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Gas Exchange of Great Basin Shrubs

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RESEARCH MEMORANDUM

RM 72-20

GAS EXCHANGE OF GREAT BASIN SHRUBS

M. M. Caldwell, R. T. Moore,
R. S. White, and E. J. DePuit



DESERT BIOME
U.S. INTERNATIONAL BIOLOGICAL PROGRAM

1971 PROGRESS REPORT

GAS EXCHANGE OF GREAT BASIN SHRUBS

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APRIL 1972

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ABSTRACT

Photosynthesis, transpiration and dark respiration were measured in the field in relation to leaf temperature, soil water potential, plant moisture stress, soil temperature, and irradiation intensity. In response to ambient environmental conditions, *Eurotia lanata*, a species possessing the C₃ photosynthetic pathway, exhibited maximum gas exchange rates during the spring months (April-May). By early August net photosynthetic activity was curtailed and transpiration rates also greatly depressed. For *Atriplex confertifolia*, a plant possessing the C₄ photosynthetic pathway, photosynthetic and transpiration rates were also at their highest levels in April and May. However, positive net photosynthesis and transpiration were maintained well into October. *Atriplex confertifolia* possessed a more favorable water use efficiency for photosynthesis under all environmental conditions in the field.

Positive net photosynthesis and transpiration activity were exhibited by both species under water stress conditions exceeding those found in the field.

Gas exchange capacity determinations were carried out for these species under predetermined environmental conditions at several times throughout the season. Transpiration and net photosynthetic activity varied greatly with phenological status and environmental history of these species. The implications of these changes in gas exchange capacity for the Desert Biome modelling effort are discussed. *Atriplex confertifolia* exhibited a much greater degree of photosynthetic acclimation as a function of leaf temperature during the season when compared to *Eurotia lanata*. On the other hand, dark respiration acclimation was much greater for *Eurotia* than for *Atriplex*.

Preliminary analysis of extensive gas exchange measurements for *Artemisia tridentata* indicate patterns of photosynthesis and transpiration similar to those found for *Atriplex* and *Eurotia*. Gas exchange capacity of this species is somewhat intermediate in acclimation potential to that of *Atriplex* and *Eurotia*.

INTRODUCTION

This process study in 1971 was a continuation from the 1970 project. Gas exchange of Great Basin shrubs in relation to relevant environmental parameters have been extensively studied in order to provide basic data for the primary productivity modelling effort of the Desert Biome. Results of this project should be correlative with studies by Dr. Neil West on growth, phenological progression and nutrient cycling in Great Basin shrub ecosystems, and the gas exchange and biomass studies of *Sitanion hystrix* by Drs. M. Hironaka and E. Tisdale.

This report includes the analysis of extensive gas exchange data collected in 1970 for *Atriplex confertifolia* and *Eurotia lanata*, with interpretive discussion of these results in the light of the Biome modelling effort. In addition, this report also contains preliminary results of gas exchange data collected for *Artemisia tridentata* during 1971.

OBJECTIVES

General goals of this project were: to relate plant gas exchange rates to plant water, status and phenology and to relevant environmental parameters in order to construct models of primary productivity and water use.

During 1971 our specific objectives were:

1. To reduce and analyze the extensive gas exchange data collected during 1970 for *Atriplex confertifolia* and *Eurotia lanata*. Budgetary limitations during 1970 prohibited these analyses during that year.
2. To carry out extensive gas exchange determinations for *Artemisia tridentata* and to initiate analysis of these data.

METHODS

Gas exchange determinations for *Atriplex confertifolia* and *Eurotia lanata* in 1970 were carried out in a mixed community of these two species in Curlew Valley, Utah. Studies during 1971 on *Artemisia tridentata* were carried out in Cache Valley near Logan, Utah. Instrumentation and methodology employed in these studies were described in detail in the 1970 progress report for the Desert Biome.

Methods as stated in the appropriate informative abstracts with appropriate DSCODES are as follows:

During 1971 and 1972, dark respiration and transpiration of *Atriplex confertifolia* and *Eurotia lanata* were measured in the field and under controlled conditions in relation to pertinent micrometeorological parameters such as solar radiation, soil and plant water potentials, and ambient vapour pressure deficit.

Air temperature was measured by a resistance thermometer, humidity with lithium chloride dew point sensors, irradiation with an Eppley pyranometer, leaf temperatures with fine wire thermocouples and a Barnes radiation thermometer, plant water stress with a pressure bomb, and leaf area with a photoelectric planimeter. The field data of the preceding parameters are stored under DSCODE A3UCB01. Soil temperatures were recorded with thermocouples and a Moeller distance thermograph (DSCODE A3UCB09), and soil water potentials with a soil psychrometer (DSCODE A3UCB10). Sampling was carried out continuously throughout the growing season.

The shoots of individual shrubs in the field were enclosed in a Siemens gas exchange chamber for gas exchange measurements following monitored ambient conditions (DSCODE A3UCB06 and CB07), and in the laboratory under constant environmental conditions while varying only 1 factor such as irradiation, temperature or humidity (DSCODE A3UCB15 and CB16). A randomized block design was used to select plants.

Potted plants of both species were used to determine plant gas exchange as a function of soil moisture depletion. Plant phenology was recorded, and leaf areas and dry weights of shoots were also sampled.

Photosynthesis and respiration of *Artemisia tridentata* were measured every month during spring and summer, 1971, under both field (DSCODES A3UCB43 and CB44) and controlled (DSCODE A3UCB41) conditions.

In the field, soil and leaf temperatures (using thermocouples) were recorded, along with ambient temperature (platinum wire thermometer) and humidity (Lithium chloride sensor), and solar radiation (with an Eppley pyranometer for the site and a silica cell within the gas analysis chamber). Phenology was monitored, and plant water stress monitored with a Scholander pressure bomb. Leaf areas and leaf weights were also measured.

The same parameters, excluding soil temperature, were measured under controlled conditions while varying only 1 factor, such as temperature or humidity.

For both field and laboratory experiments, plant foliage was measured at random.

FINDINGS

Precipitation patterns in Curlew Valley are illustrated in Fig. 1 for 1969 and 1970 and contrasted with the 10-year average (Fears, 1966) for the same area.

The progression of soil temperatures at several depths (DSCODE CB09), plant moisture stress as determined by a pressure bomb (DSCODE CB01) for *Atriplex confertifolia* and *Eurotia lanata*, and soil water potentials (DSCODE CB10) at several depths are illustrated in Fig. 2 for 1970. Precipitation for the same period is also included in this graph. The diurnal variation in plant moisture stress and soil temperatures are illustrated in Fig. 3. Detailed data on soil moisture content and soil salinity at several depths for 1970 were included in the 1970 progress report. The progression of leaf osmotic potential and leaf moisture contents for *Atriplex confertifolia* and *Eurotia lanata* are represented in Fig. 4 for 1970.

Throughout the 1970 field season, a series of simultaneous photosynthesis and transpiration measurements were conducted for *Atriplex confertifolia* and *Eurotia lanata* with the gas exchange chambers programmed to follow ambient environmental conditions (DSCODES CB06 and CB07).

Representative curves for plants for both species at several times during the season were selected and are represented in Fig. 5 to 18. Relevant leaf temperatures, irradiation intensities and in most cases vapor pressure deficit values are included in these figures (DSCODE CB01). Plant water stress and phenological status are given for each plant in the figure legends.

Gas exchange rates in most figures of this report are represented on a leaf dry weight basis. Gas exchange rates on a leaf area basis are also available and may be found in the appropriate data sets.

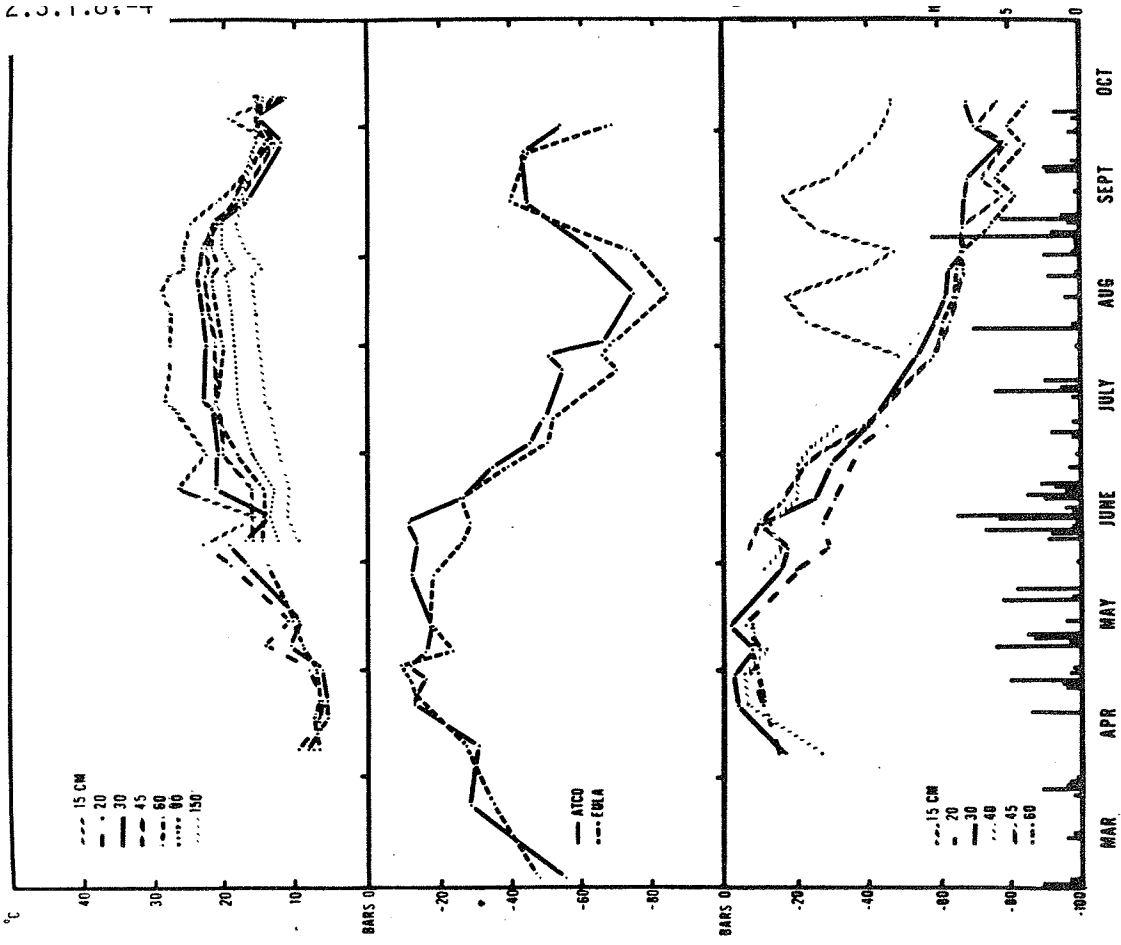


Figure 2. Soil temperatures at several depths, plant moisture stress of *A. confertifolia* and *E. lanata*, and soil water potential at several depths throughout the growing season at Curlew Valley. Precipitation for the same period is shown on the graph of soil water potential.

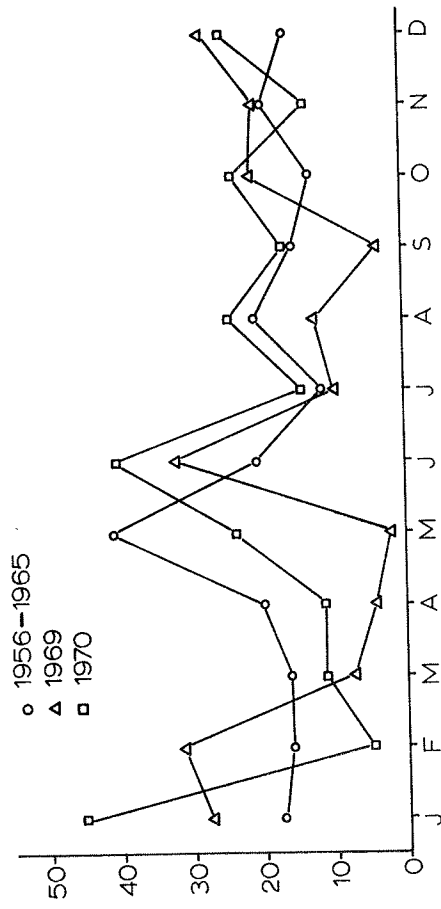


Figure 1. Monthly precipitation averages for Curlew Valley. Total yearly averages: 1956-65 = 230 mm, 1969 = 203 mm, 1970 = 257 mm.

