COMMUNITY ECOLOGY 8(1): 15-24, 2007
1585-8553/$20.00 © Akadémiai Kiadó, Budapest
DOI: 10.1556/ComEc.8.2007.1.3

Vegetation response to disturbance in a coastal marsh in Texas

J. Bhattacharjee[1†], D. Haukos[1] and J. Neaville[2*]

[1]*Department of Natural Resources Management, Texas Tech University, Lubbock, Texas, USA 79409-2125*
[2] *U.S. Fish and Wildlife Service, Anahuac National Wildlife Refuge, Anahuac, Texas, USA 77514*
[†] *Corresponding author. Recent address: Department of Biology, University of Louisiana at Monroe, Monroe, Louisiana, USA 71209-0520. E-mail: joydeep@ulm.edu*
[*] *Retired*

Keywords*:* Diversity, Intermediate coastal marsh, Muskrat, *Paspalum vaginatum*, *Scirpus olneyi, Spartina patens*.

Abstract: Disturbance is considered one of the main factors influencing plant species composition and diversity. We conducted a field study to address the plant community response in a coastal marsh to a major disturbance. In 1992, muskrats (*Ondatra zibethicus* L.) completely removed vegetation within a 450 ha area of intermediate coastal marsh in Texas, USA. We used vegetation data collected prior to the disturbance (1989-1991) as a baseline for comparison to that recorded annually for a decade (1992-2002) following the disturbance. We compared species diversity, richness, relative abundance, evenness, and species similarity between pre and postdisturbance periods to evaluate the temporal response of the disturbed plant community. Plant diversity in the study area returned to predisturbance levels after 10 years. Species diversity in the study area had two peaks following the main disturbance. These peaks are associated with fluctuations of the water levels in the area. Our results suggest that it is possible to control the sedge or grass dominance in a community by subjecting the area to a carefully timed willful disturbance (e.g., grazing or fluctuating water levels) to achieve management goals. However, vegetation composition in the area changed from a grass-dominated (predisturbance) to sedge-dominated (postdisturbance) community. At the conclusion of sampling in 2002, plant species abundance, evenness, dominance, and richness conditions reached levels similar to predisturbance. However, the species composition after a decade postdisturbance differed from that during the predisturbance period. Therefore, even though we are able to predict the return of species diversity, evenness, and richness of a community after a period following disturbance, the actual species composition of an intermediate marsh following recovery is difficult to determine accurately, as it is contingent on several biotic and abiotic conditions that prevail while the system recovers from disturbance.

Nomenclature follows: Stutzenbaker (1999) for plants and Davis and Schmidly (1994) for animals.

Introduction

All organisms within a community and other levels of ecological organization are influenced by disturbance (Connell 1978, Pickett and White 1985, Reice et al. 1990). In the past, preservation of natural plant communities included protecting them from physical disturbance (Hobbs and Huenneke 1992). However, an increasing number of ecological researchers now recognize the role of disturbance in the natural functioning of ecosystems. Petraitis et al. (1989) suggested that the relationship between disturbance and response of a community depends upon the impact that the disturbance causes: it may cause selective mortality of certain species in the community or a more catastrophic mortality in a community involving more than one species. Pickett and White (1985) distinguished disturbance components as frequency, intensity, and size. Disturbance causing selective mortality might help in maintaining diversity or richness, whereas a random disturbance may prevent vegetation from attaining community equilibrium (Petraitis et al. 1989). Furthermore, disturbance at an intermediate level tends to result in a vegetation community with maximum potential species richness (Hobbs and Huenneke 1992).

Disturbance in wetland systems is as common as in uplands (Zedler and Kercher 2004). An increase in species richness in a tallgrass prairie with increasing disturbance intensity was reported by Collins (1987). Fire on an annual basis promotes relative abundance of annual tallgrasses in Oklahoma prairies (Coppedge et al. 1998). Wetland hydrology may also be an important factor in determining vegetation response to disturbance. For example, natural cyclical patterns of vegetation change occur in the coastal wetlands of the Carolina Bays in response to rainfall cycles (Kirkman 1992) or during extended periods of drought, entire extant vegetation stands may be removed due to a fire event. Building of levees or other water-control structures affect hydrology or tidal influence, which disrupts the function of such marshes. During dry conditions, other forms of disturbance in wetlands include mechanical discing and tilling or disturbance caused by animals such as extensive rooting by hogs (Kirkman and Sharitz 1994). An important source of disturbance in coastal marsh is damage following a cyclonic or hurricane event, resulting in excessive salt influx and physical destruction of extant plant communities. In most wetland systems, there is a lack of long-term monitoring of plant communities following a disturbance, which screens much of our understanding of community recovery after disturbance.

Successful management of coastal marsh requires an understanding of plant community response to disturbance. Evaluating trends in vegetation recovery following a disturbance is of importance for insight into the fundamental processes of vegetation regeneration and development of conceptual models to predict response of vegetation to such disturbances (Keddy et al. 1989). For example, plant community response to recent (2005) hurricane events in coastal marshes of Louisiana and Texas could be predicted based on documented responses to major disturbance events. However, in most instances, long-term vegetation monitoring data are not available, making recovery predictions difficult or impossible.

