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Freshwater Inundation Effects on Emergent Vegetation of a Hypersaline Salt Marsh

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ABSTRACT: The coastal marshlands of the Nueces estuary, Texas depend upon periodic freshwater inundation to support current community structure and promote further establishment and expansion of emergent halophytes. Decades of watershed modifications have dramatically decreased freshwater discharge into the upper estuary resulting in hypersaline and dry conditions. In an attempt to partially restore inflow, the U.S. Bureau of Reclamation excavated two overflow channels re-connecting the Nueces River to the marshlands. Freshwater-mediated (precipitation and inflow) changes in tidal creek and porewater salinity and emergent marsh vegetation were examined over a 5-yr period at three stations in the upper Nueces Marsh with the aid of a Geographical Information System (GIS). Two stations were potentially subjected to freshwater inflow through the channels, while one station experienced only precipitation. Decreased tidal creek and porewater salinity were significantly correlated with increased freshwater at all stations ($R^2 = 0.37$ to 0.56), although porewater salinities remained hypersaline. GIS analyses indicated the most considerable vegetation change following freshwater inundation was increased cover of the annual succulent *Salicornia bigelovii*. Fall inundation allowed seed germination and rapid expansion of this species into previously bare areas during the subsequent winter and following spring. The station affected by both inflow and precipitation exhibited greater *S. bigelovii* cover than the station affected solely by precipitation in both spring 1999 (58.7 % compared to 27.9%) and 2000 (48.6% compared to 1.9%). Percent cover of the perennial *Batis maritima* temporarily increased after periods of consistent rainfall. The response was short term, and cover quickly returned to pre-inundation conditions within 3 mo. Prolonged inundation led to long-term (>2 yr) decreases in percent cover of *B. maritima*. Our results suggest that the timing and quantity of freshwater inundation strongly dictate halophyte response to precipitation and inflow. Brief periods of freshwater inundation that occur at specific times of year alleviate stress and promote seed germination and growth, but extended soil saturation can act as a disturbance that has a negative impact on species adapted to hypersaline conditions.

Introduction

The Nueces Marsh, located on the south Texas coast northwest of the city of Corpus Christi, is an extensive deltaic salt marsh encompassing over 75 km^2 of marshlands, channels, and mudflats (Henley and Rauschbauer 1981). As in many coastal marshes, harnessing of river water and reservoir construction to support growing municipal, agricultural, and industrial needs have dramatically reduced freshwater inflow. Since 1940, river water entering the estuary has declined over 99% (from $157,897 \times 10^3$ m^3 to 662×10^3 m^3; Bureau of Reclamation 2000), and channelization of the river has diverted flow from the marsh directly into Nueces Bay. Presently, the natural flooding threshold for the northern bank of the river is about 2.36 m above mean sea level (MSL; 1929 Datum). Only occasionally do extreme hydrographic events (e.g., tropical disturbances) cause the river to breach its bank and inundate the upper marsh (Texas Department of Water Resources 1982; Bureau of Reclamation 2000).

Natural climatological conditions exacerbate the freshwater inflow problem. The region is semi-arid with low annual rainfall (75 cm yr^{-1}) normally restricted to the fall season and driven by tropical disturbances in the Gulf of Mexico or the passage of frontal systems (Lott and Ross 1997). Hot, dry summers and prevailing southeasterly winds (mean 19 km h^{-1}) throughout the year (Armstrong 1987) combine to produce a net annual water deficit, as evaporation (152 cm yr^{-1}) exceeds precipitation (Longley 1994).

Species best able to tolerate the varying hydrological regime and resulting salinities dominate the upper Nueces Marsh although prolonged water stress and hypersalinity stunt growth and reproduction, decreasing abundance and productivity (Purer 1942; Zedler 1980, 1983; Ungar 1991; Bertness et al. 1992; Pennings and Callaway 1992; Mitsch and Gosselink 1993). These conditions require adult plants to expend considerable energy on osmoregulation which drains resources otherwise available for seed production and growth (Ungar 1962, 1991, 1995; Chapman 1974; Philipupillai

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and Ungar 1984). Bare areas can form that directly expose soils to insolation and cause additional water and salinity constraints (Zedler 1982; Bertness 1991a). Both preservation of the present halophyte community and additional expansion by seeds or vegetative growth (rhizomes) require periodic freshwater inundation to temporarily relieve salt and water stress.

Coastal marshlands are unique and valuable ecosystems. Coastal population expansion continues to threaten these areas, resulting in an inevitable conflict between human freshwater needs and preservation of these natural habitats. In October 1995, concerns about south Texas marsh productivity prompted the U.S. Bureau of Reclamation to excavate two diversion channels re-connecting the Nueces River to the upper marsh in an attempt to restore freshwater inflow events. The objectives of our study were to measure the impacts of freshwater inflow through these channels on both tidal creek and porewater salinity and attempt to understand the interactions between freshwater inundation and coincident variations in the distribution, abundance, and species composition of emergent vegetation.

