The Effect of Multiple Stressors on Salt Marsh End-of-Season Biomass

Jenneke M. Visser[1,*], Charles E. Sasser[1], and Brian S. Cade[2]

[1] *Coastal Ecology Institute, School of the Coast and Environment, Louisiana State University, Baton Rouge, Louisiana 70803*

[2] *Fort Collins Science Center, U.S. Geological Survey, Fort Collins, Colorado 80526*

ABSTRACT: It is becoming more apparent that commonly used statistical methods (e.g., analysis of variance and regression) are not the best methods for estimating limiting relationships or stressor effects. A major challenge of estimating the effects associated with a measured subset of limiting factors is to account for the effects of unmeasured factors in an ecologically realistic matter. We used quantile regression to elucidate multiple stressor effects on end-of-season biomass data from two salt marsh sites in coastal Louisiana collected for 18 yr. Stressor effects evaluated based on available data were flooding, salinity, air temperature, cloud cover, precipitation deficit, grazing by muskrat, and surface water nitrogen and phosphorus. Precipitation deficit combined with surface water nitrogen provided the best two-parameter model to explain variation in the peak biomass with different slopes and intercepts for the two study sites. Precipitation deficit, cloud cover, and temperature were significantly correlated with each other. Surface water nitrogen was significantly correlated with surface water phosphorus and muskrat density. The site with the larger duration of flooding showed reduced peak biomass, when cloud cover and surface water nitrogen were optimal. Variation in the relatively low salinity occurring in our study area did not explain any of the variation in *Spartina alterniflora* biomass.

Introduction

Many factors have been identified as production-limiting factors in salt marshes including nitrogen (Tyler 1967; Jefferies and Perkins 1977), soil drainage (Mendelssohn and Seneca 1980; Wiegert et al. 1983), soil aeration and redox potential (Howes et al. 1981; Mendelssohn et al. 1981), sulphide concentration (King et al. 1982), soil salinity (Nestler 1977; Zedler 1983), temperature (Turner 1979; Giroux and Bedard 1987), grazing (Silliman and Zieman 2001; Moon and Stilling 2002; Silliman and Bortolus 2003), and solar radiation (Morris 1982; Teal and Howes 1996). Using 5 yr of saline marsh vegetation data from a South Carolina salt marsh, Morris and Haskin (1990) showed that mean sea level and total rainfall during July and August were significantly and positively correlated with annual production. Using 13 yr of data from a salt marsh in the Netherlands, De Leeuw et al. (1990) found that the rainfall deficit during the April-June growing season was significantly correlated with the peak aboveground biomass of most salt marsh communities, while flooding frequency showed no correlation. Teal and Howes (1996) found no significant correlations using 22 yr of data from a Massachusetts salt marsh. When they used only the last 11 yr of data (the record with more extensive measurements), Teal

and Howes (1996) found positive correlations for total solar radiation and average water temperatures from June through August. Several environmental factors have been identified as controlling primary production in salt marsh angiosperms based on spatial variation or experimental manipulation. Studies of temporal variation in biomass have had limited success. There is a clear need for analysis of long-term data sets to better elucidate the importance of multiple factors controlling temporal trends in marsh primary production.

It is becoming more apparent that commonly used statistical methods, such as analysis of variance and regression, are not the best methods for estimating limiting relationships in ecology (Thomson et al. 1996; Cade et al. 1999). Cade et al. (1999) illustrated how unmeasured factors increased variation in biomass where the measured variable was less limiting. In other words, if the variable of interest was not limiting there was the opportunity for other stressors to affect biomass and large variation in biomass may be observed. Cade et al. (1999) demonstrated that the relationship with the limiting factor was near the upper edge of the data, rather than through the center of the data distribution. Linear regression correlates the average (i.e., the center of the distribution) to the limiting factor. The edge of the response variable data distribution (in the previous biomass example) is best described using quantile regression using the upper quantiles (Sharf et al. 1998; Cade and Guo

---

* Corresponding author; tele: 225/578-6377; fax: 225/578-6326; e-mail: comvss@lsu.edu
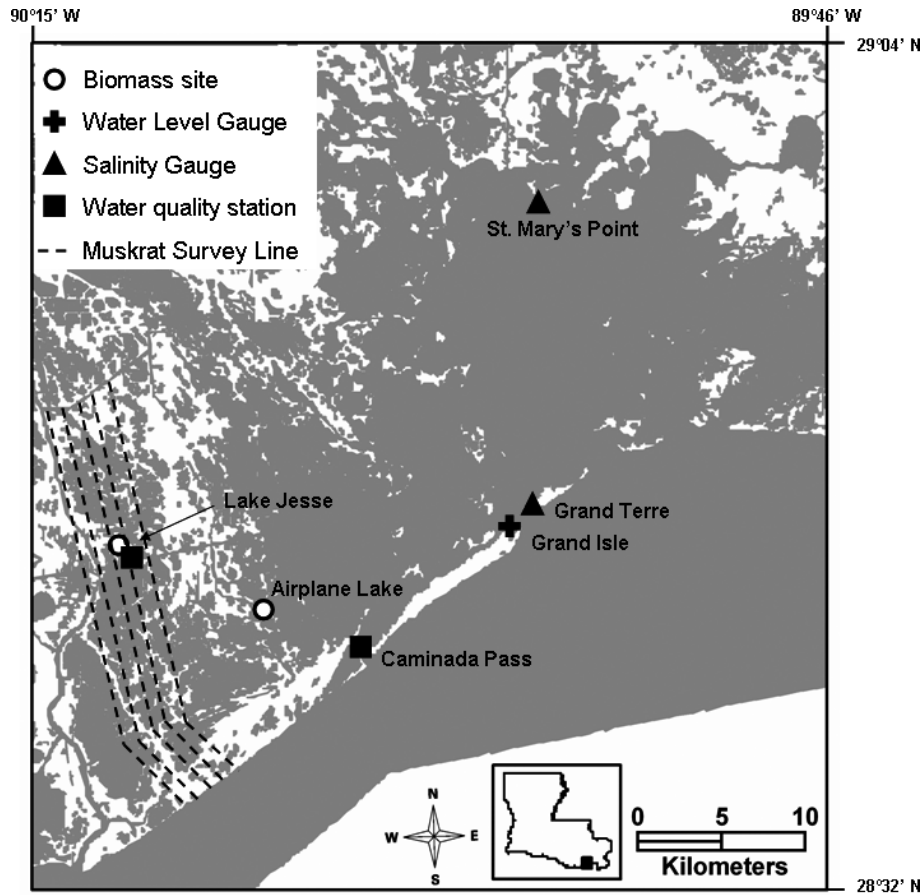
328

Fig. 1.   Location of the two study sites and data stations. Data sources are identified in the Methods section.

2000; McClain and Rex 2001). Quantile regression has a decades-long statistical history and has been only recently applied in ecology to explain environmental limitations (Terrell et al. 1996; Sharf et al. 1998; Cade et al. 1999; Cade and Guo 2000).