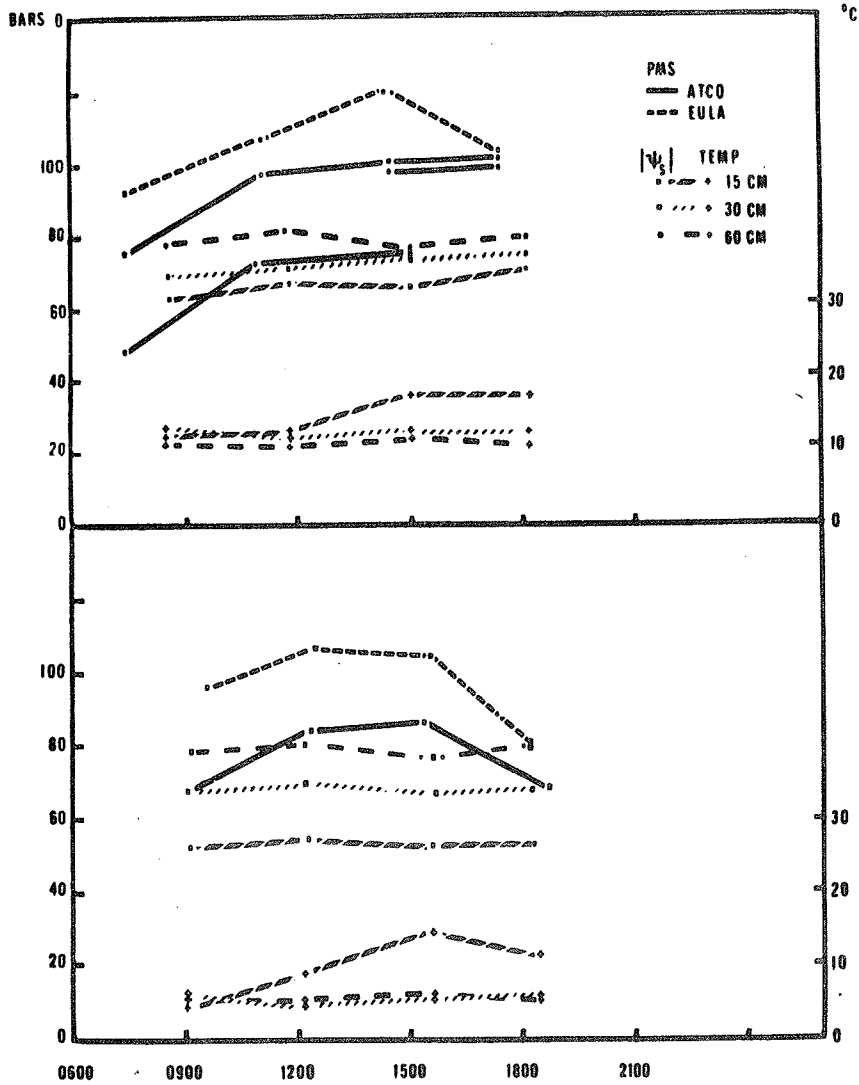


Figure 3. Typical diurnal variations in plant moisture stress, soil moisture potentials (absolute values) and soil temperatures at three depths.

2.3.1.8.-6

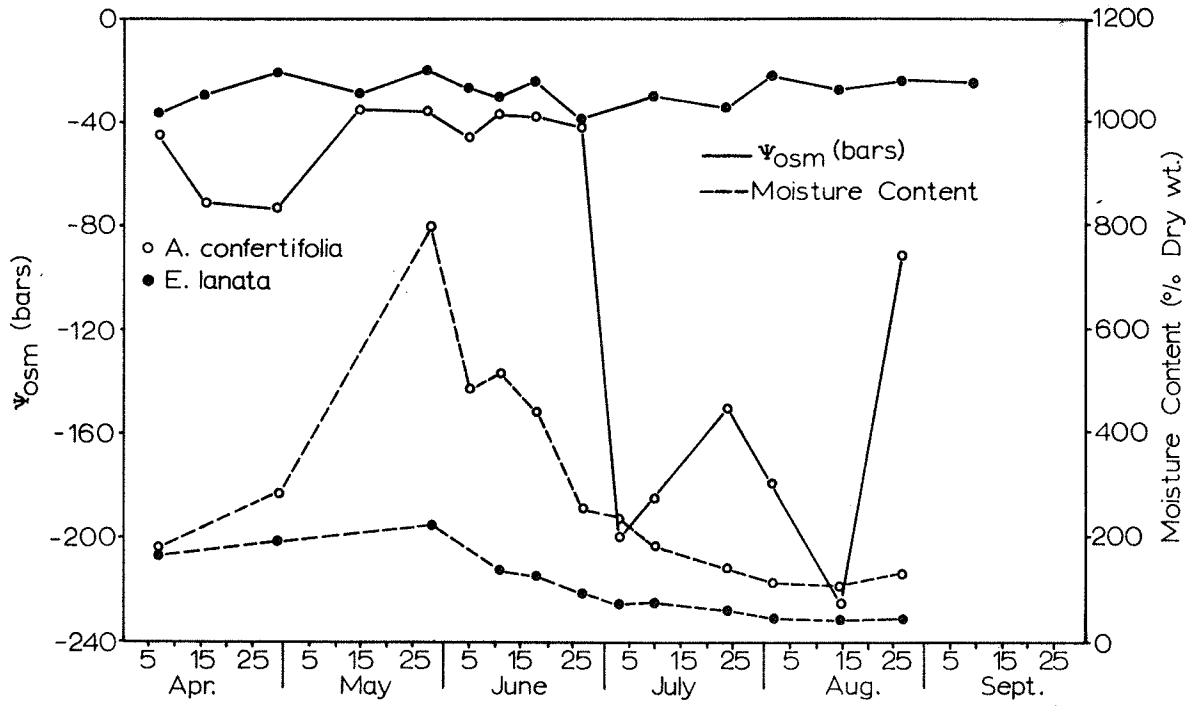


Figure 4. Seasonal progression of leaf moisture contents and osmotic potentials for *Atriplex confertifolia* and *Eurotia lanata*.

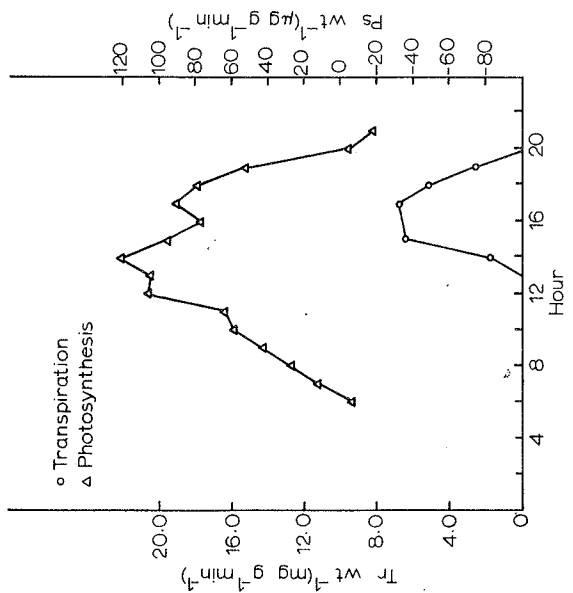
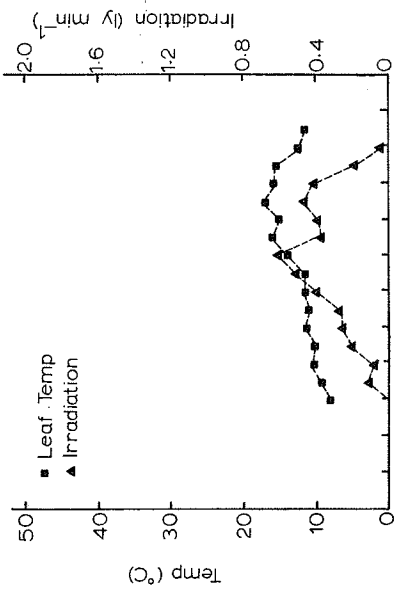


Figure 5. Transpiration and photosynthesis of a typical *A. confertifolia* plant on April 17 in relation to environmental conditions. P.M.S. - 23 bars; Phen -1.3.

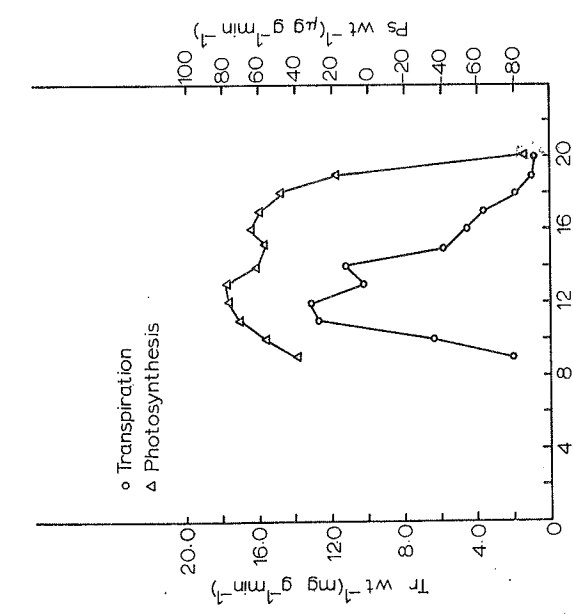
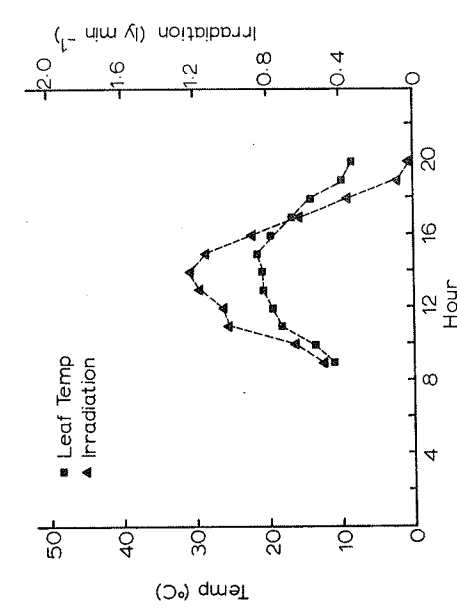


Figure 6. Transpiration and photosynthesis of a typical *A. confertifolia* plant on May 21 in relation to environmental conditions. P.M.S. - 23 bars; Phen -4.3.

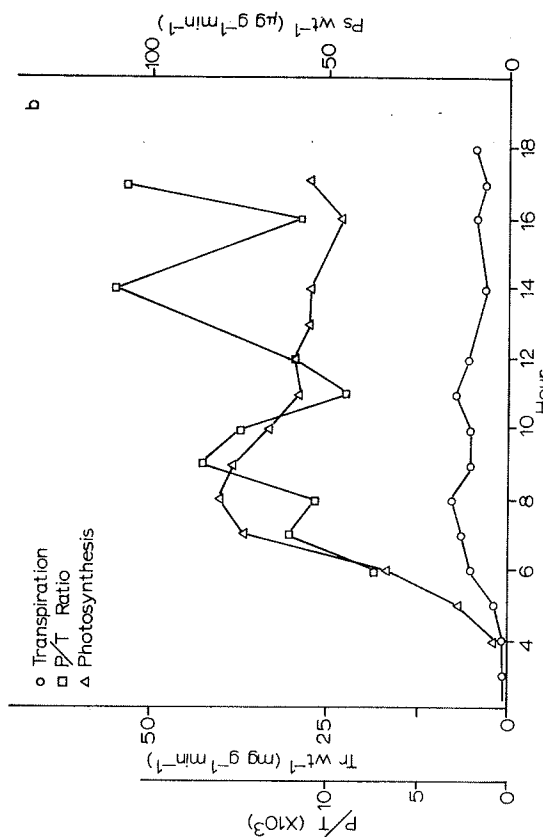
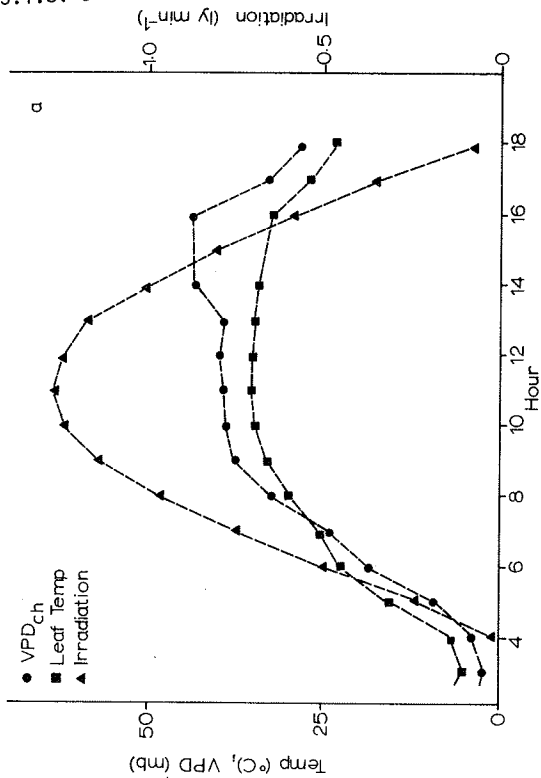


Figure 8. Transpiration and photosynthesis of a typical *A. confertifolia* plant on July 1 in relation to environmental conditions. P.M.S. - bars; Phen. -7.0.

