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Relationship Between Aboveground and Belowground Biomass of *Spartina alterniflora* (Smooth Cordgrass)

MICHAEL F. GROSS
College of Marine Studies
University of Delaware
Newark, Delaware 19716

MICHAEL A. HARDISKY
Biology Department
University of Scranton
Scranton, Pennsylvania 18510

PAUL L. WOLF
Biology Department
Lebanon Valley College
Annville, Pennsylvania 17003

VYTAUTAS KLEMAS
College of Marine Studies
University of Delaware
Newark, Delaware 19716

ABSTRACT: Aboveground and belowground biomass of *Spartina alterniflora* were harvested during the period of peak aerial biomass from six sites along a latitudinal gradient ranging from Georgia to Nova Scotia. An equation relating live aboveground to live belowground biomass for short-form plants was formulated using data collected in Delaware marshes. When data from the other sites were substituted into the equation, the mean live belowground biomass it predicted was within 15% of the value determined by harvesting at four of the five sites. At all sites, short-form plant live belowground biomass was concentrated in the upper 10 cm. Dead belowground biomass was located mostly in the top 15 cm in southern marshes, but was more evenly distributed with depth in northern marshes. Results were more ambiguous for tall-form plants, probably because of greater spatial variability in biomass distribution, and greater seasonal biomass dynamics.

Introduction

Spartina alterniflora is the dominant grass in many North American salt marshes. It often occurs as distinct height forms (Valiela et al. 1978; Niering and Warren 1980) generally regarded as being genetically similar (Mooring et al. 1971; Shea et al. 1975; Valiela et al. 1978), although results of some studies suggest genetic differences (Bertness 1988; Gallagher et al. 1988). There have been many studies of the biomass and productivity of this species (Keefe 1972; Turner 1976; Schubauer and Hopkinson 1984; Dame and Kenny 1986; among others) using traditional harvesting techniques and tagging studies. The belowground biomass component has received only limited attention, primarily because of the difficulty associated with sampling (Good et al. 1982). In a 1982 review of the literature, Good et al. found great disparity among belowground biomass/productivity estimates. Some of the observed variability is real, but some is likely the result of small core diameters, and inconsistent processing and sorting techniques among investigators. Because the quantity of belowground biomass is often much larger than the amount of aboveground material, measurements of belowground biomass are essential if accurate estimates of productivity are to be made.

An additional incentive for assessing the belowground component has come from evidence that the root material may be involved in the formation and release of sulfur gases or methane, either by providing a carbon source for microorganisms (de

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Mello et al. 1987; King 1988) or by serving as a conduit for transport of microbially produced gas between the atmosphere and the water-logged substrate (Dacey and Klug 1979; Cicerone and Shetter 1981; Seiler et al. 1984; Sebacher et al. 1985; Chanton et al. 1989; Schutz et al. 1989; Wilson et al. 1989). Knowledge of both the amount and vertical distribution of belowground biomass will be necessary to better understand the role of roots in the formation and atmospheric flux of these gases. Additionally, roots may contain substances such as dimethylsulfoniopropionate (DMSP; Dacey et al. 1987), a precursor to dimethyl sulfide (DMS). DMS may account for as much as half of the biogenic sulfur entering the atmosphere (Dacey and Blough 1987). *S. alterniflora* has been shown to be a major source of DMS release from salt marshes (Cooper et al. 1987; Dacey et al. 1987; de Mello et al. 1987). One objective of the National Aeronautics and Space Administration's (NASA) Biospherics Research Program, which funded the research described here, is to use remote sensing to measure gas flux from biogenic sources. An important step toward achieving this goal would be an ability to quantify root biomass remotely.

Recently, nondestructive estimates of *S. alterniflora* aboveground biomass and productivity have been made using remote sensing for marshes throughout eastern North America, based on the strong correlation between green biomass and its reflectance of red and near-infrared wavelengths of light (Hardisky et al. 1984; Gross et al. 1987; Bartlett et al. 1988). Remote sensing offers the advantages of being rapid, noninvasive and synoptic. Biomass estimates can be made for a particular area for an indefinite amount of time since the vegetation is not harvested and the site is not trampled or otherwise damaged. However, it is not possible to use optical remote sensing techniques to assess belowground biomass directly because visible and near-infrared light do not penetrate soil. If a relationship can be established between the aboveground and belowground biomass components, the amount of belowground biomass could perhaps be inferred from estimates of aboveground biomass made using remote sensing.

This study had two objectives: (1) harvest extensively in a Delaware marsh to develop equations relating aboveground biomass to belowground biomass and to investigate the seasonal dynamics of belowground biomass, and (2) collect additional samples in marshes from Georgia to Nova Scotia to examine latitudinal variations in the distribution of belowground biomass with depth and to evaluate the predictive accuracy of the Delaware equations. By using larger coring tubes than previous investigators, and by having one group of people process all of the samples, our data should permit a better comparison of differences among sites than is possible using literature values.

