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EFFECT OF INCREASED WATER DEPTH ON GROWTH OF A COMMON PERENNIAL FRESHWATER-INTERMEDIATE MARSH SPECIES IN COASTAL LOUISIANA

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Abstract: The response of *Sagittaria lancifolia* to increased water depths of 7.5 and 15 cm was examined in this field study. Water-depth treatments were achieved by digging sods containing one or two individual plants or ramets of *S. lancifolia* from the marsh, removing sediment from the resulting hole, and replacing the sods in their original location at the appropriate lower elevation. Plants subjected to increased water depth of 15 cm had higher mean and maximum leaf heights than disturbed control plants. Aboveground biomass was not affected by water-depth treatment; however, 15-cm treatment plants had reduced root biomass and lowered leaf tissue concentrations of Ca, Cu, Fe, Mg, and Zn. Marsh sods at 15 cm below the marsh surface had the lowest redox potential and highest interstitial water sulfide concentration, indicating that this treatment created the most stressful belowground environment. *Sagittaria lancifolia* plants responded to the level of stress imposed by the experimental conditions with an altered growth form of increased leaf height.

Key Words: environmental stress, flooding stress, freshwater wetlands, intermediate wetlands, Louisiana, plant growth, *Sagittaria lancifolia*, water-depth tolerance

INTRODUCTION

Vegetation patterns in wetland habitats are influenced by many factors, both biotic and abiotic. One process that has been suggested as a determinant of plant spatial variation along gradients is physiological specialization to different portions of the gradient (Louda 1989). Water depth is commonly recognized as a primary physical factor that varies along elevational gradients in many wetland habitats. Studies have demonstrated that increased water depth depletes soil oxygen, which in turn affects plant metabolism and growth through such mechanisms as reduced photosynthesis, altered nutrient uptake, and hormonal imbalances (Kozlowski 1984, Mendelssohn and Burdick 1988).

Emergent herbaceous marsh species demonstrate varying responses to alterations in water depth. While flooding or submergence is, in general, regarded as inhibitory to plant growth, many marsh and aquatic plants are stimulated by such conditions (Jackson and Drew 1984). The specific growth response of freshwater marsh plants to increased water depth varies depending on the species examined. Wooten (1986) studied the effect of increased water level on seedling leaf characteristics of six *Sagittaria* species, including *S. lancifolia* L. (synonymous with *S. falcata* Pursh [Godfrey and Wooten 1979]), in a greenhouse setting and found a general pattern of decreasing leaf width and leaf length and increasing petiole length with submergence. *Typha latifolia* L. and *T. angustifolia* L. showed increased allocation to leaves, greater leaf height, and decreased allocation to reproduction, both sexual and vegetative, with increased water depth in a freshwater pond (Grace and Wetzel 1982). *Typha domingensis* Pers. also increased maximum height with increasing water depth but maintained a fixed percentage of biomass in leaves (Grace 1989). In a greenhouse study, increasing water depth had the effect of increasing shoot height in *Scirpus maritimus* L. but decreasing shoot numbers and biomass (Lieffers and Shay 1981). In contrast, Seliskar (1988) found an inhibition of stem extension and decreased plant height in *Scirpus americanus* Pers. when plants subjected to a water depth of 6 cm were compared to plants in a drained treatment. McKee and Mendelssohn (1989) found that stem density and biomass of *Panicum hemitomon* Schult. were reduced by a 10-cm elevation decrease in a field experiment; these variables were not affected in *Leersia oryzoides* (L.) and *Sagittaria lancifolia.*

Wetland plants that survive and adapt to flooded conditions may have reduced vigor and, consequently, lowered productivity. They may also become more susceptible to additional stress factors, such as increased salinity. The chemical constituents of seawater increase the likelihood of phytotoxin accumulation in soils, primarily of hydrogen sulfide and reduced forms of iron and manganese (Patrick et al. 1985). Decreased soil redox potential and sulfide accumulation were suggested as major factors limiting *Spartina alterniflora* Loisel. growth in the interior of a Louisiana saltmarsh (Mendelssohn and McKee 1988a). Interacting abiotic stress factors may therefore contribute to wetland degradation and habitat loss. In Louisiana, where more than 40% of the coastal wetlands of the contiguous United States are located, wetland loss has become a major resource management issue. Marsh interior fragmentation and loss, as opposed to shoreline erosion, was described as the main cause of large scale and widespread habitat change in Louisiana (Turner and Cahoon 1987).

The objective of this field study was to describe the response of *Sagittaria lancifolia* to increased water depth. This species is a common perennial in coastal Louisiana marshes, composing 15.2% and 6.5% of the vegetation cover in fresh (< 0.5 ppt) and intermediate (0.5 to 5.0 ppt) marsh types, respectively (Chabreck 1972). It is dominant from early spring to midsummer (February–July) in many locations, especially in the freshwater-intermediate marsh transition zone of southeast Louisiana.

