Gulf of Mexico Science

Volume 27
Number 1 *Number 1*

Article 3

2009

The Effects of Flooding on Four Common Louisiana Marsh Plants

Jenneke M. Visser
Louisiana State University

Elin R. Sandy
Florida State University

DOI: 10.18785/goms.2701.03

Gulf of Mexico Science, 2009(1), pp. 21–29

The Effects of Flooding on Four Common Louisiana Marsh Plants

JENNEKE M. VISSER AND ELIN R. SANDY

The marshes of the Louisiana coastline have been deteriorating for decades as plants experience increasing levels of flooding. In this study, we determined the effects of flood duration on four of the most common marsh plants in Louisiana—*Spartina alterniflora*, *Spartina patens*, *Panicum hemitomon*, and *Sagittaria lancifolia*—by exposing them to different flooding regimes: 0%, 20%, 40%, 60%, 80%, and 100% of the time flooded. Cumulative plant height, soil redox, and soil pH were measured weekly. At the end of the experiment, above- and belowground biomass were measured. Redox measurements showed that the saturated soil (0% flooded) was slightly depleted of oxygen at a redox potential of 300 mV, whereas oxygen was depleted and nitrate and/or manganese used as electron acceptors in all the flooded treatments (20–100% flooded), which had an average soil redox potential near 200 mV. In the saturated treatment, the soil was slightly acidic (pH average 4.7), whereas the flooded treatments had neutral soil acidity (pH average 7.3). *Spartina alterniflora* biomass was significantly affected by flooding. *Spartina alterniflora* biomass in the saturated treatment was approximately twice the biomass achieved in any of the flooding treatments. *Spartina patens* showed a rapid decline in biomass with increased flood duration, reaching the lowest values in treatments that were flooded more than 50% of the time. Although aboveground biomass of *Sagittaria lancifolia* was not significantly related to flooding regime, belowground biomass decreased with increased flooding duration. The only species that showed no significant response to flooding duration was *P. hemitomon*. Our results suggest that wetland restoration techniques that reduce flooding frequency are most appropriate for organic marshes dominated by *Spartina patens* and *Spartina alterniflora*, whereas these techniques may be less appropriate for organic marshes dominated by *Sagittaria lancifolia* and *P. hemitomon*.

Accelerated sea-level rise is threatening the survival of coastal marshes throughout the world (Warren and Niering, 1993; Reed, 1995). The coastal marshes of Louisiana experience larger relative sea-level rise, as subsidence due to sediment compaction and tectonic down-warping lower the land surface, and sediment deposition from the Mississippi River is impaired (DeLaune et al., 1983; Chmura et al., 1992; Lessman et al., 1997; Gough and Grace, 1998; Reed, 2002). Restoration of these marshes is difficult because of the continuous flooding in some restoration sites (Lessman et al., 1997). Even though marsh plants tolerate saturated soils and flooded conditions, the increase in the duration of flooding is pushing the plants beyond their abilities. To improve rehabilitation and restoration project designs, it is important to know which flooding duration optimizes plant performance.

Previous studies evaluated the effects of a 100% flooding treatment vs a saturated soil condition (Mendelssohn et al., 1981; Mendelssohn and McKee, 1983; Koch and Mendelssohn, 1989; Pezeshki and DeLaune, 1993; Lessman et al., 1997), or the effect of changing marsh sod elevation under field conditions resulting in altered flooding stress (McKee and Mendelssohn, 1989; Webb et al., 1995; Grace and Ford, 1996; Gough and Grace, 1998). In general, these studies show a decrease in primary production with permanent flooding as well as with increased flooding depth. Flooding causes the soil redox potential to become more reduced as oxygen is depleted and bacteria use other electron acceptors (Patrick and DeLaune, 1972; McKee and Mendelssohn, 1989). The soil acidity is not only a function of flooding duration, but also depends on the initial soil acidity and the percentage of organic material in the soil. However, most soils tend to stabilize around neutral (pH 7) after several weeks of submergence (Ponnamperuma, 1972).

In this study, we investigated the effects of six different flooding durations, ranging from 0% to 100% of the time, on four marsh species dominating large areas along the Louisiana Gulf Coast, *Panicum hemitomon*, *Sagittaria lancifolia*, *Spartina patens*, and *Spartina alterniflora* (Visser et al., 1998). We hypothesized that an increase in flooding duration would cause 1) the soil acidity to be closer to neutral and 2) the redox potential to decrease resulting in a decrease in biomass for all species.

Methods

Panicum hemitomon, *Sagittaria lancifolia*, *Spartina patens*, and *Spartina alterniflora* were selected for this study because these species dominate a majority of the coastal marshes in Louisiana (Visser et al., 1998). Plants were collected from sites with healthy populations. Harvested sods were separated into single plants for *Sagittaria lancifolia*, and single stems for the three clonal grass species; soil material was removed from the roots. Each stem or plant was then planted into pots that contained approximately 3 liters of a 75% peat moss and 25% sand mixture. Each pot was fertilized with approximately 0.16 liter of osmocote fertilizer with 15% nitrogen and 9% phosphorus. Five replicates for each of the four species were distributed randomly among six 360-liter flood tanks, which were located outside at the Louisiana State University Aquaculture Research Station in Baton Rouge, LA. There was a sufficient space between pots and tanks so that plants did not shade one another. The total experiment consisted of 120 pots. Each tank received a different flood regime over a 7-wk period starting on 30 May 2007. The six flooding regimes were as follows: flooded 0%, 20%, 40%, 60%, 80%, and 100% of the time (Fig. 1). All tanks maintained 5 cm of water to keep the soil saturated during the nonflooded periods. In flooded conditions, tanks were filled with water to a level approximately 10–12 cm above the soil level in the pots. Flooded and drained conditions were equally spaced over the 7-wk experiment (Fig. 1). Water in the 0% and 100% flooded treatments was refreshed once a week to limit algal growth in these treatments.

