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AN EXAMINATION OF CARBON FLOW IN A BAY OF FUNDY SALT MARSH

by

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November 1995

A thesis submitted to the Faculty of Graduate Studies and Research

in partial fulfilment of the requirements of the degree of Master's of Science.

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ABSTRACT

This study examines carbon flow in the Dipper Harbour salt marsh, a macrotidal system located on the north-west coast of the Bay of Fundy, New Brunswick. The vegetated marsh surface is composed of three major zones; the *Spartina alterniflora*-dominated low marsh, the *Plantago maritima*-dominated middle marsh, and the *Spartina patens*-dominated high marsh. The total net primary production (NPP) of these dominant macrophytes is 860, 300 and 650 g C m^{-2} yr^{-1}, respectively. In all plant zones, 66% of the NPP occurs in the belowground fraction.

Empirical measurements of organic matter burial indicate that the marsh sediment acts as a carbon sink, accumulating between 75 and 105 g C m^{-2} yr^{-1}. The tidal export of aboveground plant biomass in the form of particulate organic matter accounts for a net loss of carbon ranging from 65 to 170 g C m^{-2} yr^{-1}. An experiment examining the exchange of dissolved organic carbon (DOC) suggest a net annual export of roughly 500 g C m^{-2} yr^{-1}. The forementioned fluxes are combined with estimates of surface gas exchange and algal productivity in order to construct a carbon budget. The budget predicts a DOC export term of 365 g C m^{-2} yr^{-1}, which is of the same order of magnitude as that obtained from the empirical DOC data.

The results of this study show that the *Plantago* zone plays a significant role in the circulation of carbon in the Dipper Harbour salt marsh. This suggests that the patterns of carbon circulation in northern marshes may differ considerably from those in marshes further south where no distinct *Plantago* zone has been reported.

RÉSUMÉ

Cette étude examine la circulation de carbone dans un marais salant situé sur la côte Nord-Est de la Baie de Fundy, au Nouveau Brunswick. La végétation à la surface du marais est divisée en trois zones principales; la zone du bas-marais dominé par *Spartina alterniflora*, la zone centrale dominé par *Plantago maritimo* et la zone du haut-marais dominé par *Spartina patens*. La production primaire totale de ces plantes correspond à 860, 300 et 650 g C m^{-2} an^{-1}, respectivement. La production par la fraction souterraines de ces plantes compte pour 66% de la production totale.

Des mesures empiriques démontrent que 75 à 105 g C m^{-2} an^{-1} sont enterrés dans le sédiment. L'exportation de la biomasse en surface par les marées sous forme de particule de matière organique correspond à une perte de 65 à 170 g C m^{-2} an^{-1}. Une expérience examinant les échanges de carbone organique dissoute (COD) suggèrent une exportation annuelle d'environ 500 g C m^{-2} an^{-1}. Les flux ci-mentionnés sont combinée à des estimations d'échanges gazeux de surface et de productivité d'algues afin de construire un budget de carbone. Le budget prédit une exportation en COD de 365 g C m^{-2} an^{-1}.

Les résultats de cette étude démontrent que la zone de *Plantago* joue un rôle significatif au niveau de la circulation du carbone dans le marais salant de Dipper Harbour. Par conséquence, les modèles de circulation de carbone produits pour des marais situés plus au Sud où la zone de *Plantago* n'est pas présente ne peuvent être appliqués aux marais de la Baie de Fundy.

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INTRODUCTION

Tidal salt marshes are dynamic, evolving coastal features, shaped by the interaction of water, sediment and vegetation. They usually develop on the intertidal mudflats of lagoons or estuaries, occupying a transition zone between terrestrial and marine ecosystems (Redfield 1972). In the upper intertidal zones, the flora is composed of terrestrial species adapted to the high salinity levels and flooding regimes that characterize this environment. Despite such adverse conditions, most salt marsh plant communities are highly productive (Keefe 1972, Turner 1976, Vernberg 1993). Over the past three decades, the ecological significance of tidal marshes has been the focus of some debate which has revolved around the ultimate fate of salt marsh production (Nixon 1980).

Throughout the sixties, it was assumed that salt marshes exported up to one half of their net primary production (Teal 1962) and therefore constituted a significant source of carbon with respect to adjacent coastal marine ecosystems. It was implied that nutrient export from tidal marshes provided an important source of organic carbon and other nutrients to the detrital food chain. This led to the nutrient 'outwelling hypothesis' in which Odum (1968) described salt marshes as "primary production pumps that feed large areas of adjacent waters". However, Odum and the other supporters of the 'outwelling hypothesis' had not quantitatively measured estuarine-marsh nutrient fluxes (Nixon 1980).

A substantially different view of the ecological role of salt marshes appeared when Gosselink *et al.* (1973) stated that "when nutrient-rich effluent enter a marsh the nutrients are effectively trapped by the tidal circulation pattern, and assimilated in the productive biological system". The suggestion that salt marshes act as nutrient sinks with respect to effluent input does not contradict the "outwelling hypothesis" because it places the salt marsh system directly in the transition zone between the terrestrial and marine systems. In other words, salt marshes can be considered as both sinks and sources of carbon.

To ascertain the role of a given marsh as a nutrient source or sink, total exports are subtracted from total imports. Solving this problem requires that all major nutrient fluxes and storage components be quantified in order to determine the overall budget for each nutrient. Although there is a significant amount of evidence to support the role of salt marsh systems as sinks for atmospheric carbon (Nixon 1980, Howes *et al.* 1985, Craft *et al.* 1988, Craft *et al.* 1993) and as sources of carbon for marine systems (Chrzanowski *et al.* 1983, Roman and Daiber 1989, Childers *et al.* 1993), the order of magnitude of these carbon flux estimates is highly variable, preventing any rational generalization. With the exception of Gordon *et al.* (1985) and Magenheimer *et al.* (1996), the majority of the studies on carbon flow have focused on southern marshes, from Delaware to Louisiana. This is understandable since three-fourths of the coastal marshland of eastern North America is located south of Maryland (Chabreck 1988). Information about carbon cycling in northern salt marsh systems, such as those on the coast of the Bay of Fundy, is lacking.

The tidal salt marshes along the coast of the Bay of Fundy differ considerably from those further south in both their hydrological and biological characteristics. The high tidal ranges, which are characteristic of the Fundy region, are unique to the Atlantic coast. Although it is still unclear how such extreme tidal ranges affect the cycling of nutrients in salt marsh, it has been suggested that high tidal ranges may be correlated with high levels of plant productivity (Odum and Fanning 1973, Steever *et al.* 1976). It has also been suggested that the level of energy associated with the Fundy tidal range may create very favourable conditions for the export of plant detritus (Gordon *et al.* 1985). Fundy salt marshes also differ considerably from those located further south in terms of the dominant plant populations. In general, the salt marshes of eastern North America are dominated by *Spartina alterniflora* and *Spartina patens*. *S. alterniflora* tends to occupy the lower marsh elevations near the creekbanks where the surface is most frequently flooded whereas *S. patens* tends to dominate the less frequently flooded high marsh (Redfield 1972, Pomeroy and Wiegert 1981). However, in some marshes of the Fundy region, a third structural dominant can be observed. *Plantago maritima*, a succulent forb, dominates a zone which is located in between the high and low marsh, forming a transition zone between the *Spartina* grasses at an elevation that approximates mean high water. Since *Plantago*-dominated plant communities have not been observed further south, there is very little information available in the literature concerning this forb and the role it plays in the salt marsh carbon cycle.

The purpose of this study was to examine the major carbon fluxes of a Bay of Fundy salt marsh, located at Dipper Harbour, New Brunswick. The core of this study focused on three major hypotheses, each pertaining to a specific carbon flux.

1) The net primary production of the salt marsh macrophytes represents the principal influx of carbon to the system.

II) The salt marsh sediment acts as a carbon sink; a fraction of the vascular plant production is incorporated into the soil where it is stored indefinitely.

III) There is an export of carbon from the salt marsh system to the adjacent coastal waters (i.e., the 'outwelling hypothesis').

Field data were collected over the 1994 growing season, from May to October, in order to test each of the core hypotheses. Estimates for the major flux components were determined individually and assembled in order to produce a carbon budget for the entire salt marsh ecosystem. The net primary productivity of the three dominant macrophytes at the Dipper Harbour salt marsh is the focus of chapter one. Production rates of both the above and belowground plant tissue are addressed in order to determine their overall contribution of organic carbon to the salt marsh system. Chapter two examines the rate of carbon burial within the salt marsh sediment, quantifying the sediment carbon sink. The results from an experiment designed to measure the export of dissolved organic carbon from the marsh to the adjacent coastal waters are presented in chapter three. In the final chapter, a carbon budget for the entire salt marsh system is proposed. The budget, which is based primarily upon the carbon flux estimates presented in the first three chapters, is completed by introducing flux estimates that have been presented in previously reported studies. The carbon budget is used as a tool for the examination of carbon circulation through the Dipper Harbour salt marsh.

Throughout this study, the carbon fluxes which characterize each dominant plant community are examined individually. This approach allows for a comparative analysis between the major plant zones of the Dipper Harbour salt marsh and work conducted on similar plant associations in marshes located further south. Also, since only fragmentary information about the *Plantago*-dominated marsh surface is available, this approach provides a basis for future research concerning the role this forb occupies in the biogeochemical cycles of Fundy salt marshes.

DESCRIPTION OF AREA

The Dipper Harbour salt marsh is located on the eastern coast of Point Lepreau (45°05'N, 66°26'W), a peninsula extending from the northern coast of the Bay of Fundy, 28 km southwest of Saint John, New Brunswick (Figure 1). The growing season begins in mid-April, when mean daily temperatures exceed 0°C, and can last through to mid-October, when nightly temperatures begin to drop below the freezing point.

The tidal range of the marsh varies between 6 and 8 meters. The marsh occupies a 7 hectare area located in an east-west oriented valley bottom common to the region's indented shoreline. The characteristics of the marsh closely resemble those of the "fluvial-minor" type marshes as described by Kelley *et al.* (1988). The seaward side of the marsh is bordered by a 4 m high artificial embankment, upon which sits a secondary road, Highway 790 (Figure 2). Tidal exchange is confined to an 11 m wide channel located under the highway bridge at the mouth of the creek. The drainage network is dominated by a single meandering creek which has carved the marsh surface into neat peninsulas. A few secondary creeks are present.

Figure 1 - Location of the study area in relation to the Atlantic provinces and adjacent Maine.

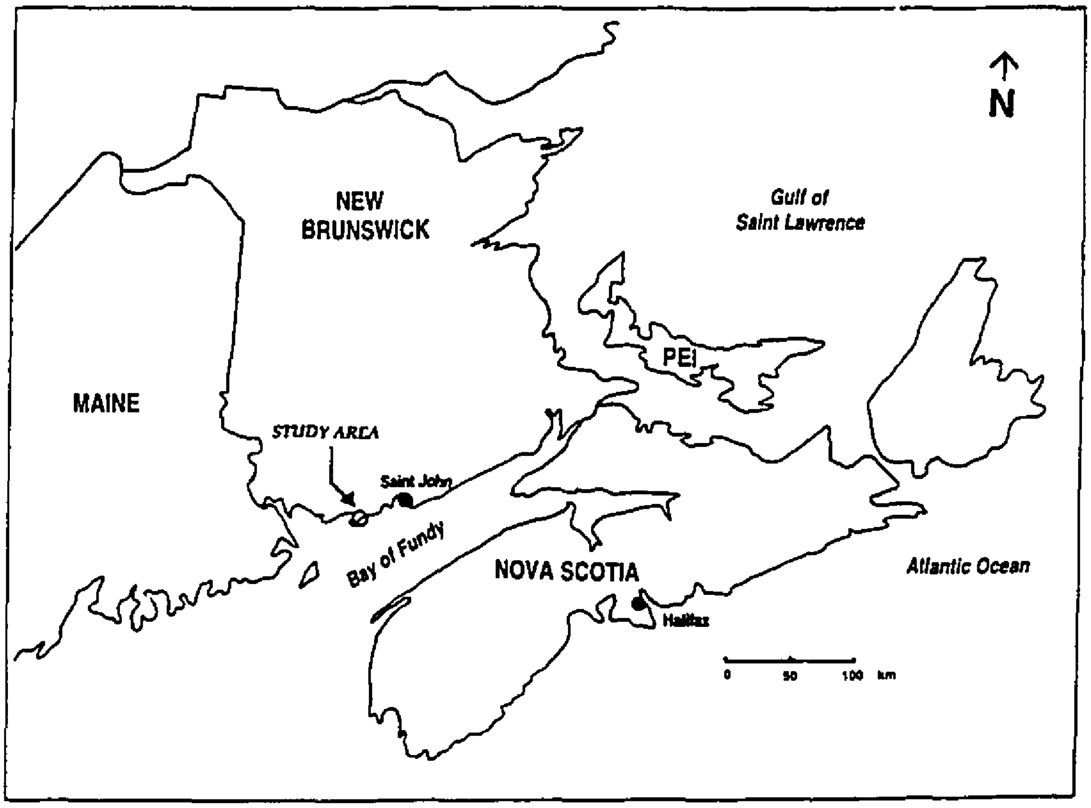
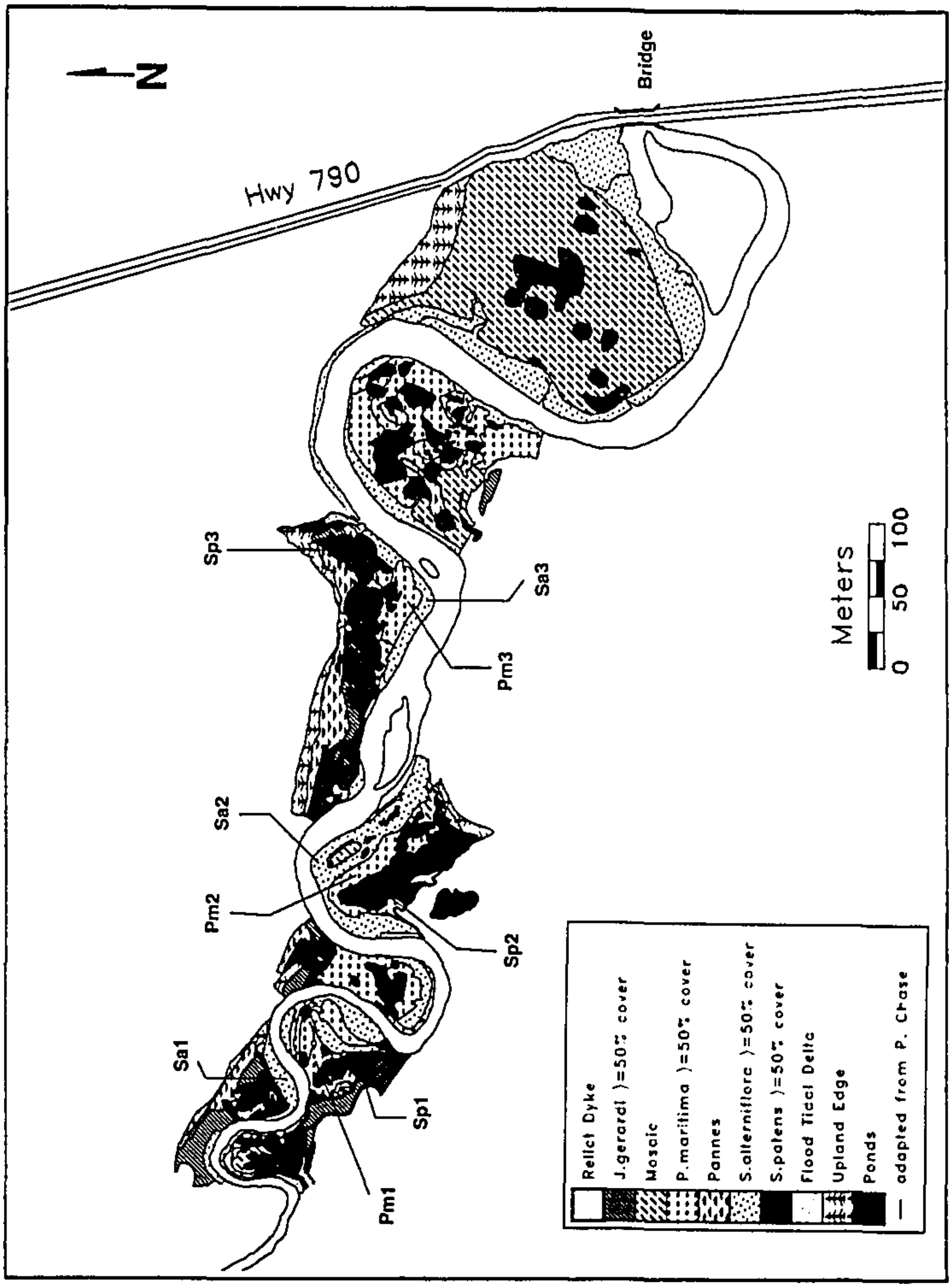


Figure 2 - Vegetation map of the Dipper Harbour salt marsh with sampling locations.



The marsh lies downstream of an 8 km^2 drainage basin occupied primarily by a mixed coniferous forest. The influence of fresh water input from the watershed is notable as water and soil salinity levels decrease inland, from about 28-35 ppt at the bridge outlet to 5-31 ppt at 1.1 km inland. Further inland, the typical high/low marsh physiography (Redfield, 1972) gives way to one resembling brackish systems.

Table 1 - Characteristics of the three dominant plant zones at the Dipper Harbour salt marsh. Flooding frequency was based on all tides between May 1 and August 30, 1994.

	Spartina alterniflora	***Spartina patens***	***Plantago maritima***
Flooding Frequency (%)	92 - 96	49 - 59	56 - 76
Area (m^2)	25662	25503	18211
Dominance (% Cover)	90 - 95	95 - 100	70 - 80

The salt marsh surface is divided into three distinct vegetation zones, which are directly related to flooding frequency (Table 1). The low marsh, dominated by monospecific stands of *Spartina alterniflora*, forms a band ranging to 2 to 20 m in width along the creekbanks. In this zone, the cover percentage of *S. alterniflora* ranges between 90% and 95%, with occasional bare patches accounting for the remaining 5-10%. *Plantago maritima*, a forb, is dominant in the intermediate elevations between low and high marsh. The cover percentage of *Plantago* varies from 70% to 80%, with the remaining surface populated by a combination of *S. alterniflora* (5%), bare patches (5-15%), and other forbs (5-15%). High marsh vegetation is dominated by *Spartina patens* which generally occurs in monospecific stands although some forb species may be present in cover percentages inferior to 5%. Other species found in abundance at the Dipper Harbour marsh include *Salicornia europaea.*, *Juncus gerardi*, *Juncus balticus*, *Triglochin maritima*, *Glaux maritima*, and *Suaeda maritima*.

CHAPTER 1 - PRODUCTIVITY OF THE DOMINANT MACROPHYTES

INTRODUCTION

Primary productivity in tidal salt marshes has received considerable attention over the past few decades. Numerous studies have focused on net aboveground primary production in salt marshes on the eastern coast of North America, from the Gulf of Mexico (Hopkinson *et al.* 1980) to Nova Scotia (Hatcher and Mann 1974). The influence of different harvesting techniques on aboveground productivity estimates has been examined by Kaswadji *et al.* (1990).

The primary production of the belowground biomass pool, which often exceeds aboveground productivity, has also been the focus of numerous studies. Yet, information concerning belowground productivity in Fundy salt marshes is greatly lacking (Gordon *et al.* 1985). *Spartina alterniflora* (smooth cordgrass), the dominant low marsh species all along the northwestern Atlantic coast, has received the greatest amount of attention. Earlier work concerning belowground productivity was reviewed by Good *et al.* (1982), and a number of additional reports have since been published. Despite the use of a variety of estimation methods, a latitudinal pattern has begun to emerge suggesting that belowground productivity decreases with increasing latitude. This pattern is not unlike that for aboveground production observed by Turner (1976).

