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AUTECOLOGY OF THE BLACK NEEDLERUSH *JUNCUS ROEMERIANUS*

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ABSTRACT *Juncus roemerianus* generally occupies the upper half of the intertidal plane and covers about 92% or 25,000 hectares of marsh in Mississippi. The vegetative canopy is best described as a series of disjunct and intergrading populations. Considerable phenotypic variation and differences in standing crop exist between populations. *J. roemerianus* has very wide environmental tolerances in comparison to all other tidal marsh angiosperms. Soil types inhabited by the rush range from very sandy to highly organic muds and peats, which may vary in the concentration of nutrient elements (nitrogen, phosphorus and potassium). Neither soil type, nutrient concentration, water content, pH nor elevation can be used to distinguish the habitat of *J. roemerianus*, because similar conditions are found in areas occupied by pure or almost pure monotypic stands of other plant species. Soil water salinity is cyclic in all populations of *J. roemerianus* examined and salinity appears to be the major edaphic factor affecting growth and distribution of the rush. The greatest concentration and fluctuation of salt content occurs in the near-surface soil layer and the lowest concentration of salt and most stable soil water regime occurs at increasingly lower depths. Experimental evidence indicates that the rush grows best in fresh water, without competition, and cannot tolerate continuous salinities greater than 30 ppt. Soil organisms which detrimentally affect the rhizomes are major factors limiting distribution of the rush into freshwater areas. Salt concentrations in the soil solution of 35–360 ppt occurs frequently in some near-surface marsh soil layers. *J. roemerianus* growing on "salt flats" apparently survives near-surface hypersaline soil water (90–360 ppt) because of deeply penetrating, specialized roots. About five billion seeds of *J. roemerianus* are produced annually in Mississippi tidal marshes, but few rush seedlings are found. Germination requires light, and seedling establishment is the vulnerable stage in the life cycle of the species. Vigorous mature stands are maintained by rhizome growth and the frequent removal of dead-standing leaves by physical factors such as storms, heavy rains, tides, and currents.

INTRODUCTION

Juncus roemerianus Scheele dominates about 25,000 hectares or 92% of tidal marsh in Mississippi (Eleuterius 1972) and about 320,000 hectares or 25% of tidal marsh throughout North America (Eleuterius 1976a). Daubenmire (1947) stated that autecological studies were important because the factors affecting the most important plants of a community, including various stages in their life cycle, must be understood before the ecology of the community can be understood. Autecological studies upon angiosperms inhabiting aquatic habitats are seriously lacking, but essential in understanding the peculiar adaptation of various species (Davis and Heywood 1963, Alexander 1971). Baker (1959) stated that discovering crucial environmental factors that affect the plant may provide valuable information concerning the evolution of the taxa. Furthermore, basic autecological information provides a foundation from which taxonomic studies, genetic studies, population biology, studies on the breeding system, and other more specific studies on ecological relationships can be initiated. An adequate understanding of adaptation and the factors regulating important species over large tracts of salt marsh would also provide the most valuable information to expediently assess and manage these complex and valuable ecosystems in view of continuous loss, pollution, and the increased pressure of human population growth on coastal areas.

The objectives of the present study are (1) to examine the general characteristics of the intertidal habitats occu-

ried by *Juncus roemerianus* and (2) to evaluate how they are related to the rush and to areas inhabited by other marsh plants. From this general examination, (3) identify and (4) provide experimental data on those exceptional factors affecting the growth and distribution of *J. roemerianus*.

This approach rapidly eliminates those minor factors, either limiting or favorable, which can not be strongly related to the distribution of the rush or account for variations in growth between populations.

MATERIALS AND METHODS

Twenty-six populations of *Juncus roemerianus* were sampled in the tidal marshes along the coast of Mississippi (Figure 1). Standing crop was determined by counting and clipping shoots from four or more rectangular (0.5 × 2.0 m) frames and square (0.25m²) frames in seven populations. Clipped samples were subsequently separated into living and dead components and the number of leaves counted. Seventy-five of the longest living leaves in each population were selected randomly and measured for stand height (average maximum leaf length attained). Standing crop of erect shoots was obtained by drying to constant weight in a forced air oven at 50°C for 24 hours and then weighing.

Soil water salinity was determined from soil cores about 50 cm in length, obtained by using thin-walled stainless steel tubes with an inside diameter of 72 mm. Three cores were taken seasonally from each habitat. Slices of the core about 2 cm thick were taken from the top or surface layer and at positions equivalent to 30 and 45 cm depths. Soil water was extracted from these slices by vacuum filtration.

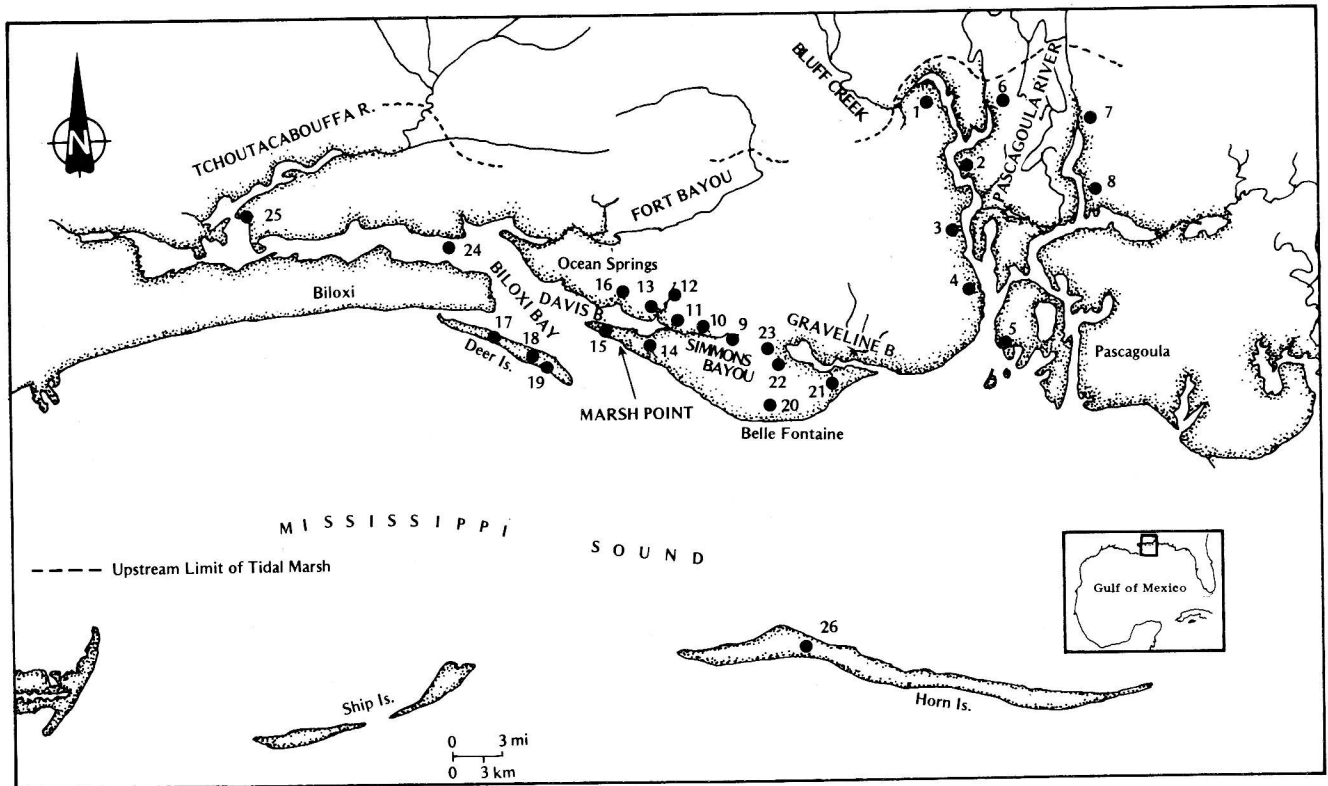


Figure 1. Map of the study area on the Mississippi coast. The location of populations of *Juncus roemerianus* studied are indicated by numbers.

