Above- and belowground emergent macrophyte production and turnover in a coastal marsh ecosystem, Georgia[1]

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Abstract

Seasonal patterns of aboveground plant mass and the depth distribution of live roots, rhizomes, and dead belowground organic matter were measured for *Spartina alterniflora* and *Spartina cynosuroides* in Georgia tidal marshes. Peak live aboveground biomass was 1.6× higher for *S. cynosuroides* than for *S. alterniflora*. Live biomass was 2.4× more belowground than aboveground for *S. cynosuroides* and 1.7× for *S. alterniflora*. Rhizomes made up 76 and 87% of live belowground biomass during the year. Mirrored patterns of biomass accumulation and loss in above- and belowground tissues during the year suggest the importance of seasonal storage and redistribution of organic matter.

Belowground production was measured with a technique that partially accounts for midseason decomposition. Total plant production was estimated to be 7,620 g dry mass·m^{-2}·yr^{-1} for *S. alterniflora* and 7,708 for *S. cynosuroides*. Belowground production was roughly 1.6× aboveground production. Turnover rates for belowground live material were 1.42·yr^{-1} for *S. cynosuroides* and 3.22·yr^{-1} for *S. alterniflora*. The fate of root and rhizome material, including the extent to which such material enters the estuarine or nearshore food webs, is not clear.

Trophic and nutrient analyses of coastal wetland ecosystems can be extremely distorted when the estimates are based on organic matter produced by aboveground portions of marsh macrophytes alone. Roots and rhizomes represent a reservoir in the energy and material cycles in which considerable energy, carbon, and nutrients are stored in estuarine wetland communities. Although the potential importance of belowground production in coastal saline and brackish marshes has been strongly suggested (Valiela et al. 1976; Stroud 1976; de la Cruz and Hackney 1977; Gallagher and Plumley 1979; Smith et al. 1979), relatively little work has actually been done to elucidate the nature of root and rhizome growth. The dearth of studies is likely attributable to a lack of uniformly satisfactory methods efficient enough for routine assessments of live and dead root and rhizome biomass. Separation of organic material from the soil matrix is difficult, and the differentiation of live and dead tissues is extremely time-consuming. Techniques suitable for forest and grassland ecosystems (Milner and Hughes 1968) do not work well in most intertidal wetlands because the soils are sticky, and direct observation of growth is precluded due to the semiaquatic, flooded condition.

The importance of organic matter produced belowground by marsh macrophytes is attested to by the magnitude of energy flow in anoxic marsh soils (Howarth and Teal 1979, 1980). In the Great Sippewissett Salt Marsh, energy flow involving inorganic reduced compounds in marsh sediments is large (as much as 2.39 W·m^{-2}·yr^{-1}), amounting to 1,800 g C·m^{-2}·yr^{-1}. That such a flow is equivalent to 885% of net aboveground primary production and 197% of root and rhizome growth (Valiela et al. 1976; Howarth and Teal 1980) clearly indicates the paramount importance of organic matter produced belowground. Future refined energy and carbon flow analyses of salt marsh ecosystems will depend on accurate measurements of the nature and form of organic matter production by the belowground portions of emergent macrophytes.

We report here static and dynamic aspects of above- and belowground biomass, turnover rates, depth profiles of root and

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rhizome material, ratios of live-to-dead plant material, and stem demography of *Spartina alterniflora* and *Spartina cynosuroides* in tidally influenced marshes along the Altamaha River. We calculated production using a technique that partially accounts for death and decomposition of plant material during the growing season. The implications of belowground primary production for energy and nutrient analyses of wetland ecosystems are discussed.

Area description and methods

Our study was done in the tidally influenced portion of the Altamaha River in coastal Georgia. Although the piedmont river watershed is the second largest on the Atlantic coast of the U.S. (37,632 km²), has a mean freshwater discharge of 382 m³·s⁻¹, and is heavily sediment laden, tidal range (2.4 m) has prevented extensive delta formation. Rather riverine sediments are mixed with offshore sands and redistributed in tidal wetlands landward of the coastal barrier islands.

The Altamaha River intersects the relatively simple coastal band of salt marsh creating brackish and freshwater tidal marshes with complex distribution patterns of vegetation. The climate in this area is nearly subtropical (yearly soil temperature range: 11°–26°C) with rainfall fairly evenly distributed through the year (133 cm).

Sampling sites (20 × 20 m) were established for nearly monospecific medium stands of the brackish water *S. cynosuroides* (31°19′48″N, 81°22′0″W; interstitial salinity 2–14‰) and the salt marsh *S. alterniflora* (31°19′02″N, 81°18′45″W; interstitial salinity 15–31‰).

Sampling was conducted about every 2 months from December 1979 to December 1980. For aboveground material, live plots were clearcut of all vegetation and the litter collected and placed into labeled plastic bags at each site: 0.25-m² plots were used for *S. alterniflora* and 0.50-m² plots for *S. cynosuroides*. In the laboratory, vegetation from each plot was sorted into the following categories: live material, four size classes—0.25 cm, 26–50 cm, 51–100 cm, and >100 cm tall; dead material on live plants; standing dead material; and surface litter. The number of culms in each size category of live material was recorded. Plant material was oven-dried at 60°C to constant mass and the mass recorded to the nearest gram.

For belowground material, five 16.3-cm-diameter cores were taken at each site (one in each clearcut plot) to a depth of 50 cm with a thin-wall, highly sharpened, stainless steel core tube. Compressed air injected from below was used to help extract the tube and its contents from the ground. Each core was then extruded in the field, cut into five 10-cm sections, and put in labeled plastic Ziploc freezer bags. Number and size of cores were largely dictated by time limitations and a desire not to compress marsh soils while coring. Cores were temporarily stored in a walk-in cold room (<6°C). Each of the sections was subsequently washed and sorted as quickly as possible. Core sections were individually placed in plastic paint cans (ca. 4 liters) and filled with a mixture of deionized water and sodium metaphosphate (to disperse the clay: Hopkinson and Dunn 1984). Core sections were shaken for 30 min on an automatic paint shaker and then washed through a set of sieves. The organic fraction retained by a 1-mm-mesh sieve was floated in a white plastic dishpan and the live roots and rhizomes separated from the dead material: living material was turgid, translucent, and creamy white to light yellow; dead material was flaccid and dull in color (deeper yellow to brown or gray). Viability stains such as tetrazolium (Stroud 1976) or chlorazol black (Valiela et al. 1976) were of little use for identifying "borderline" live or dead materials, although they did identify obviously living tissue as "living." To ensure uniformity, one of us (J.P.S.) made all the belowground separations. After the core section had been sorted, the live roots and rhizomes and the dead material were rinsed with deionized water. The materials were then oven-dried to a constant

mass at 60°C, and the mass to the nearest 0.1 g was recorded.

