Spartina alterniflora root dynamics in a Virginia marsh

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ABSTRACT: A litter bag technique was used to measure root and rhizome decomposition and production for 2 years in creekside and interior sediments in a *Spartina alterniflora* marsh on the seaside of the Delmarva Peninsula, Virginia, USA. Decay was equally rapid regardless of incubation in either creekside or interior sediments and did not vary with depth. Weight loss during the first growing season was 39 and 35 % (creekside and interior respectively). By the end of the second growing season between 81 and 88 % (creekside and interior respectively) of the starting root and rhizome material had decayed. In creekside sediments, very little root growth was measured during either year and root production was highly variable between years (1253 and 99 g m^{-2}). In the interior marsh, the patterns of root growth and the amount of root material produced were similar each year (2016 and 2269 g m^{-2}). Root and rhizome turnover was faster in the creekside sediments (2.63 yr^{-1}) than in the marsh interior (0.54 yr^{-1}). The greater root production and slower root turnover in the interior marsh occurred in sediments with elevated salinities and oxidation-reduction potentials, and lower sediment saturation. These results suggest that differences in organic matter accumulation in high and low marsh areas may be explained by differences in root production and not differences in decay processes.

KEY WORDS: Decomposition · Production · Root · *Spartina alterniflora*

INTRODUCTION

The importance of root production and decomposition to understanding net primary production, estuarine food chains/webs, nutrient cycling and biogeochemistry, and maintenance of the structural integrity of salt marshes is likely to be enormous (Good et al. 1982). Although below-ground material in salt marshes may be directly consumed by geese (Smith & Odum 1981) or fiddler crabs (Everest & Davis 1979), Good et al. (1982) suggest that removal of roots and rhizomes by grazing is not significant. Benner et al. (1991) argue that the major fate of *Spartina alterniflora* below-ground production is microbial decay. Nevertheless, because so little is known about the balance between decomposition and production of *Spartina* spp. roots and rhizomes, the extent to which this below-ground material contributes to the accumulation of sediment organic material and contributes to maintenance of marsh integrity is not clear.

Organic matter accumulation in sediments is determined by the balance between organic matter inputs, including both above- and below-ground production, and decomposition. Estimates of below-ground production of *Spartina* spp. in most cases are equal to, or exceed, values reported for above-ground production (Table 1). The contribution of above-ground materials to sediment organic matter may not be significant because little or no fallen-litter build-up occurs on the marsh surface (Chalmers et al. 1985, Morris & Whiting 1986, DeLaune & Lindau 1987, Morris 1988, Dame 1989, Newell & Fallon 1989, Cifuentes 1991, Dame et al. 1991), although Newell & Fallon (1989) estimated that at least 35 % of the original, postsenescent leaf mass reaches the sediment surface as small particulates and possibly 70 % of the total fungal-leaf system eventually is deposited on the marsh surface. Thus, it is not unreasonable to assume that in many salt marshes, organic matter inputs are primarily in the form of root and rhizome production *in situ* and that understanding the factors controlling rates of below-ground production and decay is essential to understanding sediment organic matter accumulation and the potential for salt marshes to respond to sea level rise.

Table 1. *Spartina alterniflora* and *S. cynosuroides*. Published values of below-ground net productivity (g dry wt m^{-2} yr^{-1}). NR: not reported

Sampling locale	Species	Height form	Productivity	Source
Nova Scotia, Canada	*S. alterniflora*	NR	1051[a]	Livingstone & Patriquin (1981)
Massachusetts, USA	*S. alterniflora*	NR	3500[b]	Valiela et al. (1976)
New Jersey, USA	*S. alterniflora*	Short	2300[c]	Smith et al. (1979)
Virginia, USA	*S. alterniflora*	Medium	676[d]	This study
		Short	2143[d]	This study
North Carolina, USA	*S. alterniflora*	Short	460[d]	Stroud & Cooper (1968)
		Tall	500[d]	Stroud (1976)
North Carolina, USA	*S. cynosuroides*		1860[d]	Bellis & Gaither (1985)
			2190[d]	Bellis & Gaither (1985)
South Carolina, USA	*S. alterniflora*	Short	5445[e]	Dame & Kenny (1986)
		Medium	775[e]	Dame & Kenny (1986)
		Tall	2460[e]	Dame & Kenny (1986)
Georgia, USA	*S. alterniflora*	Short	2020[c]	Gallagher & Plumley (1979)
		Tall	2110[c]	Gallagher et al. (1980)
Georgia, USA	*S. alterniflora*	Medium	4780[e]	Schubauer & Hopkinson (1984)
Georgia, USA	*S. cynosuroides*	Tall	3560[c]	Gallagher & Plumley (1979)
Georgia, USA	*S. cynosuroides*	Tall	4628[e]	Schubauer & Hopkinson (1986)

Key to productivity estimation methodology: [a]maximum functional biomass; [b]maximum-minimum mass of dead material; [c]maximum-minimum mass of total macro-organic material; [d]maximum-minimum mass of live material; [e]Smalley (1959)

The purpose of the present investigation was to measure both root (and rhizome) production and decay in adjacent marsh areas with differing tidal inundation frequency and sediment physical and chemical characteristics. The method used to measure below-ground production and decay that is discussed in this paper yields estimates of root production similar to those observed in other Atlantic coast salt marshes. In addition, the results indicate that decomposition is similar in creekside and interior sediments while below-ground production is substantially greater in the marsh interior, suggesting that differences in the rate at which salt marshes accrete organic matter can be explained by differences in root production.

