

# Production and dynamics of experimentally enriched salt marsh vegetation: Belowground biomass<sup>1</sup>

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## Abstract

Root growth increased during the early growing season in *Spartina alterniflora* salt marsh plots. While fertilization with nitrogenous fertilizer did not affect initial growth, a marked decrease in root biomass followed the spring peak particularly where nutrient doses were highest. A sharp reduction in roots occurred in enriched areas covered by *Spartina patens*, although, as with *S. alterniflora*, aboveground biomass increased. Roots disappeared during autumn leaving rhizomes as the only part of the plants to overwinter. The maximum standing crop for roots was 0–2 cm deep, for rhizomes 2–5 cm. Net annual underground production was calculated from annual increments in dead matter belowground. Total production, underground and aboveground, exceeds that of any marine vegetation, ranging from 3,900 to 6,600 g m<sup>-2</sup> yr<sup>-1</sup> in *S. alterniflora* areas and 3,200 to 6,200 g m<sup>-2</sup> yr<sup>-1</sup> in *S. patens* areas. Fertilization increased production particularly aboveground where dead plant parts are subject to export.

Although production of aboveground vegetation in salt marshes has received considerable attention, belowground production has not been studied (Keefe 1972). In salt marshes, as in other grasslands (Troughton 1957; Schuurman and Goedewaagen 1965), it has been difficult to devise satisfactory techniques for routine measurements of root and rhizome growth and production. Some methods for separation of living and nonliving materials have been suggested (Ellis and Barnes 1973; Knievel 1973; Caldwell and Camp 1974), but it is hard to differentiate live from dead underground parts. It is also difficult to wash samples completely free of adhering sediment particles (Troughton 1957; Milner and Hughes 1968). However, careful sampling and washing of samples, aided by tissue staining techniques to separate live and dead tissues, although tedious, do allow the collection of interpretable data.

We have been studying the structure and function of a Massachusetts salt marsh since 1970. A series of plots was treated with different fertilizers and the conse-

quences of the fertilization treatments have been followed through various components of the marsh ecosystem, with emphasis up to now on the aboveground vegetation (Valiela et al. 1973; Valiela and Teal 1974; Estrada et al. 1974; Banus et al. 1974; Krebs et al. 1974).

Here we give estimates of production and distribution of underground plant biomass. Our experimental design involves fertilization with urea or a sewage sludge-based fertilizer. We have identified nitrogen as the primary limiting nutrient in salt marshes (Valiela and Teal 1974); hence the urea treatment. Sewage contamination is common in coastal areas including salt marshes (Ketchum 1972), which has motivated the studies with sewage sludge fertilizer.

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## Methods

We add the mixed, commercially available sludge fertilizer (10% N, 6% P<sub>2</sub>O<sub>5</sub>, 4% K<sub>2</sub>O) and the urea (46% N) every other week to salt marsh plots 10 m in ra-

