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Seasonal changes in respiration of halophytes in salt playas in the Great Basin, U.S.A.

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Abstract

Many desert playas are covered with water in the early spring. As the weather becomes warmer and drier, water evaporates, increasing salt content of the soil from 7,000 to almost 16,000 mmol NaCl Kg^{-1}. Changes in respiratory metabolism during the growing season of four halophytes characteristic of cold desert playas was followed using calorimetry. In order of decreasing salt tolerance, the species examined were: the forbs *Salicornia rubra, S. utahensis*; the grass *Distichlis spicata*; and the shrub *Allenrolfea occidentalis*. Tissue collected in the field from sites of low and high salinity in a single playa during May, June, and August of 1997 was put in isothermal calorimeters and the metabolic heat rate (q) and respiration rate (R_{CO2}) measured. Efficiency of substrate carbon conversion (q/R_{CO2}) and predicted specific growth rate ($\Delta H_B R_{SG}$) were calculated. These species are all well-adapted to the environment in which they are found. Highest metabolism, respiration, efficiency and growth are found during May and June and are lowest during the hot, dry month of August. Differences between the species are also noted.

Introduction

In the Great Basin of the western U.S.A., the annual precipitation ranges from 10 to 20 cm, mostly as snow with relatively little spring or summer rain. Just east of the town of Goshen, Utah, are a number of playas, which in the spring are shallow lakes with a water depth of a few centimeters. During the hot, dry summer water evaporates leaving a white deposit of salt (mostly sodium chloride) in the central and lowest part of the playa. No vegetation will grow in the salt crust. However around the salt pan grow concentric circles of salt tolerant species. *Salicornia rubra*, a small annual forb is found nearest the salt pan with the perennial forb, *Salicornia utahensis*, growing on slightly less saline soil. In turn, the grass, *Distichlis spicata*, is found on higher ground, with the shrub, *Allenrolfea occidentalis*, on still higher, slightly less saline soil.

While growth of some halophytes is stimulated by salinity (Flowers et al., 1986), most species of halophytes are inhibited by high concentrations of salt with none showing optimal growth at seawater concentration (Ungar, 1991). Growth of desert species from Pakistan was promoted by low salinities (Khan et al., 1998). For instance, 425 mM NaCl promoted growth in *Cressa cretica*, while growth in 850 mM NaCl was not significantly different from control plants (Khan and Aziz, 1998). Great basin halophytes showed a similar promotion of growth at moderate salinities (400 to 600 mM NaCl) with a decline at higher salinities (Gul, 1998).

While plant growth depends on acquisition of carbon and other resources, the rate of growth is determined by the processing of resources into structural biomass as predicted by the rate and efficiency of metabolism (Hansen et al., 1998). The objective of this study was to examine differences in respiratory metabolism of field-grown material due to changing salt

Table 1. Mean concentration (mmol Kg^{-1}) and ± S.E. of soil ions at the salt playa near Goshen, Utah, during 1997.

Months	Na^+	Cl^-	K^+	Ca^{++}	Mg^{++}	NO_3
May	7030 ± 633^a	10175 ± 103^a	8.3 ± 0.74^a	439 ± 44^a	98 ± 10.0^a	7.5 ± 0.73^a
June	11470 ± 10^b	12523 ± 782^b	13.4 ± 0.7^a	497 ± 32^a	44 ± 3.9^a	2.9 ± 0.39^a
August	15870 ± 164^c	12989 ± 128^b	19 ± 1.9^a	345 ± 31^b	48 ± 0.9^a	3.3 ± 0.34^a

Values in each column having the same letter are not significantly different at $p < 0.05$, Bonferroni test.

