AN ABSTRACT OF THE THESIS OF

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Redacted for privacy

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Morphological and anatomical characteristics of Deschampsia cespitosa, Distichlis spicata, Grindelia integrifolia, Jaumea carnosa and Salicornia virginica were studied from the marsh fringing Netarts Bay, Oregon. Significant morphological differences were found along transects between upper and lower distributional limits of each species, a distance of 40 m at the most. Plants were taller in the upper, drier, portion of the marsh except for D. spicata, where the reverse was true. In certain cases stem diameter, leaf width, internode length, branching, amount of flowering and stem density were among features found to be different along the transects of the various species. Lignification of vascular bundle sheaths was greatest in stems of D. spicata from its upper zone. Larger vascular bundles of J. carnosa, more sclerenchma in G. integrifolia and less aerenchyma in S. virginica were found to be characteristic of plants from the upper distributional areas of these species.

With vertical and lateral transplants of the five species it was concluded that these species respond plastically in their morphology and anatomy to the environment. In all cases the transplanted plants took on the morphological and anatomical characteristics of the surrounding plants. Since the various morphological forms are not genetically fixed they are not considered to be ecotypes.

D. cespitosa, D. spicata, G. integrifolia and S. virginica were studied under three soil moisture treatments (saturated (SAT), field capacity (FC) and near wilting point (DRY)) in a controlled greenhouse experiment. Aerenchyma formation in S. virginica and sclerenchyma formation in G. integrifolia were affected by soil moisture in the greenhouse similarly to the way they were along the field transects. Lignification of vascular bundle sheaths of D. spicata did not appear to be controlled by soil moisture. Morphological characteristics of S. virginica in the greenhouse in relation to soil moisture were similar to those found in the field. Variability of characteristics of the other species in the field did not correlate so well with greenhouse soil moisture studies indicating that other environmental factors are influential in effecting morphology.

Above and belowground biomass of each species was measured in the greenhouse. Maximum biomass occurred under FC conditions in both cases for the four species. In the SAT treatment greatest root biomass was found in the upper 10 cm of soil for each species. Root: shoot ratios of D. cespitosa and S. virginica were not affected by changes in soil moisture while that of D. spicata was lowest in the SAT treatment and that of G. integrifolia was lowest in the DRY treatment.

# Morphological and Anatomical Responses of Selected Coastal Salt Marsh Plants to Soil Moisture

by

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## I. INTRODUCTION

Intertidal marshes are among the world's most productive natural ecosystems (Odum, 1961) with net production ranging from 485 to 5163 g dry/wt/$m^2$/yr (Gallagher, 1978). The productivity of the estuaries is certainly, in part, related to the productivity of the adjacent wetlands. In order to protect a wetland from intrusions such as filling, diking, draining, and pollution, the limits of that wetland must first be defined. In the United States, regulations set forth by the U.S. Army Corps of Engineers (COE), define wetlands as "those areas that are inundated or saturated by surface or ground water at a frequency and duration sufficient to support, and that under normal circumstances do support, a prevalence of vegetation typically adapted for life in saturated soil conditions. Wetlands generally include swamps, marshes, bogs, and similar areas." (Federal Register, July 19, 1977).

In the field, this definition alone becomes inadequate. Setting the upper limits of many wetlands has proven to be a difficult task and also one fraught with political problems. A set of criteria by which wetlands may be delineated must be agreed upon by the enforcement agencies, the U.S. Army Corps of Engineers, and the Environmental Protection Agency (EPA), who have the responsibility under Section 404 of the Federal Water Pollution Control Act Amendments of 1972 (Public Law 92-500) of setting and protecting wetland limits.

Permits are issued by these agencies for the discharge of dredge or fill material onto wetlands contiguous with navigable waters or into the waters themselves.

Several approaches have been proposed and taken to delineate wetlands. Some states define intertidal wetlands with respect to a tidal datum, e.g., mean low water (Wass and Wright, 1969, Va. Code, sec. 62. 1-13,2). The National Ocean Survey (NOS) (1975), after an investigation of eight coastal marsh sites, suggested the upper limit of the marsh be defined at 0.76 m above mean high water (MHW). With further study this was found to be satisfactory for the East and Gulf Coasts but in the West, where the ecotone at this limit spanned elevations of up to one meter, this criterion was unsatisfactory. NOS therefore set the upper marsh limit as being the average of the upper and lower limits of the transition zone which in turn was based on floristic composition.

Floristic criteria involves basing the upper wetland limits on the presence of certain species. Frenkel et al. (1978) identified the transition zone in Oregon by a strong dominance of Potentilla pacifica and the presence of Achillea millefolium, Angelica lucida, Aster subspicatus, Oenanthe sarmentosa, Trifolium wormskjoldii, and Vicia gigantea. Some statutes specify a list of indicator plants which may be used to identify a wetland (N.Y., Environ. Cons. Law, Sec 25-0103 as cited in Lagna, 1975). Frenkel, et al. (1978) used a combination of floristic and vegetational (plant coverage) criteria to establish lists of upland and wetland plants and to develop a

quantitative measure integrating floristic and vegetational data and to thus determine upland limits by shifts in plant community structure.

Remote sensing has been proposed as a means of defining wetlands for jurisdictional purposes (Reimold, et al., 1972). Different species of plants have distinct signatures on color infra-red film. Remote sensing therefore can be used as a method for obtaining a vegetational map.

Physical criteria such as soil salinity and soil moisture are possible criteria on which to base the definition of wetland limits. Salinity, however, varies diurnally, seasonally, and with depth and distance from the estuary mouth, and would therefore not provide consistent data. Soil moisture, used in the Corps of Engineers definition of a wetland, would seem a likely method for determining wetland limits, however, making the decision as to whether an area is wetland or upland cannot be based on soil moisture measurements made at a single point in time. High temporal variability caused by precipitation and tidal fluctuations would have to be overcome by taking many observations, a year's data may be required, and then computing frequency/duration values for selected depths in the marsh (Lewes and Liverman, 1979). The necessity of such a long study would be impractical for the purpose of permit evaluation.

In situations where the transition from the wetland to the upland is abrupt, it is relatively easy to determine the upper limit of the marsh. However, the problem of clear determination of the upper limit becomes paramount in areas where a wide zone of low slope separates accepted wetland from nearby upland. Depending on the

slope of the land, wide zones may take in large horizontal areas (Linthurst, 1977; Eilers, 1977), and, therefore, use of a descriptive vegetational criteria for wetland definition under such broad ecotonal situations may be quite complex and confusing. Also, in populated areas such as the New Jersey shore, large sums of money are at stake when only a few feet of area are in dispute. In such areas, a very precise method for wetland limit determination becomes important.

By their special spatial position, fringe or transition zone plants have tolerances which enable them to grow in what may be called upland at one end of the spectrum and marsh at the other. It is well established that a plant species cannot be represented by a single individual. Rather, the population approach has replaced the type categorization of a species (Clausen, 1967). The term ecotype has been used to cover a single species which possesses a variable but genetically fixed morphology, anatomy, and/or physiology in relation to a varied environment. For example, the classical experiments of Clausen, Keck, and Heisey, (1948) showed that the numerous ecotypes of Achillea millefolium collected along a transect from Bodega (8m) to Big Horn Lake (3,350m) in the Sierra Nevada retained most of their morphological characteristics when transplanted to common gardens. More recently, Watson (1969) and Watson and Fyfe (1975) studied Potentilla erecta from two contrasting habitats in Scotland and concluded that these habitats had also evolved contrasting ecotypes.

It has also been established that plants may vary plastically in morphology, anatomy, and/or physiology in relation to the environment where variation is not fixed genetically (Grant, 1975). For

example, Shea, et al., (1975) using transplant experiments found that the two growth forms of Spartina alterniflora were ecophenes as opposed to ecotypes.

There are many reports in the literature of morphological and anatomical variations within a plant species to environmental variables such as salinity, flooding, drought, mineral nutrition, wind, temperature, and light. Plant morphology and anatomy may integrate the long-term effects of the total environment under which plants are growing thus making possible the assessment of the annual moisture cycle and other environmental variables by a single set of observations. Following are examples of morphological responses to a number of selected environmental variables. Unfortunately it is only possible within the confines of this report to review a portion of the pertinent literature.

## Temperature, Light and Wind

Leaf thickness and other leaf characteristics such as succulence leaf weight, density and wax structure have been shown to be affected by temperature in studies by Duff and Beard (1974), Peet, et al. (1977), Whitecross and Armstrong (1972) and Baker (1974). With increasing light intensity leaf thickness increases (Chabot and Chabot, 1977; Aussenac and Ducrey, 1977; Penfound, 1931 and Smith and Nobel, 1978). Sanchez and Cogliatti (1975) and Njoku (1956) found leaf shape to also be affected by light intensity. Pubescence was found to be directly related to light intensities in studies done by Smith and Nobel (1978) and Hansen, et al. (1976). Wind has been shown by

Grace and Russell (1977) and Russell and Grace (1978) to cause more marginal sclerenchyma and shorter plants in Festuca arundinacea and Lolium perenne.

## Salinity

Poljakoff-Mayber (1975) reviewed the morphological and anatomical responses of plants to salinity stress. Among the structural changes ascribed to salinity are increase in succulence, change in stomata size and number, thickening of the cuticle, changes in the diameter and number of xylem vessels, development of tyloses, earlier lignification and inhibition of differentation.

Succulence is often found to increase with increasing salinity. Wignarajah, et al. (1975) found that when Phaseolus vulgaris was grown in 48 mmol/l NaCl its leaves thickened through an increase in the thickness of the spongy parenchyma layer. Also, the palisade layer was thinner than that in control leaves. Mesophyll thickness and internal to external leaf area ratio in cotton increased by about 50% as salinity rose from 0.00 to 0.30 molal NaCl (Longstreth and Nobel, 1978). This reflected longer parenchyma cells and more layers of larger spongy cells. In Salicornia herbacea succulence was induced when grown in media salinized with NaCl. Increased succulence did not occur with non-salinized substrate or in substrate containing $MgSO_4$, therefore was specific for NaCl. Succulence was due to the development of larger spongy mesophyll cells and multilayered palisade tissue (Poljakoff-Mayber, 1975).

Culms, rhizomes, and leaves were shorter and culms were less numerous in Sporobolus virginicus when stressed with salt ranging from 0 to 80 $^{o}$/oo (ppt) (Gallagher, 1979). Similar observations on the growth of S. virginicus have been reported by Breen, et al. (1977). Nestler (1977) reported that growth of Spartinia alterniflora, as measured by shoot height and wet weight, was inversely related to the interstitial salinity of the underlying sediments. Salinity was shown by Phleger (1971) to have similar effects on the growth of Spartina foliosa based on leaf size and wet and dry weight data. Reduction in total growth, due to salinity, occurs in Centaurium littorale as studied by Freijsen and VanDijk (1975). Poljakoff-Mayber (1975) reported that NaCl also induces branching and a large leaf area in Atriplex halejnus.

Mayer (1969) suggests that salinity influences the fruit size and shape of Ruppia maritima. Thick-coated seeds are produced in early summer while thin-coated seeds are produced in early fall when salinity of the marshes is higher.

Salinity retarded the development of thick cell walls in the stele of cotton roots (Gerard and Hinojosa, 1973). In tomato, as discussed by Poljakoff-Mayber (1975), the stem diameter under saline conditions was smaller than that of control plants due to reductions in the vascular tissue. The diameter of the bundles decreased with increasing salinity. Also, in the stem of Salicornia herbacea, the cortical, pith, and xylem tissues were poorly developed in the absence of NaCl while in its presence development was more normal.

At the subcellular level the mitochondria in leaf cells of Atriplex were less electrondense and had swollen cristae under saline conditions. Swelling at the granal and fret compartments occurred in the chloroplasts (Poljakoff-Mayber, 1975).

Barbour (1978) studied both the effects of competition by Lolium perenne, and salinity, on the growth of Jaumea carnosa. In monospecific flats, increasing salinity caused a decline in the growth of both species, however, the decline of Lolium was three times that of Jaumea. At low salinity, competition of Lolium on Jaumea depressed the growth of Jaumea by 52%; but at high salinity, the competitive effect was negligible. This study supports an hypothesis that halophytes grow in saline soils due to their poor competitive ability in non-saline soils.

## Mineral Nutrition

The mineral nutrition that a plant receives may also be a factor affecting its morphology. For example, root growth in lodgepole pine seedlings was found by Coutts and Philipson (1977) to respond plastically to changes in the nutrient environment. When the root systems of each plant were divided in half and one half placed in a high nutrient solution and the other in a low strength solution, those in the low regime grew slowly and became brown; the high nutrient regime stimulated growth. Upon transfer of the low regime roots to the high regime the deprived roots responded with renewed growth and an increased growth rate.

A study carried out by Keser, et al. (1975) showed the effect of aluminum on root growth of sugarbeet. Nutrient cultures containing 4, 8, and 12 ppm Al caused a reduction in root and hypocotyl growth. The lateral roots were abnormal, the primary root curved, the root cap broke away, and cells divided irregularly at the apex in nutrient cultures containing high concentrations of Al.

Cotton plants grown on deficient levels of nitrogen exhibit characteristics associated with drought resistance. Cell walls of nitrogen-deficient leaves were more rigid than those of high-nitrogen leaves and they possessed a greater crude cell wall fraction (Radin and Parker, 1979).

Valiela, et al. (1978) found a shift in plant morphology of Spartina alterniflora from its short form to the tall form in long-term fertilization experiments. Tall and short S. alterniflora had previously been shown by Shea, et al. (1975) to be genetically indistinguishable.

## Drought

Much literature is available on the effects of moisture stress or drought on plants. Hsiao (1973) reviews extensively this subject but deals mostly with physiological responses. Examples involving morphological responses to water stress follow.

Leaf size was found to be affected by moisture stress in several studies. Leaf enlargement measured before and after a 24 hour growth period, in corn, soybean, and sunflower was markedly inhibited when leaf water potential dropped to about -4 bars (Boyer, 1970). Upon

rewatering, the rate of leaf enlargement did not return to the rate in the control plants. When subjected to small water stresses, the total area of sunflower leaves decreased while in orange leaves it was the thickness that decreased (Levitt and Zaken, 1975).

Encelia farinosa, a desert shrub, lives in an environment where there exist long dry periods and then periods of high precipitation. This plant exhibits seasonal morphological variation, controlled by the moisture status of its environment. During dry periods, leaves are few, small, have more compact mesophyll, and are densely pubescent; during wet periods, the leaves are numerous, large, and less pubescent. This seasonal variation allows more photosynthate to be accumulated by the plant than would be the case if only a small amount of dense tissue were present at all times (Cunningham and Strain, 1969). Similar findings were reported by Smith and Nobel (1977) for Encelia and Hyptis.

Todd, et al. (1974) studied Impatiens balsamina under conditions of water stress. Within four days of withholding water, they observed a marked reduction in leaf thickness, and tannin and raphide sacs in the palisade and spongy parenchyma increased in size and number. After eight days of water stress there was little intercellular space in the spongy parenchyma and the vascular tissue was compressed. In the stem, vascular tissues were compressed.

Water stress in wheat leaves caused thickened cell walls and increased lignification in xylem elements and bundle sheath cells (Ridley and Todd, 1966).

The rate of leaf initiation and cell expansion was rapidly reduced in tobacco by a small water deficit, however, cell division was not so sensitive to water stress (Clough and Milthorpe, 1975). Over long exposure to water stress, though, cell division can also be inhibited (Hsiao, 1973).

Waterlogging

The subject of waterlogging is a major focus of the present research, since, in the salt marsh, soils are saturated a certain proportion of the time. Recall also that the Army Corps of Engineers wetland definition involves saturation frequency.

Development of aerenchyma is believed to be an adaptation by which plants can tolerate saturated soil conditions or a total aquatic environment. A well-developed system of aerenchyma provides for oxygen transport from leaves to roots. Barber, et al. (1962) tracked air labelled with $^{15}O$ from shoot to root in rice and barley plants and suggested that it occurs by a simple gaseous diffusion process through continuous intercellular spaces. They suggest that the size of these spaces determines the ability of the plant to withstand waterlogging. Thus with its smaller sized gas spaces, barley's survival under waterlogged conditions is poorer than that of rice. Kawase and Whitmoyer (1980) have investigated the aerenchyma development in stems of Helianthus annuus and Lycopersicon esculentum under waterlogged conditions. After 24 hours of waterlogging an increase in aerenchyma was evident and after three days very large intercellular spaces (approximately 4 cells x 8 cells in size) had formed.

The volume of root lacunae in maize and elevated fescue was found by Mingeau (1977) to increase when submitted to increasing amounts of water excess. This increase in root porosity was assumed to increase the inward transfer of oxygen. Root porosity was also shown by Das and Jat (1972 and 1977) to increase in maize and rice with increasing soil water conditions in both field and greenhouse experiments. Puccinellia, a flood-tolerant grass is suggested by Stelzer and Lauchli (1977) to be tolerant of flooded conditions due at least in part, to its well-developed system of aerenchyma.

A detrimental effect of aerenchyma formation has been proposed by the Letcombe Laboratory (1976). Investigators there are testing the possibility that aerenchyma development in roots during waterlogging may impair their ability to absorb nutrients when, subsequently, soil conditions become drier and more favorable.

Crawford and Tyler (1969) feel that the development of aerenchyma is not an entirely satisfying explanation of flooding tolerance in higher plants and they discuss metabolic adaptations, specifically patterns of organic acid accumulation, as being related to the flooding tolerance of plants. Metabolic adaptations are also discussed by Moore (1978) and Bannister (1976).

In addition to the formation of aerenchyma other morphological and anatomical features are influenced by waterlogging. Penfound (1931) observed thicker roots with more and larger xylem vessels, thicker stems with more and larger xylem vessels, thicker leaves with deeper layers of palisade and spongy chlorenchyma in sunflower,

spring wheat, and kidney wax beans when subjected to high soil water conditions as compared to drier soils.

In greenhouse experiments, three species of Achillea were observed by Dabrowska (1977) for morphological differences due to soil moisture. He found the plant's green color, plant height, the amount of stem ramification, and the number of flowers to be greater under 70% maximum capillary water capacity of the soil than at 30%.

Periera and Kozlowski (1977) studied the effects of flooding on seven woody angiosperms. They observed inhibition of root growth, alterations in root and stem morphology, including the formation of adventitious roots, and hypertrophy of the lenticels and cortex. Flooded Eucalytus globulus developed thick white roots and roots grew upward in E. camadulensis and Salix nigra.

The grass, Danthonia sericea shows morphological changes under various moisture levels. In well-drained, sandy, upland sites populations of this grass have pubescent lemmas and leaf sheaths while those found in open bogs or low wet areas bordering ponds or rivers are relatively glabrous (Quinn, 1975).

Breen, et al. (1977) found that in the salt marsh grass Sporobolus virginicus growth is inhibited by waterlogged conditions only in the small plants. As the plants become older they tolerate inundation.

Rice is a well known water-loving plant. It was found by Kawata, et al. (1977) that root system formation is affected by the drainage levels of paddy fields. Rice plants grown in an ill-drained field, with no mottling in the plow layer and no structure in the

subsoil, had root systems consisting of many roots most of which grew in the plow layer. Conversely, plants grown in a well-drained field with mottling in the plow layer and blocky structure in the subsoil had root systems consisting of many roots growing into both the plow layer and the subsoil. The latter condition produced plants with a high grain yield.

Three rice varieties were studied by Datta and Banerji (1974). In all cases within each variety, number, length, and diameter of internode, number and diameter of air sac, diameter of lumen, thickness of stem, and diameter of cortical cells were markedly larger in plants growing under deep-water conditions as compared to those growing under normal field conditions. The deep-water varieties produced three to four times more air sacs under deep-water conditions than under the usual field conditions. Therefore, differences within a variety were evident between the two soil water conditions.

Formation of adventitious roots which have a high root porosity (aerenchyma) is flood-induced in many plants and is an adaptation to waterlogged conditions by increasing the amount of root porosity. The tolerance of corn, sunflower and wheat to flooded conditions was attributed to an increase in root porosity and to an increased number of adventitious roots when compared to plants growing in non-flooded conditions (Yu, et al. 1969).

Maronek and Wott (1975) studied adventitious root formation when they subjected two to seven year old red and sugar maple trees to inundation. Sugar maple survived flooding for 30 days while red

maple survived for at least 60 days but with a 60-90% height reduction. The survivability of the red maple seemed dependent on lenticel intumenescence and/or adventitious root formation (Maronek and Wott, 1975). The formation of adventitious roots in response to flooding is also discussed by Wample and Reid (1975, 1978, and 1979) and Gill (1975).

## Purpose

The primary purpose of the present study was to evaluate the use of anatomical and morphological characteristics of five coastal wetland plant species for use in the delineation of upper wetland limits. Such criteria on morphological responses may then aid in setting Section 404 guidelines used by the enforcement agencies in setting wetland limits upon permit request. A related, secondary purpose was to determine whether any variation noted is due to ecological race formation or is a plastic response due only to local environmental conditions.

## Approach

The salt marsh fringing Netarts Bay, Oregon was selected as the site for study. Netarts Bay lies approximately 60 miles south of the mouth of the Columbia River. This site was chosen for its gentle slope from mature to immature marsh and for its proximity to Oregon State University.

Five species which exhibited differences in morphological characteristics between the upper and lower limits of their range were

selected for study. Deschampsia cespitosa (L.) Beauv., hairgrass, is known to grow in both dry and waterlogged habitats but its frequent occurrence in waterlogged habitats is thought to be due to its broad edaphic tolerance and lack of competitive ability on well drained soils (Davy and Taylor, 1974). The distribution of this species includes Alaska to Greenland, most of the U.S., northern Mexico, and Eurasia (Hitchcock and Cronquist, 1973).

Grindelia integrifolia DC. known as gumweed, is found in salt marshes and rocky shores and it is distributed coastally from Alaska to northern California (Hitchcock and Cronquist, 1973).

Distichlis spicata (L.) Greene, saltgrass, grows well on coastal beaches and salt marshes and is distributed from Vancouver Island to California and along the Atlantic Coast (Hitchcock and Cronquist, 1973).

Salicornia virginica L. can be found in coastal salt marshes and on beaches from Alaska to Baja California. It is known as the pickleweed (Hitchcock and Cronquist, 1973).

Jaumea carnosa (Less.) Gray grows on tidal flats and in salt marshes and ranges from southern Vancouver Island to southern California (Hitchcock and Cronquist, 1973).

Three research strategies were used in the study viz. 1) Plants growing in the ecotone between mudflat and upland were examined along transects for differences in morphological and anatomical features. 2) Those species noted above were transplanted in the field by exchanging position between the upper and lower part of the marsh. Lateral transplants were also made to serve as a control

of disturbance influence. Morphological and anatomical features were analyzed. 3) Four of the five species discussed above were grown in the greenhouse under three levels of soil moisture. Morphological and anatomical characteristics of these plants were analyzed.

# II. TRANSECTS

## Introduction

The initial phase of this project involved selecting marsh species demonstrating certain morphological differences between their upper and lower range within the salt marsh. Included among the characteristics measured for differences were plant length, stem diameter, internode length, leaf width, leaf number, and number of flowers. Due to their spanning, the major width of the marsh (see Figure 1) five species were selected for study. Included were Deschampsia cespitosa, Grindelia integrifolia, Distichlis spicata, Salicornia virginica, and Jaumea carnosa. Once the identified differences were shown to exist between upper and lower limits of each species, transects along these ranges of distribution were studied. Five points were identified along each of the five transects from which plants could be collected. Plants from each of these selected areas were subjected to statistical analysis to quantify apparent morphological variation.

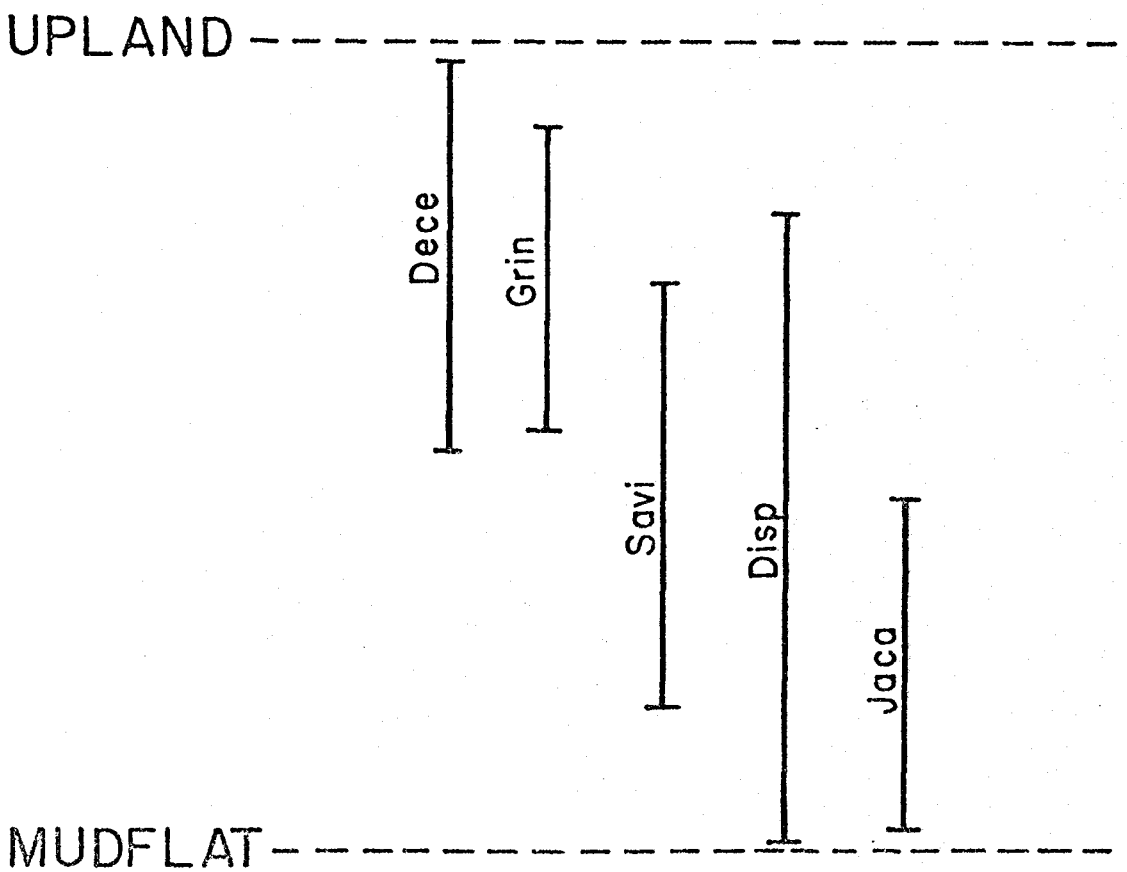



Figure 1. Schematic representation of the distribution of the five selected species (Dece = Deschampsia cespitosa, Disp = Distichlis spicata, Grin = Grindelia integrifolia, Jaca = Jaumea carnosa, Savi = Salicornia virginica).

## Materials and Methods

In August of 1978 and July, 1979, samples for anatomical and morphological analysis were collected from the upper and lower portions of the localized ranges of the five selected species. In order not to bias sampling, all plants in a specified plot were cut. In the case of Jaumea carnosa and Salicornia virginica, square 0.05 $m^2$ quadrats were used; square 0.1$m^2$ quadrats were used for Distichlis spicata and Grindelia integrifolia. Since Deschampsia cespitosa grows in clumps quadrats were not useful, therefore, typical samples, as determined by the investigator, were selected from several different clumps. In all cases, the plants were cut at ground level with a scissors.

The plant material was returned to the laboratory where the basal centimeter of each plant's stem was removed. A section was cut from each centimeter sample, placed in a vial of FAA fixative (5cc 37% formaldehyde + 5cc glacial acetic acid + 90cc 70% ethanol) and placed overnight in a vacuum dessicator to facilitate infiltration of the fixative into the plant tissue. Vials were stored until a later time when the tissue was prepared for light microscopy. Procedures for this preparation will be discussed later.

Subsequently, the following morphological measurements were taken using a meter stick, a 15 cm ruler and a metric vernier calipers, on each stem collected from the July, 1979 sampling date: 1) D. cespitosa - plant length and length of flowering shoot; 2) J. carnosa - plant length and length of the second and third internodes below the apex; 3) G. integrifolia - plant length, basal stem

diameter, number of flowers, length of woody tissue, diameter of wood at the base, length of flowering shoot and flower shoot diameter; 4) S. virginica - plant length, number of internodes, length and diameter of the fourth internode from the base, fresh and dry weights of that internode, dry weight per volume of the internode (volume determined by assuming the internode to be a cylinder having a volume equal to $\pi r^2 h$), and the numbers of primary and secondary branches per stem; and 5) D. spicata - plant length, number of internodes, lengths of the third and fourth internodes, number of leaves, width of the base of the fourth leaf from the apex, and stem diameter at the base. Statistical analysis of the data included mean, standard deviation, and t-test (Sokal and Rohlf, 1969).

On 1 September 1979, the local ranges or transects between upper and lower limits of each species were further divided giving five points along each transect except in the case of D. cespitosa where six samples were collected. See Table 1 for the sampling sites, and Figure 2 for transect location.

Using quadrats and methods as previously described, plants were harvested at each of the five points along each transect. Samples for anatomical analysis were separated from each sample as before and morphological measurements obtained, however, additional characteristics were measured at this time (see Table 2). Statistical analysis included, mean, standard deviation, one-way analysis of variance, and SNK range test (Sokal and Rohlf, 1969).

Soil moisture in the marsh was monitored by the use of Jet-Fill tensiometers manufactured by the Soilmoisture Equipment Company,

TABLE 1. SAMPLING POINTS ALONG TRANSECTS WITH ZERO BEING THE LOWER LIMIT OF SPECIES DISTRIBUTION.

| | Transect Number | Distance in meters |
|---|---|---|
| *Grindelia integrifolia* | 1 | 0, 7, 14, 21, 28 |
| *Distichlis spicata* | 2 | 0, 6, 12, 18, 24 |
| *Deschampsia cespitosa* | 3 | 0, 6, 13, 21, 31, 40 |
| *Salicornia virginica* | 4 | 0, 9.5, 19, 28.5, 38 |
| *Jaumea carnosa* | 5 | 0, 7.5, 15, 22.5, 30 |

FIGURE 2. Map of the Netarts Bay Area. Numbers1-5 indicate position of transects in the salt marsh.

#1 - *Grindelia integrifolia*

#2 - *Distichlis spicata*

#3 - *Deschampsia cespitosa*

#4 - *Salicornia virginica*

#5 - *Jaumea carnosa*

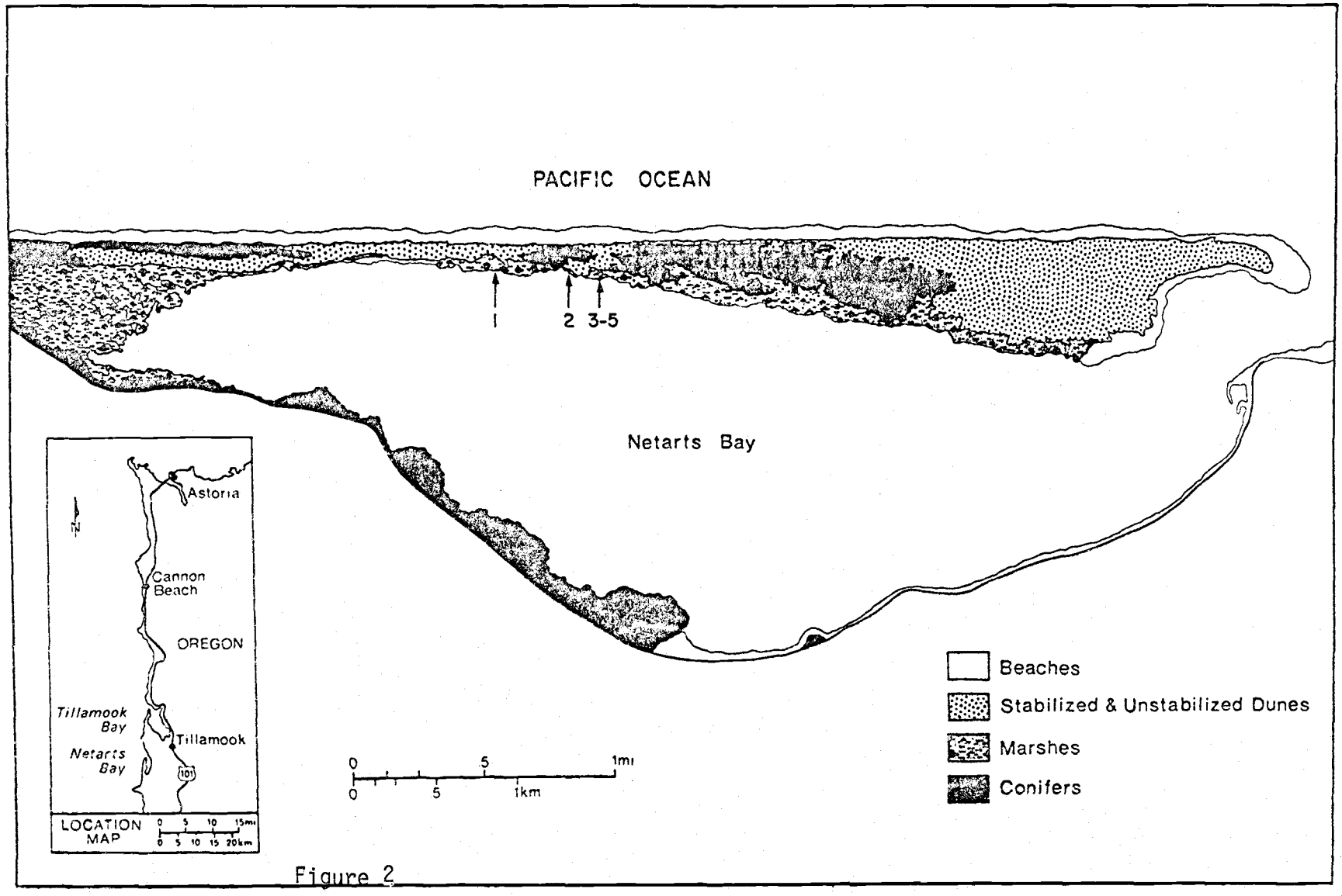

PACIFIC OCEAN
1
2
3-5
Netarts Bay
Astoria
Cannon Beach
OREGON
Tillamook Bay
Tillamook
Netarts Bay
101
LOCATION MAP
0 5 10 15mi
0 5 10 15 20km
0 5 1mi
0 5 1km
Beaches
Stabilized & Unstabilized Dunes
Marshes
Conifers

Figure 2

TABLE 2. MORPHOLOGICAL CHARACTERISTICS MEASURED FOR EACH SPECIES.

| | |
|---|---|
| *Deschampsia cespitosa*: | plant length, width of longest leaf, stem diameter, length of flowering shoot, flower shoot diameter, inflorescence length. |
| *Grindelia integrifolia*: | plant length, number of leaves, width at its widest part of third leaf from apex, stem diameter, length of flowering shoot, flower shoot diameter, number of flowers per stalk. |
| *Distichlis spicata*: | plant length, number of leaves, lengths of third and fourth internodes, width of the base of the fourth leaf from apex, stem diameter. |
| *Salicornia virginica*: | plant length, number of internodes, length, fresh and dry weight, and diameter of fourth internode from base, dry weight per volume of the fourth internode, numbers of primary and secondary branches, stem diameter, flower number. |
| *Jaumea carnosa*: | plant length, number of nodes, lengths of second and third internodes, number of leaves, leaf width and thickness of leaf in third whorl from apex, stem diameter. |

Santa Barbara, California with soil moisture tension being read in centibars. Two sizes of tensiometers were used, 12 inch and 36 inch, with the longer ones being placed in the lower parts of the marsh in order to prevent submergence at high tide. Due to cost of the instruments, it was not possible to place them at each sampling point along each transect. Two tensiometers, at depths of 10 and 25 cm below the soil surface, were located at the upper and lower ends of each transect. A pair of tensiometers was also located above the D. cespitosa zone in transect #3 on the Elmus mollis ridge which was assumed as the beginning of upland vegetation.

Elevational data for all sampling points were obtained using a Zeiss automatic level and a metric stadia rod. Data was tied to temporary National Ocean Survey (NOS) tidal bench marks which were placed in the marsh October, 1977.

Soil samples were collected at the 26 sampling sites and analyzed by the Oregon State University Soil Testing Laboratory for pH, P, K, Na, Ca, Mg, Total N, $NO_3$-N, $NH_4$-N, and "lime requirement".

Anatomical procedures were as follow. Stem samples which had been fixed in FAA were run through the tertiary-butyl alcohol series (Johannsen, 1940), followed by paraffin embedding, and sectioning. Slides were stained with a modification of the Triarch Triple Stain procedure employing safranin, fast green and gold orange (Rickson, pers. comm.).

As discussed in the Introduction environmental factors not measured in this study, such as wind, light and temperature, are known to produce morphological variability within a plant species.

However, in this particular study since the distances between the upper and lower limits of the distribution of the species are very short, 40 m at the most, these factors were assumed to be the same along the transects and were therefore not measured.

# Results and Discussion

## Upper vs Lower Distributional Limit

As described in the previous section, the initial portion of this study involved the collection of plants from the upper and lower distributional limits of the various species, in order to determine whether statistically significant morphological differences existed within a species between upper and lower marsh. Tables 3 through 7 display the results obtained for the morphological characteristics measured. The majority of the characteristics are shown to be significantly different between upper and lower ranges of the species. In Figures 3 through 6 differences in internal anatomy are also evident.