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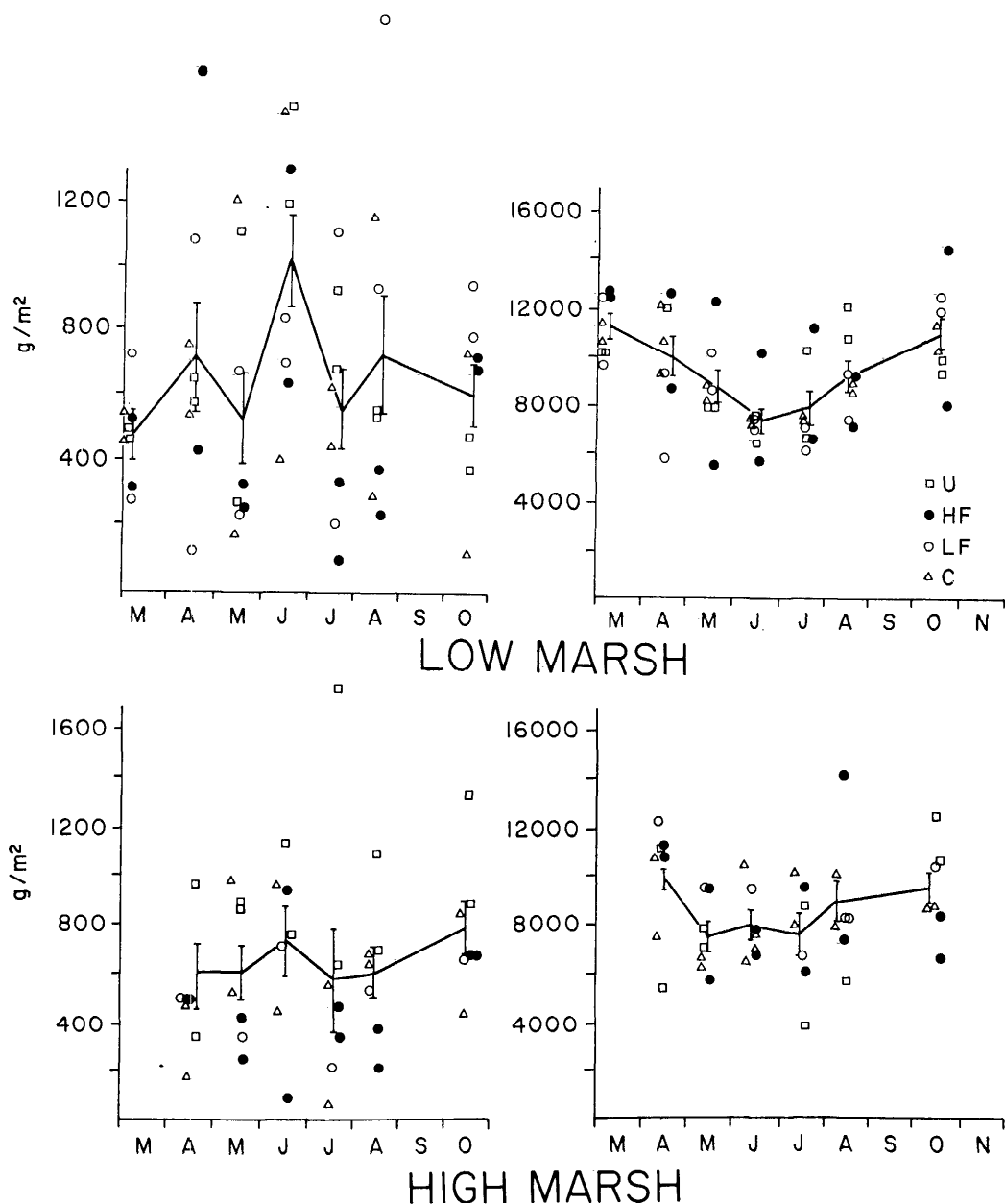


Fig. 1. Amounts of rhizomes (left) and dead matter (right) in low and high marsh under treatments. The lines show the mean  $\pm$ SE.

dus by broadcasting at low tide from May to November. We use  $25.2 \text{ g m}^{-2} \text{ wk}^{-1}$  (HF) and  $8.4 \text{ g m}^{-2} \text{ wk}^{-1}$  (LF) of the mixed fertilizer and  $5.6 \text{ g m}^{-2} \text{ wk}^{-1}$  of urea (U). There are two replicate plots for each treat-

ment, as well as two untreated controls (C). Details of the chemical makeup of the fertilizer are given elsewhere (Valiela et al. 1973; Krebs et al. 1974). The mixed fertilizer treatments began before the 1970 grow-

