Aboveground and Belowground Primary Production Dynamics of Two Delaware Bay Tidal Marshes

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Aboveground and belowground primary production dynamics of two Delaware Bay tidal marshes[1]

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ROMAN, C. T., AND F. C. DAIBER (College of Marine Studies, Univ. of Delaware, Newark, DE 19711). Aboveground and belowground primary production dynamics of two Delaware Bay tidal marshes. Bull. Torrey Bot. Club 111: 34-41. 1984.—Aboveground and belowground net primary productivity estimates of the dominant angiosperms from two tidal marshes along the Delaware Bay estuary are reported. Ash, carbon and nitrogen content of the aboveground and belowground components were also determined. Annual net aboveground production was determined by the peak live standing crop method and the Smalley (1958) method. Aerial production of tall *Spartina alterniflora* Loisel. at the Canary Creek salt marsh, employing the Smalley technique, was 1487 g m^{-2} yr^{-1}, while production of short *S. alterniflora*, *S. patens* (Ait.) Muhl. and *Distichlis spicata* (L.) Greene was, 654 g m^{-2} yr^{-1}, 1147 g m^{-2} yr^{-1}, and 785 g m^{-2} yr^{-1}, respectively. At the brackish water Blackbird Creek marsh, *Phragmites australis* (Cav.) Trin. had the highest aboveground production (2940 g m^{-2} yr^{-1}), followed by *S. patens* (1089 g m^{-2} yr^{-1}) and short *S. alterniflora* (916 g m^{-2} yr^{-1}). Belowground primary production was determined by the annual increment (max—min) method, with respective estimates of 6.5 kg m^{-2} yr^{-1}, 5.0 kg m^{-2} yr^{-1}, and 3.3 kg m^{-2} yr^{-1}, for tall *S. alterniflora*, short *S. alterniflora* and *S. patens*, at the Canary Creek marsh. Belowground estimates at the Blackbird Creek marsh were within this range.

Key words: tidal marsh, primary production, Delaware Bay, *Spartina, Distichlis, Phragmites.*

Over the past three decades numerous investigators have estimated the aboveground net primary production of salt marsh angiosperms common to the Atlantic, Gulf and Pacific coasts of the United States. This research has been reviewed in detail (Keefe 1972; Turner 1976; Kibby *et al.* 1980). Others, beginning with a study by Teal (1962), have studied the link between aboveground net primary production and energy flow dynamics within the salt marsh-estuarine ecosystem (reviewed by de la Cruz 1979). More recently, the belowground aspect of salt marsh primary productivity has received considerable attention, warranting a comprehensive review (Good *et al.* 1982). These studies have shown that belowground production and biomass estimates are significantly higher than aboveground measurements for the same species. Investigators are now beginning to speculate as to the ecological significance of this substantial belowground component (Good *et al.* 1982; Howarth and Hobbie 1982). It is apparent that such estimates of primary productivity are necessary before our complete understanding of energy flow pathways within the salt marsh-estuarine ecosystem is possible.

In this paper we report on the biomass, annual primary production and chemical composition of aboveground and belowground tissues of several common angiosperms present at two tidal marshes along the Delaware estuary. Aside from adding to a growing body of literature focusing on the magnitude and ecological role of marsh primary production, the results of this study have significant regional implications. With comprehensive biological and chemical studies currently underway in the Delaware estuary (Sharp *et al.* 1982; Biggs *et al.* 1983), it seems that the data presented in this paper will contribute to the interpretation of dynamic processes and interactions occurring between the es-

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tuary's marsh ecosystems and adjacent estuarine-coastal waters.

Study Areas. The Canary Creek salt marsh (Sussex County, Delaware) is located near the mouth of Delaware Bay (Fig. 1). The mean tidal range of this 190 ha *Spartina alterniflora* Loisel. marsh is approximately 1.0 m, with a mean annual creek water salinity at the mouth of 25–30 ppt. The Blackbird Creek marsh (New Castle County, Delaware) is about 60 km upstream from the mouth of Delaware Bay. The mean tidal range is about 1.6 m and the mean annual creek water salinity is 10–15 ppt. The hummock vegetation pattern of *S. alterniflora* and *S. patens* (Ait.) Muhl., intermixed with patches of *S. cynosuroides* (L.) Roth. and *Phragmites australis* (Cav.) Trin., is indicative of the brackish water regime of this marsh.