The majority of net belowground primary productivity estimates are based on seasonal changes in the biomass pool. The Max-Min method used by Gallagher and

Plumley (1979) and by Roman and Daiber (1984) estimates production by calculating the annual increment in total biomass (maximum biomass - minimum biomass). This method has been criticized by Schubauer and Hopkinson (1984) because it does not consider live and dead biomass separately. Another technique by Smalley (1958; *see* Turner 1976), which estimates belowground productivity by summing positive increments in both the live and dead fraction separately, has been used by Schubauer and Hopkinson (1984) and Dame and Kenny (1986). The examination of periodic changes in the live and dead biomass pool provides insight into the seasonal cycles of living and dead material, and therefore represents an essential tool for studying productivity. The processes of biomass translocation and storage can be inferred from seasonal changes in live biomass (Gallagher 1983), and changes in the dead biomass pool provide some indication of the decomposition rates and the long term accumulation of biomass. Although seasonal changes in live belowground *Spartina* biomass have been studied in southern New England (Valiela *et al.* 1976, Ellison *et al.* 1986), seasonal belowground biomass variability in marshes located on or near the Fundy coast has not been documented. Therefore, the examination of seasonal changes in the live and dead belowground biomass pools represents a major focus of this study.

The vertical distribution of underground biomass may also provide valuable insight into the growth processes involved with belowground production. Gallagher and Plumley (1979) examined vertical profiles of belowground macro-organic matter, but they did not separate living and dead tissues. In Georgia, Schubauer and Hopkinson (1984) separated belowground biomass into three fractions (roots, rhizomes, and dead material) and observed evidence of the seasonal storage and redistribution of organic matter between above and belowground *S. alterniflora* tissue. In Massachusetts, Gallagher and Howarth (1987) reported observing seasonal patterns in the distribution of recoverable underground reserves in *S. alterniflora*, but found no significant pattern in *S. patens*. Thus, the timing of peak and minimum biomass is critical to establishing translocation and/or storage dynamics. In this study, a high resolution analysis (2 cm section depth interval) is used in order to determine if similar processes and mechanisms are involved in the growth and accumulation of belowground plant tissue in salt marshes located at high latitudes.

It is the objective of this study to determine the net belowground primary productivity of three structurally dominant macrophytes in a Bay of Fundy salt marsh: *Spartina alterniflora, Spartina patens,* and *Plantago maritima.* Unlike the *Spartina* grasses, which are found in marshes all along the eastern coast of North America, *Plantago* is only dominant in northern marshes and little information about this forb has been available. Aboveground production of these three species is also determined in order to complete the examination of production and growth dynamics, and the seasonal input of carbon resulting from marcrophyte production is assessed. Finally, belowground productivity estimates from the Dipper Harbour salt marsh are compared with those from other studies conducted at different locations and evidence for a latitudinal pattern is addressed.

METHODS

Above and belowground biomass samples of *S. alterniflora, S. patens* and *Plantago* were collected on May 3, July 21, and October 2, 1994. On each of these days, biomass samples were collected at three different locations on the marsh (figure 2), providing three replicates for each species. These locations corresponded to the plant zones in which aboveground dominance (% cover) was greatest. This sampling scheme was adopted so that individual species productivity estimates could be extrapolated to the whole marsh, as a function of aboveground dominance. For the May harvest, the exact location of the sampling site within each plant zone was determined randomly. Plots harvested later in the season were located within 1 m of the May plots. Aboveground biomass was harvested in 0.1 m^2 circular clip plots. This plot size has been used in Massachsetts by Valiela *et al.* (1976) and eceeds the 0.05 m^2 used in Nova Scotia by Hatcher and Mann (1975) to determine peak standing biomass. After the dead and live fractions were separated, the live biomass was washed and dried at 60°C to constant mass, then weighed to yield a value for standing crop.

Once the vegetation had been clipped, a 16.5 cm-diameter aluminum core was twisted into the centre of the clip plot to a depth of 40 cm. Cores were cut into 2 cm sections and stored at 5°C until they could be processed. Core sections were washed over a 1 mm sieve with a garden hose. The biomass retained on the sieve was separated into live and dead fractions. Live material was turgid and light in colour, and tended to float, whereas dead material was darker, more flaccid, and tended to sink. The separated fractions were dried at 60°C to constant mass, and weighed. Unlike the *Spartina* belowground biomass, the *Plantago* biomass was dark and woody, and often broken into small fragments.

As a result, the separation of belowground *Plantago* tissue into live and dead fractions was not possible. However, the *Plantago* biomass was washed, dried, and weighed using the same technique as the *Spartina* biomass.

Although all cores were extracted to a depth of 40 cm, it became apparent through processing that only *S. alterniflora* cores maintained consistent amounts of biomass at that depth. Below 30 cm-depth, the *S. patens* cores contained mostly *S. alterniflora* and *Plantago* biomass, and therefore *S. patens* analysis was limited to the top 30 cm of the profile. For *Plantago*, the transition to another species was located at a depth of 20 cm, below which only *S. alterniflora* biomass was present.

Belowground production was estimated using the technique of Smalley (1958; *see* Turner, 1976). Although originally developed to estimate aboveground production, this method has been used to estimate belowground production (Schubauer and Hopkinson, 1984; Dame and Kenny, 1986). Smalley's technique involves summing periodic changes in the mass of live and dead material through the annual growth cycle. Annual production is assumed to be the sum of production between sampling intervals which is calculated as follows: 1) if changes between sampling intervals is positive for both live (L) and dead (D) material, the production equals the sum (L+D); 2) if L and D are negative, production is assumed to be zero; 3) if L and D are + and -, respectively, then production is equal to L; 4) if L and D are - and +, respectively, production is assumed to be equal to the sum (L+D) if the sum is greater than zero, and equal to zero if the sum is negative (Turner 1976). Since live and dead fractions were not separated in the *Plantago* samples, the Max-Min method (Gallagher and Plumley 1979) was used to determine the belowground production of this forb.

RESULTS AND DISCUSSION

Aboveground Production

Peak standing crop was observed in October for all three species although the aboveground growth of *Plantago* from July to October was not significant. Mean standing crop measurements for each sampling event are given in table 2. Increase in standing crop of aboveground *Spartina alterniflora* biomass was greater during the spring to early summer period than from July to October. Increase of *Spartina patens* was similar for both sampling intervals. It appears that the majority of *S. alterniflora* production occurs the first two to three months of growth, whereas *S. patens* production rates appear constant throughout the growing season. Average standing crop values for *Plantago* were similar for both July and October, suggesting that most aboveground production occurs prior to July. *Plantago* produced seed in late July and most stands were well into senescence by October. The onset of the senescence period for *S. alterniflora* was observed in September. During the October sampling period, *S. patens* still appeared green and healthy, suggesting that senescence had not yet begun. Therefore, values for peak standing crop of *S. patens* may be underestimated.

There was a noticeable spatial trend in standing crop measurements of *S. alterniflora*. The biomass at the site nearest to the seaward end of the marsh (Sa3) was consistently 44% higher at each sampling event than the two sites further upstream. No observable trend regarding standing crop of *S. patens* and *Plantago* was observed.

Table 2 - Standing crop measurements and net aboveground primary productivity (NAPP) estimates for the three dominant macrophyte species of the Dipper Harbour salt marsh. Numbers in brackets represent the standard deviations from the mean of three replicates.

		S. alterniflora	*S. patens*	*Plantago*
Standing Crop (g dry wt m^{-2})	May	8 (6)	0 (0)	20 (4)
	July	335 (56)	164 (19)	221 (57)
	Oct.	460 (92)	379 (82)	224 (43)
NAPP (g dry wt m^{-2})		**718 (144)**	**500 (108)**	**296 (57)**

Peak standing crop for *S. alterniflora* (Table 2) at Dipper Harbour is slightly lower than the 558 g dry wt m^{-2} reported for a salt marsh on the Atlantic coast of Nova Scotia (Hatcher and Mann, 1975), or the 563 g dry wt m^{-2} reported for marshes in the Minas Basin at the northern tip of the Bay of Fundy (Gordon *et al.*, 1985). The value reported here for *S. patens* is close to that of Gordon *et al.*, which was 371 g dry wt m^{-2}. Similar reports concerning *Plantago* were not found.

Net aboveground primary production (NAPP) was estimated as a function of peak standing crop. Peak standing crop itself is not a reliable estimate for NAPP because it does not account for leaf and stem loss during the growing season. Therefore, a suitable multiplication factor was needed to account for the loss of aboveground plant tissue during the growing season. Kaswadji *et al.* (1990) estimated that NAPP for *S. alterniflora* in Louisiana was 1.73 times greater than peak standing crop. Morris and Haskin (1990) determined that leaf and stem turnover accounted for more that 50% of their NAPP estimates for a South Carolina salt marsh, but they "expect lower leaf turnover where stem age is limited to <12 months", i.e., limited by a period of senescence. Houghton (1985) concluded that leaf and stem mortality accounted for 23-25% of *S. alterniflora* NAPP in a Long Island, New York, salt marsh. Hatcher and Mann (1975) measured a 21% loss of *S. alterniflora* live aboveground biomass over the growing season and concluded that NAPP was 1.27 times greater than peak standing crop on the eastern coast of Nova Scotia. Finally, Gordon *et al.* (1985) reported that 46% of low marsh *S. alterniflora* NAPP was lost over the growing season in the Minas Basin, as compared to 24% for species located in the high marsh.

Due to its relative proximity to the Minas Basin (roughly 200 km), the Dipper Harbour marsh is subject to very similar environmental conditions. The climatic conditions are virtually identical and the tidal range at both these sites greatly exceeds that of any other study site. It is assumed, therefore, that the loss factors observed in the Minas Basin by Gordon *et al.* (1985) can be applied to the Dipper Harbour marsh, and given that peak standing crop equals the difference between NAPP and growing season loss, NAPP at Dipper Harbour can be estimated from peak standing crop as follows:

For low marsh (*S. alterniflora*);

$$\text{NAPP} - 46\%\ \text{NAPP} = \text{Peak standing crop}$$

Thus, $\text{NAPP} = (1/.64)\ \text{Peak standing crop} = 1.56 \times \text{Peak standing crop}^{*}$

For middle and high marsh (*Plantago* and *S. patens*);

NAPP - 24% NAPP = Peak standing crop

Thus, NAPP = (1/.76) Peak standing crop = 1.32 X Peak standing crop*

* Peak standing crop is assumed equal to October standing crop.

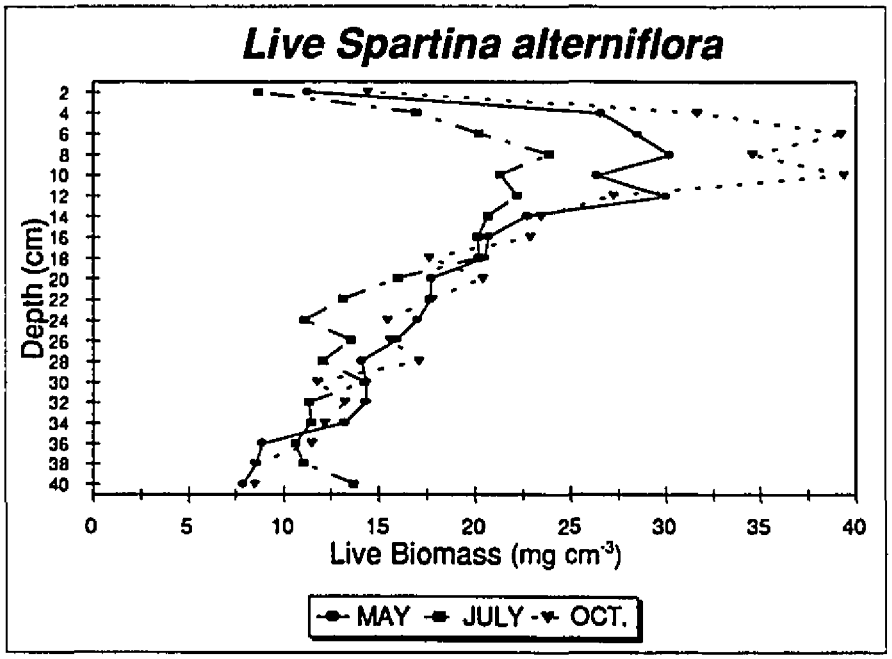
These loss factors exceed those reported for salt marshes in Long Island (Houghton, 1985) and on the Atlantic coast of Nova Scotia (Hatcher and Mann, 1975), both of which are characterized by low tidal ranges (<3 m) and the absence of a seaward barrier. The multiplication factor for the *Plantago* and *S. patens* is lower than that for the low marsh because more frequent flooding and wave action promotes more leaf loss in the low marsh (Gordon *et al.*, 1985). NAPP estimates are given in table 2.

The *S. alterniflora* NAPP estimate for the Dipper Harbour salt marsh is slightly lower than the 703 g dry wt m^{-2} reported for Maine by Turner (1976), as well as the 710 g dry wt m^{-2} and the 803 g dry wt m^{-2} measured on the Atlantic coast of Nova Scotia by Hatcher and Mann (1975) and Livingstone and Patriquin (1981), respectively. However, the *S. alterniflora* NAPP estimate from this study exceeds the 637 g dry wt m^{-2} observed in the Minas Basin by Gordon *et al.* (1985). The NAPP estimate for *S. patens* NAPP at Dipper Harbour was higher than the 403 g dry wt m^{-2} observed in the Minas Basin (Gordon *et al.* 1985). The NAPP estimates for both *Spartina* grasses fall into the lower end of the 300-3000 g dry wt m^{-2} range that characterizes salt marsh production along the Atlantic coast of North America (Turner 1976).

Seasonal Variability in the Distribution of Belowground Biomass

Throughout the growing season, belowground biomass of both *Spartina* species was relatively small in the top 2 cm (Figures 3 and 4), but increased dramatically to a maximum at 4 cm (*S. patens*) and 6-10 cm (*S. alterniflora*). In Massachusetts, Valiela *et al.* (1976) found the greatest concentration of belowground biomass at 2-5 cm for both high marsh *S. patens* and low marsh *S. alterniflora*. They concluded that these large concentrations just below the surface were adjacent to the site of optimum nitrogen fixation and absorption and at a depth where the rhizomes were protected from ice rafting. The greater depth at which *S. alterniflora* peak biomass is observed in this study may be a response to the greater extent of freezing in the Fundy region. As the process of ice rafting occurs primarily in the low marsh - below mean high water - *S. alterniflora* may exhibit a tendency to store its underground biomass reserves at a slightly greater depth than *S. patens*. However, the depth of the water table, which was not reported by Valiela *et al.* (1976), provides another possible explanation for the depth of peak biomass. A low water table may increase the redox potential in the upper portion of the sediment and enhance nitrogen fixation (Pomeroy and Wiegert, 1981). At Dipper Harbour, observations from piezometers placed within the marsh (Figure 13) indicated that the water table can drop below 40 cm., which is lower than the maximum 20 cm depth reported in the Great Sippewissett marsh by Howes *et al.* (1986). Therefore, nitrogen fixation in the Dipper Harbour sediment may be possible at a lower depth than in Massachusetts, hence accounting for the increased depth of the active rhizosphere where the greatest concentration of belowground biomass is located.

Figure 3 - Vertical profiles of belowground *S. alterniflora* biomass. Points represent the mean of three replicates.



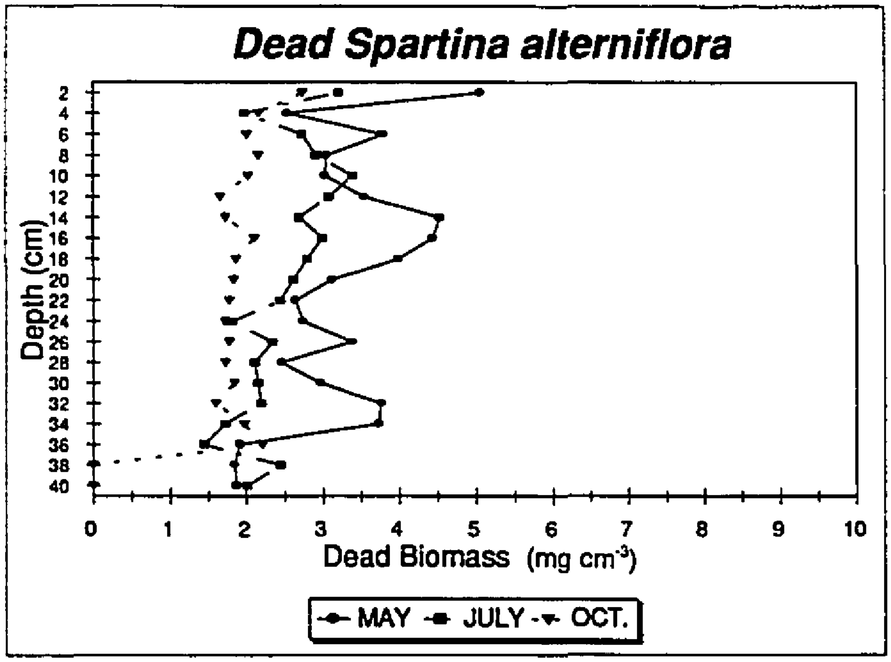
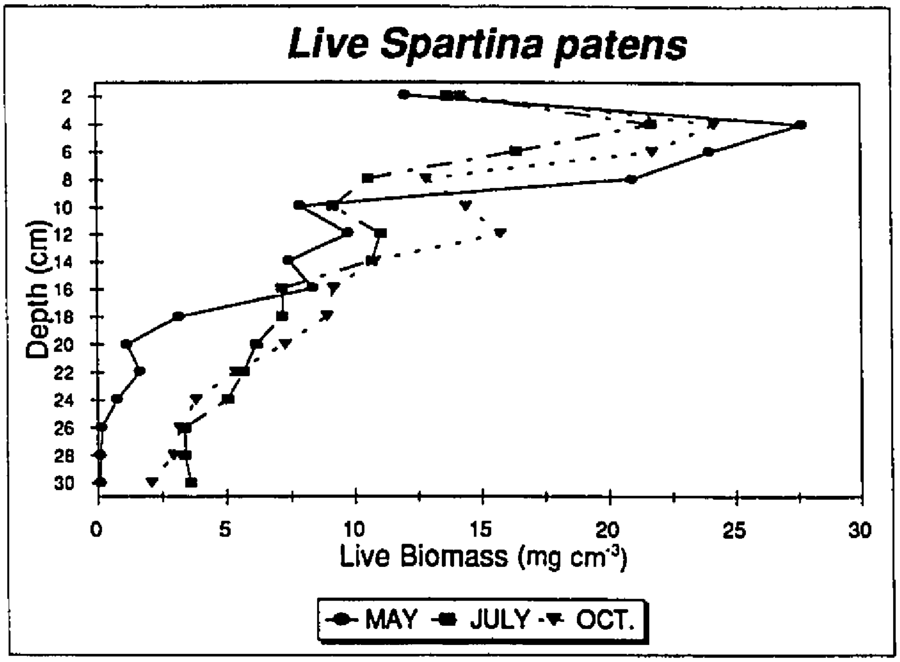
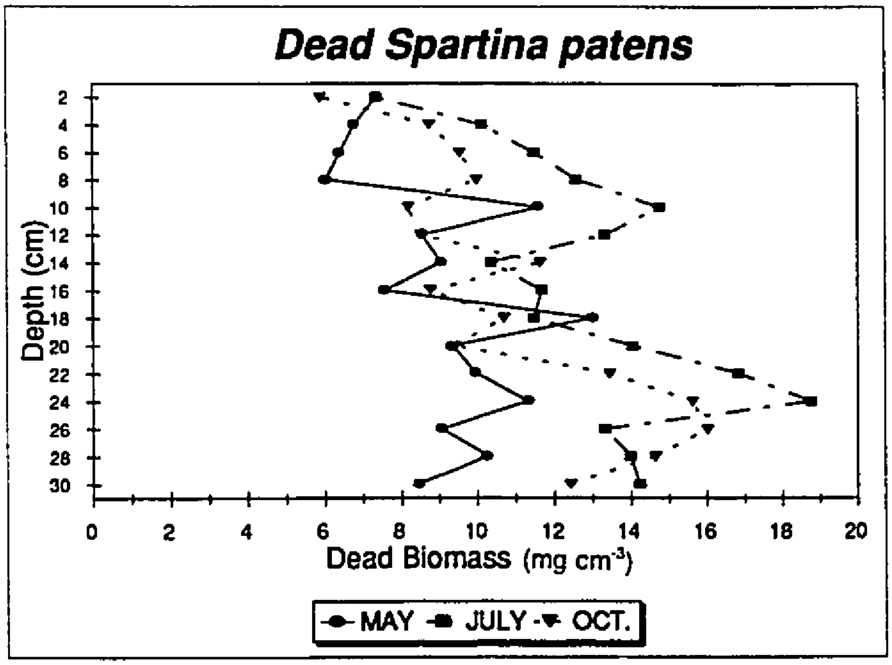


Figure 4 - Vertical profiles of belowground *S. patens* biomass. Points represent the mean of three replicates.