Aboveground productivity was determined by multiplying our measurements of seasonal biomass for each species by the seasonal production : biomass ratios calculated by Gallagher et al. (1980) for creekbank *S. alterniflora* (growing only 6 km north of our site) and by Wolf and Kinsey (unpubl. rep.) for *S. cynosuroides* (growing < 1 km west of our site).

Belowground productivity was estimated with the technique of Smalley (1958; *see* Turner 1976) which is based on summing periodic changes in the masses of live and dead material through an annual cycle. This technique underestimates production because it does not totally account for decomposition during the growing season, but it is far superior to maximum minus minimum standing crop calculations based only on dead material (Milner and Hughes 1968).

Results and discussion

Aboveground mass and demography— Statistical variation (expressed as the standard error as a percentage of the mean) for aboveground material for both species (*see* Fig. 2) averaged 17–20% for live biomass and 10–13% for dead mass. Variability was slightly less for *S. alterniflora* than for *S. cynosuroides*. These values are similar to those reported from old fields (Wiegert and McGinnis 1975) and other southeastern salt marshes (Hopkinson et al. 1978; Gallagher et al. 1980).

Live biomass exhibited clear seasonal patterns, increasing during spring and decreasing during late fall and early winter (Fig. 1). Live biomass was highest in July (733 g dry wt·m^{-2}) for *S. alterniflora* and in October (1,234 g dry wt·m^{-2}) for *S. cynosuroides*. Unlike *S. alterniflora*, *S. cynosuroides* died back completely in winter. Seasonal patterns and the level of biomass were similar to those previously reported for these species (Odum and Fanning 1973; Turner 1976; Hopkinson et al. 1978; Gallagher et al. 1980).

Aboveground dead material generally mirrored the fluctuations of the live standing crop (Fig. 1): periods of minimum standing crops of dead materials coincided
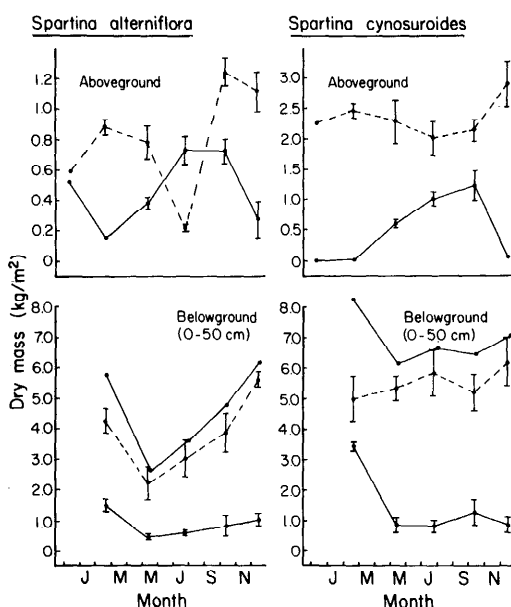

Fig. 1. Seasonal patterns of above- and belowground live and dead material standing crops for *S. alterniflora* and *S. cynosuroides* in Georgia. Each point represents a mean of five plots (December 1979, *n* = 1). Vertical lines bounded by horizontal bars represent ±1 SE. Solid lines with error bars—live material; dashed lines—dead material; solid lines without error bars—total live and dead material.

with periods of maximum live standing crops and vice versa. The mass of dead *S. cynosuroides* material was roughly 3× that of *S. alterniflora*. This difference is partly attributable to the nature of the growth form and has been observed by others (Hopkinson et al. 1978; Odum and Fanning 1973; Gallagher et al. 1980). The height and rigidity of *S. cynosuroides* culms prevent most dead material from falling onto the marsh surface where it could be periodically flooded by tidal waters. Decomposition must therefore be considerably slower (Heald 1971; McKee and Seneca 1982; Marinucci and Bartha 1982), explaining the greater year-round mass of dead material.

On an annual basis we found a very low proportion of live-to-dead material for both species. A lower live : dead ratio for *S. cynosuroides* (0.24:1) than for *S. alterniflora* (0.52:1) supports our belief that the lack of periodic flooding retards decomposition of

S. cynosuroides. Hopkinson et al. (1978) suggested that low live : dead ratios in Louisiana salt marshes were a reflection of low tidal energy and organic matter flushing. However, our ratios from Georgia are similar yet the tidal range is 8× greater. In northern marshes an apparent increase in the proportion of live-to-dead material (Turner 1976) may result from snow pressing dead material onto the sediment surface where decomposition can proceed at a faster rate due to frequent wetting and availability of nutrients.

There were substantial demographic differences between species and through the year (Fig. 2). *Spartina alterniflora* shoots grew much more densely than those of *S. cynosuroides*; *S. alterniflora* at its lowest density in late summer outnumbered *S. cynosuroides* at its highest density in late fall by almost 2 to 1. By comparison, *S. cynosuroides* was characterized by taller plants which outweighed *S. alterniflora* stems almost 2 to 1. Whereas *S. cynosuroides* died back completely in winter, *S. alterniflora* persisted year-round. The highest density of *S. alterniflora* did not coincide with its period of largest biomass, whereas the period of highest density for *S. cynosuroides* was also its period of largest biomass. Larger *S. cynosuroides* were predominant throughout most of the year with the smallest (0–25 cm) totally absent from our sampling in late spring. *Spartina alterniflora,* in contrast, was dominated by large plants only in late spring and summer, with the smallest plants always comprising some portion of the population. We do not know whether the different demographic patterns of *S. alterniflora* and *S. cynosuroides* have any adaptive significance.