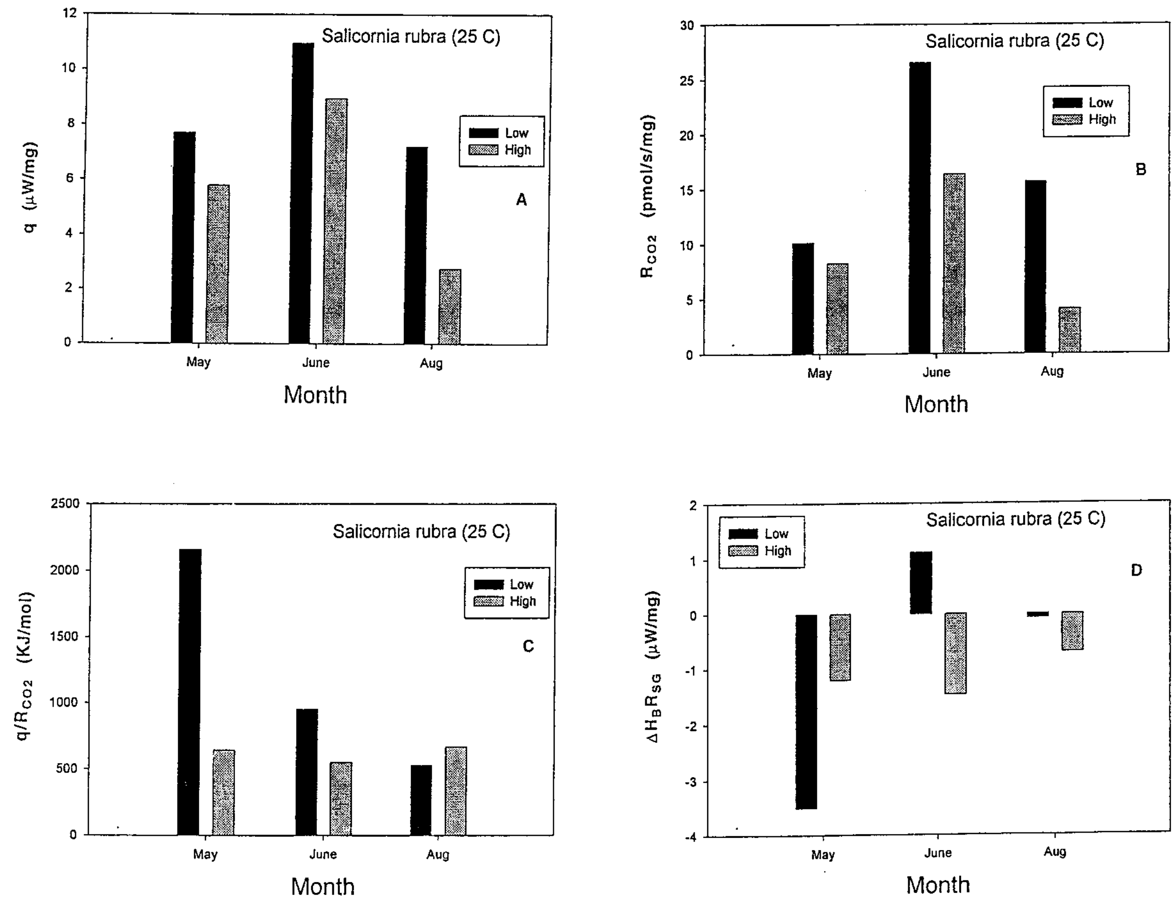

Figure 1. Salicornia rubra stem and leaf tissue was collected in the field from soil relatively high and low in NaCl in May, June, and August of 1997. Isothermal calorimetric measurements were made at 25 °C: A. Metabolic heat rates (q). B. Respiration rates. C. The ratio of metabolic heat rate to respiration rate (q/R_{CO2}) or efficiency. Smaller numbers indicate greater efficiency. D. Predicted specific growth rate ($\Delta H_B R_{SG}$).

concentrations and temperatures during the growing season (Smith et al., 1999).