Methods. The study encompassed two growing seasons, with the aboveground and belowground collections made at 1-2 month intervals, from December 1974 through October 1976. Prior to initiation of the sampling program, nearly pure stands of each vegetation type to be evaluated were delineated as study areas. At the Canary Creek marsh, *S. alterniflora* (tall form and short form), *S. patens*, and *Distichlis spicata* (L.) Greene were studied; at the Blackbird Creek marsh three vegetation types were studied: (*S. alterniflora* short, *S. paterns* and *P. australis*).

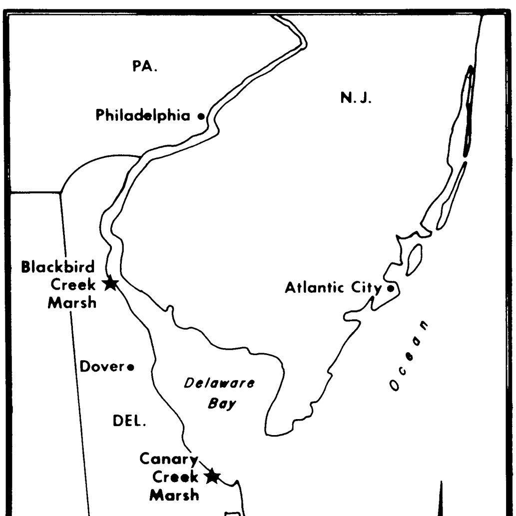

Fig. 1. The Delaware Bay estuary with location of the Canary Creek salt marsh and Blackbird Creek brackish water marsh.

For aboveground measurements five quadrats were randomly harvested from the study areas for each species. Quadrat size was dependent on stem density and varied as follows: *S. alterniflora* (tall and short) and *S. patens* at Blackbird Creek (0.25 m^2); *S. patens* at Canary Creek and *D. spicata* (0.10 m^2); *P. australis* (0.50 m^2). Aboveground material was clipped at the mud level and separated into live and dead components. Litter remaining on the marsh surface after clipping was collected separately. This surface litter component consisted primarily of degraded marsh grass. Standing live, standing dead and surface litter material were carefully washed of sediment, filamentous algae and visible animals, dried to a constant weight at 50°C, and weighed.

Annual aboveground net primary production was estimated using the peak live standing crop method and the Smalley (1958) method. The first assumes that the single highest value of standing live biomass harvested during the year represents net primary production. The Smalley method, developed specifically for use in salt marshes, is more refined and considers changes in biomass of both live and dead material over time. The relative merits and shortcomings of these methods have been reviewed (Kirby and Gosselink 1976; Linthurst and Reimold 1978; Shew *et al.* 1981).

Belowground biomass was collected following the method described by Gallagher (1974). The coring device used was a plastic (PVC) cylinder. The extracted cores were 10 cm diameter and 35 cm long. At Canary Creek the hummock vegetation pattern was noticed for both tall and short *S. alterniflora,* so three cores were taken between aerial clumps and three over aerial clumps. The Canary Creek *S. patens* and *D. spicata* study areas were fairly uniform with the hummock pattern not evident and, thus, three cores were taken on each sample date. At Blackbird Creek three cores were taken between aerial clumps and three cores over aerial clumps for the three vegetation types sampled. Except for short *S. alterniflora* at Blackbird Creek, Student's t-tests revealed no significant differences ($p < 0.05$) in biomass collected between or over aerial clumps for all vegetation types sampled; therefore, the between and over clumps data were pooled. The between and over clumps data for short *S. alterniflora* at Blackbird Creek were considered separately. All cores were washed over a 1 mm mesh screen. The retained roots and rhizomes were dried at 50°C to a constant weight. Annual belowground net primary productivity was estimated by calculating the annual increment (maximum biomass minus minimum biomass). Due to several inconsistent trends in the data, belowground biomass and production estimates for *D. spicata* at Canary Creek are not presented.

Dried plant material, both aboveground and belowground, was ground in a Wiley Mill (20-mesh screen) and ash content determined after ignition at 550°C for 3 h. Material passing through a 60-mesh screen was analyzed for organic carbon and organic nitrogen content by high temperature combustion using a Hewlett-Packard (Model 185B) CHN analyzer.

Results and Discussion. ABOVEGROUND PRODUCTION DYNAMICS. Annual aboveground net primary production of the dominant vascular plants encountered at the Canary Creek and Blackbird Creek study sites is presented in Table 1. The Smalley technique, which accounts for changes in live and dead biomass throughout the growing season, results in higher estimates of production as compared to the peak live standing crop method. Although both methods are considered to underestimate net primary production, they are relatively easy to employ and their widespread utility in salt marsh ecosystems enables meaningful comparisons with other studies.