All samples were subjected to uniform vacuum extraction (60 cm of mercury). Soil water salinity was determined with an American Optical refractometer, Model 10402 with a direct-read-out scale in ppt, and compared to determinations made with a Martex salinometer and a conductivity bridge. Soil water was also extracted by the method described by Eleuterius (1980a) and compared to the vacuum filtration method. No significant differences were found between the three methods used to determine salinity. Hydrogen ion concentration (pH) was determined in the field with a Corning model 6 portable meter and compared to wet soil samples determined with an Orion meter in the laboratory. A total of 234 soil samples were taken. The same soil cores were used for determinations of salinity, organic matter content, nitrogen, phosphorus, and potassium from the 26 populations of *Juncus roemerianus*, using standard methods described by Black (1965). Similar soil samples were also gathered and analyzed from populations of *Spartina alterniflora*, *Distichlis spicata*, *Scirpus olneyi*, and *Cladium jamaicense*.

Elevations in the marsh were determined using a surveyor's transit and stadia rod in reference to a bench mark located in the sea wall on East Beach, Ocean Springs, Mississippi, described in detail in Eleuterius and Eleuterius (1979).

To determine if light was required for germination, seeds of *Juncus roemerianus* were collected, placed on solidified agar in petri dishes in light and dark boxes at room tem-

perature and placed under Gro-lux fluorescent lamps at 3875 lux (360 foot candles). Seeds from perfect and pistillate flowers were collected from a population in the Davis Bay area. Approximately 1200 seeds were tested.

To test the general viability of seed, about 8400 seeds representing hermaphroditic and female components of seven populations were sown on solidified agar in petri plates and placed under Gro-lux lamps. Seeds were also floated on saline solutions and placed under continuous light for 6 weeks to test the effect of salinity on germination. Counts of germinated seed were made weekly.

Artificial sea mix (Rila) was used to prepare saline solutions of different concentrations to test the effect of salinity on germination of seed from both plant types and to determine the effect of salinity on vegetative growth of mature plants. Plants were selected randomly in each of several different populations and grown in a mixture of 1/2 sand and 1/2 commercial organic potting soil. Then the porous clay pots containing the plants and soil mixture were placed in large plastic buckets containing salt solutions of different concentrations. Water levels were adjusted 3 cm below the soil surface in each pot. Four replications of each treatment were used. Controls were grown in untreated tap water. Water lost through evaporation and transpiration was replaced by adding distilled water to the surface of the soil mixture. A solution of 20-20-20 soluble fertilizer (Robert Peters Co., Inc.) was used as a complete nutrient source

TABLE 1

Estimates of living shoot density (LSD), living leaf density (LLD), average maximum length of living leaves (LLL), living standing crop (LSC) and dead standing crop (DSC) and total standing leaf crops (TSC) m^{-2} , for seven different populations of *Juncus Roemerianus*.

Comparison of these data shows that some populations are structurally similar while others are very different.

See the map in Figure 1 for location of stations.

Population Location (Descriptive)	Station Number	Number m^{-2} LSD	cm		g dry wt. m^{-2}		TSC
			LLD	LLL	LSC	DSC	(LSC + DSC)
Bluff Creek	1	492 ± 73	886 ± 240	210 ± 30	1664 ± 210	416 ± 72	2080 ± 282
Upper Pascagoula River	2	572 ± 82	1258 ± 211	200 ± 41	2638 ± 201	465 ± 62	3104 ± 263
Lower Pascagoula River	5	782 ± 25	1715 ± 57	150 ± 10	3844 ± 150	430 ± 43	4275 ± 193
Grand Bayou	17	931 ± 21	2793 ± 44	180 ± 12	4225 ± 187	470 ± 32	4696 ± 187
Near salt flats	18	1680 ± 45	4032 ± 97	80 ± 8	1531 ± 120	1058 ± 127	2590 ± 247
On salt flats	19	170 ± 12	340 ± 20	30 ± 6	52 ± 3	14 ± 1	66 ± 4
Belle Fontaine	20	768 ± 17	1955 ± 31	215 ± 15	4196 ± 90	1632 ± 30	5730 ± 121

throughout the experiment. About 50 ml of a 5% solution was applied to the soil solution every 3 weeks. Plants were observed weekly and leaf length measured for 3 months.

All statistical comparisons used in this study are based upon analysis of variance (ANOVA).

RESULTS

Variation in Growth and Form

There is considerable variation in the vegetative growth and form of *Juncus roemerianus*. Generally, specific characteristics of growth can be associated with specific populations. Therefore, distinct populations of *J. roemerianus* can often be delineated on form, but not always. For example, there is a gradual change in leaf length, leaf density, and corresponding leaf production over a 9-mile stretch in the Pascagoula River marsh. However, if one samples the plant populations at intervals from the river mouth to the inland limit of marsh, differences in growth are obvious. Leaf length also increases near upland borders in most marshes. Kruczynski et al. (1978) states that both living and dead leaves, measured along a transect from the open water to the upland, increase away from the water. They also found that leaf length decreased towards the uplands. This situation also occurs in Mississippi, but it is found less often than the reverse relationship previously described. On areas that gradually slope from pine-dominated uplands to tidal marsh, the condition described by Kruczynski is generally found. However, where the elevation of the marsh is relatively low near the upland and abruptly changes to upland, the leaves of *J. roemerianus* are longer than those found seaward. In disjunct populations, separated by upland land masses and open bodies of water, more striking differences can be seen. Comparative data for seven different populations are shown in Table 1. These locations are represented by the numbered stations as shown in Figure 1. The plants of *J. roemerianus* tend to have longer leaves and fewer stems and leaves m^{-2} with decreasing salinity both up-

stream and laterally in all local estuaries. The reverse is also true with an increase in stem and leaf number (per unit of marsh surface) occurring with decreased salinity. This trend appears to be the same in the riverine populations. In a previous study, Eleuterius and Caldwell (1981) showed that the patterns and rates of growth and longevity of *J. roemerianus* varied considerably between different populations.

