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Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* Process Study

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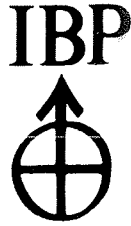
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DESERT BIOME

US/IBP ANALYSIS OF ECOSYSTEMS

1970

PROGRESS REPORT

PROCESS STUDY

Autecological Studies of *Atriplex confertifolia*
and *Eurotia lanata*

Martyn M. Caldwell, Neil E. West, and Peter J. Goodman

Utah State University

Logan, Utah

1970 PROGRESS REPORT

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PROCESS STUDY (2.3.)

Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* (2.3.2.)

Martyn M. Caldwell, Neil E. West, and Peter J. Goodman

Utah State University; Logan, Utah

Abstract

Extensive measurements of photosynthesis and transpiration have been made over a six month period in the field in relation to leaf temperatures, soil water potential and temperature, plant moisture stress, and irradiation. Other parameters such as soil salinity, leaf moisture contents and osmotic potentials, and vapor pressure of the air have also been monitored. These measurements have been made for each phenological stage for both species; they demonstrate that both species are highly variable in their photosynthetic response to environmental variables. A substantial degree of acclimation is exhibited as the plants progress through each phenological stage.

Measurements have also been made of biomass, nutrient content, growth response to environmental factors, and genetic variability in *Atriplex* and *Eurotia*. All of these factors are likely to affect the usefulness of the plants as primary producers. Biomass was measured on new and old shoots and roots of *Atriplex* and *Eurotia*. *Atriplex* produced more biomass than *Eurotia*, especially in the new shoots, and the *Atriplex* plants had more shallow roots than the *Eurotia* plants. Nutrient analyses of plant biomass and litter showed that ten times more sodium accumulated in *Atriplex* than in *Eurotia* shoots, but that *Eurotia* contained more iron, copper, and magnesium than *Atriplex*. These plant differences were reflected by similar differences in the litter nutrient contents, so that nutrient cycling varied in the two communities. In response to environmental conditions of high moisture, temperature and nitrogen supply in the soil, *Atriplex* responded more in leaf growth rate than did *Eurotia*. Finally, it has been shown that population differences exist between *Atriplex confertifolia* plants from different parts of Curlew Valley, and more noticeably, between *A. nuttallii* plants from soils with different salinities.

Objectives

To relate quantitative data on vegetative growth, water and mineral nutrient uptake, transpiration and photosynthesis to each other and to relevant environmental parameters in order to construct models of primary productivity, water use, and nutrient cycling.

Methods

Gas Exchange and Micrometeorological Studies

This year a gas exchange cuvette system has been put into operation at the Curlew Valley I.B.P. site. This system has been developed for the simultaneous measurement of photosynthesis and transpiration under precisely controlled conditions (Koch *et al.*, 1968). The system can either be used to follow ambient conditions or to establish constant conditions of temperature, humidity and irradiation. A schematic representation of this system is shown in Figure 1. By using two flow systems, a main flow stream and a bypass system, carbon dioxide and water vapor gas exchanges can be measured simultaneously and concentrations of these gases in the cuvettes can be held near ambient levels. Carbon dioxide levels are always within 10% of ambient concentrations. The concentration difference between air which has been passed through the cuvette containing the plant and air drawn directly from the environment are measured with a differential carbon dioxide infrared gas analyzer (Beckman Co.). Flow rates are also carefully measured in order to permit an absolute calculation of photosynthetic or respiratory rates. Water vapor concentrations are measured at three locations in the system (see Fig. 1) using lithium chloride sensors. The system automatically regulates the temperature of the water vapor trap in the bypass system so as to remove a quantity of water vapor which is equal to that being introduced into the system by plant transpiration. This maintains water vapor pressures within the cuvette exactly equal to those in the ambient environment. Transpiration rates are calculated from flow rates and the difference in water vapor concentrations between the chamber and the bypass system.

Temperature within the cuvette is automatically controlled to match ambient temperatures or to hold constant temperatures by the use of a Peltier heat exchanger (see Fig. 2). Air is continually circulated through the lamellae of the heat exchanger and then passed over the plant. During the daytime, the direction of electrical current in the heat exchanger causes the lamellae within the chamber to act as cooling surfaces. During the night, electrical current is reversed causing the lamellae within the chamber to act as heating surfaces in order to keep temperatures within the chamber equal to those outside of the chamber.

Air temperatures are measured continuously inside and outside the cuvette using resistance thermometers. Leaf temperatures are also measured in the cuvette using fine wire thermocouples inserted into the leaf tissue. A Barnes radiation thermometer is used to check the leaf temperatures measured with the thermocouples and to continuously record leaf temperatures of shrubs outside the chamber.

Solar irradiation is being monitored by an Eppley pyranometer. Soil temperatures are being contin-

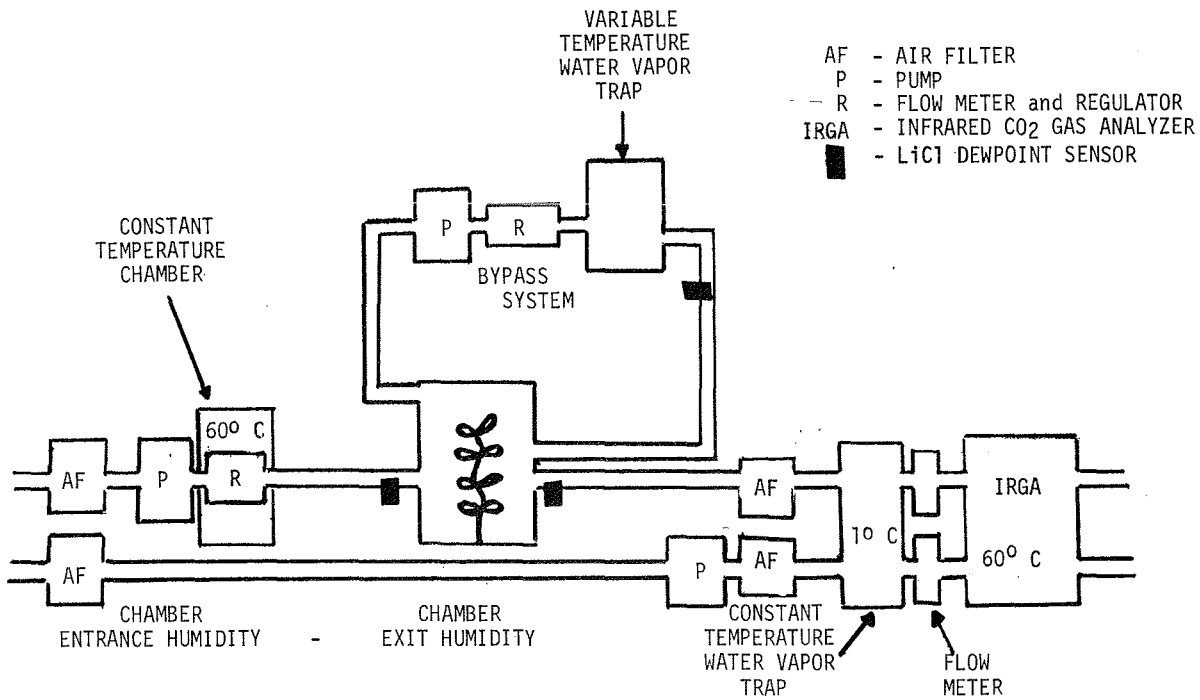
Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

Figure 1. Diagram of flow system for plant gas exchange measurements.

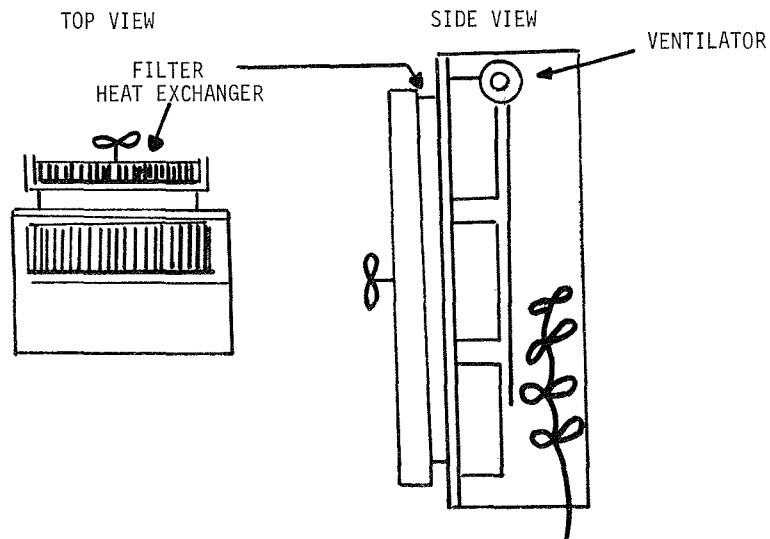


Figure 2. Plant chamber in gas exchange measurement system. Peltier controlled heat exchanger with lamellae inside chamber and outside chamber can transfer heat in either direction.

Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

checked with thermocouples at several depths to -150 cm. Soil-water potential values are being measured with soil thermocouple psychrometers as described by Rawlins and Dalton (1967). In addition, soil samples are taken for gravimetric determination of moisture in the laboratory and for water potential determination using a normal laboratory controlled-temperature thermocouple psychrometer. A neutron probe is also being used to determine bulk soil moisture at several depths. Plant water status is being determined by the Scholander pressure bomb technique (Maring and Cleary, 1967). In addition, sap is being expressed for osmotic pressure determinations using a vapor pressure osmometer. Soil salinity is also being monitored using a Beckman conductivity bridge. The vapor pressure deficit of the ambient air is being determined by lithium chloride sensors.

For the determination of plant gas exchange rates under constant environmental conditions, artificial irradiation is being used from incandescent Sylvania cool-lux bulbs. Absolute irradiation intensities and spectral compositions of artificial and natural irradiation is being determined by the use of an I.S.C.O. spectroradiometer. Branches or entire shoots of intact individuals of these two species are enclosed in the gas exchange cuvette system without disturbance of the plant root environment. Individuals are selected for sampling according to a randomized block design. Each individual plant is used for measurement of gas exchange under ambient conditions for a one-day period followed by two days of gas exchange measurements under controlled temperature, humidity and irradiation conditions. After a plant has been sampled, the leaf area, dry weight of photosynthetic tissues, phenological stage and sex of the individual and proportion of the plant included in the gas exchange chamber are recorded. Leaf areas are being determined by a photoelectric planimeter (Caldwell and Moore, 1971).

In addition, potted shrubs were used to investigate the relationship between soil moisture potential, plant moisture stress, and plant gas exchange. Potted plants are enclosed in the gas exchange chambers and exposed to artificial irradiation and varying leaf temperatures. Soil moisture potentials are monitored with four soil moisture psychrometers in each pot.

All gas exchange data and most of the microenvironmental data are recorded on strip chart recorders. These data are then semi-automatically digitized on a hybrid analog-digital computer and rendered in computer-compatible form.

Nutrient Inventory and Cycling Rates

Soil, litter, and plant samples have been collected in several communities (notably *Atriplex confertifolia* and *Eurotia lanata*) in Curlew Valley, Utah, on a seasonal basis to determine the amount of each nutrient present in the standing crop, and to determine the rate of nutrient cycling. The approach being used resembles that of McGinnis et al. (1969) in studying biomass in tropical forests. However, biomass sampling has the disadvantage of giving no indication of the capacity of the system to respond to external factors. In consequence, leaf growth rates have been compared at different levels of soil moisture, temperature, and nitrogen supply.

Another possible cause of variation in the plants' behavior may lie in their genetic composition. It seems likely that under extremes of salinity, tolerant plants will be selected, and these may well differ in other characters from the original population. Evidence has therefore been sought of differences between *Atriplex* and *Eurotia* populations in different parts of Curlew Valley and particularly where there are markedly different salinities.

Soil sampling and analysis - - Two kinds of soil samples have been taken, either at random within plots of closed plant communities, where accurate estimates of root biomass and nutrient content are required; or at points along transects, corresponding to vegetational changes, where the nature of the community is under investigation. In the closed communities, soil samples were taken systematically at depths of 0-30, 30-60, and 60-90 cm. In the transect samples, more attention was paid to changes in soil texture. Measurements were made at the surface soil, and then in successive zones of different texture. After 1 mm sieving, the soils were air-dried in preparation for analysis.

Soil conductivity was measured on moistened soil samples with a Beckman Conductivity Bridge RC 16B2. Soil pH was measured with an Orion specific ion meter 401. Dry soil samples were used for analysis of total N (semi-microkjeldahl); ammonium N (KCl extraction followed by steam distillation over MgO) and nitrate N (KCl extraction followed by steam distillation over MgO and Devarda's alloy). Soil carbon was determined by a modification of Walkley-Black's method (Schollenberger, 1927). Available Na, K, and Mg was determined by the method of Hossner and Ferrara (1967), followed in each case by measurement with a Perkin-Elmer 303 Atomic Absorption spectrometer. Total Fe, Zn, and Cu were determined by the methods of Allan (1959, 1961a, 1961b), while total P was measured after 70% perchloric acid digestion by the phospho-vanado-molybdate method (Chapman and Pratt, 1961).

Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

Litter sampling and analysis - - Litter samples were taken in both *Atriplex* and *Eurotia* plots. In *Atriplex* plots, the litter could be divided into two fractions, a coarse fraction of undecomposed woody matter, stem bases, etc.; and a fine, easily decomposable fraction of leaves and the finer stem material. Soil particles were removed by shaking the litter on a 1 mm sieve, followed by washing. In *Eurotia*, the litter was all of fine composition, so that fractionation was not possible.

Litter samples were oven dried, weighed, ground, and analysed for N, P, K, Na, Ca, Mg, Fe, Mn, Zn, and Cu, by the same techniques as were used for plant material (see below).

Litter production is also being estimated by an enclosure-platform technique devised by Mack (personal communication).

Plant Sampling -- Total biomass and annual productivity were determined for above-ground parts of plants in *Atriplex* and *Eurotia* plots. Biomass estimates were made by harvesting plants from randomly selected 1 m² plots of *Eurotia* or 4 m² plots of *Atriplex*. Plant material was dried at 60° C, weighed, and ground for analysis. Production was estimated by a technique using the ratio between old and new growth of individual plants within the communities. Forty to forty-five plants were taken at random, and separated into "new growth" (of the current year), and "old growth" fractions. Old growth : new growth ratios were expressed on a dry weight basis for each plant and enough plants were sampled to estimate the ratio ± 10% (P < 0.1). This ratio was then used to estimate annual production. The new and old fractions were also ground for analysis, as a measure of nutrient cycling rate.

Root biomass was determined from random 8.35 cm diam. core samples taken from the shoot biomass sampling plots, at depths of 0-30, 30-60, and 60-90 cm. Roots were separated from soil, using a 1 mm sieve, followed by washing and flotation. The root samples were then dried at 60°, weighed, and ground for analysis.

Plant analysis -- Dry, ground plant material was used to determine plant N (semi-microkjeldahl). For plant P, K, Na, Ca, Mg, Fe, Mn, Zn, and Cu, a 1.0 g sample stood for 2 hr. with 16 ml HNO₃ + 2.4 ml HClO₄ + 1.6 ml H₂SO₄, after which it was digested, cooled, filtered, and diluted to an appropriate volume (Chapman and Pratt, 1961). Phosphorus was determined colorimetrically as phospho-vanada-molybdate, the other elements being measured with a Perkin-Elmer 303 Atomic Absorption Spectrophotometer.

Subsidiary Studies on Growth and Nutrient Response

The effect of environmental conditions, and of differences between species and populations were investigated as follows:

The ability to grow in high concentrations of some ions (Na⁺, Cl⁻, for example) and low concentrations of others (such as NO₃⁻) must be important for survival of plants in the cold, saline desert areas such as Curlew Valley. Comparisons are therefore being made of the response of different species, and of populations within the species, to different nutrient levels. Interactions with temperature and water supply are also being tested.

Plants of *Atriplex confertifolia*, *Eurotia lanata*, and also of *Artemisia tridentata*, *Halogeton glomeratus*, and two subspecies of *Atriplex nuttallii* are being used in this study. These are being grown in a glasshouse in a standard basic nutrient solution as follows: 0.15 mM NaNO₃; 3 mM KCl; 0.8 mM NaH₂PO₄; 0.10 mM H₃BO₃; 5 mM CaCl₂; 5 mM MgCl₂; 0.1 mM FeEDTA; plus micronutrients (Shive and Robbins, 1945). The large concentrations of salt and boron in this solution were given to simulate native soil conditions, previously obtained by analysis. To date, although both cuttings and mature plants have been grown, only mature plant response to one nutrient has been measured, comparisons having been made between 0.15 mM NaNO₃ and 16.5 mM NaNO₃. However, two temperatures have been compared (25° C and 0° C) and two watering regimes (field capacity twice, or seven times weekly), and their interactions with the nitrogen levels have been tested.