We used quantile regression to elucidate multiple stressor effects on an 18-yr record of end-of-season biomass data from two salt marsh sites in coastal Louisiana. This study uses a rare long-term data set that was collected as part of a pipeline monitoring program. Because these data were not collected specifically for this analysis, environmental data from other sources that were not collected in exactly the same area were used (Fig. 1). Where data is available, we show the spatial coherence of these environmental data over distances similar to the distance between environmental monitoring sites and our biomass sites. Although spatial coherence for many environmental factors is low on a daily time scale, when integrated over a growing season, spatial variation is much smaller than interannual variation. Stressor effects estimated based on available data were flooding duration, salinity, air temperature,

grazing by muskrat (*Ondatra zibethicus*), precipitation deficit, nitrogen and phosphorus availability, and cloud cover. As with any study of this kind, many assumptions have to be made to relate one end-of-season biomass measurement to variable conditions during the growing season. We document these assumptions and previous work on these stressors in the methods section.

Methods

From 1978 through 1995, biomass was harvested in September of most years at two saline marsh sites in 0.25-m² plots (Fig. 1). The sites are named for the nearest named geographical features: Lake Jesse and Airplane Lake. Both of these lakes are connected to the myriad of waterways that are present within lower Barataria estuary and through them connected with Barataria Bay. At each site, the start of the transect (first plot) was selected through a throw of the first quadrat frame. Subsequent plots were determined by orienting the transect perpendicular to the adjacent water way and sampling at 20-m intervals. If a plot was located in open water,

the location was changed to the nearest vegetated area along the transect line. All standing plant material within each plot were clipped at ground level and placed in plastic bags. The harvested plant material was returned to the laboratory, where live plants and any attached dead leaves were separated from dead material not attached to live plants. Live plants with any attached dead material were sorted by species and oven dried at 65°C to constant weight. End-of-season biomass was determined by summing the weight of all species for each harvested plot. In this study, we only used data from plots in which >95% of the end-of-season biomass came from *Spartina alterniflora*. Two other species, *Spartina patens* and *Distichlis spicata*, were occasionally present in these samples. The resulting number of samples varied among years at Lake Jesse and ranged from a minimum of 6 samples in 1994 and 1995 to 13 samples in 1988 with an average of 9 samples per year. At Airplane Lake 10 samples were obtained each year.

The negative effects of extended flooding on the primary production of *S. alterniflora* have been well documented (Mendelssohn and Seneca 1980; Howes et al. 1986; DeLaune et al. 1984; Reed and Cahoon 1992; Pezeshki 1997). We obtained the long-term record from the National Oceanic and Atmospheric Administration (NOAA) Grand Isle Waterlevel Gauge (gauge 8761724 data down loaded from http://co-ops.nos.noaa.gov). The location of this gauge relative to the biomass sample sites is 18 km east southeast from Airplane Lake to Grand Isle and 24 km east southeast from Lake Jesse to Grand Isle. Since we only sampled vegetated plots, we assumed that the vegetated surface elevation kept up with long-term subsidence and sea-level rise (Morris et al. 2002). We estimated the long-term trend by fitting a linear regression to the Grand Isle gauge data (1955–2000). This fitted long-term trend represents apparent sea-level rise (subsidence and relative sea-level rise combined). The apparent sea-level rise was removed by subtracting the predicted value from the measured value (Fig. 2). The adjusted long-term water levels from the Grand Isle gauge were then related to marsh flooding determined using water level gauges that were deployed at each site for half a year during the winter of 1991–1992. These temporary gauges were surveyed relative to the average marsh elevation. The average daily adjusted water level at Grand Isle was plotted against the percentage of the day that the marsh was flooded and a sigmoid curve was fitted (Fig. 3). This sigmoid curve was then used to predict the daily percentage flooding at average marsh elevation of each site for the 1978 through 1995 study period. Unfortunately, the elevation of each harvested plot was not measured.

To estimate the period where different stressors could affect end-of-season biomass, we first determined the time of the growing season during which most of our harvested biomass was produced. The turnover rate of *S. alterniflora* in Louisiana is 4.6 live crops per year (Hopkinson et al. 1978), so the average lifetime of biomass is 2.6 mo. We used the 3 mo prior to harvest (June–August) as the time where a stressor could affect our end-of-season biomass. We defined the relative flooding stress during the 3 mo before harvest, as the proportion of days that each site was flooded for greater than 95% of the time.

The physiological effects of salinity on *S. alterniflora* involve complex feedbacks (Bradley and Morris 1991, 1992). *S. alterniflora* growth is greatest at salinities of 25‰ or less (Phleger 1971; Parrando et al. 1978; Drake and Gallagher 1984). We obtained the long-term salinity record from two Louisiana Department of Wildlife and Fisheries (LDWF) gauges: Grand Terre (29°27′53″N, 89°94′17″W) and St. Mary's Point (29°41′97″N, 89°94′69″W) (Fig. 2). Where data from Grand Terre were missing, we augmented the data with predicted salinity based on the correlation with the St. Mary's point data. Figure 2 shows the gaps in the data from each gauge and the strong correlation between the salinity data from these gauges, which are 16 km apart. The Grand Terre gauge is 18 km from Airplane Lake and 25 km from Lake Jesse. Salinity is spatially coherent in Barataria estuary; the area has high hydrological connectivity. Swenson and Turner (1998) used all known salinity measurements in Barataria estuary from 1980 to 1995 to generate a plot of isohaline lines. Based on these isohaline lines, both study sites should on average experience slightly lower salinity (ca. 3‰ less) than the salinity measured at Grand Terre. Although these isohaline lines shift depending on salinity of the Gulf of Mexico and runoff from local rainfall (Swenson and Turner 1998), the difference between Grand Terre and the study area remains relatively constant. Salinity at Grand Terre fluctuated between 2‰ and 34‰ during the study period (Fig. 2). The salinity stress index was defined as the proportion of time that salinity at Grand Terre exceeded 28‰.