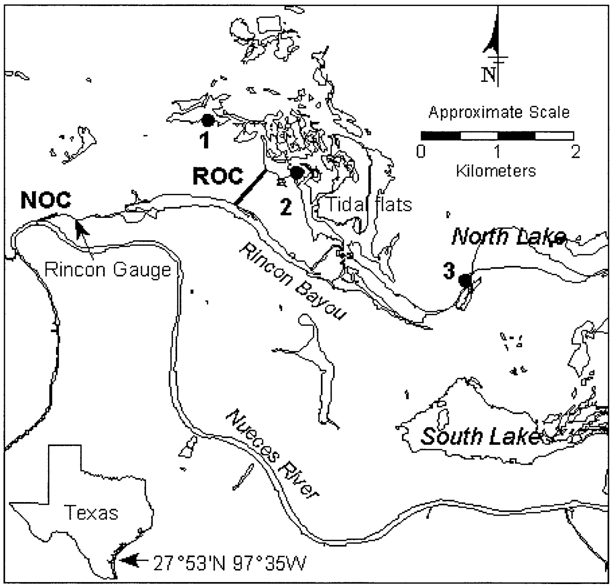

Fig. 1. Location of the Nueces Marsh, the Nueces Overflow Channel (NOC), the Rincon Overflow Channel (ROC), the U.S. Geological Survey Rincon Gauge and monitoring stations (Stations 1–3). Modified from Bureau of Reclamation (2000).

Methods

Study Area

Studies were conducted in the upper Nueces Marsh, Corpus Christi, Texas (27°53′N, 97°35′W). The study area consisted of two overflow channels and three stations chosen because of their proximity to the channels (Fig. 1). The Nueces Overflow Channel (NOC) connected the Nueces River to upper Rincon Bayou, the natural headwater of the estuary. Flow through the NOC required a minimum river water level of 0.6 m above MSL. The Rincon Overflow Channel (ROC) linked upper Rincon Bayou to an area of hypersaline tidal flats. Discharge exceeding 11.9 $m^3 s^{-1}$ and reaching levels of 1.14 m above MSL in Rincon Bayou activated the ROC.

Emergent vegetation and salinity were quantified at one reference and two treatment stations (Fig. 1). Treatment stations (stations 2 and 3) were located in areas potentially affected by freshwater diversions through the channels, and were compared to a reference station (station 1) exposed to the same meteorological influences but not affected by inflow through the channels (changes were independent of the channels). Station 1 was located 0.9 km upstream from the channels and furthest upstream from Nueces Bay. Station 2 was situated in a tidal flat area downstream from station 1 and the ROC and received freshwater from extreme inflow events that activated the ROC. Freshwater flow through the NOC potentially influenced station 3 (5.7 km distant), which was directly along Rincon Bayou but furthest from the channels.

Topographic maps created from 1993 black and white aerial photography (NAD 83 Texas State Plane) indicated station elevations well above the mean astronomical tide (0.15 m). Stations 1 and 2 were 0.75 m above MSL (1929 Datum), while station 3 was only 0.45 m above MSL. The elevations likely limited tidal flooding to spring and autumn high tides (0.60 m), although strong southeasterly winds or heavy rainfall may have produced additional flooding. The potential for marine forcing would have been greatest at station 3.

A diverse assemblage of salt-tolerant grasses, shrubs, and succulents comprised the upper delta and included both annuals and perennials. The dominant upper marsh species were *Batis maritima* (saltwort), *Borrichia frutescens* (sea ox-eye daisy), and *Monanthocloe littoralis* (shoregrass). *Distichlis spicata* (saltgrass), *Salicornia virginica* (woody glasswort), and the annual *Salicornia bigelovii* (glasswort) were periodically present.

Freshwater Inputs

River flow and precipitation from May 1996 to June 2000 were measured at the U.S. Geological Survey (USGS) Rincon Bayou Channel near Calallen (Station 08211503) gauge (Rincon Gauge) located 274 m downstream from the intersection of the Nueces River and the NOC (Fig. 1). Precipitation prior to this period were obtained from the National Climatic Data Center records for the Corpus Christi International Airport (Station 412015; 27°46′N, 97°31′W) located approximately 14 km southeast of the study area.

Sampling and Analysis

Tidal creek salinity was measured in the field using an Orion 140 conductivity meter (Orion Research Incorporated, West Germany). Two replicate soil water samples were collected using lysimeters placed within the sediments at 0, 49, and 99 m (stations 1 and 2) and 0, 47, and 103 m (station 3) from the tidal creek. Lysimeters were constructed of PVC pipes (6 cm diameter, 60 cm length) with horizontal slits cut in the lower 30 cm to allow for the passive movement of water into the pipe. Slits were cut at this depth (30–60 cm) to maximize the chances of collecting water. We recognize that this depth is likely deeper than the natural root zone of halophytes and that salinity values may underestimate the actual salinity regime experienced by the plants, but top soils were usually too dry to contain sufficient water for the analyses. If water did not collect in the lysimeters, soil samples were taken and later centrifuged at 10,000 rpm for 20 min to extract porewater. Porewater salinity was determined using a refractometer (Reichert Scientific Instruments, Buffalo, New York). On several sampling dates, porewater salinity data were not acquired due to low soil moisture.

