WETLANDS, Vol. 17, No. 2, June 1997, pp. 284–291

DISTRIBUTION OF *JUNCUS ROEMERIANUS* IN NORTH CAROLINA TIDAL MARSHES: THE IMPORTANCE OF PHYSICAL AND BIOTIC VARIABLES

Lynn Stemmy Woerner[1] and Courtney T. Hackney
Department of Biological Sciences
University of North Carolina at Wilmington
Wilmington, NC 28403

[1] *Present address:*
1222-A Hamilton Court
Cary, NC 27511

Abstract: The physical habitat of *Juncus roemerianus* was examined at nine sites along a salinity gradient in the Cape Fear River Estuary, North Carolina. Soil salinity, drainage, redox potential, pH, elevation, percent sand, percent organic matter, and above-ground plant biomass and height were measured at each site, and from these data, the habitat of *Juncus roemerianus* was determined. All parameters varied over the salinity gradient, with soils at upriver sites having a high sand fraction, low organic fraction, and highest redox potentials. Downriver, well-established marshes had low sand fractions, high organic fractions, and lowest redox potentials. Canonical Discriminant Analysis indicated that each site was statistically different from other sites due to salinity, elevation, and percent organic matter.

Mean standing live biomass was 688 g m $^{-2}$ and, despite differences in physical and chemical factors among sites, biomass of *Juncus roemerianus* did not vary. *Juncus roemerianus* was found to grow equally well within a broad range of physical and chemical habitats but did not occupy the total expanse of its potential habitat at any one site.

Extensive overlap in physical habitat occurred between *Juncus*-dominated communities and adjacent communities dominated by other species, especially in the more established marshes. However, Canonical Discriminant Analysis statistically separated short and tall form *Spartina alterniflora, Distichlis spicata, Scirpus robustus,* and *Juncus roemerianus* microhabitats based on elevation and redox potential. Thus, we found zonation in tidal marshes of the Cape Fear River Estuary was based on abiotic factors, but we recognize the importance of plant species interactions and marsh position within the landscape.

Key Words: zonation, tidal marsh, physical gradient, edaphic conditions, competition, *Juncus roemerianus,* elevation, soil salinity, *Spartina alterniflora*

INTRODUCTION

The vegetation of tidal marshes is often subject to extreme and varying environmental conditions. Consequently, tidal marshes are characterized by a low diversity of flora occurring in distinct vegetative zones. In the Southeast U.S., dominant plants include smooth cord-grass (*Spartina alterniflora* Loisel) and black needlerush (*Juncus roemerianus* Scheele), which are often found in dense monotypic stands adjacent to one another (Adams 1963, Eleuterius and Eleuterius 1979, Stout 1984, Wiegert and Freeman 1990).

Early work on zonation focused on the apparent correlation of vegetative patterns to variations in the physical environment. Adams (1963) studied North Carolina marshes and reported that zonation was associated with a gradient of edaphic factors related to tide and elevation. Salinity has also been cited as an important factor limiting distribution of marsh species (Adams 1963, Waisel 1972, Cooper 1982, Earle and Kershaw 1988). Other workers have reported that spatial patterns in their marshes were influenced by elevation and degree of inundation (Zedler 1977, Nixon 1982, Earle and Kershaw 1988); soil drainage and aeration (Mendelssohn and Seneca 1980); soil type and texture (Dawe and White 1982); nutrient availability (Pidwirny 1989), and soil redox potential (Linthurst and Seneca 1980, Mendelssohn and Seneca 1980, Mendelssohn et al. 1981, Jernigan 1990).

Changes in these physical factors over time can cause changes in vegetative patterns. DeLaune et al. (1987) suggested that increasing submergence and salinity in tidal marshes causes changes in distribution of coastal plant communities. Warren and Niering (1993) studied salt marshes in Connecticut 40 years after initial work by Miller and Egler (1950) and reported changes in community composition due to sea level rise and a decrease in accretion.

Biotic factors such as competition have also been cited as significant causes of zonation (Adams 1963, Snow and Vince 1984, Covin and Zedler 1988), and transplant studies have confirmed the existence of competition in the marsh (Stalter and Batson 1969, Bertness and Ellison 1987, Bertness 1991).

Many studies on factors determining vegetative distribution in tidal marshes have been carried out within a single site and then used as a model to represent all marshes with similar species (Adams 1963, Hackney et al. 1996). However, the presence of similar species does not necessarily indicate the same physical characteristics, hydrogeomorphic conditions, or species interactions. Physical characteristics of marshes may vary depending on marsh location (Eleuterius and Caldwell 1985) and age (Osgood and Zieman 1993).

An example of a widespread tidal marsh species that occurs in monotypic zones and also occupies a varied physical habitat is *Juncus roemerianus* (Eleuterius and Caldwell 1985). Stout (1984) described three types of habitats occupied by *J. roemerianus* communities in the northeastern Gulf of Mexico: 1) saline marshes with little significant dilution of tidal waters, 2) brackish marshes where tidal waters are diluted before flooding the marsh, and 3) the transitional community between brackish and freshwater marsh.

