Journal of Coastal Research | 26 | 5 | 901–911 | West Palm Beach, Florida | September 2010

Hurricanes, Floods, Levees, and Nutria: Vegetation Responses to Interacting Disturbance and Fertility Regimes with Implications for Coastal Wetland Restoration

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ABSTRACT

MCFALLS, T.B.; KEDDY, P.A.; CAMPBELL, D., and SHAFFER, G., 2010. Hurricanes, floods, levees, and nutria: vegetation responses to interacting disturbance and fertility regimes with implications for coastal wetland restoration. *Journal of Coastal Research*, 26(5), 901–911. West Palm Beach (Florida), ISSN 0749-0208.

A primary cause of wetland loss in the Louisiana coastal zone has been the construction of flood control levees along the Mississippi River. These levees restrict the inputs of freshwater, nutrients, and sediment that historically replenished these wetlands. Wetland loss is compounded by other factors such as storms, introduced herbivores, and saltwater intrusion. How do such simultaneous changes in fertility and disturbance regimes affect the vegetation of coastal wetlands? Will proposed restoration strategies, such as freshwater diversions and protection from herbivores, increase the productivity and accretion rates of coastal wetlands without sacrificing plant species diversity? During this 2-year study, we applied five disturbance treatments (control, fire, herbivory, single vegetation removal, and double vegetation removal) and four fertility treatments (control, sediment addition, fertilizer addition, and sediment + fertilizer addition), using a split-plot factorial design with herbivory exclosures as main plots and species richness and total aboveground biomass as dependent variables. We found that nutria, the principal vertebrate herbivore of the marsh, limited biomass production. Other disturbances decreased biomass, but only to a limited extent in the absence of herbivores. The sediment + fertilizer treatment, which simulated the additional nutrients and substrate material that a freshwater diversion might deliver, significantly increased biomass production. Fertilizer significantly increased the biomass only in the absence of herbivores. We had limited success in predicting species richness after 2 years. Only the most severe disturbance decreased species richness, whereas fertilizer addition seemed to have a minor effect ($p = 0.08$). Sediment- and nutrient-rich waters from freshwater diversions will likely mitigate negative impacts of nutria grazing on biomass and have no effect on species richness. However, it should be noted that freshwater diversions will have the most impact if nutria populations are reduced.

ADDITIONAL INDEX WORDS: *Dynamic equilibrium model, fertilizer, fire, freshwater diversion, herbivory, Huston's model of diversity, Louisiana, oligohaline marsh, sediment.*

INTRODUCTION

The Louisiana coastal zone experiences some of the highest land degradation and loss rates in the world (Boesch *et al.,* 1994; Britsch and Dunbar, 1993; Gagliano, Meyer-Arendt, and Wicker, 1981). Wetland loss is primarily driven by the construction of flood control levees along the Mississippi River during the past 2 centuries, which has severely restricted the input of freshwater, nutrients, and sediment to its delta (Day *et al.,* 2000, 2007; Martin *et al.,* 2000; Shaffer *et al.,* 1992). Coastal wetlands convert to open water if accretion does not keep pace with relative sea level rise (eustatic sea level rise + subsidence). With much of the Mississippi River watershed under strict flood control (Cowdrey, 1977), freshwater, nutrients, and sediment are not available to rebuild the rapidly submerging wetlands of the deltaic plain (Baumann, Day, and Miller, 1984; Martin *et al.,* 2000; Mossa, 1996). Wetland loss in the deltaic plain is compounded and accelerated by multiple disturbances. Hurricanes and tropical storms periodically erode protective barrier islands and directly affect wetlands through scouring, sediment and wrack deposition, and extensive salt burning of wetland vegetation (Baldwin, Mckee, and Mendelssohn, 1996; Baldwin and Mendelssohn, 1998; Boesch *et al.,* 1994; Guntenspergen *et al.,* 1995). Saltwater intrusion from dredged canals for navigation or oil exploration also leads to salt burning and loss of wetland vegetation (Boesch *et al.,* 1994; Turner, 1997). As well, herbivory from the introduced rodent, nutria, (*Myocastor coypus* [Molina]) severely reduces overall wetland biomass and can lead to the conversion of wetland to open water (Carter, Foote, and Johnson-Randall, 1999; Carter *et al.,* 1999; Conner, 1989; Ford and Grace, 1998; Taylor and Grace, 1995). Primary restoration strategies for wetlands in the delta now focus on (1) diversions of Mississippi River water across levees to augment inputs of freshwater, nutrients, and sediments to wetlands, and (2) the control of nutria populations. Hence, restoration strategies of wetlands in the delta of the Mississippi River will change both fertility and disturbance regimes.

In this study, we examined the effects of multiple disturbances and fertility enhancements upon the plant diversity of

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DOI: 10.2112/JCOASTRES-D-09-00037.1 received 8 April 2009; accepted in revision 2 July 2009.

an oligohaline marsh in the delta of the Mississippi River (Platt, 1988; Saucier, 1963). The Huston (1979) dynamic equilibrium model (DEM) of diversity was used as a conceptual framework for the design, testing, and interpretation of our experiments. We asked three questions: (1) How do simultaneous disturbance and fertility regimes affect the vegetation of coastal wetlands that are already subject to a number of perturbations and stressors, such as hurricanes, levees, and introduced herbivores? (2) Will proposed restoration strategies, such as herbivore protection and freshwater diversions, benefit (*i.e.,* increase biomass) the wetlands along the Gulf Coast? (3) Can the productivity and accretion rates of rapidly submerging coastal wetlands be increased without sacrificing plant species diversity? Our primary focus was the consequences of possible interactions of multiple disturbance and fertility treatments on species richness and biomass.

