

## SEASONAL PATTERNS IN THE BELOWGROUND BIOMASS OF *SPARTINA ALTERNIFLORA* (GRAMINEAE) ACROSS A TIDAL GRADIENT<sup>1</sup>

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### ABSTRACT

Belowground biomass of two ht forms of the salt marsh cordgrass, *Spartina alterniflora*, in a New England salt marsh exhibited a seasonal cycle. Biomass was highest in midsummer with no secondary peak in biomass corresponding with the autumn dieback of aboveground parts. Total annual biomass production and the maximum depth that living tissue penetrated into the substrate decreased with increasing tidal ht. Substrate characteristics (soil aeration, pH, nutrient levels) known to affect aboveground biomass of *S. alterniflora* also decreased with increasing tidal ht and may similarly affect belowground biomass across the same tidal gradient.

THE MAJORITY OF studies of salt marsh plants have focused on the aboveground (shoot) dynamics of the salt marsh cordgrass, *Spartina alterniflora* (hereafter referred to as "alterniflora") (e.g., Valiela, Teal and Deuser, 1978; Bertness, 1984, 1985). As one moves up the marsh from the lower intertidal to the upper intertidal, both shoot biomass and shoot ht decrease (Adams, 1963; Niering and Warren, 1980). At the extremes of this tidal gradient, two distinct ecophenes, tall-form *alterniflora* and short-form *alterniflora* have been recognized (Shea, Warren and Niering, 1975; Valiela et al., 1978). These two ht forms dramatically differ in annual production and stem density (Valiela et al., 1978). The differences in ht and production between the two forms of *alterniflora* have been correlated with nitrogen availability (Valiela et al., 1978), soil aeration or oxygen availability (e.g., Mendelssohn and Seneca, 1980) and other environmental parameters which are a function of tidal ht. Facultative mutualisms between cordgrass and the marsh mussel, *Geukensia demissa* (Bertness, 1984), and between cordgrass and fiddler crabs (*Uca pugnax*) (Bertness and Miller, 1984; Bertness, 1985) also have been shown to be im-

portant determinants of cordgrass production. The decrease in cordgrass production as tidal ht increases is directly correlated with the decrease of nutrient and oxygen availability and the declining abundance of marsh mussels and fiddler crabs with increasing tidal ht (Bertness, 1984, 1985).

Although several studies of belowground production of *alterniflora* exist (Stroud, 1976; Valiela, Teal and Persson, 1976; Gallagher and Plumley, 1979; Good, Good and Frasco, 1982; Gallagher, 1983; Gallagher, Wolf and Pfeiffer, 1984), none of these studies have examined seasonal patterns in root and rhizome production of *alterniflora* across a tidal gradient. Although numerous investigators have studied seasonal patterns in belowground production of *alterniflora* (Gallagher and Plumley, 1979; Good et al., 1982; Gallagher, 1983; Gallagher et al., 1984), only two of these studies (Gallagher and Plumley, 1979; Good et al., 1982) examined belowground production in more than one ht form of *alterniflora*. Gallagher and Plumley (1979) examined the depth profiles of root and rhizome production in both ME and GA, and found that different ht forms of *alterniflora* exhibit different belowground biomass distributions. Stroud (1976) explicitly studied belowground biomass production of the two height forms of *alterniflora* in a pair of N.C. marshes, but her results did not correspond either in pattern or production totals to those obtained for New England marshes (Gallagher and Plumley, 1979; Lytle and Hull, 1980).

Here, we present the results of a year-long study of the belowground biomass of *alterniflora* across a tidal gradient in a New England

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salt marsh. We show that amount of biomass found belowground is cyclic with a single, mid-summer peak. No second peak in the amount of belowground biomass is evident in this marsh, in contrast to results obtained from studies of southern marshes (Stroud, 1976; Gallagher and Plumley, 1976; Gallagher, 1983; Gallagher et al., 1984). The amount of belowground biomass, like that aboveground, is found to be correlated with physical parameters of the soil.