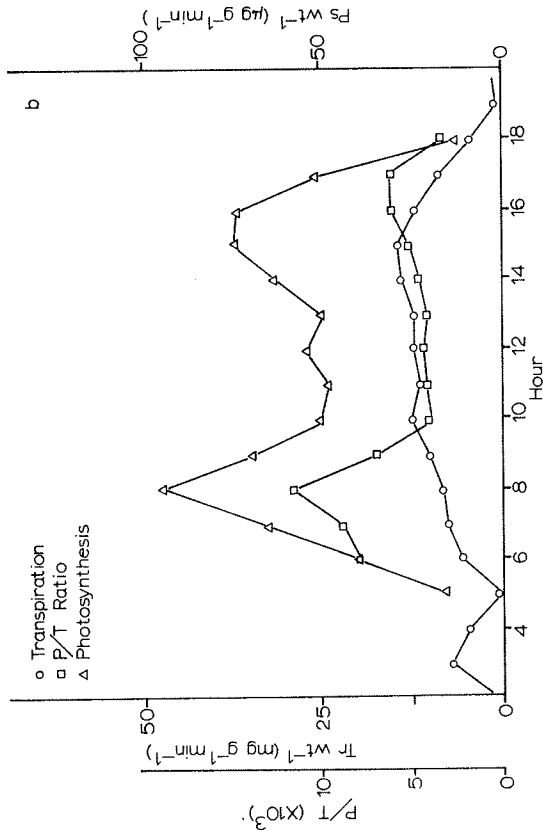
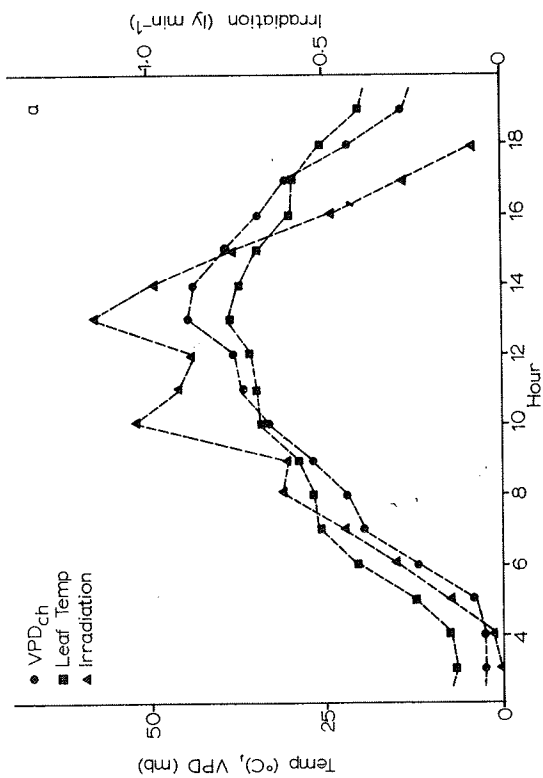


Figure 7. Transpiration and photosynthesis of a typical *A. confertifolia* plant on June 19 in relation to environmental conditions. P.M.S. - 38 bars; Phen. -6.2.

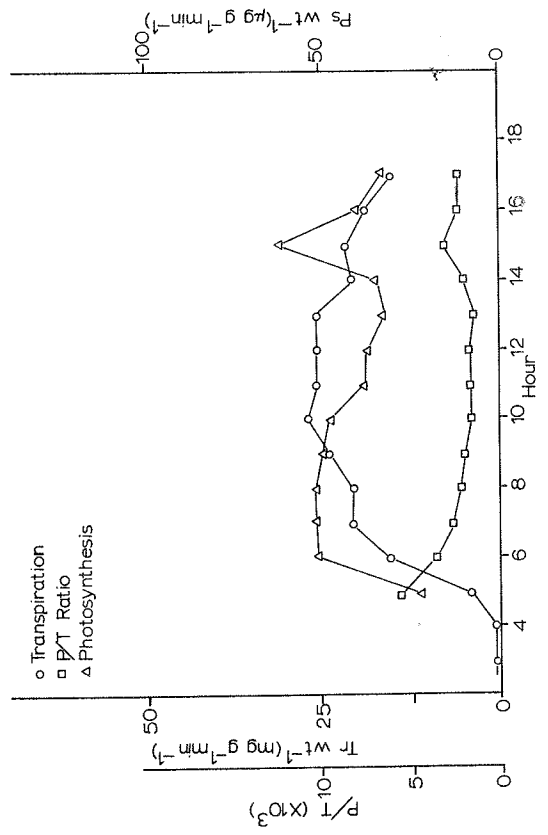
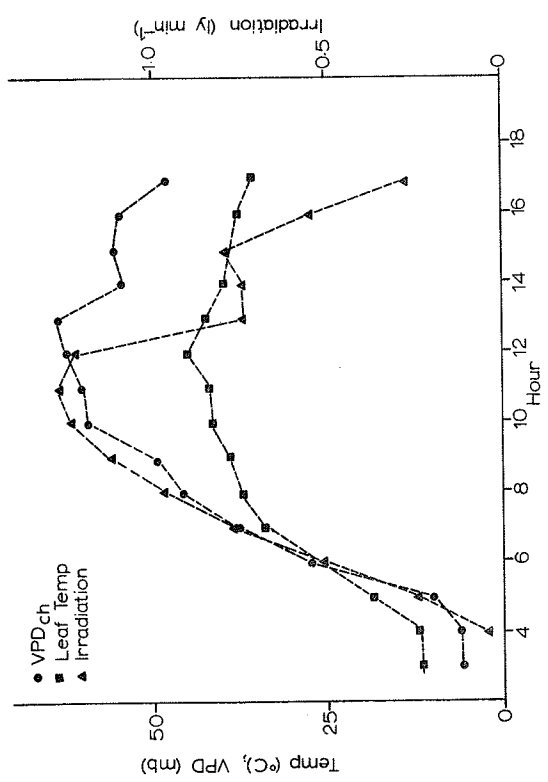


Figure 9. Transpiration and photosynthesis of a typical *A. confertifolia* plant on July 8 in relation to environmental conditions. P.M.S. - 44 bars; Phen -7.3.

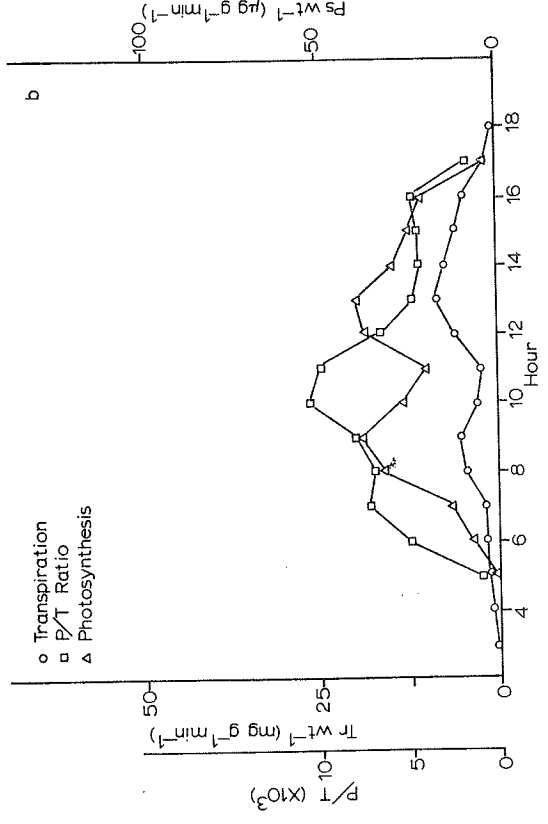
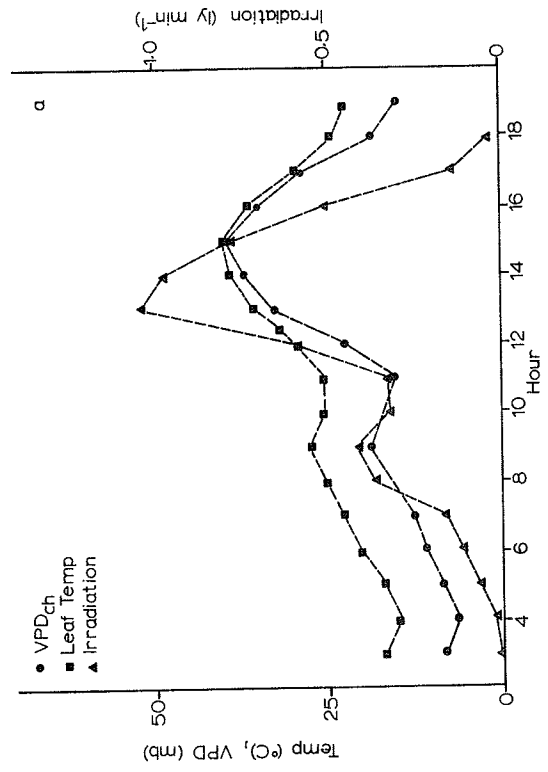


Figure 10. Transpiration and photosynthesis of a typical *A. confertifolia* plant on July 27 in relation to environmental conditions. P.M.S. -65 bars; Phen. -7.6.

2.3.1.8.-10

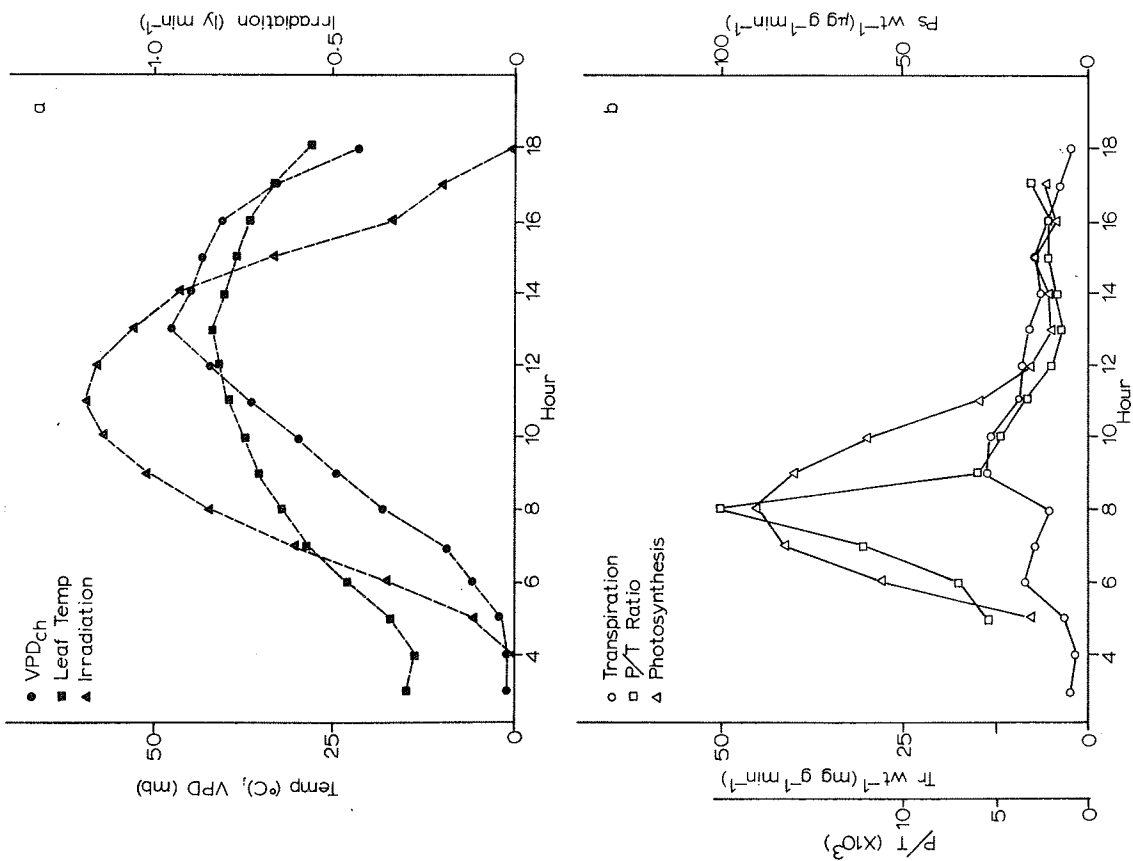


Figure 11. Transpiration and photosynthesis of a typical *A. confertifolia* plant on August 6 in relation to environmental conditions. P.M.S. - 70 bars; Phen. -7.8.

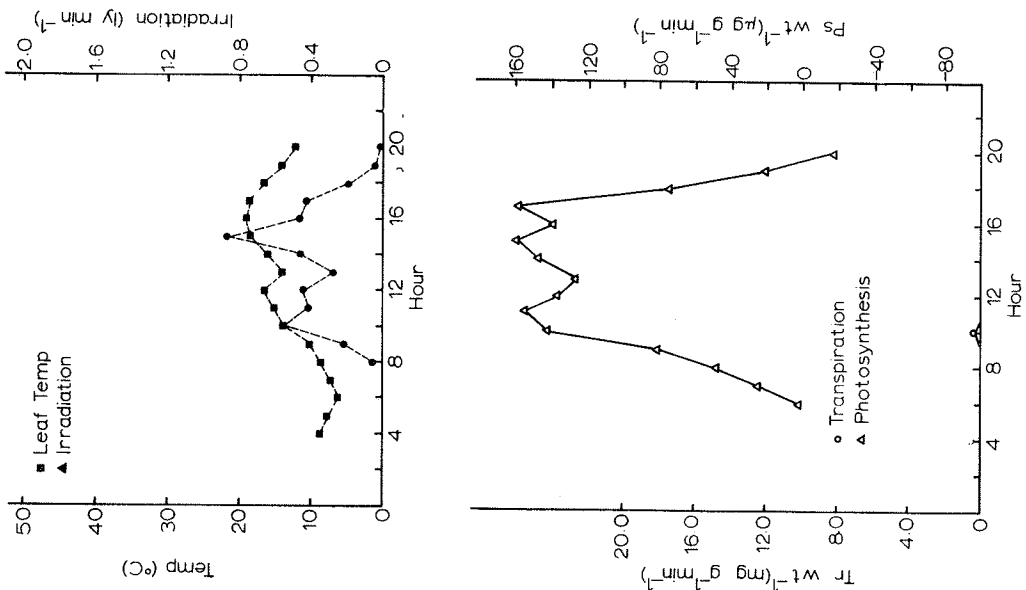


Figure 12. Transpiration and photosynthesis of a typical *Eurotia lanata* plant on April 25 in relation to environmental conditions. P.M.S. - 14 bars; Phen. -2.4.