Vertical Distribution, Tidal Range and Evaluation

Another feature of *Juncus roemerianus* is its ability to grow over a relatively wide elevational range. Although varying from place to place, the plant species seems to be restricted to the upper half of the intertidal plane. The general elevational range of *J. roemerianus*, in relation to ranges for other important marsh species, is shown in Figure 2. Considerable overlap in ranges between these four major salt marsh species was found to occur. The comparative elevations shown for *J. roemerianus* and almost pure stands of *Distichlis spicata*, *Spartina alterniflora*, and *Scirpus olneyi* indicates that unknown factors related to tidal inundation and exposure are responsible for the dominance of these species at their respective elevations. Furthermore, many other plant species can occupy the same elevations also occupied by *J. roemerianus*, attested by the greater intermixture of species in brackish and very low-salinity marshes.

Edaphic Factors in General

Juncus roemerianus occurs in a wide variety of intertidal soil types. The soils range from almost pure sand to fine silt and clay mixtures and highly organic soils, including partially decomposed peat. Soils may be homogeneous, watery, unconsolidated materials (characteristic of the riverine marshes) or the more consolidated soils composed of loosely or densely compacted sand, clay, and organic material characteristic of coastal bay and bayou marshes. Some soils may be layered or zoned especially in marshes located immediately adjacent to the coast and underlying island marshes. An intensely blue clay layer often underlies these

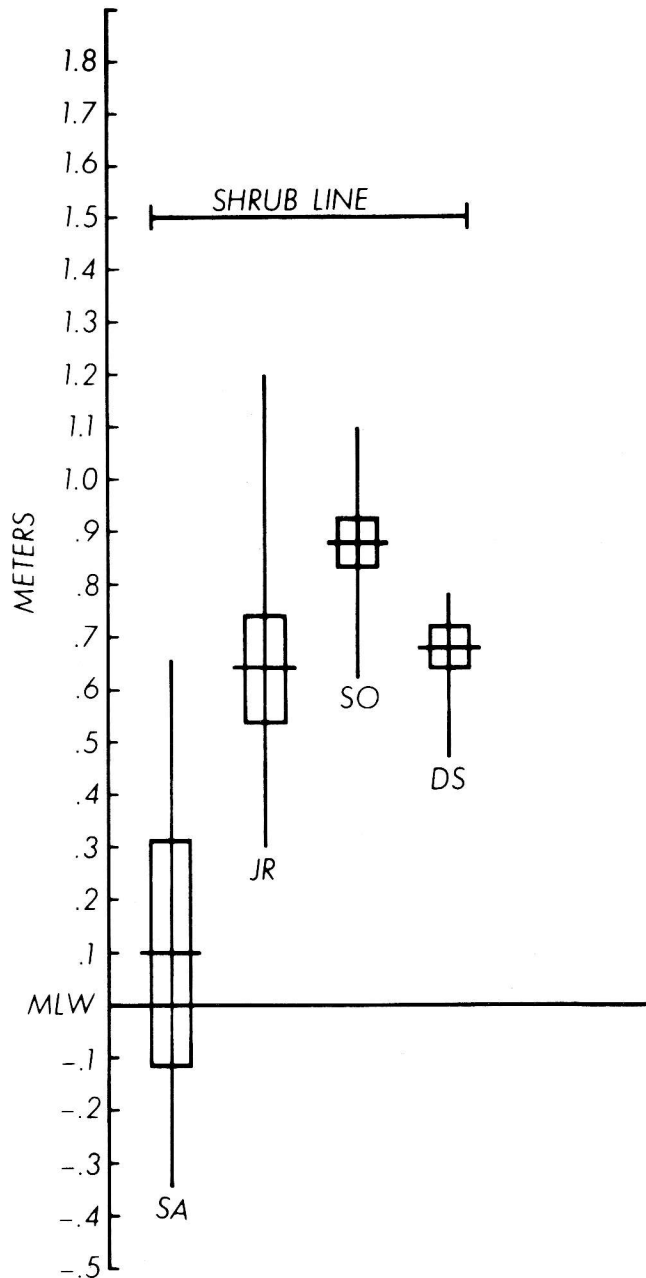


Figure 2. Elevational ranges and relationship of *Juncus roemerianus* (JR) to *Distichlis spicata* (DS), *Scirpus olneyi* (SO), *Spartina alterniflora* (SA) and mean low water (MLW).

sandy or organic surface soils. Sometimes sand is washed over organic soils in coastal and insular marshes forming layers in this fashion. *J. roemerianus* occupies a greater variety of soil types than any other marsh plant observed on the Mississippi Coast.

Soil nutrients varied considerably within and between the 26 widely separated habitats. Phosphorus (P) concentration ranged from 3 to 122 ppm, but averaged about 35 ppm in most habitats. Relatively large amounts of potassium (K) ranging from 3 to 245 ppm were found, averaging about 170 ppm for most habitats. Nitrogen (N) concentra-

tions in many habitats were not detectable; however, in those areas where determinations were obtained, the concentrations never exceeded 3 ppm. Soil pH ranged from 4.5 to 7 with most soils having a pH of 5.8. Differences in soil composition, structure, elevation, and soil water salinity prevented any meaningful correlation between concentrations of the major plant nutrients in the soil and plant growth. Soil pH could not be correlated to plant growth for the same reasons. Furthermore, comparison of the major nutrients (NPK) found in marshes occupied by *Juncus roemerianus* with those covered by *Spartina alterniflora*, *Distichlis spicata*, *Cladium jamaicense*, and *Scirpus olneyi* showed that the nutrient concentrations of the latter fell within the range for *J. roemerianus*. All of the plant habitats examined had wide variation within and between habitats. Variability in soil structure and elevation also prevented any meaningful correlation between concentrations of the major plant nutrients in the soil. Soil pH could not be correlated for the same reason. Other factors such as seasonality, soil structure, organic matter, and soil water content also influence spatial variation. Because of the wide variation between habitats, statistically significant differences in soil nutrients or pH could be found only between some populations of *J. roemerianus*. The wide variation found within each habitat indicates a gradient between them and renders any differences in nutrient concentrations meaningless. These findings indicate that *J. roemerianus* is capable of inhabiting a wide variety of soil types with variable concentrations of nutrients.

Soil Water Salinity

Soil water availability and soil water salinity are related to tidal inundation and exposure of the marsh surface. River outflow often interrupts the general tidal patterns over riverine marshes. However, in the Pascagoula River marshes soil water salinity is cyclic and variable with season, soil depth, and location in the estuary, as shown in Figure 3A and B. Small differences occur between surface and subsurface determinations and between seasons, reflecting the general low-salinity condition which prevails in these inland marshes as shown in Figure 3A. The most inland location consistently sampled (Station 2) is least influenced by the tides and shows a low concentration and correspondingly low fluctuation in soil water salinity, while the location near the mouth of the Pascagoula River shows relatively high and low concentrations of salt at various times in the annual cycle and correspondingly wide fluctuations (Station 5 as shown in Figure 3B). The soil water salinity pattern for a station in a coastal bayou marsh (Davis Bayou, Station 15), which is strongly influenced by tidal waters, is shown in Figure 3C. This pattern is similar to that found near the mouth of the Pascagoula River, but characterized by greater concentrations and fluctuations in salinity. Relatively large differences were found between surface and subsurface determinations and seasonal determinations

indicating (Figure 3C) that considerable fluctuation occurs in this marsh (Station 15).

