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FINAL REPORT

**GAS EXCHANGE, CARBON BALANCE AND PRODUCTIVITY
OF GREAT BASIN SHRUB-DOMINATED COMMUNITIES**

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ABSTRACT

Refinement of gas exchange models for *Atriplex confertifolia* and *Ceratoides lanata* was continued in 1976. The models indicate that there is little difference in total carbon fixation or transpirational water use between monospecific stands of these two shrubs. The modeled values of water transpired were verified by calculations of water extraction from the soil profile. Effects of a spring 1975 foliage removal in an *Atriplex* community were followed in 1976. In the second year following defoliation, below-ground productivity of clipped plants was about half that of control plants. Observation of relative root growth activity in *Atriplex* and *Ceratoides* communities was continued in 1976 utilizing below-ground observation chambers. Root growth of the two species growing in mixed communities is reported this year for the first time. Measurements of respiration of *Atriplex* root elements was continued in 1976. These studies indicate that there are both depth-dependent and time-dependent changes in the respiratory capacity of root system elements.

INTRODUCTION

This report is in several component parts. Substantial effort was continued on refined models of photosynthesis, dark respiration and transpiration of *Atriplex confertifolia* and *Ceratoides lanata*. Calculations of soil water extraction using soil moisture content data have been undertaken to corroborate the estimates of water loss by transpiration in these communities.

A second intensive year of study on root respiration capacity was concluded. Studies were also extended on root growth activity, soil respiration and a second phase of the study initiated in 1975 to assess the impact of partial foliage removal on above- and below-ground productivity and other elements of the carbon balance of *Atriplex confertifolia*. Studies were also continued on labile carbon components of this species.

OBJECTIVES

General goals of this project were to:

1. Relate plant gas exchange and other physiological processes of Great Basin shrubs to the productivity, water use and carbon balance of communities dominated by these plants.
2. Assess the effects of perturbations, such as partial foliage removal, on elements of the carbon balance of these plants.

During 1976, our specific objectives were to:

1. Further refine gas exchange models for *Atriplex confertifolia* and *Ceratoides lanata*.
2. Continue studies on the respiratory capacity of root elements of *Atriplex* collected in the field.
3. Continue studies on the impact of partial foliage removal in *Atriplex*-dominated communities on elements of the carbon balance.
4. Continue a second year of determinations of the labile carbon components of *Atriplex*, with and without defoliation pressure.
5. Monitor relative root growth rate activity of *Atriplex* and *Ceratoides* growing in mixed communities, using the field soil observation chambers.
6. Determine precipitation and soil moisture content levels at several depths in the communities dominated

by *Atriplex*, *Ceratoides* and a mixed community of these two species.

7. Determine soil respiration in communities dominated by *Atriplex*.

METHODS

Field studies conducted during 1976 were carried out, as in previous years, at our research site west of the Wildcat Hills in Curlew Valley.

The basic structure of the plant gas exchange model was detailed in the 1975 progress report (Caldwell et al. 1976) and will not be repeated here. The basic structure of these models has not changed; it is merely a refinement of parameters being used in the model. Similarly, all of the other techniques and experimental approaches used during 1976 have already been detailed in earlier reports of this project.

RESULTS

Refined gas exchange models for *A. confertifolia* and *C. lanata* are represented in Figure 1. These are based on the years of 1973 and 1974, which represent moist and dry 12-month periods, respectively.

Table 1 contains precipitation data for 1976 (DSCODE A3UCB39) and Table 2 reports soil moisture content values at several depths in the profile of communities of pure *Atriplex*, pure *Ceratoides* and a mixed stand of the two species (A3UCB36).

Profiles of relative root growth activity are contained in Figures 2 and 3. This is the first year in which growth activity of roots of *A. confertifolia* and *C. lanata* has been measured and reported when growing in mixed communities.

The ratio of foliage:above-ground biomass in *A. confertifolia* is reported in Table 3 (A3UCB31).