Seasonal patterns were observed in the vertical distribution of both live and dead fractions of belowground biomass (Figures 3 and 4). For *S. alterniflora*, changes in the average concentration of live belowground biomass were only significant in the top 16 cm of depth (Table 3). Live *S. alterniflora* biomass decreased by an average of 26% ($P<0.05$, *t*-test) over the 0-16 cm interval from May to July, and then increased by 51% ($P<0.01$, *t*-test) from July to October. This pattern is consistent with the translocation of live belowground biomass to aerial tissue in the earlier stages of the growing season, when the aboveground production rate is greatest (Table 2), followed by an input of biomass from photosynthesis after July, and culminating in a seasonal biomass peak in October. Gross *et al.* (1991) observed a similar pattern in Delaware in tall form *S. alterniflora*, reporting that the live belowground maximum, which occurred between September and November, was three times greater than the 800 g dry wt m^{-2} minimum which occurred in July. An identical seasonal trend has been observed in Massachusetts by Gallagher and Howarth (1987) who predict that the amount of recoverable underground reserves, and therefore the magnitude of the translocational pattern of *S. alterniflora*, increases with increasing latitude. Although this study focused on biomass rather than recoverable underground reserves, the results presented here demonstrate that the translocation of belowground biomass does play an important role in the seasonal growth pattern of *S. alterniflora* at Dipper Harbour. However, the magnitude of the translocation observed at Dipper Harbour does not exceed that reported in Delaware by Gross *et al.* (1991), suggesting that there may be a northern limit to the latitudinal pattern beyond which the pattern's amplitude ceases to increase.

In the vertical profile for live *S. patens* (Figure 4), there appears to be a drop in live biomass over the top 10 cm from May to July, but this change is not significant. This suggests that the translocation of live belowground biomass to the stems and leaves of *S. patens* from May to July is minor. Seasonal trends in the growth of aboveground biomass (Table 2) support this assumption since the production rate of *S. patens* in the May-July period (43% of peak standing crop) is much lower than that of *S. alterniflora* (78% of peak standing crop). Therefore, the need of underground reserve storage as a biomass pool for spring shoot growth by *S. patens* may be of considerably less importance than it is for *S. alterniflora*. At the 16-30 cm depth interval, live *S. patens* belowground biomass increased by 384% ($P < 0.01$, *t*-test) from May to July. The period between July and October showed no significant change in live *S. patens* biomass. Much of the difficulty encountered in establishing significant changes in the live fraction of belowground *S. patens* biomass stems from its high spatial variability; the standard errors for *S. patens* (Table 3) are much higher than for *S. alterniflora*. Nonetheless, the quantitative evidence suggests that the live fraction of belowground *S. patens* biomass exhibits only minimal seasonal variability with no distinct biomass peak. This conclusion is supported by the observations of Gallagher and Howarth (1987) who found that *S. patens* recoverable underground reserves in Massachusetts remain high throughout the summer.

Table 3 - Seasonal belowground biomass for the three dominant plant species at Dipper Harbour. The standard deviation from the mean of three replicates is given in parentheses. Negative values indicate a net decrease in biomass between two sampling periods. Significant changes in biomass, as determined by a paired Student t-test ($P<0.05$), are presented in bold type.

		BELOWGROUND BIOMASS			CHANGE IN BIOMASS			
	Depth Interval (cm)	**May**	**July**	**October**	**May - July** (g dry wt m^{-2})	(%)	**July - October** (g dry wt m^{-2})	(%)
		----------------	(g dry wt m^{-2})	----------------				
S. alterniflora	0 - 16	3926 (776)	3077 (514)	4652 (702)	**-849**	26	**1575**	51
LIVE	16 - 40	3406 (525)	3169 (509)	3392 (311)	-237	7	223	7
	total	7332 (1301)	6246 (1023)	8044 (1013)	-1086	15	1798	29
	0 - 16	600 (175)	461 (174)	332 (159)	**-139**	23	**-128**	28
DEAD	16 - 40	689 (258)	522 (201)	363 (166)	**-167**	24	**-156**	30
	total	1289 (433)	983 (375)	695 (325)	**-306**	24	**-285**	29
S. patens	0 - 16	2365 (1361)	2009 (694)	2463 (1302)	-354	15	545	23
LIVE	16 - 30	143 (74)	687 (410)	671 (285)	**545**	384	-16	2
	total	2508 (1435)	2696 (1104)	3134 (1587)	191	8	438	16
	0 - 16	1268 (498)	1836 (563)	1428 (580)	**568**	45	**-409**	22
DEAD	16 - 30	1429 (364)	2055 (911)	1846 (1516)	**625**	44	-209	10
	total	2697 (862)	3891 (1474)	3274 (2096)	**1193**	44	-618	16
Plantago LIVE + DEAD	0 - 20	2253 (1725)	1634 (736)	1606 (739)	-620	28	-28	2

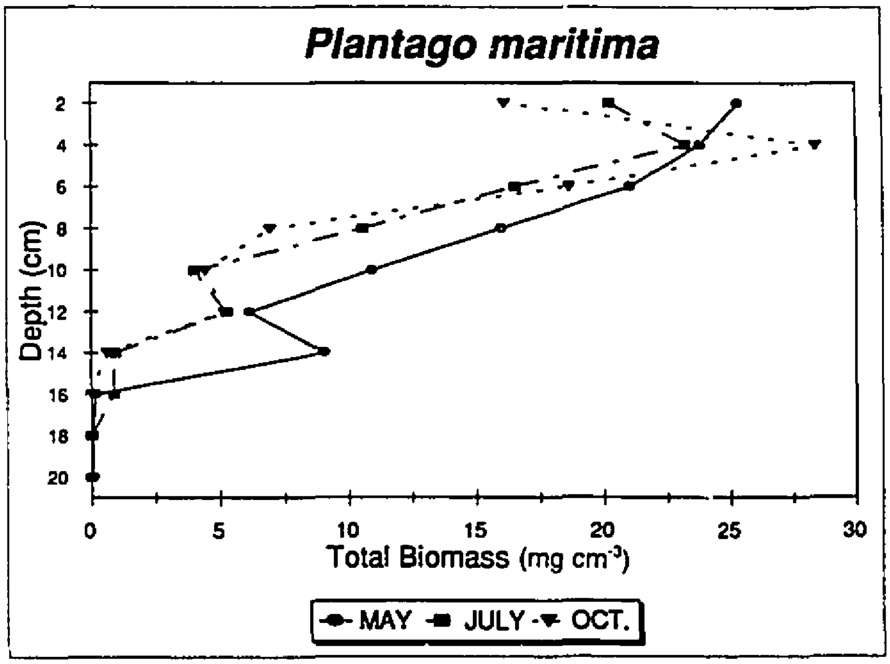
The amount of dead *S. alterniflora* biomass accounted for less than 20% of the total belowground biomass, supporting the observations by Gross *et al.* (1991) for a Nova Scotia salt marsh. At Dipper Harbour, dead *S. alterniflora* biomass decreased by 24% throughout the entire 40 cm profile ($P<0.01$, *t*-test) between May and July, followed by a second 29% loss between July and October (Table 3). These results differ from those of Valiela *et al.* (1976) who recorded an increase in dead belowground *S. alterniflora* between mid-summer and fall in Massachusetts. It appears that, during the growing season, the decomposition rate at Dipper Harbour exceeds the rate of production of new dead material (i.e., death rate of live belowground tissue), resulting in a net loss of dead material. The peak in dead belowground *S. alterniflora* biomass observed in May likely represents the accumulation of dead material over the winter, when decomposition rates are negligible.

In a litter bag study conducted in Mississippi, Hackney and De La Cruz (1980) reported that decomposition rates were twice as fast at 5 cm than at 15 cm depths, and negligible below 20 cm. However, our results indicate that the decrease in dead *S. alterniflora* biomass was significant throughout the vertical profile, seemingly independent of depth (Figure 3), implying that the net decomposition rate is equally independent of depth. The macrotidal conditions at Dipper Harbour may help to explain why the decomposition rate in the low marsh remains consistent throughout the top 40 cm of sediment. The water table in the creekbank zone can drop below 40 cm extending the depth of the oxidizing environment in the sediment to depths far greater than would be possible in Mississippi.

A different pattern was observed in the dead *S. patens* profile (Figure 4), where the dead fraction accounts for over half of the total belowground biomass pool. The average concentration of dead biomass increased by 44% ($P<0.01$, *t*-test) from May to July over the entire 30 cm profile. Between July and October, dead *S. patens* biomass decreased by 23% ($P<0.05$, *t*-test) in the top 16 cm of the profile, but no significant change was observed at the 16-30 cm depth interval (Table 3). The live/dead ratio of belowground *S. patens*, which averages 0.9 over the growing period, is much lower than that of *S. alterniflora* which ranges from 5.7 in May to 11.6 in October. Such a large concentration of dead material in the sediment of the *S. patens* zone likely results from low decomposition rates and marsh accretion. Under conditions of rising sea level, clastic sediment accretion may favour the accumulation and long term storage of belowground biomass (Mitsch and Gosselink, 1986). The presence of *S. alterniflora* biomass, which was observed at depths greater than 16 cm in all *S. patens* cores, provides evidence of this long term storage. Traces of *Plantago* biomass were also observed in several cores at depths ranging from 12 to 30 cm. Since the lower fraction of the *S. patens* belowground biomass pool contains remnants of earlier community assemblages, any changes in dead *S. patens* biomass observed in the lower core segments between sampling events may not be representative of seasonal variability. Therefore, the apparent 625 g m^{-2} increase in dead *S. patens* biomass observed from May to July in the 16-30 cm depth interval may simply be due to the spatial variability inherent in marsh sediments. The only significant loss occurs between July and October in the upper 16 cm, where it is assumed that the rate of decomposition is greatest.

No significant changes were observed in belowground biomass of *Plantago* between any of the sampling events. However, the vertical profile (Figure 5) shows a remarkable similarity between July and October, a trend suggesting that any seasonal change should occur over the first half of the growing season, before it went to seed. Spatial variability between replicate samples was high, particularly in May, as attested by the standard deviations (Table 3).

Figure 5 - Vertical profiles of belowground *Plantago* biomass. Points represent the mean of three replicates. Live and dead *Plantago* fractions were not separated.



In comparison with other species, the total belowground biomass of *Plantago* is low, accounting for less than one third that of *S. patens* and only one fourth that of *S. alterniflora*. Also, the maximum depth at which *Plantago* was observed was 22 cm, as compared to 38 cm for live *S. patens* and 45 cm for *S. alterniflora*. It would appear that the contribution of *Plantago* to the overall salt marsh belowground biomass pool is considerably smaller than that of the *Spartina* species.

Belowground Production

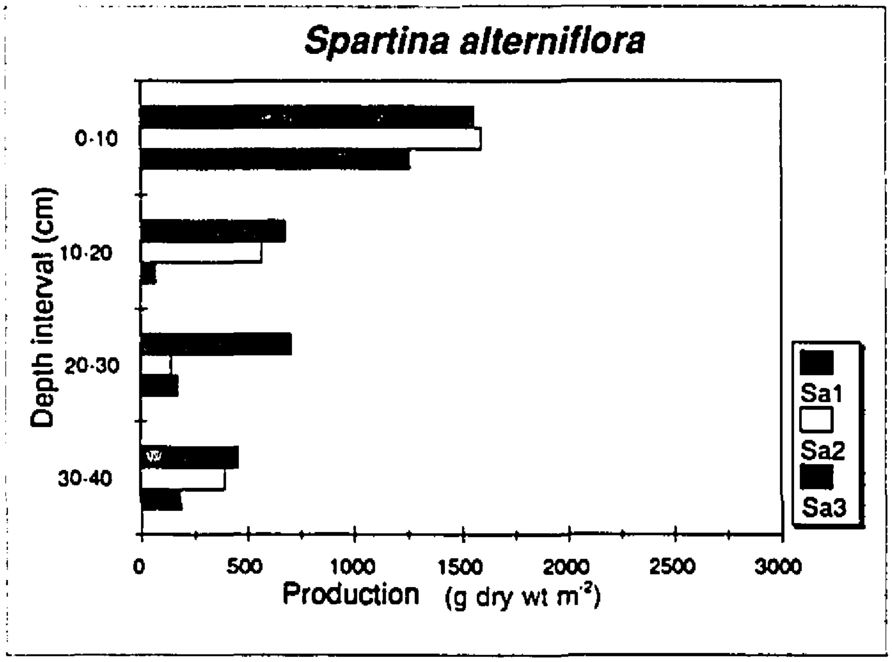
Two variations of the technique of Smalley (1958; *see* Turner, 1976) were used to estimate net belowground primary production (NBPP) for the *Spartina* species. In the first method, seasonal changes in biomass between sampling events, calculated at depth intervals of 10 cm for each replicate sample, were analyzed individually. The increases calculated for each depth interval between sampling events were summed to yield a production estimate for the entire belowground profile of each replicate. Species NBPP was then estimated by taking the mean production value obtained from the three replicates. This method corresponds to the original Smalley technique used by Schubauer and Hopkinson (1984) and Dame and Kenny (1986). The second method for estimating NBPP begins with the average biomass values in the 2 cm core sections, calculated for each species from the replicate samples (i.e., the data presented in Figures 3 and 4). Only significant increases (paired Student *t*-test) in the mean biomass of live and dead fractions were counted as production.

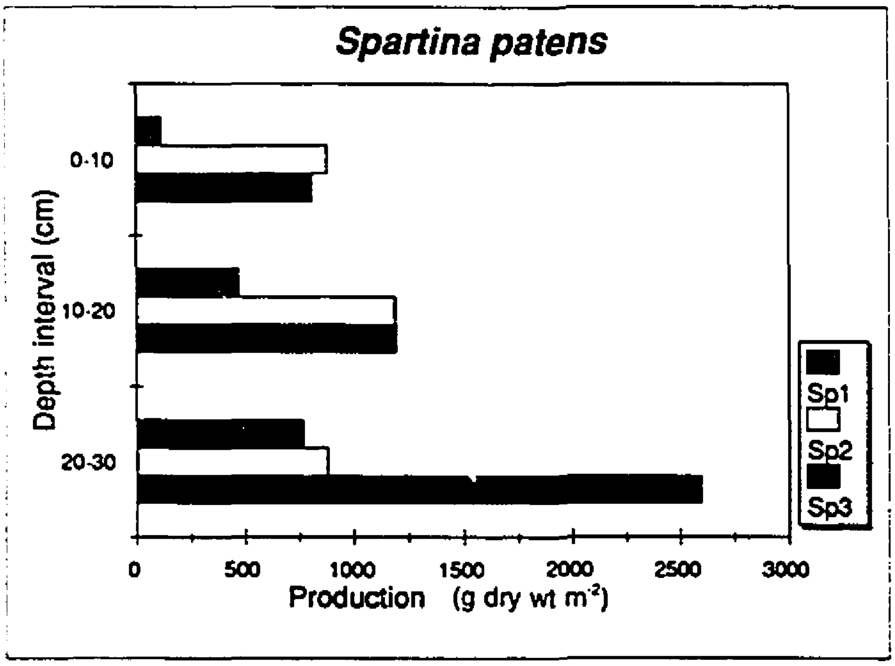
The vertical profiles were divided into two depth intervals; the top fraction at 0-16 cm depth and a bottom fraction at 16-40 cm and 16-30 cm depth for *S. alterniflora* and *S. patens*, respectively. The 16 cm level was selected to correspond to the depth where there is an obvious change in live biomass concentrations for both *Spartina* species (Figures 3 and 4). Therefore, the first method analyses seasonal changes for each replicate sample individually, yielding a productivity estimate from the mean of three individual calculations. In contrast, the second method analyses mean values in an attempt to eliminate errors due to sampling variability.

NBPP - Method I: Depth-Integrated Production Estimate (the original Smalley technique)

The depth-integrated productivity graphs (Figure 6) illustrate the differences in the growth patterns for each of the replicate samples of both *S. alterniflora* and *S. patens*. Over 60% of belowground production in *S. alterniflora* occurred in the top 10 cm where 45% of the total live biomass is located. Replicates Sa1 and Sa2 showed similar productivity values, whereas Sa3, located further down stream, was less productive. The calculated estimate for the NBPP of *S. alterniflora* is 2574 g dry wt m^{-2}. This estimate exceeds those reported in Maine (Gallagher and Plumley, 1979) and Nova Scotia (Livingstone and Patriquin, 1981), but is generally lower than production reported further south (Table 4). The NBPP of *S. alterniflora* resulted mainly from increases in live macro-organic matter concentrations between July and October, since live biomass generally decreased over the earlier part of the growing season and dead biomass decreased over the entire season. Belowground productivity of *S. alterniflora* was 4.3 times greater than estimated NAPP.

Figure 6 - Depth-integrated productivity profiles for each replicate based on increases in biomass summed over the three sampling periods (NBPP method I).





The depth-integrated productivity graph (Figure 6) shows that belowground production of *S. patens* occurs at all three depth intervals, although the Sp1 sample showed only a minimal increase in biomass in the top 10 cm. The calculated NBPP estimate for *S. patens* is 3120 g dry wt m^{-2}, which seems extremely high compared to values reported in other studies (Table 4). Nearly 40% of the *S. patens* NBPP comes from an increase in dead material between May and July, specifically between 20-30 cm depth. Such a high increase in dead biomass appears suspect. This increase may be due to spatial variability rather than actual productivity, resulting in a greatly exaggerated NBPP estimate. This assumption is particularity evident when noting the 2500 g dry wt m^{-2} production value from the Sp3 sample at the 20-30 cm depth interval (Figure 4).

NBPP - method II: Significance Tested Productivity Estimate

For *S. alterniflora*, the only significant increase occurs between July and October in the 0-16 cm depth interval of the live biomass fraction, yielding a NBPP estimate of 1575 g dry wt m^{-2} (Table 3). For *S. patens*, significant increases occur only between May and July, where live biomass increases by 545 g dry wt m^{-2} at the 18-30 depth interval and dead biomass increases by 1193 g dry wt m^{-2} over both depth intervals, yielding a preliminary NBPP estimate of 1738 g dry wt m^{-2}. However, the May-July increase in dead *S. patens* biomass at the 16-30 cm depth interval is due to an uncharacteristically high biomass concentration in the in one of the *S. patens* replicates (Sp3; *see* Figure 6) which was not present in the other replicates. As previously mentioned, it is suspected that the biomass at this depth is mainly the result of long term biomass storage since biomass from other species (*S. alterniflora* and *Plantago*) were also found at depths greater than 16 cm in the *S. patens* cores. Therefore, the increase in dead *S. patens* biomass at the 16-30 cm depth interval of the Sp3 replicate has been excluded from the overall summation, resulting in a final NBPP estimate of 1113 g dry wt m^{-2}. These NBPP estimates are considerably smaller than those from the previous method and are closer to those reported for salt marshes in Nova Scotia and Maine (Table 4). Given that the significance tested productivity estimate is based upon a more rigorous analysis of the data, it is believed that these results are more accurate than those obtained using Smalley's original technique.