In general, the results of Table 1 are within the range of production values reported for other mid-Atlantic coastal marshes (see reviews by Keefe 1972; Turner 1976; Kibby *et al.* 1980). Production of tall *S. alterniflora,* growing along creek banks at Canary Creek, was 1487 g m^{-2} yr^{-1} (Smalley method), while production of the short form was 654 g m^{-2} yr^{-1}. Production of short *S. alterniflora* at Blackbird Creek was 916 g m^{-2} yr^{-1}, considerably higher than at Canary Creek. Among other factors, the higher soil water salinities at Canary Creek probably create a more stressful environment. A similar difference in *S. patens* production between the two study sites was not evident.

The year to year variations in estimated productivity noted in Table 1 are probably due to a combination of inherent sampling variability and differing climatic conditions between the two growing seasons. Long term studies are needed to interpret the relationship between annual climatic variations and production.

Table 1. Net annual aboveground primary production estimated by the peak live standing crop method and the Smalley (1958) method. Production estimates from the two sampling years and the mean production ($\bar{x}$) are presented.

	Production (g m^{-2} yr^{-1})					
	Peak Live Method			Smalley Method		
Marsh and Species	1975	1976	$\bar{x}$	1975	1976	$\bar{x}$
CANARY CREEK MARSH						
Spartina alterniflora (tall)	893	1176	1035	1434	1539	1487
Spartina alterniflora (short)	508	558	553	561	746	654
Spartina patens	618	720	669	1136	1158	1147
Distichlis spicata	552	480	516	922	648	785
BLACKBIRD CREEK MARSH						
Spartina alterniflora (short)	702	601	652	1143	688	916
Spartina patens	779	674	727	1473	705	1089
Phragmites australis	2046	1719	1883	3664	2215	2940

Mean annual values for % ash, % carbon and % nitrogen of the aboveground live, dead and surface litter components are presented in Table 2. For each species, the % ash of the litter component appears to be consistently higher than the other components. This may be due to incomplete washing of sediment from this partially decomposed material. No consistent trends in the mean annual % carbon data were observed. In contrast, for all species, except *S. patens,* the mean annual % nitrogen levels of the standing live component were highest and the standing dead levels lowest, with the litter at intermediate levels. This suggests that upon senescence and death of the live plant, nitrogen-containing compounds are leached as dissolved materials and/or translocated to belowground plant parts, resulting in decreased nitrogen levels within the dead plant component. As the standing dead and decomposing plants become flaccid and fall to the marsh surface, microbial colonization may contribute to the increased nitrogen levels. Similar trends utilizing litterbags to document decomposition of marsh angiosperms have been noted (Odum and de la Cruz 1967; Frasco and Good 1982).

When these % composition data were studied for seasonal trends, no consistent patterns were found throughout the 22 month study period, except for % nitrogen of the standing live component. Relative nitrogen content was at a peak during the spring sampling intervals for each species except *P. australis* (Table 3). In Delaware this spring peak coincides with the period of rapid aerial growth. Generally, there was a steady decline in % nitrogen levels until a minimum was reached at the end of the growing season, although some exceptions were noted. Squires and Good (1974), studying a New Jersey *S. alterniflora* marsh, present similar results showing levels of crude protein to be highest during the spring growth period with minimum levels during the fall.

Absolute amounts of carbon and nitrogen present in the aboveground standing live, standing dead and litter pools, over two growing seasons for short *S. alterniflora* at Canary Creek, are shown in Figs. 2 and 3, respectively. Although not presented,

Table 2. Mean annual ash, carbon and nitrogen percentages of the aboveground standing live, standing dead and litter components. Each value is the mean ($\bar{x}$) and one standard error of the mean (S.E.) for all sample interval averages (n) obtained throughout the study period.

