Production Dynamics for Above and Belowground Components of a New Jersey *Spartina alterniflora* Tidal Marsh

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Above- and belowground portions of *Spartina alterniflora*, short form, from a New Jersey salt marsh, were analysed for changes in biomass, caloric content and chemical composition over an approximately 14-month period. The belowground portions of this marsh were characterized by a large biomass, averaging $11·4$ kg m^{-2} in the top 30 cm. Annual changes occurring in this layer, defined as net ecosystem production, gave a value of $2·2$ kg m^{-2}. The root to shoot ratio was $4·7$ and the turnover time, $5·5$ years.
   The distribution of photosynthetically fixed carbon in the plant tissues was determined to a depth of 50 cm by separating plant material into ash, crude protein, crude fiber, crude fat and nitrogen-free extract. Most of the tissue, on an ash-free basis, was carbohydrate; 50% nitrogen-free extract and 43% crude fiber. Seven percent entered the crude protein pathway and 1% the crude fat. Percentage of crude protein increased with depth while percent crude fiber and nitrogen-free extract decreased with depth. Aboveground portions yielded slightly lower caloric values, $4·4$ kcal/g ash-free, than those for belowground portions. Caloric content belowground increased with depth; from $4·5$ kcal g^{-1} in the top layer to $5·0$ kcal g^{-1} in the lower portions.
   High primary production, dense growth habit and root longevity, which characterize the *Spartina alterniflora* short form community, combine to form a highly stable system. Annual energy and carbon fixation by this primary producer provide a large flow of organic compounds within the estuarine ecosystem with the belowground component and its decomposition products acting as a sink.

Introduction

Data on biomass accumulation, turnover and nutrient values of the total vegetation are essential for understanding the role of salt marshes in the estuarine food web, but little information exists on belowground plant parts (Turner, 1976). Recently interest in belowground components has grown. Valiela & Teal (1974) included belowground material in a study of nutrient limitation, Stroud (1976) investigated net primary production of belowground material and carbohydrate composition of *Spartina alterniflora* and de la Cruz & Hackney (1977) studied belowground components of *Juncus roemerianus*. Belowground

productivity research has been hampered by lack of uniformly applicable methods (Iwaki & Midorikawa, 1968; Richardson, 1968; Westlake, 1968). Manual and visual separation to distinguish live and dead material which are suitable for forest ecosystems do not work well for the nature and quantity of material involved (Kucera *et al.*, 1967; Coupland, 1975). Therefore the change in biomass technique used in a Missouri prairie by Dahlman & Kucera (1965) is often used.

In this study *Spartina alterniflora* Loisel., short form, was studied over ≈ 14 months to determine the relationships of belowground biomass and chemical composition dynamics to aboveground phenomena. *Spartina alterniflora*, short form, is the dominant vascular macrophyte in New Jersey salt marshes and constituted 65% of the study area, the 1200 acre (486 ha) Manahawkin marsh along the eastern shore of Little Egg Harbor in Ocean County New Jersey. Other marsh communities in the study area included *S. patens*, *S. alterniflora*, tall form, and shrubs.

Methods

Three pure stands of *S. alterniflora*, short form, located in undisturbed portions of the marsh were chosen as sampling sites and designated as Stations 1, 2 and 3. Regular sampling, approximately monthly, was begun 5 June 1974 and continued through 22 July 1975.

Aerial and belowground plant production was measured using the harvest method (Milner & Hughes, 1968; Odum, 1971). Belowground production was determined by observing seasonal changes in the total biomass of soil-free subterranean materials (Dahlman & Kucera, 1965) Large quadrats, 3.5 m $\times$ 18.5 m, were established and 50 cm $\times$ 50 cm subplots sampled randomly. During the growing season $\approx$April–September, when both above- and below-ground samples were collected, 2 subplots were hand clipped to within less than 2 cm of the marsh surface and separated visually into live and litter portions. Litter included standing dead as well as surface litter. One 7.62 diameter $\times$ 50 cm core was removed from each subplot using a device and method similar to that described by Gallagher (1974). A sharpened copper cylinder was driven into the ground, filled with water, stoppered and lifted with a modified sleeve onto which 4 handles had been welded. Belowground material was removed from the cylinder with a wooden plunger, bagged, stored and refrigerated until processed. On occasion when differences between strata were sufficiently great to cause compression, core removal was performed in segments.