A major source of disturbance in coastal and freshwater wetlands is extensive grazing by muskrat (*Ondatra zibethicus* L.). Vegetation response to complete removal by muskrats in wetlands has received little attention compared to fire or grazing by terrestrial mammals mainly because these are common techniques in marsh management (e.g., fire as a tool to enhance pastures for the cattle industry, land management through fire or grazing removal to restore or enhance habitats for game species). However, muskrats can severely affect vegetation structure and community composition (Akkermann 1975). At low densities, they consume only minor parts of the vegetation, mostly those that are rich in carbohydrates and proteins (Danell 1977), but in higher densities muskrats can cause massive damage to vegetation structure and community composition (Weller and Fredrickson 1974). Furthermore, muskrats can cause additional disturbance in a vegetation community through an increase in soil aeration and water infiltration (Meadows and Meadows 1991, Butler 1995, Johnston 1995). Nyman et al. (1993) reported a positive correlation between species richness and muskrat activity in a coastal marsh in Louisiana. Similar results were reported by Connors et al. (2000) in a tidal marsh in the Hudson River. However, muskrats also use a considerable amount of vegetation material, mostly emergent, to make lodges for overwintering. In areas where muskrats occur at high densities, entire extant vegetation stands may be removed (Danell 1977).

To examine vegetation response to a complete removal by muskrats, we evaluated natural revegetation patterns in an intermediate coastal marsh in Texas. We expected plant diversity to increase following the disturbance, based on the disturbance-diversity hypothesis (Grime 1973a, b; Connell 1978). However, as communities exhibit some degree of resilience, we also expected the diversity to increase following disturbance and then decrease over time as the communities returned to predisturbance structure. Our primary objectives were to: (1) determine the effects of intensive disturbance on vegetation diversity of an intermediate marsh; (2) evaluate vegetation community response following disturbance and changes in species composition over time; and (3) estimate the timeframe for marsh vegetation recovery to predisturbance conditions following a major disturbance. The exclusivity of our study is the collection, monitoring, and use of long-term data, which allowed close evaluation and reporting of vegetation recovery patterns in a coastal marsh following a major disturbance. Thus, results of our study provide land managers with a tool for estimating time and pattern of vegetation recovery *a priori,* aiding future management decisions in intermediate coastal marsh.

Methods

Study site

Our study was conducted in the East Bay Bayou Marsh Unit (Tract 18), located on the east side of the East Unit on East Bay Bayou (29° 37’ 19.58" N and 94° 25’ 45.45" E) in Anahuac National Wildlife Refuge, Texas (Fig. 1). It was 1137.22 ha in size and comprised of 458.1 ha of intermediate marsh, 373.38 ha of brackish marsh, 270.94 ha of nonsaline grassland and prairie wetland, and 34.85 ha of freshwater marsh (United States Fish and Wildlife Service, unpublished data).

Based on salinity levels, coastal marsh may be classified into four types (Stutzenbaker 1999): freshwater marsh with salinity ranging from 0 to 0.5 parts per thousand (ppt), intermediate marsh with a salinity range of 0.5 to 3.5 ppt, brackish marsh with salinities ranging from 3.5

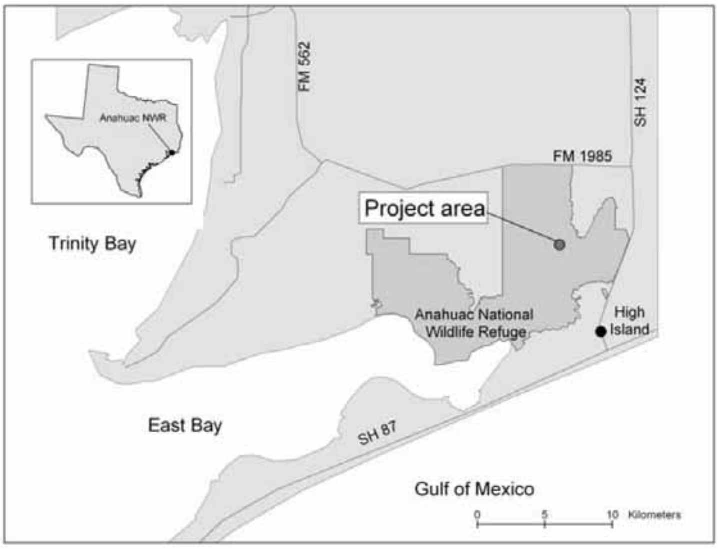

Figure 1. Map of Anahuac National Wildlife Refuge, Texas, showing the East Bay Bayou Tract.

to 10 ppt, and saline with salinity of 10 ppt and above. The East Bay Bayou was primarily an intermediate marsh; however, both salinity and water levels were dependent on prevailing winds and amount of freshwater inflow due to precipitation. Mean annual salinity during vegetation sampling from 1992-2002 in the area ranged from 0 to 6 ppt. The annual precipitation in the area ranged from 66 to 249 cm, with an average of 132 cm. Mean air temperature is 20°C with a range of 5 to 36°C (Vaughn and Fisher 1992). The 1992 muskrat disturbance occurred in intermediate marsh communities. Intermediate marsh habitats typically are comprised of a diverse community of plants. Vegetation in the East Bay Bayou Unit included grasses (e.g. *Distichilis* sp., *Paspalum* spp., *Spartina* spp.), sedges (*Cyperus* spp., *Eleocharis* spp., etc.), rushes (*Scirpus* spp., *Juncus* spp.), and cattail (*Typha domingensis*) (United States Fish and Wildlife Service, unpublished data). Plants associated with this habitat type are tolerant to a wide range of salinity values.