Plant height was measured to the nearest millimeter once a week. For *Spartina alterniflora*, *Spartina patens*, and *P. hemitomon*, the measurement was from the soil to the tip of the tallest leaf; for *Sagittaria lancifolia*, the measurement was from the soil to the tip of each green leaf with all leaves summed together. When a *Sagittaria lancifolia* leaf turned brown it was no longer measured. When new shoots emerged for any of the four species, we added their height to the height of the parent stem in the pot. The growth rate (cm/d) for each pot was determined by subtracting the cumulative stem height at the start of the experiment (30 May) from the cumulative stem height at the end of the experiment (17 July) and dividing by 48 d.

At the end of the experiment, we measured the aboveground and belowground biomass of each plant. For the aboveground biomass, all plant material was cut at the soil level and dried at 60°C for a minimum of 48 hr. For the belowground biomass, the soil was washed from the roots in a 500-μm sieve. Once the roots were washed, they were also dried at 60°C for a minimum of 48 hr. When the samples were dry, their weights were measured to the nearest gram.

In addition to the data collected from the plants, we also measured soil acidity and soil redox potential. Soil acidity (to 0.01 on pH scale), and redox potential (to the nearest 0.1 mV), was measured using a Thermo Orion 250Aplus Hand Held pH/mV meter with a silver-chloride reference electrode. The instrument was calibrated to a pH 7 buffer and a pH 4 buffer each week before taking measurements. Soil acidity was measured in each pot once a week starting 1 wk after the experiment was initiated (six sample periods). For the soil redox potential measurement, permanent platinum electrodes were placed approximately 5 cm deep in two randomly selected pots per species per treatment. Soil redox potential was measured once a week starting 2 wk after the experiment was initiated (five sample periods). The measured Eh values were corrected to the standard hydrogen electrode by adding 207 mV (Mansfeld, 2003).

We analyzed the soil data (redox potential and acidity) using analysis of variance (PROC GLM in SAS/STAT software, version 9.1 of the SAS System for Windows) with plant species and percentage of flooding as treatments. Plant species was used as a treatment in the soil data analyses, to determine if plant roots affected the soil parameters (e.g., Brix, 1987; Wright and Otte, 1999). When the analysis of variance indicated significant effects, we used Tukey's adjusted least square difference test to reveal significant differences.

The plant data were analyzed by species, because we are interested in the species-specific response to the flooding treatments. We applied both analysis of variance and regression to elucidate the effects of flooding regime. For the analysis of variance we combined all flooded treatments, because we considered them as not physiologically different (similar pH and redox potential), and compared them to the saturated treatment. Differences among flooding treatments were generally small (<0.35 pH units and <15 mV) and although some were statistically different they were considered biologically insignificant. With the regression analysis, we explored if plants were more sensitive to the flooding regimes than were our measurements of the physical soil environment. We used a