MATERIALS AND METHODS

Study area. Experiments were carried out in the marsh surrounding the upper portion of Phillips Creek (Virginia, USA) which drains into the coastal lagoon complex of Virginia's Eastern Shore (Fig. 1). The marsh area (37° 26' 38.49" N, 75° 52' 04.99" W) is located behind a relict sand ridge, and the surrounding uplands are either farm lands or pine-forest wood lots. The dominant marsh vegetation near the creek is *Spartina alterniflora*. The underlying sediments are loamy-textured with organic matter concentrations between 5 and 19% to depths of 30 cm (Barr 1989).

Two transects were established along level contours, parallel to the creekbank, using standard surveying methods (Fig. 1). One transect, designated as the interior location, was situated about 5 m from the creekbank in short-form *Spartina alterniflora* (40 cm average plant height). The other transect, referred to as the creekside location, was placed about 1 m from the creekbank in an area containing an intermediate form of *S. alterniflora* (100 cm average plant height). The creekside transect, which is 22 cm lower in elevation than the interior transect, is subject to greater frequency and duration of tidal inundation than the interior site and floods twice each day, while the interior site floods less frequently than the creekside transect.

Litter bag design and placement. Litter bags were used to measure below-ground decomposition and root growth. The bags were made from nylon mesh [Delta netting (1 × 2 mm opening), Nylon Net Company, Memphis, TN, USA] and were 50 cm long × 6.5 cm wide. The bags were filled in 10 cm sections with 12 g ± 0.5 g (wet wt) of dead roots and rhizomes per section (Fig. 1). After filling, each section was sewn closed to separate it from the adjacent section. The design of these litter bags permitted examination of the vertical distribution of below-ground decomposition without the massive disturbance of the sediments forced by burial of conventional bags at several depths in the sediment (Hackney 1987, Hemminga et al. 1988).

The root and rhizome material used to fill the litter bags was collected from large diameter cores (30.5 cm diam.) taken to a depth of 20 cm approximately 1 wk prior to the beginning of the experiment in March. The cores were returned to the laboratory where the organic matter (both live and dead) was rinsed free of
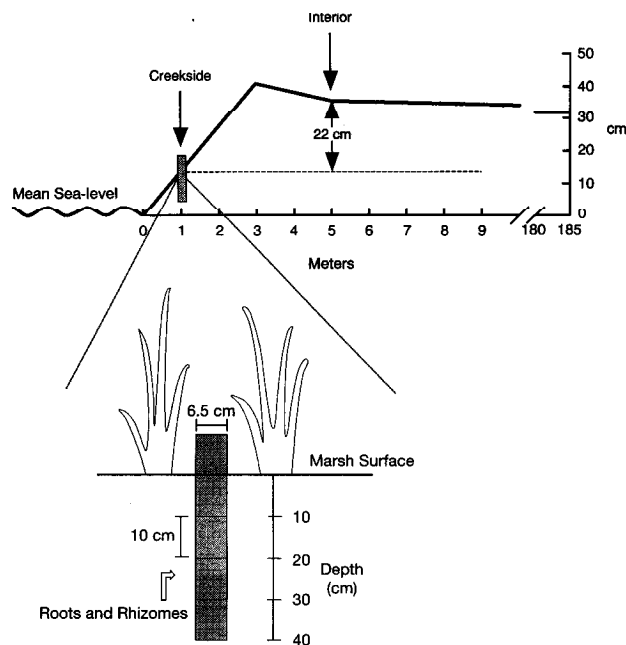
Fig. 1. Cross-section of Phillips Creek marsh illustrating the elevational differences between the creekside and interior transects. A series of litter bags was placed 1 and 5 m from the creekbank along uniform elevational contours. The inset is a schematic of the litter bag design and placement in the marsh sediment. Bags were used to measure both root decay and root in-growth

sediment. The organic material contained few live roots. Rhizomes that were easily recognized as 'live' were separated from the organic material. The remaining root and rhizome material was refrigerated in plastic bags until it was used to fill the litter bags. Approximately 12 g (wet wt) of dead root and rhizome material (and a plastic identification tag) were placed in each section of the litter bag according to the method described by Zieman (1968). Ratios of fresh weight:dry wt:ash-free dry wt were determined using the procedure of Robertson (1982). The terms below-ground material, roots, and roots and rhizomes are used interchangeably throughout this report.

