Organic Matter Fluxes and Marsh Stability in a Rapidly Submerging Estuarine Marsh

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ABSTRACT: We studied organic matter cycling in two Gulf Coast tidal, nonsaline marsh sites where subsidence causes marine intrusion and rapid submergence, which mimics increased sea-level rise. The sites experienced equally rapid submergence but different degrees of marine intrusion. Vegetation was hummocked and much of the marsh lacked rooted vegetation. Aboveground standing crop and production, as measured by sequential harvesting, were low relative to other Gulf Coast *Spartina patens* marshes. Soil bulk density was lower than reported for healthy *S. alterniflora* growth but that may be unimportant at the current, moderate sulfate levels. Belowground production, as measured by sequential harvesting, was extremely fast within hummocks, but much of the marsh received little or no belowground inputs. Aboveground production was slower at the more saline site (681 g m^{-2} yr^{-1}) than at the less saline site (1,252 g m^{-2} yr^{-1}). Belowground production over the entire marsh surface averaged 1,401 g m^{-2} yr^{-1} at the less saline site and 585 g m^{-2} yr^{-1} at the more saline site. Respiration, as measured by CO_2 emissions in the field and corrected for CH_4 emissions, was slower at the less saline site (956 g m^{-2} yr^{-1}) than at the more saline site (1,438 g m^{-2} yr^{-1}), reflecting greater contributions by *S. alterniflora* at the more saline site which is known to decompose more rapidly than *S. patens*. Burial of organic matter was faster at the less saline site (796 g m^{-2} yr^{-1}) than at the more saline site (434 g m^{-2} yr^{-1}), likely in response to faster production and slower decomposition at the less saline site. Thus vertical accretion was faster at the less saline site (1.3 cm yr^{-1}) than at the more saline site (0.85 cm yr^{-1}); slower vertical accretion increased flooding at the more saline site. More organic matter was available for export at the less saline site (1,377 g m^{-2} yr^{-1}) than at the more saline site (98 g m^{-2} yr^{-1}). These data indicated that organic matter production decreased and burial increased in response to greenhouse-like conditions brought on by subsidence.

Introduction

Hydrological conditions in tidal, nonsaline marshes are important factors regulating their biota and productivity. Hydrological conditions may change because of a greenhouse effect, which may increase the relatively slow rate of sea-level rise prevailing since the end of the last ice age (Titus 1986). Increased sea-level rise would increase submergence rates and marine influences in tidal, nonsaline marshes (Titus 1986). Such marine intrusion and submergence would require that more salt-tolerant and flood-tolerant species such as *Spartina alterniflora* Loisel establish and flourish as less tolerant species such as *Spartina patens* (Aiton) Muhl. succumb to flooding, salt, and sulfide stress.

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Also, submerging marshes must vertically accrete so that the marsh surface remains in the rising intertidal zone; otherwise, marshes may drown and convert to open water (e.g., DeLaune et al. 1983). Marsh vertical accretion is often considered synonymous with mineral sedimentation, which is ubiquitous in estuarine marshes. For instance, mineral sedimentation rates measured in inland, brackish marshes averaged 724 g m^{-2} yr^{-1} and 147 g m^{-2} yr^{-1} in Louisiana and North Carolina marshes, respectively (Craft et al. 1993; Nyman et al. 1993a). However, vertical accretion in some New England, Louisiana, and North Carolina marshes depends on the balance between organic matter production and decomposition because accumulation of soil organic matter rather than mineral sediments controls vertical accretion there (McCaffrey and Thomson 1980; Hatton et al. 1983; Bricker-Urso et al. 1989; Craft et al. 1993, Nyman et al. 1993a). Thus, the existence of some estuarine

marshes during more rapid sea-level rise may depend partly on how increased sea-level rise affects organic matter cycling within the marshes. Mineral sediments play an indirect role because they promote plant production by providing nutrients for marsh vegetation (Bricker-Urso et al. 1989; Nyman et al. 1993a).

Carbon budgets have been quantified for some estuarine marshes (e.g., Day et al. 1973; Feijtel et al. 1985), but it is not clear how organic matter fluxes in tidal, nonsaline marshes would be affected by increased submergence and marine intrusion. Even though flooding and associated stress slows productivity (Chalmers 1982), flooding should also slow soil organic matter decomposition (Nyman and DeLaune 1991) and increase the amount of production allocated to belowground tissues (Mitsch and Gosselink 1984). Thus in some marshes, organic matter accumulation may actually increase as submergence increases, which would allow the marsh surface to maintain its elevation relative to the rising intertidal zone. However, export might be altered even in marshes that maintain elevation relative to mean water levels. While this would not directly affect marsh structure, their role in organic matter flux may be altered. The purpose of this study was to estimate organic matter pools and fluxes among major components of the carbon cycle in a tidal, nonsaline marsh experiencing rapid submergence and marine intrusion. Other marshes may respond to rapid sea-level rise differently than indicated by this study because only two sites were studied; nonetheless, these data are valuable because storage, respiration, and aboveground and belowground production are rarely monitored simultaneously.

Study Area

Extensive fresh, intermediate, brackish, and saline marshes occur in southeast Louisiana adjacent to the Gulf of Mexico. Sediments deposited by the Mississippi River filled the margins of the Gulf of Mexico and built these marshes over the last several thousand years (Frazier 1967). These marshes received periodic inputs of sediments and fresh water from the Mississippi River until the early 1900s, but they are now isolated from the river by flood control and navigation levees (Frazier 1967). Even though there is no river discharge into these marshes, extensive nonsaline marshes exist where water exchange with the Gulf of Mexico is restricted because average rainfall (162 cm yr^{-1}) is faster than average evapotranspiration (102 cm yr^{-1}) (Newton 1972). This results in extensive bands of fresh, intermediate, brackish, and saline marsh that parallel Louisiana's coastline. The distance between the northern edge of the fresh marshes and the southern edge of the saline marshes varies from 24 km to 80 km (Chabreck and Linscombe 1982). *Spartina patens* is the most important plant species in Louisiana coastal marshes, and is almost twice as common as the second most important species, *S. alterniflora* (Chabreck 1970).

