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Relative Stability of Plant Communities in a South Carolina High Salt Marsh

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ABSTRACT The high marsh in southeast Atlantic coast salt marshes forms a relatively small but ecologically important transition zone between low marsh and the terrestrial shoreline. However, long-term trend data from high marshes are limited to a few studies. Permanent plots established in a high marsh near Waties Island in northeast South Carolina were measured for plant coverage from 2002–2010. At the beginning and at the end of the study, four groups of plots were identified: mixed indicated by *Borrichia frutescens*, *Distichlis spicata*, and *Fimbristylis castanea*; *Juncus* indicated by *Juncus roemerianus*; *Salicornia* indicated by *Salicornia virginica*; and *Spartina* indicated by *Spartina patens*. Ordination of the 2010 plot data and soil analyses produced clear separation of the groups along a single dominant axis with *Salicornia* and *Juncus* groups at the high end of a salinity gradient and the *Spartina* group at the high end of soil organic matter gradient. Comparison of plots classified in 2002 to the same plots in 2010 suggested both stability and change, depending on community classification. *Salicornia* and *Spartina* groups were stable. The mixed group experienced a switch in dominance from *Distichlis spicata* to *Borrichia frutescens*, whereas the *Juncus* group had gradually declining importance of *Juncus roemerianus* and gradually increasing importance of *Borrichia frutescens*. These data represent patterns and trends in a system and time period not affected by development or influenced by high intensity disturbance, and can be used as a reference for other high marshes in the immediate area experiencing environmental change.
Key words: High marsh, Myrtle Beach, permanent plots, salt marsh, South Carolina, vegetation pattern, Waties Island.

INTRODUCTION Understanding vegetation patterns and long-term change in salt marshes of the southeast Atlantic coast frequently involves the driving variables affecting a relatively small number of halophytic plant species (Pennings et al. 2005). One of the most commonly described patterns of tidal salt marshes in the southeast is the association of low marsh with high marsh (Wiegert and Freeman 1990). Low marsh, often characterized by monospecific stands of *Spartina alterniflora*, is regularly flooded; however, high marsh, often supporting usually fewer than 10 species of varying salt and inundation tolerance, is irregularly flooded (Eleuterius and Eleuterius 1979). A standard paradigm of salt marsh development is that substrate accretion through time will increase the relative proportion of high marsh at a site (Wells 1928, Wiegert and Freeman 1990). However, this trend will be influenced by rates of peat formation, sedimentation, erosion, and change in land elevation relative to sea level (Redfield 1972, de Leeuw et al. 1993).

As the southeast coastal zone experiences rapid human population growth and development pressure, new research questions have emerged regarding the important driving variables of salt marshes (Adam 2002). In contrast to the past where salt marshes were directly affected by ditching, dredging, and filling (Gedan et al. 2009), residential development along the shoreline of salt marshes now is a common direct effect and there is no evidence that such development will be curtailed in the future. Walters et al. (2010) provided a comprehensive list of salt marsh

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ecological attributes potentially changed by development. In the northeast, residential development of the shoreline has been linked to invasion of the high marsh by *Phragmites australis* (Cav.) Trin. ex Steud (Silliman and Bertness 2004), but in the southeast, impacts of development on salt marshes are not well understood and might involve both the low and high marsh (Lerberg et al. 2000, Walters et al. 2010).

On the one hand, southeast high marsh plant communities are adjacent to the terrestrial-marine boundary, where rapid landscape change is occurring. On the other hand, high marsh also potentially is affected by a rising sea level (Hackney and Cleary 1987). Although community shifts in response to a rising sea level are complex (Pennings et al. 2005), one can expect expansion of low marsh and contraction of high marsh due to increased duration and frequency of flooding in the high marsh, unless substrate accretion keeps pace with rising sea level (Redfield 1972, Warren and Niering 1993, Smith 2009). The extent of low vs. high marsh at a site is readily measured from aerial photographs; thus, Tiner (1977) estimated that salt marshes in South Carolina were 15% high marsh and 85% low marsh. Considering the relatively small extent of high marsh and its relatively high biodiversity, it is important to understand long-term changes in high marsh vegetation

The current study presents data collected from permanent plots in a northeast South Carolina high marsh. The study site was adjacent to Waties Island, an undeveloped, restricted-access barrier island that experienced no catastrophic geomorphic changes over the time period of data collection (2002–2010). Waties Island and its associated marsh provide valuable reference data for comparison to other salt marshes in the nearby and heavily developed Grand Strand area of South Carolina.