Methods

Allenrolfea occidentalis (Wats.) Kuntze, *Distichlis spicata* (L.) Greene, *Salicornia rubra* A. Nels., and *Salicornia utahensis* Tidestr. (Welsh et al., 1993) were found growing on a salt playa about one kilometer east of Goshen, Utah. Stem tips were cut from the

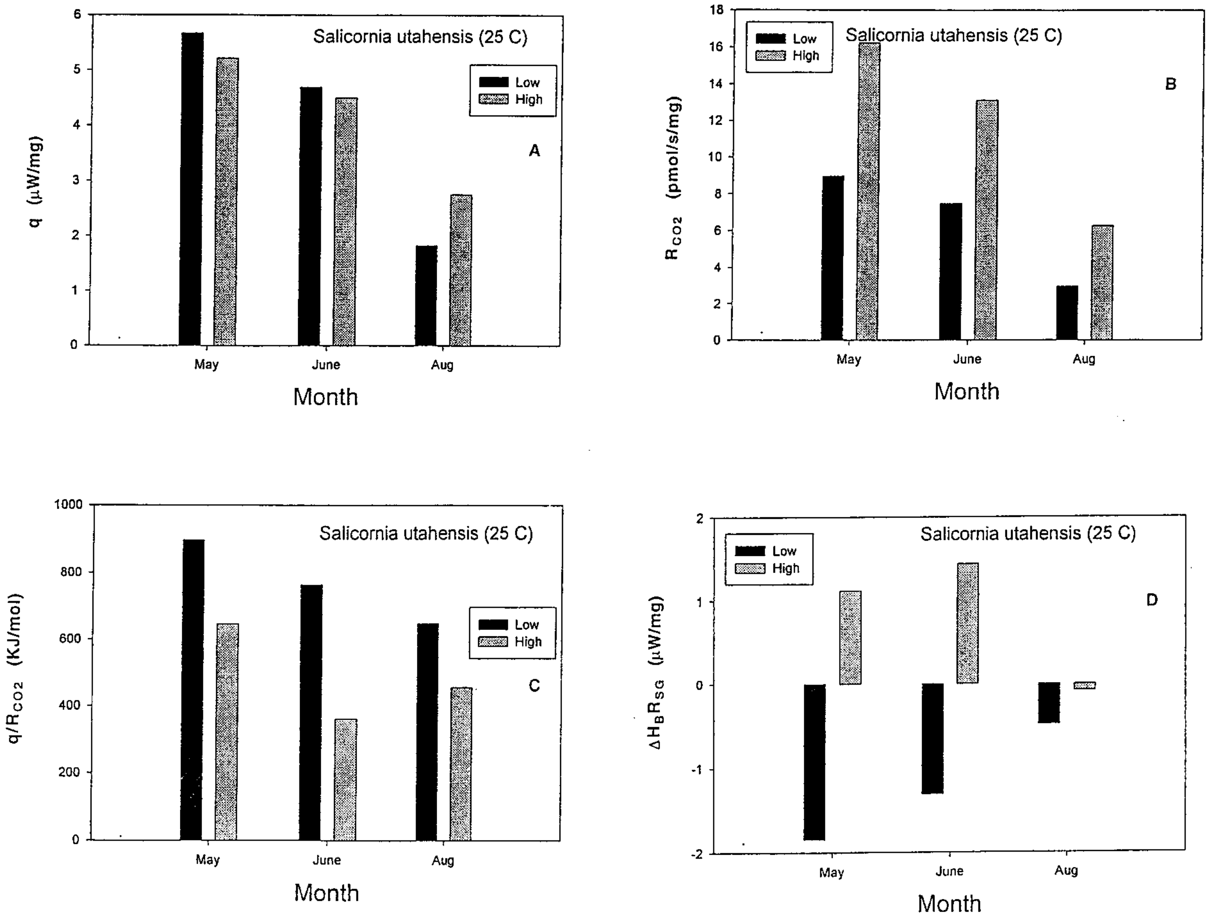

Figure 2. Salicornia utahensis stem and leaf tissue was collected in the field from soil relatively high and low in NaCl in May, June, and August of 1997. Isothermal calorimetric measurements were made at 25 °C: A. Metabolic heat rates (q). B. Respiration rates. C. The ratio of metabolic heat rate to respiration rate (q/R_{CO2}) or efficiency. Smaller numbers indicate greater efficiency. D. Predicted specific growth rate ($\Delta H_B R_{SG}$).

plants and transported on ice to the laboratory (about 1 hour) for analysis. Plant collections were made during May, June, and August of 1997. While the salt concentration increased during the season (Table 1), five plants of each species were each collected on every date from two sites expected to be high and low in salt concentration.