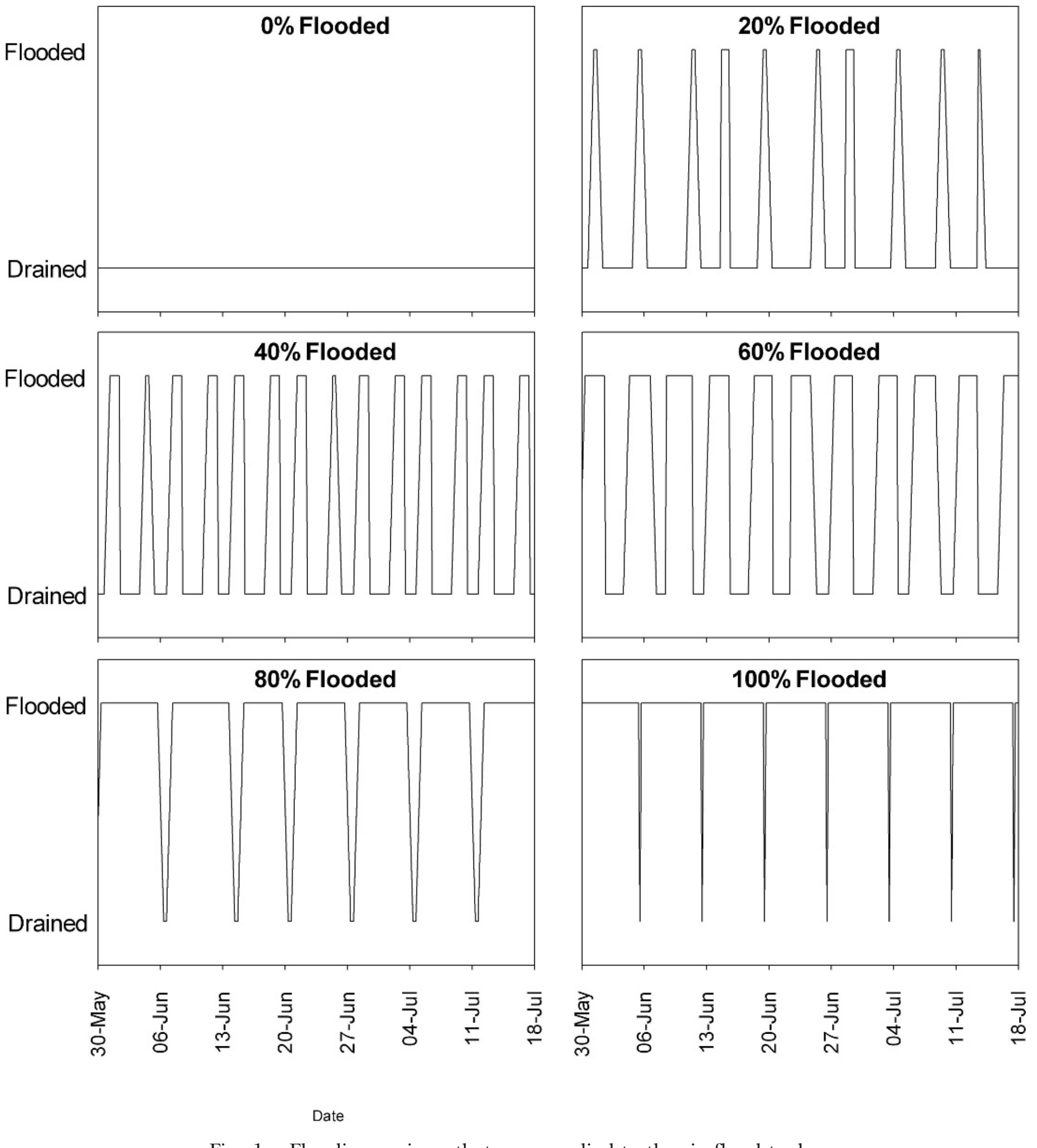

Fig. 1. Flooding regimes that were applied to the six flood tanks.

simple linear regression expecting plant growth to be increasingly negatively affected by increased flooding duration. Regression is recommended over analysis of variance because flooding duration is a continuous variable (Cottingham et al., 2005).

Results

Redox potential was statistically significant different among flooding treatments and species, but there was no significant interaction between species and flooding treatment (Table 1). On average, pots with *Sagittaria lancifolia* and *Spartina alterniflora* had higher redox potentials than pots with *P. hemitomon* and *Spartina patens*; however, these differences were extremely small (<12.5 mV) and within the error range of the redox measurements. Soil redox potential followed a similar pattern with respect to flooding treatment for all four species. Soil redox potential averaged around 331 mV for the saturated (0% flooded) treatment, then stabilized between −177 mV and 210 mV for the remaining treatments (Fig. 2).

Soil acidity was statistically significant different among flooding treatments and species, but there was no significant interaction between

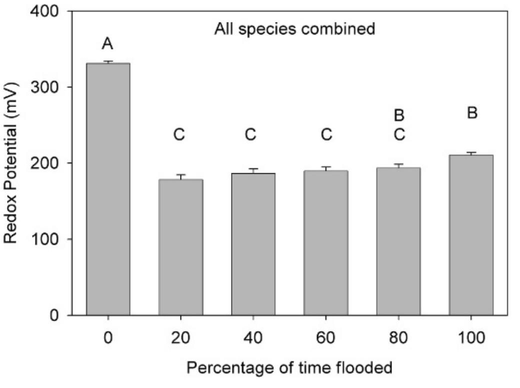

Fig. 2. Soil redox potential measured in the different flooding treatments. Each bar represents the mean of two replicate samples taken five times during the experiment for four species (n = 40). Error bars represent 1 SE. Letters indicate significant differences among treatments using Tukey's adjusted least square difference test.

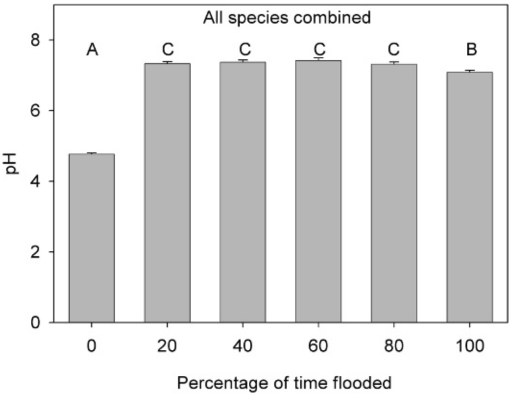

Fig. 3. Soil pH measured in the different flooding treatments. Each bar represents the mean of five replicate samples taken six times during the experiment for four species (n = 120). Error bars represent 1 SE.

species and flooding treatment (Table 1). Although soil acidity was significant different among species, Tukey's adjusted comparison of means revealed that average *Sagittaria lancifolia* soil acidity was 0.2 pH units lower than the average soil acidity for *Spartina alterniflora*, with no additional significant differences among the species. The soil in the saturated (0% flooded) treatment was acidic with a soil pH around 4.8, whereas the flooded treatments (20–100% flooded) had a neutral pH averaging between 7.1 and 7.5 (Fig. 3).