Findings

Gas Exchange and Micrometeorological Studies

Because of budgetary problems in the central Desert Biome office, analyses of the gas exchange and micrometeorological data had to be discontinued for four months. This severely limits the content of our progress report at this time. From March through October, 1970, the gas exchange and micrometeorological sensors have been in continuous operation at the field site in Curlew Valley. Seventy-nine individual plants were enclosed in the gas exchange chamber and monitored for three days. During the first day, the plants were held under essentially ambient field conditions. Following this, these individuals were exposed to artificial irradiation or total darkness while the temperature was changed to various predetermined levels. In other experiments, the temperature inside the gas cuvette was held constant while the irradiation intensities were varied. These experiments with predetermined cuvette conditions usually required two days following the ambient condition experiment. These measurements were performed for each phenological stage of both

Autecological Studies of Atriplex confertifolia and Eurotia lanata - continued

species. Since Atriplex confertifolia is a dioecious species, female and male plants were treated separately in these measurement series. Although the two sexes of Atriplex performed similarly early in the season, the gas exchange activity of these plants were quite different following the flowering stage.

The constant temperature experiments have revealed that both species possess a great deal of phenotypic plasticity in photosynthetic response to temperature. Although these data have not been statistically analyzed as yet, they can be summarized as follows: In the early spring (March) when, at night, temperatures were characteristically down to -5 to -10°, both species were able to carry on active net photosynthesis at leaf temperatures of -5° C and reached an upper thermal compensation point at 25° C. In May and June when the daily temperature regime was much higher, both species possessed upper thermal compensation points around 45° C and several individual plants of Atriplex confertifolia were found to have active photosynthesis above 50° C. The lower limit of active net photosynthesis during this period was between 0 and +5° C.

The foregoing experiments were all performed using plants in situ in the field. Soil moisture potential monitored in the rooting zone for these plants in situ suggested that the soil water potential seldom exceeded -50 to -60 atm. Although this describes the soil moisture potential in the immediate rooting zone (-30 to -60 cm in depth), there may often be roots outside of this principal rooting zone which provide access to soil moisture. We have found that roots from both of these species can be found as deep as 2.5 meters in the soil. In order to better define the photosynthetic response of these two species to soil water potential, a separate series of experiments have been carried out using potted shrubs. These experiments were initiated in the field and have been continued in the laboratory. These potted plants were sealed in the gas exchange chamber and exposed to constant artificial irradiation at several leaf temperatures. In addition, these plants were also held in darkness at varying temperatures to determine dark respiration. These experiments were carried out on several individuals of both species at soil moisture potential ranging from field capacity to soil moisture potential of -75 to -80 atm. Both species were able to exhibit active net photosynthesis and a slight amount of transpiration at the most extreme soil water potentials of -75 atm. From these studies, it appears that both species are approximately equally tolerant of very low soil moisture potentials. Statistical analyses of these data will reveal more about the characteristic functions of net photosynthesis and dark respiration in response to soil water potential and temperature.

The primary emphasis in the gas exchange studies this year has been on the influence of three primary independent variables on gas exchange processes. These three primary independent variables are leaf temperature, solar irradiation, and moisture. Most of the experiments have been designed around the influence of each of these independent variables on these two species at different times of the year. In addition to these experiments, a number of other parameters have been measured during the growing season. These parameters include soil temperature at several depths, bulk soil moisture, soil salinity, and vapor pressure deficit of the air. In addition, other relationships have also been investigated such as the relationship between precipitation and bulk soil moisture, soil salinity, plant moisture stress, plant moisture content, and osmotic potential of the expressed sap. Several of these relationships are shown in Figures 3, 4, 5, and 6.

Biomass Survey and Nutrient Inventory in Atriplex and Eurotia Communities

Biomass -- Biomass was similar in the two communities (Atriplex = 29,941 Kg/ha; Eurotia = 32,141 Kg/ha), the difference of only seven percent between them probably being less than the experimental error involved in the estimations (Table 1). Atriplex had more above-ground growth (3,806 Kg/ha) than Eurotia (3,134 Kg/ha). Atriplex had more old growth (2,511 Kg/ha), but particularly more new growth (1,295 Kg/ha) than Eurotia (old growth = 2,382 Kg/ha; new growth = 752 Kg/ha), as shown in Table 1. Eurotia had more root biomass (23,751 Kg/ha) than Atriplex (19,371 Kg/ha), but the Eurotia root biomass was equally distributed at depths of 0-30 cm and 30-60 cm, while the Atriplex root biomass was greatest at the surface (0-30 cm). There was more litter in the Atriplex community (6,764 kg/ha) than in the Eurotia (5,256 Kg/ha), and much of the Atriplex litter was in the coarse old woody material (Table 1).

Nutrient concentrations -- Nutrient analyses are summarized in Table 2, A, B, C. Mean values have been calculated so that comparisons can be made between Atriplex and Eurotia, their plant parts, and at various times in the year. More detailed comparisons of interactions are awaited from computer analyses.

Comparison of nutrient concentrations in the shoots showed that the Na content of Atriplex (0.7%) greatly exceeded (by ten times) that of Eurotia (0.07%). P and K contents were about the same in the two species, and Eurotia exceeded Atriplex in concentrations of Mn, Zn, and Ca, and considerably exceeded Atriplex (by two or three times) in Fe, Cu, and Mg (Table 2, A). Atriplex roots contained a slightly higher concentration than Eurotia of Na, K, P, Cu, and Zn (Table 2, B).

The two species showed similar distribution of nutrients other than calcium between old and new shoot growth. Shoot nutrient concentration did not change consistently in Eurotia from month to month, but in Atriplex there was an increase in July and August in Na, K, Ca, Mg, and Cu. There was a decrease in Mn and Fe during August, whereas P and Zn varied little (Table 2, A). The nutrient concentrations at different depths along the roots underwent similar changes in the two species. There was an increase in the concentrations of Na, K, Fe, Ca, Mg, and P as depth increased, while there was a decrease in the concentration of Mn with increase in depth. Cu and Zn concentrations did not change with increasing depth (Table 2, B). Root material collected in August (Atriplex) or July (Eurotia) generally contained more of each nutrient, except P, than collections made in May (Table 2, B).

Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

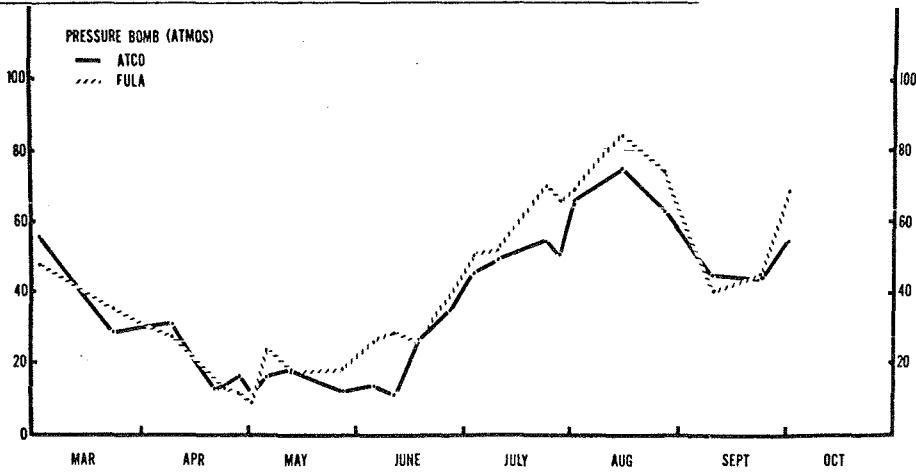


Figure 3. Plant water stress as determined by pressure bomb measurements for *Atriplex confertifolia* and *Eurotia lanata*.

