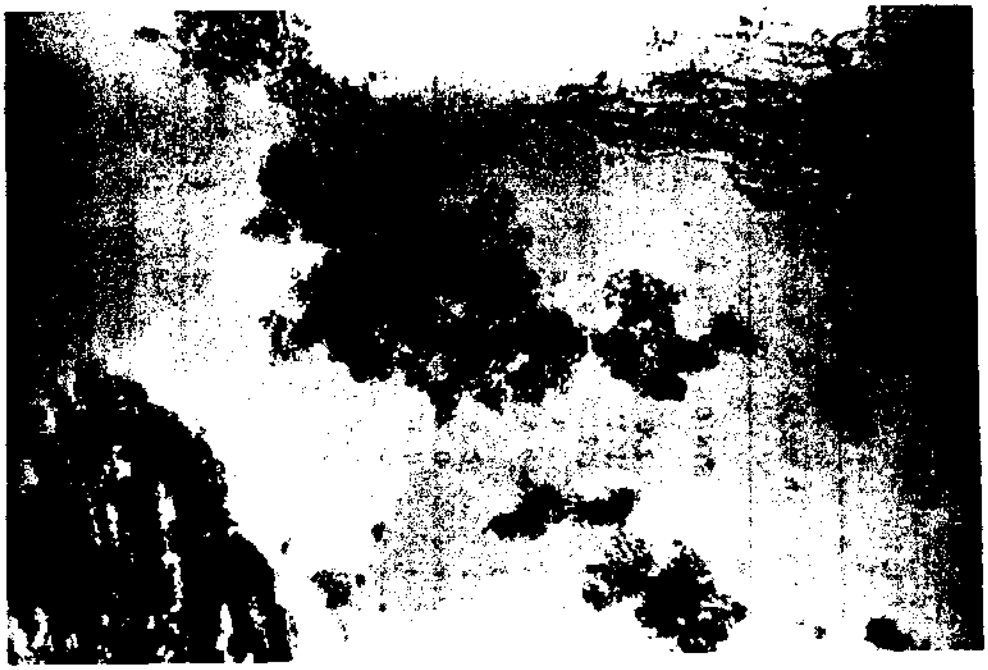

Figure a. Photomicrographs of detrital material (x160).
Top: Red mangrove leaf epidermis at right, sawgrass leaf epidermis at left of picture.

Bottom: Aggregated particles in center, *Juncus* root at lower left, sawgrass leaf epidermis at upper right.

APPENDIX III

Table 3

Monthly weights and percentages of sawgrass and *Juncus*

	Sawgrass				*Juncus*			
	Dry wt. in mg/l		% of sample wt.		Dry wt. in mg/l		% of sample wt.	
	STN A	STN C	STN A	STN C	STN A	STN C	STN A	STN C
Jan	6.7	2.0	7.2	4.4	1.8	2.4	1.9	5.3
Feb	2.6	1.1	3.5	2.5	0.0	0.6	0.0	1.4
Mar	1.9	?	9.3	?	0.0	?	0.0	?
Apr	0.7	2.3	4.8	6.1	0.1	1.8	0.6	4.8
May	3.0	12.8	13.0	10.1	1.3	5.6	5.7	4.5
Jun	0.3	?	4.9	?	0.3	?	6.3	?
Jly	0.1	0.9	4.2	6.1	0.2	0.7	12.4	4.7
Aug	0.4	0.7	3.3	6.1	1.3	0.7	9.7	6.0
Sep	0.3	0.1	4.1	4.3	1.1	0.1	15.4	3.7
Oct *	---	---	---	---	---	---	---	---
Nov	4.5	1.4	4.5	5.4	11.8	2.6	13.2	10.2
Dec	3.2	3.6	7.0	6.4	2.8	4.7	6.0	8.2

* No sample

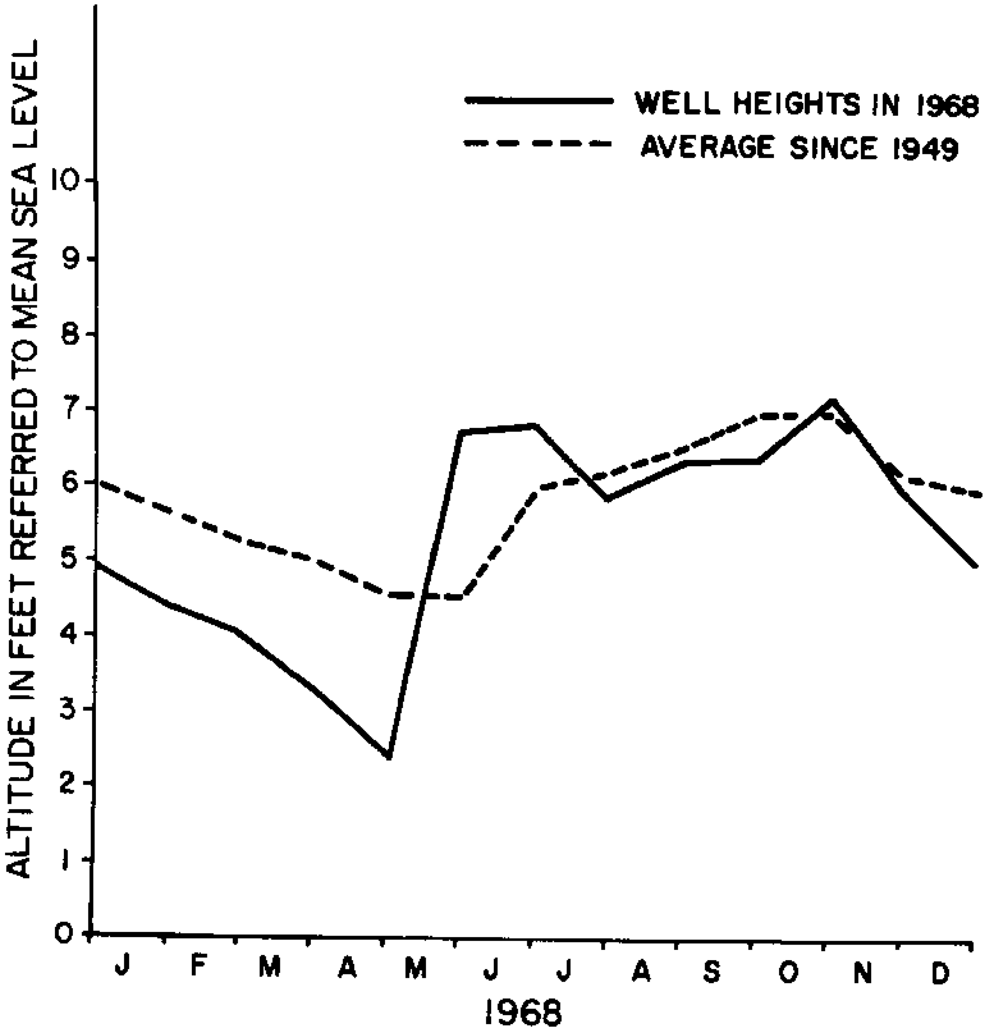

Figure b. Month-end water level in well no. G596(Everglades). (Adapted from chart prepared by U. S. Geological Survey, Water Resources Division, 1968.)

APPENDIX III

Table 4

Dark and Light Bottle Experiments

Date	Size Fraction	Net Oxygen Consumption (ml/g/hr) Light	Dark
May, 1968	over 350 microns	0.201	0.385
	150-350 "	0.646	0.666
	50-150 "	2.117	1.914
Dec, 1968	over 350 microns	0.107	0.247
	150-350 "	1.172	0.571
	50-150 "	1.720	1.656