All plants of *Spartina alterniflora*, *Sagittaria lancifolia*, and *P. hemitomon* survived the 7-wk experiment and increased in cumulative stem height as the experiment progressed. However, a few of the *Spartina patens* died and a few *Spartina patens* pots were accidently planted with *Distichlis spicata*. Therefore, the results presented below represent the average for four pots in the 0% and 40% treatments, the average for three pots in the 20% and 80% treatments, and only one pot each for the 60% and 100% flooding treatments.

TABLE 1. Summary of the results from the analyses of variance of soil data.

Dependent variable	n	Source	*P*
Acidity	636	Species	0.0002
		Flooding	$<$0.0001
		Interaction	0.3008
Redox potential	240	Species	0.0046
		Flooding	$<$0.0001
		Interaction	0.7135

Analysis of variance showed significant differences in growth between flooded and saturated treatments for *Spartina alterniflora* and *P. hemitomon* (Table 2). For *Spartina alterniflora* flooded treatments had lower growth (2.3 cm/d) than the saturated treatment (3.9 cm/d). In contrast, growth of *P. hemitomon* was greater in the flooded treatments (9.2 cm/d) than in the saturated treatment (6.8 cm/d). Regression analysis revealed that growth significantly decreased with increased flooding duration for *Spartina alterniflora* and *Spartina patens* (Fig. 4; Table 3).

The aboveground biomass for all four marsh species generally decreased with an increase in the percentage of time flooded (Fig. 5). Regression analysis showed that only *Spartina alterniflora* and *Spartina patens* had statistically significant relationships between aboveground biomass and flood duration (Table 3), whereas the relationship became significant at $\alpha = 0.10$ for *Sagittaria lancifolia*. *Panicum hemitomon* achieved its highest aboveground biomass in the 20% flooding treatment (Fig. 5). Analysis of variance contrasting flooded vs saturated treatments only revealed statistically significant differences in aboveground biomass for *Spartina alterniflora*. *Spartina alterniflora* aboveground biomass in the saturated treatment (8.1 g/pot) was approximately twice as high as in the flooded treatments (4.5 g/pot).

The belowground biomass for all four species also generally decreased with an increase in the percentage of time flooded (Fig. 6). The regression analysis showed that *Spartina alterniflora*, *Spartina patens*, and *Sagittaria lancifolia* all had a significant linear relationship between belowground biomass and flooding treatments (Ta-

TABLE 2. Summary of the results from the analyses of variance of plant data.

Species	n	Dependent variable	*P*
Panicum hemitomon	30	Aboveground biomass	0.1516
		Belowground biomass	0.9423
		Total biomass	0.9102
		Growth	0.0296
Sagittaria lancifolia	30	Aboveground biomass	0.3514
		Belowground biomass	0.0007
		Total biomass	0.0266
		Growth	0.1363
Spartina patens	16	Aboveground biomass	0.2107
		Belowground biomass	0.0091
		Total biomass	0.0579
		Growth	0.1286
Spartina alterniflora	30	Aboveground biomass	0.0008
		Belowground biomass	0.0013
		Total biomass	0.0006
		Growth	0.0158

ble 3). *Panicum hemitomon* belowground biomass did not show a significant relationship with flood duration (Table 1). Analysis of variance detected significant differences in belowground biomass between flooded and saturated treatments for all species except *P. hemitomon* (Table 2). Belowground biomass was significantly higher in saturated treatments than in flooded treatments for *Spartina alterniflora*, *Spartina patens*, and *Sagittaria lancifolia* (Fig. 6).