The greatest soil water salinity occurs on sandy "salt flats." Salinities here (Station 19) were much greater than those found in other marsh locations, but the pattern of fluctuation between surface and subsurface determinations and the general seasonal changes were similar. The wet sandy "salt flats" are apparently an amplification of salinity cycles and processes which take place throughout local tidal marshes. The soil water salinity pattern for *Juncus roemerianus* marsh areas along the edge of these "salt flats" is shown in Figure 3D. Three important facts are evident: (1) Soil water salinity varies seasonally and is cyclic in all populations; (2) the soil water salinities of the lowest depths remain the most constant; and (3) the surface layer of soil has the greatest fluctuation. The most crucial period of survival for *J. roemerianus* occurs during the summer and fall months when soil water salinity is extremely high because of evaporation and plant transpiration, especially during periods of tidal exposure in daylight hours (Eleuterius, in preparation, a).

Eleuterius and Eleuterius (1979) found that the zone of *Spartina alterniflora* in Mississippi, over an annual period, is flooded 139 times more frequently than the adjacent zone of *Juncus roemerianus* and that the duration of flooding in *S. alterniflora* was 11 times as long as that of *J. roemerianus*. Frequent tidal flooding prevents concentration of salts in the soil water, because it dilutes the soil water solution. Long periods of exposure may result in high concentration of salt, often exceeding sea strength. In many instances soil water salinity in the marsh may exceed that of the adjacent open water (bayou, bay, river, or sound). Tidal flooding also contributes to soil water salinity in those marshes under the strongest tidal influence, and when flooded by highly saline water these marshes often develop hypersaline soil water concentrations when they become exposed for long periods during summer.

Salinity, Tolerance and the Effect on Plant Growth and Form

The gradient series composed of a freshwater control (0 ppt) and seven different concentrations of salt (10–70 ppt) indicate that adaptation has occurred in plants composing some populations in the tidal marshes of Mississippi.

The salt tolerance of plants from different populations and the effect of salt on the growth of the rush can be seen by comparison of the increase in leaf length of immature plants grown in soil solutions of different salt

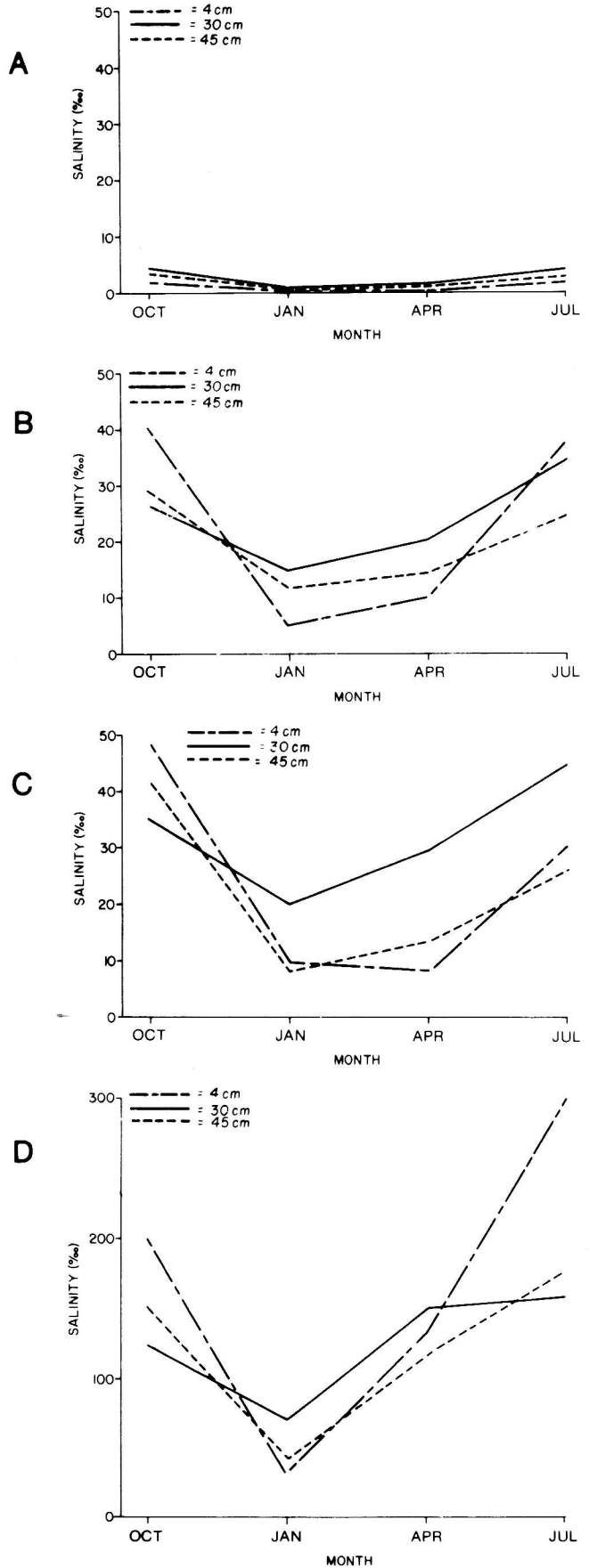


Figure 3. A. Soil water salinity as determined from soil cores from the Pascagoula River marsh near the inland limit of distribution of *Juncus roemerianus* (Station 2). B. Soil water salinity of a dense stand of *Juncus roemerianus* near the mouth of the Pascagoula River (Station 5). C. Soil water salinity of a dense stand of *Juncus roemerianus* on Marsh Point south of Davis Bay (Station 15). D. Soil water salinity of a population of *Juncus roemerianus* located on a "salt flat" on Deer Island (Station 19).

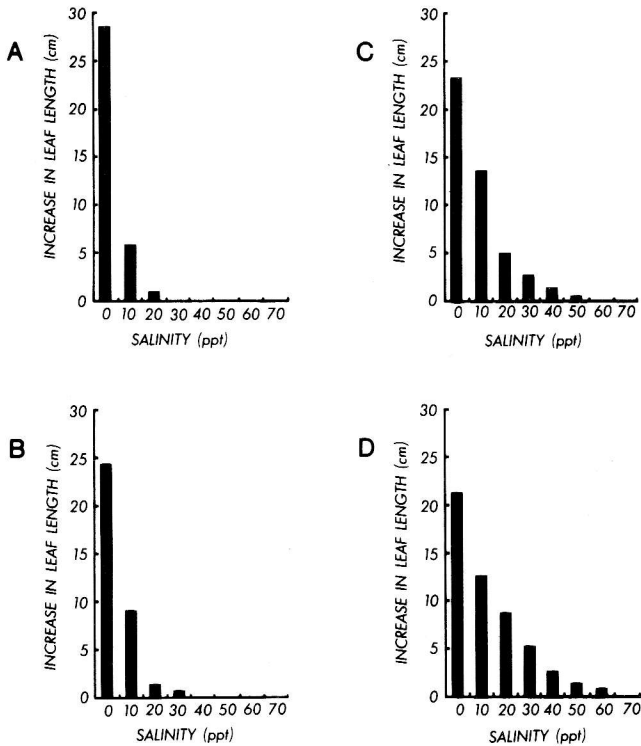


Figure 4. Growth of *Juncus roemerianus* under different salinity regimes.