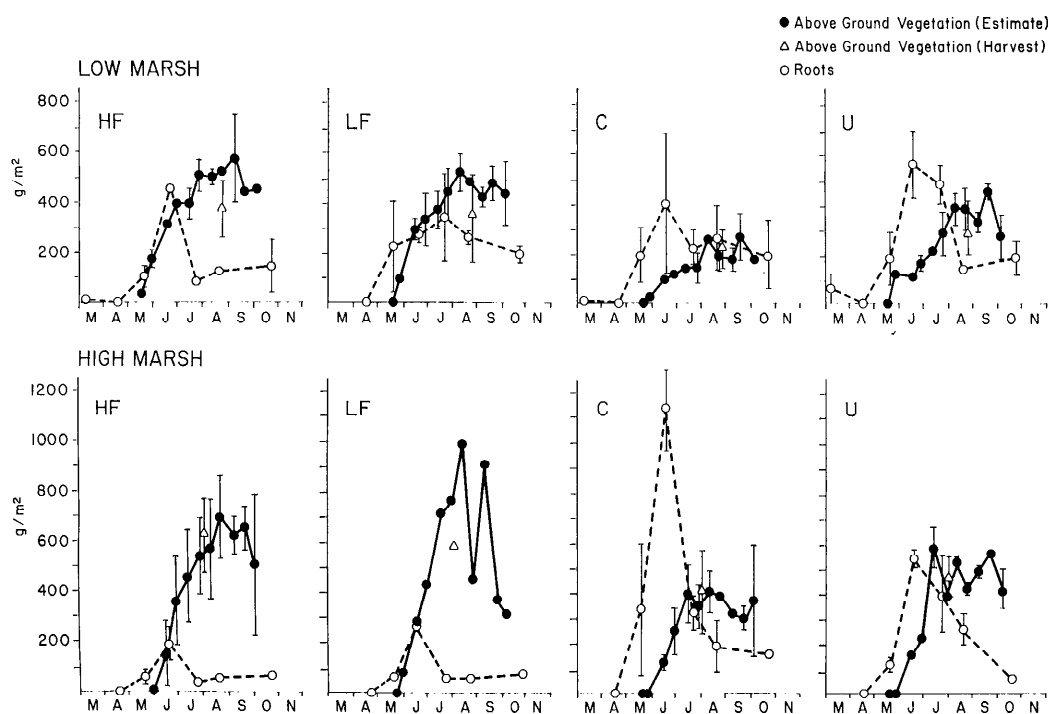


Fig. 2. Amount of aboveground vegetation and roots in low and high marsh under the treatments. The points show mean  $\pm$ SE. The values obtained by harvesting grass quadrats are shown in addition to the estimates from measurement of plant height. Where standard errors are not shown they were smaller than the symbol.

ing season; the urea plots were set up during spring 1971.

Underground plant tissues were sampled every 2 weeks from March–October by coring the sediments with a plastic tube (6.5-cm diam). The cores extended 15–25 cm deep, about the extent of root penetration (Valiela and Teal 1974). In each plot single cores were obtained from representative stands of low marsh, where *Spartina alterniflora* was virtually the only grass species, and from high marsh, the habitat where *Spartina patens* was dominant. Every plot contained high and low marsh except one subject to the LF treatment. The cores were cut in half vertically. One half was kept for chemical analyses (to be reported elsewhere) and the other half was sectioned horizontally at intervals (0–2, 2–5, 5–10, 10–15, and 15–20 cm). The sections were washed in a 0.5-mm-mesh sieve and the roots, rhizomes, and dead vegetation

separated after blotting. These materials were separated as far as possible by appearance. Live roots and rhizomes were pearl-white, translucent, and fairly rigid. Dead matter was duller gray and flaccid. When all the clearly live material had been picked out, the remainder, usually a small fraction of the total root weight, was submerged in 1 g of chlorazol black per 100 g of water, which stained dead matter but not live tissues (Williams and Williams 1974).

Every second month from March to September clean sand was introduced into core holes and recored 2 months later to estimate the growth rate of underground parts through the growing season. These values are underestimates, since growth had to take place inward from the periphery of the core hole, but were thought to give an adequate measure of relative rates of underground growth.

To obtain estimates of the aboveground

Table 1. Cumulative totals of root and rhizome biomass grown into sand cores set up as described in text. Values for high and low marsh and including the various fertilization treatments.

	Cumulative total (g/m <sup>2</sup> per growing season)	
	Roots	Rhizomes
Low marsh		
HF	56.1	130.6
LF	36.1	74.7
C	23.2	58.9
U	40.2	74.4
High marsh		
HF	15.7	71.1
LF	20.0	139.8
C	23.0	18.2
U	13.2	41.3

vegetation we measured the height of the 10 tallest plants in 0.1-m<sup>2</sup> quadrats. These values were converted to biomass using a regression of height on dry wt m<sup>-2</sup> ( $wt = 0.074 \times ht + 15.973$  for *S. alterniflora*;  $wt = 0.041 \times ht + 23.294$  for *S. patens*) (Valiela et al. 1975). Measurements were made biweekly in high and low marsh in each plot. A harvest of 0.1-m<sup>2</sup> plots in early August, followed by sorting and weighing, gave results in agreement with the nonharvest technique.

### Results and discussion

There were no effects of the fertilizer treatments on the standing crops of rhizomes in either high or low marsh (Fig. 1). No clear seasonal pattern in the abundance of rhizomes was apparent although there is a suggestion of a peak in June–July in low marsh. This is the period of maximum growth for aboveground vegetation (Fig. 2 and Valiela et al. 1975).