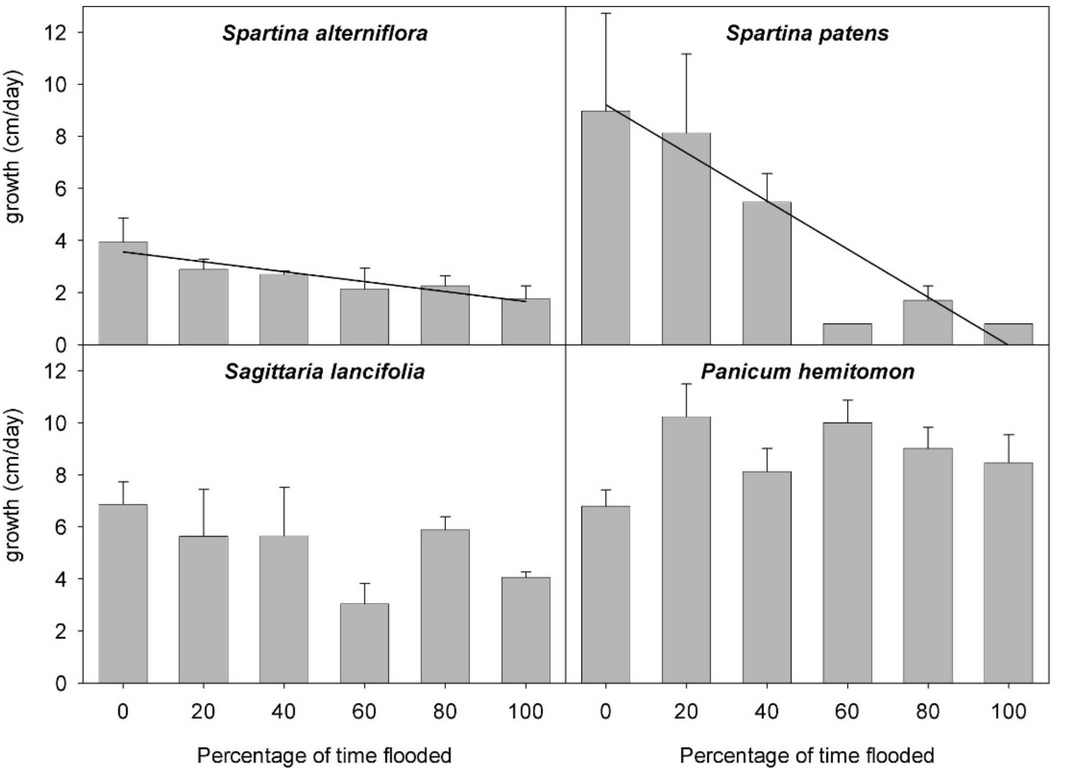

Fig. 4. Growth measured in six flooding treatments for each species. Error bars represent 1 SE. Solid lines represent significant regression fits.

TABLE 3. Summary of the results from the linear regression analysis using flooding duration as the independent variable. Significance of the relationship is indicated as follows: *** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$.

Dependent variable	Species	R^2
Growth rate	*Spartina alterniflora*	0.23**
	Spartina patens	0.37*
	Sagittaria lancifolia	0.08
	Panicum hemitomon	0.02
Aboveground biomass	*Spartina alterniflora*	0.13
	Spartina patens	0.29*
	Sagittaria lancifolia	0.12
	Panicum hemitomon	0.02
Belowground biomass	*Spartina alterniflora*	0.18*
	Spartina patens	0.31*
	Sagittaria lancifolia	0.46***
	Panicum hemitomon	<0.01

DISCUSSION

Mansfield (2003) showed a strong negative linear relationship between percentage of time flooded and redox potential in a clay soil over a 3-yr period. In his soil, redox potential decreased from approximately 500 mV in the top 10 cm of the soil, which was drained all the time, to −150mV at the 150-cm depth, which was flooded with water 95% of the time. In our experiment, flooding duration was independent of depth (i.e., the top of each pot was flooded the same amount of time as the bottom) and redox potential was measured in the top 5 cm of the substrate. Our redox measurements showed that the saturated soil (0% flooded) was slightly depleted of oxygen at a redox potential of 300 mV (Mitsch and Gosselink, 2000). In contrast, oxygen was depleted and nitrate and or manganic manganese were used as electron acceptors in the soil of all the flooded treatments (20–100% flooded), which had a redox potential near 200 mV. Tanji et al. (2003) measured changes in redox potential in a poorly drained clay soil at 5 cm and 10 cm depth in a permanently flooded rice field. Redox potential at both depths dropped rapidly in the first few days of flooding from approximately 500 mV within 24 hr after flooding to approximately 150 mV after 2 wk of flooding. Kashem and Singh (2001) evaluated the effect of flooding on mineral soils contaminated with metals in pots. They also observed drops in redox potential

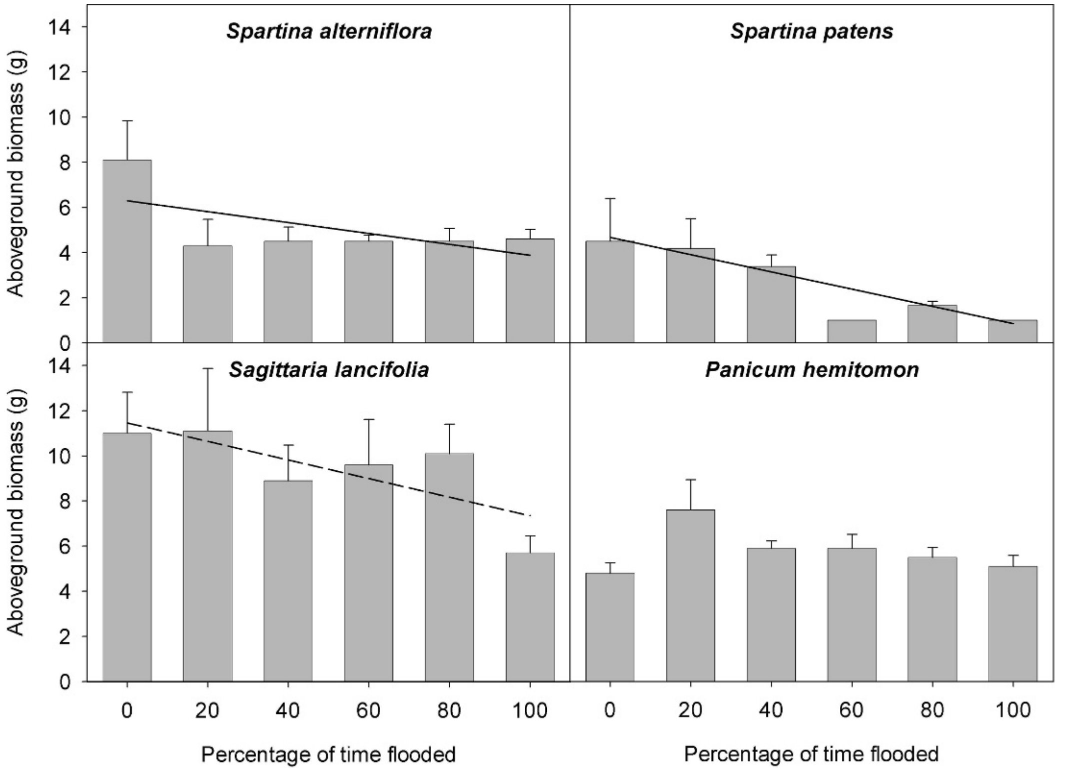

Fig. 5. Aboveground biomass of four species measured in six flooding treatments. Error bars represent 1 SE. Solid lines represent significant regression fits, dashed line represents almost significant regression fit ($P = 0.06$).

