Dynamics of above- and belowground organic matter in a high latitude macrotidal saltmarsh

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ABSTRACT: Seasonal variations in above- and belowground biomass were examined over the 1994 growing season (May to October) in the 3 major plant zones of a saltmarsh located on the Bay of Fundy. Standing crop of aboveground biomass was measured over the growing season. Belowground samples were processed at depth intervals of 2 cm, providing high-resolution vertical profiles to a depth of 40 cm. *Spartina alterniflora* showed evidence of the translocation of belowground biomass to aboveground tissue in the early part of the growing season, when the rate of aboveground growth is at a maximum. Shifts in *S. alterniflora* organic matter storage were most dynamic in the surface 16 cm. Biomass translocation generally was not significant in the *S. patens* stands, where the rate of aboveground growth was consistent throughout the growing season. All seasonal changes associated with *Plantago maritima* biomass seem to occur before July, since no changes in above- and below-ground biomass were observed between July and October. *P. maritima* contributes the least to marsh soil organic matter.

KEY WORDS: Fundy · Saltmarsh · Standing crop · *Spartina* · *Plantago*

INTRODUCTION

Wetlands, and particularly tidal saltmarshes, have long been recognized for their high rates of primary production relative to most other temperate ecosystems (e.g., Whittaker 1975). Yet most tabulations ignore belowground production, which in saltmarshes is generally higher than that produced aboveground (Good et al. 1982). The belowground component is assumed to play a critical role in the flux of greenhouse gases from marsh surfaces and, by its nature, comprises a major portion of the carbon sequestered in saltmarsh soils. To better understand the role of tidal saltmarshes in the global carbon cycle we must examine the temporal and spatial dynamics of this below-ground component. In the present study we examine the dynamics of belowground biomass for 3 dominant species in a high latitude, high tidal range saltmarsh in the outer Bay of Fundy, focussing on seasonal changes and distribution of biomass with depth. Although the majority of studies on saltmarsh production have been conducted on the eastern coast of North America, few have been situated at high latitudes or in high tidal ranges.

Belowground biomass production may contribute to the volume, hence elevation, of the marsh substrate. It is assumed that marsh elevations are in equilibrium with sea level. Thus, rising sea levels associated with greenhouse warming will require increased rates of marsh accretion, dependent, in part, on inputs from belowground production. Knowledge of temporal, spatial and species variability in the translocation of belowground biomass is essential in interpretation of the marsh accretion process.

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

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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, seasonal sampling of the live and dead belowground biomass pools is a major component of this study.

The vertical distribution of underground biomass may also provide valuable insight into the growth processes involved in belowground production. Gallagher & Plumley (1979) examined vertical profiles of belowground macro-organic matter, but they did not separate living and dead tissues. In Georgia, Schubauer & Hopkinson (1984) separated belowground biomass into 3 fractions (roots, rhizomes and dead material), and found evidence of the seasonal storage and redistribution of organic matter between above- and belowground *Spartina alterniflora* tissue. In Massachusetts, Gallagher & Howarth (1987) observed seasonal patterns in the distribution of recoverable underground reserves in *S. alterniflora*, but found no significant pattern in *Spartina patens*. Thus, the timing of peak and minimum biomass is critical to establishing translocation and/or storage dynamics. In this study, we use high resolution analysis (2 cm depth intervals) to determine if similar processes and mechanisms are involved in the growth and accumulation of belowground plant tissue in saltmarshes located at high latitudes.

The objective of the present study is to examine seasonal variations in the vertical distribution of below-

ground biomass for 3 structurally dominant macrophytes in a Bay of Fundy saltmarsh: *Spartina alterniflora*, *S. 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 information on this forb is limited. Aboveground biomass of these 3 species is also presented in order to complement the examination of production and growth dynamics.

METHODS

Study area. The Dipper Harbour saltmarsh 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 (Fig. 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 m. The marsh occupies a 7 ha area located in an east-west-oriented valley, a common feature of the region's irregular shoreline. The characteristics of the marsh closely resemble those of the 'fluvial-minor' type marshes described by Kelley et al. (1988). The seaward side of the marsh is bordered by a 4 m high artificial embankment, upon which a secondary road was constructed, Highway 790 (Fig. 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.

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 to 35 ppt at the bridge outlet to 5 to 31 ppt at 1.1 km inland. Further inland, the typical high/low marsh physiography (Redfield 1972) gives way to one resembling brackish systems.