Vegetation sampling

Vegetation sampling in the general study areas was conducted from 1989 to 2002. However, vegetation in Track 18 of the East Bay Bayou was removed completely by muskrats in 1992. Following removal of vegetation, muskrats deserted the area. To determine patterns of vegetation recovery, we annually sampled the disturbed area from 1993 to 1997 and from 2000 to 2002 during summer. We carried out vegetation sampling along 3 permanent, randomly placed line transects (each 30.48 m long). Each transect was divided into 50 equidistant points at which vegetation was sampled. At each sampling point, a pin was lowered perpendicular to ground surface and any plant species touched was recorded to calculate frequency of occurrence. If present during the vegetation sampling, water level was measured at the beginning of each transect. Similar species frequency and occurrence data collected prior to disturbance (1989 through 1991) were averaged and used as baseline data for comparison of vegetation response to removal of extant vegetation.

Data analysis

To determine vegetation community response to disturbance, we calculated species richness (*S*), evenness, diversity, dominance, abundance, relative abundance, and similarity of vegetation before and after disturbance. Evenness was calculated as $J' = H' / \ln S$ (Pielou 1966), where, H' is Shannon's index of diversity. Shannon's diversity for each year was calculated using the formula developed by Shannon and Weaver (1963). We also used Simpson's index (*D*) to measure dominance in the vegetation. It is robust against sensitivity to rare species (Magurran 1988). Simpson's index (*D*) was calculated as

$$D = \sum \frac{n_i(n_i - 1)}{N(N-1)} ,$$

where n_i is the frequency of the *i*th species and *N* is the total number of individuals. As *D* increases, diversity decreases, so we transformed *D* by 1- *D* as a second reference to diversity, which is consistent with Shannon diversity, with higher values representing higher diversity (Haukos and Smith 2004).

The degree in similarity in vegetation between years was determined by Sörensen index of similarity (Sörensen 1948). We used the formula $C_S = 2j/(a+b)$, where *j* is the number of species present in both years and *a* is the total number of species in year 1 and *b* is the total number species present in year 2.

Table 1. Average frequency of plant species in the East Bay Bayou Transects of Anahuac National Wildlife Refuge prior to (1989-1991) and following (1993-2002) vegetation removed by muskrats in 1992.

Species	Base (1989-91)	1993	1994	1995	1996	1997	2000	2001	2002
ACCU	-	6	11	-	-	-	-	-	-
AMAR	-	-	-	-	0.67	-	-	-	-
BAMO	-	-	-	0.66	-	-	-	-	-
CYAR	3.58	16	10	-	-	3.33	-	-	-
DISP	3.55	-	45	22.00	14.67	37.33	10.00	22.00	47.33
ECAL	-	-	-	-	-	6.00	-	-	-
ECCR	-	-	36	-	-	-	-	-	-
ELCE	1.45	-	50	67.33	0.67	5.33	-	-	0.67
ELMO	18.3	2	-	-	4.00	-	-	-	0.67
ELPA	2.22	-	26	-	-	-	-	-	-
GASP	-	-	-	-	-	1.33	-	-	-
IVAN	-	-	-	-	0.67	-	0.33	-	-
JURO	-	-	-	6.00	14.00	13.33	13.33	8.67	5.33
PALI	0.75	-	-	-	-	-	-	-	-
PAVA	48	12	62	76.67	88.67	82.00	96.67	70.00	56.67
PLPU	-	-	4	-	-	2.67	-	-	-
SCOL	8.16	-	15	23.33	42.67	69.33	72.00	84.00	94.67
SCRO	-	2	-	-	-	1.33	-	-	-
SCVA	2.22	-	-	-	-	-	-	-	-
SPPA	44	44	56	32.00	42.67	49.33	10.00	22.00	6.67
SPSP	1.33	-	-	-	-	0.67	-	-	-
TYDO	1.09	-	2	20.00	43.33	37.33	4.00	1.33	30.67
VILU	-	-	-	-	-	0.67	-	-	-

Species represented in the table are: ACCU =*Acnida cuspidata*, AMAR = *Ambrosia artemisiifolia*, BAMO = *Bacopa monnieri*, CYAR = *Cyperus articularis*, DISP = *Distichilis spicata*, ECAL = *Eclipta alba*, ECCR = *Echinochloa crusgalli*, ELCE = *Eleocharis cellulosa*, ELMO = *Eleocharis montevidensis*, ELPA = *Elocharia parvula*, GASP = *Galium* sp., IVAN = *Iva annua*, JURO = *Juncus roemerianus*, PAVA = *Paspalum vaginatum*, PALI = *Paspalum lividum*, PLPU = *Pluchea purpurascens*, SCRO = *Scirpus robustus*, SCOL = *Scirpus olneyi*, SCVA = *Scirpus validus*, SPPA = *Spartina patens*, SPSP = *Spartina spartinae*, TYDO = *Typha domingensis*, and VILU = *Vigna luteola*. A " – " indicates absence.

