



Growth, ionic and osmotic relations of an *Allenrolfea occidentalis* population in an inland salt playa of the Great Basin Desert

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Variation in growth, physiology and ionic relations patterns of *Allenrolfea occidentalis*, a perennial halophyte of dry habitats, was studied under field conditions from May 1996 to November 1997. An *A. occidentalis* community has a characteristic soil pH of 7.3–8.3. During the two years, the population was exposed to great variations in soil salinity, from 29 to 146 dS m⁻¹, and soil moisture, ranging from drought (9.2%) to wet (19%). The salt concentrations were significantly higher in the surface soil layers than in the subsurface layers. Seasonal changes in dry weight are directly related to soil salinity stress. *Allenrolfea occidentalis* had greater growth and biomass production under saline conditions. Na⁺ and Cl⁻ ions were accumulated in plant tissues in much greater amounts than K⁺, Ca²⁺, and Mg²⁺. Soil salinities were significantly reduced at the end of the growing season. Water potentials of the shoots decreased significantly with increasing salinity. The plant (F_v/F_m ratio) was more affected by salinity and irradiation levels during the summer period.

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Introduction

Many semi-arid regions in the world contain soils and water resources that are too saline for most common economic crops (Nerd & Pasternak, 1992). The utilization of halophytic plants in saline soils for pasture and fodder production is the only economic solution presently available (Yeo & Flowers, 1980). These group of plants not only tolerate high level of salinity (Flowers, 1972) but display optimal growth in saline conditions (Ungar, 1991). Some stem- and leaf-succulent halophytes grow larger and benefit from an NaCl concentration that is above the minimal amount required as micronutrients in plants (Boucaud & Ungar, 1976; Flowers, 1972; Kefu *et al.*, 1995; Khan & Aziz, 1998; Khan *et al.*, 1998). Internal osmotic and water potential generally become increasingly negative with increases in salinity (Khan *et al.*, 1998). Tissue water

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concentration increases at lower salinity and then gradually decreases with increases in salinity (Khan *et al.*, 1998). Halophytic species commonly exhibit quite high concentrations of several ions in various plant organs or the entire plant (Ungar, 1991). Although the salt-accumulating nature of halophytes has been recognized for many years, now it has been established that sodium is essential for the growth of most of the Chenopodiaceae (Moore & Caldwell, 1972; Naidoo & Rughunanan, 1990). 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 & Yeo, 1986; Cheeseman, 1988). Potassium accumulation is generally of little importance in their osmotic adjustment, for example, K^+ accounted for just 4% of the cation contribution to the osmotic adjustment of *Sarcocornia natalensis* grown on 500 mol m^{-3} NaCl (Naidoo & Rughunanan, 1990) and 4.4–9.2% of the adjustment of 10 other euhalophytes grown on 540 mol m^{-3} (Glenn & O'Leary, 1984). *Allenrolfea occidentalis* is a C_3 plant and is found in an environment where halomorphic soil induces extreme osmotic stress, with erratic and low precipitation during the growing seasons (Trent *et al.*, 1997). During drought, this species has a low net assimilation rate, leaf conductance and transpiration in comparison to years with high moisture. *Allenrolfea occidentalis* is restricted to a few communities directly at the margin of playas, where soils are often poorly drained and have high soil salinity (Hansen & Weber, 1975; Skougard & Brotherson, 1979). *Allenrolfea occidentalis* (S. Wats.) Kuntze is a stem-succulent, sodium-accumulating shrub associated with saline soils in the Great Basin Desert (Ungar, 1973). It ranges from 30 cm to 1 m in height. This woody perennial plant grows in environmental conditions beyond the potential of almost any salt-tolerant species in a desert ecosystem (Young *et al.*, 1995). Seeds of this halophyte tolerate high salinity and warm temperature stress without losing viability (Gul, 1998), and seeds germinate at 800 mM NaCl. *Allenrolfea occidentalis* plants require 600 mM NaCl for optimal growth under laboratory conditions (Gul, 1998). They tolerate high salinity in the field (1M NaCl) (Jensen & Parfitt, 1977) and under laboratory conditions ($>1\text{M NaCl}$) (Gul, 1998). The distribution of plant species in saline environments of the 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 *et al.*, 1995). There are certain areas in western Utah, where the salt forms thick crusts on the top of the soil, making plant growth of any kind almost impossible. In such areas some of the more salt tolerant plants survive with little or no competition, and *A. occidentalis* is one of them (Quigley, 1956). The growing season of *A. occidentalis* spans seven months (from May to November), during which plants are subjected to a great variation in edaphic conditions (Trent *et al.*, 1997).

The objective of this study was to investigate the growth, water relations, ionic contents and photosynthesis of an *A. occidentalis* population every month during the growing seasons of 1996 and 1997. This information will be useful in determining the potential for growing *A. occidentalis* on saline soils.

Materials and methods

The study was conducted in a salt playa east of Goshen, in north-eastern Utah. It is a low lying flat ground in the bottom of fairly wide valley, which was an area of ancient Lake Bonneville. The site is situated between the Wasatch mountains to the east and the Tintic range to the west. Soil type of the area is Jordan loam, and soil salinity ranges from 27 to 145 dS m^{-1} . The water table varies from 1 to 3 m below the surface. The area contains numerous salt marshes and salt playas with nearly pure stands of *Salicornia utahensis*, *Salicornia rubra*, *Distichlis spicata*, and *A. occidentalis*.