The saltmarsh surface is divided into 3 distinct vegetation zones, which are directly related to flooding frequency (Table 1). The low marsh, dominated by monospecific stands of *Spartina*
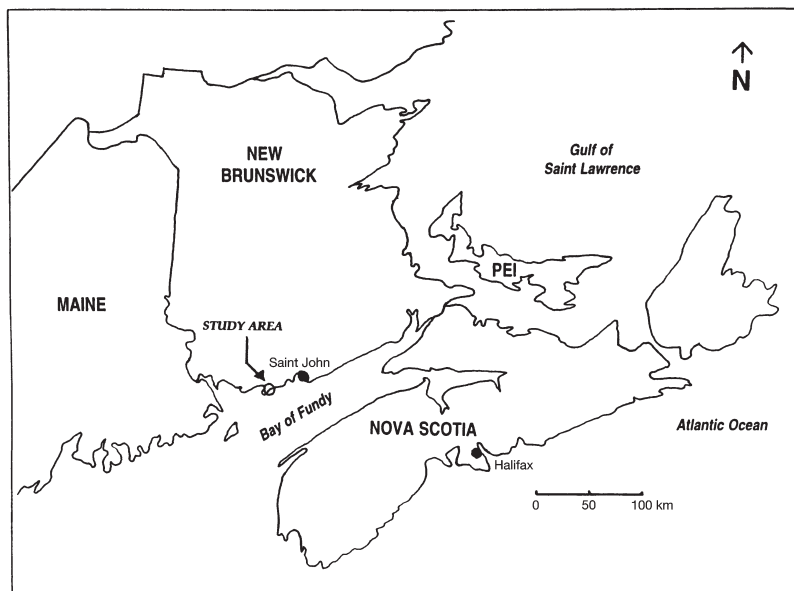

Fig. 1. Location of the study area in New Brunswick (Canada) in relation to the province of Nova Scotia (Canada) and the state of Maine (USA)
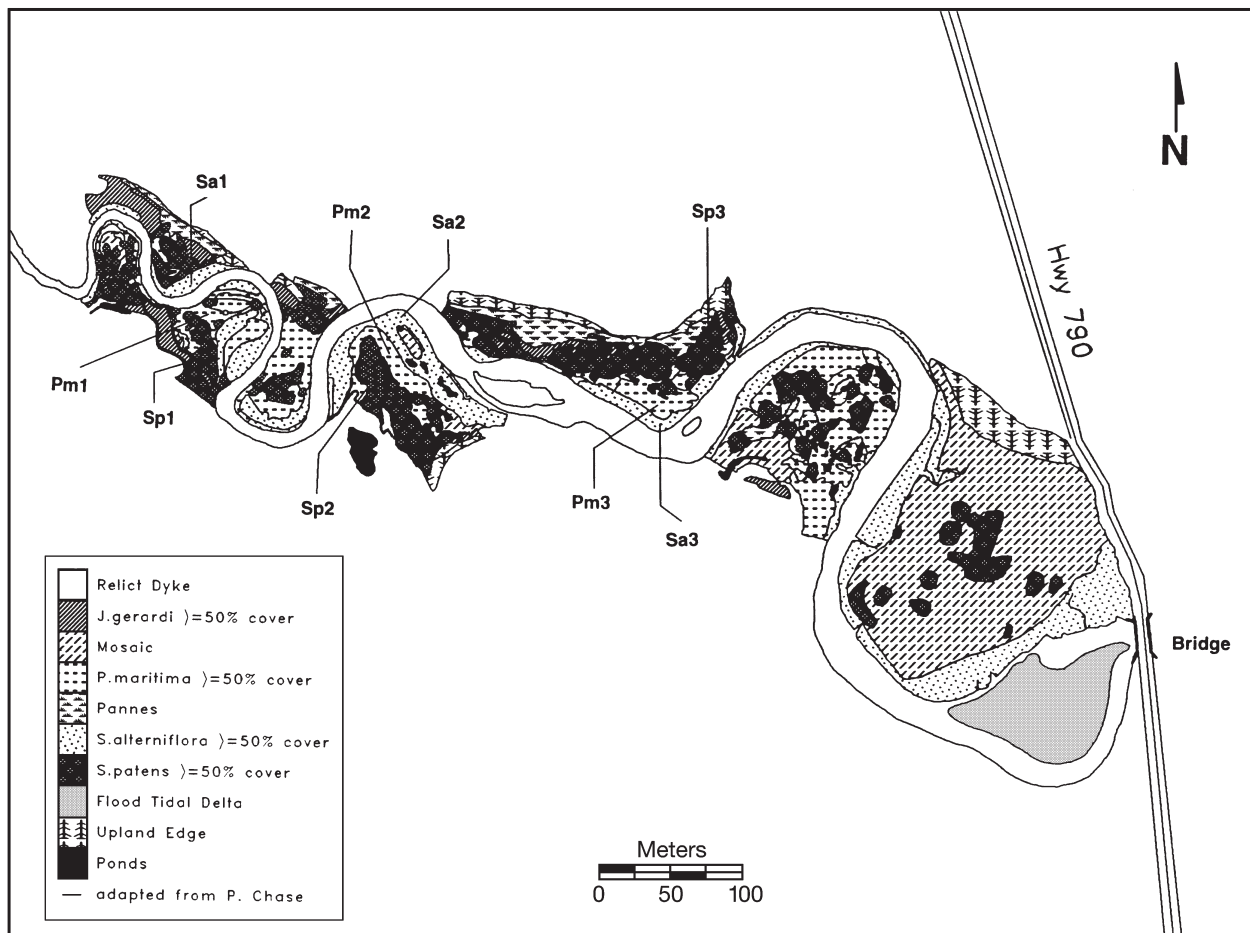
Fig. 2. Vegetation map of Dipper Harbour saltmarsh. Sample locations are noted for each species. Numbers refer to profiles from individual stands. Designations used in the following figures: Sa, *Spartina alterniflora*; Sp, *Spartina patens*; Pm, *Plantago maritima*