S. alterniflora uses the C_4 biochemical pathway of photosynthesis with a temperature optimum between 30°C and 35°C (Giurgevich and Dunn 1979). We obtained the long-term air temperature record from the National Weather Service (NWS) station at the New Orleans airport (29°59′34″N 09°15′03″W) (Fig. 2). The distance from the New Orleans weather station to Airplane Lake is 86 km south and to Lake Jesse is 81 km south. We defined the proportion of days on which the maximum air
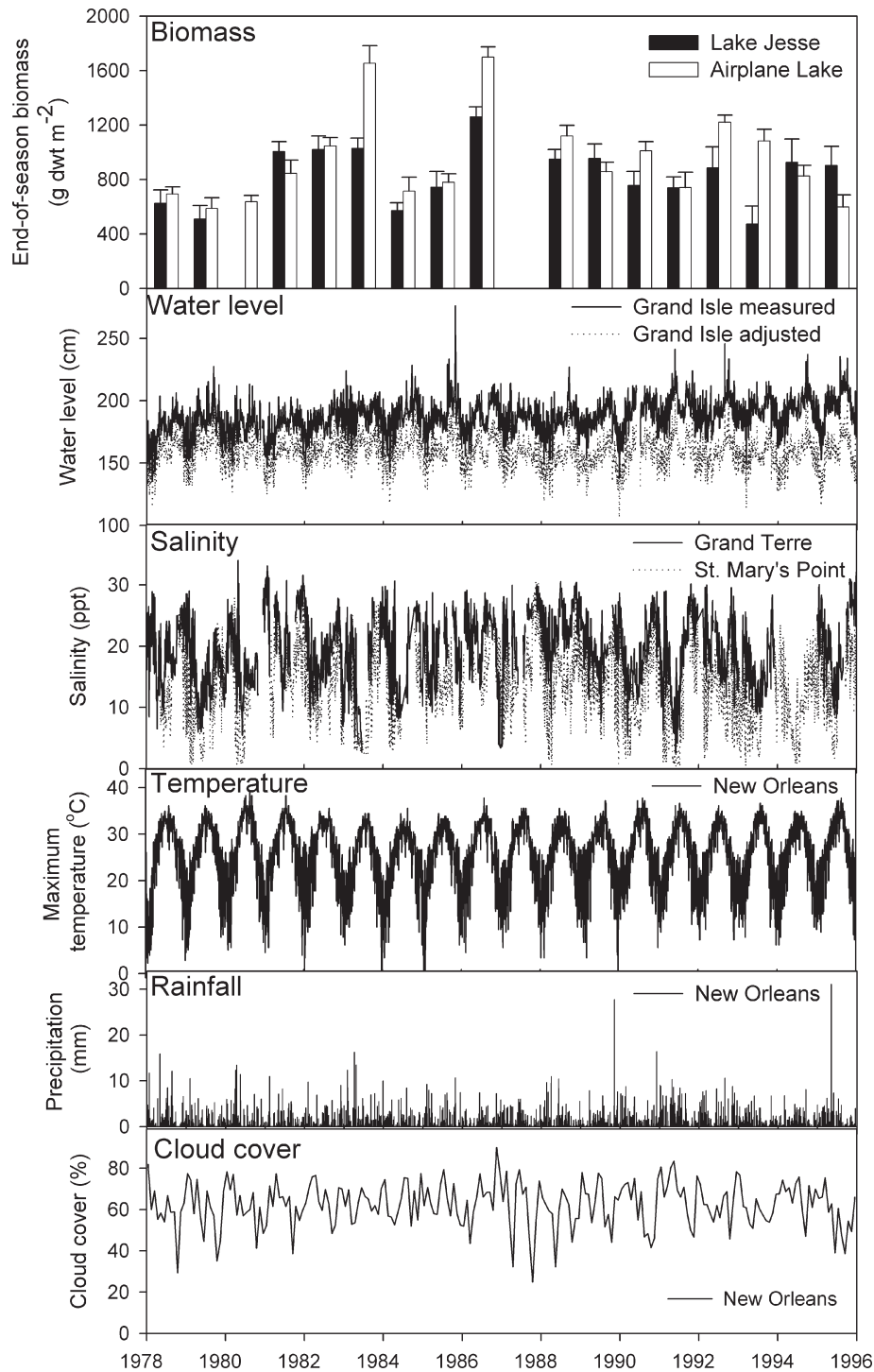
Fig. 2.   Biomass, water level, salinity, temperature, rainfall, and cloud cover recorded during the period of study. Data sources are identified in the Methods section.

temperature exceeded 35°C as the temperature stress index. To evaluate the usefulness of climate data collected 80 to 86 km from the site, we used climate data from Grand Isle (86 km from New Orleans and 17 to 23 km from the sites) that was only collected from 1951 through 1962 (the only years with sufficient data at Grand Isle) and found a highly significant positive correlation between
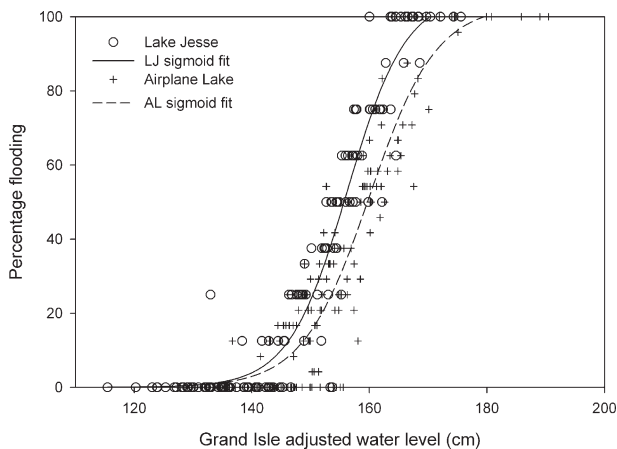
Fig. 3. Muskrat house density, total Kjeldahl nitrogen, and total phosphorus recorded during the period of study. Data sources are identified in the Methods section.

temperature stress at Grand Isle and New Orleans. On average, Grand Isle had 1.4 more days exceeding 35°C during the growing season than New Orleans. Over the study period, the number of days exceeding 35°C during the 92-d growing season ranged from 0 to 33 at New Orleans.

Muskrat is a known grazer in Louisiana salt marshes. Muskrat houses (active and inactive) were counted on aerial surveys over 1,197 ha of saline marsh near the two biomass sites in March of each year (for details see Visser et al. 1994). Active muskrat house density in the study area varied between 0.06 to 1.47 houses ha^{-1} (Fig. 4). To scale the muskrat grazing stress index to a 0 to 1 value, we defined it as the active house density divided by 2. This assumes that the maximum density of muskrat houses is 2 houses ha^{-1}.

Rainfall deficits are associated with decreased biomass production in salt marshes (De Leeuw et al. 1990). In coastal Louisiana water surpluses occur during the winter months, but during the summer precipitation and evaporation tend to be closely balanced, with occasional deficits in May through August (Gosselink 1984). We obtained the long-term precipitation record from the NWS station at the New Orleans airport (Fig. 2). We used the Thornthwaite equation (Chow 1964) to calculate the potential evaporation at the study sites from the temperature record. Then the precipitation deficit was obtained by subtracting precipitation from potential evaporation. The highest average deficit from June through August over the period of climate data evaluated (1948–2002) occurred in 1990 (108 mm mo^{-1}). We used climate data from Grand Isle that was only collected from 1951 through 1957 and in 1961 (the only years with sufficient data) and found a significant positive correlation between annual precipitation
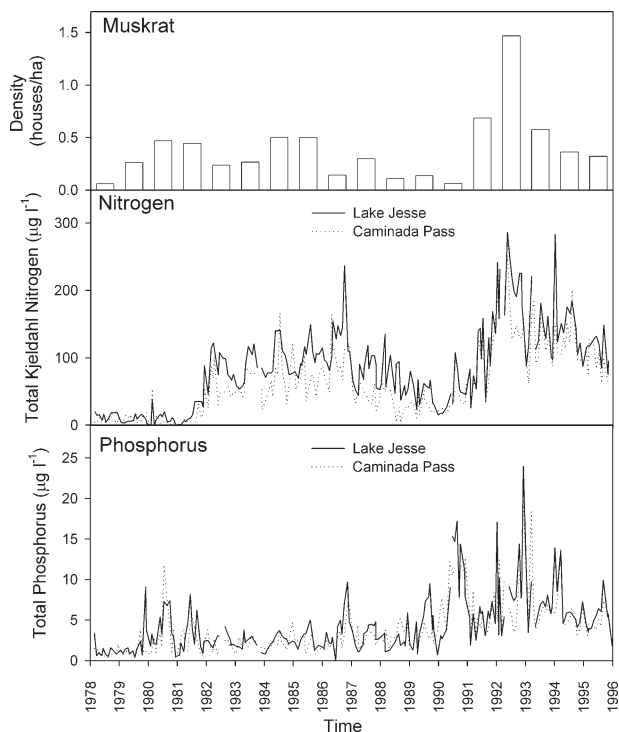

Fig. 4. Relationship between marsh flooding at each site and the long-term NOAA water level gauge at Grand Isle.

deficit at Grand Isle and New Orleans. The precipitation deficit at Grand Isle was lower than the precipitation deficit at New Orleans in 5 of the 6 years in which a precipitation deficit occurred at New Orleans. This spatial difference averaged 21 mm, while the precipitation deficit at New Orleans ranged from 0 to 108 mm during the study period. Since a precipitation surplus should not be stressful to the plants, we defined the precipitation deficit stress index as 0 when precipitation exceeded potential evaporation, and as the precipitation deficit divided by 150 (to scale between 0 and 1, estimating the true maximum deficit at 150 mm) when a deficit occurred.