Materials and Methods

The primary test site (DE) was the Great Marsh, located at Lewes, Delaware, near the mouth of the Delaware Bay (Fig. 1). To assess the effect of coring tube size on the variability of the belowground biomass estimate, a homogeneous area of short-form (hereafter referred to as short) *S. alterniflora* (defined as being less than 90 cm tall at peak height) was divided into 121 contiguous 25 cm by 25 cm subplots. Using a randomized design, one core from each subplot was taken using a stainless steel coring tube either 3.7 cm (100 subplots), 10.2 cm (13 subplots), 16.5 cm (5 subplots), or 21.5 cm (3 subplots) in diameter, such that the total area sampled using each coring tube was approximately 0.11 m^2. All sampling was done during one day in July 1987. Each coring tube had a stainless steel flange welded to the top, and two horizontal stainless steel handles used to twist the tube into the substrate. After being driven into the soil, a 3 cm-thick wooden disk with a 0.5 cm-thick rubber sheet glued onto one side was fastened to the flange (rubber side down) using C-clamps to create an airtight seal. While one individual pulled the coring tube upward by the handles, another individual injected pressurized air into the substrate underneath the cores to aid in core extraction. This was accomplished using a 1 m long, 0.5 cm diameter stainless steel tube with a perforated tip, attached to a pressurized (20.7×10^6 N m^{-2}, or 3,000 psi) air tank. Some distortion/compaction of the cores was observed when the two smallest coring tubes were used. Preliminary sampling had indicated that little macroorganic matter was located below 30 cm in short-form areas, or below 50 cm in tall-form areas. Consequently, core material from the Great Marsh site that was extracted from depths greater than 30 cm was discarded. Cores were cut in the field into 0–5 cm, 5–10 cm, 10–15 cm, 15–20 cm, and 20–30 cm sections using a knife. This was done to facilitate processing of the root material, and to measure the vertical distribution of belowground biomass. Substrate was removed from the core sections by washing the cores over a 2 mm-mesh sieve. Belowground materials retained by the mesh were separated into live and dead fractions and dried at 60°C to constant mass. Material was considered live if it was white and turgid. The mean, standard error (SE), and coefficient of variation (c.v.) of the estimate of belowground biomass resulting from cores of each diameter were computed and compared.

Within the Great Marsh, five permanent plots

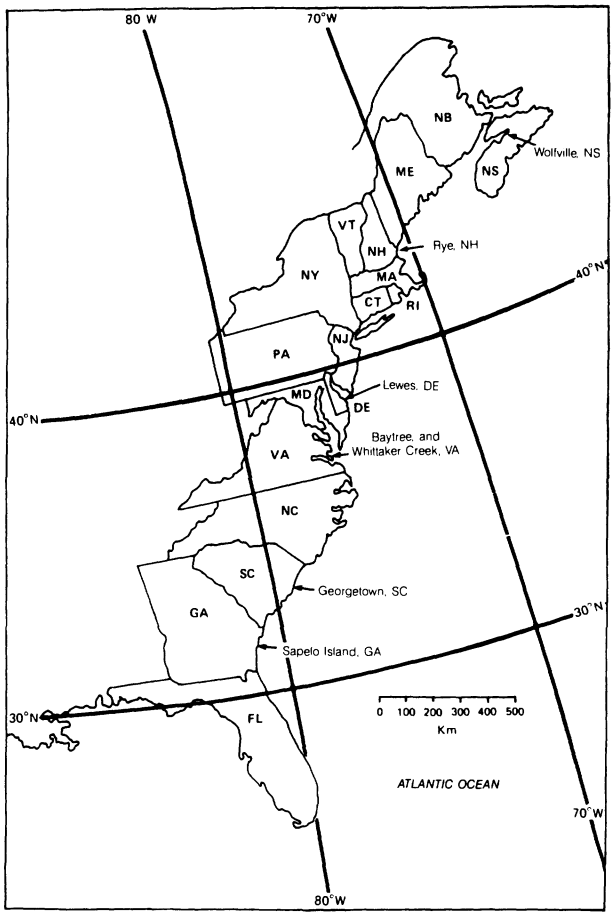

Fig. 1. Location of the six sampling sites.

of short *S. alterniflora*, and three permanent plots of tall-form (greater than 90 cm tall at peak height; hereafter referred to as tall) plants were sampled in June, July, August, September, and November 1987, and March 1988 to provide information on the seasonal pattern of live and dead aboveground and belowground standing crop biomass. The plots were 10 m^2 in size and were distributed throughout the 580-ha marsh. One site, in a low salinity area, contained only tall plants. At two other sites, both tall and short plants were sampled. At the other sites, only short plants were sampled. On each date, a different portion of the plot was harvested. One sample was gathered per plot per date.

Additional samples (58 short, 23 tall) were taken in the summers of 1987, 1988, and 1989 from sites in the marsh that were not sampled seasonally. An effort was made to obtain samples from as many parts of the marsh as possible, and to have the samples encompass the range (as determined by visual inspection) of biomass, height, and stem density found in the marsh. The number of samples acquired on each sampling trip was governed by the desire to obtain equal numbers of samples from each summer month, and the ability to process the belowground parts of the samples within two weeks.

At each plot, mean canopy height, defined as distance from the substrate surface to the top of most of the stems, was measured. All aboveground biomass from an area 0.25 m^2 in size was harvested. Then, three cores were obtained from within the 0.25 m^2 square. The results of the preliminary study on the effects of core tube diameter on the belowground biomass estimate suggested that 16.5 cm diameter cores were large enough to overcome the inherent spatial variability in the distribution of root material in the short plants. Visual observation, and other preliminary coring, indicated that biomass in tall plots was unevenly distributed over a larger spatial area than in short plots. Therefore, the 16.5 cm coring tube was used for short plots, and the 21.5 cm tube for tall plots. The decision to obtain three cores per plot was based on other preliminary data indicating that little decrease in the c.v. of the belowground biomass estimate was achieved by extracting more than three cores from a plot. The coring technique was identical to that described above, except that in tall plant areas, belowground material extracted from depths greater than 50 cm was discarded, and the cores were cut into 0–10 cm, 10–20 cm, 20–30 cm, and 30–50 cm sections. In the laboratory, belowground materials were processed as described above. Aerial tissues were separated into live leaves, live stems plus inflorescences, and dead material, and the number of live stems was counted. All biomass components were dried at 60°C to constant mass.