alterniflora, forms a band ranging from 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 to 10%. *Plantago maritima*, a forb, is dominant in the intermediate elevations between low and high marsh. The cover percentage of *P. maritima* varies from 70 to 80%, with the remaining surface populated

by a combination of *S. alterniflora* (5%), bare patches (5 to 15%) and other forbs (5 to 15%). High marsh vegetation is dominated by *S. patens*, which generally occurs in monospecific stands although some forb species may be present in cover percentages <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* (see Chmura et al. 1997 for additional details). Preliminary observations suggested to us that downstream gradients in production might be present. Thus, we subdivided the marsh into 3 units: Unit 1 was the furthest upstream, i.e. the furthest away from the tidal inlet, and Unit 3 was closest to the tidal inlet.

Sampling. Above- and belowground samples of *Spartina alterniflora*, *S. patens* and *Plantago maritima* were collected on May 3, July 21 and October 2, 1994. At each sampling event, 3 replicates per species were

Table 1. Characteristics of the 3 dominant plant zones in the Dipper Harbour saltmarsh. Flooding frequency was based on the number of tides between May 1 and August 30, 1994

	Spartina alterniflora	Spartina patens	Plantago maritima
Flooding frequency (%)	90–95	50–60	55–75
Area (m^2)	25 662	25 503	18 211
Dominance (% cover)	90–95	95–100	70–80

taken from different locations on the marsh (Fig. 2). The sampling sites were located, if possible, in monospecific stands. In *P. maritima* stands densities were greater than 30 plants per 0.1 m². The position of each quadrat within the sampling location was chosen by random toss. Aboveground biomass was harvested in 0.1 m² clip plots. 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 the standing crop.

Once the vegetation had been clipped, a 15 cm diameter aluminum core was gently twisted into the centre of the clip plot to a depth of 40 cm. Compaction in all cores was minimal, never exceeding 1 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. 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 maritima* biomass was dark and woody, and often broken into small fragments. As a result, the separation of belowground *P. maritima* tissue into live and dead fractions was not possible. However, the *P. maritima* 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 *Spartina alterniflora* cores maintained consistent amounts of biomass at that depth. Below 30 cm depth, the *S. patens* cores contained mostly *S. alterniflora* and *Plantago maritima* fragments, and therefore *S. patens* analysis was limited to the top 30 cm of the profile. For *P. maritima*, the transition to another species was located at a depth of 20 cm, below which only *S. alterniflora* fragments were present.

RESULTS AND DISCUSSION

Aboveground biomass

Peak standing crop was observed in October for all 3 species, although the aboveground growth of *Plantago maritima* 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 *S. patens* was similar for both sampling intervals. It appears that *S. alterniflora* production primarily occurs in the first 2 to 3 mo

Table 2. Average seasonal standing crop (g dry wt m^{-2}) for the 3 dominant macrophyte species in the Dipper Harbour saltmarsh. SE: standard error

| | *Spartina alterniflora* | | *Spartina patens* | | *Plantago maritima* | |
	Avg.	SE	Avg.	SE	Avg.	SE
May	8	6	0	0	20	4
July	335	56	164	19	221	57
Oct	460	92	379	82	222	43

of growth, whereas *S. patens* production rates appear constant throughout the growing season. Average standing crop values for *P. maritima* were similar for both July and October, suggesting that most aboveground production occurs prior to July. *P. maritima* 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 the 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 2 sites further upstream. No observable trends regarding the standing crops of *S. patens* and *P. maritima* were observed.

Peak standing crop for *Spartina alterniflora* (Table 2) at Dipper Harbour is similar to the 558 g dry wt m^{-2} reported for a saltmarsh on the Atlantic coast of Nova Scotia (Hatcher & Mann 1975), and the 563 g dry wt m^{-2} reported for marshes in the Minas Basin, at the head of the Bay of Fundy (Gordon et al. 1985). Our measurement for *S. patens* is close to that of Gordon et al., who reported 371 g dry wt m^{-2}. No reports for *Plantago maritima* were found for the western Atlantic, but the maximum of 466 g dry wt m^{-2} reported by Ketner (1972, as cited by Groenendijk & Vink-Lievaart 1987) for a Dutch marsh is considerably higher than that measured at Dipper Harbour.