We compared differences in vegetation diversity (using software PAST version 1.38, Hammer et al. 2006) between consecutive years to examine vegetation changes in the area and the length of time required for the vegetation to return to predisturbance levels. Diversity comparisons between any two years (*A* and *B*) were carried out by first pooling the diversity data from the years and then 1000 random pairs of samples (A_i, B_i) with the same number of data points in the original two years are taken from this pool. For each replicate pair, the diversity indices $div(A_i)$ and $div(B_i)$ were computed. The number of times $|div(A_i) - div(B_i)|$ exceeds or equals $|div(A) - div(B)|$ indicated that the observed difference could have occurred by random sampling from one year to another as estimated by the pooled sample. Finally, we used correspondence analysis (CORRESP procedure in SAS® 9.1; SAS 2003) to explore patterns of plant community composition across years. We plotted species and year scores from the first two dimensions to examine patterns in species distribution and identify plant species that contributed to relative separation of years.

Results

Prior to disturbance, vegetation in the area was dominated by two grasses *Spartina patens* and *Paspalum vaginatum*, and a rush *Eleocharis montevidensis* (Table 1). Among other species present in relatively lower abundance were *Eleocharis cellulosa*, *Paspalum lividum, Spartina spartinae, Eleocharis parvula*, and *Typha domingensis*.

We recorded 23 species of plants in the area (Table 1). Annual species richness ranged from 6 (2001) to 14 (1997). Frequency of individual species ranged from 0 to 96.67 (*Paspalum vaginatum*). Although not frequent in our samples, *Spartina patens* was one of only two species (the other being *Scirpus olneyi*) recorded in the area in the predisturbance period and annually throughout the 10-year postdisturbance period (Table 1). Species such as

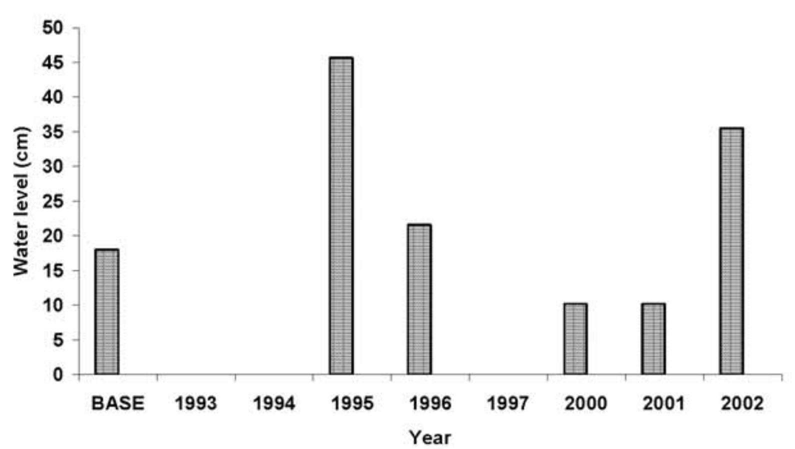

Figure 2. Average water level measurements in the study area in predisturbance period (base: 1989-91) and during successive sampling in the East Bay Bayou Tract of Anahuac National Wildlife Refuge. No data were collected during 1998 and 1999.

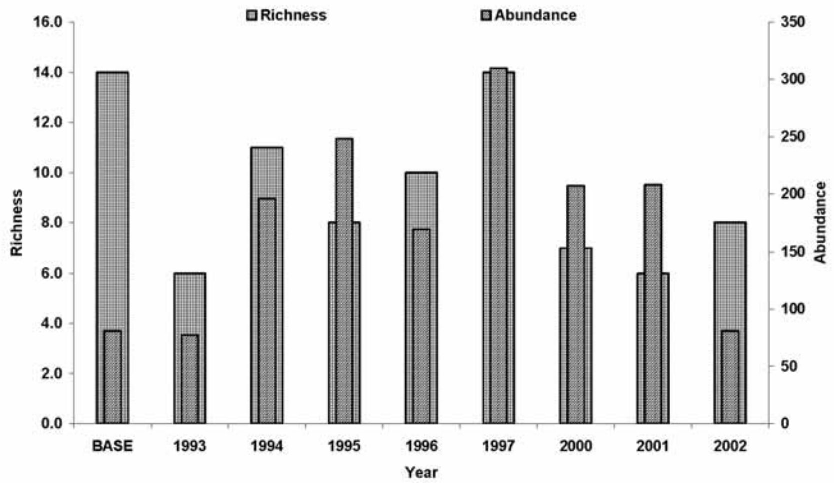

Figure 3. Plant species richness and abundance before (base: 1989-91) and following removal of vegetation in 1992 in the East Bay Bayou Tract of Anahuac National Wildlife Refuge.

Cyperus articularis, Eleocharis montevidensis, and *Eleocharis parvula* had higher abundances in predisturbance periods than following disturbance. Water level at the time of sampling ranged from 0 to 45 cm in the area. No standing water was present during sampling for the years 1993, 1994, and 1997, whereas 1995 had the highest water level, followed by 2002 (Fig. 2).

The 5 most abundant species in the area, pre and post-disturbance, were *Paspalum vaginatum, Distichilis spicata, Scirpus olneyi, Spartina patens*, and *Typha domingensis*. However, *Paspalum vaginatum,* and *Spartina patens* were the only 2 out of the 5 most abundant species to reappear immediately after disturbance. Although the above 2 species reappeared sooner than did others following disturbance, the abundance of *Paspalum vaginatum* increased steadily from 1993 to 2000 and by 2001- 2002 had declined to predisturbance levels. The abundance of *Spartina patens* declined during 1994-2002 period. However, abundance of the sedge *Scirpus olneyi* increased following the disturbance. *Typha domingensis* abundance was higher following years of relatively higher water levels in the area. The high abundance of *Typha domingensis* during 1996 and 1997 may be due to relatively high water levels in the area during 1995 and 1996. Similarly, relatively higher water level in 2001 and 2002 might have resulted in higher abundance of *Typha domingensis* in 2002.