The Huston (1979) DEM is particularly appropriate for studying coastal wetlands in the Mississippi River delta, because both historic anthropogenic changes have, and proposed restoration strategies will, alter fertility and disturbance regimes. The DEM postulates that measurable relationships exist between two fundamental factors of ecological communities: disturbance and fertility (Grime, 1979; Southwood, 1977). The DEM also offers probable mechanisms: the rate at which biomass accumulation causes competitive displacement, and the rate at which biomass loss allows coexistence. As such, low disturbance rates require low recovery rates (low fertility) to maintain high biological diversity, but equally, high disturbance rates require high recovery rates (high fertility) to maintain high biological diversity. The Huston (1979) model includes both the intermediate disturbance hypothesis (Connell, 1978) and the unimodal productivity–diversity hypothesis (Grime, 1973, 1979), producing a synthesis of two well-supported diversity models.

The DEM assumes that (1) the subject community is not at equilibrium, as a result of periodic population reductions (disturbances); (2) its component species have different population growth rates; and (3) some environmental changes affect all competing species in the same way (Huston, 1979). Wetlands along the Gulf Coast, particularly oligohaline marshes, are certainly subject to multiple disturbances (storms, high salinity pulses, herbivory; *e.g.,* Boesch *et al.,* 1994), which reduce populations of plant species. They are also dominated by different functional types, including annuals and perennial emergents and herbaceous vines (McFalls, 2004), with fundamentally different population growth rates. As well, environmental changes, such as increases in fertility through nutrient input from Mississippi floodwaters or salt burning from hurricane storm surges, affect all the component species similarly at any one site (*e.g.,* Boesch *et al.,* 1994). As such, many wetlands along the Gulf, and particularly, the oligohaline marshes, should be particularly suited to the DEM.

Rationale for Treatments

Disturbance Treatments

Disturbances, defined as events that destroy plant biomass (Grime, 1977, 1979), strongly influence species diversity and biomass patterns by creating heterogeneity in ecological communities (Brewer, Levine, and Bertness, 1998; Connell, 1979; Shumway and Bertness, 1994; Watt, 1947). This heterogeneity is created from the differential survival and recovery of species based on life history strategies, reduced competitive exclusion, and the changes that occur in edaphic factors due to the disturbance (*e.g.,* Al-Mufti *et al.,* 1977; Grime and Hunt, 1975; Grubb, 1977; Skellam, 1951). Disturbance intensity, measured as the proportion of biomass killed (Grime, 1979; Sousa, 1984), dictates how far the system is perturbed. In this study, we applied disturbance treatments of increasing intensity in the following postulated order: control, fire, herbivory, single vegetation removal treatment, and double vegetation removal treatment.

Fire is a natural process in coastal wetlands, and prescribed burning has been used historically as a management tool in Louisiana marshes (Nyman and Chabreck, 1995). Fire is generally used as a technique to increase diversity, but it can also decrease biological diversity in wetlands if organic matter in the soil is ignited, creating new depressions with increased flooding (Lane, Day, and Day, 2006; Vogl, 1973; White, 1994).

Herbivory can have significant effects on species composition in wetlands, especially at small spatial scales (Bakker, 1985; Bazely and Jeffries, 1986). Nutria are herbivores of particular concern in Louisiana because they exert pressure on an already stressed coastal system (Conner, 1989; Nyman, Chabreck, and Kinler, 1993; Rejmanek, Gosselink, and Sasser, 1990; Taylor and Grace, 1995). Nutria not only destroy large expanses of vegetation, but they may subsequently prevent regeneration in these areas (Carter, Foote, and Johnson-Randall, 1999; Shaffer *et al.,* 1992). Herbivory was expected to be a stronger disturbance than fire based on the selective nature of herbivores and the many published studies on the effects of nutria grazing and grubbing (Ford and Grace, 1998; Llewellyn and Shaffer, 1993; Myers, Shaffer, and Llewellyn, 1994; Shaffer *et al.,* 1992; Taylor *et al.,* 1994). Nutria have a yearlong effect on vegetation, whereas fire is a one-time disturbance.

Vegetation removal treatments were included to simulate extreme disturbances that can occur in deltaic wetlands, such as erosion, wrack deposition, and salt burning, associated with hurricane damage (Guntenspergen *et al.,* 1995). A single vegetation removal treatment was a pulse disturbance designed to cause 100% mortality in adult plants, but to allow regeneration from buried propagules. Although not a topic of this article, the regeneration would allow an examination of the role of the seed bank in vegetation recovery. Once again, although not a topic of this article, the double vegetation removal treatment was designed to examine the role of propagule dispersal and colonization in vegetation recovery. Plants were allowed to regenerate, but they were periodically killed before producing seed. The vegetation removal treatments using herbicide were expected to be the two strongest disturbances because all aboveground and belowground biomass was killed, whereas nutria herbivory and fire treatments were expected to primarily remove aboveground biomass only.

Fertility Treatments

Increases in biomass production are brought about by increases in available resources (Grime, 1979). Such increases not only have profound effects on community interactions, composition, and species richness (Grime, 1973, 1977, 1979) but also can fundamentally alter ecosystem processes, such as decomposition, nutrient cycling, and accretion (Craft and Richardson, 1993). Fertility treatments were designed to include factors that might affect both production and accretion in Louisiana's rapidly submerging coastal areas. The fertility treatments serve, in part, to evaluate the potential for restoring coastal wetlands by means of diversions of sediment and nutrient-rich freshwater from the Mississippi River. Fertility treatments of hypothesized increasing intensity were applied: no fertility enhancement (control), sediment addition, fertilizer addition, and sediment + fertilizer addition.