Marsh and Species	Sampled Component	Ash %		Carbon %		Nitrogen %	
		$\bar{x}$ (S.E.)	n	$\bar{x}$ (S.E.)	n	$\bar{x}$ (S.E.)	n
CANARY CREEK MARSH							
Spartina alterniflora (tall)	Live	11.7(0.5)	16	41.0(0.9)	14	1.52(0.16)	14
	Dead	11.3(0.8)	18	41.3(0.6)	16	0.98(0.04)	16
	Litter	12.2(0.7)	15	41.9(0.4)	16	1.20(0.09)	16
Spartina alterniflora (short)	Live	11.4(0.4)	15	41.6(0.6)	13	1.23(0.09)	13
	Dead	11.9(0.1)	17	41.2(0.7)	16	0.91(0.05)	16
	Litter	12.1(0.8)	16	42.1(0.6)	15	1.14(0.10)	15
Spartina patens	Live	6.3(0.3)	13	43.8(0.8)	13	0.89(0.09)	13
	Dead	5.9(0.4)	17	45.1(0.8)	16	0.67(0.03)	15
	Litter	7.6(0.7)	15	44.8(0.6)	15	0.98(0.05)	15
Distichlis spicata	Live	5.8(0.3)	13	44.2(0.9)	13	1.22(0.14)	12
	Dead	5.9(0.3)	17	44.5(0.5)	17	0.86(0.05)	17
	Litter	10.6(1.1)	15	42.7(0.5)	15	1.15(0.28)	15
BLACKBIRD CREEK MARSH							
Spartina alterniflora (short)	Live	9.2(0.5)	13	42.8(0.8)	14	1.51(0.24)	14
	Dead	10.4(0.9)	17	42.8(0.8)	16	0.98(0.04)	16
	Litter	15.8(2.0)	17	39.4(1.2)	16	1.42(0.05)	16
Spartina patens	Live	6.1(0.3)	12	44.3(1.0)	12	0.94(0.12)	12
	Dead	6.4(0.6)	18	45.7(0.5)	18	0.80(0.04)	18
	Litter	8.4(0.6)	16	44.2(0.5)	16	1.18(0.06)	16
Phragmites australis	Live	7.6(0.4)	10	42.8(0.9)	10	1.36(0.18)	8
	Dead	6.1(0.3)	16	44.6(0.5)	15	0.50(0.04)	15
	Litter	11.4(0.5)	18	41.5(0.7)	17	0.98(0.05)	17

Table 3. Seasonal variation in % nitrogen of aboveground standing live biomass. Maximum and minimum % nitrogen values and the month each value was recorded are presented. For comparisons, the mean annual % nitrogen values for this component are shown (from Table 2).

Marsh and Species	% Nitrogen Maximum (month)	Minimum (month)	Annual Mean
CANARY CREEK MARSH			
Spartina alterniflora (tall)	2.92 (March)	0.95 (June)	1.52
Spartina alterniflora (short)	2.04 (May)	0.89 (October)	1.23
Spartina patens	1.55 (April)	0.50 (October)	0.89
Distichlis spicata	1.86 (May)	0.69 (September)	1.22
BLACKBIRD CREEK MARSH			
Spartina alterniflora (short)	3.70 (May)	0.88 (September)	1.51
Spartina patens	2.08 (May)	0.64 (October)	0.94
Phragmites australis	1.83 (July)	0.67 (June)	1.36

similar trends were generally observed for the other vegetation types at both Canary Creek and Blackbird Creek. Maximum carbon and nitrogen accumulation in the live component corresponded with peak live biomass which occurred in mid to late summer. Fluctuations in the standing dead and litter components are noted but, in general, there appears to be a fairly constant supply of plant detrital material available for exchange between the marsh surface and creek waters.

BELOWGROUND PRODUCTION DYNAMICS. The maximum recorded belowground standing crops at the Canary Creek marsh were 19.3 kg m^{-2}, 12.4 kg m^{-2}, and 6.0 kg m^{-2}, for short *S. alterniflora*, tall *S. alterniflora* and *S. patens*, respectively (Table 4). At Blackbird Creek the maximum biomass for *S. patens* was 20.8 kg m^{-2}, considerably higher than at the more saline Canary Creek marsh, 17.8 kg m^{-2} for short *S. alterniflora* and 11.0 kg m^{-2} for *P. australis*. Smith *et al.* (1979), studying a salt marsh of similar geographic location, report a maximum belowground standing crop for short *S. alterniflora* of 12.3 kg m^{-2}.