Seasonal variability in the distribution of belowground biomass

Throughout the growing season, live belowground biomass of both *Spartina* species was generally low in the top 2 cm (Figs. 3 & 4), but increased dramatically to maximums between 4 to 12 cm (*S. alterniflora*) and 4 to 8 cm (*S. patens*). In Massachusetts, Valiela et al. (1976)
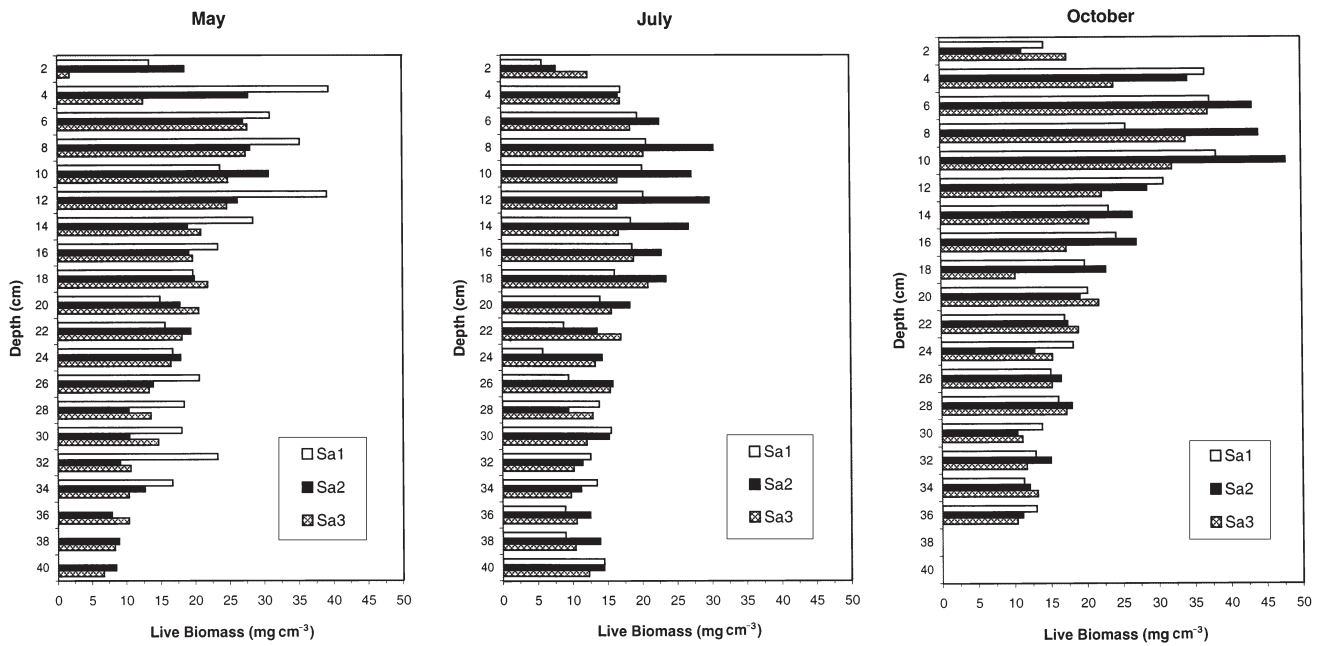
Fig. 3. *Spartina alterniflora.* Live belowground biomass in individual stands as recorded over the 3 sampling periods
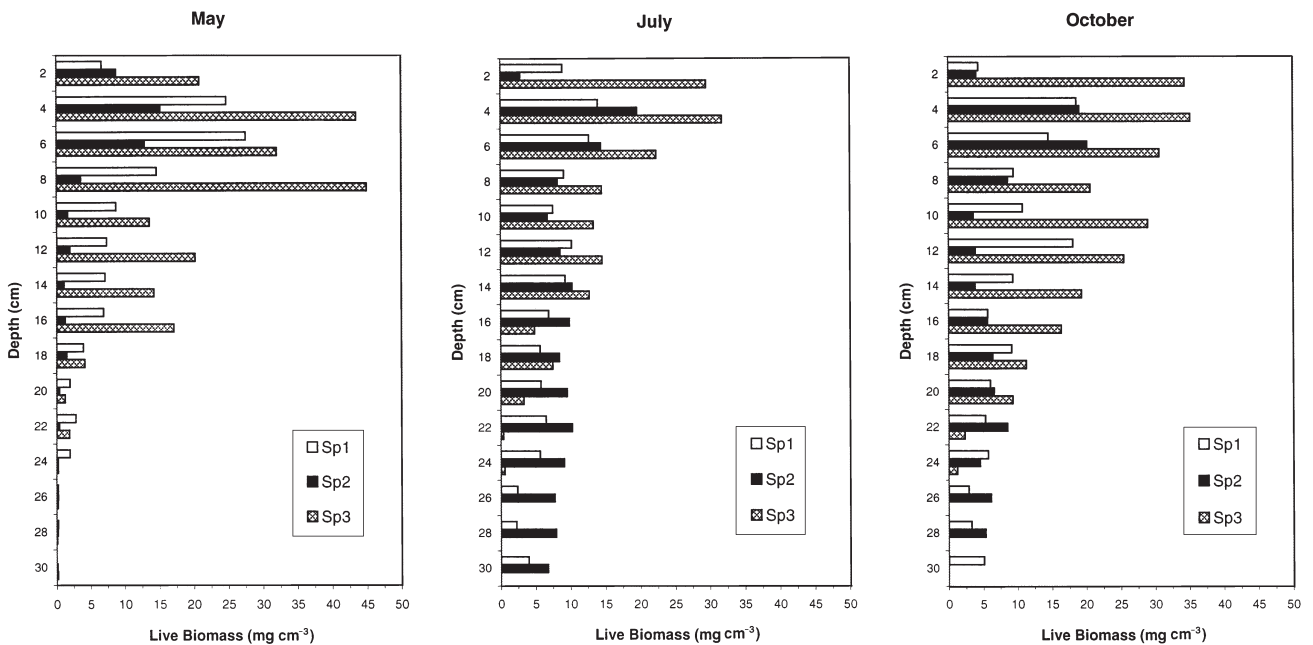