Marshes in five other geographical areas were selected for sampling based on latitude, existence of historical data compiled by other investigators, accessibility, and the availability of laboratory space for processing of samples (Fig. 1). Samples were collected from marshes on Sapelo Island, Georgia (GA), marshes adjacent to the Belle W. Baruch Institute for Marine Biology and Coastal Research, South Carolina (SC), the Whittaker Creek and Bay Tree marshes near the York River, Virginia (VA), marshes near Rye, New Hampshire (NH), and from Bay of Fundy marshes near Wolfville, Nova Scotia (NS). Vegetation from each site was sampled in July or August, close to the period of peak aboveground biomass. Virginia sites were sampled in 1986–1987, Georgia and South Carolina in 1987, Nova Scotia in 1988, and New Hampshire in 1989. Only the 16.5 cm and 21.5 cm coring tubes were utilized. Samples were processed as described above, and an attempt was made to collect samples that spanned the range of biomass resident at each site, as estimated by visual inspection. Most of the sampling effort focused on the short-height form, since most

TABLE 1. Effect of core diameter on measured belowground biomass.[a]

	Core Diameter (cm)			
	3.7 n = 100	10.2 13	16.5 5	21.5 3
Live	1,060 (0.59)[b]	1,383 (0.22)	1,629 (0.08)	1,759 (0.11)
Dead	7,220 (0.23)	8,482 (0.06)	8,096 (0.09)	9,547 (0.10)

[a] Biomass values are dry biomass means expressed in g m^{-2}.
[b] Number in parentheses is the coefficient of variation.

euhaline marshes in eastern North America are dominated by short *S. alterniflora.*

Results

The study to investigate the effect of various core sizes on estimates of belowground biomass indicated that the lowest estimates of both live and dead belowground biomass were generated from data from the 3.7 cm diameter cores (Table 1). Also, biomass estimates from the smallest cores exhibited the largest c.v. Live belowground biomass estimates seemed to be approaching an asymptote for the 16.5 cm and 21.5 cm diameter cores.

The data from the five short DE seasonal plots show that there were no significant seasonal differences in live belowground biomass or dead belowground biomass (Fig. 2). Since this paper focuses on belowground biomass, aboveground data are included for informational purposes only and have not been statistically analyzed.

The seasonal changes in biomass were much more dramatic in the tall plant plots (Fig. 3). Live belowground biomass was lowest in June and July, and highest in September and November. It exhibited a large and significant decrease between November and March, returning to the June level. The live belowground maximum was about three times as large as the live belowground minimum. This is in contrast to the short plants, where there was no significant difference in live belowground biomass from month to month.

Correlation coefficients (r) between DE short plant aboveground and belowground biomass components were computed for samples spanning a number of time intervals (e.g., May through October, June through September, June through August, etc.). The correlation coefficients for samples collected from June 10 through September 10 are listed in Table 2. When samples collected on dates either earlier than June 10 or later than September 10 were included in the database, the correlations between aboveground and belowground biomass became weaker, although gradually at first (data not shown). For example, expanding the time window to include samples gathered from June 10 to October 1 resulted in an average drop in r of about 0.02, but a further reduction of 0.08 resulted when samples from late May and early June were included. Throughout the rest of the paper, the results derived from using the mid-June through mid-September samples will be emphasized. There were very strong correlations between all aerial biomass components and live belowground biomass. Note in particular that ln(live aboveground biomass) and ln(total aboveground biomass) exhibit the highest correlations with ln(live belowground biomass). Although significant, correlations were weak between aboveground biomass and dead or total belowground biomass. For tall plants, all correlations were very weak (data not shown), regardless of how the data were transformed. The strongest correlation was between ln(leaf biomass) and ln(live belowground biomass): r = 0.51 for 29 samples. Figure 4 shows ln(live belowground biomass) plotted against ln(live aboveground biomass) for all DE samples collected between June 10 and September 10. Note that most of the tall plot values do not overlay the short plot values.

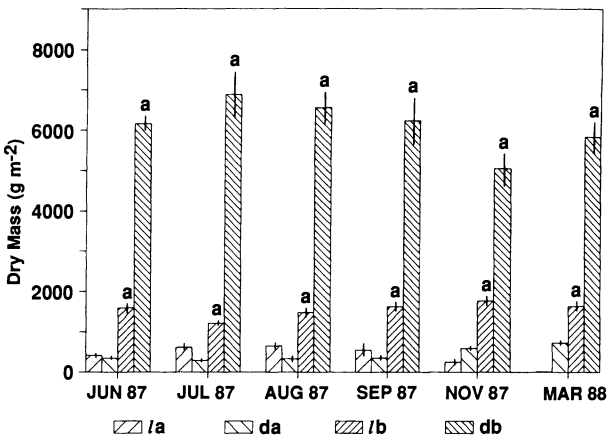

Fig. 2. Seasonal pattern of mean live aboveground (la), dead aboveground (da), live belowground (lb), and dead belowground (db) biomass for five short-form plots harvested in Delaware. Vertical lines represent one SE of the mean. Similar letters above columns within a belowground biomass category indicate no significant difference in the mean (Duncan's multiple range test, p = 0.05).

