Population Dynamics of a Perennial Halophyte *Allenrolfea occidentalis*

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Abstract—Demography and population biology of a perennial halophyte, *Allenrolfea occidentalis,* was studied during the growing seasons (May to November) of 1996 and 1997. Soil samples were collected monthly from the playa throughout the growing seasons for two years and analysed to determine the conductivity, pH, soil moistures and ions. During the study period, the population was exposed to wide variations in soil salinity from low to high and soil moisture ranging from very wet to drought levels. Seasonal changes in dry weight was directly related to soil salinity stress. When salinity levels become low, the dry matter production increases. The population of *A. occidentalis* suffered heavy mortality in 1996 due to the high salinity and temperature stress. Plant growth reached its maximum in July and succulence decreased with aging of plants. Results indicate that community vegetation respond differently to the environmental changes in 1996 and in 1997. Salinity, temperature and precipitation have a major effect on the survival and growth of *A. occidentalis* under field conditions.

The distribution of plant species in saline environments of inland western United States is closely associated with soil water potentials and other factors influencing the level of salinity stress, including microtopography, precipitation, and depth of water table (Young and others 1995). There are certain areas in western Utah, where the salt content is high enough to form thick salt crusts on the top of the soil making plant growth of any kind impossible, on such areas some of the more salt tolerant plants survive with little or no competition and *Allenrolfea occidentalis* (Wats.) Kuntze is one of them (Quigley 1956). *Allenrolfea occidentalis* is a perennial chenopod, which colonizes extremely saline habitats of the temperate desert basins. Plant communities dominated by *A. occidentalis* offer the extreme in adaptations to survival and growth under moisture stress (Young and others 1995). During the growing season *A. occidentalis* plants are subjected to a great variation in edaphic conditions (Trent and others 1997). Seasonal variation in soil salinity in saline habitats is well documented and is directly influenced by the fluctuations in soil moisture levels (Ungar 1973, 1978a; Waisel 1972). Young and others (1995) showed that the

A. occidentalis plants have to allow salts to enter through root membranes and the physiology of the plant changes from the wet to dry years due to the increase in soil salinity. Flanagan and Jefferies (1988) reported that as salinity increased, photosynthesis in *Plantago maritima* declined 17 to 14 μmol m^{-2}.S^{-1} while leaf conductance dropped markedly. Transpiration and photosynthesis involve gas exchange between the plant and atmosphere through the stomata and are well known to decrease with water stress (Fisher 1976) or salinity (Khan and others 1976).

Halophytic species commonly exhibit quite high concentrations of several salt ions in various plant organs or the entire plant. Although the salt accumulating nature of halophytes has been recognized for many years, now it has been proven that sodium is essential to the growth of most of the chenopodiaceae (Brownwell and Wood 1957; Brownwell 1965; Moore and Caldwell 1972; Naidoo and Rughunanan 1990; Khan and others 1998). Terrestrial halophytes utilize the controlled accumulation and sequestration of inorganic ions, chiefly Na$^+$ and K$^+$ balanced by Cl$^-$, as the basic mechanism by which they adjust the osmotic potential of their internal tissue to the external salinity (Flowers and Yeo 1986; Cheeseman 1988).

In this study, the environmental conditions as they affect growth of a natural population of *Allenrolfea occidentalis* during the growing seasons in an inland salt playa of the Great Basin desert, are reported. The objective of this study was to study the effect of variation in soil salinity and temperature on the growth and ecophysiology of *A. occidentalis* under natural conditions.

Materials and Methods _____

Study site

The site chosen for this study is a salt playa east of Goshen, northwestern Utah. It is an area of flat, low-lying ground in the bottom of a fairly wide valley that spreads out at the southern end into a vast stretch of flat, salt incrusted plain. The area contains numerous salt marshes and salt playas with nearly pure stands of *Allenrolfea occidentalis*.

The point centered quarter method (Cottam and Curtis 1956) was used to sample the vegetation over 20 random points and relative frequencies were calculated for each species in the community. During the spring of 1996, three transects were established in the salt playa. These transects ran through the community and were approximately parallel to the marsh. Fifteen permanent quadrats (100 x 100 m^2) were established on three transects, three replicates on each

site. The number of plants surviving in each plot and their cover were counted monthly throughout the growing season from May to November 1996 and 1997. In order to reduce disturbance in quadrats, ten equal sized plants were randomly collected from the area in the vicinity of each quadrat every month of the growing season for two years. Plants were separated into leaves, stem and root. *Allenrolfea occidentalis* does not have true leaves but they form jointed, seemingly leafless stems. The green leafy succulent portion is considered here as leaf while woody portion as stem. Fresh and dry weight of the plants was recorded before and after drying the material in an oven at 80°C for 48 h.