Fig. 4. *Spartina patens.* Live belowground biomass in individual stands as recorded over the 3 sampling periods

found the greatest concentration of live belowground biomass at 2 to 5 cm for both low marsh *S. alterniflora* and high marsh *S. patens*. 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 depths at which

S. alterniflora peak biomass are observed in this study may be a response to the greater extent of freezing in the Fundy region. As erosion by 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*.
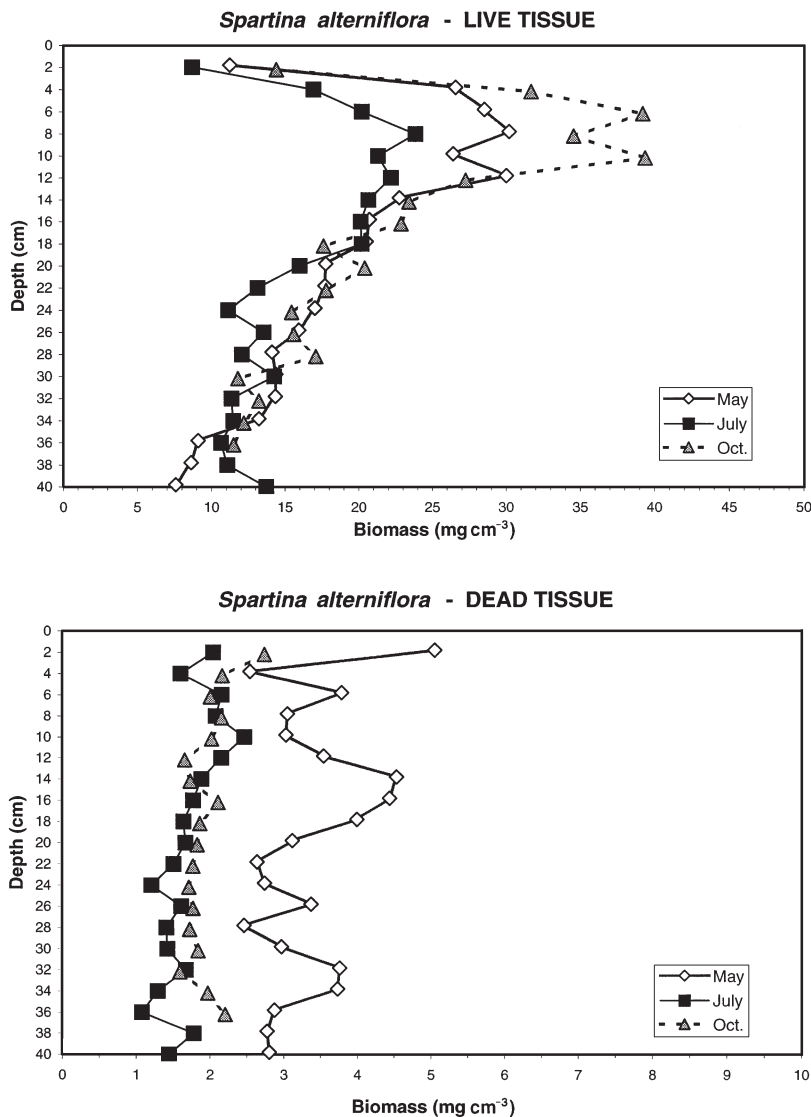
Fig. 5. *Spartina alterniflora.* Vertical profiles of belowground biomass. Points represent the mean of 3 replicates. Standard errors are reported in Appendix 1

Seasonal patterns were observed in the vertical distribution of both live and dead fractions of belowground biomass for both *Spartina* species (Figs. 5 & 6). For *S. alterniflora*, changes in the average concentration of live belowground biomass were only significant in the top 16 cm (Table 3). Live *S. alterniflora* biomass decreased by an average of 22% (p < 0.05, *t*-test) over the 0 to 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 the tall form of *S. alterniflora*, reporting that the live belowground maximum, which occurred between September and November, was 3 times greater than the 800 g dry wt m^{-2} minimum which occurred in July. A similar seasonal trend was observed in Massachusetts by Gallagher & Howarth (1987), who predicted that the amount of recoverable underground reserves, and therefore the magnitude of the translocational pattern of *S. alterniflora*, increases with increasing latitude. Although the Dipper Harbour study focussed on biomass rather than recoverable underground reserves, the results presented here support the hypothesis that the translocation of belowground biomass does play an important role in the seasonal growth pattern of *S. alterniflora*.

The amount of dead *Spartina alterniflora* biomass accounted for <20% of the total belowground biomass, supporting the observations by Gross et al. (1991) for a Nova Scotian saltmarsh. 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 midsummer and fall in Massachusetts. It appears that, during the growing season, the decomposition rate at Dipper Harbour may exceed the death rate of live belowground tissue, resulting in no net gain in dead material. The peak in dead belowground *S. alterniflora* biomass observed in May cannot be explained directly from our data, but is likely to result from the accumulation of dead material over the winter, when decomposition rates are reduced due to low temperatures and freezing of the soil.