The precipitation largely occurs in the cold winter months. Temperature and precipitation values were obtained from a Utah State weather collection station at Goshen, which is a few miles from the site.

The 2-ha community was sampled using the point centered quarter method (Cottam & Curtis, 1956) by taking 20 random points. At each of the random points, the relative frequencies of each species were determined. During the spring of 1996, three transects were established and were approximately parallel to the marsh. Fifteen permanent quadrats were established on the three transects with three replicates on each site. The number of plants surviving in each plot and their cover were determined monthly throughout the growing season. Thirty equal-sized plants were randomly collected along the each transect every month of the growing season for two years. Plants were separated into leaves, stems and roots. *Allenrolfea occidentalis* does not have true leaves but they form jointed, seemingly leafless stems. The green cylindrical portion is considered here as leaf and the woody portion as stem. Weight of plants was recorded before and after drying the material in an oven at 80°C for 48 h. The net photosynthesis rate of four replicates per quadrat along the transects was taken around 10 am each time with a LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). Light intensity was determined at the time photosynthetic measurements were made. The level of stress in plants growing in field conditions was measured with a CF-1000 chlorophyll fluorescence measurement system. The stress was measured as a ratio of F_v (variable fluorescence) to F_m (maximum fluorescence). The water potential was measured at midday using a plant moisture stress instrument (PMS Instrument Co, Corvallis, OR) on randomly collected plants. The measurements involved reversing the water flow using a pressure chamber. The water potential was measured on 10 plants, with each plant replicated three times to give a measurement based on 30 determinations.

Ions were determined from both plant and soil samples. Plant material (0.5 g) was boiled in 25 ml of distilled water for 2 h at 100°C (Clifton, NJ, U.S.A.) using a dry heat bath. This hot water extract was cooled and filtered using Whatman no. 2 filter paper. One millilitre of hot water extract was diluted with distilled water for ion analysis. Ten surface (to a depth of 15 cm) and 10 subsurface (to a depth of 15–30 cm) soil samples were collected monthly near the plants along the three transects from the *A. occidentalis* community during the growing season. Soil moisture was measured by weighing 12 g of each sample, oven drying at 136°C for 24 h and reweighing to determine the water loss. Per cent soil moisture was calculated as percentage weight of water in dry soil. For the determination of organic content 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. Soil conductivity (model 10 portable conductivity meter) and pH (pH meter) were measured. Chloride, nitrate and sulfate ion contents were measured with a DX-100 ion chromatograph. Cation contents Na^+ , K^+ , Ca^{2+} and Mg^{2+} of the plant organs were analyzed using a Perkin Elmer (Norwalk, CT, U.S.A.) model 360 atomic absorption spectrophotometer.

The results 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

Temperatures fluctuated consistently throughout the growing season. The temperatures gradually increased from May to August (Fig. 1). A peak was reached during July, followed by a gradual decrease from August to November. The precipitation was much higher during 1997 in comparison with 1996 (Fig. 1). There was hardly any rain during the summer of 1996, but a lot of rain during 1997.