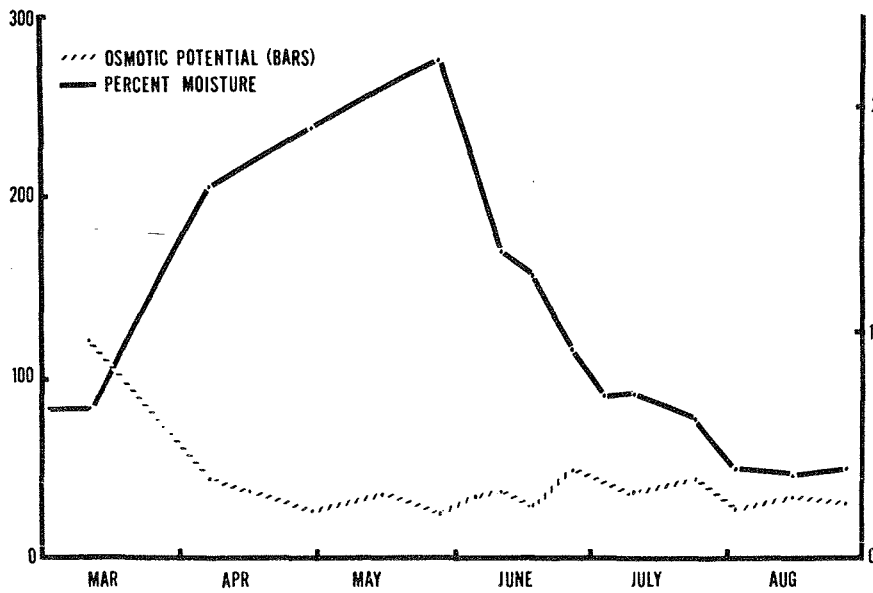
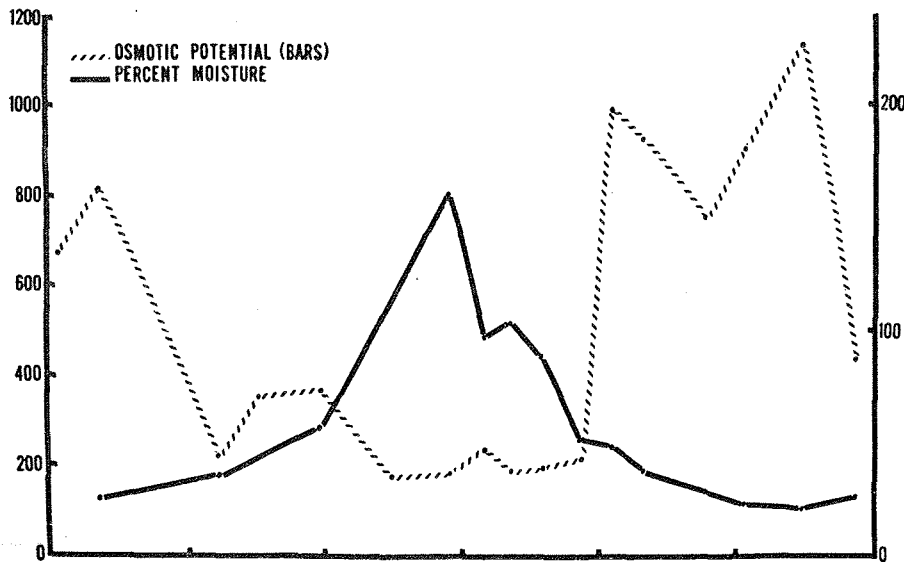
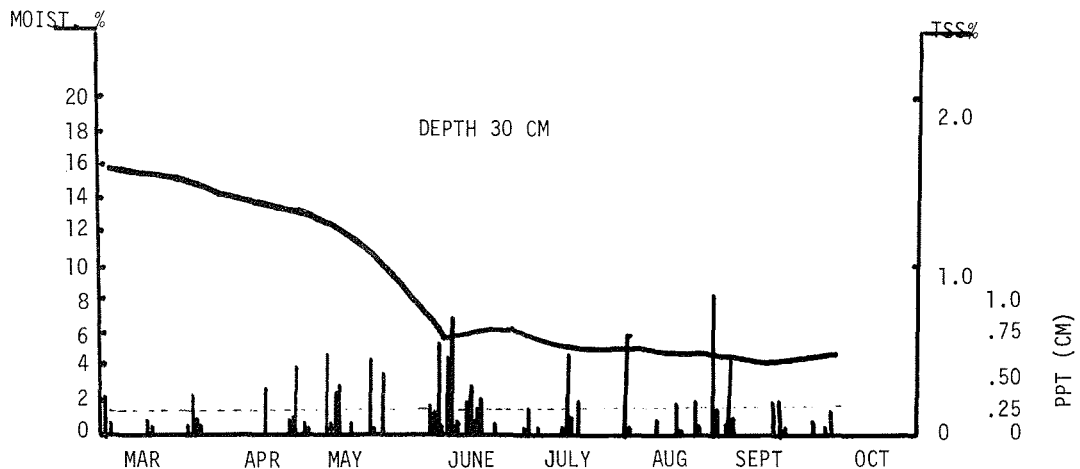
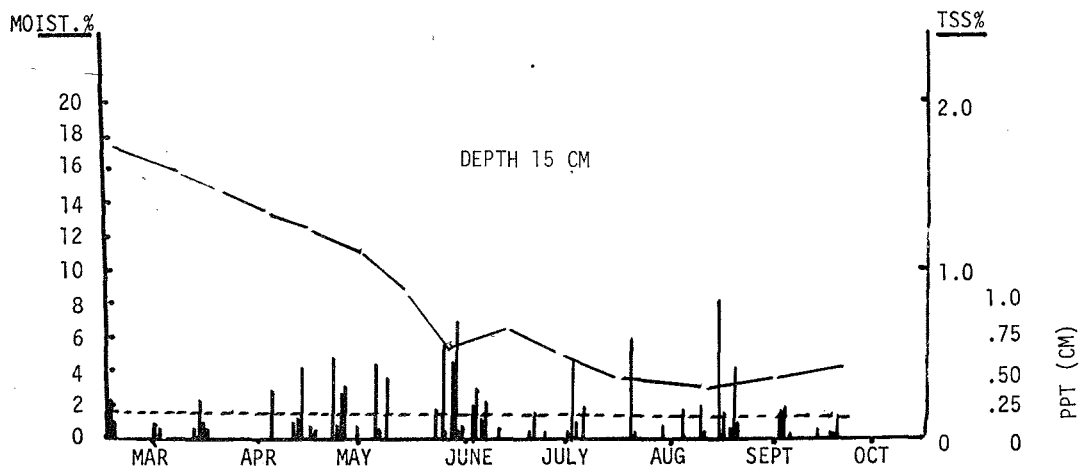
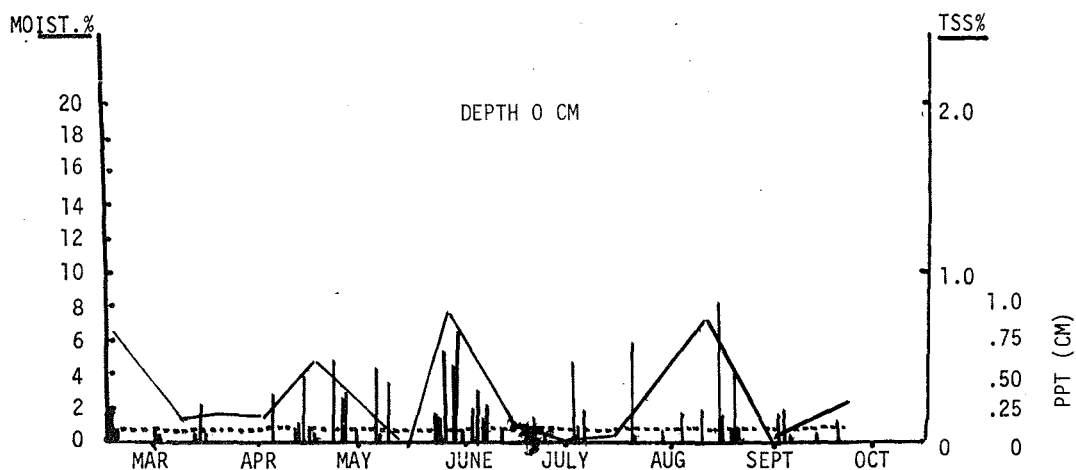


Figure 4. Leaf moisture content and osmotic potential throughout the season for *Eurotia lanata*.



Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued



Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

Figure 6. - continued

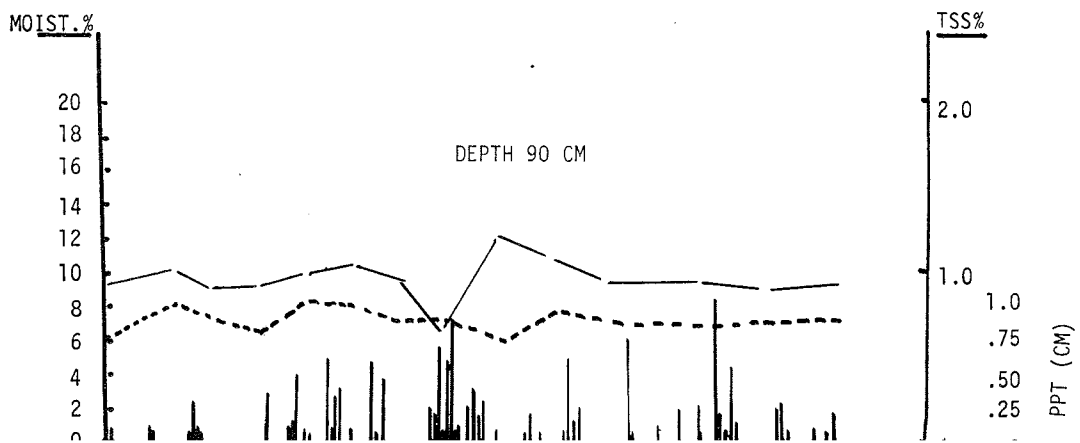
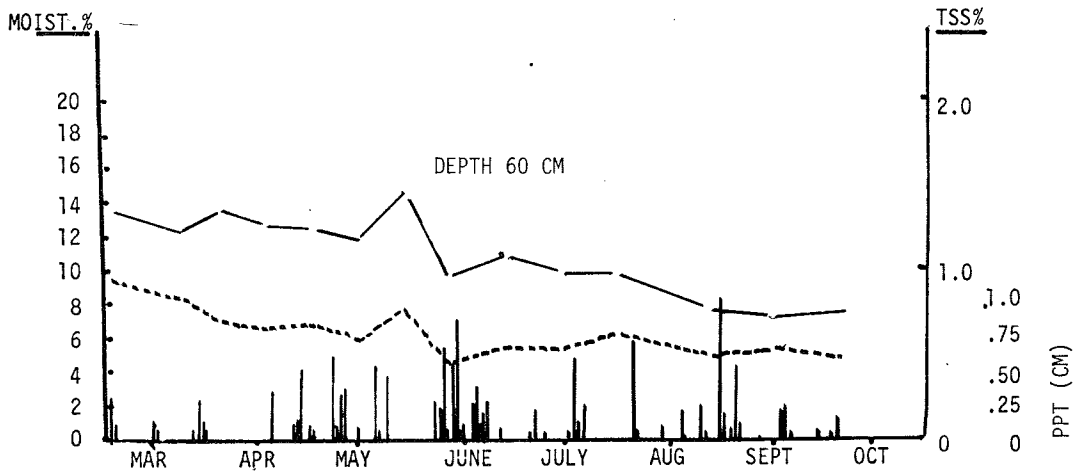
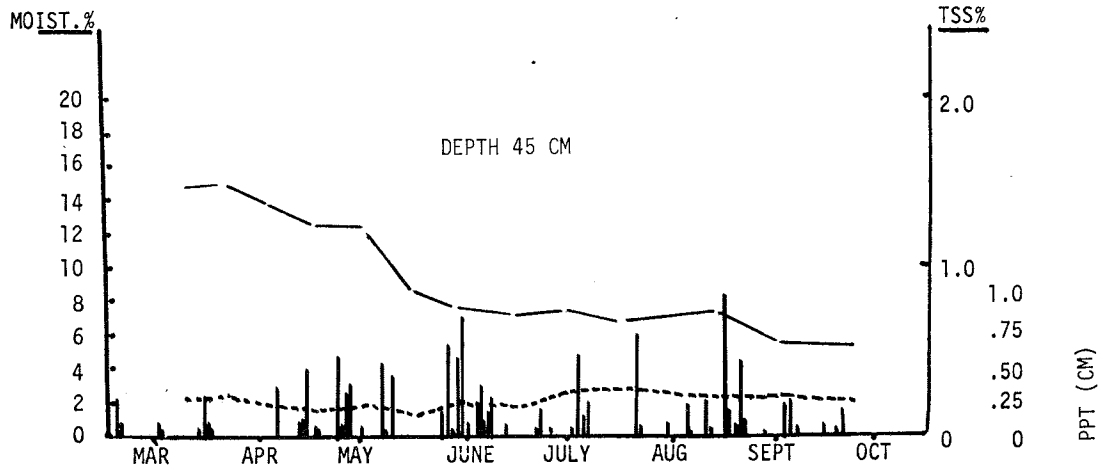


Figure 6. - continued

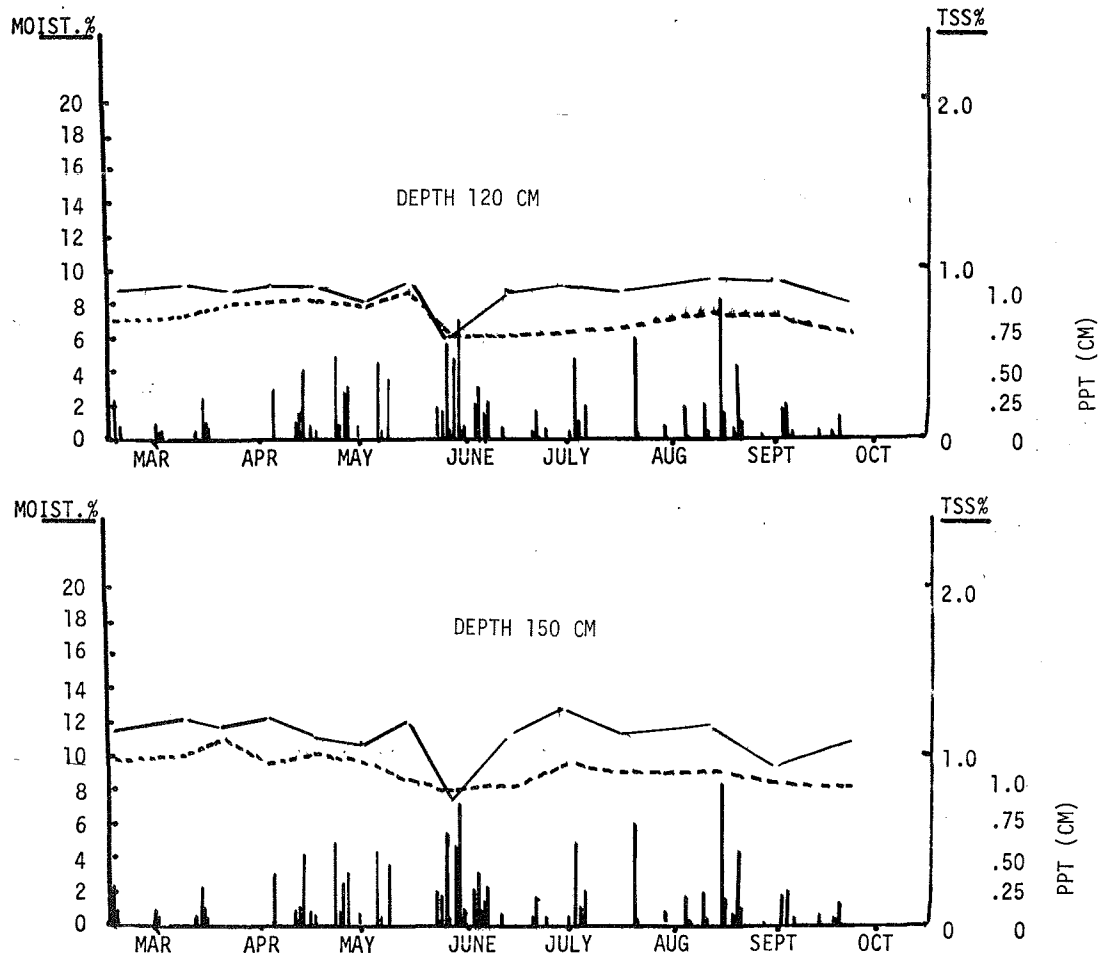


Table 1. *Atriplex confertifolia* and *Eurotia lanata* biomass estimates for various plant parts and litter, 1970.

ITEM	Depth - cm	<i>Atriplex</i> - Biomass Kg/ha.	<i>Eurotia</i> - Biomass Kg/ha.
<u>Shoots</u>	---	3,806	3,134
New growth	---	1,295	752
Old growth	---	2,511	2,382
TOTAL		<u>3,806</u>	<u>3,134</u>
<u>Roots</u>	0-30	13,838	10,193
	30-60	4,166	9,402
	60-90	1,367	4,166
TOTAL		<u>19,371</u>	<u>23,751</u>
<u>Litter</u>			
coarse		4,128	---
fine		2,636	5,256
TOTAL		<u>6,764</u>	<u>5,256</u>
PLANT COMMUNITY TOTAL		29,941	32,141

Autecological Studies of Atriplex confertifolia and Eurotia lanata Continued
 Table 2.