Over 200 litter bags were placed in Phillips Creek marsh (PCM) on March 26, 1988. For the creekside transect, a flat spade was inserted in the sediment to approximately 60 cm depth and a bag slid into the sediment along the blade of the spade. Bags were placed vertically so that the top 10 cm section remained on the surface and the bottom of each bag was approximately 40 cm deep (Fig. 1). The sediment was then pressed back in around each bag. In the interior marsh, cores were augered, a bag was placed vertically in each hole, and the sediment removed by coring was returned to the core hole beside the bag to insure an environment similar to the pre-existing one. Along

each transect, individual bags were inserted into the sediment at approximately 30 cm intervals. Each bag was assigned an identification number. Bags were selected for sampling a priori using a random number table. Three bags for simultaneous measurement of decomposition and root in-growth were collected twice each month during the first year and every 2 mo during the second year. All litter bags were returned to the lab where they were refrigerated and processed within 1 wk of collection.

Determination of root in-growth and decay. The rate of litter decay was measured as the loss of ash-free dry weight (AFDW) over time. To minimize live root loss from the bags during sampling, we carefully slid a hand into the sediment along the outside of the bag. When roots were encountered, they were broken off outside of the bag. In the laboratory, each bag was separated into 10 cm sections and washed free of sediments. The material in the bags was hand-sorted and all live roots were separated from the dead material based on turgor, color, and in some cases microscopic examination. Live and dead materials were handled separately. All organic materials were dried at 80 °C to a constant weight (approximately 24 h). The AFDW was determined as the weight loss after combustion (500 °C for 12 h) of each separate material for each 10 cm section of each bag.

Sediment collection. To determine the relationship between sediment properties and below-ground biological processes, sediment platinum electrode potential, sediment temperature, pH, pore-water salinity, soil moisture, bulk density, and soil water retention over a tidal cycle were measured. Depth profiles of platinum electrode potential (an indicator of relative redox status) and temperature were determined every 2 mo in duplicate core samples for both transect locations. Cores were taken immediately adjacent to the first bag sampled from each transect. To minimize disturbance of the sediments, the hole left by the core extraction was filled with a sediment core taken from an adjacent area of the marsh where a similar growth form of Spartina alterniflora was found. Sediment cores were taken in steel tubes 5.2 cm in diameter and 60 cm in length. Each core tube had holes, 1.3 cm in diameter, drilled into the side so that the center of each hole was spaced 2 cm apart. The holes were sealed with silicone sealant (Dow-Corning) to create an air impermeable membrane. After the core was taken, the relative redox potential was measured by inserting a platinum wire electrode through the silicone plug, placing a silver-silver chloride reference electrode in the overlying water, and reading the resulting voltage with a digital millivolt meter (Bell et al. 1990). The platinum wire electrode was calibrated in the field using Zobell's Solution (Zobell 1946, Nordstrom 1977).

After the redox potential was measured, the membrane was removed, and the soil temperature was measured by inserting a standard soil thermometer into the sediment.

On 3 separate occasions, additional cores were taken for extraction of pore water to measure vertical distribution of salinity and pH. The cores were collected within 1 m of the transect line near the bags sampled on that date, and the holes were filled with sediment from another location in the marsh. After collection of the cores, the ends of the tubes were sealed with rubber stoppers, and the cores were placed on ice and returned to the lab for analysis. Two cores were collected for each site on each of the dates sampled. Samples were taken on May 17 (53 d from inception of the experiment), July 16 (112 d), and October 4 (193 d). In the laboratory, the sediment cores were extruded and cut into 4 cm sections. Pore water was squeezed out of each sediment layer through a #3 Whatman filter paper using N_2 gas at a pressure of 30 to 40 psi (ca 2 to 2.7×10^5 Pa) in a Reeburgh-type squeezer (Reeburgh 1967) and collected in 20 ml glass liquid-scintillation vials. The pH was measured with a combination electrode, and the salinity was measured with a hand-held refractometer.

Additional cores (2 along each transect) were collected on a monthly basis at each site for soil moisture determinations. Stoppered cores were returned to the laboratory where they were extruded into 4 cm sections and placed into tared holders made from PVC pipe (5.2 cm inside diameter) covered at one end with a fine mesh netting (0.03 cm^2) to contain the sample while allowing water to pass. The samples in their PVC holders were weighed and placed in muffin tins. The samples were then flooded with water so that all sections were subjected to equal hydrostatic pressures, allowed to saturate for 24 h, and weighed again (the mesh on the PVC holders allowed complete drainage of superfluous water upon removal from the muffin tin). The difference in weight was the amount of water needed to bring each section to saturation. Next, each 4 cm core section was dried at 80°C to a constant weight and the moisture content determined as the weight loss per unit of dry sediment weight (data not shown). The percent saturation was calculated as the field wet weight of each section divided by the weight of the saturated core section multiplied by 100.

The degree of saturation of the sediments was also determined at 2 h intervals over a complete tidal cycle at each transect once during the 2 yr experiment. Cores were collected as described for the salinity/pH determinations except that the top 5 cm (volume 106.3 cm^3) were removed from the cores in the field and placed into preweighed PVC holders as described above. The samples were wrapped completely in plastic wrap and

placed on ice to maintain field moisture conditions until they were returned to the lab. In the lab, the samples were handled as described above.