Solar radiation may limit salt marsh productivity (Morris 1982; Teal and Howes 1996). No solar radiation data were available, instead we used daily average percentage cloud cover obtained from the NWS station at the New Orleans airport (Fig. 2). We calculated cloud cover stress as the average percentage cloud cover during the growing season. No data were available to test the applicability of the New Orleans cloud cover data to estimate cloud cover at our site. We have found significant correlation at a similar distance for interannual variation in other climatic factors (see above).

The availability of nutrients, particularly nitrogen and phosphorus, is important for the productivity of

a salt marsh (Mitsch and Gosselink 2000). *S. alterniflora* is primarily nitrogen limited (Valiela and Teal 1974; Patrick and DeLaune 1976; Smart and Barko 1980). In Louisiana, *S. alterniflora* biomass was positively correlated to both total nitrogen and total phosphorus density (TP) in the soil (DeLaune and Patrick 1979). The tidal water is an important source of nitrogen for the salt marsh (Valiela and Teal 1979; Childers et al. 1993). We obtained the results from two water quality stations (Lake Jesse (29°15′18″N 90°11′22″W) and Caminada Pass (29°12′21″N, 90°02′44″W)) sampled by LDWF near our study sites (Turner et al. 1998). This data set contained monthly measurements of ammonia, nitrate-nitrite, total Kjeldahl nitrogen (TKN), phosphate, and TP. We used correlation analysis between the two stations to determine if the measurements were coherent over relatively large spatial distances. TKN and TP showed strong correlations between the two stations (Fig. 4), indicating that these measurements could be used to estimate the surface water nutrient concentration at our study sites. Based on the geographical distribution, we used the Lake Jesse water quality station for the Lake Jesse marsh and the average from the Lake Jesse and Caminada Pass water quality stations for the Airplane Lake marsh. We used the average of the June, July, and August samples, and TKN and TP were scaled by dividing them by an estimated maximum value: 300 μg at l^{-1} for TKN and 20 μg at l^{-1} for TP.

Cade et al. (1999) illustrated that changes near the maxima provide the best estimate of the response to a single limiting factor, when considering the fact that multiple limiting factors are expected to affect the response. Quantile regression is the preferred technique to estimate this model (Cade et al. 1999; McClain and Rex 2001). We applied quantile regression using the QUANTREG package in R (Venables and Smith 2004). We selected among candidate quantile regression models by computing small sample adjusted Akaike Information Criteria (AIC_c) for seven quantile levels (τ = 0.50, 0.60, 0.70, 0.80, 0.90, 0.95, and 0.975) following Cade et al. (2005). To facilitate comparisons, we always referenced AIC_c for models with selected stressor variables to AIC_c for the model with just a single parameter for the intercept. Larger differences in AIC_c (ΔAIC_c) for each quantile were indicative of a model that explained more variation when adjusted for the number of estimated model parameters. Our selection process was to first consider models with a single stressor variable with common slopes and intercepts across sites (fewest parameters), then with a single stressor variable with separate intercepts and slopes for sites (two more parameters), and then models that included addi-

tional stressor variables added to the best single stressor variable model. We examined candidate single variable models graphically to determine whether linear or nonlinear forms were more appropriate. Models that had the largest ΔAIC_c across most quantiles were selected to explore further by examining coefficient estimates and their precision. Where ΔAIC_c differed by <2 across most quantiles for multiple candidate models, we examined coefficients of these equivalent candidate models. We used this model selection approach to suggest candidate models to explore further by examining coefficient estimates and their precision. We used the xy pairs bootstrap method in the R Quantreg library with 1,000 resamples to estimate standard errors of estimated coefficients.

Results

Substantial variation in average end-of-season biomass was observed at both sites (Fig. 2), with Airplane Lake having a slightly higher average of 916 g m^{-2} than the 869 g m^{-2} at Lake Jesse. Although the two sites behaved slightly differently over time the mean end-of-season biomass at both sites were significantly correlated (Pearson correlation coefficient: r = 0.61, p = 0.012). Average end-of-season biomass was highest at both sites in 1986 (1698 g m^{-2} at Airplane Lake, 1,261 g m^{-2} at Lake Jesse). The lowest average biomass was observed at Lake Jesse in 1993 (473 g m^{-2}) and at Airplane Lake in 1979 (587 g m^{-2}). Maximum end-of-season biomass peaked in 1983 at Airplane Lake (2,536 g m^{-2}), with the second highest maximum observed at this site in 1986 (2,068 g m^{-2}). At Lake Jesse, maximum end-of-season biomass peaked in 1986 at 1,710 g m^{-2}, with the second highest maximum observed at this site in 1994 (1,664 g m^{-2}). The lowest maximum end-of-season biomass occurred in 1980 (818 g m^{-2}), when only the Airplane Lake site was sampled. At Lake Jesse the lowest maximum end-of-season biomass occurred in 1979 (907 g m^{-2}); this year had the second lowest maximum biomass recorded at Airplane Lake (1,012 g m^{-2}).

Louisiana has a subtropical climate. During our study period average high temperatures exceeded 30°C during the months of June, July, August, and September (Fig. 2). The highest temperature stress during the period of study occurred in 1980, when 36% of the growing season days had maximum temperatures that exceeded 35°C. Temperature stress was also relatively high in 1981, 1990, and 1995. Rainfall is relatively evenly distributed over the year, but June and July tend to be slightly wetter with 17 to 18 cm mo^{-1}. Precipitation deficits occurred in only 5 of the 18 growing seasons, with the highest deficit occurring in 1990. Cloud cover averaged around 40% during the growing season,
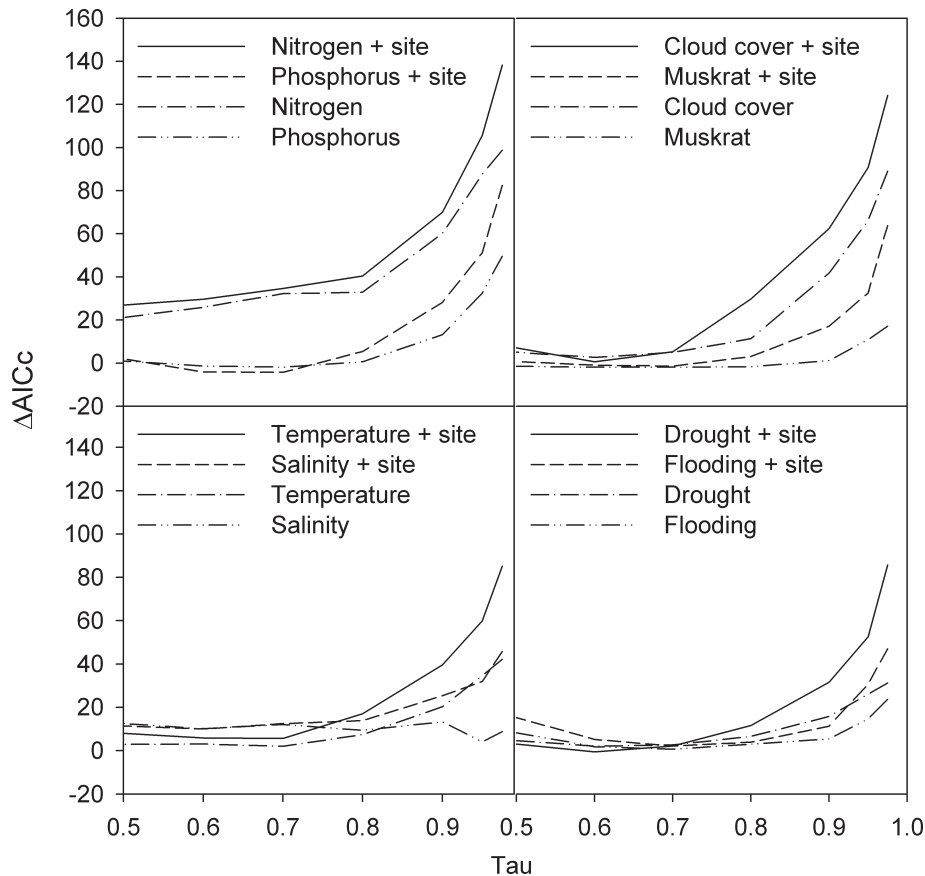
Fig. 5.   Fit of one parameter models as estimated by small sample adjusted change in Akaike Information Criteria (ΔAIC_c). Models with different slopes and intercepts for each site are indicated by the parameter name + site.