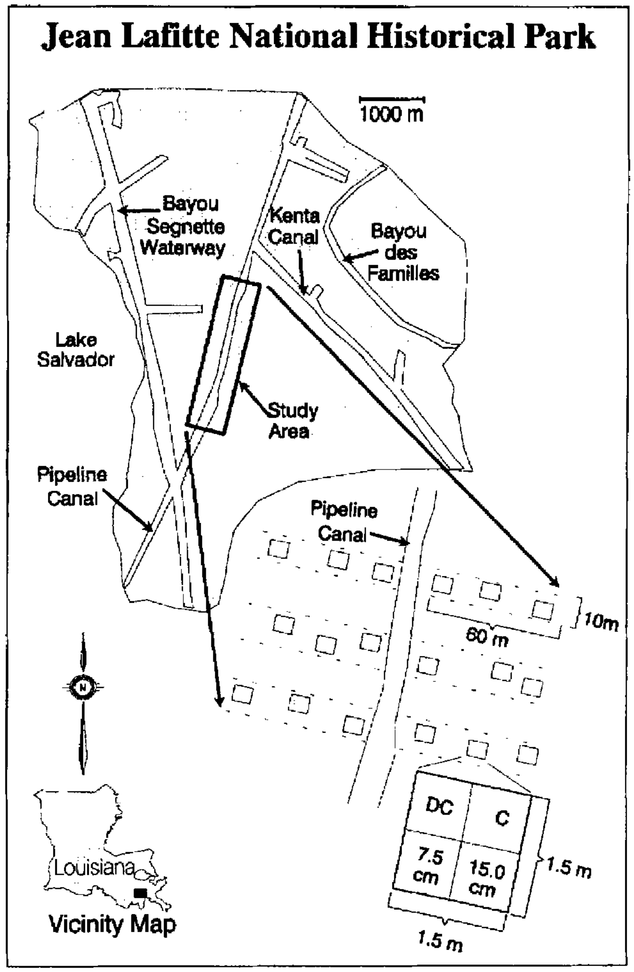

Figure 1. Location of the Barataria Unit of Jean Lafitte National Historical Park and Preserve and experimental design. Sampling sites were randomly placed within three 10-m wide zones along Pipeline Canal. Water-depth treatments were control (C), disturbed control (DC), and reduced elevations of 7.5 cm and 15.0 cm.

STUDY AREA

The site for this study was the Barataria Preserve Unit of Jean Lafitte National Historical Park and Preserve (29°45'N, 90°10'W), which covers an area of about 8,000 ha in the Barataria Basin of southeast Louisiana (Figure 1). The Barataria Basin is an interdistributary estuarine-wetland system located between the natural levees of the active Mississippi River and the abandoned Bayou Lafourche distributary (Conner and Day 1987). The basin has been essentially isolated from river flow since leveeing of the Mississippi River in the 1930-40s. Jean Lafitte National Historical Park and Preserve is located mid-basin, where wetlands are tidally influenced and wind, rainfall, and evapotranspiration act as primary hydrologic forcing functions (Conner and Day 1987).

Hydrologic alterations in the park were described in Taylor et al. (1989); these alterations range from small canals created in the late 18th century to drain agricultural lands and transport lumber, to the Bayou Segnette Waterway, a major navigation canal constructed in 1958. Since the late 1950s, the Park has experienced a sediment deficit and a slight increase (1.2 ppt) in mean salinity (Taylor et al. 1989). Documentation of vegetation change from freshwater to intermediate and brackish marsh species was provided in Taylor et al. (1989). Maps created from aerial photographs taken in 1953 and 1983 indicated a 53% decrease in freshwater marsh, a 100% increase in intermediate marsh, and a 195% increase in open water area during this time period (U.S. Fish and Wildlife Service 1983). The change in marsh vegetation was described as an increase in *Spartina patens* (Ait.) cover, which is characteristic of brackish marshes. The Park location is currently considered to be a transitional region from primarily freshwater to primarily saltwater conditions in the Barataria Basin (Demcheck 1991).

The study was conducted in an intermediate marsh dominated by *Sagittaria lancifolia* and *Spartina patens*; other species present included *Scirpus americanus, Vigna luteola* (Jacq.) Benth., *Polygonum punctatum* Ell., *Eleocharis* spp., *Hydrocotyl* spp., and *Panicum* spp. Portions of the study site were floating marsh, as described in Swarzenski et al. (1991).

METHODS

Experimental Design

The study began in April 1989 and concluded in July 1990. The experimental design is illustrated in Figure 1. Three 10-m-wide zones (north, mid, and south) were established along Pipeline Canal, extending perpendicularly from each side of the canal into the marsh. A 10-m-wide buffer strip parallel to the canal was removed from consideration to exclude canal and levee effects on vegetation. Eighteen 1.5-m^2 sampling sites were randomly selected from the edge of the buffer up to 50 m into the marsh interior; six sampling sites were located within each of the three zones, three on each canal side. The eighteen sites were therefore blocked on side and distance from the canal to remove hydrologic differences.

