

ABSTRACT

A. Clark Gaither. BELOWGROUND BIOMASS IN SIX SALT MARSH PLANT COMMUNITIES. (Under the direction of Vincent J. Bellis.) Department of Biology, May, 1985.

Belowground standing crop, net annual production, distribution of macro-organic matter with depth, turnover time, and belowground/aboveground biomass ratios were estimated for six salt marsh plant communities bordering estuarine tributaries of South Creek in Beaufort County, North Carolina. Estimates were derived from macro-organic matter (MOM) values derived from analysis of core samples obtained at monthly intervals throughout 1982.

Mean belowground standing crop values ($\text{kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) were: herbaceous annuals 5.53, Cladium jamaicense 7.44, Spartina cynosuroides 8.34, Typha domingensis 2.65, Juncus roemerianus 7.80, and Distichlis spicata 2.61. MOM within these plant communities was not evenly distributed throughout the soil profile. The bulk of this material resided within the 0 to 30.0 cm depth increment which contained most of the living roots and rhizomes.

Three indices of net annual production (NAP) were also evaluated. Estimates of NAP based on maximum minus minimum values from periodic regression analysis (PRA) were judged to be most reliable. NAP values ($\text{kg}\cdot\text{m}^{-2}$) based on PRA were: herbaceous annuals 1.34, Cladium jamaicense 2.33, Spartina cynosuroides 2.16, Typha domingensis 3.55, Juncus roemerianus 1.52, and Distichlis spicata 3.69. Generally, these values fell within the range of belowground production values for comparable

marshes along the Atlantic and Gulf Coasts. Belowground NAP within these communities ranged from two to four times greater than aboveground production.

BELOWGROUND BIOMASS
IN SIX SALT MARSH PLANT COMMUNITIES

A Masters Thesis

Presented to

The Graduate Faculty of the Department of Biology
East Carolina University

In Partial Fulfillment
of the Requirements for the Degree
Master of Science in Biology

by

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DEDICATION

For their continued love and support, I would like to dedicate this work to my Mom and Dad, Mena Bell and Dent Turner Gaither.

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CONTENTS

	<u>Page</u>
LIST OF FIGURES.	i
LIST OF TABLESii
INTRODUCTION	1
DESCRIPTION OF STUDY AREA.	5
MATERIALS AND METHODS.14
RESULTS AND DISCUSSION21
Belowground Standing Crop21
Net Annual Production23
Computations.23
Comparison With Other Studies26
Belowground Biomass Pathways.35
General Seasonal Pattern.37
Herbaceous Annuals Community.38
<u>Cladium jamaicense</u> Community.39
<u>Spartina cynosuroides</u> Community.39
<u>Typha domingensis</u> Community40
<u>Juncus roemerianus</u> Community.41
<u>Distichlis spicata</u> Community.41
Distribution of Macro-organic Matter with Depth42
Turnover Time45
Belowground/Aboveground Biomass Ratio47
SUMMARY AND RECOMMENDATIONS50
LITERATURE CITED52

LIST OF FIGURES

- Figure 1. Location map of South Creek study area.
- Figure 2. Vegetative cover map of Jacks Creek tributary marsh showing sampling sites for herbaceous annuals (A), Spartina cynosuroides (S), Cladium jamaicense (C), Typha domingensis (T), Juncus roemerianus (J), and the marsh water level recorder (R).
- Figure 3. Vegetative cover map of Jacobs Creek tributary marsh showing the sampling site for Distichlis spicata (D).
- Figure 4. Coring apparatus for sampling marsh type sediments, modified from Gallagher (1974).
- Figure 5. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the herbaceous annuals community.
- Figure 6. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the Cladium jamaicense community.
- Figure 7. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the Spartina cynosuroides community.
- Figure 8. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the Typha domingensis community.
- Figure 9. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the Juncus roemerianus community.
- Figure 10. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the Distichlis spicata community.
- Figure 11. Pathways open to belowground biomass, modified from Good et al. (1982).

LIST OF TABLES

- Table 1. Vegetative cover of Jacks Creek marsh.
- Table 2. Vegetative cover of Jacobs Creek marsh.
- Table 3. Estimates of belowground standing crop for six salt marsh plant communities. Estimates derived from this study are based upon yearly means in $\text{kg}\cdot\text{m}^{-2}$ to a depth of 30.0 centimeters.
- Table 4. Comparison of belowground productivity among six salt marsh plant communities using four methods of estimating net annual production.
- Table 5. Periodic regression models for macro-organic matter in six salt marsh plant communities.
- Table 6. Belowground productivity estimates for salt marsh plant communities along the western Atlantic and Gulf Coasts modified from Good et al. (1982).
- Table 7. Distribution of macro-organic matter (MOM) with depth in six salt marsh plant communities.
- Table 8. Belowground biomass turnover times (years) for six salt marsh plant communities.
- Table 9. Belowground/aboveground biomass ratio for six salt marsh plant communities.

INTRODUCTION

Over the past twenty years, salt marsh ecosystems have received considerable attention from biologists. Salt marsh productive capacity became of interest to estuarine ecologists following the publication of a paper by John Teal (1962) describing energy flow in a salt marsh at Sapelo Island, Georgia. Teal concluded that 45% of the marsh's production was removed by tidal flux to estuarine waters, thus contributing to the detrital based food web. This view was expanded by Eugene P. Odum (1968) who six years later introduced the term "outwelling" to describe the transport of nutrients from the salt marsh to estuarine based consumers. Since that time, numerous research efforts on salt marsh ecosystems have produced a moderate body of data on aboveground production. These data have been summarized in literature reviews by Keefe (1972), Turner (1976), and most recently by Nixon (1980) in which he questioned earlier assertions that all salt marshes are exporters of organic matter to coastal waters. Nixon's assessment of available data indicated that salt marshes must be considered individually, some as exporters and others as sinks of nutrients and/or organic carbon. How then can salt marshes be simultaneously considered as both exporters and sinks of organic carbon? This question is currently being debated among estuarine ecologists.

After the conceptual model of "outwelling" was introduced, ecologists directed a greater amount of research effort toward measuring aboveground primary production in salt marsh ecosystems. This usually entailed the use of clipped plot techniques originally developed for use in terrestrial plant communities. Results from these studies have shown southern (Gulf Coast) marshes to be one order of magnitude more

productive than those in the extreme northern latitudes. Net annual aboveground production values of 1-2 kg·m⁻² were obtained from southern marshes while annual production in northern Canada was estimated at 0.3 kg·m⁻². A gradient of production values has been shown to exist between these two extreme locations, supporting the contention that greater productivity is correlated with longer growing seasons (Turner, 1976).

Most early investigators of salt marsh primary productivity have, however, failed to consider the relative contribution of belowground components (stem bases, roots, and rhizomes) to overall productivity. Good et al. (1982) concluded that this failure has occurred simply because aboveground components are more accessible. If one is to gain an understanding of the salt marsh and marsh/estuarine interactions, should not the total vegetative component be considered when assessing primary productivity? Kucera et al. (1967), in a study of a tallgrass prairie, stressed the importance of assessing both above and belowground components in order to fully appraise plant productivity. In a study of a New Jersey tidal marsh, Smith et al. (1979) noted the need for data on biomass, turnover time, and nutrient value of the **total** vegetative component as a necessary prerequisite for understanding the ecological dynamics of salt marshes and their degree of interaction with estuarine food webs.

It is only within the past ten years that ecologists have turned their attention to salt marsh production belowground. John L. Gallagher was the first to advance our ability to measure the belowground vegetative component in a salt marsh, a component difficult to measure and evaluate even in terrestrial plant communities (Dahlman and Kucera, 1965). Marsh soils often remain, or are intermittently, inundated and

can be quite soft. As a result, traditional terrestrial sampling techniques are inappropriate. However, Gallagher (1974) devised a coring apparatus and technique for sampling the belowground biomass (BGB) in salt marsh soils which allowed the collection of suitable samples.

After Gallagher's 1974 paper was published, other ecologists (Stroud, 1976; de la Cruz and Hackney, 1977; Whigham et al. 1978; Smith et al., 1979; and others) began to report the significance of this vegetative component with respect to overall primary productivity and total standing crop. Good et al. (1982) have recently reviewed the available literature on BGB in salt marsh ecosystems. They concluded that the belowground marsh component is at least equal to, and often exceeds, the aboveground component in terms of production and standing crop. For instance, de la Cruz and Hackney (1977) reported belowground standing crop 4-5 times greater than average aboveground standing crop in a Mississippi Juncus roemerianus Scheele marsh, while Gallagher (1974) in a study of short form Spartina alterniflora Loisel at Sapelo Island, Georgia, reported a belowground/aboveground biomass ratio of 48.9:1. Good et al. (1982) further reported that the potential significance of the typically large belowground component to food chains or webs, nutrient cycling, and structural maintenance of the marsh is "enormous." For example, de la Cruz and Hackney (1977) sampled estuarine seston from the aforementioned J. roemerianus marsh in Mississippi which contained root and rhizome material indicating that marsh rhizospheric components were entering the estuary, thereby contributing to the detrital food web. They suggested that this organic input might be significant in marsh-estuarine trophic interactions and

concluded that physical, chemical, and biological parameters should be considered along with the distribution of belowground components with depth when studying total primary production of marsh vegetation. Also, Gardner (1975) reported that through seepage there was a probability of rhizospheric productivity leaving the marsh in the form of dissolved organic matter. That belowground components may serve as a potential energy and nutrient source for estuarine-dependent consumers was recognized by Hackney and de la Cruz (1980), prompting a decomposition study of roots and rhizospheric materials from two species of tidal marsh plants in a Mississippi Gulf Coast marsh. Their findings revealed a large BGB of decaying plant material which maintained a stable, highly nutritious energy supply available for consumption.

Before any role may be defined for salt marshes as either sinks or sources of organic carbon, the belowground component must be more adequately assessed. Currently, the amount of data available on BGB within these important ecosystems is small and fragmentary. Considerably more information concerning aboveground and belowground biomass dynamics from a variety of salt marshes must be obtained in order to define the relative contribution of belowground biomass production to total salt marsh productivity.

The primary purpose of this investigation was to expand the available data base on belowground biomass (BGB) by simultaneously measuring this component in each of six different salt marsh plant communities with accompanying computations of turnover times and belowground/aboveground biomass ratios. Secondary objectives were to determine the distribution of BGB with depth among vegetation types and to assess whether observed seasonal patterns could be explained in terms

of the life history of the plants involved. Coincidentally, several alternative methods for estimating belowground net annual production were tested and compared.

DESCRIPTION OF STUDY AREA

For this investigation two marshes were selected for study. These marshes border Jacks and Jacobs Creeks and are located in Beaufort County near Aurora, North Carolina (Figure 1). Both creeks are small, lateral, brackish tributaries of South Creek. Each watershed exhibits a vegetative cover gradient beginning with upland forest at the headwaters, passing through swamp forest, then abruptly changing to brackish marsh. Both creeks open to the larger estuarine system of South Creek and then into the Pamlico River.

The historical development of the study streams has been established from our stratigraphic studies and carbon-14 age determinations of subfossil organic matter recovered from marsh peat (Bellis and Gaither, manuscript in preparation). Both Jacks and Jacobs Creeks originated from drainage patterns established by erosion of the Yorktown formation between two and six million years ago. This was followed by several successive transgressive/regressive cycles and depositional episodes. The present basin, sculptured during the Wisconsin glaciation some thirty to fifty thousand years ago, assumed its present level within the last five to fifteen thousand years (early Holocene) (Eames, 1983 and Copeland et al., 1983).