The purpose of this study was to examine the physical and chemical habitat associated with tidal marshes along a salinity gradient. The physical habitat of *Juncus roemerianus* was described, including elevation, soil salinity, drainage, redox potential, pH, and texture. The physical environment was also compared with that of adjacent plant communities to determine if distribution of *J. roemerianus* was controlled by tolerance to physical conditions.

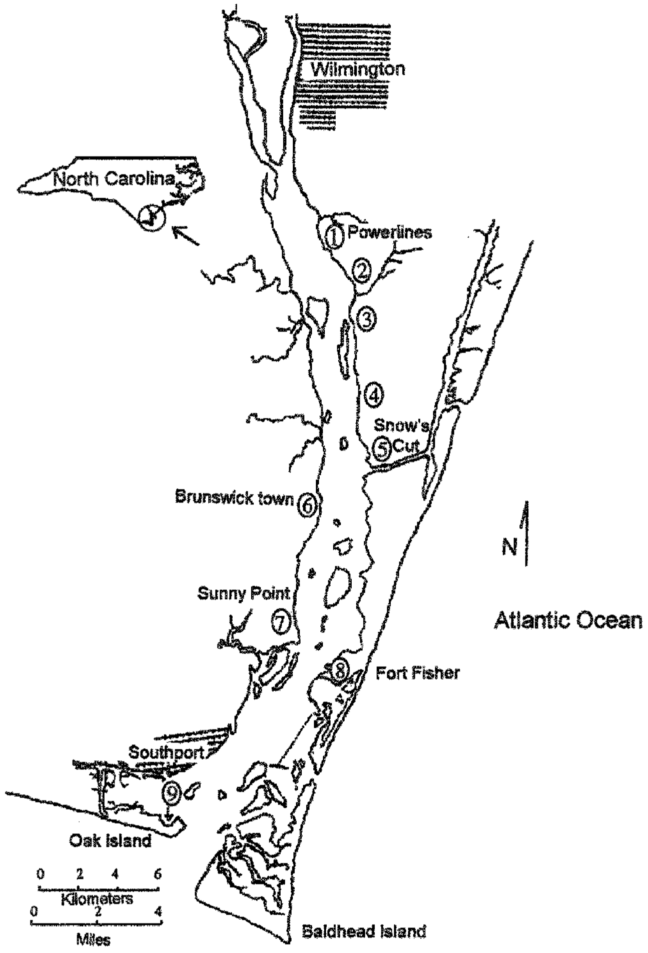

Figure 1. Locations of study sites along the lower Cape Fear River, North Carolina. GPS coordinates for the study sites were: Site 1: 34°09.140′N and 77°56.611′W, Site 2: 34°09.088′N and 77°55.822′W, Site 3: 34°06.420′N and 77°55.490′W. Site 4: 34°05.096′N and 77°55.291′W, Site 5: 34°03.197′N and 77°55.060′W, Site 6 (Fort Fisher): 33°57.658′N and 77°56.493′W, Site 7 (Brunswick Town State Historic Site) 34°02.381′N and 77°56.645′W, Site 8 (Sunny Point Military Ocean Terminal): 34°00.210′N and 77°57.290′W, and Site 9 (Fort Caswell Baptist Assembly): 33°53.596′N and 78°01.279′W.

STUDY AREA

The Cape Fear River flows 320 km southeast through North Carolina and drains 14624 km². Saltwater intrusion occurs up to 32 km upstream (Giese et al. 1985). Nine sites were selected along a salinity gradient from the mouth to 20 km upriver (Figure 1). Marshes along this gradient were selected that were characterized by stands of *Juncus roemerianus* adjacent to U.S.G.S. vertical datum benchmarks (NGVD). Salinity ranged from 0.5 ppt at the upriver site to 35 ppt at the mouth, and all sites had a mean tidal amplitude of 1.43 m (NOAA 1995).

METHODS

A 100-m transect was established through the middle of each site. Every 10 m along the transect, a permanent station was established for a total of 8–10 stations per site. For small stands of *J. roemerianus* (sites 1 and 2), stations were located every five meters to attain 8–10 stations per site.

The largest adjacent vegetative zone dominated by a plant other than *J. roemerianus* was selected, and a transect along the edge where these two zones met was established. Every 10 m, two stations were established, one meter within and one meter outside of the *Juncus* zone, for 8–10 pairs of stations.

At each station (in both *J. roemerianus* and adjacent vegetative zones), soil salinity, drainage, redox potential, and pH were measured once each season: late winter (March), spring (May), summer (July), and fall (September). Elevation, percent sand, and percent organic matter were measured in July. Percent organic matter, above-ground biomass, and plant height were also measured in July at *J. roemerianus* stations.

At each station, a 7.3 cm (dia.) × 20 cm sediment core was removed at low tide. Holes were covered with a ring to prevent surface water from entering. After interstitial water refilled the hole, water depth was measured to determine soil drainage, and salinities were recorded to the nearest 0.5 ppt.