https://aquila.usm.edu/goms/vol27/iss1/3
DOI: 10.18785/goms.2701.03

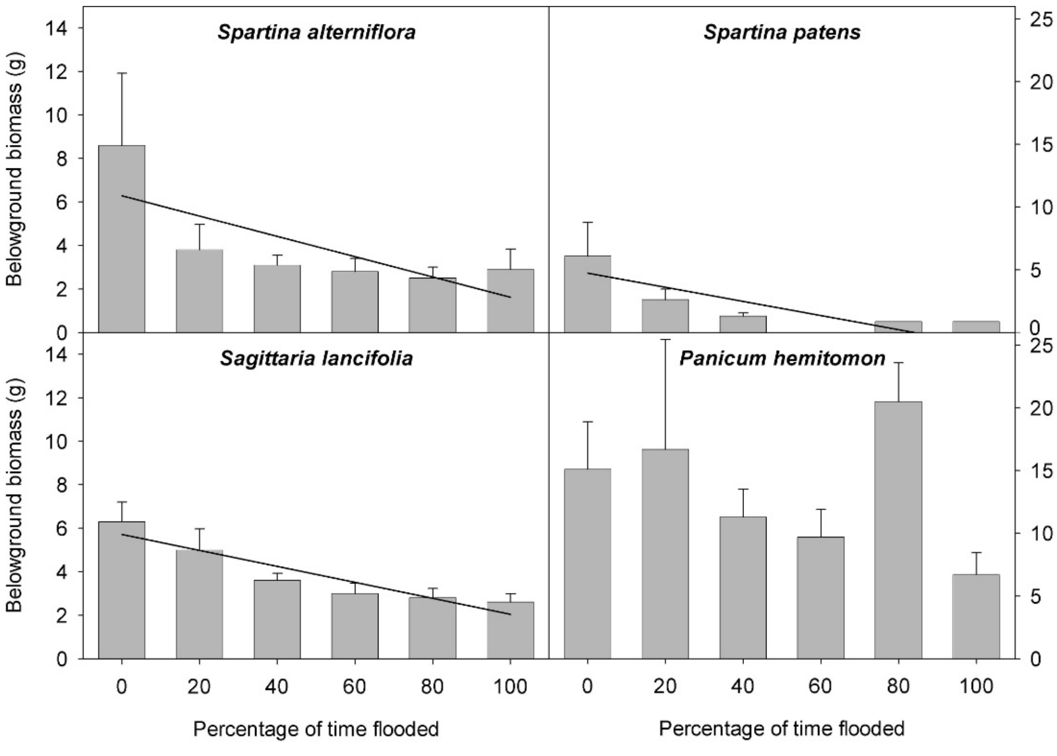

Fig. 6. Belowground biomass of four species measured in six flooding treatments. Error bars represent 1 SE. Solid lines represent significant regression fits.

(150 mV to −300 mV) within the first week of flooding in two treatments; however, for one treatment that had a high nitrate content the drop of redox potential was much more gradual. Field soils may have higher redox potential than potted soils because of several factors, including a better developed rhizosphere and bioturbation. All of our flooding treatments flooded the pots for less than a week (Fig. 1). Even our 20% flooding treatment, which had a flood duration of approximately 34 hr per flood cycle, significantly reduced the redox potential in our organic soil. Willis and Hester (2004) found that full reduction of redox potential took 5 wk of flooding, with no significant effect of soil type on redox potential. Our once-a-week refreshing of the surface water in the 100% flooding treatment may have prevented the development of lower redox conditions in this treatment.

The soil acidity for all four marsh species showed a similar pattern in relation to the flooding treatments as observed for redox potential. In the saturated treatment soils were slightly acidic (pH 4.7). In contrast, all the flooded treatments had neutral soils (pH 7.3). These differences are large enough to affect nutrient availability to the plants (Larcher, 1995). Ponnamperuma (1972) showed that soil acidity in organic soils with high iron content increased from acidic levels (pH $<$ 4) in drained conditions to a neutral level (pH 6–7) after 2 wk of continuous flooding. Our results show that this trending toward neutral soil acidity can be achieved with flooded conditions for as little as 20% of the time. Our first measurements were taken 2 wk after the start of the experiment and soil acidity changed little over the following 5 wk. The more neutral soil conditions in the flooded treatments should increase nutrient availability in the soil. However, the congruent reduction in oxygen availability probably limits the ability of the more sensitive plants (*Spartina patens*, *Spartina alterniflora*, and *Sagittaria lancifolia*) to respond. The slight increase in growth of *P. hemitomon* in the flooded treatments may be related to this increased nutrient availability.