Richness and abundance

Peaks in diversity and abundance corresponded to zero water levels. Richness peaked in 1994 with 11 species, in 1997 with 14 species, and 5 years following disturbance (Fig. 3). There was a gradual increase in richness from 1993 through 1997, with an exception in 1994 when there was a sharp increase to 11 species from 6 species in

1993. After the peak in 1997, there was a sharp decline by 2000, which continued until 2001 when there were only 6 species present. There was a slight increase in species richness by 2002. Average species richness in the predisturbance period was 14 and in 2002, it was 8. Similar to richness, species abundance had two peaks, one in 1995 (248 individuals/transect) and the other in 1997 (310 individuals /transect), but abundance declined thereafter, reaching 81 individuals by 2002, which was similar to the predisturbance period (80 individuals /transect).

The five dominant plant species (highest frequencies in a given year) species before and after the disturbance consisted of three grasses (*Distichilis spicata*, *Paspalum vaginatum*, and *Spartina patens*), a sedge (*Scirpus olneyi*), and cattail (*Typha domingenisis*). The overall change in the relative abundance of the dominant species indicated a transition from a grass-dominated (*Spartina patens*) community immediately following disturbance to a more sedge-dominated (*Scirpus olneyi*) plant community by the end of the vegetation sampling in 2002 (Fig. 4). There were two species, *Paspalum lividum* and *Scirpus validus*, which did not reestablish in the area after the disturbance. Following disturbance, *Paspalum vaginatum* had the highest relative abundance in 1993. This was the only year where 3 of the 5 most frequently recorded species were absent. As other species recovered after the disturbance, relative abundance of *Paspalum vaginatum* declined. In 1997, when diversity peaked for the second time, the relative abundances of the 5 dominant species were between 12-28 (Fig. 4).

Diversity

Following the same bimodal pattern of abundance and richness, plant diversity peaked in 1994 and 1997 during

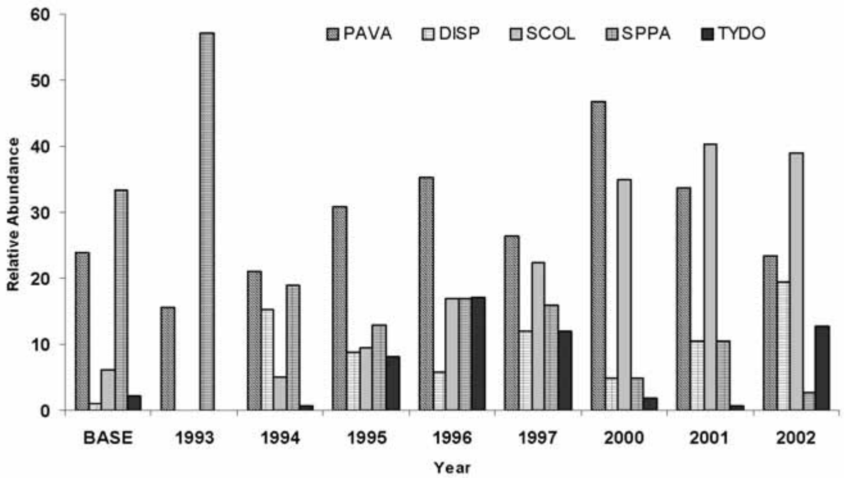

Figure 4. Relative abundance of the five dominant species in the East Bay Bayou Transect of Anahuac National Wildlife Refuge. Predisturbance period is denoted as base (1989-91). Species represented are DISP=*Distichilis spicata*, PAVA=*Paspalum vaginatum*, SCOL= *Scirpus olneyii*, SPPA= *Spartina spartinae*, and TYDO = *Typha domingensis.*

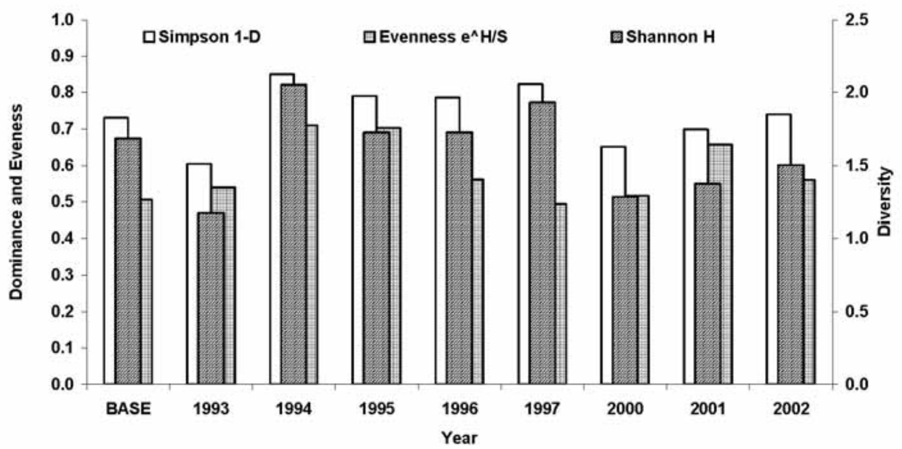

Figure 5. Plant species diversity, dominance, and evenness before (base: 1989-91) and following muskrat removal of vegetation in 1992 in the East Bay Bayou Tract of Anahuac National Wildlife Refuge.