Characteristics of plants from all sites are summarized in Table 3. Notable among-site short plant differences include greater values for height and all aboveground biomass parameters for the GA samples, and a very low, dead aboveground biomass value for NS samples. Stem density was lower at the three southernmost sites than for the DE, NH, and NS samples. Dead belowground biomass was greatest for DE and NH samples, and least for NS samples. Mean live belowground biomass was

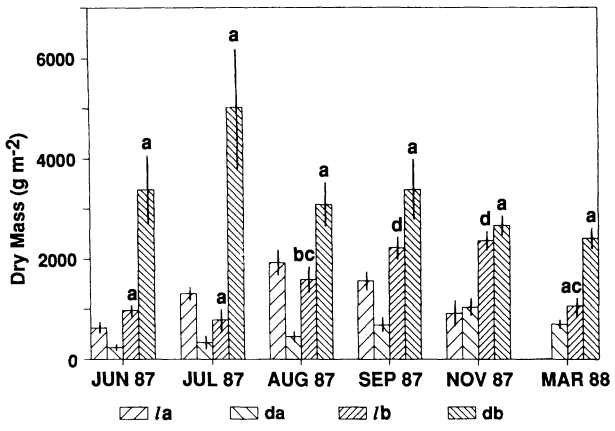

Fig. 3. Seasonal pattern of mean live aboveground (la), dead aboveground (da), live belowground (lb), and dead belowground (db) biomass for three tall-form plots harvested in Delaware. Vertical lines represent one SE of the mean. Similar letters above columns within a belowground biomass category indicate no significant difference in the mean (Duncan's multiple range test, p = 0.05).

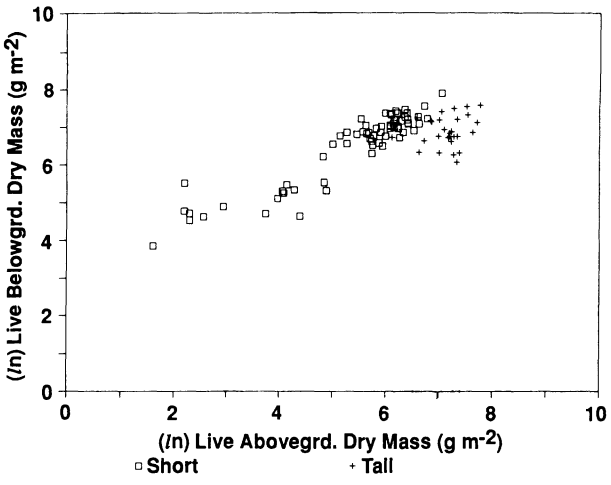

Fig. 4. Relationship between ln(live aboveground) and ln(live belowground) biomass for short-form (n = 68) and tall-form (n = 29) DE samples collected between June 10 and September 10.

remarkably similar at all sites, as was mean live aboveground (except for GA). Root : shoot ratios were smallest in GA and greatest in DE. In comparison to short plant plots, tall plots generally had similar live belowground biomass, lower stem densities, lower dead belowground biomass, and lower root : shoot ratios, but higher live aboveground biomass. Tall data from non-DE sites have been grouped together because of the small number of samples processed at each site (n = 3 to 10).

For the short plants collected from all locations between mid-June and mid-September, the c.v. between the belowground biomass estimates computed from each of the three cores per plot was about 20% for the live and dead components, and about 15% for the total (live plus dead) belowground biomass measurement (Table 4). The c.v. from the tall plants was about 35% for live and 30% for dead and total.

Equations to predict live belowground biomass from various aboveground components, formulated from short plant samples collected in Delaware from mid-June through mid-September, appear in Table 5. When aboveground biomass data from the other five study sites were substituted into the DE live aboveground or live leaf equations, the mean predicted live belowground biomass was within 15% of the measured value determined by harvesting for the SC, VA, NH, and NS short plant samples (Table 6). The equations resulted in large overestimates of live belowground biomass for the GA samples. The equation based on live leaf biomass was the most accurate predictor of live belowground biomass at four sites, resulting in prediction errors of 7% or less for the SC, VA, NH, and NS samples. Mean live belowground biomass of tall plants was poorly predicted (errors of 30% or greater) regardless of what type of predictive equation was used (short plant equations, tall plant equations, or equations based on both height forms combined). Tall plant equations and their predictive accuracies are not shown due to the poor correlations between tall plant aboveground and belowground biomass.

TABLE 2. Pearson correlation coefficient[a] between aboveground and belowground biomass components for DE short-form samples (harvested from June 10 through September 10).[b]

Belowground	Aboveground				
	ln(Live)[c]	ln(Leaves)	ln(Stems)	ln(Dead)	ln(Total)
ln(Live)	0.93	0.92	0.88	0.90	0.93
ln(Dead)	0.34	0.30	0.42	0.31	0.33
ln(Total)	0.49	0.45	0.55	0.45	0.48

[a] significant at p = 0.01.
[b] n = 68.
[c] Live aboveground = leaves + stems.