On one occasion a set of 2 cores from each site was collected and returned to the lab for analysis of the soil bulk density characteristics. Samples were extruded into 4 cm sections, and then dried at 80°C. The dry weight was obtained and used to calculate the soil bulk density based on the volume of the section (85 cm^3).

Calculation of root productivity and turnover. Root productivity is generally expressed as g m^{-2} yr^{-1} integrated over some depth, frequently the depth of the rooting zone. The litter bag technique described here yields measures of root growth into 10 cm vertical sections of the bag that were not uniform in all dimensions at all depths; they resembled a vertical stack of pillow-shaped compartments. Therefore, it was necessary to determine the cross-sectional area of the litter bags. As a result of the pillow-shaped geometry, the cross-sectional area of the bag compartments was some value between zero and an area computed on the basis of the maximum diagonal dimensions of the compartments. Because the actual distribution of diagonal dimensions could not be determined directly, a value equal to one-half the maximum cross-sectional area was used for converting depth integrated values to an areal basis. Productivity was calculated as the difference between the minimum (March samples) and maximum (August–September) values of live roots (Stroud 1976) and ignores root death that may have occurred between sampling intervals. Root turnover times were derived by dividing the calculated below-ground productivity (mean of 2 growing seasons) by root and rhizome standing stock. Estimates of below-ground standing stocks were calculated based on measures of rhizome biomass (183 and 1735 g m^{-2}, creekside and interior respectively) done at PCM assuming that 44 % of the biomass was comprised of rhizomes in the interior marsh and 71 % in the creekside marsh (Valiela et al. 1976). The proportions of total below-ground biomass comprised of rhizomes for low marsh *Spartina alterniflora* reported by Valiela et al. (1976) for a Massachusetts, USA, marsh are very similar to those reported by Schubauer & Hopkinson (1984) for a Georgia, USA, salt marsh.

RESULTS

Sediment properties

Temperature, pH, and bulk density did not differ significantly (ANOVA, $p > 0.10$) between the interior and creekside locations. Temperature was measured

at 2 cm intervals, from 2 to 30 cm. Temperatures never varied by more than 3 °C over the entire depth of the profiles. Average temperatures did vary with season and ranged from 2 to 31 °C. There was no significant difference in the average sediment bulk density between the 2 sites (0.945 ± 0.166 SD and 0.861 ± 0.089 SD g cm^{-3} for the interior and creekside sediments respectively). However, at both sites there was an increase in bulk density with increasing depth in the sediments. The values ranged from about 0.8 g cm^{-3} at the surface to about 1.1 g cm^{-3} at 30 cm. These values are similar to those reported by Barr (1989) who worked in the same location in the Phillips Creek

marsh. There were no significant differences in the pH of pore water between the locations or with depth or season (the overall range for 20 samples was 7.8 to 8.4). The lack of differences in pH, temperature, and bulk density between the 2 locations was not unexpected given the close proximity of the 2 transects.

