Taximetric Analysis of Female and Hermaphroditic Plants Among Populations of Juncus Roemerianus Under Different Salinity Regimes

Lionel N. Eleuterius

Botany Section
Gulf Coast Research Laboratory
Ocean Springs, MS 39564-7000, USA

ABSTRACT


The gynodioecious salt marsh rush, Juncus roemerianus Scheele, entails considerable phenotypic variation. Phenograms constructed from cluster analysis of 32 morphological characteristics measured in seven widely separated populations of the J. roemerianus were used to show that these populations are distinct entities adapted to different soil water salinities. Populations in marsh habitats with prevailing low salinity soil water are composed of plants with the longest leaves, largest inflorescences and they have more flowers and seeds. A population of dwarfed J. roemerianus growing in hypersaline soil water is very distinct from all other populations. Reproductive isolation of the seven rush populations is caused by geographical features (distance and water barriers) and restricted pollen dispersal. Elements within a cluster had a high degree of natural association and are considered distinct from other clusters. This taximetric study shows that plants bearing pistillate flowers could not be separated from those bearing perfect flowers or identified to sex based only on vegetative characteristics. Salinity is a strong natural selective force on populations of J. roemerianus. Ecological information is also shown to be important in understanding adaptation and taxonomic relationships among salt tolerant plants.

ADDITIONAL INDEX WORDS: Juncus roemerianus, salt marshes, gynodioecious, marsh rush, intertidal plant populations, tidal marshes, phenotypic variation.

INTRODUCTION

Observations and related field studies carried out for a number of years have indicated that considerable phenotypic variation exists in natural populations of the tidal marsh rush, Juncus roemerianus Scheele and in different places throughout the range of the species (Eleuterius, 1972, 1976). Vegetative morphology, inflorescence size, and seed production obviously differ among populations. For example, in Mississippi Juncus roemerianus plants grow very tall with leaves over 2 meters in height in certain very low salinity marshes whereas, they remain short with leaves less than 30 centimeters, in hypersaline marshes (Eleuterius, 1984). Furthermore, in a previous publication (Eleuterius, 1978) I pointed out that some of the reference manuals used to identify and describe J. roemerianus, differ in their taxonomic descriptions (Chapman, 1860; Small, 1933; Fernald, 1950; Gleason, 1952; Radford, et al., 1968; Correll and Johnston, 1972; Long and Lakela, 1972; Correll and Correll, 1975).

The objectives of the present study were to determine (i) whether or not the local populations of Juncus roemerianus could be distinctly separated on the basis of morphological characteristics, and (ii) if the morphological units were distinct, could they be grouped in such a manner that detected phenotypic plasticity or genetic adaptation to different salinity regimes.

The study area (Figure 1), was located on the Gulf of Mexico (30° 23' N latitude, 88° 43' W longitude). Populations 1, 2, and 3 were located in the riverine marshes of the Pascagoula River over a distance of 24 kilometers (15 miles) and
were not separated by terrestrial land masses. Here, the soil water salinity varied from 0 to 5 ppt. The other four populations were disjunct. Population 4 was located behind the sand dunes and land masses (forests) in a relatively low salinity marsh area at Belle Fontaine Point, while population 5 was situated on Marsh Point. The soil water salinity in population 4 varied from 6 to 12 ppt, and in population 5, from 15 to 25 ppt. The remaining two populations (6 & 7) were located 3.2 kilometers (2 miles) apart from each other at two hypersaline locations on Deer Island, which is off the mainland at a distance of 4.0 kilometers (2.5 miles). The soil water salinity at the Grand Bayou population (6) ranged from 20-35 ppt, and the soil water salinity was often recorded greater than 65 ppt at the Salt Flats population (7). Each of the seven populations were composed of two plant types based on the production of imperfect (I) or perfect flowers (P).

METHODS

Numerical (counts) and linear, volumetric, and dry weight measurements of leaf and floral structures were made on perfect and pistillate flowering plants from each population. Each determination was made 75 times in the field or laboratory on living materials. Counts and linear metric measurements need no explanation. Volume displacement was determined in cm³ by submerging the entire inflorescence in graduated cylinders filled with water. Plant specimens from each population were collected twice, once when they were in flower and a second time when they had matured and produced seed. The means of each vegetative, floral, or
seed measurement were calculated for both components of each population. Analysis of variance (ANOVA) was used to determine whether or not differences within and between populations were statistically significant (0.05 level). A least significant difference (LSD) test was then used to determine differences between means of each variable.

