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EFFECTS OF SOIL DRAINAGE ON VERTICAL DISTRIBUTION OF SUBSURFACE TISSUES IN THE SALT MARSH MACROPHYTE *SPARTINA ALTERNIFLORA* LOIS.

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Abstract: *Spartina alterniflora* was propagated in buckets of modified salt marsh soil with near-natural cyclic flood/drain regimes to determine effects of soil drainage on the vertical distribution of subsurface tissues. There was a significant correlation between aerial biomass and drainage during the first year but not during the second. No statistically significant correlation was found between soil drainage depth and subsurface tissue distribution either at the end of the first growing season or the second. Well-drained soils led to more uniform vertical distribution, but in general, soil drainage depth had no consistent effect either on distribution of subsurface plant biomass or on aerial:subsurface tissue ratios.

Key Words: *Spartina alterniflora*, cordgrass, salt marsh restoration, soil drainage, biomass

INTRODUCTION

The ecological function of saltmarsh cordgrass (*Spartina alterniflora* Lois.) in U. S. Atlantic and Gulf Coast salt marshes has become increasingly apparent through time. Not only does it provide habitat for estuarine invertebrates, birds, fishes, and mammals (Teal 1962, Boesch and Turner 1984), but it also governs the abundance of their food supply (Bourn and Cottam 1950, Odum and de la Cruz 1967, Moy and Levin 1991, Posey et al. 1997).

Despite the fact that most cordgrass research to date has dealt with aerial tissues, 60% or more of its total biomass is known to be below the marsh surface in the form of an extensive root and rhizome network (see review in Good et al. 1982). The abundance of its subsurface tissues has prompted a recent series of diverse investigations aimed at elucidating the physiology and growth strategies of this plant within the largely anoxic soil environment. Notable among these are reports on nitrogen metabolism (De Laune et al. 1984), distribution of aerenchyma (Teal and Kanwisher 1965, De Laune et al. 1983), root to shoot ratios (Gross et al. 1991), and vertical distribution of root mass in soil (Gallagher 1974, Gallagher and Plumley 1979, De Laune et al. 1983, Gross et al. 1991). Although our understanding of the adaptation of this plant to the marsh soil environment is increasing, there still remain large gaps in our knowledge.

The present investigation explores one of those gaps—namely, the relationship of soil drainage to vertical proliferation of cordgrass subsurface tissues. Our primary objective was to determine how survival of cordgrass transplants would be influenced by cyclic soil flooding/drainage so that transplant growth might be enhanced by appropriate soil drainage when created salt marshes are designed.

MATERIALS AND METHODS

Individual plants were removed from a 10 m^2 short-form cordgrass plot in the Bradley Creek salt marsh (New Hanover County, NC 34°12′30″ N by 77°49′12″ W) for transplantation into 96, 30-cm-diam. × 30-cm-high polypropylene buckets. The soil mix used consisted of one part washed builders sand to two parts natural salt marsh soil that had been sieved through a 3-mm^2 mesh wire screen prior to sand addition. Sieving was done to remove any original plant material from the soil that might become entwined in cordgrass roots, causing artificially high estimates of subsurface plant biomass during later harvest. Our decision to amend this soil with builders sand was based on initial experiments that demonstrated which of several soil mixtures yielded the desired drainage characteristics. Prior consultation with the U. S. Army Corps of Engineers district office (Wilmington, NC) revealed that there currently are no regulations concerning the composition of fill material that can be used to construct new salt marshes other than that they be devoid of