Belowground mass—Both *S. alterniflora* and *S. cynosuroides* were characterized by large standing crops of belowground organic matter. In contrast to the aboveground material, we observed 3.5× and 2.3× more live and dead mass belowground for *S. alterniflora* and *S. cynosuroides* (Fig. 1). Sampling variability was also somewhat higher with the belowground components, averaging 15 and 16% for dead material and 27 and 23% (expressed as the standard error as a percentage of the mean) for live *S. alter-*

niflora and *S. cynosuroides.* The level of variability is less than that in some reports (Gallagher and Plumley 1979; Valiela et al. 1976; Smith et al. 1979), probably because we used a larger 0.02-m^2 coring device instead of the smaller, more commonly used, 0.004-m^2 core tube.

Seasonal patterns in the quantity of belowground materials were clearly evident for both marsh grass species (Fig. 1). Total material was at a minimum in late spring and at a maximum during winter, a pattern in accordance with that previously observed for *S. alterniflora* (Valiela et al. 1976; Smith et al. 1979). Gallagher and Plumley (1979) observed similar timing for the minimum quantity of macro-organic matter for *S. cynosuroides* but their period of maximum mass preceded ours by several months.

Temporal trends in dead material were similar to the total of live and dead material for *S. alterniflora* but deviated substantially during late winter for *S. cynosuroides.* On an annual basis dead material comprised 83% (3,780 g·m^{-2}) of the total belowground mass of *S. alterniflora* and 80% (5,470 g·m^{-2}) of total *S. cynosuroides* mass. The relative importance and seasonality of dead matter in the Altamaha marshes were similar to those observed in a Massachusetts *S. alterniflora* marsh but the absolute quantity of material was only about 50% of that in the northern marsh (Valiela et al. 1976). This may be indicative of more rapid decomposition of belowground dead material in the warmer marshes of the south.

The seasonal pattern of belowground live biomass (roots and rhizomes) did not mirror that of the dead mass as was observed for aboveground material, rather there was a general similarity. For both grasses, biomass reached major peaks in February followed by smaller secondary peaks in the fall. Of great interest is the temporal asynchrony between the biomass of aboveground and belowground live tissues. Belowground biomass peaked when aboveground mass was at its lowest level. The much smaller secondary peak in the belowground biomass in the fall coincided with a time of high mortality of aerial plant parts. Apparently belowground tissue mass is built up during late fall–early winter, following the period of high
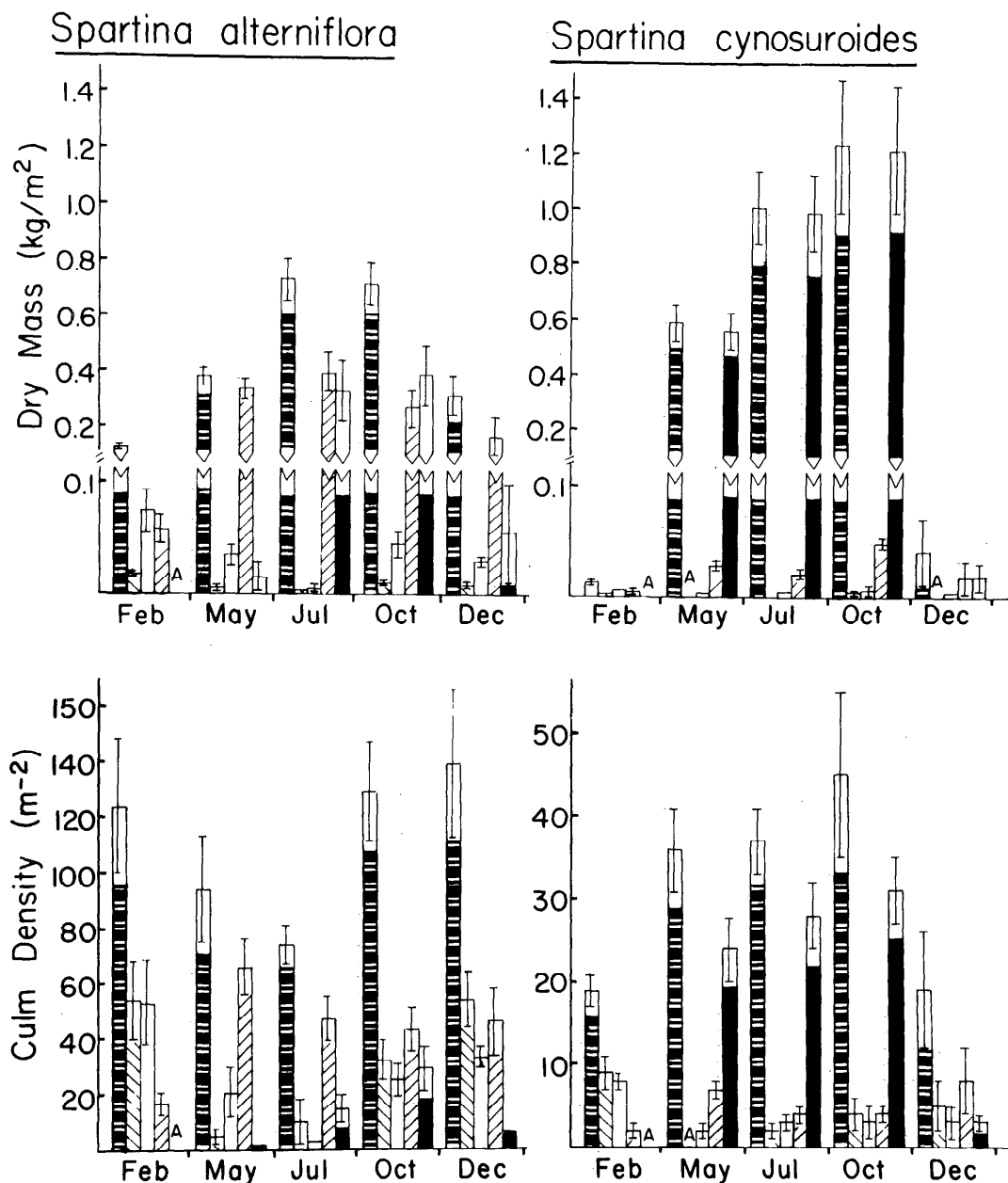
Fig. 2. Seasonal density and size structure of live culms of *S. alterniflora* and *S. cynosuroides* in Georgia. Each group of five bars for each sampling date represents the mean of five plots and (from left to right) the following categories: total (all size classes), 0–25 cm, 26–50 cm, 51–100 cm, and >100 cm. Missing bars indicate the absence of plants of this height. Vertical lines bounded by horizontal bars represent ±1 SE.

aerial mortality, and reaches its highest level just before the time of maximum shoot emergence (Fig. 2) and aboveground production. With the onset of rapid spring growth of aboveground tissues the biomass belowground promptly declines.