Louisiana's microtidal coastal marshes do not exhibit the high marsh/low marsh characteristics of many other tidal marshes (e.g., Daiber 1986). Instead, *S. alterniflora* marsh gradually gives way to *S. patens* marsh over several km, with only a few centimeters difference between them in elevation relative to mean water levels. *Spartina alterniflora* marsh averages ~4 cm below mean water levels and *S. patens* marsh averages ~2 cm above mean water levels (Sasser 1977). In Louisiana, *S. patens* marsh typically floods 120 times per year and is flooded 43% of the time whereas *S. alterniflora* marsh typically floods 190 times per year and is flooded 55% of the time (Sasser 1977). In recent years, there has been an inland migration of saline marsh into formerly brackish marsh areas (Chabreck and Linscombe 1982). Some of this may result from the canals constructed throughout the marshes that increase water exchange between interior marshes and the Gulf of Mexico, but much of the inland migration of saline marsh likely results from increasing marine intrusion and flooding associated with the natural cycle of delta building and delta decay (Coleman and Gagliano 1964; Morgan 1967).

The study area was in southeast Louisiana, between Bayou Terrebonne and Bayou Barre (Fig. 1). This area was selected because it is in the advanced stages of the delta lobe cycle, which is characterized by sediment starvation and continued compaction of the underlying sediments that leads to subsidence and transgression (i.e., marine intrusion) (Morgan 1967; Coleman 1988). Massive sediment introductions and associated wetland creation ended long ago and the Gulf has been reclaiming this lobe for centuries. Although wetland deterioration is a natural part of this stage of the delta lobe cycle, flood control measures constructed on the Mississippi River in 1928 deprives this lobe of annual introductions of fresh water and sediments. Such annual flooding may slow wetland loss by relieving plant stress and providing nutrients. Canal dredging in Louisiana marshes is also believed to have contributed substantially to wetland loss (see Boesch et al. 1994 for a thorough discussion), but our study area lacks canals and spoilbanks that inhibit drainage or sediment introduction from the Gulf of Mexico.

Two sites were selected that were separated by approximately 3 km (Fig. 2). Site selection was constrained by the opposing goals of being near each
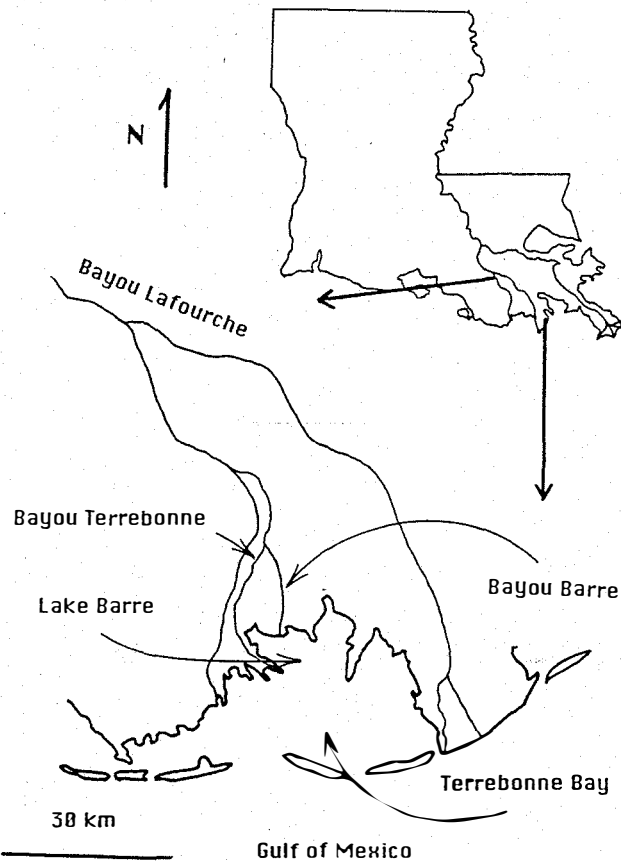
Fig. 1. Location of the general study area in southeast Louisiana where organic matter cycling was studied during 1990 and 1991.

Fig. 2. Location of the sites sampled in the study area.

other to minimize differences between them in subsidence rates, but far from each other to maximize differences between them in marine intrusion. The sites will be referred to as the less saline site and the more saline site, with the more saline site being more southerly and more closely linked to the Gulf of Mexico (Fig. 2). Since 1974, a large area of marsh, approximately 2 km SW of our southern site, converted to open water.