For ion measurements 0.5 gram of plant material was boiled in 25 ml of water for two hours at 100°C using a dry heat bath. This hot water extract was cooled and filtered using Whatman no. 2 filter paper. One ml of hot water extract was diluted with distilled water for ion analysis. Chloride, nitrate and sulphate ions contents were measured with a DX-100 ion chromatograph. Cation contents Na^+, K^+, Ca^{2+} and Mg^{2+} of the plant organs were analysed using a Perkin Elmer model 360 atomic absorption spectrophotometer. The net photosynthesis rate of four replicates per quadrat were taken with an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). The level of stress in plants growing in field conditions were measured with CF-1000 chlorophyll fluorescence measurement system. The water potential was measured using a Plant Moisture Stress Instrument (PMS Instrument Co.).

Ten surface soil (to a depth of 15 cm) and 10 subsurface (to a depth of 30 cm) soil samples were collected monthly from the *A. occidentalis* community during the growing season. Soil moisture was measured by weighing 12 g of samples, oven drying them at 136°C for 24 h and reweighing them to determine the water loss. Percent soil moisture was calculated as percentage weight of water in dry soil. Then for the determination of organic contents of the soil these samples were dried at 360°C for 24 h.

Five grams of soil mixed with 25 ml of distilled water were shaken and filtered using Whatman no. 1 filter paper. PH (pH meter) and soil conductivity (model-10 portable conductivity meter) were measured. The results of growth, ion contents, net photosynthesis, water potential and stress were analysed using three way ANOVA. A Bonferroni test was carried out to determine if significant (P <0.05) differences occurred between individual treatments (SPSS 1996).

Results

A three way ANOVA showed a significant individual effect of quadrats F = 28.71, (P <0.0001) and years F = 7.02, (P <0.001), while months were not significant in affecting basal area. Interactions between quadrats, years and months were also significant (P <0.0001). Phytosociological survey showed that the salt playa community has an almost pure population of *A. occidentalis* a few individuals of *Salicornia rubra*, *Salicornia utahensis* and *Distichlis spicata* were present. Quantitative data indicated that *A. occidentalis* had consistently high cover in the intermediate plots throughout the growing season of 1996 (fig. 1). The overall cover of the plants in the *A. occidentalis* community was higher in 1996 than 1997.
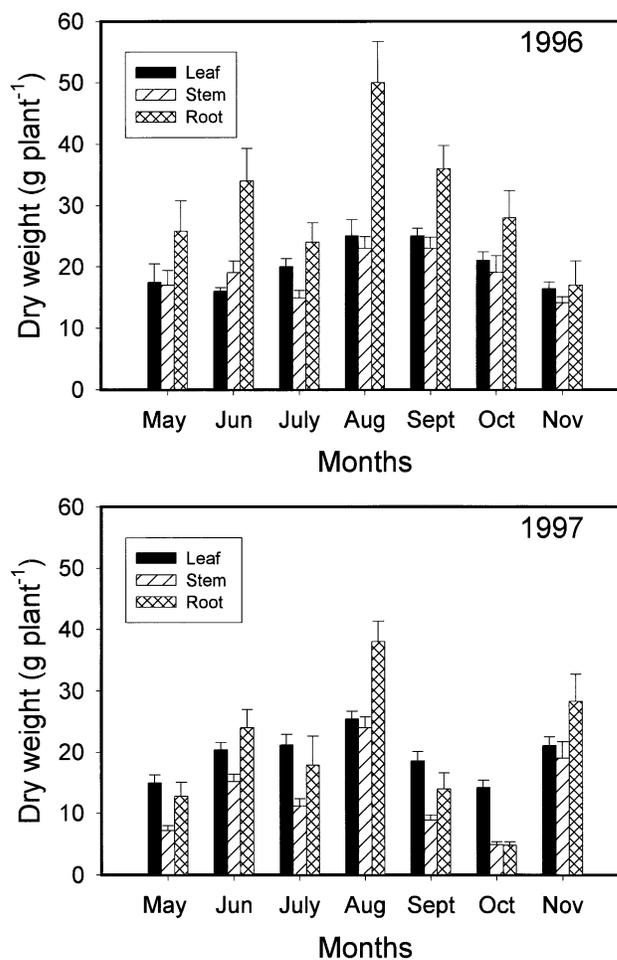

Figure 1—Seasonal pattern of dry weight (g plant^{-1}) of leaf, stem and root of plants collected from an *Allenrolfea occidentalis* community. Bar represents mean ± S. E.