In a litter bag study conducted in Mississippi, Hackney & 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 *Spartina alterniflora* biomass was significant throughout the vertical profile,
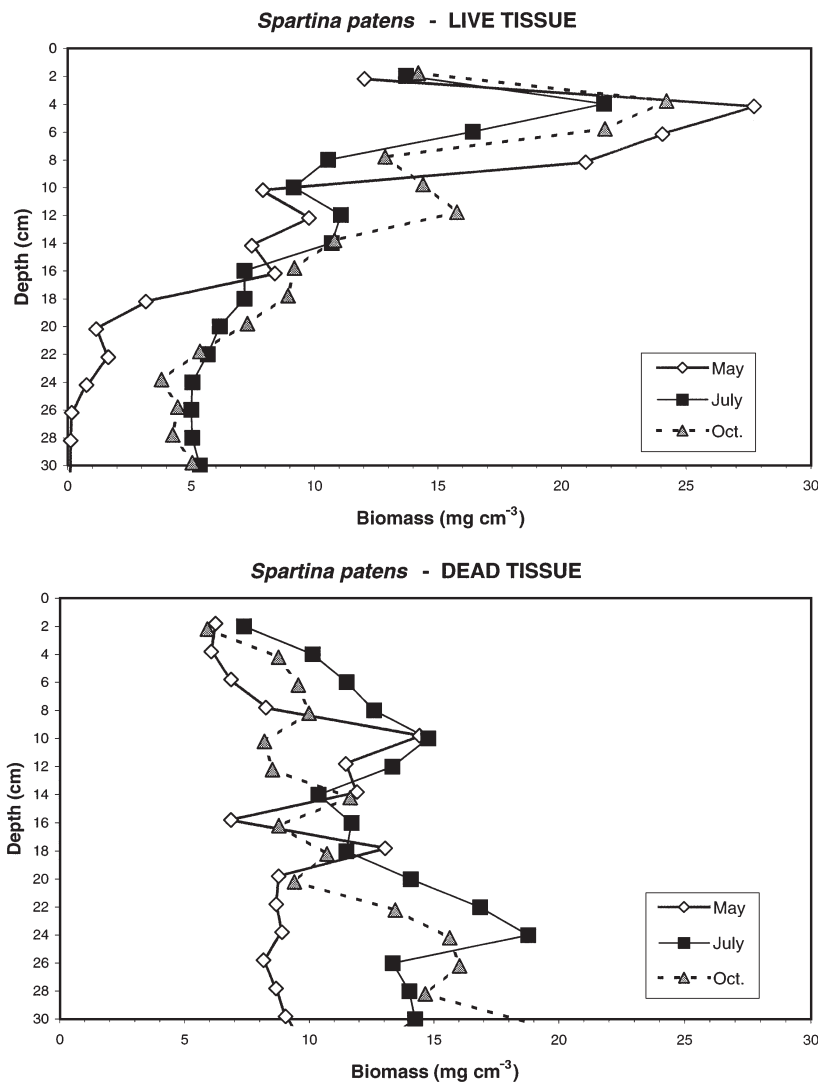
Fig. 6. *Spartina patens.* Vertical profiles of belowground biomass. Points represent the mean of 3 replicates. Standard errors are reported in Appendix 1

patens from May to July. Seasonal trends in the growth of aboveground biomass (Table 2) indicate that the aboveground production rate of *S. patens* in the May to July period (43% of peak standing crop) is much lower than that of *S. alterniflora* (78% of peak standing crop). It would appear that the need of underground reserve storage as a biomass pool for spring shoot growth by *S. patens* may be less important than it is for *S. alterniflora*. At the 16 to 30 cm depth interval, live *S. patens* belowground biomass increased by 380% ($p < 0.01$, 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*.

Dead tissue accounts for well over $\frac{1}{2}$ of the total belowground biomass pool in the *Spartina patens* zone (Fig. 6). 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 22% ($p < 0.05$, t-test) in the top 16 cm of the profile, but no significant change was observed at the 16 to 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 may result 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 & Gosselink 1986). The presence of *S. alterniflora* biomass, which was observed at depths >16 cm in all *S. patens* cores, provides evidence of this long-term storage. Traces of *Plantago maritima* 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,

seemingly independent of depth (Fig. 5, Table 3), implying that the net decomposition rate is equally independent of depth. The macrotidal conditions at Dipper Harbour may help to explain why the apparent 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 (Connor 1995), extending the oxidizing environment in the sediment to depths far greater than would be possible in Mississippi, where microtidal conditions limit such large fluctuations in the marsh water table.