At all sites, the greatest amount of live belowground biomass in the short plants was located in the top 10 cm (Fig. 5), and decreased with depth after that. In SC and VA, the proportion found below 10 cm was particularly small, and the largest amount was found in the top 5 cm. Depth profiles of dead belowground biomass show a different pattern (Fig. 6). The three southernmost sites (GA, SC, and VA) show similar profiles, with most of the biomass located in the top 15 cm. At the three northernmost sites (DE, NH, and NS), the profile is strikingly different, with dead biomass being minimal in the top 5 cm, and remaining at high, fairly constant levels with depth between 5 and 30 cm. Tall plant biomass depth profiles are not pre-

TABLE 3. Characteristics of samples collected from six sites.[a]

	Short						Tall	
	GA	SC	VA	DE	NH	NS	DE	Other[b]
n =	15	16	23	68	10	23	29	30
Aboveground								
Height (cm)	67	52	45	37	39	43	121	109
	(8)	(5)	(2)	(2)	(5)	(2)	(6)	(8)
Leaves	345[c]	160	216	235	185	186	761	342
	(38)	(12)	(24)	(20)	(30)	(14)	(46)	(35)
Stems	306	163	182	120	80	165	588	571
	(54)	(18)	(23)	(10)	(12)	(12)	(46)	(86)
Live	651	323	398	356	266	351	1,349	912
	(89)	(29)	(46)	(29)	(41)	(21)	(82)	(119)
Dead	459	282	284	291	261	64	393	378
	(70)	(30)	(24)	(25)	(45)	(12)	(36)	(56)
Stem density	331	565	647	1,038	1,139	1,029	314	373
(stems m^{-2})	(93)	(59)	(60)	(100)	(230)	(100)	(35)	(48)
Belowground								
Live	831	765	893	913	754	875	1,044	832
	(77)	(44)	(53)	(64)	(127)	(51)	(77)	(55)
Dead	3,421	3,253	4,320	5,925	6,549	1,960	2,968	1,694
	(233)	(403)	(445)	(256)	(682)	(152)	(476)	(264)
Ratios of Belowground to Aboveground								
Live below/	1.42	2.55	2.64	3.71	3.16	2.59	0.84	1.18
(leaves + stems)	(0.11)	(0.19)	(0.22)	(0.44)	(0.44)	(0.13)	(0.08)	(0.12)
Live below/	2.55	4.99	4.79	5.94	4.70	4.96	1.45	2.84
(leaves)	(0.18)	(0.30)	(0.38)	(0.77)	(0.76)	(0.26)	(0.11)	(0.25)

[a] Values are means, with one SE of the mean in parentheses.
[b] Other tall includes tall plants harvested from GA, SC, VA, NH, and NS.
[c] Units of biomass are g dry mass m^{-2}.

sented because the small number of samples processed per site does not permit meaningful between-site comparisons.

Discussion

The importance of using large core diameters is evident from our study utilizing coring tubes of four different sizes (Table 1). The variability in measured biomass in cores of the same size is reflected in the c.v. The high c.v. for live biomass measured using data from the two smallest coring tubes is probably a reflection of heterogeneity in live biomass on a small spatial scale resulting from the occurrence of stems in clumps, rather than being evenly spaced. In short plant areas, the larger diameter (16.5 cm and 21.5 cm) cores sample an area large enough to overcome the "clump effect," and therefore exhibit a low c.v. The similarity between the c.v. values obtained using the 16.5 cm tube vs. the 21.5 cm tube indicates that the 16.5 cm tube is adequate for sampling short plants. A danger in using small diameter coring tubes is that inaccurate estimates of biomass are likely unless the investigator ensures that the proportion of cores taken over culms vs. the proportion taken between culms is representative of the marsh.

The c.v. for live biomass measurements made from three cores per plot (Table 4) suggests that the real average variability in live belowground biomass on a small spatial scale (0.02 m^2, the area sampled with one 16.5 cm diameter coring tube) is around 20% for short plants. The actual variability is probably somewhat less than 20%, since some error was introduced by having several people sort the roots. The degree of spatial variability seems to be similar between sites. The larger c.v. for tall plots (Table 4), despite using a coring tube that samples a 50% larger area, indicates that the real spatial variability in belowground biomass is quite large for tall plants. This is undoubtedly due to the uneven spacing of culms that characterizes areas of tall *S. alterniflora*. The large c.v. is probably a contributing factor to our finding of poor correlations between above and belowground biomass

TABLE 4. Mean coefficient of variation of belowground biomass measured from three cores per aboveground sample.

	Short						Tall	
	GA	SC	VA	DE	NH	NS	DE	Other[b]
n =	15[a]	16	23	68	10	23	29	30
Live	0.29	0.20	0.20	0.26	0.22	0.20	0.40	0.32
Dead	0.14	0.22	0.10	0.13	0.25	0.28	0.35	0.22
Total	0.11	0.16	0.10	0.12	0.18	0.15	0.32	0.23

[a] n = number of plots sampled. Number of cores = 3 times n.
[b] Other tall includes samples from GA, SC, VA, NH, and NS combined.

TABLE 5. Equations to predict live belowground biomass from aerial biomass components.[a] $p < 0.001$ for all three equations.

ln(Live Below, g) = 0.718 × ln(Live Above, g) + 2.646, $r^2 = 0.86$
ln(Live Below, g) = 0.700 × ln(Live Leaves, g) + 3.051, $r^2 = 0.85$
ln(Live Below, g) = 0.713 × ln(Total Above, g) + 2.235, $r^2 = 0.86$

[a] Equations were computed from 68 short-form samples collected in Delaware between June 10 and September 10.
[b] Live Above = live leaves + live stems.
[c] Total Above = all live above + all dead above.

for tall plants. If we were to repeat the tall plant study, we would sample larger aboveground and belowground areas in each plot.

Our study of short plant belowground biomass in DE indicates that the seasonal changes in the live component are statistically insignificant (Fig. 2). In the tall plants, however, there were some significant seasonal changes in live biomass (Fig. 3). The accumulation of live material near the end of the growing season probably represents translocation to increase reserves for storage over the winter and for regrowth in the spring. This reasoning is consistent with Gallagher (1983) and Gallagher and Howarth's (1987) finding that recoverable underground reserves (RUR) were minimal in the summer, and that tall plants displayed much larger seasonal changes in RUR than did short plants. It is interesting to note that, in the abovementioned studies, RUR of short DE plants did undergo seasonal changes, whereas our measurements of live belowground biomass of short DE plants show no significant seasonal trends. An investigation of the relationship between RUR and biomass is needed.