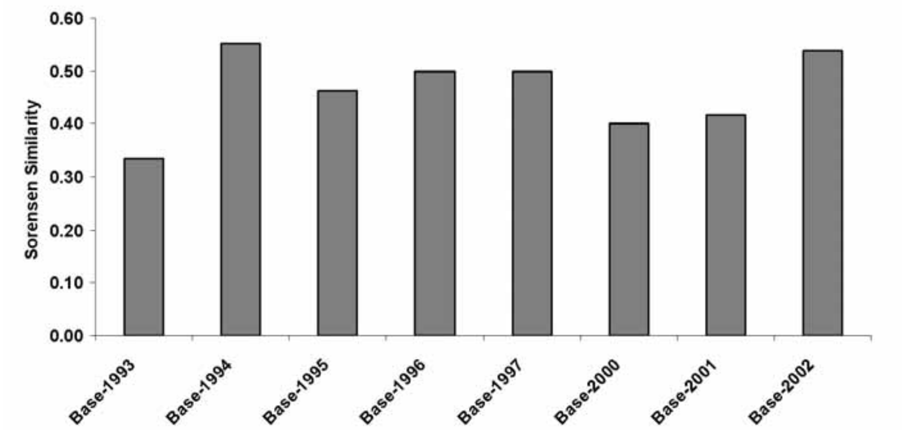

Figure 6. Vegetation similarity (Sörensen's index) compared between the predisturbance period (base: 1989-91) and successive annual vegetation sampling in the East Bay Bayou Tract of Anahuac National Wildlife Refuge.

the 10-year period following initial disturbance (Fig. 5). After the 1994 peak, diversity declined in 1995 and 1996 before peaking again in 1997, followed by a long-term decline to predisturbance values by 2001 (Fig. 5). In 1993, a year after disturbance, plant diversity as measured by Shannon's index decreased compared to predisturbance levels. However, diversity was higher than predisturbance levels during the following 4 years (1994-1997); diversity increased from 1993 to 1994 (t_2 = -10.34, P < 0.001). Diversity in 1995 declined relative to 1994 (t_2 = 5.59, P < 0.001). There was no change (t_2 = 0.41, P = 0.68) in diversity between 1995 and 1996 (Fig. 5). Following the second peak of diversity in 1997, there was a sharp decline in diversity by 2000 (t_2 = 8.45, P < 0.001) (Fig. 5). Plant diversity in the area during 2001 and 2002 approached diversity levels of the predisturbance period (predisturbance - 2001 t_2 = 1.07, P = 0.28 and predisturbance – 2002 t_2 = 0.35, P = 0.73). Simpson's dominance followed the same distribution patterns as diversity, with the first peak in 1994 and the second peak in 1997. Species evenness increased following disturbance and peaked in 1995, followed by a decline until 1997. Evenness values reached 0.56 by 2002, a decade after disturbance, which was close to the predisturbance value of 0.51.

Sörensen index of similarity

We compared similarity in vegetation species composition between the predisturbance period and each year sampled following the disturbance. The vegetation similarity between the predisturbance period and one year after the disturbance dropped to about 33% (Fig. 6). Vegetation similarity in the area then experienced both increasing and decreasing trends during the 10-year period. At the end of the 10-year period, species composition in the community was only 54% similar to what it was before the disturbance.

Ordination

The first two dimensions in the correspondence analysis accounted for 63% of the variation. Individuals or small groups of species separated years along the two axes (Fig. 7). The species *Paspalum lividum* and *Scirpus validus* occurred only in the base years, when freshwater conditions dominated (J. Neaville, unpublished data) and spatially separating it from the rest. Species that separated 1993 from other years were *Cyperus articularis*, *Paspalum lividum*, *Scirpus robustus*, and *Acnida cuspidata*. The presence of *Echinochloa crusgalli*, *Eleocharis parvula*, and *Pluchea purpurascens* isolated 1994 from others years. Similarly, *Bacopa monnieri* occurred only in 1995 separating this year from the rest. Years 1996 and 1997 were grouped based on the species *Ambrosia artemisiifolia*, *Gallium* sp., *Vigna luteola*, and *Eclipta alba,* whereas years 2000 through 2002 were grouped based on the common presence of *Iva annua*, *Scirpus olneyi*, *Typha domingensis*, *Juncus roemerianus*, and *Paspalum vaginatum*.

Two species, *Paspalum lividum* and *Scirpus validus*, which were present prior to grazing, did not reestablish in the area after the disturbance likely because of the lack of consistent freshwater necessary to support these species. Following grazing, it took about 2 years for the sedge *Scirpus olneyi* to reappear in the area. After that, there was a steady increase in abundance of *Scirpus olneyi*, and the species dominated the community by the end of vegetation sampling in 2002. Plant communities from 1994 through 2000 were dominated by the grass *Paspalum vaginatum,* which declined after 2000.