In the laboratory, cores were sliced in half vertically and subdivided horizontally, into 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, 20–30 cm, 30–40 cm and 40–50 cm segments. One half was washed in a 1 mm mesh sieve by hand, pulling apart the mat of roots, rhizomes and decomposing fragments; the second half was not washed. Washing was deemed complete when washed material yielded no further apparent soil particles on flotation in a white enamel pan. All separated aboveground, washed belowground, and unwashed belowground materials were dried in a force draft oven at 80 °C for 48 h. After being weighed, dried materials were ground and passed through a 60 mesh screen on a Wiley Mill and stored, frozen, until further analysis.

Salinity of surface muds was monitored throughout the study period using the method of Good (1965) to extract the soil solution and a SoluBridge Conductivity meter and tables to determine salinity.

Plant density at each station was determined by counting the number of culms present in duplicate 25 cm $\times$ 25 cm quadrats. Peak mean dry weight per culm was calculated from sampling on 25 June 1975 and 11 December 1975.

Energy content was measured by burning processed material in a Parr 1222 adiabatic calorimeter with a temperature controller according to the Parr method (Parr, 1960). Reported results are within a 2% variation of duplicate 1-g samples. Ash content was determined by igniting desiccated samples for 2 h at 600 °C in a Temco F-1635 muffle furnace (Reiners & Reiners, 1972). Because of variation in the mineral content of plants, both seasonally and in response to physiological demands, ash content was determined for each sample individually.

Samples from the same depth interval and date were pooled to provide sufficient quantities for chemical analysis. Coefficients of variation conducted on test runs to determine whether pooling of material would yield valid results, were positive. All analyses were conducted on duplicate desiccated samples and the results presented on an ash-free basis. Crude protein content was determined by the standard macro-Kjeldahl method (AOAC, 1965) of total organic nitrogen determination with a boric acid finish. Estimated crude protein content was obtained by multiplying Kjeldahl nitrogen by 6·25 (AOAC, 1965). Crude fiber determinations were performed using an acid-alcohol extraction of soluble compounds followed by ashing of the residue (Cusmano & Scotton, 1951). Crude fat content was determined by petroleum ether extraction for 3 h in a Goldfisch extractor (AOAC, 1965), while nitrogen-free extract was determined by subtracting the sum of the 3 previous percentages from 100.

Periodic regression analysis, using Biomed program, BMD104R, (Dixon, 1973) was used to analyse biomass data for the 0–30 cm layer. Periodic regression analysis, a useful tool where a rhythmic biological response is associated with a period of determinate length (Bliss, 1970), was carried to 5 harmonics. Actual data were interpolated to provide the evenly spaced intervals required for the analysis. In addition to actual or interpolated data, estimated dry weights (dummy variables) were used to complete 2 full annual cycles. Three series of possible dummy variables were tested to determine which would produce the least biased information. Regression curves presented for Year I+Year II data include dummy values which duplicate values from corresponding dates of the previous year.

Estimation of root longevity and, consequently, the length of time required for replacement (turnover) of the belowground complex was calculated. The per cent of the total biomass which changes annually was determined using the method of Dahlman & Kucera (1965) which is shown by the following equation:

$$\frac{\text{Net primary production}}{\text{Maximum biomass}} = \text{Per cent turnover.}$$

Results

Biomass

The *Spartina alterniflora*, short form, belowground community is characterized by a large standing crop and large annual net primary production. The top 30 cm layer was comprised

TABLE 1. Mean quantities (kg m^{-2}), range and maximum biomass present in layers of *Spartina alterniflora*, short form. Data are presented for a 1 year period

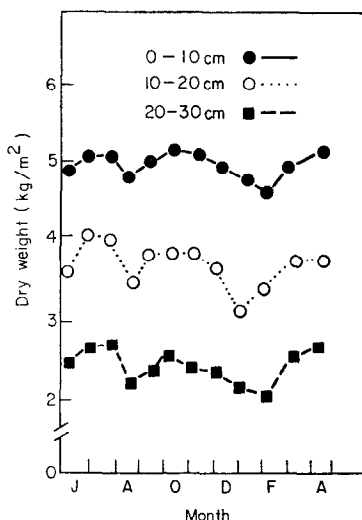|	0–10 cm (kg m^{-2})	10–20 cm (kg m^{-2})	20–30 cm (kg m^{-2})	0–20 cm (kg m^{-2})	0–30 cm (kg m^{-2})
Mean	5·0	3·7	2·5	8·7	11·2
Range	0·9	0·9	0·9	1·3	2·3
Maximum	5·4	4·0	2·9	9·3	12·3

Figure 1. Regression curves of predicted annual cycle for 3 layers of belowground biomass in *Spartina alterniflora*, short form, for Years I and II combined.