Stem and leaf tissue were placed in ampules and run in triplicate. Isothermal calorimetric measurements of metabolic heat (q) rates and respiration rates (R_{CO2}) were made at 15 and 25 °C. Measurements were made in the Calorimetry Sciences Corporation multi-cell model 4100 MC DSC or the very similar predecessor of this instrument, the Hart Scientific model 7707 DSC. Metabolic heat rates were measured on 10 to 30 mg dry weight of tissue. Respiration rates were measured with the addition of an NaOH trap and consequent heat of carbonate formation (Criddle et al., 1997; Hansen et al., 1998).

Metabolic heat rate (q) is expressed as microwatts (μW) per mg dry weight. Respiration rate (R_{CO2}) is expressed as picomoles (moles^{-12}) per second per mg dry weight. The ratio q/R_{CO2} is inversely proportional to the efficiency of conversion of substrate carbon to biomass. Low values for the ratio indicate higher efficiency. The predicted specific growth rate (R_{SG}) comes from: $\Delta H_B R_{SG} = 455 R_{CO2} - q$, where the constant 455 kJ/mol of O_2 is from Thornton's rule (Smith et al., 1999). Thus from the two measured quantities, respiration rate and metabolic heat loss, both efficiency and predicted growth can be calculated.

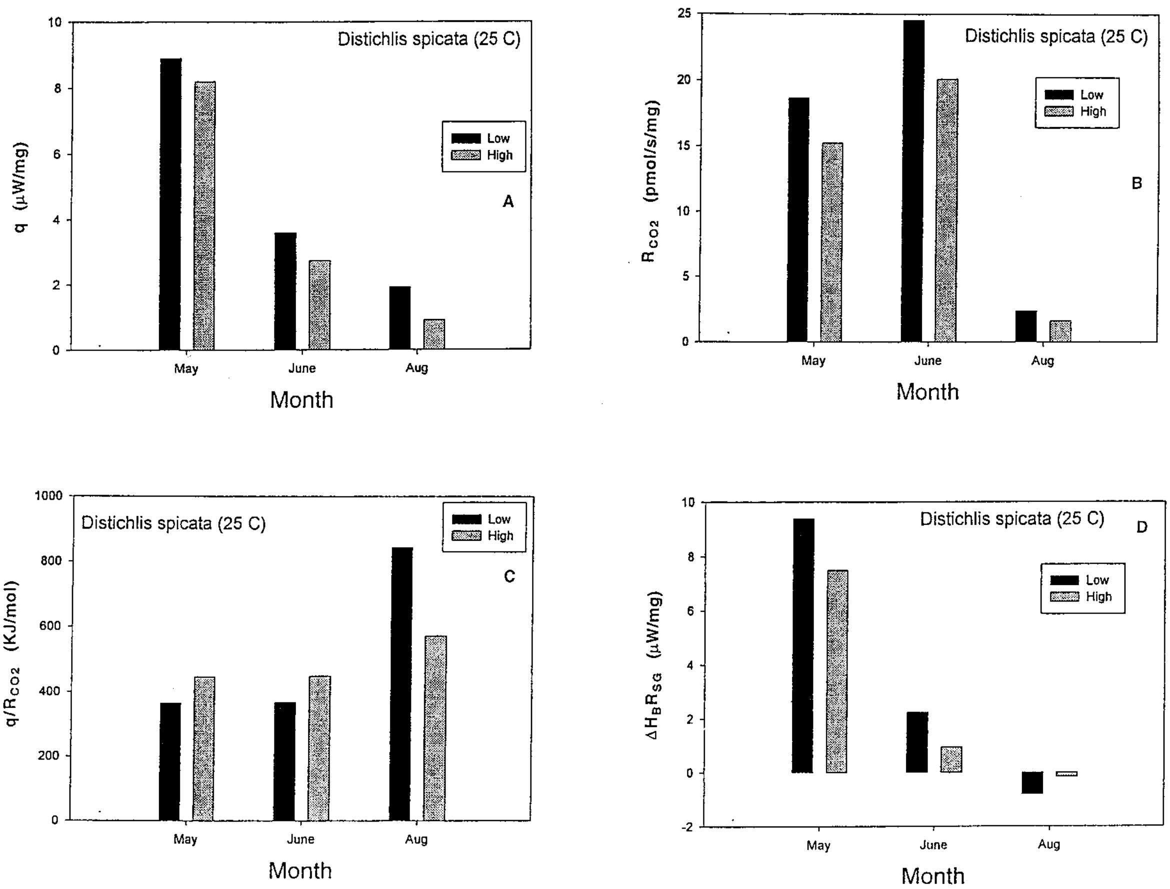

Figure 3. Distichlis spicata stem and leaf tissue was collected in the field from soil relatively high and low in NaCl in May, June, and August of 1997. Isothermal calorimetric measurements were made at 25 °C: A. Metabolic heat rates (q). B. Respiration rates. C. The ratio of metabolic heat rate to respiration rate (q/R_{CO2}) or efficiency. Smaller numbers indicate greater efficiency. D. Predicted specific growth rate ($\Delta H_B R_{SG}$).