There exists a large variability within a species in its response to stressors (Hester et al., 2001). Our results, like most others, reflect the response of a single population of each species. Our results show that *Spartina alterniflora* biomass was significantly affected by flooding duration and it was the only of the evaluated species in which both above- and belowground biomass production showed the same pattern as soil redox potential and acidity. *Spartina alterniflora* biomass in the saturated treatment was approximately twice the biomass achieved in any of the flooding treatments. Mendelssohn and McKee (1988) showed with a reciprocal transplant study that permanently flooded *Spartina alterniflora* plants had significantly lower biomass than plants growing in irregularly flooded streamside locations. Mendelssohn and McKee (1988) related the decrease in aboveground biomass to decreased soil redox potential as well as to increased interstitial sulfide and ammonium concentrations, whereas soil acidity was not a significant factor controlling growth. *Spartina alterniflora* aboveground biomass increased when its elevation in the marsh was raised by 20–30 cm, which drastically reduced the frequency of flooding (Wilsey et al., 1992; Webb et al., 1995).

Spartina patens in our study showed a rapid decline in biomass with increased flooding, reaching the lowest values in treatments that were flooded more than 50% of the time. This indicates that the 20% flooding duration inhibited growth less than the 40% flooded treatment even though soil redox potential was essentially the same in these two treatments. However, redox-potential measurements may not be sensitive enough to capture all soil redox reactions (Tanji et al., 2003) to which *Spartina patens* is responding. Burdick et al. (1989) studied three zones in a brackish marsh with a mixture of *Spartina patens*, *Spartina alterniflora*, and *D. spicata*: a lower-elevation (most flooded) inland zone, a high-elevation (least flooded) berm zone, and an intermediate-elevation stream-edge zone. Soil redox potential was highest in the more porous stream edge, intermediate in the berm, and lowest in the inland zone. This illustrates the influence of soil porosity on the effect of flooding on soil redox potential. *Spartina patens* biomass was four times higher in the berm zone than in the edge and inland zone. Competition with *Spartina alterniflora* as well as differences in sulfide and ammonium concentrations may have contributed to the reduced biomass at the edge. In our study, competition was absent and soil porosity constant among the different flooding treatments. Webb et al. (1995) showed that the aboveground biomass of *Spartina patens* increased fourfold when marsh sods were raised 20 cm above the ambient marsh surface, which increased the soil redox at 2 cm depth from ~−100 mV to ~+125 mV. We found *Spartina patens* aboveground biomass at 0% and 20% flooding to be four times higher than the aboveground biomass of >50% flooded treatments.

Although aboveground production of *Sagittaria lancifolia* was not significantly related to flooding regime, belowground biomass decreased with increased flooding duration in our experiment. Howard and Mendelssohn (1995) lowered *Sagittaria lancifolia* marsh sods by 7.5 cm and 15 cm, which resulted in a linear decrease in the average soil redox at 2 cm below the marsh surface. *Sagittaria lancifolia* response with decreased elevation included an increase in mean height, no effect on aboveground biomass, and no effect on total belowground biomass (roots and rhizomes), although root biomass decreased. Howard and Mendelssohn postulated that responses from the tuberous rhizomes maybe very slow since they persist for many years. The *Sagittaria lancifolia* plants we harvested were relatively young with minimal rhizome development and therefore most of our belowground biomass for this species consisted of roots. Martin and Shaffer (2005) exposed mature *Sagittaria lancifolia* plants to 5 cm and 30 cm permanent flooding depth in a greenhouse setting and found no significant differences in above- and belowground biomass.

The only species that showed no significant response to flooding duration was *P. hemitomon*. Willis and Hester (2004) compared saturated with permanently flooded treatments and found no significant effects on above- and belowground biomass of *P. hemitomon*. Willis and Hester (2004) measured larger adventitious root biomass in the deeper-flooded treatment. We observed adventitious root development in the longer-flooded treatments, but did not separate adventitious roots from the aboveground biomass.

Our results suggest that wetland restoration techniques that reduce flooding frequency are most appropriate for organic marshes dominated by *Spartina patens* and *Spartina alterniflora*, whereas these techniques may be less appropriate for organic marshes dominated by *Sagittaria lancifolia* and *P. hemitomon*. Results from similar experiments using mineral soils are needed before a more general recommendation is made. Our experiment focused on duration of flooding with fresh water, whereas *Spartina alterniflora* and *Spartina patens* occur in saline environments. Additional experiments are needed to test for the effect of flooding using water with different salinities.

Literature Cited

Brix, H. 1987. Treatment of wastewater in the rhizosphere of wetland plants—the root-zone method. Water Sci. Technol. 19:107–118.

Burdick, D. M., I. A. Mendelssohn, and K. L. McKee. 1989. Live standing crop and metabolism of the marsh grass *Spartina patens* as related to edaphic factors in a brackish, mixed marsh community in Louisiana. Estuaries 12:195–204.

Chmura, G. L., R. Costanza, and E. C. Kosters. 1992. Modeling coastal marsh stability in response to sea level rise: a case study in coastal Louisiana, USA. Ecol. Model. 64:47–64.

Cottingham, K. L., J. T. Lennon, and B. L. Brown. 2005. Knowing when to draw the line: designing more informative ecological experiments. Front. Ecol. Environ. 3:145–152.

Delaune, R. D., R. H. Baumann, and J. G. Gosselink. 1983. Relationships among vertical accretion, coastal submergence and erosion in a Louisiana Gulf Coast marsh. J. Sediment. Petrol. 53:147–157.

Gough, L., and J. B. Grace. 1998. Effects of flooding, salinity, and herbivory on coastal plant communities, Louisiana, United States. Oecologia 117:527–535.