**MATERIALS AND METHODS**—We studied the belowground biomass of *alterniflora* at Rumstick Cove, a small, protected embayment of Smith Cove in Barrington, Bristol Co., R.I. (US). The seaward border of the marsh is dominated by a roughly 5 m wide band of tall-form *alterniflora* (mean ht 150 cm). Above this zone, a band of short-form *alterniflora* (mean ht 80 cm) (Valiela et al., 1978) about 3 m wide extends to the mean high water line. (A complete description of Rumstick Cove is given in Bertness, 1984.) In our work, we have distinguished three zones of *alterniflora*. The seaward edge of the marsh, extending 1 m inland from the point where *alterniflora* first appears, and where littoral marsh expansion occurs (Redfield, 1972; Bertness, 1984) is referred to as the marsh edge (+0.1 m to +0.6 m mean tidal ht). The remaining area of the low marsh dominated by tall-form *alterniflora*, approximately 4 m wide, is referred to as the marsh flat (+0.6 m to +1.0 m mean tidal ht). The zone of short-form *alterniflora* is referred to as the short *alterniflora* zone (+1.0 m to +1.2 m mean tidal ht). *Spartina patens* Muhl. dominates the marsh vegetation above +1.2 m mean tidal ht.

To quantify belowground biomass, 8 soil cores were taken in each of the three zones monthly for 1 yr (May 1983 through April 1984). Cores were taken at haphazard locations in each of these three zones using a 6.5 cm inner diam plunger-type coring device (Gallagher, 1974). All cores were taken on obvious clumps of *alterniflora* culms. Cores obtained were normally 30–50 cm in length. Cores were extruded from the corer, wrapped intact in aluminum foil, and returned to the laboratory where the cores were cut into 5 cm long horizontal sections. Each section was washed through a 2 mm mesh sieve to remove mud, soil and fine particulate matter. The remaining organic matter was separated into rhizomes, roots and debris (non-living organic matter). Living and dead matter were distinguished by color and texture (Valiela et al., 1976; Barbor, 1981). Rhizomes, roots and debris were dried (50 C for 5 days) and weighed ( $\pm 0.01$  g).

Each month, an additional five cores were taken in each of the three *alterniflora* zones to measure total root system length and associated aboveground biomass. The shoots of each core were cut at ground level, dried and weighed. The entire core (unsectioned) was then rinsed free of mud and soil. Debris was removed carefully with water and forceps. The freed root system was separated into rhizomes and adventitious roots. The adventitious roots were sorted into two groups: seeker-type roots (roots lacking root hairs and/or secondary branching) and fine roots (roots with copious root hairs and/or extensive branching) (Sutherland and Eastwood, 1916; Anderson, 1974). Lengths of all of these parts were measured ( $\pm 1$  cm). Only the main axis of the fine roots was measured. No cores were taken in December 1983 or January 1984.

Annual decomposition rate in each of the three zones was also quantified. Ten mesh bags ("litter bags," Weider and Lang, 1982), containing a known quantity of living root and rhizome tissue were buried at three depths (5, 10 and 20 cm) in each of the three zones in April 1983 (see Bertness, 1985, for details of the method used). After one yr, the bags were excavated, the contents washed free of soil and other decayed particulate matter through a 2 mm mesh sieve, and the remaining organic material was dried and weighed.

The following physical parameters of the substrate also were measured in each of the three marsh zones using published techniques: soil redox potential (Eh) (Howes et al., 1981; Bertness, 1984), water percolation rate through the sediment (Mendelssohn and Seneca, 1980; Bertness, 1985), substrate hardness (Bertness and Miller, 1984), and soil pH (Linthurst, 1980). Soil samples in each zone were also analyzed for the following nutrients: Magnesium, Phosphorus, Potassium, and total Kjeldahl Nitrogen (Bertness, 1984).

All results are presented in grams dry wt per core. The appropriate multiplicative conversion factor to  $g/m^2$  is 301.36.