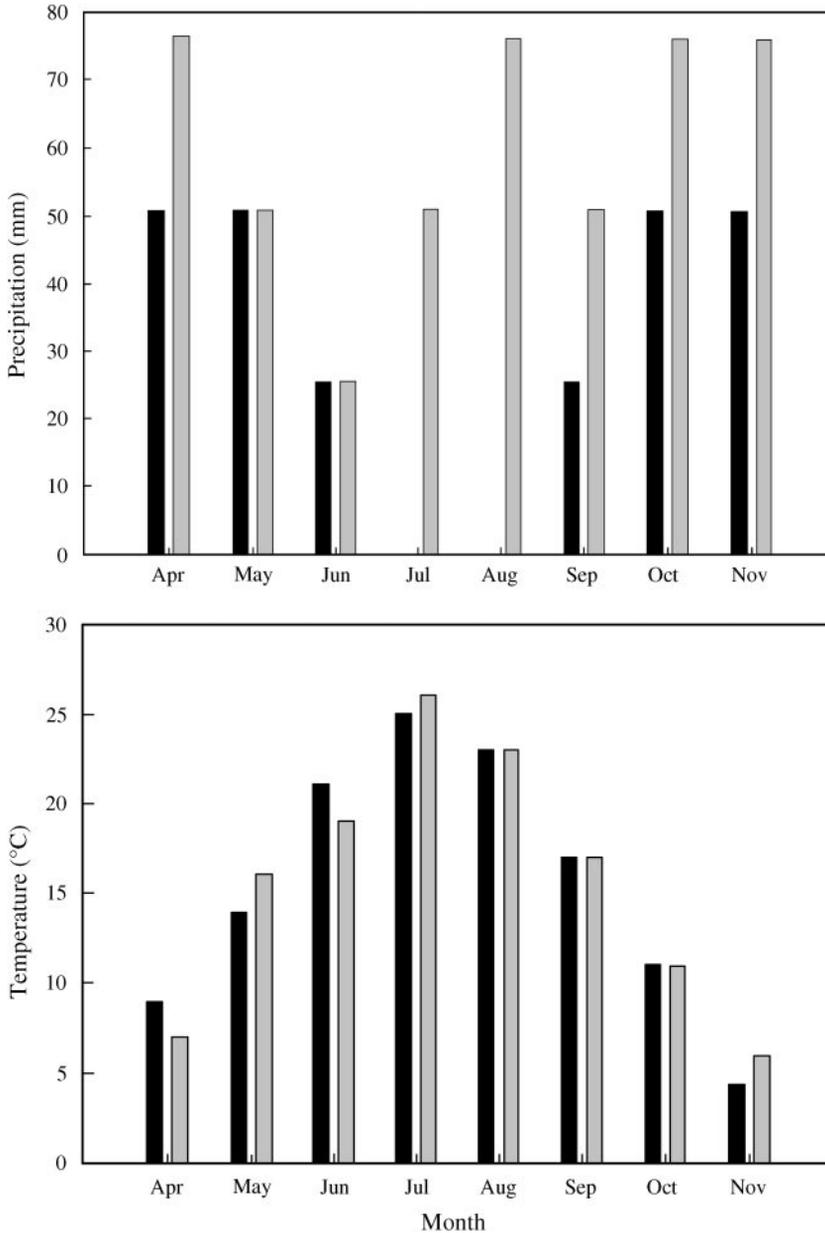


Figure 1. Monthly precipitation (cm) and field temperature (°C) recorded during 1996 (■) and 1997 (□).

A three-way ANOVA showed a significant individual effect of plant parts, years and months and their interactions in affecting dry weight, succulence and ion content of *A. occidentalis* plants (Table 1).

Plants collected from the field were separated into leaves, stem and root. Fresh and dry weights were determined. *Allenrolfea occidentalis* plants collected on August 1996 had greater dry weights than plants collected in other months (Fig. 2). The highest dry

Table 1. Results of three-way ANOVA of plant characteristics by month (M), plant part (P), and Year (Y) treatments

Independent variable	M	P	Y	M × P	M × Y	P × Y	P × M × Y
Fresh weight	42***	234***	28***	7.8***	17***	7.1**	2.2*
Dry weight	21***	43***	43**	3.6***	10.9***	12***	1.31 ^{n.s.}
Tissue water	58***	694***	8.7***	24***	19***	3.1*	7.6***
Na ⁺	20.4***	404***	3221***	20***	5.6***	49***	8.9***
Cl ⁻	1.9*	2739***	20***	2.1*	1.5 ^{n.s.}	4.2*	0.65 ^{n.s.}
K ⁺	54***	26***	227***	35***	2.4*	0.16 ^{n.s.}	1.55 ^{n.s.}
Ca ²⁺	39***	64***	59***	12***	10.3***	19***	8.2***
Mg ²⁺	31***	29***	409***	4.9***	22***	37***	3.8***

Note: Numbers represent *F*-values: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; n.s. = not significant.

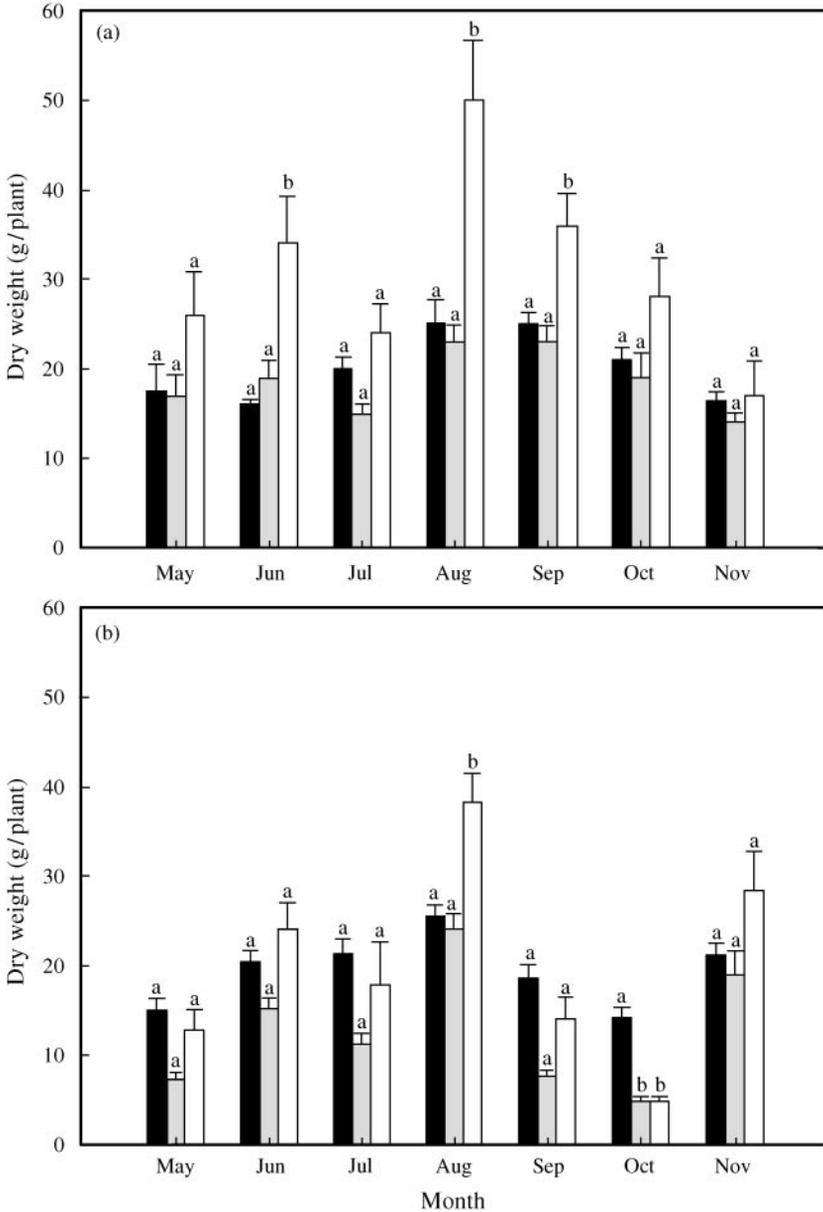


Figure 2. Seasonal pattern of dry weight (g/plant) of leaf (■), stem (▒) and root (□) of plants collected from an *Allenrolfea occidentalis* community in (a) 1996 and (b) 1997. Bars represent mean \pm S.E. Different letters above bars represent significant differences between treatments.

weight was recorded for roots (Fig. 2) in 1996 and in 1997. The lowest weight of stem and root was recorded in October 1997.