concentrations for a period of 3 months. The total leaf length of the test seedlings was about 25 cm, based on measurements of all leaves present at the start of the experiment. Seedlings were selected with five leaves and leaves of similar length. An increase in the number of new leaves produced by each plant corresponds with a decrease in salinity. Transplants from the low-salinity area (Station 2) died in the highest salinities at the end of 2 weeks (Figure 4A), while others from Station 5 and Station 15 had a greater tolerance and survived a longer period of time in the higher concentrations of salt. Dwarfed transplants from the hypersaline salt flats (Station 19) exhibit the greatest tolerance (Figure 4D). The growth of all surviving transplants regardless of marsh location is decreased with increasing salinity. Survival of mature plants of *J. roemerianus* in the marsh probably occurs through two processes. One process concerns the "duration" or the length of the period of time that the plants are exposed to high salt concentration. In most populations of *J. roemerianus*, nearest the coast, relatively high concentrations of salt in soil water is not con-

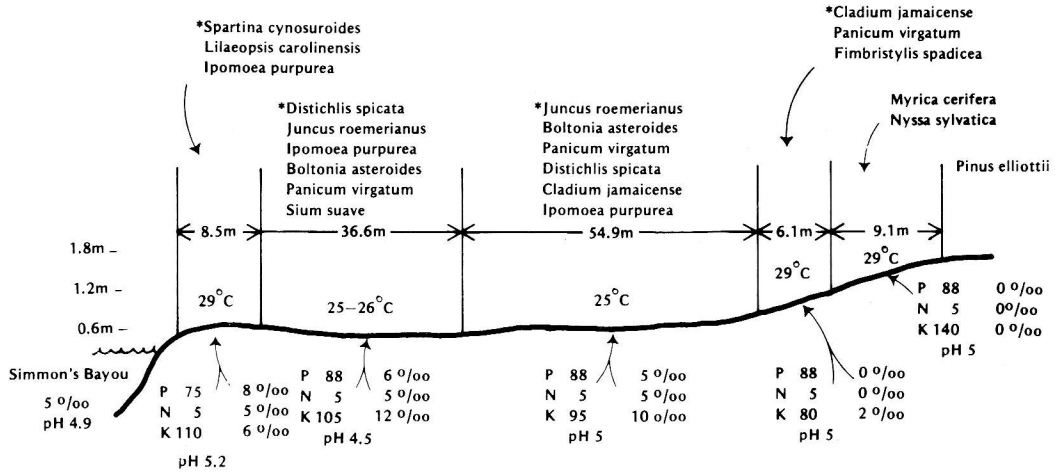
tinuous. Therefore, *J. roemerianus* is able to survive these relatively "brief" periods of intense salt concentration. The second process concerns a peculiar biological attribute of *J. roemerianus*. Two kinds of roots are generally produced by *J. roemerianus* (Eleuterius 1976b). In hypersaline marshes, specialized, deeply penetrating roots (6 to 8 feet) may allow the plants to draw less saline water which occurs at lower depths. The absence of fibrous, absorbing roots produced on plant shoots near the soil surface may indicate that high concentrations of salt in the upper soil layers inhibits their formation. However, *J. roemerianus* appears to have a much greater tolerance to salt than most plants inhabiting brackish or saline marshes.

Profile Diagrams

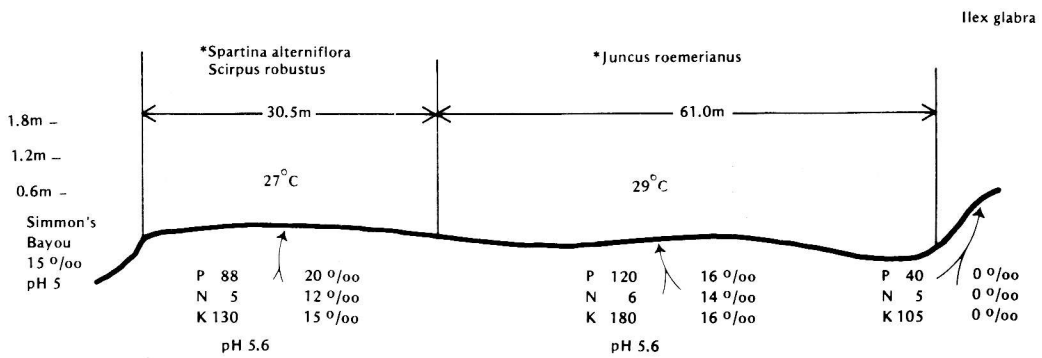
The profiles shown in Figure 5 diagrammatically show the elevation, edaphic characteristics, plants, and plant assemblages associated with *Juncus roemerianus* taken on three subsequent days during midsummer at three different estuarine locations. These illustrations simultaneously summarize several segments of new information. Relationships between habitats of *J. roemerianus* and adjacent ones occupied by other plant species, can be readily shown from these profile diagrams by comparing plant zones, and distance and ecological, especially edaphic, data. Plant community composition and plant zonation of pure stands in low- and high-salinity regimes in the Davis Bay estuarine system are shown in Figure 5A and 5B, respectively. Some differences are found in available soil nitrogen, phosphorus, and potassium between zones or habitats at each location or between locations. Statistically significant differences are found between some zones while no differences are found between others. Substantial differences in soil water salinity were found between some zones. The soil water salinity of "salt flats" is significantly different from that of all other vegetational zones. Soil pH is significantly higher in the more saline areas. The very sandy (0.1 to 2.5% OM), barren "salt flat" on Deer Island (Station 19) is flanked by habitats with higher ratios of organic matter to sand ranging from 0.4 to 6.0% (Figure 5C). These insular habitats are often underlain at a depth of 2 m by a stratum of blue clay. The diagrams and corresponding ecological data show that *J. roemerianus* grows in a variety of habitats and occurs closely associated with several vascular plant species known to be highly salt tolerant (see associated species listed in Figure 5C). Based on edaphic data, the sites occupied by other species on Deer Island also appear to be suitable for the growth of

Figure 5. A. Profile diagram of an inland, relatively low-salinity marsh along Simmons Bayou (Station 9) showing the vegetation composition and related edaphic conditions. Elevations are shown approximately and not to scale. Soluble nutrients (NPK) are expressed in ppm, and soil water (interstitial) salinities are shown as isohalines in ppt. B. Profile diagram of a relatively high salinity marsh, seaward of the location shown in Figure 5A, near the mouth of Simmons Bayou (Station 11). The vegetation composition and related edaphic conditions are shown. C. Profile diagram of salt marshes and related areas on the eastern portion of Deer Island (Station 19). Plant species composing the plant populations and communities are shown with corresponding edaphic data. The "barren salt flat" is devoid of vegetation. Dwarf plants occur in zones immediately adjacent to the hypersaline barren zone. Soluble plant nutrients (NPK) are expressed in ppm, while soil salinities at different depths (isohalines) are shown as ppt.