**RESULTS AND DISCUSSION**—The amount of total belowground biomass distinctly peaked in midsummer, concurrent with the peak in aboveground biomass (Fig. 1). Studies of southern marshes have documented two peaks in belowground biomass; one in early summer at the time of maximal aboveground growth (as we report here), and another in late fall following the winter dieback of aboveground parts (Stroud, 1976; Gallagher, 1983). The length of the growing season is much shorter in New England than it is further south (Gal-

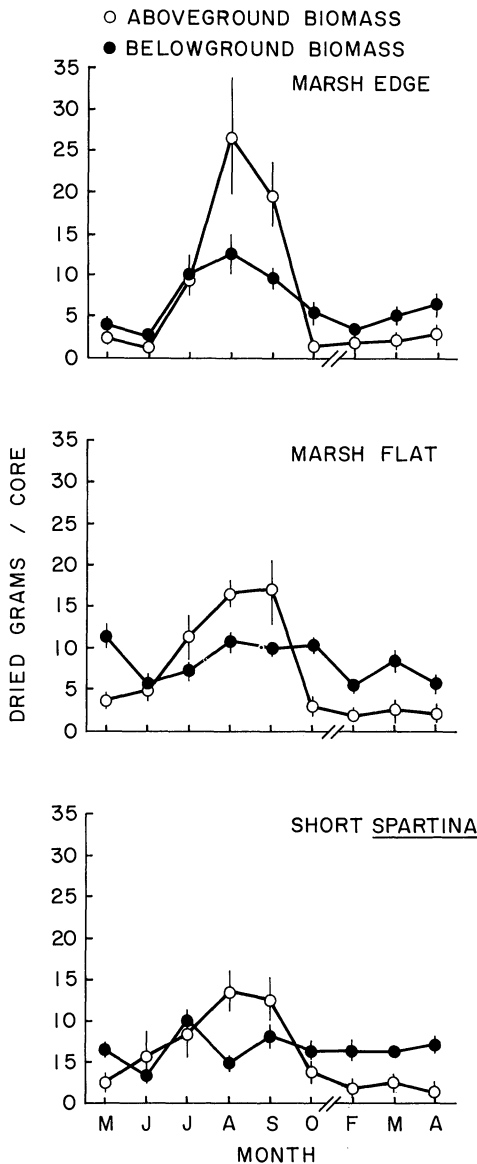


Fig. 1. Total aboveground and belowground biomass of *S. alterniflora* (g/core) in each of the three marsh zones over the course of the year (top: tall-form alterniflora on the marsh edge; middle: tall-form alterniflora on the marsh flat; bottom: short-form alterniflora). Values are means with one S.E. bar.

lagher, 1983). The shortened New England growing season may compress the time available for root growth and eliminate the summer "depression" in belowground biomass seen in southern marshes. Root : shoot biomass ratios declined markedly through the summer as aboveground biomass dramatically increased, but total root biomass/month varied much less than did shoot biomass (Fig. 1).

Total belowground production, determined

by subtracting the minimum monthly belowground biomass from the maximum monthly belowground biomass (Stroud, 1976), decreased with increasing tidal ht (marsh edge: 9.94 g/core [2,995.50 g/m<sup>2</sup>], marsh flat: 5.54 g/core [1,669.53 g/m<sup>2</sup>], short alterniflora zone: 6.76 g/core [2,037.18 g/m<sup>3</sup>]). Total belowground production was significantly greater on the marsh edge than in the other two zones ( $P < 0.05$ , Scheffé test), but total belowground production on the marsh flat was not significantly different from that in the short alterniflora zone ( $P > 0.05$ , Scheffé test). Similarly, total aboveground production decreased with increasing tidal ht. On the marsh edge total aboveground production was 25.04 g/core (7,547.19 g/m<sup>2</sup>), on the marsh flat, 14.89 g/core (4,486.02 g/m<sup>2</sup>) and on the short alterniflora zone, 12.01 g/core (3,620.67 g/m<sup>2</sup>). Total aboveground production in each zone was significantly different from that in the other two zones ( $P < 0.05$ , Scheffé test). Although the data presented here were gathered over but a single yr, the environmental conditions of that year were normal for the region. Our method of deliberately taking core samples from obvious clumps of alterniflora culms could lend an upward bias to our results, but our estimates of total above- and belowground production at Rumstick Cove are comparable to those reported for other New England salt marshes (Valiela et al., 1976; Lytle and Hull, 1980) and the aboveground production is similar to that of other years at Rumstick Cove (Bertness and Ellison, unpubl. data).