NBPP of Plantago

Seasonal changes in total belowground biomass of the *Plantago* replicates (Figure 7) show no apparent trend, so it is impossible to identify any seasonal pattern involving the belowground growth of *Plantago*. The root tissue of *Plantago* is dense and woody, usually found as a single twisted "stalk", in contrast to the fibrous rhizome mat produced by the *Spartina* grasses. Therefore, the potential for belowground growth of a mature individual may be very small in comparison with that of a *Spartina* stand. The above to belowground ratio of *Plantago* averaged 0.14 for both July and October, suggesting that the belowground biomass fraction may play a considerable role in production dynamics in the northern salt marshes where this forb is found in abundance. Since live and dead fractions in the belowground biomass of *Plantago maritima* were not separated, the Max-Min method (Gallagher and Plumley, 1979) was used to estimate a NBPP of 648 g dry wt m^{-2} (Table 3). Maximum total biomass, taken from the mean of the three replicates, was observed in May, and minimum total biomass in October. This estimation method resembles the depth-integrated productivity method because no attempt is made to isolate significant changes. Therefore, the NBPP value reported here for *Plantago* should be considered as an overestimate.

Figure 7 - Total belowground biomass in each of the replicate samples of *Plantago* for each sampling period.

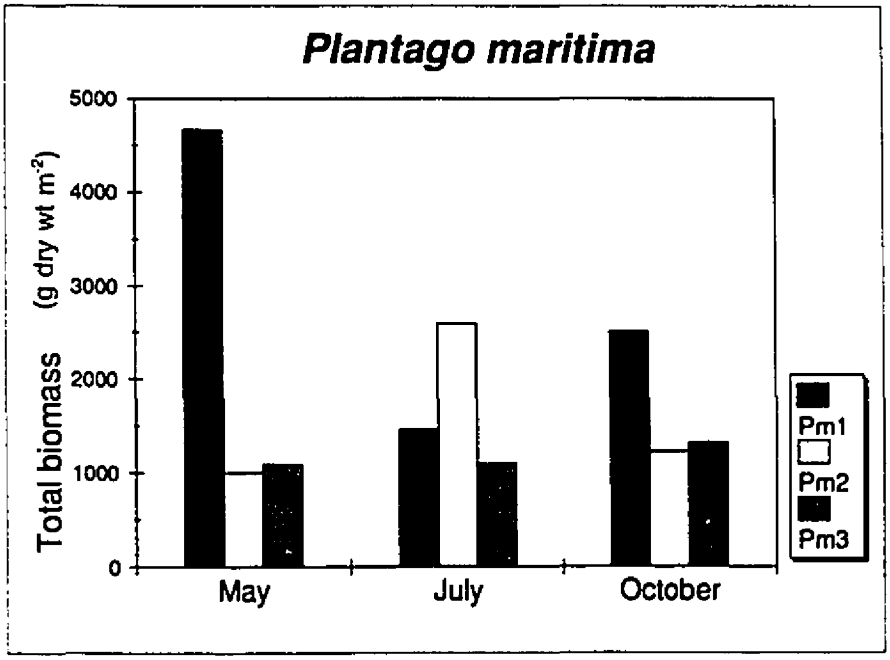


Table 4 - Belowground productivity estimates for several locations along the eastern coast of North America, including this study, presented in order of decreasing latitude.

	NBPP (g dry wt m^{-2})	Location	Method	Source
S. alterniflora	**2574**	**New Brunswick**	**Smalley**	**This Study**
	1575	**New Brunswick**	**Smalley (STP)**	**This Study**
	1050	Nova Scotia	Growth habit	Livingstone and Patriquin (1981)
	226	Maine	Max-Min	Gallagher and Plumley (1979)
	3500	Massachusetts	Colonization	Valiela et al. (1976)
	2200	New Jersey	Max-Min	Smith et al. (1979)
	6500	Delaware	Max-Min	Roman and Daiber (1984)
	2363	S. Carolina	Smalley	Dame and Kenny (1986)
	2100	Georgia	Max - Min	Gallagher and Plumley (1979)
	4780	Georgia	Smalley	Schubauer and Hopkinson (1984)
S. patens	**3120**	**New Brunswick**	**Smalley**	**This Study**
	1113	**New Brunswick**	**Smalley (STP)**	**This Study**
	540	Maine	Max - Min	Gallagher and Plumley (1979)
	2500	Massachusetts	Colonization	Valiela et al. (1976)
	310	Georgia	Max - Min	Gallagher and Plumley (1979)
	470	Delaware	Max - Min	Gallagher and Plumley (1979)
	3300	Delaware	Max - Min	Roman and Daiber (1984)
Plantago	**648**	**New Brunswick**	**Max - Min**	**This Study**

Carbon Input from Macrophyte Production

The annual input of carbon from net primary productivity to the salt marsh system is dependant upon the carbon content of the plant tissues, which may vary slightly from one species to another. The carbon content of *S. alterniflora* and *S. patens* tissue was estimated by taking the average of values from previously published reports (Table 5). Since no published data for *Plantago maritima* was available, the carbon content in *Plantago* tissues was measured using a Leco Total Carbon Analyzer at the Soil Chemistry Laboratory of McGill University. Three replicate samples of both above- and belowground tissue were ignited, and the mean carbon content and standard deviation are presented in table 5.

For *S. alterniflora*, the average carbon content of live belowground biomass has been estimated at 37.6%, and the aboveground biomass at 41.1%. The estimate for *S. patens* carbon content is 37.8% and 44.1% in live belowground and aboveground tissue, respectively. The carbon content of *Plantago* biomass was measured at 43.5% (± 1.0%) and 41.7% (± 1.2%) for above- and belowground tissue, respectively.

The carbon input to the marsh system from the net primary production of above- (NAPP) and belowground (NBPP; significance tested productivity estimate) fractions of the three dominant macrophytes is presented in table 6. These carbon input terms were obtained by multiplying the productivity estimates with the percent carbon content of the associated live plant tissue. The most productive plant species, *S. alterniflora*, is responsible for the greatest carbon input, followed by *S. patens* and *Plantago*.

Table 5 - Carbon content of above- and belowground biomass of the dominant salt marsh macrophytes. Values for *S. alterniflora* and *S. patens* were obtained from previously reported studies. Values for *Plantago* were determined through laboratory analysis. The standard deviation from the mean of three *Plantago* replicates are given in parentheses.

S. alterniflora	**% carbon**	**location**	
Aboveground	42.7	Fundy (N.S.)	Gordon et al. (1985)
	41.0	Delaware (a)	Roman and Daiber (1984)
	42.8	Delaware (b)	Roman and Daiber (1984)
	38.3	N. Carolina	Keefe (1972)
	40.8	Georgia	Keefe (1972)
Average	**41.1**		
Belowground	36.6	Maine	Gallagher and Plumley (1979)
	36.5	Delaware (a)	Roman and Daiber (1984)
	40.9	Delaware (b)	Roman and Daiber (1984)
	36.5	Georgia	Gallagher and Plumley (1979)
Average	**37.6**		

S. patens	**% carbon**	**location**	**source**
Aboveground	43.8	Delaware (a)	Roman and Daiber (1984)
	44.3	Delaware (b)	Roman and Daiber (1984)
Average	**44.1**		
Belowground	40.6	Maine	Gallagher and Plumley (1979)
	31.8	Delaware	Gallagher and Plumley (1979)
	37.9	Delaware (a)	Roman and Daiber (1984)
	39.9	Delaware (b)	Roman and Daiber (1984)
	38.8	Georgia	Gallagher and Plumley (1979)
Average	**37.5**		

Plantago	**% carbon**	**location**	**source**
Aboveground	43.5 (1.0)	Fundy (N.B.)	This study
Belowground	41.7 (1.2)	Fundy (N.B.)	This study

Table 6 - Input of carbon from the net above- and belowground primary productivity (NAPP & NBPP) of the three dominating macrophytes.

	Macrophyte Productivity ---- (g dry wt m^{-2} yr^{-1}) ----		Associated Carbon Production ---- (g C m^{-2} yr^{-1}) ----		
	NAPP	NBPP	NAPP	NBPP	NPP
S. alterniflora	718	1575	295.1	592.2	**887.3**
S. patens	500	1113	220.5	420.7	**641.2**
Plantago	296	648	128.8	270.2	**399.0**

CONCLUSIONS

In addition to yielding estimates of above and belowground net primary production for *S. alterniflora*, *S. patens*, and *Plantago maritima*, this study has also provided some insight into the mechanisms involved in the seasonal growth patterns of these salt marsh macrophytes. Aboveground productivity at Dipper Harbour resembles the NAPP estimates reported for other northern salt marshes. The NAPP results reported here are lower than those reported for southern salt marshes, supporting the latitudinal gradient hypothesis proposed by Turner (1976). At Dipper Harbour, the *Spartina* dominated associations each cover about 37% of the marsh surface area with *Plantago* dominated associations accounting for the remaining 26%. Located at the lower elevations near the creekbanks, *S. alterniflora* had the greatest aboveground productivity (718 g dry wt m^{-2}) followed by high marsh *S. patens* (500 g dry wt m^{-2}). *Plantago*, which occupies the transition zone between the two

Spartina zones, was the least productive (296 g dry wt m^{-2}).

A similar pattern was observed in the production estimates of the belowground fraction. Again, *S. alterniflora* had the highest NBPP value (1575 g dry wt m^{-2}) followed by *S. patens* (1113 g dry wt m^{-2}) and *Plantago* (648 g dry wt m^{-2}). The NBPP estimates presented here for the *Spartina* grasses are those obtained using the significance tested productivity (STP) method which was derived from Smalley's original technique. Previously reported studies of belowground plant production used Smalley's technique to examine changes in biomass over depth intervals of 5 or 10 cm (Valiela *et al.* 1976, Schubauer end Hopkinson 1984, Gross *et al.* 1991). In this study of the Dipper Harbour salt marsh, core samples were processed over 2 cm depth intervals, allowing for a highly detailed analysis of the vertical distribution of belowground biomass. The STP method uses this high resolution data to provide a more accurate estimate of NBPP than that obtained by Smalley's technique.

The NBPP estimate for *Plantago*, obtained using the Max-Min method, indicates that this forb is not inconsequential in relation to the overall production of the Dipper Harbour salt marsh. The root/shoot ratio of *Plantago* (defined as NBPP/NAPP) was 2.19. This value closely resembles those of *S. alterniflora* and *S. patens* which were 2.19 and 2.23, respectively. Other reported root/shoot ratios vary considerably, ranging from 0.97 for *S. alterniflora* in South Carolina (Dame and Kenny 1986) to 8.2 for *S. alterniflora* in Massachussetts (Valiela *et al.* 1976). Although the apparent similarity between the root/shoot ratios of all three macrophytes in this study is striking, comparisons between *Plantago* and the *Spartina* grasses must be interpreted with caution as very little information is as yet available concerning the growth patterns of *Plantago*.

In addition to increasing the accuracy of the NBPP estimates, the high resolution vertical profiles provided information concerning the amplitude of seasonal changes as well as the depths at which these changes occurred. For *S. alterniflora*, evidence of biomass translocation between May and July was observed from changes in live biomass, as was evidence of the accumulation of biomass for winter storage between July and October. The dead *S. alterniflora* fraction decreased consistently From May to October, suggesting that decomposition may be consistent throughout the growing season. The vertical profiles of *S. patens* showed live belowground biomass concentrations remaining constant close to the surface and production occurring at depths below 16 cm. The *Plantago* profiles, which do not extend below 20 cm in depth, displayed no evidence of any seasonal trend.

Since cores were extracted from monospecific stands, the presence of tissue from other plant species (*Plantago* and *S. alterniflora*) at depths below 16 cm in the *S. patens* cores raises a number of questions. Assuming that these macrofossils were deposited by vegetation associations different from that of the community sampled, when did this change in community occur? What effects do changes in community structure have on measurements of belowground plant productivity? Are changes in community structure specific to salt marshes in the Bay of Fundy region? The findings reported here suggest a substantive caveat for future studies, and perhaps, for a new interpretation of previous studies.

Finally, there is some evidence of a latitudinal trend for belowground productivity since NBPP estimates reported here for the Dipper Harbour salt marsh are generally lower than those from Massachusetts to Georgia (Table 4). However, our estimates from the STP method are considerably higher than those reported in Maine (Gallagher and Plumley, 1979) and Nova Scotia (Livingstone and Patriquin, 1981). Such an inconsistency in the NBPP estimates for northern salt marshes is likely due in part to the different methods that were used in each of these study. It is hoped that the results presented in this study will stimulate further research into the belowground productivity of northern salt marshes, particularly with respect to *Plantago*.

CHAPTER 2 - SEDIMENTARY CARBON BURIAL

INTRODUCTION

Tidal salt marshes along the eastern coast of North America are accreting environments (Redfield 1972). The rate of vertical growth of salt marshes is believed to be in equilibrium with relative sea level rise (Redfield 1972, Pomeroy and Wiegert 1981, Mitsch and Gosselink 1986). Marsh accretion results from a combination of two factors; the deposition of clastic sediment on the marsh surface and the *in situ* production and accumulation of organic material derived from net primary production (Redfield 1972, Nixon 1980, Craft *et al.* 1993). Due to this tendency for accumulating organic matter, it has been suggested that the salt marsh sediment acts as an atmospheric carbon sink (Pomeroy and Wiegert 1985, Stevenson *et al.* 1986, Craft *et al.* 1993). The rates of accumulation of organic material are influenced by the rates of productivity and decomposition, as well as by the rates of tidal export of coarse and particulate aboveground vegetation (Redfield 1972, DeLaune *et al.* 1978, Bricker-Urso *et al.* 1989, Craft *et al.* 1993). Inorganic sedimentation is controlled by physical factors, the most important of which is the local hydrology. The deposition of mineral sediment can contribute to the vertical accretion of the marsh surface (Redfield 1972, Pomeroy and Wiegert 1981, Mitsch and Gosselink 1986). Mineral sediment may originate from material suspended in the tidal water and/or from upland runoff.

The area of coast surrounding Dipper Harbour is characterised by a series of cliffs composed of red conglomerate and siltstone (Geological Survey of Canada 1963). The erosion from these cliffs produces an abundant supply of fine sediment to the adjacent coastal waters. Unlike the estuarine or deltaic salt marshes where the inorganic sediment originates from upland runoff (Mitsch and Gosselink 1986), the input of clastic sediment to the Dipper Harbour salt marsh is more likely to result from the deposition of material suspended in tidal water, given the relatively small size of the surrounding drainage basin. Therefore, tidal energy plays an important role in regulating the magnitude of inorganic sediment deposition. In a comprehensive review of the literature, Stevenson *et al.* (1986) have noted a strong correlation between the local tidal range and the accretionary balance (vertical accretion minus local average sea level rise).

The purpose of this study is to estimate the rate of carbon burial within the salt marsh sediment at Dipper Harbour under present day conditions, in order to quantify the sediment carbon sink. The rate of carbon accumulation in salt marsh sediments can be inferred by combining soil carbon content with marsh accretion rates. Although many researchers have addressed the subject of marsh accretion, relatively few have focused on the rate at which organic material accumulates in the sediment, and information concerning carbon burial in the salt marshes of Atlantic Canada is particularly lacking.

In Rhode Island, Bricker-Urso *et al.* (1989) calculated that organic dry solids contribute 29% and 54% to the sediment mass accumulation of low and high marsh, respectively. In Louisiana, Delaune *et al.* (1981) report percent soil organic carbon contents of 11.2% in streamside salt marshes, and 15.6% in brackish marshes located further inland. Both these studies suggest that the soil organic matter content of sediments located near creekbanks is inferior to that in sediments located further inland. However, in North Carolina salt marshes, Craft *et al.* (1993) have suggested that flooding frequency was far more important in determining soil carbon content than was the position of the sample cores (i.e., streamside vs. backmarsh). They observed that carbon content in the regularly flooded marshes in North Carolina (<6%) was significantly lower than that in the irregularly flooded marshes (22-40%). The results from these studies suggest that in the macrotidal environment of the Dipper Harbour salt marsh where flooding frequency is closely related to the distance from creekbank, there should be an increase in sediment carbon content along an elevational gradient running from low to high marsh. Therefore, under conditions where the vertical accretion rate is uniform over the entire marsh surface, the net rate of carbon burial should be lower in the frequently flooded low marsh dominated by *S. alterniflora* than in the infrequently flooded *S. patens* dominated high marsh. This study examines whether this pattern exists for sediments in the Dipper Harbour salt marsh by combining measurements of total sediment carbon content from the three major plant vegetation zones with marsh accretion rates.

METHODS

Sediment samples were obtained in July from surfaces dominated by *S. alterniflora*, *S. patens*, and *Plantago* using a 16.5 cm diameter aluminum core. For each plant zone, three replicate cores were extracted to a depth of 40 cm, with the exception of two cores from the *Plantago* zone which only reached 32 cm in depth. The cores were cut into 2 cm thick sections between the 0-20 cm depth interval, and into 4 cm thick sections between at depths of 20-40 cm. A subsample of 21.5 cm^3 in volume was taken from the centre of each section, dried at 60° C to constant mass and, weighed in order to calculate bulk density (mass/volume). Root matter was not removed from the sediment samples. Loss on ignition (LOI) was measured for every section using the method outlined by Craft *et al.* (1991). The following regression equation (Craft *et al.* 1991) was used to estimate the percent organic carbon content from the LOI results:

$$\text{Organic C} = (0.40 \pm 0.01)\text{LOI} + (0.0025 \pm 0.0003)\text{LOI}^2$$

The concentration of soil organic carbon (mass of carbon/volume) was calculated for each subsample by multiplying the bulk density by the percent organic carbon content. Since each subsample represented a depth interval of only 2 or 4 cm, this approach produced highly detailed vertical profiles of sediment carbon content.

The rate of marsh accretion at Dipper Harbour was estimated from ^{137}Cs-dating. The 1964 ^{137}Cs peak concentration was located at a depth of 5.7 cm, providing an accretion rate of 1.9 mm yr^{-1} over the past 30 years (Chmura, unpublished data). Although the core used for ^{137}Cs dating was extracted from an area located in the *S. patens* dominated high marsh, it is assumed that the 1.9 mm yr^{-1} accretion rate is representative of the entire vegetated marsh surface. This accretion rate is supported by macrofossil analysis of sediments located in the other major vegetation zones (Chmura, unpublished data).

Figure 8 - Depth profiles of percent soil organic carbon in the *S. alterniflora* (a), *S. patens* (b), and *Plantago* (c) dominated vegetation zones at Dipper Harbour. The line represents the mean of the three replicate samples. Symbols identify each replicate.