Soil redox potential was measured at low tide using a method similar to de la Cruz et al. (1989). A mini pH meter and six platinum tipped electrodes were used to measure redox potential of the substrate at depths of 5 and 10 cm for each station. Sediment temperature was recorded at 5 and 10 cm depths. Sediment pH was also recorded within the first 5 cm at each station using the pH meter and an Ag/AgCl standard gel-filled electrode also calibrated in the lab with standard 7.0 buffer solution. Elevation was measured using a transit, referenced to a U.S.G.S. elevational benchmark, and recorded in meters relative to mean sea level (MSL).

At each station, two sediment cores were collected and homogenized. From each sample, percent organic material was determined by drying, then ashing in a muffle furnace at 600°C for 4.5 h. Percent sand content was determined using the methods outlined in Folk (1974); sandy samples were separated by dry seiving, and samples with more than a few percent of silt and clay were separated by wet sieving.

Above-ground live biomass for *Juncus* was determined during peak growing season (July) by selecting six random 0.25 m^2 plots along transects. Plants were clipped at ground level early in July. Leaves were then sorted into live and dead; leaves that were more than 50% green were considered to be live. The live leaves were dried at 103°C and weighed.

Statistical Analyses

All statistical analyses used SAS version 6.0, and significance was determined at $\alpha = 0.05$ (SAS Institute Inc. 1989). Principle Component Analysis was used to determine if correlations existed among parameters. Redox potential at 5 and 10 cm were highly correlated ($r^2 = 0.92$); therefore, Eh at 10 cm was removed from further analysis. Data were tested for normality (using PROC Univariate normal), and log and arcsin transformations were made where appropriate. Student-Newman-Keuls tests were used to determine differences between sites for each parameter. Analysis of Variance followed by pairwise comparisons (using Tukey's studentized range test) determined differences among sites and seasons for individual variables.

Table 1. Habitat characteristics of marshes dominated by *Juncus roemerianus*. Values are the mean and standard deviation from all sites combined. Ranges are in parentheses.

Elevation (m above MSL)	0.68 ± 0.13 (0.27–0.92)
Sand content (%)	65.9 ± 34 (10.3–100)
Organic content (%)	14.8 ± 14 (0.5–50.7)
Salinity (ppt)	17.3 ± 9.3 (0.5–38.0)
Redox potential (mV)	117.2 ± 164.9 (−230.8–+510.5)
pH	7.00 ± 0.55 (5.72–8.93)
Drainage (cm)	11.92 ± 6.9 (0–20)

Multiple regression via the GLM procedure determined if any of the physical parameters (redox potential, salinity, drainage, pH, elevation, percent organic matter, or percent sand) were related to biomass and height of *Juncus roemerianus*.

Juncus roemerianus Compared with Other Zones

Analysis of variance and pairwise comparisons (using Tukey's test) were made between *J. roemerianus* and other vegetative zones by site and season to determine if differences in variables occurred between zones. Canonical Discriminant Analysis was used to determine if separation existed between *Juncus roemerianus* and other vegetative zones. This separation was determined using the Wilks' Lambda multivariate test statistic. Canonical variables were examined to determine which of the parameters measured (redox potential, salinity, soil drainage, pH, percent sand, or elevation) were most important in determining this separation. (Mardia et al. 1979, Johnson 1994).

RESULTS

Soil characteristics of *Juncus roemerianus* communities are summarized in Table 1. Sites, originally selected along a salinity gradient, were arranged according to mean salinity on all figures. The mean elevation for *Juncus roemerianus* was 65 cm with most stations within 0.6 to 0.8 m above msl (Figure 2). Even with this narrow elevation range, we found significant variation among sites for elevation ($F = 25.86$, d.f. = 8/71, $P < 0.0001$). In addition, a Student-Newman-Keuls test showed that elevation was the same at all sites

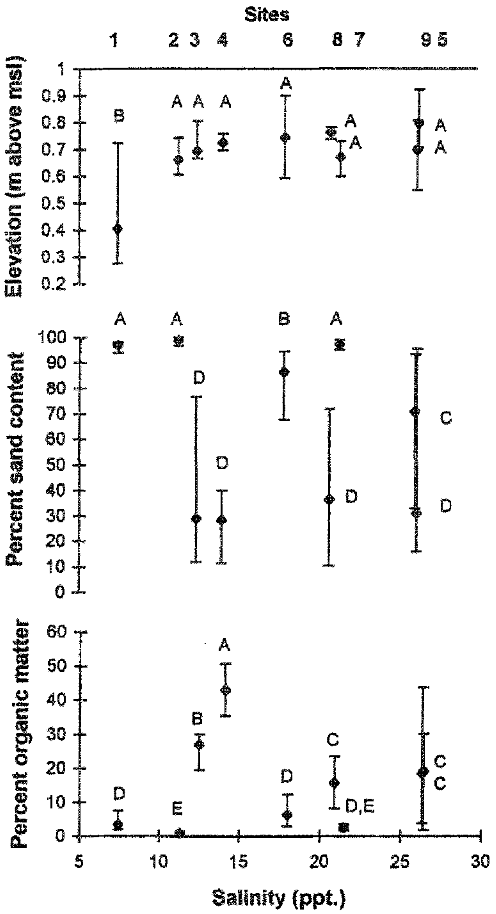

Figure 2. Soil characteristics from nine marshes along a salinity gradient dominated by *Juncus roemerianus*. Values are means and ranges. Values with the same letters are not significantly different based on Student-Newman-Keuls tests.