The depth profiles of belowground biomass are consistent with the pattern in seasonal biomass at all tidal hts (Fig. 2), showing decreasing penetration of roots and rhizomes into the marsh substrate with increasing tidal ht. On the marsh edge, when belowground biomass was at its maximum (July–August 1983), live roots and rhizomes were present to the greatest depths (up to 20 cm underground). During the rest of the year, live belowground biomass was concentrated in the top 10–15 cm of the substrate (Fig. 2). On the marsh flat, we observed a similar pattern. Throughout the year, roots were restricted to the upper 15 cm of the marsh, but rhizomes extended to greater depths in midsummer than during the rest of the year (Fig. 2). In the short alterniflora zone, the bulk of the belowground biomass occurred in the upper 10 cm of the marsh throughout the year, and only rhizomes extended deeper into the substrate (Fig. 2). There was no clear seasonal change in the depth distribution of live belowground biomass in the short alterniflora zone over the 1-yr sampling period.

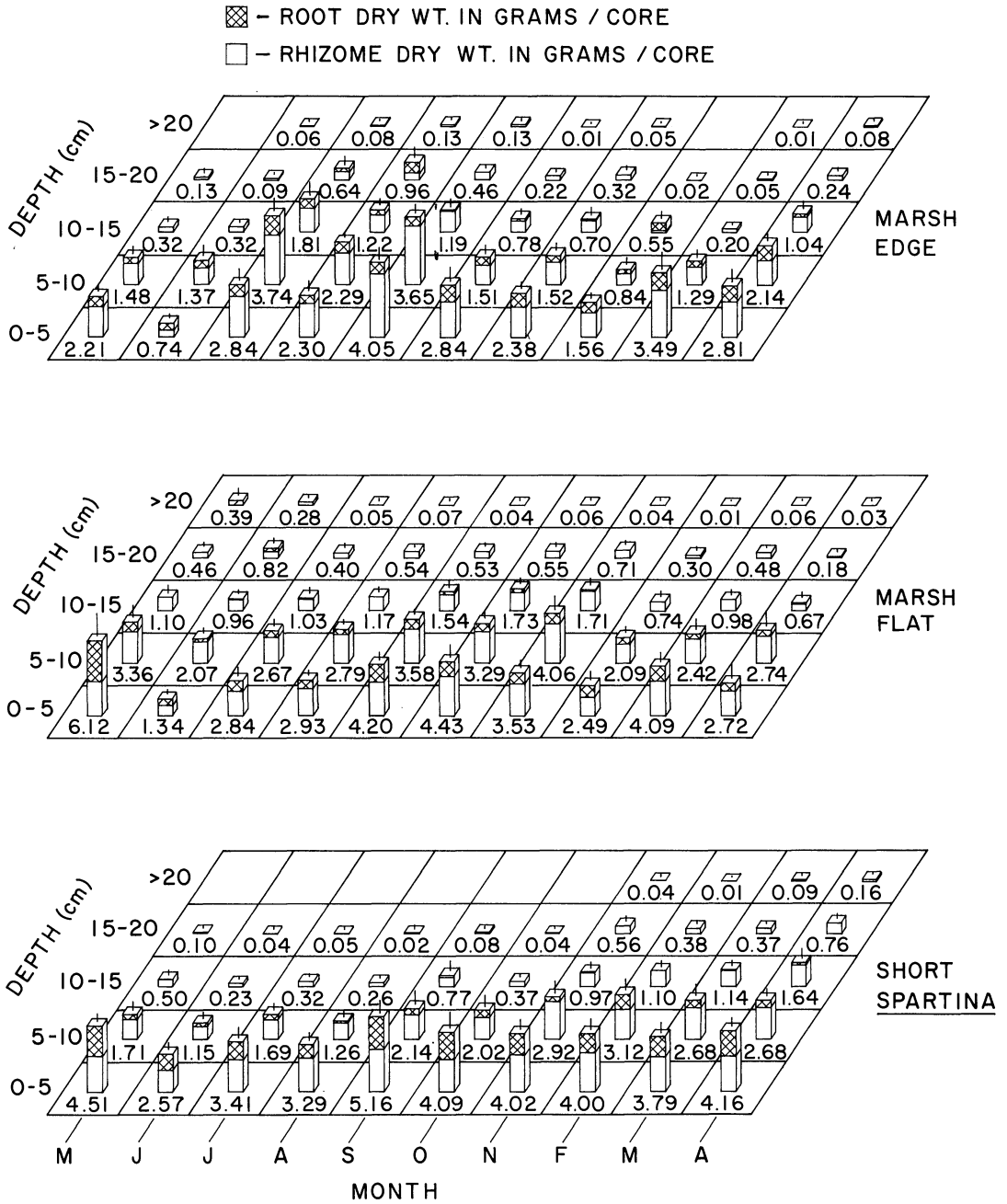


Fig. 2. Depth profiles of belowground biomass of *S. alterniflora* in each of the three marsh zones separated into roots and rhizomes. The value below each block is the mean total biomass (g/core) at that depth (roots + rhizomes). S.E. bars are for total biomass at the given depth.

Total length of the root and rhizome systems also showed clear seasonal patterns which varied over the tidal gradient (Fig. 3). The length of the rhizome system was greater in the marsh flat than in the other two zones (Fig. 3), and tended to be greatest in midsummer. More variation in overall rhizome length was ap-

parent on both the marsh edge and flat, while the rhizome length in the short *alterniflora* zone was relatively stable throughout the year. Seeker root length was greatest in the short *alterniflora* zone in all months except for July, but in all zones, seeker root length showed a dramatic decline over the course of the summer