As mentioned previously, the poor correlation between aboveground and belowground biomass for tall plants is probably a result, in part, of large spatial variability in biomass distribution. However, the dynamic nature of the tall plants (larger seasonal swings in biomass than in the shorter plants) may make it inherently impossible to derive belowground biomass prediction equations for tall *S. alterniflora* that are accurate over an entire season. The differences in seasonal biomass dynamics between tall and short plants may be partially a response to the physical properties of the subsurface environment, and to the age of the plant population. Our tall plants were usually sampled from creekbank locations, whereas short samples came from the backmarsh. Smart (1986) hypothesizes

TABLE 6. Accuracy of DE live belowground biomass prediction equations when applied to other sites.[a]

Mean Live Below (g)	GA n = 15	SC 16	VA 23	NH 10	NS 23
Actual[b]	781	748	853	689	840
Predicted 1[c]	1,352 (+73%)[f]	859 (+15%)	945 (+11%)	708 (+3%)	915 (+9%)
Predicted 2[d]	1,188 (+52%)	718 (−4%)	833 (−2%)	738 (+7%)	785 (−7%)
Predicted 3[e]	1,248 (+60%)	864 (+16%)	915 (+7%)	723 (+5%)	659 (−22%)

[a] Equations are listed in Table 5.
[b] The Table 6 "actual" means differ slightly from those shown in Table 3, because the means in Table 6 were transformed from mean logarithmic values.
[c] Predicted 1: predicted using live aboveground equation.
[d] Predicted 2: predicted using live leaves equation.
[e] Predicted 3: predicted using total aboveground equation.
[f] Percent over or under estimate.

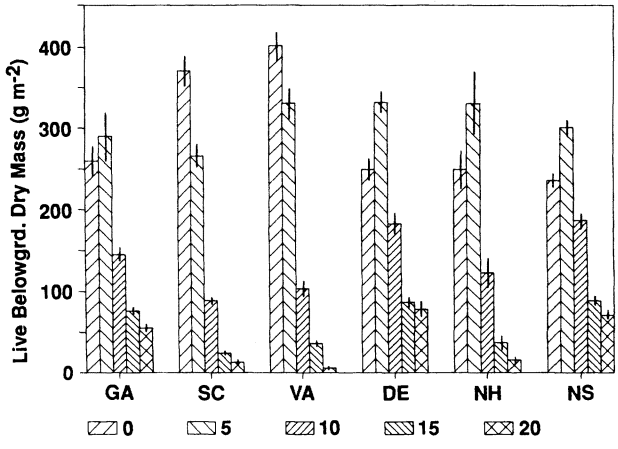

Fig. 5. Depth profile of mean live belowground biomass of short-form plants at each of six sites: GA (n = 15 plots), SC (n = 16), VA (n = 23), DE (n = 68), NH (n = 10), and NS (n = 23). In the legend, 0 = 0–5 cm, 5 = 5–10 cm, 10 = 10–15 cm, 15 = 15–20 cm, and 20 = 20–30 cm. Vertical lines represent one SE of the mean.

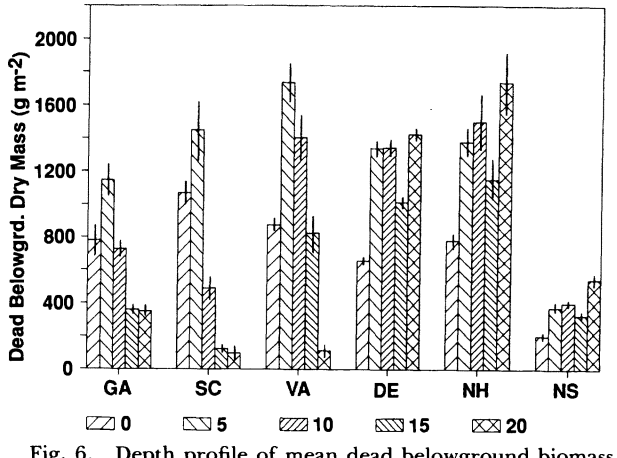

Fig. 6. Depth profile of mean dead belowground biomass of short-form plants at each of six sites: GA (n = 15 plots), SC (n = 16), VA (n = 23), DE (n = 68), NH (n = 10), and NS (n = 23). In the legend, 0 = 0–5 cm, 5 = 5–10 cm, 10 = 10–15 cm, 15 = 15–20 cm, and 20 = 20–30 cm. Vertical lines represent one SE of the mean.

that disturbance (e.g., sedimentation, erosion, ice-scouring, and slumping) at creekbank sites keeps the plant population young and the competition for nutrients to a minimum, minimizing the amount of root material required. In static backmarsh sites, intense competition for nutrients results in increased allocation of biomass to root material. As roots die and decay, peaty material accumulates, retaining nutrients, and the competition becomes even greater and still more roots are produced. Using this hypothesis, one can argue that the ability of a plant in the short *Spartina* zone to survive competition from its neighbors would be enhanced if the plant maintained a substantial amount of live root mass year-round, as short DE plants do.