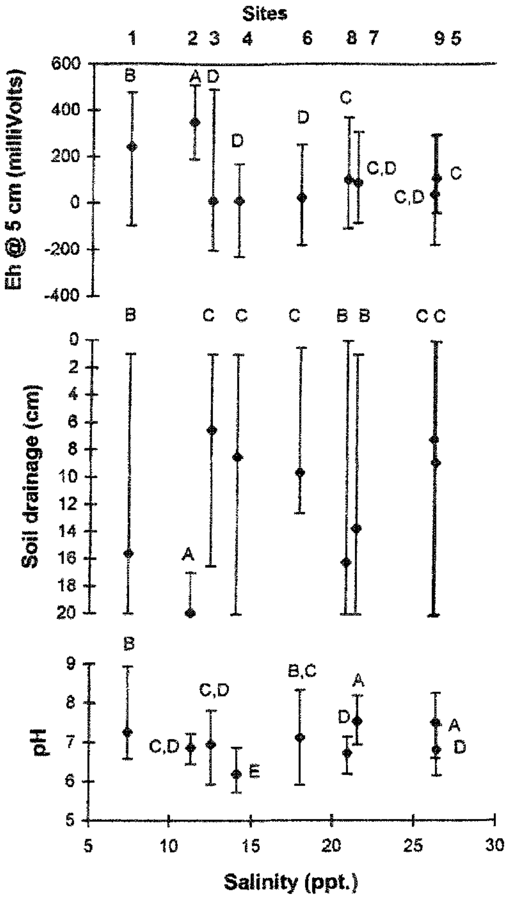

Figure 3. Annual means of *Juncus roemerianus* marsh soil characteristics along a salinity gradient. Values are means and ranges. Values with the same letters are not significantly different according to Student-Newman-Keuls tests.

except site 1, which was significantly lower. Sites varied considerably with respect to percent sand ($F = 47.33$, d.f. = 8/71, $P < 0.0001$) and organic matter ($F = 51.59$, d.f. = 8/71, $P < 0.0001$).

Percent sand generally decreased over the gradient (Figure 2), with sites 1, 2, and 7 grouped together with a very large (>95%) sand fraction. Sites 3, 4, 5, and 8 were also grouped together with a low sand fraction (<30%), containing a large amount of silt and clay. Percent organics varied inversely with sand content (Figure 2), with sites 1, 2, 6, and 7 having the lowest values compared to sites 3 and 4, with 8, 9, and 5 intermediate.

There were also significant differences among sites ($P < 0.0001$) for all parameters that had been measured seasonally. Sites 1 and 2, which consistently had the lowest salinities, also had the highest redox potentials (Figure 3). Downriver sites (5 to 7) had the greatest salinities. Sites 3, 4, 6, 7, and 9 had the lowest redox potentials. Drainage was less consistent, but the sites with greater sand content typically had greater soil drainage (Figure 3).

Mean biomass was 688 g m^{-2} and did not vary significantly over sites ($F = 137$, d.f. = 8/45, $P < .2342$), but showed wide variation within sites. Height did vary significantly over sites ($F = 8.49$, d.f. = 8/45, $P < 0.0001$), with the tallest plants found at sites 1 and 3 (Figure 4).

Multiple regression of the dependent variable biomass on the elevation, percent organic matter, and percent sand content showed biomass weakly correlated ($r^2 = 0.21$, $F = 8.0$, $P < 0.0001$) with these parameters. Only percent sand was significantly correlated ($F = 42.79$, $P < 0.0001$) with biomass. Height was correlated with the parameters measured ($r^2 = .61$, $F = 47.83$, $P < 0.0001$); height was negatively correlated with elevation ($F = 163.53$, $P < 0.0001$), salinity ($F = 86.56$, $P < 0.0001$), redox potential ($F = 19.78$, $P < 0.0001$), and percent sand ($F = 15.05$, $P < 0.0001$); and height was positively correlated with percent or-

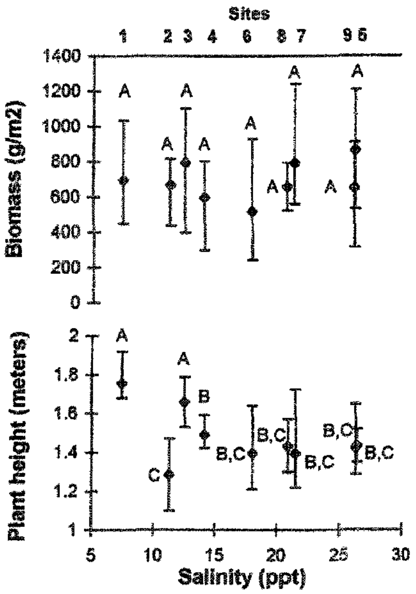

Figure 4. Biomass and height of *Juncus roemerianus* during peak growing season along a salinity gradient. Values are means and ranges. Values with the same letter are not significantly different.

ganic matter (F = 43.25, $P < 0.0001$) and pH (F = 6.57, $P < 0.01$).