The patterns of biomass accumulation and loss above- and belowground during the year
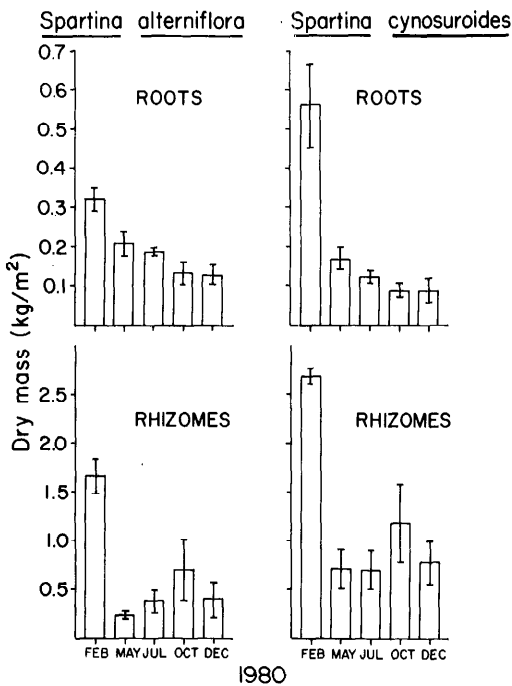
Spartina alterniflora · Spartina cynosuroides

Fig. 3. Seasonal patterns of the standing crops of belowground live roots and live rhizomes for *S. alterniflora* and *S. cynosuroides* in Georgia. Each bar is the mean of five cores (0–50 cm). Vertical bars bounded by horizontal bars represent ±1 SE.

suggest the importance of seasonal storage and redistribution of organic matter. Hull et al. (1976) and Lytle and Hull (1980*a,b*), measuring photosynthate distribution in various organs of *S. alterniflora* through the year, observed similar seasonal patterns of organic distribution. They found relatively little photosynthate incorporation in belowground tissues during summer (slow growth) but substantial transfer belowground upon the onset of aboveground tissue senescence in the fall. They noted that during the early growing season plants drew heavily on energy stored over winter in belowground tissue.

Ratios of belowground live-to-dead material were similar for the two species (0.20:1 for *S. alterniflora* and 0.26:1 for *S. cynosuroides*). The low values for both plants are indicative of the recalcitrant nature of most of the mass of dead roots and rhizomes and their slow weight-specific rate of decomposition.

Seasonal patterns of root and rhizome biomass were similar for the two species (Fig. 3): root biomass rapidly declined at the outset of the growing season while rhizome tissue declined precipitously after the midwinter peak and then reached a smaller secondary peak at the end of summer. This contrasts the pattern of a midsummer-only rhizome peak observed in the Massachusetts marsh by Valiela et al. (1976).

On an annual basis, we found that rhizomes made up by far the greatest portion of the belowground biomass. The importance of the rhizome as the overwintering storage tissue is suggested by the seasonal pattern of its relative contribution to total biomass. In both marsh grasses the percentage of total belowground tissue mass due to rhizomes increased in fall when culm mortality is highest and carbohydrate translocation to storage organs is greatest (Lytle and Hull 1980*a*). For *S. cynosuroides,* rhizomes made up from 90–94% of live material in fall; during the rapid aboveground growth in spring, the amount and proportion of rhizome tissue decreased sharply. In *S. alterniflora,* the relative amount of rhizome material fell from 78 to 53% in spring. The seasonality of root biomass, which we found to be similar in both species, may be related to the availability and demand for plant nutrients. A large investment in root biomass in winter would enable the plant to take advantage of the high ammonium concentrations in the soil in early spring (Chalmers 1977).

The greatest mass of total macro-organic material was centered 10–30 cm below the sediment surface on an annual basis (Fig. 4). In general, mass increased from the surface to 20 or 30 cm and decreased below that. *Spartina cynosuroides* roots were an exception to this pattern as the greatest quantity was in the top 10 cm. There was more live material mass close to the surface than there was dead matter. Valiela et al. (1976) found *S. alterniflora* roots to have maximum standing crops in the surface 2 cm, rhizomes had maximum standing crops 2–5 cm deep, and little or no biomass by 20 cm. They considered the subsurface maximum rhizome mass to be a protective response of the plant to ice-rafting in winter.
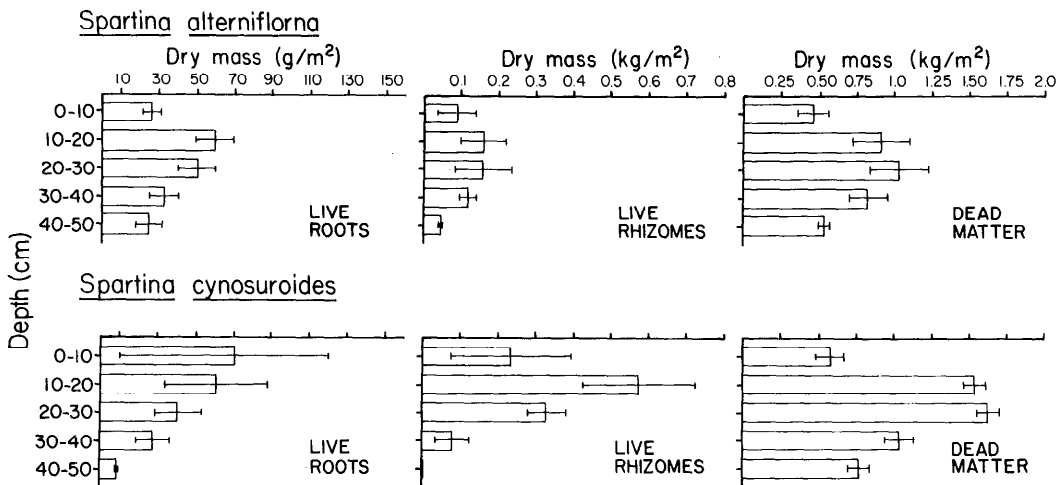
Fig. 4. Vertical distribution of rhizomes, roots, and dead matter in *S. alterniflora* and *S. cynosuroides* marshes. Horizontal lines—SE.