MATERIALS AND METHODS

Study Site

Waties Island (33°50′43″N, 78°35′12″W) is the terminus of the Grand Strand, generally defined as a 97-km section of beach stretching from Little River, South Carolina to Winyah Bay near Georgetown, South Carolina. This island is ca. 0.5 km wide and 4.0 km in length, although these dimensions have historically changed due to geomorphic processes. The north end of Waties Island is delimited by Little River Inlet and the south end is delimited by Hog Inlet. Between Waties Island and the mainland is an ocean-dominated lagoonal marsh with tidal creeks fed and drained by the two inlets. The tidal regimen is semidiurnal with a maximum range of 2.6 m. This study focused on a high marsh site (1–2 m above sea level) located adjacent to the southern end of Waties Island (Figure 1). Vibracores taken from this high marsh indicate the historical presence of both subtidal and intertidal environments. Infilling from island washover and transport associated with Hog Inlet likely created the current high marsh and embedded raised areas (Wright et al. 2003).

Plant Community and Soil Sampling

In 1998, a 100 × 100-m grid was established on the island and in the high marsh by Dr. Eric Pauley (formerly in the Department of Biology at Coastal Carolina University). Points of grid line intersection were used to establish sample areas marked by single sections of PVC pipe. At each sample area, four 1-m^2 plots were established 5 m from the PVC pipe in the four cardinal directions. This study focused on 18 sample areas and 66 plots located in the high marsh, and monitored beginning in 2002. Plant coverages in these plots were measured in late summer of 2002, 2004, 2007, and 2010. Variation in measurement was minimized by involving a single person (JOL) throughout the entire study (Pascal and Antoine 2007). Total plant coverage in each plot initially was estimated and then the contributions of individual species to this total were determined. Importance values of species were calculated as relative coverage (i.e., coverage of a species divided by total plant coverage) and these were used in all subsequent analyses. This approach allowed uniform assessment of different plant growth forms but might have missed ephemeral or rare species. In 2010, four surface-soil samples (upper 10 cm) were collected from each plot, composited, air-dried and then sent to the Clemson University Agricultural Service Lab for standard soil testing and measurement of organic matter, nitrate, and soluble salts. Soluble soil components likely change with

Figure 1. The southern end of Waties Island in northeast South Carolina. The high marsh research site (outlined in white) is located between the relatively high ground of Waties Island and three unnamed islands adjacent to the low marsh.

season and thus this analysis of soil is best viewed as a snapshot during the time when plants were actively growing.

Data Analyses

Recent (i.e., 2010) relationships among plant communities, soil properties, and community attributes were developed with nonmetric dimensional scaling (NMS) following the guidelines of Peck (2010). This "free ordination" approach allowed the placement of plots and species within a few axes so that redundant patterns could be graphically presented. Cluster analysis (75% of information remaining as the cutoff) followed by indicator species analysis (Peck 2010) of plot data collected in 2010 were used to further clarify community patterns. The three axes of this ordination were used to examine relationships between axis scores and soil properties, and between axis scores and community attributes.

Changes in plant communities from 2002 to 2010 were assessed by grouping plots from 2002 with cluster analysis (75% of information remaining as the cutoff) followed by indicator species analysis. This produced four groups of plots, each with at least one significant indicator species (Peck 2010). Community attributes (i.e., Shannon Weiner diversity, H′ and richness) of these four groups in 2002 were compared with one-way analysis of variance. Then, communities of these four groups were compared between 2002 and 2010 with blocked nonmetric multiresponse permutation procedure (MRPP), a nonparametric multivariate test of difference between groups (Lesica and McCune 2004) and Per-Manova (Peck 2010). Plots were the blocks and years were the groups. When strong significant group differences between years were indicated, trends of relative coverage of relatively important individual species were presented for the entire study period. All multivariate community analyses were done with PC-ORD version 6.0 (McCune and Mefford 2011).