Juncus roemerianus Compared with Other Vegetative Zones

Spartina alterniflora was the dominant vegetation in the adjacent zones, except at site 3 where *Distichlis spicata* Greene dominated the adjacent area. At site 4, *S. alterniflora* initially dominated the entire adjacent zone. However, in spring, *Scirpus robustus* Pursh invaded about half of this zone and became the dominant adjacent flora for the remainder of the study.

Elevation was significantly lower for *S. alterniflora* than *J. roemerianus* at the two sites furthest upriver (Site 1, F = 9.04, $P < 0.0076$; Site 2, F = 144.8, $P < 0.0001$). There was also a significant difference between *Juncus* and *Distichlis* stands at site 4 (F = 9.34, $P < 0.01$), with *Distichlis* being significantly higher in elevation (Figure 5).

Redox potential was consistently greater in *Juncus* soils vs. *Spartina* soils (Figure 5). Sites that showed significant differences ($P < 0.05$) between stands with respect to redox potentials were upriver sites (1 and 2), which corresponded to the significant elevation differences. Pairwise comparisons revealed no significant differences in salinity or percent sand content between *Juncus roemerianus* and stands of adjacent vegetation at any site (all P values >0.05).

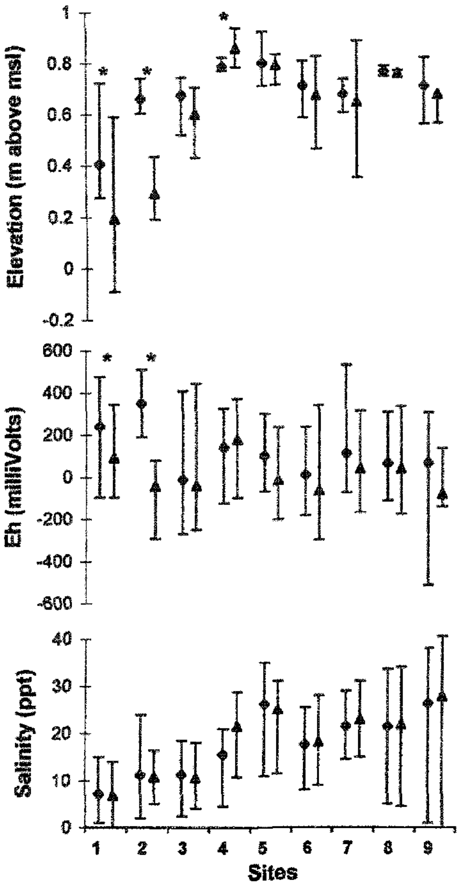

Figure 5. Pairwise comparisons of physical characteristics of stands of *Juncus roemerianus* and adjacent stands of vegetation. All adjacent stands were dominated by *Spartina alterniflora* except site 4, which was dominated by *Distichlis spicata*. Values are means and ranges. Pairs indicated by an * are significantly different ($P < 0.05$).

Canonical Discriminant Analysis revealed separation ($P < 0.0001$) between *Juncus roemerianus* and *Spartina alterniflora* for all seasons. When *Spartina alterniflora* was separated into short and tall forms, there was significant separation of the two height forms and *Juncus* based on elevation and redox potential. When *Distichlis spicata* and *Scirpus robustus* were added, there was significant separation (Wilk's Lambda = 0.417, df = 20/1848, $P < 0.0001$) of the different vegetative zones (Figure 6). The first two canonical variables were responsible for 90.1% of this separation. The first canonical variable (CAN 1) was responsible for 67.1% of the separation, with elevation as the only highly weighted variable (standardized coefficient of 1.26) The highly weighted variable in the second canonical variable (CAN 2) was redox potential, which had a standardized coefficient of 0.997.

DISCUSSION

Physical Habitat of *Juncus roemerianus*

Juncus roemerianus occurs over a wide range of physical and chemical variables. In Mississippi marsh-

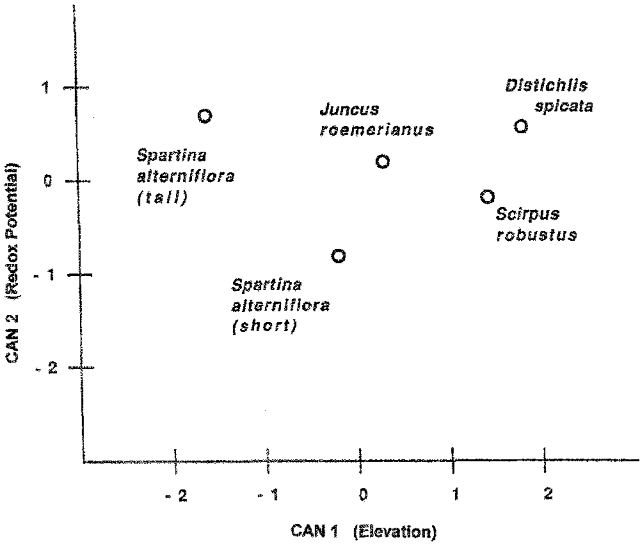

Figure 6. Separation of vegetative types and relative position of each species along canonical axes. Values are class means. Heavily weighted variables were elevation in CAN 1, and redox potential in CAN 2.

es, monotypic stands of *Juncus* have been found to occupy a variety of marsh habitats that have significant differences in salinity, organic matter, percent sand content, soil water content, and nutrient concentrations (Hackney and de la Cruz 1978, Eleuterius and Caldwell 1985). The ability of this species to occupy a variety of soil types allows for its wide distribution in tidal marshes in the Southeastern United States.