The impact of partial foliage removal on *A. confertifolia* was assessed again during 1976. This experiment was initiated in 1975. In late spring of 1975, several plots of a nearly monospecific community of *A. confertifolia* were subjected to partial foliage removal. The objectives of this

experiment were to observe the effects of this foliage removal on several aspects of the carbon balance of these communities over a two-year period. During 1976, the second year of this experiment, several parameters were measured in these communities. The accumulated litter deposition of control plants and plants subject to pruning in 1975 is represented in Figure 4 (A3UCB38). The seasonal distribution of this litter drop is represented for pruned and control plants in Figure 5. Figure 6 contains the 1976 values of soil respiration for the control and treatment plots of the *Atriplex* community (A3UCB25).

Plants within the pruned and control treatment areas were labeled with $^{14}\text{CO}_2$ in the spring of 1976 as part of the below-ground turnover assay. The relative radioactivity of $^{14}\text{CO}_2$ efflux from the soil surface following this labeling period is contained in Table 4 (A3UCB34) for the control and pruned treatment plots.

The below-ground turnover coefficients, early season biomass and below-ground productivity are shown in Table 5 (A3UCB27). Table 6 contains the average weight of foliage and stem materials from the plants that were used in the litter deposition determinations. These plants were harvested in the fall of 1976. Plant materials from both the pruned and control plants in this experiment were also subjected to labile carbon analysis several times during the year. Labile carbon in the form of percentage sugars and starch are given for these two groups of plants in Table 7 (A3UCB34).

Studies of *Atriplex* root element respiration were continued in 1976. As in 1975, the respiration rates of excised root elements from three depth intervals in the soil profile were assayed at 12 C. Sampling was repeated at two-week intervals from mid-April until late July. The results of these measurements are shown in Figure 7 (A3UCB37), which also depicts patterns of temperature and water content in the soil profile.

Table 1. Average precipitation in the *Atriplex confertifolia* study plot (A3UCB39)

Collection dates	Precipitation (mm)
12-8-75 to 4-2-76	48
4-2-76 to 4-21-76	29
4-21-76 to 5-5-76	7
5-5-76 to 5-17-76	16
5-17-76 to 6-4-76	14
6-4-76 to 6-14-76	0
6-14-76 to 7-21-76	0
7-21-76 to 8-13-76	0
8-13-76 to 9-2-76	22
9-2-76 to 9-15-76	9
9-15-76 to 10-5-76	30
10-5-76 to 11-23-76	0
11-23-76 to 12-13-76	0

Table 2. Mean soil moisture percentage by volume at several depths under (a) *Atriplex confertifolia*, (b) *Ceratoides lanata* and (c) a mixed stand composed of both species (A3UCB36)

a. <i>Atriplex confertifolia</i>									
Depth (cm)	Apr 19	May			Jun 30	Jul 21	Aug 13	Sep 2	Oct 5
		5	15	28					
10	4.5	3.5	3.5	2.5	1.5	1.5	1.0	1.5	4.1
20	11.5	11.5	9.0	6.0	1.0	1.0	0.5	2.0	6.9
30	21.0	21.0	20.0	15.0	7.0	6.0	5.5	6.5	9.6
40	17.5	18.5	18.5	15.0	8.5	8.0	7.5	7.5	7.9
50	12.0	13.0	13.5	11.5	8.0	8.0	7.5	7.5	7.4
60	8.5	10.0	10.5	9.5	7.5	7.5	7.5	7.5	7.4
70	7.5	8.5	9.0	8.5	7.0	8.0	7.5	7.5	7.9
80	7.5	9.0	9.5	8.5	8.0	9.0	8.5	8.5	8.5
90	9.0	10.5	10.5	9.5	9.5	10.5	10.0	10.0	10.1
100	10.0	11.5	12.0	11.0	11.0	12.0	11.5	11.5	11.2

b. <i>Ceratoides lanata</i>									
Depth (cm)	Apr 20	May 5	Jun		Jul 21	Aug 13	Sep 2	Oct 5	
			14	30					
15	2.5	.5	.8	.5	.5	.5	.5	1.4	
30	13.3	8.5	3.5	.8	.5	.9	1.4	5.2	
45	12.8	10.6	5.8	3.5	3.5	3.0	3.0	4.1	
60	8.5	9.5	7.9	5.8	5.8	5.8	5.2	6.2	
90	9.0	10.1	9.5	9.0	8.5	8.5	8.5	9.5	
120	8.5	9.5	9.0	8.5	8.5	8.0	8.5	10.1	