with the lowest cloud cover occurring in 1995 (23%). Growing season cloud cover was also low in 1990 at 25%. All of the climate variables (temperature stress, precipitation deficit, and cloud cover) were significantly correlated to each other. Temperature stress was negatively correlated with cloud cover ($r = -0.68$, $p = 0.0025$) and positively correlated with precipitation deficit ($r = 0.84$, $p < 0.0001$). Cloud cover was negatively correlated with precipitation deficit ($r = -0.70$, $p = 0.0020$).

From January 1978 through December 1995, salinity at Grand Terre fluctuated between 2‰ and 34‰ and averaged 19‰ (Fig. 2). In approximately half of the study years, salinity at Grand Terre exceeded 28‰ for <1% of the growing season. The highest salinity stress, with 20% of the summer salinity observations at Grand Terre exceeding 28‰, occurred in 1988. Figure 3 shows that the Lake Jesse marsh floods at lower water levels than the Airplane Lake marsh. On average, the Airplane Lake site experienced 6% of the growing season's days where the marsh was continuously flooded, while Lake Jesse experienced on average 19% of continuous flooding days during the growing season. The

highest flooding occurred in 1995, with 40% of the growing season days flooded at the Lake Jesse site and 22% of the growing season days flooded at the Airplane Lake site.

Muskrat house density averaged 0.39 houses ha⁻¹ during the study period, with a population explosion reaching a density of 1.47 houses ha⁻¹ in 1992 (Fig. 4). TKN and TP concentrations in the surface water were relatively low in the early 1980s and peaked in the early 1990s. Both nutrients indices were significantly positively correlated with year, indicating that nutrient levels in general increased over the study period. The growing season nitrogen index was also positively correlated with the muskrat index ($r = 0.56$, $p = 0.0193$).

The comparison of one-parameter models, revealed that models that used separate slopes and intercepts for the two sites always provided a better fit for the upper quantiles (Fig. 5). The model comparison showed poor model fit for all one-parameter models using the 0.5 quantile. The 0.5 quantile regression represents the fit of the conditional median, an alternative measure of central tendency to the conditional mean of least squares
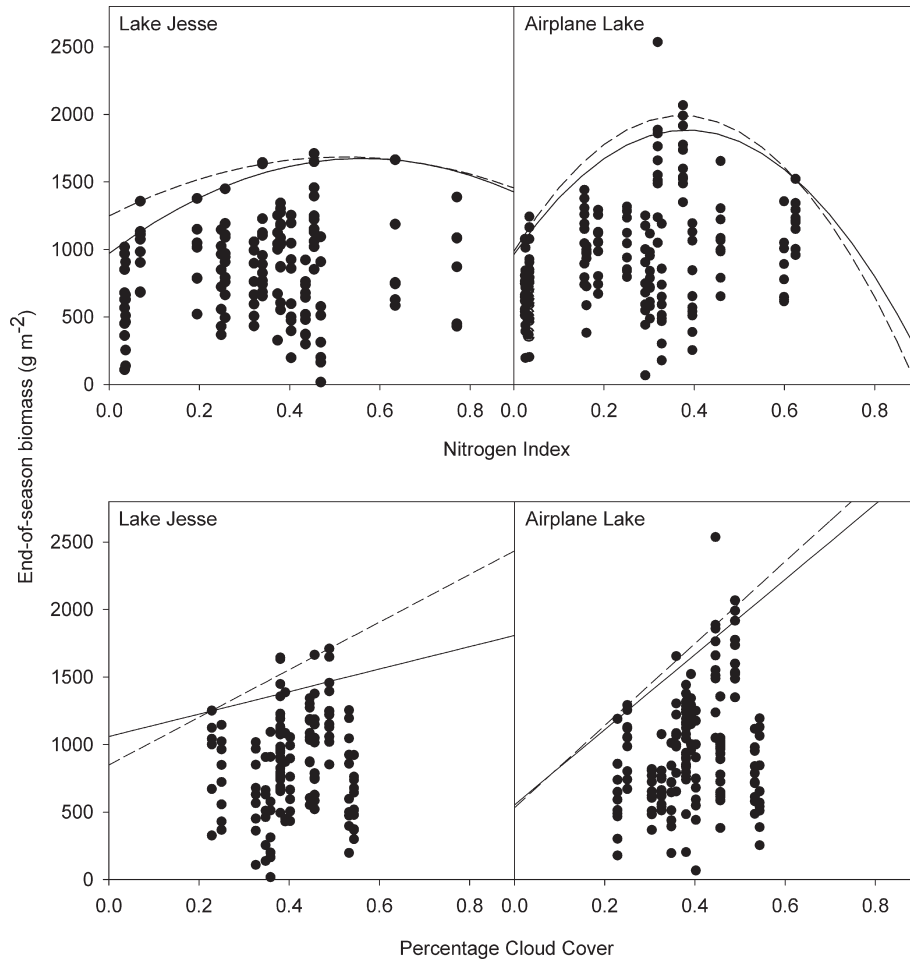
Fig. 6.   Biomass data for all plots graphed as a function of the nitrogen index and as a function of cloud cover. Each year is represented with a letter symbol, starting with an A for 1978 and ending with R for 1995. The solid lines show the model fit at τ = 0.95 and the dashed lines show the model fit at τ = 0.975.

regression. Of the one-parameter models, nitrogen provided the best fit for all quantiles. This model used a second order polynomial fit (Fig. 6, Table 1). Maximum biomass was greatest at a nitrogen stress index of 0.35 at Airplane Lake, which corresponds with a surface water TKN of 105 µg at l^{-1}, while the maximum at Lake Jesse occurs at 0.5 or 150 µg at l^{-1}. The second-best one-parameter model for upper quantiles was a linear relationship with cloud cover. Years with higher cloud cover had higher maximum biomass (Fig. 6).