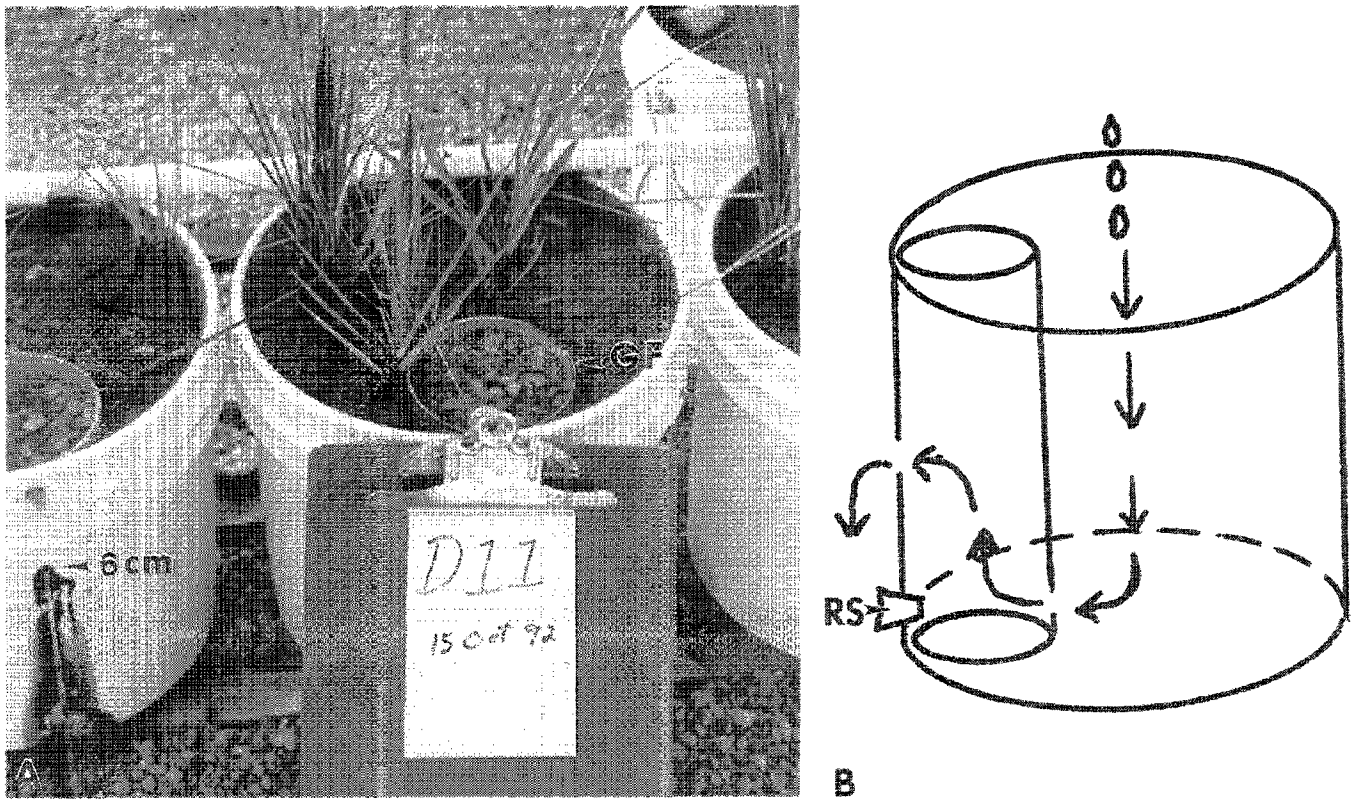

Figure 1. Close-up view of sample bucket. A) Note gravel filter (GF) and 6-cm external drain hole (EDH) in bucket shown at far left. Dark streak beneath EDH is cyanobacterial growth. B) Schematic diagram of bucket design indicating path of flooding water as it filled, then exited the bucket via the GF and EDH. Note lower external hole (plugged with rubber stopper "RS"). Periodic removal of RS allowed complete draining of bucket to prevent hypersaline conditions from developing in waterlogged soil.

toxins. Our soil composition was considered "typical."