c. Mixed stand									
Depth (cm)	Apr 20	May 5	Jun		Jul 21	Aug 13	Sep 2	Oct 5	
			14	30					
15	1.5	.5	.5	.5	.5	.5	.5	.5	
30	14.0	6.2	3.5	.5	.5	.5	1.0	6.2	
45	15.0	10.1	5.8	3.5	3.0	2.5	2.5	4.1	
60	12.4	10.6	8.5	6.3	5.8	5.2	5.2	4.5	
90	9.5	8.5	10.1	9.5	9.0	9.0	8.5	7.9	
120	10.5	8.5	10.1	10.6	10.2	9.5	9.5	7.9	

Table 3. Foliage:shoot dry weight ratios for *Atriplex confertifolia* of different size classes (A3UCB31)

Date of Collection	<i>Atriplex confertifolia</i>		
	Small (10-50 g)	Intermediate (50-150 g)	Large (150-300 g)
4-2-76	0.19 ±	0.12 ±	0.10 ±
σ ²	0.02	0.02	0.01
4-21-76	0.24 ±	0.12 ±	0.13 ±
σ ²	0.03	0.03	0.03
5-17-76	0.31 ±	0.26 ±	0.16 ±
σ ²	0.04	0.05	0.03
6-4-76	0.35 ±	0.29 ±	0.29 ±
σ ²	0.03	0.02	0.02
6-30-76	0.27 ±	0.31 ±	0.22 ±
σ ²	0.03	0.03	0.04
8-13-76	0.28 ±	0.25 ±	0.26 ±
σ ²	0.04	0.02	0.03
9-15-76	0.27 ±	0.25 ±	0.20 ±
σ ²	0.04	0.03	0.03

Table 4. Carbon dioxide efflux and relative ^{14}C activity of CO_2 efflux from small plots (A3UCB34)

Plot series	Dates	Treatment	$\text{mg CO}_2 \cdot \text{m}^{-2} \cdot \text{day}^{-1}$		$\text{dpm} \cdot \text{m}^{-2} \cdot \text{day}^{-1}$	
			Under shrub	Between shrubs	Under shrub	Between shrubs
Not applicable	4-2 to 4-21-76	unclipped	3.05×10^3	3.26×10^3	--	--
Not applicable	4-21 to 5-5-76	unclipped	3.33×10^3	3.31×10^3	--	--
Not applicable	5-5 to 5-17-76	unclipped	3.93×10^3	3.86×10^3	--	--
A	5-17 to 6-4-76	clipped	3.53×10^3	3.43×10^3	5.77×10^6	5.14×10^6
B	5-17 to 6-4-76	unclipped	3.74×10^3	3.75×10^3	1.44×10^7	1.42×10^7
A	6-4 to 6-14-76	clipped	3.04×10^3	3.06×10^3	2.77×10^6	2.78×10^6
B	6-4 to 6-14-76	unclipped	3.26×10^3	3.26×10^3	5.49×10^6	4.89×10^6
A	6-14 to 6-30-76	clipped	2.54×10^3	2.48×10^3	3.17×10^5	3.29×10^5
B	6-14 to 6-30-76	unclipped	2.32×10^3	2.25×10^3	6.12×10^5	5.75×10^5
A	6-30 to 7-21-76	clipped	1.75×10^3	1.74×10^3	2.02×10^4	2.04×10^4
B	6-30 to 7-21-76	unclipped	1.84×10^3	1.85×10^3	3.00×10^4	2.88×10^4
A	7-21 to 8-13-76	clipped	1.48×10^3	1.54×10^3	5.28×10^3	6.43×10^3
B	7-21 to 8-13-76	unclipped	1.60×10^3	1.58×10^3	8.93×10^3	8.93×10^3
A	8-13 to 9-2-76	clipped	1.40×10^3	1.33×10^3	4.55×10^3	4.53×10^3
B	8-13 to 9-2-76	unclipped	1.48×10^3	1.51×10^3	7.83×10^3	7.45×10^3
A	9-2 to 9-15-76	clipped	1.48×10^3	1.42×10^3	4.34×10^3	4.08×10^3
B	9-2 to 9-15-76	unclipped	1.56×10^3	1.58×10^3	5.00×10^3	5.50×10^3
A	9-15 to 10-5-76	clipped	1.40×10^3	1.36×10^3	2.30×10^3	2.55×10^3
B	9-15 to 10-5-76	unclipped	1.49×10^3	1.49×10^3	2.83×10^3	2.85×10^3