No obvious seasonal trends in belowground biomass were observed. Others have shown cycles for *S. alterniflora* with peak biomass occurring in late spring/summer (Valiela *et al.* 1976; Smith *et al.* 1979). Gallagher and Plumley (1979) show some seasonal cycles, however they also present some complex and often erratic cycles. The heterogeneous distribution of be-

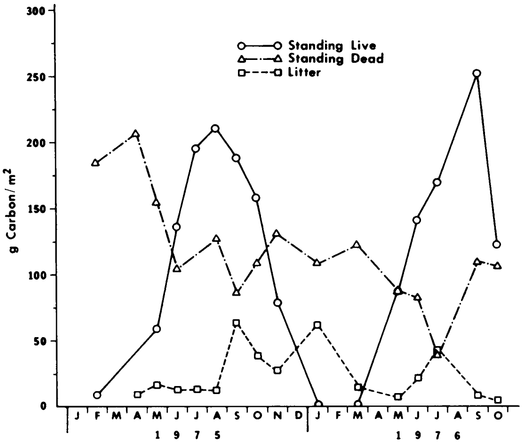

Fig. 2. Seasonal patterns of carbon accumulation (g m^{-2} of marsh) for short *Spartina alterniflora* at the Canary Creek marsh. The standing live, standing dead and litter components are presented.

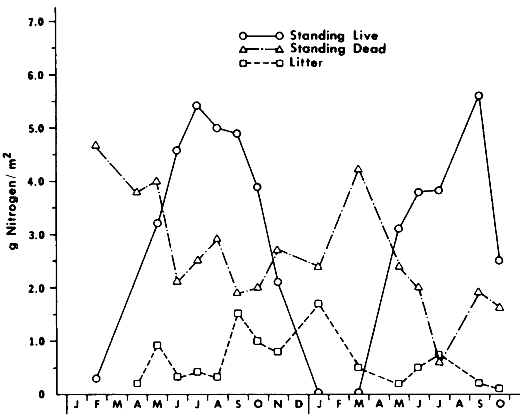

Fig. 3. Seasonal patterns of nitrogen accumulation (g m^{-2} of marsh) for short *Spartina alterniflora* at the Canary Creek marsh. The standing live, standing dead and litter components are presented.

Table 4. Estimates of maximum and minimum belowground biomass, with one standard error of the mean (S.E.) and number of cores (n), for the two years of sampling. Belowground net primary production was estimated as the annual increment (max - min) and the mean ($\bar{x}$) production determined.

		Biomass (kg m^{-2})		
Marsh and Species	Year	Max(S.E., n)	Min(S.E., n)	Production (kg m^{-2} yr^{-1})
CANARY CREEK MARSH				
Spartina alterniflora (tall)	1975	12.4(1.3, 6)	4.7(0.3, 6)	7.7
	1976	9.4(1.4, 6)	4.1(0.6, 6)	5.3
				$\bar{x}$ = 6.5
Spartina alterniflora (short)	1975	19.3(0.9, 6)	13.7(0.8, 6)	5.6
	1976	14.3(1.1, 6)	9.9(0.7, 6)	4.4
				$\bar{x}$ = 5.0
Spartina patens	1975	6.0(0.6, 3)	3.5(0.3, 3)	2.5
	1976	4.7(0.7, 3)	0.6(0.4, 3)	4.1
				$\bar{x}$ = 3.3
BLACKBIRD CREEK MARSH				
Spartina alterniflora (short)				
BC[a]	1975	8.5(0.4, 3)	3.8(1.0, 3)	4.7
	1976	9.2(1.1, 3)	4.0(0.1, 3)	5.2
				$\bar{x}$ = 5.0
OC	1975	17.8(0.8, 3)	11.2(1.2, 3)	6.6
	1976	12.1(1.4, 3)	7.8(0.4, 3)	4.3
				$\bar{x}$ = 5.5
Spartina patens	1975	20.8(0.9, 6)	13.5(1.4, 6)	7.3
	1976	12.1(2.2, 6)	7.6(0.9, 6)	4.5
				$\bar{x}$ = 5.9
Phragmites australis	1975	11.0(1.4, 6)	4.6(0.4, 6)	6.4
	1976	10.0(1.5, 6)	4.9(1.0, 6)	5.1
				$\bar{x}$ = 5.8

[a] Cores taken between aerial clumps (BC) and over aerial clumps (OC).

lowground material throughout the study areas, and incomplete or excessive washing of cores could result in variability significant enough to mask any seasonal patterns. As noted in Table 4, there was substantial variability in our biomass data, and thus the biomass and productivity estimates are interpreted with caution. Perhaps with a larger sample size and a more frequent sampling interval seasonal biomass patterns would have been observed. De la Cruz and Hackney (1977), studying a *Juncus roemerianus* Scheele tidal marsh, determined that 19 belowground core samples per monthly collection interval were needed to minimize variability.