Grace, J. B., and M. A. Ford. 1996. The potential impact of herbivores on the susceptibility of the marsh plant *Sagittaria lancifolia* to saltwater intrusion in coastal wetlands. Estuaries 19:13–20.

Hester, M. W., I. A. Mendelssohn, and K. L. McKee. 2001. Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora*: morphological and physiological constraints. Environ. Exp. Bot. 46:277–297.

Howard, R. J., and I. A. Mendelssohn. 1995. Effect of increased water depth on growth of a common perennial freshwater-intermediate marsh species in coastal Louisiana. Wetlands 15:82–91.

Kashem, M. A., and B. R. Singh. 2001. Metal availability in contaminated soils: i. effects of flooding and organic matter on changes in Eh, pH, and solubility of Cd, Ni, and Zn. Nutr. Cycl. Agroecosyst. 61:247–255.

Koch, M. S., and I. A. Mendelssohn. 1989. Sulphide as a soil phytotoxin: differential responses in two marsh species. J. Ecol. 77:565–578.

Larcher, W. 1995. Physiological plant ecology. Springer, Berlin, Germany.

Lessman, J. M., I. A. Mendelssohn, M. W. Hester, and K. L. McKee. 1997. Population variation in growth response to flooding of three marsh grasses. Ecol. Eng. 8:31–47.

Mansfeld, T. 2003. In situ long-term redox potential measurements in a dyked marsh soil. J. Plant Nutr. Soil Sci. 166:210–219.

Martin, S. B., and G. P. Shaffer. 2005. *Sagittaria* biomass partitioning relative to salinity, hydrologic regime, and substrate type: implications for plant distribution patterns in coastal Louisiana, United States. J. Coast. Res. 21:167–174.

McKee, K. L., and I. A. Mendelssohn. 1989. Response of a freshwater marsh plant community to increased salinity and increased water level. Aquat. Bot. 34(4):301–316.

Mendelssohn, I. A., and K. L. McKee. 1983. Root metabolic response of *Spartina alterniflora* to hypoxia, p. 239–253. *In:* Plant life in aquatic and amphibious habitats. R. M. M. Crawford (ed.). British Ecological Society, Special Publication 5. Wiley-Blackwell, Oxford, United Kingdom.

———, and ———. 1988. *Spartina alterniflora* die-back in Louisiana: time-course investigation of soil waterlogging effects. J. Ecol. 76:509–521.

———, ———, and W. H. Patrick Jr. 1981. Oxygen deficiency in *Spartina alterniflora* roots: metabolic adaptation to anoxia. Science 214:439–441.

Mitsch, W. J., and J. G. Gosselink. 2000. Wetlands. 3rd ed. John Wiley and Sons, Inc., New York.

Patrick, W. H., Jr., and R. D. Delaune. 1972. Characterizations of the oxidized and reduced zones in flooded soil. Proc. Soil Sci. Am. 36:573–576.

Pezeshki, S. R., and R. D. Delaune. 1993. Effects of soil hypoxia and salinity on gas exchange and growth of *Spartina patens*. Mar. Ecol. Prog. Ser. 96:75–81.

Ponnamperuma, F. N. 1972. The chemistry of submerged soils. Adv. Agron. 24:29–96.

Reed, D. J. 1995. The response of coastal marshes to sea-level rise: survival or submergence? Earth Surface Process. Landforms 20:39–48.

———. 2002. Sea-level rise and coastal marsh sustainability: geological and ecological factors in the Mississippi Delta plain. Geomorphology 48:233–243.

Tanji, K. K., S. Gao, S. C. Scardaci, and A. T. Chow. 2003. Characterizing redox status of paddy soils with incorporated rice straw. Geoderma 114:333–353.

Visser, J. M., C. E. Sasser, R. H. Chabreck, and R. G. Linscombe. 1998. Marsh vegetation types of the Mississippi River deltaic plain. Estuaries 21:818–828.

Warren, R. S., and W. A. Niering. 1993. Vegetation change on a northeast tidal marsh: interaction of sea-level rise and marsh accretion. Ecology 74:96–103.

Webb, E. C., I. A. Mendelssohn, and B. J. Wilsey. 1995. Causes for vegetation dieback in a Louisiana salt marsh: a bioassay approach. Aquat. Bot. 51:281–289.

Willis, J. M., and M. W. Hester. 2004. Interactive effects of salinity, flooding, and soil type on *Panicum hemitomon*. Wetlands 24:43–50.

Wilsey, B. J., K. L. McKee, and I. A. Mendelssohn. 1992. Effects of increased elevation and macro- and micronutrient additions on *Spartina alterniflora* transplant success in salt-marsh dieback areas in Louisiana. Environ. Manage. 16:505–511.

Wright, D. J., and M. L. Otte. 1999. Wetland plant effects on the biogeochemistry of metals beyond the rhizosphere. Biol. Environ. Proc. R. Ir. Acad. 99(B):3–10.

(JMV) Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana 70803; and (ERS) Department of Biological Sciences, Florida State University, Tallahassee, Florida 32306. Present addresses: (JMV) Department of Renewable Resources, University of Louisiana Lafayette, P.O. Box 44650, Lafayette, Louisiana 70504; and (ERS) Department of Oceanography and Coastal Sciences, Louisiana State University, Baton Rouge, Louisiana 70803. Send reprint requests to JMV. Date accepted: October 23, 2009.