The comparison of two-parameter models, showed that the better models include nitrogen and any of the other variables with different slopes and intercepts for the two sites (Fig. 7). The best fit for the upper quantiles based on the ΔAIC_c is provided by the models that combine nitrogen with either precipitation deficit or cloud cover. The smaller standard errors of parameter estimates for

the model that combines nitrogen and precipitation deficit (Table 2) suggest that it is the best model of the upper quantiles.

Discussion

We show here the use of the quantile regression method in unraveling the multiple stressors that affect *S. alterniflora* biomass. A previous attempt at analyzing the same data using regression based approaches found no statistically significant relationships, similar to the results of Teal and Howes (1996). Based on the literature there are many factors that may limit *S. alterniflora* growth. Our quantile regression based results indicate that total nitrogen concentration in the surface water explains most of the variation in peak biomass at our two sites. TKN measures both the available nitrogen for plant uptake (ammonium and nitrate) and organic nitrogen. Inorganic nitrogen in surface waters is

TABLE 1. Description of the two best one-parameter quantile regression models. These models are graphed in Fig. 6. AL = Airplane Lake, LJ = Lake Jesse.

Coefficient	τ = 0.950			τ = 0.975		
	Value	Standard Error	p	Value	Standard Error	p
Nitrogen model						
Intercept AL	962	105	<0.0001	986	94	<0.0001
TKN index AL	4,808	933	<0.0001	5416	1,400	0.0001
TKN index^2 AL	−6,264	1,420	<0.0001	−7,297	2,155	0.0008
Intercept difference LJ	9	195	0.9616	263	197	0.1831
TKN index difference LJ	−2,305	1,633	0.1590	−3,738	1,810	0.0397
TKN index^2 difference LJ	4,038	2,333	0.0845	5,682	2,692	0.0356
Cloud cover model						
Intercept AL	555	216	0.0108	533	188	0.0048
Cloud index AL	2,783	597	<0.0001	3,036	666	<0.0001
Intercept difference LJ	506	344	0.1419	316	451	0.4841
Cloud index difference LJ	−1,951	936	0.0380	−1,274	1,157	0.2714

rapidly transformed to organic forms or lost to the atmosphere through denitrification as water floods the marsh surface (Childers et al. 1993). The available nitrogen in the surface water is highly variable due to uptake by phytoplankton, benthic algae, and emergent plants. The in situ mineralization of organic nitrogen is one of the sources of nitrogen available for plant growth in addition to the available nitrogen in the surface water (Morris and Bowden 1986). Mineralization of nitrogen in Louisiana salt marsh soils is sufficient to provide the nitrogen requirements for *S. alterniflora*, but much of this is lost through denitrification (Patrick and DeLaune 1976). It is not surprising that we identified total surface water nitrogen as an important factor that affects *S. alterniflora* biomass. The curvilinear relationship between TKN and maximum end-of-season biomass indicates that as nitrogen increases biomass increases up to a point. Decreases beyond this point may be due to the

positive correlation between surface water nitrogen and muskrat density during our study period. Increased muskrat density should translate to higher grazing pressure and result in a lower *S. alterniflora* biomass. Experiments that control the interaction among nitrogen availability to the plants and grazing are necessary to fully interpret this result.

Morris (1982) found that almost half of the variation in leaf growth of *S. alterniflora* could be explained by solar radiation alone, with increasing growth as solar radiation increased. The same positive correlation between solar radiation and *S. alterniflora* biomass was found by Teal and Howes (1996). Both of these studies were performed in Massachusetts. We found that cloud cover, which should be inversely related to solar radiation, was positively correlated with maximum biomass in Louisiana. Our data showed a strong negative correlation between percentage cloud cover and
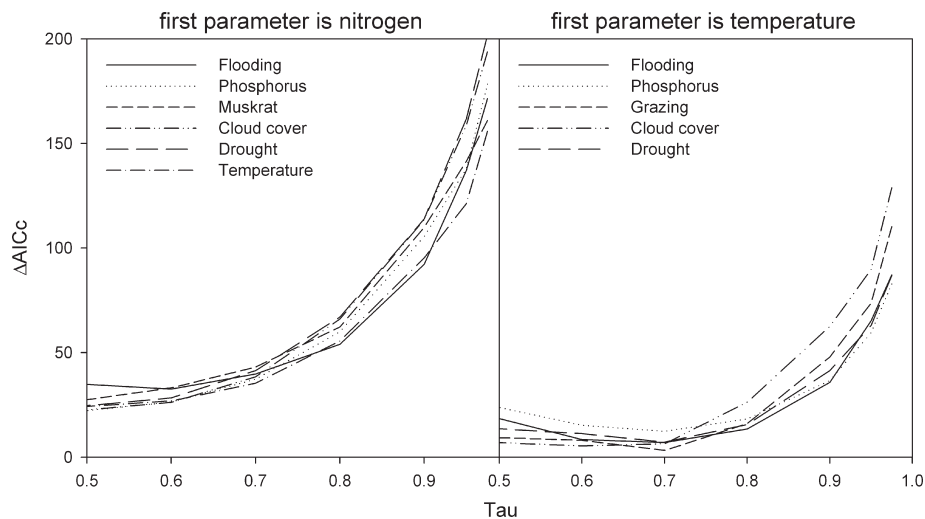

Fig. 7. Fit of two parameter models as estimated by small sample adjusted change in Akaike Information Criteria (ΔAIC_c).

TABLE 2.   Description of the two best two-parameter quantile regression models. AL = Airplane Lake, LJ = Lake Jesse.

Coefficient	$\tau = 0.950$			$\tau = 0.975$		
	Value	Standard Error	p	Value	Standard Error	p
Nitrogen + precipitation deficit model						
Intercept AL	1,006	71	<0.0001	1,026	75	<0.0001
TKN index AL	4,777	660	<0.0001	5,245	1,310	<0.0001
TKN index^2 AL	−6,326	1,122	<0.0001	−7,126	2,055	0.0006
Precipitation deficit AL	−588	118	<0.0001	−648	114	<0.0001
Intercept difference LJ	−37	178	0.8363	217	179	0.2267
TKN index difference LJ	−2,235	1,375	0.1051	−3,467	1,641	0.0354
TKN index^2 difference LJ	4,026	1,934	0.0382	5,371	2,459	0.0297
Precipitation deficit difference LJ	153	226	0.4977	50	194	0.7974
Nitzrogen + cloud cover model						
Intercept AL	178	208	0.3923	187	380	0.6226
TKN index AL	3,560	759	<0.0001	3,458	1,130	0.0024
TKN index^2 AL	−4,544	1,161	0.0001	−4,598	1,822	0.0121
Clouds AL	2,282	565	<0.0001	2475	1,015	0.0154
Intercept difference LJ	352	453	0.4376	918	539	0.0895
TKN index difference LJ	−2,037	1,462	0.1645	−1,711	1,561	0.2738
TKN index^2 difference LJ	3,443	2,033	0.0913	2,816	2,283	0.2182
Clouds difference LJ	−945	1,172	0.4209	−2,109	1,461	0.1499

precipitation deficit as well as our temperature stress index. Without a doubt, these relationships are different in temperate regions such as Massachusetts. Cloud cover, temperature, and drought stressors may become more important as climate is predicted to change (IPCC 2001). The Hadley global climate model generally depicts a warmer and wetter future climate in the southeastern United States, while the Canadian global climate model depicts a hotter and drier future climate for the same region (Twilley et al. 2001).