Rapid subsidence causes rapid marsh submergence in southeast Louisiana (Penland and Ramsey 1990). Our study sites experienced rapid submergence, as indicated by tide gauge analyses; submergence averaged 1.38 cm yr^{-1} since 1964 at six tide gauges surrounding the basin containing our study sites (Penland et al. 1988). This time period was used because it is the same time span over which we estimated vertical accretion. The actual submergence rate at the study sites may be even faster because the tide gauges are anchored in more stable levee sediments adjacent to major Mississippi River distributaries. The levee sediments are more consolidated than the bay fill and marsh
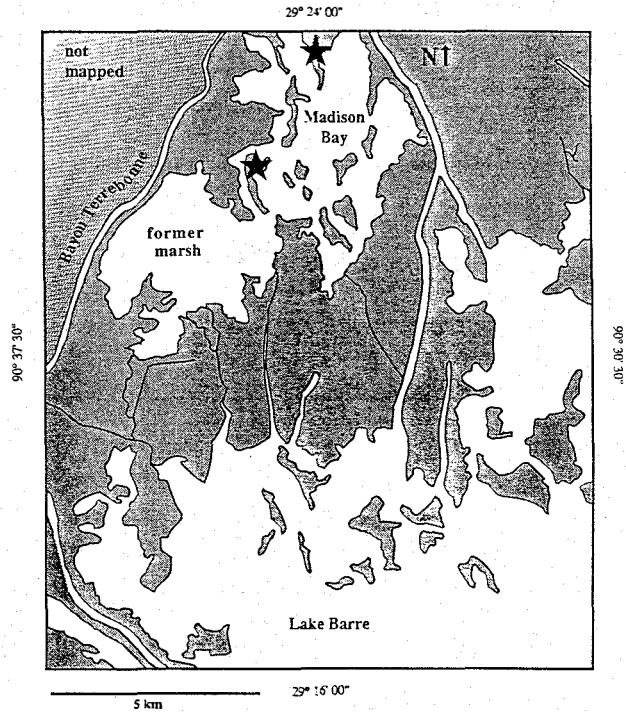
deposits typical of the interdistributary basins. We assumed that the two sites experienced equal submergence because of their proximity, but there was no way to test that assumption. Marsh vertical accretion is not keeping pace with submergence in this study basin (Nyman et al. 1993a) and flooding frequencies >90% were measured in the southern portion of this basin (unpublished data, D. Reed. Louisiana Universities Marine Consortium, Chauvin, Louisiana).

Marine intrusion is also common in southeast Louisiana. Chabreck (1970) compared a vegetative map made in the 1940s to one made in 1968 and found that the saline marsh type had moved inland an average of 3.4 km during the interim. Both of our sites were located in areas that were brackish marsh in the 1940s (O'Neil 1949) and whose soil was classified as brackish marsh, deep peat in the 1950s (United States Department of Agriculture 1956). However, the border between saline and brackish marsh has been migrating northward such that it was 2–3 km south of our more saline site in the 1940s (O'Neil 1949), at our more saline site in 1978 (Chabreck and Linscombe 1978), and at our less saline site in 1988 (Chabreck and Linscombe 1988). Thus, marine intrusion occurred at both sites but was more advanced at the more saline site.

Hydrological data were not collected at our study sites. Unless noted otherwise, the following

information is from a salt marsh bayou ~2.8 km south of our more saline site (Wang et al. 1993). Tides are diurnal and with a range of 30 cm to 60 cm. However, water levels are predictable only during calm weather because wind energy is often sufficient to modify or overpower the weak tidal energy. Peak channel flows of 40 cm s^{-1} have been measured and water velocity on the marsh surface is 10–20% slower than that in adjacent bayous. Sediment concentrations range from 10 mg l^{-1} to 30 mg l^{-1}. Tidal currents are insufficient to resuspend sediments deposited on the marsh, but some recently deposited sediments may be eroded during storms. Storm flooding apparently causes more mineral sedimentation on the marsh than does tidal flooding (Reed 1989; Wang et al. 1993). Mineral sedimentation is still an active process even though the area is in the advanced stages of the delta lobe cycle. Mineral sedimentation averaged 1,992 g m^{-2} yr^{-1} in salt marsh surrounding the bayou studied by Wang et al. (1993) and 724 g m^{-2} yr^{-1} in brackish marsh that included the sites used for this study (Nyman et al. 1993a).

During preliminary visits, we noted that rooted plant stems were clumped rather than distributed uniformly or randomly. Plants were rooted only in elevated hummocks, with hummocks being separated by up to 2 m. Hummocks consisted of pillars of densely packed living roots generally less than 50 cm in diameter. The decumbent stems from robust hummocks might cover 2 m^2 however. We estimated that 87% of the marsh surface had no rooted stems. Decumbent *S. patens* stems covered much of the area lacking rooted stems at the less saline site but not at the more saline site. Smaller hummocks were light enough to be picked up and moved with no apparent damage to living roots. Marsh soil was very weak between hummocks; it was not uncommon to sink thigh or even waist deep when walking. Much sampling was done from a pirogue (a flat-bottomed, canoe-like boat).

Methods

ABOVEGROUND PRODUCTION

Biomass was harvested for 2 yr. Litter and all rooted stems were harvested spring (March), summer (June/July), and fall (September) during 1990. Seven harvests were made in 1991: March, April, May, June, July, August, and October. Four plots were harvested from each marsh during each visit. Previous researchers in Louisiana brackish marshes harvested from 0.25-m^2 plots (White et al. 1978) and 0.1-m^2 plots (Hopkinson et al. 1978). We used larger plots to prevent samples lacking vegetation. In 1990, 1-m^2 plots were harvested, but in 1991 plot size was reduced to 0.5 m^2 to reduce sample processing time. Samples were returned to the laboratory, refrigerated for storage, and classified as live or dead culms by species. Samples were then oven-dried. Median live biomass by species and total live and dead biomass were compared between marshes using Wilcoxon's Signed Rank test (Steele and Torrie 1980). This test for paired observations is nonparametric and therefore does not require that data are normally distributed. Annual aboveground production over the 2-yr period was estimated from the oven-dried weight of live and dead material with Smalley's method (Shrew et al. 1981).