There was also no response to treatment in the amount of dead plant matter for either high or low marsh (Fig. 1) but there was minimum material in June–July, followed by a new accumulation in autumn. This implies in situ decomposition during spring and summer followed by accumulation of dead organic matter by death of roots and rhizomes during fall.

In contrast to rhizomes and underground

dead matter, fertilization distinctly affected the quantity of roots, which was correlated with aboveground live vegetation (Fig. 2). In low marsh all plots showed a peak standing crop in June or July (observed in other grasses by Stuckey 1941) followed by a reduction, more marked where nitrogen was abundant (IIF and U plots). This trend is more striking in high marsh, where fertilized plots had much lower standing crops of roots than controls at all times. In presenting the data we have shown the standard errors but have not tested the results statistically. The observed differences among treatments and over time seemed large enough to be taken as real.

Though they resulted in less root biomass, the fertilization treatments increased aboveground vegetation (Fig. 2 and Valiela et al. 1975). The peak standing crops of roots during June coincide with the fastest growth of plant tops. This is also the time of greatest depletion of pore-water nitrogen (Valiela and Teal 1974).

The amounts of roots and rhizomes that grew into the sand cores were converted to growth rates and a cumulative total calculated (Table 1). In low marsh the totals were higher in fertilized plots than in the controls. Growth of rhizomes was slow at first, peaking about the end of June or later followed by reduced growth toward the end of August. Roots peaked earlier, mid-May to mid-June.

In high marsh root growth in the control plots was greater than but similar to that in the fertilized plots (Table 1). We have no explanation for the high value for rhizome growth in the LF treatment in high marsh.

Root growth as measured with sand cores was not sufficient to result in the root biomass found in June–July. Since the sand core method provided a good estimate of relative growth rates but a low estimate of total growth, we needed another procedure for the latter. The seasonal pattern of dead biomass (Fig. 1) suggests that after mid-summer there is an accumulation of roots and rhizomes that grew and died in that growing season. We estimated under-

Table 2. Estimates of annual production ( $\text{g m}^{-2}$ ) by the various components of salt marsh grasses under the treatments. The values for HF, LF, and C are means for 3 years; the urea plots are means for 2 years.

	Annual production ( $\text{g m}^{-2}$ )			
	HF	LF	C	U
Low marsh				
above-ground	1,320.9	956.4	423.7	834.3
rhizomes	2,943.0	5,490.0	3,291.0	4,014.0
roots	372.0	147.0	207.0	414.0
total	4,635.9	6,593.4	3,921.7	5,262.3
High marsh				
above-ground	1,255.6	1,379.5	631.8	1,193.5
rhizomes	3,384.0	3,402.0	1,614.0	4,505.0
roots	156.0	210.0	906.0	474.0
total	4,795.6	4,991.5	3,211.8	6,172.5

ground production by taking the mean minimum value of dead matter in Fig. 1 and subtracting this from the mean maximum value to the right of the minimum for each treatment (Table 2). We then estimated the amount of roots from the peaks in Fig. 2. The difference between the value for increments of dead biomass and peak for roots must be the contribution by rhizomes, since there was no other apparent source of dead plant material. Root production was greater than shown in Table 2 since some would have died before maximum root biomass was reached. The estimates of rhizome production are therefore low. The total underground production should also be an underestimate, since decomposition of dead underground plant parts must have decreased the maximum accumulation.

We estimated the total net production by marsh vegetation by adding to the roots and rhizomes production the aboveground production calculated in Valiela et al. (1975).

The vertical distribution of roots, rhizomes, and dead matter did not vary seasonally. The data from the various dates were pooled in Fig. 3. Roots have maximum standing crops near the surface of the marsh sediment in both low and high marsh, while rhizomes have maximum standing crops between 2–5 cm deep. This difference may serve to place the roots nearest

the site of nitrogen fixation and adsorption while protecting the rhizomes from removal by ice-rafting in winter, a common occurrence in low marsh at our latitude. The root distributions of Fig. 3 also show the reduction apparently prompted by fertilization in the high and low marsh relative to the controls. Dead matter increases down to about the depth of root penetration. The gradient probably reflects increased decay toward the surface. Below 10–15 cm the decayed materials are small enough for significant amounts to be washed through our 0.5-mm sieves during processing of the samples.