Vegetation percent cover was censused seasonally from June 1995 to June 2000 at 265 points along three permanent transects (one per station; Bertness and Ellison 1987). Transects were 99-m long and 8-m wide (792 m^2; n = 65) at stations 1 and 2, and 103-m long and 8-m wide (824 m^2; n = 75) at station 3. All extended perpendicularly from the vegetation line at the water's edge. Transects were sampled at 3-m intervals near the tidal creeks and at about 10-m intervals elsewhere along perpendicular transect lines. The lines were spaced closest together near the water because this area was expected to show the greatest variation in inundation. Transect elevation above the tidal creek was measured at each sampling interval using a transit and stadia rod. At each interval, vegetation sampling occurred at 2-m intervals along an 8-m transect line parallel to the shoreline. A 0.25-m^2 quadrat subdivided into 100 5 × 5 cm cells allowed visual estimation of percent cover of each species and bare area at each sampling point. Cells with no vegetation, covered with water, or consisting of wrack (dead plant material >2 cm thick) were considered bare area. Percent cover data for station 3 on June 2000 were not collected because livestock had destroyed the transect.

To facilitate spatial analyses, we used a Geographical Information System (GIS) to supplement data synthesis. The GIS allowed point data acquired in the field to be geographically represented, interpolated into grids, and spatially presented in a visual context that aided the detection of patterns and trends. Percent cover maps were created to determine changes in species cover and bare area for the sampling date prior to and at least two sampling dates following an inflow event. Initial maps depicting interpolated cover of each species and bare area were created using the Spatial Analyst extension and Inverse Distance Weighting function in ArcView GIS 3.2 (ESRI, Inc. 1999). The method uses data acquired in the field as reference points and assumes that the measurement at each sampling point has a local influence that diminishes with distance. Areas closest to the field measurement would have a more similar value than those more distant.

Final vegetation maps were created by querying individual interpolated maps to locate areas within the transect where percent cover of each species or bare area exceeded 50%. Individual maps of cover greater than 50% for each species or bare area were then merged into one map for each station on each sampling date. This approach facilitated comparisons of changes in species dominance across the entire length of the transect by allowing vegetation cover for all species and bare area to be mapped simultaneously. The percent of the transect area covered by greater than 50% cover was used to evaluate changes. Ground-truthing of maps indicated interpolation errors at the 50% level of only ±3%. While the conversion of field data into interpolated surfaces is by no means exact, the method allows for analyses in a spatially coherent, three-dimensional manner, which naturally represents the data.

Porewater salinity data were analyzed using a general linear model procedure (SPSS Inc. 2000). Significant differences among sampling dates were determined using a one-way analysis of variance (ANOVA). When significant differences for a main effect occurred ($p < 0.05$), a Tukey Multiple-comparison test was used to determine significant differences between sampling dates.

Results

Freshwater Inputs

Monthly river flow past the Rincon Gauge varied between study years (Fig. 2). Only three large freshwater inflow events occurred during the study: June–July 1997 (summer 1997), October 1998, and September 1999. These events produced high flow ($>493 \times 10^3$ m^3) and activated the ROC.

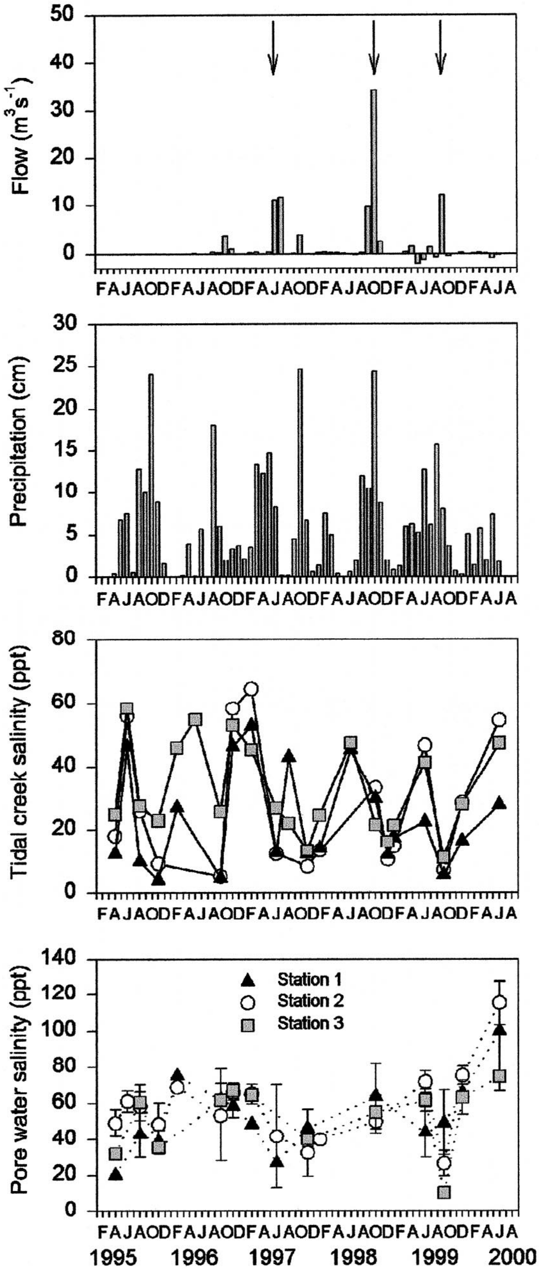

Fig. 2. Monthly river flow, precipitation, and seasonal tidal creek and mean porewater salinity in the upper Nueces Marsh between January 1995 and June 2000. Monthly precipitation prior to May 1996 are from the Corpus Christi International Airport. Precipitation and flow values from May 1996 to June 2000 are from the U.S. Geological Survey Rincon Gauge located downstream from the intersection of the Nueces River and the Nueces Overflow Channel. Error bars represent mean ± SE. Arrows indicate freshwater inflow events.