A comprehensive review of belowground net primary production literature (Good *et al.* 1982) reveals a broad range of reported values (tall *S. alterniflora,* 0.2 to 3.5 kg m^{-2} yr^{-1}; short *S. alterniflora,* 0.6 to 6.2 kg m^{-2} yr^{-1}; *S. patens,* 0.3 to 3.3 kg m^{-2} yr^{-1}; *P. australis,* 2.8 to 3.7 kg m^{-2} yr^{-1}). Our estimates are generally higher than these previously reported values, yet seem reasonable (Table 4). However, a striking disparity was found when comparing Gallagher and Plumley's (1979) estimate of *S. patens* belowground production at Canary Creek (0.47 kg m^{-2} yr^{-1}) with our estimate (3.29 kg m^{-2} yr^{-1}). Nearly identical methods were employed. Although the Gallagher and Plumley (1979) estimate appears low when compared to our value and others (3.27 kg m^{-2} yr^{-1}, Good and Frasco 1979; 2.5 kg m^{-2} yr^{-1}, Valiela *et al.* 1976), this clearly points to the intra-marsh variability associated with sample core location and the need to provide for adequate sample size in this heterogeneous environment.

A summary of mean annual ash, carbon and nitrogen content of the belowground biomass is shown in Table 5. The % carbon and % nitrogen values are generally comparable with those reported by others (Gallagher and Plumley 1979). Smith

Table 5. Mean annual ash, carbon and nitrogen percentages of the belowground biomass component. Each value is the mean ($\bar{x}$) and one standard error of the mean (S.E.) for all sample interval averages (n) obtained throughout the study period.

Marsh and Species	Ash %		Carbon %		Nitrogen %	
	$\bar{x}$ (S.E.)	n	$\bar{x}$ (S.E.)	n	$\bar{x}$ (S.E.)	n
CANARY CREEK MARSH						
Spartina alterniflora (tall)	22.8(1.5)	18	36.5(0.9)	17	1.04(0.04)	17
Spartina alterniflora (short)	17.9(1.2)	18	39.8(0.8)	16	0.95(0.04)	16
Spartina patens	24.3(2.3)	15	37.9(1.3)	15	1.14(0.04)	15
Distichlis spicata	22.7(1.7)	18	38.0(1.0)	17	0.98(0.04)	17
BLACKBIRD CREEK MARSH						
Spartina alterniflora (short)						
BC[a]	20.6(1.9)	18	39.4(1.0)	16	1.38(0.05)	16
OC	14.6(1.5)	18	40.9(1.2)	16	1.16(0.04)	16
Spartina patens	23.0(1.5)	18	39.9(1.1)	16	1.06(0.03)	16
Phragmites australis	19.8(1.2)	16	36.1(0.7)	15	1.17(0.05)	15

[a] Cores taken between aerial clumps (BC) and over aerial clumps (OC).

et al. (1979) found a mean annual % ash of 14.5 for *S. alterniflora* belowground biomass. Our ash content values for *S. alterniflora* and the other species sampled are somewhat higher, again suggesting a less vigorous washing during sample processing or less organic accumulation. As with the aboveground component, no apparent seasonal trends in these percent elemental data were observed. However, when specifically analyzing belowground roots and rhizomes for carbohydrate storage compounds, others have shown seasonal variations, suggesting translocation as a link between aboveground and belowground primary production in *S. alterniflora* marshes (Stroud 1976; Smith *et al.* 1979; Lytle and Hull 1980).

SIGNIFICANCE OF BELOWGROUND PRODUCTION. Belowground reserves of energy may become available for exchange within the marsh-estuarine environment by several pathways. Howarth and Teal (1979, 1980) have studied the relationship between belowground biomass, its decomposition by anaerobic sulfate reduction, and energy flow in salt marshes. They suggest that the energy available from oxidation of reduced inorganic sulfur compounds (i.e., end products of sulfate reduction) represents an important mechanism for the transfer of energy from the productive belowground component to marsh-estuarine energy flow pathways. Another exchange mechanism could be the leaching of dissolved organic materials from both live and dead belowground biomass, with subsequent seepage or diffusion to marsh surface waters and creek waters. Processes by which particulate organic materials may be mobilized from underground and incorporated into estuarine food webs include: bioturbation by invertebrates or small mammals; the physical uprooting of belowground materials by waterfowl and muskrat activities (Lay and O'Neil 1942; Lynch *et al.* 1947; Smith and Odum 1981); daily erosion from unstable creek banks or more severe erosion during storms; and, the eroding of marsh peat chunks during periods of ice thaw. In addition to becoming an integral part of the marsh-estuarine trophic structure, a portion of this belowground biomass remains as peat and contributes to marsh accretion.

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