The manipulative design for water-level treatments was similar to that devised by Mendelssohn and McKee (1988a, 1988b). Each sampling site was divided into four quadrats, and the following treatments were randomly applied within a quadrat: an undisturbed control, a disturbed control (sod of vegetation dug up and replaced at original elevation), and two levels of increased flooding stress (sods replaced 7.5 cm and 15 cm below original elevation) (Figure 1). The experimental sods contained one or two individual plants or ramets of *S. lancifolia* and were about 0.30 m in diameter and 0.20-m deep. After flooding treatment sods were dug up, enough sediment was removed from the resulting hole to allow sod replacement at the appropriate lower elevation. Each sod was placed in plastic mesh netting that surrounded the bottom and sides to facilitate harvest at the conclusion of the experiment, to allow for the free-flow of interstitial water, and to retard ingrowth of rhizomes from plants in the surrounding marsh. Because the marsh in the study area varied from freely floating to partially attached mats, the sods were secured into position in the mat by using plastic-coated aluminum wire. Vegetation within 0.25 m of the sods and the controls was clipped to the marsh surface to standardize shading effects, and other plant species were removed periodically from the sods. To prevent nutria (*Myocastor coypus* Molina) herbivory, each of the 18 sample sites was surrounded by a wire exclosure.

Data Collection

Number of individual plants or ramets, total leaf number, leaf height above the sediment surface, and leaf blade width and length were used as indicators of plant response to flooding. Experimental sites were visited over a 4-day period every 6 to 8 weeks during the growing season on the following dates: May 23, July 11, and August 22 in 1989, and March 20, May 15, and July 10 in 1990. Sampling was started earlier in the second growing season to allow harvest at peak biomass. Because of time constraints in the field, data on plant number, leaf number, and leaf height were collected at only nine of the 18 sites during the second and third visits of the first growing season. Similarly, repeated leaf blade measurements were made just two times each growing season and also at only nine sites during the first year.

Plants were harvested in late July 1990 and oven-dried to a constant weight at 75 °C for biomass determination. Belowground material was harvested from the east side of the canal only; this material was separated into root and rhizome fractions. Young leaf tissue was collected at harvest from plants in each water-depth treatment. After rinsing in deionized water, drying to a constant weight, and grinding in a Wiley mill (60-mesh sieve), the leaf tissue was digested in nitric acid and analyzed for concentration of elemental Na and the essential nutrients Ca, Cu, Fe, K, Mg, Mn, P, and Zn using inductively coupled argon plasma spectrometry (ICP) techniques. Total leaf carbon and nitrogen content were also determined for each leaf sample using a CHN analyzer.

Environmental parameters were monitored at each treatment during all six site visits. Soil redox potential was measured within 2 cm of the sediment surface and at 15 cm below the surface using a brightened platinum electrode with a calomel reference electrode. Interstitial soil-water samples were collected using a syringe and plastic tubing (McKee et al. 1988) at 15 cm below the sod surface. Sulfide concentration was obtained by immediately placing 5 ml of interstitial water into an equal volume of antioxidant buffer and using an ion sensitive electrode to analyze the sample within 24 hr (Lazar Research Lab, Inc. application note, ISM-146 micro-electrode). The remainder of the sample was placed on ice and returned to the laboratory for measurement of pH and salinity within 1 week. A subsam-

Table 1. Plant response variables by water treatment: height in centimeters, biomass in grams per sod (0.071 m^2). LEAFHT = total leaf height, MEANHT = mean left height, MAXHT = maximum leaf height, NOPLNT = number of plants in sod, NOLEAF = number of leaves in sod, AG:BG = ratio of aboveground live to belowground biomass, AGL = aboveground live biomass, AGD = aboveground dead biomass, ROOT = root biomass, RHIZ = rhizome biomass, and BG = belowground biomass (ROOT + RHIZ).

	Water-Depth Treatment			
Variable	Control	Disturbed Control	7.5 cm	15.0 cm
LEAFHT	1691.80 (153.39)[1]	1515.48 (142.36)	1331.35 (120.84)	1521.71 (127.20)
MEANHT	86.28 (1.75)	82.19 (2.40)	87.78 (2.65)[2]	94.56 (2.69)[2]
MAXHT	114.70 (3.19)	109.65 (2.48)	115.48 (3.06)	124.71 (2.63)[2]
NOPLNT	3.00 (0.33)	2.39 (0.23)	2.39 (0.26)	2.56 (0.18)
NOLEAF	19.53 (1.76)	18.44 (1.76)	15.17 (1.41)	16.00 (1.22)
AG:BG[3,4]	0.64 (0.06)[2]	0.89 (0.06)	0.86 (0.09)	0.78 (0.09)
AGL	60.85 (6.75)	53.60 (5.79)	43.97 (4.06)	53.98 (5.19)
AGD	24.88 (3.01)[2]	17.41 (1.80)	16.57 (1.35)	19.03 (2.57)
BG[3]	88.02 (16.97)	68.48 (7.66)	66.29 (5.94)	77.10 (9.82)
ROOT[3]	12.53 (2.10)	12.67 (1.73)	9.41 (0.78)	8.50 (0.93)[2]
RHIZ[3]	75.49 (14.90)	55.81 (6.42)	56.88 (5.67)	68.61 (9.25)

[1] Mean (standard error), n = 18.
[2] Treatment mean is significantly different ($p < 0.05$) than disturbed control mean.
[3] n = 9.
[4] Analysis of log transformed data.

ple of interstitial water was filtered through a 0.45 micron filter, a portion of this filtered water was frozen for analysis of $N\text{-}NH_4$ (EPA 350.1, colorimetric automated phenate method), and the remainder was acidified for ICP analysis of soluble Ca, Cu, Fe, K, Mg, Mn, Na, P, and Zn concentrations.