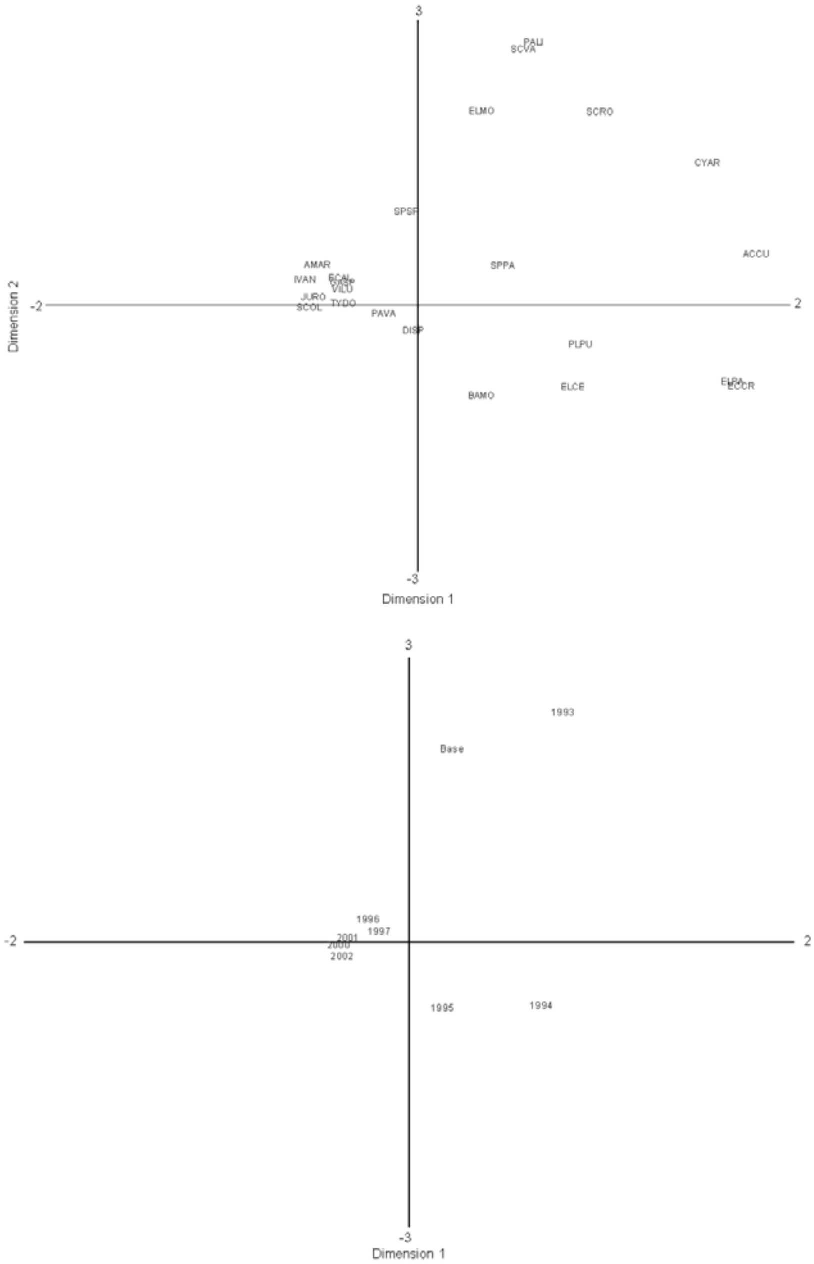

Figure 7. Position of scores for years and species along the first two dimensions obtained using correspondence analysis of vegetation and year (1992, 1993, 1994, 1995, 1996, 1997, 2000, 2001, and 2002) in the East Bay Bayou Tract, Anahuac National Wildlife Refuge, Texas. Species are ACCU =*Acnida cuspidata*, AMAR = *Ambrosia artemisiifolia*, BAMO = *Bacopa monnieri*, CYAR = *Cyperus articularis*, DISP = *Distichilis spicata*, ECCR = *Echinochloa crusgalli*, ECAL = *Eclipta alba*, ELCE = *Eleocharis cellulosa*, ELMO = *Eleocharis montevidensis*, GASP = *Gallium* sp., IVAN = *Iva annua*, JURO = *Juncus roemerianus*, PALI = *Paspalum lividum,* PAVA = *Paspalum vaginatum*, PLPU = *Pluchea purpurascens*, SCRO = *Scirpus robustus*, SCOL = *Scirpus olneyi*, SPPA = *Spartina patens*, SPSP = *Spartina spartinae*, TYDO = *Typha domingensis*, and VILU = *Vigna luteola*.

Correspondence analysis of vegetation data and year indicated that vegetation community in the marsh changed over time. During the first three years following disturbance, there were very few common species among years. From 1996 through 2002, the plant community had more species in common (appeared clustered) among years, however, the plant community composition differed from what was found in the area before disturbance.

Discussion

The diversity of plant species in the disturbed area initially increased to values greater than that during predisturbance period but then declined over time and returned to predisturbance values in about a decade. Similarly, during the first 4 years following the disturbance, species evenness and dominance were higher than predisturbance levels but both declined and were close to predisturbance levels by the end of 10-year sampling period.