of a mean 11·2 kg m^{-2} (Table 1). Almost half of this material, 5·0 kg m^{-2}, occurred in the top 10 cm layer with 3·7 kg m^{-2} in the 10–20 cm stratum and 2·5 kg m^{-2} in the 20–30 cm zone (Table 1). The 30–40 cm stratum was similar to the 20–30 cm zone with respect to weight of the belowground biomass containing an average 2·3 kg m^{-2} over the study period. The material in this layer, however, was becoming noticeably more fragmentary and less resilient than that of the layers above it. In the 40–50 cm zone the belowground biomass was greatly reduced (1·8 kg m^{-2}). The extent of decomposition, apparent at all levels, increased with depth. In many instances the 40–50 cm zone contains a distinct boundary between the root mass-decomposition product stratum and the mud-silt sedimentation layer overlying the hard sand marsh bottom. The 30–40 and 40–50 cm segments were deleted from biomass analysis because of the erratic nature of samples. Minor differences in mean biomass were observed among the 3 study sites at all levels.

A general increase in belowground biomass occurred from late winter until July with the greatest rates of increase in March prior to shoot emergence and in June as shown by the regression curves (Figure 1).

High belowground biomass levels reached in early summer are, in general, maintained until November. A declining trend occurred from December through February, with the greatest rate of decrease in December and January. During this winter period the surface was periodically frozen and ice-covered. Biomass decline in August, corresponded to a period of very hot weather, low precipitation and highly saline (32–83‰) conditions during July and early August of 1974.

A peak for belowground biomass was reached on 25 June 1975, culminating a general increase from the late winter minimum point. Regression curves obtained by the inclusion of all actual data plus estimated variables to complete a 2-year period, predict 0–20 cm and 10–20 cm peaks from 1 July to 1 August; on 1 May in 0–10 cm and 20–30 cm layers and, for the entire 30 cm layer, peak times on 1 May, 1 July and 1 August (Figure 1).

Secondary peaks for the 0–10 cm and 20–30 cm layers coincided with the primary peaks for the lower layers (30–40 and 40–50). An autumn secondary high peak for the entire below-ground biomass occurred during October and November with the 10–20 cm layer having

a major influence (Figure 1). Aboveground plant parts became senescent by the end of November.

Net ecosystem production estimates were based on the premise that the combination of decomposition rates and growth rates will undergo proportional changes from year to year and, that harvesting conducted regularly over a year's time will detect those changes. Regression equations calculated on the basis of 16 samplings were computed to 5 harmonics. Changes in the 30 cm layer totaled 2·3 kg m^{-2} for Year I and 2·2 kg m^{-2} for Year I+II. Changes within the 0–10 cm strata were identical for Year I and Year I+II calculation periods at 0·9 kg m^{-2} (Table 2). The 20–30 cm layer also was the same, 0·9 kg m^{-2}, for each computation. The 10–20 cm zone, however, ranged from 0·9 kg m^{-2} for Year I to 1·1 kg m^{-2} for Year I+II. Because the 10–20 cm layer variation fell within the limits of fluctuation in the whole 30 cm subterranean community for Year I, no overall increase in net ecosystem production was measured for Year I+II. This general pattern of increased biomass accumulation in the 1975 growing season, which accounts for the higher mean biomass reported for Year I+II, does not result in an increased range.

TABLE 2. Annual turnover of the belowground portion of *Spartina alterniflora*, short form

		Belowground Change (kg m^{-2})	Belowground Maximum (kg m^{-2})	Turnover (%)	Rate (years)
0–10 cm	Year I	0·9	5·4	17·5	5·7
	Year I+II	0·9	5·5	17·4	5·7
10–20 cm	Year I	0·9	4·0	22·0	4·5
	Year I+II	1·1	4·2	26·3	3·8
20–30 cm	Year I	0·9	2·9	30·5	3·3
	Year I+II	0·9	2·9	30·4	3·3
0–30 cm	Year I	2·3	12·3	18·3	5·5
	Year I+II	2·2	12·3	18·1	5·5

Aboveground production averaged 525 g m^{-2} in 1974 and 429 g m^{-2} in 1975 for the 3 stations. Stations 1 and 2 yielded similar peak standing crops for each year with the Station 3 value somewhat lower. Plant density was greater at Station 1 with about 2590 culms m^{-2}, Station 2 had only 1340 culms m^{-2} and Station 3 was intermediate with about 1760 culms m^{-2}. The average weights per culm were 0·19 g at Station 1, 0·36 g at Station 2 and 0·24 g at Station 3. Lower peak standing crop at Station 3 is at least partially due to large tidal deposits, frequently observed at that location.