Water depth was not monitored at each treatment. However, water depth above the marsh surface was measured at six locations at 4 to 6 week intervals using staff gauges anchored in the mineral substrate below the vegetation mat. The stations were located in each of the three zones along Pipeline Canal (north, mid, and south) on both the east and west sides of the canal.

Statistical Analysis

The general linear model approach to analysis of variance (ANOVA) (SAS Institute, Inc. 1991) was used to compare plant and environmental response means over the four water-depth treatments. To remove any variation due to position along the canal and distance perpendicular to the canal, the 18 sampling sites were treated as blocks in all analyses. The following predetermined contrasts were examined: 1) undisturbed control versus disturbed control (C vs. DC), 2) 7.5-cm water depth versus disturbed control (7.5 vs. DC), and 3) 15.0-cm water depth versus disturbed control (15 vs. DC). Data were transformed when necessary to meet ANOVA assumptions of variance homogeneity. Significance level was $p < 0.05$ unless otherwise indicated.

Repeated measures ANOVA with the Wilk's lambda test criterion (SAS Institute, Inc. 1991) was used to test for differences in plant response treatment means over time and to determine if differences over time depended on water-depth treatment. In these analyses, water-depth treatments represented the between-subject main effect, and time represented the within-subject factor. The appropriateness of the univariate approach to repeated measures analysis was tested with Mauchly's criterion (Moser et al. 1990, Potvin et al. 1990). Where the hypothesis of sphericity of the covariance matrices could not be met, adjusted significance levels (Greenhouse-Geisser or Huynh-Feldt) were used when only mild violation was present. In most cases, however, nonsphericity of the covariance matrices made multivariate repeated measures analyses necessary (Moser et al. 1990, Potvin et al. 1990). All repeated measures analyses were performed using site as blocks, and the two growing seasons were analyzed separately.

RESULTS

Plant Response

No treatment differences were found between initial (pre-treatment) plant measurements. At harvest, plants subjected to a 15-cm increased water depth (decreased elevation) had significantly greater mean and maximum leaf heights compared to disturbed controls, and 7.5-cm treatment plants had significantly greater mean height (Table 1). Biomass measures affected by treatment were root biomass, which was significantly re-

Table 2. Nutrient concentration in leaf tissue. Elemental concentrations are reported as ppm, and total C and N concentrations are reported as mg/g. C = control, DC = disturbed control.

	Water-Depth Treatment			
Variable	C	DC	7.5 cm	15.0 cm
Total C	413.53[1]	409.79	411.54	412.47
	(1.28)	(2.01)	(1.51)	(1.82)
Total N	18.04	19.33	18.28	18.80
	(0.60)	(0.80)	(0.49)	(0.87)
K	29574.45	30392.91	28772.67	31892.42
	(2368.23)	(2279.39)	(1847.90)	(2745.80)
Ca	4164.60	4287.31	3533.95	3460.49[2]
	(248.56)	(261.95)	(283.69)	(150.55)
Mg	3028.60	3095.01	2890.70	2733.56[2]
	(174.33)	(144.55)	(116.25)	(97.48)
P	1894.04	1935.42	1877.73	2109.77
	(72.22)	(104.55)	(78.36)	(154.49)
Na	20936.41	21767.23	21327.75	19812.44
	(643.10)	(1295.47)	(931.18)	(1064.56)
Fe[3]	52.54	64.22	51.77	49.40[2]
	(4.89)	(8.61)	(2.68)	(3.21)
Mn	71.89	75.79	68.02	62.44
	(6.54)	(7.41)	(5.18)	(6.78)
Zn[3]	73.06	94.10	42.23[2]	41.12[2]
	(7.19)	(23.16)	(5.02)	(5.64)
Cu	24.06	26.27	23.18[2]	20.37[2]
	(1.31)	(1.46)	(1.23)	(1.21)

[1] Mean (standard error), n = 18.
[2] Treatment mean is significantly different ($p < 0.05$) than disturbed control mean.
[3] Analysis of log transformed data.

duced in the 15-cm treatment, and aboveground-to-belowground ratio, which was higher in the disturbed control compared to the undisturbed control (control). There was also a significantly lower aboveground dead biomass in the disturbed control sod compared to the control.

Analyses of elemental concentrations in leaf tissue indicated that plants in the 15-cm treatment had significantly lower leaf concentrations of Ca, Cu, Fe, Mg, and Zn than the disturbed controls (Table 2). Tissue samples from the 7.5-cm treatment also had lower Cu and Zn than disturbed controls. Total C and N analyses showed no significant treatment effect. Mean leaf nutrient concentrations in the disturbed control did not significantly differ from those in the control.

Repeated measures ANOVA indicated a significant time effect in each growing season for all plant measurements, with the exception of number of plants during the first year. The time-treatment interaction was significant in the first year for mean leaf height, maximum leaf height, blade width, and blade length; this interaction was significant in the second year for leaf number only. Of these variables with significant time-treatment interaction, only mean and maximum height showed significant treatment effects overall. Mean height changed differently over time depending on water-depth treatment the first growing season, with plants in the 15-cm treatment becoming taller (Figure 2a). When measurements were initiated in the second growing season, the mean height of 15-cm treatment plants already exceeded that of the other treatments. The treatments thereafter changed similarly over time. This pattern is also apparent in the maximum height data; the significant difference between the 15-cm treatment and the disturbed control was established in the first growing season, and the treatments behaved similarly over time during the second year (Figure 2b).