RESULTS

Species, Plant Communities and Soil Properties: 2010

Among the eight important high marsh species, *Borrichia frutescens*, *Limonium caroli-*

Table 1. Frequencies, indicator values, and group assignments for plant species found in a high marsh community at Waties Island, South Carolina during 2002–2010

Species	Code	Frequency (%) 2002, 2010	2002 Indicator value (p)	2010 Indicator value (p)	2002 Group assignment	2010 Group assignment
Borrichia frutescens (L.) Augustin de Candolle	BOFR	75, 71	45.1 (0.0082)	53.4 (0.0002)	Mixed	Mixed
Limonium carolinianum P. Miller	LICA	68, 69	43.4 (0.0078)	37.7 (0.0474)	*Salicornia*	Mixed
Distichlis spicata (Linnaeus) Greene	DISP	75, 58	80.4 (0.0002)	54.7 (0.0004)	Mixed	Mixed
Spartina patens (Aiton) Muhlenberg	SPPA	45, 46	90.9 (0.0002)	87.9 (0.0002)	*Spartina*	*Spartina*
Salicornia virginica Linnaeus, Samphire	SAVI	32, 38	95.7 (0.0002)	95.8 (0.0002)	*Salicornia*	*Salicornia*
Juncus roemerianus Scheele	JURO	32, 34	91.5 (0.0002)	87.6 (0.0002)	*Juncus*	*Juncus*
Fimbristylis castanea (Michaux) Vahl	FICA	11, 26	15.5 (0.2314)	34.9 (0.0072)	Mixed	Mixed
Spartina alterniflora Loiseleur	SPAL	14, 11	16.4 (0.1460)	12.3 (0.2595)	*Salicornia*	*Juncus*

nianum, and *Distichlis spicata* occurred at highest frequencies in 2010, and *Spartina alterniflora* and *Fimbristylis castanea* occurred at lowest frequencies (Table 1). Cluster analysis of plant communities suggested the presence of four groups, three of which were dominated and strongly indicated (importance value [IV] > 87) by single species: a *Juncus* group indicated by *Juncus roemerianus*, a *Salicornia* group indicated by *Salicornia virginica*, and a *Spartina* group indicated by *Spartina patens* (Table 1). The fourth group, mixed, was indicated by *Borrichia frutescens*, *Distichlis spicata*, and *Fimbristylis castanea*. Mean plot-level richness of the groups ranged from 2.9–4.6 species $plot^{-1}$ ($F = 9.92$, $p < 0.001$) in 2010. Plots classified as mixed in 2010 had higher richness and higher H′diversity than the other three groups.

The NMS ordination (final stress = 11.593, final instability = 0.0026) included three axes with a cumulative r^2 of 0.842. Axis 1 accounted for ca. 50% of cumulative variation and

Table 2. Pearson correlations (r) between soil or plot variables measured in 2010 and nonmetric multidimensional scaling axes 1–3 derived from the Waties Island high marsh community in 2010. Significant correlations are in bold. N = 66

Variables	Axis 1 r	Axis 2 r	Axis 3 r
Soil pH	**0.591**	−0.154	−0.067
Soil organic matter	**−0.595**	−0.048	0.048
Soil nitrate nitrogen (N)	**−0.338**	−0.101	−0.129
Soil phosphorus (P)	**0.813**	−0.192	0.098
Soil potassium (K)	**0.735**	−0.143	**0.351**
Soil soluble salts	**0.770**	−0.236	**0.389**
Plot richness	−0.039	**0.271**	**-0.433**
Plot H′	0.098	**0.293**	**-0.459**

represented gradients in soil nutrients, soluble salts, and organic matter. Generally, plot scores for axis 1 were positively associated with pH, phosphorus (P), potassium (K), and soluble salts, and negatively associated with nitrate nitrogen (N) and organic matter (Table 2). Plots located at the upper end of axis 1 included two relatively tight clusters of plots classified as *Juncus* or *Salicornia* and a small, less-tightly clustered subset of plots classified as mixed (Figure 2). Plots located at the lower end of axis 1 were generally tightly clustered and classified as *Spartina*. Plot scores for axis 3 were negatively associated with richness and H′ diversity, with plots located at the lower end of axis 3 broadly distributed and classified as mixed (Figure 2).