Other sediment properties with the potential to influence plant and microbial growth and productivity were quite different between sites, particularly in the top 20 cm where most of the live roots are found. Platinum electrode potentials for the sites showed that in the top 20 cm, the interior marsh sediments were more oxidized than at the creekside location (Fig. 2a).
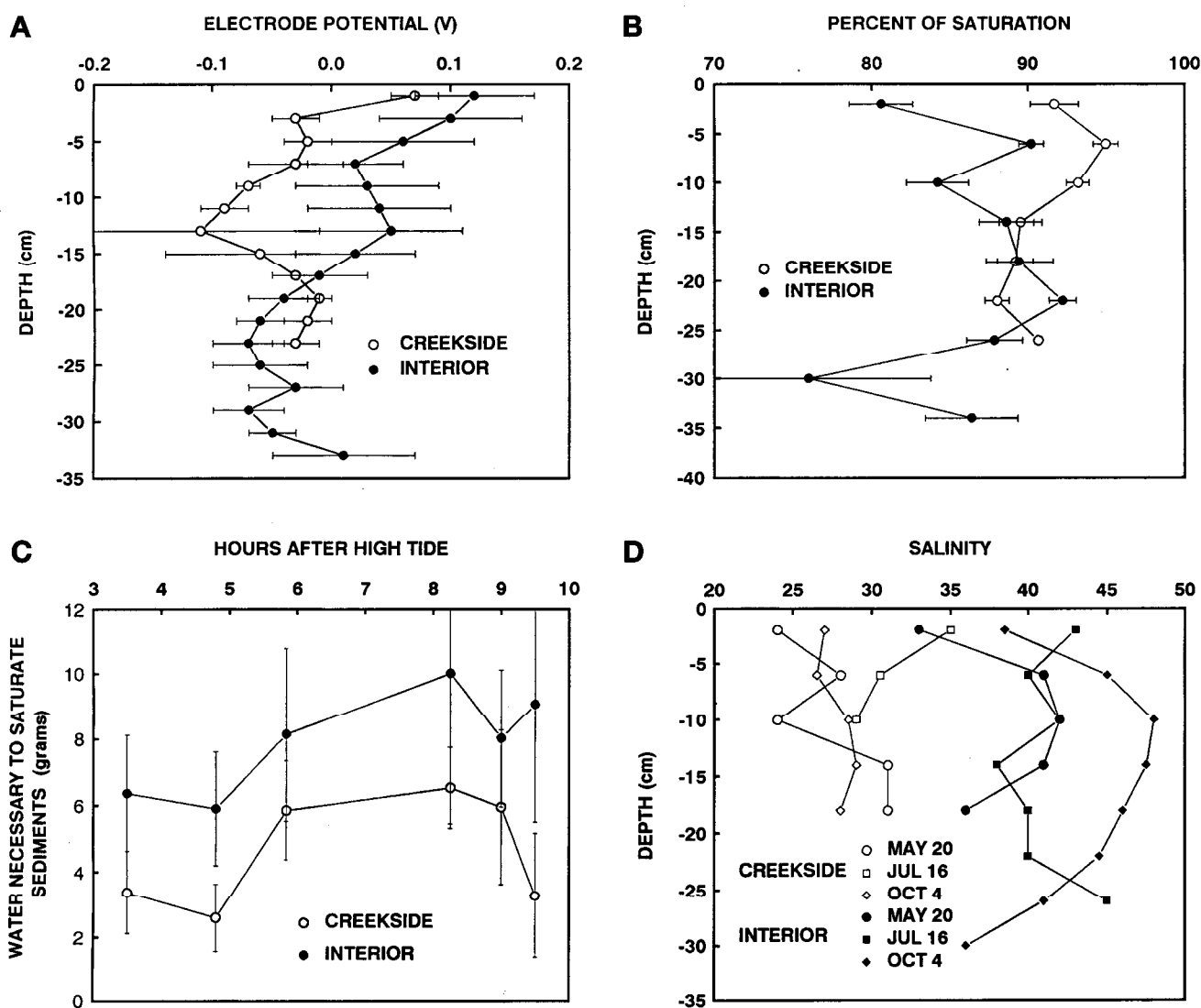

Fig. 2. Comparison of creekside and interior sediment characteristics. For all panels, error bars indicate 1 SD except where SD is less than the size of the symbol. (A) Platinum electrode potential, a relative index of sediment redox potential, as a function of depth. Samples were collected bimonthly for 2 yr. (B) Sediment saturation as a function of depth. Saturation was measured monthly for 2 yr. (C) Sediment saturation expressed as the grams of water necessary to fully saturate the top 5 cm (volume = 106.3 cm^3) of sediment during a falling tide (n = 2). (D) Pore-water salinities in May, July and October as a function of depth in sediments (n = 2)

A Student's paired *t*-test indicated the differences were significant (p = 0.031). At depths greater than 20 cm, the relative redox state of the sediments was quite similar at about 0 mV. The values in Fig. 2a are time-averaged and accurately reflect the relationship between the relative redox conditions along the transects regardless of season or the amount of time since high tide (an index of the aeration of the marsh soil). ANOVA results using data from all depths and times for each site yielded no significant depth effect, although platinum electrode potential tended to decrease with depth at both sites. A strong seasonal trend in redox potential was observed (data not shown); the highest values occurred during the winter and the lowest values were observed from late May through August.

The percent of sediment saturation was consistent with the redox estimates. The moisture content in the top 20 cm of the creekside sediments was always greater in the rooting zone than at corresponding depths in the interior marsh (Fig. 2b). Time- and depth-averaged saturation values for each site were significantly different (p = 0.0005, *t*-test). The average percent saturation (± SD) was 86.9 ± 9.50 % and 91.6 ± 6.22 % for the interior and creekside marshes respectively. The degree of saturation was, as expected, highly dependent on the tidal cycle (Fig. 2c); however throughout the tidal cycle the amount of water required to saturate the sediment cores (5.2 cm diam, 5 cm length) was always greatest for the interior marsh.

Major differences in pore-water salinity between the 2 sites were observed throughout the year (Fig. 2d). A 2-way ANOVA indicated that the effect of site was significant (p = 0.0005), but that the effect of depth in the soil was not. The mean salinity for the interior location was 41 ± 4 ppt while the mean creekside salinity (28 ± 3 ppt) approximated the salinity of the water in Phillips Creek. Pore-water salinities as high as 50 ppt were measured during the summer at the interior location and were consistent with salinities measured in piezometers with a calibrated YSI salinometer.