Sediment additions were designed to simulate the regular sediment deposition that would occur during a normal year if spring flooding occurred (Saucier, 1963). Sediment input provides both mineral substrate and nutrients (Frey and Basan, 1978; Johnston *et al.,* 1984; Niering and Warren, 1980). The high productivity of riverine and deltaic wetlands is often attributed to the regular deposition of nutrient-rich mineral sediments in floodwaters (Day *et al.,* 2000; Gorham and Pearsall, 1956; Mitsch and Gosselink, 2000; Ranwell, 1964). However, sediment input in wetlands does not only provide nutrients. It can also have negative effects by filtering out species unable to cope with burial (Dittmar and Neely, 1999; Jurik, Wang, and Van Der Valk, 1994; Keddy, 2000; Neely and Wiler, 1993; Van Der Valk, Swanson, and Nuss, 1983) and can, therefore, act as a disturbance under the DEM, depending on the thickness of deposited sediment. Over time, continued sediment additions will increase elevation and reduce flooding, potentially increasing the pool of colonists (Gough and Grace, 1998).

Fertilizer additions simulated the higher nutrient loadings that would probably accompany spring flooding if water control structures were not in place along the Mississippi River. Increases in nutrients alone may also increase accretion in wetlands through peat accumulation (Craft and Richardson, 1993). Additions of both sediment and fertilizer were designed to more accurately simulate a spring flooding event, where dissolved nutrients and suspended sediments are deposited on the wetland surface. The actual extent of nutrient and sediment inputs into wetlands from river diversions will depend on the rate and timing of inputs, the landscape position of wetlands, and the distance of wetlands from distributaries.

METHODS

Study Area

The research was conducted at Turtle Cove Experimental Marsh (30°17′ N, 90°20′ W; 0.3 m elevation National Geodetic Vertical Datum), located in the wetlands south of Southeastern Louisiana University's Turtle Cove Environmental Research Station, 35 km northwest of New Orleans, Louisiana (Figure 1). This marsh is on the Manchac land bridge, a 10-km strip of wetland that separates Lake Pontchartrain and Lake Maurepas in the Lake Pontchartrain basin of southeast Louisiana. At Hammond, Louisiana, 28 km to the north, mean annual temperature is 19.3 °C (January, 9.9 °C; July, 27.6 °C), and mean annual precipitation is 162.6 cm, based on 1971–2000 average climate temperatures from the Southern Regional Climate Center (SRCC, 2004a, 2004b). The site receives minor tidal influence (0.05–0.15 m), but wind-driven water level fluctuations dominate (2002–2003 90% interval, 0.60 m; maximum interval, 1.59 m; USACE, 2004). Short-lived peaks in water levels are associated with tropical storms and hurricanes. Mean salinity during 2002–2003 at the Louisiana Universities Marine Consortium Lake Pontchartrain station, 5 km to the east, was 1.66 ppt (range, 0.00–4.59 ppt; LUMCON, 2004)—making it an oligohaline marsh (Cowardin *et al.,* 1979). The flora has been documented by Platt (1988), and the vegetation in our study area was dominated by three species: *Schoenoplectus americanus* (Pers.) Volk. ex Schinz & Keller (39.0%), *Polygonum punctatum* Ell. (18.9%), and *Sagittaria lancifolia* L. Nomenclature follows the Integrated Taxonomic Information System (ITIS) used by the U.S. Department of Agriculture (ITIS, 2005).

Experimental Design

This experiment was a randomized block design with a split-plot factorial. Herbivore exclosures or areas open to mammalian herbivory (40 × 60 m) were the main plot treatments. Herbivory as the main plot is justified because nutria are ubiquitous in coastal Louisiana, and as such, any research or management decisions should include the effects of these mammalian herbivores. Factorial combinations of fertility treatments and disturbance treatments (besides herbivory) were randomly allocated to 3 × 3-m subplots. A boardwalk, 335 m in length, provided access to the main plots. Access inside of main plots was provided by 670 m of catwalk, constructed to minimize damage to the organic soil.

Treatments

Herbivory Exclosures

In early 2002, three 40 × 60-m herbivore exclosures were constructed and paired with three parallel areas of equal size open to herbivory. Exclosures were designed to prevent nutria, the principal vertebrate herbivores of the marsh, from entering the plots, but the exclosures also excluded other less-common herbivores, such as feral hogs (*Sus scrofa* L.), marsh rabbits (*Sylvilagus aquaticus* L.), and muskrats (*Ondatra zibethicus* L.). Exclosures consisted of approximately 1.5-m-tall wire fences supported by pressure-treated wooden posts. They were constructed from 1.83-m-tall, vinyl-coated, welded, 2-mm wire fencing with 5 × 10-cm openings. The fencing was inserted at least 45 cm into the substrate to prevent nutria from burrowing into the exclosures. Where exclosures crossed drainage areas, we reinforced them with additional fencing. Additional fencing, at least 60 cm wide, was also placed on the soil surface and attached to the fence to further discourage burrowing. The few nutria that managed to enter the exclosures were generally removed within a week.