Sets of 12 buckets were drained by gravity to one of the following depths (measured from the soil surface) on each ebb tide cycle: 0, 3, 6, 9, 12, 15, 18, and 21 cm. Hereafter, this experimental parameter will be referred to simply as "drainage depth." Each bucket was engineered with an internal filter (Figure 1) that regulated drainage to the desired depth by the end of each 6-h ebb tide cycle, yet prevented soil from clogging the external drainage holes (EDH). Our original design did not include a filter, but repeated EDH clogging with soil particles disrupted drainage to the extent that soil was continuously waterlogged in all cases. Filters consisted of 10-cm-diameter, gravel-filled, PVC pipes attached vertically to the inside circumference of each bucket (tangent to the EDH). This arrangement required all flooding water first to percolate through the soil then pass through the filter before exiting the bucket via the EDH (see schematic diagram of water pathway in Figure 1). We ensured that the filter did not serve as a source of soil aeration by drilling only four 3-mm-diameter holes in its wall, through which pore water could escape the soil. These holes were drilled in the lower edge on the side opposite where its circumference contacted the bucket wall; thus, soil aeration via the filter was precluded by the "head" of standing water that extended from the bucket bottom to the level of each EDH.

Each bucket was provided with an additional 1-cm-diameter hole that was plugged with a rubber stopper at all times. Whereas soil in each bucket was continuously saturated at depths below the EDH, these stoppers were removed for two full tidal cycles about every 10 days to prevent hypersaline soil conditions from developing due to evaporation.

Buckets were flooded to overflow with unfiltered, natural seawater on a repeating, simulated tidal cycle (6-h flood: 6-h ebb: 6-h flood, etc.). This was accomplished by an overhead 1.3-cm-diameter PVC pipe system (Figure 2) through which seawater flow was controlled by a solenoid valve attached to an electrical timer. A single 2-mm-diameter hole was drilled in the underside of this fill-pipe above each bucket such that water dripped directly onto the soil surface during the "flood" cycle.