Decomposition

Analysis of variance indicated no significant overall depth effect on AFDW loss for either the interior or the creekside marsh sites below-ground. However, there appeared to be a more rapid loss of material from the portion of the bags left on the surface at both sites. All below-ground data for a given site were pooled since there was no depth effect on weight loss. The pooled data were used to compare decomposition in the below-ground portion of the bags with that occurring in the portion of the bags on
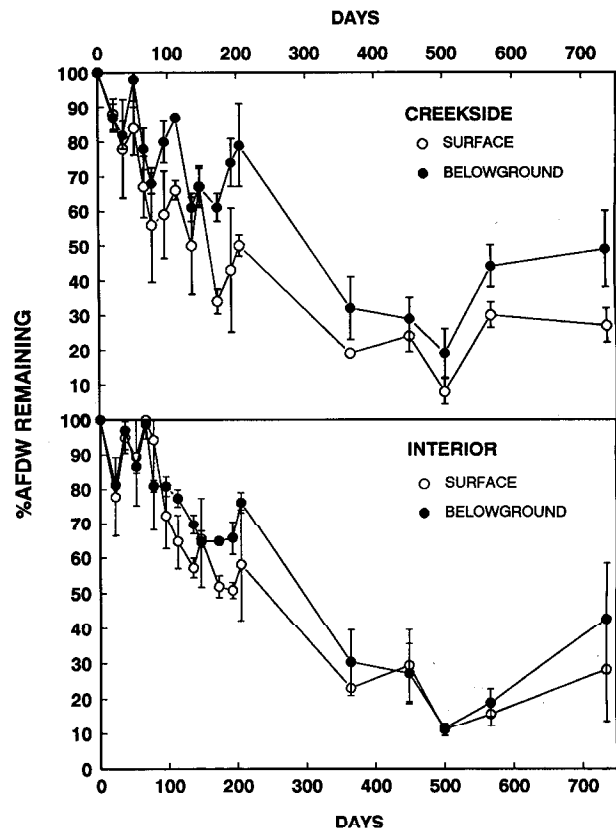

Fig. 3. *Spartina alterniflora*. Root and rhizome weight loss (expressed as percentage of ash-free dry wt remaining) on the sediment surface (O) and below ground (●) for litter bags incubated near the creekside and in the interior marsh. Error bars are 1 SD (n = 3) except where SD is less than the size of the symbol

the marsh surface (Fig. 3, Table 2). For both sites, weight loss of root and rhizome material incubated on the sediment surface was more rapid than for the similar material incubated below the sediment surface (Student's paired *t*-test, p = 0.0005 for the creekside and p = 0.013 for the interior). Surface decay was faster at the creekside than the interior (34 and 52 % remaining respectively) and was greater than below-ground weight loss (Table 2). Although major differences were observed in sediment properties between the creekside and interior transects, no differences in below-ground decomposition between the sites were observed (Fig. 3, Table 2). During the first growing season (March–August, Days 0 to 172), the amount of material remaining in the bags was 65 and 61 %, for the interior and creekside marshes respectively. By the end of October of the second year (Day 501) only 12 and 19 % of the original AFDW (interior and creekside respectively) remained in the litter bags. At the end of each growing season, the increase in AFDW in the bags (Fig. 3, Days 201

Table 2. Above- and below-ground weight loss (% ± SD) and decay constants (k) for each growing season

| | Creekside | | | Interior | | |
	AFDW remaining	k (d^{-1})	r^2	AFDW remaining	k (d^{-1})	r^2
First growing season						
Above-ground	34 ± 4	−0.0047	0.75	52 ± 3	−0.0036	0.73
Below-ground	61 ± 4	−0.0025	0.65	65 ± 1	−0.0025	0.77
Second growing season						
Above-ground	8 ± 4	−0.0050	0.88	11 ± 2	−0.0056	0.87
Below-ground	19 ± 7	−0.0045	0.98	12 ± 0	−0.0046	0.96

and 501) can be accounted for by the death of the root material that grew into the bags during that summer (recall that live material had been picked out prior to the weight determinations and was handled separately).

Decay-rate coefficients and regression values were determined for each site and for above- and below-ground decay for each growing season (Table 2). Both linear and first-order exponential model decay constants were computed but only the first-order exponential decay coefficients are presented because, based on the r^2 values, more of the variance in the data was explained by the exponential model. During the first 172 d (March–August) the decay constants for the below-ground materials were −0.0025 d^{-1} for both sites, while the coefficients for surface decay were −0.0047 and −0.0036 d^{-1} for the creekside and interior respectively. The second year's decay coefficients were calculated between Days 204 to 501. The coefficients were greater for the second year (−0.0050 and −0.0045 creekside above and below-ground respectively; −0.0046 and −0.0056 interior above and below-ground respectively) than for the first year.