A three way ANOVA showed a significant individual effect of plant parts, years and months and their interactions in affecting dry weight of *A. occidentalis* plants. Plants collected from the field were analysed for leaves, stem and root fresh and dry weights. *Allenrolfea occidentalis* plants collected on August 1996 had greater dry weights than plants collected in other months (fig. 1). The fresh and dry weights of the plants increased gradually from May to September and then decreased.

A three way ANOVA showed a significant individual effect of months (P <0.0001) and years (P <0.0001), while soil layers were not significant in affecting pH (table 2). The surface soil pH was generally higher and fluctuated more than the corresponding subsurface pH. The subsurface pH of the soil changed very little during the growing season (table 1 and 2). The decrease in pH of the surface soil appeared to be correlated to the amount of rainfall. A decrease in the pH of the surface soil occurred in May to July 1997 due to heavy rainfalls, it was generally inversely proportional to the increase in subsurface pH.

Table 1—Seasonal variation in the pH, conductivity (ds/m), moisture content (%) and organic content (%) of the soil from *Allenrolfea occidentalis* community during the year of 1996.

Months	Soil layers	pH	Conductivity ds/m	Moisture contents	Organic contents
				- - - - - - *Percent* - - - - - -	
May	Surface	8.0 ± 0.01	135 ± 19	14 ± 1.2	3.8 ± 0.9
	Subsurface	8.2 ± 0.09	78 ± 13	19 ± 1.5	2.7 ± 0.9
June	Surface	7.5 ± 0.04	132 ± 8.5	11 ± 0.37	2.2 ± 0.22
	Subsurface	7.6 ± 0.07	137 ± 22	14 ± 0.64	2.4 ± 0.27
July	Surface	8.2 ± 0.02	160 ± 16	12 ± 0.7	1.8 ± 0.34
	Subsurface	8.1 ± 0.03	118 ± 9.0	15 ± 1.3	3.0 ± 1.3
August	Surface	7.9 ± 0.03	161 ± 6.0	12 ± 1.1	3.0 ± 2.6
	Subsurface	7.7 ± 0.05	91 ± 13	14 ± 0.51	1.3 ± 0.71
September	Surface	7.9 ± 0.02	99 ± 21	12 ± 1.8	3.1 ± 1.5
	Subsurface	7.6 ± 0.06	74 ± 7.0	12 ± 1.9	3.4 ± 0.81
October	Surface	8.3 ± 0.08	109 ± 7.0	11.4 ± 0.88	2.1 ± 0.28
	Subsurface	8.2 ± 0.08	73 ± 5.0	16 ± 1.2	2.4 ± 0.33
November	Surface	8.2 ± 0.02	87 ± 8.0	12 ± 0.61	1.9 ± 0.60
	Subsurface	8.1 ± 0.03	78 ± 4.0	16.2 ± 1.1	1.8 ± 0.39

Table 2—Seasonal variation in the pH, conductivity (ds/m), moisture content (%) and organic content (%) of the soil from *Allenrolfea occidentalis* community during the year of 1997.