Five grams of soil were mixed with 25 ml of distilled water, shaken and filtered through Whatman #1 paper. Chloride and nitrate ions were measured with a DX-100 ion chromatograph. Na^+, K^+, Ca^{2+}, and Mg^{2+} cation concentrations were measured with a Perkin-Elmer model 360 atomic absorption spectrophotometer. Data obtained were analyzed using three way ANOVA. A Bonferroni test was used to determine significance ($p < 0.05$) of differences between individual treatments (SPSS, 1999).

Results

Salt content in the playa (Table 1) was mostly sodium chloride which increased in concentration as water evaporated during the spring and summer months. Other ions increased only slightly or even decreased in concentration during the same period.

Other than a normal increase in metabolism with an increase in temperature (Q_{10} of 2 or higher) there seemed to be few differences in our results at 15 and 25 °C so we will only present data for 25 °C. The four species considered seem to grow best in late spring. *Salicornia rubra* (Figure 1) had the highest metabolic activity and predicted growth in June on low salt soils. Greatest carbon conversion efficiency was in August.

Salicornia utahensis (Figure 2) consistently had higher respiration rates and predicted growth rates in high rather then low salt soils, especially in May and June. Efficiency was greatest in June on high salt soils. All metabolic measures (Figure 3) were consistently higher for *Distichlis spicata* in May and June on low salt soil. Efficiency was best in August on low salt