The succulence of the leaves increased progressively during both growing seasons and then declined during early fall (Fig. 3). Stem succulence peaked in September during the 1996 growing season, and in August in 1997. Root succulence remained unaffected during both seasons.

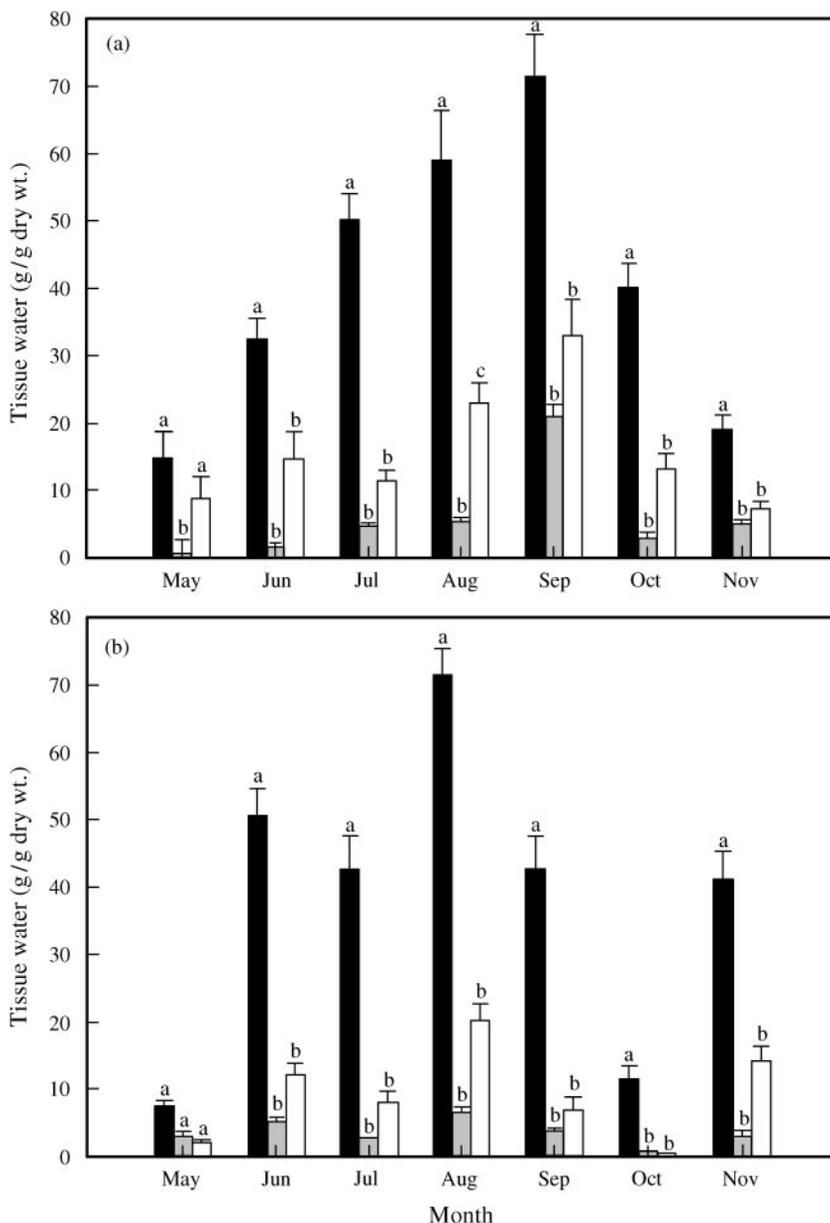


Figure 3. Seasonal pattern of tissue water content (g g⁻¹ dry wt.) of leaf (■), stem (▒) and root (□) of plants collected from an *Allenrolfea occidentalis* community in (a) 1996 and (b) 1997. Bars represent mean ± S.E. Different letters above bars represent significant differences ($p < 0.05$) between treatments.

The Cl⁻ ion content in *A. occidentalis* tissues (leaf, stem and root) remained constant throughout most of the 1996 growing season (Fig. 4). Na⁺ ion concentration gradually increased from 1000 μM to 35,000 μM in 1996, however in 1997 it increased to 28,000 μM (Figs 4 and 5). K⁺ ion concentration in leaves was significantly higher in August (Figs 4 and 5). However, K⁺ concentration was significantly lower in the stem as compared with the leaves and roots. The K⁺ ions in leaves and roots decreased