However ice-rafting is nonexistent in Georgia marshes and maximum rhizome biomass is still subsurface and below the region of maximum root biomass. Perhaps the depth at which rhizomes grow is related to protection from freezing temperatures in the northern marshes and to overheating, dehydration, or both in the southern marshes. We can only speculate about the factors controlling the depth distribution of marsh grass roots and rhizomes. The deeper distribution of dead material than of biomass may reflect the lower rate of microbial activity at depth in marsh sediments (Christian and Wiebe 1978; Howarth and Hobbie 1982) and hence a decreased rate of decomposition (Hackney and de la Cruz 1980). Live material may be centered nearer the surface, where remineralization and supposedly nutrient supply are greatest, but deep enough to avoid damage due to seasonal changes in microclimatology.

The depth distribution of roots and rhizomes through the year provides insight into the vertical zonation of growth. Figure 5 shows that the temporal pattern of *S. alterniflora* root biomass integrated over depth (Fig. 4) is largely attributable to changes in the 10–30-cm zone: roots at other depths exhibited no clear seasonal pattern and were uniformly dynamic. A general asynchrony of seasonal patterns of root mass with depth

indicates that growth did not occur simultaneously at all depths but at different depths at different times of year. Perhaps this is in response to seasonal changes in the depth distribution of growth inhibitors (such as H_2S, increased salinity, etc.) or in nutrient availability. The most dynamic changes in rhizome standing crop were in the top 30 cm, especially the top 20 cm. The lack of substantial changes below 30 cm may indicate that growth and mortality were in constant balance or that there was little growth there. Dead material profiles indicate the 10–40-cm zone to be the most dynamic; below 40 cm there were minor seasonal changes, reflecting more constant death of roots and rhizomes and less seasonal change in decomposition. This is not unexpected because the factors controlling decomposition such as temperature and soil moisture content (*see also* Howarth and Hobbie 1982) are more constant (Hopkinson unpubl. data) deep in the marsh soils.

Seasonal depth profiles of belowground organic matter for *S. cynosuroides* were similar to those for *S. alterniflora* and indicate that activity is confined primarily to the upper 30 cm (Fig. 6). The temporal randomness of root biomass at different depths in the sediment seen with *S. alterniflora* was not seen for *S. cynosuroides*. Rather biomass seemed to increase and decrease si-
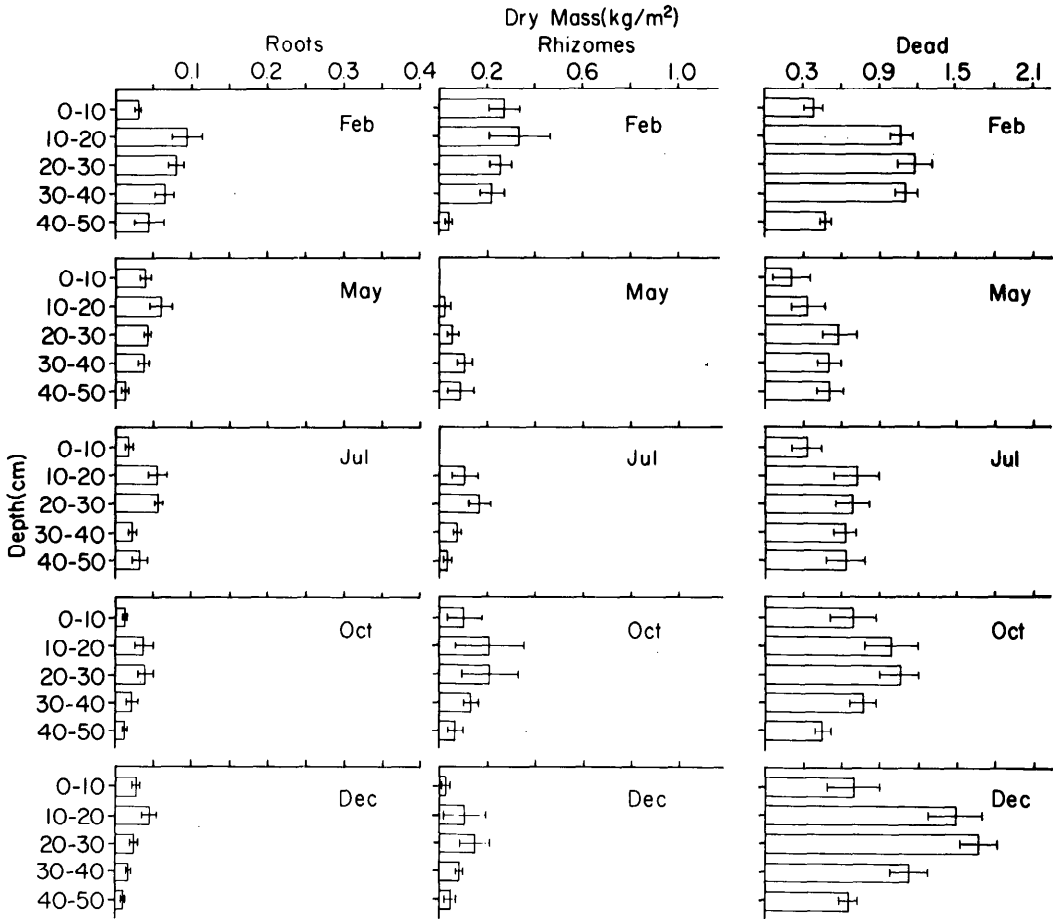
Fig. 5. Seasonal patterns of *S. alterniflora* root, rhizome, and dead matter depth distributions. Horizontal bars—SE.

multaneously at all depths above 40 cm (Fig. 6). The most active zone for rhizome tissue was between 10 and 30 cm. The large amount of dead material at all depths tended to mask any substantial changes in standing crop through the year.