Root in-growth, productivity and turnover

In order to obtain good estimates of root decay and to estimate root growth, live roots were removed from the litter bags and the amount of live root material growing into the bags at each depth was evaluated. Occasionally live rhizomes grew into the bags: it was not uncommon to observe a single rhizome extending completely through the width of a bag. When live rhizomes were encountered, they were included in estimates of root growth. Live roots were infrequently encountered at depths >20 cm for both the creekside and interior marsh. Greatest root growth occurred at 1 to 10 cm depth in the marsh interior and at 10 to 20 cm depth along the creekbank. Over all the depths examined, the total amount of live root material in the bags at any given depth was greatest for those bags incubated in the

marsh interior (Fig. 4). The biomass of roots in the bags reached similar peaks in August of both years (2626 and 2489 g m^{-2}) in the marsh interior. The peak for the creekside was 1352 g m^{-2} the first year and only 198 g m^{-2} the second. Regardless of location in the marsh, by March 78 to 89% of the live roots found in the bags the previous August was gone. Root productivity was estimated from the root in-growth data to be 2016 and 2269 g dry wt m^{-2} yr^{-1} in the marsh interior compared to 1253 and 99 g dry wt m^{-2} yr^{-1} in the creekside marsh for the first and second growing seasons respectively. Variation in the amount of live root mass recovered from the bags was much greater the second year especially for the interior marsh samples. Estimated below-ground biomass turnover rates based on the mean productivity estimates for both growing seasons were 2.63 and 0.54 yr^{-1} creekside and interior respectively and are included here only to illustrated the effect of similar decay constants, but different root productivities, on organic matter accumulation in creekside and interior sediments.
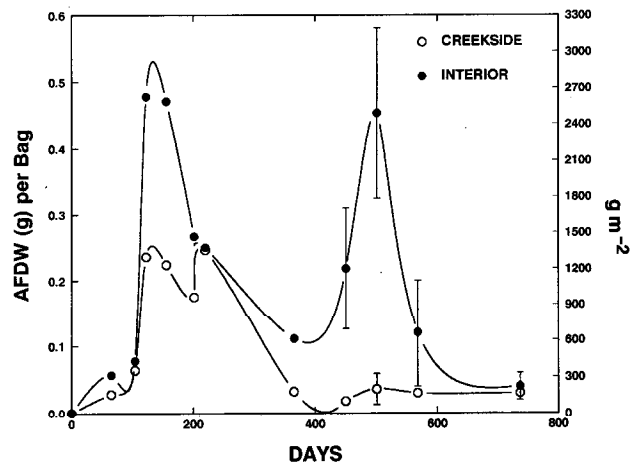

Fig. 4. *Spartina alterniflora*. Root in-growth into litter bags incubated in creekside (○) and interior (●) marsh sediments. Error bars are 1 SD (n = 3) except where SD is less than the size of the symbol. Curves were fit by eye to illustrate general trends

DISCUSSION

Simultaneous measurement of root decay and production using the method described here yielded results that are consistent with those of other studies in which either root decay (Hackney 1987) or root production (Dame & Kenny 1986) were measured. At PCM, root decay on the marsh surface was more rapid than below-ground, similar to the results reported by others (Hackney & de la Cruz 1980, van der Valk and Attiwill 1983, Valiela et al. 1984). However, at PCM there were no differences in root decay with depth in the sediment or between the creekside and the interior. Hackney (1987) also found root decomposition to be greater above- than below-ground and that differences in sediment redox potential or drainage had little effect on below-ground decay. The weight loss data reported for PCM fall within published values for below-ground root and rhizome decay, although rates of weight loss vary greatly within and between studies from approximately 80 % remaining after 1 yr to 45 % remaining after 1.5 yr (Hackney & de la Cruz 1980 and Benner et al. 1991 respectively).

There are a number of methods that have been used to calculate above-ground primary productivity in *Spartina alterniflora* salt marshes (reviewed in Turner 1976). The method applied below-ground here, the max-min approach, is a conservative estimate of production (Turner 1976) in comparison to Smalley's method (1959) because the max-min method ignores root death and decay. Because most literature reports are based on a form of the max-min method, the production data from the present study were calculated using the max-min method for comparative purposes.

Root production along the creekside and in the marsh interior at PCM (680 and 2140 g dry wt m^{-2}, respectively) are also within the range of values reported in the literature (Table 1). Production estimates for *Spartina alterniflora* vary from 460 to 5445 g dry wt m^{-2}. Between-year variation in *Spartina* spp. root production has been examined in only one other study (Bellis & Gaither 1985) where above- and below-ground productivity for 6 marsh plants, including *S. cynosuroides* but not *S. alterniflora*, were measured. For *S. cynosuroides* during an 18 mo study, Bellis & Gaither (1985) reported low between year variation in peak below-ground biomass. During the 2 years that root production was measured at PCM, production along the creekside was highly variable (1250 and 99 g dry wt m^{-2}, first and second year respectively) while below-ground production in the marsh interior was much less variable (2270 and 2020 g dry wt m^{-2}). The great difference between the 2 years at the creekside site might be attributed to the susceptibility of the creekside plants to changes in the environment or to

the greater degree of spatial heterogeneity in above-ground plant and below-ground biomass distribution observed in the creekside location. Studies of above-ground productivity (Dame & Kenny 1986, Morris & Haskin 1990) have shown that variation in *S. alterniflora* aerial production is greater at creekbank sites than in mid-marsh and interior sites. Dame & Kenny (1986) suggest that areas with higher infiltration, such as creekbanks, will exhibit greater variation in pore water salinities as a result of year-to-year variations in rainfall and upland run-off and thus greater variation in productivity. Variation in annual production in creekside locations may also be related to the greater spatial heterogeneity in plant distribution there. The creekside location at PCM is typified by large, less numerous plants (46 vs 103 plants m^{-2}, 156.34 vs 60.72 g dry above-ground wt m^{-2}, creekside and interior respectively; W. E. Odum unpubl. data) with patchy rhizome distribution (183 ± 93 SD g dry wt m^{-2}, CV = 0.508, n = 6; and 1735 ± 480 SD g dry wt m^{-2}, CV = 0.277, n = 6; creekside and interior respectively) as compared to the interior marsh so that root and rhizome production is likely to be more heterogeneous at the creekbank as well.