BELOWGROUND PRODUCTION

Belowground biomass was sampled at the same times that aboveground biomass was sampled. Cores (15-cm diameter, 20 cm long) were collected from each harvested plot. Previous estimates of belowground biomass typically used cores ranging from 6.0 cm to 10 cm diameter (de la Cruz and Hackney 1977; Jordan et al. 1989). Cores were collected from hummocks (vegetated) and unvegetated marsh soil during 1990. Unvegetated marsh was not sampled after 1990 because live biomass was rarely encountered in those samples. During 1990, samples were washed with water and sodium metaphosphate to remove soil; live and dead material were separated according to the methods of Hopkinson and Dunn (1984). Live and dead biomass were clearly distinguishable in some samples, but in most samples there appeared to be a gradient from live to dead, with much biomass appearing somewhere in between. Other workers also found live-dead separation techniques to be inadequate and therefore reported belowground biomass as a combination of live and dead material (see Good et al. 1982); thus, we also report these data as total belowground biomass. A different technique was therefore used in 1991. Cores were dried, weighed to determine bulk density, ground, and samples were combusted to estimate percent organic matter (Davies 1974). Total organic matter content of the cores was then estimated from soil bulk density and percent organic matter. Median belowground biomass was compared between marshes with Wilcoxon's Signed Rank test (Steele and Torrie 1980). Data collected in 1990 were also tested for differences in belowground biomass between vegetated and unvegetated marsh using Wilcoxon's Signed Rank test (Steele and Torrie 1980). Annual belowground production over the 2-yr period was estimated from changes in total belowground biomass in a manner similar to Smalley's method. If the change in total biomass was positive, then production for that interval equaled that change; if the

change was zero or negative, then production was zero.

RESPIRATION

Carbon dioxide emission rates were determined from vegetated and unvegetated marsh soil at both sites in April 1990 and September 1990. Emission rates were measured with a flow-through Infrared Gas Analyzer as described by Nyman and DeLaune (1991), with the exception that these measurements were made from the marsh surface rather than from intact cores in the laboratory. These field measurements were made over litter as well as soil. The CO_2 emission rate measured in the field was corrected for seasonal differences and for annual CH_4 emission (as noted by Smith et al. 1983) to estimate total C emissions. A factor of 1.724 was used to estimate organic matter from carbon (Wilson and Staker 1932).

BURIAL

Two cores (15 cm diameter, 50 cm long) were collected from hummocks in each marsh. These cores were among 30 collected to study sedimentation throughout this area (Nyman et al. 1993a). Cores were returned the laboratory and sectioned into 3-cm increments. Soil bulk density was determined from the oven-dried weight of soil increments. Vertical accretion was estimated with the ^{137}Cs dating technique (DeLaune et al. 1978). That technique locates the 1963 marsh surface, which contains peak levels of   Cs fallout. Soil increments that contained the 1963 marsh surface, and all overlying increments were ground. Samples from each increment were combusted to determine percent organic matter (Davies 1974). The amount of organic matter in each soil increment was then estimated from the soil bulk density and percent organic matter of each increment. Annual burial rates were then estimated from the total amount of organic matter buried since 1963 and the number of years (27) between core collection and 1963.

EXPORT

Export was estimated from the difference between production and the sum of decomposition and burial. Other studies have estimated export indirectly, for example, Day et al. (1973) estimated export from the difference between production and respiration. Nonetheless, our export estimates should be judged cautiously because they depend on the assumptions that other measurements are accurate and that all organic matter flows were measured.

EDAPHIC CONDITIONS

Water salinity was measured either in the adjacent bayou or on the marsh surface during most site visits using a YSI salinometer. Differences in salinity between bayou water and water standing on the marsh surface were negligible. Soil water salinity was not measured. Salinity was also recorded at these sites when sampling was conducted for other studies in this area; thus there often were more than one salinity measurement for each month, and these were averaged to obtain monthly estimates. Water salinity was compared between sites using Wilcoxon's Signed Rank test, pairing on month (n = 8). Soil Eh was recorded during spring and fall 1990 site visits (using duplicate platinum electrodes as described by Faulkner et al. 1989) in vegetated and bare soil at −1 cm, −5 cm, and −10 cm depth. Soil Eh was compared between marshes with Wilcoxon's Signed Rank test, pairing on depth and sampling date (n = 6). Depth of water standing on the marsh surface was also recorded. These data were used to estimate average flooding depth as well as hummock elevation relative to the unvegetated marsh surface.

Results

Hummocks appeared more robust at the less saline site and averaged 15 cm above bare soil; hummocks averaged 13 cm above bare soil at the more saline site. *S. patens* greatly dominated the less saline site but not the more saline site (Fig. 3). Total live standing crop was greater at the less saline site than at the more saline site (P > T⁺ = 0.0137) as was live *S. patens* (P > T⁺ = 0.0010) and total dead biomass (P > T⁺ = 0.0332). The more saline site had more *S. alterniflora* biomass (P > T⁺ = 0.0244) than the less saline site (Table 1). No difference was detected between the sites in biomass of *Distichlis spicata* (L.) Greene (P > T⁺ = 0.1162); no other species were harvested. Aboveground production was faster at the less saline site than at the more saline site (Table 2).