We found that stands of *Juncus roemerianus* in North Carolina marshes also occur over a wide range of physical and chemical variables, including salinity, elevation, percent sand content, percent organic matter, redox potential, and soil drainage (Figures 2, 3, and 4). Significant differences in soil organics, elevation, and sand content were found between *Juncus* marshes along the salinity gradient. Variations in these physical characteristics may be due to factors including marsh age or maturity and physical setting within the landscape (Redfield 1972, Osgood and Zieman 1993). Although marsh age is not known in this study, recent activities such as dredging in the Cape Fear River have allowed for salt intrusion further upriver. This increase in salinity has led to establishment of *Spartina* and *Juncus* marshes further upstream where bald cypress (*Taxodium distichum* Richard) was once dominant (Hackney and Yelverton 1990). The two sites furthest upriver are likely younger than the other marshes studied and have not had an opportunity to accumulate sediment or organic material. Osgood and Zieman (1993) studied barrier islands of Virginia and reported that sediments of younger marshes were coarser and had a greater sand content and a lower percentage of organics than older marshes. They also found that younger marshes had higher redox potentials, which was attributed to better drainage and a steeper elevational grade that older sites. The stands of *Juncus roemerianus* at the upriver sites (1 and 2) as well as Site 7 (Sunny Point) occurred as narrow bands along the river's edge. The marshes at sites 1 and 2 occurred on a steeper elevational grade than the other sites, with significant differences in elevation and redox potential between vegetative zones (Figure 5). The vegetation in these areas was exposed to regular inundation by twice-daily tides and better drainage (Figure 3), which may prevent buildup of fine grained sediment and organic material. In the majority of the other sites (3, 4, 5, 8, and 9), the stands of *Juncus* were located in irregularly flooded, protected embayments. These well-established marshes have accumulated more sediment, and as a result, the finer grained sediment content was significantly greater in these marshes.

Despite differences in physical characteristics, *J. roemerianus* achieved similar biomass throughout its range. Although differences in plant height were detected between sites, there were no significant differences in standing biomass for any of the sites along gradients of salinity, elevation, redox potential, or percent organic matter (Figure 4). Similarly, Christian et al. (1990) found no differences in growth of *Juncus* along gradients of hydroperiod and salinity.

While there were no significant differences in biomass, we found a negative effect of sand content on biomass and height. We also found a negative effect of redox potential on height. Smart and Barko (1978) found that *Spartina alterniflora* and *Distichlis spicata* grew best on silt and clay soils with low biomass on sandy soils. This difference in growth was attributed to nutrient limitations of growth in sandy soils. In this study, plant height was negatively correlated with elevation and salinity. *S. alterniflora* also has its taller height forms in zones of lower elevations and lower soil salinity then the short form (Adams 1963). Although the height differences shown by *Juncus roemerianus* are not as apparent as in *S. alterniflora,* the effects of inundation and salinity are similar.

Zonation

It has been well documented that distribution of vegetation in the tidal marsh is dependent on species' varying tolerance to physical factors. (Adams 1963, Cooper 1982, Earle and Kershaw 1988). Hackney et al. (1996) found distinct differences in some physical characteristics that could be used to statistically separate vegetative zones. We found similar differences between vegetative zones in the lower salinity marshes studied. In the marshes with the lowest salinity (sites

1 and 2), the narrow bands of *Juncus* were found growing at significantly lower elevations than the adjacent stands of *Spartina alternifora.* Redox potential in the *Juncus* zone was greater in these areas. The *Juncus* at these upriver sites may be restricted from the lower intertidal zone due to inundation. At site 2, a stand of *Juncus roemerianus* was observed along the river's edge in the high intertidal zone shoreward of an area of bare sand, indicating that *Juncus* was restricted from the lower elevation by inundation. In the spring of 1994, *Spartina alterniflora* established in this bare area. The *Spartina* grew vigorously but did not invade higher elevations occupied by *Juncus.*

Restriction of *Spartina alterniflora* to the regularly inundated low marsh has been well-documented. Bertness and Ellison (1987) conducted transplant studies in New England marshes and showed that *S. alterniflora* was able to grow vigorously along the entire marsh elevation gradient but was restricted from the high marsh due to competitive exclusion by *Spartina patens* Muhl. They reported that the superficial rhizome and root mat of *S. patens* inhibited penetration and seedling establishment by *S. alterniflora. Distichlis spicata* may also restrict *Juncus roemerianus* from higher elevations. In the present study, *Distichlis spicata* occupied a region adjacent to *Juncus* at Site 4. The elevation of this zone was significantly higher than that of *Juncus* with some overlap (Figure 5).