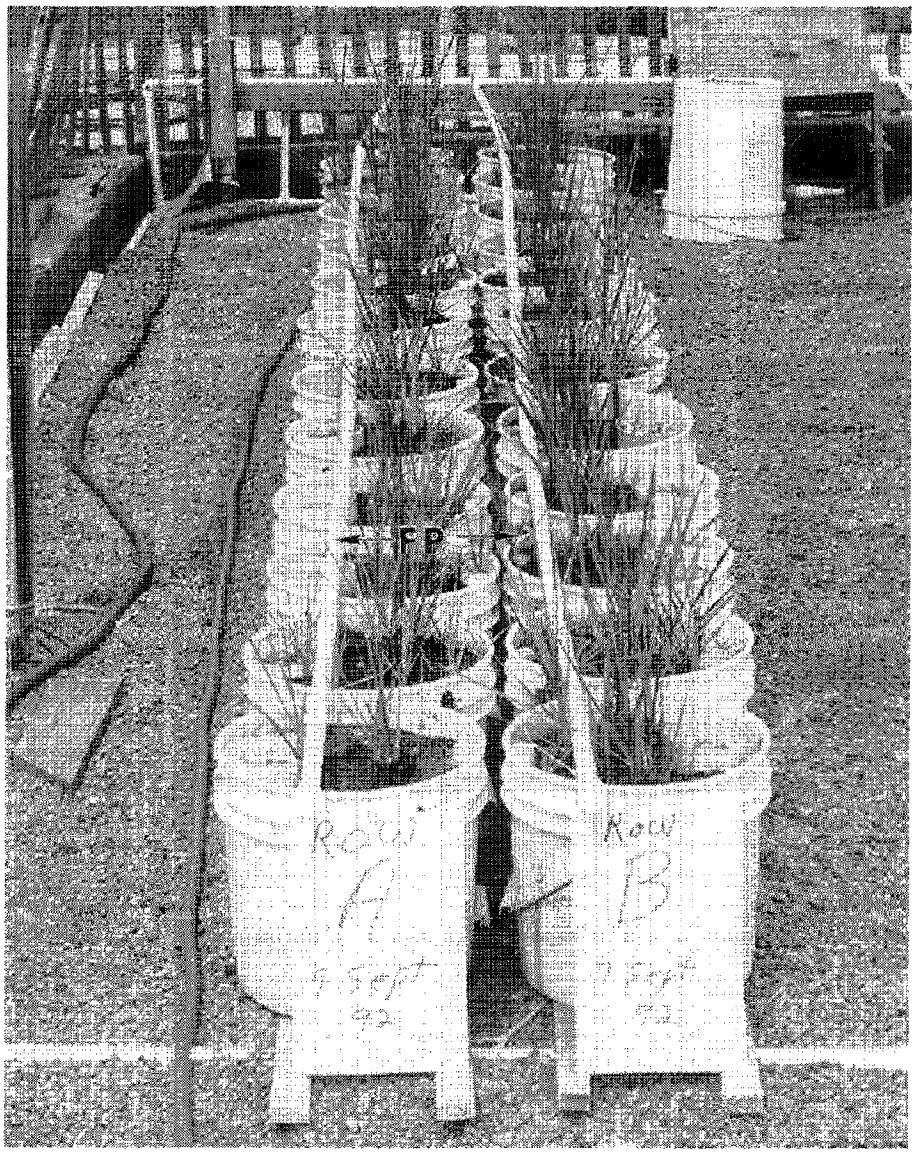

Figure 2. Double row of buckets one month prior to year 1 harvest. Note seawater fill-pipes (FP) that carried flooding water to each row. Buckets filled via 2-mm-diameter holes on the underside of FP, which dripped water directly onto soil surface. FP of left-most bucket line passed over edge of gravel filter, but fill holes were positioned to drip water onto soil surface rather than directly into filter.

Each of the 96 buckets was planted in early May 1992 with a single clump of cordgrass. Prior to planting, all subsurface tissues were washed with unfiltered seawater to remove original soil and minimize the chance that a residual soil effect would influence subsequent growth. To the extent possible, we planted equal-sized clumps in a central hole that was five cm in diameter by 10 cm deep.

To stimulate transplant growth, each bucket received one half teaspoon of Royster 16-4-8 granular fertilizer (2% iron content) once each two weeks for the first month. Thereafter, plants were not fertilized for the remainder of the two-year experiment.

After planting, buckets were positioned outdoors in eight rows of 12 at the UNC Wilmington Seawater Facility at Wrightsville Beach, North Carolina. Positioning within each row was done without regard to drainage depth but with the overall objective that four complete rows would contain six replicates of each drainage depth. All buckets sat on an 8-cm-deep layer of gravel, which covered a concrete pad (Figure 2). To reduce the likelihood that solar radiation would heat contained soil to unnaturally high temperatures, the entire experimental plot was covered with a single thickness of 1-mm-mesh polypropylene shade cloth that re-

duced light intensity by 50% without altering light quality.

Four complete rows of buckets (six replicates of each drainage depth) were harvested at the end of the first full growing season (October 1992) and represented year 1 accumulated biomass. The remaining four rows were harvested in October 1993 and represented biomass accumulated during two growing seasons. Only buckets with live plants were harvested, which reduced sample size to five replicates for each drainage depth and each harvest year.

Immediately before harvest, each bucket was photographed to document the physical appearance of above-ground plant tissues. All stem and leaf tissue was cut at ground level and oven dried (103°C). Buckets were then inverted and tapped on the side to loosen the soil cylinder. Even by the end of the first year, there was sufficient subsurface biomass in most buckets so that the soil cylinder remained intact and easy to section into discrete 3-cm-thick slabs (cut horizontally using a standard carpenter's hand saw). These slabs hereafter will be referred to as "depth increments." All plant tissue in each 3-cm depth increment was washed free of soil, oven dried, and weighed. No attempt was made to separate living from dead tissue or root from rhizome during harvest.