Wetland vegetation encroached the basins of Jacks and Jacobs Creeks some 4,000 years before present with brackish marsh in residence for

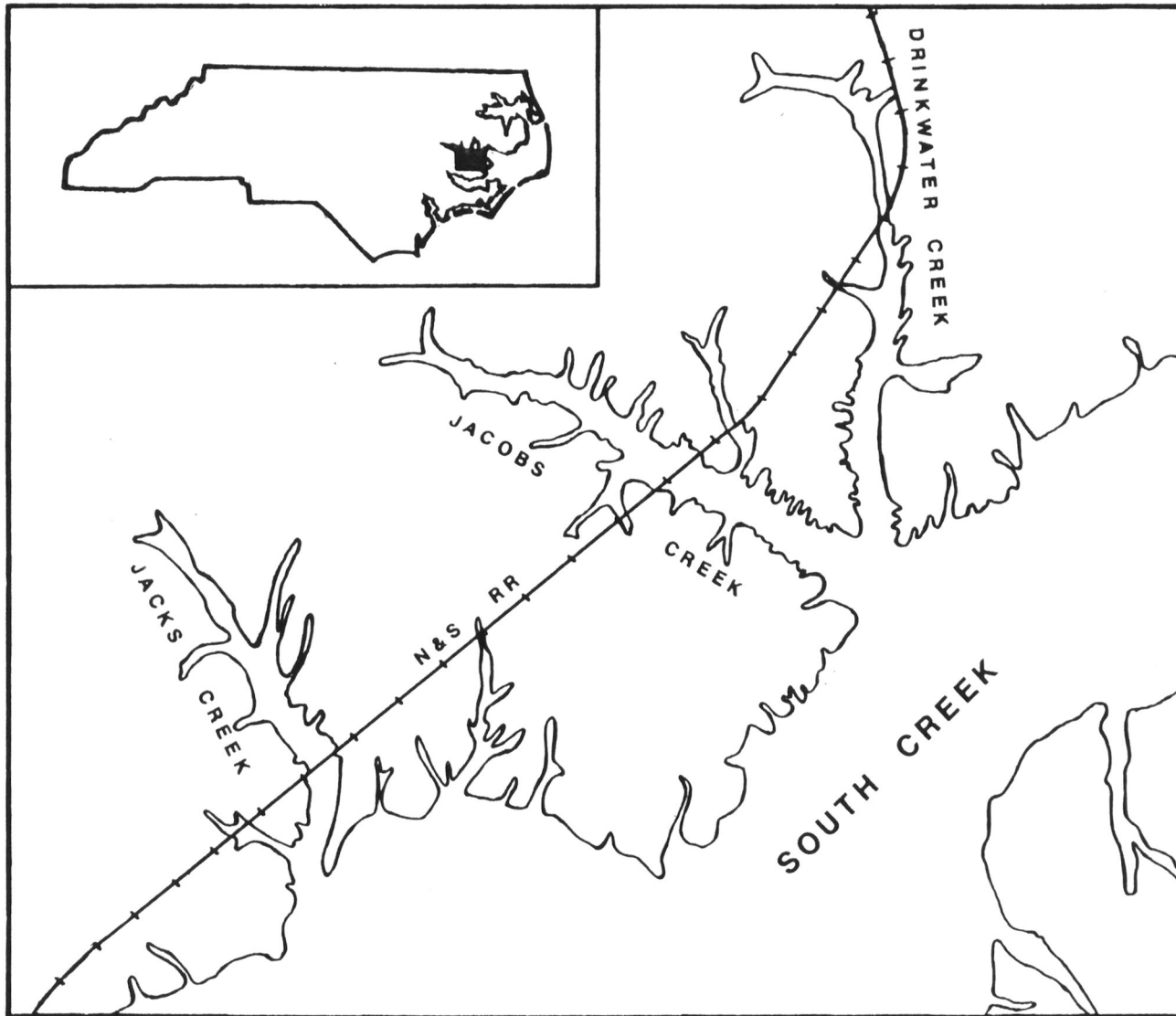


Figure 1. Location map of South Creek study area (Lat. $35^{\circ}20'$, Long. $76^{\circ}46'$).

less than 3,000 years. Vertical accumulation of marsh peat within the study marshes has averaged approximately 0.8 meters per thousand years. Organic sediment accretion coupled with slow lateral expansion of marsh, faster upstream expansion, and downstream erosion should persist as long as sea level continues to rise.

The open water channel of Jacks Creek (Figure 2) is approximately 850 m long and 90 m wide at its mouth but only 7-15 m wide along the greater portion of its length. Jacobs Creek (Figure 3) has an open water channel 975 m long and a breadth which gradually widens from 4.5 m at the headwaters to 106 m at the mouth. Channel depths varied from 1.3-1.5 m at their mouths to 0.6-0.9 m in the upper reaches. Each marsh is situated in a basin having relatively steep lateral slopes (rise to run ratios of 1:4-1:6 for Jacks Creek) of mineral soil which may reach 3.0 m in elevation above mean sea level.

Aerial photos supported by ground truth observations of Jacks Creek have revealed a vegetative cover consisting of a mosaic pattern of discrete vegetative communities. In contrast, the vegetative cover of Jacobs Creek presented a much less conspicuous mosaic pattern with a tendency for the plant cover to form complex, continuously intergrading mixtures of vegetation. Also, the vegetative cover of Jacobs Creek marsh exhibited a greater number of species than were encountered at Jacks Creek marsh.

Eight vegetative communities, based on dominance of aerial coverage, were identified at Jacks Creek (Figure 2). These were Juncus roemerianus, Spartina cynosuroides (L.) Roth, Cladium jamaicense Crantz, Typha domingensis Persoon, Hibiscus moscheutos Linnaeus, mixed marsh (mixtures of the aforementioned types), mixed herbaceous annuals

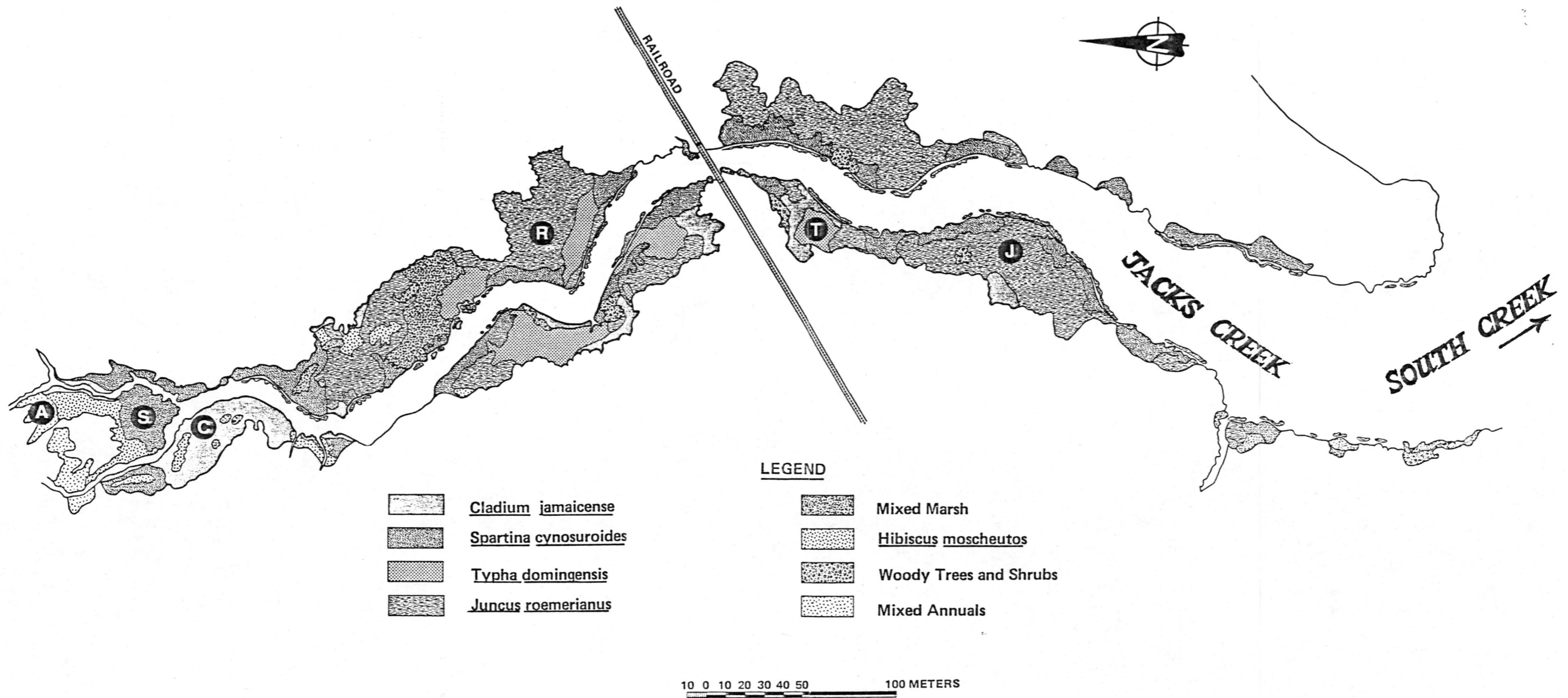


Figure 2. Vegetative cover map of Jacks Creek tributary marsh showing sampling sites for herbaceous annuals (A), Spartina cynosuroides (S), Cladium jamaicense (C), Typha domingensis (T), Juncus roemerianus (J), and the marsh water level recorder (R).

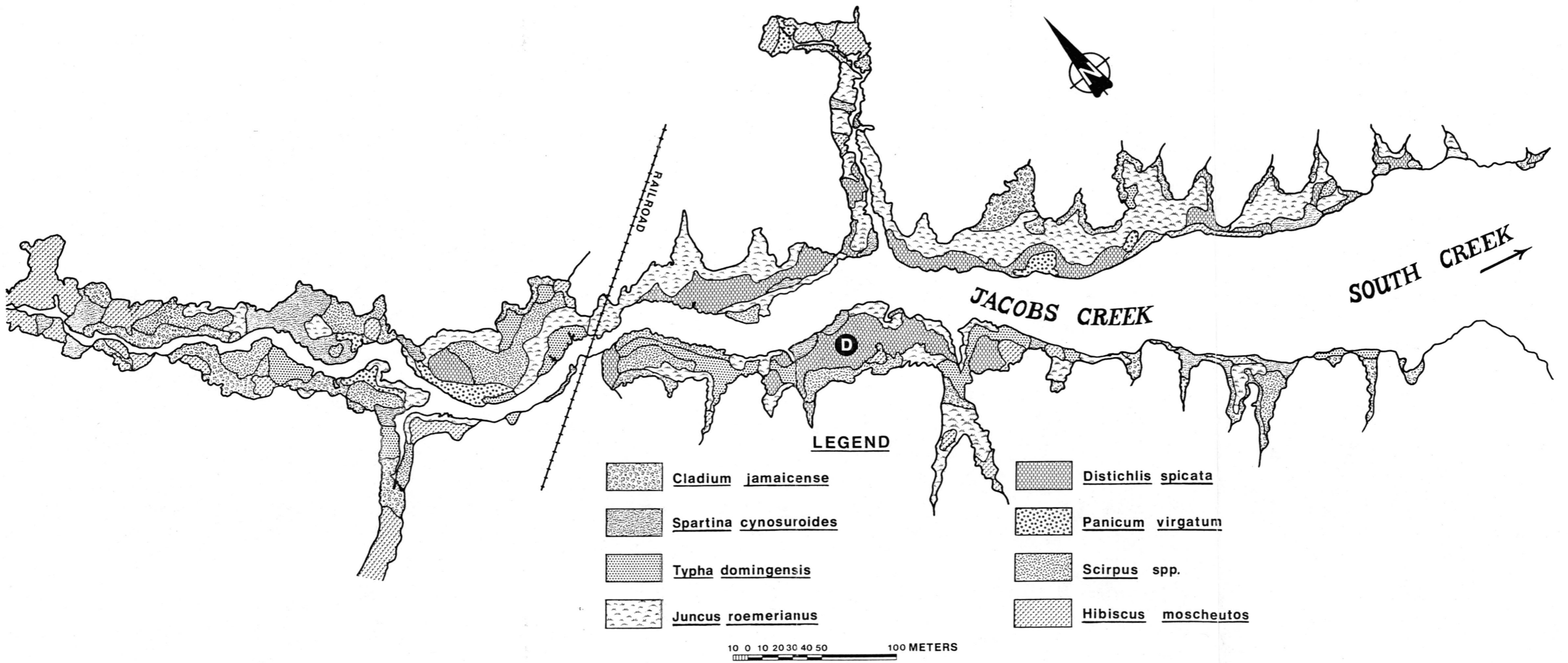


Figure 3. Vegetative cover map of Jacobs Creek tributary marsh showing the sampling site for *Distichlis spicata* (D).

(usually Aster subulatus Michaux, Amaranthus cannabinus (L.) J. D. Sauer, Eleocharis obtusa (Willdenow) Schultes, Osmunda regalis (Willdenow) Gray, and Pluchea purpurascens (Swartz) de Candolle), and woody trees and/or shrubs (usually Pinus taeda Linnaeus and Baccharis halimifolia Linnaeus). Relative aerial coverage by each vegetation type is given in Table 1. Within the stream itself, open water covers an area of 2.49 hectares with 2.88 hectares of bordering marsh. The marsh border was variable in width and ranged from 1.5 - 4.6 m at the headwaters to 30 m near the midpoint of the creek.

The vegetative cover of Jacobs Creek (Figure 3), although similar in composition to Jacks Creek, was a more heterogeneous mixture of vegetation. Only relatively small areas of marsh were dominated by any one vegetation type while large areas of mixed vegetation were apparent. Seven aerially important cover types were identified on Jacobs Creek in addition to those previously listed for Jacks Creek. These were Spartina patens (Aiton) Muhlenberg, S. alterniflora, Distichlis spicata (L.) Greene, Scirpus spp., Panicum virgatum, A. cannabinus, and Phragmites communis Trinius. Figure 3 shows aerial coverage for the dominant species only. Minor plant communities in terms of aerial coverage were not omitted but were incorporated in to the closest dominant vegetation type. Relative aerial coverage by each vegetation type is given in Table 2. The open water surface area of Jacobs Creek consisted of 4.91 hectares with an adjacent 5.85 hectares of bordering marsh. Marsh border varied in width from 6-30 m along the length of the stream.