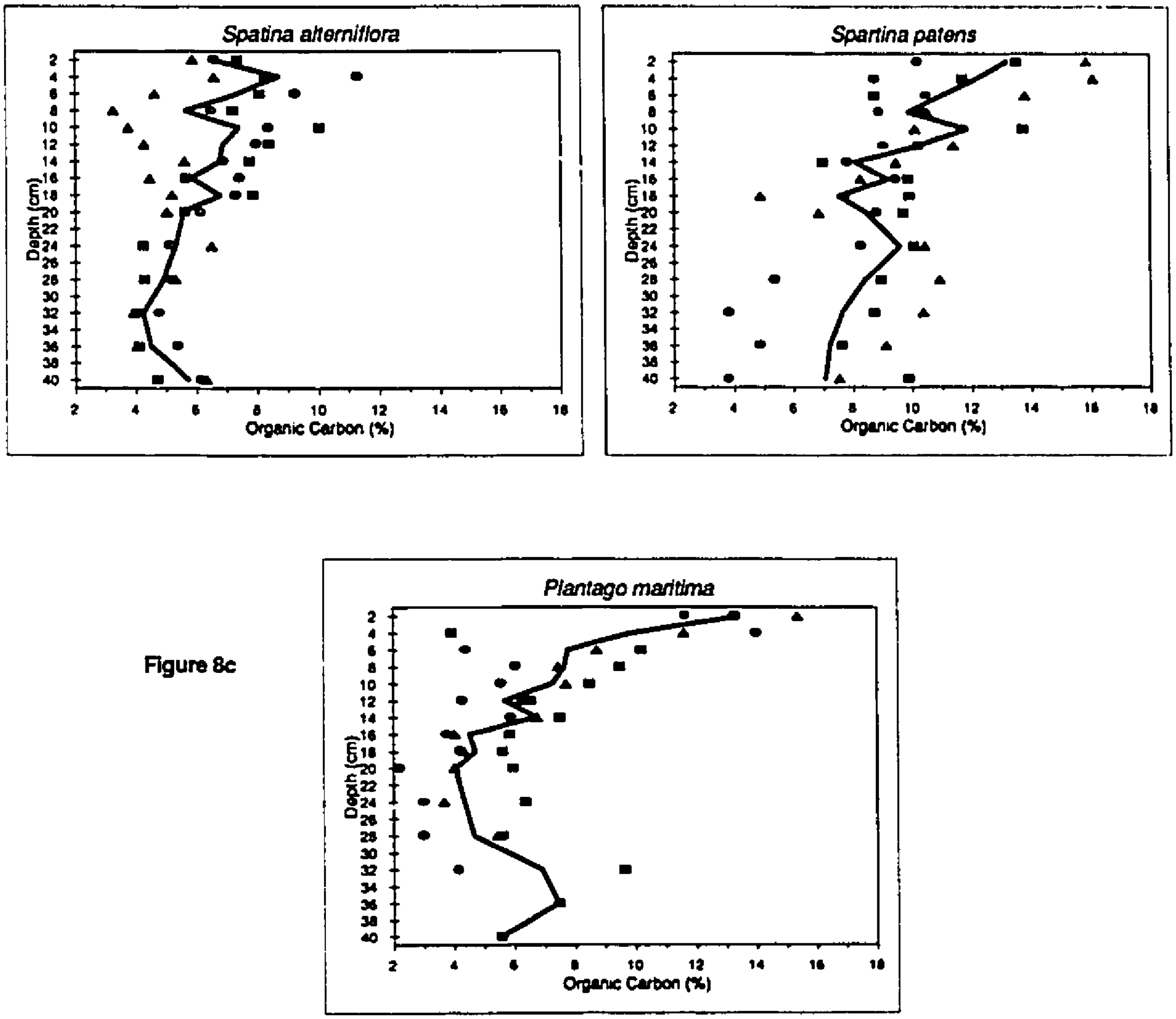


Figure 8a

Figure 8b

Figure 8c

Figure 9 - Depth profiles of sediment bulk density in the *S. alterniflora* (a), *S. patens* (b), and *Plantago* (c) dominated vegetation zones at Dipper Harbour. The line represents the mean of the three replicate samples. Symbols identify each replicate.

Figure 9a

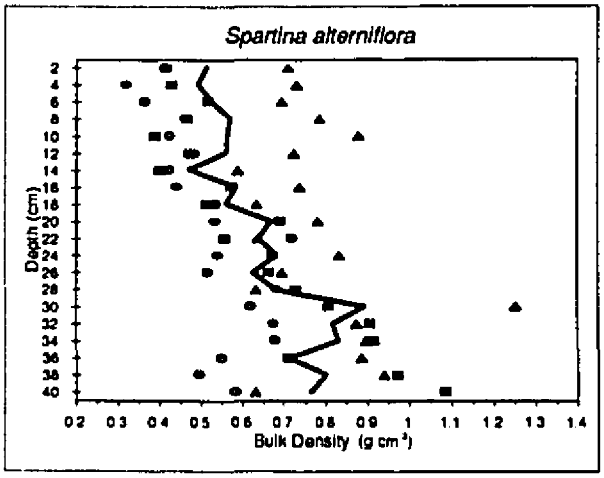


Figure 9b

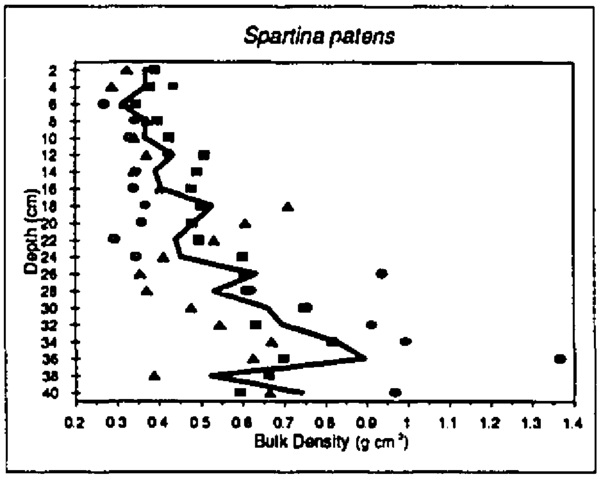


Figure 9c

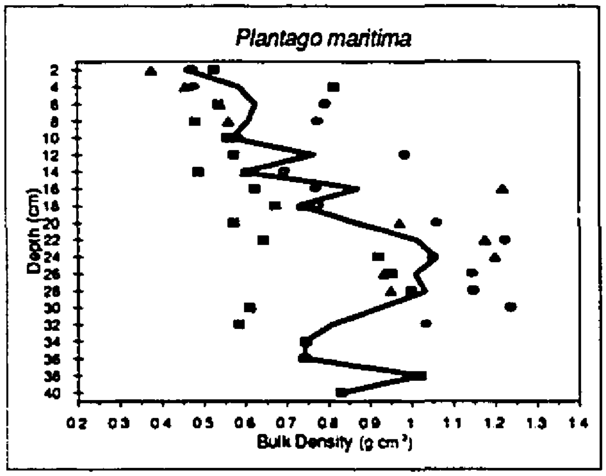


Figure 10 - Depth profiles of soil organic carbon concentrations (mass of carbon per unit volume) in the *S. alterniflora* (a), *S. patens* (b), and *Plantago* (c) dominated vegetation zones at Dipper Harbour. The line represents the mean of the three replicate samples. Symbols identify each replicate.

Figure 10a

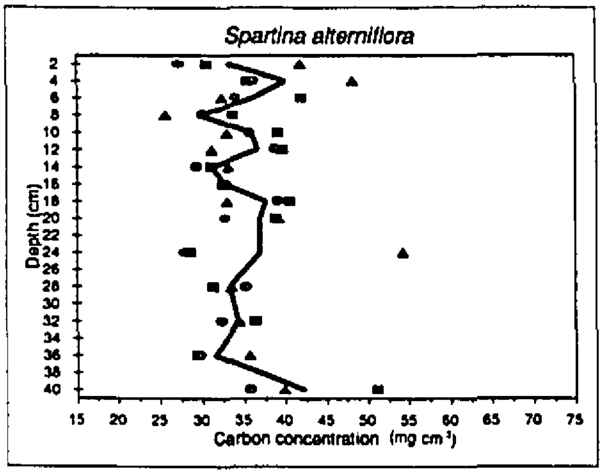


Figure 10b

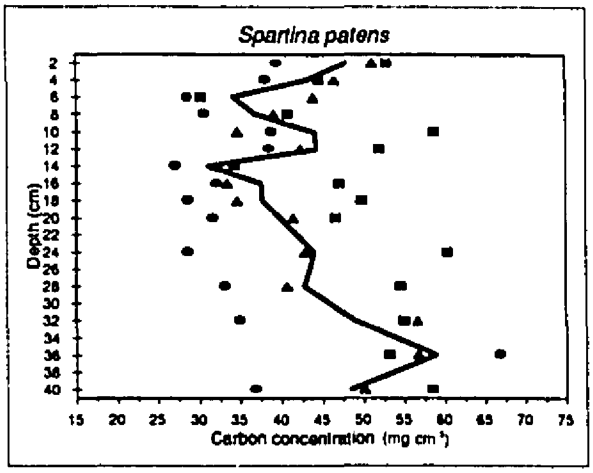
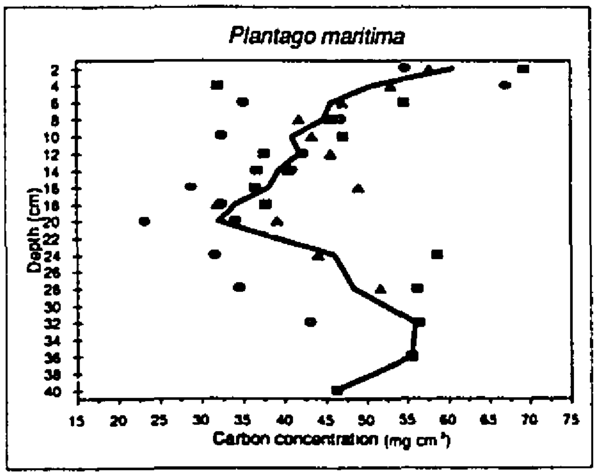


Figure 10c



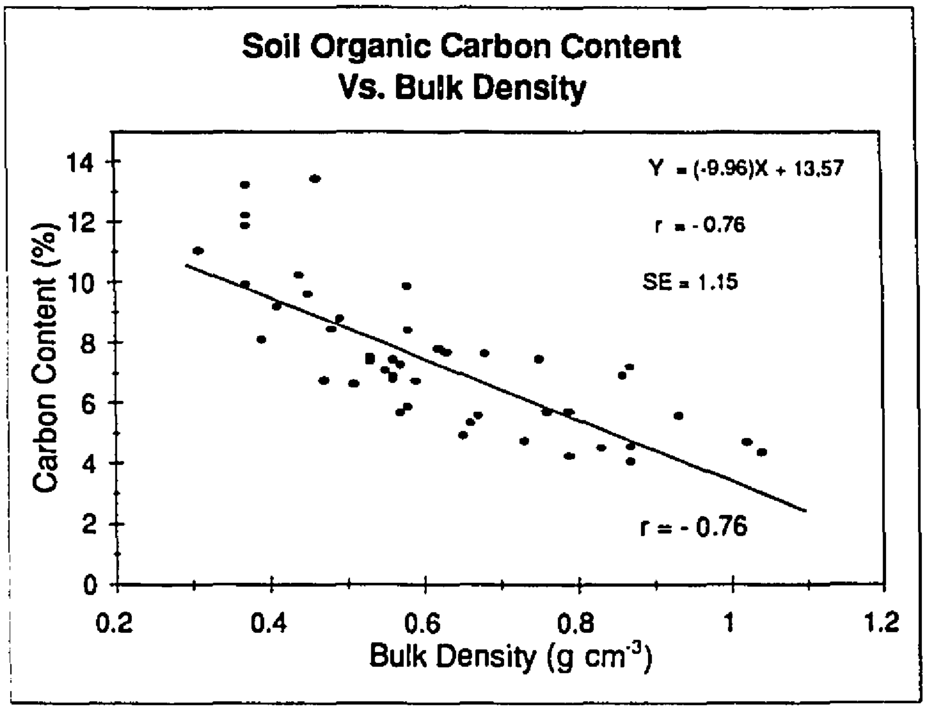
RESULTS

Percent soil organic carbon content was lowest in the *S. alterniflora* zone, averaging 7.2% in the top 10 cm of sediment (Figure 8) and ranging between 6.9% (10-12 cm) and 4.3% (28-32 cm) at depths below 10 cm. Soil bulk density in the *S. alterniflora* zone was relatively constant in the top 18 cm of sediment, averaging between 0.5 and 0.6 g cm^{-3} (Figure 9). Below this level, soil bulk density tended to increased with depth, reaching 0.8 g cm^{-3} at the 28-40 cm level. The concentration of soil organic carbon in the *S. alterniflora* zone averaged 36.9 mg cm^{-3} (Figure 10) over the 40 cm profile, ranging between 31.8 mg cm^{-3} (12-14 cm) and 45.2 mg cm^{-3} (36-40 cm).

The highest percent soil organic carbon content was observed in the *S. patens* zone, averaging 11.6% in the top 10 cm and 7.7% between 10 and 40 cm depth (Figure 8). Soil bulk density ranged consistently between 0.3 and 0.5 g cm^{-3} in the top 24 cm of the *S. patens* profile (Figure 9). Although there was much variation in the bulk density of replicate samples located below a depth of 24 cm, the bulk density values tented to be greater in this depth interval. The concentration of soil organic carbon in the *S. patens* sediment ranged between 31.2 mg cm^{-3} (12-14 cm) and 62.6 mg cm^{-3} (32-36 cm), averaging 43.2 mg cm^{-3} over the entire 40 cm profile (Figure 10).

Percent soil organic carbon content in the *Plantago* zone also tended to decrease with depth, averaging 9.2% in the top 10 cm and 5.0% between 10 and 30 cm in depth (Figure 8). The bulk density of the *Plantago* sediment tended to increase with depth in the profile from under 0.5 g cm^{-3} in the top 2 cm to 1.0 g cm^{-3} at depths below 20 cm (Figure 9). The concentration of soil organic carbon in the *Plantago* zone averaged 47.3 mg cm^{-3} over the 40 cm profile (Figure 10), ranging between 34.5 mg cm^{-3} (16-18 cm) and 61.8 mg cm^{-3} (0-2 cm).

Figure 11 - Graph of percent soil organic carbon content Vs. bulk density. Sediment from all three dominant plant zones are included.



For all three plant zones, percent soil carbon content was highest in the top 10 cm, tending to decrease with depth. Conversely, bulk density tended to increase with depth, resulting in a strong negative correlation between percent carbon content and bulk density (r = -0.76; *see* Figure 11). Craft *et al.* (1993) reported a similar relationship between bulk density and soil organic carbon. The percent sediment carbon content observed for the Dipper Harbour salt marsh are lower than those reported in Louisiana by Delaune *et al.* (1978) and in Rhode Island by Bricker-Urso *et al.* (1989). They are also inferior to those from the infrequently flooded marshes reported in North Carolina by Craft *et al.* (1993).

DISCUSSION

When averaged over the 40 cm profiles, the percent carbon content of sediments was lowest in the low marsh *S. alterniflora* zone (6.2%), followed by the middle marsh *Plantago* zone (6.7%) and the high marsh *S. patens* zone (9.4%). These results suggest that the percent carbon content in soils at the Dipper Harbour salt marsh increase with distance from the creekbank, and with decreasing flooding frequency, thus supporting the conclusions made by Bricker-Urso *et al.* (1989), Delaune *et al.* (1981), and Craft *et al.* (1993). However, the results reported here do not supply any direct evidence as to the mechanisms responsible for this spatial trend. In their examination of microtidal salt marshes in North Carolina, Craft *et al.* (1993) suggested that higher carbon accumulation rates in the irregularly flooded marshes can be attributed to: (1) reduced rates of decomposition due to waterlogging, (2) reduced tidal flushing and export of detritus, (3) higher net primary production, and (4) a higher resistance to decomposition by the emergent high marsh vegetation. However, in the Dipper Harbour system, waterlogging of high marsh sediments is only a factor during periods of spring tides or rain events, net primary production is greatest in the low marsh, and no evidence has been found suggesting differences in the resistance to decomposition between low marsh *S. alterniflora* and high marsh *S. patens*. Given that the Dipper Harbour system is macrotidal, it would appear likely that tidal flushing of soil organic matter may be the primary mechanism responsible for creating the high to low marsh percent soil carbon content gradient observed in this study.

The plant zone with the highest soil carbon concentration (i.e., on a mass per volume basis) was *Plantago* which averaged 47.3 mg C cm^{-3} over the top 40 cm of sediment. This was surprising given that the *Plantago* zone is characterized by the lowest productivity of above- and belowground biomass as well as the lowest macro-organic matter (MOM) content (see Chapter 1). The lowest soil carbon concentration was observed in the *S. alterniflora* sediment. Although the average percent carbon content of the *Plantago* sediment was inferior to that of the *S. patens* sediment, the mean bulk density of the *Plantago* zone sediment (0.75 g cm^{-3}) was sufficiently greater than that of the *S. patens* zone (0.48 g cm^{-3}), resulting in a higher concentration of carbon.

Potential Origin of Sedimentary Carbon

The contribution of belowground macro-organic matter to the sediment carbon pool was relatively low in all three plant zones. Macro-organic matter (MOM) is defined as here as the portion of belowground organic matter retained by a 1 mm sieve. The MOM concentration was determined from the belowground biomass data presented in chapter 1. In both *Spartina* zones, the MOM accounted for 19% of the total soil carbon concentration (Figure 12a). Craft *et al.* (1988) observed similar relative contributions of MOM to total sediment carbon pools for *S. alterniflora*-dominated marshes along the coast of North Carolina, ranging between 6% and 45%. In the *Plantago* zone, the MOM accounted for only 9.6 % of the absolute soil carbon content. These results suggest that the amount of MOM represents only a small fraction of the total carbon present in the salt marsh sediment, and that MOM can not be used as a sole predictor of the total carbon stored in the soil. The low MOM to soil carbon ratio in the sediments of the Dipper Harbour salt marsh may be due, in part, to an abundance of very fine particles of organic matter that were not retained by the 1 mm sieve used in separating MOM from the sediment. Such particles could include fine roots and partially decomposed plant material, as well as dissolved organic compounds which may adhere to the surfaces of the clastic sediment particles.

Figure 12 - The contribution of macro-organic matter (MOM) to the total sediment carbon in the top 40 cm (a) and top 6 cm (b) of the three major plant zones of the Dipper Harbour salt marsh.

Figure 12a

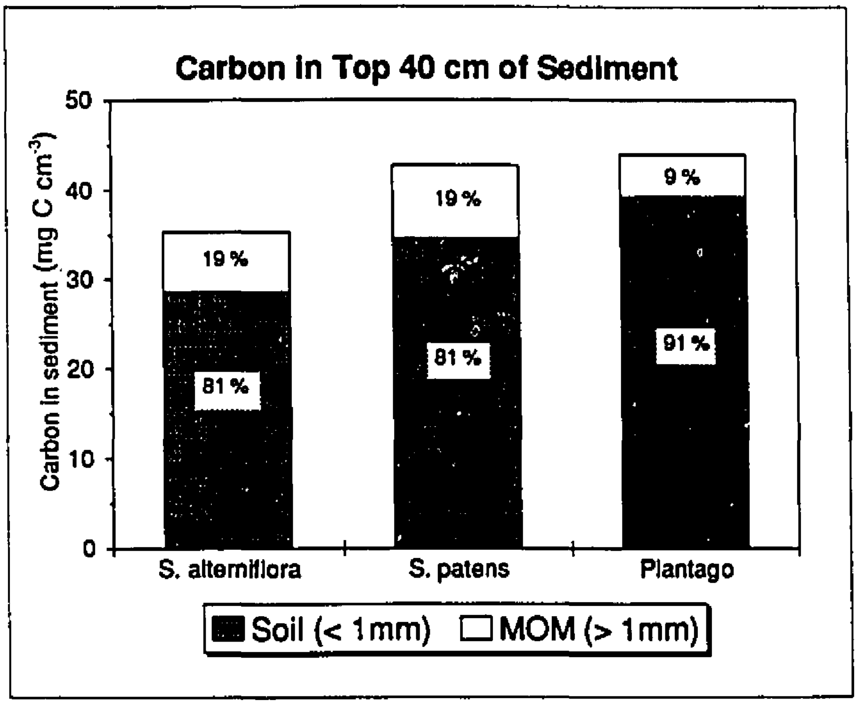


Figure 12b

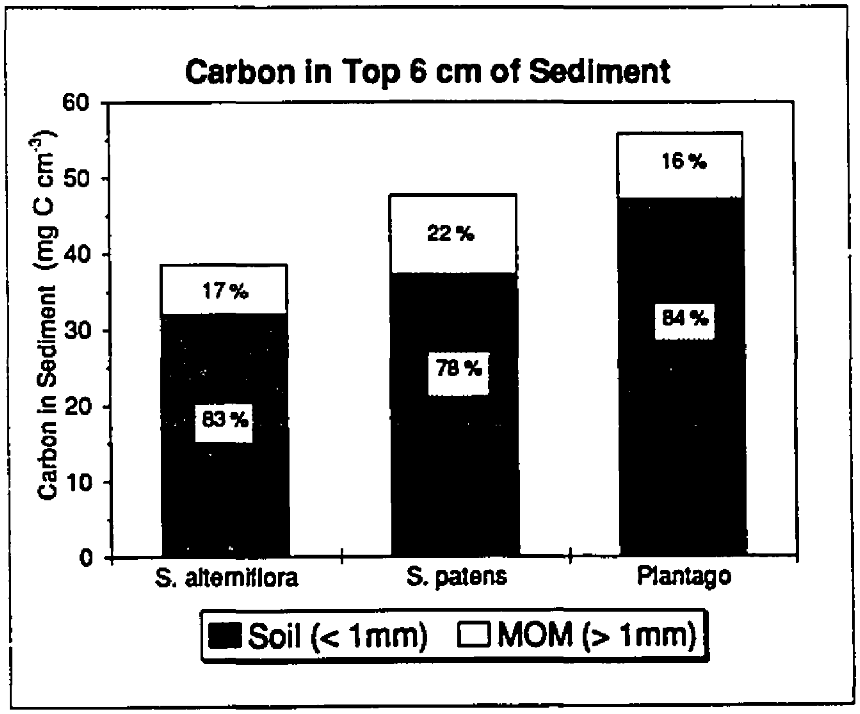


Table 7 - Net primary productivity estimates of algae in coastal systems along the eastern coast of North America.