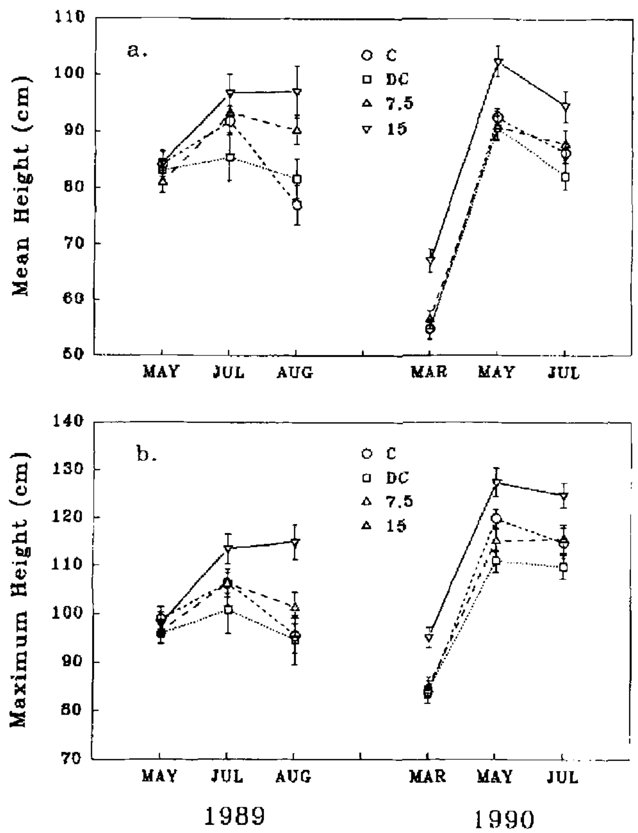

Figure 2. Mean (a) and maximum (b) leaf heights over time for the 1989 and 1990 growing seasons. Water-depth treatments were control (C), disturbed control (DC), and reduced elevations of 7.5 cm (7.5) and 15.0 cm (15).

Environmental Response

Water-depth measurements at the six staff gauges indicated seasonal variations in depth, with lowest water levels occurring during the winter (Figure 3). The sites ranged from an essentially freely-floating (north-

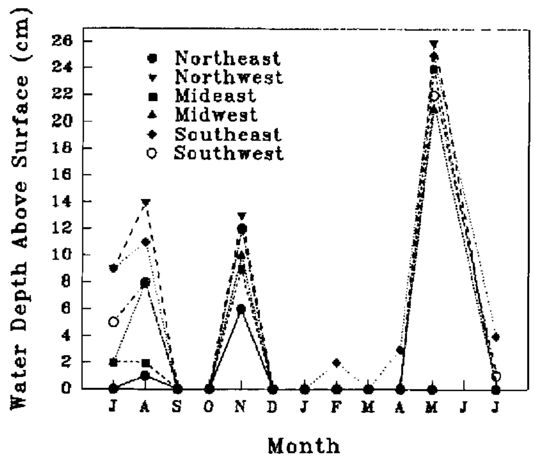

Figure 3. Water depth above marsh surface at six locations along Pipeline Canal from July 1989 to July 1990.

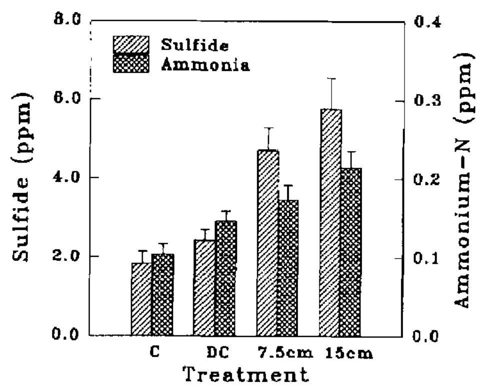

Figure 4. Post-treatment mean interstitial water sulfide and ammonium-N concentrations. Analyses performed on log transformed data.

east) to attached (northwest and southeast) vegetation mats. Despite this variation, the experimental treatments remained anchored at lower elevations in the mat throughout the study. It was noted, however, that even the 15-cm reduced elevation treatment lacked standing water during some of the low-water periods.

Analysis of initial (pre-treatment) environmental variables showed no treatment differences. Data were not collected to test for initial differences in interstitial soil water nutrient status at the surface compared to 15 cm. Establishment of the marsh sods, with no increased flooding, significantly decreased Fe, Mg, and Na concentrations and salinity/conductivity (Table 3) and increased ammonia and sulfide (Figure 4). Interstitial water surrounding the roots of plants subjected to a decreased elevation of 15 cm had significantly higher concentrations of K, Mg, Mn, Na, and P, as well as higher salinity and conductivity, than the disturbed controls (Table 3). However, interstitial water Fe and Zn were reduced at lowered elevations. Mean redox potential (Eh) was significantly lower in the 7.5- and 15-cm treatments as compared to the disturbed control (Figure 5). Trends of increasing sulfide and ammonia concentrations in interstitial water followed decreased elevation and redox potentials (Figure 4). Treatment differences in Eh were most dramatic in March 1990, for measurements at both 2 cm and 15 cm, and were less distinct at other times (Figure 6). Interstitial water sulfide concentrations, however, re-

Table 3. Elemental analyses of soil interstitial water (ppm) and soil-water pH, salinity (ppt), and conductivity (micromhos/cm × 10^4 at 25° C). Data were means for five post-treatment measurements. C = control, DC = disturbed control.