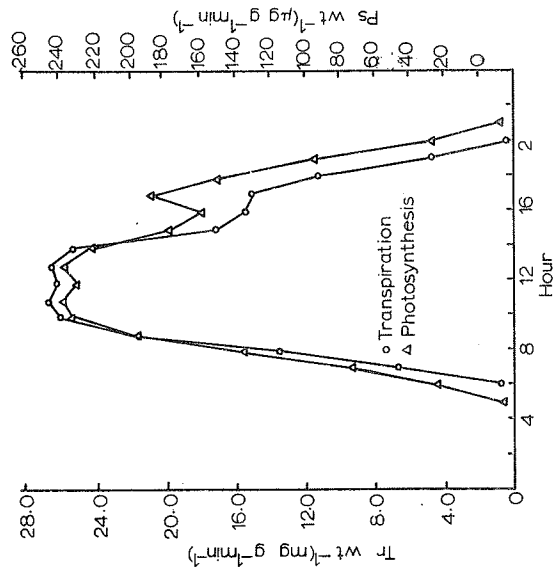
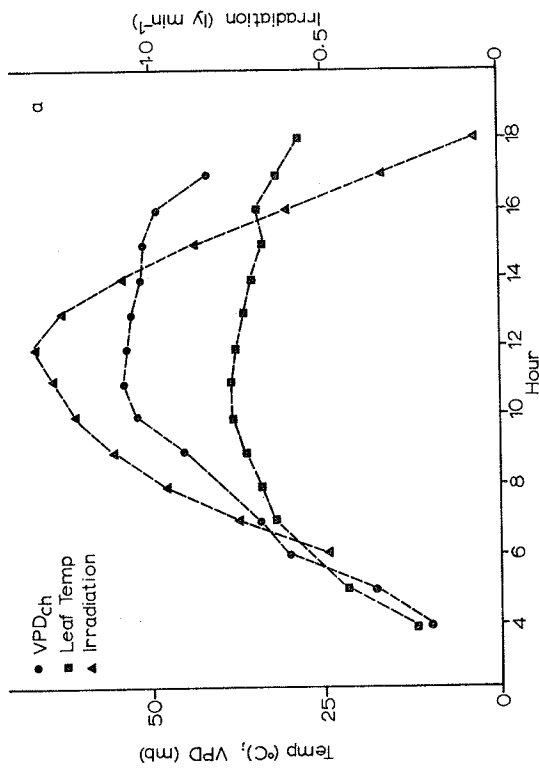


Figure 13. Transpiration and photosynthesis of a typical *Euphorbia lanata* plant on May 29 in relation to environmental conditions. P.M.S. - 28 bars; Phen. -2.0.

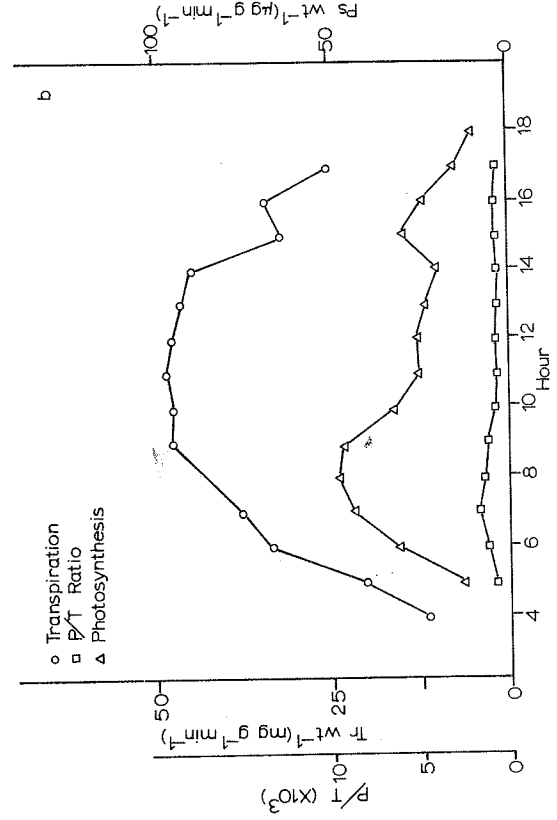
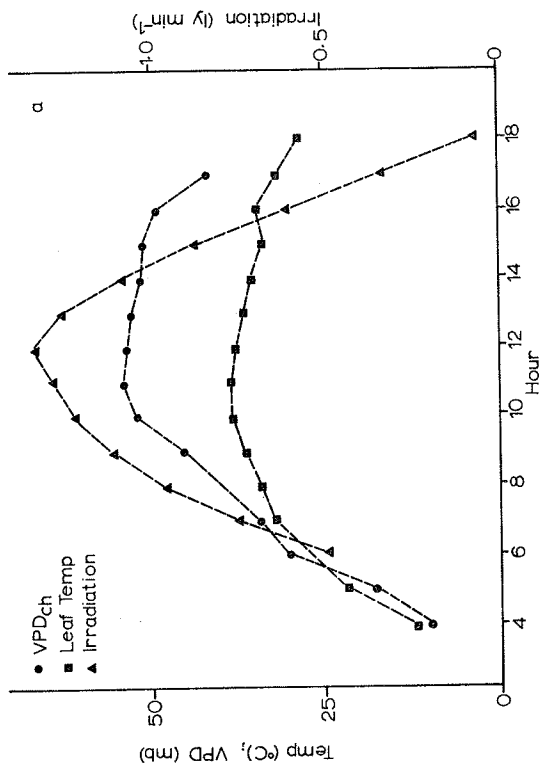


Figure 14. Transpiration and photosynthesis of a typical *E. lanata* plant on June 21 in relation to environmental conditions. P.M.S. - 30 bars; Phen. -5.8.

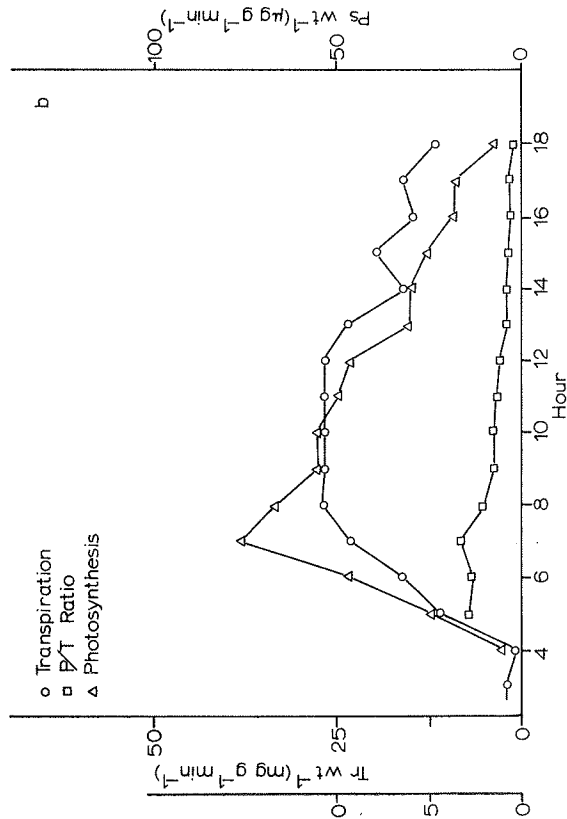
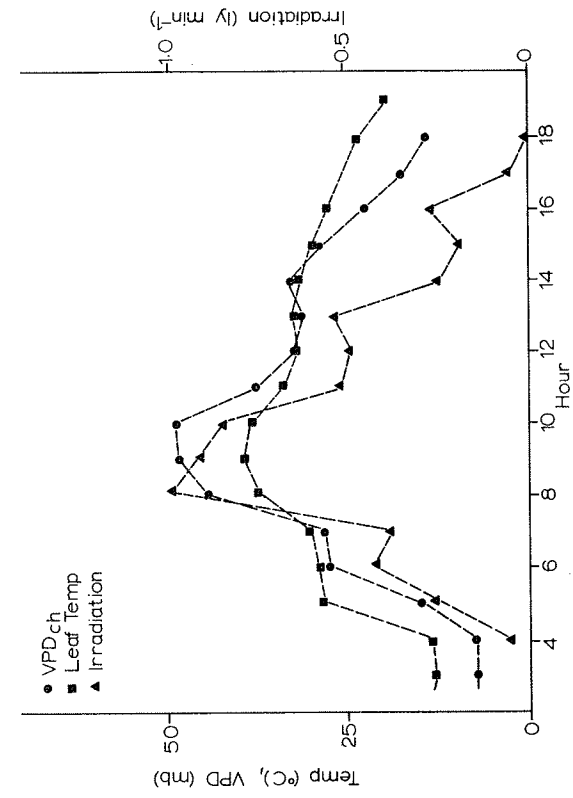


Figure 15. Transpiration and photosynthesis of a typical *Euxotia lanata* plant on July 1 in relation to environmental conditions. P.M.S. - 41 bars; Phen. -7.0.

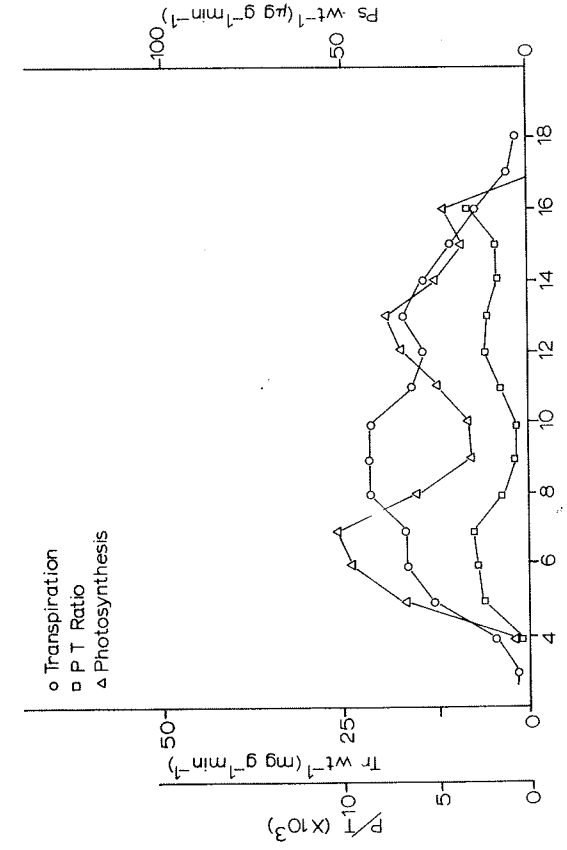
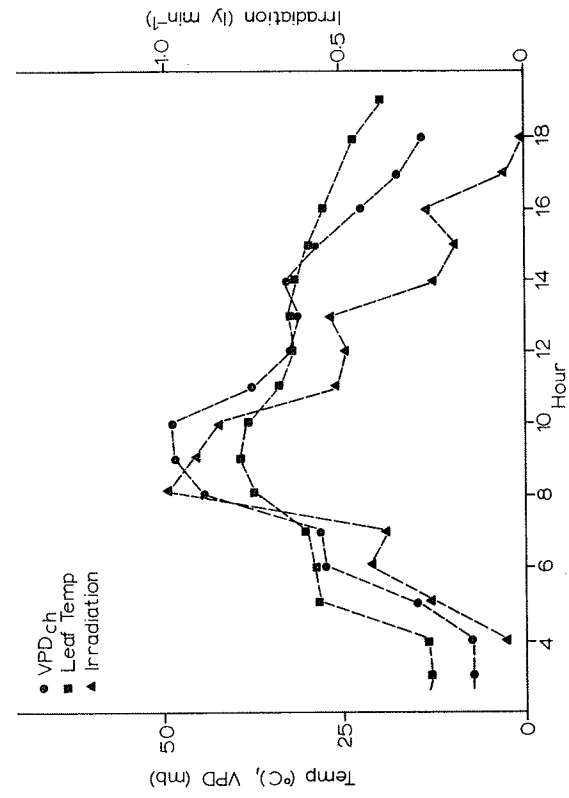


Figure 16. Transpiration and photosynthesis of a typical *E. lanata* plant on July 9 in relation to environmental conditions. P.M.S. - 50 bars; Phen. -6.7.