Salinity and flooding are the two factors most frequently assumed to affect saline marsh productivity (Howes et al. 1981; Mendelssohn et al. 1981; King et al. 1982; Wiegert et al. 1983; Zedler 1983). Significant variation exists in the response of different *S. alterniflora* populations to hypersalinity (Pezeshki and DeLaune 1995; Hester et al. 1998, 2001). In Louisiana salinity in the saline marsh area rarely exceeds the salinity tolerance of even the most sensitive populations. It is not surprising that we found salinity a poor predictor for *S. alterniflora* biomass at our sites.

We found our flooding index to be a poor predictor of *S. alterniflora* biomass, while model fit significantly improved by using different models for each site. The flooding index we developed suffers from the lack of elevation data for each harvested plot and may be an inadequate estimator of the actual flooding that occurred at the site. The major difference between the two sites is that one site is more frequently flooded then the other (Fig. 4) and this difference may be captured by fitting different models for each site. During optimum nitrogen and cloud cover conditions, maximum biomass at the more frequently flooded site is lower than at the less

frequently flooded site. Maximum biomass is similar at both sites under extreme nitrogen as well as low cloud cover conditions.

Surface water phosphorus explained very little of the variation in *S. alterniflora* biomass. Most salt marsh soils have adequate phosphorus for plant growth (Pomeroy et al. 1972; Patrick and DeLaune 1976; Paludan and Morris 1999) and no input from surface water is necessary. It has been shown that water flooding the marsh has a lower inorganic phosphorus content than the subsurface return flow (Childers et al. 1993) and only 1% of added phosphorus was taken up in a fertilization experiment (Patrick and DeLaune 1976).

We demonstrated that quantile regression is a useful statistical tool to ascertain the stressors that best explain interannual variation in biomass. Precipitation deficit combined with surface water nitrogen provided the best two-parameter model to explain variation in the peak biomass with different models for the two study sites. Precipitation deficit, cloud cover, and temperature were significantly correlated with each other. Surface water nitrogen was significantly correlated with surface water phosphorus and muskrat density. The site with the larger duration of flooding, showed reduced peak biomass, when cloud cover and surface water nitrogen were optimal. Salinity did not explain the variation in biomass.

study area. NOAA's Coastal Ocean Program MULTISTRESS Award No. NA16OP2670 supported J. Visser and C. Sasser's effort to prepare this manuscript. This manuscript benefited significantly from the extensive critical reviews from three reviewers.

LITERATURE CITED

BRADLEY, P. M. AND J. T. MORRIS. 1991. The influence of salinity on the kinetics of NH₄⁺ uptake in *Spartina alterniflora*. *Oecologia* 85: 375–380.

BRADLEY, P. M. AND J. T. MORRIS. 1992. Effect of salinity on the critical nitrogen concentration of *Spartina alterniflora* Loisel. *Aquatic Botany* 43:149–161.

CADE, B. S. AND Q. GUO. 2000. Estimating effects of constraints on plant performance with regression quantiles. *Oikos* 91:245–254.

CADE, B. S., B. R. NOON, AND C. H. FLATHER. 2005. Quantile regression reveals hidden bias and uncertainty in habitat models. *Ecology* 86:786–800.

CADE, B. S., J. W. TERRELL, AND R. L. SCHROEDER. 1999. Estimating effects of limiting factors with regression quantiles. *Ecology* 80: 311–323.

CHILDERS, D. L., H. N. MCKELLAR JR., R. DAME, F. SKLAR, AND E. BLOOD. 1993. A dynamic nutrient budget of subsystem interactions in a salt marsh estuary. *Estuarine Coastal and Shelf Science* 36:105–131.

CHOW, V. T. (ed.). 1964. Handbook of Applied Hydrology. McGraw-Hill, New York.

DELAUNE, R. D. AND W. H. PATRICK JR. 1979. Nitrogen and phosphorus cycling in a Gulf Coast salt marsh, p. 143–151. *In* V. S. Kennedy (ed.), Estuarine Perspectives. Academic Press, New York.

DELAUNE, R. D., C. J. SMITH, AND M. D. TOLLEY. 1984. The effect of sediment redox potential on nitrogen uptake, anaerobic root respiration and growth of *Spartina alterniflora* Loisel. *Aquatic Botany* 18:223–230.

DE LEEUW, J., H. OLFF, AND J. P. BAKKER. 1990. Year-to-year variation in peak above-ground biomass of six salt-marsh angiosperm communities as related to rainfall deficit and flooding frequency. *Aquatic Botany* 36:139–151.

DRAKE, B. G. AND J. L. GALLAGHER. 1984. Osmotic potential and turgor maintenance in *Spartina alterniflora* Loisel. *Oecologia* 62: 368–375.

GIROUX, J. F. AND J. BEDARD. 1987. Factors influencing aboveground production of *Scirpus* marshes in the St. Lawrence estuary, Quebec, Canada. *Aquatic Botany* 29:195–204.

GIURGEVICH, J. R. AND E. L. DUNN. 1979. Seasonal patterns of CO₂ and water vapor exchange of the tall and short forms of *Spartina alterniflora* Loisel in a Georgia salt marsh. *Oecologia* 43:139–156.

GOSSELINK, J. G. 1984. The Ecology of Delta Marshes of Coastal Louisiana: A Community Profile. U.S. Fish and Wildlife Service, FWS/OBS-84/09. Washington, D.C.

HESTER, M. W., I. A. MENDELSSOHN, AND K. L. MCKEE. 1998. Intraspecific variation in salt tolerance and morphology in *Panicum hemitomon* and *Spartina alterniflora* (Poaceae). *International Journal of Plant Science* 159:127–138.

HESTER, M. W., I. A. MENDELSSOHN, AND K. L. MCKEE. 2001. Species and population variation to salinity stress in *Panicum hemitomon*, *Spartina patens*, and *Spartina alterniflora*: Morphological and physiological constraints. *Environmental and Experimental Botany* 46:277–297.

HOPKINSON, C. S., J. G. GOSSELINK, AND R. T. PARRONDO. 1978. Aboveground production of seven marsh plant species in coastal Louisiana. *Ecology* 59:760–769.

HOWES, B. L., J. W. H. DACEY, AND D. D. GOEHRINGER. 1986. Factors controlling the growth form of *Spartina alterniflora*: Feedbacks between above-ground production, sediment oxidation, nitrogen, and salinity. *Journal of Ecology* 74:881–898.

HOWES, B. L., R. W. HOWARTH, J. M. TEAL, AND I. VALIELA. 1981. Oxidation-reduction potential in a salt marsh: Spatial patterns and indications with primary production. *Limnology and Oceanography* 26:350–360.

INTERGOVERNMENTAL PANEL ON CLIMATE CHANGE (IPCC). 2001. Climate Change 2001: The Scientific Basis. Cambridge University Press, Cambridge, United Kingdom.

JEFFERIES, R. L. AND N. PERKINS. 1977. The effects on the vegetation of the additions of inorganic nutrients to salt marsh soils at Stiffkey, Norfolk. *Journal of Ecology* 65:867–882.

KING, G. M., M. J. KLUG, R. G. WIEGERT, AND A. G. CHALMERS. 1982. Relation of sulphide concentration to *Spartina alterniflora* production in a Georgia salt marsh. *Science* 218:61–63.

MCCLAIN, C. R. AND M. A. REX. 2001. The relationship between dissolved oxygen concentration and maximum size in deep-sea turrid gastropods: An application of quantile regression. *Marine Biology* 139:681–685.