For all statistical analyses, year 2 data were obtained by subtracting the mean of year 1 for a given treatment depth from the total biomass measured at the end of year 2. This was done before calculating mean values since each raw data point obtained after two years actually represented total biomass accumulated over a two-year period. Significance was tested at the $\alpha=0.05$ level. Aerial:subsurface ratios for each harvest were analyzed by two-way ANOVA after log transformation to normalize data. Subsurface biomass from each depth increment was analyzed by two-way ANOVA where year and drainage depth were main effects. A one-way ANOVA was used when significant depth-by-year interaction was found.

RESULTS

Mean total (i.e., all depth increments lumped) subsurface biomass increased through time for each drainage depth (Table 1). In addition, more biomass was produced close to the surface in all drainage depths (Figure 3). There was a significant increase ($F_{15\times64}=10.26$; $P_r>F=0.0001$) in subsurface total biomass for year two compared to year one. The same statistical statement is true for each depth increment as well.

A year × drainage depth interaction indicated a different response to drainage depth by plants between years. One way ANOVA (by year) was used to determine if drainage depth influenced biomass accumulation at different depths. There was no significant effect of drainage depth on subsurface biomass accumulation by the end of year one, but significant differences were noted for year two (Table 2). These differences did not, however, represent a predictable pattern. For instance, in the 0- to 3-cm depth increment, the mean biomass in buckets drained to 3 cm was significantly different from that in buckets drained to 15 or 21 cm but did not differ from those drained to 18 cm. This unpredictable pattern continued in all increments from the soil surface to the bucket bottom. However, the relative peak of belowground biomass occurred at the increment just above the drainage depth for 4 (i.e., 3, 6, 12, and 18 cm) of the possible 7 treatments (0 cm drainage would require aerial roots).

Table 1. Mean total subsurface biomass in replicate buckets (n = 5) as a function of soil drainage depth. Year 2 values represent total mass present at year 2 harvest less mean of year 1 values for same drain depth.

Soil drained to (cm)	Total subsurface biomass (g, ± SE)	
	Year 1	Year 2
0	22.3 (4.42)	83.1 (16.71)
3	18.7 (3.48)	92.2 (14.89)
6	23.7 (1.62)	63.3 (9.43)
9	23.6 (2.75)	103.9 (15.06)
12	19.4 (4.22)	124.0 (22.69)
15	23.2 (3.53)	50.6 (13.66)
18	25.0 (5.05)	90.4 (3.30)
21	17.3 (2.38)	45.9 (10.62)

Comparisons of aerial to subsurface mass for both years are presented in Table 3. Above- ground biomass was significantly correlated with drainage depth ($r=0.84$, $n=40$) for the first year (i.e., the greater the drainage, the more above-ground tissue was produced) but not for year 2 ($r=0.14$, $n=40$). There was no significant change in the aerial:subsurface ratio from year one to year two. There also was no effect of drainage depth on aerial:subsurface ratio for either year.

DISCUSSION

We were surprised that drainage had no overriding effect on growth and accumulation of belowground plant biomass at the various depth increments. Less drainage did not favor accumulation of subsurface tissue closer to the surface, nor did deeper drainage favor proliferation at greater depths. Despite the statistically significant differences between some individual depth increments (Table 2), the apparent randomness of these differences suggests that they do not represent a biologically significant pattern. We conclude from these