Total primary production for the above- and belowground portions of the *Spartina alterniflora*, short form, study sites was 2·8 kg m^{-2} for Year I and 2·7 kg m^{-2} for Year I+II, yielding root to shoot ratios of 4·37 and 4·71 respectively. The calculated per cent turnover increased with depth (Table 2). About 18% of the 0–30 cm zone is replaced annually and turnover time averaged 5·5 years.

Ash content
Percentage ash appeared to increase slightly with depth. The 0–10 cm layer contained 11·5%; the 10–20 cm, 13·5%; the 20–30 cm, 14·8%; 16·5% in the 30–40 cm and 16·2% in the 40–50 cm layer. Ash content values were not significantly different due to the con-

siderable variation in samples from any given depth. Consistent seasonal differences were not apparent. Aboveground ash content of live material averaged 13·7% and litter, 26·5%.

Energy content

Energy content varied according to component and stratum. Although not statistically tested, calorimetric measurements of the aboveground plant yielded lower values, 4·4 kcal/g ash-free for live material and 4·2 kcal/g ash-free for litter material, than those obtained for the below-ground portions. Mean caloric content for the belowground complex was 4·5 kcal/g ash-free in the 0–5 cm layer; 4·6 kcal/g in the 5–10 cm stratum; 4·8 kcal/g for the 10–15 cm layer and 5·0 kcal/g for each of the four deepest segments; 15–20 cm, 20–30 cm, 30–40 cm and 40–50 cm.
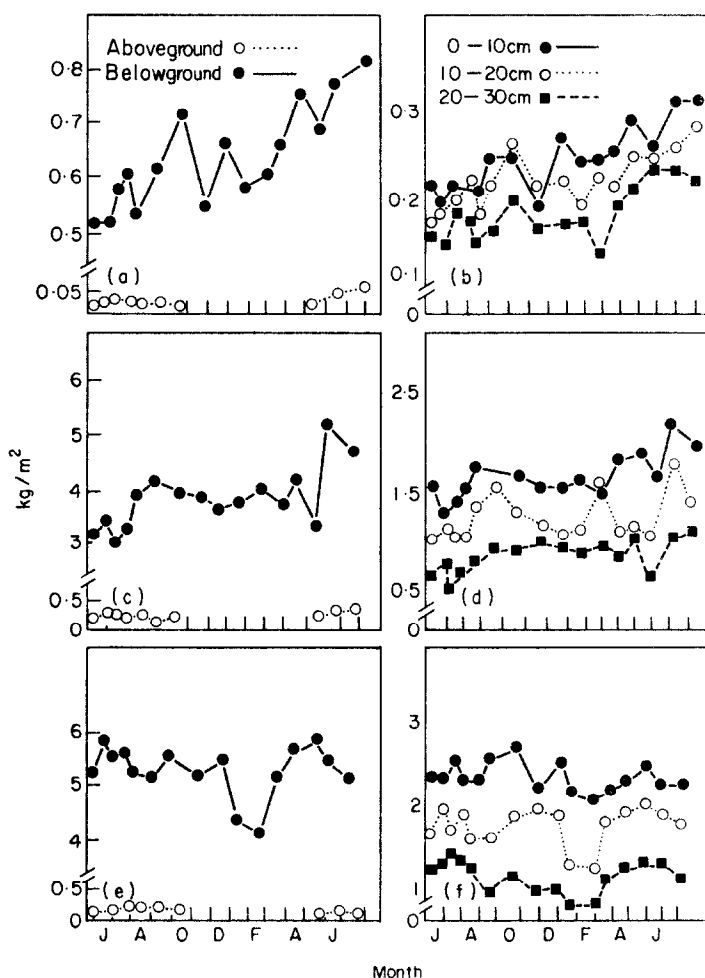

Figure 2. Proximate analysis in kg m^{-2} for *Spartina alterniflora*, short form, from June 1974–July 1975: (a) crude protein present in the aboveground and 30 cm belowground portions; (b) crude protein in the belowground zones; (c) crude fiber in the aboveground and 30 cm belowground portions; (d) crude fiber in the belowground zones; (e) nitrogen-free extract in the aboveground and the 30 cm belowground portions; and (f) nitrogen-free extract in the belowground zones.