## Morphology

Deschampsia cespitosa plants (Table 3) are considerably larger in the upper marsh than they are at the lower range of their distribution. This is evident for both vegetative and floral portions of the plant. Conversely, Distichlis spicata (Table 4) plants are taller with larger stem diameters and longer internodes in the lower marsh zone. However, stem density is greater in the upper marsh. Also, a greater percentage of D. spicata plants are in flower, (7.5% vs 3.8%) in the upper marsh zone. Plants of Grindelia integrifolia (Table 5) are larger in the upper than in the lower part of the marsh. Total plant length along with length of individual parts, i.e. flowering shoots and vegetative rosettes, is greatest in the upper marsh. There is also

TABLE 3. *Deschampsia cespitosa*. MORPHOLOGICAL MEASUREMENTS OF PLANTS FROM THE UPPER AND LOWER DISTRIBUTIONAL LIMITS (measurements in cm).

| | | Plant length | Flowering shoot length |
|---|---|---|---|
| upper | $\bar{X}$ | 50.7 | 99.9 |
| | SD | 8.1 | 13.2 |
| | N | 142 | 36 |
| lower | $\bar{X}$ | 39.0 | 80.2 |
| | SD | 5.4 | 9.2 |
| | N | 125 | 19 |
| level of significant difference | | .001 | .001 |

TABLE 4. *Distichlis spicata*. MORPHOLOGICAL MEASUREMENTS OF PLANTS FROM THE UPPER AND LOWER DISTRIBUTIONAL LIMITS (measurements in cm).

| | | Plant length | No. internodes | Length 3rd internode | Leaf width | Stem diameter | % with flowers | Stem density |
|---|---|---|---|---|---|---|---|---|
| upper | $\bar{X}$ | 7.0 | 5.8 | 0.4 | 0.2 | 0.10 | 7.5% | 3710/$m^2$ |
| | SD | 3.5 | 2.5 | 0.2 | 0.1 | .02 | | |
| | N | 103 | 103 | 103 | 103 | 103 | | |
| lower | $\bar{X}$ | 13.4 | 6.2 | 1.3 | 0.3 | 0.12 | 3.8% | 2120/$m^2$ |
| | SD | 7.0 | 2.7 | 0.6 | 0.1 | 0.04 | | |
| | N | 106 | 106 | 106 | 104 | 106 | | |
| level of significant difference | | .001 | N.S. | .001 | .001 | .001 | | |

TABLE 5. *Grindelia integrifolia*. MORPHOLOGICAL MEASUREMENTS OF PLANTS FROM THE UPPER AND LOWER DISTRIBUTIONAL LIMITS (measurements in cm).

| | | Overall plant length | No. flower stalks per plant | No. vegetative rosettes per plant | Flowering shoot length | Flowering shoot diameter |
|---|---|---|---|---|---|---|
| upper | $\bar{X}$ | 41.6 | 1.7 | 1.1 | 36.5 | 0.24 |
| | SD | 10.0 | 2.6 | 0.7 | 4.5 | 0.06 |
| | N | 17 | 17 | 17 | 28 | 28 |
| lower | $\bar{X}$ | 24.7 | 0.7 | 1.2 | 27.2 | 0.29 |
| | SD | 5.4 | 0.8 | 1.0 | 4.7 | 0.09 |
| | N | 31 | 31 | 31 | 21 | 21 |
| level of significant difference | | .001 | .05 | N.S. | .001 | .05 |

TABLE 5. (continued). *Grindelia integrifolia*. MORPHOLOGICAL MEASUREMENTS OF PLANTS FROM THE UPPER AND LOWER DISTRIBUTIONAL LIMITS (measurements in cm).

| | | No. flowers per flower stalk | Length vegetative rosette | Stem diameter | Length wood | Diameter wood |
|---|---|---|---|---|---|---|
| upper | $\bar{X}$ | 1.6 | 23.0 | 0.24 | 9.0 | 0.46 |
| | SD | 0.8 | 6.0 | 0.10 | 3.5 | 0.13 |
| | N | 28 | 22 | 21 | 19 | 19 |
| lower | $\bar{X}$ | 2.0 | 19.0 | 0.35 | 1.4 | 0.54 |
| | SD | 0.8 | 2.8 | 0.15 | 0.8 | 0.20 |
| | N | 21 | 34 | 34 | 15 | 15 |
| level of significant difference | | N.S. | .005 | .005 | .001 | N.S. |

more woody tissue in upper marsh plants, but stem and flowering shoot diameter is greatest in plants of the lower marsh.

Larger plants were also found at the upper limit of the distribution of Jaumea carnosa (Table 6). Here plant length, internode number and length, and leaf width were greatest. At the sampling dates, 12.9% of the plants in the lower marsh were flowering while in the upper marsh no flowers were produced. Stem density (stems/$m^2$) was greatest in the lower marsh. In general, the upper plants of J. carnosa were elongated, non-flowering and of lower density than their counterparts lower in the marsh which were short, in flower, and almost three times as dense.

Salicornia virginica (Table 7) followed the same growth pattern as did D. cespitosa, G. integrifolia, and J. carnosa. Plants at the upper limit of its distribution in the marsh were greater in length and internode number, and showed more branching. Eighty-eight percent of the upper plants displayed primary branching compared to 24% for the lower marsh. Secondary branching occurred in the upper plants, 6%, while none was found in the lower plants. Stem density was greatest in the lower marsh.

It was hypothesized that the differences observed in morphology may be a result of differences in soil moisture. It must be realized, however, that other mutually correlating factors such as salinity and nutrients as well as various other variables, as discussed in the Introduction, are probably also involved.

Stem diameter of D. spicata and G. integrifolia was greater in the lower marsh zone and may be due to the higher soil moisture in this area and thus the greater moisture content of the plant stems. Work

TABLE 6. *Jaumea carnosa*. MORPHOLOGICAL MEASUREMENTS OF PLANTS FROM THE UPPER AND LOWER DISTRIBUTIONAL LIMITS (measurements in cm).

| | | Plant length | No. internodes | Length 3rd internode | Leaf width | Stem diameter | % Stems with flowers | Stem density |
|---|---|---|---|---|---|---|---|---|
| upper | $\bar{X}$ | 18.4 | 6.7 | 3.2 | 0.5 | 0.11 | 0% | 1200/$m^2$ |
| | SD | 3.8 | 2.4 | 0.8 | 0.1 | 0.02 | | |
| | N | 60 | 61 | 60 | 61 | 61 | | |
| lower | $\bar{X}$ | 6.6 | 4.4 | 1.3 | 0.3 | 0.11 | 12.9% | 3420/$m^2$ |
| | SD | 3.0 | 1.7 | 0.4 | 0.1 | 0.03 | | |
| | N | 170 | 97 | 140 | 97 | 97 | | |
| level of significant difference | | .001 | .001 | .001 | .001 | N.S. | | |

TABLE 7. Salicornia virginica. MORPHOLOGICAL MEASUREMENTS OF PLANTS FROM THE UPPER AND LOWER DISTRIBUTIONAL LIMITS (measurements in cm).

| | | Stem length | No. green internodes | wt/vol internode | No. primary branches | % stems with primary branches | % stems with secondary branches | Stem density |
|---|---|---|---|---|---|---|---|---|
| upper | $\bar{X}$ | 20.2 | 14.7 | 0.09 | 13.9 | 88.0% | 6.0% | 4040/$m^2$ |
| | SD | 5.9 | 2.9 | 0.02 | 10.2 | | | |
| | N | 50 | 50 | 50 | 50 | | | |
| lower | $\bar{X}$ | 8.6 | 11.3 | 0.13 | 2.1 | 24.0% | 0.0% | 6020/$m^2$ |
| | SD | 2.9 | 2.8 | 0.03 | 4.2 | | | |
| | N | 50 | 50 | 50 | 50 | | | |
| level of significant difference | | .001 | .001 | .001 | .001 | | | |

by Todd, et al. (1974) describes compression of cortical and vascular tissues in stems of Impatiens under dry soil conditions. Under high soil water content, Penfound (1931) describes increased stem diameter due to more and larger xylem vessels and thicker-walled phloem and wood fibers.

Plant length, except in the case of D. spicata, was greatest in the upper marsh zone. Here the soil is drier and the salinity is less, both due to less frequent tidal inundation. Under dry soil conditions growth is reduced (Bannister, 1976) however this is with water potentials of 1.0 bar and greater. In the upper marsh zone at Netarts, soil water tension was always less than 1.0 bar. Since waterlogging or salinity can cause reduction in growth (Nestler, 1977; Phleger, 1971; Freysen and Van Dijk, 1975; Gallagher, 1979 and Breen, et al., 1977) and as previously mentioned, salinity is greater in the lower marsh zone, the observed reduction in growth may be caused by a combination of waterlogging and high salinity. Perhaps salinity does not effect D. spicata in this manner due to its many ecological adaptations, salt glands being one example (Hansen, et al., 1976). As for the saturated soil, the large aerenchymatous network throughout this plant adapts it to the waterlogged conditions.

Leaf enlargement is retarded by both water stress (Boyer, 1970, Levitt and Zaken, 1975, Cunningham and Strain, 1969, and Smith and Nobel, 1977) and salinity (Phleger, 1977). Salinity, however, has been shown to induce a large leaf area in Atriplex halejnus (Poljakoff-Mayber, 1975). In J. carnosa, leaf width was greatest in the upper marsh zone where drier soil and lower salinity occur. However,

the reverse was true for D. spicata. Recall that for plant length, D. spicata had results opposite to those found in the other species.

For D. spicata the percentage of stems in flower and for G. integrifolia the number of flowering shoots per plant, were greater in the upper zone at the time of sampling (7.5% vs 3.8% and 1.7 vs 0.7, respectively) than in the lower zone. In the case of J. carnosa flowering was greater in the lower zone (12.9% vs 0.0% for the upper zone). Dabrowska (1977) found that Achillea produced more flowers when the soil was near field capacity than when at a much drier value, however, he did not test against waterlogged conditions. Since flowering response was not similar within the three species, I find it difficult to attribute the reason to soil moisture, salinity or elevation. One speculation could involve the effects of competition. In two instances where flowering was greatest, there was lower competition from other species (D. spicata was a mono-specific stand). Barbour (1978) reported that the growth of J. carnosa was markedly depressed by competition at lower salinities, while at higher salinities the previous competitor was no longer competitive. Recall that in the lower marsh zone the salinity is higher. For now this idea must remain as speculation since this research does not include data on competition and community structure.

Anatomy

Stem cross sections were successfully obtained for Distichlis spicata, Grindelia integrifolia, Jaumea carnosa, and Salicornia virginica. Figures 3A and 3B are cross sections of D. spicata. From

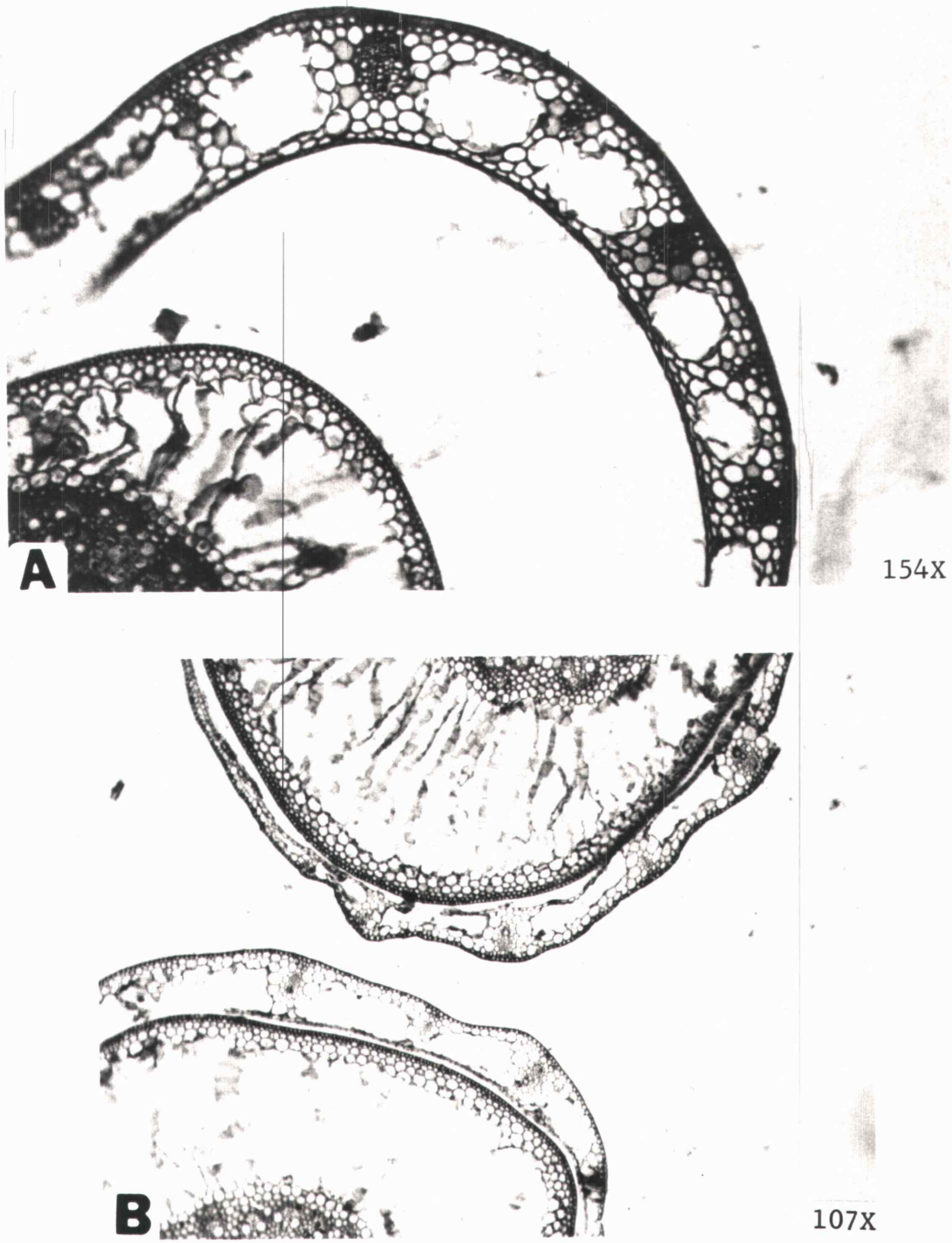



Figure 3. Stem cross sections of Distichlis spicata from its upper and lower distributional limits (A = upper, B = lower).

these Figures it can be seen that there is greater lignification (assumed due to increased cell wall thickness and increased staining ) in the bundle sheath cells of the plants from the high marsh zone (3A) than in those from the low zone (3B). Poljakoff-Mayber (1975) attributes earlier occurrence of lignification to increased salinity, however, since my findings indicate the greater lignification in the upper zone of the marsh where the salinity is less and if I assume previous work to be correct, I must conclude that increased lignification in this case is due to an environmental factor other than salinity.

Stem cross sections of G. integrifolia are displayed in Figures 4A and 4B. Here the most notable difference between stems taken from the species' upper and lower distributional limits is the greater amount of secondary xylem from plants of the upper marsh region. Grace and Russel (1977) report more sclerenchyma in drought-grown Festuca but as previously discussed, upper marsh conditions are not so extreme as drought conditions therefore explanation of this phenomenon probably lies in some other environmental variable.

Vascular bundles of J. carnosa are greater in diameter and vessel number in stem sections taken from this species' upper distributional limit (Figure 5A) than they are in sections from the lower zone (Figure 5B). Salinity and high soil water conditions are known to cause changes in the amount of vascular tissue. Increase in salinity causes a reduction in the amount of total vascular tissue (Poljakoff-Mayber, 1975) while high soil water content causes an increase in the size and number of xylem vessels (Penfound, 1931). In the case of J. carnosa it would appear that the vascular tissue was responding more

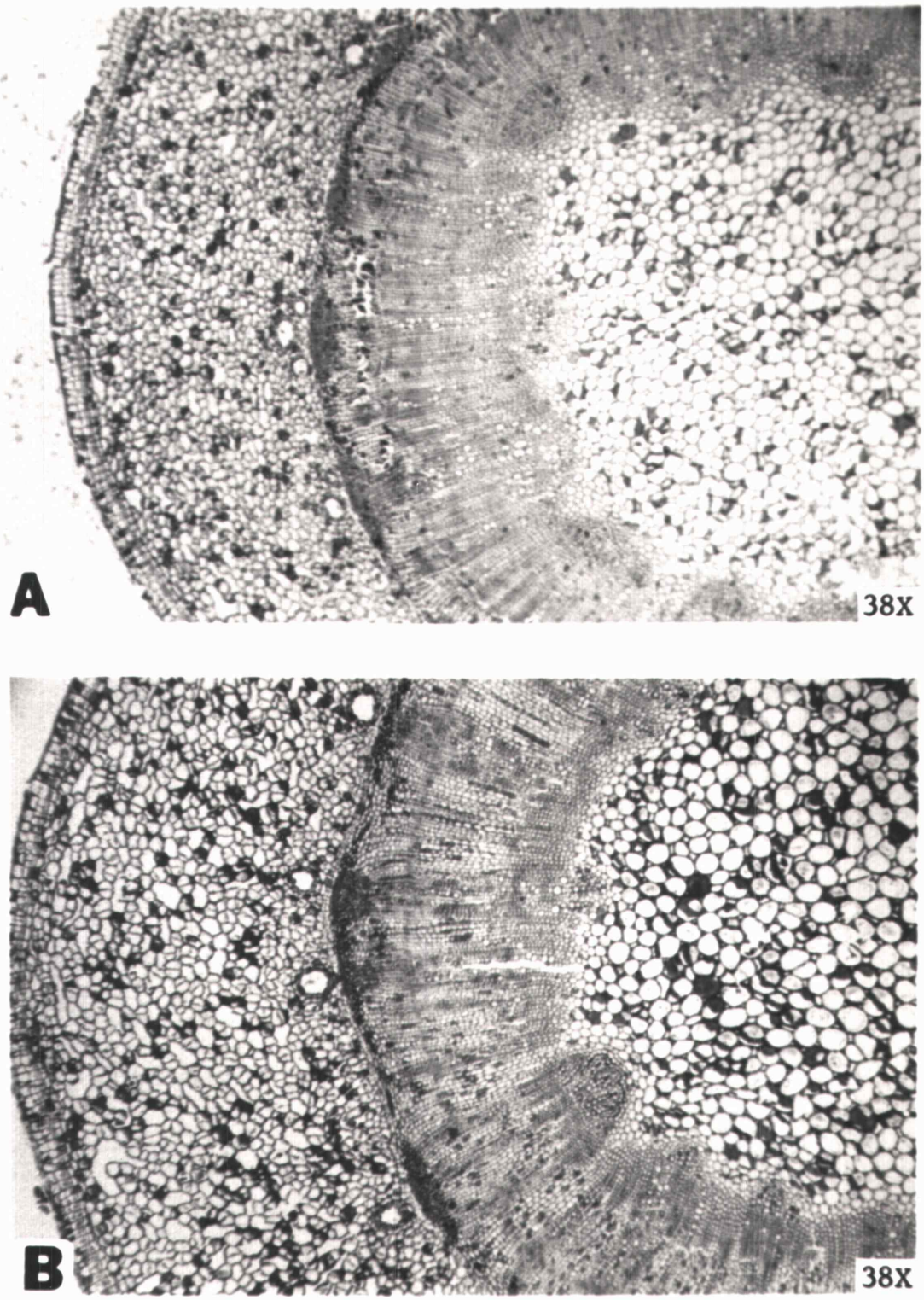
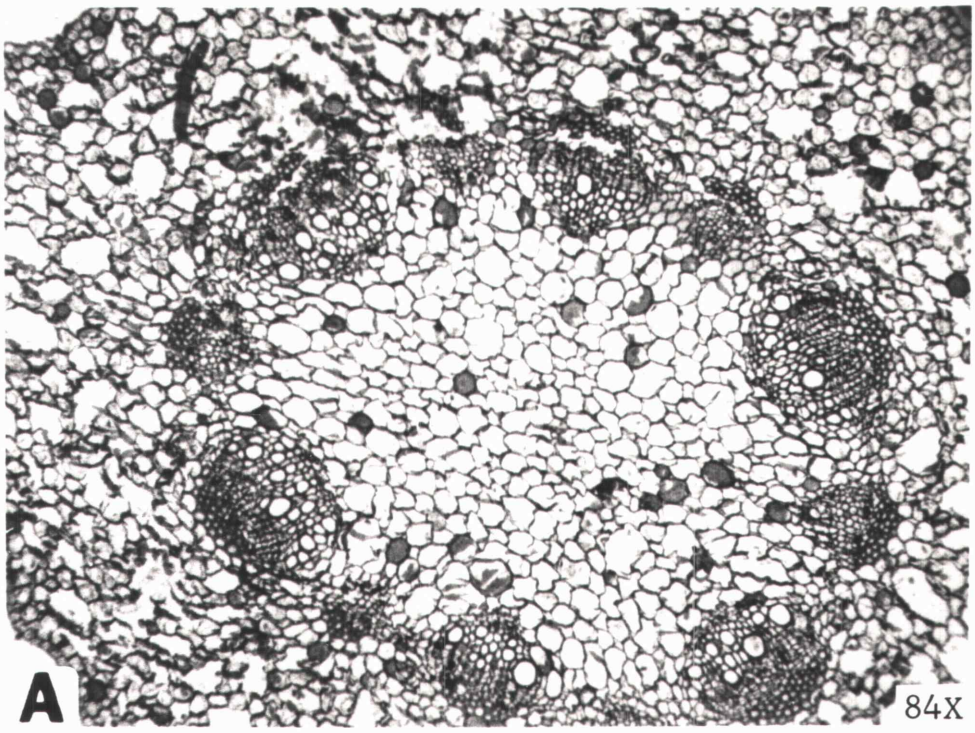



Figure 4. Stem cross sections of Grindelia integrifolia from its upper and lower distributional limits (A = upper, B = lower).



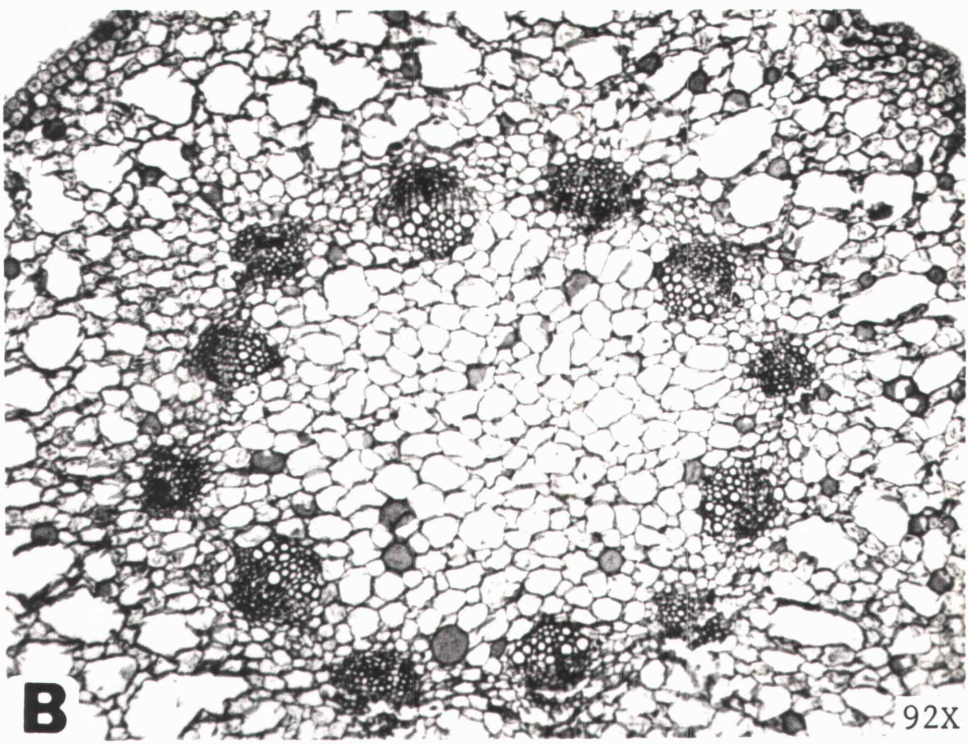




Figure 5. Stem cross sections of Jaumea carnosa from its upper and lower distributional limits (A = upper, B = lower).

to decreased salinity in the upper marsh zone than to increased soil moisture in the lower area, since vascular bundles are largest at the plant's upper distributional limit.

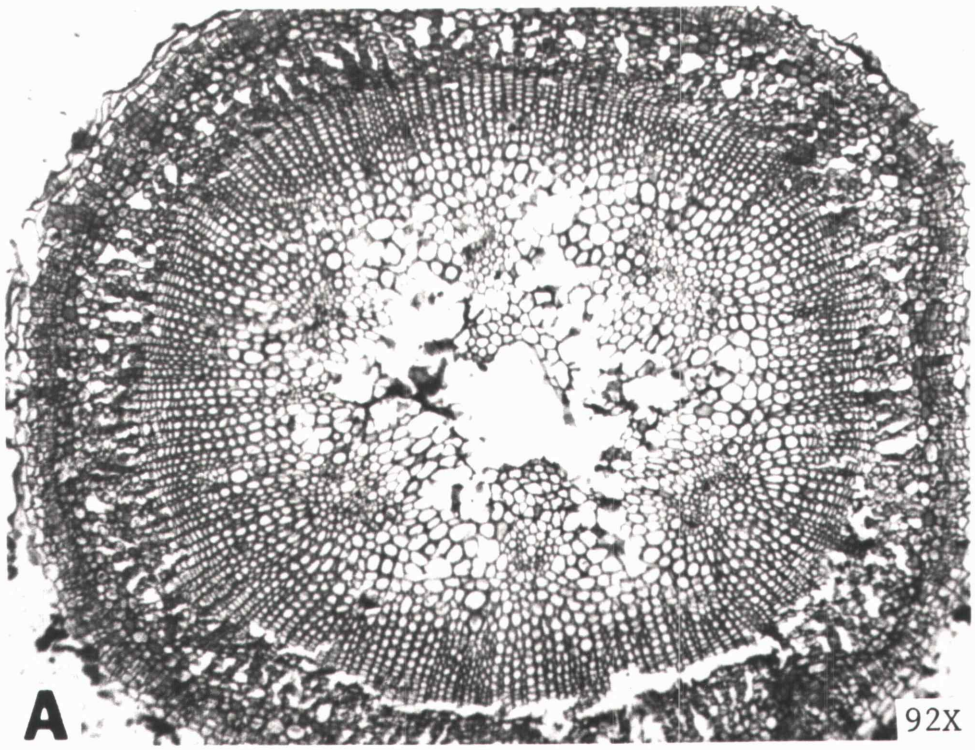
As discussed in the Introduction, there is much evidence for the formation of aerenchymatous tissue in the adaptation of plants to waterlogged environments (Barber, 1962; Kawase and Whitmoyer, 1980; Mingeau, 1977; Das and Jat, 1972 and 1977; and Stelzer and Lauchli, 1977). This adaptation is exemplified in this research by S. virginica. It can be seen from Figures 6A and 6B that the amount of aerenchyma in stem sections from the frequently saturated, lower marsh zone is noticeably greater than in sections from the upper zone.

## Differences Along the Transects

In view of the preceding evidence of intraspecific differences between upper and lower marsh plants, plants along a transect, between and including the upper and lower sites of each species, were also studied in order to find a more precise indication of where along the transect changes occurred.

### Morphology

Table 8 indicates which characteristics differed significantly along the transect of Deschampsia cespitosa. An SNK range test was carried out on each set of significant variables with results being displayed in Table 9. With all SNK range tests, transect points are arranged in increasing order. Plant length of D. cespitosa increases with distance up the marsh. Its greatest length occurs at 0.761 m



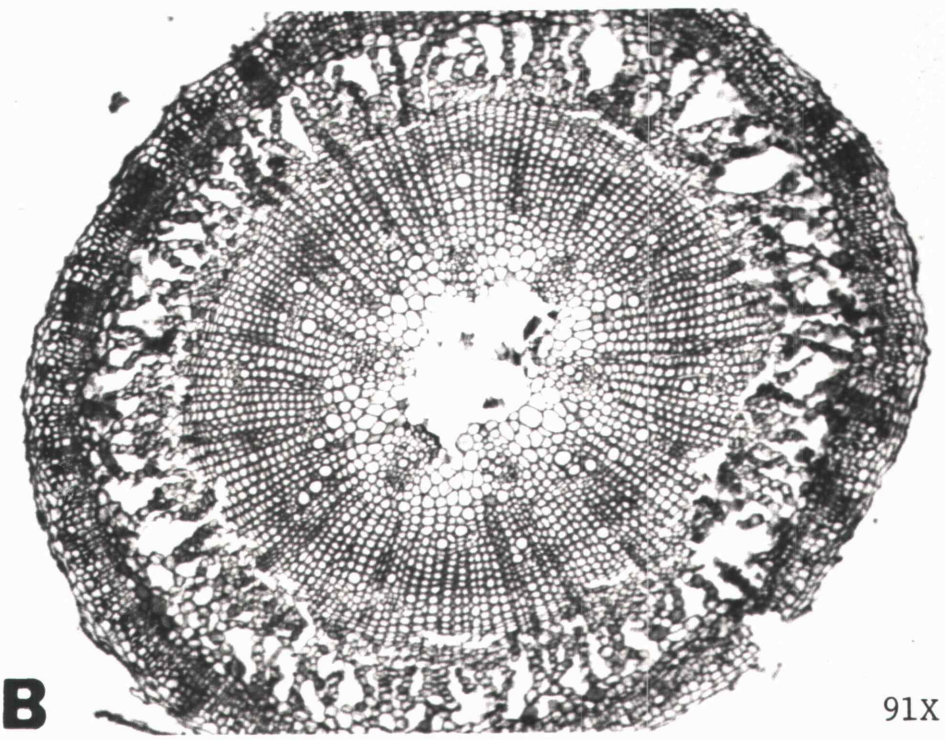




Figure 6. Stem cross sections of Salicornia virginica from its upper and lower distributional limits (A = upper, B = lower).

TABLE 8. Deschampsia cespitosa. MORPHOLOGICAL MEASUREMENTS OF PLANTS ALONG TRANSECT (cm).

| Distances along transect | | Plant length | Stem diameter | Leaf width | Flowering shoot length | Flowering shoot diameter | Inflorescence length |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | 45.2 | 0.12 | 0.22 | 73.8 | 0.20 | 16.3 |
| 0m | SD | 9.2 | 0.03 | 0.04 | 5.1 | 0.05 | 2.3 |
| | N | 68 | 68 | 68 | 4 | 7 | 4 |
| | $\bar{X}$ | 51.5 | 0.12 | 0.24 | 80.5 | 0.19 | 16.0 |
| 6m | SD | 9.5 | 0.03 | 0.05 | 13.1 | 0.05 | 3.8 |
| | N | 45 | 46 | 45 | 10 | 11 | 11 |
| | $\bar{X}$ | 52.7 | 0.13 | 0.25 | 102.2 | 0.18 | 21.0 |
| 13m | SD | 7.3 | 0.04 | 0.05 | 7.4 | 0.06 | 3.7 |
| | N | 43 | 45 | 45 | 4 | 4 | 6 |
| | $\bar{X}$ | 61.6 | 0.13 | 0.24 | 99.1 | 0.19 | 21.3 |
| 21m | SD | 14.8 | 0.04 | 0.04 | 10.7 | 0.02 | 1.9 |
| | N | 19 | 19 | 19 | 8 | 8 | 8 |
| | $\bar{X}$ | 64.1 | 0.16 | 0.27 | 92.8 | 0.23 | 21.0 |
| 31m | SD | 14.6 | 0.04 | 0.07 | 13.5 | 0.04 | 7.1 |
| | N | 43 | 43 | 43 | 6 | 8 | 8 |

TABLE 8 (continued). Deschampsia cespitosa. MORPHOLOGICAL MEASUREMENTS OF PLANTS ALONG TRANSECT (cm).

| Distances along transect | | Plant length | Stem diameter | Leaf width | Flowering shoot length | Flowering shoot diameter | Inflorescence length |
|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | 77.1 | 0.14 | 0.24 | 111.0 | 0.20 | 20.4 |
| 40m | SD | 11.3 | 0.05 | 0.06 | 4.8 | 0.04 | 3.2 |
| | N | 38 | 39 | 39 | 6 | 11 | 9 |
| level of significant difference | | .001* | .001* | .001* | .001* | .50 | .05* |

*considered significant

TABLE 9. Deschampsia cespitosa. SNK RANGE TEST OF SIGNIFICANT VARIABLES (numbers represent distance along transect with 0 being the lower limit of distribution).

| | | | | | |
|---|---|---|---|---|---|
| PLANT LENGTH | | | | | |
| 0m | 6m | 13m | 21m | 31m | 40m |
| STEM DIAMETER | | | | | |
| 0m | 6m | 13m | 21m | 40m | 31m |
| LEAF WIDTH | | | | | |
| 0m | 6m | 21m | 40m | 13m | 31m |
| FLOWERING SHOOT LENGTH | | | | | |
| 0m | 6m | 31m | 21m | 13m | 40m |

above MHW which is lower in elevation than the 31 m site (see Table 10). Therefore greatest plant length occurs at an elevation less than the highest elevation at which the species occurs. Stem diameter is greatest at the highest elevation and greatest leaf width also occurs at this point and also at 13 m which is 0.478 m above MHW. Flower stalk length at the two lowest elevations is the same and is significantly less than length at the four higher points, which are statistically the same (Table 9).

Statistically significant morphological differences were found along the transects of D. cespitosa and the remaining species to be discussed. As would be expected for such a transect, a continuim exists thus making it difficult to draw a line dividing any two transect points such that all differences in morphological characteristics coincide at these points. Perhaps the best way to make such data useful is to select those characteristics that would be most obvious to an observer and relate this to an environmental parameter such as elevation. For example, with D. cespitosa, tallest plants are found at 40 m which has an elevation of 0.761 m above MHW (Table 10). Therefore, it may be possible to extrapolate this data to another marsh and postulate that the point where one finds the tallest D. cespitosa has an elevation of approximately 0.76 m above MHW.

In Table 11, it can be seen that all morphological characteristics of Distichlis spicata differed significantly at various points along the transect. From the SNK range tests of Table 12, it is evident that the upper, middle range (18 m or 0.322 m above MHW) is a significant location in terms of growth characteristics. Here the plant length,

TABLE 10. ELEVATIONAL DATA FOR TRANSECT POINTS (m above MHW).

| | | |
|---|---|---|
| Deschampsia caespitosa | 0m: | 0.324 |
| | 6m: | 0.416 |
| | 13m: | 0.478 |
| | 21m: | 0.673 |
| | 31m: | 0.766 |
| | 40m: | 0.761 |
| Distichlis spicata | 0m: | -0.494 |
| | 6m: | -0.318 |
| | 12m: | 0.053 |
| | 18m: | 0.322 |
| | 24m: | 0.809 |
| Grindelia integrifolia | 0m: | 0.361 |
| | 7m: | 0.488 |
| | 14m: | 0.478 |
| | 21m: | 0.539 |
| | 28m: | 0.641 |
| Jaumea carnosa | 0m: | -0.045 |
| | 7.5m: | 0.149 |
| | 15m: | 0.230 |
| | 22.5m: | 0.250 |
| | 31m: | 0.416 |
| Salicornia virginica | 0m: | 0.126 |
| | 9.5m: | 0.281 |
| | 19m: | 0.354 |
| | 28.5m: | 0.417 |
| | 38m: | 0.498 |

TABLE 11. Distichlis spicata. MORPHOLOGICAL MEASUREMENTS OF PLANTS ALONG TRANSECT (cm).

| | | Plant length | No. leaves | Length 3rd internode | Length 4th internode | Leaf width | Stem diameter |
|---|---|---|---|---|---|---|---|
| 0m | $\bar{X}$ | 13.7 | 10.4 | 0.94 | 0.83 | 0.24 | 0.08 |
| | SD | 6.8 | 4.4 | 0.36 | 0.39 | 0.05 | 0.03 |
| | N | 32 | 32 | 27 | 26 | 30 | 32 |
| 6m | $\bar{X}$ | 9.6 | 11.6 | 0.44 | 0.48 | 0.23 | 0.10 |
| | SD | 4.2 | 3.5 | 0.24 | 0.18 | 0.04 | 0.02 |
| | N | 61 | 58 | 53 | 53 | 53 | 61 |
| 12m | $\bar{X}$ | 12.2 | 10.8 | 0.48 | 0.60 | 0.28 | 0.09 |
| | SD | 4.2 | 3.6 | 0.28 | 0.23 | 0.04 | 0.04 |
| | N | 52 | 50 | 44 | 44 | 45 | 52 |
| 18m | $\bar{X}$ | 5.6 | 9.4 | 0.30 | 0.30 | 0.28 | 0.11 |
| | SD | 2.1 | 2.5 | 0.13 | 0.12 | 0.06 | 0.03 |
| | N | 49 | 47 | 43 | 41 | 45 | 48 |
| 24m | $\bar{X}$ | 9.7 | 8.3 | 0.52 | 0.59 | 0.25 | 0.08 |
| | SD | 3.9 | 2.5 | 0.26 | 0.26 | 0.06 | 0.03 |
| | N | 82 | 78 | 70 | 55 | 77 | 78 |
| level of significant difference | | .001 | .001 | .001 | .001 | .001 | .001 |

TABLE 12. *Distichlis spicata*. SNK RANGE TEST OF SIGNIFICANT VARIABLES (numbers represent distance along transect with 0 being the lower limit of distribution).

| PLANT LENGTH | | | | |
|---|---|---|---|---|
| 18m | 6m | 24m | 12m | 0m |

| NO. LEAVES | | | | |
|---|---|---|---|---|
| 24m | 18m | 0m | 12m | 6m |

| LENGTH 3RD INTERNODE | | | | |
|---|---|---|---|---|
| 18m | 6m | 12m | 24m | 0m |

| LENGTH 4TH INTERNODE | | | | |
|---|---|---|---|---|
| 18m | 6m | 24m | 12m | 0m |

| LEAF WIDTH | | | | |
|---|---|---|---|---|
| 6m | 0m | 24m | 12m | 18m |

| STEM DIAMETER | | | | |
|---|---|---|---|---|
| 0m | 24m | 12m | 6m | 18m |

leaf number, and third and fourth internode lengths are greatest. Also at this upper, middle position, leaf width and stem diameter are least. Therefore, measuring these characteristics might give an indication of approximately where in the marsh the elevation of 0.3 m above MHW is located.

With Grindelia integrifolia only three characteristics proved to be statistically significantly different along the transect (Tables 13 and 14). Vegetative rosette length and flowering shoot length were both greatest at 21 m (upper middle range) at an elevation of 0.539 m above MHW. Stem diameter was greatest at 0 m (0.361 m above MHW). Perhaps greatest vegetative and flowering shoot length could be used in this marsh as an indication of an elevation of approximately 0.5 m above MHW.

All morphological characteristics measured on Jaumea carnosa were found to be significantly different along the transect (Tables 15 and 16). In five out of the eight characteristics measured, 7.5 m (0.149 m above MHW) appeared to be an important point along the transect. Here plant length, stem diameter, number of nodes and leaf number were the least and leaf thickness was the greatest. Perhaps such morphological characteristics should be used to find that area of the marsh approximately 0.15 m above MHW.