Zonation and monospecific stands of certain species do not always coincide with the apparent gradient of physical factors, and the presence of certain species does not necessarily indicate the existence of specific edaphic characteristics. Wiegert and Freeman (1990) reported that *Juncus roemerianus* dominates primarily where low interstitial salinity prevails. However, we found that salinity alone did not seem to limit distribution of *Juncus roemerianus* nor was it responsible for zonation patterns of *Juncus* and *Spartina* (Figure 4). Interstitial salinity for both species ranged from 5 to 25 ppt and was not significantly different for the two species at any location.

Juncus roemerianus also has a wide range of tolerance to other physical factors measured, and we found that the physical characteristics associated with stands of *Juncus* overlapped with other vegetative zones. Although the plants occur in monotypic stands with little or no mixing of species, percent sand content, soil drainage, and pH were not significantly different between vegetative zones at any of the locations. In all marshes but site 2, we found considerable overlap of redox potential and elevation between zones indicating that abiotic factors may be partly responsible for distribution patterns.

While biotic factors were not examined in this study, the role of these factors may help to explain the apparent overlap of habitats. It has been suggested that plants may alter their environment to exclude other species (Howes et al. 1986, Bertness and Ellison 1987, Pidwirny 1989, Hackney et al. 1996). We found significant differences in elevation and redox potential between zones in some marshes. Statistical separation of different vegetative zones occurred primarily due to differences in elevation (Figure 6), which may be controlled by the plants. Other biotic factors such as preemption (Grace 1987) and alteration of microhabitats through mechanisms such as allelopathy (as summarized by Rice (1974)) have been documented in other habitats and may deserve further investigation in the tidal marsh.

Describing the physical and chemical factors of the tidal marsh can delineate the potential habitat of a species, as long as biotic interactions do not exclude species. Van der Valk (1981) and Mitsch and Gosselink (1986) maintain that distribution patterns in the tidal marsh are due to tolerance of environmental conditions as well as competitive plant interactions. Current theory suggests that the importance of competition changes along environmental gradients. At the harsh end of the gradient, such as the frequently flooded low marsh, species distribution is limited by tolerance to physical factors. At the benign end, such as the high marsh, interspecific competition is more important in determining distribution patterns (Snow and Vince 1984, Pennings and Calloway 1992). In general, *J. roemerianus* occupies a slightly different, but overlapping part of the intertidal physical/chemical habitat than other species (Figure 6). The exact positions of boundaries between different vegetative zones, however, are not clearly related to these variables (as there is considerable overlap between habitat occupied by different species), which may be due to short- and long-term physical changes as well as biotic interactions.

ACKNOWLEDGMENTS

We thank N. Woerner, O. Rutten, F. Hernandez, and D. Swearingen for help in the field. We thank M. Posey and L. Cahoon for their helpful comments during the preparation of this manuscript and M. LaSalle for a final review. This work was supported in part by a grant from the North Carolina Academy of Sciences and also by the Environmental Monitoring and Assessment–Wetlands Program (EMAP).

LITERATURE CITED

Adams, D.A. 1963. Factors influencing vascular plant zonation in North Carolina salt marshes. Ecology 44:445–456.

Bertness, M.D. 1991. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72:138–148.

Bertness, M.D. and A.M. Ellison. 1987. Determinants of pattern in a New England salt marsh community. Ecological Monographs 57:129–147.

Christian, R.R., W.L. Bryant, and M.M. Brinson. 1990. *Juncus roemerianus* production and decomposition along gradients of salinity and hydroperiod. Marine Ecology Progress Series 68:137–145.

Cooper, A. 1982. The effects of salinity and waterlogging in the growth and cation uptake of salt marsh plants. New Phytologist 90:263–275.

Covin, J. D. and J. B. Zedler. 1988. Nitrogen effects on *Spartina foliosa* and *Salicornia virginica* in the salt marsh at Tijuana Estuary, CA. Wetlands 8:51–63.

Dawe, N.K. and E.R. White. 1982. Some aspects of the vegetation ecology of the Little Qualicum River estuary, British Columbia. Canadian Journal of Botany 60:1447–1460.

de la Cruz, A.A., C.T. Hackney, and N. Bhardwaj. 1989. Temporal and spatial patterns of redox potential (Eh) in three tidal marsh communities. Wetlands 9:181–190.

DeLaune, R.D., S.R.Pezeshki, and W.H. Patrick, Jr. 1987. Responses of coastal plants to increase in submergence and salinity. Journal of Coastal Research 3:535–546.

Earle, J.C. and K.A. Kershaw. 1988. Vegetation patterns in James Bay coastal marshes. III. Salinity and elevation as factors influencing plant zonations. Canadian Journal of Botany 67:2967–2974.

Eleuterius, L.N. and J.D. Caldwell. 1985. Soil characteristics of four *Juncus roemerianus* populations in Mississippi. Gulf Research Reports 8:9–13.

Eleuterius, L.N. and C.K. Eleuterius. 1979. Tide levels and salt marsh zonation. Bulletin of Marine Science 29:394–400.