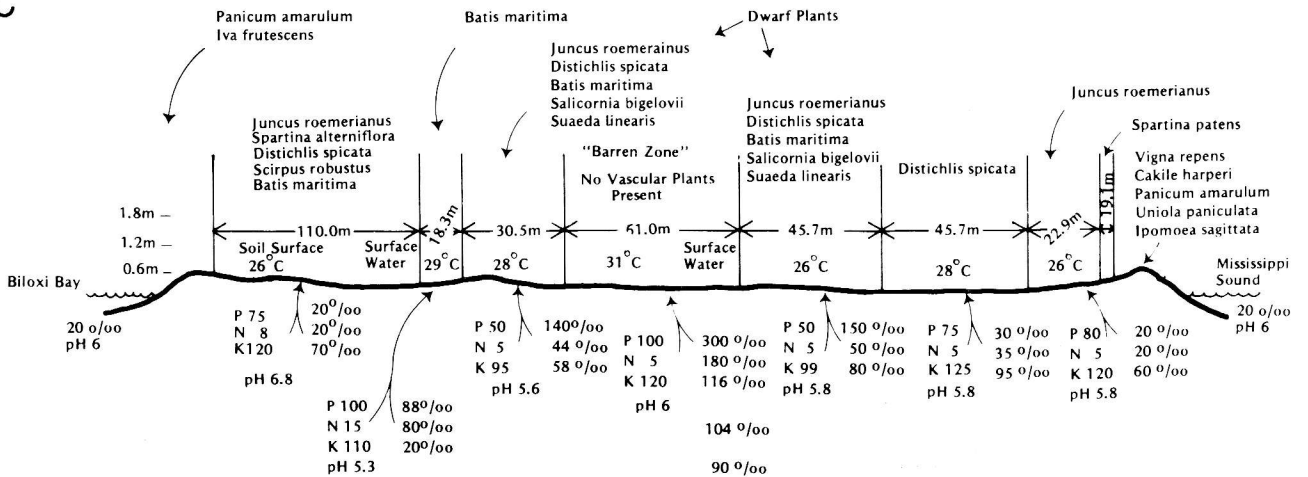
A



B



C



J. roemerianus indicating that considerable overlap in habitat characteristics occurs between these species.

Attention should be drawn to the fact that mature plants of *Juncus roemerianus* exist as "dwarfs" along the edge of hypersaline "salt flats" (Figure 5C). *Distichlis spicata* also grows in a dwarf form here. The "dwarf" plants of *J. roemerianus*, which flower each spring, are also associated with the succulents *Salicornia bigelovii*, *Suaeda linearis*, and *Batis maritima*.

Phenotypic variation of *Juncus roemerianus* may be caused by one or more edaphic factors, elevation in relation to tidal inundation, other environmental factors, or genetic differentiation. Soil water salinity is most certainly one of the major environmental factors affecting the growth and form of *J. roemerianus*. However, phenotypic variation in *J. roemerianus* may be the result of genetic differentiation (ecotypic adaptation) because entire populations often share the same characteristics, such as leaf length, shoot density, inflorescence size, etc., but no statistically significant correlation between these plant features and edaphic factors could be found.

Other Factors Affecting Growth

Another factor affecting plant growth is the accumulation of large amounts of dead-standing plant material, that is, leaves which have died but remain upright (see DSC in Table 1). Generally in most marsh areas, this dead material is periodically swept away by tidal waters, wave action, river discharge, fire, and the high winds of hurricanes and storms. However, in many protected marshes, especially near the adjacent uplands and in the upper region of bayous, which are not under strong tidal influence, large amounts of dead-standing leaf material accumulates over several years and progressively suppresses plant growth by reducing the amount of light reaching the living leaves. Thus, this accumulation of dead leaf material detrimentally affects the growth of *Juncus roemerianus*. Grazing by nutria (*Myocastor coypus*) and sometimes muskrats (*Ondatra zibethicus*) often detrimentally affect the growth of *J. roemerianus*, because they excavate and consume the rhizomes. The upper portion of the leaves of *J. roemerianus* in brackish and saline marshes are often stripped by meadow grasshoppers: *Orchelimum fidicinium*, *O. concinnum*, *Conocephalus hygrophilus*, *C. fasciatus*, *Paroxya claviliger*, *Orphulella olivacea*, *O. pelidna*, *Clinocephalus elegans*, *Meromiria intertesta* and *Dichromorpha viridis*. The grasshoppers occur in great numbers, or swarms, composed of several species. In some years, a definite pattern of succession of grasshopper species seems to occur. However, observations over a 16-year period clearly indicates that grasshopper swarms in tidal marshes of Mississippi are generally composed of mixed species which persist throughout the warmer months of the year. These grasshoppers do not feed extensively on nor do they permanently damage *J. roemerianus*. Extensive damage to *J. roemerianus* is prevented by the presence of many

thick, tough fibrous strands that run lengthwise in the leaves (Eleuterius 1976b). The large grasshopper *Romalea microptera* also occurs abundantly in marshes of *J. roemerianus*, but this insect feeds on the succulent leaves of *Sagittaria lancifolia*, *Pontederia cordata*, *Crinum americanum*, *Hymenocallis occidentalis*, and *Iris virginica*.

One of the most important factors limiting the distribution of *Juncus roemerianus* into freshwater habitats is the difference in numbers and kinds of soil organisms found in freshwater habitats compared to those found in brackish and saline areas. Plants of *J. roemerianus* dug out of low-salinity marshes near the limit of inland distribution always have poorly developed rhizomes. The protective rhizome scales (Eleuterius 1976b) are generally decomposed or eaten away. The rhizomes also appear blackened with ragged scale fragments. Numerous observations carried out over many years (10+) indicate that the rhizomes are also perforated with holes made by what appears to be several or more different kinds of small animals that bore into and through the rhizomes of *J. roemerianus*. Rhizome destruction by soil organisms appears to limit distribution of *J. roemerianus* inland by hindering its spread and restricting its growth to isolated clumps. Competition with *Cladium jamaicense* and other herbaceous plants and swamp trees such as cypress (*Taxodium distichum*) and black gum (*Nyssa sylvatica*) is an obvious major limiting factor in the upper regions of the bayous and rivers. In each river system on the Mississippi coast *J. roemerianus* is replaced by *C. jamaicense* or it grades into tree-covered swamps.

Seed Production and Germination

About five billion seeds are produced annually by *Juncus roemerianus* in Mississippi. Plants bearing pistillate flowers generally produce more seed than plants with perfect flowers. Light is required for germination. Seeds buried under mud or organic soil will not germinate. Seeds germinate totally submerged under clear water in the presence of light with an intensity of 2153 lux (200 foot candles) or greater. Germination is decreased with increasing salinity and inhibited by salinities above 15 ppt (Table 2). However, many of the salt-inhibited seeds, which were subsequently rinsed thoroughly in fresh water, germinated under freshwater conditions. Also, seedling growth decreased with increased salinity. Seeds from plants bearing pistillate flowers were more viable than those bearing perfect flowers. Germination of seed from pistillate flowers ranged from 24 to 100% and those from perfect flowers ranged from 0 to 96%. However, there was a significant difference between the two seed groups. Ninety-five percent (95%) of all seed samples from plants with pistillate flowers germinated within a range of 65 to 85%, with an average of 75%. Ninety-five percent (95%) of all seed samples from perfect flowers germinated within the range of 42 to 77%, with an average of 60%. Perfect flowers may be self-pollinated and the lower seed viability may represent an inbred weakness.