In spite of the great variation in creekside root production, it is clear that root production at PCM is much greater in the marsh interior than along the creekbank. Dame & Kenny (1986) also observed greater root production in short-form than in tall-form *Spartina alterniflora* (5445 and 2363 g dry wt m^{-2} respectively). The interior marsh vegetation at PCM is similar to the high marsh, short-form *S. alterniflora* at the site used in Dame & Kenny (1986), but the creekside vegetation at Bread & Butter Creek (Dame & Kenny's study) is tall-form *S. alterniflora* while at PCM the creekside *S. alterniflora* is an intermediate height form. Regardless of the differences in height form, the pattern of root production is similar between the creekside and interior marsh locations observed in these studies from 2 different marshes.

It is apparent from the results of this study that while decomposition did not vary between the creekside and interior marsh locations or with depth in the sediment, root production, and root and rhizome standing crop did. Sediment temperature, pH, and bulk density were not significantly different between the creekside and interior. Nutrients were not monitored during this study, but measurements made at another location in PCM suggest that pore-water concentrations of ammonium and phosphate are similar in the creekside and interior portions of the marsh (Chambers 1990) and are not likely to be directly responsible for the differences in root production that were observed. Sediment redox potential, drainage, and salinity were also measured during the course of this work at PCM and were found

to be very different between the interior and creekside areas (Fig. 2).

The results presented here from PCM and those of others (Valiela et al. 1982, 1984, Bertness 1985, Hackney 1987) indicate that decomposition is not affected by redox conditions or conditions associated with low redox potential. However, the effects of redox on root production by *Spartina alterniflora* are not clear. Field studies with *S. alterniflora* indicate that short-form below-ground productivity may be decreased under reduced drainage conditions, but much less so than tall-form (Linthurst & Seneca 1980, Mendelssohn & Seneca 1980). Increasing sediment aeration resulted in increased below-ground productivity with the response of the tall-form being greater than that of short-form (Linthurst & Seneca 1981). However, short-form *S. alterniflora* root production was increased in response to reduced drainage conditions laboratory studies (Mendelssohn & Seneca 1980). At PCM higher redox potentials and lower moisture contents existed in the sediments with much greater rates of root production and higher salinities.

At PCM pore-water salinities were commonly above the values that are thought to depress root production by *Spartina alterniflora*. During July when root biomass was nearing its peak, salinities in the root zone ranged from 38 to 48 ppt for the interior location and those along the creekside ranged from 27 to 35 ppt. The pore-water salinities at both locations are within the range (30 to 45 ppt) that Linthurst & Seneca (1981) found reduced below-ground biomass by as much as 61 % in comparison to salinities between 15 and 30 ppt. At PCM, the range of salinities that interior marsh grass was exposed to was greater than for creekside plants. This wide range of salinities in the interior marsh may stress *S. alterniflora* more than elevated salinities alone and result in greater plant investment in root production (Valiela et al. 1976, Schubauer & Hopkinson 1984) in conditions where water and nutrient uptake per unit root is low.

Results from PCM where root production is greatest in the interior marsh and decay is constant between interior and creekside also suggest that organic matter accumulation should be most rapid in the high marsh. These results support Armentano & Woodwell's (1975) observations that organic matter accumulation is greater in the high marsh. Additionally, estimates of root turnover in PCM interior are lower than those for the creekside sediments (0.54 and 2.63 yr^{-1} respectively). Good et al. (1982) in New Jersey, USA, and Gallagher & Plumley (1979) in Georgia have found turnover of roots and rhizomes to be faster in creekbank zones of tall *Spartina alterniflora* than in short-form cord grass. Good et al. (1982) attribute these differences between high and low marsh to differences

in decay. Yet, in this study at PCM, decay rates (and by inference microbial activities) are similar but root production is quite different and are consistent with Howarth & Teal's (1979) work in Sippewissett Marsh (MA, USA) where microbial sulfate reduction rates (and by implication decomposition) were found to be similar regardless of the growth form of *S. alterniflora*. Howarth & Hobbie (1982) suggest that root and rhizome turnover could be faster in the tall zones even if the rates of heterotrophic microbial activity are similar if the pool size of dead roots is less along the creekbanks. They hypothesize that the amount of root and rhizome material produced in the interior marsh is greater than the creekbank while microbial activity (in terms of the present study, decay) is similar. Thus, differences in organic matter accumulation in high and low marsh areas may be explained by differences in root production (and factors controlling that production) and not decomposition processes.

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