Location	**Types of Algae**	**Algal NPP** ($g\ C\ m^{-2}\ yr^{-1}$)	**Source**
Georgia	Salt marsh benthic algae: pennate diatoms, green filamentous, and blue-greens.	180	Pomeroy (1959)
Delaware	Salt marsh edaphic algae: blue-greens, diatoms, filamentous and foliaceous greens.	80	Gallagher and Daiber (1974)
Massachusetts	Salt marsh epibenthic algae: green filamentous.	53	Van Raalte et al. (1976)
Fundy (N.S.)	Benthic microalgae on intertidal mudflats (sediments located 50-100 m below S. alterniflora marshes).	47-83	Hargrave et al. (1983)

Microfloral productivity provides a possible explanation for the low MOM to total soil carbon ratio, particularly in the *Plantago* zone where the ratio is smallest. The structure of the aboveground fraction of the *Plantago* vegetation and the relatively sparse cover of the *Plantago*-dominated assemblages allows for a greater penetration of light to the surface of the sediment than do the *Spartina* grasses. This may in turn favour the growth of microflora, hence increasing the amount of carbon on the surface of the sediment. However, for the microfloral community to contribute substantially to the accumulation of carbon in the sediment, the production rate of the microflora must be sufficiently important in relation to that of *Plantago*, and surface conditions must favour the burial of the carbon derived from this productivity. One of the microfloral communities that may potentially fulfil these requirements is that of the benthic algae.

Epiphytic and epibenthic algae are believed to contribute significantly to the net primary production of salt marshes (Pomeroy and Wiegert 1981, Wiegert and Freeman 1990). Although the total biomass of the benthic algae is small compared to that of the macrophytes, they have a much higher turnover rate and respond more rapidly to environmental changes which increases their potential for productivity (Wiegert and Freeman 1990). The majority of microalgal production occurs during ebb tide, and surfaces with less abundant macrophyte biomass, such as bare creekbanks, tend to be the most productive (Pomeroy and Wiegert 1981, Hargrave *et al.* 1983). The results from four different studies, presented in table 7, appear to show a trend of decreasing algal productivity with increasing latitude. In the three studies conducted over salt marsh sediments, algal productivity estimates ranged from 53 g C m^{-2} yr^{-1} (assuming 1 g C = 2 g dry wt.) in Massachusetts (Van Raalt *et al.* 1976) to 180 g C m^{-2} yr^{-1} in the Sapelo Island marshes of Georgia (Pomeroy 1959). These values corresponding to between one-third to one-fourth that of the aboveground productivity of vascular plants. In the upper Bay of Fundy, Hargrave *et al.* (1983) estimated the net primary productivity of epibenthic microalgae on intertidal sediments located 50-100 m beyond the lower edge of a *S. alterniflora* marsh to be between 47 and 83 g C m^{-2} yr^{-1}. However, since these mudflats are unvegetated and subjected to a far greater level of submergence, the algal communities on the mudflats may be quite different from those present on the surface of the adjacent salt marshes. It is therefore unlikely that the microalgal productivity estimates reported by Hargrave *et al.* are representative of salt marsh sediments for the same region.

The burial of the aboveground tissue of vascular plants may represent another source of carbon for the salt marsh sediment. In the two plant zones dominated by the *Spartina* grasses, some dead vegetation was observed in May on the marsh surface. The upper layer of dead vegetation consisted of tissue from the previous season which was underlain by a second layer of older tissue. These observations suggest that a fraction of *Spartina* aboveground biomass is eventually buried in the salt marsh sediment. However, the fraction of the NAPP carbon input (i.e., the NAPP which is not exported) can be different for each *Spartina* species. In the Cumberland Basin, Gordon *et al.* (1985) estimated a loss of 23% NAPP in the frequently flooded *S. alterniflora* dominated low marsh over the winter period (Nov.-Apr.). In the same study, no overwinter loss was observed in the high marsh *S. patens* zone.

In order to estimate the fraction of aboveground plant production which remains on the marsh surface after one year, new dead vegetation (three replicates for each plant species) was sampled in May. The results from this study are presented in table 8. The difference between the mass of new dead vegetation and maximum standing crop showed that only 60% of *S. alterniflora* peak standing crop remains on the marsh surface on an annual basis. Assuming that this remaining aboveground biomass is eventually buried within the marsh substrate, this burial term accounts for 115 g C m^{-2} yr^{-1}, which is equal to 40% of *S. alterniflora* NAPP. In the high marsh zone, 80% of the *S. patens* peak standing crop from the previous year remained on the surface through to May. Therefore, carbon burial term originating *S. patens* aboveground production is 130 g C m^{-2} yr^{-1}, which is equal to 60% of *S. patens* NAPP. In the *Plantago* zone, no vegetation cover was observed in early May as the sediment surface was completely bare. Therefore, it is assumed that all aboveground *Plantago* biomass is eventually exported from the marsh on an annual basis, and that the contribution of carbon to the marsh sediment by *Plantago* NAPP is nil.

It would appear from these results that the burial of aboveground biomass does not help explain the low MOM to soil carbon ratio observed in the sediments of the Dipper Harbour salt marsh. Also, it should be noted that during the processing of sediment samples for the analysis of carbon content, very few traces of aboveground tissue were observed.

Table 8 - Fate of aboveground plant biomass as a function of net aboveground primary productivity (NAPP).

	NAPP	Peak Standing Crop	Overwintering Dead	% NAPP Buried	% NAPP Exported	Annual export
	(g dry wt m^{-2} yr^{-1})	------- (g dry wt m^{-2})	-------			(g C m^{-2} yr^{-1})
S. alterniflora	690	460	275	40	60	171.8
S. patens	495	380	300	60	40	65.2
Plantago	290	225	0	0	100	126.6

Estimated value of the sediment carbon sink

In order to estimate the rate of the carbon accumulation in the Dipper Harbour salt marsh sediment, the ^{137}Cs accretion rate of 1.9 mm yr^{-1} over the past 30 years was combined with the soil carbon concentration in the top 6 cm of soil for each dominant plant zone (Figure 12b). The 6 cm cut-off depth was chosen to ensure that the soil carbon concentration data was representative of the edaphic characteristics associated with the dominant plant communities. In addition, the ^{137}Cs determined accretion rate is only valid for the top 6 cm of sediment. The dated core was taken from a zone dominated by *S. patens*, located north of the creek, approximately half way between the Pm2 and Sp1 sample sites (Figure 2). Although rates may be spatially variable, the dated core represents the only data available for estimating modern rates of marsh accretion in this region. I have therefore, for the purpose of this exercise, chosen to use this rate under the assumption that it is typical of the accretion rates over the entire marsh.

The estimated rate of carbon burial was highest in the *Plantago* zone (106.0 g C m^{-2} yr^{-1}), intermediate in the *S. patens* zone (81.1 g C m^{-2} yr^{-1}) and lowest in the *S. alterniflora* zone (73.3 g C m^{-2} yr^{-1}). These values fall within the ranges estimated in North Carolina by Craft *et al.* (1993) of 21-59 g C m^{-2} yr^{-1} and 106-146 g C m^{-2} yr^{-1} for regularly and irregularly flooded marshes, respectively. The estimates obtained in this study closely resemble the 89 g C m^{-2} yr^{-1} carbon burial term reported for *S. alterniflora* sediments in Massachusetts by Howes *et al.* (1985) who based their estimate on a local accretion rate of 1.5 mm yr^{-1}.

CONCLUSIONS

The rates of carbon burial reported here were not proportional to the net primary productivity rates of the dominant macrophytes. The most productive plant zone, dominated by *S. alterniflora*, was characterized by the lowest sediment carbon accumulation rate, and the highest carbon burial rate was found in the least productive plant zone dominated by *Plantago*. Belowground macro-organic matter (MOM) represented only a small fraction of the carbon stored in the top 6 cm of the sediment, accounting for only 16% of the total soil carbon content in zones dominated by *Plantago*, and 17% and 22% in zones dominated by *S. alterniflora* and *S. patens* respectively (Figure 12b). The ratio of MOM to total sediment carbon in the top 6 cm of marsh substrate did not differ significantly from that calculated for the top 40 cm in the zones dominated by *Spartina*. However, the 15% MOM to total sediment carbon ratio in the top 6 cm of the *Plantago* cores was significantly greater (*t*-test; $P < 0.05$) than the 10% ratio calculated over the 40 cm depth profile. This can be attributed to the relatively high concentration of belowground biomass observed in the upper portions of the *Plantago* sediment.

The results of this study support the assumption that the accreting sediment of the Dipper Harbour salt marsh acts as carbon sink. However, unlike similar studies that have concluded that the net primary production of salt marsh macrophytes represents the principal source of carbon to the sediment (DeLaune *et al.* 1981, Bricker-Urso *et al.* 1989, Craft *et al.* 1993), the results presented here indicate that the direct contribution of MOM to the sediment carbon pool is relatively small. The majority of the carbon stored in the sediment of the Dipper Harbour salt marsh (over 80%) appears to be constituted of small organic particles (< 1 mm). Evidence suggests that the net primary production of microfloral communities may be responsible for a fraction of the particulate carbon observed in the sediment, particularly in the *Plantago* zone where surface condition may favour the growth of benthic microalgae, and where the burial of aboveground *Plantago* biomass is negligible.

At Dipper Harbour, a gradient of increasing percent soil carbon content was observed from low to high marsh, supporting the observations by Craft *et al.* (1993) who attributed this trend to flooding frequency. Increased flooding frequency can result in the increased leaching of organic carbon from the sediment. However, the soil carbon concentrations observed in this study where greatest in the sediments of the *Plantago* zone, which is located in between the *S. alterniflora* low marsh and the *S. patens* dominated high marsh. The sediment in this zone was characterized by a relatively high bulk density which is likely to decrease the hydrological conductivity of the substrate and hence impede the leaching of organic material. Assuming this is the case, the sediment of *Plantago* zone may "capture" a fraction of the carbon that leaches through the soil from the high marsh sediment. Therefore, the high relatively high soil carbon concentrations observed in the *Plantago* zone may not necessarily originate from the *in situ* production of the dominant plants, as has been suggested for systems located further south where *Plantago* dominated zones are absent. The results of this study suggest that the mechanisms involved in the sedimentary flow of carbon in salt marshes located in Fundy salt marshes may be considerably different then in those located on the eastern coast of the United States.

CHAPTER 3 - DISSOLVED ORGANIC CARBON FLUX

INTRODUCTION

The movement of organic carbon from salt marshes to adjacent coastal waters has been considered as a major flux component of the overall salt marsh carbon cycle (Pomeroy and Wiegert 1981, Craft *et al.* 1993). Given the high rates of primary productivity, it has been hypothesized that a significant fraction of this production is eventually exported to near shore waters by the tides (Teal 1962, Odum 1968). However, studies designed to test this 'outwelling hypothesis' have met with mixed results, and the importance of the tidal carbon export term remains enigmatic (Woodwell *et al.* 1977, Nixon 1980, Williams *et al.* 1992).

The organic carbon susceptible to tidal export can be divided into two distinct forms. The first, dissolved organic carbon (DOC), corresponds to carbon-based substances which are not retained by a 0.45 μm filter. All other forms of suspended organic matter, ranging in size from 0.45 μm to several centimetres, are categorized as particulate organic carbon (POC). The salt marsh DOC pool is composed primarily of organic acids leached from plant tissue or derived from the microbial degradation of plant detritus (Wolaver and Spurrier 1988, Moran and Hodson 1990), whereas the POC pool is made up mostly of fragments of aboveground plant tissue. This study focuses on the transport of DOC through the Dipper Harbour salt marsh.

In order to estimate this carbon flux over a single tidal cycle, DOC concentrations in both flood and ebb waters must be monitored with respect to tidal stage and weighted in terms of water volume discharge. The principal source of experimental error associated with such a study originates from the estimation of tidal discharge (Roman 1984). Since the DOC in the tidal prism is measured as a concentration, an accurate measurement of tidal discharge is essential in determining the mass of the carbon exchanged between the salt marsh system and the adjacent coastal waters. The magnitude and direction of the carbon exchange may fluctuate over consecutive tidal cycles, since DOC concentrations have been shown to vary diurnally (Roman and Daiber 1989), and tidal amplitude is rarely constant from one tide event to another. Therefore, an estimation of the tidal carbon flux, even over short periods of time, requires the monitoring and sampling of numerous tidal cycles. The problem of repetitive sampling is compounded when attempting to monitor the tidal carbon flux over seasonal or annual periods, as tidal amplitude and hence water volume discharge is constantly changing due to solar, lunar, and climatic influences (Hutchinson and Sklar 1993). Although many authors have attested to this problem of inherent diurnal and seasonal variability, a number of net annual tidal carbon flux estimates have been reported and there is a general agreement that salt marshes export DOC (Chrzanowski *et al.* 1983, Chalmers *et al.* 1985, Wolaver and Spurrier 1988, Roman and Daiber 1989).

Annual DOC flux estimates between salt marshes and adjacent waters may vary considerably within a similar region. For example, the annual DOC export term for a marsh in the North Inlet region of South Carolina estimated in 1983 by Chrzanowski *et al.* (416 g m^{-2} yr^{-1}) is an order of magnitude greater than the 1988 estimate by Wolaver and Spurrier (33.3 g m^{-2} yr^{-1}) for a marsh in the same region. Despite such inconsistencies concerning the order of magnitude of the net annual DOC flux estimates, a few observations regarding the factors that influence the transport of DOC have been reported. Increases in the organic carbon concentrations of ebb and slack low tide runoff have been observed shortly after storm and rain events (Chalmers *et al.* 1985, Wolaver and Spurrier 1988, Sedell and Dahm 1990). Roman and Daiber (1989) noted that the ebb tide transport of POC and DOC after a storm event was 5 to 6 times greater than normal. The import of carbon from terrestrial sources to the marsh system may also influence the estimated carbon export flux (Chrzanowski *et al.* 1983, Roman and Daiber 1989). Wolaver *et al.* (1986) found DOC concentrations to vary inversely with salinity, suggesting the importance of a fresh water DOC source. Williams *et al.* (1992) found that freshwater inputs accounted for about 11% of the observed carbon export from a marsh in the North Inlet area (South Carolina).

The objective of this study was to determine the magnitude of the tidal DOC flux at the Dipper Harbour salt marsh, testing the outwelling hypothesis proposed by Odum (1968). The DOC exchange flux was measured over 18 tide events from May to August 1994, and both diurnal and seasonal variability was considered. In order to examine the processes involved in the circulation of DOC within the salt marsh system, DOC concentrations were also measured in the marsh sub-surface groundwater, in the freshwater entering the marsh system from the terrestrial drainage basin, and in the slack low tide runoff.

METHODS

Hydrological exchanges between the Dipper Harbour marsh and the adjacent coastal waters were monitored at a 11.5 m wide bridge, located at the outlet of the marsh creek (figure 2). The geometrical uniformity of the bridge channel provided excellent conditions for monitoring tidal water volume discharge.

A Marsh-McBirney electromagnetic current meter, affixed to a Campbell Scientific 10X datalogger, was installed under the bridge to record instantaneous current velocities. The current meter probe was positioned in the location which best represented the average current velocity of both flood and ebb flows. This 'ideal' position was determined using the method described by Roman (1984), in which a dense spatial array of current meters is established over a cross-section of the channel. The array was repeated for tidal cycles over three consecutive days and bivariate linear regression analysis was used to determine the best possible position for the current meter. The error term associated with this method is estimated at 7-11%. A stage recorder located under the bridge monitored the tidal amplitude. When coupled with the data from a stage recorder (also located under the bridge) and measurements of channel width, the instantaneous current velocities provided a constant record of tidal water volume discharge from early June to late August 1994.

The tidal water DOC concentrations were monitored in the flood and ebb flows over three periods in order to account for seasonal variability. The first set of water samples was collected from May 27 to June 5. The second and third set of water samples were collected from July 23 to August 1, and from August 21 to August 31, respectively. During each of these sampling periods, three diurnal tidal cycles (1 day, 1 night) were sampled for DOC, each corresponding to spring, mean, and neap tides. As a result, six tides were sampled over each period, accounting for a total of 18 tides over the entire season.

Tidal water was collected with a 10 l stainless steel bucket from the centre of the channel under the bridge during both flood and ebb flows. Using a rope attached to the top of the bridge, the bucket was lowered to the bottom of the channel before being returned to the surface. A brick was attached to the outside of the bucket to reduce buoyancy. Water samples were collected at stage intervals of 25 cm. Therefore, more samples were collected during the spring (18-20) and mean tides (14-16) than during the neap tides (8-12). A water sample was also taken from the bridge channel at slack low tide in order to record the DOC concentrations in runoff and seepage water.

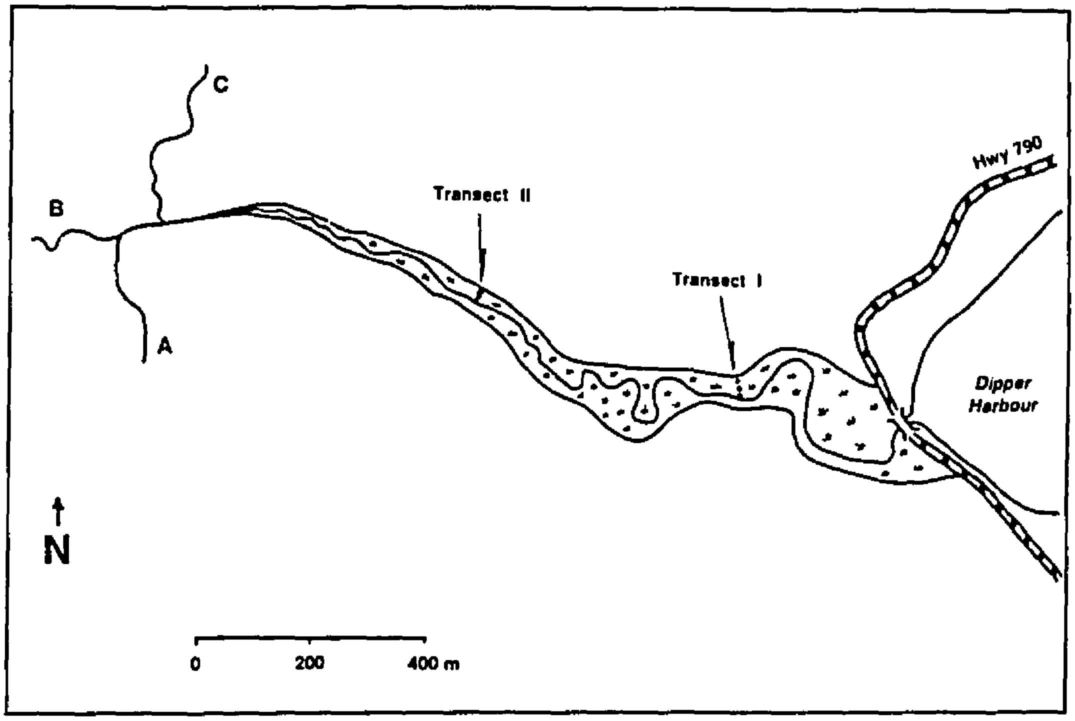
The fraction of the total discharge associated with individual water samples was used to weight DOC concentrations. Since each water sample was collected at specific tidal stage (at 25 cm increments), it was possible to associate DOC concentrations from individual water samples with a representative volume of water. The water volume associated with each water sample was calculated for neap, mean, and spring tides from the discharge data that was available for similar tides that occurred throughout the summer. Spring tides were defined as those reaching heights equal or greater than 7.5 m above sea level (ASL), mean tides were defined as those reaching between 6.7 and 6.9 m ASL in height, and neap tides were defined as those whose maximum height was less than 6.2 m ASL. Water volume data from tidal events which did not fall within any of these categories were not included in the calculation of representative water volume because they did not correspond to any of the tidal events that were sampled. Once the tidal DOC data had been coupled with the stage related water volume, estimates of the flood and ebb DOC fluxes were available. To assess the significance of any apparent import or export term, a paired Student *t*-test was conducted on the DOC concentrations for each flood/ebb cycle.