Variable	Water-Depth Treatment			
	C	DC	7.5 cm	15.0 cm
Element				
K	3.880 (0.506)	3.914 (0.340)	4.951 (0.341)[2]	5.945 (0.336)[2]
Ca	26.022 (1.406)	24.390 (0.923)	24.669 (1.189)	26.171 (1.265)
Mg	36.666 (2.049)[2]	31.759 (1.486)	33.227 (1.932)	35.556 (2.242)[2]
P	0.106 (0.015)	0.098 (0.005)	0.120 (0.007)	0.129 (0.009)[2]
Na	285.367 (17.979)[2]	240.151 (13.649)	270.952 (17.815)[2]	273.798 (18.066)[2]
Fe[3]	1.011 (0.346)[2]	0.298 (0.043)	0.259 (0.102)[2]	0.176 (0.032)[2]
Mn	0.037 (0.009)	0.042 (0.005)	0.049 (0.007)	0.059 (0.008)[2]
Zn[3]	0.098 (0.052)	0.053 (0.009)	0.030 (0.002)[2]	0.031 (0.003)[2]
Cu	0.011 (0.002)	0.008 (0.002)	0.010 (0.003)	0.010 (0.002)
pH	6.086 (0.019)	6.115 (0.021)	6.095 (0.018)	6.121 (0.015)
Salinity	1.212 (0.061)[2]	1.126 (0.049)	1.181 (0.057)	1.251 (0.062)[2]
Conduct.	0.199 (0.010)[2]	0.184 (0.008)	0.195 (0.009)[2]	0.204 (0.010)[2]

[1] Mean (standard error), n = 18.
[2] Treatment mean significantly different ($p < 0.05$) than disturbed control mean.
[3] Analysis of log transformed data.

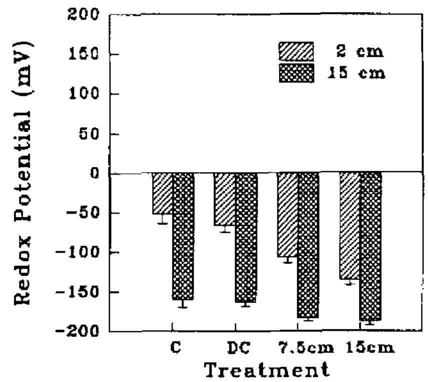

Figure 5. Post-treatment mean oxidation-reduction potential at 2- and 15-cm depths.

mained higher in the reduced elevation treatments throughout both growing seasons (Figure 7).

DISCUSSION

Because *Sagittaria lancifolia* is a common wetland plant in coastal Louisiana, it is apparently well-adapted to fluctuating water regimes. This experiment dem-

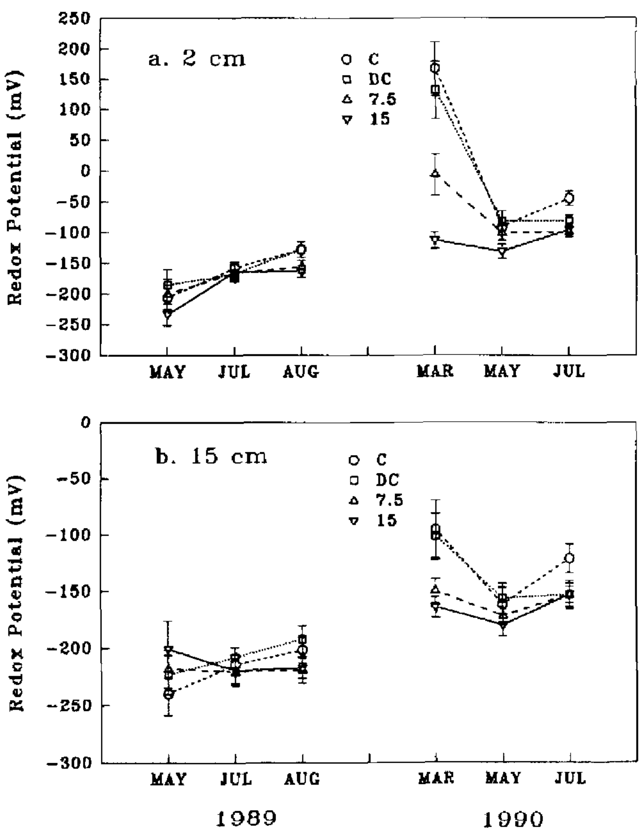

Figure 6. Eh measurements over time obtained at depths of 2 cm (a) and 15 cm (b). Water-depth treatments were control (C), disturbed control (DC), and reduced elevations of 7.5 cm (7.5) and 15.0 cm (15).