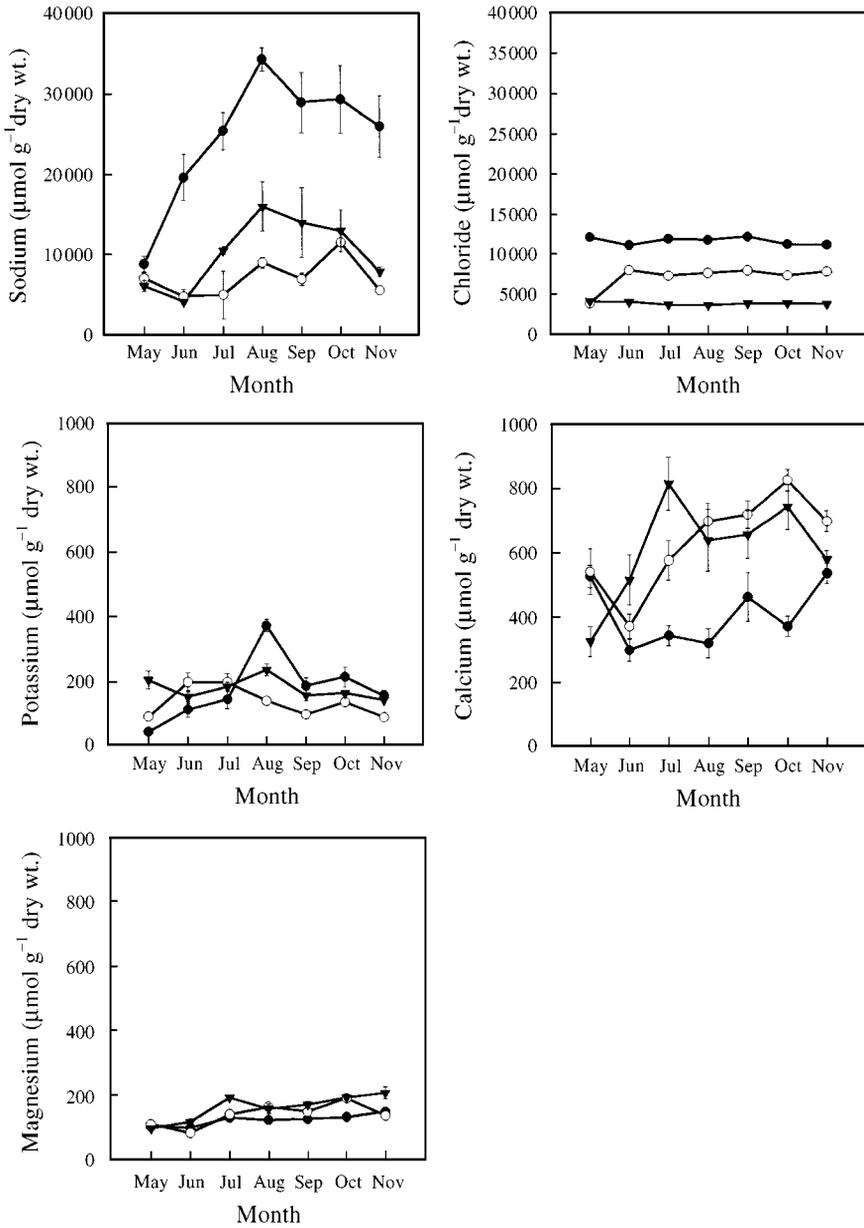


Figure 4. Monthly variation in ion contents of leaf (●), stem (○) and root (▼) of *Allenrolfea occidentalis* during 1996.

significantly during the months of low salinity. The major cations Ca^{2+} and Mg^{2+} differed in their availability patterns throughout the growing seasons (Figs 4 and 5).

Photosynthesis rates were significantly higher in August than in the other months, which did not significantly differ from each other (Table 2). The monthly values of F_v/F_m were always low, and indicated 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 *A. occidentalis* was