Community Change: 2002 to 2010

Comparison of species frequencies, indicator values, and group assignments between 2002 and 2010 suggested stability among the species and communities found in the entire study site (Table 1). Exceptions included a decrease in frequency of *Distichlis spicata* and an increase in frequency of *Fimbristylis castanea*. However, when groups of plots classified in 2002 were compared to the same groups in 2010, there was evidence for community change in two of the groups: *Juncus* and mixed (Table 3). In both of these sets of plots, dominant indicator species (*Juncus roemerianus* in the *Juncus* group; *Distichlis spicata* in the mixed group) showed gradual declines in relative cover, whereas other subordinate species showed gradual increases in relative cover (Figure 3). In plots classified as *Salicor-*

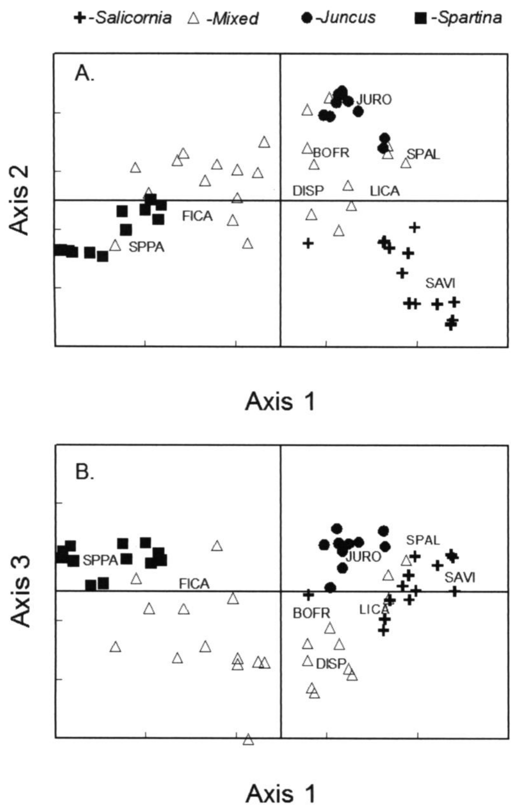

Figure 2. A. Axis 1 vs. axis 2, B. and axis 1 vs. axis 3 of the nonmetric dimensional scaling (NMS) ordination derived from Waties Island high marsh plots in 2010. Plot symbols represent the results of cluster analysis. Codes for species are listed in Table 1.

nia or *Spartina* there were no detectable community changes during the study period.

DISCUSSION

Species and Soil Properties

A broad base of previous research suggests that high marsh species and thus high marsh communities of the southeast are influenced by several factors, including but not limited to, inundation, salt stress, nutrient limitation, soil oxygen, and interspecific interactions (Adams 1963, Woerner and Hackney 1997; Pennings et al. 2005). These factors can produce visible vegetation zones when elevation gradients from low marsh to high marsh are clear cut. Or, in the case of the Waties Island high marsh, where elevation gradients are complex, these factors can produce vegetation patches varying in extent, composition, and stability.

Some of the plant community patterns at the Waties Island high marsh can be explained by responses of species to soil properties or effects of species on soil properties as observed in other southeast marshes. For example, *Salicornia virginica* commonly is found associated with high interstitial salinities (Stalter and Batson 1969, Wiegert and Freeman 1990). Waties Island high marsh plots dominated by this species occurred in shallow depressions where evaporation increased soil salinity. Patches dominated by *Salicornia* can intergrade with bare salt pans (Wiegert and Freeman 1990). *Spartina patens* is a productive species capable of forming an organic root mat that can in turn inhibit invasion by other species (Bertness and Ellison 1987, Leonard et al. 2010). Plots dominated by this species at the Waties Island high marsh were associated with high soil organic matter and few other associated species. *Distichlis spicata* is a community associate on highly saline sites and also is a colonizer of disturbances (Bertness 1991, Wiegert and Freeman 1990). At Waties Island, *Distichlis spicata* was found as a component of the mixed community at relatively high salinities. *Juncus roemerianus* at Waties Island was associated with relatively high salinities. Wiegert and Freeman (1990) suggested that *Juncus* should be associated with lower salinities, although Woerner and Hackney (1997) found this species across a wide range of marsh environments.

Table 3. Results of blocked nonmetric multiresponse permutation procedure (MRPP) and PerManova (effect of year) for comparisons of Waties Island high marsh communities between 2002 and 2010. Groups were identified in 2002 by cluster analysis

Group	Blocked MRPP		PerManova (effect of year)	
Juncus	A = 0.32	P < 0.001	F = 12.82	P < 0.001
Mixed	A = 0.13	P < 0.001	F = 12.27	P < 0.001
Salicornia	A = 0.75	P = 0.072	F = 2.96	P = 0.052
Spartina	A = 0.06	P < 0.05	F = 2.32	P = 0.078