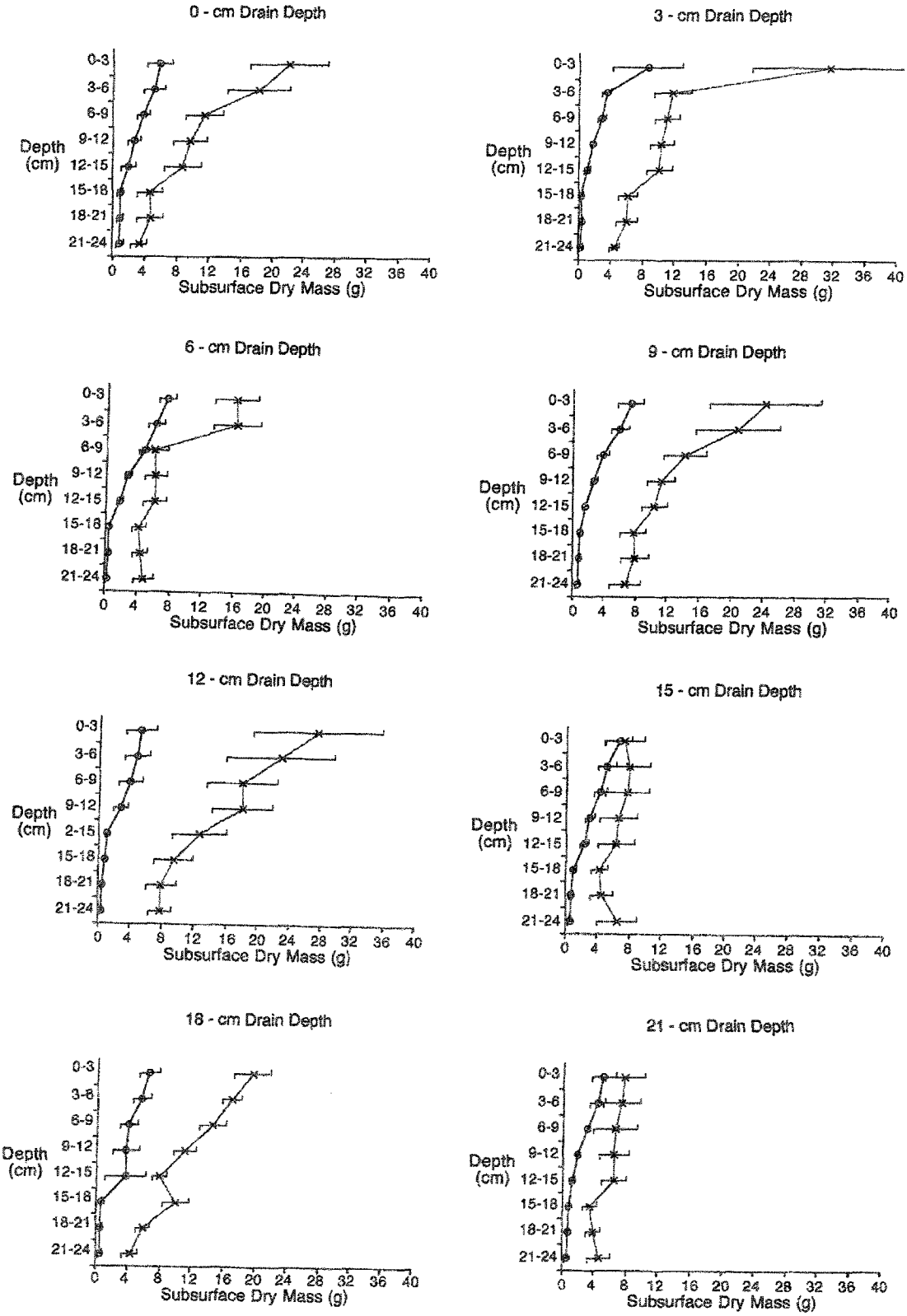

Figure 3. Mean dry weights of subsurface tissue (n=5) in each 3-cm depth increment. Horizontal bar at each data point represents standard deviation. Drain depths for each graph indicated above plot. Year 1 profile indicated by -o- and year 2 by -x-.

Table 2. Significant (α = 0.05) differences between subsurface biomass in each depth increment as related to drainage treatments for year two data. Bars connecting treatments represent no significant difference. Drain depths for each sampling increments are arranged in order of decreasing subsurface biomass differences from left to right.