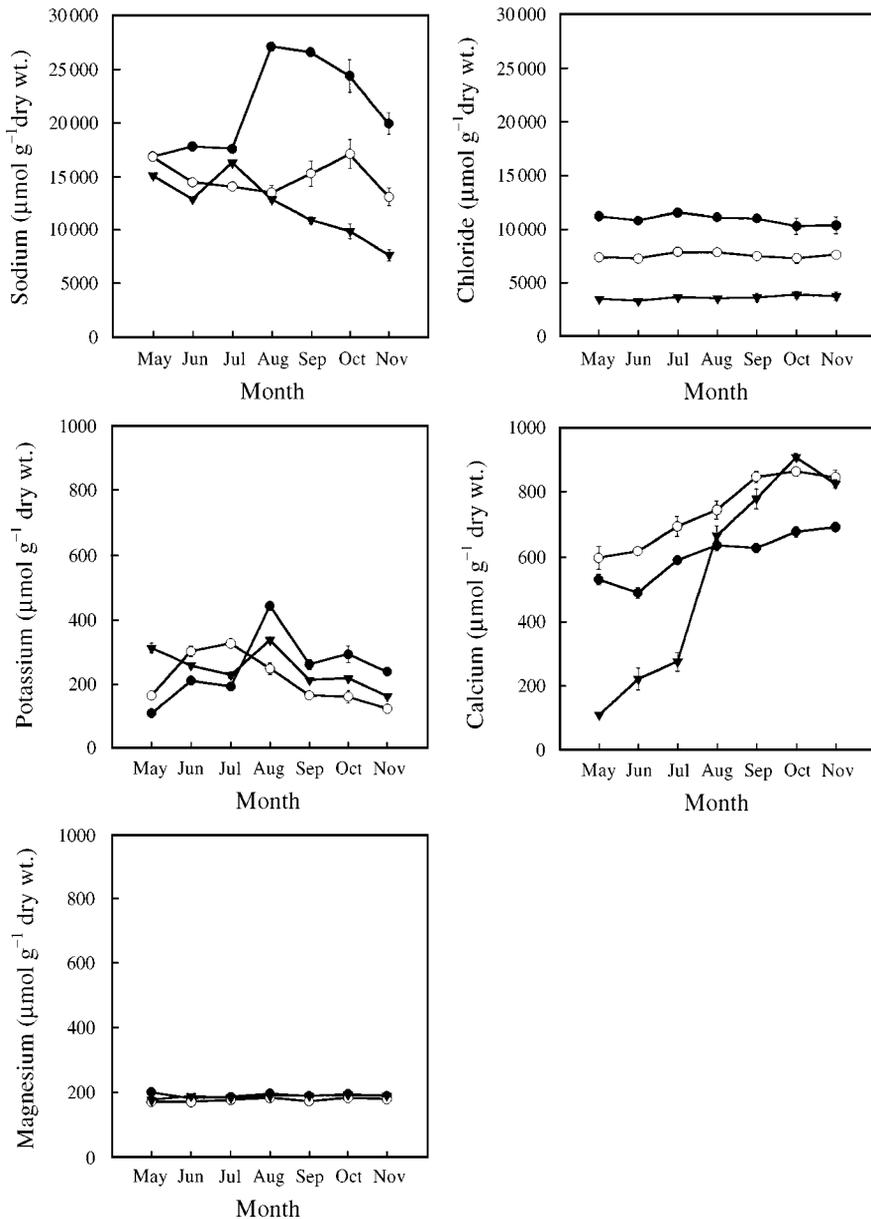


Figure 5. Monthly variation in ion contents of leaf (—●—), stem (—○—) and root (—▼—) of *Allenrolfea occidentalis* during 1997.

significantly greater from July to October (Table 2). Water potentials of shoots decreased significantly with increase in salinity (Table 2).

A three-way ANOVA showed significant individual effects of soil layer, year, month and their interactions in affecting the ion contents of *A. occidentalis* (Table 3). Individual ion analysis of soil samples from surface and sub-surface layers showed that Na^+ and Cl^- were the two ions responsible for most of the salinity of the soil (Tables 4 & 5). The Na^+ and Cl^- ion content in the surface and subsurface soil layers fluctuated considerably. The concentration of Na^+ and Cl^- were highest during

Table 2. Mean \pm S.E. for water potential, photosynthesis and stress under field conditions for 1997 season

Months	Water potential (- Mpa)	Stress (F_v/F_m)	Net photosynthesis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)	Conductivity of the soil surface (d S m^{-1})
May	36.8 \pm 1.2	0.50 \pm 0.035	3.8 \pm 0.43	109 \pm 4.0
June	42.6 \pm 1.3	0.69 \pm 0.037	4.1 \pm 0.49	147 \pm 11
July	70.6 \pm 5.4	0.74 \pm 0.032	5.1 \pm 1.2	145 \pm 12
August	87.6 \pm 4.3	0.75 \pm 0.032	9.2 \pm 1.2	135 \pm 13
September	88.8 \pm 0.86	0.58 \pm 0.033	5.7 \pm 0.57	106 \pm 12
October	82.4 \pm 3.6	0.46 \pm 0.046	0.0 \pm 0.0	109 \pm 7.0
November	34.4 \pm 3.6	0.52 \pm 0.031	0.0 \pm 0.0	87 \pm 8.0

the summer (Tables 4 & 5). The levels of Ca^{2+} and Mg^{2+} ions were fairly constant throughout the growing season. The Ca^{2+} ion concentration was considerably higher in 1997 than in 1996 (Tables 4 & 5). The surface Ca^{2+} , Mg^{2+} , K^+ , NO_3^- and SO_4^- ion concentrations were higher than sub-surface concentrations.

Discussion

An *A. occidentalis* community of a Great Basin Desert playa was exposed to stressful conditions throughout the growing seasons of 1996–1997. The year 1996 was considerably drier in comparison to 1997. Dry matter production of *A. occidentalis* increased, reaching its peak during August. High moisture availability during 1997 had no significant effect on biomass production. Conductivity of the soil ranged from 80 to 160 d S m^{-1} . Halophytes often exhibit stunted growth when found under saline conditions approaching their tolerance limits, indicating that increased salinity stress during the late summer could account for the decreased growth (Khan & Ungar, 1998; McGraw & Ungar, 1981; Waisel, 1972). In August, the salinity in *A. occidentalis* was highest, soil salinity was near its highest level, plant stress indicator (F_v/F_m) was highest, but photosynthesis and dry wt. values were also near maximum. Gul (1998) found *A. occidentalis* showed optimal growth at 600 mM NaCl, and a further increase in salinity decreased the growth.

Allenrolfea occidentalis is a stem-succulent halophyte, and showed a progressive increase of succulence that peaked during August. Succulence is thought to contribute to salt regulation by increasing the vacuolar volume available for ion accumulation (Albert, 1982; Greenway & Munns, 1980; Ungar, 1991). Salinity increased the water content of *Suaeda torreyana* (Glenn & O'Leary, 1984), *Salsola kali* (Reimann & Breckle, 1995), *Arthrocnemum fruticosum* (Eddin & Doddema, 1986), *Halopyrum mucronatum* (Khan *et al.*, 1998). Gul (1998) reported that succulence in *A. occidentalis* did not vary significantly with the increase in salinity. Plants which were grown in the greenhouse only faced more negative osmotic potential (Gul, 1998), while field populations in the present study were also subjected to matric potential. It seems that low availability of water induced succulence in *A. occidentalis*, rather than high salinity concentration. There is an adaptive capability of *A. occidentalis* to grow better in high salinity areas (Young *et al.*, 1995). Marks (1950) reported that *A. occidentalis* in the lower Colorado Desert forms 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 salt concentration of the soil surface layers was considerably higher than the salt concentration in the sub-surface soil layers during the hot summer months. Spring rain