Seven of the eight characteristics measured on Salicornia virginica proved to differ significantly along the transect (Table 17). Table 18 illustrates, with SNK range tests, where these differences occurred. In every case, those plants at 0 m (0.126 m above MHW) possessed the lowest values. So, it is possible that finding such

TABLE 13. Grindelia integrifolia. MORPHOLOGICAL MEASUREMENTS OF PLANTS ALONG TRANSECT (cm).

| | | Flowering shoot length | Flowering shoot diameter | No. flowers per stalk | Stem length | Stem diameter | No. leaves | Leaf width | Total length wood |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | 25.6 | 0.19 | 1.0 | 19.3 | 0.47 | 5.4 | 2.1 | 16.0 |
| 0m | SD | 1.9 | 0.02 | 0.0 | 1.5 | 0.14 | 1.0 | 0.3 | |
| | N | 4 | 4 | 4 | 9 | 9 | 9 | 8 | |
| | $\bar{X}$ | 26.1 | 0.24 | 1.7 | 20.9 | 0.31 | 5.7 | 1.9 | 41.0 |
| 7m | SD | 4.6 | 0.05 | 0.5 | 3.2 | 0.09 | 1.3 | 0.6 | |
| | N | 9 | 9 | 9 | 15 | 15 | 15 | 13 | |
| | $\bar{X}$ | 29.2 | 0.24 | 1.9 | 21.0 | 0.33 | 5.0 | 2.1 | 89.0 |
| 14m | SD | 5.2 | 0.10 | 1.3 | 3.0 | 0.09 | 1.6 | 0.3 | |
| | N | 17 | 17 | 17 | 19 | 19 | 19 | 16 | |
| | $\bar{X}$ | 33.1 | 0.25 | 1.7 | 23.9 | 0.31 | 5.0 | 1.8 | 154.0 |
| 21m | SD | 5.8 | 0.05 | 0.6 | 3.9 | 0.09 | 1.2 | 0.5 | |
| | N | 18 | 18 | 18 | 21 | 21 | 21 | 17 | |
| | $\bar{X}$ | 32.2 | 0.20 | 1.7 | 19.6 | 0.31 | 6.3 | 1.5 | 162.0 |
| 28m | SD | 6.1 | 0.07 | 1.0 | 1.1 | 0.08 | 2.5 | 0.4 | |
| | N | 27 | 27 | 27 | 9 | 9 | 9 | 7 | |
| level of significant difference | | .01* | .25 | .75 | .001* | .001* | .25 | .05* | |

*considered significant

TABLE 14. Grindelia integrifolia. SNK RANGE TEST OF SIGNIFICANT VARIABLES (numbers represent distance along transect with 0 being the lower limit of distribution).

| STEM LENGTH | | | | |
|---|---|---|---|---|
| 0m | 28m | 7m | 14m | 21m |

| STEM DIAMETER | | | | |
|---|---|---|---|---|
| 7m | 21m | 28m | 14m | 0m |

| FLOWER STALK LENGTH | | | | |
|---|---|---|---|---|
| 0m | 7m | 14m | 28m | 21m |

TABLE 15. *Jaumea carnosa*. MORPHOLOGICAL MEASUREMENTS OF PLANTS ALONG TRANSECT (cm).

| | | Plant length | Stem diameter | No. nodes | Length 2nd internode | Length 3rd internode | No. leaves | Leaf width | Leaf thickness |
|---|---|---|---|---|---|---|---|---|---|
| 0m | $\bar{X}$ | 15.2 | 0.16 | 8.7 | 1.0 | 1.3 | 20.7 | 0.25 | 0.12 |
| | SD | 4.2 | 0.03 | 3.0 | 0.4 | 0.5 | 5.8 | 0.06 | 0.04 |
| | N | 98 | 60 | 60 | 58 | 57 | 59 | 52 | 52 |
| 7.5m | $\bar{X}$ | 11.5 | 0.14 | 6.1 | 1.4 | 2.0 | 14.7 | 0.31 | 0.16 |
| | SD | 2.9 | 0.03 | 2.2 | 0.6 | 0.7 | 4.3 | 0.07 | 0.03 |
| | N | 75 | 60 | 60 | 60 | 58 | 60 | 60 | 55 |
| 15m | $\bar{X}$ | 15.8 | 0.15 | 7.7 | 1.5 | 2.1 | 17.8 | 0.43 | 0.14 |
| | SD | 5.0 | 0.03 | 3.3 | 0.6 | 0.7 | 6.7 | 0.11 | 0.03 |
| | N | 37 | 37 | 37 | 37 | 35 | 37 | 30 | 29 |
| 22.5m | $\bar{X}$ | 21.0 | 0.16 | 10.1 | 1.3 | 1.4 | 22.6 | 0.40 | 0.10 |
| | SD | 4.5 | 0.02 | 3.5 | 0.5 | 0.3 | 7.1 | 0.09 | 0.00 |
| | N | 34 | 13 | 13 | 13 | 12 | 13 | 13 | 11 |
| 30m | $\bar{X}$ | 23.7 | 0.14 | 9.7 | 1.7 | 2.1 | 22.2 | 0.45 | 0.10 |
| | SD | 7.8 | 0.03 | 3.5 | 0.4 | 0.5 | 7.1 | 0.09 | 0.02 |
| | N | 43 | 36 | 36 | 36 | 35 | 36 | 27 | 22 |
| level of significant difference | | .001* | .025* | .001* | .001* | .001* | .001* | .001* | .001* |

*considered significant

TABLE 16. *Jaumea carnosa*. SNK RANGE TEST OF SIGNIFICANT VARIABLES (numbers represent distance along transect with 0 being the lower limit of distribution).

| PLANT LENGTH | | | | |
|---|---|---|---|---|
| 7.5m | 0m | 15m | 22.5m | 30m |

| STEM DIAMETER | | | | |
|---|---|---|---|---|
| 7.5m | 30m | 15m | 22.5m | 0m |

| NO. NODES | | | | |
|---|---|---|---|---|
| 7.5m | 15m | 0m | 30m | 22.5m |

| LENGTH 2ND INTERNODE | | | | |
|---|---|---|---|---|
| 0m | 22.5m | 7.5m | 15m | 30m |

| LENGTH 3RD INTERNODE | | | | |
|---|---|---|---|---|
| 0m | 22.5m | 7.5m | 30m | 15m |

| NO. LEAVES | | | | |
|---|---|---|---|---|
| 7.5m | 15m | 0m | 30m | 22.5m |

| LEAF WIDTH | | | | |
|---|---|---|---|---|
| 0m | 7.5m | 22.5m | 15m | 30m |

| LEAF THICKNESS | | | | |
|---|---|---|---|---|
| 30m | 22.5m | 0m | 15m | 7.5m |

TABLE 17. *Salicornia virginica*. MORPHOLOGICAL MEASUREMENTS OF PLANTS ALONG TRANSECT (cm).

| | | Stem length | No. internodes | Internode length | No. primary branches | No. secondary branches | Dry wt/vol internode | Stem diameter | No. flowers |
|---|---|---|---|---|---|---|---|---|---|
| | $\bar{X}$ | 19.6 | 16.2 | 1.2 | 6.3 | 1.8 | 0.10 | 0.10 | 0.6 |
| 0m | SD | 4.5 | 3.4 | 0.2 | 6.2 | 6.3 | 0.03 | 0.02 | 2.3 |
| | N | 44 | 44 | 44 | 44 | 44 | 14 | 44 | 44 |
| | $\bar{X}$ | 24.7 | 13.4 | 1.3 | 9.4 | 8.9 | 0.12 | 0.10 | 3.1 |
| 9.5m | SD | 5.2 | 3.8 | 0.2 | 4.4 | 10.0 | 0.03 | 0.03 | 3.1 |
| | N | 14 | 14 | 14 | 14 | 14 | 8 | 14 | 14 |
| | $\bar{X}$ | 24.7 | 15.0 | 1.3 | 15.0 | 2.1 | 0.13 | 0.13 | 3.4 |
| 19m | SD | 4.4 | 3.4 | 0.2 | 4.4 | 4.3 | 0.03 | 0.03 | 3.7 |
| | N | 32 | 32 | 32 | 32 | 32 | 19 | 32 | 32 |
| | $\bar{X}$ | 34.2 | 22.2 | 1.4 | 28.7 | 19.9 | 0.12 | 0.12 | 0.9 |
| 28.5m | SD | 8.6 | 6.4 | 0.4 | 10.0 | 26.2 | 0.04 | 0.03 | 1.6 |
| | N | 15 | 15 | 15 | 15 | 15 | 10 | 15 | 15 |
| | $\bar{X}$ | 30.4 | 20.6 | 1.4 | 21.2 | 2.0 | 0.11 | 0.11 | 0.8 |
| 38m | SD | 9.2 | 5.8 | 0.3 | 12.1 | 6.4 | 0.02 | 0.04 | 1.6 |
| | N | 25 | 25 | 25 | 25 | 25 | 13 | 25 | 25 |
| level of significant difference | | .001* | .001* | .001* | .001* | .001* | .10 | .001* | .001* |

*considered significant

TABLE 18. *Salicornia virginica*. SNK RANGE TEST OF SIGNIFICANT VARIABLES (numbers represent distance along transect with 0 being the lower limit of distribution).

| STEM LENGTH | | | | |
|---|---|---|---|---|
| 0m | 19m | 9.5m | 38m | 28.5m |

| NO. INTERNODES | | | | |
|---|---|---|---|---|
| 9.5m | 19m | 0m | 38m | 28.5m |

| INTERNODE LENGTH | | | | |
|---|---|---|---|---|
| 0m | 9.5m | 19m | 28.5m | 38m |

| NO. PRIMARY BRANCHES | | | | |
|---|---|---|---|---|
| 0m | 9.5m | 19m | 38m | 28.5m |

| NO. SECONDARY BRANCHES | | | | |
|---|---|---|---|---|
| 0m | 38m | 19m | 9.5m | 28.5m |

| STEM DIAMETER | | | | |
|---|---|---|---|---|
| 0m | 9.5m | 38m | 28.5m | 19m |

| NO. FLOWERS | | | | |
|---|---|---|---|---|
| 0m | 38m | 28.5m | 9.5m | 19m |

values would be indicative of an elevation around 0.13 m above MHW. For five of the seven characteristics, 28.5 m gave the greatest values, therefore, such values for the various characteristics would possibly be useful in locating this higher elevation, 0.42 m above MHW.

For an explanation of the morphological differences found along these transects the possible reasons discussed in the previous section, entitled "Upper vs Lower Distributional Limit", would hold true here also. Most cases in the literature, however, report results from much more extreme situations, i.e., the distances between points along the transects in this study are minute when compared to those in previous studies (for example, Clausen, Keck and Heisey, 1948). Finding such large and statistically significant differences in morphological characteristics within these "micro-transects" reflects the large environmental gradients found in a wetland ecosystem.

Anatomy

Stem cross sections from plants collected at each transect point were made of Distichlis spicata, Grindelia integrifolia, Jaumea carnosa, Salicornia virginica, and Deschampsia cespitosa. No differences in stem anatomy of D. cespitosa were found along its transect.

Cross sections of D. spicata can be seen in Figures 7A-E. Lignification of the vascular bundle sheath is greatest in plants from the upper marsh zone (7A) and lessens with progression down the marsh.

Figures 8A-C are stem cross sections of G. integrifolia. Here once again greatest secondary xylem formation occurs in plants from the upper marsh zone (8A). The amount of secondary xylem tissue is

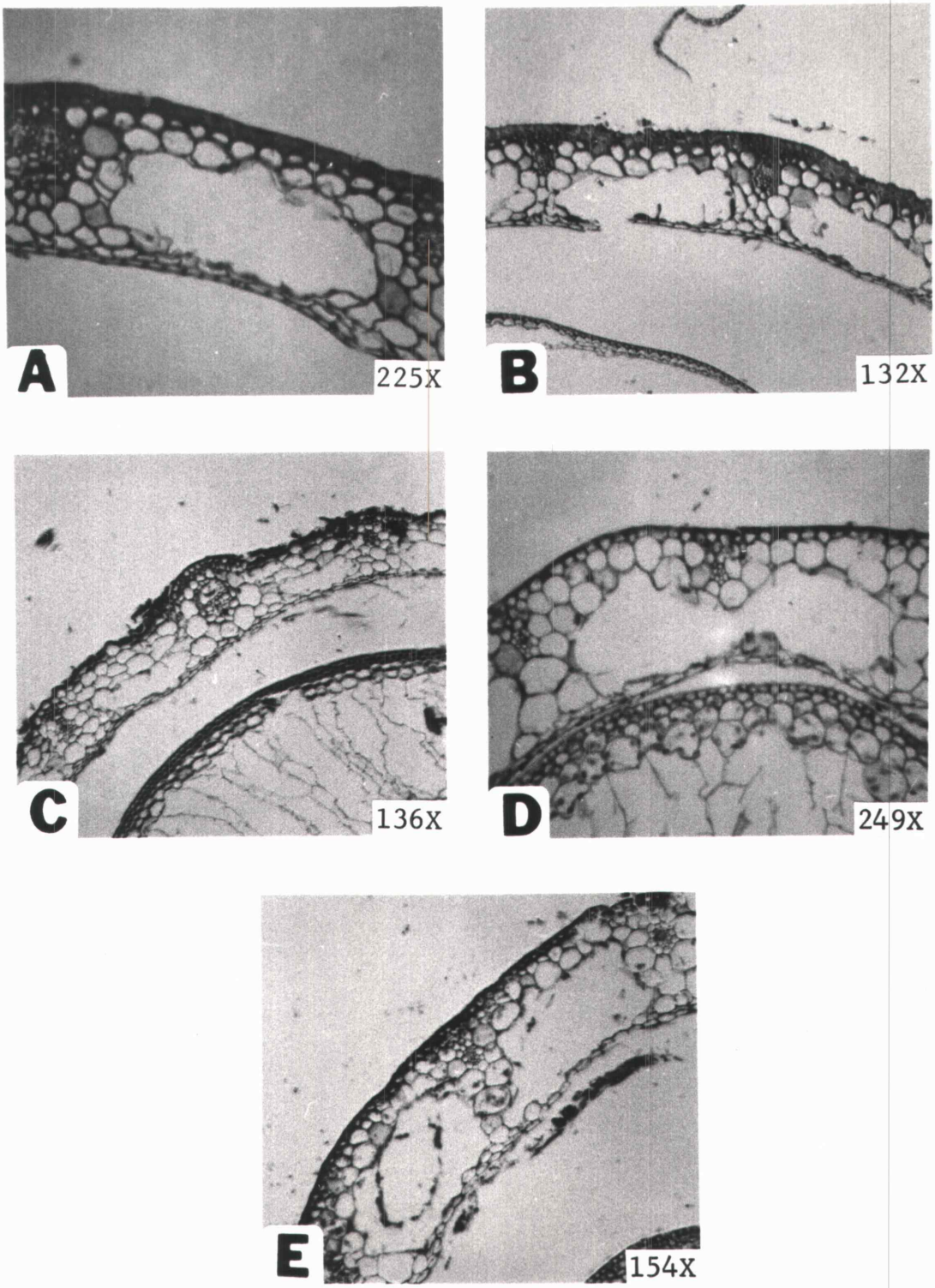



Figure 7. Stem cross sections of Distichlis spicata along transect (A = 24 m, B = 18 m, C = 12 m, D = 6 m, E = 0 m).

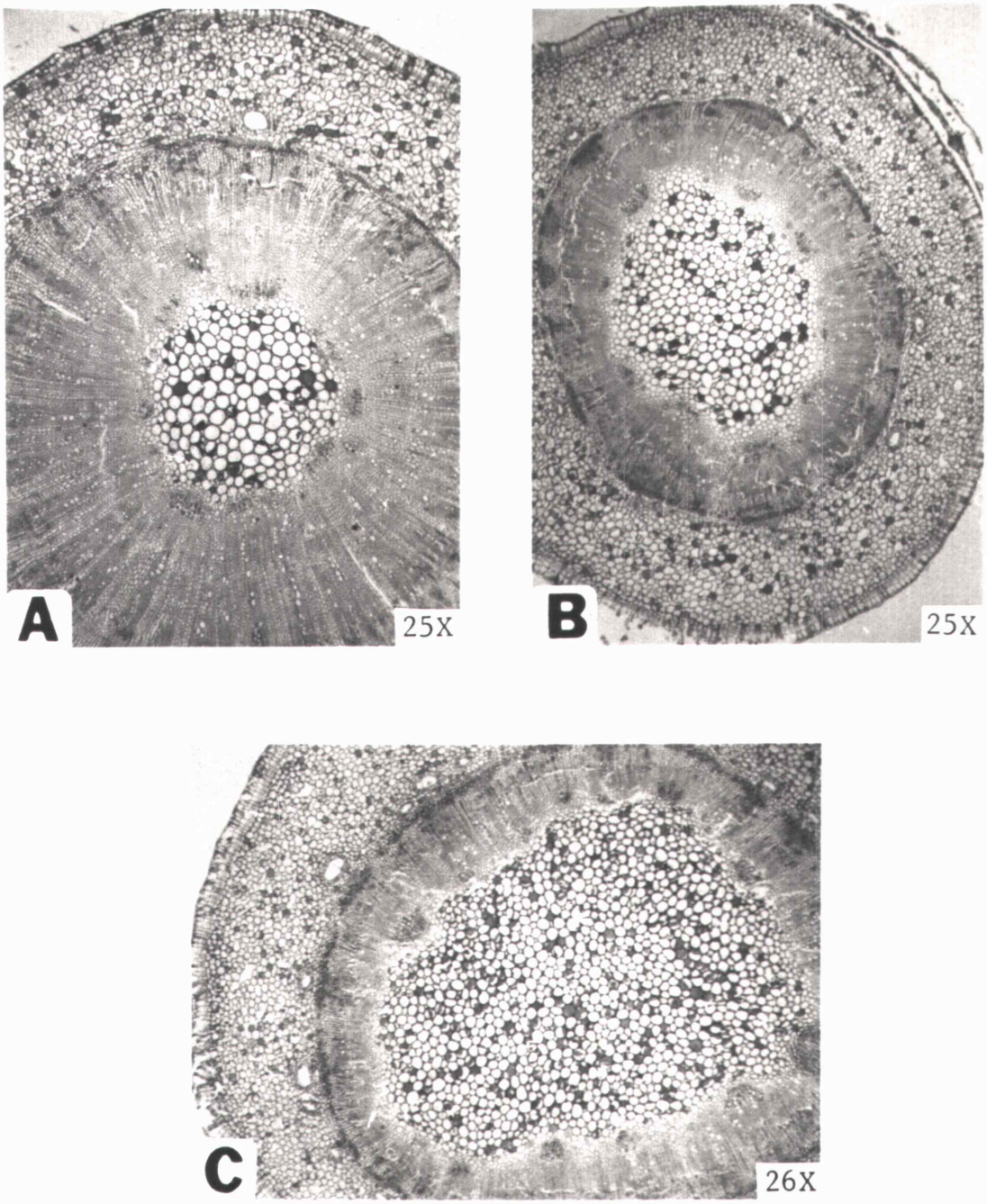



Figure 8. Stem cross sections of Grindelia integrifolia along transect (A = 28 m, B = 14 m, C = 0 m).

least at the lower limit (8 C) and intermediate in the middle of the transect (8 B).

Vascular bundles in stems of J. carnosa from the species' upper distributional limit are greater in their diameter and number of xylem vessels (Figure 9 A) than in those stems from the lower limit (Figure 9). At the transect's midpoint bundle size is intermediate (Figure 9B).

Cross sections of stems of S. virginica collected along the transect are displayed in Figures 10A-C. Aerenchyma formation is greatest in those plants from the lower marsh zone (10C) while such extensive development of this tissue is not obvious in plants from the upper distributional limit (10A). An intermediate amount of aerenchyma is seen in those sections taken from plants at the transect's midpoint (10B). Possible explanations of the observed phenomena were discussed in the "Upper vs Lower Distributional Limit" section of this thesis.

## Soil Moisture

Soil moisture data for the upper and lower limits of each transect are discussed in the transplant section of this thesis. However, it is possible to consolidate these data and obtain a picture of soil moisture in the north marsh site at various points along a wide transect ranging in elevation between upland and mudflat. Figure 11 illustrates these data for May through November, 1979, at the 10 cm depth. The solid line (#1) (the highest elevation studied, 1.014 m above MHW) indicates soil moisture as measured by centibars tension (the greater the value, the drier the soil) at the base of a ridge covered with

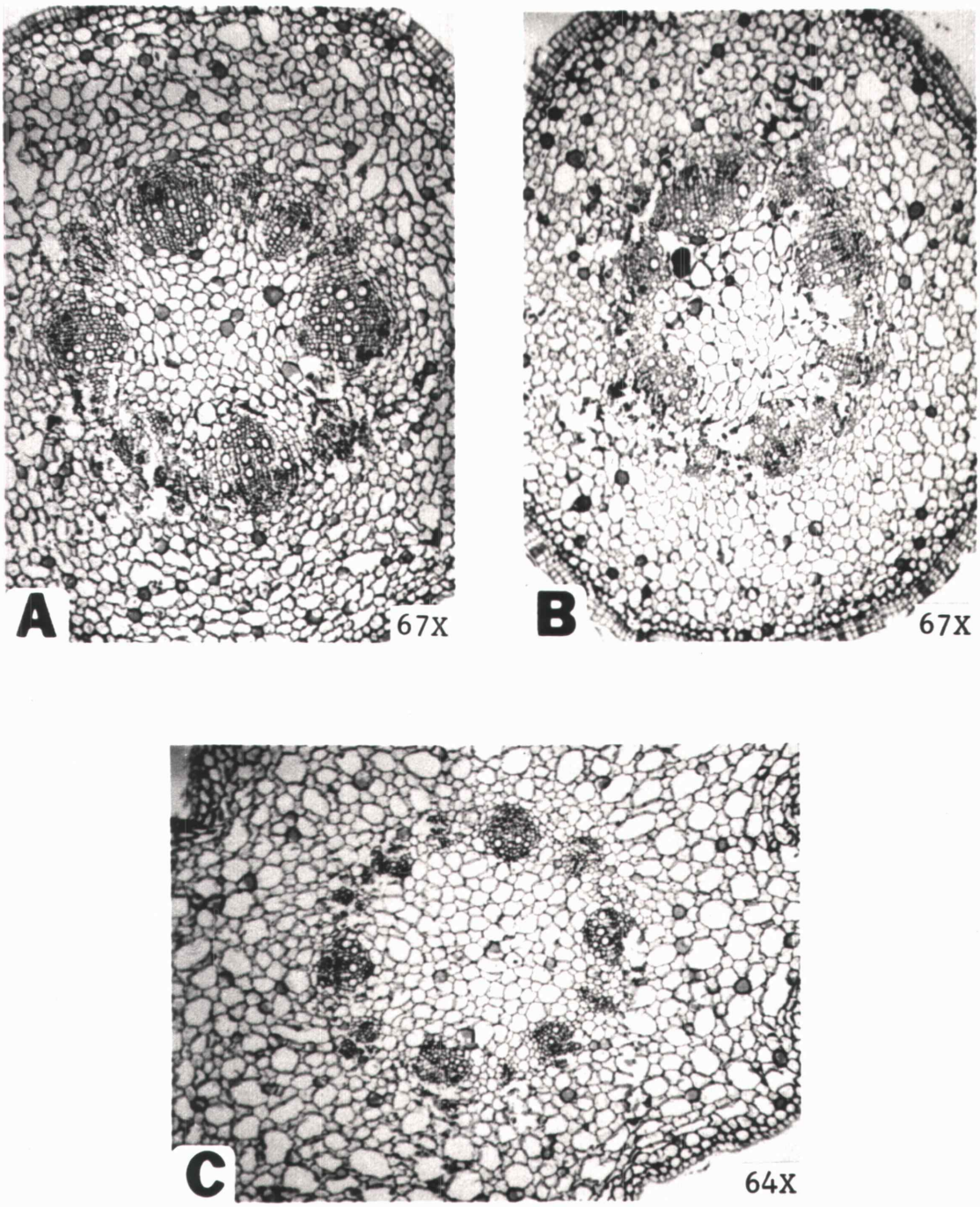



Figure 9. Stem cross sections of Jaumea carnosa along transect (A = 31 m, B = 15 m, C = 0 m).

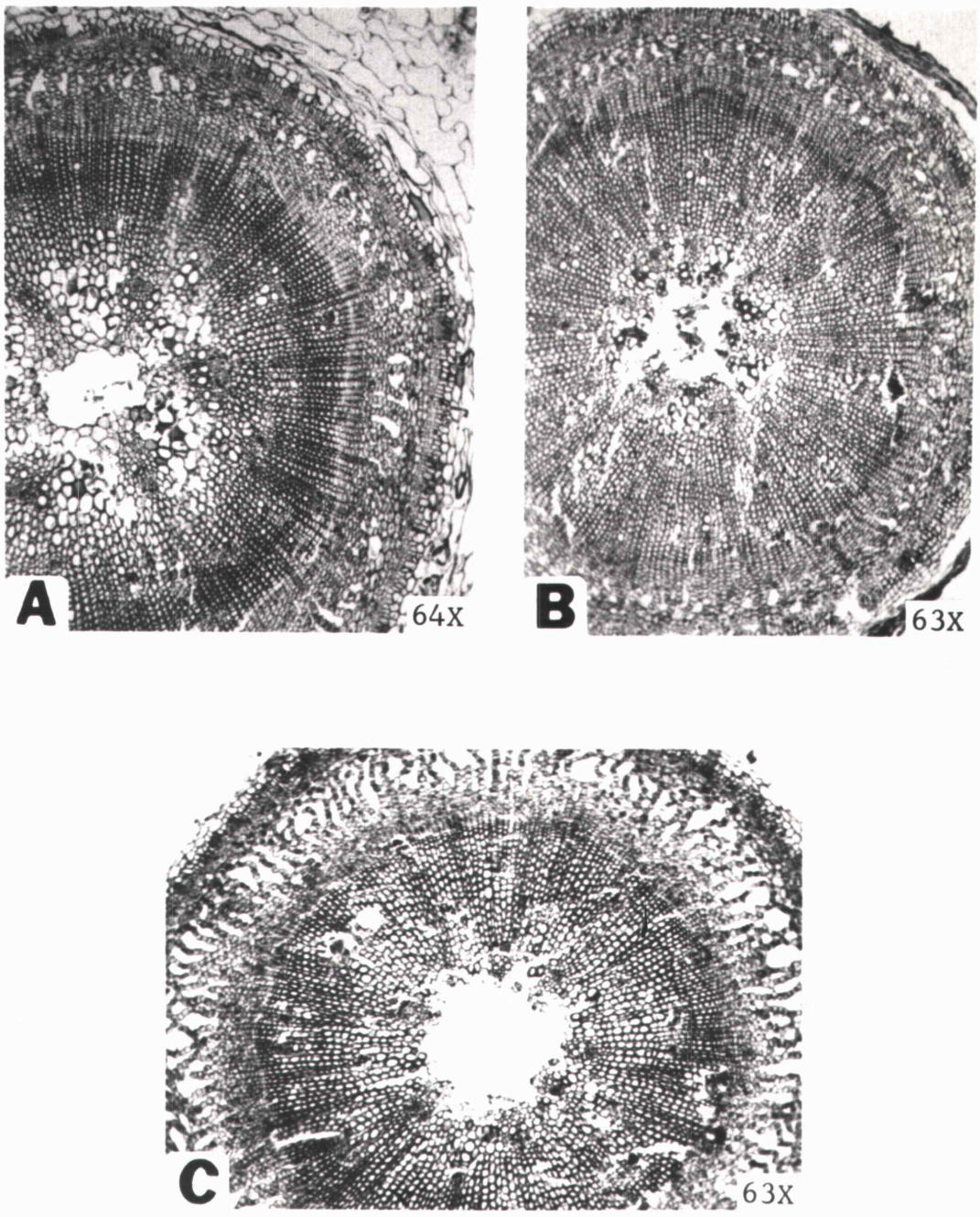



Figure 10. Stem cross sections of Salicornia virginica along transect (A = 38 m, B = 19 m, C = 0 m).

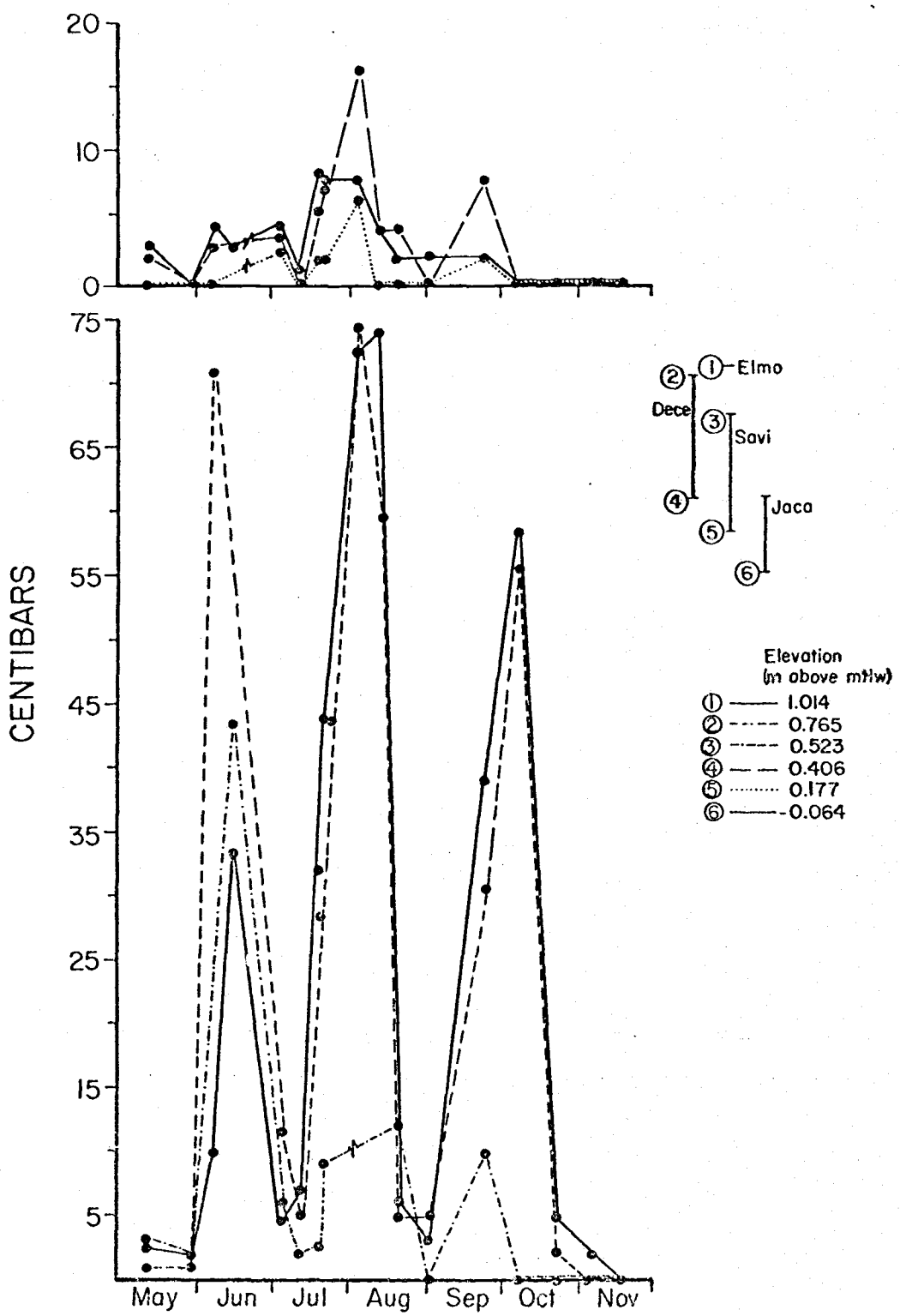



Figure 11. Soil moisture tension for the north sampling area, May-November, 1979 (depth = 10 cm).

*Elymus mollis* - assumed in this project to start upland vegetation. The reason for a low June value at this site is unknown. The next highest point along the transect is located at the upper distributional limit of *Deschampsia cespitosa* (0.765 m above MHW) and is represented in the figure as a dashed line (#2). The upper distributional limit of *Salicornia virginica* (0.523 m above MHW) is below the *D. cespitosa* level. This point is represented by the dotted-dashed line.(#3). The remaining three transect points are represented in the upper portion of the figure. Included, in the order of decreasing elevation, are the lower distributional limit of *D. cespitosa* which coincides with the upper *Jaumea carnosa* limit (0.406 m above MHW), the lower distributional limit of *S. virginica* (0.177 m above MHW), and the lower limit of *J. carnosa* (0.064 m below MHW).

In general, soil moisture increases with a decrease in elevation. This is not the case with transect point #5 (Figure 11), however. Here the dotted line representing the lower *S. virginica* site at 0.177 m above MHW occurs below the solid line (#6), -0.064 m above MHW. This is explained by the fact that at the lower *S. virginica* site the tensiometers were situated in a small valley or pool which prevented normal drainage from the slope.

With each elevation, the peaks in soil dryness occurred at the same time of year, but to a different degree. Dry periods occurred during mid June, late July/early August and late September/early October. Thus, the wet periods were May, early July, late August/early September, and November.

To determine what caused these fluctuations, precipitation data for Tillamook, Oregon (10 miles NE of Netarts) (Figure 12) (NOAA, 1979) and predicted tidal data for Netarts Bay (Figure 13) (NOAA, 1978) were studied. From Figure 12, which illustrates precipitation in inches, it can be seen that the wet periods, as seen in the tensiometer data, coincide with the wettest periods in terms of precipitation. Tidal data for these months is represented in Figure 13 and although in some places the highest tides coincide with high soil moisture it is believed precipitation is the main influence in the fluctuation.

It can be seen from Figure 11 that the conclusion of Lewis and Liverman (1979) concerning the inability to delineate wetlands using only one or a few soil moisture measurements is true. Soil moisture fluctuations throughout a season are great.

## Soil Chemical Properties

Certain trends can be extracted from the chemical property data displayed in Tables 19 through 23, even though replicate soil samples were not analyzed. Salinity in each case, as measured by K and Na, decreases from low to high marsh. This occurs because tidal inundation is most frequent at the lower elevations and salt water is continually flushing the soil. At higher elevations precipitation has a chance to dilute the salt from the previous inundation.

Total nitrogen is very low in the Distichlis spicata sites (Table 20). This is not surprising since the soil at this particular site consisted totally of sand. K, Ca, and Mg are also low in this sandy soil. The buffered pH ($pH^B$) is highest in D. spicata soil

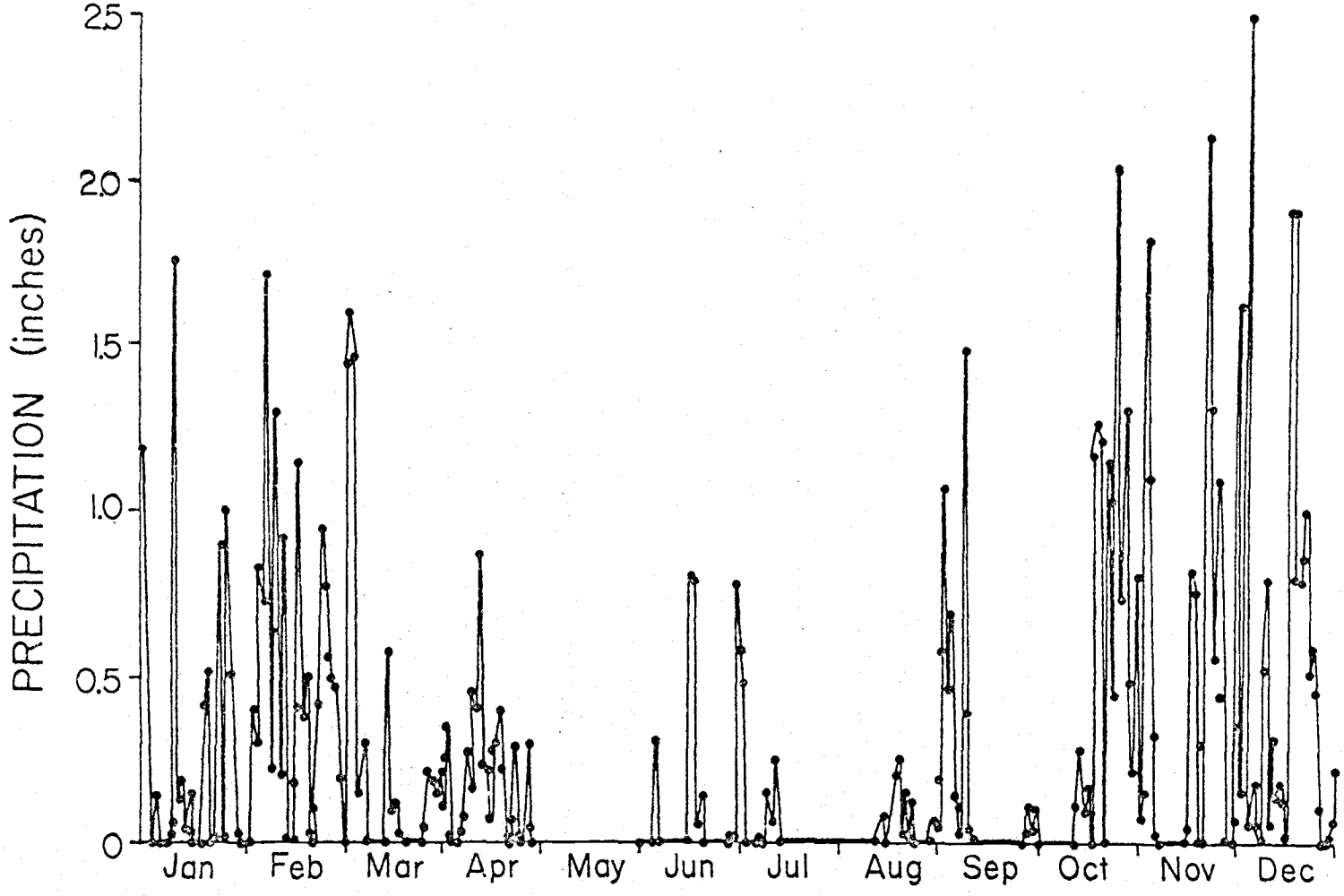



Figure 12 1979 precipitation for Tillamook, Oregon.