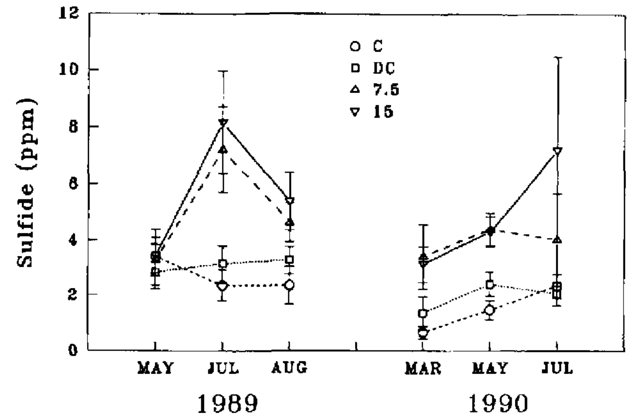

Figure 7. Interstitial water sulfide concentration over time. Water-depth treatments were control (C), disturbed control (DC), and reduced elevations of 7.5 cm (7.5) and 15.0 cm (15).

onstrated that up to 15 cm of increased water depth did not affect the standing crop of *S. lancifolia,* as indicated by aboveground and total belowground biomass determinations at the conclusion of the second growing season. The reduced net photosynthesis found for this species in a greenhouse study by Pezeshki et al. (1987) after about 2 months exposure to 5 cm of increased freshwater flooding is apparently a short-term response that does not affect biomass accumulation. Additional evidence for the ability of this species to adapt to flooding stress was provided in the field study by McKee and Mendelssohn (1989), where a 10-cm increase in water depth was found to have no effect on biomass or stem density after one growing season. A greenhouse study of the freshwater species *Justicia lanceolata* (Chapm.) Small indicated a qualitative reduction in biomass with increased water depth in the first 15 weeks of exposure to flooding; this effect, however, was not quantitatively significant at the conclusion of the experiment 8 weeks later (Llewellyn and Shaffer 1993). It should be noted that the field experiments involving *S. lancifolia* did not necessarily involve the continuous flooding stress associated with greenhouse studies or other field designs where water depth is closely controlled. In this study, natural water-level fluctuations in the tidally influenced marshes of Jean Lafitte National Historical Park and Preserve periodically drew water levels down below the surface of even the 15-cm reduced elevation treatment.

Interpretation of the aboveground-to-belowground biomass ratio results is difficult. This ratio was significantly higher in the disturbed control compared to the control, but differences between the disturbed control and the water-depth manipulation treatments were not significant. The process of digging up the sods may have caused a shift in allocation from belowground to aboveground material or simply reduced belowground production. This interpretation, however, is not substantiated by separate analyses of aboveground and belowground biomass; in these analyses, no significant treatment differences were found (Table 1).

Although total belowground (root plus rhizome) biomass of *S. lancifolia* was not affected by water depth treatment, the separation of belowground material into fractions allowed the detection of decreased root biomass in the 15-cm treatment. Mature individuals of this species have thick, tuberous rhizomes that persist for many years, so it is likely that an adverse belowground growth response would become manifested in young root material first. Root biomass was also significantly decreased in *Spartina patens* by lowered Eh in a rhizotron study (Bandyopadhyay et al. 1993). In a field study by Mendelssohn and Seneca (1980), the tall and medium growth forms of *S. alterniflora* had reduced root, rhizome, and aboveground biomass in restricted drainage treatments.

The growth form of *S. lancifolia* was affected by water-depth treatment, with greater maximum and mean leaf heights in plants subjected to a 15-cm increase in water depth and greater mean height in those subjected to a 7.5-cm increase. Expression of this morphological response required two to three months exposure to the flooding conditions in the first growing season but was apparent very early in the second growing season. McKee and Mendelssohn (1989) found that leaf elongation of this species in a greenhouse study was stimulated at low salinity (< 2.4 ppt) levels by increased water depth over a 35-day period, but mean height data were not presented.

A driving force behind the morphological response of increased leaf height was proposed by Grace (1989). This scenario is based on an increasing importance of light limitation on plant growth as water depth increases. Grace (1989) stated that a plant of a given height would have a decreasing proportion of its total biomass capable of substantial photosynthetic activity and an increasing proportion contributing to its respiratory burden as water depth is increased. Therefore, increasing height is a response that can maintain or increase the proportion of assimilatory tissue. This theory was supported by Squires and van der Valk (1992); they related the distribution of seven emergent species along a water-depth gradient in a Manitoba marsh to the individual species' ability to adjust shoot length for maintenance of sufficient shoot area above the water surface. In the present study, both suspended solids in the water and shading from the sides of the hole created to simulate the water-depth increase were probable sources of light limitation. Leaves of *S. lancifolia* in the 15-cm treatment had mean and maximum leaf heights at harvest exceeding those of the disturbed control by 12.37 cm and 15.06 cm, respectively. Although blade length and width measurements were not obtained at harvest, repeated measures analysis of data obtained before harvest indicated no overall treatment differences in leaf blade dimensions. The leaf height increase was therefore due to increased petiole length, a response to increased water depth also indicated in the greenhouse study of *S. lancifolia* seedlings by Wooten (1986). The height increase was achieved without an increase in biomass or decrease in leaf number; this could be accomplished by greater production of aerenchyma tissue in the petioles.