TABLE 2

Inhibition and germination of seeds in various concentrations of sea salt solutions at room temperature and under 360 foot candles of light. Approximately 100 seeds were placed on each plate.

Salt Concentration ppt	Percent Germination		Number of days for germination to occur
	♀	♂	
Distilled water	73	52	7
1	67	47	7
2	58	36	7
5	34	20	14
7	17	11	21
10	6	2	30
15	0	0	
20	0	0	
25	0	0	
30	0	0	

Many seed samples from perfect flowers were not viable. The seeds from plants with pistillate flowers are round in cross section, full, robust, dark brown or reddish brown. However, the seeds from plants with perfect flowers are often flattened, thin, transparent, light brown, tan or yellowish in color. A few seeds in each capsule may be robust, but generally they are slightly smaller in size (Eleuterius 1975).

Seedling Establishment

A conspicuous aspect of all populations of *Juncus roemerianus* is the absence of seedlings. Perhaps the dense vegetative canopy reduces light below the required intensity for germination. Furthermore, none have been found on muddy or organic substrates, vegetated or barren, probably because the seeds are easily buried. Seedlings have been found on sand substratum. A sandy substratum probably favors germination, because sufficient light penetrates through the thin layer of sand covering the seeds and the seeds are not easily covered by sand. On sandy shores and sandy areas resulting from dredging operations, seedlings often become established, but few plants reach maturity. About 20 seedlings were observed on a sandy shore, near the high tide lines (4 feet above MLW), several years ago. About 75% were subsequently lost because of erosion from heavy rains, storm waves, and currents. Most of the seedlings were washed away, others were buried. Later, drought or salt concentrations in the soil probably caused the death of the remaining seedlings. In other instances, I have seen a few seedlings become established and develop into mature stands, but always associated with great mortality of seedlings. The seedlings of *J. roemerianus* are obviously much more sensitive to environmental stress than mature plants.

The vulnerable stages in the life cycle of *Juncus roemerianus* are, therefore, germination and seedling establishment. Once seedlings reach maturity, the rush becomes an aggressive colonizer. Mature plants of *J. roemerianus* maintain a

dense stand by vigorous rhizome growth. The rate of rhizome growth is not rapid in comparison to many other tidal marsh plants, but on new terrain and in the best developed stands, the production of new rhizomes is prolific. Mature plants are steadfast, strong competitors, persistent in growth, and are therefore aggressive colonizers.

DISCUSSION

The availability of the major soluble nutrients, nitrogen (N), phosphorus (P), and potassium (K) cannot be used to delineate the habitat of *Juncus roemerianus* from that of *Spartina alterniflora*, *Distichlis spicata*, *Scirpus olneyi*, and *Cladium jamaicense*. Furthermore, NPK concentrations could not be used to separate morphologically distinct populations of *J. roemerianus*. The spatial variation of NPK within and between *J. roemerianus* populations and habitats of other plants indicates that nutrient availability is influenced by soil water salinity, season, elevation, soil structure, organic matter content (Boyd 1970), and the frequency and duration of the tides. Relatively large amounts of K and P are readily available in all tidal marsh soils sampled and certainly do not seem to be a limiting factor. Available N was not detected in most soil samples. However, N transformation in wetland soils and the effect on the vegetation has been the subject of intensive research (Waring and Bremner 1964, Tyler 1967, Maye 1972, Ponnaperuma 1972, Engler and Patrick 1974, Delaune, et al. 1976). How *J. roemerianus* and many other tidal marsh plants obtain a sufficient supply of N remains, at present, unknown. Researchers have recently shown that some aquatic plants are capable of nitrogen fixation (Patriquin and Knowles 1972). However, it should be pointed out that the distribution of other soil nutrients, such as sulfur, iron, cobalt, zinc, and magnesium, may differ significantly between populations of *J. roemerianus* and those of other marsh plants. I conclude this section on soil nutrition by pointing out that in the inland, low-salinity regions of tidal marshes in Mississippi, more than 50 species of plants occupy the same wetland terrain as *J. roemerianus* (Eleuterius 1972, Eleuterius and McDaniel 1978, and Eleuterius 1980b). These species occur intermixed with *J. roemerianus* at the same elevation, soil structure and nutrient concentration. Because of their abundance, the major soil elements utilized as nutrients by *J. roemerianus*, do not seem to be a limiting factor for the growth and distribution of the rush. The amount of water composing a soil sample is a nebulous measurement because of the ebb and flood of the tide and fluctuation caused by evaporation. However, the amount of water composing the solution is important in relation to the concentration of soil nutrients. Thus, the concentration of plant nutrients in the soil solution is obviously in a constant state of fluctuation. This may account for the difficulty in relating plant growth to nutrient concentrations in soil solutions in tidal marshes. Ho (1971) found that seasonal changes occurred in the water and sediment of an estuary in Louisiana. The

soil data obtained in the present study compare favorably with those of marshes found in Louisiana, Florida, and Georgia (Chabreck 1972, Maye 1972, Stewart, et al. 1973, Burpbacher, et al. 1973, Volk, et al. 1975, and Steward and Ornes 1975). It is concluded that *J. roemerianus* is capable of inhabiting a variety of soil types with different nutrient concentrations.

Elevation is an important factor in the seaward distribution of *Juncus roemerianus*. *Spartina alterniflora* can tolerate considerably more tidal flooding in comparison to *J. roemerianus* which is clearly shown in the present study and by previous research (Kurz and Wagner 1957, Adams 1963, Eleuterius and Eleuterius 1979). *J. roemerianus* has a wide vertical range above mean low water, which means that it grows at the same elevation as many other tidal marsh plants. In the lower regions of riverine marshes where tidal influence is greatest, *J. roemerianus* grows at the same elevation as almost pure stands of *Distichlis spicata* and *Scirpus olneyi*, and in some places at the same elevations as almost monotypic stands of *Spartina alterniflora*, *Spartina patens*, *Spartina cynosuroides*, and *Cladium jamaicense*. In the inland, low-salinity riverine regions, *J. roemerianus* occurs, as stated above, at the same elevation as 50+ species of tidal marsh plants. Therefore, elevation, per se, can not delineate individual populations or the overall habitat of *J. roemerianus* from that of many other plants. Eleuterius and Eleuterius (1979) showed that other factors are obviously involved in delineating a habitat of *J. roemerianus* from *Spartina alterniflora*, but the factors were not defined. *J. roemerianus* was shown to occupy the upper 40% of the intertidal plane in an estuarine marsh strongly influenced by the tide at a single location in Mississippi.