Months	Soil layers	pH	Conductivity ds/m	Moisture contents	Organic contents
				- - - - - - *Percent* - - - - - -	
May	Surface	8.0 ± 0.03	109 ± 4.0	9.2 ± 1.3	2.9 ± 0.46
	Subsurface	8.1 ± 0.09	88 ± 2.0	15 ± 1.4	2.4 ± 0.08
June	Surface	7.8 ± 0.11	147 ± 11	10.2 ± 1.4	3.4 ± 0.18
	Subsurface	8.1 ± 0.08	107 ± 12	11.8 ± 1.4	4.1 ± 0.19
July	Surface	7.9 ± 0.02	138 ± 11	14 ± 12	2.9 ± 0.19
	Subsurface	8.1 ± 0.06	93 ± 9.0	14 ± 0.53	3.7 ± 0.40
August	Surface	7.5 ± 0.07	145 ± 12	12.1 ± 0.50	2.9 ± 0.16
	Subsurface	7.8 ± 0.08	108 ± 8.0	11 ± 0.36	3.7 ± 0.40
September	Surface	7.3 ± 0.02	135 ± 13	13.3 ± 0.95	2.0 ± 0.19
	Subsurface	7.3 ± 0.04	68 ± 9.0	14.3 ± 0.76	3.5 ± 0.75
October	Surface	7.3 ± 0.02	122 ± 12	10.7 ± 0.65	2.2 ± 0.28
	Subsurface	7.4 ± 0.01	96 ± 11	15.4 ± 1.07	2.8 ± 0.33
November	Surface	7.5 ± 0.05	106 ± 12	12.9 ± 0.55	1.3 ± 0.60
	Subsurface	7.4 ± 0.02	83 ± 9.0	16.1 ± 0.86	2.4 ± 0.20

Soil conductivity remained high throughout the growing season except for the period when it received summer rains (table 1 and 2). A decrease in soil solution conductivity occurred in the fall to levels found in early spring (table 1 and 2).

The sub-surface moisture content was higher than the surface soil moisture throughout the growing season except for the months of October 1996 and July 1997, when the salt playa had an increase in surface soil moisture due to the rainfall (table 1 and 2).

A three way ANOVA showed significant individual effects of plant parts, years, months and their interactions in affecting the ion contents of *A. occidentalis* except for the interactions of Cl⁻ ion. The Cl⁻ ion content in *A. occidentalis* tissues (leaf, stem and root) remained constant throughout most of the growing season of 1996 and 1997 (fig. 2). Na ion
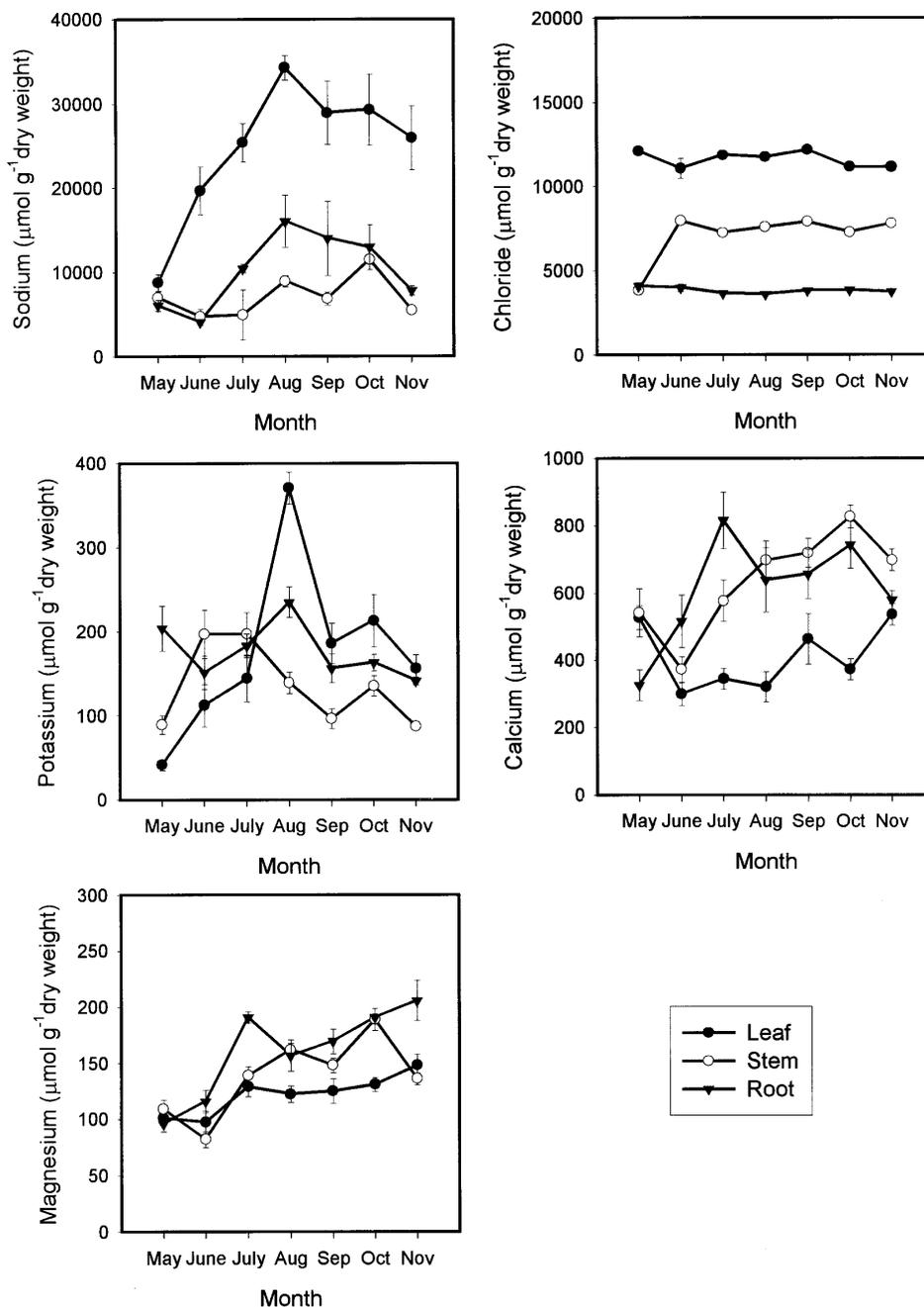
1996