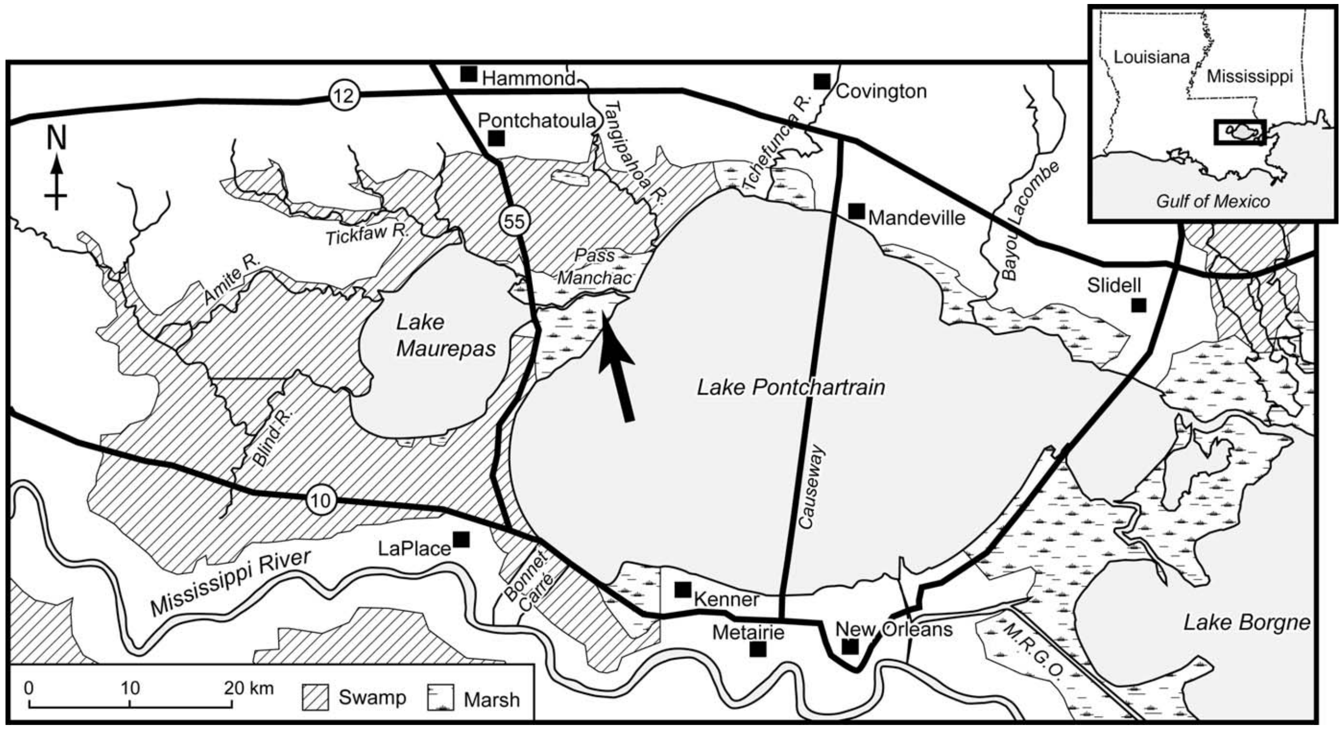

Figure 1. Study area. Location of Turtle Cove Environmental Marsh (TCEM) noted by arrow.

Fire

Prescribed burns were applied annually in late winter (April 23, 2002, and February 1, 2003) when water levels were low and a large amount of natural fuel in the form of standing litter was present. Fires were set using a propane torch designed for vegetation burning (Model VT3-30C, Flame Engineering Inc., LaCrosse, Kansas).

Vegetation Removal

A standard backpack sprayer and the manufacturer recommended levels of Rodeo aquatic-approved herbicide were applied until complete mortality of vegetation was achieved. For the single vegetation removal treatment, herbicide was applied in May 2002. For the double vegetation removal treatment, herbicide was first applied in May 2002 and then reapplied in September 2002, May 2003, and July 2003.

Sediment Addition

Soil for the sediment treatment was obtained from bottomland sources in southeast Louisiana by local contractors. It was hand-applied annually to a depth of 1 cm across the entire plot, in late February to early March. This is similar to the sediment-loading rates to wetlands from Mississippi River delta diversions at Caernarvon and at West Pointe à la Hache, Louisiana, which deliver 0.75–1.57 cm/y and 1.24–1.84 cm/y, respectively (Lane, Day, and Day, 2006). These diversion projects have pulses of discharge with most maxima in the spring (Lane, Day, and Day, 2006), and as such, sediments are also delivered as pulses in the spring, as in this study, but extending over a several weeks, in contrast to this study. Sediment in 2003 was analyzed by Louisiana State University's AgCenter Soil and Plant Test Laboratory for calcium (874 mg/L), magnesium (110 mg/L), phosphorus (41.5 mg/L), potassium (58.3 mg/L), sodium (57.3 mg/L), pH (4.84), and organic matter (2.3%) (McFalls, 2004).

Fertilizer Addition

Slow release Osmocote 18–6–12 (N–P–K) was applied annually at a rate of 215 g/m^2, which provided 38.7 g N/m^2/y, 12.9 g P/m^2/y, and 25.8 g K/m^2/y. It was applied once prescribed burns were finished in early spring. These loading rates are higher than the Mississippi River diversion at Caernarvon, Louisiana, which deliver 8.9–23.4 g N/m^2/y and 0.9–2.0 g P/m^2/y throughout a 260-km^2 marsh (Lane, Day, and Thibodeaux, 1999), but inputs at Caernarvon, Louisiana, are heterogenous throughout the 260-km^2 marsh, and some areas received far higher loadings (Mitsch *et al.,* 2005). Our N loading rates are similar to those modeled for the Maurepas diversion of 8.4–87.7 g N/m^2/y (Lane *et al.,* 2003), which would feed the study marsh once it became operational.

Fertilizer and Sediment Addition

The sediment + fertilizer treatment followed the same protocols as the individual applications. Plots were fertilized, and then, sediment was applied.