Net production—Net aerial production for *S. alterniflora* and *S. cynosuroides* was 2,840 and 3,080 g dry wt·m^{-2}·yr^{-1}. The turnover rates (production/mean biomass) used to calculate these estimates were 5.09·yr^{-1} for *S. alterniflora* (Gallagher et al. 1980) and 5.35·yr^{-1} for *S. cynosuroides* (Wolf and Kinsey unpubl. rep.). This kind of calculation does not provide any information on the seasonal pattern of productivity but does

provide a reliable annual estimate of a very dynamic process. Measurements of peak standing biomass without supportive information on turnover rates underestimate true net production (Turner 1976; Hopkinson et al. 1978). Our rate of production for *S. alterniflora* is comparable to estimates similarly calculated for other southeastern marshes (Keefe 1972; Turner 1976; Hopkinson et al. 1978; Gallagher et al. 1980), while our estimate for *S. cynosuroides* is substantially higher than that calculated by Odum and Fanning (1973) and by Hopkinson et al. (1978).

Summing periodic mass changes in live and dead belowground organic matter, we
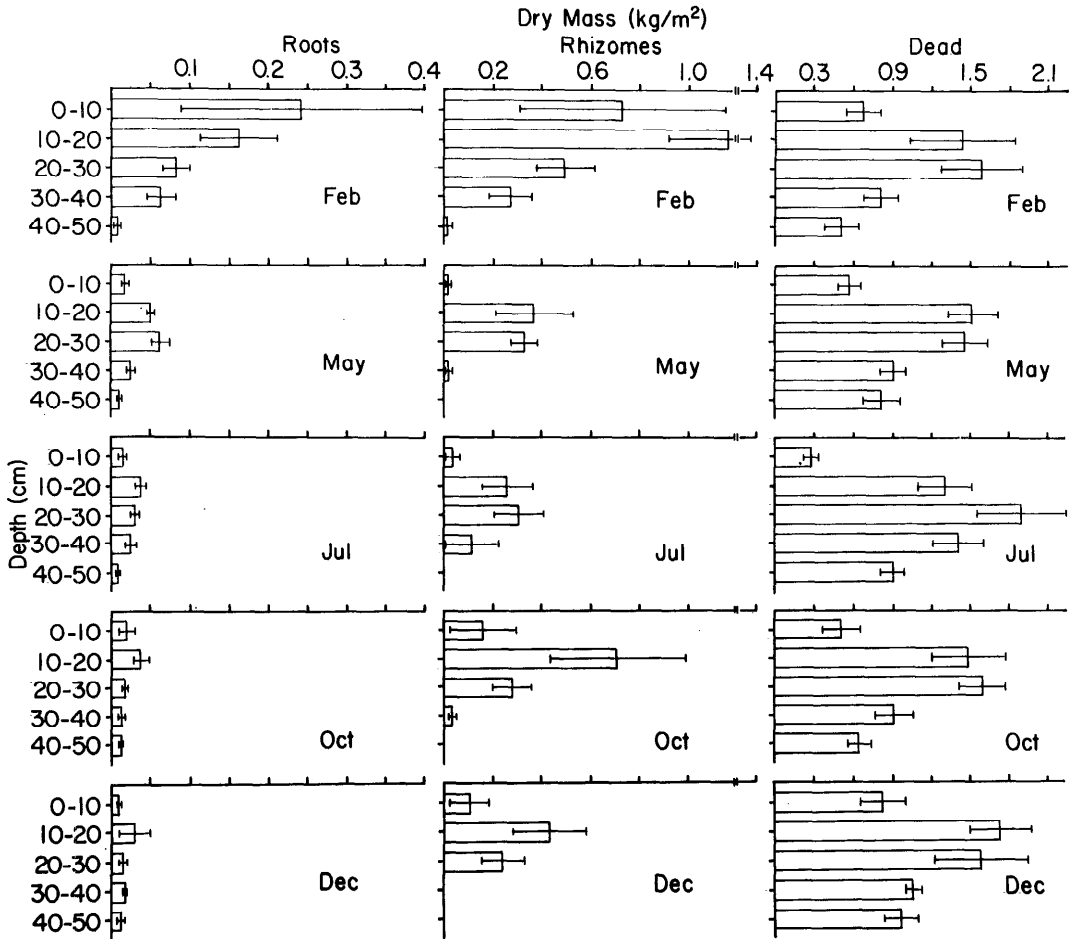
Fig. 6. As Fig. 5, but of *S. cynosuroides.*

estimate root and rhizome productivity to be 4,780 g dry mass·m^{-2}·yr^{-1} for *S. alterniflora* and 4,628 for *S. cynosuroides.* Compared to estimates in the literature (Table 1), these rates are high. Published productivity estimates for *S. alterniflora* range from 460 to 3,900 g·m^{-2}·yr^{-1} (Stroud and Cooper 1968; Livingstone and Patriquin 1981). There is only one previous published estimate of *S. cynosuroides* belowground production; this is 3,560 g·m^{-2}·yr^{-1} (Gallagher and Plumley 1979).

Our relatively high productivity values may reflect the sensitivity of the Smalley (1958) technique. Due to the difficulty and large investment of labor and time needed to conduct studies of root growth in flooded

soils, no completely satisfactory techniques have been developed to measure belowground productivity, although there are several successful methods available for aerial production (e.g. Wiegert and Evans 1964; Lomnicki et al. 1968; Hopkinson et al. 1980; Williams and Murdoch 1972; Singh et al. 1975). To date all but one estimate of belowground production in wetlands (Livingstone and Patriquin 1981) has been calculated as the difference between maximum and minimum mass of either total belowground macro-organic matter (Gallagher and Plumley 1979; de la Cruz and Hackney 1977; Smith et al. 1979) or total dead material (Valiela et al. 1976). Both techniques may give an inaccurate measure

Table 1. Published values of above- and belowground net productivity for *S. alterniflora* and *S. cynosuroides* estimated with harvest techniques.