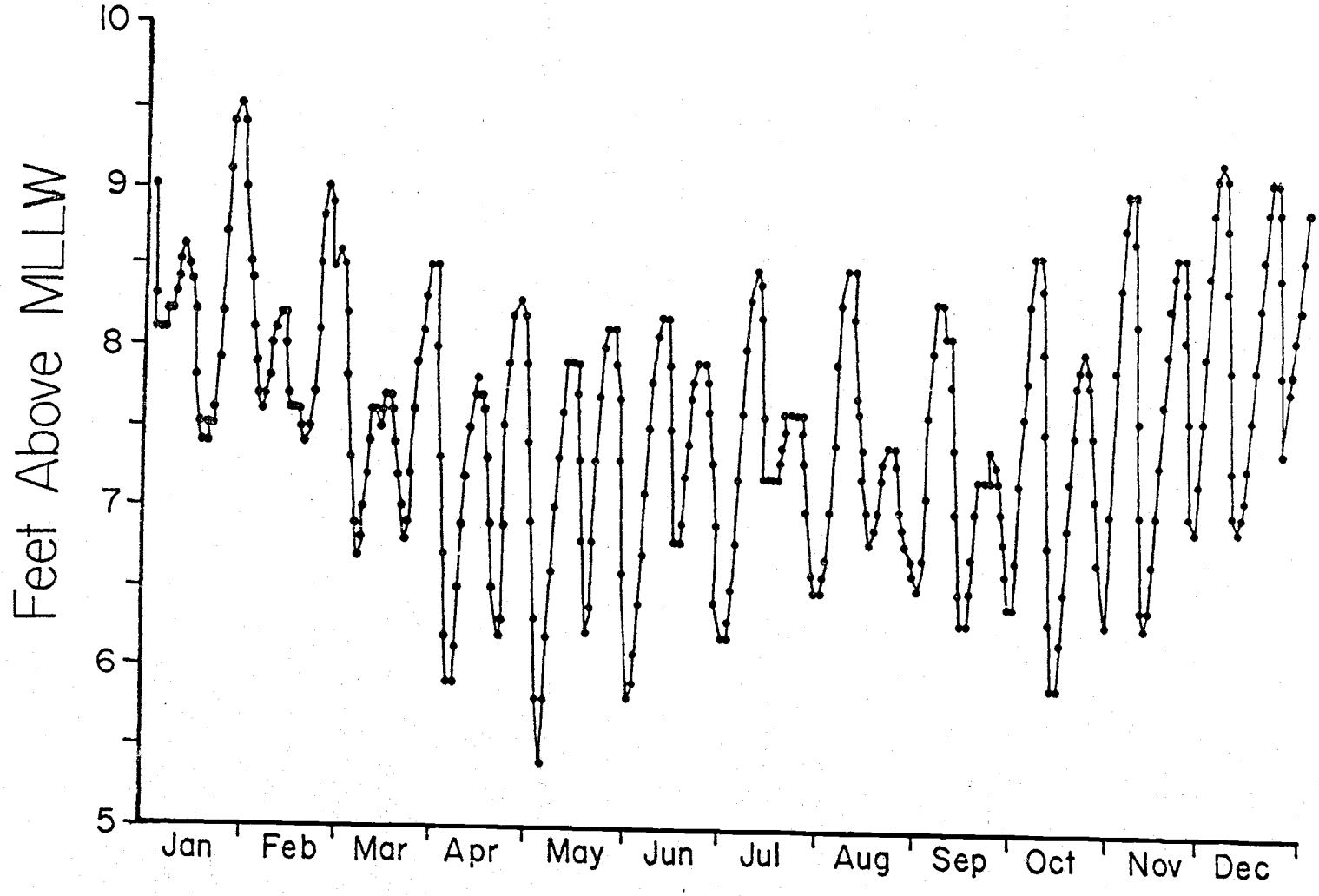



Figure 13. 1979 high tides at Netarts Bay, Oregon.

TABLE 19. SOIL CHEMICAL PROPERTIES ALONG THE *Deschampsia cespitosa* TRANSECT (0 = lower distributional limit).

| Distance (m) | $pH^W$ | $pH^B$ | P (ppm) | K (ppm) | Ca (meq/100g) | Mg (meq/100g) | Na (meq/100g) | Total N (%) | $NO_3$ (ppm) | $NH_4$ (ppm) |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 6.0 | 6.6 | 17 | 1872 | 8.8 | 26.0 | 57.0 | 0.56 | 84.24 | 14.04 |
| 13 | 6.2 | 6.6 | 20 | 1646 | 9.7 | 28.0 | 44.0 | 0.76 | 69.52 | 14.84 |
| 21 | 6.5 | 6.8 | 22 | 858 | 6.3 | 14.0 | 14.7 | 0.60 | 24.60 | 4.82 |
| 31 | 7.1 | 6.9 | 19 | 725 | 5.3 | 11.0 | 10.5 | 0.44 | 14.36 | 4.42 |
| 40 | 6.8 | 6.8 | 19 | 605 | 5.9 | 13.0 | 10.2 | 0.62 | 18.22 | 6.02 |

TABLE 20. SOIL CHEMICAL PROPERTIES ALONG THE *Distichlis spicata* TRANSECT (0 = lower distributional limit).

| Distance (m) | $pH^W$ | $pH^B$ | P (ppm) | K (ppm) | Ca (meq/100g) | Mg (meq/100g) | Na (meq/100g) | Total N (%) | $NO_3$ (ppm) | $NH_4$ (ppm) |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 5.9 | 7.3 | 21 | 195 | 0.9 | 1.9 | 5.0 | 0.02 | 0.90 | 5.22 |
| 6 | 6.1 | 7.3 | 17 | 289 | 1.6 | 4.1 | 15.3 | 0.09 | 0.90 | 8.83 |
| 12 | 6.6 | 7.4 | 19 | 199 | 1.1 | 2.6 | 7.4 | 0.03 | 6.28 | 2.61 |
| 18 | 6.6 | 7.4 | 19 | 129 | 1.0 | 1.9 | 6.8 | 0.01 | 0.68 | 1.30 |
| 24 | 6.8 | 7.4 | 20 | 90 | 0.9 | 1.1 | 0.83 | 0.02 | 0.90 | 4.61 |

TABLE 21. SOIL CHEMICAL PROPERTIES ALONT THE *Grindelia integrifolia* TRANSECT (0 = lower distributional limit).

| Distance (m) | $pH^W$ | $pH^B$ | P (ppm) | K (ppm) | Ca (mgq/100g) | Mg (meq/100g) | Na (meq/100g) | Total N (%) | $NO_3$ (ppm) | $NH_4$ (ppm) |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 5.8 | 6.6 | 26 | 1755 | 6.6 | 22.0 | 54.0 | 0.42 | 1.34 | 5.62 |
| 7 | 5.9 | 6.6 | 24 | 1677 | 6.7 | 20.0 | 35.5 | 0.54 | 9.86 | 14.04 |
| 14 | 6.1 | 6.6 | 17 | 1416 | 7.0 | 19.0 | 33.0 | 0.48 | 36.78 | 13.64 |
| 21 | 6.1 | 6.8 | 20 | 1221 | 6.0 | 17.0 | 25.4 | 0.56 | 0.92 | 9.22 |
| 28 | 6.4 | 7.0 | 19 | 542 | 4.0 | 8.6 | 11.1 | 0.60 | 1.80 | 8.82 |

TABLE 22. SOIL CHEMICAL PROPERTIES ALONG THE *Jaumea carnosa* TRANSECT (0 = lower distributional limit).

| Distance (m) | $pH^W$ | $pH^B$ | P (ppm) | K (ppm) | Ca (meq/100g) | Mg (meq/100g) | Na (meq/100g) | Total N (%) | $NO_3$ (ppm) | $NH_4$ (ppm) |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 6.2 | 7.1 | 9 | 608 | 2.5 | 6.8 | 254.0 | 0.16 | 0.67 | 0.80 |
| 7.5 | 6.1 | 6.9 | 18 | 1872 | 7.4 | 21.0 | 70.0 | 0.38 | 2.24 | 14.84 |
| 15 | 5.9 | 6.7 | 15 | 2301 | 7.5 | 24.0 | 63.0 | 0.52 | 7.18 | 10.04 |
| 22.5 | 6.0 | 6.4 | 21 | 2106 | 10.5 | 27.0 | 68.0 | 0.82 | 92.26 | 27.68 |
| 30 | 6.1 | 6.6 | 17 | 1747 | 9.5 | 26.0 | 51.0 | 0.66 | 92.26 | 11.64 |

TABLE 23. SOIL CHEMICAL PROPERTIES ALONT THE *Salicornia virginica* TRANSECT (0 = lower distributional limit).

| Distance (m) | $pH^W$ | $pH^B$ | P (ppm) | K (ppm) | Ca (meq/100g) | Mg (meq/100g) | Na (meq/100g) | Total N (%) | $NO_3$ (ppm) | $NH_4$ (ppm) |
|---|---|---|---|---|---|---|---|---|---|---|
| 0 | 5.8 | 6.6 | 25 | 2184 | 8.2 | 25.0 | 76.0 | 0.60 | 25.06 | 35.30 |
| 9.5 | 5.8 | 6.5 | 18 | 1950 | 8.3 | 24.0 | 55.0 | 0.50 | 12.56 | 8.42 |
| 19 | 5.9 | 6.5 | 17 | 1911 | 8.8 | 25.0 | 59.0 | 0.64 | 56.50 | 10.84 |
| 28.5 | 6.1 | 6.6 | 16 | 1794 | 9.7 | 28.0 | 54.0 | 0.64 | 100.28 | 11.64 |
| 38 | 6.6 | 6.8 | 22 | 1466 | 9.4 | 23.0 | - | 0.70 | 42.82 | 10.84 |

indicating a lower capacity factor of soil acidity for this soil, which is expected of sand.

The soil pH increases slightly from lower to upper marsh in the case of each species. Since ammonia ion concentration increases from upper to lower marsh it is somewhat surprising that the soils at the lower end of the transects are less basic than those at the upper end. $NH_4$ ion concentration is therefore not the determining factor here. If pH had been taken directly in the field it would be understandable that the wetter soil would have a more basic pH since the hydronium ions displace the $Na^+$ ions which, under drier conditions, saturate the soil cation exchange capacity. Thus more hydroxyl ions remain in the water combining with the displaced $Na^+$ ions giving NaOH, a base. However, soil samples were dried, ground and analyzed, therefore, equilizing moisture content.

Following are trends in the morphology of each plant species in relation to the soil chemical properties.

Stem diameter and leaf width of Deschampsia cespitosa is greatest at 31 m (0.766 m above MHW) where total N, $NO_3$, $NH_4$, and Mg are lowest (Tables 9 and 19). Plant length is greatest at 40 m (0.761 m above MHW) where these factors are also on the low side. This is somewhat surprising since one would expect less growth where nitrogen is low. Valiela, et al. (1978), showed that with fertilization, there was a shift in the morphology of Spartina alteniflora from the short form to the tall form.

Stem diameter and leaf width of D. spicata are greatest at 18 m (0.322 m above MHW) where the nitrogen variables are lowest (Tables 12

and 20). Plant length, leaf number, and internode lengths, however, are lowest at this site. These same morphological features appear to be intermediate in value (Table 12) under the high salinity conditions which occur at 6 m (-0.318 m above MHW) (Table 19). Of the species they studied, Parrondo, et al. (1978) found D. spicata to be the most tolerant of increasing salinity as measured by its growth. Morphological characteristics, therefore, appear to be affected differently by these several environmental variables.

Stem length and flower stalk length of Grindelia integrifolia are greatest at 21 m (0.539 m above MHW) (Table 14). Here $NO_3$ levels are lowest (Table 21) which is again surprising considering the previously mentioned findings of Valiela, et al. (1978). No other correlations are obvious.

For Jaumea carnosa 7.5 m (0.149 m above MHW) seems to stand out along the transect with respect to morphological variables (Table 16). Here plant length, stem diameter, node number and leaf number are least. At 7.5 m, there seems to be a large jump in K, P, Mg, Na, and $NH_4$ (Table 22) which may account for the significant difference in morphological features between those plants at 7.5 m and those at the other distances along the transect.

All morphological measurements of Salicornia virginica were lowest at 0 m (0.126 m above MHW) (Table 18). Here P, K, Na, and $NH_4$ were greatest and Ca was lowest (Table 23). At 28.5 m (0.417 m above MHW) six of seven morphological features (all except flower number) had their highest values. At this point Ca, Mg, and $NO_3$ were greatest and P, K and Na were low.

## Conclusions

1. Statistically significant morphological differences were found within each of the five species, not only between the species' upper and lower distributional limits, but also between points along the transects between upper and lower limits. Differences were found within very short distances reflecting the steep environmental gradients existing within a wetland ecosystem.
2. Anatomical differences within species were also present, for instance, greater lignification of vascular bundle sheath cells occurred in the upper zones while greater aerenchyma formation occurred in the lower zones. With further investigation and verification, such morphological and anatomical characteristics could be useful in determining elevations in other marsh systems.
3. Soil moisture, salinity and other chemical properties of the soil are among environmental variables found to change along the transects.

# III. TRANSPLANTS

## Introduction

In order to ascertain whether the differences in morphological and anatomical characteristics within a species along transects from upper to lower marsh were determined genetically or the result of plant plasticity due to environmental influence, a transplant experiment involving the five species Deschampsia cespitosa, Grindelia integrifolia, Distichlis spicata, Salicornia virginica, and Jaumea carnosa was carried out. Field transplants were made between the upper and lower ranges of each species and laterally at each site to serve as a control of disturbance influence.

## Materials and Methods

Transplant methods similar to those of Shea, et al. (1975) were employed. Transplants were made on 21 October 1978 when the plants were becoming dormant, which allowed for approximately one year subsequent growth in the field. Transplants were located at the upper and lower limit of distribution (on transects 1-5) of each species and were marked with wooden stakes. Using a garden spade 16 transplants, each 20 $cm^2$ and approximately 30 cm in depth, were made for Jaumea carnosa, Distichlis spicata and Salicornia virginica. Each block of excavated marsh contained numerous plants. The design allowed for four lateral transplants at the upper limit and lower limit, four vertical transplants from the upper to the lower limit, and from lower to the upper limit, giving four replicates of each situation. Transplants were positioned as schematically illustrated in Figure 14.

Modified procedures were used for Deschampsia cespitosa and Grindelia integrifolia. Since D. cespitosa is distributed in scattered clumps, individual young clumps were transplanted, while in the case of G. integrifolia, where the distribution is that of scattered individuals, transplants were made of individual plants. In both cases there were four replicates each of lateral and vertical transplants with transplants being excavated in the same manner as with the other three species. Due to the death of many of the G. integrifolia transplants over the winter, transplants of this species were repeated on 7 June 1979.

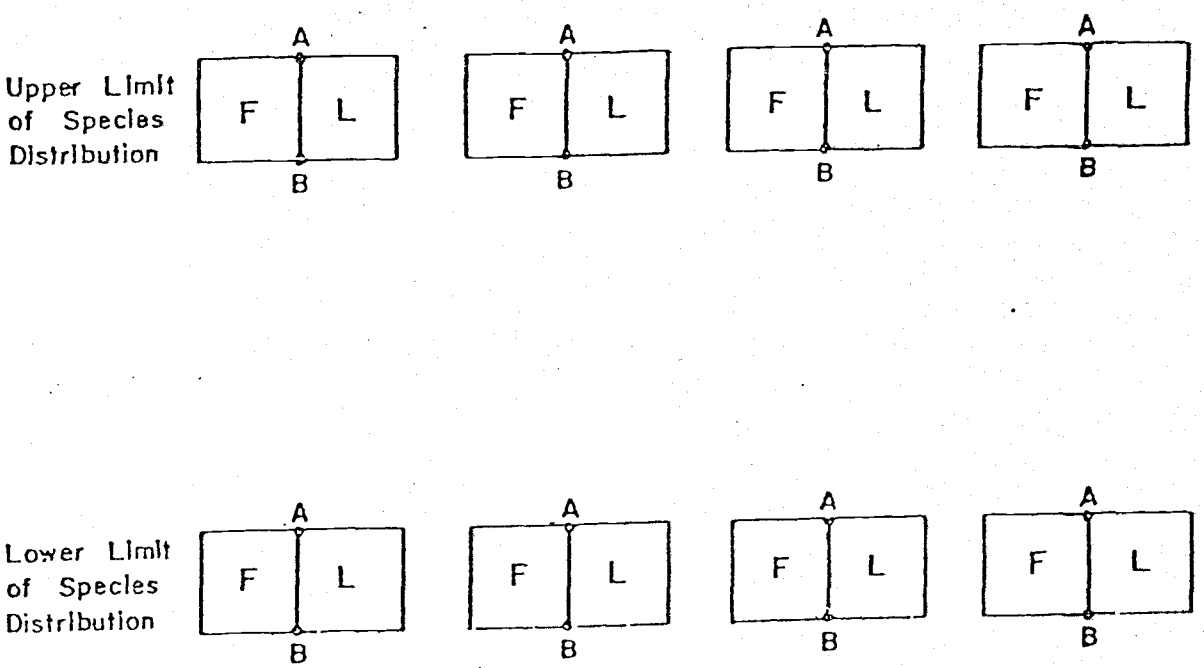



Figure 14. Design of transplant experiment for Jaumea carnosa, Distichlis spicata and Salicornia virginica (F = foreigner, L = lateral, A and B = numbered stakes).

Plastic garden edging, 20 cm in depth, was placed around the transplants of rhizome-producing species, i.e., all except D. cespitosa, in an attempt to prevent rhizomes of surrounding plants from penetrating the transplants and subsequently being confused with the experimental plants.

Soil moisture was monitored at the transplant sites via the tensiometers located at the upper and lower ends of each transect as described in the previous section. Elevational data and soil samples for nutrient analysis were also gathered for each transplant in the manner described previously.

Transplants were harvested on 1 September 1979. The entire block of transplanted marsh was carefuly eased out of the ground in order to thoroughly examine for rhizomes that may have come in from outside the transplant. Only D. spicata proved to be a problem in which case considerable effort was taken to exclude rhizomes that grew over the top of the plastic edging.

Plant stems were then cut with a scissors at the soil surface and placed in labeled plastic bags. Upon return to the laboratory, samples for anatomical analysis were taken from each stem as described in Section II. Those morphological characteristics listed in Table 2 of Section II were measured on each stem of the five transplanted species. Statistical analysis included mean, standard deviation, one-way analysis of variance and SNK range test (Sokol and Rohlf, 1979).

## Results and Discussion

Tables 25, 28, 31, 34 and 37 contain mean measurements for the morphological characteristics of each species. More detailed data on mean and N values can be found in Tables A-E of the appendix.

### Deschampsia cespitosa

Figure 15 illustrates the soil moisture differences between the upper and lower transplant sites of Deschampsia cespitosa. The y-axis is in centibars, a measure of soil tension (the greater this value the drier the soil). Soil moisture is greater in the lower marsh where inundation is more frequent. The elevation of the upper transplant site is 0.778 m above Mean High Water (MHW) and that of the lower site is 0.368 M above MHW (Table 24) giving a difference of 0.410 m. Elevation and soil moisture are of course related. Nutrient data was not collected for the D. cespitosa transplants since no edging had been placed around them making it difficult to determine exactly what soil had been transplanted.

Plant length, length of the flowering shoot, and inflorescence length vary significantly within the four transplants of Deschampsia cespitosa (see Table 25). Table 26 illustrates, by use of the Student-Newman-Keuls (SNK) range test, where the significant differences occur for these three morphological characteristics. In all SNK Tables, transplants are arranged in increasing order.

Flowering shoot length of the lower foreigner (LF) transplanted from the upper to the lower marsh, and the lower lateral (LL) are not significantly different. The upper foreigner (UF) transplanted from

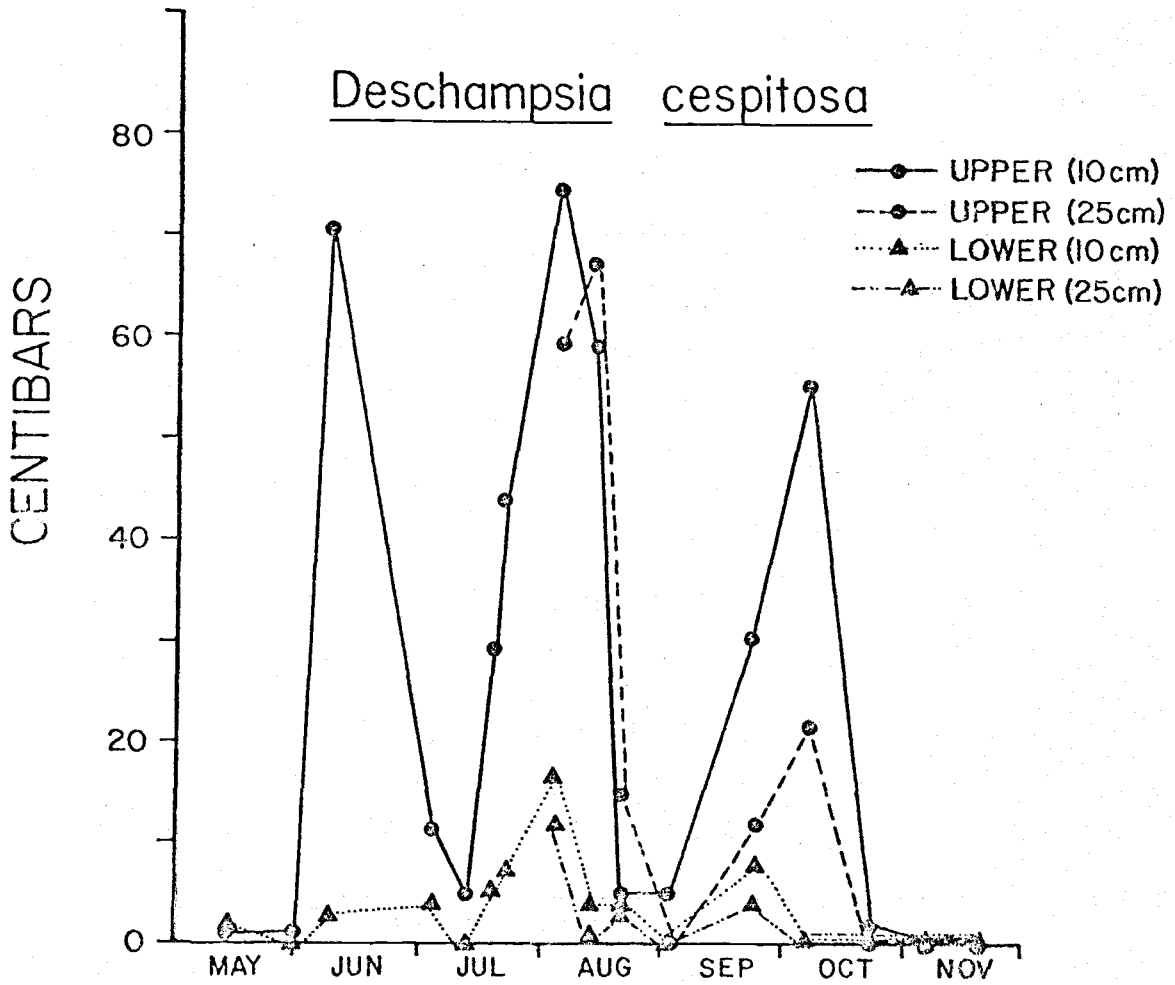



Figure 15. Soil moisture tension of upper vs lower Deschampia cespitosa transplants.

TABLE 24. ELEVATIONAL DATA FOR TRANSPLANTS (m above MHW).

| | |
|---|---|
| *Deschampsia cespitosa* | upper: 0.778<br>lower: 0.368 |
| *Distichlis spicata* | upper: 0.793<br>lower: -0.552 |
| *Grindelia integrifolia* | upper: 0.591<br>lower: 0.387 |
| *Jaumea carnosa* | upper: 0.417<br>lower: -0.069 |
| *Salicornia virginica* | upper: 0.515<br>lower: 0.120 |

TABLE 25. *Deschampsia cespitosa* TRANSPLANTS - MORPHOLOGICAL MEASUREMENTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) $\bar{X}$cm ± SE.

| | Plant length | Stem diameter | Leaf width | Flowering shoot length | Flowering shoot diameter | Inflorescence length |
|---|---|---|---|---|---|---|
| UL | 47.4 ± 5.3 | 0.14 ± 0.00 | 0.26 ± 0.03 | 94.6 ± 9.6 | 0.23 ± 0.02 | 17.8 ± 1.3 |
| UF | 66.6 ± 6.4 | 0.14 ± 0.01 | 0.26 ± 0.01 | 102.5 ± 7.8 | 0.21 ± 0.01 | 20.7 ± 1.2 |
| LL | 41.2 ± 5.8 | 0.12 ± 0.00 | 0.22 ± 0.00 | 67.0 ± 1.6 | 0.16 ± 0.01 | 15.2 ± 0.8 |
| LF | 38.0 ± 3.2 | 0.11 ± 0.01 | 0.21 ± 0.01 | 64.2 ± 2.8 | 0.19 ± 0.00 | 14.7 ± 0.3 |
| level of significant difference | .025* | .10 | .25 | .025* | .10 | .025* |

*considered significant

TABLE 26. *Deschampsia cespitosa* Transplants. SNK range test of significant variables, alpha = 0.05 (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner).

PLANT LENGTH

| LF | LL | UL | UF |
|---|---|---|---|

FLOWERING SHOOT LENGTH

| LF | LL | UL | UF |
|---|---|---|---|

INFLORESCENCE LENGTH

| LF | LL | UL | UF |
|---|---|---|---|

the lower to the upper marsh, and the upper lateral (UL) also possess similar length.

LF, LL, UL are not significantly different for plant length but UF does differ. LF here, as in the previous case of flowering shoot length, has developed the shorter stature of its surrounding neighbors in its new location.

A somewhat similar result was obtained for inflorescence length. LF, LL, and UL did not differ, and UL and UF were also similar. Therefore, differences occurred between the lower transplants and the UF. The LF responded similarly to its location as did the LL by displaying a short inflorescence length.

These results indicate that transplanted plants develop characteristics of the surrounding plants. D. cespitosa, therefore, responds plastically to environmental conditions.

Distichlis spicata

Soil moisture was greatest at the lower sites of Distichlis spicata over the growing season (see Figure 16). The lower transplants were 1.345 m below the upper transplants in elevation (Table 24).

Various chemical properties of the transplanted soil were also measured. Table 27 illustrates trends (since replicates were not obtained, significant differences cannot be assumed) between the four transplants. Quantities close in value for each property measured have been underlined. With most of the properties measured, the soils of the upper transplants were similar, as were those of the lower

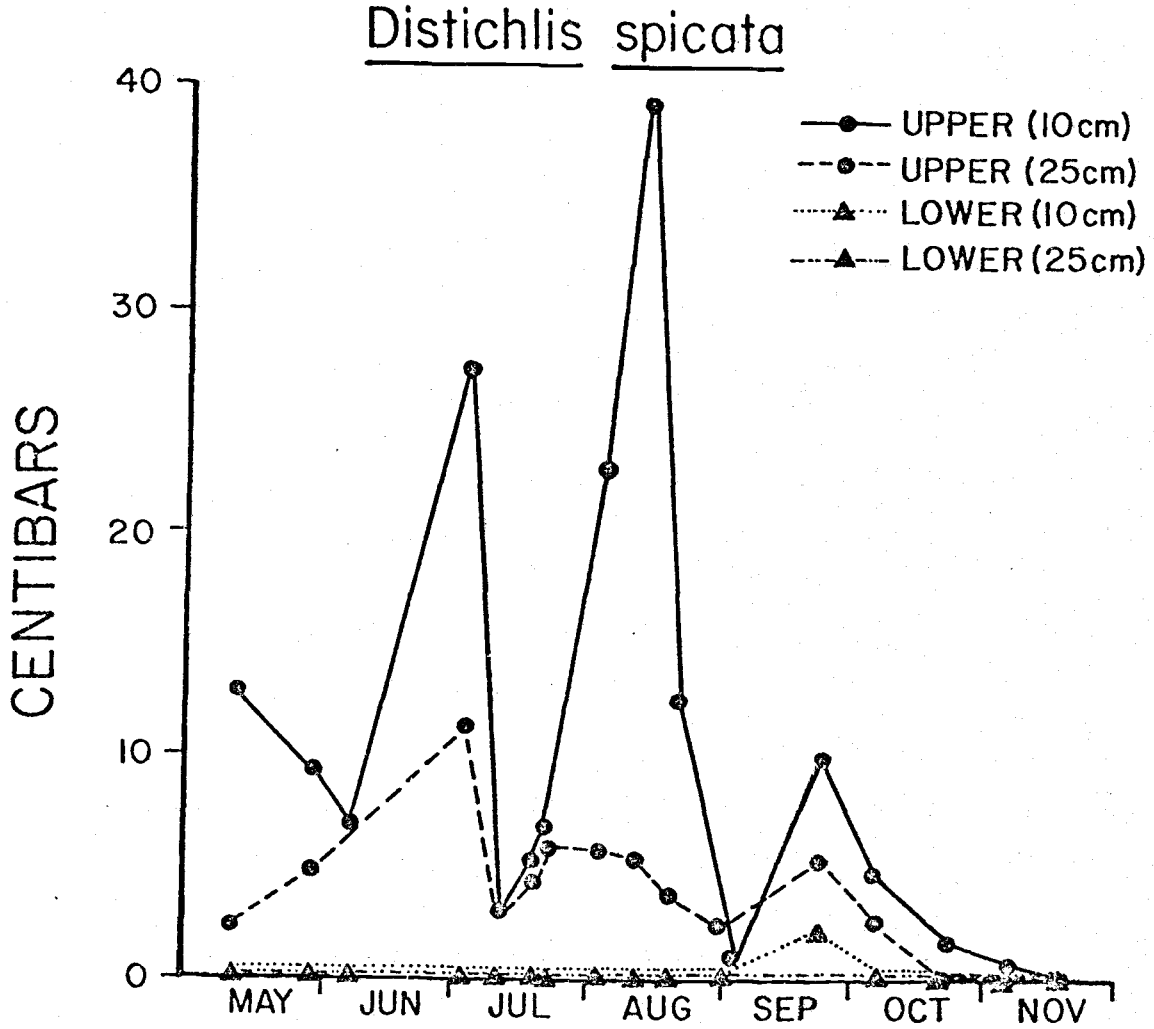



Figure 16. Soil moisture tension of upper vs lower Distichlis spicata transplants.

TABLE 27. *Distichlis spicata*. CHEMICAL PROPERTIES OF TRANSPLANTED SOIL.

| | UL | UF | LL | LF |
|---|---|---|---|---|
| pH | 6.7 | 5.7 | 4.1 | 4.9 |
| $pH^B$ | 7.1 | 7.0 | 6.9 | 7.1 |
| P (ppm) | 22 | 13 | 12 | 20 |
| K (ppm) | 90 | 133 | 254 | 203 |
| Na (meq/100g) | 0.88 | 1.73 | 8.7 | 7.1 |
| Ca (meq/100g) | 0.5 | 0.7 | 1.7 | 1.8 |
| Mg (meq/100g) | 0.8 | 1.1 | 4.1 | 3.6 |
| Total N (%) | 0.02 | 0.02 | 0.04 | 0.03 |
| $NO_3N$ (ppm) | 0.46 | 0.46 | <0.50 | <0.50 |
| $NH_4N$ (ppm) | 0.80 | 2.61 | 8.02 | 6.42 |

transplants. The sandy soil at this site in the marsh probably allowed for rapid change in chemical properties.

For D. spicata, plant length, length of the third internode and stem diameter differed significantly between the transplants (see Table 28). In all three cases the SNK range test (Table 29) showed the difference to be between the upper and lower transplants.

The internal anatomy of D. spicata gave similar results. The lignification of the bundle sheaths of UL and UF appears to be very similar (see Figure 17A and B). Less lignification is seen in LL and LF (Figures 17C and D).

Those plants moved from the upper to lower marsh developed as did those in the surrounding lower site; those transplanted from the lower to upper marsh developed as those in the upper zone. From these results it is evident that D. spicata responds plastically in its morphology and anatomy to the environment. During the same time period the soil properties also took on values resembling those of the new site. Therefore it may be that D. spicata is responding in its morphology to the soil chemical properties.

## Grindelia integrifolia

Differences in soil moisture between the upper and lower transplant sites are illustrated in Figure 18. The elevational difference between the two sites is 0.20 m (Table 24). Chemical properties measured in the transplanted soil of G. integrifolia also show some similarities between the UF and LL (Table 30).

TABLE 28. *Distichlis spicata* TRANSPLANTS - MORPHOLOGICAL MEASUREMENTS. (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) $\bar{X}$cm + SE.

| | Plant length | No. leaves | Length 3rd internode | Length 4th internode | Leaf width | Stem diameter |
|---|---|---|---|---|---|---|
| UL | 6.8 ± 0.3 | 7.4 ± 0.3 | 0.4 ± 0.0 | 0.4 ± 0.0 | 0.25 ± 0.01 | 0.10 ± 0.00 |
| UF | 6.9 ± 0.9 | 8.0 ± 0.1 | 0.4 ± 0.1 | 0.4 ± 0.2 | 0.25 ± 0.01 | 0.10 ± 0.00 |
| LL | 11.2 ± 1.4 | 7.0 ± 0.0 | 1.4 ± 0.2 | 1.2 ± 0.0 | 0.27 ± 0.01 | 0.08 ± 0.01 |
| LF | 10.3 ± 0.8 | 7.0 ± 0.6 | 1.0 ± 0.2 | 0.8 ± 0.2 | 0.24 ± 0.01 | 0.08 ± 0.00 |
| level of significant difference | .01* | .50 | .005* | .10 | .50 | .001* |

*considered significant

TABLE 29. *Distichlis spicata* TRANSPLANTS. SNK RANGE TEST OF SIGNIFICANT VARIABLES, alpha = .05 (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner).

PLANT LENGTH

| | | | |
|---|---|---|---|
| UL | UF | LF | LL |

LENGTH 3RD INTERNODE

| | | | |
|---|---|---|---|
| UF | UL | LF | LL |

STEM DIAMETER

| | | | |
|---|---|---|---|
| LL | LF | UL | UF |

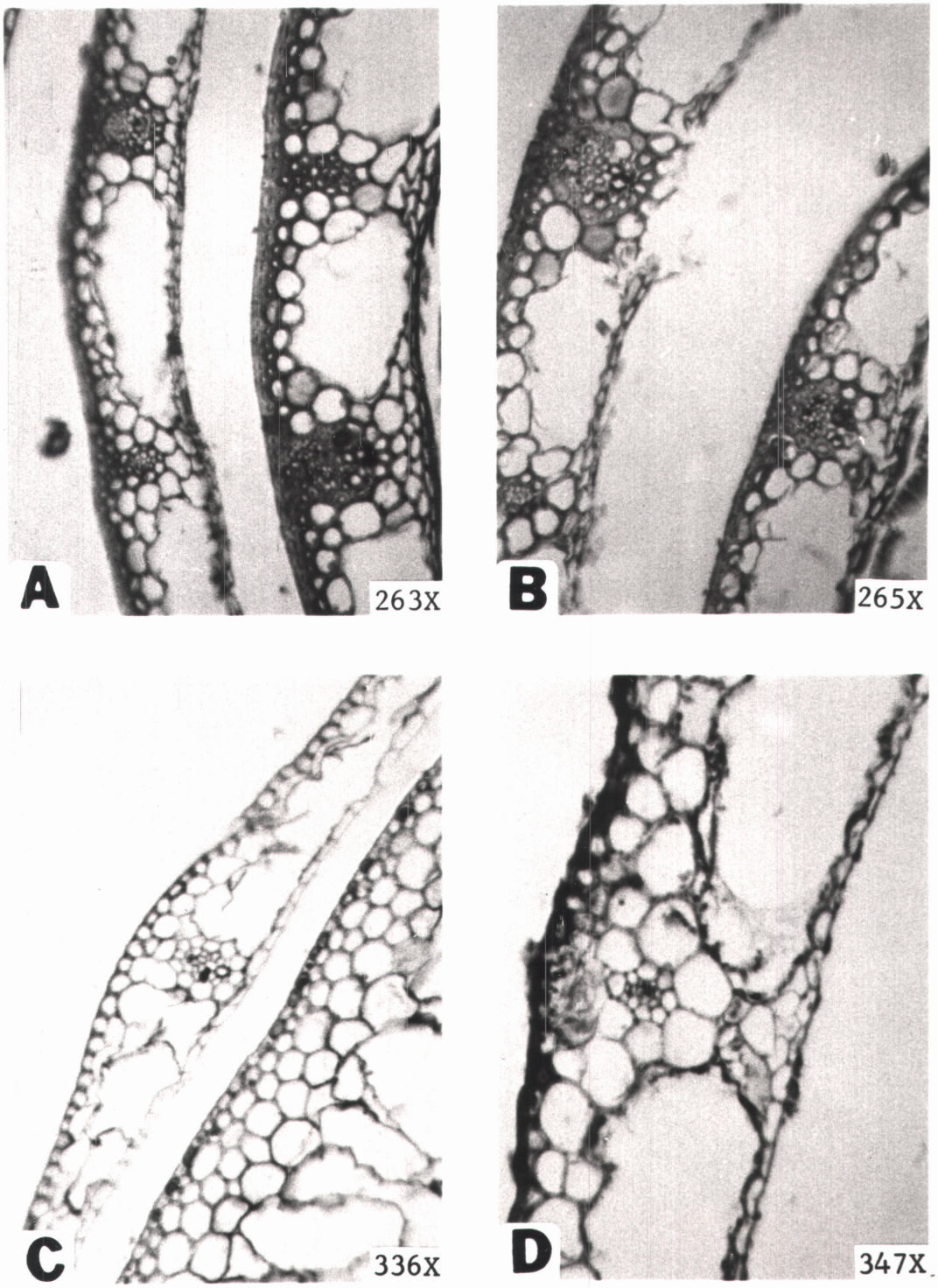



Figure 17. Stem cross sections of transplanted Distichlis spicata (A = UL, B = UF, C = LL, D = LF).

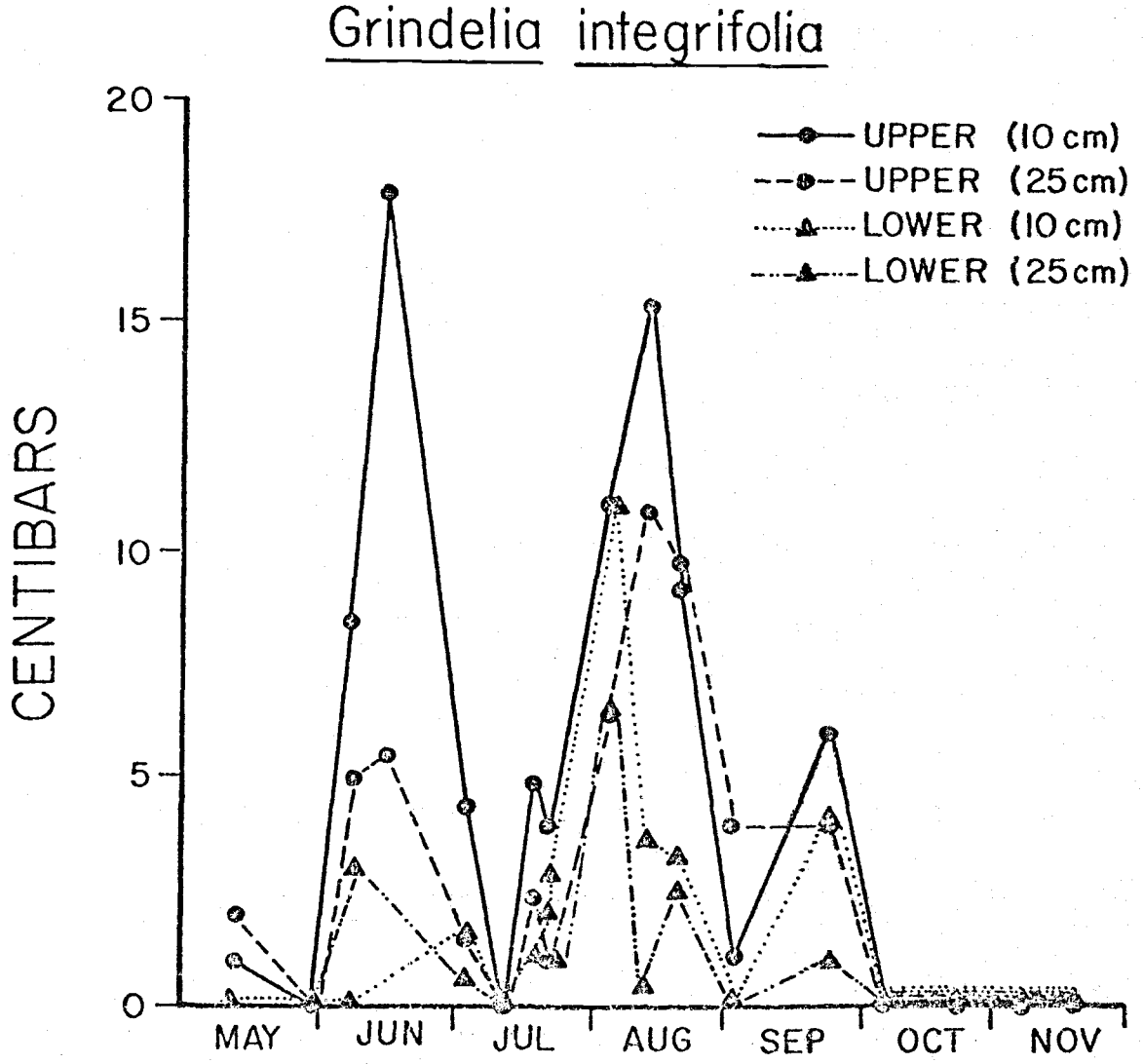



Figure 18. Soil moisture tension of upper vs lower Grindelia integrifolia transplants.