Table 1. Vegetative cover of Jacks Creek marsh.

Marsh community type ¹	Area (ha)	Relative coverage (percent of total)
1. <u>Juncus roemerianus</u> (stand)	1.10	38.13
<u>Juncus roemerianus</u> (fringe)	0.08	2.92
2. <u>Spartina cynosuroides</u> (stand)	0.70	24.21
3. <u>Cladium jamaicense</u> (stand)	0.27	9.53
<u>Cladium jamaicense</u> (fringe)	<0.01	<0.05
4. <u>Typha domingensis</u> (stand)	0.26	8.97
5. Mixed (no dominant)	0.15	5.08
6. <u>Hibiscus moscheutos</u> (clumps)	0.13	4.36
7. Woody trees and shrubs	0.12	4.31
8. Herbaceous annuals ²	<u>0.07</u>	<u>2.44</u>
SUBTOTAL	2.88	100.00
Open water	2.49	46.31
Marsh	<u>2.88</u>	<u>53.69</u>
TOTAL	5.37	100.00

¹named after dominant species comprising 51 percent or more of living biomass of sample

²principally Amaranthus cannabinus and Aster sublatus

Table 2. Vegetative cover of Jacobs Creek marsh.

Marsh community type ¹	Area (ha)	Relative coverage (percent of total)
1. <u>Juncus roemerianus</u>	1.51	25.79
2. <u>Distichlis spicata</u>	1.01	17.29
3. <u>Cladium jamaicense</u>	0.75	12.77
4. <u>Scirpus</u> spp.	0.57	9.76
5. <u>Spartina cynosuroides</u>	0.46	7.89
6. Woody trees and shrubs	0.45	7.60
7. <u>Typha domingensis</u>	0.36	6.14
8. <u>Panicum virgatum</u>	0.32	5.49
9. <u>Hibiscus moscheutos</u>	0.30	5.15
10. <u>Spartina patens</u>	0.06	1.08
11. <u>Phragmites communis</u>	0.04	0.68
12. <u>Spartina alterniflora</u>	0.01	0.20
13. <u>Amaranthus cannabinus</u>	<u>0.01</u>	<u>0.16</u>
SUBTOTAL	5.85	100.00
Open water	4.91	54.39
Marsh	<u>5.85</u>	<u>45.61</u>
TOTAL	10.76	100.00

¹named after dominant species comprising 51 percent or more of living biomass of sample

Surface water movement within these two stream systems was controlled by several factors including lunar tides, wind tides, and freshwater runoff. Wind tides (primarily northeasterly) exerted the greatest influence on water level with each stream. Due to the essentially flat topography of these marsh systems, complete flooding occurs when wind-driven tides push a sufficient amount of water from the Pamlico estuary into the study streams such that storage capacity is exceeded. During the period of study these marshes were inundated well over half of the time with single flood events lasting from several weeks to more than a month. The extreme range in recorded water level was from approximately 1.5 m, one meter above the marsh surface to one-half meter below. Water level was also recorded in a well located at Jacks Creek at a point 40.0 m north of the stream channel within a stand of J. roemerianus (Figure 2). This instrument recorded water level within the marsh soil during non-flood conditions. Between November, 1981 and April, 1983, this recorder documented a water level range from 0.94 m above the marsh surface to 0.11 m below its surface. Both Jacks and Jacobs Creeks are meso-oligohaline with salinities ranging from 0 ‰ to 15 ‰.

The term "tributary marsh" has been proposed (Bellis and Gaither, unpublished manuscript) to describe these and similar brackish marsh systems exhibiting the following characteristics:

- (1) narrow configuration of the marsh basin,
- (2) presence of a single open water channel draining adjacent uplands as well as the marsh itself,
- (3) relatively high ratio of marsh edge per unit area,
- (4) mosaic pattern in the distribution of plant communities, and

(5)a tendency for these mosaic patterns to form as bands parallel to the long axis of the marsh.

These characteristics serve to distinguish the tributary marsh from the more extensive "estuarine fringe marshes".

MATERIALS AND METHODS

Procedures for collecting and processing belowground biomass (BGB) samples have been reported previously by Gallagher (1974). These procedures were used in this investigation with slight modification of the coring apparatus. The coring device (Figure 4) was constructed from a 0.5 m section of 7.4 cm diameter aluminum irrigation pipe. The bottom end of the core tube was sharpened and serrated to facilitate coring. A handle was attached to the opposite end with adjustable thumb screws. Notches were filed into one side of the coring tube at one decimeter intervals to facilitate control over the depth of insertion into the marsh sediments. A three inch diameter (7.6 cm) plumber's test plug was used to cap the corer during extraction from the marsh. A vent pipe was constructed from a 1.0 m section of half-inch electrical conduit. The bottom end of this pipe was tightly plugged with a rubber stopper above which a series of small holes (1/16 in. dia.) were drilled.

Coring was accomplished by inserting the core tube into the marsh sediments while alternately twisting the handle clockwise, then counter-clockwise, and exerting a downward force. The core tube was inserted into the marsh in one decimeter increments. After each decimeter increment of penetration, a meter stick was placed inside the top end of the corer until it came to rest atop the sediments inside. From the

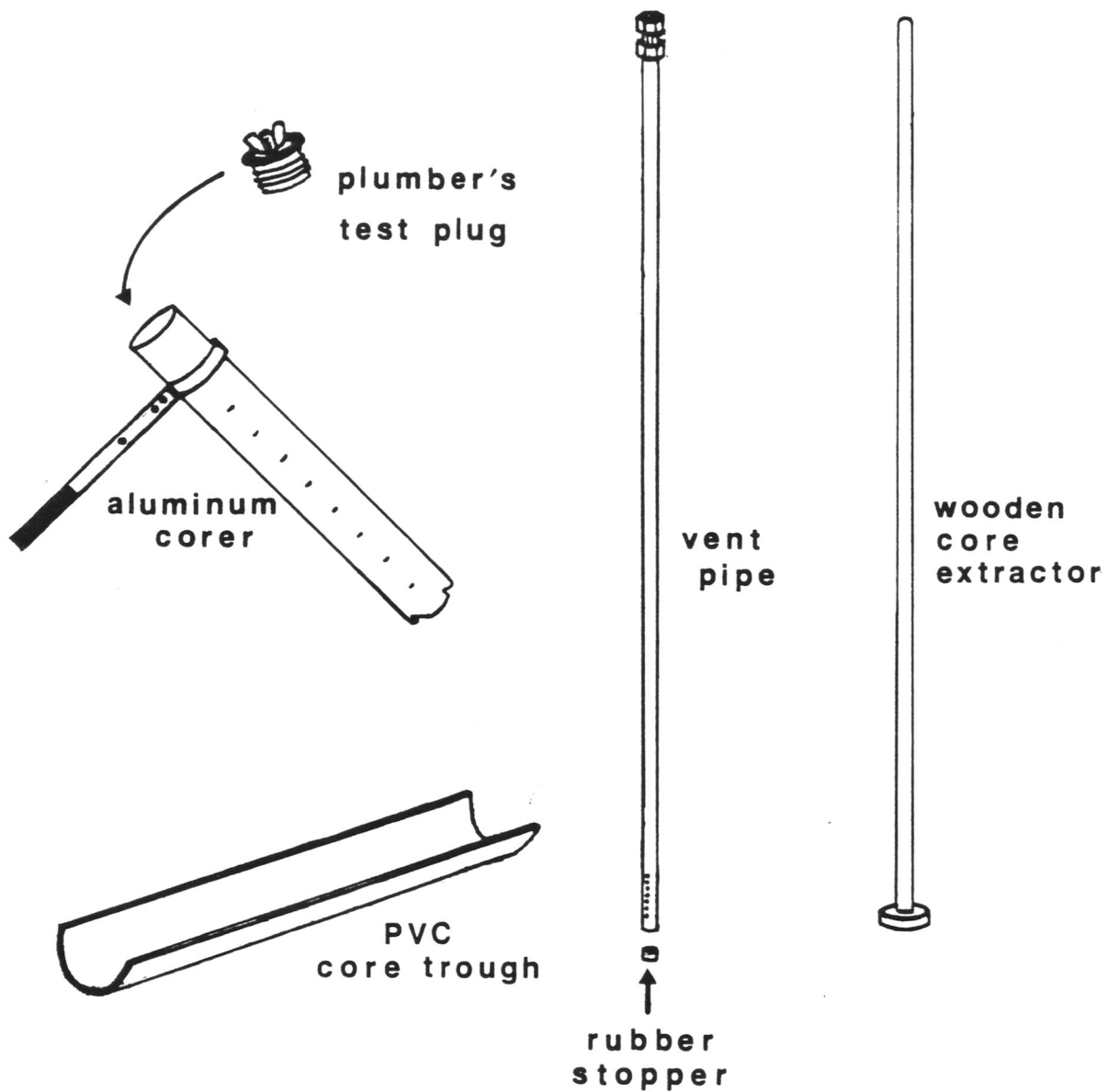


Figure 4. Coring apparatus for sampling marsh type sediments, modified from Gallagher (1974).

length of the core tube (0.5 m), the depth of insertion, and by observing the meter stick reading at the tube's rim, the amount of core compression was computed for each successive increment of penetration. The core was inserted to a final depth of four decimeters in every sampling attempt.

Gallagher (1974) noted that the barrel of the core tube acts as a resonator such that any change in sound indicates a change in soil density. Cutting thorough underground stems and rhizomes could not only be heard but felt through the hands as well. These observations helped determine the proper amount of downward force applied to the top end of the coring tube, thereby serving to lessen the effects of core compaction.

After coring was completed but before the core tube was extracted from the sediments, a plumber's test plug was inserted into the open top end and tightened to form an air tight seal. The vent pipe was then introduced parallel to, and along the entire length of, the core tube. The small vent holes at the sediment end of the vent pipe allowed air to enter the void created beneath the core tube during extraction, thereby equalizing the pressure. In this manner, the core tube was more easily removed with minimal loss of core material.

Upon recovery of the core, a wooden piston type core extractor was used to remove the intact core from the corer. Cores were pushed out into a trough constructed from a 1.0 m long split section of 10.8 cm (outside dia.) polyvinylchloride pipe. Final core length and core hole depth were recorded in order to document core compaction. All cores were trimmed to a final length of 30.0 cm and sectioned into three 10.0 cm increments. Good et al. (1982) has reviewed the literature

concerning measurements of marsh belowground biomass and concluded that the bulk of all living vascular plant material resides 30.0 cm or less in depth within the sediments, and in a study of a New Jersey S. alterniflora tidal marsh, Smith et al. (1979) found half as much belowground material at the 20-30 cm increment of depth as compared to the 0-10 cm increment. Based on these findings, living vascular plant biomass below 30.0 cm of depth was considered to be insignificant and was not sampled in this study.

Breakage of a core occasionally occurred within the 20-30 cm increment. Recovered cores less than 30.0 cm, but longer than 20.0 cm, in length were retained and trimmed to a final length of 20.0 cm resulting in only two 10.0 cm increments after sectioning. It was concluded that these cores were satisfactory for analysis because breakage usually occurred at a well defined interface between contiguous, intertwined, living roots and rhizomes and decomposing plant tissues having less structural integrity. Thus, nearly all of the living material present was recovered within these "short cores". Cores less than 20.0 cm in length before sectioning were discarded and replaced by other cores of suitable length.

After sectioning, each core increment was placed into an individually labeled plastic bag (Dow Ziplock^R sandwich bags, 16.5 cm x 14.9 cm), sealed, and returned to the laboratory. Cores were kept at 4 C until further processing.

No attempt was made to separate living from dead tissues. Separation techniques based on differential staining (Knieval, 1973) and differences in color and turgidity (Valiela et al., 1976) were found inappropriate for some plant species (de la Cruz and Hackney, 1977).

Because such methods are also tedious, dependent upon judgements by technicians, and time consuming (especially when large numbers of samples are involved), many investigators have reported BGB as a combination of living and dead tissues (Gallagher, 1974; de la Cruz and Hackney, 1977; Good and Frasco, 1979; and Smith et al., 1979).

Processing entailed washing each core increment free of very fine mineral and organic matter. Core increments were hand washed with tap water over a Wildco brass screen sieve having a 520 μm pore size. Washing was considered complete when water passing through the material atop the sieve ran clear. All material retained by the sieve has been defined as macro-organic matter or MOM (Gallagher and Plumley, 1979) and represents the BGB within the salt marsh soils sampled. This material consisted of both living and dead roots, stem bases, and rhizomes.

MOM from each core increment was oven dried for not less than 48 hours at 85 C, weighed to the nearest milligram (Mettler P120 N single pan balance), and recorded as $\text{mg}\cdot\text{cm}^{-3}$ (a 10.0 cm core increment obtained from a core tube having an inside diameter of 7.4 cm contains 430 cm^3). After MOM from each core increment had been dried and weighed the material was stored in individually labeled plastic bags should future access be required. Incremental biomass values in $\text{mg}\cdot\text{cm}^{-3}$ were summed for each individual core and were extrapolated to a per meter square basis to a depth of 30.0 cm using a conversion factor of 232.56, which is the number of cores potentially obtainable from 1.0 m^2 using a corer with an inside diameter of 7.4 cm. A similar conversion was used by de la Cruz and Hackney (1977).