Belowground biomass (P > T⁺ = 0.0420) also was greater at the less saline site than at the more saline site (Table 1). Belowground biomass was not significantly correlated to aboveground biomass within the range we sampled (unpublished data), and there was 7.5 times and 10.4 times more belowground biomass than aboveground biomass at the less saline and more saline sites respectively. There was roughly twice as much belowground biomass in hummocks as in areas lacking rooted stems (P > T⁺ = 0.0156). Annual belowground production was 281 g m⁻² and 0 g m⁻² in unvegetated marsh at the less saline and more saline sites respectively. Annual belowground production in
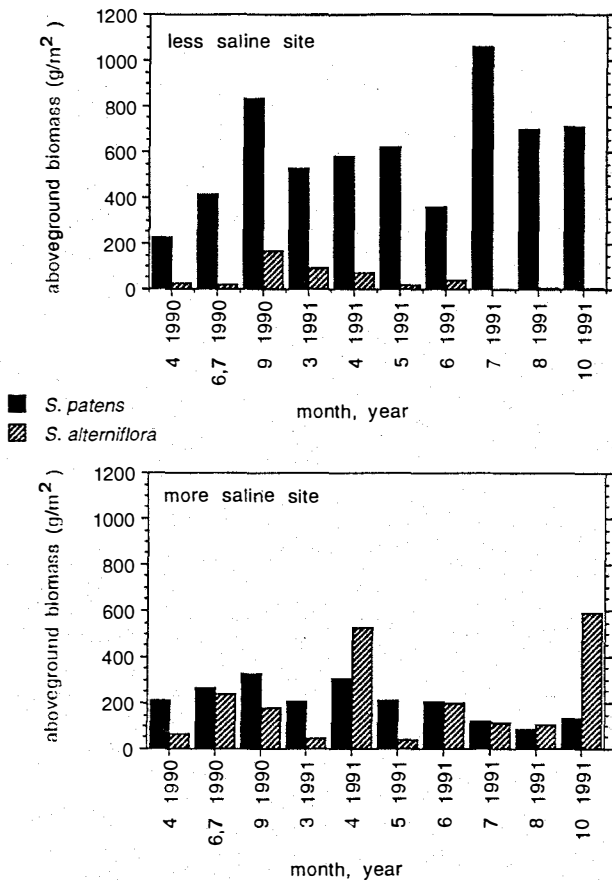
Fig. 3. Live biomass of *Spartina patens* and *Spartina alterniflo-ra* on sampling dates in 1990 and 1991 at two tidal, nonsaline marshes in southeast Louisiana.

hummocks was extremely high: 8,960 g m^{-2} at the less saline site and 4,678 g m^{-2} at the more saline site. Annual belowground production reflects the relative contributions of hummocks and bare marsh to marsh surface area (Table 2).

TABLE 1. Vegetation biomass (g m^{-2}) at Billy Goat Bay, Louisiana: 10 sampling dates between March 1990 and October 1991.

Species	Mean	Median	Range
North Madison Bay marsh			
Live *Spartina patens*	604	598	226–1,063
Live *Spartina alterniflora*	46	25	2–167
Live *Distichlis spicata*	101	89	25–275
Total live biomass	769	747	304–1,288
Total dead biomass	642	570	266–1,352
Belowground biomass	10,620	9,924	8,140–14,788
West Madison Bay marsh			
Live *Spartina patens*	208	209	89–324
Live *Spartina alterniflora*	164	111	37–596
Live *Distichlis spicata*	63	50	18–154
Total live biomass	437	418	247–755
Total dead biomass	508	333	171–1,218
Belowground biomass	9,810	9,487	7,473–12,030

TABLE 2. Organic matter cycling (g m^{-2} yr^{-1}) at less saline and more saline sites in rapidly submerging estuarine marsh, Terrebonne Parish, Louisiana, 1990–1991.

	Less Saline	More Saline
Aboveground production	1,252	681
Belowground production	1,401	585
Total production	2,653	1,266
Soil respiration	483	734
Burial	796	434
Export	1,377	98

Some of the differences in plant community structure and function may be related to differences in flooding and salinity (i.e., marine intrusion between the sites). Soil was more reduced at the more saline site than at the less saline site (P > T$^+$ = 0.0156), suggesting more flooding at the more saline site (Fig. 4). Soil Eh averaged over depth was -17 ± 42 mV at the less saline site and -126 ± 15 mV at the more saline site. Continuous water-level data were not collected, but observed water depths averaged 2 cm over hummocks at the less saline site and 8 cm over hummocks at the more saline site during our site visits. Water salinity also appeared higher at the more saline site. When salinity estimates differed between the sites by more than 0.5‰ (5 of 8 months) salinity was always higher at the more saline site (Fig. 5). However, salinity at the more saline site (6.2‰) was not significantly different (P > T$^+$ = 0.0977) from that at the less saline site (5.2‰). Salinity was observed to fluctuate greatly, particularly at the more saline site. For instance, salinity at the more saline site increased from 6.2‰ to 12.5‰ over a period of 7 d during April 1990. Such fluctuations may be more of a factor on plant growth than mean salinity, but too few data were collected to evaluate that effect. Salinity also appeared lower in 1991 than in 1990 (Fig. 5), but that effect was not evaluated.
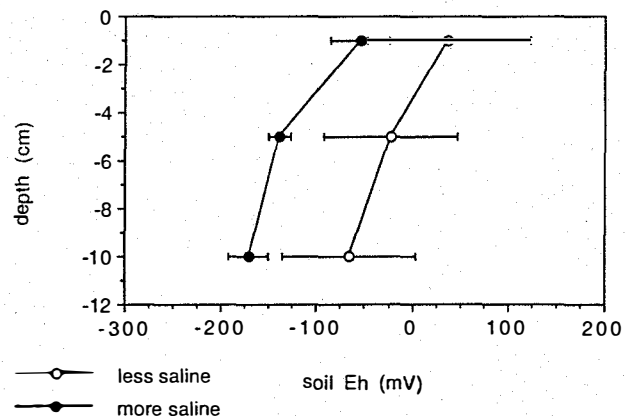