Crude protein

The 0-30 cm layer contained an average 639 g m^{-2} crude protein and underwent several rapid changes which in some instances were coincident with identifiable phenological or environmental events [Figure 2(a)]. Increase or decrease of crude protein for the 30 cm layer and each of its subdivisions corresponded to biomass changes except during the month of December when crude protein content rose while biomass declined. A comparison of June and July 1974 crude protein percentages and dry weights with those of June and July, 1975, showed that both were greater in 1975. Thus, in addition to the greater biomass, the rate increased about 1%, yielding 207 g m^{-2} more crude protein in June and July of 1975. Both years were characterized by a high aboveground tissue level of crude protein at the onset of the growing season, as observed by Squiers & Good (1974).

Percentage of crude protein (but not absolute amounts) generally increased with depth down to 40 cm with a 1% decrease occurring in the 40-50 cm stratum. The curves describing the ash-free dry weight of crude protein are characterized by numerous rapid fluctuations and a lack of synchronization between layers [Figure 2(b)].

Crude Fiber

The 30 cm summary curve [Figure 2(c)] displays rapid increases during August 1974 and June 1975, strong decreases in May and July 1975, a relatively static condition between growing seasons and a mean crude fiber content of 3·7 kg m^{-2}. Examination of crude fiber content within the 3 strata [Figure 2(d)] reveals some differences in trend among levels. The 0-10 cm layer, containing a mean 1734 g m^{-2} crude fiber, follows, in overall aspect, the summary pattern of rapid accumulation during and after biomass increase. Additional distinct decreases occurred June 1974 and February 1975. The 10-20 cm layer demonstrated dramatic increases during August–September and June 1974 and an additional increase in February 1975. The latter is directly opposed to the top layer decrease. This layer also exhibited a rapid crude fiber decrease from September to January, a trend entirely different from those shown in the other zones. The 20-30 cm zone, with a mean 795 g m^{-2} demonstrated growing season changes similar to those in the upper layers. The mid-July to December time period is one of steady increase in crude fiber for the 20-30 cm layer.

The mean percentage of crude fiber present in the entire 40 cm layer is uniformly near 38·5%, with no differences among levels, although absolute quantities decrease with depth. The differences between growing seasons noted for the crude protein fraction, were also present in the crude fiber data. Higher percentages, approximately 7%, as well as greater dry weights were observed in the 1975 growing season.

Nitrogen-free extract

The nitrogen-free extract fraction forms the largest proximate analysis component, 54%, or a mean of 6844 g m^{-2} in the 30 cm layer. This component, comprised primarily of storage compounds, may include small amounts of cellulose, hemicellulose or lignin depending on the extent of the crude fiber digestion (Squiers & Good, 1974; Hinds, 1975).

Seasonal dry weight fluctuation of belowground quantities of nitrogen-free extract showed close correlation with biomass standing crop changes [Figure 2(e)]. Peaks occurred in July and November–December 1974 and May–June 1975 with a low point during February 1975 for each layer.

Percentage of nitrogen-free extract averaged ≈54% throughout the top 30 cm and decreased to 45% at 40-50 cm. The percentage of fluctuation within each layer showed a distinct increase with depth. The greatest change in weight occurred in the 10-20 cm layer.

Net change in the top layer was 402 g m^{-2} (16%); 764 g m^{-2} (44%) in the 10–20 cm zone and 628 (54%) of the 20–30 cm layer [Figure 2(f)].

Comparing growing seasons, June and July 1974 produced less dry weight but a higher percentage (9·2%) of nitrogen-free extract than June and July of 1975, in opposition to crude fiber and crude protein production which increased in both percentage and dry weight in 1975. Aboveground peaks occurred in late July during 1974 and 1975 and were 286 g m^{-2} and 246 g m^{-2} respectively.

Crude fat

Quantities of fats and lipids in the 0–30 cm belowground layer are low, 1·13%, and follow no apparent seasonal pattern. Trends in the ether extract component during seed development did not occur in this community. Percentages are higher in the 0–10 cm and 10–20 cm layers, 1·25% and 1·13% respectively, than the lower layers which contained 0·88%, 0·83% and 0·76%. Dry weights decreased with depth. Differences in dry weights and percentage between June and July 1974 and 1975 were random and no general trends were apparent within or between growing seasons.