Core samples were collected monthly from six different vegetative cover types from January through December, 1982. Five sample sites were

located on Jacks Creek (Figure 2) and included the vegetation types herbaceous annuals, C. jamaicense, S. cynosuroides, T. domingensis, and J. roemerianus. An additional sample site containing D. spicata located on nearby Jacobs Creek (Figure 3) comprised the sixth vegetative community selected for study.

Kucera et al. (1967) reported that seasonal development of standing crop [above or belowground], cessation of growth [senescence], and transfer to the litter stage are complex occurrences and that within a multispecies community the phenological development, and thus the time of maximum biomass, may not coincide for all components. For this reason large, uniform, nearly monospecific stands of vegetation representative of the dominant marsh vegetative types were selected for study.

Cores for the assessment of BGB were recovered from plots simultaneously sampled by another investigator (Bellis, personal communication) assessing aboveground biomass. This procedure facilitated estimates of total (above and belowground) biomass and annual production based on concurrent sampling. In practice, all cores for BGB determinations were drawn from within the last of three contiguous 0.5m² aboveground clipped plots within each vegetative community. Gallagher and Plumley (1979) selectively sampled marsh plant communities by taking cores either over stems or between stems resulting in two measures of BGB for the same stand of vegetation. Because a measure of mean BGB was desired for each community type independent of their respective, relative stem densities, no such selectivity was applied in this study.

For the first six months of 1982, five cores were removed each

month from each vegetative community. In July, 1982, the number of cores recovered monthly was increased to ten in order to reduce the effects of statistical variation between consecutive cores. This sampling regime continued for the remainder of 1982. Altogether, a total of 90 cores were removed from each plant community giving an annual total of 540 cores.

Aboveground samples were individually placed in plastic trash bags (Hefty^R two-ply) at harvest, returned to the laboratory, and stored at 4 C until processed. Live and dead vegetation within each bag was separated by species and weighted to the nearest 10.0 gm using a Pesola 1 kg hanging scale. After recording total wet weight of a sample, each portion was subsampled (approximately 100 g). Subsamples were placed in #8 brown paper bags, weighed to the nearest gram (Mettler P 120 N single pan balance), oven dried to constant weight at 85 C, and reweighed to the nearest gram. Total dry weight of the original sample was computed and reported as g·m⁻².

Statistical analyses were performed using packaged program procedures accessible through the Statistical Package for the Social Sciences (SPSS) including summary statistics, and one-way analyses of variance (Nie et al., 1975). Periodic regression analysis (Hackney and Hackney, 1977 and Hackney and Hackney, 1978) was performed on BGB data using release 79.6 of SAS (SAS is a registered trademark of the SAS Institute, Cary, North Carolina) computer programs. The one-term periodic regression model used was:

$$Y_j = \alpha_0 + \alpha_1 \sin (CX_j) + \beta_1 \cos (CX_j)$$

where

Y_j = dependent variable (BGB)

α_0 = constant parameter

α_1, β_1 = coefficients of the harmonic function of X.

C = $2\pi/n$

X_j = ith independent variable (numbered day of the year)

RESULTS AND DISCUSSION

Belowground Standing Crop

The surface texture of salt marsh sediments appeared to be closely correlated with plant stem density and the configuration of the roots and rhizomes. Mean macro-organic matter standing crop varied from a low of 5.53 kg·m⁻² for the herbaceous annuals community to approximately twice that value (12.63 kg·m⁻²) for the D. spicata community (Table 3). Highest macro-organic matter standing crop values were obtained for the Distichlis and Juncus communities which grew from shallow rhizomes bearing short internodes. The closely spaced, upright stems and associated adventitious roots produced a fibrous, firm surface. Conversely, Cladium and Typha communities were often associated with a discontinuously textured surface characterized by scattered clumps of stems and associated rhizomes. The Spartina community was intermediate in both standing crop (8.34 kg·m⁻²) and texture between that of Cladium/Typha and Juncus/Distichlis. Herbaceous annuals produced the lowest belowground standing crop values as would be expected from a plant community which is non-rhizomatous and therefore stores no food reserves.

Few published estimates are available for comparisons of belowground standing crop data (Table 3). Of the values that are

Table 3. Estimates of belowground standing crop for six salt marsh plant communities. Estimates derived from this study are based upon yearly means in kg.m⁻² to a depth of 30.0 centimeters.

Plant community	Belowground Standing crop Annual Mean (kg.m ⁻²)	Location	Source
Herbaceous annuals	5.53	North Carolina	This study
<u>Cladium jamaicense</u>	7.44	North Carolina	This study
<u>Spartina cynosuroides</u>	8.34 10.90 ¹	North Carolina Mississippi	This study de la Cruz, 1974
<u>Typha domingensis</u>	2.65 ¹ 9.19	Texas North Carolina	McNaughton, 1966 This study
<u>Juncus roemerianus</u>	7.80 ¹ 8.53 ² 11.38	Mississippi Georgia North Carolina	de la Cruz, 1974 Gallagher, 1974 This study
<u>Distichlis spicata</u>	2.61 ² 12.63	Georgia North Carolina	Gallagher, 1974 This study

¹to a depth of 20.0 cm

²published values that were adjusted to reflect a depth profile of 30.0 cm

available, some represent only a single sampling effort (McNaughton, 1966 and Gallagher, 1974) and/or sampling was completed to a depth of only 20.0 cm (McNaughton, 1966 and de la Cruz, 1974). These inconsistencies make strict comparisons impossible. Currently there is simply insufficient information to support broad conclusions concerning possible floristic or geographic general patterns of belowground biomass distribution.

Although belowground standing crop biomass estimates obtained from this study (5.53-12.63 kg·m⁻²) were generally of the same order of magnitude as those reported elsewhere (2.61-10.90 kg·m⁻²), estimates for the same plant species at different locations were quite divergent. For instance, McNaughton (1966) reported a standing crop biomass for T. domingensis of 2.65 kg·m⁻², an estimate nearly four times greater (9.19 kg·m⁻²) was obtained from this study.

Net Annual Production

Computations

Several methods were used to estimate net annual production (NAP) for each vegetation type. All NAP estimates (Table 4) were derived from variations of the maximum/minimum technique in which NAP is defined as the difference between the maximum and the minimum macro-organic matter measurements obtained during one complete growth cycle.

The maximum/minimum technique using monthly means has been the most frequently used method for estimating NAP. The main disadvantage of this type of data treatment is that it relies on only two extreme values taken from an entire collection cycle. A NAP value derived from

Table 4. Comparison of belowground productivity among six salt marsh plant communities using four methods of estimating net annual production.

Marsh community type	MOM ¹ standing crop annual mean (kg·m ⁻²)	Belowground production (kg·m ⁻² ·yr ⁻¹ to a depth of 30.0 cm)			
		Max. - min. of monthly means	PRA ²	Running means	Duncan's range
Herbaceous annuals	5.53	2.72	1.34	1.01	0.68
<u>Cladium jamaicense</u>	7.44	6.33	2.33	2.38	5.12
<u>Spartina cynosuroides</u>	8.34	4.88	2.16	1.86	0.75
<u>Typha domingensis</u>	9.19	3.39	3.55	2.81	1.26
<u>Juncus roemerianus</u>	11.38	3.28	1.52	2.46	2.41
<u>Distichlis spicata</u>	12.63	3.89	3.69	2.75	0.51

¹macro-organic matter

²periodic regression analysis

this method could not be expected to adequately account for variation inherent in sampling. Periodic regression analysis (PRA) has the advantage of using all values in a data set, not just extreme or averaged values. A periodic curve fitted to all data points will produce maximum and minimum predicted estimates derived from all data points. One disadvantage of the PRA technique is that more harmonics may be required to gain a statistically significant fit than can be explained biologically in terms of seasonal development. If this occurs, other methods of data analysis may be more appropriate (Hackney and Hackney, 1978).

The use of running means effectively reduced the influence of extreme values, thereby, smoothing out cyclical patterns. In this method of analysis individual monthly means were averaged for successive three month periods. In each case the resultant mean was reported for the central month. NAP was then estimated from the difference between annual maximum and minimum running mean values. This type of analysis generally yielded lower NAP values (Table 4) than periodic regression analysis or the maximum/minimum of monthly means. The most conservative estimates of NAP were obtained from Duncan's multiple range test. This method often grouped chronologically non-sequential months into two or more statistically related subgroups, thus interrupting the continuum of the natural growth cycle and making biological interpretation difficult. Duncan's range test was also employed to estimate NAP. This test arranged monthly means into two or more subgroups which were significantly different from one another statistically ($\alpha = 0.05$). NAP was then estimated as the difference between the means of the highest and lowest subgroups. NAP estimates generated using Duncan's range test

were among the lowest obtained (for four of the six vegetation types) and were judged to represent gross underestimates. While it is true that any method which fails to account for decomposition will underestimate NAP, this method seemed especially conservative. It was concluded that predicted NAP values generated by PRA provided the most accurate assessment of BGB. At the very least this method allowed for a more realistic assessment of sample variation even where statistical significance was lowered in terms of actual data to curve fit.

Given the high degree of variation among monthly macro-organic means (Figures 5-10), any estimate of NAP based on the simple maximum/minimum technique using the monthly means was considered to be statistically inappropriate. Less value was placed on NAP values derived from the running means and Duncan's multiple range test because these values seemed too conservative for use. However, their use is not precluded where variability is low and where cyclical patterns are well defined.

Table 5 presents the periodic models for each vegetation type. All prediction curves were carried through two harmonics as these were the only models which could be readily interpreted biologically in terms of a seasonal cycle of development.

Comparison With Other Studies

NAP values obtained in this study were compared to published values available in the literature (Table 6). The NAP values listed here for the present study were not generated using the preferred PRA technique, but rather from the maximum/minimum of monthly means - values which

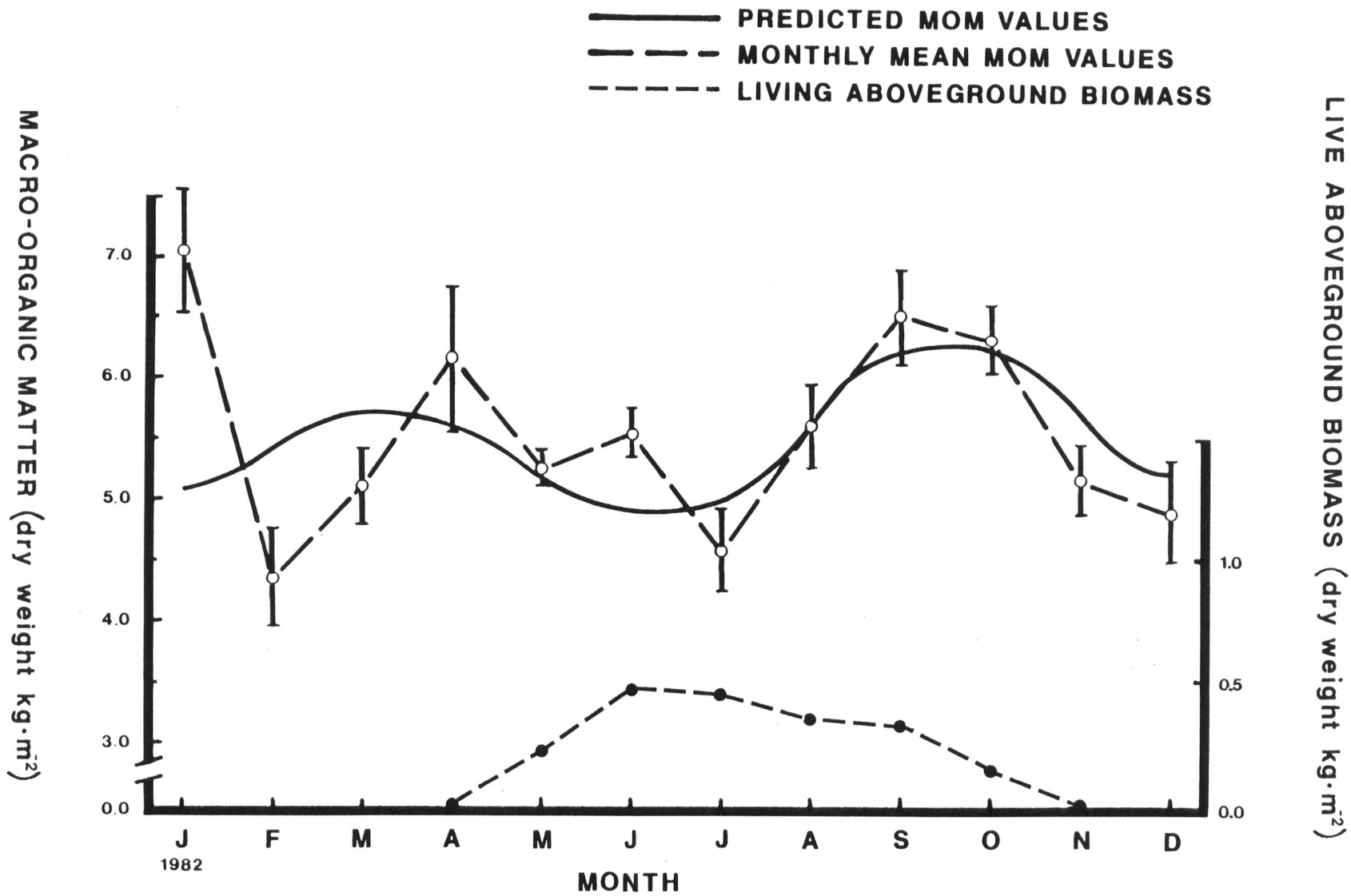


Figure 5. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the herbaceous annuals community. Vertical bars represent ± 1 standard error.