The values for salt marsh production obtained (Table 1) exceed any comparable measurement in natural marine vegetation. Mann (1973) calculated that net primary production in beds of kelp—the most productive marine plants—reached a maximum of about  $2,300 \text{ g m}^{-2} \text{ yr}^{-1}$ , making kelp beds important sources of organic matter for the coastal environment. Although salt marsh production was greater than that of kelp, we assume that only the aboveground vegetation is subject to export mechanisms (Teal 1962; Odum and de la Cruz 1967), so that only aboveground parts of salt marsh plants contribute organic matter to other parts of the coastal ecosystem.

Odum (1959) listed a variety of terrestrial plants that have high production rates, with little mention of belowground produc-

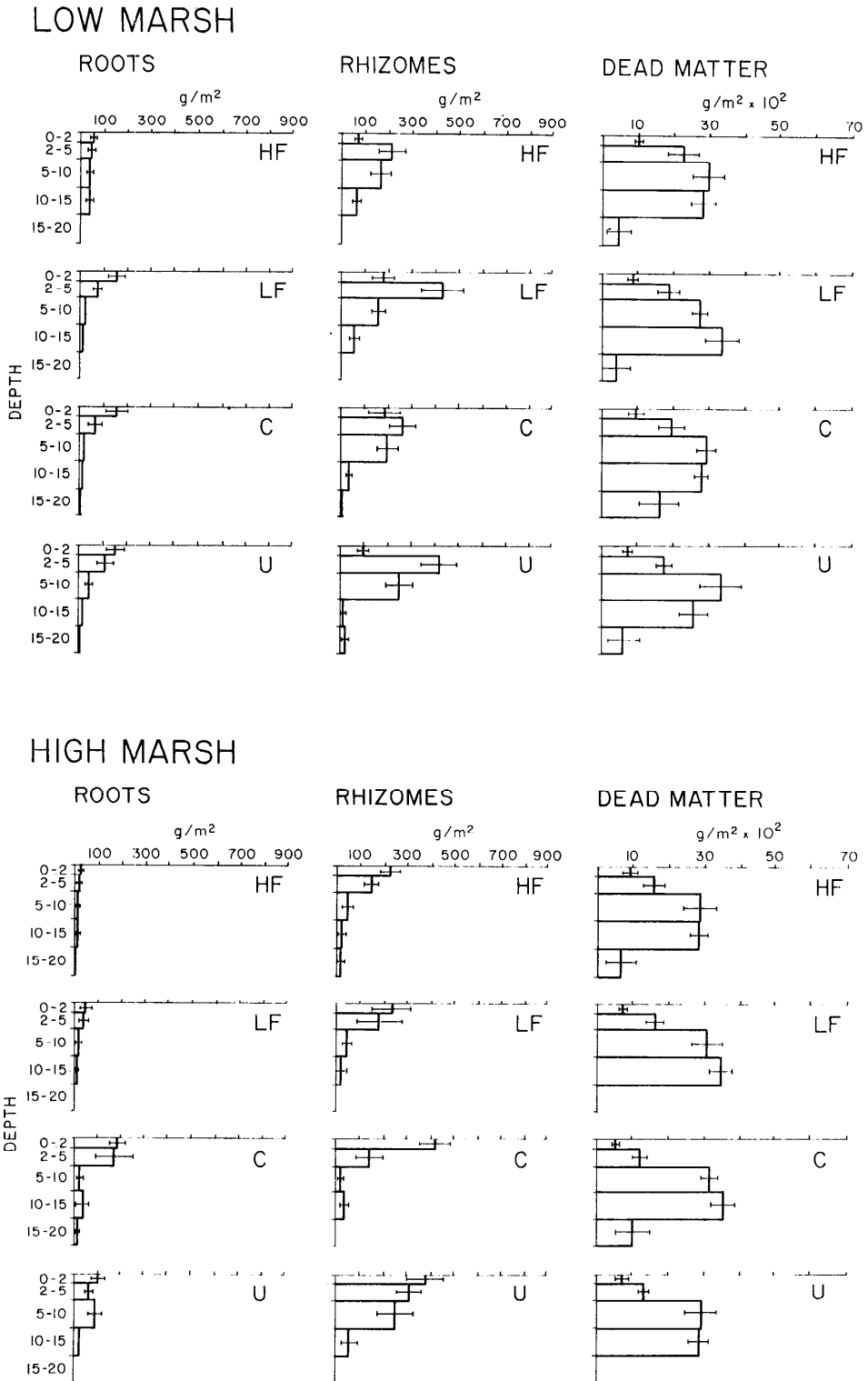


Fig. 3. Vertical distribution of rhizomes, roots, and dead matter in low and high marsh under the treatments. The horizontal lines are standard errors. Depth is in centimeters.