Figure 2—Monthly variation in ion contents of leaf, stem and root of *Allenrolfea occidentalis* during the year of 1996.

concentration gradually increased from 1,000 mM to 35,000 mM in 1996, and 28,000 mM in 1997 (fig. 2 and 3). K^+ ion concentration in leaves was significantly higher in August. However, K^+ concentration was significantly lower in stem as compared to the leaves and roots. The K^+ ions in leaves and roots decreased significantly during the months of low salinity. The major cation macronutrients Ca^{++} and Mg^{++} differed in their availability patterns throughout the growing seasons (fig. 2 and 3).

Photosynthesis rates was significantly higher in August than the other months, which did not significantly differ from each other (table 3). The monthly values of F_v/F_m were always low and showed high stress in the field plants. Water relation parameters of the plants were measured to see if they might be related to the differences in plant growth in field conditions. Water potential of the *A. occidentalis* was significantly greater in July to October (table 3). Water
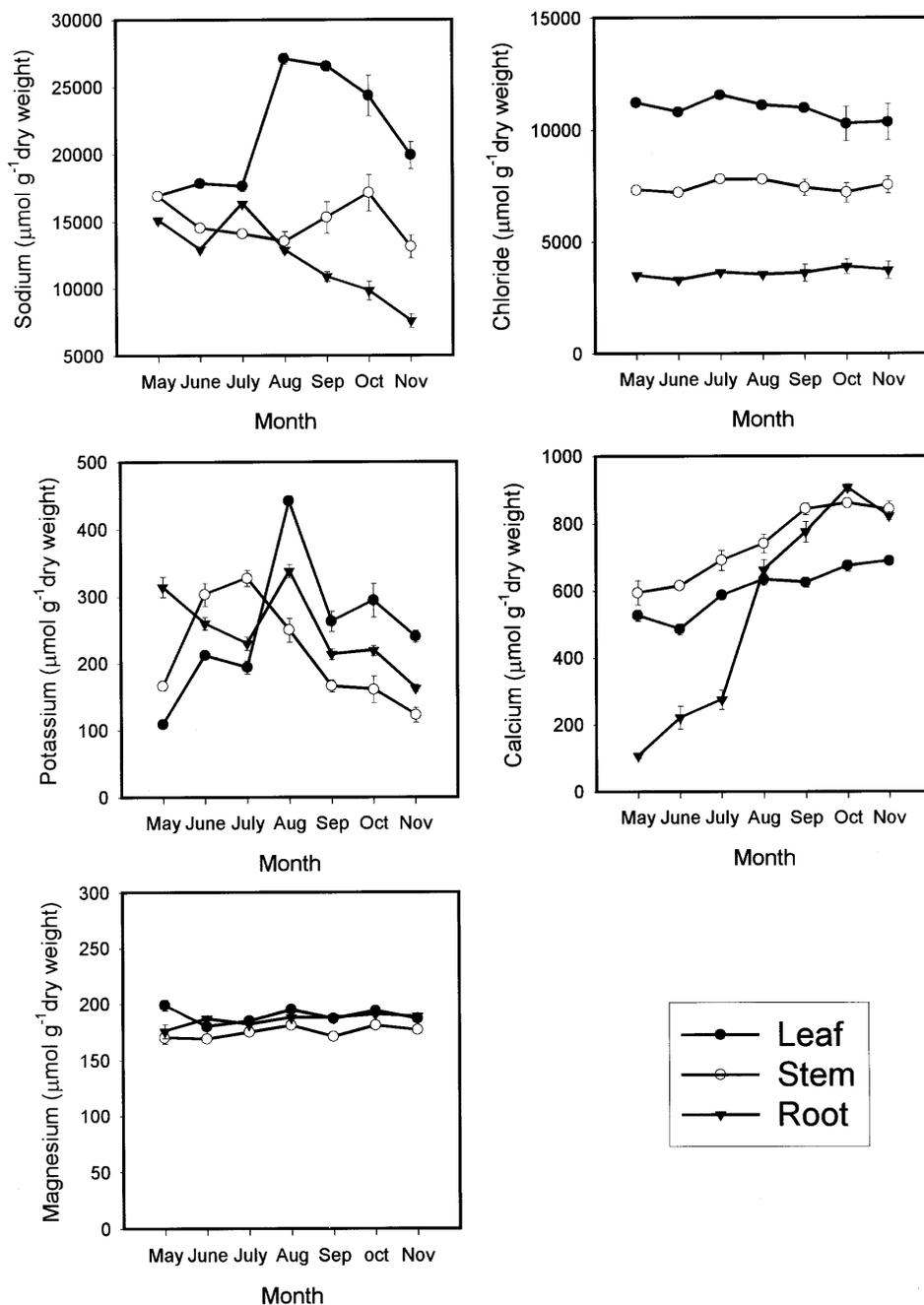
1997