In the vertical profile of live *Spartina patens* (Fig. 6), there was no significant change in live biomass over the upper 16 cm from May to July (Table 3). Therefore, our results do not offer any evidence of translocation of live belowground biomass to the stems and leaves of *S.*

Table 3. Seasonal belowground biomass (g dry wt m^{-2}) for the 3 dominant plant species at Dipper Harbour. Negative values indicate a net decrease in biomass between 2 sampling periods. Significant changes in biomass, as determined by a paired Student's *t*-test (p < 0.05), are presented in bold type. SE: standard error

| | Depth interval (cm) | Belowground biomass | | | | | | Change in biomass | | | |
| | | May | | Jul | | Oct | | May–Jul | | Jul–Oct | |
		Avg.	SE	Avg.	SE	Avg.	SE	(g m^{-2})	(%)	(g m^{-2})	(%)
Spartina alterniflora	0–16	3926	606	3077	431	4652	476	**–849**	22	**1575**	51
(live)	16–40	3406	72	3169	259	3392	110	–237	7	223	7
	Total	7332	603	6246	652	8044	562	–1086	15	1798	29
S. alterniflora	0–16	600	107	461	147	332	156	**–139**	23	**–128**	28
(dead)	16–40	689	148	522	182	363	162	**–167**	24	**–156**	30
	Total	1289	182	983	321	695	318	**–306**	24	**–285**	29
Spartina patens	0–16	2365	1322	2009	603	2463	1248	–356	15	454	23
(live)	16–30	143	66	687	393	671	125	**544**	380	–16	2
	Total	2508	1354	2696	370	3134	1124	188	7	438	16
S. patens	0–16	1268	262	1836	419	1428	419	**568**	45	**–409**	22
(dead)	16–30	1429	231	2055	893	1846	1491	**626**	44	–209	10
	Total	2697	253	3891	1232	3274	1504	**1194**	44	–617	16
Plantago maritima (live + dead)	0–20	2253	1704	1634	604	1606	553	–619	27	–28	2

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 626 g m^{-2} increase in dead *S. patens* biomass observed from May to July at the 16 to 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. Although loss may also be the result of spatial variability, the decomposition rate is likely to be greater in the upper 16 cm than in the 16 to 30 cm depth interval.

The vertical profiles of *Plantago maritima* (Fig. 7) show a remarkable similarity between July and October, suggesting that any seasonal change should occur over the first $\frac{1}{2}$ of the growing season, before the forb goes to seed (late July to early August). Spatial variability between replicate samples was high, particularly in May, as attested by the standard errors (Table 3). In comparison with other species, the total belowground biomass of *P. maritima* is low, accounting for <$\frac{1}{3}$ that of *Spartina patens* and only $\frac{1}{4}$ that of *S. alterniflora*. Also, the maximum depth at which *P. maritima* 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 *P. maritima* to the overall saltmarsh belowground biomass pool is considerably smaller than that of the *Spartina* species.

Conclusions

The present work provides some insight into the mechanisms involved in the seasonal growth patterns of *Spartina alterniflora*, *S. patens* and *Plantago maritima*. In this study of the Dipper Harbour saltmarsh, core samples were processed over 2 cm depth
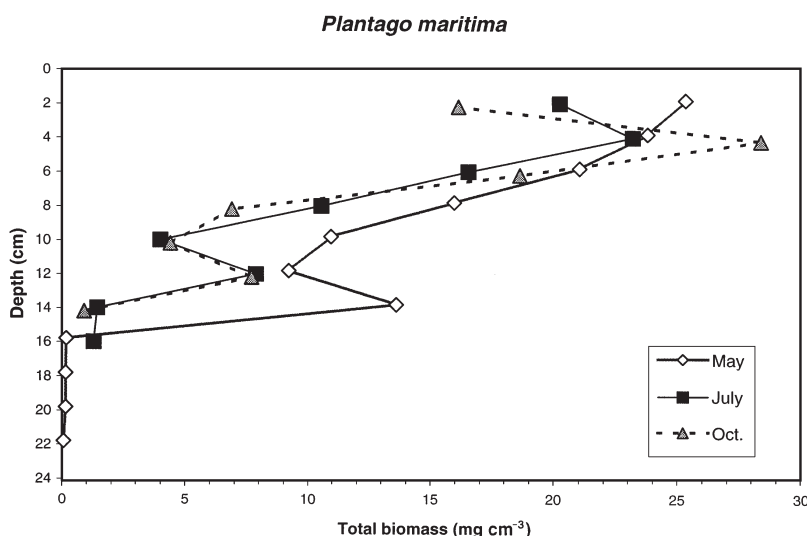

Plantago maritima

Fig. 7. *Plantago maritima*. Vertical profile of belowground biomass. Points represent the mean of 3 replicates. Live and dead *P. maritima* fractions were not separated. Standard errors are reported in Appendix 1

intervals, allowing for a highly detailed analysis of the vertical distribution of belowground biomass.

The high-resolution vertical profiles provide information on the amplitude of seasonal changes as well as the depths at which these changes occurred. For *Spartina 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 maritima* 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 (*Plan-*

tago maritima and *Spartina 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 saltmarshes in the Bay of Fundy region? The findings reported here suggest a substantive caveat for future studies and, perhaps, a new interpretation of previous studies.