Table 3. Results of three-way ANOVA of soil characteristics by month (M), soil layer (S), and Year (Y) treatments

Independent variable	M	S	Y	M × S	M × Y	S × Y	S × M × Y
PH	42***	3.7*	194***	0.955 ^{n.s.}	47***	17***	2.3*
Conductivity	5.6***	13.4***	85***	2.3*	4.5***	1.5 ^{n.s.}	4.3***
Na ⁺	33***	22***	121***	4.7***	5.4***	8.6***	4.4***
Cl ⁻	3.3**	5.4*	0.3 ^{n.s.}	2.7*	3.3**	5.4*	2.0*
K ⁺	33***	23***	121***	4.7***	5.4***	8.6**	4.5***
Ca ²⁺	39***	64***	59***	12***	10.3***	19***	8.2***
NO ₃ ⁻	28***	11.3**	626***	5.1***	20.6***	8.7**	4.3***
SO ₄ ⁻	35***	52***	591***	3.3***	35***	52***	3.3***
Mg ²⁺	11***	1.8 ^{n.s.}	438***	1.4 ^{n.s.}	37***	000 ^{n.s.}	0.79 ^{n.s.}

Note: Numbers represent *F*-values: **p* < 0.05; ***p* < 0.01; ****p* < 0.001; n.s. = not significant.

Table 4. Seasonal changes in soil extract elemental composition ($\mu\text{mol g}^{-1}$ dry wt.) at the salt playa near Goshen Utah, during 1996 (mean \pm S.E.)

Months	Soil layers	Na ⁺	Cl ⁻	K ⁺	Ca ²⁺	Mg ²⁺	NO ₃ ⁻
May	Surface	3700 \pm 54 ^a	9992 \pm 144 ^a	4.3 \pm 0.63 ^a	169 \pm 30 ^a	66 \pm 7.2 ^a	5.6 \pm 0.59 ^a
	Sub-surface	3800 \pm 42	1291 \pm 954	4.5 \pm 0.49	151 \pm 26	61 \pm 5.0	6.2 \pm 0.57
June	Surface	6000 \pm 61 ^b	12857 \pm 128 ^b	7.1 \pm 0.71 ^a	178 \pm 29 ^a	79 \pm 8.0 ^a	9.0 \pm 1.9 ^a
	Sub-surface	6080 \pm 71	12718 \pm 117	7.2 \pm 0.84	184 \pm 23	87 \pm 7.4	7.0 \pm 0.48
July	Surface	4070 \pm 312 ^c	16035 \pm 690 ^c	4.8 \pm 0.36 ^a	184 \pm 15 ^a	73.3 \pm 3.2 ^a	5.5 \pm 0.22 ^a
	Sub-surface	3870 \pm 220	10427 \pm 516	4.6 \pm 0.25	213 \pm 32	75.8 \pm 5.3	5.3 \pm 0.26
August	Surface	11400 \pm 92 ^d	10762 \pm 148 ^d	13.4 \pm 1.1 ^a	261 \pm 61 ^a	135 \pm 9.4 ^b	9.0 \pm 0.36 ^a
	Sub-surface	11130 \pm 87	10096 \pm 134	13.0 \pm 1.6	270 \pm 20	119 \pm 11	9.8 \pm 1.2
September	Surface	9223 \pm 87 ^e	10413 \pm 997 ^d	11.0 \pm 1.1 ^a	293 \pm 45 ^a	131 \pm 8.3 ^b	7.5 \pm 1.0 ^a
	Sub-surface	8624 \pm 55	11125 \pm 142	10.0 \pm 0.7	279 \pm 30	125 \pm 7.6	7.2 \pm 0.64
October	Surface	11460 \pm 16 ^d	10716 \pm 105 ^d	14.0 \pm 2.0 ^a	317 \pm 45 ^a	118 \pm 1.0 ^b	9.9 \pm 1.1 ^a
	Sub-surface	8470 \pm 77	11588 \pm 119	9.9 \pm 0.89	301 \pm 29	116 \pm 13	8.3 \pm 1.3
November	Surface	6840 \pm 92 ^b	14647 \pm 150 ^c	8.1 \pm 1.1 ^a	274 \pm 28 ^a	108 \pm 9.0 ^b	6.3 \pm 0.64 ^a
	Sub-surface	6240 \pm 53	11399 \pm 176	7.3 \pm 0.62	243 \pm 20	105 \pm 6.4	6.1 \pm 0.63

Values in each column for surface sample with the same superscript are not significantly different at $p < 0.05$, Bonferroni test.

Table 5. Seasonal changes in soil extract elemental composition ($\mu\text{mol g}^{-1}$ dry wt.) at the salt playa near Goshen Utah, during 1997 (mean \pm S.E.)