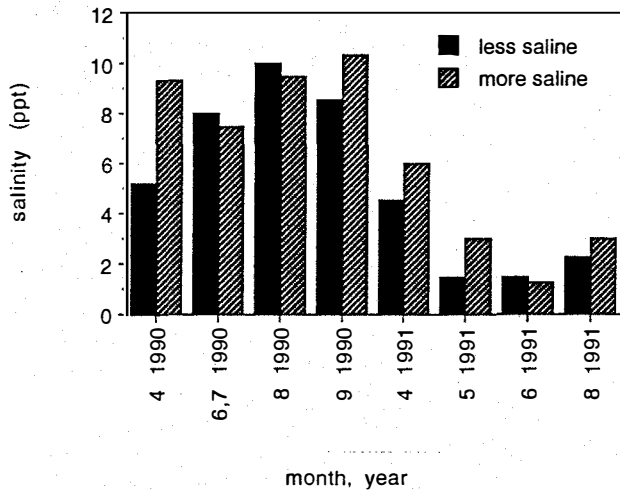Fig. 4. Soil Eh over depth at two tidal, nonsaline marshes in Louisiana.

Fig. 5.   Salinity observed at two tidal, nonsaline marshes in Louisiana.

Cs-137 acitivity (counts per section)

Cs-137 activity (counts per section)

Fig. 6. ^{137}Cs activity with depth in replicate cores from two tidal, nonsaline marshes in Louisiana. Peak ^{137}Cs activity marks the 1963 marsh surface.

Respiration was more rapid at the more saline site than the less saline site, in spite of more reducing conditions at the more saline site (Table 2). Respiration was generally faster over hummocks than over bare marsh soil, but too few samples were collected for statistical analysis. Organic matter burial and organic matter available for export were also slower at the more saline site than at the less saline site. Vertical accretion was slower at the more saline site (0.85 cm yr^{-1}) than at the less saline site (1.3 cm yr^{-1}); ^{137}Cs data are profiled in Fig. 6.

Discussion

Spartina patens biomass was generally lower than reported in Gulf Coast brackish marshes (Hopkinson et al. 1978; White et al. 1978), especially at the more saline site. *Spartina patens* biomass did not show strong season patterns, which is in agreement with previous work on the Gulf Coast (Hopkinson et al. 1978). *Spartina alterniflora* biomass was also lower than previously reported in Gulf Coast saline marshes, even at the more saline site where it was more common. Low plant biomass is commonly related to flooding and associated stresses (Chalmers 1982). Flooding frequencies over 90% were measured at a saline site several km south of these studies site (unpublished data, D. Reed. Louisiana Universities Marine Consortium, Chauvin, Louisiana), and, as noted, our sites appeared to be almost continually flooded.

Root:shoot ratios at both sites were greater than previously reported for monospecific *S. patens* (Knox 1986). High root:shoot ratios are indicative of unfavorable soil conditions (Knox 1986) and are further evidence that these marshes flooded excessively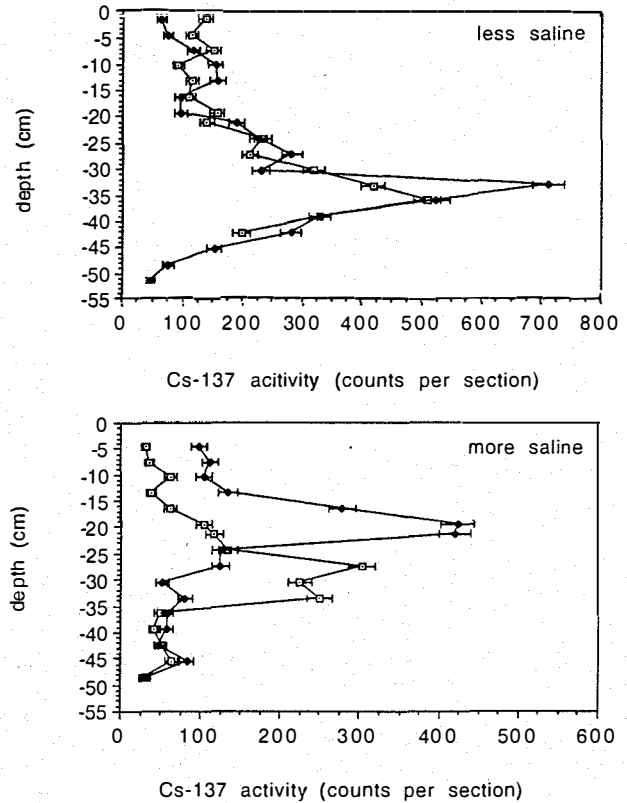. Marsh plants appear to put more energy into root production under unfavorable soil conditions (Mitsch and Gosselink 1984), perhaps because unfavorable soil conditions require more root surface to service each unit of aboveground biomass (Good et al. 1982).

Excessive flooding was also indicated by the low soil Eh. DeLaune et al. (1983) observed soil Eh in the upper 10 cm of soil in a short *S. alterniflora* marsh approximately 100 mV more oxidized than we observed at our less saline site, where Eh was higher. The difference in soil Eh between the less saline and more saline site indicated that the more saline site was more flooded than the less saline site. This flooding difference was assumed to result from the observed difference in vertical accretion rather from a difference in the underlying subsidence rate between the two sites. It should be noted that the lower soil Eh at the southern site may also partly result from the greater amount of *S. alterniflora* at that site. Nyman and DeLaune (1991) showed that Eh could be lower in *S. alterniflora* marsh soil than in *S. patens* marsh soil even when soil drainage was the same, likely because *S. alterniflora* is less resistant to decomposition.

The sites differed in the amounts of *S. patens* and

TABLE 3. Organic matter fluxes previously reported in *Spartina patens*-dominated marshes, with emphasis on Gulf of Mexico marshes.