A. SHOOT MINERAL CONTENT (%)

	Na	K	Mn	Fe	Zn	Ca	Mg	Cu	P
<u>Shoot Mean</u>									
<u>Atriplex</u>	.739	1.055	.0139	.124	.0020	1.139	.233	.0021	.056
<u>Eurotia</u>	.071	.919	.0187	.324	.0028	1.774	.418	.0043	.057
<u>Distribution</u>									
old growth	.562	.887	.0140	.131	.0022	1.787	.317	.0021	.047
<u>Atriplex</u>									
new growth	.806	2.171	.0069	.060	.0027	3.099	.553	.0021	.054
old growth	.079	.658	.0188	.356	.0029	2.221	.355	.0019	.057
<u>Eurotia</u>									
new growth	.091	1.240	.0096	.205	.0027	1.948	.396	.0019	.057
<u>Seasonal Change</u>									
April	.656	.905	.0160	.1516	.0022	.779	.179	.0020	.060
May	.782	.970	.0139	.1417	.0021	.771	.186	.0017	.057
<u>Atriplex</u>									
June	.609	.950	.0160	.1467	.0021	.756	.179	.0018	.058
July	.808	1.288	.0120	.0885	.0020	1.675	.330	.0021	.063
Aug.	.841	1.161	.0116	.0903	.0017	1.704	.293	.0028	.043
April	.076	.895	.0215	.286	.0029	2.414	.513	.0031	.058
May	.092	1.131	.0186	.259	.0025	2.371	.469	.0038	.052
<u>Eurotia</u>									
June	.070	1.134	.0177	.274	.0024	2.014	.449	.0038	.051
July	.047	.735	.0184	.415	.0026	1.192	.401	.0051	.061
Aug.	.071	.690	.0174	.384	.0035	.880	.266	.0055	.063

Table 2. Continued

B. ROOT MINERAL CONTENT (%)

	Na	K	Mn	Fe	Zn	Ca	Mg	Cu	P
<u>Root Mean</u>									
<u>Atriplex</u>	.502	.650	.0150	.458	.0032	3.654	.558	.0045	.081
<u>Eurotia</u>	.296	.510	.0157	.379	.0035	5.113	.621	.0037	.075
<u>Distribution</u>									
1'	.426	.623	.0166	.415	.0033	3.156	.535	.0047	.073
2'	.500	.656	.0143	.464	.0032	3.328	.558	.0044	.083
<u>Atriplex</u>									
3'	.581	.671	.0142	.494	.0030	4.477	.580	.0044	.088
1'	.180	.501	.0186	.294	.0036	4.749	.500	.0038	.069
<u>Eurotia</u>									
2'	.349	.517	.0141	.413	.0035	5.289	.670	.0037	.075
3'	.360	.511	.0143	.429	.0035	5.300	.692	.0037	.081
<u>Seasonal Change</u>									
May	.390	.527	.0155	.375	.0031	2.826	.343	.0044	.080
<u>Atriplex</u>									
Aug.	.614	.773	.0185	.540	.0032	4.316	.771	.0046	.080
May	.180	.457	.0157	.343	.0030	5.132	.589	.0037	.074
<u>Eurotia</u>									
July	.413	.562	.0156	.414	.0040	4.086	.652	.0037	.075

C. LITTER MINERAL CONTENT (%)

	Na	K	Mn	Fe	Zn	Ca	Mg	Cu	P
<i>Atriplex</i> coarse (July only)	.210	.379	.0160	.126	.0020	1.671	.238	.0023	.047
<i>Atriplex</i> fine (July only)	.178	.296	.0167	.152	.0023	1.568	.257	.0022	.076
<i>Eurotia</i> (July only) total	.058	.426	.0220	.247	.0031	1.462	.308	.0042	.045
<u>Seasonal Change</u>									
<i>Atriplex</i> (coarse fraction only)									
April	.194	.375	.0181	.132	.0024	1.482	.276	.0025	.043
May	.214	.393	.0156	.111	.0021	1.526	.277	.0022	.051
June	.193	.357	.0184	.123	.0019	1.606	.250	.0024	.045
July	.210	.379	.0160	.126	.0020	1.671	.238	.0023	.047
August	.165	.289	.0149	.144	.0019	1.650	.230	.0023	.045
<i>Eurotia</i> (total)									
April	.048	.351	.0191	.221	.0030	1.524	.261	.0031	.062
May	.054	.354	.0185	.214	.0031	1.574	.267	.0030	.061
June	.054	.433	.0198	.230	.0029	1.340	.249	.0032	.046
July	.058	.426	.0220	.247	.0031	1.462	.308	.0042	.045
August	.036	.403	.0175	.352	.0033	1.763	.347	.0035	.068

Eurotia litter contained more Mn, Mg, Fe, Zn and Cu, and almost as much Ca as *Atriplex* litter. Only in Na and P did *Atriplex* litter exceed *Eurotia* litter (Table 2 C). The nutrient concentration in litter under *Eurotia* apparently reached a maximum in July or August, while the seasonal pattern of change was less marked in *Atriplex*; some nutrients in *Atriplex* reaching peaks in July and August, but others (e.g. Zn and Cu) scarcely changing (Table 2 C).

Subsidiary Projects: Growth and Nutrient Response in Species and Ecotypes

Since one of the objectives of the I.B.P. Desert Program is to predict the effects of perturbations of the system, it was considered necessary to supplement the biomass and nutrient inventory with an investigation of plant response to environmental changes. As a first step, the effects of varying temperature, moisture and nitrogen supply have been studied, using leaf growth rate to measure response. *Atriplex confertifolia* and *Eurotia lanata* were used in this work. The growth rates of different populations of these species and of *A. nuttallii* have also been compared but, as yet, only in one environmental condition.

Effects of varying temperature and water supply on *Atriplex* and *Eurotia* -- Over a three week period in October and November, 1970, plants of the two species were given a) either 0.15 mM or 16.5 mM NaNO₃ twice weekly b) either a mean temperature of 2°C (outdoors) or 27°C (temperature controlled glasshouse) c) either water to field capacity once weekly or seven times weekly. Relative leaf growth rates were calculated, as a non-destructive measure of shoot growth, by the formula

$$\bar{R}_L = \frac{\text{Loge } L_2 - \text{Loge } L_1}{t_2 - t_1}$$

where \bar{R}_L = Relative leaf growth rate; L_1 and L_2 are leaf areas, at times t_1 and t_2 respectively. The leaf areas were measured by rating, using Xerox leaf images.

Effects of treatments on the two species (Fig. 7) show that neither water nor nitrogen increase stimulated growth at low temperature. In hot, but dry conditions, nitrogen increased growth somewhat, particularly in *Atriplex*. Without nitrogen, relative leaf growth rate was small in both species even in hot and wet conditions. The greatest growth response to nitrogen occurred in hot and wet conditions. *Atriplex* was more responsive than *Eurotia* to each factor (Fig. 7).

Population differences: Samples of each of six mature plants were taken along two transects in Curlew Valley, potted at least 6 weeks before the experiments began, and maintained in a glasshouse at 27°C, with daily watering, and basic nutrients plus 16.5mM NaNO₃.