The October 1998 and September 1999 events coincided with heavy precipitation (~24 cm). During summer 1997, 955 × 10^3 m^3 of freshwater entered the upper marsh, representing 83% of the positive inflow into the area for the year. The October 1998 event (our sampling during this month occurred prior to the event) was the largest of the study period (1,419 × 10^3 m^3 or 72% of the annual positive net flow).

During late summer 1999, two separate flooding events occurred (Fig. 2). At the end of August, the tidal surge of Hurricane Bret flooded all transects with saltwater from the bay. About 2 wk later, freshwater entered the channels and flooded station 2 and possibly station 3. The September 1999 freshwater inflow event was small (511 × 10^3 m^3) compared to the other events. Our September 1999 sampling occurred following the tidal surge but before the freshwater inflow event so that any changes observed in September 1999 were in response to the tidal surge and direct precipitation and not the mid-September inflow event.

Currently, the Texas Natural Resource Conservation Commission permit for the two main-stem reservoirs on the Nueces River (Lake Corpus Christi and Choke Canyon) requires the release of 112,258 × 10^3 m^3 annually of freshwater to the Nueces estuary through a combination of reservoir spills and releases. During this study, monthly reservoir releases produced some freshwater inflow into the delta (Bureau of Reclamation 2000), but flow was minimal compared to the three large flooding events and did not appear to impact emergent halophytic vegetation.

Interannual variation in precipitation was high (Fig. 2). Rainfall was greatest in 1995 (92.7 cm) although about 60% of the rain fell between August and November. Approximately 50 cm less fell in 1996. In 1997, annual precipitation (90.5 cm) closely resembled the value for 1995. In 1998, 75% of the annual precipitation (73.7 cm) occurred during the fall. In 1999, rainfall totaled only 66.3 cm but was distributed throughout the year with each month from March to September receiving >5 cm.

SALINITY

Salinity fluctuated considerably among and within stations (Fig. 2). Mean porewater salinity (10.5–115.4‰) usually exceeded tidal creek salinity (4.0–64.7‰; Fig. 2). Porewater salinity changes reflected those of tidal creeks at stations 2 and 3 (Fig. 3). Significant correlations between tidal creek and porewater salinity were obtained at stations 2 ($R^2 = 0.47$; $p = 0.004$) and 3 ($R^2 = 0.59$; $p = 0.003$), but not at station 1 ($R^2 = 0.12$; $p = 0.246$).

Both tidal creek and porewater salinity exhibited correlations between decreasing salinity and increasing precipitation (Fig. 4). Decreased tidal creek salinity was significantly ($p = 0.001$) correlated with increased cumulative precipitation at all

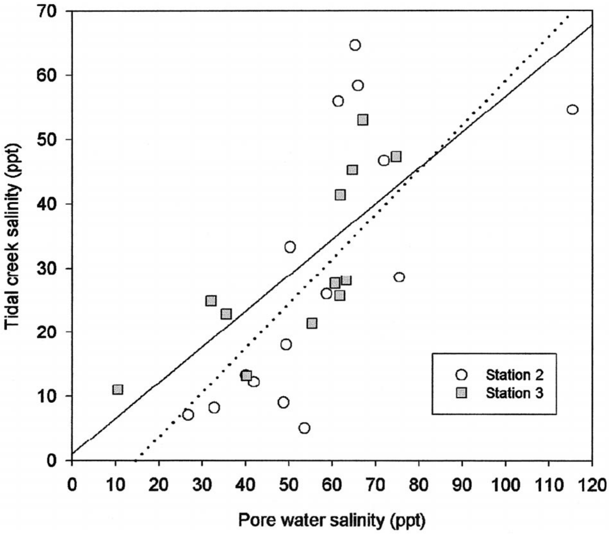

Fig. 3. Relationship between tidal creek and porewater salinity at stations 2 and 3. $R^2 = 0.47$ and 0.59 at stations 2 (solid line) and 3 (dotted line), respectively. No statistical relationship was observed at station 1 ($R^2 = 0.12$).

stations ($R^2 = 0.47$, 0.56, and 0.44 for stations 1, 2, and 3, respectively; Fig. 4a). Linear regressions also showed a significant correlation ($p < 0.05$) between decreased porewater salinity and increased cumulative precipitation at all stations ($R^2 = 0.37$, 0.41, and 0.52 for stations 1, 2, and 3, respectively; Fig. 4b). Cumulative precipitation is the sum of precipitation for the three months prior to a sampling date. This interval was chosen because tidal creek salinity remained depressed for up to three months following precipitation events (Fig. 2; e.g., November 1997–January 1998). Inflow and salinity regressions could not be performed because heavy inflow always coincided with or followed heavy precipitation and could not be distinguished separately. Time series of salinity data (Fig. 2) indicate decreased tidal creek and porewater salinity at stations 2 and 3 following inflow events and high salinities during dry, hot periods. Only one mean porewater salinity value (pooled for all samples) was significantly higher ($p < 0.05$, ANOVA) at one station on one sampling date (station 2, June 2000).