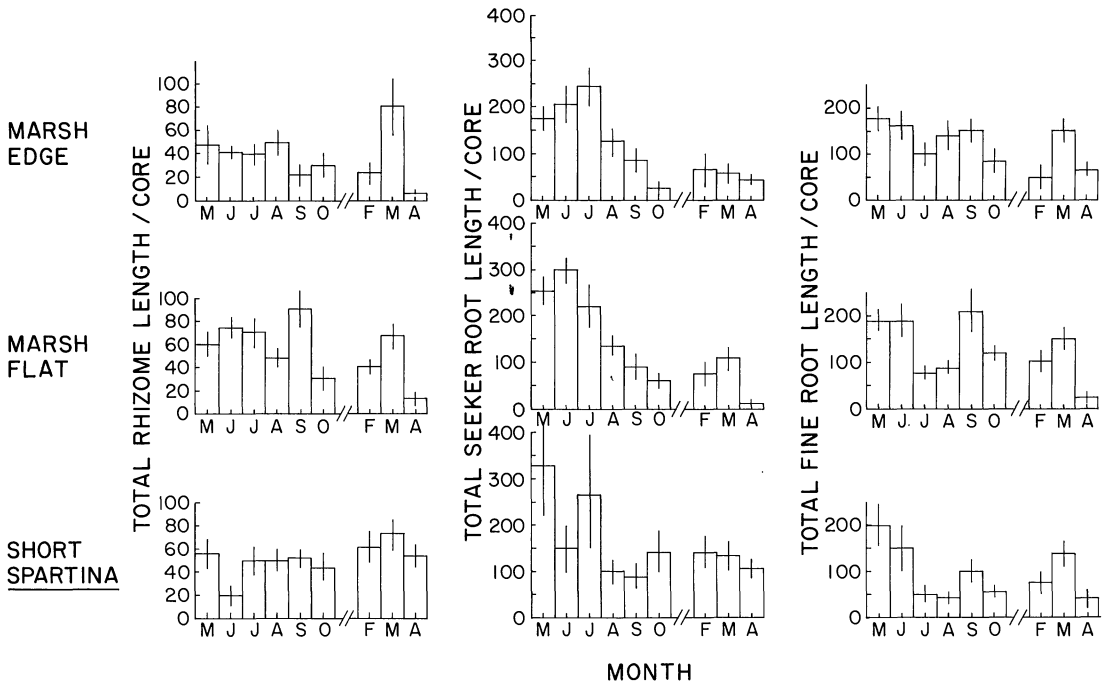


Fig. 3. Total lengths (cm/core) of rhizomes, seeker roots and fine roots of *S. alterniflora* in each of the three marsh zones. Bars are means  $\pm$  one S.E.

(Fig. 3). Seeker roots most likely serve to search the substrate for areas amenable to growth (Sutherland and Eastwood, 1916; Anderson, 1974). The short *alterniflora* zone is relatively nutrient-poor, while the marsh flat and marsh edge are richer in nutrients and soil oxygen (see below). Seeker roots may have to travel a longer distance to find suitable areas of growth in the short *alterniflora* zone than in the other two zones.

We suggest that when seeker roots encounter a suitable area for growth, fine roots develop for nutrient absorption (Sutherland and Eastwood, 1916; Anderson, 1974). Our data show that fine root length is highest when seeker root length is lowest (Fig. 3), and that fine root length is highest in nutrient rich areas. On both the marsh edge and the marsh flat, fine root length is much higher than in the short *alterniflora* zone (Fig. 3). Seeker root elongation proceeds