Taxonomic data were subjected to cluster analysis to show associations among populations on the basis of vegetative, floral, and seed characteristics. Elements within a cluster have a high degree of natural association and are considered distinct from other clusters. The Bray-Curtis coefficient of similarity was used for these analyses. This coefficient can be expressed as either a similarity or dissimilarity index. In testing four common similarity indices against each other and a theoretical distribution, BLOOM (1981) found that only the Bray-Curtis index accurately reflects similarity. The equation form used in this study is:

\[ S = \frac{\sum (X_y - X_q)}{\sum X_y + X_q} \]

RESULTS

Considerable phenotypic variation was found between the seven populations of *Juncus roemerianus* (Figure 2). Plants bearing pistillate or perfect flowers could not be separated based on vegetative characteristics alone. Both hermaphroditic and female plants had similar vegetative characteristics. There are, however, distinct differences in the form and size of the inflorescence, flowers and seeds of hermaphroditic plants in comparison to those of female plants (See G-P, Figure 2). The major results obtained from statistical analyses are summarized below.

The similarity of the seven populations is based on (1) vegetative characteristics only (Figure 3A), (2) vegetative and inflorescence characteristics (Figure 3B), (3) vegetative, inflorescence, and flower characteristics (Figure 3C), and (4) all 16 characteristics including vegetative, inflorescence, flower, and seed data (Figure 3D). The similarity between populations changes as additional characteristics are considered. When all taximetric data are used, population 7 located on the Deer Island Salt Flats, is shown to be distinctly and completely different from all other populations. These later populations are shown to be separated into two main groups, which grow under hypersaline conditions. The first group includes 6, 3 and 5, while the second includes 4, 1 and 2. Populations with similar soil water salinity regimes had similar morphological characteristic or phenotypic expressions. The two inland populations of *Juncus roemerianus* in the Pasca-goula River (1 and 2) and the population at Belle Fontaine Point (4) were in relatively low salinity marshes. Plants in these three populations are characterized by very long leaves and large inflorescences, many flowers and seeds. The populations at the mouth of the Pas-cagoula River (3), the Marsh Point population (5) and the Grand Bayou (6) population are similar in morphological characteristics.

DISCUSSION

Quantitative data show that the seven populations of *Juncus roemerianus* are extremely and distinctly different based on a number of morphological characters. Whether or not the phenotypic variation between these populations is caused by a predominance of environmental or genetic factors is not completely known. However, three selective mechanisms in the present study appear to be involved: reproductive isolation caused by water and land barriers, a peculiar breeding system which may favor genetic adaptation and differentiation, and exposure of some populations to extremely stressful environmental conditions caused by very salty soil water. Soil water salinity has been shown to affect time and rate of germination, the size of plants in *Juncus roemerianus* (ELEUTERIUS, 1984) as well as branching, leaf size and anatomy in other halophytes (POLJAKOFF-MAYBER and GALE, 1975). Interstitial salinity was also considered to be the cause of ecophenes in *Spartina alterniflora* by NESTLER (1977). The genotype may, according to prevalent environmental factors, give rise to different phenotypes (DAVIS and HEYWOOD, 1973). In some examples, the phenoplasticity may be so wide that it overlaps and even obscures the genotype variability. However, each genotype has a range in plasticity which is genetically determined. In some populations, the range of expression is narrow, the plants are termed stenoplastic; or broad, the
Figure 2. Taximetric diagrams of quantitative data of vegetative (A-F), inflorescence (G-K), flowers (L-M), and seed (N-P) characteristics of plants bearing perfect (P) and imperfect (I) flowers from seven populations of Juncus roemerianus. Values shown are means and the standard error of the mean.
Figure 3. Phenograms showing the relative similarity between seven populations of *Juncus roemerianus* based only on vegetative characteristics (A), based on vegetative and inflorescence characteristics (B), based on vegetative, inflorescence and flower characteristics (C), and based on vegetative, inflorescence, flower, and seed characteristics (D).
plants being called euryplastic. Therefore, the classical view holds that the genetic constitution produces the character of the phenotype, not just the environment. Recent experimental work indicates that *Juncus roemerianus* tends to be broad in phenotype or euryplastic (EULITERIUS, In Press).