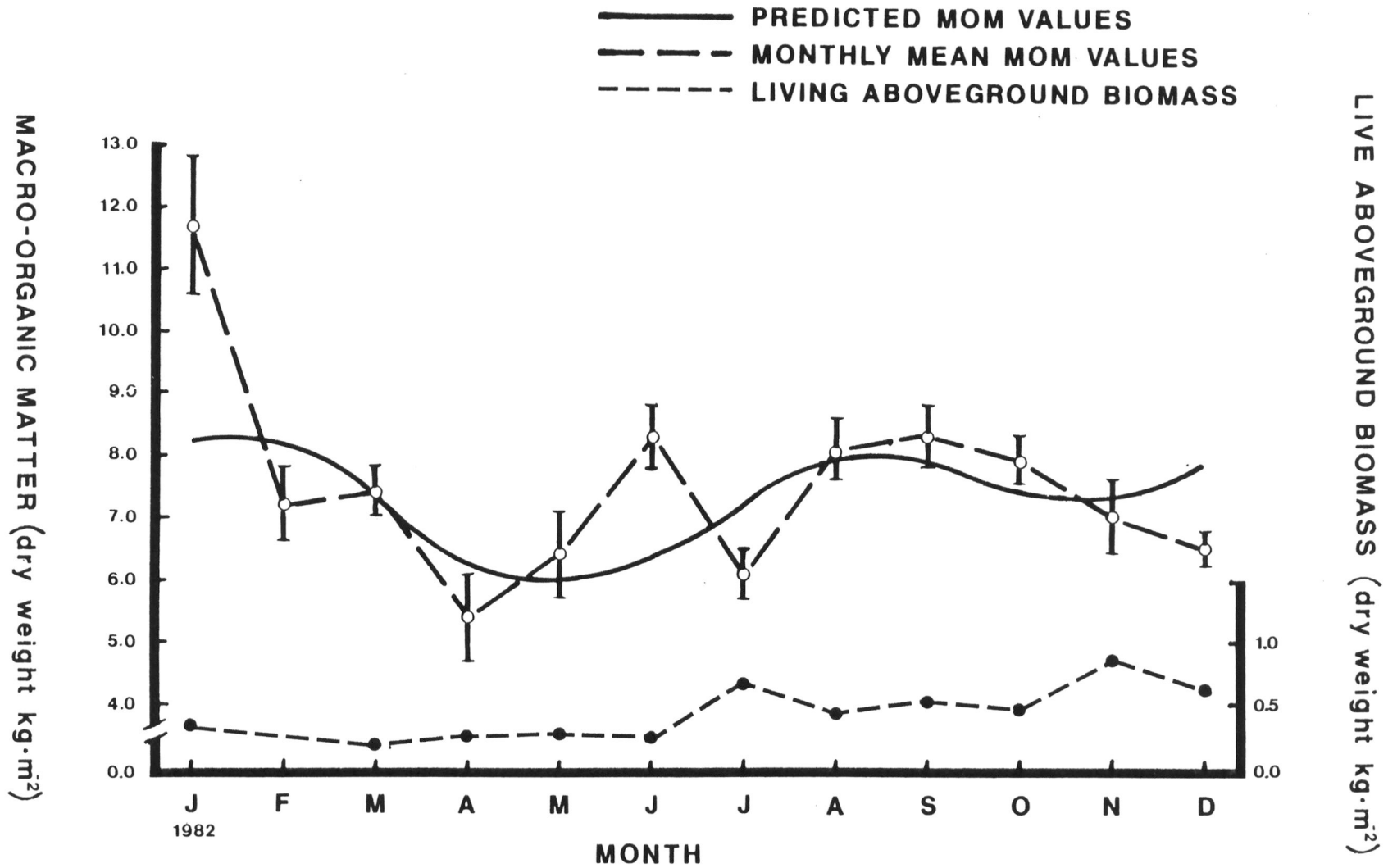


Figure 6. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the *Cladium jamaicense* community. Vertical bars represent ± 1 standard error.

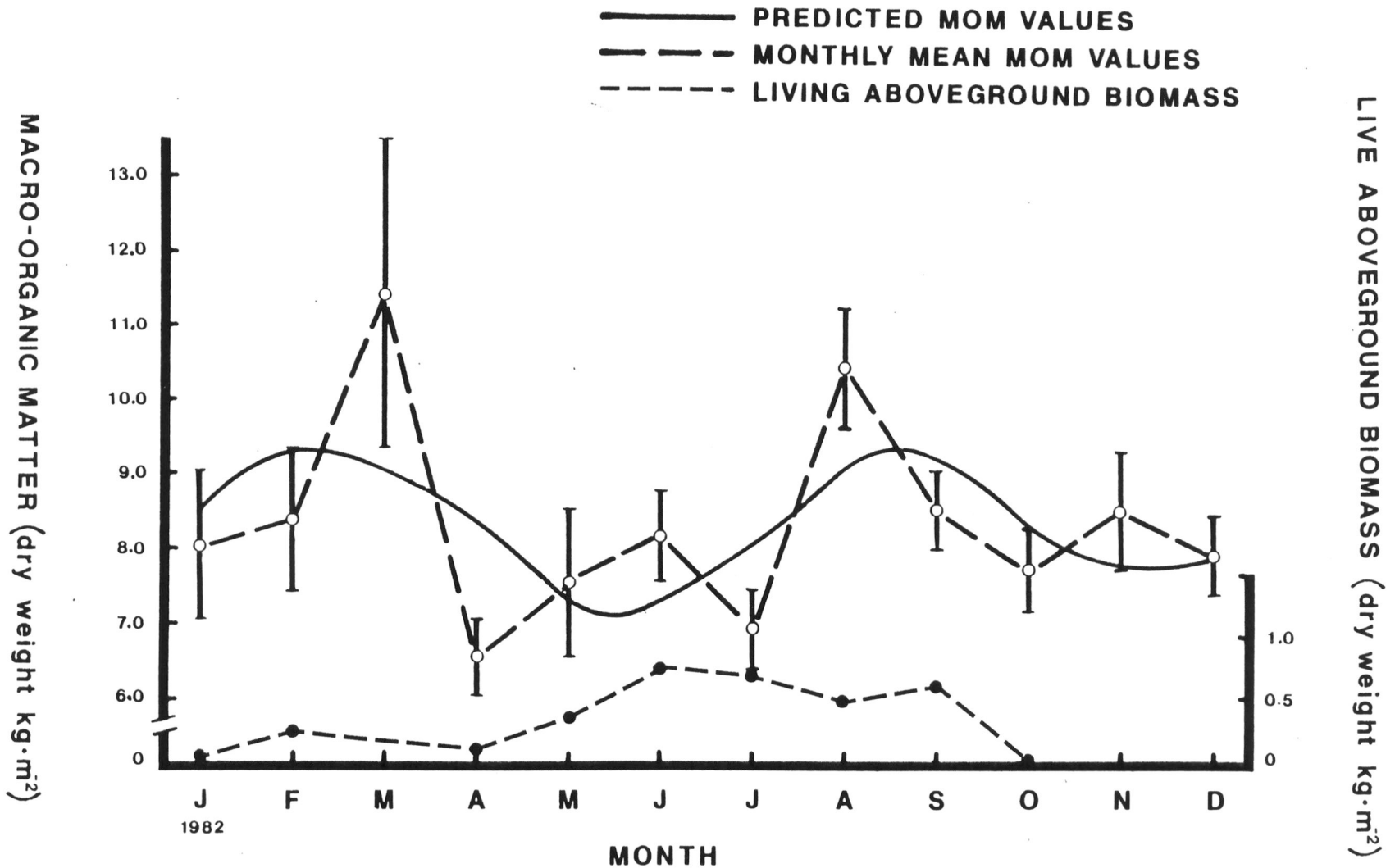


Figure 7. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the *Spartina cynosuroides* community. Vertical bars represent ± 1 standard error.

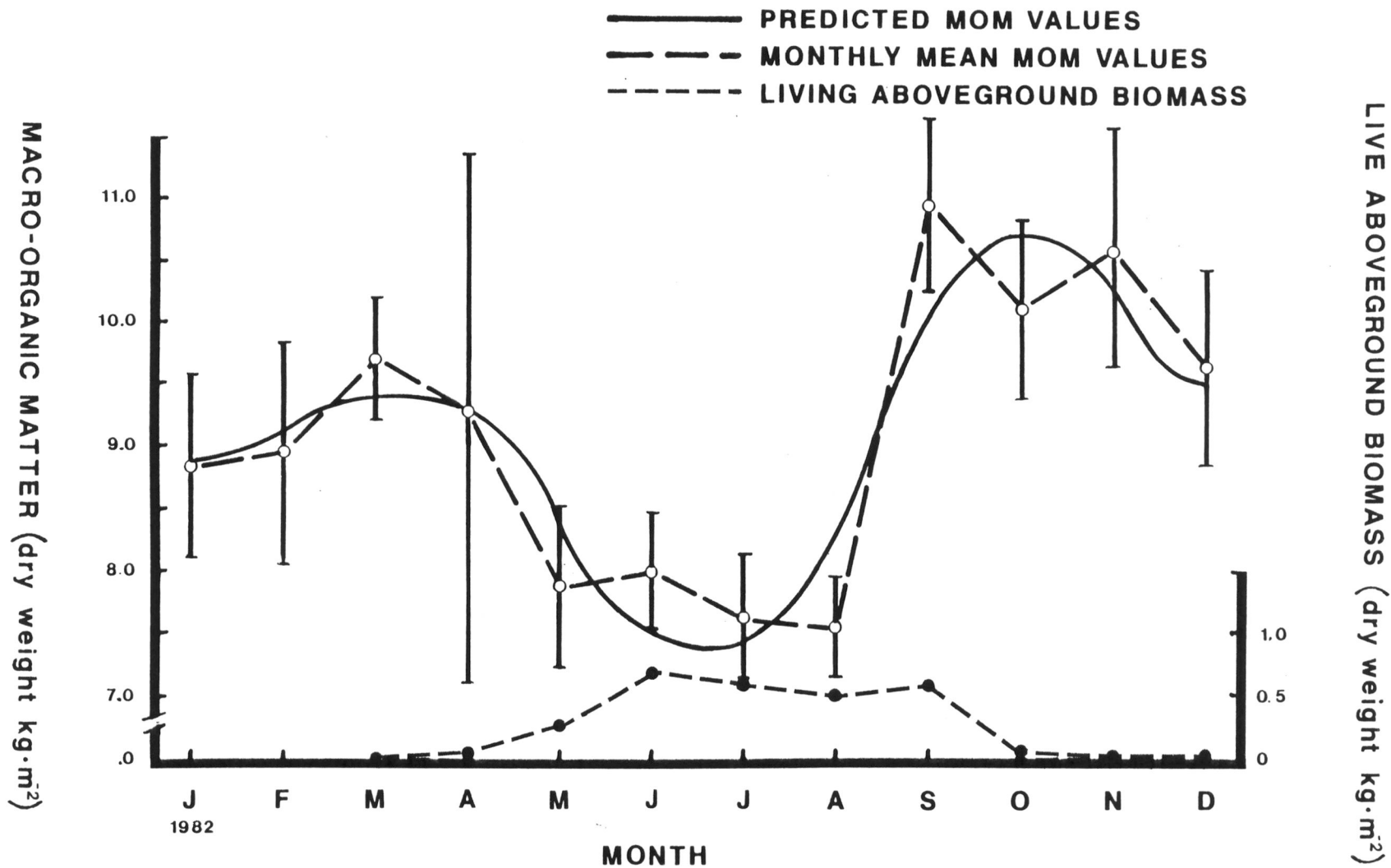


Figure 8. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass the the *Typha domingensis* community. Vertical bars represent ± 1 standard error.