Discussion

The belowground complex of live and dead roots and rhizomes and decomposing fragments of *S. alterniflora*, short form, total some 112 t ha^{-1} in the top 30 cm. The biomass is comparable to that reported by de la Cruz (1974) of 90–160 t ha^{-1} for 6 types of communities in a Mississippi salt marsh and 97–124 t ha^{-1} for *Juncus roemerianus* (de la Cruz & Hackney, 1977). Good & Smith (1975) reported biomass values for other Manahawkin marsh community types as 70 t ha^{-1} for *S. alterniflora*, tall form, 80 t ha^{-1} for *Distichlis spicata* (L.) Greene and 90 t ha^{-1} for *Spartina patens* (Ait.) Muhl. Our estimates are considerably higher than the belowground estimates of 34·9 t ha^{-1} for *S. alterniflora* high marsh in Massachusetts reported by Valiela *et al.* (1976) and estimates of 10·8–59·4 t ha^{-1} for *S. alterniflora* in North Carolina reported by Stroud (1976). Belowground estimates for Manahawkin communities are also much higher than those reported by Good & Good (1975) for New Jersey tidal freshwater marshes along the Delaware River which were 18–31 t ha^{-1} for perennial species and 8·9 t ha^{-1} for the annual *Zizania aquatica*.

Total above- and belowground net primary production was estimated to be 28 t ha^{-1}, approximately 23 t ha^{-1} of which is belowground production. Total production is quite similar to that of *Zizania aquatica*, 25 t ha^{-1}, (Good & Good, 1975) although in *Zizania* the bulk (16 t) of the material is aboveground. Dry weight changes in belowground biomass reflect not only growth-induced changes but also changes related to translocation, consumption and decomposition. Weight changes in the 0–10 and 10–20 cm portions of the root-rhizome system are of similar magnitude comprising about 20 t ha^{-1} together. Activity in the 20–30 depth interval is markedly lower, accounting for about 15% of belowground production, but is still large (3 t ha^{-1}) in comparison to aboveground production. Annual productivity was estimated to be 1·36 kg m^{-2} (13·6 t ha^{-1}) by de la Cruz & Hackney (1977) for *Juncus roemerianus* with the top 20 cm layers accounting for 94% of belowground productivity. Our belowground biomass shows several peaks, the first in late winter-early spring (March–April) before aboveground growth is very active, a second in June and a third in autumn which is probably related to translocation from senescing aboveground parts although active tillering also occurs at this time in New Jersey. The spring and early summer peaks are separated by a period of loss (May) as shoot growth becomes active. Midsummer was an

inactive period for both above- and belowground growth. A measurable decline in below-ground biomass during an unfavorable hot, dry period indicates that belowground biomass is relatively sensitive to even short stress periods.

The high root to shoot ratio found for *Spartina alterniflora* (4·7) here has been suggested by others. Gallagher (1974) found root to shoot ratios of 1·43, 11·24 and 50·0 for tall, medium and short *S. alterniflora*, respectively. Stroud (1976) reported root to shoot ratios of 5·5 and 18·0 for 2 *S. alterniflora* short form populations. Adaptive significance has been ascribed to high root to shoot ratios for some communities. Water and nutrient uptake per unit root surface is diminished by low soil temperature, low nutrient levels, low soil oxygen and high soil moisture, requiring greater root surface for each aboveground unit (Shaver & Billings, 1975; Wielgolaski, 1975). Valiela *et al.* (1976) found that nitrogen fertilizers reduced root mass in *S. alterniflora*, suggesting an inverse relationship between root biomass and available nitrogen. Haines & Dunn (1976) found decreased allocation to roots with the addition of nitrogen. Salinity provides an additional stress for which abundant belowground growth is a adaptive benefit. Maintenance of water flow from the soil solution toward the plant is dependent upon high cell sap osmotic concentration which is developed by halophytes under saline conditions. Because of possible toxicity from increased osmotic concentration, the established water potential is often of a magnitude providing low water potential. Mech-anisms counteracting the effects of low potential are larger root to shoot ratios and a reduced water requirement for plants such as *S. alterniflora* which uses the C-4 photosynthetic pathway (Odum, 1974; Black, 1971). An early study of halophyte species (Repp, 1939) reported very large root to shoot ratios; *Suaeda maritima* (64·3), *Camphorosma ovata* (35·5), *Aster pannonicus* (7·1) and *Triglochin maritimum* (3). Waisel (1972) cited additional studies showing rapid root growth to be a common halophyte physiological characteristic.

The turnover period of 5·5 years calculated for the top 30 cm layer is slightly longer than that reported for prairie or tundra communities (Weaver, 1958; Dahlman & Kucera, 1965;
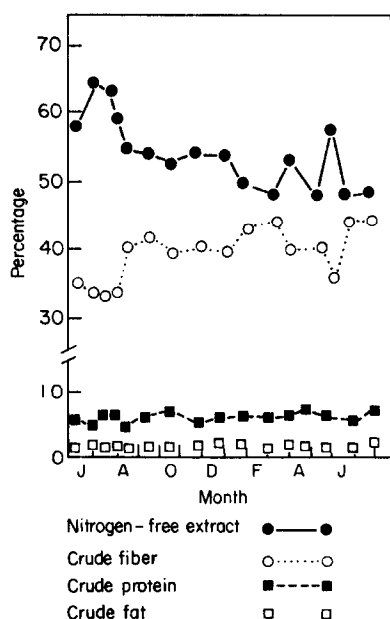

Figure 3. Proximate analysis components on an ash-free basis in the top 30 cm belowground zone of *Spartina alterniflora*, short form, from June 1974–July 1975.