Figure 3—Monthly variation in ion contents of leaf, stem and root of *Allenrolfea occidentalis* during the year of 1997.

potentials of shoots decreased significantly with increase in salinity (table 3).

Discussion

An *Allenrolfea occidentalis* population in a Great Basin salt playa was exposed to great variations in environmental conditions. This exposure to soil salinity varying from 29-146 dS m^{-1} and soil moisture ranging from drought to very wet levels affected the growth of *A. occidentalis*. Young and others (1995) reported that the *A. occidentalis* communities of the salt deserts in Great Basin are distributed continuously, with inclusion of stable sand dunes that rise 5 to 10 m above the lake plain. He also concluded that the mounds on the playa surface that predominantly support *A. occidentalis* plants are successionally dynamics.

Table 3—Mean ± S. E. for water potential, photosynthesis and stress under field conditions.

Months	Water potential (−Mpa)	Stress (F_v/F_m)	Net photosynthesis (μmol m^{-2} s^{-1})
May	36.8 ± 1.2	0.50 ± 0.035	3.8 ± 0.43
June	42.6 ± 1.3	0.69 ± 0.037	4.1 ± 0.49
July	70.6 ± 5.4	0.74 ± 0.032	5.1 ± 1.2
August	87.6 ± 4.3	0.75 ± 0.032	9.2 ± 1.2
September	88.8 ± 86	0.58 ± 0.033	5.7 ± 0.57
October	82.4 ± 3.6	0.46 ± 0.046	0.0 ± 0.0
November	34.4 ± 3.6	0.52 ± 0.031	0.0 ± 0.0

Dry matter production under saline conditions increases with decreases in salinity (Chapman 1974; McGraw and Ungar 1981; Gul and Khan 1994). Seasonal changes in dry weight accumulation observed in this investigation appear to be directly related to soil salinity stress. The greatest increase in dry matter production in August and September appear to be related to increased photosynthesis and maintenance of osmotic balance despite high soil salinity.

The salt playa community of *A. occidentalis* faces stressful conditions throughout the growing season. During drought conditions the saline soils become dry and were more stressful to the plants. During such conditions the dry mass production of plants affected by salinity, pH and conductivity increased which shows that dry season promotes salinity increases and affects the plant growth. There is an adaptive capability of *A. occidentalis* to grow better in high salinity areas (Young and others 1995). Marks (1950) reported that *A. occidentalis* in the lower Colorado desert form pure dense stands on the moist saline soils. It is usually an indicator of soils which are heavy textured ranging from silt loam to clay.