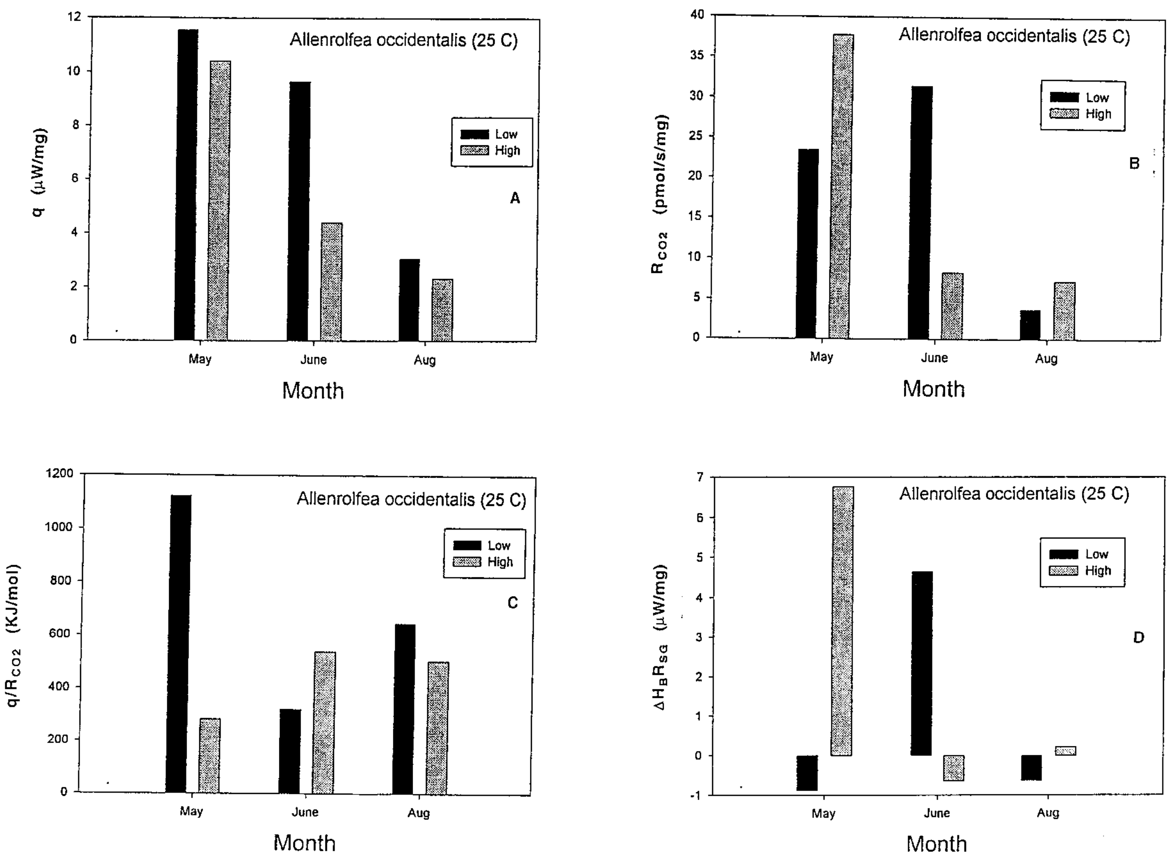

Figure 4. Allenrolfea occidentalis stem and leaf tissue was collected in the field from soil relatively high and low in NaCl in May, June, and August of 1997. Isothermal calorimetric measurements were made at 25 °C: A. Metabolic heat rates (q). B. Respiration rates. C. The ratio of metabolic heat rate to respiration rate (q/R_{CO2}) or efficiency. Smaller numbers indicate greater efficiency. D. Predicted specific growth rate ($\Delta H_B R_{SG}$).

soil. Predicted growth, however, was much higher in May. *Allenrolfea occidentalis* (Figure 4) had the highest respiration rate in May on high salt soil, which led efficiency to be best and predicted growth to be highest under those conditions.

Discussion

Desert shrub species differ in growth response to salinity (Dodd and Donovan, 1999). Plants submitted to drought and saline stress generally have reduced biomass compared to control plants (De Herralde et al., 1998). Some plants seem to be able to accumulate osmolytes to overcome this problem (Hare et al., 1998) which has stimulated interest in using new molecular approaches to improving salt tolerance (Winicov, 1998).

Salt stress has been shown to diminish water use and photosynthetic efficiency in C_3 (Farquhar et al., 1982) as well as C_4 plants (Zhu and Meinzer, 1999). Growth depression by sodium chloride has been shown to be not directly related to respiration (Kasai et al., 1998). Nonetheless, inhibition of metabolism by NaCl was shown to be responsible for decreased growth of barley roots (Criddle et al., 1989).

Predicted growth and efficiency for all species in this study (Figures 1–4) is lowest during the hot, dry month of August when soil salinity is at a maximum (Table 1). Milder conditions in May and June seem to be preferred. While there are common trends during the growing season, differences occur as well. Clearly much work needs to be done in both field and laboratory for an understanding of the biological processes and ecological meaning of these preliminary results.

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