Shaver & Billings, 1975). Direct calculation of the data without regression analysis would indicate a turnover of about 4 years. Turnover estimated for *Spartina alterniflora*, tall form, for the same marsh system is faster; about 2·55 years (Good & Smith, 1975). Differences in turnover between the 2 forms result in a larger standing belowground crop (maximum 12 300 g m^{-2}) for the short form compared to the tall form (maximum 8500 g m^{-2}) although the annual increment for the short form (2300 g m^{-2}) is considerably below that of the tall form (3300 g m^{-2}).

Energy content per unit of dry matter in the *Spartina alterniflora* community was within the range described in the literature (Golley, 1961; Kucera *et al.*, 1967; Odum, 1971; Squiers & Good, 1974; Hinds, 1975; Stroud, 1976). The aboveground caloric level of 4·44 kcal g^{-1} was similar to that of 4·5 kcal g^{-1} found by Squiers & Good (1974) for another *S. alterniflora*, short form, community in New Jersey; of 4·5 kcal g^{-1} found by Kucera *et al.* (1967) in a Missouri tallgrass prairie and of 4·4 kcal g^{-1} found by Hinds (1975) in a Washington *Bromus tectorum* community.

The total annual energy fixation of 12 700 kcal m^{-2} includes 2090 kcal m^{-2} for aboveground parts and 10 610 kcal m^{-2} for belowground parts. The inclusion of belowground production in these comparisions is useful primarily in providing perspective into the magnitude of the root-rhizome system, emphasizing the need for additional investigation into the fate of this large component.
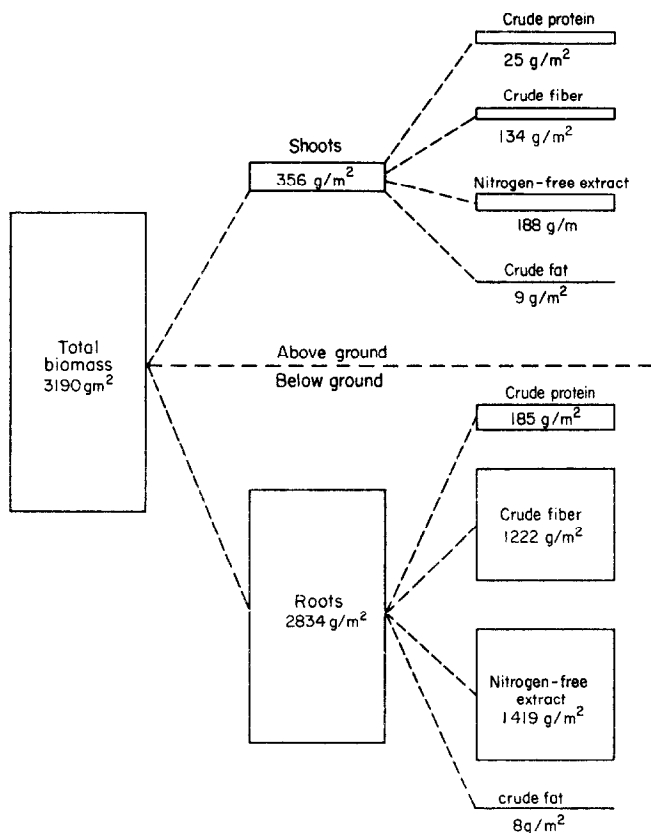

Figure 4. Flux of photosynthetically fixed material into 4 carbon pathways in *Spartina alterniflora*, short form, from 5 March to 25 June 1975.

Most of the photosynthetically fixed carbon in this belowground community became storage or structural carbohydrate (50% and 43% respectively), 7% entered the crude protein pathway and 1% the crude fat (Figure 4). These results are similar to those of Hinds (1975) for roots of mature *Bromus tectorum*. Aboveground percentages were very similar to those of Squiers & Good (1974). Crude protein, crude fiber, nitrogen-free extract and crude fat were 7, 38, 53, and 3% respectively. Udell *et al.* (1969) found larger percentages of crude protein and a lower percentage of crude fiber for *S. alterniflora*, short form.