The lowest porewater salinities occurred in September 1999 immediately following the tidal surge of Hurricane Bret (Fig. 2). The flooding of soils, albeit with salt water, appeared to flush the soils of salts at least temporarily. Porewater salinity at stations 2 (26.7‰) and 3 (10.5‰) were lowest on this sampling date, but values quickly increased and reverted back to pre-flood levels (75.4‰ and 63.2‰) by December 1999. Porewater salinity at station 1 actually increased by about 5‰ after the tidal surge.

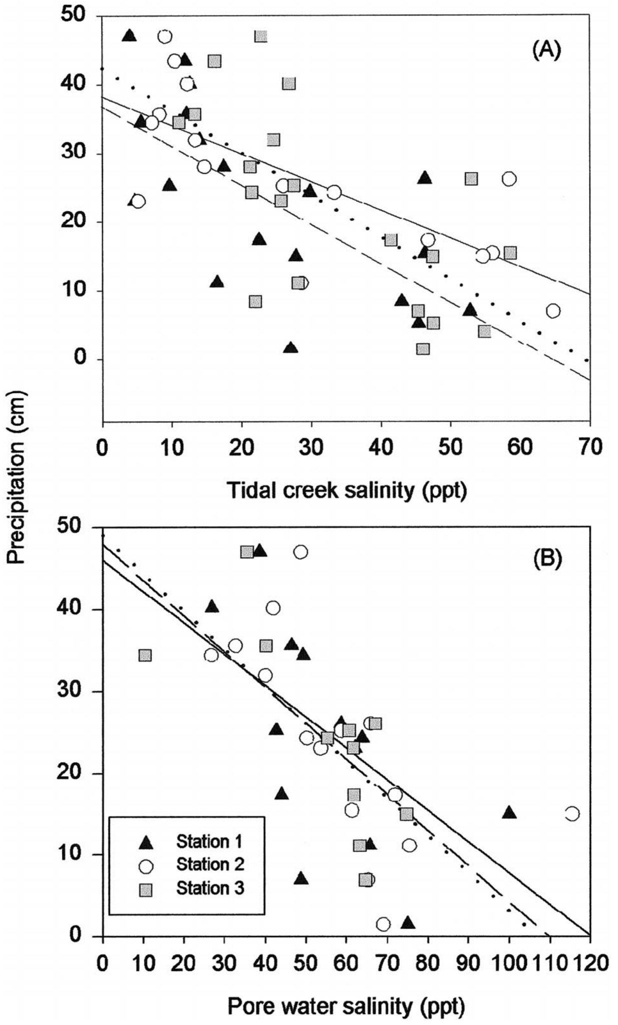

Fig. 4. Correlation between tidal creek (A) and mean porewater salinity (B) with cumulative precipitation for the three months prior to sampling at the three stations. $R^2 = 0.47$, 0.56, and 0.44 for tidal creek and 0.37, 0.41, and 0.52 for porewater salinity regressions at stations 1 (dashed line), 2 (solid line), and 3 (dotted line), respectively.

TRANSECT ELEVATION

Elevation along the transects varied between ca. 0 and 0.7 m above the tidal creek (Fig. 5). Station 2 exhibited minimal elevation change, facilitating flooding by inflow through the ROC. Elevation at stations 1 and 3 increased to 0.2 m above the tidal creek at 3 m, which limited inundation to periods of high flow. An elevation drop of 0.3 m between 40 and 60 m at station 1 was due to a saltpan. A small creek intersected the transect at station 3 between 50 and 57 m. The creek bank at 57 m was eroded, creating a steep increase in elevation.

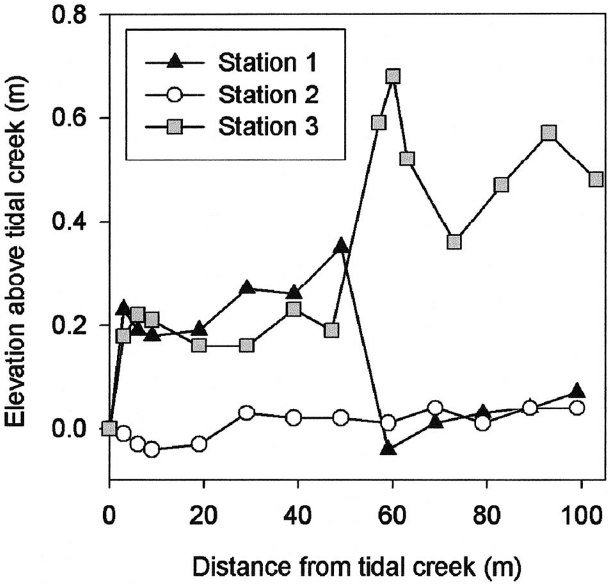

Fig. 5. Elevation changes along transects as a function of distance from the tidal creek. Note the increase in elevation at the 3 m mark at stations 1 and 3.