Competition with other flowering plants is an important factor in the distribution of *Juncus roemerianus*. The leaves become longer, but shoot density decreases as the number of competitor plants increases upstream and inland in riverine marshes and in the upper ends of bayous strongly influenced by the tides. Penfound and Hathaway (1938), O'Neal (1949), and Gillham (1957) reported similar distributional patterns. The overall effect of competition is a reduction in growth and production of the rush. Plants representing the limit of inland distribution are also in competition with an array of microflora not found in the more saline downstream marshes.

Plant zones in hypersaline areas appear almost stabilized, based on observations over a number of years. Invasion of a zone by plants from an adjacent zone does not readily occur. The plant zones appear to represent plant populations in a state of balanced existence unique to tidal marshes.

Soil water salinity is the most important factor affecting the growth and distribution of *Juncus roemerianus*. Salinity was also determined to be the major factor affecting plant zonation in tidal marshes by Reed (1947), Jackson (1952), Kurz and Wagner (1957), and Adams (1963). Soil water salinity operates in two ways to favor the growth of *J. roe-*

merianus. One way is the removal of competing flowering plants, which are less salt tolerant than *J. roemerianus*. Death of less salt tolerant competitors favors the growth and spread of *J. roemerianus* by providing more space and reducing competition for nutrients and light. Soil water salinity reaches annual peaks in August and October. Observations made over a number of years indicate that the August peak may be modified by heavy summer rains, but the October peak has consistently occurred locally without interruption for the past decade. Therefore, the greatest upstream penetration and effect of salt water in bayous and rivers occurs during October and early November of each year. This relatively brief period (3 to 6 weeks) of salt water intrusion also benefits *J. roemerianus* by the modifying effect on the soil microorganisms. The introduction of salt into the soils of these otherwise freshwater-dominated tidal marshes obviously kills or reduces the number of harmful microorganisms (Eleuterius, in preparation, b). Thus, tidal influence also delineates salt marshes on an areal basis by the direct introduction of sea salt into the soil solution. In Mississippi, the tidal amplitude is relatively small with an 1.8 foot range between high and low tides. However, the annual cycle of highs and lows may extend over a vertical range of 5 feet or more (Eleuterius and Eleuterius 1979). Therefore, seasonal patterns of tides are important and represent a complex relationship to plant distribution (Chapman 1976). *J. roemerianus* extends 10–15 miles inland along the river estuaries. A similar pattern is also found in coastal bayous, where the number of associated species increases with decreased salinity. In Mississippi, the rush dominates 92% or about 25,000 hectares of tidal marsh (Eleuterius 1972). This extensive coverage also suggests that the rush has relatively wide environmental tolerances.

Soil water salinity has pronounced effects on the growth, form, and the physiological adaptation of *Juncus roemerianus* and also inhibits germination. Phlegher (1971) also found that salt concentration in sand cultures reduced the growth of *Spartina foliosa* Trin. In the present study, where the entire root mass was included in the test container and the salinity of the soil water remained constant, the test plants from different populations were shown to have different tolerances to salt, but each test group had definite limits to their ability to withstand high concentrations of salt. These data indicate that different populations of *J. roemerianus* have different tolerances to salt. Furthermore they strongly suggest that physiological adaptation has occurred in the different populations studied. In nature, however, soil water salinity fluctuates and the soil water salinity decreases with increasing depth. The hypersaline soil water regime found on the salt flats appears to be an amplification or an exaggeration of the same process that takes place in other habitats of *J. roemerianus*.

Comparison of the effects of salinity on germination with tolerances of mature plants indicates that tolerance to

salt obviously increases with maturity. Absence of seedlings in vegetated tidal marshes may also result from the failure of seed to germinate, because the seeds are quickly buried in muddy substratum, or they become coated with fine mud particles, where without the presence of light they can not germinate, or they are simply swept out to sea. Richards and Clapham (1941), Lazenby (1955), Tadmor, et al. (1958), and Welch (1966, 1967) found that other species of *Juncus* required light for germination. Furthermore, the low ambient temperature of winter and more frequent rainfalls indirectly result in lower soil water salinity and reduce stresses on *J. roemerianus*. Low temperatures reduce evaporation and transpiration. The low temperatures and low-salinity regimes of winter favor germination and seedling growth.

Chapman (1942) presented data on the germination of *Juncus maritimus* after 23 days in tap water and various concentrations of salt. Germination in tap water was 50%, 10 ppt—18%, 20 ppt—5%, and 33 ppt—0%. He also showed that germination of an unidentified species of *Salicornia* was reduced with increased salinity, but 12% germination occurred in 100 ppt NaCl. Ungar (1962) indicated that the limiting factor for seed germination of *Salicornia* under high salinities was chiefly osmotic. This appears to be true also for *J. roemerianus*. Ayers (1951) also reported a steady drop in *Salicornia* germination with increased salinity. Ungar (1962) reported an abrupt decrease in *Salicornia* germination when a 50 ppt salt concentration was reached. The retardation and prevention of germination of *J. roemerianus* by high salinity in the present study is obviously caused by osmotic factors.

Salinity is known to affect many aspects of the metabolism of plants and to induce changes in their anatomy and morphology (Uphof 1941, Bernstein and Hayward 1958, Nestler 1977). These changes are often considered to be adaptations which increase the chances of the plant to endure stress imposed by salinity (Waisel 1972, Poljakoff-Mayber and Gale 1975). Numerous investigations into the constitution of various species of plants from different ecological groups showed that only a few phenotypical adaptations, such as ecads, actually exist. Most of the populations investigated went through the action of natural selection to form genetically fixed ecotypes (Turesson 1922, 1931, Stebbins 1950, Waisel 1959). Salt-resistant forms have evolved in *Typha angustifolia* L. and *T. latifolia* L. in soil containing high concentrations of salt (McMillan 1959, McNaughton 1966). Similar results were obtained for *Phragmites communis* Trin. (Waisel 1972). In order for evolutionary change to occur, there must be a source of genetic variation and a driving force (Grant 1971, Jones and Luchsinger 1977).

Soil water salinity appears to exert a selective pressure on *Juncus roemerianus*, which has resulted in physiological and perhaps genetic differentiation. Physiological and genetic variation may account, in part, for the phenotypic variation between different populations of *J. roemerianus*. Paradoxically, the absence of seedlings in the marsh does not provide the number of progeny of different genotypes upon which a selective force, such as soil water salinity, can work. This conflict in operative mechanisms may be deceptive since the selective process is a slow one which may have occurred ages ago. Corroborative support for this possibility is the present maintenance of the mature stands of *J. roemerianus* by vigorous vegetative growth for long periods of time. These results and interpretations have evolutionary implications and raise important questions regarding the future survival of *J. roemerianus*.

Other factors affecting the growth of *Juncus roemerianus*, described in this study, are of minor importance. However, I should point out in closing this discussion that there looms on the horizon a greater threat to survival of *J. roemerianus* and all other components of tidal marshes, both plant and animal. Although both federal and state agencies are charged with the responsibility to safeguard our estuaries and tidal marshes, domestic and other forms of pollution continue unabated, and estuarine water quality continues to decline. A continuation of this trend may have a severe effect on the future of *J. roemerianus* and other estuarine organisms well adapted to relatively pristine environments.

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