Table 1. *Split-plot analysis of variance table of aboveground biomass and species richness in 2003, in the second year of treatments of herbivory (Herbiv), disturbance (Dist), fertilizer addition (Fert), and sediment addition (Sed). Covariables are proximity to closest flowing water (Prox) and relative elevation (Relev) of plots. Analyses were made on square root–transformed biomass and untransformed species richness. Bolded* p *values are smaller than 0.10.*

		Biomass			Richness		
Source	df	MS	*F*	*P*	MS	*F*	*P*
Block	2	15.8	3.78	0.206	4.98	2.16	0.314
Herbiv	1	331.9	78.83	**0.010**	1.01	0.44	0.574
Error A	2	4.2			2.31		
Dist	3	232.5	33.20	**0.000**	25.16	12.73	**0.000**
Fert	1	99.0	14.14	**0.000**	6.27	3.17	**0.080**
Sed	1	23.5	3.35	**0.072**	0.03	0.01	0.909
Herbiv × Dist	3	42.5	6.06	**0.001**	0.98	0.50	0.687
Herbiv × Fert	1	86.6	12.36	**0.001**	0.00	0.00	0.974
Herbiv × Sed	1	2.8	0.40	0.532	1.77	0.90	0.348
Dist × Fert	3	9.3	1.33	0.275	0.34	0.17	0.914
Dist × Sed	3	1.5	0.22	0.883	3.77	1.91	0.138
Fert × Sed	1	28.8	4.11	**0.047**	0.04	0.02	0.889
Herbiv × Dist × Fert	3	8.3	1.18	0.325	1.84	0.93	0.432
Herbiv × Dist × Sed	3	35.0	5.00	**0.004**	1.38	0.70	0.555
Herbiv × Fert × Sed	1	0.4	0.06	0.815	1.20	0.61	0.440
Dist × Fert × Sed	3	0.2	0.03	0.993	2.01	1.02	0.392
Herbiv × Dist × Fert × Sed	3	12.4	1.78	0.162	0.48	0.24	0.868
Prox	1	40.0	5.71	**0.020**	0.04	0.02	0.889
Relelev	1	11.6	1.65	0.204	3.58	1.81	0.183
Error B	58	7.0			1.98		

Data Collection

In July 2003, all aboveground biomass was clipped from two systematically chosen 0.25-m^2 areas just inside the 9-m^2 plot perimeters. Samples were held in cold storage (5 °C) less than 3 weeks before they were sorted into live *vs.* dead material, dried to a constant weight in a forced air oven at 80 °C for at least 48 hours, and weighed on a digital laboratory balance to the nearest 0.01 g. Species richness was assessed visually in the inner 4 m^2 (2 m × 2 m) of each plot by collecting percentage of cover data by species on April 28, June 25, July 29, August 27, and October 17, 2003.

Statistical Analysis

Separate analyses were conducted first on biomass, and second, on richness, averaged over the five sampling times. They were analyzed as a 2 × 4 × 4 randomized block design with split-plot factorial analyses of covariance (ANCOVA). A randomized block design was used because of the large spatial area of the experiment. For the split plot, the main plot disturbance fixed effect was herbivory (two levels: no herbivory, by means of the exclosure; or herbivory, without exclosure). In the subplots, fixed effects were factorial combination of other disturbances (four levels: control, fire, single vegetation removal, or double vegetation removal), fertilizer addition (2 levels: none, fertilizer), and sediment addition (two levels: none, sediment). We measured relative elevation of individual plots, as measured in the center of the plot using a laser surveying system, and proximity of the center of the plot to the nearest flowing water as covariables because these factors can influence flood level and duration.

Analyses were performed using general linear models in SPSS Version 15.0. Homogeneity of variance was verified using plots of residuals *vs.* predicted values, and normality was verified by evaluating histograms of residuals. Biomass data were square root–transformed to achieve homogeneity of variance, and richness data were not transformed. No interactions between blocks or covariables and the fixed effects were included in the model.

RESULTS

Aboveground Biomass

Herbivory significantly reduced biomass ($p = 0.010$; Table 1; Figure 2). On average, areas protected from nutria herbivory had 1.4 times the biomass of areas open to herbivory.

Other disturbances also significantly affected biomass ($p < 0.001$), but there was a strong and significant interaction with herbivory ($p = 0.001$; Table 1; Figure 3). When nutria herbivory was combined with an additional disturbance, such as fire, single vegetation removal, or double vegetation removal, the effect of the other disturbances was amplified. Without herbivores, fire had no effect relative to the control, and single and double herbicide treatments were reduced in a similar manner (open histograms, Figure 3). In the presence of herbivores, there was a downward trend in biomass production in our hypothesized order of disturbance intensity (control < fire < herbivory < single vegetation removal < double vegetation removal).

Sediment addition only slightly increased biomass ($p = 0.072$; Table 1), whereas fertilizer significantly increased biomass by 1.3 times that of control plots ($p < 0.001$). However, there was a significant interaction between sediment and fertilizer additions ($p = 0.047$; Table 1; Figure 4). The addition of sediment alone did not increase biomass above control plots, but the addition of sediment with fertilizer, which simulated Mississippi River flooding events proximal to the outfall, resulted in increased biomass compared with plots with only fertilizer addition. The order of response in biomass production

Figure 2. Overall effect of herbivory on aboveground biomass in July 2003 (mean ± 1 SE).

provides evidence that the hypothesized ranking of fertility treatments was generally correct (control < sediment only < fertilizer only < sediment + fertilizer).

There was also a significant interaction between herbivory and fertilizer addition ($p = 0.001$; Table 1; Figure 5). Where herbivory was allowed, nutria significantly reduced biomass of the fertilized plots—to the point that those plots were not different from nonfertilized plots.