VEGETATION MAPS

Summer 1997 Inflow Event

The summer 1997 event produced variable vegetative responses (Fig. 6). Most notably, vegetative expansion of the perennial *B. maritima* led to a temporary increase in cover at all stations despite the stations being affected differently by freshwater inundation. The increase was 7-fold at station 1 (from 1.7% of the transect having cover greater than 50% in June to 12.1% in August) and corresponded to a 4-fold decrease (2.3% to 0.5%) in *B. frutescens* and bare area decline from 38% to 33%. At station 2, both *B. maritima* and *M. littoralis* nearly doubled between June and August 1997, and bare area decreased from 75.4% to 64.4%. At station 3, *B. maritima* increased 3-fold (from 13.7% in June to 35.5% in August) and coincided with reduced bare area (from 29.9% in June to 20.3% in August) and decreased *B. frutescens* (from 10% in June to 3.1% in August). The effects were temporary with changes quickly reverting to pre-flood levels by November.

October 1998 Inflow Event

The principal change after the October 1998 event was increased cover of the annual *S. bigelovii* the following spring (Fig. 6). The plant's annual life cycle dictates that the increased cover was due to seed germination and expansion earlier in the season. The increase occurred at stations 1 and 2 only and was greatest at station 2, which had the lowest transect elevation and was affected by both inflow and precipitation compared to only precipitation at station 1. At station 1, increased *S. bigelovii* cover (from 0% to 27.9%) coincided with decreased bare area (44.5% in January to 8% in June 1999). At station 2, *S. bigelovii* expansion (from 0% to 58.7%) was twice that seen at station 1 with a resultant decline in bare area from 86.3% in October 1998 to 14.1% in June 1999. At both stations, *M. littoralis* cover ultimately decreased following *S. bigelovii* expansion.

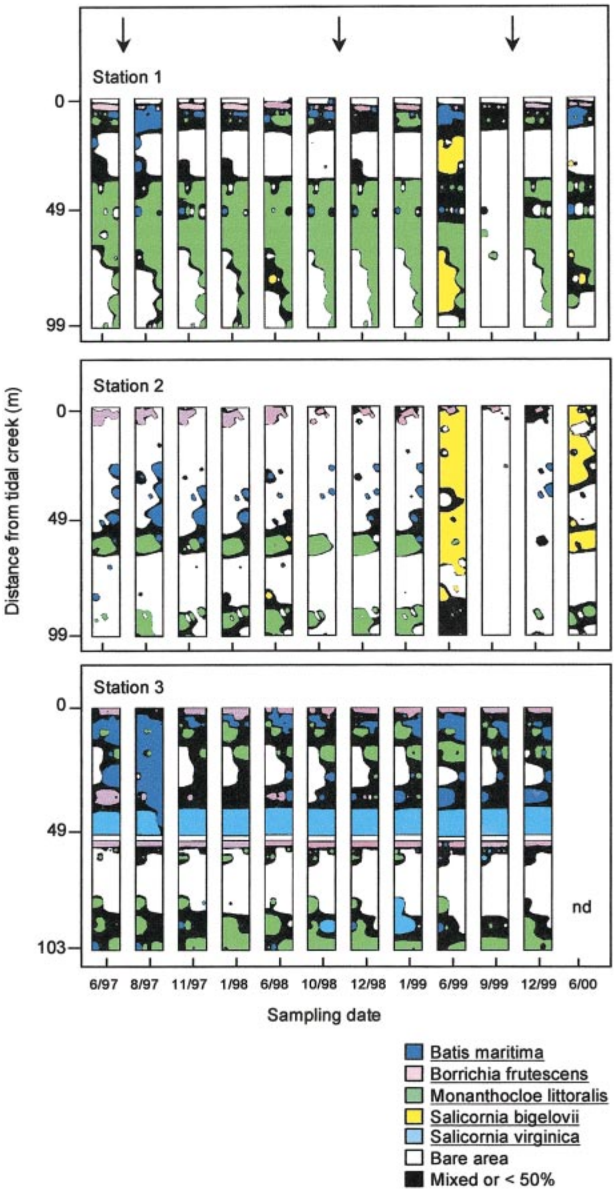

Fig. 6. Species percent cover and bare area at the three stations for the sampling date prior to a freshwater inflow event and at least two subsequent visits. Mapped areas are covered by at least 50% of listed species or bare area (see methods). Arrows indicate inflow events. nd = no data.

At stations 1 and 3, which were affected only by precipitation, vegetative cover of perennial succulents increased following the event (Fig. 6). *B. maritima* increased 13-fold (from 0.5% to 6.4%) and 4-fold (from 3% to 12.6%) at stations 1 and 3, respectively. At station 3, *S. virginica* appeared toward the end of the transect in January 1999.