Comparison of our results with those of other investigators who attempted to measure belowground biomass (rather than RUR) is difficult because of the variability in sorting techniques (separation of live and dead, or just measurement of all macro-organic matter [MOM]), diameter, size, number of cores taken per plot, and sampling frequency. Dead macroorganic matter is of variable age and may contain material produced many years, if not decades, before sampling occurs. In addition, the quantity of dead material often dwarfs the amount of live material (Fig. 2). In studies in which live was not separated from dead (Haines 1979; Smith et al. 1979; Buresh et al. 1980; Gordon et al. 1985, for example), relatively small changes in the amount of dead material may have obscured trends in the live component. Consequently, our discussion will focus on live belowground biomass. Valiela et al. (1976), working in Massachusetts (MA), reported peaks in live belowground biomass in the summer, with no peak toward the end of the growing season. Ellison et al. (1986) reported a similar pattern in a Rhode Island (RI) marsh, but took cores only directly over culms, which may have affected their results. In SC, live belowground biomass was maximal in the autumn and minimal in late winter (Dame and Kenny 1986). In GA, Schubauer and Hopkinson (1984) found a peak in November and a minimum in May. The timing of maxima and minima in DE seems to agree more with those of southern marshes than with those from New England. However, for studies in which biomass in both short and tall plants was assessed, our report of larger seasonal changes for tall plants is similar to that of Ellison et al. (1986), but in contrast to that of Dame and Kenny (1986), who measured large seasonal swings in live belowground biomass in short plants.

Investigators have reported significant linear relationships between natural logarithms of live shoot and root dry mass for a number of species, including forest understory species (Piper 1989), pasture grasses and clover (Davidson 1969), and carrot, parsnip, radish, and red beet (Hole et al. 1984). Whigham and Simpson (1978) formulated linear regression equations relating root and shoot biomass in 15 annual and perennial freshwater tidal wetland macrophytes. For many of the species mentioned above, the nature of the relationship changed during the growing season. It was encouraging to see that the correlation between live aboveground and live belowground biomass for short *S. alterniflora* in our study remained very strong for at least three consecutive months (Table 2), particularly since the samples were obtained during a three-year period. The stability of this relationship accounts for the success of using aboveground biomass to estimate belowground biomass. The decrease in the strength of the correlation between live aboveground and belowground biomass early and late in the growing season was not unexpected. Seasonal changes in belowground biomass are not as dramatic as those in aboveground biomass in DE. Early and late in the growing season, the aboveground component is quite small, whereas the belowground component varies relatively little for short plants (Fig. 2). Including samples from either end of the growing season increases scatter in the relationship between the two biomass components and weakens the correlation.

Correlations between aerial biomass and dead belowground biomass were poor (Table 2), probably because dead material may be present from growth that occurred many years earlier. Since the quantity of dead belowground material was often several times larger than the quantity of live roots and rhizomes, the dead biomass accounted for most of the total subterranean biomass, which explains the poor correlations between aerial and total belowground biomass.

The accurate predictions of live belowground biomass made using the DE equations at other sites (Table 6) indicate that sites that differ greatly in latitude, soil characteristics, and climate may still be fundamentally similar in terms of the relationship between aboveground and belowground biomass (Table 3), even when the data are gathered during different years. The success of the DE equations at the SC site was somewhat surprising, since Dame and Kenny (1986), working in the same marsh, measured similar July/August short *S. alterniflora* live aboveground biomass (about 250–300 g, as opposed to our mean of 323 g), but vastly greater live belowground biomass (about 3,300–4,200 g, versus our mean of 765 g). Our dead belowground measurements are almost identical to theirs for the July/August time period, so the explanation does not seem to be a difference in dis-

tinguishing between live and dead belowground material. We are unable to explain the discrepancy. Our biomass values for nearby GA are, however, similar to those measured by Schubauer and Hopkinson (1984). Although we used a 2-mm-mesh sieve, both Dame and Kenny (1986) and Schubauer and Hopkinson (1984) used 1-mm-mesh sieves, so sieve size alone cannot explain the difference between our SC data and those of Dame and Kenny.

We can only speculate as to why the DE equations do not work on the GA data (Table 6). Part of the GA disparity is a result of those plants being taller than the plants from the other sites. As Table 3 illustrates, tall plants tend to have less live root biomass per g of shoot biomass (the root : shoot ratio is less). However, even when the taller samples were removed from the GA data set, making the mean height similar to that of the other sites, the DE equations still resulted in large overestimates of belowground biomass (data not shown). The variability is not a simple function of latitude, since there was little difference between mean live aboveground and belowground biomass in SC, VA, DE, NH, and NS. Seneca (1974) reported differences in root : shoot ratios as a function of photoperiod and thermoperiod among seedlings grown from seed collected from various populations, but his Sapelo Island, GA, plants did not show unusual responses. Thus, there is no evidence that the anomalous GA ratios have a genetic basis. It is possible that differences in soil characteristics, such as nitrogen availability, are responsible. The root : shoot ratio of *S. alterniflora* often decreases when the plants are fertilized with nitrogen (Good et al. 1982). A higher level of available nitrogen in GA soils could explain the different GA root : shoot ratio. Levin et al. (1989) show that root : shoot ratios of many plants decrease with increasing internal nitrogen concentrations, so perhaps the GA plants had higher tissue nitrogen levels. Although we did not measure nitrogen levels, a review of the literature seems to indicate that Sapelo Island, GA, is not unusual with respect to either substrate nitrogen or plant tissue nitrogen levels (Mendelssohn and Marcellus 1976; Patriquin and McClung 1978; Chalmers 1979; Haines 1979; Buresh et al. 1980; Ellison et al. 1986; Smart 1986; Bertness 1988; Mendelssohn and McKee 1988; Pezeshki et al. 1988; Curtis et al. 1989).