TABLE 1. Substrate characteristics in the marsh edge, flat, and short *S. alterniflora* habitats at the study site. Measurements with different superscripts are significantly different ( $P < 0.05$ , Scheffé test). See text for methods

	Marsh edge	Marsh flat	Short <i>S. alterniflora</i> zone
Percolation rate <sup>a</sup> ml/hr $\pm$ S.E. (N)	73.1 $\pm$ 20 <sup>b</sup> (24)	91.1 $\pm$ 16 <sup>b</sup> (25)	12.5 $\pm$ 2 <sup>c</sup> (23)
Substrate hardness <sup>a</sup> kg $\pm$ S.E. (N)	23.2 $\pm$ 2 <sup>b</sup> (15)	30.2 $\pm$ 2 <sup>c</sup> (15)	61.2 $\pm$ 3 <sup>d</sup> (15)
pH $\pm$ S.E. (N) <sup>a</sup>	6.77 $\pm$ 0.1 <sup>b</sup> (10)	6.26 $\pm$ 0.1 <sup>c</sup> (10)	5.55 $\pm$ 0.2 <sup>d</sup> (10)
Magnesium <sup>a</sup> $\mu$ g/g $\pm$ S.E. (N)	4,023.1 $\pm$ 129 <sup>b</sup> (10)	3,218.0 $\pm$ 121 <sup>c</sup> (10)	3,268.7 $\pm$ 397 <sup>c</sup> (10)
Phosphorus <sup>a</sup> $\mu$ g/g $\pm$ S.E. (N)	28.0 $\pm$ 6 <sup>b</sup> (10)	71.5 $\pm$ 8 <sup>c</sup> (10)	95.0 $\pm$ 11 <sup>c</sup> (10)
Potassium $\mu$ g/g $\pm$ S.E. (N)	1,503.0 $\pm$ 80 (10)	1,350.0 $\pm$ 73 (10)	1,278.1 $\pm$ 185 (10)
Kjeldahl Nitrogen % $\pm$ S.E. (N)	0.89 $\pm$ 0.1 (10)	0.93 $\pm$ 0.1 (10)	0.65 $\pm$ 0.1 (10)

<sup>a</sup>  $P < 0.05$ , ANOVA among marsh zones.