Two of the populations (6, 7) are insular with the nearest *Juncus roemerianus* populations on the mainland about 4.8 kilometers (3 miles) away. The body of water surrounding the island serves as a barrier and mechanism for reproductive isolation. The distance between the Grand Bayou population (6) and Salt Flat population (7) is approximately 3.2 kilometers (2 miles) and the distance between these populations and that at Belle Fontaine Point (4) is about 9.6 kilometers (6 miles). This Belle Fontaine Point population (4) is land-locked and extremely isolated. One of the populations at Marsh Point (5) is on a peninsula. The three riverine populations are intergrading, but separated by numerous open water segments of the river. These three populations are separated by several kilometers, therefore distance and water may have caused plants of *Juncus roemerianus* within parts of this large 700 hectare marsh to become differentiated.

Most plant species are subdivided by their distribution and breeding patterns into small populations (GRANT, 1963). This provides an ideal situation in which natural selection may operate on the genetic variation without interference from gene flow from nearby populations. Thus, populations may differentiate ecologically and geographically and eventually form genetically different ecotypes. Such ecotypes, or races, may be the basis of a subspecies or variety (GRANT, 1971). Phenotypic adaptation should be theoretically sufficient for enabling plants to evade and survive the pressure of natural selection without genotypical changes (CLEMENTS *et al.*, 1950). However, numerous investigations into the constitution of various species of plants from different ecological groups have shown that few phenotypic adaptations, such as ecads, actually exist. Most of the populations investigated have apparently gone through the action of natural selection to form genetically fixed ecotypes (TURESSON, 1922a; STEBBINS, 1950; WAISEL, 1959; McMILLAN, 1959; McNAUGHTON, 1966). The first modern definition of ecotypes was based on populations of coastal halophytes by TURESSON, (1922b) and the present study suggests that more systematic work needs to be carried out on other tidal marsh plants.

*Juncus roemerianus* is wind pollinated, and because of the wet conditions of the marsh surface, damp vegetation and humid air above the marsh, pollen does not travel very far. Once shed, it apparently becomes heavy with moisture and lost from the air currents. Moreover, the culm is consistently much shorter than the leaves in every population examined. This places the inflorescences deep within the dense stands of upright rush leaves, a factor which further hinders pollen dispersal, and probably results in inbreeding of some populations.

The three riverine populations apparently represent populations within a cline in response to the salinity gradient of the Pasca-goula River. The Grand Bayou (6) and the Salt Flat populations (7) on Deer Island are responses to very saline (20-35 ppt) and hypersaline (65 ppt +) soil water salinities, respectively. The flowering period of the later population is relatively short (1 month) and occurs earlier in the year than the other populations. The land-locked Belle Fontaine Point population (4) has relatively low soil water salinity (6-12 ppt). And the Marsh Point population (5) has a soil water salinity of 15-25 ppt. Soil water salinity is obviously a stressful selective force acting on some of the populations. Those populations, not exposed to extremely high salinity water for prolonged periods, are composed of larger plants while those under the stressful influence of salt are smaller.

In conclusion, the cause of the phenotypic variation and differences found in the seven populations, based on circumstantial evidence of isolation, inbreeding and the presence of strong selective pressure caused by salinity of the soil medium, suggests that genetic differentiation has probably occurred in some of the rush populations studied. Furthermore the study indicates that *Juncus roemerianus* marshes, which are homogeneous vegetatively, may be composed of a mosaic of genetically distinct populations.

**ACKNOWLEDGEMENTS**

I greatly appreciate the assistance of John Caldwell in preparing the graphs and helping
me get this paper into the proper form. Helen Gill and Cindy Dickens typed early drafts of this manuscript and Kathy Butler, expertly typed the final draft. I thank all of them. Thanks are also due Dr. Terry McBee and Walt Brehm, for their computer expertise and for performing the statistical analyses.

LITERATURE CITED


TURESSON, G., 1922a. The genotypical responses of the plant to the habitat. Hereditas, 3, 211-250.

TURESSON, G., 1922b. The species and variety as ecological units. Hereditas, 3, 100-113.