A complex, significant interaction occurred between herbivory, disturbance, and sediment addition ($p = 0.004$; Table 1; Figure 6). In the absence of herbivores, sediment addition increased biomass only in the fire treatments. In the presence of herbivores, sediment addition increased the biomass of the control treatments only. For some reason, it appears that nutria determine whether added sediment will affect the biomass of control or burned plots.

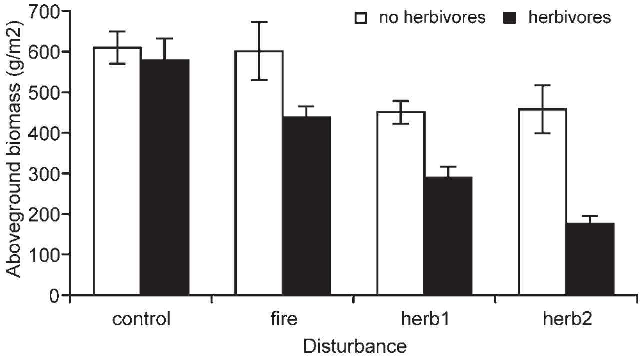

Figure 3. Effect of herbivory and other disturbance types on aboveground biomass in July 2003 (mean ± 1 SE).

Species Richness

Herbivory did not cause any significant change in mean species richness ($p = 0.57$; Table 3), although other disturbances did ($p < 0.001$; Figure 7). Specifically, only the double herbicide treatment reduced the mean species richness compared with the control. Fertilizer addition decreased species richness slightly, although it was not quite statistically significant ($p = 0.080$; Figure 8). Sediment addition had no effect ($p = 0.909$) on species richness. There were no interactions.

DISCUSSION

Effects of Interactions of Fertility and Disturbance on Biomass

We were successful in establishing a sequence of treatments with increasing rates of biomass gain through the application of sediment and fertilizer. As our predicted intensity of fertility increased, biomass increased monotonically (control < sediment addition < fertilizer addition < sediment and fertilizer addition). We also successfully set up a sequence of treatments with increasing rates of biomass loss through the application of increasing disturbances. As our predicted disturbance intensity increased, biomass decreased monotonically (control > fire > herbivory > single vegetation removal > double vegetation removal).

The two-way and three-way interactions between herbivory, other disturbance treatments, and fertility treatments did not always follow the monotonic patterns shown by the main treatment effects. Biomass decreased monotonically with increasing disturbance when also exposed to herbivory, but this decrease was less marked and not monotonic inside the exclosures. Apparently, herbivory by nutria had an effect on

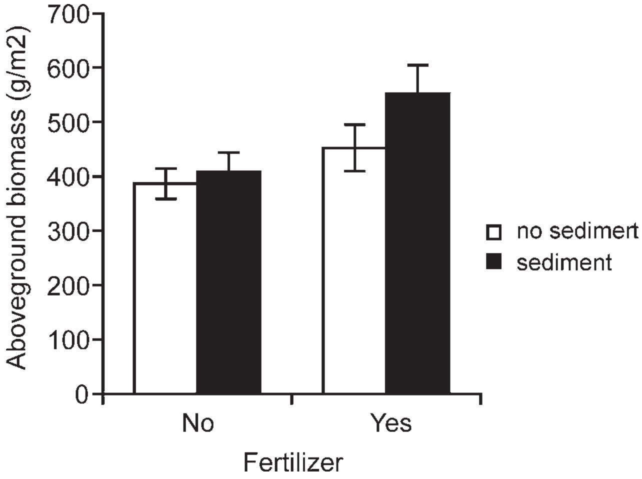

Figure 4. Effect of fertilizer and sediment additions on aboveground biomass in July 2003 (mean ± 1 SE).

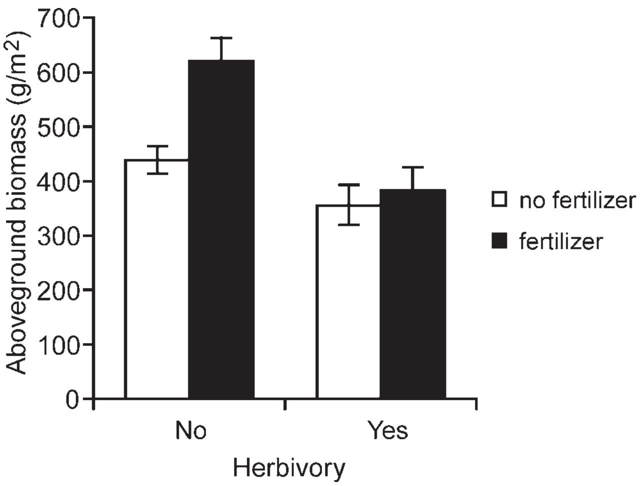

Figure 5. Effect of herbivory and fertilizer addition on aboveground biomass in July 2003 (mean ± 1 SE).

biomass if another disturbance was also present. Similar interactions of nutria herbivory and disturbances have been observed in other studies in the Louisiana coastal marshes and swamps (*e.g.,* Brewer, Levine, and Bertness, 1998; Gough and Grace, 1998). However, unlike some previous studies (Taylor *et al.,* 1994; Ford and Grace, 1998), we did detect a negative interaction between herbivory and fire. Nutria apparently selectively consumed biomass in burned plots, particularly if the plot had a fertility enhancement.