We have other evidence suggesting that soil characteristics may affect root : shoot ratios. We previously sampled another marsh in NH, growing on borrow pit material and located next to a road (i.e., probably a disturbed marsh, perhaps having poor soil) that exhibited very large root : shoot ratios, and consequently poor estimates of live belowground biomass using the DE equations (data not shown).

It must be emphasized that the data in this study were obtained from closely spaced sites in each state or province: it is possible that there is more variability in biomass levels and root : shoot ratios among several marshes in the same state, than among the six systems sampled in this study. Nonetheless, it is important and significant that there are some basic similarities in biomass characteristics among marshes located in such different climatic regimes. Despite differences in DNA content (Freshwater 1988), phenology of flowering (Somers and Grant 1981), height, color, length of growing period, and morphology (Seneca 1974), *S. alterniflora* populations growing at different latitudes appear to have similar root : shoot ratios near peak aerial biomass when growing in their native environments.

Gallagher and Plumley (1979) grouped belowground biomass profiles into three categories: Type 1, showing an even distribution with depth; Type 2, having most macroorganic matter concentrated near the surface; and Type 3, demonstrating a relatively low concentration near the surface, the highest amount somewhat below the surface, and then a decease with depth. Our live biomass profiles for short plants seem to be closest to Type 2 profiles at all sites (Fig. 5). The concentration of live root material near the substrate surface is probably a response to saturated soil conditions (Seliskar 1983), and makes short the distance that oxygen diffusing into the roots from the aerial tissues must travel. Dead biomass shows a change from Type 2 to Type 3 (the decrease with depth occurs below 30 cm) as one moves from south to north (Fig. 6). The change in the dead belowground biomass profile is very abrupt and occurs between VA and DE. This is also where a dividing line between northern and southern canopies occurs with respect to the relationship between aboveground biomass and reflectance of electromagnetic radiation (Bartlett et al. 1988). Research is needed to identify what factors are responsible for these latitudinal differences. Two other latitudinal studies of *S. alterniflora* did not find distinct differences between northern (DE and north) and southern (VA and south) populations: Freshwater (1988) reported a gradual increase in DNA amount with latitude, and Seneca (1974) identified four broad population groupings (New England—Massachusetts, Rhode Island, and Connecticut; Mid-Atlantic—New York, Virginia and North Carolina; South Atlantic—Georgia, Florida; Gulf Coast—Mississippi, Texas). The change in the dead biomass vertical profile cannot be at-

tributed to a change in the vertical distribution of live roots, since the live belowground biomass profiles were similar at all sites (Fig. 5). Decomposition proceeds faster at warmer temperatures (Howes et al. 1985), so one might expect the proportion of dead belowground biomass found deep in the substrate to increase with latitude because of slower decomposition in response to lower temperatures and a shorter growing season. Although this pattern was indeed observed, the abruptness of the change, and the similarity among the three northernmost profiles, would not be expected if temperature were the only important factor. The temperature hypothesis appears more reasonable, however, as an explanation of the trend toward increasing amount of total dead belowground biomass with increasing latitude (Table 3). The abnormally small amount of dead material found in the Nova Scotia marshes may be related to the abnormally large tidal range (in the vicinity of 15 m) in the Bay of Fundy. The volume of water washing over the marsh may replenish pore waters with nutrients that could be used to accelerate decomposition, and may remove toxins or metabolites that can slow decomposition (Howarth and Hobbie 1982). Other possible explanations for the diversity in dead belowground biomass include variation in how refractory the roots are from different populations, and changes in the types of decomposer organisms living at different latitudes.

Despite the similarities between the quantities of biomass measured by Schubauer and Hopkinson (1984) and our study in GA, Schubauer and Hopkinson report different biomass profiles, with biomass maxima being located deeper. Core compaction in their study, which could explain the disparity, is unlikely, since they used a 16.3-cm diameter coring tube, and our core extraction technique was similar to theirs. Our NH vertical live biomass profiles do not resemble those of Bertness (1985) and Ellison et al. (1986) for a RI marsh, but our dead biomass profiles do. The distributions reported for the control short plant plots of Valiela et al. (1976) in MA are more similar to those of the RI marsh than to our NH profiles. In light of the among-site similarities that we have found, it seems likely that some of the diversity in belowground biomass profiles reported by other investigators working in various parts of the country is a result of differences in core size, and in coring and sorting technique.

Conclusions

Live aboveground *S. alterniflora* biomass can be used to accurately estimate live belowground biomass of short plants between the time the canopy becomes full, and the beginning of senescence (June–September in DE). The relationship between live aboveground and live belowground biomass is similar for marshes sampled in SC, VA, NH, and NS.

In DE, belowground biomass showed more seasonal variation for short plants than for tall plants. At all geographical locations, the live belowground biomass of the short plants was concentrated in the top 10 cm of substrate. Dead belowground biomass was mostly in the upper 15 cm for southern marshes, but was more evenly distributed with depth in northern marshes.

Relative to the goals of NASA's Biospheric Research Program, the ability to estimate live belowground biomass from live aboveground biomass is useful because spectral data gathered using satellites are highly correlated with live aboveground biomass of *S. alterniflora* for marshes throughout eastern North America (Hardisky et al. 1983; Gross et al. 1987; Bartlett et al. 1988). It would therefore be possible to use satellite images to derive rapid, nondestructive estimates of live aboveground and live belowground standing crop *S. alterniflora* biomass for entire marshes located between SC and NS. Although such estimates would be subject to some error, they would be a vast improvement over estimates based on extrapolations from a limited number of samples processed using traditional, destructive, harvesting methods.

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