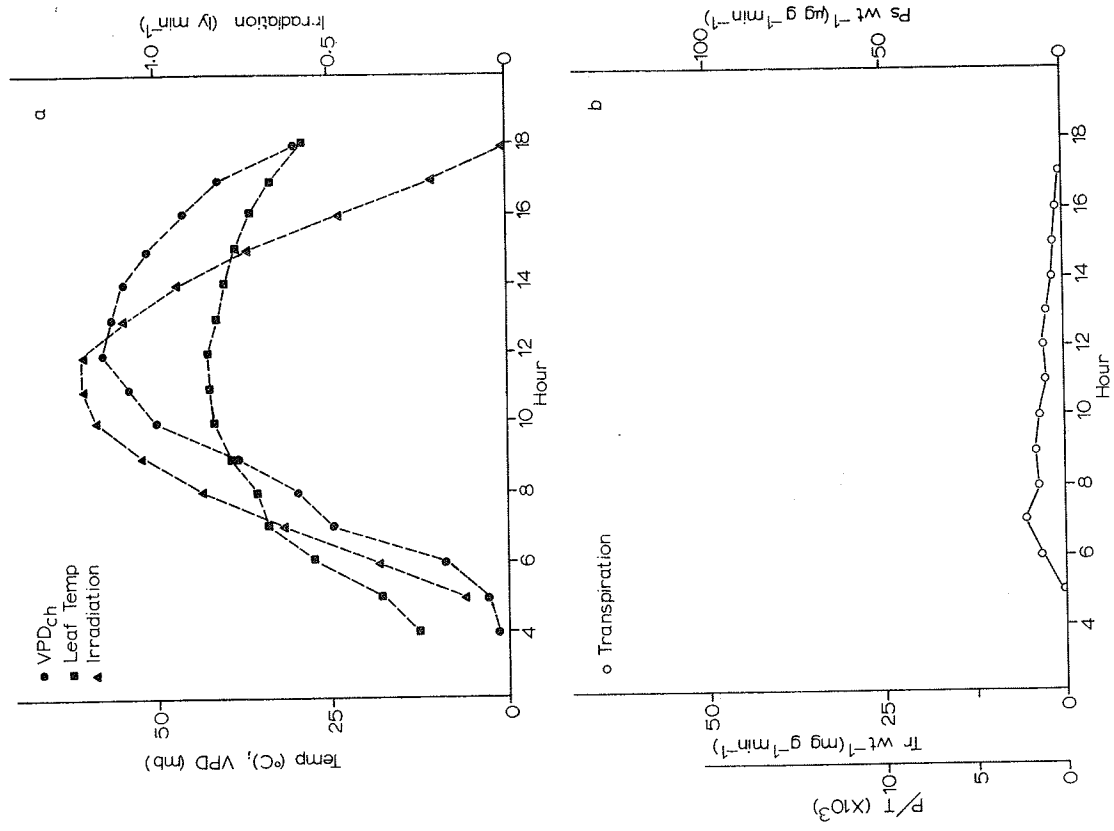


Figure 17. Transpiration and photosynthesis of a typical *Euxotia lanata* plant on July 27 in relation to environmental conditions. P.M.S. - P.M.S. - 69 bars; Phen. - 7.3.

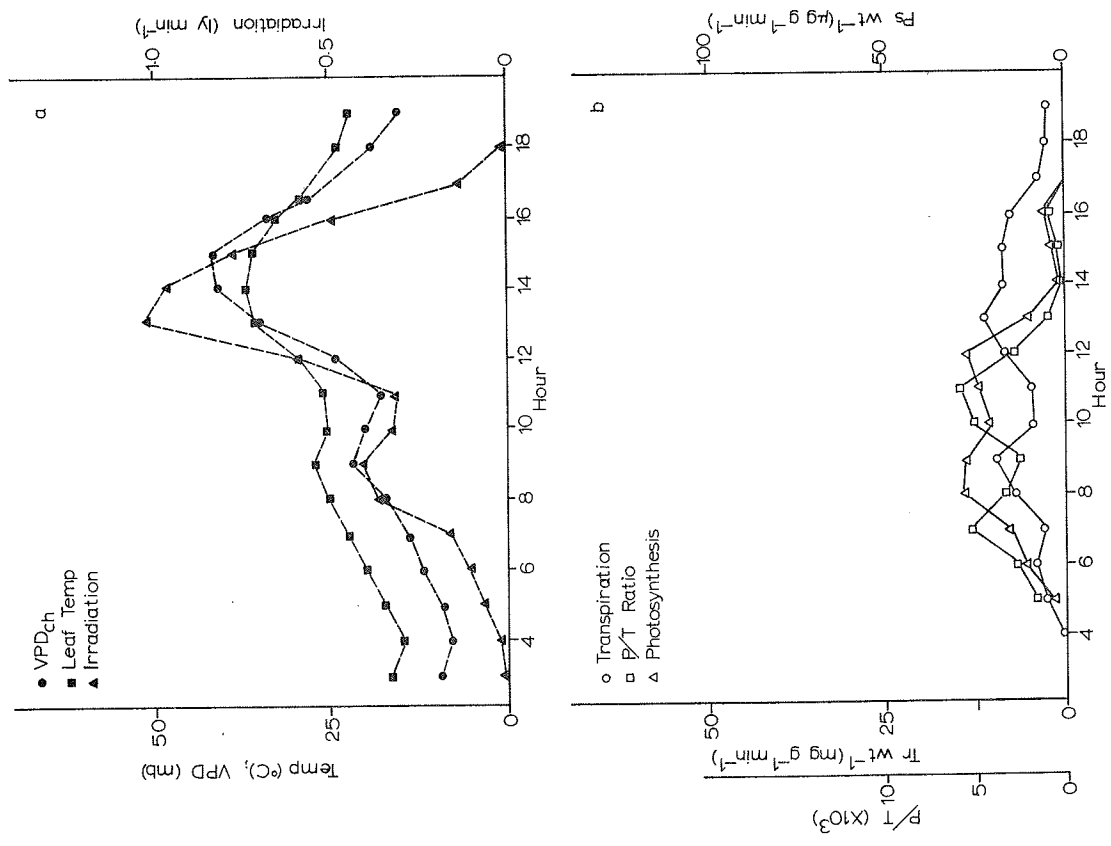


Figure 18. Transpiration and photosynthesis of a typical *E. lanata* plant on August 7 in relation to environmental conditions. P.M.S. - 78 bars; Phen. - 6.7. (No net photosynthesis during the entire day).

The correlation between plant moisture stress and soil moisture potentials are represented for *Atriplex confertifolia* and *Eurotia lanata* in Fig. 19. The correlation between plant moisture stress and phenological status of these two species is represented in Fig. 20. The phenological index employed is similar to that described by West and Wein (1971) and is explained in detail in Table 1.

The progression of plant gas exchange as a function of ambient environmental parameters is certainly instructive in approximating plant performance in the natural environment. However, for the construction of predictive models for water loss, net photosynthesis and dark respiration of these shrubs, experiments were conducted whereby all environmental factors which might alter plant gas exchange were varied independently (DSCODE CB15 and CB16). From these data, regression equations have been derived. Figures representing partial regressions from multiple regression equations may be found in the Ph.D. dissertations of R.T. Moore (1971) and R.S. White (incomplete). Transpiration as determined for plants in the field as a function of plant moisture stress, phenological status, vapor pressure deficit, and leaf temperature are represented for *Atriplex confertifolia* and *Eurotia lanata* in Figures 21 and 22, respectively. Since plant moisture stress and phenological status were highly correlated throughout the season in the field (see Figure 20) these two independent variables were varied simultaneously in the development of these partial regression equations. Similarly, because of the close correlation of leaf temperature and vapor pressure deficit, these two parameters were varied simultaneously much as would be expected in the field. All other independent variables were held constant near their means in these partial regression equations. A similar series of transpiration determinations under constant controlled environmental conditions were conducted in the laboratory. In this situation the same individual plants could be used for transpiration determinations at several states of water stress. Since the same plants were used it was impractical to use the pressure bomb for determination of plant moisture stress. Therefore, soil moisture stress was determined by four or five thermocouple psychrometers in each pot. There exists a close correlation between soil moisture stress measured in this method and plant moisture stress as determined by pressure bomb (see Figure 19). In these laboratory determinations all plants were in the same phenological stage, "post-fruiting, vegetative" phenological stage. Transpiration as a function of soil water potential, vapor pressure deficit, and leaf temperature are represented in Figures 23 and 24 for *Atriplex confertifolia* and *Eurotia lanata*.

Both species were evidenced to exhibit active transpiration and positive net photosynthesis at extreme water stress conditions. Absolute values of photosynthesis and transpiration are reported for three individuals of each species at extreme plant moisture stress as indicated in Table 2. These values of plant moisture stress exceed those ever evidenced in the field during 1970 (Fig. 2).

To investigate possible submodels for the Desert Biome ecosystem model, we have surveyed the applicability of existing models of plant transpiration to desert plant data collected in 1970. One such model by Norero (1969) seemed particularly appropriate. Plant transpiration rates predicted from Norero's model are compared with actual values measured in the laboratory and in the field for *Atriplex confertifolia* and *Eurotia lanata* in Figures 25 through 28. Predictability under laboratory conditions seems to be greater than for transpiration under field conditions.

Representative net photosynthetic behavior as a function of leaf temperature is shown in Figures 29 and 30 for *Atriplex confertifolia* and *Eurotia lanata* at three times during the season. These net photosynthetic curves are plotted on both an absolute basis and also as photosynthesis as a percent of maximum rate at a particular phenological stage. Corresponding response of dark respiration as a function of leaf temperature at three times during the season are represented in Figures 31 and 32.

Efforts have also been directed during the past year toward multiple regressions which may serve as the basis for submodels of photosynthetic behavior. A three dimensional diagram of partial regressions derived from one such multiple regression is represented in Figure 33 for *Eurotia lanata*.

Data from the gas exchange measurement of *Artemisia tridentata* taken during 1971 are presently in a final analysis stage (DSCODES CB41 and CB43). These will be reported in detail in the 1972 annual report. Preliminary analyses indicate that the progression of net photosynthesis and dark respiration through the course of the season are very similar in pattern to that of *Eurotia lanata*.

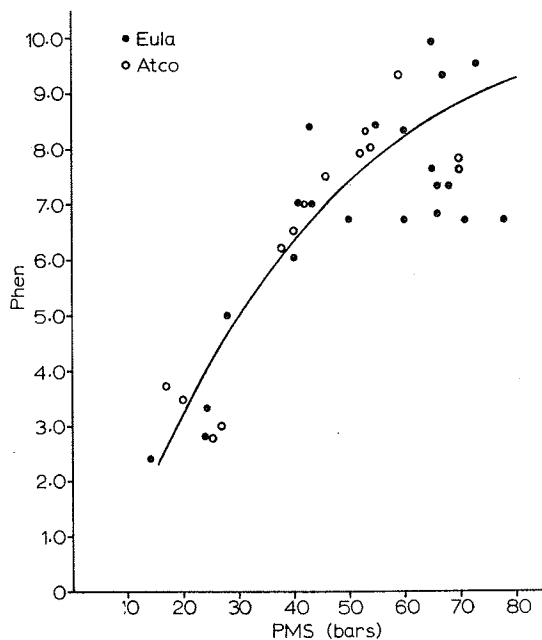


Figure 19. Scatter diagram of plant moisture stress versus phenology of *A. confertifolia* and *E. lanata*. Correlation coefficients: Atco, $r = .84$; Eula, $r = .73$ (visually estimated regression curve).

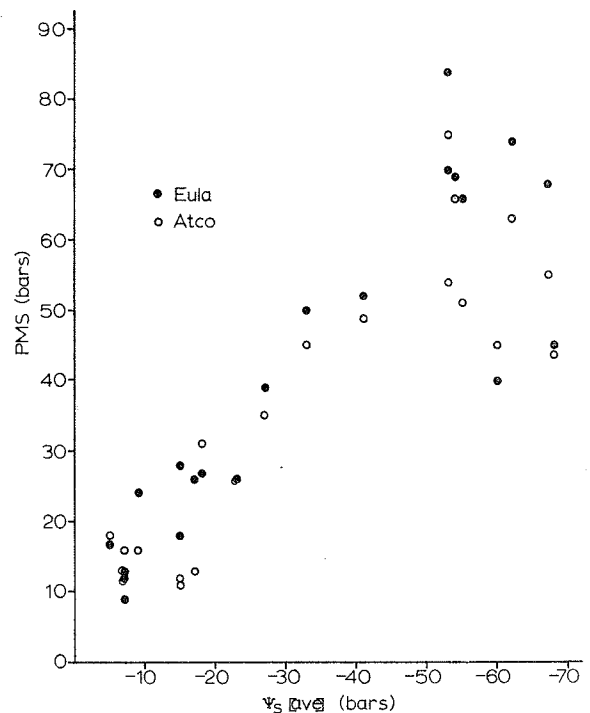


Figure 20. Scatter diagram of plant moisture stress of *A. confertifolia* and *E. lanata* versus average soil water potential. Correlation coefficients: Atco, $r = -.87$; Eula, $r = -.88$.