Appendix 1. Average biomass (g dry wt m^{-2}) calculated as mean of 3 replicates. SE: standard error

Depth (cm)	Live biomass						Dead biomass					
	May		Jul		Oct		May		Jul		Oct	
	Avg.	SE	Avg.	SE	Avg.	SE	Avg.	SE	Avg.	SE	Avg.	SE
Spartina alterniflora												
2	11.24	7.01	8.68	2.73	14.40	2.53	5.06	1.12	2.05	0.16	2.75	1.50
4	26.56	11.02	16.91	0.16	31.67	5.49	2.55	0.27	1.60	0.70	2.17	1.82
6	28.52	1.70	20.20	1.80	39.20	2.84	3.79	1.08	2.16	1.27	2.01	1.18
8	30.20	3.55	23.85	4.65	34.55	7.53	3.06	0.32	2.08	0.57	2.16	1.09
10	26.39	3.08	21.30	4.43	39.37	6.50	3.04	0.69	2.47	0.89	2.03	0.71
12	29.99	6.48	22.19	5.60	27.24	3.64	3.55	0.57	2.16	1.10	1.66	0.36
14	22.76	4.09	20.66	4.40	23.40	2.48	4.54	2.31	1.89	0.93	1.74	0.61
16	20.72	1.87	20.14	1.93	22.88	4.11	4.44	2.38	1.78	0.44	2.11	0.73
18	20.51	0.97	20.20	3.08	17.62	5.37	4.00	1.58	1.65	0.24	1.87	1.01
20	17.76	2.31	15.99	1.76	20.41	1.06	3.12	0.83	1.67	0.09	1.83	0.66
22	17.71	1.56	13.12	3.35	17.79	0.80	2.64	0.33	1.51	0.41	1.77	0.49
24	17.04	0.61	11.12	3.78	15.45	2.18	2.75	0.64	1.21	0.35	1.72	0.83
26	15.93	3.31	13.55	2.90	15.59	0.64	3.38	0.74	1.61	0.32	1.77	0.65
28	14.11	3.30	12.05	1.91	17.10	0.77	2.46	0.21	1.41	0.47	1.73	0.76
30	14.38	3.09	14.26	1.59	11.79	1.48	2.97	0.65	1.42	0.37	1.84	0.94
32	14.35	6.33	11.36	0.98	13.22	1.38	3.76	1.85	1.67	0.62	1.59	0.71
34	13.22	2.62	11.46	1.55	12.20	0.77	3.74	0.83	1.29	0.44	1.97	1.03
36	9.08	1.44	10.64	1.47	11.50	1.12	2.87	1.19	1.08	0.35	2.21	1.21
38	8.62	0.34	11.06	2.07			2.77	1.63	1.78	0.72		
40	7.58	1.05	13.71	1.03			2.80	1.93	1.44	0.70		
Spartina patens												
2	12.03	6.22	13.71	11.39	14.21	14.21	6.07	3.07	10.15	0.76	8.77	3.62
4	27.72	11.74	21.72	7.40	24.22	7.71	6.86	4.91	11.51	2.88	9.57	3.68
6	24.06	8.17	16.41	4.18	21.74	6.68	8.26	4.39	12.61	4.64	10.00	3.11
8	20.97	17.50	10.56	2.79	12.87	5.46	14.43	4.81	14.78	5.63	8.21	2.69
10	7.91	4.87	9.16	2.93	14.40	10.67	11.47	4.93	13.34	3.25	8.53	4.39
12	9.78	7.66	11.07	2.54	15.77	8.94	11.92	3.77	10.38	6.21	11.65	3.78
14	7.45	5.35	10.71	1.45	10.81	6.41	6.86	0.73	11.71	3.57	8.78	5.52
16	8.39	6.56	7.16	2.06	9.19	5.05	13.05	3.55	11.49	2.02	10.72	2.59
18	3.16	1.20	7.16	1.15	8.92	1.98	8.77	3.76	14.07	4.30	9.41	3.46
20	1.16	0.63	6.16	2.55	7.28	1.43	8.67	1.14	16.85	6.90	13.45	10.21

Appendix 1. (continued)

Depth	Live biomass						Dead biomass					
(cm)	May		Jul		Oct		May		Jul		Oct	
	Avg.	SE	Avg.	SE	Avg.	SE	Avg.	SE	Avg.	SE	Avg.	SE
Spartina patens (continued)												
22	1.65	0.98	5.67	4.08	5.36	2.54	8.91	0.45	18.77	7.30	15.63	14.67
24	0.76	0.80	5.05	3.51	3.80	1.89	8.15	1.20	13.34	7.65	16.03	17.30
26	0.17	0.02	5.01	3.10	4.46	1.88	8.65	4.20	14.01	7.46	14.65	15.24
28	0.12	0.07	5.04	3.30	4.26	1.16	9.04	2.61	14.24	9.96	18.66	12.30
30	0.11	0.03	5.35	1.60	5.04		9.75	4.67	12.63	9.90		
Plantago maritima (total biomass)												
2	25.37	15.26	20.27	4.57	16.16	3.34						
4	23.83	6.89	23.22	9.31	28.39	8.39						
6	21.07	13.29	16.56	5.50	18.66	8.40						
8	15.99	16.96	10.57	7.90	6.92	4.06						
10	10.96	12.57	4.01	3.46	4.42	5.43						
12	9.24	10.18	7.90	1.67	7.73	7.88						
14	13.63	15.41	1.43	1.06	0.91	0.78						
16	0.17		1.29	1.39								

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