From 5 March to 25 June 1975, a total of 3190 g m^{-2} of ash-free dry matter (raw values; not derived from regression analysis) was accumulated in the *Spartina alterniflora*, short form, community. Of this, 2834 g m^{-2} (88·8%) entered the belowground component. Determination of carbon flux by proximate analysis showed 1419 g m^{-2} (50·1%) of this to be nitrogen-free extract, 1222 g m^{-2} (43·1%) crude fiber, 185 g m^{-2} (6·5%) crude protein and 8 g m^{-2} (0·3%) to be crude fat (Figure 4).

Striking correspondence between seasonal biomass changes, both in the 30 cm layer and in the sub-levels and seasonal nitrogen-free extract changes, indicate a direct relationship between biomass and nitrogen-free extract (storage compounds). Inter-relationships among nitrogen-free extract, crude fiber and crude protein percentage changes suggest that the storage compound component acts as a reservoir of fixed carbon, releasing amounts as needed for other plant functions. Nitrogen-free extract and crude fiber dynamics show essentially opposite trends throughout the year (Figure 3). Percentage increases in soluble carbon compounds occur in sharp spurts followed by sharp decreases during periods of rapid growth. The companion process of crude fiber dynamics follows as the major deposition site for nitrogen-free extract compounds. The crude fiber fraction composed primarily of the insoluble structural compounds characteristic of secondary cell walls is present in much greater percentage during maturation than growth. Loss of crude fiber dry weight would reflect disintegration of older plant parts.

Seasonal change phenomena of the crude protein component reflects the dynamic and sensitive nature of protein metabolism. Instances of opposing trends between layers undoubtedly document protein breakdown in one location and synthesis in another of higher priority. Crude protein percentage increase with depth is elucidated somewhat by amino acid analyses of decomposing material revealing a discrepancy between crude protein values and amino acid totals (de la Cruz & Poe, 1975). Non-protein compounds which are lumped into the crude protein fraction have been shown to include fungal chitin (Odum, W. E., personal communication). The other nitrogen compounds which have yet to be identified may serve as buffers and chelators maintaining the year-round nutrient supply which is known to exist. Crude protein content was higher than that measured by Valiela & Teal (1974) for either urea-enriched or untreated plots or rhizomes and roots of a *Spartina alterniflora* community in Massachusetts.

Stresses to the *S. alterniflora*, short form, community in terms of nutrient limitation, salinity, waterlogging and fluctuating water level are substantial. New growth is limited or absent during much of the summer, visible yellowing may accompany dry periods and flowering is absent. *S. alterniflora*, short form, seems to be occupying an essentially unfavorable habitat which is probably beyond the tolerance limit of potential competing species. The concept of tidal subsidy as outlined by Odum (1974) probably does not apply consistently to the short form communities where inundation is irregular. Opportunities for import of nutrients and export of detritus between portions of the ecosystem are much more limited than in *S. alterniflora*, tall form. Storms may account for a significant amount of the interaction between the short form communities and the rest of the system. Short form

communities are likely to function more often as a sink or reservoir of materials. Data from a Long Island *S. alterniflora* marsh reported by Armentano & Woodwell (1975) suggest that marsh sediments represent a major sink for the flux of carbon. Litter from the previous year is typically present in the spring in short form communities in contrast to its absence in tall form communities, further supporting the dominant role of in situ decomposition and the lesser importance of export during typical tidal cycles. The large percentage of belowground material would also seem to make export, at least in easily recognizable forms, more difficult. The annual energy and carbon fixation by this community presents a substantial flow of organic compounds within the system. Much of the material, both living and in various states of decomposition, is present in the belowground component. Compounds derived from these materials by anaerobic and aerobic processes constitute a large potentially available nutrient pool. The mechanisms of utilization remain unclear.

In *S. alterniflora*, short form, the belowground component appears to be more dynamic than the aboveground; changes in biomass and chemical composition can be quite rapid. Patterns probably vary somewhat from year to year, depending primarily on rainfall and temperature. Stroud (1976) found the rhizomes to be the most variable plant part in regard to carbohydrate composition. Variations were related to marsh location, ecophenal height forms and phenophase events. Above-belowground relationships of these ecophenes reflect differences of their roles in the marsh system as a whole as well as differences in adaptive strategies. It is increasingly clear that comparisons of marsh types based on data from aboveground parts alone can yield only a very incomplete and probably somewhat distorted view of the interaction between various parts of the ecosystem and functional roles of constituent communities.

Acknowledgements

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