Manipulating the elevation of the sods altered two physical/chemical conditions. In addition to the desired increase in relative height of the water column above the sod surface in comparison to the surrounding marsh, sod sediment was brought into contact with deeper surrounding sediment. It was not possible to separate the effects of exchange with this deeper sediment from the effects of increased water depth alone on soil-water chemical characteristics. Results indicated that the water-depth treatments affected soil-water chemistry as well as plant morphology. Patrick et al. (1985) described the general patterns of nutrient changes in soils subjected to increased flooding. They noted higher concentrations of Ca, Cu, Fe, K, Mg, Mn, P, and Zn resulting from biological reduction and associated chemical reactions, including factors such as the greater solubility of some metals in reduced form. Ammonia concentrations also increase because mineralization of organic nitrogen proceeds under reduced conditions, and sulfates present are reduced to sulfides. While no change was noted in this study for Ca or Cu concentration, K, P, Mg, Mn, Na, ammonium, and sulfide did have increased concentrations in one or both of the flooded treatments compared to the disturbed control. Decreased Fe and Zn concentrations in flooded treatments may be due to reaction of hydrogen sulfide with reduced forms of these elements to produce insoluble metal sulfides (DeDatta 1981). Conductivity and salinity were significantly greater in the 15-cm treatment than in the disturbed control, but this small salinity effect is biologically insignificant.

The disturbance effect of digging up the marsh sods caused a statistically significant decrease in a number of environmental variables (Table 3). With the exception of Fe, however, the magnitude of the change was relatively minor. When sods were subjected to increased flooding, Fe concentrations were reduced further, probably due to precipitation with sulfide that also increased with flooding (Figure 4). The statistically significant increase in sulfide and ammonium due to digging was also small compared to further increases with flooding.

The effect of water-level treatments on interstitial water nutrient concentrations was not necessarily reflected in leaf tissue nutrients. Despite increased availability of K, Mg, Mn, Na, P, and N (measured as ammonium) in the interstitial water of the 15-cm treatment, tissue concentrations did not increase. In fact, Mg tissue content was lower in the 15-cm treatments. However, the decreased Fe and Zn availability in interstitial water was reflected in the leaf tissue. Leaf Ca and Cu were reduced with greater water depth, while interstitial water concentrations were not affected. The general tissue nutrient effects described are similar to those found for *P. hemitomon,* where decreased concentrations of leaf Ca, Mg, P, Fe, Mn, and Zn were found in flooded treatments of a 35-day greenhouse study (McKee and Mendelssohn 1989). In contrast, the brackish marsh species *S. patens,* when grown in flooded freshwater rhizotron conditions, had elevated tissue content of Fe and Mn and no change in Na, K, Ca, Mg, Zn, and Cu (Bandyopadhyay et al. 1993).

A possible interpretation of the nutrient patterns in *S. lancifolia* leaf tissue versus the soil water solution is that of decreased nutrient uptake by the plant. Because nutrient uptake is an active process, it will be affected by a lowered root energy status, which can result as a consequence of flooding stress (Mendelssohn et al. 1981, Koch et al. 1990). Several recent studies have linked reduced nitrogen uptake with low sediment oxygen concentrations (Morris and Dacey 1984, Howes et al. 1986, Bandyopadhyay et al. 1993). Lower root energy production as a consequence of anaerobic root metabolism, root carbon deficits resulting from increased glucose consumption during anaerobic respiration (Pasteur Effect), and carbon loss through ethanol diffusion from roots are plausible mechanisms by which N uptake may be negatively impacted by flooding stress (Mendelssohn et al. 1981, Mendelssohn and McKee 1987, Koch et al. 1990).

The trend of increasing sulfide with decreasing surface elevation and redox potential may have implications for nutrient uptake and plant growth as well. Koch et al. (1990) found that leaf elongation in the freshwater marsh species *P. hemitomon* was significantly slower in an anoxic compared to aerated treatment and was further reduced by sulfide levels above 1 mM (32 ppm). Increasing sulfide concentration inhibited root alcohol dehydrogenase activity, the enzyme that catalyzes the final step in alcoholic fermentation, and was associated with a decreased adenylate energy charge ratio and decreased nitrogen uptake (Koch et al. 1990). Although mean sulfide levels found in this study were comparatively low (maximum of 5.77 ppm), concentrations up to 40 ppm were occasionally measured. If reduced soil conditions and/or raised sulfide concentrations led to decreased nutrient uptake, however, conditions were not sufficiently stressful to adversely affect plant vigor as measured by aboveground standing crop.

In summary, *S. lancifolia* adapted to the degree of stress imposed by a 15-cm increase in water depth with increased mean and maximum leaf height and no change in aboveground biomass. These results, however, do not indicate that water depth increases of less than 15 cm will not adversely affect biomass of this species across the coastal region of southeast Louisiana. Additional factors need to be considered before any practices that alter water depth are instituted, including composition of the marsh plant community and the associated seed bank and the relative flood tolerance of all the species represented. Other plant species were selectively removed from the experimental units in this study. Therefore, interspecific competitive effects on growth of *S. lancifolia* under increased flooding regimes were removed. Additionally, similar results would not necessarily be expected in areas where water levels are permanently increased and where increased water levels coincide with increased surface water salinities; the experimental design of this study did not interfere with the normal, tidally influenced hydrologic regime of the study site. The potential for elevated soil salinity and its effects on flood tolerance and competitive interactions must also be considered.

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