Months	Soil layers	Na ⁺	Cl ⁻	K ⁺	Ca ²⁺	Mg ²⁺	NO ₃ ⁻
May	Surface	7030 \pm 633 ^a	10175 \pm 103 ^a	8.3 \pm 0.74 ^a	439 \pm 44 ^a	98 \pm 10.0 ^a	7.5 \pm 0.73 ^a
	Sub-surface	5268 \pm 506	8546 \pm 575	6.5 \pm 0.59	176 \pm 26	80 \pm 3.9	6.5 \pm 0.47
June	Surface	11470 \pm 10 ^b	12523 \pm 782 ^b	13.4 \pm 0.7 ^a	497 \pm 32 ^a	44 \pm 3.9 ^a	2.9 \pm 0.39 ^a
	Sub-surface	9180 \pm 76	11339 \pm 810	8.2 \pm 0.64	248 \pm 38	49 \pm 3.8	1.5 \pm 0.18
July	Surface	16400 \pm 76 ^c	13116 \pm 481 ^c	19 \pm 0.9 ^a	444 \pm 48 ^a	40 \pm 1.7 ^a	4.2 \pm 0.31 ^a
	Sub-surface	8030 \pm 73	10154 \pm 490	9.6 \pm 0.86	167 \pm 24	37 \pm 1.9	2.8 \pm 1.6
August	Surface	15870 \pm 164 ^d	12989 \pm 128 ^b	19 \pm 1.9 ^a	345 \pm 31 ^b	48 \pm 0.9 ^a	3.3 \pm 0.34 ^a
	Sub-surface	11930 \pm 108	9710 \pm 186	14.0 \pm 1.3	123 \pm 59	34 \pm 1.7	3.4 \pm 0.33
September	Surface	9560 \pm 59 ^e	13750 \pm 118 ^c	11.0 \pm 0.7 ^a	381 \pm 37 ^b	36 \pm 1.9 ^a	2.7 \pm 1.4 ^a
	Sub-surface	6195 \pm 68	15633 \pm 112	14.0 \pm 1.2	161 \pm 24	47 \pm 1.0	2.5 \pm 0.2
October	Surface	16851 \pm 190 ^c	13200 \pm 93 ^c	20 \pm 2.3 ^a	338 \pm 40 ^b	48 \pm 0.7 ^a	3.5 \pm 0.69 ^a
	Sub-surface	12140 \pm 97	11190 \pm 171	14 \pm 1.14	236 \pm 37	34 \pm 1.3	3.4 \pm 0.2
November	Surface	10040 \pm 72 ^f	12967 \pm 109 ^b	12 \pm 0.9 ^a	302 \pm 50 ^b	38 \pm 2.1 ^a	2.8 \pm 0.14 ^a
	Sub-surface	11980 \pm 67	13644 \pm 610	14 \pm 1.36	324 \pm 51	46 \pm 2.4	2.7 \pm 0.63

Values in each column for surface sample with the same superscript are not significantly different at $p < 0.05$, Bonferroni test.

reduces the salt concentration in the soil surface layer. During the hot summer months, soil surface layers were often encrusted with deposits of white salt, which gave the impression that the plants were surrounded by extremely high concentrations of salt when, in fact, the rooting zones or layers were relatively less saline (Ungar, 1978a; Waisel, 1972).

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, occurring largely during the winter when temperatures are too low for growth (Trent *et al.*, 1997). Sodium and chloride were the two principal ions responsible for increases in osmotic potential of soil samples (Hansen & Weber, 1975). In most saline environments, including Great Basin salt playas, external Na^+ and Cl^- concentrations far exceed those of Ca^{2+} , Mg^{2+} or K^+ .

Many species in the Chenopodiaceae accumulate a large amount of Na^+ and Cl^- when the external salinity is high (Albert, 1975; Flowers & Yeo 1986; Tiku, 1975; Ungar, 1978b). High substrate Na^+ , in addition to any direct toxic effects, presents both water relations and a nutritional challenge for plants (Niu *et al.*, 1995). Donovan *et al.* (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 level of Na^+ accumulation and tolerance for *S. vermiculatus*. Na^+ uptake, necessary for osmoregulation in halophytes, could start as soon as the seed germinates, and allow the seedling to maintain water uptake, turgor and growth (Eddleman & Romo, 1987; Romo & Haferkamp, 1987). In saline and alkaline soils, availability of the cations like K^+ , Ca^{2+} and Mg^{2+} may also be limited (Marschner, 1995; Vasek & Lund, 1980). Leaf K^+ , Ca^{2+} and Mg^{2+} data were consistent with other published reports (Donovan *et al.*, 1997; Glenn & O'Leary, 1984; Rickard, 1982; Rickard & Keough, 1968; Wallace *et al.*, 1973).

Water potential of *A. occidentalis* shoots became extremely negative with increase in growth of the plant; it peaked during August and September. This increase in plant water potential appears to be linked with the increase in soil salinity. Antlfinger & Dunn (1983) found that species growing in higher salinities had a more negative water potential than those growing in low saline areas. Trent *et al.* (1997) showed that water potential of *A. occidentalis* dropped significantly during the dry seasons. Our data showed a similar response. Photosynthesis decreases with the increase in salinity (Flanagan & Jefferies, 1988; Percy & Ustin, 1984). Low rainfall increases drought and salinity stress and thereby reduces the photosynthesis rate. Changes in F_v/F_m stress ratio shows that plants are under a high degree of stress during summer, and this could be due to either drought or high irradiance (Jimenez *et al.*, 1997; Larcher *et al.*, 1990; Sharma & Hall, 1998).

In conclusion, an inland salt marsh population of *A. occidentalis* was found to be very 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. Na^+ and Cl^- were accumulated in, rather than excluded from, the tissues. Reduced growth at high salinity is apparently due to an insufficient supply of photosynthate to support growth, less than favorable water relations in shoots, or differences in ionic relations in different environmental conditions.

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