There was a change in the species abundance following the disturbance from a grass-dominated community for the first 8 years after the graze-out event to that of sedge-dominated composition by 2001. From the response patterns it can be concluded that following a disturbance in an intermediate marsh, grasses recover faster than sedges. This may also be due to the fact that grasses colonize disturbed areas sooner because of the presence of abundant propagules, and once they colonize, they ameliorate conditions for the sedges to recruit.

Among all species, *Typha domingensis* took the longest time to reappear following the vegetation removal by muskrats. This may be the result of muskrats using the whole plant including leaves for building lodges and digging out tubers for food (Danell 1977). Any remaining *Typha domingensis* bulbs in the soil did not emerge until there was sufficient standing freshwater to initiate regrowth. However, once *Typha domingensis* appeared in the vegetation, its abundance was regulated more by water level in the area than by any other measured factor having higher abundance in or following years that had higher water levels (between 25-45 cm).

A bimodal diversity curve was obtained in our study as the system recovered from disturbance. This is somewhat contrary to the findings of several studies (Pickett and White 1985, Huston 1994) that support the intermediate disturbance hypothesis (Connell 1978) of a unimodal diversity-disturbance curve. Water level fluctuated in the area because of operation of water control structures in the Bayou and was zero during sampling in 1993, 1994, and 1997. Thus, we were evaluating a system recovering from a major disturbance (i.e., complete grazeout), followed by two more disturbances (complete drying of the ground during two different periods). The two diversity peaks in 1994 and 1997 were when there was no standing water in the area at the time of vegetation sampling. The increase in diversity during these periods is explained by the lack of water that allowed more species to colonize the area under drier mudflat conditions. High water levels during 1995 and 1996 eliminated species that could not grow under inundated conditions; there was a corresponding decrease in diversity during these years. Thus, additional lesser disturbances during community recovery may affect temporal diversity patterns.

As expected of a system recovering after disturbance, we observed that diversity initially increased and then decreased to predisturbance levels over time. Similar to what others have found in different wetland systems (Nyman et al. 1993, Connors et al. 2000), our study showed species diversity increases following disturbance by muskrats in intermediate coastal marsh. However, through the analysis of long-term vegetation data, we were able to document the return of diversity levels to predisturbance levels because of community resilience. Therefore, an increase in diversity reported after disturbance in several studies may actually show a declining trend in time if data were collected for a longer time frame.

Resilience allowed plant communities to reach predisturbance levels of diversity, evenness, and dominance after a decade following muskrat removal of vegetation. As we monitored vegetation, it was difficult to exempt the marsh under study from any further disturbance. However, this allowed a better understanding of the importance of water levels on determining the vegetation composition in the area. Hydrologic regimes primarily drive vegetation changes in wetlands (Kirkman and Sharitz 1994) and based on our results, we conclude that it is possible to control the sedge or grass dominance in the community by subjecting the area to a carefully timed willful disturbance (grazing, fire, or fluctuating water levels) to achieve management goals.

The result of our study puts forward the concept that even though the quantitative measures of a plant community such as diversity, richness, evenness, and abundance, reach predisturbance levels after a period, plant species composition of the area might not return to predisturbance levels. The plant community composition present several years following disturbance is regulated more by the factors that prevail while the system is recovering. In our study, the hydrologic fluctuations following the main disturbance led to conditions favorable for a different set of plant species to become established.

For vegetation recovery in areas set aside with predetermined management objectives such as to obtain or maintain maximum vegetation productivity or high plant diversity, we suggest induction of a major disturbance every 4-5 years to achieve desired results. Based on the type of vegetation and area to be managed, either cattle grazing or fire may be used as the source of disturbance.

Major catastrophic disturbance in coastal marsh (i.e., recent hurricane hits in 2005 from Ivan, Rita, Katrina, etc.) regions of Louisiana, Florida, and Texas have caused major concerns as vegetation in these areas have been damaged due to the physical impact of the water surge, long-term inundation of marshes, and in some cases high influx of soil salinities due to evaporation of water in stagnant areas. Such areas are potential sites for studying vegetation recovery, however, based on our study we strongly recommend long-term monitoring and data collection (for at least a decade) to be able to draw meaningful conclusions on the vegetation recovery process. Several short-term studies in the past have tried to interpret vegetation recovery patterns following a disturbance and have reported unanimous trends of increase in diversity with disturbance with disturbance (Connors et al. 2000, Feldman and Lewis 2005, etc.). Such results may be true but only reflect a pattern that is ephemeral and changes within a short time period. Most of such results and conclusions are precarious and might have been different if monitored for a longer period. Thus, even if disturbance such as hurricanes, flood, fire, etc. are short-lived, it can take several years of continued monitoring to understand how a vegetation community responds to such events.

Acknowledgments. We thank the staff and management at the Anahuac National Wildlife Refuge for logistic support. Research was supported by the U.S. Fish and Wildlife Service. We appreciate help provided by P. Walther, M. Whitbeck, J. Couch, J. Fontenot, B. Dawson, J. Thompson, T. Neaville, C. Neaville, and J. Storey for their assistance in fieldwork. We also thank Dr. N. McIntyre and M. Tulbure for their comments. This is manuscript T-9-1124 of the College of Agricultural and Natural Resources at Texas Tech University. The views presented in this paper are those of the authors and do not necessarily reflect the views of the U.S. Fish and Wildlife Service.

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Received June 20, 2006
Revised Fenruary 2, 2007
Accepted February 23, 2007