Sampling locale	Species	Height form	Net primary production* (g dry mass·m⁻²·yr⁻¹)			Reference
			Above	Below	Total	
Nova Scotia	*S. alterniflora*	Not reported	803[1]	1,051[7]	1,851	Livingstone and Patriquin 1981
Massachusetts	*S. alterniflora*	Not reported	420[2]	3,500[4]	3,920	Valiela et al. 1976
New Jersey	*S. alterniflora*	Short	500[6]	2,300[3]	2,800	Smith et al. 1979
North Carolina	*S. alterniflora*	Short	650[5]	460[5]	1,110	Stroud and Cooper 1968;
		Tall	1,300[5]	500[5]	1,800	Stroud 1976
Georgia	*S. alterniflora*	Short	1,350[1]	2,020[3]	3,370	Gallagher and Plumley
		Tall	3,700[1]	2,110[3]	5,810	1979; Gallagher et al. 1980
Georgia	*S. alterniflora*	Medium	2,840[1]	4,780[2]	7,620	This study
Georgia	*S. cynosuroides*	Tall	2,200[1]	3,560[3]	5,760	Gallagher and Plumley 1979; Wolf and Kinsey unpubl. rep.
Georgia	*S. cynosuroides*	Tall	3,080[1]	4,628[2]	7,708	This study

* Key to productivity estimation methodology: 1—incorporating turnover; 2—Smalley 1958; 3—maximum − minimum mass of total macro-organic material; 4—maximum − minimum mass of dead material; 5—maximum − minimum mass of live material; 6—not reported; 7—maximum functional (live) biomass.

of true net production, the former more so than the latter. The latter underestimates production by the degree to which the pool size turns over. Use of the technique during the growing season requires the assumption that decomposition (assumed equal to production) occurs only when the quantity of dead material declines. In temperate or subtropical marshes, however, decomposition is a year-round process (Pomeroy and Wiegert 1981) even though mortality of live material may periodically exceed decomposition so that the mass of dead material increases. Production estimates based on the annual change in total mass must be used with extreme caution. For example, if live and dead materials have asynchronous mass patterns, with true production of 1,000 g C, then [max live (1,100 g) + min dead (100 g)] − [max dead (1,000 g) + min live (100 g)] yields a production estimate of 100. On the other hand, biomass patterns may be synchronous, in which case [max live (1,100 g) + max dead (1,000 g)] + [min live (100 g) + min dead (100 g)] equals 1,900 g C. Without knowledge of the seasonal cycles of the quantity of live and dead materials we cannot determine what these changes represent. To account for some of these shortcomings, we used the Smalley (1958) technique which is based on periodic

changes in the masses of live and dead material separately so that it partially accounts for material that grows and dies during the annual cycle.

Because different methodologies have been used to calculate belowground production (Table 1), comparisons between our results and others must be interpreted with caution. Is production in the marshes we analyzed truly higher or are our results an artifact of the technique? To facilitate comparison we have recalculated our belowground productivities by the commonly used max-min methodology (Table 2). For both grasses, productivity estimated with the Smalley technique is from 1.4 to 4.6 times higher than estimates calculated with alternative techniques. Proportional differences in estimates between techniques are not consistent from one species to the other. For *S. alterniflora,* estimates based on total material and dead material are comparable while production based on live material is substantially lower. With *S. cynosuroides,* however, estimates based on total and live material are similar while the productivity based on dead material is considerably different. Consistent differences between techniques for different species should not be expected, however, since factors such as turnover rates and seasonal patterns of bio-

Table 2. Production and turnover estimates for belowground portions of *S. alterniflora* and *S. cynosuroides*.

Production technique	Production estimate*	Turnover rate (yr⁻¹)†		
		1	2	3
S. alterniflora				
Smalley 1958	4,780	0.77	3.22	0.85
Total material‡	3,510	0.57	2.36	0.63
Dead‡	3,425	0.55	2.31	0.61
Live‡	1,048	0.17	0.71	0.19
S. cynosuroides				
Smalley 1958	4,628	0.56	1.42	0.75
Total	2,043	0.25	0.63	0.33
Dead	1,173	0.14	0.36	0.19
Live	2,412	0.29	0.74	0.39

* g dry mass·m⁻²·yr⁻¹.
† Turnover rate—production/unit weight of (1) maximum weight of live and dead material, (2) maximum live biomass, and (3) maximum dead material mass.
‡ Maximum − minimum mass over an annual period.

mass of live and dead material probably vary between species as mentioned earlier. The range of estimates in Table 2 should nearly bracket "true" net production; however, even the Smalley method probably underestimates the true belowground production.

Our calculation of *S. alterniflora* productivity from seasonal differences in total belowground organic matter is considerably higher than estimates so calculated by Stroud and Cooper (1968), Stroud (1976), Gallagher and Plumley (1979), and Smith et al. (1979). However, our estimate based on dead material changes is similar to that of Valiela et al. (1976). Our total organic matter calculation for *S. cynosuroides* is much lower than that of Gallagher and Plumley (1979). The broad range of production estimates and the lack of consistent results even with the same methods precludes the drawing of generalities concerning patterns of production, geographic variability, or species differences. Such comparisons will be impossible until considerably more work has been done on the belowground system. In an ecosystem in which detrital pathways are as important as they are in marsh ecosystems, it is quite remarkable that research in marsh production has generally omitted belowground measurements.

Ratios of production per unit biomass

presented in Table 2 suggest the presence of two organic matter pools that have considerably different turnover dynamics in marsh sediments. Both the Georgia and Massachusetts marshes are characterized by large, slowly turning over pools of dead material and smaller and more rapidly turning over pools of live material. Turnover times of live material are 3.8 times faster than for *S. alterniflora* dead matter and 1.9 times faster for *S. cynosuroides*. The slower turnover time for dead organic matter reflects the recalcitrant nature of most of the material and its generally slow rate of decomposition (*see* Howarth and Hobbie 1982).

Rates of belowground production were similar for *S. alterniflora* and *S. cynosuroides* but because the latter has a greater maximum biomass it also has a slower turnover rate. The turnover rate of live material was $3.2 \cdot yr^{-1}$ for *S. alterniflora* and $1.42 \cdot yr^{-1}$ for *S. cynosuroides*. Turnover times of dead material were less than unity for both species. Tremendous differences in productivity reported in other belowground investigations preclude rigorous comparisons of turnover rates, but in general the turnover rates of most of the dead belowground plant materials are considerably slower than those for aboveground tissues (Hopkinson et al. 1978; Valiela et al. 1976; Gallagher and Plumley 1979). A slower rate of decomposition of belowground organic matter is expected because of structural polymeric material in roots, oxygen limitation of grazing meiofauna, and a buildup of metabolites and toxins (Howarth and Hobbie 1982).