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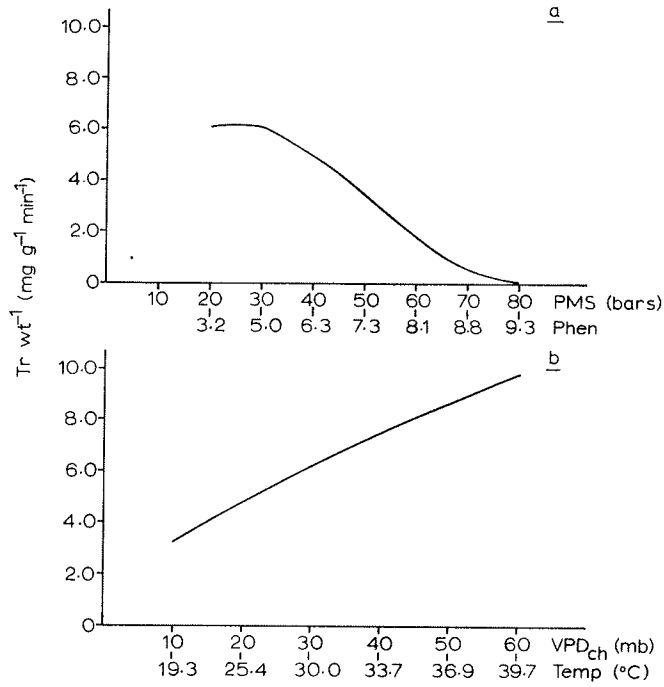


Figure 21. Transpiration of *A. confertifolia* (field) versus; (a) plant moisture stress and phenology, and (b) vapor pressure deficit and leaf temperature.

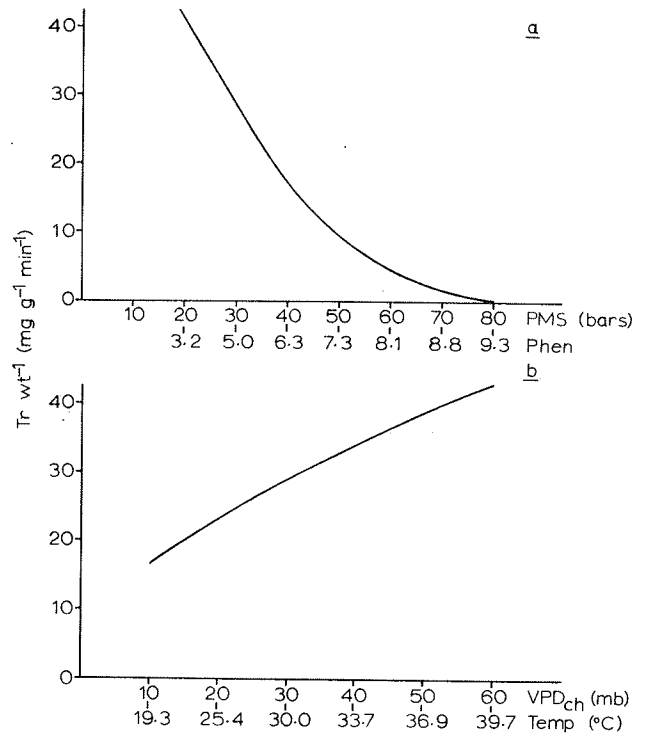


Figure 22. Transpiration of *E. lanata* (field) versus; (a) plant moisture stress and phenology, and (b) vapor pressure deficit and leaf temperature.

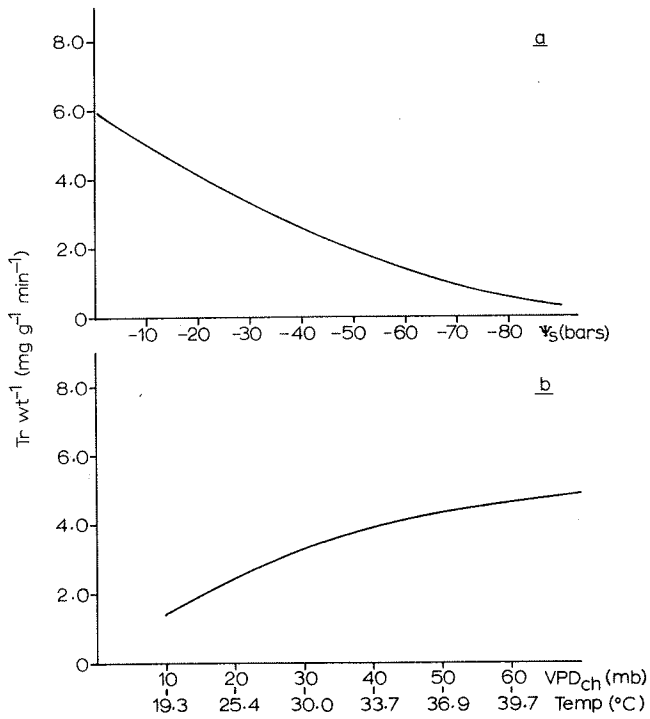


Figure 23. Transpiration of *A. confertifolia* (laboratory) versus; (a) soil water potential, and (b) vapor pressure deficit and leaf temperature.

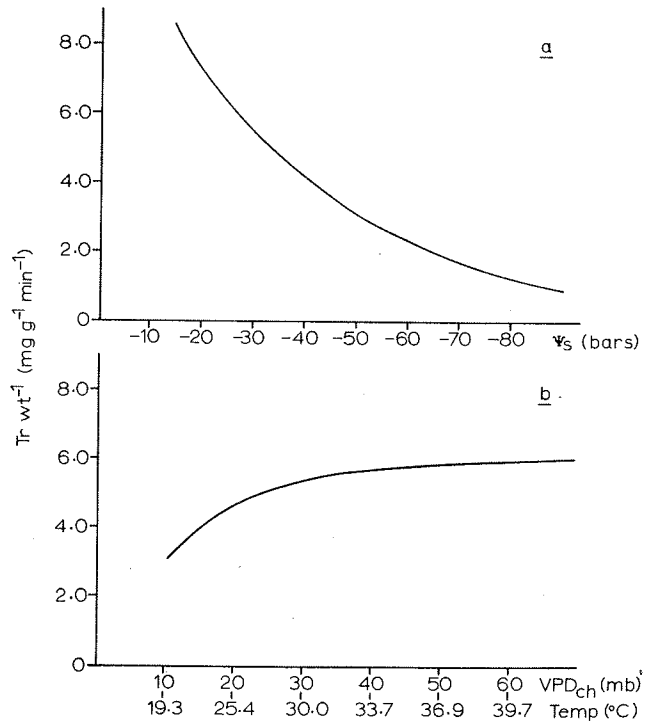


Figure 24. Transpiration of *E. lanata* (laboratory) versus; (a) soil water potential, and (b) vapor pressure deficit and leaf temperature.

Table 1. Phenology Scoring Criteria.

Phenology	Description	
	<i>A. confertifolia</i>	<i>E. lanata</i>
0.0	-----Spring dormancy-----	
1.0	-----Vegetative buds not open, no twig elongation-----	
2.0	-----Vegetative bud partially open, no twig elongation-----	
3.0	-----Buds partially open, twigs elongating-----	
4.0	-----Floral buds developing-----	
5.0	-----Flowering-----	
6.0	Fruit developing, male flowers withering	Fruit developing, twigs becoming woody
7.0	(Male) Twigs woody and yellow (Female) Some woody tissue in new growth	Woody tissue in new growth
8.0	(Male) Leaves turning red (Female) Fruit turning red	Fruit developed, primary leaves dropping
9.0	Primary leaves dropped, secondary leaves present	Secondary leaves present
9.9	-----Fall dormancy-----	

Table 2. Transpiration and Photosynthesis at Extreme PMS.

Species/Plant	Temp	VPD	PMS bars	Photosynthesis mg cm ⁻² min ⁻¹	mg g ⁻¹ min ⁻¹	Transpiration mg cm ⁻² min ⁻¹
<i>A. confertifolia</i>						
A	30.4	23	96	30.4	5.7	112
B	41.2	53	97	-0.3	0.9	16
C	25.5	21	114	5.9	0.7	16
<i>E. lanata</i>						
A	18.6	8	120	2.3	2.2	26
B	30.6	28	105	6.1	4.1	36
C	30.0	29	95	-8.9	5.1	40

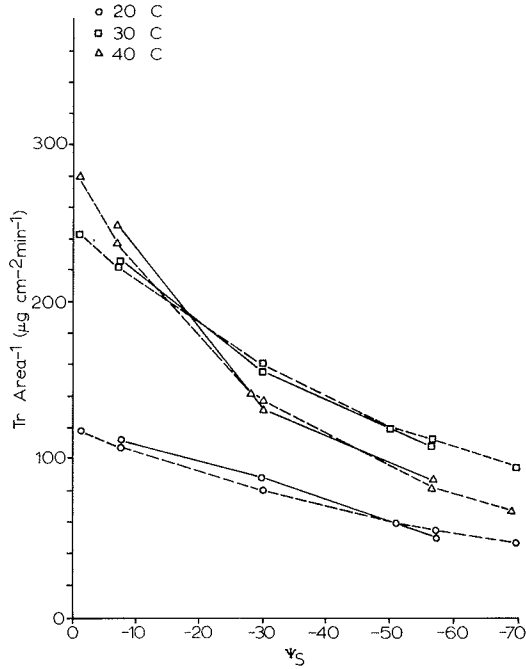


Figure 25. Comparison of laboratory observations of transpiration by *A. confertifolia* (solid lines) with predictions from Norero's (1969) model (dashed lines).

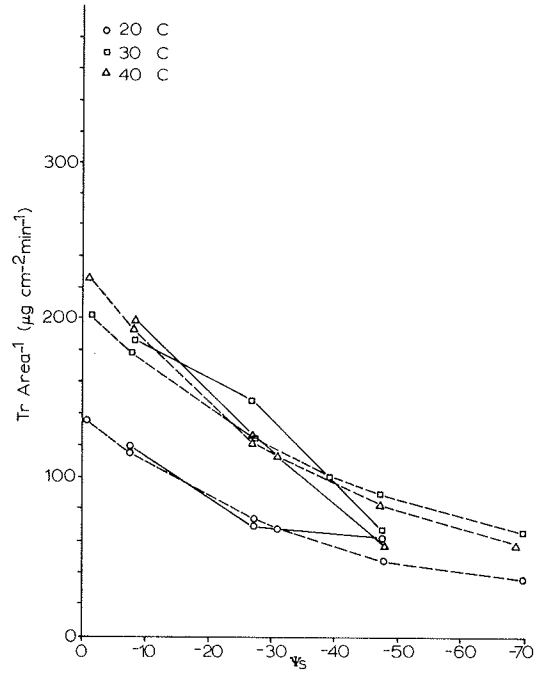


Figure 26. Comparison of laboratory observations of transpiration of *E. lanata* (solid lines) with predictions from Norero's (1969) model (dashed lines).

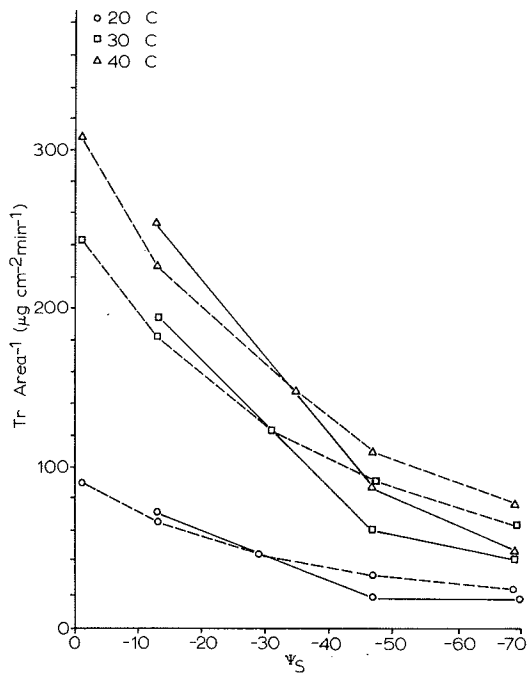


Figure 27. Comparison of field observations of transpiration by *A. confertifolia* (solid lines) with predictions from Norero's (1969) model (dashed lines).

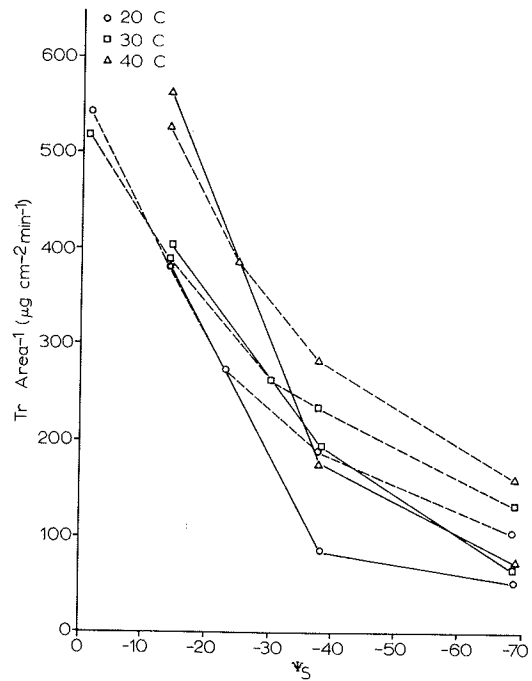


Figure 28. Comparison of field observations of transpiration of *E. lanata* (solid lines) with predictions from Norero's (1969) model (dashed lines).