TABLE 30. *Grindelia integrifolia*. CHEMICAL PROPERTIES OF TRANSPLANTED SOIL.

| | UL | UF | LL | LF |
|---|---|---|---|---|
| pH | 6.2 | 5.9 | 5.7 | 6.1 |
| $pH^B$ | 7.0 | 6.5 | 6.5 | 7.0 |
| P (ppm) | 15 | 16 | 17 | 19 |
| K (ppm) | 339 | 1412 | 1646 | 998 |
| Na (meq/100g) | 7.1 | 27.6 | 50.0 | 32.9 |
| Ca (meq/100g) | 2.5 | 5.8 | 6.8 | 6.1 |
| Mg (meq/100g) | 5.3 | 17.0 | 22.0 | 17.0 |
| Total N (%) | 0.23 | 0.44 | 0.42 | 0.34 |
| $NO_3$-N (ppm) | 0.92 | 1.82 | 3.64 | 21.87 |
| $NH_4$-N (ppm) | 7.22 | 13.64 | 13.24 | 12.44 |

Stem diameter and length of the stem excluding new growth differed significantly among the Grindelia integrifolia transplants (Table 31). The SNK range test showed LL and UF to be essentially equal to each other in these two characteristics and UL and LF also to be similar to each other (Table 32). For stem diameter, LF and UL are similar to LL.

The data in Tables 31 and 32 were obtained from the second set of G. integrifolia transplants. Recall that these transplants were made in June and not the previous fall as were the other species, therefore, these plants did not have as long a period of time to adapt and respond to their new environment as did the other species, and this possibly explains the similarity of UL to LF and of LL to UF. It is not thought that these morphological characteristics are fixed genetically, but rather that length of time for a plastic response was not sufficient.

Stem sections, obtained to observe internal anatomy, were taken from the survivors of the first transplanting of G. integrifolia. Here, as in D. spicata, those features characteristic of the new environment were taken on by the foreigners. Figures 21A and 21B show for UL and UF the greater secondary xylem formation typical of upper marsh plants. LL and LF (Figures 19C and D) show reduced development of secondary xylem.

Jaumea carnosa

As seen in Figure 20, soil moisture differs for the two Jaumea carnosa transplant sites, being greater in the lower area. Table

TABLE 31. *Grindelia integrifolia* TRANSPLANTS - MORPHOLOGICAL MEASUREMENTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) $\bar{X}$cm + SE.

| | Stem length | Stem diameter | No. leaves | Leaf width | Total length wood |
|---|---|---|---|---|---|
| UL | 14.0 ± 1.4 | 0.31 ± 0.04 | 4.4 ± 0.8 | 1.7 ± 0.1 | 26.9 ± 12.3 |
| UF | 18.2 ± 1.8 | 0.50 ± 0.04 | 4.7 ± 0.4 | 1.9 ± 0.1 | 5.6 ± 2.1 |
| LL | 17.8 ± 1.5 | 0.41 ± 0.05 | 5.6 ± 0.5 | 1.7 ± 0.2 | 3.8 ± 0.7 |
| LF | 11.8 ± 0.2 | 0.29 ± 0.04 | 3.6 ± 0.2 | 1.4 ± 0.2 | 30.4 ± 3.6 |
| level of significant difference | .10 | .05* | .25 | .50 | .05* |

*considered significant

TABLE 32. *Grindelia integrifolia* TRANSPLANTS. SNK RANGE TEST OF SIGNIFICANT VARIABLES, alpha = .05 (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner).

STEM DIAMETER

| LF | UL | LL | UF |
|---|---|---|---|

TOTAL LENGTH WOOD

| LL | UF | UL | LF |
|---|---|---|---|

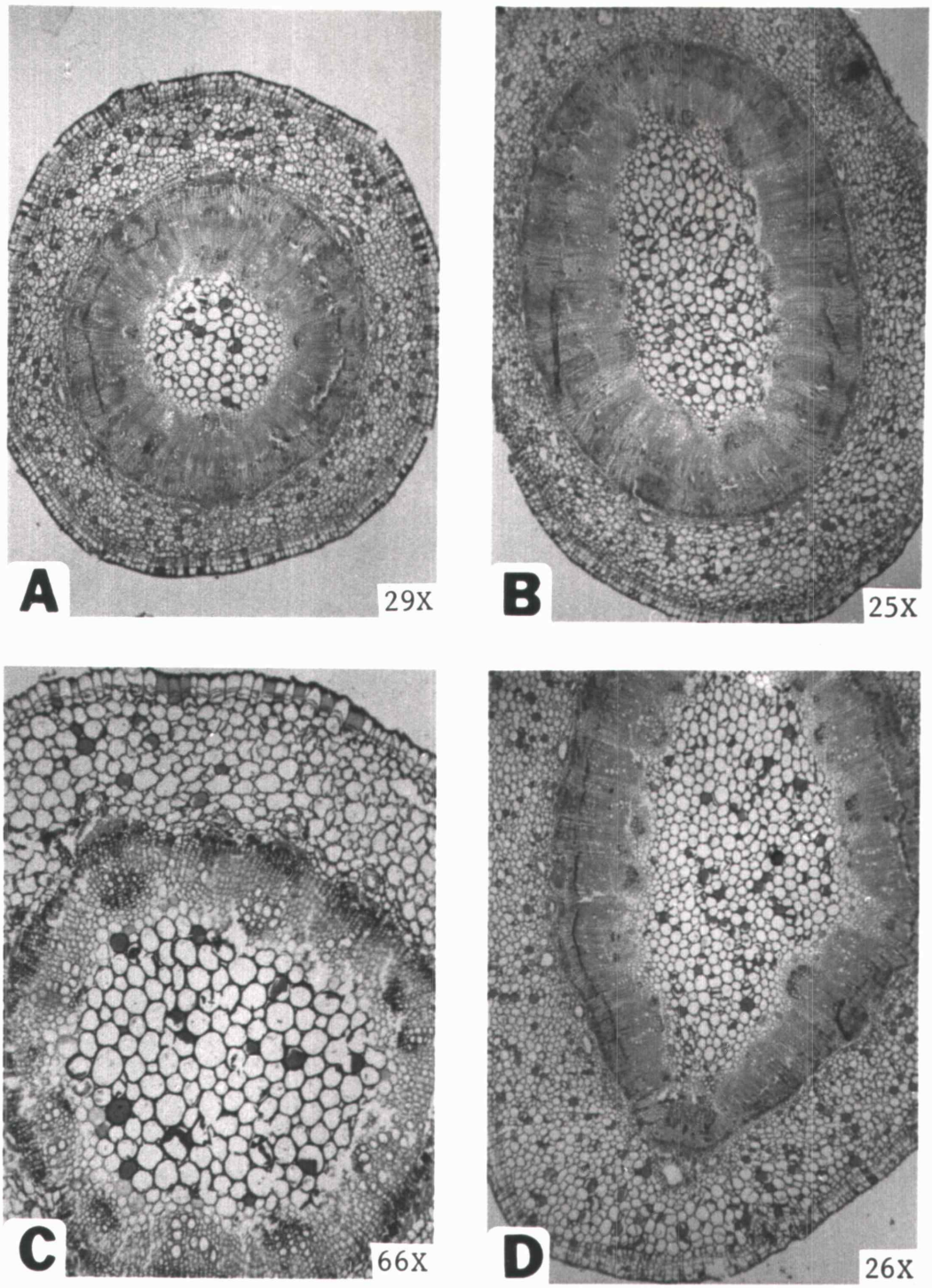



Figure 19. Stem cross sections of transplanted Grindelia integrifolia (A = UL, B = UF, C = LL, D = LF).

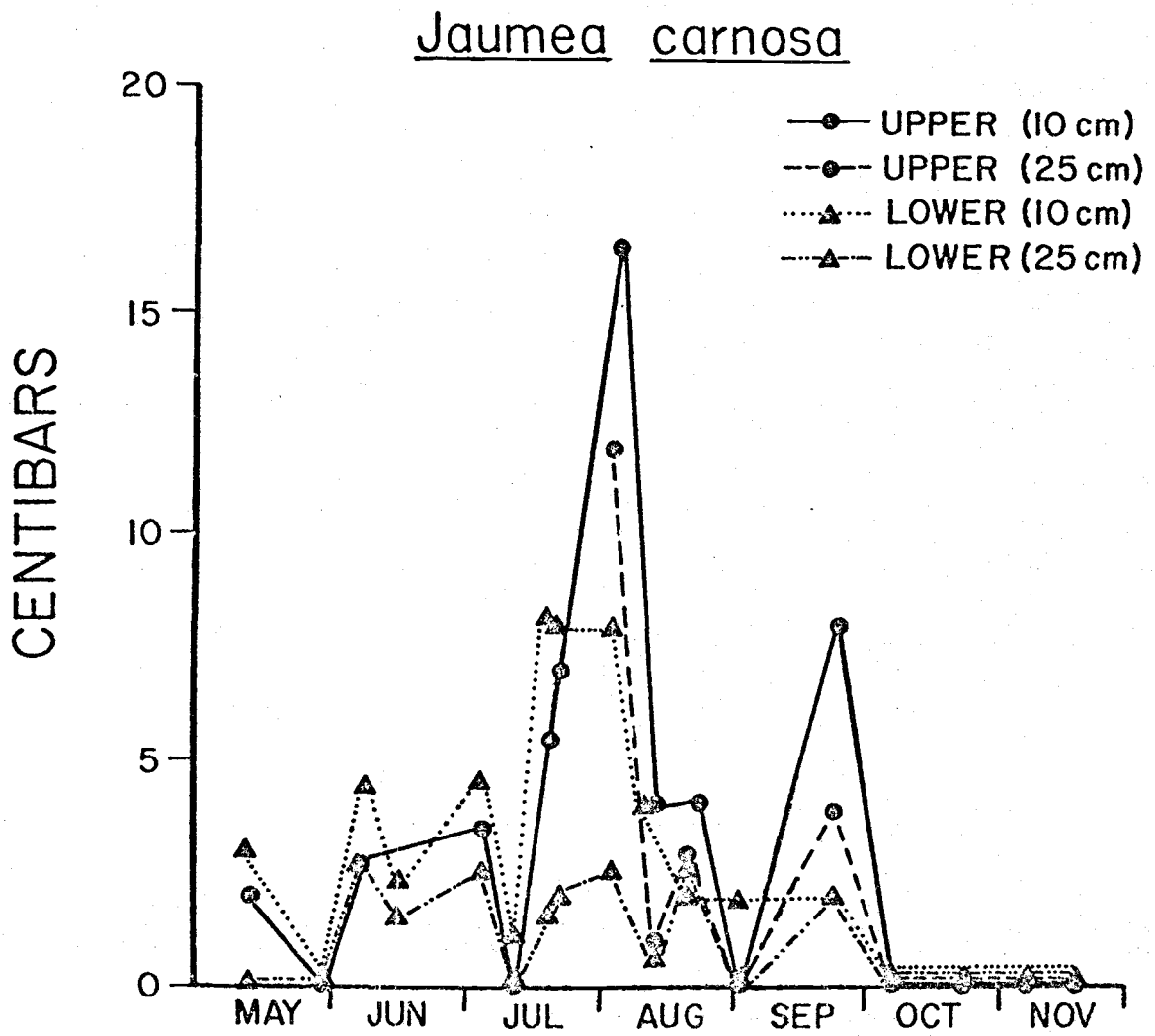



Figure 20. Soil moisture tension of upper vs lower Jaumea carnosa transplants.

24 indicates that the lower transplants were 0.486 m below the upper ones in elevation.

Data on the soil chemical properties (Table 33) showed similarities between UF and LL and between UL and LF except for pH which shows the upper transplants to be similar and the lower transplants to be similar. Therefore, in the case of J. carnosa soil moisture, elevation, or pH may be the important factors affecting the plant's morphology but statistical evaluation of these relationships was not done.

J. carnosa showed significant differences in plant length and length of its second and third internodes between the transplants (Table 34). For plant length, LF developed similarly to LL but UF was not found to differ from LF or LL (Table 35). For internode length, LL and LF were similar as were UL and UF.

Vascular bundle size in stems of J. carnosa tended to be larger in UL and UF transplants (Figures 21A and 21B) and somewhat smaller in LL and LF (Figures 21C and 21D). Thus, overall, as expressed by these morphological and anatomical characteristics, J. carnosa responded plastically to the environment.

## Salicornia virginica

Differences in soil moisture between the upper and lower transplant sites of Salicornia virginica can be seen in Figure 22. Soil moisture is greater in the lower area. The elevation of the upper transplants was 0.515 m above MHW while that of the lower transplants was 0.120 m above MHW, a difference of 0.395 m (Table 24).

TABLE 33. *Jaumea carnosa*. CHEMICAL PROPERTIES OF TRANSPLANTED SOIL.

| | UL | UF | LL | LF |
|---|---|---|---|---|
| pH | 6.2 | 6.0 | 6.5 | 6.5 |
| $pH^B$ | 6.7 | 6.9 | 7.2 | 6.9 |
| P (ppm) | 16 | 12 | 13 | 22 |
| K (ppm) | 1755 | 920 | 1100 | 1872 |
| Na (meq/100g) | 56 | 28.6 | 33.8 | 70 |
| Ca (meq/100g) | 8.9 | 4.5 | 4.6 | 10.0 |
| Mg (meq/100g) | 28.0 | 14.0 | 15.0 | 30.0 |
| Total N (%) | 0.60 | 0.18 | 0.18 | 0.56 |
| $NO_3$-N (ppm) | 85.66 | 20.64 | 7.28 | 91.12 |
| $NH_4$-N (ppm) | 17.66 | 6.82 | 5.62 | 17.26 |

TABLE 34. *Jaumea carnosa* TRANSPLANTS - MORPHOLOGICAL MEASUREMENTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) $\bar{X}$cm ± SE.

| | Plant length | Stem diameter | No. nodes | Length 2nd internode | Length 3rd internode |
|---|---|---|---|---|---|
| UL | 18.3 ± 1.9 | 0.15 ± 0.01 | 7.2 ± 0.8 | 1.9 ± 0.1 | 2.2 ± 0.2 |
| UF | 14.2 ± 2.6 | 0.14 ± 0.00 | 6.6 ± 0.7 | 2.0 ± 0.2 | 2.2 ± 0.2 |
| LL | 8.9 ± 0.4 | 0.14 ± 0.00 | 6.6 ± 0.4 | 1.1 ± 0.0 | 1.1 ± 0.0 |
| LF | 11.4 ± 1.0 | 0.16 ± 0.00 | 6.4 ± 0.2 | 1.2 ± 0.1 | 1.6 ± 0.1 |
| level of significant difference | .025* | .10 | .50 | .001* | .005* |

*considered significant

TABLE 34 (continued). *Jaumea carnosa* TRANSPLANTS - MORPHOLOGICAL MEASUREMENTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) $\bar{X}$cm ± SE.

| | No. leaves | Leaf width | Leaf thickness |
|---|---|---|---|
| UL | 16.8 ± 1.9 | 0.39 ± 0.05 | 0.09 ± 0.01 |
| UF | 15.4 ± 1.4 | 0.28 ± 0.03 | 0.08 ± 0.01 |
| LL | 15.6 ± 1.0 | 0.31 ± 0.02 | 0.11 ± 0.00 |
| LF | 15.2 ± 0.3 | 0.37 ± 0.02 | 0.10 ± 0.00 |
| level of significant difference | ..50 | .25 | .25 |

*considered significant

TABLE 35. Jaumea carnosa TRANSPLANTS. SNK RANGE TEST OF SIGNIFICANT VARIABLES, alpha = .05 (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner).

PLANT LENGTH

| LL | LF | UF | UL |
|---|---|---|---|

LENGTH 2ND INTERNODE

| LL | LF | UL | UF |
|---|---|---|---|

LENGTH 3RD INTERNODE

| LL | LF | UF | UL |
|---|---|---|---|

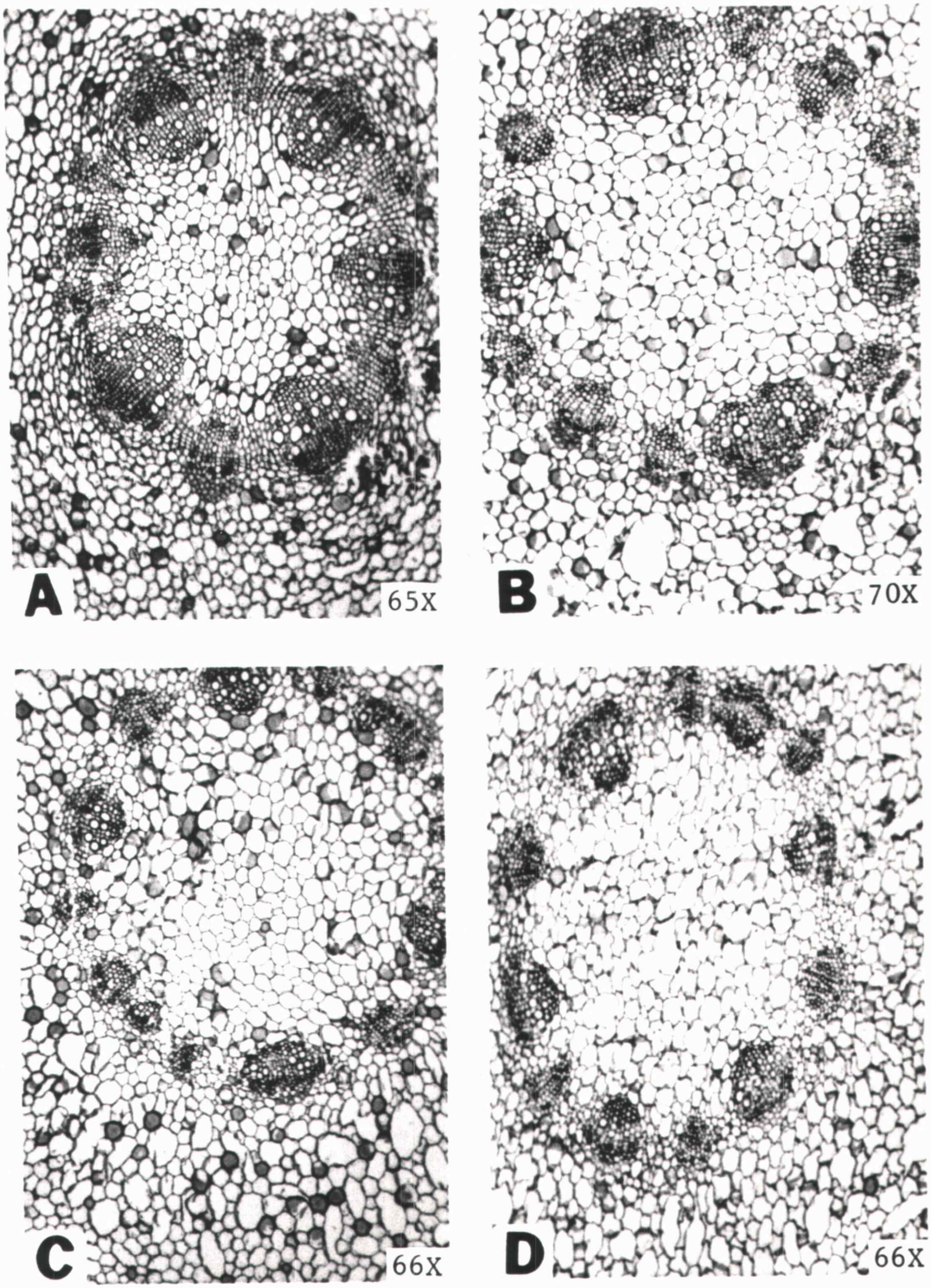



Figure 21. Stem cross sections of transplanted Jaumea carnosa (A = UL, B = UF, C = LL, D = LF).

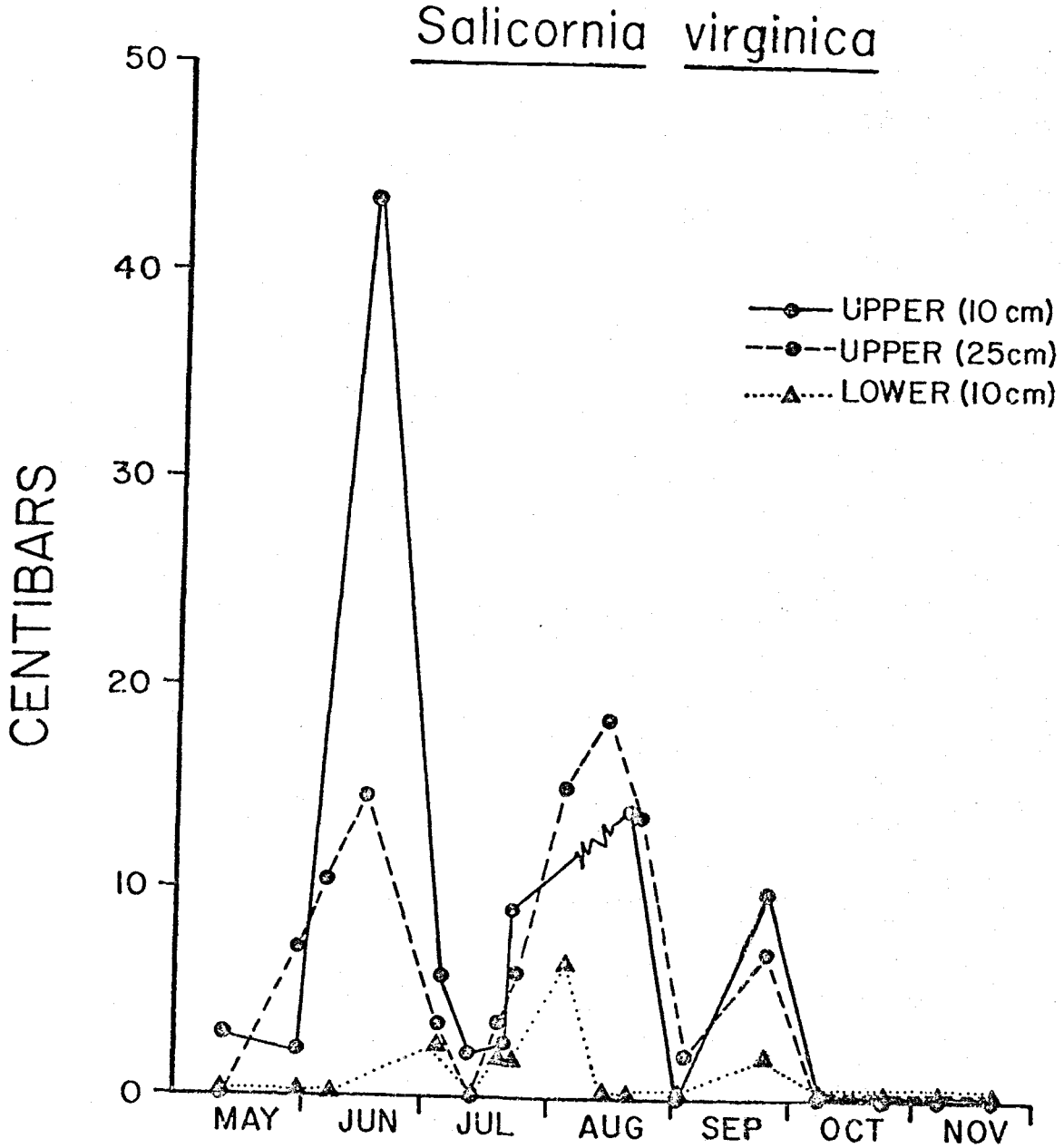



Figure 22 Soil moisture tension of upper vs lower Salicornia virginica transplants.

The soil's chemical property data indicate that for the most part UL and UF are similar and LL and LF are similar (Table 36). Thus, all the environmental variables measured in this case show differences between upper and lower sites and may therefore all be causes of morphological variance seen between upper and lower marsh.

Stem length, internode length, number of primary branches and stem diameter proved to be significantly different between transplants of Salicornia virginica (Table 37). Stem length differs between LL and UL only. The foreigners were intermediate in length and not significantly different from either LL or UL (Table 38).

UF and UL were similar in internode length, however, LF was not statistically significantly different from these. LL and LF were equal in internode length. Here a trend toward responding plastically to their new locations is evident.

UF and UL had essentially the same number of primary branches, however, these two did not differ from LL. The LF had significantly more primary branches than the other three.

With stem diameter UF and LF differed significantly.

Anatomically, growth plasticity of the plants to the new environment was demonstrated. The amount of aerenchymatous tissue in stems of LL and LF (Figures 23C and 23D) was greater than in those of UL and UF (Figures 23A and 23B). More aerenchyma was formed by plants in the lower, wetter environment.

Possible causes of the morphological and anatomical differences observed between upper and lower marsh zones were discussed in the Transect section of this thesis. Worthy of discussion are a few transplant experiments exemplifying the possible outcomes.

TABLE 36. *Salicornia virginica*. CHEMICAL PROPERTIES OF TRANSPLANTED SOIL.

| | UL | UF | LL | LF |
|---|---|---|---|---|
| pH | 6.6 | 6.2 | 6.0 | 5.8 |
| $pH^B$ | 6.9 | 6.8 | 6.6 | 6.5 |
| P (ppm) | 24 | 25 | 26 | 25 |
| K (ppm) | 1271 | 1022 | 1950 | 1802 |
| Na (meq/100g) | 27 | 23.6 | 62 | 62 |
| Ca (meq/100g) | 6.7 | 5.0 | 8.3 | 9.8 |
| Mg (meq/100g) | 18.0 | 13.0 | 26.0 | 31.0 |
| Total N (%) | 0.40 | 0.31 | 0.45 | 0.66 |
| $NO_3$-N (ppm) | 57.86 | 34.62 | 29.16 | 80.22 |
| $NH_4$-N (ppm) | 14.44 | 17.66 | 17.66 | 17.66 |

TABLE 37. *Salicornia virginica* TRANSPLANTS - MORPHOLOGICAL MEASUREMENTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) $\bar{X}$cm ± SE.

| | Stem length | No. internodes | Length internode | No. primary branches | Dry wt/vol internode | Stem diameter |
|---|---|---|---|---|---|---|
| UL | 27.3 ± 2.7 | 20.7 ± 3.0 | 1.4 ± 0.1 | 11.4 ± 2.5 | 0.09 ± 0.01 | 0.11 ± 0.01 |
| UF | 22.0 ± 2.2 | 15.7 ± 0.6 | 1.6 ± 0.2 | 6.0 ± 1.3 | 0.10 ± 0.00 | 0.08 ± 0.01 |
| LL | 16.8 ± 1.2 | 15.6 ± 0.9 | 1.0 + 0.0 | 6.4 ± 0.8 | 0.10 + 0.00 | 0.10 + 0.00 |
| LF | 22.8 ± 1.1 | 17.8 ± 0.3 | 1.2 ± 0.0 | 16.1 ± 0.6 | 0.12 ± 0.01 | 0.14 ± 0.01 |
| level of significant difference | .025* | .25 | .025* | .005* | .25 | .001* |

*considered significant

TABLE 38. Salicornia virginica TRANSPLANTS. SNK RANGE TEST OF SIGNIFICANT VARIABLES, alpha = .05 (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner).

STEM LENGTH

| LL | UF | LF | UL |
|---|---|---|---|

LENGTH INTERNODE

| LL | LF | UL | UF |
|---|---|---|---|

NO. PRIMARY BRANCHES

| UF | LL | UL | LF |
|---|---|---|---|

STEM DIAMETER

| UF | LL | UL | LF |
|---|---|---|---|

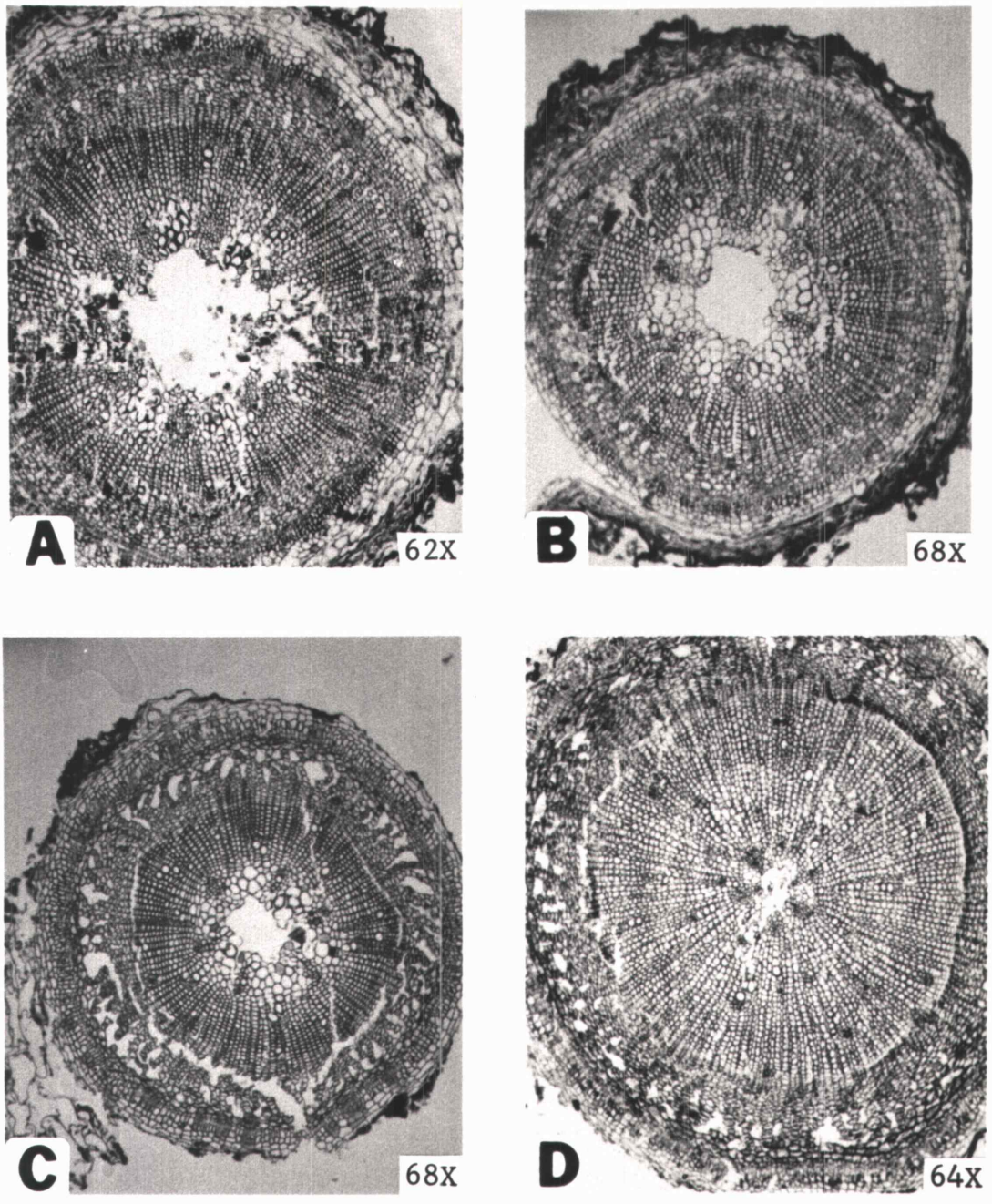



Figure 23. Stem cross sections of transplanted Salicornia virginica (A = UL, B = UF, C = LL, D = LF).

Quinn (1975) made reciprocal transplants of the perennial grass, Danthonia sericea, from bog and upland populations. Populations having pubescent lemmas and leaf sheaths are characteristic of well-drained, upland sites while glabrous populations are found in low, wet areas or open bogs. The reciprocal transplants were observed for six growing seasons. At the wetland site, upland populations rapidly lost vigor and died by the middle of the first growing season. Survival at the upland site by wetland populations was better at the end of one year, but stress was observed. At the end of five years only 17% of the wetland plants in the upland site were surviving compared to 83% of the pubescent plants transplanted at the same site. The transplanted populations never developed the morphological characteristics or the tolerances of the surrounding plants and therefore it was concluded that definite ecotypes exist in these populations of D. sericea.

Another example of ecotypes of a species from contrasting habitats is provided by the work of Watson and Fyfe (1975). Transplants and seedling material of Potentilla erecta from two sites in Scotland were studied. Plant diameter was used to show that transplants from one population were significantly larger than those from another. Using canonical analysis they confirmed their hypothesis that contrasting ecotypes had evolved within the contrasting habitats.

The other possible outcome in transplant experiments is a finding that ecotypes do not exist as is the case in the present research. This result was obtained with the tall form (from the intertidal area) and short form (from the panne area) of Spartina

alterniflora, a salt marsh grass, by Shea, et al. (1975). Following the reciprocal transplanting of the two forms of S. alterniflora it was observed that the short plants, when growing in the intertidal area, were 1.5 times as tall at the end of the growing season as were the normal panne forms. The tall forms growing in the panne areas grew at the same rate and reached the same terminal height as did the surrounding panne plants. This result, along with electrophoretic comparisons of enzymes and total soluble proteins, led Shea, et al. to conclude that the tall and short forms of S. alterniflora are genetically indistinguishable and should therefore be considered as ecophenes rather than ecotypes.

## Conclusions

1. Results of the transplant experiments on *Deschampsia cespitosa*, *Distichlis spicata*, *Grindelia integrifolia*, *Jaumea carnosa* and *Salicornia virginica* suggest that the morphological and anatomical characteristics found to differ in these species, as found in *Spartina alterniflora*, by Shea, et al. (1975) are not genetically fixed. These plants are responding plastically to their environment. The different forms of each species used in the present study would, therefore, not be considered ecotypes but ecophenes.
2. Soil moisture, salinity and other chemical properties of the soil are all thought to be possible environmental variables affecting the plant's morphology. The soil of *J. carnosa* is the only one that did not show evidence of changing (except for pH) to become more like the soil in its new location yet the plant's morphology did change. Here soil moisture may be significant in effecting the plant's morphology.

# IV. GREENHOUSE

## Introduction

It was hypothesized that soil moisture was the main cause of the morphological and anatomical differences observed between the upper and lower portions of the marsh. In order to ascertain whether or not this was the case, a controlled moisture experiment was designed and conducted in the greenhouse where conditions other than soil moisture level were kept constant. In order to study the two extremes, and a midpoint, three moisture treatments were established - saturated, field capacity and near wilting point. Four of the five species studied in the previous two sections were selected for study in this experiment - Deschampsia cespitosa, Grindelia integrifolia, two upper and transition zone marsh species, and Distichlis spicata and Salicornia virginica, two species from the lower marsh.

## Materials and Methods

Plants were grown in pots 36 cm in height and 15 cm in diameter. These were constructed from PVC (polyvinyl chloride) irrigation pipe with an 18 $cm^2$ PVC plate cemented to the bottom of each. A 0.8 cm hole was drilled into each pot 0.5 cm above the base to allow for drainage. For each species the pots were arranged on the greenhouse bench in a random block design with ten replicates of each moisture treatment.

The pots were filled to a depth of 35 cm (Gallagher, 1974) with river sand supplied by the OSU greenhouse. For Deschampsia cespitosa the pots were planted with seeds collected the previous fall from Netarts spit. Rhizomes of Salicornia virginica and Distichlis spicata were collected at Netarts the day before planting, brought back to the greenhouse where they were washed free of mud with tap water and four, approximately equal size sections were placed in each of the respective pots. In the case of Grindelia integrifolia, both seeds, collected the previous fall, and young plants collected at Netarts the day prior to planting were used. Thirty young G. integrifolia plants, each approximately 5 cm in height were sorted and one was placed in each pot. Seeds were then planted around the transplant.

The substrate surface of each pot was covered with 1 cm of peat to aid in maintaining moisture. To allow for germination and equilibration, the pots were watered with tap water every other day and with North Carolina State University (NCSU) nutrient solution (Downs and Hellmers, 1975) once every two weeks.

After four weeks, the plants were watered with their appropriate concentrations of artificial seawater, Rila Marine Mix (Barbour, 1978). In an attempt to duplicate natural field conditions, G. integrifolia and D. cespitosa, the upper marsh plants, were kept at a constant salinity of 8 °/oo while D. spicata and S. virginica, from the lower marsh, were maintained at 16 °/oo (Liverman, pers. comm.). These salinities were maintained throughout the experiment. Salinity was measured with an American Optical refractometer (Behrens, 1965).

Moisture treatments were begun at the start of the fifth week. All the pots were flushed with their appropriate concentration of seawater. Five hundred ml of the NCSU nutrient solution were then added to each pot and allowed to drain. At this point, the drainage holes in the saturated pots were stoppered with rubber serum vial caps. Seawater was then added until saturation was reached, i.e., water was standing on the substrate surface. Water was maintained on the surface throughout the experiment except once a month when the pots were reflushed in the manner described above. The plants growing under saturated conditions were watered as needed with tap water to avoid the addition of more salts and to replace that water lost by evaporation.