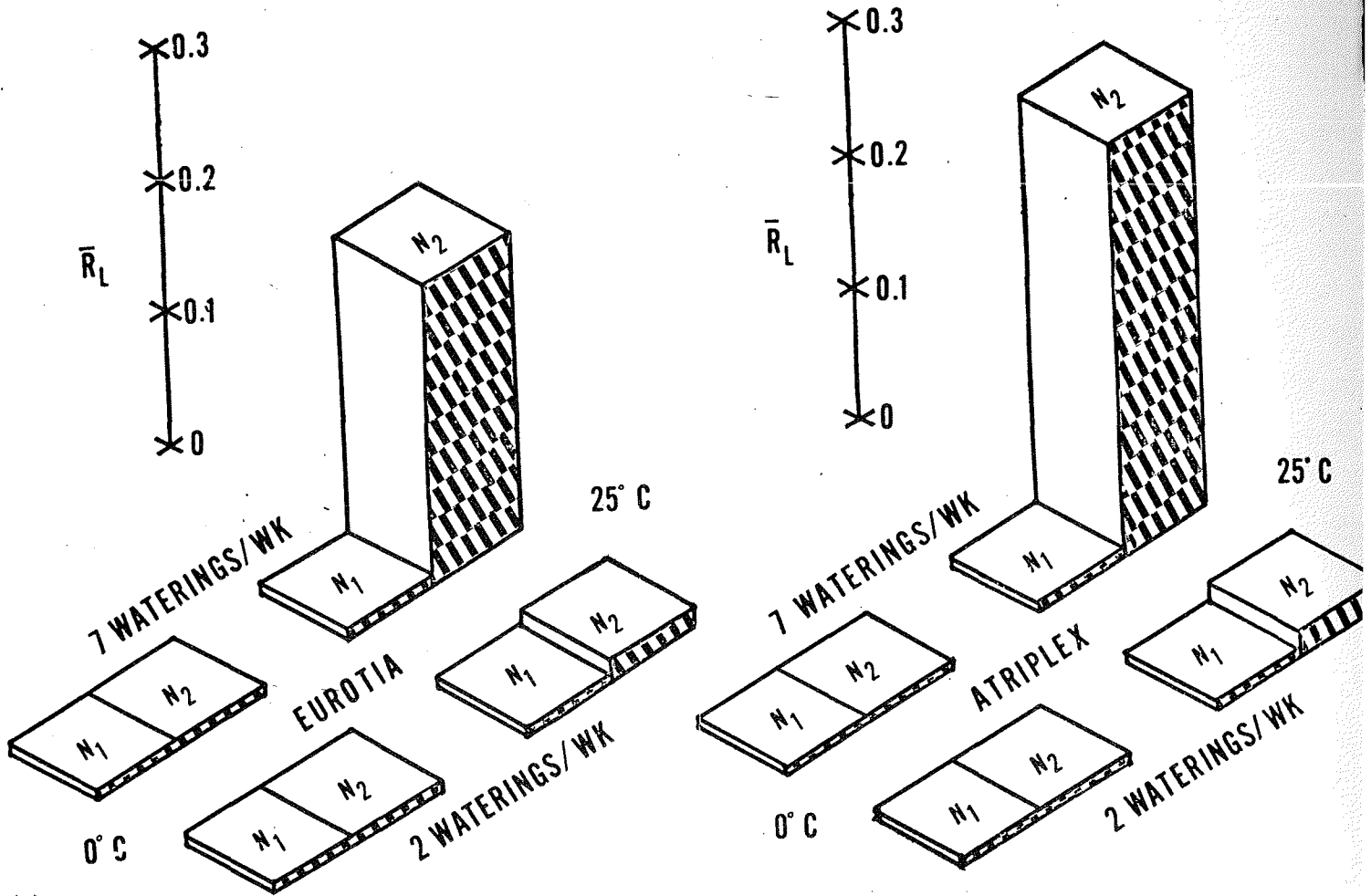


Fig. 7. Relative leaf growth rate of *Atriplex confertifolia* and *Eurotia lanata* in different environments.

(a) Four sites were sampled for *Atriplex confertifolia* and for *Eurotia lanata* on a W-E transect, at the following points (W of Valley): (i) "pure stands" of *Atriplex* and *Eurotia*, (ii) a "mixed plot" of *Atriplex* and *Eurotia*, (iii) an area of mainly *Atriplex nuttallii* subsp. *falcata*, (iv) a "grass plot" (E of Valley). The locations are shown on the map (Fig. 8).

(b) Four sites were sampled for *Atriplex nuttallii* on a N-S transect at the following points (N of Valley): (i) the area of *A. nuttallii* subsp. *falcata* sampled in the W-E transect, (ii) near the ranch house on the Kelton road, (iii) at Kelton, (iv) on the edge of the Great Salt Lake (Fig. 8). A sample was also taken (v) in a grazed, fenced field near the Logan City airport.

Relative leaf growth rates were calculated (as above), and sample new shoot dry weights (either half plant weights, or 150 shoot weights) were taken (Table 3). Owing to the differences in plant size (and hence shoot number), dry weights were expressed as mean dry weight per shoot (in mg).

In the W-E transect, relative leaf growth rate and dry weight were less in *Atriplex* plants from pure stands than in *Atriplex* from other sites. Conversely, pure stand *Eurotia* slightly out-yielded *Eurotia* from other sites. The pure stand *Atriplex* was found in an area which (for this transect) had a high conductivity (Table 3).

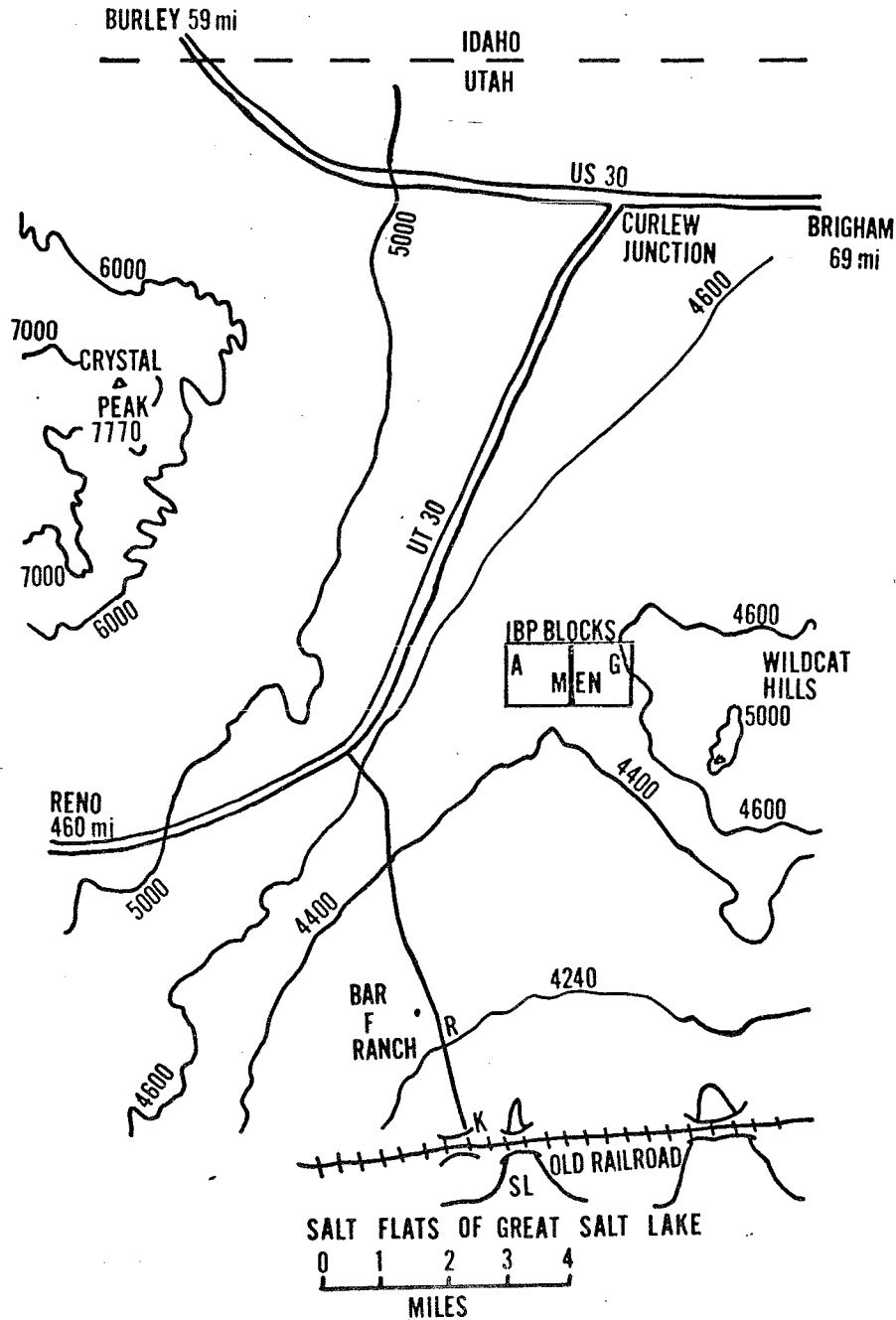


Figure 8. SKETCH MAP OF CURLEW VALLEY SHOWING PLANT SAMPLING POINTS

A pure *Atriplex Confertifolia*
 M mixed *Atriplex/Eurotia*
 E pure *Eurotia*
 N *Atriplex nuttallii*
 Subsp. *fulcata*

R "RANCH" SITE *A. nuttallii*
 Subsp. *gardneri*
 K "Kelton" SITE *A. nuttallii*
 Subsp. *gardneri*
 SL "Salt Lake" SITE *A. nuttallii*
 Subsp. *gardneri*

Table 3. Population Differences -- Mean RLGR and Dry wt/shoot.