Production (g m^{-2} yr^{-1})	Location	Source
	Aboveground	
1,341	Louisiana	White et al. (1978)
1,945	Louisiana	DeLaune and Smith (1984)
4,159	Louisiana	Hopkinson et al. (1980)
6,043	Louisiana	Hopkinson et al. (1978)
	Belowground	
2,520	Massachusetts	Valiela et al. (1976)
120	Georgia	Gallagher and Plumley (1979)
150	Delaware	Gallagher and Plumley (1979)
220	Maine	Gallagher and Plumley (1979)
	Respiration	
436	Louisiana	DeLaune and Smith (1984)
	Burial	
510	Louisiana	DeLaune and Smith (1984)
	Export	
998	Louisiana	DeLaune and Smith (1984)

S. alterniflora they contained. Bertness (1991) showed that when these two species occur together, *S. patens* dominates less flooded sites by out growing *S. alterniflora,* and *S. alterniflora* dominates more flooded sites that *S. patens* cannot tolerate. Thus the differences between the sites in species composition indicates that the more saline site was more flooded than the less saline site, in agreement with the difference in Eh between sites. As noted, the difference in flooding was assumed to result from the different vertical accretion rates. Given that *S. alterniflora* was not limited by *S. patens* at the more saline site, an unanswered question was what limited *S. alterniflora* at the more saline site?

Aboveground production was faster than that generally reported for *S. patens* on the Atlantic Coast of the United States, but only about half that generally reported on the Gulf Coast (Table 3). Also, Pezeshki et al. (unpublished data) found slower *S. patens* carbon assimilation rates in this area than at other Louisiana brackish marsh areas. Belowground production at both sites was faster than the three estimates by Gallagher and Plumley (1979) on the Atlantic Coast, but less than that in Massachusetts reported by Valiela et al. (1976) (Table 3). Belowground production was 1.1 times and 0.9 times aboveground production at our less saline and more saline sites, respectively. In a Georgia *S. alterniflora* marsh, belowground production was 1.6 times aboveground production (Schubauer and Hopkinson 1984), but we are unaware of similar estimates from Gulf Coast or other *S. patens* marshes.

We expected respiration would be less than previously reported for brackish marsh because of the frequent flooding at these sites. However, the previous estimate of respiration in brackish marsh (from data in DeLaune and Smith 1984) was similar to that at our less saline site, and less than that at our more saline site (Table 3). It should also be noted that our respiration rates may slightly underestimate actual respiration. We observed many crustaceans and small fish on the marsh surface. Their density appeared high, but we did not measure respiration with any animals enclosed in our chambers.

The faster respiration at the more saline site likely resulted from the greater amount of *S. alterniflora* there. Soil respiration is faster in saline marsh soil than in brackish marsh soil (Smith et al. 1983; Nyman and DeLaune 1991), most likely because *S. patens* is more resistant to decomposition than *S. alterniflora*. In fact, organic matter lost through respiration at the more saline site was more similar to that previously reported for saline marsh, 728 g m^{-2} yr^{-1} (from data in Feijtel et al. 1985), than to that reported for brackish marsh.

Burial was faster at these sites than at other sites for which estimates are available (Table 3). This likely resulted from the rapid belowground production in hummocks, much of which was apparently buried and subsequently elevated the hummocks above the surrounding soil that lacked rooted stems. However, vertical accretion was still inadequate to counter the estimated submergence rate of 1.38 cm yr^{-1}. This vertical accretion deficit is the most likely cause of the excessive marsh flooding, and was greater at the more saline site. If submergence continues to be more rapid than vertical accretion, then these marshes will gradually drown and convert to open water. A more extensive study of vertical accretion indicated that since 1964, this general area has lost at least 11 cm elevation relative to mean water levels (Nyman et al. 1993a). Given that vertical accretion depends on the amount of organic matter accumulation rather than the amount of mineral sedimentation (McCaffrey and Thomson 1980; Hatton et al. 1983; Bricker-Urso et al. 1989; Nyman et al. 1993a), then the cause of inadequate vertical accretion was inadequate accumulation of soil organic matter. Apparently, even the extremely rapid belowground production that occurred in hummocks was not adequate. This indicates that the maximum amount of submergence that some marshes can perpetually tolerate is less than occurs at this site, and is further evidence of a postulated positive feedback loop between inadequate vertical accretion and inadequate plant production (Nyman et al. 1993a).

As noted, both sites were characterized by elevated hummocks surrounded by soil almost devoid of rooted vegetation. Hummock elevation appeared to result from vigorous root growth by *S. patens* at culm bases immediately above the hummock surface; roots from one stem appeared to link up with roots from adjacent stems to form a more elevated surface that captured silt. Adventitious root production in response to flooding is widely recognized. Although death often results in the deeper parts of the plant where anoxia develops, ethylene production stimulates adventitious root growth in the hypoxic portions of the soil surface (Hook 1984; Kozlowski and Pallardy 1984; Jackson 1985). This has been noted in *S. patens* (Naidoo et al. 1992). We also noted root growth and production of upright stems from decumbent stems of *S. patens,* but they never persisted. Their failure to persist might result from salinity fluctuations; Naidoo et al. (1992) noted that production of negatively gravitropic roots was inversely related to salinity. *S. patens* growth at the more saline site was never great enough to form large mats like those at the less saline site. We have noted at Marsh Island, Louisiana, that such mats may exceed 10 cm in thickness and give rise to persistent, upright stems; however, that apparently requires more drying, lower salinity, or both, than occurs at our sites. We have occasionally noted layers of horizontal stems in cores collected from brackish marsh for ^{137}Cs dating. Thus although root production appears to be most important for soil formation, such mat production may also partly counter submergence in *S. patens* marsh. *S. alterniflora* also exhibited some adventitious root growth at both sites but never formed floating mats.