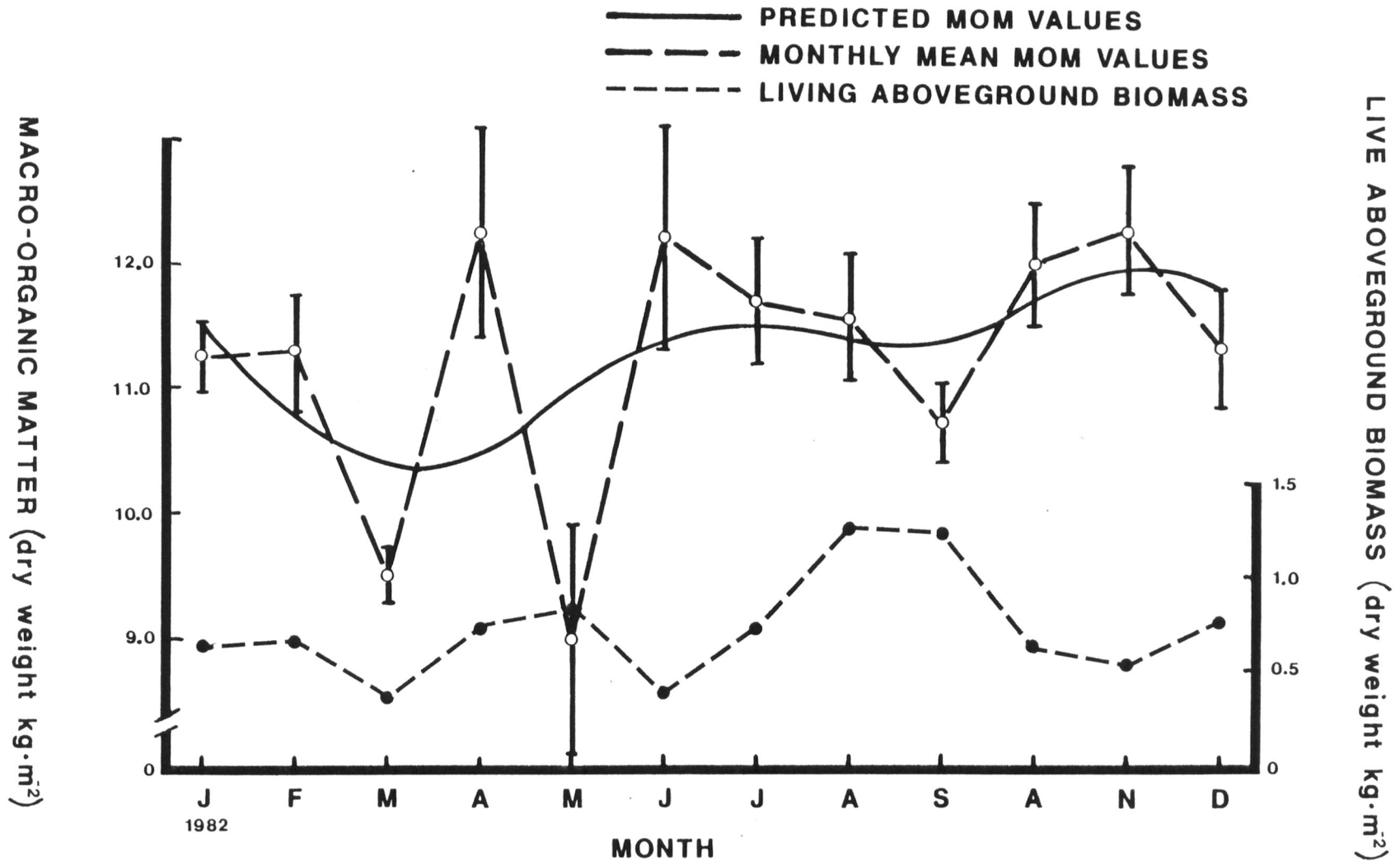


Figure 9. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the Juncus roemerianus community. Vertical bars represent ± 1 standard error.

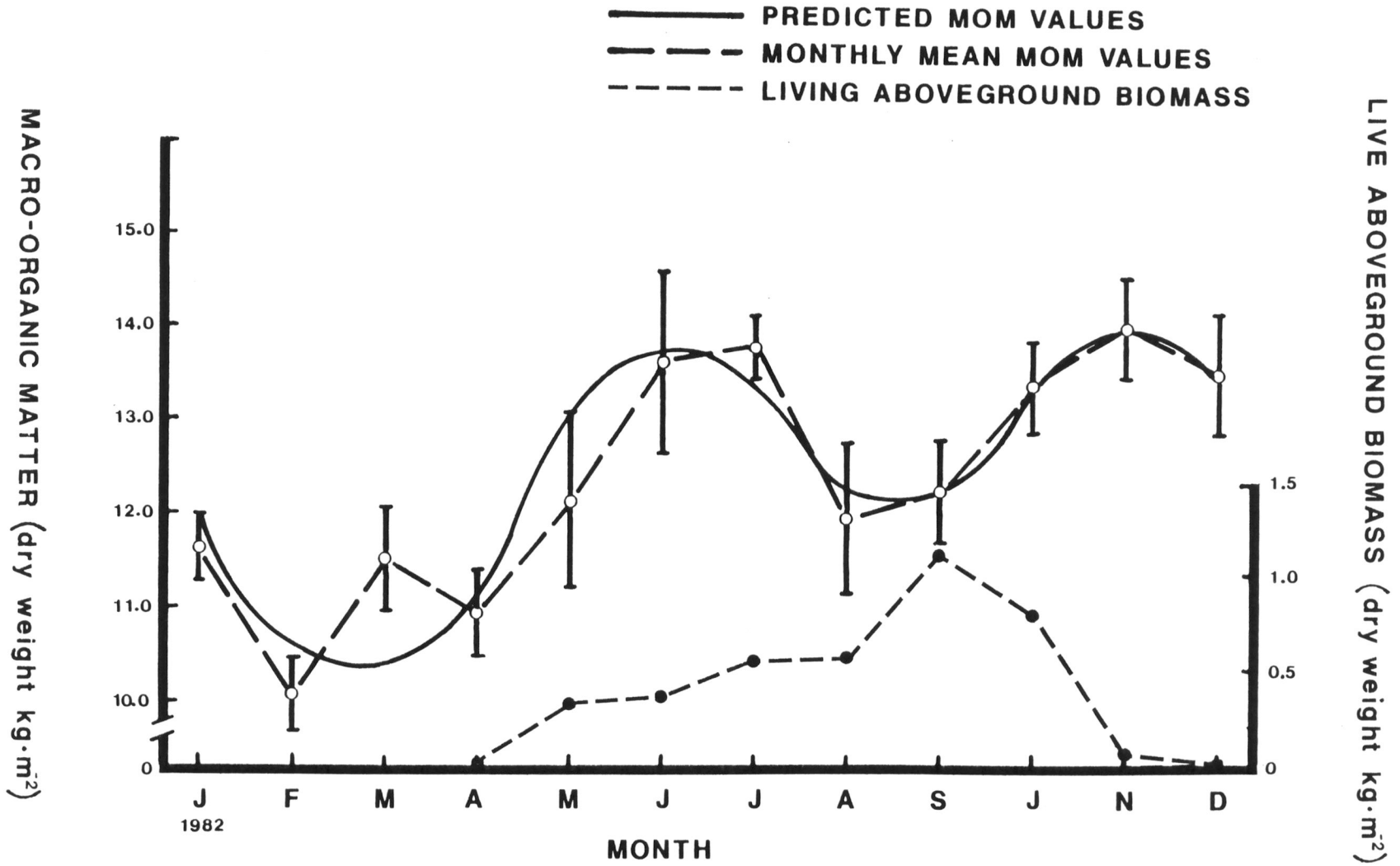


Figure 10. Living aboveground biomass, actual macro-organic matter biomass, and predicted macro-organic matter biomass for the *Distichlis spicata* community. Vertical bars represent ± 1 standard error.

Table 5. Periodic regression models for macro-organic matter in six salt marsh plant communities.

Marsh community type	Probability of > F	R ²	Periodic model ($y=g \cdot m^{-2}$)	Annual mean ($g \cdot m^{-2}$)
Herbaceous annuals	0.0437	0.11	$y=5494.3-295.9\sin(CX_i)+93.1\cos(CX_i)-49.0\sin(2CX_i)-467.4\cos(2CX_i)$	5,532
<u>Cladium jamaicense</u>	0.0671	0.10	$y=7367.4-359.6\sin(CX_i)+612.1\cos(CX_i)+694.3\sin(2CX_i)-45.5\cos(2CX_i)$	7,436
<u>Spartina cynosuroides</u>	0.1708	0.07	$y=8379.0-57.7\sin(CX_i)+222.2\cos(CX_i)+743.3\sin(2CX_i)-579.5\cos(2CX_i)$	8,335
<u>Typha domingensis</u>	0.0009	0.20	$y=9089.1-443.5\sin(CX_i)+1012.7\cos(CX_i)-474.4\sin(2CX_i)-797.8\cos(2CX_i)$	9,194
<u>Juncus roemerianus</u>	0.1895	0.07	$y=11266.7-522.6\sin(CX_i)+121.4\cos(CX_i)-129.0\sin(2CX_i)+344.0\cos(2CX_i)$	11,381
<u>Distichlis spicata</u>	0.0001	0.29	$y=12466.2-939.7\sin(CX_i)-117.5\cos(CX_i)-751.2\sin(2CX_i)+991.8\cos(2CX_i)$	12,629

$$C=2\pi/365$$

X_i =the number of the specific day of the year (1-365) for which a predicted value is desired

Table 6. Belowground productivity estimates for salt marsh plant communities along the western Atlantic and Gulf Coasts, modified from Good et al. (1982).

Marsh community type	Net annual productivity (kg·m ⁻²)	Location	Source
Herbaceous annuals	2.72	North Carolina	This study
<u>Cladium jamaicense</u>	6.33	North Carolina	This study
<u>Spartina cynosuroides</u>	2.20	Mississippi	de la Cruz and Hackney, 1977
	3.56	Georgia	Gallagher and Plumley, 1979
	4.88	North Carolina	This study
<u>Typha domingensis</u>	3.39	North Carolina	This study
<u>Juncus roemerianus</u>	1.36	Mississippi	de la Cruz and Hackney, 1977
	3.28	North Carolina	This study
	3.36	Georgia	Gallagher and Plumley, 1979
	4.4-7.6	Alabama	Stout, 1978
<u>Distichlis spicata</u>	1.07	Georgia	Gallagher and Plumley, 1979
	2.78	New Jersey	Good and Frasco, 1979
	3.40	Delaware	Gallagher and Plumley, 1979
	3.89	North Carolina	This study

tended to be zero to three times larger than PRA estimates. These values, although considered less reliable, are presented because all other published figures are based on the maximum/minimum technique and comparisons should be made free from the bias imposed by a different technique. Estimates of NAP for the S. cynosuroides (4.88 kg·m⁻²) and D. spicata (3.89 kg·m⁻²) communities were greater than values reported in any previous study of these two species (Table 6). NAP for the Juncus community (3.28 kg·m⁻²) was most comparable to an estimate from a Juncus community in Georgia. Both of these values were intermediate compared to extreme NAP estimates from Mississippi and Alabama. No data are available in the literature for comparison of NAP values obtained for T. domingensis and C. jamaicensis (3.39 and 6.33 kg·m⁻², respectively).

As with the belowground standing crop, limited data precludes comparisons, generalizations, and predictions concerning NAP estimates versus geographic location and associated climatic conditions. Good et al. (1982) has reviewed the literature on the NAP of these and other salt marsh species and also concluded that the available data is too fragmentary and variable to enable the delineation of trends. However, they did conclude that belowground production does not seem to follow the trend of gradual increase from north to south apparent in aboveground biomass production. Data from this study when compared with other studies (Table 6) also supports this conclusion.