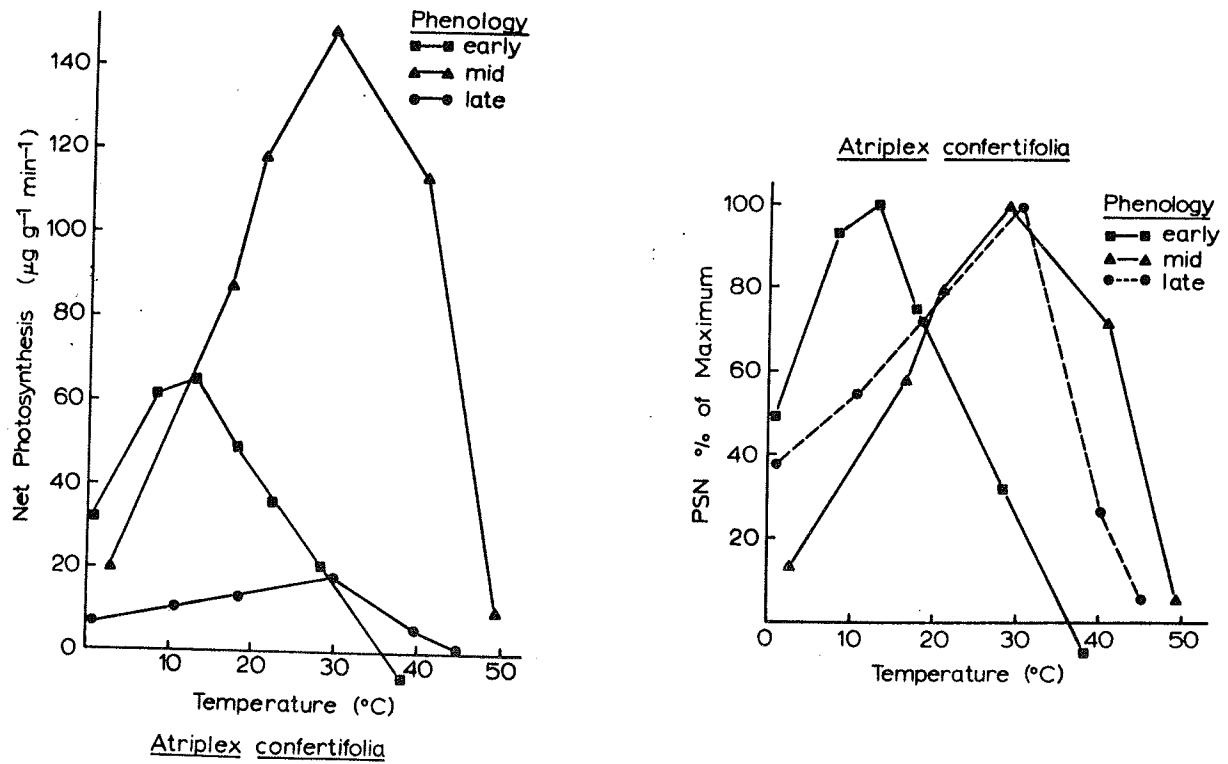


Figure 29. Net photosynthesis of *Atriplex confertifolia* plotted as a function of leaf temperature at three phenological stages: early (April), mid (May-June), and late (August-September). Figure 29a represents photosynthesis in absolute units and Figure 29b represents photosynthesis as a percent of the maximum value for a particular phenological stage.

2.3.1.8.-20

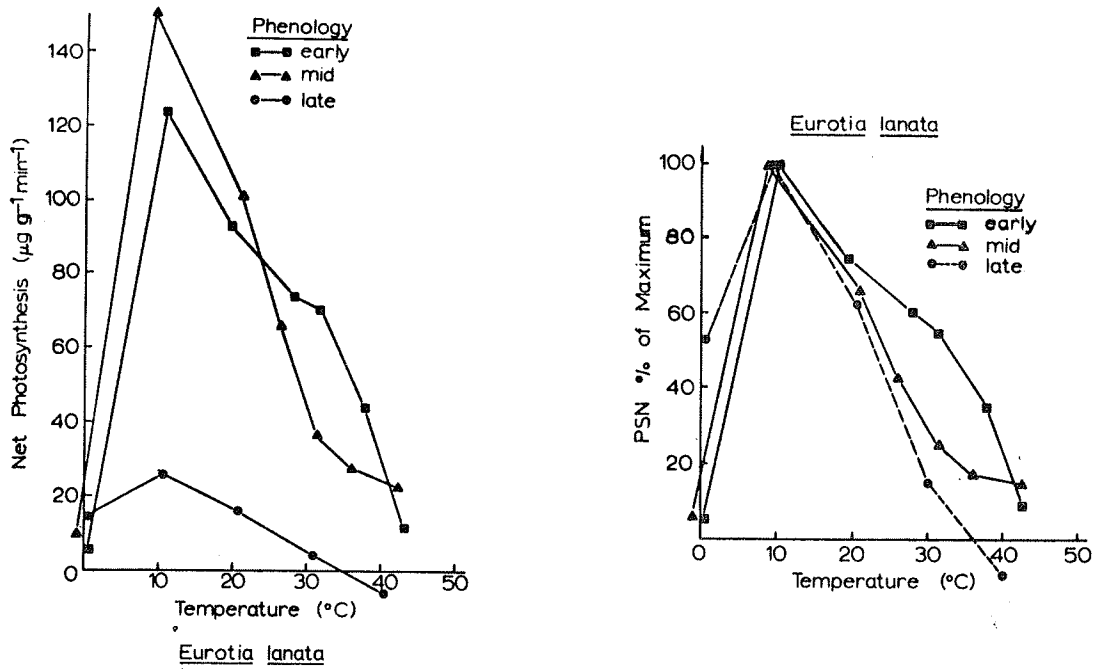
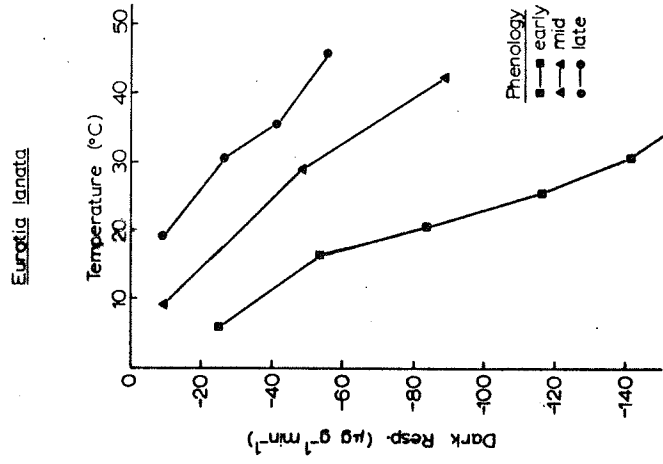


Figure 30. Net photosynthesis of *Eurotia lanata* plotted as a function of leaf temperature at three phenological states: early (April), mid (May-June), and late (August-September). Figure 30a represents photosynthesis in absolute units and Figure 30b represents photosynthesis as a percent of the maximum value for a particular phenological stage.



2.3.1.8.-21

Figure 32. Dark respiration of *Euzotia lanata* plotted as a function of temperature at three phenological stages.

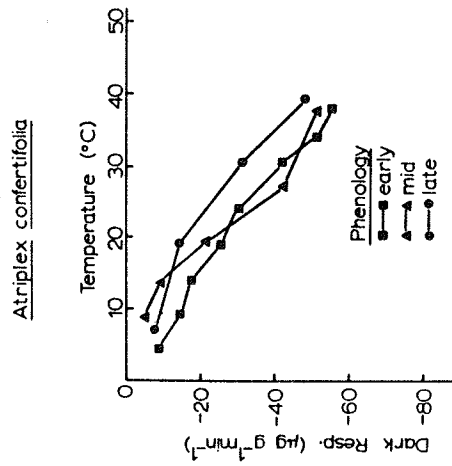


Figure 31. Dark respiration of *Atriplex confertifolia* plotted as a function of temperature at three phenological stages.

2.3.1.8.-22

$$\hat{Y} = B_0 + B_1X_1 + B_2\left(\frac{1}{X_1}\right) + B_3\sqrt{X_2} + B_4X_1X_2 + B_5X_3$$

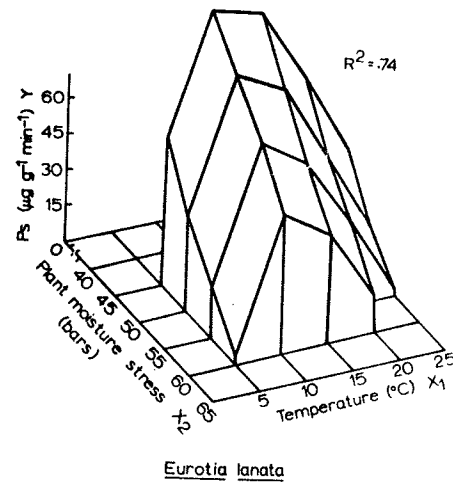


Figure 33. Net photosynthesis of *Eurotia lanata* during early summer in relation to temperature and plant moisture stress as computed by reanalysis.

DISCUSSION

During the favorable season for physiological activity (early March through October) *Atriplex confertifolia* and *Eurotia lanata* progress through at least ten easily recognized phenological stages as described in Table 1. With this progression of phenology are changes in the composition of leaves of different ages and physiological states, increasingly severe plant moisture stress (Figs. 2 and 20), and usually decreasing leaf moisture contents (Fig. 4). These biological changes reflect a seasonal progression of solar irradiation, temperature and decreasing soil moisture potentials (Fig. 2). Plant water stress values do undergo diurnal fluctuations. Apparently these fluctuations are in response to changes in atmospheric moisture stresses since soil temperatures and moisture potentials undergo little diurnal variation at depths greater than 15 cm (Fig. 3). These variations in plant moisture stress on a daily basis are, however, quite small when compared to the increasing plant moisture stress that develops in these species throughout the progression of the season. This trend is reversed in late August and early September when plant moisture stresses decrease in response to fall precipitation and decreased atmospheric moisture stress.

Although plant moisture stress increases during the progression of the season, there seems to be a lesser change in leaf osmotic potentials for *Eurotia lanata* (Fig. 4). For *Atriplex confertifolia* there is apparently little change until late June when osmotic potentials plummet to very low values. This abrupt decrease in leaf osmotic potential probably reflects the maturation and rupture of vesicular epidermal hairs on the leaf surfaces. These hairs have been observed on many species of this genus and appear to function as a mechanism of salt excretion from the leaf (Osmond et al., 1969; Mozafar and Goodin, 1970).

Precipitation patterns during this intensive year of study (1970) were reasonably representative of those during the past decade (Fig. 1).

With changes in plant phenological status, moisture stress and environmental conditions through the progression of the season, it is not surprising that the plant gas exchange activity and the capacity for plant gas exchange also undergo dramatic changes. In the construction of primary productivity models for the Desert Biome it is paramount that these changes be taken into account for a reasonably predictive modelling effort.

The gas exchange response of *Atriplex confertifolia* on several selected days throughout the season are shown in Figures 5 through 11. In these cases, the gas exchange chambers were programmed to track ambient environmental conditions. Important environmental parameters are also shown in these figures. Correlative representations for *Eurotia lanata* are found in Figures 12 through 18. For both species, optimal photosynthetic rates were evidenced in the spring months (April and May) when leaf temperatures seldom exceeded 20°C. At this time of the year, too, plant water stress values were reasonably small (Fig. 2). As the season progressed, rates of net photosynthesis were greatly reduced. This is particularly true for *Eurotia lanata* which curtailed all positive net photosynthetic activity by the first part of August. Net photosynthesis in *Atriplex* continued much later in the season at a more vigorous pace (Fig. 11). Photosynthetic activity for *Atriplex* did continue well into the month of October, although this was prominent only during the morning hours. During the afternoon hours net photosynthesis usually became negative for *Atriplex*. The pattern displayed in Figure 11 was quite typical throughout the later fall period. Transpiration rates remained about the same order of magnitude for *Atriplex* throughout the season. For *Eurotia lanata*, transpiration rates were initially quite high and then exhibited curtailment parallel to the gradual cessation of net photosynthetic activity in late July and August. The water use efficiency of photosynthesis is expressed by photosynthesis/transpiration ratios (P/T) in most of these Figures. Throughout the season P/T ratios are much more favorable for *Atriplex* than for *Eurotia* under a variety of environmental conditions.

The variation in gas exchange activity of these species throughout the season certainly reflects in part the changing environment during the course of the year. However, phenological status of these plants and the environmental history also contribute to substantial differences in the gas exchange capacity under predetermined environmental conditions. Much effort was therefore directed in these studies to determining the gas exchange capacity at various times of the year. These capacity values represented as regression functions should be most helpful in the Biome modelling effort.

The capacity for transpiration is represented in Figures 21 to 24. In the field determinations for *Atriplex* and *Eurotia*, transpiration is represented as a function of plant moisture stress and phenology since these two independent variables were always highly correlated in these determinations. Radiation intensities during these determinations were constant at $2.5 \text{ g cal cm}^{-2} \text{ min}^{-1}$. Under these conditions the transpiration capacity of *Eurotia lanata* was also substantially higher than that of *Atriplex*. This correlates well with the performance of these two species under ambient environmental conditions.

Similar transpiration capacity determinations were carried out in the laboratory when the plants were in a constant phenological condition in the late fall. In this situation, irradiation intensities were held constant at $1.1 \text{ g cal cm}^{-2} \text{ min}^{-1}$. Functional relationships in these laboratory determinations are very similar to those obtained under field conditions. The magnitude of transpiration capacity for *Eurotia*, however, was in the same order of magnitude as for *Atriplex*. This abrupt drop in transpiration capacity in these laboratory plants probably reflects the late season phenological condition of the plants which were used for these determinations.