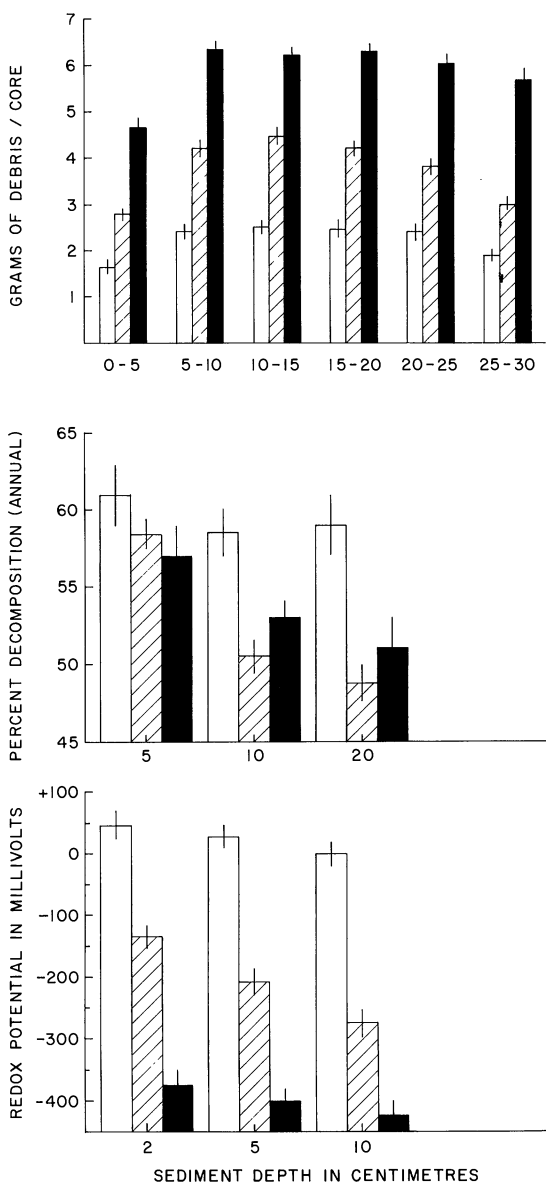


Fig. 4. Depth profiles of quantity of debris (g/core) percent annual decomposition and soil redox potential in the three marsh zones. Bars are means  $\pm$  one S.E. in the marsh edge (open bars), marsh flat (cross-hatched bars), and the short alterniflora zone (solid bars). See text for methods.

most rapidly in the early spring prior to the onset of rapid aboveground growth, followed by fine root elongation in the summer and early fall.

Soil nutrients (except for Phosphorus), pH, percolation rate, decomposition rate and oxygen levels (redox) all decrease, while belowground dead plant material (debris) and substrate hardness increase with increasing tid-

al ht (Fig. 4, Table 1). Decreases in nutrients and soil oxygenation and increases in soil acidity and peat accumulation parallel the decrease in above- and belowground production as tidal ht increases. Live roots and rhizomes placed into small mesh bags decomposed more rapidly on the marsh edge and marsh flat than they did in the short alterniflora zone (Fig. 4). Although the live root and rhizome tissue which we used in our experiment may have decayed more rapidly than naturally senescent tissue would have, the pattern of decreased decomposition rate with increasing tidal ht is consistent at all three depths examined and appears to be real. The more rapid rate of decomposition on the edge and the flat and the consequent decrease in belowground debris may both increase soil nutrient levels and increase available space for root growth and water movement in these zones. As a result of marsh mussels depositing nitrogenous wastes on the marsh edge, and to a lesser extent on the marsh flat, above- and belowground alterniflora production is stimulated (Bertness, 1984). High mussel densities on the marsh edge may, at least in part, be responsible for the high production found on the marsh edge (Bertness, 1984). Similarly, fiddler crab burrowing activities have been shown to increase above- and belowground production on the marsh flat by increasing soil aeration and oxygen levels (Bertness and Miller, 1984; Bertness, 1985). The abundance of both fiddler crabs and marsh mussels decreases with increasing tidal ht (Bertness, 1984, 1985; Bertness and Miller, 1984). Physical characteristics of the substrate which may be influenced by the animals in the marsh appear to be the major determinants of both above- and belowground alterniflora productivity in this New England salt marsh.

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