As we increased fertility through fertilizer addition, biomass increased only in the exclosures where herbivory was absent. This suggests that nutria consume a great deal of the increased vegetation that results from enhanced fertility, perhaps because of an increased nutritive value of higher fertility plots (White, 1993). Nutria are known to select specific species of plants in their diet (Wilsey, Chabreck, and Linscombe, 1991), although it is not known how this is related to their food quality. The increase of marsh biomass with fertilization but without herbivores has three important implications. First, it is possible that increased fertility of coastal marshes might not, in the long run, lead to more plant biomass but to more nutria biomass. Second, it is a reminder that trophic effects may be underestimated in coastal wetlands; in more saline habitats, snails may replace nutria as agents that control biomass (Silliman and Bertness, 2002). Third, it suggests that the effects of alligators as predators on nutria might have significant top-down effects by decreasing nutria and increasing sensitivity of marshes to fertilization (Keddy *et al.,* 2009).

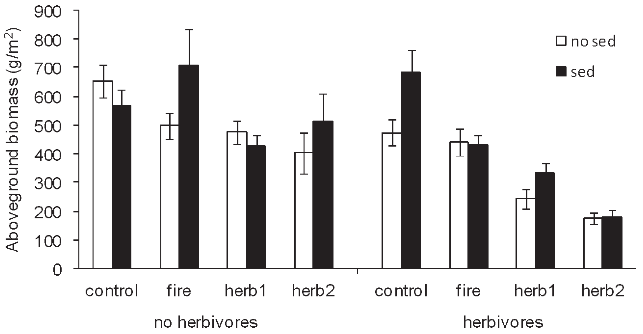

Figure 6. Effect of herbivory, other disturbances, and sediment addition on aboveground biomass in July 2003 (mean ± 1 SE).

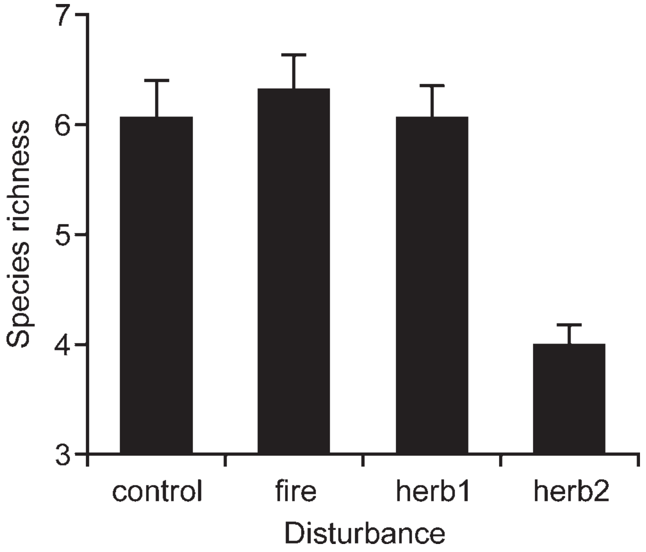

Figure 7. Effect of other disturbances on species richness averaged over five sampling periods in April, June, July, August, and October 2003 (mean ± 1 SE).

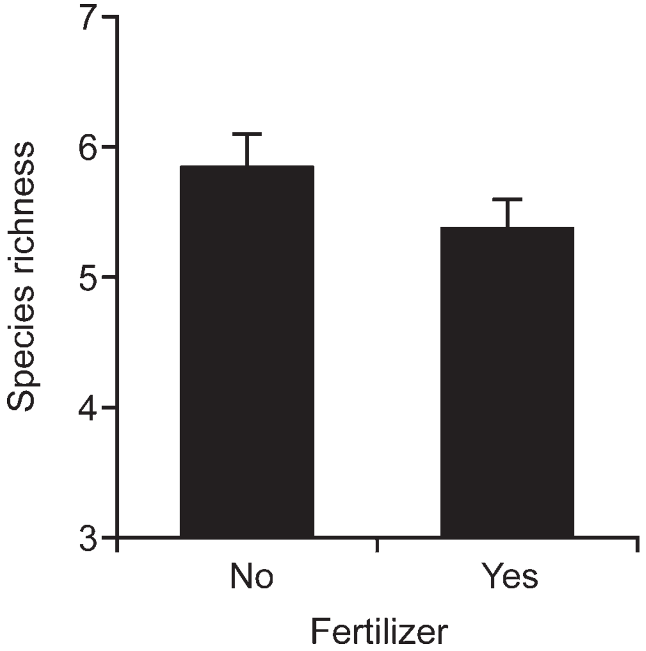

Figure 8. Effect of fertilizer addition on species richness averaged over five sampling periods in April, June, July, August, and October 2003 (mean ± 1 SE).

Effects of Interactions of Fertility and Disturbance on Species Richness

The DEM did not usefully predict the effects of the treatments on species richness after 2 years of treatments. Increased disturbance intensity did decrease species richness, but only in the most severe disturbance treatment—double vegetation removal by herbicide. Simultaneous disturbances (herbivory with other disturbances) had no effect on species richness.

Fertilizer addition had a slight but nonsignificant effect on richness, and there was no interaction between fertility and any disturbance, contrary to what is predicted by the DEM. There was support for the individual components of the Huston model, for the Connell (1978) intermediate disturbance hypothesis, and for the Grime (1973, 1979) unimodal productivity–diversity hypothesis. Competitive displacement as a result of fertilizer addition only slightly reduced species richness in this Louisiana oligohaline marsh during our 2-year study. This may indicate that these oligohaline marshes are more like the systems described by the intermediate disturbance hypothesis portion of the DEM—systems with high growth rates, such as intertidal zones and coral reefs (Connell, 1978; Sousa, 1984). Despite herbivory being shown to be an intermediate disturbance in this study, at least as measured by effects on biomass, it did not significantly affect species richness during the course of this study. The Manchac area also has intermediate to high disturbance rates, like systems best described by the Grime (1973, 1979) model. Frequently, high-disturbance rates in the experiment resulted in diversity levels that might suggest a unimodal productivity–diversity curve. Species richness only slightly decreased with fertilizer addition, providing further evidence that the diversity patterns within the community were controlled primarily by disturbance regimes during the course of this study. Species richness patterns indicate that the Manchac area has high growth rates, like systems that are best described by the intermediate disturbance hypothesis. This information gives support to the two components of the DEM, but when combined, they were not able to accurately predict species richness responses after 2 years of treatments. However, Bakker (1985), who examined herbivory in salt marshes, needed 3 years of data to detect a diversity change, and Turkington *et al*. (2002) needed almost a decade to see diversity changes. We expect that ongoing monitoring of this experiment will lead to clearer trends.