In addition to tidal and slack low tide runoff water, fresh water from the surrounding drainage basin was collected from three streams at the inland limit of the Dipper Harbour marsh, located approximately 1.8 km from the bridge (Figure 13). Fresh water runoff was collected during each diurnal sampling event. Three additional fresh water samples were taken after storm events over the summer. These streams, flowing from the south, west and north, represent the three most important tributaries of fresh water to the Dipper Harbour salt marsh system. The fresh water discharge from these streams was measured using a "pygmy" Price Meter. Discharge was monitored at the same location that the water samples were collected. The "pygmy" Price Meter was also used to measure the slack low tide discharge under the bridge during each diurnal sampling event.

Groundwater was sampled along two transects oriented from creek to upland, located approximately 0.4 km and 1.3 km from the bridge (Figure 13). Three pairs of piezometers were located on each transect; in the low marsh, middle marsh, and high marsh. At each location, one piezometer sampled groundwater at a depth of 0.4 m, the other at 1.0 m. Groundwater was collected six times over the summer; June 10, June 16, July 23, July 31, August 22, and August 30.

All individual samples of tidal water, fresh water and groundwater were collected in 1 l Nalgene bottles and placed in a cooler. Once returned to the lab, water samples were filtered through a 0.45 μm fibreglass filter. The filtrate was stored and shipped frozen. The DOC concentrations were measured using a Shimadzu TOC-5050 Total Organic Carbon Analyzer by Mike Dalva of the McGill University Geography Department.

Figure 13 - Location of the three main fresh water tributaries (A, B, and C) and the groundwater transects (I and II).



RESULTS AND DISCUSSION

Tidal Water

The water volume associated the different stages of spring, mean, and neap tide events are presented in table 9. The values of instantaneous discharge measured at a specific stage height tended to be greater during the flood cycle than during the ebb. The overall duration of the flood cycle (160 min.) averaged 15 minutes less than that of the ebb cycle (175 min.). The total volume of water associated with spring tides averaged 115050 (± 35750) m^3 and 103200 (± 39220) m^3 for flood and ebb flows, respectively. The volume of water exchanged during mean tides averaged 63000 (± 23270) m^3 on the flood and 58350 (± 25490) m^3 on the ebb. Neap tides averaged 27000 (± 14850) m^3 on the flood and 25650 (± 12670) m^3 on the ebb. A similar difference between the water volume of flood and ebb cycles was observed by Roman and Daiber (1989) who noted an 11% flood-directed residual in their analysis of mean tide events. The authors suggested that this difference was due to experimental error. However, this residual term may be the result of water retention by the marsh sediment, since the value of the residual decreases with decreasing tidal amplitude. During spring tide events, when the entire marsh surface is flooded, the data shows a flood-directed residual of 10%. The residual term drops to 7% under mean tidal amplitudes and to 5% at neap tide, when only a small fraction of the marsh is flooded. It seems likely that this excess flood water is responsible, at least in part, for the slack low tide runoff observed throughout the summer.

Table 9 - Water volume exchange during spring, mean, and neap tides, based on the average discharge (avg Q) and the time elapsed between sampling intervals. The proportion of the water volume exchange for a specific stage interval over the total volume of the flood or ebb cycle represents the factor (or "weight") by which each individual DOC sample is multiplied in order to obtain the net DOC exchange for a given tide event.

SPRING TIDE

	Flood Cycle				Ebb Cycle			
Sample or Stage Marker (cm)	Time interval (min)	avg Q ($m^3 s^{-1}$)	Volume (m^3)	Proportion (%)	Time interval (min)	avg Q ($m^3 s^{-1}$)	Volume (m^3)	Proportion (%)
25	25	5	7500	6.5	15	5	4500	4.4
50	15	12.5	11250	9.8	15	6.5	5850	5.7
75	10	15	9000	7.8	15	7.5	6750	6.5
100	10	17	10200	8.9	15	9.5	8550	8.3
125	15	17.5	15750	13.7	15	12.5	11250	10.9
150	15	18	16200	14.1	15	13.5	12150	11.8
175	15	15	13500	11.7	15	14	12600	12.2
200	20	14	16800	14.6	20	14	16800	16.3
225	20	10.5	12600	11.0	25	13.5	20250	19.6
250	15	2.5	2250	2.0	25	3	4500	4.4
Total	**160**		**115050**	**100**	**175**		**103200**	**100**

MEAN TIDE

	Flood Cycle				Ebb Cycle			
Sample or Stage Marker (cm)	Time interval (min)	avg Q ($m^3 s^{-1}$)	Volume (m^3)	Proportion (%)	Time interval (min)	avg Q ($m^3 s^{-1}$)	Volume (m^3)	Proportion (%)
25	25	4	6000	9.5	25	3	4500	7.7
50	20	5	6000	9.5	25	4.5	6750	11.6
75	20	7	8400	13.3	20	5	6000	10.3
100	15	8.5	7650	12.1	20	6.5	7800	13.4
125	20	10.5	12600	20.0	20	7.5	9000	15.4
150	20	10	12000	19.0	25	9	13500	23.1
175	25	6	9000	14.3	25	6	9000	15.4
200	15	1.5	1350	2.1	15	2	1800	3.1
Total	**160**		**63000**	**100**	**175**		**58350**	**100**

Table 9 - Continued.

NEAP TIDE

Sample or Stage Marker (cm)	Flood Cycle				Ebb Cycle			
	Time interval (min)	avg Q ($m^3 s^{-1}$)	Volume (m^3)	Proportion (%)	Time interval (min)	avg Q ($m^3 s^{-1}$)	Volume (m^3)	Proportion (%)
25	30	1	1800	6.7	35	1.5	3150	12.0
50	30	2.5	4500	16.7	30	2.5	4500	17.1
75	30	4	7200	26.7	30	3.5	6300	24.0
100	30	4.5	8100	30.0	35	3.5	7350	28.0
125	35	2.5	5250	19.4	40	2	4800	18.3
150	5	0.5	150	0.6	5	0.5	150	0.6
Total	**160**		**27000**	**100**	**175**		**26250**	**100**

Concentrations of DOC in individual tidal water samples varied enormously within single flood/ebb events, as indicated by the standard errors included in table 10. There was no apparent pattern in the distribution of the DOC data within a given flood or ebb cycle, and the variability seemed random. However, despite this variability, a number of the weighted values were similar for single tidal events as well as for a few diurnal cycles. In May, the differences in the net DOC concentration between flood and ebb tides was less than 3 mg l^{-1} for all three tidal ranges, suggesting that the tidal DOC exchange was minimal. In July, the weighted DOC concentrations in the ebb cycle were consistently higher than those in the flood for all three tidal ranges, suggesting a net import of DOC. However, establishing the actual value of this import flux would be premature given that the differences between the individual DOC concentrations in flood and ebb waters were not significant (paired Student *t*-test). The August sampling events were the only ones to contain evidence of the tidal export of DOC. These occurred during the day spring tide and the night neap tide cycles. Results from all other tide cycles from the August sampling period suggest an import of DOC. Again, due to the high degree of variability between individual samples, none of these fluxes proved to be significant.

One notable difference between this and other similar studies is the remarkably high DOC concentrations observed in the tidal prism at Dipper Harbour. Previously published mean flood water DOC concentrations range from 1.5 mg l^{-1} (Roman and Daiber 1989) to 18.6 mg l^{-1} (Wolaver and Spurrier 1988). At Dipper Harbour, mean DOC values frequently exceed 100 mg l^{-1}, with some individual concentrations reaching 200 mg l^{-1}. The reason for such high DOC concentrations remains unclear. One possible factor may be the presence of a large lobster pound located just below the mean low water level in Dipper Harbour. However, water sampled from different locations along the Bay of Fundy coast of New Brunswick, from St-Andrew's to Point Lepreau, also contained DOC concentrations exceeding 100 mg l^{-1}, suggesting that high DOC concentrations are characteristic of the region.

Table 10 - Concentrations of DOC in tidal water. DOC concentrations from individual tidal water samples were weighted in terms of the proportional stage related water volume (table 9) and summed in order to estimate a net DOC concentration for the entire flood or ebb cycle.

Spring Tides

	DAY				NIGHT			
DATE	Flood		Ebb		Flood		Ebb	
	DOC (mg/l)	SE	DOC (mg/l)	SE	DOC (mg/l)	SE	DOC (mg/l)	SE
May 27	36.4	18.8	35.6	30.6	33.8	16.2	34.5	9.5
July 23	91.9	35.3	91.1	54.1	93.5	28.3	86.7	46.4
August 21	50.0	21.6	75.6	36.6	125.1	30.1	102.1	32.1

Mean Tides

	DAY				NIGHT			
DATE	Flood		Ebb		Flood		Ebb	
	DOC (mg/l)	SE	DOC (mg/l)	SE	DOC (mg/l)	SE	DOC (mg/l)	SE
May 31	69.4	31.9	70.9	36.4	76.8	37.6	78.3	23.2
July 27	138.0	24.0	101.5	56.1	92.8	58.5	64.7	51.0
August 26	132.2	38.5	110.3	27.2	113.1	34.0	82.8	26.7

Neap Tides

	DAY				NIGHT			
DATE	Flood		Ebb		Flood		Ebb	
	DOC (mg/l)	SE	DOC (mg/l)	SE	DOC (mg/l)	SE	DOC (mg/l)	SE
June 5	74.6	41.3	74.8	36.6	96.6	12.2	98.9	11.8
August 1	163.1	20.9	155.0	22.1	162.2	43.6	136.9	46.5
August 31	11.9	9.7	7.9	2.6	12.1	0.9	36.5	8.0

Groundwater

As with the DOC concentrations measured in tidal water, the groundwater DOC concentrations were highly variable. There was no significant difference in the groundwater DOC between the two transects, nor was there any significant difference between individual piezometers along each transect. In June and July, mean concentrations of DOC in groundwater ranged from 72 mg l^{-1} to 87 mg l^{-1} at both depths (Table 11). The August DOC groundwater values were significantly lower ($P < 0.05$) than those observed earlier in the season, averaging 38 mg l^{-1} and 51 mg l^{-1} in the 0.4 m and the 1.0 m water tables, respectively.

Fresh Water Tributaries

The discharge from fresh water streams entering the marsh system varied from 0.01 $m^3\ s^{-1}$, recorded on August 10 under extremely dry conditions, to 5.45 $m^3\ s^{-1}$, recorded on August 22 after an intense and prolonged rain event. These values represent the sum of the discharge from the three most important fresh water streams. Over the entire season, fresh water discharge averaged 0.3 $m^3\ s^{-1}$. Slack low tide runoff at the marsh outlet (under the bridge) showed a slightly higher range of discharges, averaging 0.45 $m^3\ s^{-1}$ over the summer. It is assumed that the 0.15 $m^3\ s^{-1}$ difference between these two averages represents the discharge associated with water drained from the marsh sediment, which will hereafter be termed 'marsh seepage'. When extrapolated to cover the mean duration of the slack low portion of a single 12 hour tidal cycle (385 min), the average volume of water accounted for by marsh seepage is 3,450 m^3 per tide cycle. Although this water volume is less than the estimated flood-directed residual estimated for spring tides (11,850 m^3), it is of the same order of magnitude with the residual terms estimated for mean (4,650 m^3) and neap tides (1,350 m^3).

Table 11 - Concentrations of DOC in groundwater from the Dipper Harbour salt marsh.

DEPTH	Transect	Distance from Creek (m)	DOC Concentrations (mg/l)					
			June 10	June 16	July 23	July 31	August 22	August 30
0.4m	I	5	70.9	76.2	62.2	128.9	38.0	14.4
	I	20	10.8	117.0	8.1	16.7	111.7	12.6
	I	50	9.0	52.2	25.2	12.8	32.6	23.3
	II	1	92.9	258.2	50.5	194.1	30.5	5.6
	II	9	73.5	110.1	48.0	106.8	61.3	10.5
	II	25	119.8	55.7	129.9	84.0	88.4	24.6
1.0m	I	5	83.2	81.3	22.3	5.0	63.9	34.5
	I	20	32.0	88.2	55.9	103.9	108.0	12.0
	I	50	149.3	104.8	47.5	167.2	20.1	6.5
	II	1	59.2	48.8	82.2	130.2	81.6	15.6
	II	9	38.1	65.0	77.7	133.4	103.1	66.0
	II	25	147.8	125.5	100.1	64.1	68.9	30.6

Table 12 - Concentrations of DOC in water from the three principal fresh water tributaries and from the channel under the bridge at outlet of the Dipper Harbour salt marsh during slack low tide. All values are in mg l^{-1}.

	— Fresh water streams —			Watershed	Marsh outlet
Date	A	B	C	(weighted)	
5/27	33.9	31.7	28.9	31.5	36.6
5/30	67.4	81.6	74.8	76.3	93.9
6/02	83.3	11.2	136.2	60.5	92.0
6/04	97.9	15.1	26.6	38.7	56.6
6/14	67.9	9.2	187.1	68.4	147.0
7/08	40.4	57.8	73.1	57.2	29.7
7/23	14.1	26.1	26.8	23.3	54.0
7/27	131.6	67.6	121.2	97.0	106.6
7/31	119.6	51.2	189.8	103.0	149.3
8/22	89.7	55.2	100.5	75.2	27.9
8/26	11.5	22.7	13.7	17.6	26.3
8/30	12.7	34.8	28.8	27.8	33.7
Mean	**64.2**	**38.7**	**83.9**	**56.4**	**71.1**
SD	**40.0**	**22.6**	**60.6**	**27.5**	**43.6**

The DOC concentrations in the fresh water streams, as well as those in the slack low tide runoff under the bridge are presented in table 12. In order to obtain an overall estimate of the DOC concentration in the fresh water input, individual DOC values from each stream were weighted in terms of the stream's contribution to the overall discharge. The DOC from central stream B, which was the major contributor of fresh water, accounted for 50% of the overall runoff (hence DOC) from the drainage basin. The discharge from streams

A (flowing from the south) and C (from the north) each accounted for 25% of the overall input of DOC.

With the exception of the measurements taken July 7 and August 22, the DOC concentrations observed at the marsh outlet (under the bridge) were greater than the weighted DOC concentrations in the fresh water streams. Over the season, DOC concentrations averaged 56.4 (± 27.5) mg l^{-1} in the fresh water streams and 71.1 (± 43.6) mg l^{-1} in the slack low tide runoff (Table 12). This translates into a 20% increase in the DOC of stream water as it flowed through the marsh system. One possible explanation for such an increase may be related to a contribution in DOC by marsh seepage. As stated earlier, the volume of water associated with marsh seepage during slack low tide can account, on average, for 3,450 m^3 per tide cycle. In order to account for the increase in DOC that was observed between the upland limit of the marsh creek and the outlet, the average DOC concentration in marsh seepage would be 100 mg l^{-1}, and marsh seepage would account for a DOC export of 350 kg per slack tide event (assuming a mean tide). In comparison, the DOC export term for the surrounding fresh water drainage basin (8.5 km^2) is approximately 390 kg DOC per slack tide event.

CONCLUSIONS

Due to the high level of variability in the DOC concentrations of tidal water, the magnitude of the net annual DOC export flux from the Dipper Harbour salt marsh remains uncertain. Replicate analyses for [DOC] were performed on each sample and there appears to be no consistant error in the determination of the concentration. However, this study has generated some interesting observations concerning the processes that govern the transport of DOC through the marsh system.

It would appear that the principal mechanism involved in the export of DOC from the marsh involves marsh seepage during slack low tide. The magnitude of marsh seepage export term (assuming two tidal cycles per day) is estimated at roughly 700 kg DOC per day. Considering the surface area of the vegetated marsh (69,575 m^2) and extrapolating over a 200 day growing season, the marsh seepage DOC export term accounts for a loss of 2,000 g DOC m^2 yr^{-1}. This term seems rather large and may be an overestimate. However, analysis of the tidal water suggests that the marsh may import DOC during tidal inundation since the concentrations of DOC in the flood water tend to be greater than those in the ebb water. In South Carolina, similar observations were made by Wolaver and Spurrier (1988) who reported a 'statistically insignificant' DOC import to the vegetated marsh during tidal inundation, and exports of DOC from the marsh via runoff and seepage during low tide exposure. Therefore, it is not impossible that the import of DOC observed during tidal inundation at Dipper Harbour may counter the slack low tide export, hence reducing the net DOC export from the marsh to the adjacent waters. When extrapolated for two tidal cycles per day over a 200 day growing season for the entire vegetated marsh surface, the overall tidal DOC import term (i.e., the difference between flood and ebb) accounts for about 1,500 g DOC m^{-2} yr^{-1}. Although this is only a crude estimate that is by no means conclusive, it suggests that the tidal import of DOC may balance out a significant proportion of the low tide export of DOC, resulting in a net annual DOC export in the order of 500 g C m^{-2} yr^{-1}.

CHAPTER 4 - CARBON BUDGET

INTRODUCTION

Although most studies of salt marsh carbon have focused on one major flux component, there have been some attempts to model the flow of carbon through the entire system. One of the primary objectives for modelling carbon flow through coastal salt marshes has been to test the "outwelling hypothesis" (Teal 1962, Odum 1968, Nixon 1980) which states that a significant proportion of the net production is exported from the marsh to the estuarine waters. Pomeroy and Wiegert (1981) examined various carbon fluxes in the salt marshes of Sapelo Island, Georgia, compiling an extensive amount of data into what remains today as one of the most complete and comprehensive studies of salt marsh nutrient cycling. However, in the final analysis, their estimate for vascular plant (*S. alterniflora*) and algal productivity was greater than the sum of the carbon lost (through respiration and tidal transport) and stored (through sedimentation). As a result, their annual carbon budget did not balance, and a residual export term of 178 g C m^{-2} yr^{-1} remained unaccounted for in the data. The authors suggested that this export term was the result of herbivory by macroconsumers. In a similar study of two tidal marshes of the Gulf Coast (Louisiana), Nyman *et al.* (1995) used measurements of plant productivity, soil respiration and sediment burial to construct a budget which solved for organic matter export.

Carbon budgets have also been used as a tool for estimating flux terms other than tidal export. In the Great Sippewissett Salt Marsh of Massachusetts, Howes *et al.* (1985)

constructed an annual belowground carbon budget for sediments supporting short *S. alterniflora* in order to determine the belowground production rate of *S. alterniflora*. Their budget was constructed from measurements of carbon dioxide and methane emissions from the sediment to the atmosphere, inorganic carbon exchanges in porewater, leaching of dissolved organic carbon from the sediment profile, and sediment burial.

In northern salt marshes, such as those along the coast of the Bay of Fundy, there is only fragmentary information available concerning the mechanisms and the magnitude of the major flux components involved in carbon cycling. In an examination of salt marshes located in the Cumberland Basin, Gordon *et al.* (1985) suggested that the majority of aboveground plant biomass produced in these systems is eventually exported to adjacent coastal waters. However, no direct empirical evidence concerning the tidal export of carbon was presented. The authors refer to observations showing the widespread distribution of *Spartina* detritus as the most convincing evidence, postulating that the high tidal ranges in the Fundy region may provide the energy necessary for exporting plant material from the marsh surface. Since information concerning belowground plant production and the fate of dissolved organic carbon (DOC) was lacking, Gordon *et al.* (1985) did not attempt to quantify the carbon export term.