Depth increment (cm)	Drainage depth (cm)	$F_{7\times39}$	Pr > F
0–3	3 12 9 0 18 6 21 15	2.86	0.0196
3–6	12 9 0 18 6 3 15 21	2.76	0.0231
6–9	12 18 9 0 3 15 21 6	3.17	0.0115
9–12	12 9 18 3 0 15 21 6	3.92	0.0034
12–15	12 9 3 0 18 15 21 6	1.64	0.1596
15–18	18 12 9 3 0 15 6 21	3.59	0.0058
18–21	9 12 3 18 0 15 6 21	1.59	0.1749
21–24	12 9 15 6 3 21 18 0	1.21	0.3263
Mean total mass/bucket	12 9 3 18 0 6 15 21	3.02	0.0149

data that the depth to which soil drains has no marked effect on proliferation of subsurface tissues of newly transplanted *S. alterniflora,* at least during the first two seasons of growth.

Statistically, however, there was a significant correlation between accumulation of aerial biomass (leaves and stems) and drainage depth during the first year but not during the second. Plants in better-drained soils were able to transfer a greater portion of their gross primary productivity into growth of aerial tissues during year one. Howes et al. (1981) noted that plants may gain better access to nutrients in a more aerobic environment by spending less energy maintaining roots. Under poorly drained conditions (0–6 cm depths), perhaps establishment of belowground tissue in year one allowed greater aerial production in year two. The fact that aerial tissue production in the present study correlated with drainage during the first year but not the second may, accordingly, relate to the initial use of high-iron fertilizer early in our study but not during year two.

Table 3. Mass (g) of aerial tissue and aerial : subsurface mass (A : S) ratios.

Drain depth (cm)	Mean dry wt. aerial tissue (g) (±SE)		A : S* ratio	
	yr 1	yr 2	yr 1	yr 2
0	7.7 (1.41)	34.6 (6.42)	0.34	0.42
3	6.7 (0.58)	28.9 (3.43)	0.35	0.31
6	9.4 (0.78)	26.9 (4.31)	0.39	0.42
9	10.4 (0.96)	39.0 (5.32)	0.43	0.38
12	11.3 (1.96)	40.5 (4.92)	0.59	0.33
15	10.6 (1.54)	27.1 (4.39)	0.45	0.54
18	12.4 (1.70)	36.7 (2.34)	0.49	0.41
21	10.8 (1.06)	24.2 (10.05)	0.62	0.53

* Ratio calculated using mean of total subsurface tissue in all replicates (n = 5).

It is apparent that the magnitude of increase in aerial as well as subsurface tissue during the second growing season suggests that a longer period of time is required before a biomass plateau would be reached. Broom et al. (1986), for instance, monitored cordgrass biomass changes for a prolonged period following transplantation on a North Carolina barrier island and reported that subsurface biomass did not reach equilibrium until the fourth growing season. It seems likely, however, that the time required for roots and rhizomes to fully stabilize new soil would vary as a function of soil composition. To our knowledge, there are no published reports of the effect of soil composition on the rate of subsurface plant growth, but we believe that such a study would be of significant environmental value in light of the absence of regulations governing the composition of fill material that can be used to create new marshes.

Our data suggest that altering soil drainage to facilitate establishment of cordgrass subsurface tissues after transplantation is unnecessary. While it seems intuitively reasonable that increased drainage (e.g., by ditching) may enhance soil oxygen content and thereby maximize root growth, our results argue that the effect would be minimal for sites planted with monocultures of cordgrass. Indeed, ditching may well have a destabilizing long-term effect on marsh community health as shown by Bourn and Cottam (1950). Their investigation compared vegetational diversity and density in an unditched Delaware salt marsh compared to an adjacent site that had been drained by mosquito-control ditching. They reported a pronounced decrease in macrophyte community diversity and plant spacing

and a corresponding decrease in associated fauna in the ditched area. They did not, however, present data on changes in aerial or subsurface plant biomass. Warren and Niering (1993) noted that ditching can, in fact, increase soil inundation in some instances where ditches cut through creek-bank levees and provide a path for tidal water to enter high marsh areas where it otherwise would not reach.

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