Root-to-shoot ratios (mean annual live biomass of roots and rhizomes : mean annual live aboveground biomass) are usually high in plants growing under harsh environmental conditions (Shaw 1952; Kucera et al. 1967; Shaver and Billings 1975; Valiela et al. 1976; Smith et al. 1979). Our ratios for *S. alterniflora* (1.7) and *S. cynosuroides* (2.5) are similar to comparably calculated ratios for *S. alterniflora* (1.7: Valiela et al. 1976; 1.8: Patriquin and McClung 1978; 2.4: Livingstone and Patriquin 1981) and are consistent with the hypothesis relating harshness of environmental conditions to the investment in belowground tissues by plants. Root-to-shoot ratios based

on production rather than biomass are similarly greater than unity (2.1:1—*S. alterniflora* and 1.5:1—*S. cynosuroides*). Ratios for the Georgia marshes are considerably lower than that reported by Valiela et al. (1976) for a Massachusetts marsh (8.2:1) but similar to that reported by Livingstone and Patriquin (1981) for a Nova Scotia marsh (1.6). The high root-to-shoot ratios characteristic of *Spartina* appear to be an adaptive response by the plants to harsh environmental conditions such as low nitrogen availability, waterlogged soils, anoxic soils, periodic plant inundation, high toxin concentrations, and saline water (Hopkinson and Schubauer 1984). Factors such as these act to decrease the effective uptake of water and nutrients by a unit of root surface (Shaw 1952). Consequently each unit of aboveground tissue requires a greater root surface than would be needed under more favorable conditions (Shaver and Billings 1975). Haines and Dunn (1976), Valiela et al. (1976), and Morris (1980, 1982) observed decreased root production with increased nitrogen availability.

Conclusions

Our estimates of total net primary production for *S. alterniflora* and *S. cynosuroides* (7,620 and 7,708 g dry mass·m^{-2}·yr^{-1}) are larger than any previously reported productivity values for salt and brackish marsh macrophytes based on harvest techniques. This intertidal coastal marsh system is one of the most productive ecosystems in the world, exceeding the productivity of most intensively managed agricultural crops (Odum 1971). Even so, our estimates should be considered conservative because the Smalley (1958) production technique that we used does not fully account for decomposition of dead material during the sampling interval nor does it measure above- or belowground exudate production. Our production estimate for *S. alterniflora* is 87% of that predicted by a linear regression of aboveground biomass on net primary productivity estimated by the CO_2 exchange technique (Giurgevich and Dunn 1982). This close approximation lends support to the utility of our harvest-based technique. Apparently the limitations of the Smalley

(1958) technique are not severe for these wetland ecosystems.

For both species, belowground organic matter production exceeded aerial production (68 and 60% of total production for *S. alterniflora* and *S. cynosuroides*). This result is in general agreement with observations from other belowground investigations in wetlands (Valiela et al. 1976; Smith et al. 1979; Gallagher and Plumley 1979; Livingstone and Patriquin 1981; de la Cruz and Hackney 1977). However, some of our results strongly contrast with the observations of Livingstone and Patriquin (1981); we inferred (as did Valiela et al.) that there was substantial belowground turnover during the growing season and that root production constitutes a minor fraction of belowground production.

Presently the fate of root and rhizome material, including the extent to which such material enters the estuarine or nearshore food webs, is not clear. Except for the small quantity of organic matter added to marshes along with sediment (Armentano and Woodwell 1975), the quantity of sediment organic matter is not increasing, which indicates that an amount of material equal to primary production is lost from the system annually. However, the annual carbon budget for the Duplin River marshes of Georgia (Pomeroy and Wiegert 1981; Hopkinson and Hoffman in press) indicates that only about 50% of marsh macrophytic net production is metabolized to CO_2 and CH_4. The balance is not totally accounted for. There is some evidence that a large amount is flushed from the marsh and then hydrologically exported from the Duplin River (Pomeroy and Wiegert 1981), but Haines (1977) strongly challenged the idea that substantial quantities of the exported carbon are of *Spartina* origin. Even if culm detritus is tidally exported, the contribution from the belowground organic pool is probably limited due to restricted water exchange in marsh soils, leaving its fate uncertain at best. The carbon and energy budgets for the Great Sippewissett Marsh in Massachusetts are more in balance with primary production (Howarth and Teal 1980). Organic carbon produced by plants is largely lost as CO_2 while plant energy content is transferred to

reduced inorganic sulfur compounds (Howarth and Teal 1979), some of which is exported (Howarth and Teal 1980; Howarth et al. 1983). However budgets for both systems are erroneous to the extent to which net belowground primary production has been underestimated. Our results indicate that the error could be substantial for the Georgia salt marsh system, as the organic carbon budget (Pomeroy and Wiegert 1981) is based on productivities calculated using a technique of maximum minus minimum sediment macro-organic matter mass (Gallagher and Plumley 1979).

Our study points out the difficulty of measuring belowground production and the need to find an appropriate and standardized technique to facilitate intercomparison of marsh systems. All methodologies that have been used are extremely laborious and time-consuming, especially the techniques which entail separation of live material. The technique of maximum minus minimum total macro-organic matter may be the most straightforward, but the resulting production estimate does not necessarily bear any relation to true production. Without a priori information on seasonal cycles of living and dead material, results with this technique should be interpreted cautiously. A technique that may prove useful is to separate only live rhizomes from the total macro-organic matter and include the roots with the dead material. As about 80% of the total time required to separate live and dead materials was used in separating roots, a considerable saving could be realized with this approach. By lumping roots with dead material and then applying the Smalley (1958) production technique, we found total belowground production to be only slightly underestimated (4.1%) for *S. alterniflora.* Because root biomass is so much less than rhizome or dead material mass in Georgia, its inclusion with dead material is not likely to influence production estimations substantially even if seasonal biomass patterns are completely asynchronous.

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