Belowground Biomass Pathways

Several biological processes could cause belowground biomass to

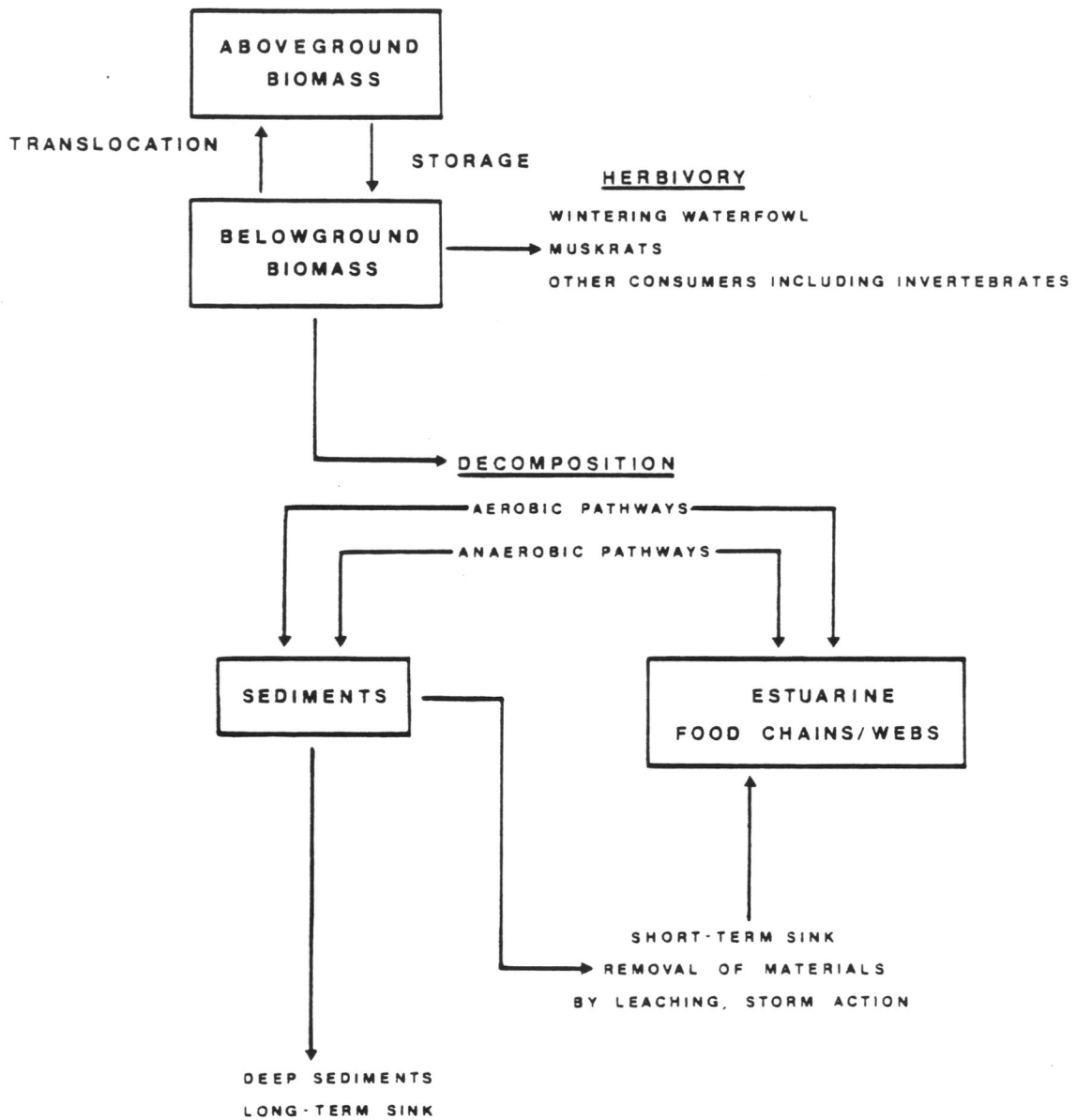


Figure 11. Pathways open to belowground biomass, modified from Good et al. (1982).

increase or decrease (Figure 11). Excess photosynthate might be stored belowground as reserves. Senescence of aboveground plant parts might also contribute to storage. Both processes serve as input modes to belowground biomass. The leaching of roots and rhizomes, decomposition of belowground biomass, new growth of plant parts aboveground, environmental stress on above or belowground vegetation, inflorescence, and seed production could constitute modes of output, all decreasing belowground biomass. Additional reported output modes such as herbivory by geese (Smith and Odum, 1981), muskrats (Lynch et al., 1974) or the burrowing activity of invertebrates like the fiddler crab (Katz, 1980) were not evident within the marshes studied.

General Seasonal Pattern

A single pattern relating actual and predicted BGB values to living aboveground biomass (AGB) was apparent for most of the vegetation types. S. cynosuroides (Figure 9) was a good example of this general pattern. Exceptions to this pattern will be discussed separately.

In late spring living AGB increased as BGB declined. Translocation of nutrients stored in belowground rhizomes upward to support newly initiated shoots could account for the observed spring decrease in BGB. As AGB approached a summer maximum, BGB began to increase, presumably because excess photosynthate was being stored belowground. Maximum BGB typically occurred during summer or late summer. A decline in BGB then ensued coincident with inflorescence production. Translocation of nutrients to reproductive structures from belowground could explain this decrease in BGB. With reproduction completed, AGB rapidly declined with

the coming of winter. As aboveground components senesced, BGB began to increase. With the onset of winter, BGB declined and continued to do so as storage products were lost to leaching, decomposition, or both.

Predicted BGB values based on the PRA model sometimes failed to correspond closely to actual data points based on monthly mean BGB values. In several instances slight increases in BGB were apparent from the PRA model during periods of the year when little or no living aboveground vegetation was present, as in S. cynosuroides (January - March). It was concluded that these apparent increases in BGB should be considered as distortions resulting from extreme variation among actual monthly mean values.

Herbaceous Annuals Community. The herbaceous annuals community, located adjacent to the swamp forest at the headwaters of Jacks Creek (Figure 5), exhibited comparatively high stem density but lower BGB than any of the other vegetation types. Lower BGB values were expected because this was a non-rhizomatous plant community. Initial sampling showed an unusually high BGB content in January (Figure 7) followed by a sharp decline. While decomposition of the previous seasons root mass could account for this decline, the increase in BGB from February to April cannot be accounted for because of the complete absence of living AGB. In fact, sporadic increases and decreases in BGB were seen following the appearance of living AGB in April. This inconsistent pattern was attributed primarily to the more than occasional presence of varying amounts of subfossil wood in the lower core segments. If the steady increase in BGB from July to September is real it appears to correspond to the growth peak of living AGB. Living AGB began to decrease rapidly in September until none remained in November.

Coincident with this decrease was the steady decline in BGB beginning in September, presumably due to decomposition.

PRA of the data is represented in Figure 7. Given a probability of a greater F ($P > F$) of 0.0437 the model (Table 5) should be a good predictor of BGB in this vegetative community, subfossil wood notwithstanding.

Cladium jamaicense Community. This plant community typically consisted of unevenly spaced clumps or culms and exhibited relatively low stem density. This vegetation type is one of two studied here in which portions of the leaves remain green throughout the winter months. Belowground stem bases and rhizomes were typically large and tough. Rhizomes were found to be evenly spaced between culms and were often continuous with adjacent culms.

This plant community followed the general seasonal pattern previously described with respect to BGB and living ABG (Figure 6), the only notable exception being January's comparatively high mean value. Variation was great but not great enough to account for this initially high BGB value. Reinspection of the stored MOM obtained from each of the five cores revealed that a greater number of cores were taken over stem bases rather than between stems. Two of these stem bases were especially large in size. It was felt that the weight contribution of these plant parts raised total BGB to a higher value than would have been obtained otherwise.

PRA of the data offered a reasonably good fit ($P > F = 0.0671$). It would seem that the model (Table 5) might be sensitive to the effects of January's initially high BGB value and that a better fit would be obtained had sampling been more homogeneous.

Spartina cynosuroides Community. The relatively large sample variance that occurred in this vegetative community (Figure 7), was attributed to its habit of belowground growth. Although plants were widely but uniformly spaced aboveground, belowground rhizomes were not. Rhizomes, typically deeply buried, were horizontally elongate and ran from culm to culm as previously noted by Eleuterius (1981). Successful recovery of viable rhizomatous material was mainly dependent upon sampling in close proximity to a stem base or directly over one.

Overall this vegetative community followed the general seasonal pattern with respect to BGB and living AGB. The major deviations in actual BGB values from predicted values (Figure 7) occurred where variation was greatest as in the months of March and August. Due to this variation, PRA yielded a $P > F$ of 0.1708 (Table 5) and, therefore, the data does not fit the model well. Additional harmonics did produce a better fit but the model did not then fit biologically logical seasonal patterns in BGB in relation to living AGB.

Typha domingensis Community. The greatest amount of variation occurred in this vegetative community (Figure 8) for the same reasons discussed for S. cynosuroides in regard to its habit of belowground growth. Stem bases were comparatively tougher, larger, more fibrous, and heavier. Disproportionate sampling over or between stem base could cause a great deal of variation among replicate cores. Aboveground, culms were unevenly spaced while stem density was low.

It is interesting to note that even with extreme variation, PRA yielded an exceptionally good fit to a two harmonic model with a $P > F$ of 0.009 (Table 5). The first cosine term of the model explained most of the data in terms of fit. It would appear that a large amount of

variation among replicate samples worked for the model where the fit may not have been as good at other points throughout the year. One sample value could shift the phase angle of the curvilinear plot sufficiently to gain a good fit. In this particular instance, the model should be used with reservation for prediction purposes.

BGB followed the same general patterns in relation to living AGB as as previously described with no notable exceptions.

Juncus roemerianus Community. The J. roemerianus community exhibited a high stem density aboveground and turgid, tightly interwoven roots and rhizomes belowground. This plant community did deviate from the general pattern at several points. Typically, this community type experienced two peaks in living AGB during the summer months, and a large portion of this component remained alive throughout the winter months (Figure 9). The prediction curve for BGB did not always correspond closely to the actual data ($P > F = 0.1895$). Divergence from the prediction model was greatest when variation among replicate core samples was greatest, as in the months of April through June. Given the compactness of the cores from this community coupled with an inherently high stem density, one might not have expected such great variability among replicate cores. One possible explanation for the observed variation during spring could be that relatively small variations in aboveground stem density may result in large changes in BGB. This cannot be confirmed as we did not record stem density at the time of sampling.

Distichlis spicata Community. D. spicata was characterized by dense growth and high stem density aboveground and small tightly intertwined roots and rhizomes belowground. Such growth characteristics,

indicative of this vegetative community, resulted in the largest annual mean standing crop ($12.63 \text{ kg}\cdot\text{m}^{-2}\cdot\text{yr}^{-1}$) of all the plant communities sampled here.

Unlike the other vegetation types, the prediction curve for this plant community corresponded closely to actual monthly means throughout the entire year (Figure 10). The prediction model exhibited a $P > F$ of 0.0001.

D. spicata also differed from the other plant communities in that as living ABG increased BGB did also. It wasn't until July that BGB started to decline. By that time the aboveground vegetation had become well established. The decline in BGB continued until September when living ABG reached a maximum. The sharp increase in living ABG between August and September could have been caused by an upward translocation of stored reserves to support inflorescence and seed production consequently decreasing BGB. Belowground reserves depleted and reproduction complete, living ABG declined rapidly from September to November. It was hypothesized that as aboveground plant parts senesced, nutrients were translocated into the rhizomes, thereby restocking depleted reserves. Decomposition could account for the slight decline in BGB between November and December.

Distribution of Macro-Organic Matter with Depth

Macro-organic matter (MOM) was not evenly distributed throughout the soil profile within the various vegetative community types (Table 7). MOM decreased with depth within the first twenty centimeters in the herbaceous annuals community, but exhibited an increase below the root

Table 7. Distribution of macro-organic matter (MOM)¹ with depth in six salt marsh plant communities.

Marsh community type	Annual mean MOM values with depth (kg.m ⁻²)		
	0-10 cm	10-20 cm	20-30 cm
Herbaceous annuals	2.51(0.07)	1.26(0.06)	1.76(0.12)
<u>Cladium jamaicense</u>	2.52(0.11)	2.36(0.09)	2.62(0.08)
<u>Spartina cynosuroides</u>	3.58(0.13)	2.87(0.11)	1.67(0.06)
<u>Typha domingensis</u>	3.09(0.12)	3.07(0.13)	3.16(0.10)
<u>Juncus roemerianus</u>	3.82(0.10)	3.83(0.09)	3.72(0.09)
<u>Distichlis spicata</u>	5.54(0.14)	4.30(0.08)	2.71(0.06)

¹mean (standard error)

zone in the 20.0 to 30.0 cm increment. This discontinuous pattern of MOM distribution appeared to have resulted from the fact that these samples were collected near the headwater swamp forest at Jacks Creek. Marsh vegetation has only recently encroached this area and little peat had formed within the silty swamp forest soils. The sudden apparent increase in MOM within the 20.0 to 30.0 cm increment was caused by an abundance of subfossil wood buried at this level which was not a factor at other sample sites.

For J. roemerianus, T. domingensis, and C. jamaicense, MOM values appeared to remain relatively uniform with depth through the 30.0 cm profile. This would be a Type I profile as described by Gallagher and Plumley (1979). Conversely, S. cynosuroides and D. spicata MOM values declined continuously with increasing depth to 30.0 cm, Gallagher and Plumley's (1979) Type 2 profile. Differences in MOM distribution belowground could reflect varying rates of decomposition at different depths in the peat as was demonstrated by Hackney and de la Cruz (1980), to differing habits of growth belowground, or to changing patterns of vegetative cover. A combination of these three factors would be the most likely explanation.

Except in the herbaceous annuals community most of the seasonal variation in MOM occurred within the 0-20.0 cm increment, and it was within this zone of the soil profile that most of the living roots and rhizomes were found. Living roots and rhizomes held cores intact. Because few rhizomes penetrate further than 20.0 cm, breakage of the core sometimes occurred within the 20.0 to 30.0 cm increment as it was extracted from the marsh.

Turnover Time

Belowground biomass turnover times were derived by dividing the maximum monthly MOM value by the annual biomass increment of growth (NAP based on the maximum/minimum of the monthly means) giving a turnover time in years. While turnover rates may give insight concerning relative rates of decomposition, they do not offer details of the process itself (Good et al., 1982). Turnover times for each vegetation type studied are given in Table 8. NAP estimates based on the maximum/minimum of the monthly mean MOM values rather than those based on periodic regression analysis were used to calculate turnover times, because the former method was used by all previous investigators and, thus, should yield turnover times more comparable to those already published.