In order to achieve field capacity conditions without the loss of nutrients due to the frequent watering of these plants, the field capacity pots were set up in a manner similar to that used by Parrondo, et al. (1978). Each pot was placed on a 6" x 6" x 2" block of wood with a styrofoam cup positioned under the drainage hole of each (see Figure 4). These plants were watered every other

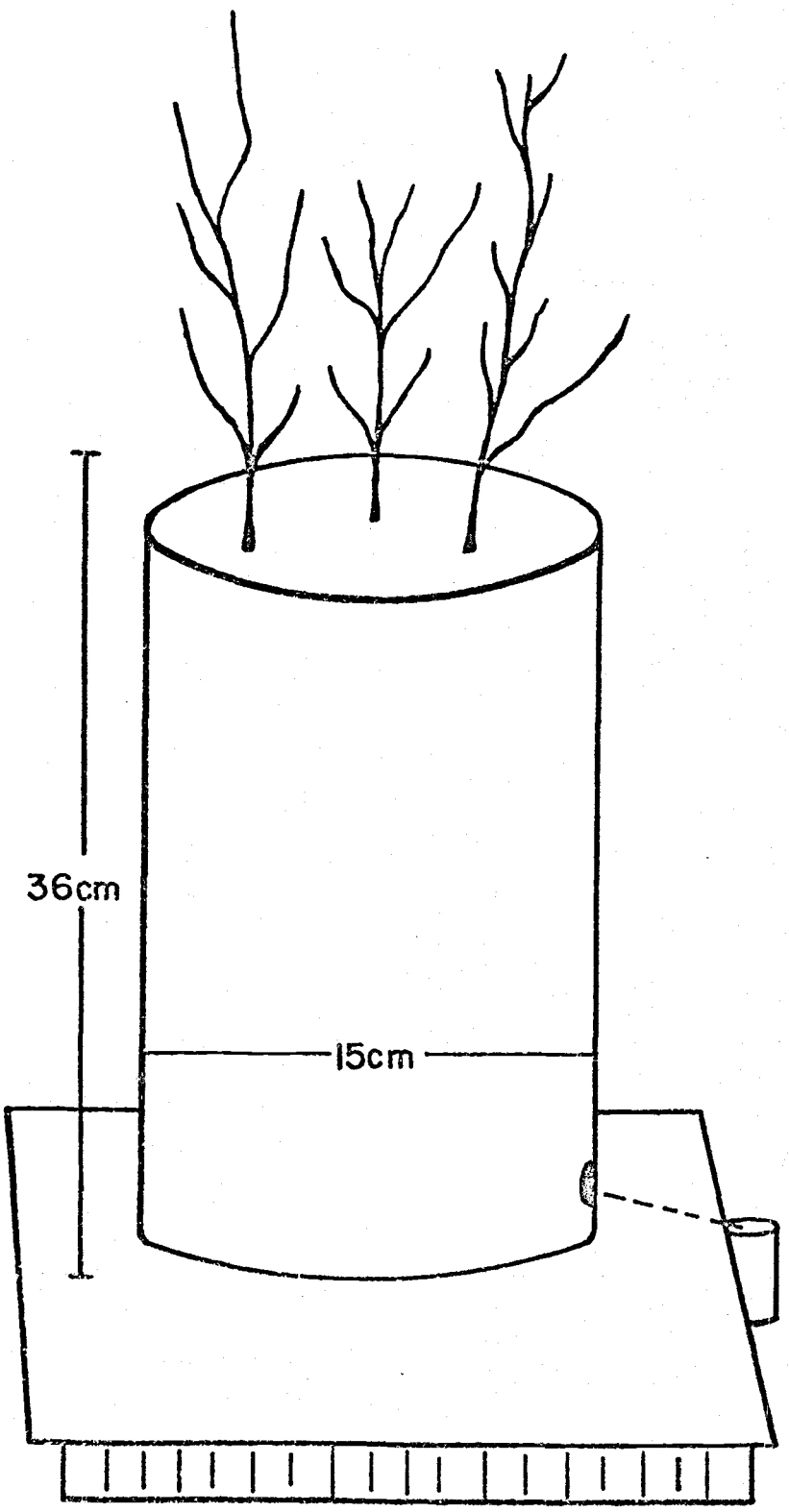



Figure 24. Design of field capacity pot.

day with tap water after which the drained water was recycled by pouring it back into the top of the pot. Thus, the amount of nutrients and salts in the saturated and dry pots remained constant.

The plants under dry conditions were watered only frequently enough to keep the moisture level above wilting point. This was determined by taking a soil core with a 10 cc syringe from each of three random pots and calculating the percent moisture on a dry weight basis. When this value reached approximately wilting point (3.8% moisture at 15 bars tension) as read from a moisture tension curve for the river sand, (Figure 25), the plants were watered. Watering was necessary only about once a month and when this level was reached, all pots received their monthly reflushing. During the hottest summer weeks the greenhouse temperature rose above the usual $75^{o}$ F. At these times, it was necessary to give the plants a frequent sprinkling of tapwater to prevent wilting.

The greenhouse experiment continued through mid-November 1979, with the four species being harvested at different times to allow time for the processing of samples. The harvest dates were: S. virginica-2 Oct., D. spicata-11 Oct., G. integrifolia-30 Oct. and D. cespitosa-19 Nov.

For each species, all plants were cut from each pot at substrate level with a scissors and placed in labeled plastic bags. In the laboratory, sections were taken from each stem for anatomical analysis.

Those morphological characteristics listed in Table 2 of Section II were measured on every plant except for D. cespitosa

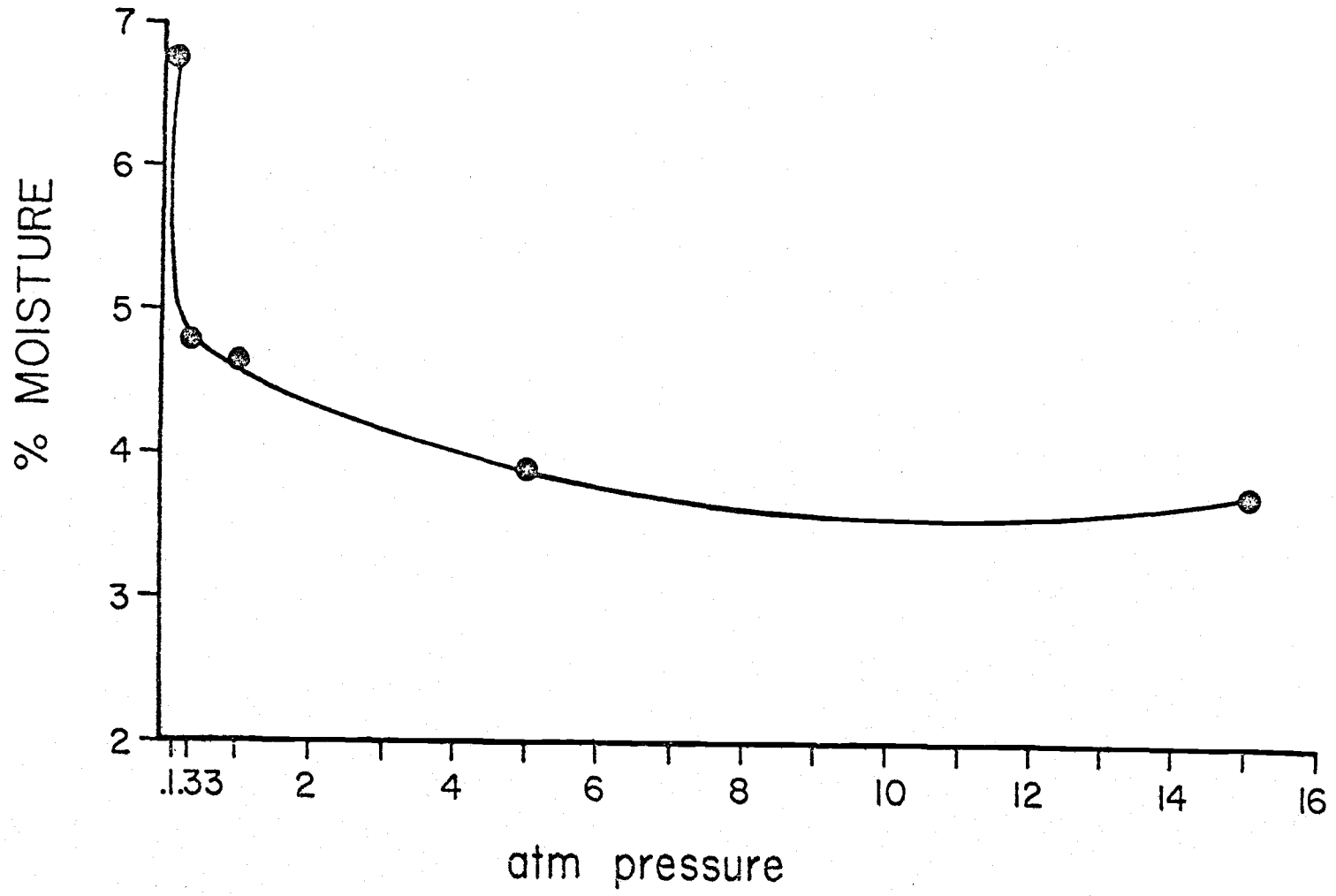



Figure 25. Soil moisture tension curve for greenhouse river sand.

where measurements were taken on subsamples. Statistical analysis included mean, standard deviation, one-way analysis of variance and SNK range test (Sokal and Rohlf, 1969).

The aerial biomass was determined for each sample by drying in an oven at $60^{o}$ C and weighing on a Mettler balance. Statistical analysis of biomass was as described above.

Belowground biomass and its distribution were determined for each pot. Due to the variable sized sand particles and the presence of peat, a rather long and intricate method of washing was necessary. Initially, using fingers and forceps, as much peat as possible was removed from the sand surface. With a piece of hardware cloth covering the soil surface, water was run into the pot to float off more of the peat and to thoroughly wet the sand. The pot was then inverted and slipped off the soil column. The soil column was laid on its side and cut with a knife and/or scissors into sections, 0-10 cm, 10-20 cm, and 20-35 cm (or to pot bottom - not always 35 cm due to settling) from the soil surface.

The sections were washed individually. Each section was placed in a tub and covered with water; gentle shaking allowed the larger roots to come free of sand and remaining peat. The remaining mixture of sand, roots, and water was poured into a 1.0 mm mesh sieve and washed with running water until all sand less than 1.0 mm in size was removed. The mixture left in the sieve was placed in a tub of water where the roots were picked out with forceps. The water and suspended material were then decanted into a sieve from which the

remaining roots were collected. Roots from each section were combined, placed in aluminum foil boats and dried in a $60^{o}$ C oven. Statistical analysis, as described previously in this section, was performed.

## Results and Discussion

### Morphology and Anatomy

Tables 39, 41, 43 and 45 contain data on the morphological measurements made on the four species used in the present study. More detailed information on the mean and N values can be found in Tables F-I of the appendix.

Deschampsia cespitosa - Plant length and stem diameter showed significant differences between the three soil moisture levels (Table 39). As can be seen in Table 40, an SNK range test indicated that there was no significant difference between field capacity (FC) and saturated (SAT) conditions. The shortest plants occurred in the dry (DRY) soil.

This is in opposition to what was found in the marsh where the tallest plants occurred in the upper, less wet portion of the transect. This could be explained by the fact that the "dry" portion of the marsh is closer in moisture level to FC than to the extreme DRY (near wilting point) conditions used in the greenhouse study. Unlike in the field, a difference between saturated and field capacity conditions did not result in a difference in plant length.

Distichlis spicata - Differences in morphological characteristics correlated with moisture level appeared in plant length, number of leaves, length of third and fourth internodes, stem diameter, and stem density of Distichlis spicata (Table 41). According to the SNK range test (Table 42) significant differences occur with each moisture level in the case of the first, second, and last

TABLE 39. *Deschampsia cespitosa* - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) $\bar{X}$cm ± SE.

| | Plant length | Stem diameter |
|---|---|---|
| DRY | 20.8 ± 0.7 | 0.02 ± 0.00 |
| FC | 35.6 ± 1.1 | 0.08 ± 0.00 |
| SAT | 34.8 ± 0.8 | 0.08 ± 0.00 |
| level of significant difference | .001* | .001* |

*considered significant

TABLE 40. *Deschampsia cespitosa* - GREENHOUSE. SNK RANGE TEST OF SIGNIFICANT VARIABLES, $\alpha$ = .05 (DRY = near wilting point, FC = field capacity, SAT = saturated).

PLANT LENGTH

| DRY | SAT | FC |
|---|---|---|

STEM DIAMETER

| DRY | FC | SAT |
|---|---|---|

TABLE 41. *Distichlis spicata* - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) $\bar{X}$cm + SE.

| | Plant length | No. leaves | Length 3rd internode | Length 4th internode | Leaf width | Stem diameter | Stem density |
|---|---|---|---|---|---|---|---|
| DRY | 24.0 ± 1.3 | 13.1 ± 0.6 | 1.5 ± 0.1 | 2.0 ± 0.1 | 0.22 ± 0.01 | 0.06 ± 0.00 | 50.6 ± 3.7 |
| FC | 28.2 ± 1.2 | 14.8 ± 0.3 | 1.3 ± 0.1 | 1.5 ± 0.1 | 0.21 ± 0.00 | 0.06 ± 0.00 | 89.0 ± 7.5 |
| SAT | 20.1 ± 0.4 | 12.5 ± 0.2 | 1.0 ± 0.0 | 1.3 ± 0.0 | 0.22 ± 0.00 | 0.08 ± 0.00 | 110.5 ± 5.9 |
| level of significant difference | .001* | .005* | .001* | .001* | .75 | .001* | .001* |

*considered significant

TABLE 42. *Distichlis spicata* - GREENHOUSE. SNK RANGE TEST OF SIGNIFICANT VARIABLES, $\alpha$ = .05 (DRY = near wilting point, FC = field capacity, SAT = saturated).

PLANT LENGTH

| SAT | DRY | FC |
|---|---|---|

NO. LEAVES

| SAT | DRY | FC |
|---|---|---|

LENGTH 3RD INTERNODE

| SAT | FC | DRY |
|---|---|---|

LENGTH 4TH INTERNODE

| SAT | FC | DRY |
|---|---|---|

STEM DIAMETER

| DRY | FC | SAT |
|---|---|---|

STEM DENSITY

| DRY | FC | SAT |
|---|---|---|

characteristics just mentioned. Length of the third internode and stem diameter are similar in FC and DRY conditions. For the fourth internode, length at FC and SAT are not significantly different.

The fact that in the greenhouse experiment, plant length and internode length are least in the SAT conditions and stem density (no. stems/pot) is least in the DRY conditions (all of which are opposite of what occurs in the field) indicates that soil moisture is probably not the sole environmental factor influencing the morphology of D. spicata.

Recall that in the field an increase in lignification of the vascular bundle sheaths was evident with an increase in distance up the D. spicata transect. From results of the greenhouse experiment it appears that soil moisture is not the determining environmental factor for this anatomical characteristic. Figures 26A through C show stem cross sections from the DRY, FC, and SAT treatments, respectively. No differences in the amount of lignification are obvious between the three treatments.

Grindelia integrifolia - Significant differences in leaf number and stem density (Table 43) were observed in Grindelia integrifolia. Leaf number for FC and DRY were similar, while significant differences between each treatment were found for stem density (Table 44).

Leaf number was not a significant variable with G. integrifolia in the field transect study, perhaps because in the field, G. integrifolia grows in the upper portion of the marsh where saturated conditions are reached infrequently during the growing season. It is, therefore, not surprising that the SAT treatment produced a significant difference in leaf number in the greenhouse study. Since stem

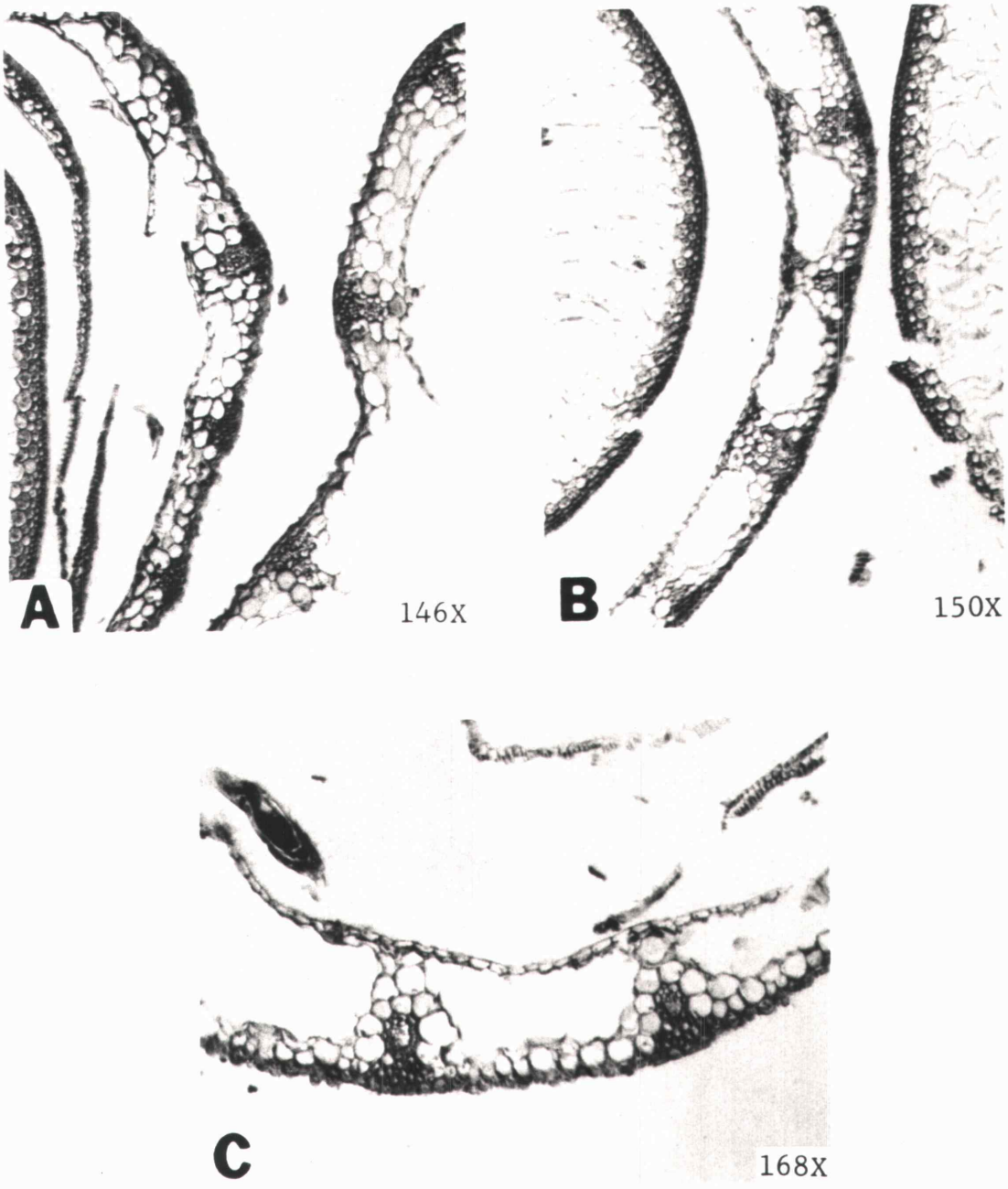



Figure 26. Stem cross sections of Distichlis spicata from the greenhouse experiment (A = DRY, B = FC, C = SAT).

TABLE 43. *Grindelia integrifolia* - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) $\bar{X}$cm ± SE.

| | Stem length | Stem diameter | No. leaves | Leaf width | Stem density |
|---|---|---|---|---|---|
| DRY | 17.7 ± 0.7 | 0.48 ± 0.02 | 6.6 ± 0.3 | 1.4 ± 0.0 | 12.9 ± 1.3 |
| FC | 17.7 ± 0.7 | 0.46 ± 0.02 | 6.4 ± 0.2 | 1.3 ± 0.1 | 23.9 ± 1.4 |
| SAT | 15.9 ± 0.4 | 0.45 ± 0.02 | 4.8 ± 0.2 | 1.2 ± 0.0 | 20.2 ± 1.4 |
| level of significant difference | .10 | .50 | .001* | .25 | .001* |

*considered significant

TABLE 44. *Grindelia integrifolia* - GREENHOUSE. SNK RANGE TEST OF SIGNIFICANT VARIABLES $\alpha = .05$ (DRY = near wilting point, FC = field capacity, SAT = saturated).

NO. LEAVES

| SAT | FC | DRY |
|---|---|---|

STEM DENSITY

| DRY | SAT | FC |
|---|---|---|

density was not measured in the field a comparison between field and greenhouse cannot be made. However, saturated soil does affect this factor.

Stem cross sections of G. integrifolia (Figures 27A-C) display differences in anatomy for the three treatments. As in the field, secondary xylem development is greater in those plants subjected to drier conditions (27A). In the DRY treatment less pith is present. Stems from FC and SAT treatments (27B and C) appear to be fairly similar in pith and secondary xylem development.

Salicornia virginica - Six of the eight characteristics measured on Salicornia virginica were shown to be significant with a one-way analysis of variance (Table 45). S. virginica was the only species in the greenhouse experiment that did not grow with consistent success. Plants died in six of the 30 pots and this was not limited to any particular moisture level. Healthy growth was not consistent with moisture level either, therefore, this should be kept in mind when reviewing the data. Measurements increased with decreasing moisture in all characteristics except stem density where the opposite occurred, and internode length where FC was greater than DRY. FC and SAT were indistinguishable for internode number, number of primary and secondary branches, and stem density (Table 46). No difference was found between FC and DRY for stem length or number of secondary branches.

The characteristics of S. virginica measured in this experiment follow fairly closely the results found in the field and therefore indicate that soil moisture is probably an important environmental factor affecting this species' morphology.

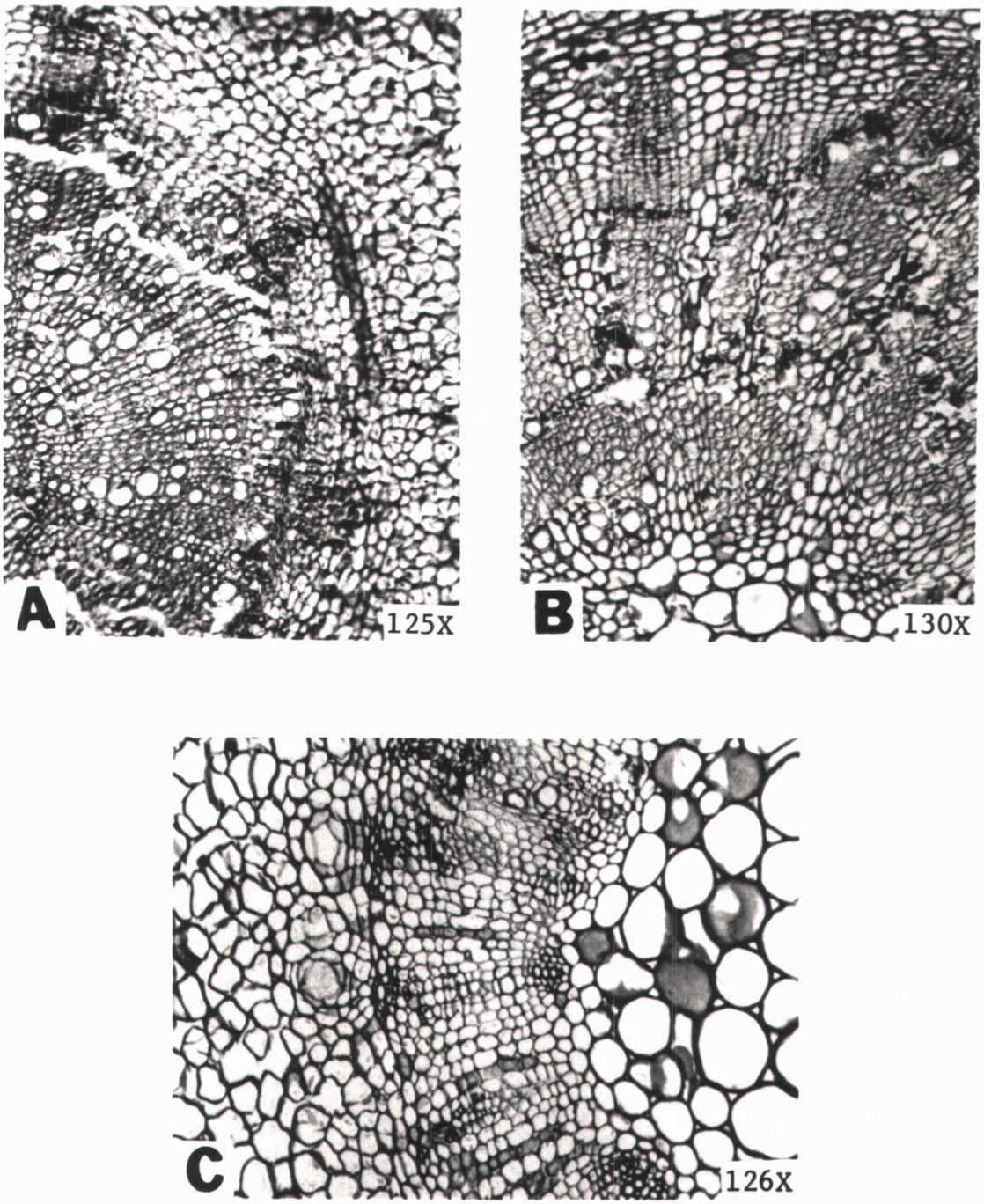



Figure 27. Stem cross sections of Grindelia integrifolia from the greenhouse experiment (A = DRY, B = FC, C = SAT).

TABLE 45. *Salicornia virginica* - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) $\bar{X}$cm ± SE.

| | Stem length | No. internodes | Length internode | No. primary branches |
|---|---|---|---|---|
| DRY | 27.4 ± 1.0 | 18.5 ± 1.1 | 1.3 ± 0.1 | 19.2 ± 2.0 |
| FC | 26.8 ± 1.9 | 12.0 ± 1.3 | 1.6 ± 0.1 | 13.1 ± 1.7 |
| SAT | 15.5 ± 0.7 | 11.4 ± 1.0 | 1.1 ± 0.0 | 8.9 ± 0.9 |
| level of significant difference | .001* | .001* | .001* | .001* |

*considered significant

TABLE 45 (continued). *Salicornia virginica* - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) $\bar{X}$cm ± SE.

| | No. secondary branches | Stem diameter | No. flowers | Stem density |
|---|---|---|---|---|
| DRY | 43.7 ± 11.7 | 0.13 ± 0.01 | 10.1 ± 3.2 | 5.1 ± 0.8 |
| FC | 31.2 ± 7.2 | 0.13 ± 0.01 | 10.3 ± 1.8 | 12.2 ± 4.4 |
| SAT | 5.8 ± 1.0 | 0.12 ± 0.00 | 3.4 ± 0.4 | 14.9 ± 1.8 |
| level of significant difference | .01* | .50 | .10 | .025* |

*considered significant

TABLE 46. Salicornia virginica - GREENHOUSE. SNK RANGE TEST OF SIGNIFICANT VARIABLES, $\alpha = .05$ (DRY = near wilting point, FC = field capacity, SAT = saturated).

STEM LENGTH

| SAT | FC | DRY |
|---|---|---|

NO. INTERNODES

| SAT | FC | DRY |
|---|---|---|

LENGTH INTERNODE

| SAT | DRY | FC |
|---|---|---|

NO. PRIMARY BRANCHES

| SAT | FC | DRY |
|---|---|---|

NO. SECONDARY BRANCHES

| SAT | FC | DRY |
|---|---|---|

STEM DENSITY

| DRY | FC | SAT |
|---|---|---|

As in the field, the amount of aerenchymatous tissue present in the stems of S. virginica coincides with soil moisture. It can be seen from Figures 28A through C that the amount of aerenchyma in stems of the SAT treatment (28C) far exceeds the amount in stems of the other two treatments. It is also evident that the amount of this tissue is greater in stems under the FC treatment than those under the DRY treatment. Since, in the greenhouse experiment, other environmental variables were kept constant, soil moisture is shown to be the factor affecting aerenchyma formation.

Experiments conducted by Penfound (1931) and Dabrowska (1977) have also illustrated the effect of soil moisture on plant morphology and anatomy. In his study of sunflower, wheat and bean, in which plants were grown under three moisture treatments, Penfound reported that plant height and leaf area increased in direct ratio to the water content of the soil. Root depth was greatest in the moist soil (middle treatment). With higher water content, roots and stems were thicker having more and larger xylem vessels; and leaves were thicker having more palisade and spongy parenchyma.

Dabrowska (1977) studied three species of Achillea under conditions of 30% and 70% maximum capillary water capacity of the soil. Plants under higher soil water content displayed a greener color, greater height, greater flower number and a large amount of ramification. From these experiments, along with the results discussed in this thesis, it is evident that soil moisture plays an important role in influencing plant morphology.

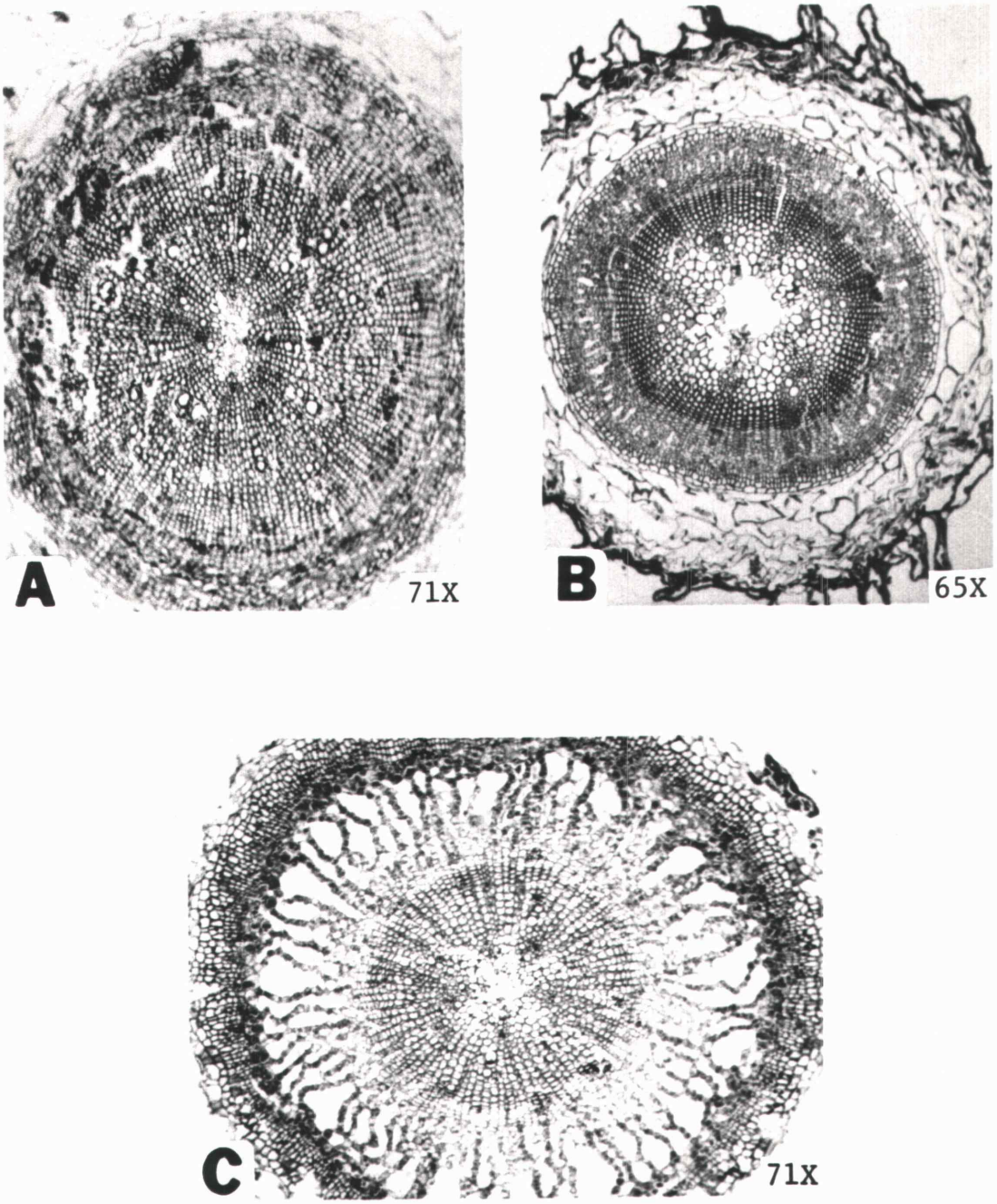



Figure 28. Stem cross sections of Salicornia virginica from the greenhouse experiment (A = DRY, B = FC, C = SAT).

Aerial Biomass

To get an idea of how soil moisture affects plant production in each of the four species, the aboveground biomass was measured from each pot and the dry weight and percent dry weight were calculated.

Deschampsia cespitosa - Each moisture treatment brought about a significant difference in dry weight and percent dry weight for Deschampsia cespitosa (Table 47). This provides evidence that soil moisture plays a significant role in biomass production with FC offering optimal conditions. As would be expected, percent dry weight of the plant increased with decreasing moisture.

Distichlis spicata - Dry weight was greatest in the FC and SAT treatments of Distichlis spicata but the differences were not statistically significant (Table 48). This species is known to flourish in saturated soils. Percent dry weight increased with decreasing soil moisture. Production of D. spicata is thus also significantly affected by soil moisture.

Grindelia integrifolia - As with Deschampsia cespitosa the biomass production of Grindelia integrifolia was greatest under FC conditions and is significantly different under each of the three moisture levels (Table 49). Percent dry weight, as in the previous two cases, increased with decreasing soil moisture.

Salicornia virginica - In the case of Salicornia virginica, no significant differences were found in either dry weight or percent dry weight (Table 50). This is believed to be due to the inconsistent growth of the plants under greenhouse conditions as previously discussed.

TABLE 47. Deschampsia cespitosa - GREENHOUSE. AERIAL BIOMASS (g dry wt.) (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X} \pm SD$

| DRY | | FC | | SAT | |
|---|---|---|---|---|---|
| DRY WT. | % DRY WT. | DRY WT. | % DRY WT. | DRY WT. | % DRY WT. |
| 14.4 ± 1.4 | 54.7 ± 5.9 | 43.9 ± 5.5 | 33.8 ± 1.9 | 32.5 ± 3.1 | 29.6 ± 1.9 |

b) level of significant difference:

DRY WT. = .001
% DRY WT. = .001

c) SNK Range Test ( $\alpha$ = .05):

| DRY WT. | | | % DRY WT. | | |
|---|---|---|---|---|---|
| DRY | SAT | FC | SAT | FC | DRY |

TABLE 48. *Distichlis spicata* - GREENHOUSE. AERIAL BIOMASS ( g dry wt.) (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X} \pm SD$

| DRY | | FC | | SAT | |
|---|---|---|---|---|---|
| DRY WT. | % DRY WT. | DRY WT. | % DRY WT. | DRY WT. | % DRY WT. |
| 6.3 ± 0.9 | 57.4 ± 3.2 | 13.0 ± 1.8 | 53.1 ± 1.7 | 11.7 ± 1.9 | 50.5 ± 1.3 |

b) level of significant difference:

DRY WT. = .001
% DRY WT. = .001

c) SNK Range Test ($\alpha$ = .05)

| DRY WT. | | | % DRY WT. | | |
|---|---|---|---|---|---|
| DRY | SAT | FC | SAT | FC | DRY |

TABLE 49. Grindelia integrifolia - GREENHOUSE. AERIAL BIOMASS (g dry wt.) (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X} \pm SD$

| DRY | | FC | | SAT | |
|---|---|---|---|---|---|
| DRY WT. | % DRY WT. | DRY WT. | % DRY WT. | DRY WT. | % DRY WT. |
| 6.9 ± 1.1 | 16.1 ± 1.0 | 10.6 ± 1.6 | 15.4 ± 1.0 | 5.5 ± 1.5 | 10.9 ± 1.1 |

b) level of significant difference:

DRY WT. = .001
% DRY WT. = .001

c) SNK Range Test ( $\alpha$ = .05):

| DRY WT. | | | % DRY WT. | | |
|---|---|---|---|---|---|
| SAT | DRY | FC | SAT | FC | DRY |

TABLE 50. *Salicornia virginica* - GREENHOUSE. AERIAL BIOMASS (g dry wt.) (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X} \pm SD$

| DRY | | FC | | SAT | |
|---|---|---|---|---|---|
| DRY WT. | % DRY WT. | DRY WT. | % DRY WT. | DRY WT. | % DRY WT. |
| 6.4 ± 2.4 | 36.0 ± 8.9 | 8.4 ± 7.5 | 32.3 ± 16.1 | 4.9 ± 1.8 | 24.4 ± 4.0 |

b) level of significant difference:

DRY WT. = .50 NS
% DRY WT. = .10 NS

Growth studies of plants growing under varying soil moisture conditions have been carried out by several other investigators. Breen, et al. (1977) found that small, one month old seedlings of the salt marsh grass, Sporobolus virginicus died when the soil surface was covered with 3 cm of water. Growth of larger plants, three months old, however, improved with increased inundation so, once established, S. virginicus grows well in waterlogged conditions.

Shoot weights of four populations of Danthonia sericea were significantly less under saturated and dry conditions than they were at moist levels (Quinn, 1975). Similar results occurred with Deschampsia cespitosa and Grindelia integrifolia in this study with the FC treatment offering optimal conditions for these species.

Underground Biomass and Distribution

It was observed throughout the experiment that in the SAT treatment, roots accumulated on the soil surface. It was therefore, decided to collect data on root distribution as well as root biomass with the thought that this may prove to be another feature of possible use in the delineation of wetlands.

Total underground biomass, like aerial biomass, was greatest under FC conditions for every species (see Tables 51-54). Root biomass was significantly different with each treatment in the cases of Deschampsia cespitosa and Distichlis spicata (see SNK range test results - Tables 51-54). No difference was found between SAT and DRY treatments of Grindelia integrifolia and Salicornia virginica, but FC was different than the other two treatments.

TABLE 51. *Deschampsia cespitosa* - GREENHOUSE. UNDERGROUND BIOMASS (g dry wt.) AND DISTRIBUTION (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X}$, SD, N

| | DRY | | | | FC | | | | SAT | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-10cm | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL |
| $\bar{X}$ | 1.1 | 0.5 | 0.3 | 2.0 | 3.3 | 1.7 | 1.3 | 6.4 | 3.1 | 1.0 | 0.2 | 4.2 |
| SD | 0.4 | 0.2 | 0.1 | 0.5 | 1.0 | 0.5 | 0.4 | 1.6 | 0.4 | 0.1 | 0.0 | 0.5 |
| N | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 |

b) level of significant difference between totals = .001

c) SNK range test between totals ( $\alpha$ = .05):

DRY SAT FC

TABLE 52. Distichlis spicata - GREENHOUSE. UNDERGROUND BIOMASS (g dry wt.) AND DISTRIBUTION (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X}$, SD, N

| | DRY | | | | FC | | | | SAT | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-10cm | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL |
| $\bar{X}$ | 5.0 | 2.8 | 4.1 | 11.9 | 8.4 | 7.1 | 9.8 | 25.3 | 9.7 | 3.0 | 1.7 | 14.4 |
| SD | 0.7 | 0.3 | 0.8 | 1.4 | 1.4 | 1.3 | 2.2 | 3.7 | 1.9 | 0.6 | 0.4 | 2.2 |
| N | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 10 | 0.2 | 0.1 | 0.7 |

b) level of significant difference between totals = .001

c) SNK range test between totals ($\alpha$ = .05):

DRY SAT FC

TABLE 53. Grindelia integrifolia - GREENHOUSE. UNDERGROUND BIOMASS (g dry wt.) AND DISTRIBUTION (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X}$, SD, N

| | DRY | | | | FC | | | | SAT | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-10cm | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL |
| $\bar{X}$ | 2.8 | 1.9 | 2.0 | 6.7 | 6.1 | 4.8 | 8.0 | 19.0 | 5.9 | 1.6 | 0.1 | 7.7 |
| SD | 0.8 | 0.6 | 0.7 | 1.6 | 1.5 | 1.3 | 1.6 | 3.9 | 2.0 | 0.7 | 0.1 | 2.8 |
| N | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 | 8 |

b) level of significant difference between totals = .001

c) SNK range test between totals ($\alpha$ =.05):

DRY SAT FC

TABLE 54. *Salicornia virginica* - GREENHOUSE. UNDERGROUND BIOMASS (g dry wt.) AND DISTRIBUTION (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) $\bar{X}$, SD, N

| | DRY | | | | FC | | | | SAT | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | 0-10cm | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL | 0-10 | 10-20 | 20-35 | TOTAL |
| $\bar{X}$ | 1.9 | 0.8 | 0.4 | 3.1 | 3.3 | 1.4 | 1.8 | 6.5 | 2.3 | 0.13 | 0.03 | 2.4 |
| SD | 0.7 | 0.2 | 0.2 | 0.8 | 2.3 | 0.8 | 1.4 | 4.1 | 0.6 | 0.10 | 0.02 | 0.7 |
| N | 9 | 9 | 9 | 9 | 7 | 7 | 7 | 7 | 9 | 9 | 9 | 9 |

b) level of significant difference between totals = .005

c) SNK range test between totals:

SAT DRY FC

Soil moisture is thus a significant factor in root biomass production as well as in aerial biomass production.