The transpiration capacity relationships of these two halophytic species are consistent with the reports of other workers. Slatyer (1956, 1957) found a progressive decline in transpiration in several mesophytic species as θ_s and ψ_s decreased. Bahrani and Taylor (1961) reported a sharp reduction in transpiration of alfalfa (*Medicago sativa*) as ψ_s decreased from -.3 bars to -4 bars, with only a slight reduction beyond that point. Several other mesophytic plants have been reported to exhibit a steadily decreasing transpiration rate with decreasing ψ_s within the ψ_s range of -1 to -15 bars (Gavande and Taylor, 1967; Pallas, Michel and Harris, 1967; Babalola, Boersma and Youngberg, 1968).

Denmead and Shaw (1962) and Gardner and Ehlig (1963), on the contrary, reported transpiration to be relatively unaffected by changing water stress until ψ_s dropped low enough to induce "turgor loss" or "wilting". That ψ_s level was dependent upon soil, atmospheric, and plant conditions. Below that point there was an almost linear decrease in transpiration with decreasing θ_s , or a curvilinear decrease with decreasing ψ_s . Ehlig and Gardner (1964) found relative transpiration rates of four mesophytic species to decrease sharply with decreases in leaf water potential from -5 to -15 bars. Below -15 bars the rates tended to reach a stable minimum value. The initial decline in transpiration rate occurred at higher θ_s and ψ_s levels as the potential transpiration rate increased, indicating a greater sensitivity to ψ_s under such conditions. Since ψ_s is normally quite low and potential transpiration rather high at Curlew Valley, conditions for the "plateau" of maximum transpiration as visualized by Denmead and Shaw (1962) and Gardner and Ehlig (1963) would rarely occur for *A. confertifolia* and *E. lanata*. Thus, the question of whether these two species would exhibit a plateau of maximum transpiration at very high ψ_s is somewhat immaterial.

Palmer, Trickett, and Linacre (1964) reported that within the ψ_s range of -10 to -60 bars, the falling transpiration rate of *Atriplex nummularia* was almost linearly related to the logarithm of ψ_s . Two other *Atriplex* species, *A. hastata* (a coastal species) and *A. spongiosa* (an arid species), have been shown to transpire under conditions of severe moisture stress (Slatyer, 1970a). *Atriplex hastata* showed relatively stable transpiration with increasing stress until the relative tissue water content reached approximately 65 percent where transpiration decreased abruptly. Transpiration by *A. spongiosa*, would appear to be very similar to the response of *A. confertifolia*.

Active transpiration of *A. confertifolia* and *E. lanata* was observed at extreme values of ψ_s and PMS (Table 2). Similar activity at extreme ψ_s levels has been shown for four other halophytes from near Great Salt Lake (Detling, 1969). They also exhibited gradual decreases in photosynthetic activity without sharp changes at any particular point. Transpiration was not measured in Detling's study.

Transpiration by these halophytic species at extreme Ψ_s levels and the progressive decrease in transpiration and photosynthesis with decreasing Ψ_s supports the concept that no common constant exists (in terms of θ_s and Ψ_s) which characterizes either a sharp change in the transpiration curve or the lower limit of moisture extraction by all plants (Gardner and Ehlig, 1963; Gardner and Nieman, 1964). It is evident that these halophytic plants are able to extract sufficient moisture to transpire and photosynthesize at Ψ_s levels at which most mesophytic species would not survive.

Net photosynthetic capacity of these two species are represented in Figures 29 and 30 as a function of changing leaf temperature at constant irradiation intensities ($2.5 \text{ cal}^{-2} \text{ min}^{-1}$). In both species there are dramatic changes in the absolute net photosynthetic values with progression of the season. As was reflected in photosynthetic data under ambient conditions, the photosynthetic capacity is greatly depressed during the latter part of the growing season. A similar pattern was exhibited in net photosynthetic capacity data for *Artemisia tridentata* in 1971.

When plotted as a percent of maximum photosynthesis at any given phenological stage, the temperature acclimation of these species for net photosynthesis become apparent. For *Eurotia lanata* there is little apparent acclimation taking place in terms of relative photosynthesis at different leaf temperatures during the course of the season. For *Atriplex*, however, there is a dramatic shift both in the optimal temperature for photosynthesis and also in the upper and lower limits of photosynthetic activity. For example, during the early season optimal photosynthesis is occurring at approximately 12°C leaf temperature and the upper thermal compensation point for photosynthesis is reached at 37°C . During the mid-season when leaf temperatures are expected to be maximal, the optimal photosynthetic rate takes place at leaf temperatures of 32°C and the upper thermal compensation point is 50°C . In a few individuals the upper thermal compensation point even exceeded 50°C leaf temperature. It was reported in the 1970 annual report that both *Eurotia* and *Atriplex* were able to carry on positive net photosynthesis at leaf temperatures of -5°C . This is not represented in Figures 29 and 30 but certainly was apparent in most individual plants studied.

Temperature acclimation for net photosynthesis in *Artemisia tridentata* appears to be more similar to that of *Eurotia lanata*. There is a small shift in the optimal temperature for photosynthesis but not nearly so dramatic as for *Atriplex*.

These photosynthetic capacity values provide new insights in the photosynthetic behavior of wildland plants which possess the C_4 and C_3 photosynthetic pathways. *Atriplex confertifolia* fixes carbon via the C_4 pathway while *Eurotia lanata* and *Artemisia tridentata* apparently use the normal C_3 pathway (Welkie and Caldwell, 1970). Generalizations in the literature for agronomic species suggest that C_4 plants have very high optimal temperatures for photosynthesis (35 to 40°C) and very high net photosynthetic rates as opposed to C_3 species (Hatch and Slack, 1970). Data presented in this report do take exception to these generalizations. For the same season of the year the absolute values of net photosynthetic capacity for *Atriplex confertifolia*, *Eurotia lanata* and *Artemisia tridentata* are all in the same ranges of magnitude. The C_4 plant does not appear to be superior in net photosynthetic rates. *Atriplex confertifolia* does not possess a high optimum temperature for photosynthesis, particularly during the early season. If C_4 plants do have an advantage in the cold desert environment, it may be in the immense acclimation potential for net photosynthesis as exhibited by *Atriplex*. Plants possessing the C_4 pathways are reported to have a greater water use efficiency for photosynthesis (Hatch and Slack, 1970; Slatyer, 1970b). This generalization does seem to hold for *Atriplex confertifolia* and *Eurotia lanata* based on the ambient field data (Figs. 5 to 18).

The capacity for dark respiration is represented in Figures 31 and 32 for *Atriplex* and *Eurotia* at three phenological stages during the course of the season. In this situation, *Atriplex* does not appear to undergo acclimation in terms of dark respiration potential as a function of leaf temperature during the course of the year. *Eurotia*, on the other hand,

does experience abrupt shifts in dark respiration rates as a function of leaf temperature at different times of the year. At any given temperature dark respiration rates are much less at later, and usually warmer, periods of the growing season. High respiration rates at cooler leaf temperatures in the early season may certainly be adaptive in permitting active growth of these plants when prevailing temperatures are quite cool. During the later season reduced respiration rates at higher temperature would seem to be beneficial for conservation of energy. The lack of dramatic shifts in dark respiration for *Atriplex confertifolia* is quite perplexing in this regard since *Atriplex* initiates shoot growth and metabolic activity as early in the season as does *Eurotia lanata*. Data from 1971 for *Artemisia tridentata* reveal dark respiration capacity performance as somewhat intermediate between that of *Eurotia* and *Atriplex*.

We do wish to extend strong recommendation to the Biome modelling effort that close attention be paid to the changes in gas exchange capacity (net photosynthesis, dark respiration and transpiration) which these species undergo during the course of the active season of growth and physiological activity. Reasonably predictive models would need to incorporate the plasticity and acclimation which these species exhibit in the course of the year.

Although not under the specific contract of our process study, we have taken an adjunct interest in the sub-models which might be sufficiently predictive of desert plant gas exchange behavior so as to be useful in the overall desert ecosystem models. Specifically, we have investigated the applicability of several models for plant transpiration as a function of environmental parameters to our desert plant data. One particularly promising model is that of Norero (1969) who presented a model for evapotranspiration which, from his supporting data at least, appeared to be valid for much of the transpiration data in the literature. Norero's equation for actual transpiration (ET_a) is based on maximum transpiration (ET_{max}) as modified by soil water potential (ψ) and a plant, soil and climate adjustment factor (k):

$$ET_a = \left[1 + \frac{\psi^k}{\psi'} \right]^{-1} ET_{max} \quad (1)$$

where:

$$k = \frac{2.56}{\log \left[\frac{\psi_{min}}{\psi_{max}} \right]} \quad (2)$$

and:

$$\psi' = \psi \text{ at which } ET_a = 1/2 ET_{mas} \quad (3)$$

Based on the transpiration data of Palmer et al. (1964), Norero lists k values for *Atriplex* of 1.227 for low evaporative demand (1.9 mm day^{-1} , $\psi' = -40$) and 0.877 for high evaporative demand (6.2 mm day^{-1} , $\psi' = -95$). He has also apparently calculated ψ_{min} values of -1100 for *Atriplex* which would appear to be rather extreme for *A. confertifolia* and *E. lanata*.

Direct testing of Norero's model with the data from this study is possible only in a limited manner. The model assumes constancy in all environmental variables other than ψ_s . Thus, ET_{max} , ET_a , ψ' , and ψ_{min} would all have to be determined under equivalent conditions of VPD, temperature, irradiation and phenology. These conditions were most closely approximated with the laboratory experiments. The field experiments under controlled conditions met most of the criteria, except that phenology varied and ψ_s data are available only indirectly.

If one assumes ψ_{max} values of -0.5 to -1 bar (based on the studies with potted plants), and considers ψ_{min} to be in the range of -90 to -120 bars for both species (since transpiration appeared to become negligible in that range), k values for both species would range from 1.07 to 1.31 which agrees well with Norero's calculations for *Atriplex nummularia*.

Values of ET_a were calculated from averaged data for several plants of each species for the potted and field data. The individual observations were adjusted so that the resultant means were for "equivalent" conditions. These measurements along with the ET_a curves from Norero's model are shown in Figures 25-28. The ET_{max} values were based on an estimated intercept of $\psi_{max} = -1$.

From comparisons of the actual data and the values predicted by the model, it is evident that for response curves shaped similar to those in Figure 25 the model is quite accurate. However, for convex response curves, such as at 30°C in Figure 26, the model begins to depart from the observations since it is based on the generally valid assumption that the most rapid reduction in transpiration occurs at relatively high ψ_s .

Although Norero's model provides a sound functional description of the response curves, its predictive value seems to be rather limited. One must first measure at least both ends and the center of the response curves to obtain the parameters required by the model. It might then be used to predict values for completing the curves.

Numerous other models have been proposed for estimating transpiration, most of which apply primarily to stands of field crops rather than individual plants and which assume a rather high ψ_s level. Penman (1949) postulated that actual evapotranspiration would equal potential ET until the available moisture was virtually exhausted. More recent evidence indicates that actual transpiration begins to fall below potential transpiration quite early in the drying process. This has been taken into account quite well by Makkink and Van Heemst (1956) and Norero (1969). Idle (1970) presented one of the most comprehensive models available, incorporating radiation, humidity, air temperature, leaf temperature, and leaf size. He did, however, make some assumptions regarding the effects of water stress which would likely limit the model's accuracy in arid situations.

Numerous models have relied primarily on an energy balance approach (Penman, 1952; Thornthwaite, 1948; Blaney and Criddle, 1950). Several of the systems for estimating potential evapotranspiration were evaluated by Stanhill (1965) and found to be of limited value in arid regions where plant characteristics become more important. As pointed out by Brouwer (1956), the transpiration process is more than mere physical evaporation and such approaches must consider plant factors interacting with the energy supply. Lemon, Glaser, and Satterwhite (1957) accurately evaluate the problem in their statement:

"The soil, the plant, and the atmosphere form a single system for the transfer of water. Such terms as transpiration, translocation, adsorption, and availability of soil moisture all refer simply to various aspects of this transfer. More attention has been given to the individual elements of this system than to the system as a whole. It is the resultant of the interaction of the three components of the system, not their absolute values, which influences the growth and behavior of plants and thus warrants intensive study."

(Lemon, Glaser, and Satterwhite, 1957, p. 468)

Efforts are also currently underway to apply photosynthetic data to previously existing or newly devised sub-models which may be useful in the overall Desert Biome modelling effort. This application of desert photosynthetic data to sub-models will be under the auspices of the Ph.D. dissertation by Richard White to be completed in 1972.

Preliminary attempts to derive relationships for photosynthesis as a function of plant and environmental parameters by routine regression analyses have been carried out in 1971. One such representation for photosynthesis of *Eurotia lanata* as a function of plant moisture stress and leaf temperature is represented in Figure 33.

EXPECTATIONS

During 1972, gas exchange data for *Artemisia tridentata* taken in 1971 will be completely analyzed and represented in Figures. Further analysis of photosynthetic data from *Eurotia lanata* and *Atriplex confertifolia* will be carried out; however, Desert Biome funds will not be used for these analyses. A major effort will be directed towards development of methods for determination of translocation and root growth in relation to gas exchange as described in our 1972 proposal. Once the methodology is thoroughly proven for desert plants, initial attempts will be made to carry out the measurements in field situations during 1972. Details of methodology and experimental plans to be applied may be found in the 1972 proposal.

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