The bare areas between hummocks were observed to be flooded almost permanently. The soil conditions expected to result from such flooding are the most likely reason that these areas did not support rooted vegetation, and were not colonized by new plants during this study. Drainage of the low areas between hummocks was observed only during prevailing north winds that occur during winter and spring and that cause extremely low tides. At normal low tides, the surface of most of hummocks were barely exposed, and the surface of bare soil was flooded by 10–20 cm of water. Plants rooted in hummocks were thus protected somewhat from flooding stress by their elevation. Plants rooted in the hummocks may have been further protected from anoxia by the extremely dense root network and lack of dead material in the hummocks; which might partially counter anoxia via the loss of relatively oxidized substances (Chalmers 1982).

Previous field studies indicated that marshes can export organic matter, including dissolved organic carbon (Craft et al. 1989 and articles cited therein). But our export estimates were greater than generally reported and more similar to modeling results that yield exports of 1,000 g C m^{-2} yr^{-1} (Mitsch and Gosselink 1984). Our estimate may not be accurate given the method we used, or our estimate may be high because our study sites were dominated by *S. patens*. Previous studies have generally been made in *S. alterniflora* marshes, which are less productive (Pezeshki and DeLaune 1991), usually omitted belowground production from their budgets (Feijtel et al. 1985), or assumed that belowground production equaled that buried and assumed that respiration recycled only aboveground production (e.g., Day et al. 1973).

Mineral sediments provide nutrients for salt marsh vegetation (DeLaune et al. 1981), and plant biomass is related to soil nutrient content in Gulf Coast and Atlantic Coast salt marshes (Broome et al. 1975; DeLaune and Pezeshki 1988). Soil bulk density depends on mineral sediment content (Hatton et al. 1983), thus plant biomass is related to soil bulk density in Louisiana salt marshes (DeLaune and Pezeshki 1988) and brackish marshes (Nyman et al. 1994). In addition to nutrients, soil mineral matter contains Fe, which likely buffers against sulfide toxicity (King et al. 1982). However, within the range sampled, no relationship was detected between biomass of either of these species and soil bulk density in this area (unpublished data), suggesting that factors other than nutrient availability regulated plant growth. Regardless, average soil bulk density at these sites, 0.09 g cm^{-3}, is too low to support healthy *S. alterniflora* marsh, which appears to require at least 0.25 g cm^{-3} (DeLaune et al. 1990). Thus it does not appear that these *S. patens*-dominated marshes will convert to *S. alterniflora*-dominated marshes in response to continuing increases in flooding, salinity, and sulfate unless mineral sedimentation also increases so that soil bulk density increases. Insufficient soil mineral matter for brackish marsh to convert to saline marsh partly explains the large area of open water where brackish marsh previously existed southwest of our more saline site.

For marshes that are submerging as rapidly as those observed in this study area, there appear to be few management options available to insure their continued existence. Any measure that does not cause vertical accretion to equal submergence will likely fail within several decades, but any attempt to make vertical accretion equal to submergence at this late stage of the delta lobe cycle is counter to the natural driving forces and is likely to be very expensive. Sediment introductions to restore the lost elevation, and thereby reduce flood-

ing stress, would require 88 kg m^{-2} of sediment (Nyman et al. 1993b). An additional 0.7 kg m^{-2} yr^{-1} would be needed to supplement the natural mineral sedimentation rate to prevent vertical accretion deficits from redeveloping (Nyman et al. 1993b). However, the energy needed to transport these sediments is likely unjustifiable, thus the most common management goal may therefore be to prolong the existence of these marshes by reducing flooding or salinity. Levees could be constructed so that rain water could be pumped out. This would reduce flooding as well as salinity stress by prohibiting Gulf water from entering the area. This option suffers from high costs, the loss of estuarine exchange, and the likelihood of failure within several decades because the marsh would be below sea level. Another option is to restore spring flooding from the river. The major benefit of this option is that salts and sulfides could be flushed from the marshes each spring as would occur naturally. Such annual flushing should reduce plant mortality and increase plant production. This is the only option that can be applied regionally but suffers from high costs as well as from the level of cooperation required from many public and private interests. It is likely that all these options will be applied to various degrees in southeastern Louisiana. Outside Louisiana, such efforts may help maintain estuarine marshes in the event of moderate increases in the rate of global sea-level rise. However, should the rate of submergence exceed 1.08 cm yr^{-1} (the average vertical accretion rate observed at these sites), it is almost certain that estuarine marshes will drown and be replaced by shallow bays within 75 yr. Outside Louisiana, such marsh loss may be permanent. Louisiana, on the other hand, benefits from the magnitude of the Mississippi River and a new round of the delta lobe cycle could be initiated once bays were deep enough to accommodate sufficient river flow.

Conclusions

All indications were that flooding was excessive in these marshes because of greenhouse-like conditions brought on by subsidence. This flooding, which resulted from inadequate marsh vertical accretion, reduced production and stimulated organic matter burial. Reduced production and increased burial presumably limited export to the adjacent estuary, but export data from similar marshes are not available for comparison. Although burial was stimulated, it was not stimulated enough to cause adequate vertical accretion. Thus, these marshes may slowly drown over the coming decades. We speculate that negative effects of greenhouse-like conditions on production, burial, and export were greater where marine intrusion was

more advanced, but studies specifically designed to test those hypotheses are required before conclusions can be made regarding marine intrusion.

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