Root distribution is best viewed as percent of total dry weight (see Table 55). In the SAT treatment for each species, by far the greatest percentage of root mass is in the upper 10 cm of the soil column, 95.8% in the case of S. virginica. Root biomass was also greatest in the upper 10 cm of the DRY treatment but not nearly to the extent as in the SAT treatment. Under FC conditions root biomass was more evenly distributed probably due to the more even distribution of water and oxygen.

With such a large percentage of the roots in the upper ten centimeters, under saturated conditions, the measurement of root distribution may provide a method for one-time sampling to determine saturated soil conditions. Recall the problems of a one-time physical measurement discussed in the Introduction. Field verification would of course be necessary.

## Root:Shoot Ratios

Root:shoot ratios indicate changes in allocation of photosynthate under varying environmental conditions. Ratios for the four species used in the greenhouse experiment are shown in Tables 56 through 59.

Deschampsia cespitosa - The root:shoot ratios for Deschampsia cespitosa were not significantly different for the three treatments (see Table 56). As seen previously from Tables 47 and 51 the dry weight of both above- and belowground biomass increased in the

TABLE 55. GREENHOUSE - UNDERGROUND BIOMASS DISTRIBUTION MEASURED AS % OF TOTAL GRAMS DRY WT. (DRY = near wilting point, FC = field capacity, SAT = saturated).

a) *Deschampsia cespitosa*

| Depth (cm) | DRY | FC | SAT |
|---|---|---|---|
| 0-10 | 55.0 | 51.6 | 73.8 |
| 10-20 | 25.0 | 26.6 | 23.8 |
| 20-35 | 15.0 | 20.3 | 4.8 |

b) *Distichlis spicata*

| Depth (cm) | DRY | FC | SAT |
|---|---|---|---|
| 0-10 | 42.0 | 33.2 | 67.4 |
| 10-20 | 23.5 | 28.1 | 20.8 |
| 20-35 | 34.4 | 38.7 | 11.8 |

c) *Grindelia integrifolia*

| Depth (cm) | DRY | FC | SAT |
|---|---|---|---|
| 0-10 | 41.8 | 32.1 | 76.6 |
| 10-20 | 28.4 | 25.3 | 20.8 |
| 20-35 | 29.8 | 42.1 | 1.3 |

d) *Salicornia virginica*

| Depth (cm) | DRY | FC | SAT |
|---|---|---|---|
| 0-10 | 61.3 | 50.8 | 95.8 |
| 10-20 | 25.8 | 21.5 | 5.4 |
| 20-35 | 12.9 | 27.7 | 1.2 |

TABLE 56. ROOT:SHOOT RATIO FOR *Deschampsia cespitosa* IN THE GREENHOUSE.

| | DRY | FC | SAT |
|---|---|---|---|
| $\bar{X}$ | 0.14 | 0.15 | 0.13 |
| SD | 0.04 | 0.04 | 0.01 |
| N | 8 | 8 | 8 |

level of significant difference = .50, N.S.

following order: DRY, SAT, FC. Since the ratio does not change, both roots and shoots are affected equally.

Distichlis spicata - The SAT treatment significantly decreased the root:shoot ratio of Distichlis spicata from 1.97 (FC) to 1.24 (SAT) (Table 57). Saturated conditions therefore inhibit root growth more than shoot growth while with the other two treatments (FC and DRY) both plant parts are affected similarly.

Grindelia integrifolia - In each treatment of Grindelia integrifolia the root:shoot ratios are affected differently (Table 58). Ratios significantly increase from DRY (0.98) to SAT (1.42) with FC having the largest value (1.85). The proportion of roots relative to shoots is therefore greatest under field capacity conditions. Unlike Distichlis spicata where root growth is most inhibited by saturated soil, root growth of G. integrifolia is most inhibited by dry soil.

Salicornia virginica - The root:shoot ratios of Salicornia virginica, as with Deschampsia cespitosa, are not affected by soil moisture treatment (Table 59).

Shoot:root ratios of Spartina cynosuroides, a salt marsh grass occupying the high marsh and of Spartina alterniflora, found in the low marsh, were studied by Parrondo, et al. (1978) in a controlled, greenhouse, soil moisture experiment. Constantly flooded sediment reduced growth of S. cynosuroides however did not affect the shoot:root ratio. In other words, the degree of inhibition due to flooding was the same for shoots and roots. Root growth of S. alterniflora was reduced under drained conditions giving a shoot:root ratio in the drained environment twice that of plants under flooded conditions.

TABLE 57. ROOT:SHOOT RATIO FOR Distichlis spicata IN THE GREENHOUSE.

| | DRY | FC | SAT |
|---|---|---|---|
| $\bar{X}$ | 1.93 | 1.97 | 1.24 |
| SD | 0.34 | 0.29 | 0.16 |
| N | 10 | 10 | 10 |

level of significant difference = .001

SNK range test:

| SAT | DRY | FC |
|---|---|---|

TABLE 58. ROOT:SHOOT RATIO FOR *Grindelia integrifolia* IN THE GREENHOUSE.

| | DRY | FC | SAT |
|---|---|---|---|
| $\bar{X}$ | 0.98 | 1.85 | 1.42 |
| SD | 0.17 | 0.27 | 0.33 |
| N | 8 | 8 | 8 |

level of significant difference = .001

SNK range test:

DRY SAT FC

TABLE 59. ROOT:SHOOT RATIO FOR *Salicornia virginica* IN THE GREENHOUSE.

| | DRY | FC | SAT |
|---|---|---|---|
| $\bar{X}$ | 0.47 | 0.47 | 0.48 |
| SD | 0.17 | 0.15 | 0.09 |
| N | 9 | 6 | 9 |

level of significant difference = 1.0, N.S.

The differences seen between the two species correlate well with their distribution in the natural environment.

Results similar to those observed by Parrondo for S. cynosuroides were seen in Deschampsia cespitosa and Salicornia virginica in this research. Here soil moisture treatment did not affect the root:shoot ratios. Comparing only FC and SAT treatments (similar to Parrondo's drained and flooded conditions) for Distichlis spicata and Grindelia integrifolia, root growth was inhibited more than shoot growth by the saturated soil. This is not surprising for G. integrifolia, since it is a high marsh plant, however one would think that for D. spicata, a low marsh species, results similar to Parrondo's S. alterniflora would have been found. Perhaps metabolic conditions within the substrate played a significant role in determining root growth. It could be, however, that what occurred in the greenhouse is not what happens in the field. Recall that aerial biomass in the greenhouse was opposite of that found in the field.

## Conclusions

1. Soil moisture significantly affected the morphology and anatomy of the four salt marsh species studied in the greenhouse experiment. As seen with Salicornia virginica greenhouse results correlate well with those of the field indicating that soil moisture may be the cause of morphological variations observed in the field. In other cases, such as Distichlis spicata results opposite of those occurring in the field were found in the greenhouse. Here environmental variables other than soil moisture must be causing the observed morphological and anatomical differences.
2. Aerial biomass production along with belowground biomass production are significantly affected by soil moisture. For all species the FC treatment offered optimal growth conditions for both above- and belowground plant parts.
3. After further investigation in the field, root distribution may prove to be a useful criteria for integrating soil moisture over a period of time. For all four species studied, by far the greatest percentage of root mass occurred in the upper 10 cm of the soil under SAT conditions.
4. Root:shoot ratios of Deschampsia cespitosa and S. virginica were not affected by changes in soil moisture. Ratios for D. spicata were lowered by saturated soils while those for Grindelia integrifolia were lowest under dry conditions.

# V. SUMMARY

Three research strategies were used to study morphological and anatomical responses of five salt marsh plant species to ecological variables. Species included were Deschampsia cespitosa, Distichlis spicata, Grindelia integrifolia, Jaumea carnosa, and Salicornia virginica from the marsh fringing Netarts Bay, Oregon. The study was designed to search for information that would be useful to the U.S. Environmental Protection Agency in setting Section 404 guidelines for the delineation of upper wetland limits.

Along a transect from its upper to its lower distributional limits (40 m at the most) significant morphological differences were found for each species. Soil moisture, measured with tensiometers, increased from the upper to the lower zones. Plant heights were greater in the upper, drier portion of the marsh, except for D. spicata where the reverse was true. Differences were also seen in stem diameter, internode length, branching, leaf width and amount of flowering. Anatomically, greater lignification of the vascular bundle sheaths of D. spicata was evident in plants from the upper distributional zones. In the upper areas vascular bundle size of J. carnosa was larger, the amount of secondary xylem was greater in G. integrifolia and aerenchymatous tissue of S. virginica was decreased. The identification of the significant characteristics and their relationship to elevation may prove useful in determining elevation in wetlands where tidal data are not available.

Based on the results of vertical and lateral transplants, differences found in morphology and anatomy within each of the five

species appeared not to be genetically fixed. Since upon transplanting the plants took on those morphological and anatomical characteristics of the plants in the surrounding area, it was concluded that these species respond plastically to their environment. The various morphological states are therefore, not considered to be ecotypes. Evidence for the change in chemical properties of the transplanted soil was also found and may thus be a significant facter affecting the plants' morphology.

In a controlled greenhouse experiment the morphological and anatomical responses along with biomass production of four of the species, D. cespitosa, D. spicata, G. integrifolia and S. virginica, were studied at three different moisture levels (field capacity (FC), saturated (SAT), and near wilting point (DRY)). S. virginica responded similarly to soil moisture in the greenhouse as it did in the field, for example, more aerenchyma was formed by plants under SAT conditions. Secondary xylem formation in G. integrifolia was greatest in the DRY treatment which is also in agreement with field results. Results opposite of those occurring in the field were found however for D. spicata. Here plant height was least in the SAT treatment and soil moisture did not appear to affect the amount of lignification of vascular bundle sheaths. Plant height of D. cespitosa under FC and SAT treatments was not found to be significantly different while, in the field, differences were seen between soil moistures similar to these. In view of these results, it is concluded that other environmental factors such as salinity and nutrients affect the plants' morphology and anatomy in the salt marsh.

With each species maximum above and belowground biomass production was found in the FC treatment. Root:shoot ratios of D. cespitosa and S. virginica were not affected by changes in soil moisture while those of D. spicata and G. integrifolia were. For all the species under the SAT treatment the greatest percentage of root mass occurred in the upper 10 cm of the soil. Perhaps root distribution may provide a useful index reflecting the integrated soil moisture over a period of time.

Recommendations for Future Research

1. Those morphological characteristics measured that proved to be insignificant and should not be included in future studies or for wetland boundary determination were the following: Deschampsia cespitosa - flowering shoot diameter, Distichlis spicata - number of internodes, Grindelia integrifolia - number of vegetative rosettes, leaf number, flower number and flowering shoot diameter, Jaumea carnosa - stem diameter, Salicornia virginica - dry weight/volume of an internode. Significant characteristics that would be useful in future work are: D. cespitosa - plant length, stem diameter, leaf width, flowering shoot length, and inflorescence length, D. spicata - plant length, leaf number, length of third and fourth internodes, leaf width and stem diameter, G. integrifolia - plant length, length of the flowering shoot, length of vegetative rosettes, length of woody tissue, stem diameter and leaf width, J.

carnosa - plant length, number of nodes, lengths of second and third internodes, leaf number, leaf width, and leaf thickness, S. virginica - stem length, internode number and length, number of primary and secondary branches, stem diameter, and flower number.

2. Results of this study suggest that it may be possible to use morphological characteristics to determine elevation. To verify this hypothesis another field study is necessary. Elevation should be determined in a selection of marshes for the sites of significant morphological change and then correlated to those elevations found in this study. High correlations would prove this method to be a valid one.

3. In the greenhouse experiment at least 67% of the underground biomass of D. cespitosa, D. spicata, G. integrifolia and S. virginica was located in the upper 10 cm of the soil when grown under saturated conditions. Such root distribution may provide EPA with a one-time measurement for the determination of saturated soils. A field study would be necessary. Tensiometers should be set out for at least one year in upper (drier) and lower (wetter) marsh sites to determine the percentage of time that the soils are saturated in these areas. Replicate soil cores must then be taken at the tensiometer sites using a coring device such as the one described by Gallagher (1974). The cores should be sectioned and washed in a 1 mm sieve and the root distribution determined upon oven drying. If results

similar to those in the greenhouse are found, root distribution would be very useful in delineating upper wetland limits according to soil moisture.

# VI. LITERATURE CITED


Aussenac, G. and M. Ducrey. 1977. Etude bioclimatique d'une futaie feuillue (Fagus silvatica L. et Quercus sessiliflora Salisb.) de l'Est de la France. I. Analyse des profils microclimatiques et des caractéristiques anatomiques et morphologiques de l'appareil foliaire. Ann. Sci. Forest. 34(4): 265-284.

Baker, E. A. 1974. The influence of environment on leaf wax development in Brassica oleracea var. gemmifera. New Phytol. 73(5): 955-966.

Bannister, P. 1976. Introduction to physiological plant ecology. John Wiley & Sons: New York. 273 pp.

Barber, D. A., M. Ebert and N. T. S. Evans. 1962. The movement of $^{15}O$ through barley and rice plants. J. Exp. Bot. 13: 397-403.

Barbour, M. G. 1978. The effect of competition and salinity on the growth of a salt marsh plant species. Oecologia (Berl.) 37: 93-99.

Barbour, M. G. and T. M. DeJong. 1977. Response of West Coast beach taxa to salt spray, sea water inundation, and soil salinity. Bull. Torr. Bot. Club 104(1): 29-34.

Behrens, E. W. 1965. Use of the Goldberg refractometer as a salinometer for biological and geological field work. J. Mar. Res. 23: 165-171.

Boyer, J. S. 1970. Leaf enlargement and metabolic rates in corn, soybean, and sunflower at various leaf water potentials. Plant Physiol. 46: 233-235.

Breen, C. M., C. Everson and K. Rogers. 1977. Ecological studies on Sporobolus virginicus (L.) Kunth. with particular reference to salinity and inundation. Hydrobiologia 54(2): 135-140.

Chabot, B. F. and J. F. Chabot. 1977. Effect of light and temperature of leaf anatomy and photosynthesis in Fragaria vesca. Oecologia (Berl.) 26: 363-377.

Clausen, J. 1967. Stages in the evolution of plant species. New York: Hafner Publishing Co.

Clausen, J. D., D. Keck, and W. M. Hiesey. 1948. Experimental studies on the nature of the species. III. Environmental responses of climatic races of Achillea. Publ. Carneg. Inst. No. 581.

Clough, B. F. and F. L. Milthorpe. 1975. Effects of water deficit on leaf development in tobacco. Aust. J. Plant Physiol. 2: 291-300.

Coutts, M. P. and J. J. Philipson. 1977. The influence of mineral nutrition on the root development of trees. III. Plasticity of root growth in response to changes in the nutrient environment. J. Exp. Bot. 28(106): 1071-1075.

Crawford, R. M. M. and P. D. Tyler. 1969. Organic acid metabolism in relation to flooding tolerance in roots. J. Ecol. 57: 237-246.

Cunningham, G. L. and B. R. Strain. 1969. Ecological significance of seasonal leaf variability in a desert shrub. Ecology 50: 400-408.

Dabrowska, J. 1977. Effect of soil moisture on some morphological characters of Achillea collina Becker, A. millefolium L. ssp. millefolium and A. pannonica Scheele. Ekol. pol. 25(2): 275-288.

Das, D. K. and R. L. Jat. 1972. Adaptability of maize to high soil water conditions. Agron. J. 64(6): 849-850.

Das, D. K. and R. L. Jat. 1977. Influence of 3 soil water regimes on root porosity and growth of 4 rice varieties. Agron J. 69(2): 197-200.

Datta, S. K. and B. Banerji. 1974. Anatomical variations of flood resistance and deep-water rice under field and deep-water conditions. Phytomorphology 24(3-4): 164-174.

Davy, A. J. and K. Taylor. 1974. Water characteristics of contrasting soils in the Chiltern Hills and their significance for Deschampsia caespitosa (L.) Beauv. J. Ecol. 62(2): 367-378.

Downs, R. J. and H. Hellmers. 1975. Environment and the Experimental Control of Plant Growth. New York: Academic Press. 145 pp.

Drew, A. B. and W. K. Ferrell. 1977. Morphological acclimation to light intensity in Douglas fir seedlings. Can. J. Bot. 55(15): 2033-2042.

Duff, D. T. and J. B. Beard. 1974. Supraoptimal temperature effects upon Agrostis palustris I. Influence on shoot growth and density, leaf blade width and length, succulence, and chlorophyll content. Physiologia Pl. 32(1): 14-17.

Eilers, H. P. 1975. Plants, plant communities, net production and tide levels: the ecological biogeography of the Nehalem salt marshes, Tillamook County, Oregon. Ph.D. Thesis, Oregon State University, Corvallis, Oregon. 368 pp.

Federal Register, July 19, 1977. Title 33.

Federal Water Pollution Control Act. 1972. Public Law 92-500.

Freijsen, A. H. J. and A. VanDijk. 1975. Differences in growth rate and salt tolerance between varieties of the halophyte Centaurium littorale (Turner) Gilmour, and their ecological significance. Acta Bot. Neerl. 24(1): 7-22.

Frenkel, R. E., T. Boss, and S. R. Schuller. 1978. Transition zone vegetation between intertidal marsh and upland in Oregon and Washington. Final report prepared for the U.S. Environmental Protection Agency. Department of Geography, Oregon State University, Corvallis, Oregon.

Frenkel, R. E. and H. P. Eilers. 1976. Tidal datums and characteristics of the upper limits of coastal marshes in selected Oregon estuaries. Pilot study of the Environmental Protection Agency, Final report. Department of Geography. Oregon State University, Corvallis, Oregon.

Gallagher, J. L. 1974. Sampling macro-organic profiles in salt marsh plant root zones. Soil Sci. Soc. Amer. Proc. 38(1): 154-155.

Gallagher, J. L. 1978. Estuarine angiosperms: productivity and initial photosynthate dispersion in the ecosystem. In: Estuarine Interactions, M. L. Wiley (ed.). Academic Press: New York. 603 pp.

Gallagher, J. L. 1979. Growth and element compositional responses of Sprorbolus virginicus (L.) Kunth to substrate salinity and nitrogen. Amer. Midl. Nat. 102(1): 68-75.

Gerard, C. J. and E. Hinojosa. 1973. Cell wall properties of cotton roots as influenced by calcium and salinity. Agron. J. 65(4): 556-560.

Gill, C. J. 1975. Ecological significance of adventitious rooting as a response to flooding in woody species, with special reference to Alnus glutinosa (L.) Gaertn. Flora 164(1): 85-98.

Grace, J. and G. Russell. 1977. The effect of wind on grasses. J. Exper. Bot. 28(103): 268-278.

Grant, V. 1975. Genetics of flowering plants. Columbia University Press: New York. 514 pp.

Hansen, D. J., P. Dayanandan, P. B. Kaufman, and J. D. Brotherson. 1976. Ecological adaptations of salt marsh grass, Distichlis spicata (Gramineae), and environmental factors affecting its growth and distribution. Amer. J. Bot. 63(5): 635-650.

Hawkes, A. L. 1966. Coastal wetlands--problems and opportunities: North Amer. Wildlife Conf. Trans., 31: 59-77.

Hitchcock, C. L. and A. Cronquist. 1973. Flora of the Pacific Northwest. Seattle: University of Washington Press. 730 pp.

Hsiao, T. C. 1973. Plant responses to water stress. Ann. Rev. Plant Physiol. 24: 509-570.

Johannsen, D. A. 1940. Plant Microtechnique. New York: McGraw-Hill Co. 523 pp.

Kawase, M. and R. E. Whitmoyer. 1980. Aerenchyma development in waterlogged plants. Amer. J. Bot. 67(1): 18-22.

Kawata, S. I., M. Katano, and K. Yamazaki. 1977. Root system formation in rice plants in ill-drained and well-drained paddy field conditions. Jap. J. Crop Sci. 46(2): 261-268.

Keser, M., B. F. Neubauer, and F. E. Hutchinson. 1975. Influence of aluminum ions on developmental morphology of sugarbeet roots. Agron. J. 67(1): 84-88.

Langa, L. 1975. The relationship of Spartina alterniflora to Mean High Water: Marine Science Research Center, State University. New York at Stony Brook New York Sea Grant Institute, NYSSGP-RS-75-002.

Letcombe Laboratory. 1976. Response of plants to waterlogging and anaerobic soil conditions. Agricultural Research Council Letcombe Laboratory Annual Report, pp. 64-67.

Levitt, J. and R. Ben Zaken. 1975. Effects of small water stresses on cell turgor and intercellular space. Physiologia Pl. 34(3): 273-279.

Lewis, D. H. and M. Liverman. 1979. Evaluation of soil moisture conditions in a coastal wetland. A progress report prepared by the U.S. Environmental Protection Agency, Corvallis, Oregon.

Linthurst, R. H. 1977. An evaluation of biomass, stem density, net aerial primary production (NAPP) and NAPP estimation for selected estuarine angiosperms in Maine, Delaware, and Georgia. M.S. Thesis. Department of Botany, North Carolina State University at Raliegh.

Longstreth, D. J. and P. S. Nobel. 1978. Salinity-induced changes in leaf anatomy and photosynthesis. Plant Physiol. 61(4 suppl.): 94.

Maronek, D. M. and J. A. Wott. 1975. Morphological and physiological responses of Acer rubrum L. and Acer saccharum Marsh. to inundation. Abst. Hort. Science. 10(3): Sect. 2, 24-25.

Mayer, F. L. S., Jr. 1969. Influence of salinity on fruit size in Ruppia maritima L. Proc. Utah Acad. Sci. Arts Lett. 46(2): 140-143.

Mingeau, M. 1977. Parasite racinaire et tolerance a l'ennoyage. Ann. Agron. 28(2): 171-183.

Moore, P. D. 1978. Adaptations to waterlogged environments. Nature 271(5642): 207.

National Oceanic and Atmospheric Administration (NOAA). 1975. The relationship between the upper limit of coastal marshes and tidal datum, Rockville, National Ocean Survey (a pilot study conducted for the EPA).

National Oceanic and Atmospheric Association (NOAA). 1978. Tide Tables 1979, West Coast of North and South America.

National Oceanic and Atmospheric Association (NOAA). 1979. Climatological Data, January-December, 1979. 85(1-12): 5.

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

Njoku, E. 1956. The effect of light intensity on leaf shape in Ipomoea caerulea. New Phytol. 55: 91-110.

Odum, E. P. 1961. The role of tidal marshes in estuarine production. The Conservationist 15: 12-13.

Parrondo, P. T., J. G. Gosselink and C. S. Hopkinson. 1978. Effects of salinity and drainage on the growth of three salt marsh grasses. Bot. Gaz. 139(1): 102-107.

Peet, M. M., J. L. Ozbun, and D. H. Wallace. 1977. Physiological and anatomical effects of growth temperature on Phaseolus vulgaris L. cultivars. J. Exper. Bot. 28(102): 57-69.

Penfound, W. T. 1931. Plant anatomy as conditioned by light intensity and soil moisture. Amer. J. Bot. 18: 558-572.

Pereira, J. S. and T. T. Kazlowski. 1977. Variations among woody angiosperms in response to flooding. Physiol. Plant 41: 184-192.

Phleger, C. 1971. Effect of salinity on growth of a salt marsh grass. Ecology 52: 908-911.

Poljakoff-Mayber, A. M. 1975. Morphological and anatomical changes in plants as a response to salinity stress. In: Plants in Saline Environments, A. Poljakoff-Mayber and J. Gale (eds.). Springer-Verlag: New York. 213 pp.

Quinn, J. A. 1975. Variation among Danthonia sericea (Gramineae) populationsin responses to substrate moisture levels. Amer. J. Bot. 62(8): 884-891.

Radin, J. W. and L. L. Parker. 1979. Water relations of cotton plants under nitrogen deficiency. I. Dependence upon leaf structure. Plant Physiol. 64: 495-498.

Reimold, R. J., J. L. Gallagher and D. E. Thompson. 1972. Coastal mapping with remote sensors. pp. 99-112. In: Proceedings of a symposium on coastal mapping. Amer. Soc. Photogrammetry, Washington, D.C. 319 pp.

Ridley, E. J. and G. W. Todd. 1966. Anatomical variations in the wheat leaf following internal water stress. Bot. Gaz. 127: 235-238.

Rohlf, F. J. and R. R. Sokal. 1969. Statistical Tables. W. H. Freeman and Company: San Francisco. 253 pp.

Russell, G. and J. Grace. 1978. The effect of wind on grasses. IV. Some influences of drought or wind on Lolium perenne. J. Exp. Bot. 29(108): 245-255.

Sanchez, R. A. and D. Cogliatti. 1975. The interaction between phytochrome and white light irradiance in the control of leaf shape in Taraxacum officinale. Bot. Gaz. 136(3): 281-285.

Shea, M. L., R. S. Warren, and W. A. Niering. 1975. Biochemical and transplantation studies of the growth form of Spartina alterniflora on Connecticut salt marshes. Ecology 56(2): 461-466.

Smith, D. 1972. Effect of day-night temperature regimes on growth and morphological development of Timothy plants derived from winter and summer tillers. J. Br. Grassld. Soc. 27: 107-110.

Smith, W. K. and P. S. Nobel. 1977. Influences of seasonal changes in leaf morphology on water-use efficiency for three desert broadleaf shrubs. Ecology 58(5): 1033-1043.

Smith, W. K. and P. S. Nobel. 1978. Influence of irradiation, soil water potential, and leaf temperature on leaf morphology of a desert broadleaf, Encelia farinosa Gray (Compositae).

Sokal, R. R. and F. J. Rohlf. 1969. Biometry. W. H. Freeman and Company: San Francisco. 775 pp.

Stelzer, R. and A. Läuchli. 1977. Salt and flooding tolerance of Puccinellia peisonis II. Structural differentiation of the root in relation to function. Zeitschrift fur Pflanzenphysiologie. 84(2): 95-108.

Todd, G. W., P. E. Richardson, and S. P. Sengupta. 1974. Leaf and stem anatomical anomalies in drought-susceptible species Impatiens balsamina, under conditions of drought stress. Bot. Gaz. 135(2): 121-126.

Valiela, I., J. M. Teal, and W. G. Deuser. 1978. The nature of growth forms in the salt marsh grass Spartina alterniflora Amer. Nat. 112(985): 461-470.

Wample, R. L. and D. M. Reid. 1975. Effect of aeration on the flood-induced formation of adventitious roots and other changes in sunflower (Helianthus annus L.). Planta (Berl.) 127: 263-270.

Wample, R. L. and D. M. Reid. 1978. Control of adventious root production and hypocotyl hypertrophy of sunflower (Helianthus annus) in response to flooding. Physiol. Plant. 44: 351-358.

Wample, R. L. and D. M. Reid. 1979. The role of endogenous auxins and ethylene in the formation of adventitious roots and hypocotyl hypertrophy in flooded sunflower plants (Helianthus annus). Physiol. Plant. 45: 219-226.

Wass, M. L. and T. D. Wright. 1969. Coastal wetlandsof Virginia. Glouster Point: Virginia Institute of Marine Science.

Watson, P. J. 1969. Evolution in closely adjacent plant populations. VI. An entomophilous species, Potentilla erecta, in two contrasting habitats. Heredity 24: 407-422.

Watson, P. J. and J. L. Fyfe. 1975. Potentilla erecta in two contrasting habitats - a multivariate approach. Heredity 34(3): 417-422.

Whitecross, M. I. and D. J. Armstrong. 1972. Environmental effects on epicuticular waxes of Brassica napus L. Aust. J. Bot. 20: 87.

Wignarjah, K., D. H. Jennings, and J. F. Handley. 1975. The effect of salinity on growth of Phaseolus vulgaris L. I. Anatomical changes in the first trifoliate leaf. Ann. Bot. 39(164): 1029-1038.

Yu, P. T., L. H. Stolzy, and J. Letey. 1969. Survival of plants under prolonged flooded conditions. Agron. J. 61: 844-847.

# VII. APPENDIX

TABLE A. *Deschampsia cespitosa* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Plant length | Stem diameter | Leaf width |
|---|---|---|---|
| UL-66 | 42.3 (n = 22) | 0.13 (n = 22) | 0.21 (n = 22) |
| UL-65 | 59.7 (n = 20) | 0.13 (n = 20) | 0.23 (n = 20) |
| UL-67 | 35.6 (n = 31) | 0.13 (n = 31) | 0.34 (n = 31) |
| UL-68 | 52.2 (n = 28) | 0.15 (n = 28) | 0.25 (n = 28) |
| $\bar{X}$ | 47.4 | 0.14 | 0.26 |
| SD | 10.6 | 0.01 | 0.06 |
| SE | 5.3 | 0.00 | 0.03 |
| UF-61 | 70.6 (n = 32) | 0.12 (n = 37) | 0.24 (n = 37) |
| UF-62 | 54.0 (n = 52) | 0.15 (n = 54) | 0.27 (n = 54) |
| UF-64 | 75.2 (n = 27) | 0.14 (n = 27) | 0.28 (n = 27) |
| $\bar{X}$ | 66.6 | 0.14 | 0.26 |
| SD | 11.2 | 0.02 | 0.02 |
| SE | 6.4 | 0.01 | 0.01 |
| LL-49 | 35.4 (n = 31) | 0.12 (n = 31) | 0.22 (n = 31) |
| LL-37 | 47.0 (n = 22) | 0.12 (n = 22) | 0.22 (n = 22) |
| $\bar{X}$ | 41.2 | 0.12 | 0.22 |
| SD | 8.2 | 0.00 | 0.00 |
| SE | 5.8 | 0.00 | 0.00 |
| LF-8 | 45.7 (n = 9) | 0.13 (n = 9) | 0.22 (n = 9) |
| LF-41 | 33.9 (n = 30) | 0.09 (n = 30) | 0.19 (n = 30) |
| LF-3 | 31.6 (n = 120) | 0.11 (n = 120) | 0.20 (n = 120) |
| LF-44 | 41.0 (n = 13) | 0.11 (n = 13) | 0.22 (n = 13) |
| $\bar{X}$ | 38.0 | 0.11 | 0.21 |
| SD | 6.5 | 0.02 | 0.02 |
| SE | 3.2 | 0.01 | 0.01 |

TABLE A (continued). *Deschampsia cespitosa* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Flowering shoot length | Flowering shoot diameter | Inflorescence length |
|---|---|---|---|
| UL-66 | 107.8 (n = 3) | 0.23 (n = 12) | 18.9 (n = 12) |
| UL-65 | 89.1 (n = 6) | 0.18 (n = 6) | 16.2 (n = 6) |
| UL-67 | 69.8 (n = 3) | 0.22 (n = 3) | 15.2 (n = 3) |
| UL-68 | 111.5 (n = 2) | 0.28 (n = 2) | 21.1 (n = 3) |
| $\bar{X}$ | 94.6 | 0.23 | 17.8 |
| SD | 19.2 | 0.04 | 2.7 |
| SE | 9.6 | 0.02 | 1.3 |
| UF-61 | 88.4 (n = 5) | 0.20 (n = 5) | 23.0 (n = 4) |
| UF-62 | 115.2 (n = 9) | 0.22 (n = 9) | 20.0 (n = 11) |
| UF-64 | 104.0 (n = 6) | 0.21 (n = 6) | 19.1 (n = 6) |
| $\bar{X}$ | 102.5 | 0.21 | 20.7 |
| SD | 13.5 | 0.01 | 2.0 |
| SE | 7.8 | 0.01 | 1.2 |
| LL-49 | 68.6 (n = 6) | 0.17 (n = 6) | 16.0 (n = 6) |
| LL-37 | 65.5 (n = 5) | 0.16 (n = 5) | 14.4 (n = 6) |
| $\bar{X}$ | 67.0 | 0.16 | 15.2 |
| SD | 2.2 | 0.01 | 1.1 |
| SE | 1.6 | 0.01 | 0.8 |
| LF-8 | 69.9 (n = 7) | 0.19 (n = 7) | 13.8 (n = 7) |
| LF-41 | 57.2 (n = 10) | 0.18 (n = 10) | 15.2 (n = 10) |
| LF-3 | 62.4 (n = 26) | 0.19 (n = 26) | 14.6 (n = 26) |
| LF-44 | 67.3 (n = 11) | 0.18 (n = 11) | 15.1 (n = 10) |
| $\bar{X}$ | 64.2 | 0.19 | 14.7 |
| SD | 5.6 | 0.01 | 0.6 |
| SE | 2.8 | 0.00 | 0.3 |

TABLE B. *Distichlis spicata* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Plant length | No. leaves | Length 3rd internode | Length 4th internode | Leaf width | Stem diameter |
|---|---|---|---|---|---|---|
| UL-12/18 | 6.7 (n = 50) | 8.2 (n = 34) | 0.4 (n = 32) | 0.4 (n = 26) | 0.25 (n = 34) | 0.11 (n = 34) |
| UL-13/15 | 7.1 (n = 67) | 7.3 (n = 33) | 0.4 (n = 26) | 0.6 (n = 19) | 0.28 (n = 32) | 0.10 (n = 33) |
| UL-11/17 | 7.5 (n = 48) | 7.1 (n = 32) | 0.5 (n = 24) | 0.5 (n = 17) | 0.25 (n = 32) | 0.10 (n = 32) |
| UL-26/28 | 6.0 (n = 34) | 6.8 (n = 34) | 0.4 (n = 22) | 0.4 (n = 18) | 0.23 (n = 32) | 0.10 (n = 34) |
| $\bar{X}$ | 6.8 | 7.4 | 0.4 | 0.4 | 0.25 | 0.10 |
| SD | 0.6 | 0.6 | 0.05 | 0.10 | 0.02 | 0.00 |
| SE | 0.3 | 0.3 | 0.02 | 0.05 | 0.01 | 0.00 |
| UF-11/17 | 6.0 (n = 56) | 7.9 (n = 47) | 0.4 (n = 42) | 0.3 (n = 35) | 0.23 (n = 45) | 0.10 (n = 47) |
| UF-26/28 | 6.7 (n = 49) | 7.7 (n = 30) | 0.3 (n = 23) | 0.4 (n = 18) | 0.27 (n = 30) | 0.11 (n = 30) |
| UF-13/15 | 9.4 (n = 50) | 8.0 (n = 30) | 0.6 (n = 22) | 0.9 (n = 15) | 0.25 (n = 30) | 0.11 (n = 30) |
| UF-12/18 | 5.4 (n = 57) | 8.2 (n = 38) | 0.3 (n = 30) | 0.2 (n = 25) | 0.23 (n = 38) | 0.09 (n = 38) |
| $\bar{X}$ | 6.9 | 8.0 | 0.4 | 0.4 | 0.25 | 0.10 |
| SD | 1.8 | 0.2 | 0.14 | 0.3 | 0.02 | 0.01 |
| SE | 0.9 | 0.1 | 0.07 | 0.2 | 0.01 | 0.00 |

TABLE B (continued). *Distichlis spicata* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Plant length | No. leaves | Length 3rd internode | Length 4th internode | Leaf width | Stem diameter |
|---|---|---|---|---|---|---|
| LL-27/25 | 12.5 (n = 2) | 7.0 (n = 2) | 1.7 (n = 1) | 1.2 (n = 1) | 0.28 (n = 2) | 0.08 (n = 2) |
| LL-30/29 | 9.8 (n = 13) | 7.1 (n = 10) | 1.2 (n = 6) | 1.1 (n = 5) | 0.26 (n = 8) | 0.07 (n = 13) |
| $\bar{X}$ | 11.2 | 7.0 | 1.4 | 1.2 | 0.27 | 0.08 |
| SD | 1.9 | 0.1 | 0.4 | 0.1 | 0.01 | 0.01 |
| SE | 1.4 | 0.0 | 0.2 | 0.0 | 0.01 | 0.01 |
| LF-19/20 | 8.1 (n = 10) | 5.4 (n = 9) | 1.5 (n = 5) | 0.8 (n = 5) | 0.24 (n = 7) | 0.07 (n = 10) |
| LF-14/16 | 11.5 (n = 7) | 7.0 (n = 7) | 1.2 (n = 4) | 1.1 (n = 4) | 0.21 (n = 6) | 0.08 (n = 7) |
| LF-30/29 | 10.0 (n = 25) | 7.2 (n = 24) | 0.9 (n = 15) | 1.0 (n = 15) | 0.26 (n = 19) | 0.08 (n = 25) |
| LF-27/25 | 11.5 (n = 2) | 8.5 (n = 2) | 0.6 (n = 2) | 0.2 (n = 1) | 0.25 (n = 2) | 0.08 (n = 2) |
| $\bar{X}$ | 10.3 | 7.0 | 1.0 | 0.8 | 0.24 | 0.08 |
| SD | 1.6 | 1.3 | 0.4 | 0.4 | 0.02 | 0.00 |
| SE | 0.8 | 0.6 | 0.2 | 0.2 | 0.01 | 0.00 |