Evidence presented in the previous chapter suggests that the Dipper Harbour salt marsh exports DOC to the adjacent coastal waters. A crude estimate of the DOC export term (500 g C m^{-2} yr^{-1}) was obtained by subtracting the net tidal exchange import term (1,500 g C m^{-2} yr^{-1}) from the export term estimated for slack low tide runoff (2,000 g C m^{-2} yr^{-1}). Although this estimate supports the outwelling hypothesis, the results remain inconclusive due to the variability in the measurements.

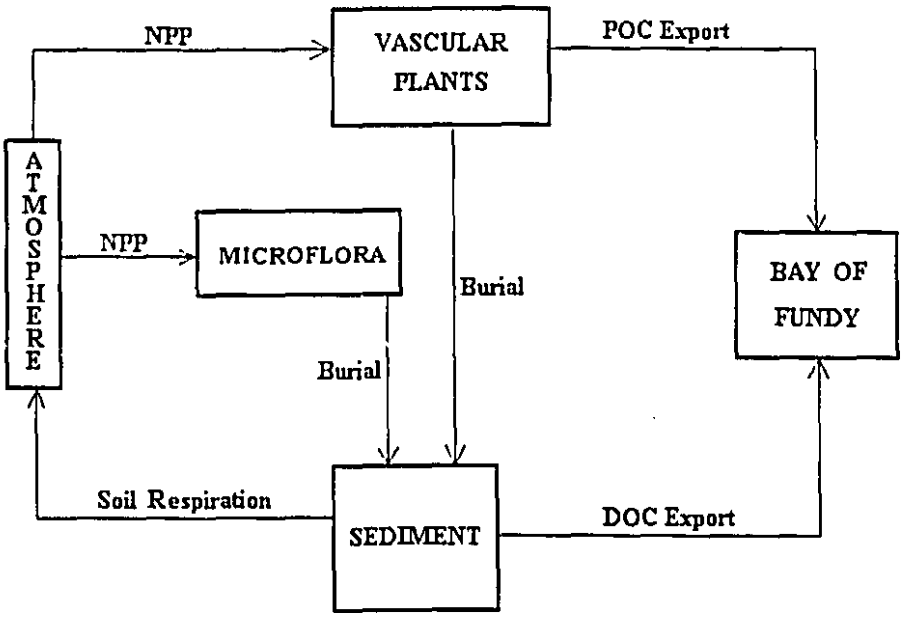
This final chapter presents a carbon budget for the Dipper Harbour salt marsh which estimates the DOC export term. The DOC export term predicted by the budget is compared to that obtained from the DOC study in an attempt to produce the best possible estimate of the magnitude of the DOC flux. The approach used to construct this carbon budget is similar to that used by Nyman *et al.* (1995). In addition to carbon flux estimates related to the net primary production (NPP) of the dominant macrophytes, to the rates of sediment carbon burial, and to the tidal export of particulate organic carbon (POC), other fluxes such as soil respiration and algal productivity are estimated from data available in the literature.

As both NPP and the rate of carbon burial vary with vegetation zone, a carbon budget presented for each of the three major plant zones; *S. alterniflora, S. patens,* and *Plantago.* Hence, the role of each dominant plant is addressed in terms of the overall salt marsh carbon cycle. Surfaces over which macrophyte productivity was assumed to be negligible, such as creekbanks, pans and pools, are not included in the budget.

CARBON FLUX MODEL

Figure 14 is a box model representation of the major carbon fluxes on the salt marsh system upon which the carbon budget is based. In this model, the carbon fixed by the production of macrophytes can follow one of two pathways. One fraction, principally composed of coarse and particulate fragments of aboveground plant tissue (POC), can be exported directly to the adjacent coastal waters via tidal flushing. The remaining portion, which includes the remaining aboveground tissue as well as all belowground plant biomass, is incorporated into the sediment (i.e., the model considers all remaining dead aboveground plant material as part of the sediment). The salt marsh substrate itself is a dynamic system in which many biogeochemical processes occur and from which many of the carbon fluxes originate. Through the process of microbial decomposition, a fraction of the organic matter stored in the soil is mineralized to carbon dioxide (CO_2) and returned to the atmosphere via soil respiration. Another fraction of organic matter can be buried within the salt marsh substrate, resulting in a long term storage flux in which the sediment acts as a carbon sink. Finally, the remaining fraction of the organic matter pool, composed mainly of soluble carbon-based compounds such as humic acids, can be leached from the sediment via tidal inundation or low tide seepage and runoff and eventually exported to the adjacent coastal waters. This last export term, corresponding to the DOC flux, represents the unknown term which is estimated by the budget.

Figure 14 - Compartmental model of the principal carbon fluxes, reservoirs, and storage terms in the Dipper Harbour salt marsh system. The carbon budget is based on this model.



BUDGET COMPONENTS

Production

The input of carbon to the Dipper Harbour system from the net primary productivity of the vascular plants is presented in chapter 1. The greatest source of carbon to the salt marsh systems is the belowground productivity of the macrophytes (NBPP), which accounts for over 60% of the total input of carbon for all three dominant plant species (Table 13). Since production of this macro-organic matter occurs below the surface of the sediment, it is not likely to be exported quickly from the system and can be considered to have relatively long residence time. The turnover periods for the live belowground biomass pool in the Dipper Harbour marsh, which were estimated at 2.5 years for *Plantago* and *S. patens* and at 4.5 years for *S. alterniflora*, support this assumption. Although no direct relationship between NBPP and DOC export has been identified, it has been made clear that the input of carbon from belowground production greatly influences the model. For example, a 25% decrease in NBPP would result in a 30% decrease in DOC export.

Aboveground plant productivity (NAPP) accounts for roughly 30% of the system's total input of carbon. However, because the aboveground plant biomass is subjected to the rigors of climate and tidal inundation, it is far more likely to be dislodged from the marsh surface and exported as particulate matter than the belowground biomass. The plants that are located in the areas that are most frequently flooded or that are subjected to disturbances such as ice rafting are more susceptible to biomass loss than those plants which are located in less frequently flooded areas. Therefore, changes in NAPP may not affect the DOC estimate as much as changes in NBPP. For example, a 25% decrease in NAPP would result in a 15% decrease in DOC export.

Benthic algae living on the sediment surface are believed to contribute significantly to the net primary production. The results from four different studies of algal productivity are presented in table 7. It has been observed that algal productivity represents between 25% and 33% of the productivity by aboveground macrophytes (Mitsch and Gosselink

1986). Assuming that the ratio of algal productivity to NAPP at the Dipper Harbour salt marsh is similar to those in previously reported studies, the input of carbon from benthic algae has been estimated at 50 g C m^{-2} yr^{-1}. The values assigned to algal productivity in the carbon budget represent between 5% and 11% of the total input of carbon to the different vegetation zones (Table 13). Since this estimate was based on results from previous research conducted at different locations, it represents the carbon input term with the greatest level of uncertainty. However, the uncertainty related to this flux estimate does not grealty increase the uncertainty level of the model. Even if the value of algal productivity were to triple, the estimated DOC export would only increase by 27%.

Overall net primary productivity, as determined by the sum of NAPP, NBPP and algal production, varies considerably between each major plant zone. The *S. alterniflora*-dominated low marsh is characterized by the greatest annual influx of carbon (922 g C m^{-2} yr^{-1}) followed by the *S. patens*-dominated high marsh (704 g C m^{-2} yr^{-1}). The middle marsh, dominated by *Plantago*, is characterized by the lowest productivity rate (449 g C m^{-2} yr^{-1}). Therefore, in order to establish a carbon budget for other salt marshes in the Fundy region, the surface area occupied by each of the dominant plant species must be determined.

Sediment Burial

The rates of carbon burial in the sediments of each of the major plant zones are presented in chapter 2. The zone dominated by *Plantago* is characterized by the highest burial rate (106 g C m^{-2} yr^{-1}), followed by the *S. patens*-dominated high marsh sediments (81 g C m^{-2} yr^{-1}). The sediments of the *S. alterniflora*-dominated low marsh have the lowest soil carbon accumulation rate (73 g C m^{-2} yr^{-1}). Although this flux term is associated with a large potential for error (due to the fact that accretion rates were based upon a single ^{137}Cs profile), the model's sensitivity towards this flux is rather small. For example, if the accretion rate were to double, hence doubling the carbon burial rate, the predicted DOC export would only decrease by 23%.

Table 13 - Carbon budget for each of the major plant zones of the Dipper Harbour salt marsh. The budget for the overall vegetated marsh surface was obtained by weighting the flux values for each plant zone by the percentage of area dominated by each macrophyte. All values are in g C m^{-2} yr^{-1}.

	Plant Zone			
	S. alterniflora	***S. patens***	***Plantago***	**Overall marsh**
NAPP	295	221	129	**224**
NBPP	577	433	270	**443**
Algal NPP	50	50	50	**50**
Total Production	**922**	**704**	**449**	**718**
Tidal export of NAPP (POC)	172	65	127	**121**
Sediment Burial	73	81	106	**85**
Soil Respiration	146	129	150	**141**
Total export and storage	**391**	**276**	**383**	**346**
Predicted DOC export	**531**	**428**	**66**	**371**

Export of Particulate Organic Carbon

Throughout the year, a portion of the aboveground biomass pool is lost from the marsh surface and exported by the ebb tide. This loss corresponds to the particulate organic carbon (POC) export term. During the growing season from early May to early October, some leaves and stems can be dislodged from the plants and exported. The loss of plant material can also occur during the period of senescence, from mid-October to late April. The magnitude of winter export flux can vary from one year to the next, since it is greatly dependant upon the frequency of disturbance events, primarily ice rafting. Dionne (1989) observed that erosion by ice occurred across the marsh surface, but was most prominent in a narrow strip located between the high and low marsh. At Dipper Harbour, the zone most likely to be disturbed by ice rafting is that dominated by *Plantago*, located between the low and high marsh. In early May, no vegetation cover was observed in this plant zone as the sediment surface was completely bare. Therefore, it is assumed that the annual export term for aboveground *Plantago* biomass is equal to the NAPP value estimated for this species, which is 126.6 g C $m^{-2} yr^{-1}$. Estimates for the export of POC are represented in table 8.

In the two other major plant zones, dominated by the *Spartina* grasses, only a fraction of the aboveground biomass pool is exported. The remaining portion is assumed to be buried in the marsh sediment. The annual export term for *S. alterniflora* is estimated at 172 g C $m^{-2} yr^{-1}$, which corresponds to 60% of *S. alterniflora* NAPP. The export of POC from the *S. patens* zone is estimated at 65 g C m^{-2} yr^{-1}, which corresponds to 40% of the NAPP. When compared to the estimated DOC export term, the overall POC export term is small, representing only 25% of the carbon exported to the Bay of Fundy. Under extreamly harsh climatic conditions where the POC export term were to double, the estimated DOC flux would likely fall by 33%.

Soil Respiration

The surface to atmosphere CO_2 flux was the focus of a study conducted by Magenheimer *et al.* (1996) at the Dipper Harbour salt marsh. Gas flux measurements were obtained using a static chamber technique over a period from mid-July to early September 1993. Although these flux measurements were taken one year prior to the other measurements reported in this study, it is assumed that they are representative of the system. Magenheimer *et al.* also measured the efflux of methane (CH_4), but these were found to be several orders of magnitude lower than the CO_2 effluxes and therefore have not been included in the Dipper Harbour carbon budget.

Table 14 - CO_2 flux measurement from the vegetated surface of the Dipper Harbour salt marsh (from Magenheimer *et al.* 1996).

	— Carbon dioxide flux —		
	daily ($g\ m^{-2}\ d^{-1}$)	annual ($g\ m^{-2}\ yr^{-1}$)	annual C export ($g\ C\ m^{-2}\ yr^{-1}$)
S. alterniflora	2.67	534	145.6
S. patens	2.37	474	129.3
Plantago	2.75	550	150.0

The results from the Magenheimer *et al.* study are presented in table 14. The greatest mean daily efflux of CO_2 was measured in the *Plantago* zone (2.75 g CO_2 m^{-2} d^{-1}), followed by *S. alterniflora* (2.67 g CO_2 m^{-2} d^{-1}), and *S. patens* (2.37 g CO_2 m^{-2} d^{-1}). Because the measurements obtained by the static chamber technique include the CO_2 flux from respiration by vascular plants and microflora, these values represent overestimates of soil respiration. However, Magenheimer *et al.* reported that their measurements were likely to underestimate the total gas flux since their measurements did not account for episodic gas releases and the degassing of porewater. Also, the covered chambers may have repressed the conductive action of the plants.

In order to derive an annual estimate of the soil respiration export term, the mean daily CO_2 flux rate for each dominant plant zone was integrated over 200 days. Although Magenheimer *et al.* assumed that the summer emission rate covered a period of 150 days, an extra 50 days of emission were added in order to account for emissions that may occur over the remaining seasons. The estimates for the annual carbon flux attributed to soil respiration for the Dipper Harbour marsh range between 129.3 g C m^{-2} yr^{-1} for the *S. patens* zone and 150.0 g C m^{-2} yr^{-1} for the *Plantago* zone (Table 14). The annual CO_2 fluxes reported here are slightly lower than those reported in previous studies, which have ranged between 180 and 640 g C m^{-2} yr^{-1} in Louisiana, South Carolina, Long Island and Massachusetts (Howes *et al.* 1985, Smith *et al.* 1983, Houghton and Woodwell 1980, Morris and Whiting 1986). The model's sensitivity towards the soil respiration flux is similar to that of the POC export flux, since the magnitude of both fluxes is similar.

Budget predicted DOC export term

When the export and storage terms are subtracted from the total production (Table 13), there remains a residual which has not been accounted for in the quantitative analysis of the major salt marsh carbon fluxes. It is believed that this residual approximates the export flux associated with the removal of dissolved organic carbon (DOC) from the system. The DOC flux predicted by the budget for both *S. alterniflora* and *S. patens* (522 g C m^{-2} yr^{-1} and 425 g C m^{-2} yr^{-1} respectively) is of the same order of magnitude as the net flux estimated from the field data (500 g C m^{-2} yr^{-1}) for the entire vegetated marsh surface. The DOC flux predicted for *Plantago* is much lower than for the other zones, accounting for only 64 g C m^{-2} yr^{-1}. This is because the sum of tidal export of NAPP, soil burial, and soil respiration terms in the *Plantago* zone were high, and total production was low. These results suggest that the cycling of carbon in *Plantago*-dominated salt marsh sediment may differ considerably from that in the *Spartina*-dominated marsh sediment.

In order to obtain an overall carbon budget for the entire vegetated salt marsh, the different flux estimates made for each dominant plant zone were weighted as a function of the area occupied by each species. Of the total 69375 m^2 surface of the Dipper Harbour salt marsh, 37.0% is dominated by *S. alterniflora*, *S. patens* and *Plantago* dominate 36.8% and 26.2%, respectively. The area weighted carbon flux estimates for the overall marsh surface are presented in table 13. The final budget of the entire vegetated salt marsh surface predicts a mean DOC export flux of 366 g C m^{-2} yr^{-1}.

CARBON CIRCULATION

The Spartina-Dominated Zones

At the Dipper Harbour salt marsh, each major plant zone is characterized by different physical conditions relating primarily to flooding frequency, influence soil characteristics such as mineral composition, bulk density, and hydrological conductivity. The dominant plants themselves are also likely to influence the edaphic conditions.

Despite the different physical conditions, many of the carbon flux terms which characterize the *S. patens*-dominated high marsh and the *S. alterniflora*-dominated low marsh are similar. Both these zones have relatively high rates of macrophyte production, and the rates of sediment carbon burial and soil respiration in both zones are similar. The difference in production between these two plant communities (roughly 200 g C m^{-2} yr^{-1}) is accounted for by differences in the export of particulate organic matter and DOC. As suggested by Gordon *et al.* (1985), the greater flooding frequency in the low marsh is likely to promote the removal of aboveground plant tissue, hence increasing the potential for the export of carbon from this zone. Also, soil saturation due to tidal flooding increases the potential for the leaching of DOC from the sediment. The principal mechanism involved with DOC export appears to be slack low tide runoff, during which the tidal water that had filled the sediment pore spaces is leached from the soil into the creek and exported from the marsh. Hence, the greater DOC export from the frequently flooded *S. alterniflora* zone predicted by the model is supported by the field observations.

The Plantago-Dominated zones

The carbon flux terms associated with the *Plantago* zone are considerably different from those in the *Spartina*-dominated communities. This zone is characterized by the lowest NPP and highest rates of tidal export of particulate matter and soil respiration. As a result, the organic carbon pool available for sediment burial and DOC export is relatively low. Yet, the rate of carbon accumulation in the soil of the *Plantago* zone is roughly 25% greater than that of the *Spartina* zones. One plausible hypothesis for such a high sedimentary carbon accumulation rate may relate to the edaphic conditions which regulate carbon circulation within the sediment of the *Plantago* zone. Given that the bulk density of the *Plantago* sediment is greater than that observed in the other vegetation zones, it is possible that the *Plantago* sediment acts as a barrier which restricts the belowground circulation of carbon between the high and low marsh. Under such conditions, a fraction of the DOC which is leached from the high marsh sediment may become trapped in the *Plantago* sediment where it is stored.

Microfloral productivity represents another possible explanation for the high sediment carbon accumulation rates observed in the *Plantago* zone. The surface coverage of *Plantago* is not as high as that of the *Spartina* associations and, as a result, a greater amount of solar insolation reaches the sediment surface, promoting microfloral productivity. In salt marshes to the south, it has been observed that the net primary production of microalgal communities located in *S. alterniflora*-dominated marshes represents 25%-33% of the aboveground productivity of the macrophytes (Mitsch and Gosselink 1986). Given the increased availability of sunlight beneath the *Plantago* canopy, it seems reasonable to assume that the potential for microalgal growth in this plant zone exceeds that of the *Spartina* zones. Microbial activity in the *Plantago* associations may also explain the relatively high level of soil respiration observed in this zone by Magenheimer *et al.* (1996), as one would expect lower soil respiration rates in the least productive sites. The sediment "barrier" hypotheses and the microfloral production hypothesis for explaining the high sediment carbon accumulation rates observed in the soil of the *Plantago* zone are not exclusive.

Analysis of the carbon budget of the Dipper Harbour salt marsh suggest that tidal export of organic material, in both particulate and dissolved form, accounts for 65%, 52%, and 48% of the net primary productivity of *S. alterniflora*, *S. patens*, and *Plantago* respectively. However, unlike the *Spartina*-dominated vegetation zones for which the budget predicts a relatively large DOC export term, most of the organic material exported from the *Plantago* zones appears to be in coarse or particulate form. These results support the "outwelling hypothesis" proposed by Teal (1962) who suggested that about 45% of the production by salt marsh macrophytes was exported to adjacent coastal waters. Although an attempt at measuring the export of DOC though field observation was not entirely conclusive, the DOC export term predicted by the budget is of the same order of magnitude as the crude estimate obtained by the field data. These results also support the observations reported by Gordon *et al.* (1985) who suggested that coastal tidal salt marshes play a major ecological role in the Bay of Fundy, supplying carbon to the adjacent coastal ecosystem.

In the future, the carbon budget could be refined by a further examination of soil respiration, since the rates presented here do not distinguish between the CO_2 produced by decomposition and that produced by the macrophyte and microfloral respiration. The accuracy of the Dipper Harbour salt marsh carbon budget would also be increased if further information concerning the growth dynamics of the microfloral communities was made available. Although only fragmentary information is available concerning *Plantago*, it has become increasingly evident that this forb plays a significant role in the circulation of carbon throughout the Dipper Harbour salt marsh. The results of this study suggest that carbon cycling in northern marshes which possess a *Plantago* dominated "middle marsh" habitat may be quite different from that in marshes located further south where which have served as models for previous carbon budgets.

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