A. W-E Transect						
Site	Soil Conductivity	Growth of <u>Atriplex</u>		Soil Conductivity	Growth of <u>Eurotia</u>	
	m mhos	dw mg	RLGR (\bar{R}_L)	m mhos	dw mg	RLGR (\bar{R}_L)
Pure Stand	10.00	7.8	0.15	0.80	16.4	0.35
Mixed Plot	0.80	12.2	0.35	0.80	15.8	0.24
Nuttall Site	1.43	15.7	0.38	1.43	16.2	0.15
Grass Plot	1.00	11.6	0.38	1.00	16.3	0.18
Standard Error		1.8	0.10		3.4	0.08

B. N-S Transect				
Site	Conductivity m mhos	<u>A. nutallii</u>		Sub species identity
		dw mg	RLGR	
Nuttall Site	1.43	9.7	0.39	(probably subsp <u>falcata</u>)
Ranch house	5.20	14.8	0.60	(probably subsp <u>gardneri</u>)
Kelton	96.00	15.4	0.60	(probably subsp <u>gardneri</u>)
Great Salt Lake	121.00	13.4	0.42	(probably subsp <u>gardneri</u>)
Logan City Airport	17.5	20.0	0.52	(probably subsp <u>gardneri</u>)
Standard Error		3.2	0.06	

In the N-S transect, A. nutallii subsp. falcata yielded less than the other subspecies (gardneri). The yield of the Great Salt Lake population was less than that of the other populations of subsp. gardneri. The Logan population was heavily grazed, and may have a dwarfed habit as a result of selection (Table 3).

Discussion

Gas Exchange and Micrometeorological Studies

Although the data analysis of the gas exchange and micrometeorological studies are incomplete at this time because of the aforementioned budgetary limitations, our data do suggest that these two cold desert shrub species exhibit a surprisingly great degree of phenotypic plasticity. The photosynthetic response to temperature has been demonstrated to vary with temperature pretreatment in a number of species (Semikhatova, 1960; Mooney and West, 1964; Strain and Chase, 1966; Mooney and Shropshire, 1967; and Strain, 1969). The degree of plasticity exhibited by these two cold desert species far exceeds the range of change demonstrated in the earlier literature. This substantial degree of phenotypic plasticity is of utmost importance in building a realistic model of primary productivity for the cold desert ecosystem. It would not be unreasonable to assume that differences in photosynthetic rates of individuals of the same species would be much more variable at different times of the year than between different ecotypes of the same species. That is, phenotypic plasticity is probably far more important than ecotypic differences.

Once statistical analyses of these data have been completed, relationships of photosynthesis and transpiration as functions of leaf temperature, irradiation intensity, and moisture stress will be available for each phenological stage of both species.

Composite trends of the moisture stress of each species as measured by the pressure bomb are shown in Figure 3. Water stress was minimal in both species in a period from mid-April to mid-June. Values during this period were only -10 to -20 atm. Maximal stresses were reached in mid-August when values of

Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

-75 to -85 atm were reached. Both species exhibited remarkably similar curves. These trends in plant moisture stress reflect soil moisture depletion in the 15 to 60 cm zone in the soil profile (see Fig. 6). Plant water stress values also rather closely reflected precipitation levels (see Fig 6). Although soil moisture at the soil surface closely paralleled precipitation patterns, soil moisture in the primary rooting zone was relatively unaffected by precipitation during the period from March until September. Within the rooting zone, soil moisture decreased from about 15% moisture in March to a stable level of 4% at 15 cm to 8% at 60 cm. This low level was maintained from mid-June until September. The apparent correspondence between precipitation and plant water stress is probably due to reduced transpirational losses during periods of precipitation rather than due to any immediate change in soil moisture per se.

Total soluble salts were also followed at each depth in the soil throughout the season (Fig. 6). Salt concentration increases with depth in the soil but does not vary throughout the season. Soil water potentials at each depth closely reflect soil moisture content and soluble salt concentrations.

The moisture content of the leaves of both species reached a peak in late May (275% of dry weight for *Eurotia lanata* and 800% for *Atriplex confertifolia*) and decreased rapidly thereafter (see Fig. 4 and 5). These percentages reached rather stable levels by early August (50% for *Eurotia lanata* and about 100% for *Atriplex confertifolia*). The osmotic potential of *Eurotia lanata* leaves approached a level of -35 to -45 atm. Measurements after July 1 were seriously confounded by external salt accumulations on the leaves (see Fig. 5).

Nutrients and Biomass

The plant community biomass for *Atriplex* (29,941 Kg/ha) and *Eurotia* (32,141 Kg/ha) were remarkably similar. The main differences between the *Atriplex* and *Eurotia* communities (Table 1) appear to be caused by the woody nature of *Atriplex*. The new growth in *Atriplex* is supported on old woody material, while that of *Eurotia* is virtually from the base of the plant. The rooting habit also differs (Table 1). *Atriplex* has almost a surface rooting habit (0-30 cm), while in *Eurotia*, an equal amount of root material is found at 30-60 cm depth. The woodiness and surface rooting of *Atriplex* clearly separate it environmentally from *Eurotia*; and particularly in times of drought, snowfall and other adverse conditions. The woody, spiny nature of *Atriplex* obviously also increases its persistence under grazing, compared with *Eurotia*.

Another important difference between the species is in their shoot sodium content (Table 2 A). The large sodium content of *Atriplex* shoots compared with *Eurotia* may imply that it is more tolerant of salinity, but alternatively, it may show that *Eurotia* can more effectively exclude sodium from its metabolism. Add to this the large content of other nutrients in *Eurotia*, and the difference is a most important one, making *Eurotia* more important from a nutritional standpoint, as well as easier to graze through its lack of spines.

The observation that new growth exceeds old growth in Na, K and Mg shows that these nutrients are labile within both species (Table 2 A). This is important in making the greatest use of nutrients in relatively short supply (e.g. K) compared with Na. It is physiologically interesting that the two plants differ in calcium distribution between old and new growth, since calcium metabolism has recently been linked with salinity tolerance (Epstein and La Haye, 1969). Presumably the plants differ in their Ca:Na ratios and in their tolerance mechanisms. The large amount of calcium in the new growth of *Atriplex* may mean that it is an important source of this nutrient, if it is available to the grazing animal; or alternatively, if it is deposited immediately in coarse spicules, it would be both unavailable and unpalatable. This point would seem to be worth further investigation.

Seasonal change in nutrient content is presumably related to water availability. Accumulation occurs in July and August when water stress is probably greater than earlier in the year (Table 2 A).

One complication in interpreting these analyses is the use of a steel mill, which may have contributed to the contents of iron and manganese in the samples, which were highly lignified, calcified, and presumably siliceous. While abrasion of the mill may have contributed somewhat to apparent variation in stem iron content, a greater contamination of iron seems to have occurred in the roots (Table 2 B) where very large apparent iron contents were found. Whether this iron was on the root surface, or contained within the roots, is debatable.

Phosphorus contents of shoots (Table 2 A) and roots (Table 2 B) were low, and this observation needs further investigation, whether this is an artifact of analysis (by absorption or interference), whether the plants have low P requirements, or whether P is in limited supply in the soil.

The growth and nutrient response studies (Fig. 7; Table 3) show that *Atriplex confertifolia* is more responsive to environmental conditions of water, temperature and nitrogen supply than is *Eurotia*. This is important if perturbations of the system are being considered, as changes in the environment would seem likely to alter the balance between *Atriplex* and *Eurotia*.

Atriplex confertifolia shows more differentiation between populations than does *Eurotia*; and *A. confertifolia* apparently grows on soil with a wide range of conductivity (Table 3). For these reasons also, *Atriplex* is potentially more successful than *Eurotia*, and is able to fit into a wide range of environments either by acclimation or genetic variability.

Autecological Studies of *Atriplex confertifolia* and *Eurotia lanata* - continued

By all the criteria used here it seems that *A. confertifolia*, *E. lanata* and also *A. nuttallii* are highly adapted halophytes, differing in their means of survival (for example, *Eurotia* by resisting salt uptake, *Atriplex* by accumulating salt). All in all, the spiny, tolerant species *A. confertifolia*, and probably even more so, *A. nuttallii* subsp. *gardneri*, which seems very variable genetically (Table 3), are better able to survive in extreme environmental conditions of drought and salinity, than is *Eurotia lanata*.

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