September 1999 Floods

Two separate flooding events inundated the marsh during September 1999 (Fig. 2). Just prior to early September sampling, the tidal surge of Hurricane Bret flooded all stations. We measured dramatic decreases in *M. littoralis, B. maritima,* and *S. bigelovii* and consequent increases in bare area at stations 1 and 2 (Fig. 6), but the impact was not seen at station 3. About 2 wk later, freshwater flooded the marsh through both channels. December 1999 and June 2000 sampling revealed a rapid recovery of plant cover (Fig. 6). At station 1, *M. littoralis* quickly expanded into almost half the bare area, and *B. frutescens* cover more than doubled. Bare area decreased from December 1999 (45.1%) to June 2000 (37.7%), and both *B. maritima* and *S. bigelovii* increased. At station 2, *S. bigelovii* invaded previously bare areas (almost 50% of the transect), reducing bare area from 85.4% in December 1999 to 46.2% by June 2000. *M. littoralis* tripled (from 1.3% in December 1999 to 3.5% in June 2000), reaching levels greater than the previous spring (0.7%). No data were obtained for June 2000 at station 3 due to destruction of the transect by cattle.

Discussion

Salinity Changes

Along the Texas Gulf Coast, low freshwater inundation, infrequent tidal flushing, and high evaporation lead to hypersaline and dry conditions (Mitsch and Gosselink 1993). In this study, tidal creek salinities were up to two times higher than normal sea water, and porewater salinity exceeded values of 100‰. Dunton (unpublished data) frequently measured high soil salinities (maximum of 112‰) in the upper delta between 1994 and 1999. High values typically coincided with drought periods. Heavy precipitation and inflow reduced salinities, but changes were typically short term and quickly reversed. Comparable effects in a hypersaline marsh were noted in the Tijuana estuary, California (Zedler 1983; Zedler et al. 1986).

Variations in soil salinity reflected corresponding changes in tidal creek salinity at stations 2 and 3. The trend is similar to that described by Hackney and De la Cruz (1978) for a Mississippi tidal marsh. The lack of a response at station 1 may be indicative of the station's location. Station 1, unlike station 2, was not impacted by freshwater flooding through the channels and was not subjected to tidal flushing as often as station 3.

Freshwater Effects on the Annual Halophyte *S. bigelovii*

The timing, type (precipitation versus inflow), and quantity of freshwater inundation had variable effects on percent cover of *S. bigelovii,* an annual succulent. Seed germination and plant expansion following fall inundation rapidly increased cover the subsequent spring. Lower air temperatures and evaporation rates common during late fall and winter likely facilitated this response (i.e., soils remain moist with a lower salinity for a longer time). Seeds may have germinated following inundation during warmer periods, but seedling survival was ultimately dependent on additional freshwater input to periodically moisten soils and maintain lower salinities. Seeds sprout near the soil surface, and salinity exposure is 2 to 100 times that of the subsoil (Ungar 1978). Seedlings are generally more sensitive to elevated salinities than mature plants (Ungar 1995). Droughts and hypersaline soils common in summer inhibit sexual reproduction and have led to near extinctions of *S. bigelovii* in California salt marshes (Zedler and Beare 1986). Fall inundation ensures that annual plants attain a sufficient size to withstand the harsher conditions common during spring and summer.

S. bigelovii cover increased more at station 2, which was affected by both inflow and precipitation, than at station 1, which was affected solely by precipitation. In June 1998, following heavy rains in fall 1997 (32 cm) but no inflow event, cover at stations 1 and 2 were similar (0.9–1.0%; Fig. 6). During June 1999, following heavy fall rains (35 cm) in combination with an inflow event (October 1998), cover at station 2 (58.7%) was twice that seen at station 1 (27.9%). Following a fall with little precipitation (4.6 cm) but an inflow event (September 1999), cover at station 2 in June 2000 was 48.6% compared to 1.9% at station 1.

The enhancement of *S. bigelovii* cover following flooding events compared to precipitation alone may reflect differences in the duration of soil saturation. Flooding is associated with much larger volumes of water that completely saturate soils and keep them moist for longer periods. Kuhn and Zedler (1997) observed that two or more weeks of soil saturation were required for seed germination of the California native halophyte, *S. subterminalis* at salinities typical of hypersaline soils (>35‰). Seedlings required an additional 2 to 3 wk of high moisture to survive. Kuhn and Zedler (1997) further noted that only the germination and establishment phases were dependent upon freshwater inundation, but that soil saturation lasting longer than 8 wk caused pronounced declines in growth and production, indicating again the importance of inundation timing and duration.

Transect elevation appeared to affect *S. bigelovii* cover. At station 3, cover was below the 50% mapping level on each sampling date. The mean vegetation lines are 0.2 and 0.7 m higher than at station 2, indicating that freshwater inflow events must rise to a higher level to flood the station 3 transect and elicit a vegetative response. In June 1999 and 2000, we observed extensive cover of *S. bigelovii* near the station 3 transect in previously bare areas along the tidal creek at lower elevations. Some freshwater may have reached this area but did not rise sufficiently to inundate our transect. The enhanced growth of *S. bigelovii* at lower elevations near station 3 suggests again that precipitation alone is not sufficient to elicit the same response as inflow.