MENDELSSOHN, I. A., K. L. MCKEE, AND W. H. PATRICK JR. 1981. Oxygen deficiency in *Spartina alterniflora* roots: Metabolic adaptation to anoxia. *Science* 214:439–441.

MENDELSSOHN, I. A. AND E. D. SENECA. 1980. The effect of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. *Estuarine Coastal and Marine Science* 2:27–40.

MITSCH, W. J. AND J. G. GOSSELINK. 2000. Wetlands, 3rd edition. John Wiley and Sons, New York.

MOON, D. C. AND P. STILING. 2002. The influence of species identity and herbivore feeding mode on top-down and bottom-up effects in a salt marsh system. *Oecologia* 133:243–253.

MORRIS, J. T. 1982. A model of growth responses by *Spartina alterniflora* to nitrogen limitation. *Journal of Ecology* 70:25–42.

MORRIS, J. T. AND W. B. BOWDEN. 1986. A mechanistic, numerical-model of sedimentation, mineralization, and decomposition for marsh sediments. *Soil Science Society of America Journal* 50:96–105.

MORRIS, J. T. AND B. HASKIN. 1990. A 5-yr record of aerial primary production and stand characteristics of *Spartina alterniflora*. *Ecology* 71:2209–2217.

MORRIS, J. T., P. V. SUNDARESHWAR, C. T. NIETCH, B. KJERVE, AND D. R. CAHOON. 2002. Responses of coastal wetlands to rising sea level. *Ecology* 83:2869–2877.

NESTLER, J. 1977. Interstitial salinity as a cause of ecophenic variation in *Spartina alterniflora*. *Estuarine Coastal and Marine Science* 5:707–714.

PALUDAN, C. AND J. T. MORRIS. 1999. Distribution and speciation of phosphorus along a salinity gradient in intertidal marsh sediments. *Biogeochemistry* 45:197–221.

PARRONDO, R. T., J. G. GOSSELINK, AND C. S. HOPKINS. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. *Botanical Gazette* 139:102–107.

PATRICK, JR., W. H. AND R. D. DELAUNE. 1976. Nitrogen and phosphorus utilization by *Spartina alterniflora* in a salt marsh in Barataria Bay, Louisiana. *Estuarine and Coastal Marine Science* 4: 59–64.

PEZESHKI, S. R. 1997. Photosynthesis and root growth in *Spartina alterniflora* in relation to root zone aeration. *Photosynthetica* 34: 107–114.

PEZESHKI, S. R. AND R. D. DELAUNE. 1995. Variations in the response of two US Gulf coast populations of *Spartina alterniflora* to hypersalinity. *Journal of Coastal Research* 11:89–95.

PHLEGER, C. F. 1971. Effect of salinity on the growth of a salt marsh grass. *Ecology* 52:908–911.

POMEROY, L. R., L. R. SHENTON, R. D. JONES, AND J. R. REIMOLD. 1972. Nutrient flux in estuaries, p. 274–291. *In* G. E. Likens (ed.), Nutrients and Eutrophication. American Society of Limnology and Oceanography Special Symposium. Allen Press, Lawrence, Kansas.

REED, D. J. AND D. R. CAHOON. 1992. The relationship between marsh surface-topography, hydroperiod, and growth of *Spartina alterniflora* in a deteriorating Louisiana salt-marsh. *Journal of Coastal Research* 8:77–87.

SHARF, F. S., F. JUANES, AND M. SUTHERLAND. 1998. Inferring ecological relationships from the edges of scatter diagrams: Comparison of regression techniques. *Ecology* 79:448–460.

SILLIMAN, B. R. AND A. BORTOLUS. 2003. Underestimation of *Spartina* productivity in western Atlantic marshes: Marsh invertebrates eat more than just detritus. *Oikos* 101:549–554.

SILLIMAN, B. R. AND J. C. ZIEMAN. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology* 82:2830–2845.

SMART, R. M. AND J. W. BARKO. 1980. Nitrogen nutrition and salinity tolerance of *Distichlis spicata* and *Spartina alterniflora*. *Ecology* 61:630–638.

SWENSON, E. M. AND R. E. TURNER. 1998. Past, present and probable future salinity variations in the Barataria estuarine system. Report prepared for the Louisiana Department of Natural Resources, Baton Rouge, Louisiana.

TEAL, J. M. AND B. L. HOWES. 1996. Interannual variability of a salt-marsh ecosystem. *Limnology and Oceanography* 41:802–809.

TERRELL, J. W., B. S. CADE, J. CARPENTER, AND J. M. THOMPSON. 1996. Modeling stream fish habitat limitations from wedged-shaped patterns of variation in standing stock. *Transactions of American Fisheries Society* 125:104–117.

THOMSON, J. D., G. WEIBLEN, B. A. THOMSON, S. ALFARO, AND P. LEGENDRE. 1996. Untangling multiple factors in spatial distributions: Lilies, gophers, and rocks. *Ecology* 77:1698–1715.

TURNER, R. E. 1979. A simple model of the seasonal growth of *Spartina alterniflora* and *Spartina patens*. *Contributions in Marine Science* 22:137–147.

TURNER, R. E., E. M. SWENSON, M. KASPRZAK, AND T. ROMAIRE. 1998. Water Chemistry, Volume 2, p. 1–68. *In* C. E. Sasser and J. M. Visser (eds.), LOOP Marine and Estuarine Monitoring Program, 1978–1995. Report to LOOP, Inc., New Orleans, Louisiana.

TWILLEY, R. R., E. J. BARRON, H. L. GHOLZ, M. A. HARWELL, R. L. MILLER, D. J. REED, J. B. ROSE, E. H. SIEMANN, R. G. WETZEL, AND R. J. ZIMMERMAN. 2001. Confronting Climate Change in the Gulf Coast Region: Prospects for Sustaining our Ecological Heritage. Union of Concerned Scientists, Cambridge, Massachusetts.

TYLER, G. 1967. On the effect of phosphorus and nitrogen supplied to Baltic shore-meadow vegetation. *Botaniska Notiser* 120:433–447.

VALIELA, I. AND J. M. TEAL. 1974. Nutrient limitation in salt marsh vegetation, p. 547–563. *In* R. J. Reimold and W. H. Queen (eds.), Ecology of Halophytes. Academic Press, New York.

VALIELA, I. AND J. M. TEAL. 1979. The nitrogen budget of a salt marsh ecosystem. *Nature* 280:652–656.

VISSER, J. M., D. E. EVERS, G. O. HOLM JR., C. E. SASSER, G. W. PETERSON, AND J. G. GOSSELINK. 1994. 1993 Annual report, LOOP, Inc., Environmental monitoring program Louisiana Offshore Oil port Pipeline. Report to LOOP, Inc., New Orleans, Louisiana.

WIEGERT, R. G., A. G. CHALMERS, AND P. F. RANDERSON. 1983. Productivity gradients in salt marshes: The response of *Spartina alterniflora* to experimentally manipulated soil water movement. *Oikos* 41:1–6.

ZEDLER, J. B. 1983. Freshwater impacts in normally hypersaline marshes. *Estuaries* 6:346–355.

SOURCES OF UNPUBLISHED MATERIALS

KOENKER, R. 2004. The quantreg package. http://www.econ.uiuc.edu/~roger/research/rq/rq.html.

VENABLES, W. N. AND D. M. SMITH. 2004. An Introduction to R. http://www.r-project.org/.