TABLE C. *Grindelia integrifolia* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Plant length | Stem diameter | No. leaves | Leaf width | Total length wood |
|---|---|---|---|---|---|
| UL-F | 15.8 (n = 1) | 0.30 (n = 1) | 3.0 (n = 1) | 1.9 (n = 1) | 25.2 |
| UL-H | 15.1 (n = 4) | 0.26 (n = 4) | 4.5 (n = 4) | 1.5 (n = 3) | 49.0 |
| UL-D | 11.2 (n = 2) | 0.38 (n = 5) | 5.8 (n = 5) | 1.7 (n = 5) | 6.5 |
| $\bar{X}$ | 14.0 | 0.31 | 4.4 | 1.7 | 26.9 |
| SD | 2.5 | 0.06 | 1.4 | 0.2 | 21.3 |
| SE | 1.4 | 0.04 | 0.8 | 0.12 | 12.3 |
| UF-E | 15.9 (n = 3) | 0.42 (n = 3) | 4.0 (n = 3) | 2.0 (n = 2) | 1.2 |
| UF-B | 14.3 (n = 3) | 0.50 (n = 3) | 4.0 (n = 3) | 1.6 (n = 3) | 10.0 |
| UF-G | 21.7 (n = 5) | 0.48 (n = 5) | 5.6 (n = 5) | 1.9 (n = 5) | 8.5 |
| UF-C | 21.1 (n = 4) | 0.59 (n = 4) | 5.2 (n = 4) | 2.2 (n = 4) | 2.7 |
| $\bar{X}$ | 18.2 | 0.50 | 4.7 | 1.9 | 5.6 |
| SD | 3.7 | 0.07 | 0.8 | 0.2 | 4.3 |
| SE | 1.8 | 0.04 | 0.4 | 0.1 | 2.1 |

TABLE C (continued). *Grindelia integrifolia* TRANSPLANTS (UL = lower lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Plant length | Stem diameter | No. leaves | Leaf width | Total length wood |
|---|---|---|---|---|---|
| LL-N | 18.5 (n = 5) | 0.47 (n = 5) | 5.4 (n = 5) | 1.9 (n = 5) | 5.5 |
| LL-L | 20.6 (n = 5) | 0.37 (n = 5) | 5.2 (n = 5) | 1.7 (n = 5) | 2.9 |
| LL-M | 13.5 (n = 1) | 0.30 (n = 1) | 7.0 (n = 1) | 1.1 (n = 1) | 2.5 |
| LL-P | 18.8 (n = 1) | 0.50 (n = 1) | 5.0 (n = 1) | 2.1 (n = 1) | 4.2 |
| $\bar{X}$ | 17.8 | 0.41 | 5.6 | 1.7 | 3.8 |
| SD | 3.0 | 0.09 | 0.9 | 0.4 | 1.4 |
| SE | 1.5 | 0.05 | 0.5 | 0.2 | 0.7 |
| LF-K | 12.0 (n = 9) | 0.25 (n = 9) | 3.4 (n = 9) | 1.2 (n = 5) | 34.0 |
| LF-I | 11.6 (n = 8) | 0.32 (n = 8) | 3.9 (n = 8) | 1.7 (n = 7) | 26.8 |
| $\bar{X}$ | 11.8 | 0.29 | 3.6 | 1.4 | 30.4 |
| SD | 0.3 | 0.05 | 0.4 | 0.4 | 5.1 |
| SE | 0.2 | 0.04 | 0.2 | 0.2 | 3.6 |

TABLE D. *Jaumea carnosa* TRANSPLANTS (UL = upper later, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Plant length | Stem diameter | No. nodes | Length 2nd internode |
|---|---|---|---|---|
| UL-22/21 | 18.9 (n = 8) | 0.16 (n = 8) | 7.4 (n = 8) | 1.9 (n = 7) |
| UL-24/23 | 15.2 (n = 17) | 0.15 (n = 17) | 6.0 (n = 17) | 2.0 (n = 15) |
| UL-47/48 | 15.6 (n = 8) | 0.15 (n = 8) | 6.0 (n = 8) | 2.1 (n = 8) |
| UL-45/50 | 23.4 (n = 5) | 0.13 (n = 5) | 9.2 (n = 5) | 1.6 (n = 5) |
| $\bar{X}$ | 18.3 | 0.15 | 7.2 | 1.9 |
| SD | 3.8 | 0.01 | 1.5 | 0.2 |
| SE | 1.9 | 0.01 | 0.8 | 0.1 |
| UF-47/48 | 14.7 (n = 18) | 0.14 (n = 18) | 6.6 (n = 18) | 2.3 (n = 17) |
| UF-45/50 | 11.0 (n = 23) | 0.14 (n = 22) | 5.6 (n = 23) | 1.7 (n = 19) |
| UF-22/21 | 21.2 (n = 4) | 0.15 (n = 4) | 8.5 (n = 4) | 2.6 (n = 4) |
| UF-24/23 | 9.8 (n = 97) | 0.13 (n = 27) | 5.8 (n = 27) | 1.6 (n = 25) |
| $\bar{X}$ | 14.2 | 0.14 | 6.6 | 2.0 |
| SD | 5.1 | 0.01 | 1.3 | 0.5 |
| SE | 2.6 | 0.00 | 0.7 | 0.2 |
| LL-33/40 | 9.1 (n = 27) | 0.14 (n = 27) | 7.0 (n = 26) | 1.1 (n = 27) |
| LL-35/31 | 9.0 (n = 9) | 0.14 (n = 9) | 6.1 (n = 9) | 1.2 (n = 8) |
| LL-34/32 | 7.8 (n = 21) | 0.14 (n = 21) | 5.9 (n = 21) | 1.0 (n = 20) |
| LL-38/36 | 9.7 (n = 28) | 0.15 (n = 15) | 7.5 (n = 15) | 1.0 (n = 15) |
| $\bar{X}$ | 8.9 | 0.14 | 6.6 | 1.1 |
| SD | 0.8 | 0.00 | 0.8 | 0.1 |
| SE | 0.4 | 0.00 | 0.4 | 0.0 |
| LF-34/32 | 13.4 (n = 4) | 0.15 (n = 4) | 6.8 (n = 4) | 1.3 (n = 4) |
| LF-35/31 | 11.6 (n = 9) | 0.17 (n = 9) | 6.6 (n = 9) | 1.5 (n = 9) |
| LF-38/36 | 11.8 (n = 4) | 0.15 (n = 4) | 6.0 (n = 4) | 1.2 (n = 4) |
| LF-33/40 | 8.8 (n = 23) | 0.16 (n = 23) | 6.0 (n = 23) | 1.0 (n = 23) |
| $\bar{X}$ | 11.4 | 0.16 | 6.4 | 1.2 |
| SD | 1.9 | 0.01 | 0.4 | 0.2 |
| SE | 1.0 | 0.00 | 0.2 | 0.1 |

TABLE D (continued). *Jaumea carnosa* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Length 3rd internode | No. leaves | Leaf width | Leaf thickness |
|---|---|---|---|---|
| UL-22/21 | 2.3 (n = 7) | 17.2 (n = 8) | 0.43 (n = 5) | 0.10 (n = 3) |
| UL-24/23 | 2.4 (n = 15) | 13.6 (n = 17) | 0.45 (n = 11) | 0.10 (n = 11) |
| UL-47/48 | 2.7 (n = 7) | 14.2 (n = 8) | 0.23 (n = 3) | 0.05 (n = 1) |
| UL-45/50 | 1.6 (n = 5) | 22.0 (n = 5) | 0.43 (n = 5) | 0.10 (n = 5) |
| $\bar{X}$ | 2.2 | 16.8 | 0.39 | 0.09 |
| SD | 0.5 | 3.8 | 0.10 | 0.02 |
| SE | 0.2 | 1.9 | 0.05 | 0.01 |
| UF-47/48 | 2.6 (n = 14) | 15.0 (n = 18) | 0.20 (n = 11) | 0.05 (n = 6) |
| UF-45/50 | 2.0 (n = 17) | 13.4 (n = 23) | 0.29 (n = 13) | 0.08 (n = 6) |
| UF-22/21 | 2.5 (n = 4) | 19.5 (n = 4) | 0.35 (n = 2) | 0.10 (n = 1) |
| UF-24/23 | 1.7 (n = 23) | 13.7 (n = 27) | 0.29 (n = 18) | 0.09 (n = 9) |
| $\bar{X}$ | 2.2 | 15.4 | 0.28 | 0.08 |
| SD | 0.4 | 2.8 | 0.06 | 0.02 |
| SE | 0.2 | 1.4 | 0.03 | 0.01 |
| LL-33/40 | 1.2 (n = 26) | 15.7 (n = 27) | 0.30 (n = 27) | 0.11 (n = 27) |
| LL-35/31 | 1.2 (n = 8) | 14.2 (n = 9) | 0.36 (n = 8) | 0.11 (n = 8) |
| LL-34/32 | 1.1 (n = 19) | 14.2 (n = 21) | 0.28 (n = 19) | 0.11 (n = 17) |
| LL-38/36 | 1.0 (n = 15) | 18.3 (n = 15) | 0.29 (n = 14) | 0.09 (n = 14) |
| $\bar{X}$ | 1.1 | 15.6 | 0.31 | 0.11 |
| SD | 0.1 | 1.9 | 0.04 | 0.01 |
| SE | 0.0 | 1.0 | 0.02 | 0.00 |
| LF-34/32 | 1.8 (n = 4) | 15.5 (n = 4) | 0.40 (n = 4) | 0.11 (n = 4) |
| LF-35/31 | 1.5 (n = 8) | 15.9 (n = 9) | 0.41 (n = 8) | 0.09 (n = 8) |
| LF-38/36 | 1.7 (n = 4) | 15.0 (n = 4) | 0.38 (n = 4) | 0.11 (n = 4) |
| LF-33/40 | 1.2 (n = 18) | 14.5 (n = 23) | 0.30 (n = 22) | 0.10 (n = 21) |
| $\bar{X}$ | 1.6 | 15.2 | 0.37 | 0.10 |
| SD | 0.3 | 0.6 | 0.05 | 0.01 |
| SE | 0.1 | 0.3 | 0.02 | 0.00 |

TABLE E. *Salicornia virginica* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | Stem length | No. internodes | Length internode |
|---|---|---|---|
| UL-71/54 | 28.4 (n = 13) | 19.0 (n = 13) | 1.5 (n = 12) |
| UL-69/70 | 32.0 (n = 3) | 26.7 (n = 3) | 1.1 (n = 3) |
| UL-56/57 | 29.4 (n = 29) | 24.0 (n = 29) | 1.5 (n = 29) |
| UL-72/42 | 19.4 (n = 4) | 13.2 (n = 4) | 1.4 (n = 4) |
| $\bar{X}$ | 27.3 | 20.7 | 1.4 |
| SD | 5.5 | 5.9 | 0.2 |
| SE | 2.7 | 3.0 | 0.1 |
| UF-71/54 | 20.2 (n = 16) | 16.8 (n = 16) | 1.2 (n = 16) |
| UF-72/42 | 28.6 (n = 2) | 16.5 (n = 2) | 2.0 (n = 2) |
| UF-56/57 | 21.0 (n = 20) | 15.2 (n = 20) | 1.5 (n = 20) |
| UF-69/70 | 18.4 (n = 9) | 14.4 (n = 9) | 1.5 (n = 9) |
| $\bar{X}$ | 22.0 | 15.7 | 1.6 |
| SD | 4.5 | 1.1 | 0.3 |
| SE | 2.2 | 0.6 | 0.2 |
| LL-7/4 | 19.0 (n = 64) | 13.0 (n = 63) | 1.0 (n = 62) |
| LL-9/2 | 18.8 (n = 43) | 16.8 (n = 43) | 1.1 (n = 43) |
| LL-5/10 | 14.8 (n = 92) | 17.1 (n = 19) | 0.9 (n = 45) |
| LL-1/6 | 14.8 (n = 61) | 15.5 (n = 38) | 1.0 (n = 38) |
| $\bar{X}$ | 16.8 | 15.6 | 1.0 |
| SD | 2.4 | 1.9 | 0.1 |
| SE | 1.2 | 0.9 | 0.0 |
| LF-7/4 | 21.4 (n = 11) | 17.4 (n = 11) | 1.2 (n = 10) |
| LF-5/10 | 21.5 (n = 11) | 18.1 (n = 11) | 1.2 (n = 11) |
| LF-9/2 | 26.0 (n = 28) | 18.5 (n = 28) | 1.3 (n = 28) |
| LF-1/6 | 22.3 (n = 23) | 17.0 (n = 22) | 1.3 (n = 23) |
| $\bar{X}$ | 22.8 | 17.8 | 1.2 |
| SD | 2.2 | 0.7 | 0.1 |
| SE | 1.1 | 0.3 | 0.0 |

TABLE E (continued). *Salicornia virginica* TRANSPLANTS (UL = upper lateral, UF = upper foreigner, LL = lower lateral, LF = lower foreigner) measurements in cm.

| | No. Primary branches | Dry wt/vol internode | Stem diameter |
|---|---|---|---|
| UL-71/54 | 13.7 (n = 13) | 0.10 (n = 8) | 0.12 (n = 12) |
| UL-69/70 | 11.7 (n = 3) | 0.08 (n = 3) | 0.10 (n = 3) |
| UL-56/57 | 15.8 (n = 29) | 0.09 (n = 11) | 0.12 (n = 29) |
| UL-72/42 | 4.5 (n = 4) | - | 0.08 (n = 3) |
| $\bar{X}$ | 11.4 | 0.09 | 0.11 |
| SD | 4.9 | 0.01 | 0.02 |
| SE | 2.5 | 0.01 | 0.01 |
| UF-71/54 | 2.4 (n = 16) | 0.10 (n = 5) | 0.08 (n = 15) |
| UF-72/42 | 8.0 (n = 2) | - | 0.10 (n = 2) |
| UF-56/57 | 5.7 (n = 20) | - | 0.08 (n = 18) |
| UF-69/70 | 7.9 (n = 9) | - | 0.07 (n = 9) |
| $\bar{X}$ | 6.0 | 0.10 | 0.08 |
| SD | 2.6 | 0.00 | 0.01 |
| SE | 1.3 | 0.00 | 0.01 |
| LL-7/4 | 8.6 (n = 64) | 0.10 (n = 20) | 0.10 (n = 64) |
| LL-9/2 | 6.3 (n = 43) | 0.10 (n = 27) | 0.09 (n = 42) |
| LL-5/10 | 5.4 (n = 45) | 0.10 (n = 13) | 0.09 (n = 44) |
| LL-1/6 | 5.1 (n = 38) | 0.11 (n = 19) | 0.10 (n = 38) |
| $\bar{X}$ | 6.4 | 0.10 | 0.10 |
| SD | 1.6 | 0.00 | 0.01 |
| SE | 0.8 | 0.00 | 0.00 |
| LF-7/4 | 15.0 (n = 11) | 0.11 (n = 10) | 0.14 (n = 9) |
| LF-5/10 | 15.2 (n = 11) | 0.09 (n = 5) | 0.15 (n = 11) |
| LF-9/2 | 17.1 (n = 28) | 0.13 (n = 17) | 0.14 (n = 28) |
| LF-1/6 | 17.1 (n = 23) | 0.13 (n = 14) | 0.12 (n = 23) |
| $\bar{X}$ | 16.1 | 0.12 | 0.14 |
| SD | 1.2 | 0.02 | 0.01 |
| SE | 0.6 | 0.01 | 0.01 |

TABLE F. Deschampsia cespitosa - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) measurements in cm.

| DRY: | Plant length | Stem diameter |
|---|---|---|
| 1 | 19.6 (n = 50) | 0.02 (n = 50) |
| 2 | 23.9 (n = 50) | 0.02 (n = 50) |
| 3 | 18.2 (n = 50) | 0.02 (n = 50) |
| 4 | 20.4 (n = 50) | 0.03 (n = 50) |
| 5 | 25.2 (n = 50) | 0.02 (n = 50) |
| 6 | 21.4 (n = 50) | 0.01 (n = 50) |
| 7 | 20.2 (n = 50) | 0.02 (n = 50) |
| 8 | 18.6 (n = 50) | 0.02 (n = 50) |
| 9 | 19.2 (n = 50) | 0.02 (n = 50) |
| 10 | 21.3 (n = 50) | 0.02 (n = 50) |
| $\bar{X}$ | 20.8 | 0.02 |
| SD | 2.2 | 0.00 |
| SE | 0.7 | 0.00 |

| FC: | Stem length | Stem diameter |
|---|---|---|
| 1 | 39.2 (n = 50) | 0.08 (n = 50) |
| 2 | 37.6 (n = 50) | 0.08 (n = 50) |
| 3 | 29.5 (n = 50) | 0.08 (n = 50) |
| 4 | 34.4 (n = 50) | 0.09 (n = 50) |
| 5 | 39.6 (n = 50) | 0.07 (n = 50) |
| 6 | 30.6 (n = 50) | 0.08 (n = 50) |
| 7 | 35.3 (n = 50) | 0.08 (n = 50) |
| 8 | 34.8 (n = 50) | 0.08 (n = 50) |
| 9 | 38.7 (n = 50) | 0.08 (n = 50) |
| 10 | 36.1 (n = 50) | 0.08 (n = 50) |
| $\bar{X}$ | 35.6 | 0.08 |
| SD | 3.4 | 0.00 |
| SE | 1.1 | 0.00 |

| SAT: | Stem length | Stem diameter |
|---|---|---|
| 1 | 33.7 (n = 50) | 0.08 (n = 50) |
| 2 | 31.4 (n = 50) | 0.09 (n = 50) |
| 3 | 31.9 (n = 50) | 0.07 (n = 50) |
| 4 | 38.1 (n = 50) | 0.09 (n = 50) |
| 5 | 32.8 (n = 50) | 0.08 (n = 50) |
| 6 | 35.5 (n = 50) | 0.08 (n = 50) |
| 7 | 37.2 (n = 50) | 0.09 (n = 50) |
| 8 | 37.6 (n = 50) | 0.07 (n = 50) |
| 9 | 35.7 (n = 50) | 0.08 (n = 50) |
| 10 | 34.3 (n = 50) | 0.09 (n = 50) |
| $\bar{X}$ | 34.8 | 0.08 |
| SD | 2.4 | 0.01 |
| SE | 0.8 | 0.00 |

TABLE G. Distichlis spicata - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting, FC = field capacity, SAT = saturated) measurements in cm.

| | Plant length | No. leaves | Length 3rd internode |
|---|---|---|---|
| DRY: | | | |
| 1 | 22.9 (n = 61) | 11.0 (n = 19) | 1.7 (n = 19) |
| 2 | 24.1 (n = 40) | 16.0 (n = 12) | 1.4 (n = 12) |
| 3 | 23.5 (n = 56) | 13.4 (n = 43) | 1.8 (n = 43) |
| 4 | 21.6 (n = 62) | 12.5 (n = 21) | 1.4 (n = 21) |
| 5 | 29.7 (n = 38) | 16.6 (n = 12) | 1.8 (n = 12) |
| 6 | 16.6 (n = 71) | 10.6 (n = 20) | 0.8 (n = 20) |
| 7 | 31.5 (n = 36) | 13.2 (n = 12) | 2.1 (n = 12) |
| 8 | 22.0 (n = 48) | 13.5 (n = 14) | 1.2 (n = 14) |
| 9 | 25.3 (n = 48) | 12.2 (n = 16) | 1.9 (n = 15) |
| 10 | 22.4 (n = 46) | 12.4 (n = 14) | 1.2 (n = 14) |
| $\bar{X}$ | 24.0 | 13.1 | 1.5 |
| SD | 4.2 | 1.9 | 0.4 |
| SE | 1.3 | 0.6 | 0.1 |
| FC: | | | |
| 1 | 27.1 (n = 96) | 15.2 (n = 39) | 1.4 (n = 39) |
| 2 | 28.2 (n = 97) | 14.8 (n = 22) | 1.4 (n = 22) |
| 3 | 28.9 (n = 83) | 15.7 (n = 20) | 1.3 (n = 20) |
| 4 | 25.2 (n = 134) | 12.8 (n = 32) | 1.3 (n = 31) |
| 5 | 30.2 (n = 66) | 14.4 (n = 58) | 1.5 (n = 56) |
| 6 | 31.5 (n = 65) | 16.0 (n = 13) | 1.0 (n = 12) |
| 7 | 23.3 (n = 117) | 13.8 (n = 52) | 1.3 (n = 51) |
| 8 | 35.1 (n = 62) | 15.1 (n = 62) | 1.6 (n = 62) |
| 9 | 23.2 (n = 96) | 14.5 (n = 22) | 1.2 (n = 22) |
| 10 | 29.2 (n = 74) | 15.3 (n = 37) | 1.1 (n = 36) |
| $\bar{X}$ | 28.2 | 14.8 | 1.3 |
| SE | 3.7 | 0.9 | 0.2 |
| SD | 1.2 | 0.3 | 0.1 |
| SAT: | | | |
| 1 | 18.3 (n = 127) | 11.7 (n = 37) | 0.9 (n = 37) |
| 2 | 20.1 (n = 129) | 12.7 (n = 54) | 1.0 (n = 54) |
| 3 | 19.2 (n = 107) | 11.9 (n = 26) | 1.1 (n = 25) |
| 4 | 20.2 (n = 114) | 12.5 (n = 20) | 0.9 (n = 19) |
| 5 | 22.2 (n = 100) | 13.1 (n = 48) | 1.1 (n = 47) |
| 6 | 21.4 (n = 111) | 12.4 (n = 22) | 0.9 (n = 22) |
| 7 | 18.8 (n = 98) | 12.2 (n = 51) | 1.2 (n = 51) |
| 8 | 20.5 (n = 123) | 12.9 (n = 23) | 0.9 (n = 23) |
| 9 | 21.0 (n = 68) | 12.9 (n = 16) | 1.2 (n = 16) |
| 10 | 19.4 (n = 128) | 13.0 (n = 27) | 1.0 (n = 27) |
| $\bar{X}$ | 20.1 | 12.5 | 1.0 |
| SD | 1.2 | 0.5 | 0.1 |
| SE | 0.4 | 0.2 | 0.0 |

TABLE G (continued). Distichlis spicata - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) measurements in cm.

| | Length 4th internode | Leaf width | Stem diameter | Stem density |
|---|---|---|---|---|
| DRY: | | | | |
| 1 | 2.1 (n = 16) | 0.20 (n = 19) | 0.07 (n = 19) | 61 |
| 2 | 2.0 (n = 12) | 0.19 (n = 12) | 0.07 (n = 13) | 40 |
| 3 | 2.0 (n = 42) | 0.28 (n = 42) | 0.06 (n = 56) | 56 |
| 4 | 1.7 (n = 21) | 0.22 (n = 21) | 0.06 (n = 21) | 62 |
| 5 | 2.6 (n = 12) | 0.21 (n = 12) | 0.06 (n = 12) | 38 |
| 6 | 1.3 (n = 20) | 0.20 (n = 20) | 0.06 (n = 24) | 71 |
| 7 | 2.6 (n = 12) | 0.23 (n = 12) | 0.06 (n = 12) | 36 |
| 8 | 1.5 (n = 14) | 0.20 (n = 14) | 0.06 (n = 16) | 48 |
| 9 | 2.0 (n = 14) | 0.23 (n = 16) | 0.06 (n = 16) | 48 |
| 10 | 1.7 (n = 14) | 0.22 (n = 14) | 0.07 (n = 16) | 46 |
| $\bar{X}$ | 2.0 | 0.22 | 0.06 | 50.6 |
| SE | 0.4 | 0.03 | 0.00 | 11.6 |
| SD | 0.1 | 0.01 | 0.00 | 3.7 |
| FC: | | | | |
| 1 | 1.6 (n = 39) | 0.20 (n = 39) | 0.06 (n = 39) | 96 |
| 2 | 1.5 (n = 21) | 0.21 (n = 21) | 0.06 (n = 24) | 97 |
| 3 | 1.6 (n = 19) | 0.21 (n = 20) | 0.06 (n = 22) | 83 |
| 4 | 1.8 (n = 29) | 0.21 (n = 32) | 0.06 (n = 32) | 134 |
| 5 | 1.6 (n = 56) | 0.25 (n = 58) | 0.06 (n = 66) | 66 |
| 6 | 1.3 (n = 12) | 0.21 (n = 13) | 0.07 (n = 13) | 65 |
| 7 | 1.5 (n = 49) | 0.21 (n = 52) | 0.08 (n = 58) | 117 |
| 8 | 1.8 (n = 62) | 0.22 (n = 62) | 0.06 (n = 62) | 62 |
| 9 | 1.3 (n = 21) | 0.20 (n = 22) | 0.06 (n = 24) | 96 |
| 10 | 1.2 (n = 34) | 0.20 (n = 36) | 0.07 (n = 37) | 74 |
| $\bar{X}$ | 1.5 | 0.21 | 0.06 | 89 |
| SE | 0.2 | 0.01 | 0.01 | 23.7 |
| SD | 0.1 | 0.00 | 0.00 | 7.5 |
| SAT: | | | | |
| 1 | 1.1 (n = 37) | 0.23 (n = 37) | 0.07 (n = 37) | 127 |
| 2 | 1.2 (n = 54) | 0.20 (n = 54) | 0.08 (n = 54) | 129 |
| 3 | 1.1 (n = 25) | 0.21 (n = 25) | 0.08 (n = 28) | 107 |
| 4 | 1.2 (n = 18) | 0.22 (n = 20) | 0.07 (n = 23) | 114 |
| 5 | 1.2 (n = 45) | 0.22 (n = 47) | 0.09 (n = 49) | 100 |
| 6 | 1.2 (n = 22) | 0.21 (n = 22) | 0.07 (n = 23) | 111 |
| 7 | 1.5 (n = 51) | 0.22 (n = 51) | 0.08 (n = 51) | 98 |
| 8 | 1.3 (n = 23) | 0.22 (n = 23) | 0.08 (n = 25) | 123 |
| 9 | 1.5 (n = 16) | 0.23 (n = 16) | 0.03 (n = 17) | 68 |
| 10 | 1.3 (n = 27) | 0.21 (n = 27) | 0.07 (n = 28) | 128 |
| $\bar{X}$ | 1.3 | 0.22 | 0.08 | 110.5 |
| SE | 0.1 | 0.01 | 0.01 | 18.8 |
| SD | 0.0 | 0.00 | 0.00 | 5.9 |

TABLE H. Grindelia integrifolia - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) measurements in cm.

| DRY: | Stem length | Stem diameter | No. leaves | Leaf width | Stem Density |
|---|---|---|---|---|---|
| 1 | 17.0 (n = 11) | 0.58 (n = 11) | 7.4 (n = 11) | 1.3 (n = 11) | 11 |
| 2 | 16.9 (n = 14) | 0.47 (n = 14) | 6.8 (n = 14) | 1.2 (n = 14) | 14 |
| 3 | 18.8 (n = 17) | 0.41 (n = 17) | 5.5 (n = 17) | 1.5 (n = 17) | 17 |
| 4 | 20.1 (n = 9) | 0.54 (n = 9) | 7.7 (n = 9) | 1.5 (n = 9) | 9 |
| 5 | 17.2 (n = 15) | 0.45 (n = 15) | 6.2 (n = 15) | 1.2 (n = 15) | 15 |
| 6 | 21.7 (n = 6) | 0.52 (n = 6) | 6.8 (n = 6) | 1.7 (n = 6) | 6 |
| 7 | 14.0 (n = 14) | 0.47 (n = 14) | 7.3 (n = 14) | 1.2 (n = 14) | 14 |
| 8 | 17.5 (n = 19) | 0.41 (n = 19) | 4.9 (n = 19) | 1.5 (n = 19) | 19 |
| 9 | 16.0 (n = 15) | 0.43 (n = 15) | 5.9 (n = 15) | 1.4 (n = 15) | 15 |
| 10 | 18.2 (n = 9) | 0.56 (n = 9) | 8.1 (n = 9) | 1.3 (n = 9) | 9 |
| $\bar{X}$ | 17.7 | 0.48 | 6.6 | 1.4 | 12.9 |
| SD | 2.1 | 0.06 | 1.0 | 0.2 | 4.0 |
| SE | 0.7 | 0.02 | 0.3 | 0.0 | 1.3 |
| FC: | | | | | |
| 1 | 16.2 (n = 28) | 0.45 (n = 28) | 6.9 (n = 28) | 1.1 (n = 28) | 28 |
| 2 | 17.9 (n = 20) | 0.52 (n = 20) | 7.8 (n = 20) | 1.2 (n = 20) | 20 |
| 3 | 20.5 (n = 19) | 0.43 (n = 19) | 5.4 (n = 19) | 1.4 (n = 19) | 19 |
| 4 | 20.6 (n = 25) | 0.45 (n = 25) | 5.4 (n = 25) | 1.6 (n = 25) | 25 |
| 5 | 15.9 (n = 21) | 0.48 (n = 21) | 6.3 (n = 21) | 1.4 (n = 21) | 21 |
| 6 | 15.0 (n = 28) | 0.43 (n = 28) | 5.8 (n = 28) | 1.3 (n = 28) | 28 |
| 7 | 20.7 (n = 16) | 0.58 (n = 16) | 7.1 (n = 16) | 1.7 (n = 16) | 16 |
| 8 | 16.7 (n = 26) | 0.43 (n = 26) | 6.0 (n = 26) | 1.2 (n = 26) | 26 |
| 9 | 16.1 (n = 29) | 0.46 (n = 29) | 6.8 (n = 29) | 1.1 (n = 29) | 29 |
| 10 | 17.5 (n = 27) | 0.39 (n = 27) | 6.6 (n = 27) | 1.1 (n = 27) | 27 |
| $\bar{X}$ | 17.7 | 0.46 | 6.4 | 1.3 | 23.9 |
| SD | 2.2 | 0.05 | 0.8 | 0.2 | 4.5 |
| SE | 0.7 | 0.02 | 0.2 | 0.1 | 1.4 |

TABLE H (continued). *Grindelia integrifolia* - GREENHOUSE. MORPHOLOGICAL MEASURMENTS (DRY) = near wilting point, FC = field capacity, SAT = saturated) measurements in cm.

| DRY: | Stem length | Stem diameter | No. leaves | Leaf width | Stem Density |
|---|---|---|---|---|---|
| 1 | 15.4 (n = 23) | 0.38 (n = 23) | 4.6 (n = 23) | 1.3 (n = 23) | 23 |
| 2 | 16.1 (n = 17) | 0.44 (n = 17) | 4.1 (n = 17) | 1.2 (n = 17) | 17 |
| 3 | 16.3 (n = 15) | 0.41 (n = 15) | 5.1 (n = 15) | 1.2 (n = 15) | 15 |
| 4 | 17.0 (n = 17) | 0.38 (n = 17) | 4.1 (n = 17) | 1.3 (n = 17) | 17 |
| 5 | 16.9 (n = 19) | 0.57 (n = 19) | 6.6 (n = 19) | 1.3 (n = 19) | 19 |
| 6 | 13.9 (n = 22) | 0.43 (n = 22) | 5.1 (n = 22) | 1.1 (n = 22) | 22 |
| 7 | 14.6 (n = 25) | 0.44 (n = 25) | 5.3 (n = 25) | 1.1 (n = 25) | 25 |
| 8 | 13.9 (n = 16) | 0.54 (n = 16) | 4.6 (n = 16) | 1.4 (n = 16) | 16 |
| 9 | 18.0 (n = 19) | 0.42 (n = 19) | 4.2 (n = 19) | 1.3 (n = 19) | 19 |
| 10 | 16.7 (n = 29) | 0.45 (n = 29) | 4.8 (n = 29) | 1.2 (n = 29) | 29 |
| $\bar{X}$ | 15.9 | 0.45 | 4.8 | 1.2 | 20.2 |
| SD | 1.4 | 0.06 | 0.8 | 0.1 | 4.5 |
| SE | 0.4 | 0.02 | 0.2 | 0.0 | 1.4 |

TABLE I. *Salicornia virginica* - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) measurements in cm.

| | Stem length | No. internodes | Length internode | No. primary branches |
|---|---|---|---|---|
| DRY: | | | | |
| 1 | 28.4 (n = 6) | 21.2 (n = 6) | 1.4 (n = 6) | 29.0 (n = 6) |
| 2 | 26.6 (n = 6) | 23.7 (n = 6) | 1.4 (n = 6) | 25.0 (n = 6) |
| 3 | 29.2 (n = 3) | 18.0 (n = 4) | 1.4 (n = 4) | 13.2 (n = 4) |
| 4 | 23.0 (n = 6) | 14.2 (n = 5) | 1.4 (n = 5) | 17.4 (n = 5) |
| 5 | 25.8 (n = 10) | 16.4 (n = 10) | 1.3 (n = 10) | 11.3 (n = 10) |
| 6 | 25.3 (n = 6) | 18.0 (n = 5) | 0.9 (n = 6) | 13.8 (n = 6) |
| 7 | 24.5 (n = 5) | 17.6 (n = 5) | 1.4 (n = 5) | 20.6 (n = 5) |
| 8 | 32.9 (n = 3) | 22.0 (n = 3) | 1.1 (n = 3) | 19.3 (n = 3) |
| 10 | 30.6 (n = 1) | 15.0 (n = 1) | 1.2 (n = 1) | 23.0 (n = 1) |
| $\bar{X}$ | 27.4 | 18.5 | 1.3 | 19.2 |
| SD | 3.2 | 3.2 | 0.2 | 5.9 |
| SE | 1.0 | 1.1 | 0.1 | 2.0 |
| FC: | | | | |
| 1 | 22.0 (n = 32) | 10.0 (n = 32) | 1.6 (n = 32) | 10.7 (n = 32) |
| 3 | 29.6 (n = 3) | 15.3 (n = 3) | 1.7 (n = 3) | 15.7 (n = 3) |
| 5 | 22.5 (n = 11) | 10.9 (n = 11) | 1.5 (n = 11) | 11.6 (n = 11) |
| 8 | 34.2 (n = 2) | 7.5 (n = 2) | 2.0 (n = 2) | 7.0 (n = 2) |
| 9 | 24.6 (n = 11) | 13.1 (n = 10) | 1.4 (n = 11) | 15.2 (n = 11) |
| 10 | 27.7 (n = 14) | 15.4 (n = 14) | 1.3 (n = 14) | 18.6 (n = 14) |
| $\bar{X}$ | 26.8 | 12.0 | 1.6 | 13.1 |
| SD | 4.7 | 3.1 | 0.2 | 4.2 |
| SE | 1.9 | 1.3 | 0.1 | 1.7 |
| SAT: | | | | |
| 1 | 17.2 (n = 8) | 11.0 (n = 8) | 1.1 (n = 7) | 10.8 (n = 8) |
| 2 | 13.5 (n = 12) | 11.8 (n = 12) | 1.0 (n = 12) | 8.3 (n = 12) |
| 3 | 15.3 (n = 13) | 8.4 (n = 13) | 1.2 (n = 12) | 7.7 (n = 13) |
| 4 | 17.2 (n = 14) | 13.3 (n = 14) | 1.1 (n = 14) | 12.4 (n = 14) |
| 5 | 12.2 (n = 17) | 7.1 (n = 17) | 1.0 (n = 15) | 5.6 (n = 17) |
| 6 | 18.2 (n = 15) | 15.1 (n = 15) | 1.0 (n = 15) | 13.9 (n = 15) |
| 8 | 13.9 (n = 19) | 10.6 (n = 19) | 1.0 (n = 19) | 6.1 (n = 19) |
| 9 | 15.1 (n = 26) | 9.5 (n = 26) | 1.0 (n = 23) | 8.1 (n = 26) |
| 10 | 16.8 (n = 10) | 16.0 (n = 10) | 1.1 (n = 10) | 7.4 (n = 10) |
| $\bar{X}$ | 15.5 | 11.4 | 1.1 | 8.9 |
| SD | 2.0 | 3.0 | 0.1 | 2.8 |
| SE | 0.7 | 1.0 | 0.0 | 0.9 |

TABLE I (continued). Salicornia virginica - GREENHOUSE. MORPHOLOGICAL MEASUREMENTS (DRY = near wilting point, FC = field capacity, SAT = saturated) measurements in cm.

| DRY: | No. secondary branches | Stem diameter | No. flowers | Stem density |
|---|---|---|---|---|
| 1 | 10.0 (n = 6) | 0.13 (n = 6) | 7.5 (n = 6) | 6 |
| 2 | 14.0 (n = 6) | 0.11 (n = 6) | 2.7 (n = 6) | 6 |
| 3 | 38.8 (n = 4) | 0.13 (n = 4) | 2.5 (n = 4) | 4 |
| 4 | 44.4 (n = 5) | 0.14 (n = 5) | 6.2 (n = 5) | 5 |
| 5 | 10.4 (n = 10) | 0.10 (n = 10) | 3.7 (n = 10) | 10 |
| 6 | 52.7 (n = 6) | 0.14 (n = 6) | 7.7 (n = 6) | 6 |
| 7 | 35.2 (n = 5) | 0.12 (n = 5) | 19.0 (n = 3) | 5 |
| 8 | 67.0 (n = 3) | 0.13 (n = 3) | 32.0 (n = 3) | 3 |
| 10 | 121.0 (n = 1) | 0.20 (n = 1) | 10.0 (n = 1) | 1 |
| $\bar{X}$ | 43.7 | 0.13 | 10.1 | 5.1 |
| SD | 35.0 | 0.03 | 9.6 | 2.5 |
| SE | 11.7 | 0.01 | 3.2 | 0.8 |
| FC: | | | | |
| 1 | 18.7 (n = 32) | 0.11 (n = 32) | 7.0 (n = 32) | 32 |
| 3 | 9.3 (n = 3) | 0.10 (n = 3) | 4.7 (n = 3) | 3 |
| 5 | 30.7 (n = 11) | 0.10 (n = 11) | 9.6 (n = 11) | 11 |
| 8 | 31.0 (n = 2) | 0.18 (n = 2) | 13.5 (n = 2) | 2 |
| 9 | 36.4 (n = 11) | 0.14 (n = 11) | 17.0 (n = 11) | 11 |
| 10 | 61.4 (n = 14) | 0.13 (n = 14) | 9.9 (n = 14) | 14 |
| $\bar{X}$ | 31.2 | 0.13 | 10.3 | 12.2 |
| SD | 17.8 | 0.03 | 4.4 | 10.8 |
| SE | 7.2 | 0.01 | 1.8 | 4.4 |
| SAT: | | | | |
| 1 | 11.0 (n = 8) | 0.11 (n = 8) | 5.0 (n = 8) | 8 |
| 2 | 2.7 (n = 12) | 0.12 (n = 12) | 1.9 (n = 12) | 12 |
| 3 | 3.0 (n = 13) | 0.10 (n = 13) | 2.2 (n = 13) | 13 |
| 4 | 6.5 (n = 14) | 0.13 (n = 14) | 2.9 (n = 14) | 14 |
| 5 | 8.0 (n = 17) | 0.11 (n = 17) | 5.8 (n = 17) | 17 |
| 6 | 2.3 (n = 15) | 0.11 (n = 15) | 3.5 (n = 15) | 15 |
| 8 | 3.6 (n = 19) | 0.11 (n = 19) | 2.5 (n = 19) | 19 |
| 9 | 7.6 (n = 26) | 0.11 (n = 26) | 2.6 (n = 26) | 26 |
| 10 | 7.8 (n = 10) | 0.14 (n = 10) | 4.3 (n = 10) | 10 |
| $\bar{X}$ | 5.8 | 0.12 | 3.4 | 14.9 |
| SD | 3.0 | 0.01 | 1.4 | 5.4 |
| SE | 1.0 | 0.00 | 0.4 | 1.8 |