Generally, plant communities in this study which exhibited relatively low stem density also exhibited a lower MOM turnover time. Such communities included C. jamaicense (1.85 years), S. cynosuroides (2.34 years), and T. domingensis (3.23 years). Alternatively, the D. spicata (3.59 years) and J. roemerianus (3.74 years) communities exhibited comparatively high stem density and revealed longer turnover times. The herbaceous annuals (2.60 years) exhibited the third longest turnover time, however, this elevated value was considered an artifact caused by an abundance of subfossil wood in the 20-30 cm increment.

Some data on turnover time were available in the literature for purposes of comparison. Hackney and de la Cruz (1980) obtained turnover times of 2.33 years for S. cynosuroides and 3.67 yrs. for J. roemerianus from salt marshes in Georgia. These values are in close agreement with

Table 8. Belowground biomass turnover times (years) for six salt marsh plant communities.

Marsh community type	Max. monthly MOM value (kg.m ⁻²)	Annual increment of growth (kg.m ⁻² .yr ⁻¹)	Turnover time (years)
Herbaceous annuals	7.07	2.72	2.60
<u>Cladium jamaicense</u>	11.68	6.33	1.85
<u>Spartina cynosuroides</u>	11.42	4.88	2.34
<u>Typha domingensis</u>	10.95	3.39	3.23
<u>Juncus roemerianus</u>	12.28	3.28	3.74
<u>Distichlis spicata</u>	13.98	3.89	3.59

those derived from this study (Table 8). For D. spicata, studies in Georgia and Delaware (Gallagher and Plumley, 1979) revealed a turnover time of 3.33 years at each location. Again, these values are quite comparable to the turnover time derived from this study for D. spicata (3.59 years). One might expect a longer turnover time from the Delaware study where generally cooler ambient temperatures might slow the rate of decomposition. In a study of New Jersey D. spicata marsh, Good and Fransco (1979) did, in fact, obtain a longer turnover time of 4.50 years. Currently, such differences cannot be readily explained, but it would seem that physical and chemical properties of individual salt marshes might significantly influence decomposition rate, not just temperature.

Belowground/Aboveground Biomass Ratio

Concurrent sampling of belowground biomass (BGB) and aboveground biomass (AGB) has allowed the computation of BGB/AGB ratios for each plant community studied (Table 9). While BGB/AGB ratios may not be strictly comparable to root/shoot ratios available in the literature (Good et al., 1982) they do confirm the findings of previous investigators that greater amounts of fixed carbon reside within the soils of salt marshes than in the aboveground vegetative component. For the salt marsh plants studied here, observed ratios ranged from 4.9 for C. jamaicense to 10.3 for T. domingensis. The herbaceous annuals exhibited a BGB/AGB ratio of 13.8:1, a high value probably due to the presence of subfossil wood within the 20.0 to 30.0 cm increment.

Studies of D. spicata in Georgia (Gallagher, 1974) and New Jersey

Table 9. Belowground/aboveground biomass ratio for six salt marsh plant communities.

Marsh community type	Belowground biomass annual mean (kg.m ⁻²)	Aboveground biomass annual mean (kg.m ⁻²)	B:A ratio
Herbaceous annuals	5.53	0.04	13.8
<u>Cladium jamaicense</u>	7.44	1.51	4.9
<u>Spartina cynosuroides</u>	8.34	1.62	5.1
<u>Typha domingensis</u>	9.19	0.89	10.3
<u>Juncus roemerianus</u>	11.38	1.60	7.1
<u>Distichlis spicata</u>	12.63	1.97	6.4

(Good and Frasco, 1979) revealed root/shoot ratios of 7.2 and 4.5, respectively. An intermediate BGB/AGB ratio of 6.4 was obtained from this study of Distichlis. The BGB/AGB ratio of 7.1 obtained from the J. roemerianus community was most comparable to a root/shoot ratio of 8.2 obtained from a Georgia Juncus marsh (Gallagher, 1974). Much lower ratios were obtained from Juncus marshes in Mississippi (de la Cruz and Hackney, 1977) and Alabama (Stout, 1978), 0.80 and 3.26, respectively.

Investigations by Good et al. (1982) have shown that large root/shoot ratios within salt marsh plant communities result from a disproportionately larger amount of belowground biomass as compared to aboveground biomass. Data from this study supports this observation.

Why is the belowground component so disproportionately large? It has been suggested that a portion of this component might be necessary for the structural integrity and maintenance of the marsh (Good et al., 1982). Roots and rhizomes containing stored food reserves needed for the initiation of new growth, maintenance of aboveground tissues or during periods of extreme environmental stress form another significant fraction of the belowground component. Yet, superficially, it would appear that much more photosynthate is stored than is necessary for winter survival and subsequent rejuvenation. Unfortunately, there are not yet enough data on the belowground component of the salt marsh to adequately assess its complete function and interactions with the estuarine environment.

SUMMARY AND RECOMMENDATIONS

Estimates of belowground standing crop and net annual production from two low salinity marshes of Jacks and Jacobs Creeks fell within the range of values reported for similar marshes along the Atlantic and Gulf Coasts. Net annual production estimates derived from periodic regression analysis were judged to be more realistic than those derived from the simple maximum/minimum technique using monthly means because all data points were used to generate the prediction models.

Macro-organic matter was not evenly distributed throughout the soil profile within the various plant communities. The bulk of this material resided within the 0-20.0 centimeter depth increment which contained most of the living roots and rhizomes.

Relatively lower turnover times were obtained from plant communities which exhibited relatively low stem density while higher turnover times were obtained from plant communities having comparatively high stem density. Turnover times derived from this study were comparable to other published values.

While BGB/AGB ratios are not strictly comparable to root/shoot ratios, they did confirm reports by previous investigators that greater amounts of fixed carbon are produced within the soils of salt marshes than in the aboveground component.

Based on these and other studies it would appear that much more photosynthate is stored belowground than seems necessary for initiation of new growth the following season. Currently, the functional

significance for this apparent excess storage is unclear. Additional studies needed to clarify this phenomenon include: "in situ" decomposition of roots and rhizomes, measurement of belowground biomass and its distribution with depth, the "in situ" growth response to selected stress factors (salinity, hydroperiod, photoperiod, etc.), and quantification of the contribution of living tissues to total belowground biomass for many more salt marshes in different geographic locations. In order to account for the variation inherent in sampling BGB in narrowly confined 0.5 m² plots, it is recommended that concurrent, random sampling be performed to evaluate variation. Also, confirmation of predicted MOM values would be indicated in order to fully evaluate periodic regression analysis modeling.

Studies such as these would help to elucidate the role of the belowground component in the salt marsh and any function the total vegetative component may have in marsh-estuarine interactions.

LITERATURE CITED

- Bellis, V. J. Personal Communication. Department of Biology, East Carolina University, Greenville, North Carolina.
- Bellis, V. J. and A. C. Gaither. Unpublished manuscript. Department of Biology, East Carolina University, Greenville, North Carolina.
- Copeland, B. J., R. G. Hodson, S. R. Riggs and J. E. Easley, Jr. (1983). The ecology of Albemarle Sound, North Carolina: an estuarine profile. U.S. Fish and Wildlife Service, Division of Biological Services, Washington, D.C. FWS/OBS-83/01. 68 pp.
- Cruz, A. A. de la (1974). Primary productivity of coastal marshes in Mississippi. Gulf Res. Rep. 4:351-356.
- Cruz, A. A. de La and C. T. Hackney (1977). Energy value, elemental composition, and productivity of belowground biomass of a Juncus tidal marsh. Ecology 58:1165-1170.
- Dahlman, R. C. and C. L. Kucera (1965). Root productivity and turnover in native prairie. Ecology 46:84-89.
- Eames, G. B. (1983). The late Quaternary seismic stratigraphy, lithostratigraphy, and geologic history of a shelf-barrier-estuarine system, Dare County, North Carolina. Masters Thesis. East Carolina University, Greenville, North Carolina.
- Eleuterius, L. E. (1981). Tidal Marsh Plants. Mississippi - Alabama Sea Grant Consortium, Ocean Springs, Miss. publication number MASGP-77-039. 131 pp.
- Gallagher, J. L. (1974). Sampling macro-organic matter profiles in salt marsh plant root zones. Soil Sci. Soc. Amer. Proc. 38:154-155.
- Gallagher, J. L. and F. Gerald Plumley (1979). Underground biomass profiles and productivity in Atlantic coastal marshes. Amer. J. Bot. 66(2):156-161.
- Gardner, L. R. (1975). Runoff from an intertidal marsh during tidal exposure-recession curves and chemical characteristics. Limnol. Oceanogr. 20:81-89.
- Good, R. E. and B. R. Frasco (1979). Estuarine evaluation study; a four year report on production and decomposition dynamics of salt marsh communities; Manahawkin marshes, Ocean County, New Jersey. Report to N.J.D.E.P. Div. Fish, Game and Shelfisheries. 105 pp.

- Good, R. E., N. F. Good, and B. R. Frasco (1982). A review of primary production and decomposition dynamics of the belowground marsh component. pp. 139-157. In: Estuarine Comparisons, (Ed.) Victor S. Kennedy. Academic Press, New York. 709 pp.
- Hackney, C. T. and A. A. de la Cruz (1980). In situ decomposition of roots and rhizomes of two tidal marsh plants. Ecology 61(2): 226-231.
- Hackney, C. T. and O. P. Hackney (1978). An improved, conceptually simple technique for estimating the productivity of marsh vascular flora. Gulf Research Reports 6(2):125-129.
- Hackney, O. P. and C. T. Hackney (1977). Periodic regression analysis of ecological data. Journal Miss. Academy Sci. XXII:25-33.
- Katz, L. C. (1980). Effects of burrowing of the fiddler crab, Uca pugnax (Smith). Estuar. Coastal Mar. Sci. 11:233-237.
- Keefe, C. W. (1972). Marsh production: a summary of the literature. Contrib. Mar. Sci. 16:163-181.
- Kniefel, D. P. (1973). Procedure for estimating ratio of live to dead root dry matter in root core samples. Crop Sci. 13:124-126.
- Kucera, C. L., R. C. Dahlman, and M. R. Koelling (1967). Total net productivity and turnover on an energy basis for tallgrass prairie. Ecology 48(4):536-541.
- Lynch, J. J., T. O'Neil and D. W. Lay (1974). Management significance of damage by geese and muskrats to Gulf Coast marshes. J. Wildl. Man. 11:50-76.
- McNaughton, S. J. (1966). Ecotype function in the Typha community type. Ecol. Monogr. 36:297-325.
- Nie, N. H., C. H. Hull, J. Jenkins, K. Steinbrenner, and D. H. Bent (1975). Statistical Package for the Social Sciences. McGraw-Hill, New York. 675 pp.
- Nixon, S. W. (1980). Between coastal marshes and coastal waters - a review of twenty years of speculation and research on the role of salt marshes in estuarine productivity and water chemistry. pp. 437-525. In: P. Hamilton and K.B. MacDonald (Eds.) Estuarine and Wetland Processes, Plenum Press, New York.
- Odum, E. P. (1968). A research challenge: evaluating the productivity of coastal and estuarine water. In: Proceedings of the Second Sea Grant Conference. Univ. of Rhode Island, October, 1968. pp. 63-64.

- Smith, K. K., R. E. Good, and N. F. Good (1979). Production dynamics for above and belowground components of a New Jersey Spartina alterniflora tidal marsh. Estuarine and Coastal Mar. Sci. 9:189-201.
- Smith, T. J., III and W. E. Odum (1981). The effects of grazing by Snow Geese on coastal salt marshes. Ecology 62(1):98-106.
- Stout, J. P. (1978). An analysis of annual growth and productivity of Juncus roemerianus Scheele and Spartina alterniflora Loisel in coastal Alabama. Doctoral dissertation. The University of Alabama.
- Stroud, L. M. (1976). Net primary production of belowground material and carbohydrate patterns of two height forms of Spartina alterniflora in two North Carolina marshes. Doctoral dissertation. North Carolina State University, Raleigh, North Carolina.
- Teal, J. M. (1962). Energy flow in the salt marsh ecosystem of Georgia. Ecology 43:614-624.
- Turner, R. E. (1976). Geographic variation in salt marsh macrophyte production: a review. Contrib. Mar. Sci. 20:47-68.
- Valiela, I., J. M. Teal, and N. Y. Persson (1976). Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass. Limnol. Oceanogr. 21(2):245-252.
- Whigham, D. F., J. McCormick, R. E. Good, and R. L. Simpson (1978). Biomass and primary production in freshwater tidal wetlands of the Middle Atlantic Coast. In: R.E. Good, D.F. Whigham, and R.L. Simpson (Eds.), Freshwater Wetlands: Ecological Processes and Management Potential. Academic Press, New York, pp. 3-20.