Overall, the extensive marshes of the Manchac area have relatively low diversity (Boshart, 1997; Gough and Grace, 1998; Thomson, 2000), on average just over 5 species *per* 4 m^2 in our experiment. The study area was dominated by just three species (*S. americanus, P. punctatum,* and *S. lancifolia*), all of which can produce dense canopies and become, dominants in fertile areas (Boshart, 1997). Transplant experiments in these marshes showed that competition from existing plants has a negative effect on other species that might establish (Geho, Campbell, and Keddy, 2007). The cover of existing plants, and therefore, of these competition effects, might be reduced by natural disturbances, from the small scale (herbivory) to the large scale (hurricanes), but contrary to expectations, none of our disturbance treatments increased plant diversity. The Manchac area appears to already be at maximal diversity, as shown by the highest richness in control plots. Why, then, is the mean species richness so low? Gough, Grace, and Taylor (1994) suggested that the abiotic stressors of increased salinity and flooding kept the species pool at very low levels in the Manchac area. Selective feeding by herbivores might compound this effect by reducing establishment of species, such as southern cattail (*Typha domingensis* Pers. (Geho, Campbell, and Keddy, 2007). Finally, it may be that dispersal of new species may require decades to occur.

MANAGEMENT IMPLICATIONS

In summary, during 2 years, nutria decreased biomass, but they had a neutral effect on species richness. The treatments simulating a freshwater diversion apparently reduced the negative effects of nutria on biomass. However, the small increase in biomass when fertilizer was applied in the presence of herbivores indicates that nutria consumed a large proportion of the extra biomass produced. The extra, potentially more nutritious, food created by enhanced fertility, suggests that increasing fertility throughout a large area may lead to larger nutria populations (White, 1993). These results are consistent with other evidence that predators, such as alligators, may increase marsh biomass by reducing effects of herbivory (Keddy *et al.,* 2009). In our study, it appears that the effects of herbivores did not completely remove the added production because enhanced fertility increased biomass somewhat, even in the presence of herbivores (that is, outside of the exclosures). Because the highest biomass was achieved when both fertilizer and sediments were applied, floodwaters from the Mississippi River may mitigate the negative effects of nutria grazing. However, it should be noted that freshwater diversions will have the most effect if nutria populations are reduced.

Based on the species richness data, there was no concomitant decrease observed in diversity when productivity is increased. This is positive information in terms of proposed freshwater diversions, given that enhanced productivity generally yields lower biological diversity (*e.g.,* Auclair, Bouchard, and Pajaczkowski, 1976; Grime, 1979; Rosenzweig, 1971). It is surprising that we found no decrease in species richness in response to our fertility treatments. This suggests, however, that potential eutrophication from freshwater diversions may not have negative effects on plant diversity, at least in the short term. More experimentation is needed to determine the long-term effects of freshwater diversion nutrients on species richness.

Fire in areas of high nutria abundance should be avoided if fertility is increased. The combination of fire and the additional nutrients seems to promote heavy, localized herbivory, which could lead to a positive feedback cycle of reduced accretion and increased inundation. Other studies have also found that fire tends to increase grazing pressure (Mcnaughton, 1984; Smith and Kadlec, 1985; Smith, Kadlec, and Fonesbeck, 1984; Svejcar, 1989; Woolfolk *et al.,* 1975).

The most important general conclusion may lie, not in the details of the interactions, but in the sheer number and complexity of them. That is, no single factor—nutria grazing, sediment, or fire—emerged as the dominant controlling factor on either biomass or species richness. Although it is often tempting to try to manage wetlands as if single controls were dominant, these data suggest otherwise. The sheer number of interactions suggests that we need to view wetlands as arising out of multiple, interacting factors, some of which we understand, and some of which remain unknown. Hence, multiple working hypotheses need to be entertained in planning future research. For coastal wetlands as a whole, interactions among the factors we manipulated, combined with possible interactions from others that we did not manipulate (*e.g.,* salinity and alligator predation), need continuing attention both at the level of basic science and in habitat management.

ACKNOWLEDGMENTS

We are indebted to the U.S. Environmental Protection Agency for funding through the Wetland Protection and Development Grant Program (R-82898001-01, R-82898001-02, and R-82898001-03). Additional funding was provided by The National Oceanic and Atmospheric Administration through the Lake Pontchartrain Act. We offer our sincere thanks to Dr. Nick Norton and to the entire Southeastern Louisiana University Pontchartrain Basin Research Program. This project could not have been completed without much field assistance from M. Broussard Lombard, T. Menzel, J. Smith, M. Clark, J. Zoller, M. Kaller, A. Roth, D. Dardis and her teacher–research associate program, and many others. Special thanks to R. Moreau and H. Reno at Turtle Cove Environmental Marsh (TCEM) Research Station for all of their support. Thanks also to the Louisiana Department of Wildlife and Fisheries for permission to construct TCEM and to conduct research on their land. Thanks to M. Huston, M. White, R. Miller, M. Clark, M. Kaller, and J. Willis for their comments on earlier drafts.

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