The rapid establishment of *S. bigelovii* following freshwater inundation may reflect the seed bank composition in the upper marsh. Although no studies have been performed for this area, Ungar (2001) hypothesized that a large persistent seed bank may exist in hypersaline soils because seeds germinate only if stressful conditions are alleviated. Annual plants may use seed banks to maximize survival potential in perennially dominated salt marshes (Ungar 2001). Seed banks are an important factor in determining community structure in salt marshes following disturbance (Ungar 1982). Allison (1996) noted rapid post-flood establishment in areas with a nearby seed supply and reduced soil salinity.

In salt marsh habitats, halophyte sexual reproduction is critical to community success (Ungar 1991; Allison 1996). Seeds allow establishment at locations distant from neighbors, while vegetative growth is limited to a particular area (Adam 1990). In this study, *S. bigelovii* seeds sprouted in previously bare areas. Similar colonization of bare space was documented for the annual *S. europaea* (Bertness and Ellison 1987; Bertness 1991b). Seeds facilitate rapid bare area re-establishment following the loss of adult populations from disturbances like flooding, drought, or burial (Allison 1996). These early colonizers passively shade the soil surface, reducing porewater salinity and increasing soil moisture (Bertness 1991a). Eventually, competitively dominant and persistent perennial species invade (Bertness and Ellison 1987; Bertness 1991a; Bertness et al. 1992), providing stable habitat and food for a variety of primary and secondary consumers (Henley and Rauschbauer 1981).

PERENNIAL RESPONSE TO FRESHWATER INUNDATION

The most notable perennial response to freshwater inundation was increased cover of the succulent *B. maritima* following consistent rainfall and decreased cover after prolonged inundation. At all stations, cover temporarily peaked during August 1997 following heavy spring rains (52 cm in 5 mo) and the summer 1997 inflow event. Inundation likely lessened the stressful summertime conditions, allowing short-term vegetative expansion. This peak contrasts to measurements obtained in the lower Nueces Marsh during summer 1997 where *B. maritima* cover decreased in response to direct precipitation (Weilhoefer 1998). Dunton et al. (2001) also noted decreased cover in the low marsh following heavy rains and speculated that precipitation served as a temporary physical disturbance reducing vegetation cover over a relatively short period.

The different response between the two marsh areas likely results from a combination of salinity and soil moisture. Heavy rains alleviate water and salinity stress in the upper marsh, but do not waterlog soils. Tidal inundation is periodic, and soils do not remain moist even though frequent tidal inundation in the low marsh keeps soils wet. Excessive flooding produces anoxic soils and forces belowground tissues to rely on anaerobic metabolism (Mendelssohn et al. 1981). We hypothesize that succulent halophytes highly adapted to hypersaline and dry conditions (e.g., *B. maritima*) are relatively intolerant of continuously waterlogged soils. The continual suppression of *B. maritima* at station 2 after the initial flood in summer 1997 supports this idea. Unlike station 1 and probably station 3, station 2 was flooded by freshwater on three occasions. The station's relatively low transect elevation facilitated flooding. Similar freshwater-mediated growth limitations have been observed in *S. virginica* (Zedler and Beare 1986; Allison 1996, 1996; Pennings and Callaway 1992; Weilhoefer 1998) and *S. subterminalis* (Kuhn and Zedler 1997).

Cover of most species decreased at stations 1 and 2 following the September 1999 tidal surge of Hurricane Bret. During the tidal surge, thick, green cyanobacterial mats were lifted from the marsh soils and then dropped onto the vegetation when the water retreated (Alexander personal observation). The thick mats shaded emergent plants and reduced air flow, creating stagnant conditions that resulted in a loss of plant cover. The physical disturbance associated with this inundation event created bare space that clearly contributed to the spatial heterogeneity and high plant species diversity characteristic of the Nueces Marsh.

Conclusions

In the absence of any change in the frequency of pulsed flooding events, the hypersaline and dry conditions in the upper Nueces Marsh will persist as reflected in an emergent plant community that alternates between annual dominance and perennial persistence in both time and space. If freshwater inflow is increased and sustained through permanent diversions, halophyte productivity in the upper delta may increase to some threshold (Zedler 1983) value before plant dominance shifts from marine to freshwater species. The community structure shift in the upper marsh would be offset by increased halophyte growth and expansion in the low marsh facilitated by freshwater dilution of tidal waters from the bay.

Our study demonstrates the effects of freshwater inundation, both precipitation and inflow, on salinity and emergent vegetation characteristics over broad temporal and spatial scales. Brief periods of freshwater inundation at specific times of year alleviated stress in hypersaline and dry soils and promoted seed germination and expansion of *S. bigelovii.* Prolonged soil saturation following flooding acted as a disturbance and resulted in reduced cover of *B. maritima,* a perennial halophyte adapted to hypersaline environments. Our results emphasize the dynamic role of hydrological events in determining community structure and the mosaic patterns characteristic of salt marsh emergent vegetation assemblages.

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