The high moisture content of the soil and the subsequent evaporation may have had a cooling effect upon the temperature of the soil. Both lower temperatures and high relative humidity would have a favorable effect on plant growth. An increase in moisture stress throughout the season primarily due to increases in salt from underground sources and slight decreases in soil moisture.

Many species in the chenopodiaceae accummulate large amounts of Na and Cl when the external salinity is high (Albert 1975; Tiku 1975; Ungar 1978b; Flowers and Yeo 1986). Sodium and chloride were the two principal ions responsible for increases in osmotic potential of soil samples (Hansen and Weber 1975). They were also responsible for 85 to 95 percent of the osmotic potentials of *Salicornia utahensis*. Donovan and others (1997) reported the similarity of high leaf sodium in *Sarcobatus vermiculatus* from different sites throughout the growing season. They concluded that high leaf Na$^+$ similarity throughout the growing season indicates a dominance of Na$^+$ nutrition over the entire gradient, and a possible upper boundry of Na accumulation and tolerance for *S. vermiculatus*. Na$^+$ uptake necessary for osmoregulation in halophytes, can start as soon as seedlings germinate, allowing the seedlings to maintain water uptake, turgor and growth (Eddleman and Romo 1987; Romo and Haferkamp 1987). Concentration of Na$^+$ was lower in *A. occidentalis* root and shoot cells in comparison with the external solution. It is possible that the permeability of *A. occidentalis* root and shoot to Na$^+$ is low and that the Na$^+$ entering the root by passive diffusion is probably removed by active efflux. This further supports the idea of root control over the inflow of Na$^+$ in higher salinity modalities. In saline and alkaline soils, availability of the cation macronutrients, K$^+$, Ca^{++}, and Mg^{++} may also be limited (Marschner 1995; Vasek and Lund 1980). Leaf K$^+$, Ca^{++}, and Mg^{++} were all consistent in *Sarcobatus* (Rickard and Keough 1968; Glenn and O' Leary 1984; Rickard 1982; Donovan and others 1997).

Great Basin desert plants establish and persist in an environment where halomorphic soils induce extreme osmotic stress and atmospheric precipitation is very low and erratic and occurs largely during the winter when temperatures are too low for growth (Trent and others 1997). The effect of soil water potential on photosynthesis, stress and water potential of the shoots from the *A. occidentalis* community is inconclusive. We suspect that the plant physiological changes in the field can be explained by an increase in soil salinity. Flanagan and Jefferies (1988) reported that as salinity increased, photosynthesis in *Plantago maritima* declined. Increased soil salinity cannot fully explain the dramatic decrease in photosynthesis. Pearcy and Ustin (1984) suggested that increased salinity primarily reduced photosynthesis within the mesophyll and secondarily as a result of reduced leaf conductance. Our data showed a larger reduction in photosynthesis with seasonal changes. The water potential of *A. occidentalis* plants was extremely negative throughout the growing season. Trent and others (1997) reported that xylem water potential of *A. occidentalis* dropped significantly during dry seasons. Changes in F_v/F_m stress ratio were more evident when plants were exposed to a high stress. When plants were exposed to high irradiance (direct sunlight) they were strongly photoinhibited (Jimenez and others 1997). In our study low F_v/F_m values in *A. occidentalis* plants were found even in low temperatures, although the lowest values logically appeared in the higher salinity months. This is in accordance with Sharma and Hall (1998) and Larcher and others (1990) who only found a decrease in this ratio when stress was added.

In conclusion, an inland salt marsh population of *A. occidentalis* has been shown to be highly salt tolerant. Growth enhancement by salinities was related to an increase in biomass of the plants, presumably due to the stimulating effect of NaCl on plants of inland salt marsh populations. Na$^+$ and Cl$^-$ were accumulated in, rather than excluded from, the tissues; the cellular NaCl tolerance may

be related to the capacity to accumulate betains as compatible solutes. Reduced growth at high salinity apparently is due to an insufficient supply of photosynthate to support growth, or less than favorable water relations in shoots or differences in ionic relations in different environmental conditions.

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