tion. The net total production of a tall grass prairie in Missouri, including above- and belowground parts, was estimated at about 1,000–2,000 g m<sup>-2</sup> yr<sup>-1</sup> (Kucera et al. 1967), considerably below our production values. In sites within the U.S. IBP Grassland Biome study, total net annual production averaged only 104–699 g m<sup>-2</sup> (Sims and Singh 1971). Redmann (1975) found root standing crops of 4–6 kg m<sup>-2</sup> in North Dakota grasslands—values comparable to our measurements. A rough check on our present results can be made from CO<sub>2</sub> uptake data collected during the energy balance measurements of Teal and Kanwisher (1970) which give an annual fixation equivalent to a production by *S. alterniflora* of 3,500 g m<sup>-2</sup> yr<sup>-1</sup> for an unfertilized marsh at West Falmouth, about 2 km north of Great Sippewisset marsh. This agrees very well with the measurements of 3,900 g m<sup>-2</sup> yr<sup>-1</sup> made in our control creeks (Table 2).

The ratio between below- and aboveground parts in grasses varies substantially (Bray 1963; Kucera et al. 1967; Sims and Singh 1971), increasing to considerably over 1 : 1 as the habitat becomes drier. Our ratios exceed 1 : 1 (Table 2, Figs. 1, 2), and thus salt marshes could be conceived as a xeric environment for an angiosperm. We have observed repeatedly that *Spartina* grasses show greening and increased growth following a substantial rainfall.

The lack of measurable response to treatment by the rhizomes may have been at least partly due to the smallness of the core used in sampling. It would seem better to have used a surface area closer to that used in sampling aboveground vegetation (0.1 m<sup>2</sup>). However, this would have made the processing of samples too laborious and destructive to the marsh. It may also be that rhizome biomass is not very sensitive to changes in available nutrients. Since rhizomes are the perennial portion of the marsh grasses and its anchor in the mud, there may be a premium in providing for a high bulk of rhizome tissue, even if nutrient supplies were not sufficient to allow maximal growth of plant tops.

We did not expect the marked decay in

dead matter seen in Fig. 1, and supported by the gradient of Fig. 3, since we supposed that decomposition in anoxic sediments would be slow. However, dead parts still attached to the living plant would be supplied with oxygen from the plant's air spaces (Teal and Kanwisher 1966), so that aerobic oxidation could occur. The volume of underground plant parts involved in accumulation and decomposition is large enough that the surface of the marsh would rise and fall about 1 cm each year. (This figure was calculated from Fig. 1, an average organic matter of 20% for marsh sediments in the fall, and a weight of 1 g of sediment cm<sup>-3</sup>.) Such elevational differences may be important in an environment where the difference between sites supporting low or high marsh vegetation may be less than a centimeter.

The roots in both high and low marsh showed a seasonal pattern of growth in spring, near-disappearance during winter, and clear responses to the treatments. The disappearance of roots after the summer growth peak is found to a lesser extent in other grasses (Sims and Singh 1971; Stuckey 1941). The reduction of root standing crops, seen especially in high marsh, is similar to that found by Power and Alessi (1971) in a North Dakota grassland subject to nitrogen fertilization. Barley roots may increase following nitrogen additions but the root : shoot ratio is reduced (Welbank and Williams 1964). It seems as if some grasses manufacture enough roots to process needed nitrogen and no more. The amount of root is therefore inversely proportional to the available nitrogen in the sediment.

The total production estimates (Table 1) showed a good response to fertilization with urea compared to controls. In both high and low marsh the lower dose of sewage sludge fertilizer generated greater production than the higher dosage, as if some deleterious material were depressing growth at the high level of contamination. This may be due to a multiplicity of factors unrelated to contamination, such as the specific balance between decomposition and

production in roots and rhizomes in each treatment, a feature which our data cannot elucidate. The important points regarding this are that the aboveground production is not much smaller in the HF plots relative to LF plots after 5 years of treatment, and both are substantially higher than the controls, and that the difference between HF and LF involves mainly underground production, not aboveground parts, so that the smaller total production under high levels of contamination is immaterial for those components of the ecosystem dependent on organic matter exported from the salt marsh surface.

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