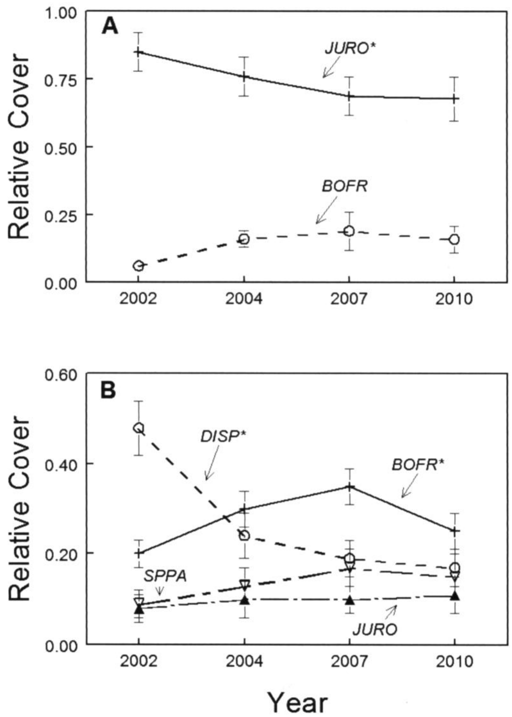

Figure 3. Trends in relative cover (means ± SE) of important plant species in Waties Island high marsh plots. A. Data from plots classified as *Juncus* in 2002. B. Data from plots classified as mixed in 2002. Codes for species are provided in Table 1. Indicator species are marked with *.

Two species found at the Waties Island high marsh were notable for different reasons. *Borrichia frutescens* is a common species of high marshes in the southeast (Wiegert and Freeman 1990; Perry and Atkinson 1997), but is limited by several factors (Stalter and Batson 1969). This species at Waties Island had the highest overall frequency and was an important component of two communities, perhaps indicating relative maturity of this high marsh site (Wiegert and Freeman 1990). *Spartina alterniflora*, the sole dominant engineer of the low marsh (Wiegert and Freeman 1990), was found at low frequencies and low importance in the Waties Island high marsh, suggesting that this site has gone through the lengthy developmental processes where *Spartina alterniflora* was displaced by other species (Pennings et al. 2005).

Although high marsh communities in the northeast have experienced dramatic changes in extent and composition through time (Smith 2009), long-term trends for southeast salt marshes are less clear (Walters et al. 2010). Community stability at the Waties Island high marsh varied depending on community classification with patches dominated by *Salicornia virginica* and *Spartina patens* showing no change, whereas the mixed and *Juncus* communities did change. Evidence for change through time in the mixed community was likely driven by the decline in *Distcihlis spicata*. A similar trend was noted by Brinson and Christian (1999) in a Virginia marsh and might be related to the dependence of this species on recent disturbance, such as wrack deposition or sedimentation (Bertness and Ellison 1987, Tolley and Christian 1999). In contrast to the results of Brinson and Christian (1999), *Juncus roemerianus* patches at Waties Island showed changes in composition, although such changes were variable and could not be attributed to consistent upward or downward trends of important individual species through time other than the gradual decline in relative coverage of the dominant species, *Juncus roemerianus*.

Relatively high community stability was suggested for those high marsh communities at opposite ends of salinity and soil organic matter gradients. However, mechanisms for this stability might differ. *Spartina patens* often dominated plots through high coverage (mean of 90%) and thus was likely able to compete successfully with potential plot invaders (Leonard et al. 2010). In contrast, *Salicornia virginica* also dominated plots but with low coverage (mean of 26%) suggesting that stability here was the result of salt or inundation stress (Pennings et al. 2005). Communities in the midsection of the salinity and soil organic matter gradients were susceptible to change, perhaps indicating the presence of a suite of species capable of tolerating these intermediate high marsh environmental conditions.

Data presented in this study represent communities and community change in a single high marsh during a time period when allogenic factors such as overwash, erosion, wrack deposition, and inlet modification were small or not present. However, such processes have influenced this high marsh in the past and will likely influence it in the future (Tolley and Christian 1999). The relatively minor changes in the high marsh measured in this study during a period of environmental stability should be interpreted cautiously, because a single site might not be representative of all high marshes in the region. However, the species assemblage and community pattern at Waties Island were similar to other salt marshes both locally (Stalter and Batson 1969, Morris et al. 2005, Walters et al. 2010) and regionally (Wiegert and Freeman 1990, Tolley and Christian 1999). Future studies should focus on the mechanisms imparting relative stability to southeastern high marsh communities, particularly as compared to similar but less stable salt marsh systems in the northeast (Silliman and Bertness 2004, Pennings et al. 2005).

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