Folk, R.L. 1974. Petrology of Sedimentary Rock. Hemphill's, Austin, TX, USA.

Giese, G. L., H. B. Wilder, and G. G. Parker. 1985. Hydrology of major estuaries and sounds of North Carolina. U. S. Geological Survey Water-Supply Paper 2221.

Grace, J. B. 1987. The impact of preemption on the zonation of two *Typha* species along lakeshores. Ecological Monographs 57: 283–303.

Hackney, C.T., S. Brady, L. Stemmy, M. Boris, C. Dennis, T. Hancock, M. O'Bryon, C. Tilton, and E. Barbee. 1996. Does intertidal vegetation indicate specific soil and hydrologic conditions. Wetlands 16:89–93.

Hackney, C.T. and A.A. de la Cruz. 1978. Changes in intersitial water salinity of a Mississippi tidal marsh. Estuaries 1:185–188.

Hackney, C.T. and G.F Yelverton. 1990. Effect of human activities and sea level rise on wetland ecosystems in the Cape Fear River estuary, North Carolina, USA. p. 55–63. *In* D.F. Whigham, R.E. Good, and J. Kvet (eds.) Wetland Ecology and Management: Case Studies. Kluwer Academic Publishers, The Hague, Netherlands.

Howes, B.L., J.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.

Jernigan, L.S. 1990. Factors influencing the distributional patterns of *Juncus roemerianus* in two North Carolina salt marshes. Ph.D Dissertation. North Carolina State University, Raleigh, NC, USA.

Johnson, D.E. 1994. Applied Multivariate Methods. Kansas State University, Manhattan, KS, USA.

Linthurst, R.A. and E.D. Seneca. 1980. The effect of standing water and drainage potential on the *Spartina alterniflora*-substrate complex in a North Carolina salt marsh. Estuarine and Coastal Marine Science 11:27–40.

Mardia, K.V, J.T, Kent, and J.M. Bibby. 1979. Multivariate Analysis. Academic Press, New York, NY, USA.

Mendelssohn, I.A. and E.D. Seneca. 1980. The influence of soil drainage on the growth of salt marsh cordgrass *Spartina alterniflora* in North Carolina. Estuarine and Coastal Marine Science 11: 27–40.

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.

Miller, W.R. and F.E. Egler. 1950. Vegetation of the Wequetequock-Pawcatuck tidal marshes, Connecticut. Ecological Monographs 20:147–171.

Mitsch, W.J. and J.G. Gosselink. 1986. Wetlands. Van Nostrand Reinhold, New York, NY, USA.

Nixon, S.W. 1982. The ecology of New England high salt marshes: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-81/55.

NOAA. 1995. Tide Tables for North Carolina. Office of Oceanography and Marine Assessment. Washington, DC, USA.

Osgood, D.T. and J. C. Zieman. 1993. Spatial and temporal patterns of substrate physicochemical parameters in different-aged barrier island marshes. Estuarine, Coastal and Shelf Science 37:421–436.

Pennings, S.C. and R.M. Callaway. 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73:681–690.

Pidwirny, M.J. 1989. Plant zonation in a brackish tidal marsh: descriptive verification of resource-based competition and community structure. Canadian Journal of Botany 68:1689–1697.

Redfield, A.C. 1972. Development of a New England salt marsh. Ecological Monographs 42:201–237.

Rice, E.L. 1974. Allelopathy. Academic Press, New York, NY, USA.

SAS Institute Incorporated. 1989. SAT/STAT User's Guide, Version 6, 4th Edition. Vol. 1. Cary, NC, USA.

Smart, R.M. and J.W. Barko. 1978. Influence of sediment salinity and nutrients on the physiological ecology of selected salt marsh plants. Estuarine and Coastal Marine Science 7:487–495.

Snow, A.A. and S.W. Vince. 1984. Plant zonation in an Alaskan salt marsh. Journal of Ecology 72:669–684.

Stalter, R. and W.T. Batson. 1969. Transplantation of salt marsh vegetation, Georgetown, South Carolina. Ecology 50:1087–1089.

Stout, J.P. 1984. The ecology of irregularly flooded salt marshes of the northeastern Gulf of Mexico: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-85/7.1.

van der Valk, A.G. 1981. Succession in wetlands: a Gleasonian approach. Ecology 62:688–696.

Waisel, Y. 1972. Biology of Halophytes. Academic Press, New York, NY, USA.

Warren, R.S. and W.A. Niering. 1993. Vegetation change on a northeast tidal marsh: interaction of sea-level rise and marsh accretion. Ecology 74:96–103.

Wiegert, R.G. and B.F. Freeman. 1990. Tidal salt marshes of the Southeast Atlantic Coast: a community profile. U.S. Fish and Wildlife Service, Office of Biological Services, Washington, DC, USA. FWS/OBS-85/7.29.

Zedler, J.B. 1977. Salt marsh community structure in the Tijuana Estuary, California. Estuarine and Coastal Marine Science 5:39–53.

Manuscript received 4 January 1996; revisions received 27 December 1996 and 10 March 1997; accepted 11 March 1997.