Table 5. Below-ground turnover coefficients, biomass and productivity in 1976 of *Atriplex confertifolia* plots subjected to partial foliage removal in 1975 with comparable values for control plots (A3UCB27)

Depth (cm)	Pruned			Control		
	Turnover coefficient	Biomass ($\text{g} \cdot \text{m}^{-2}$)	Production ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)	Turnover coefficient	Biomass ($\text{g} \cdot \text{m}^{-2}$)	Production ($\text{g} \cdot \text{m}^{-2} \cdot \text{yr}^{-1}$)
5-30	0.047	983.9	46.2	0.103	818.8	84.3
30-60	0.052	415.2	21.6	0.086	440.5	37.9
60-90	0.029	234.1	6.8	0.092	238.4	21.9
Total profile	0.043	1633.2	74.6	0.094	1497.7	144.1

Table 6. Average weight of above-ground plant parts for individual *Atriplex* plants (A3UCB21)

Plant parts	Average weight (g)	
	Pruned	Control
Foliage	23.3	32.3
Stems	179.8	283.5

Table 7. Percent labile carbon in ethanol-soluble (sugars) and acid-hydrolyzable (starch) components based on tissue dry weight for the *Atriplex*-dominated community (A3UCB34)

Plant organs	Treatment	4-21-76		5-5-76		5-17-76		6-4-76		6-30-76		9-15-76	
		% sugar	% starch	% sugar	% starch	% sugar	% starch	% sugar	% starch	% sugar	% starch	% sugar	% starch
Winter leaves	Unclipped	0.34	5.92	--	--	--	--	--	--	--	--	--	--
	Clipped	0.60	7.28	0.30	4.97	--	--	--	--	--	--	--	--
New-growth leaves	Unclipped	--	--	--	--	--	--	1.17	6.39	--	--	1.06	5.81
	Clipped	--	--	0.32	0.46	--	--	--	--	--	--	0.40	3.74
New-growth stems	Unclipped	0.59	0.97	--	--	--	--	1.86	1.25	--	--	0.89	5.47
	Clipped	0.73	5.61	--	--	--	--	--	--	--	--	1.04	5.06
Old-growth stems	Unclipped	0.97	2.42	0.59	2.65	0.78	6.37	1.54	1.37	7.35	8.05	1.20	6.19
	Clipped	0.55	5.19	0.30	9.04	--	--	1.46	8.36	<0.02	4.86	0.94	5.00
New-growth leaves and stems	Unclipped	--	--	0.42	5.14	0.96	6.65	--	--	1.48	7.14	--	--
	Clipped	--	--	--	--	1.45	5.63	1.55	1.41	<0.02	8.92	--	--
Taproot	Unclipped	--	--	0.92	0.91	1.87	10.56	2.64	6.92	4.55	10.47	6.09	9.02
	Clipped	--	--	0.53	1.81	1.17	6.93	2.78	7.40	0.71	3.29	3.12	6.72
Diffuse root (5-30 cm)	Unclipped	--	--	--	--	<0.02	3.43	--	--	--	--	3.07	6.26
	Clipped	--	--	--	--	<0.02	6.26	--	--	--	--	1.94	4.10
Diffuse root (30-50 cm)	Unclipped	--	--	--	--	<0.02	3.88	--	--	--	--	1.69	5.80
	Clipped	--	--	--	--	<0.02	4.63	--	--	--	--	1.32	3.08
Diffuse root (50-70 cm)	Unclipped	--	--	--	--	<0.02	4.10	--	--	--	--	2.60	4.05
	Clipped	--	--	--	--	<0.02	4.76	--	--	--	--	1.71	3.09

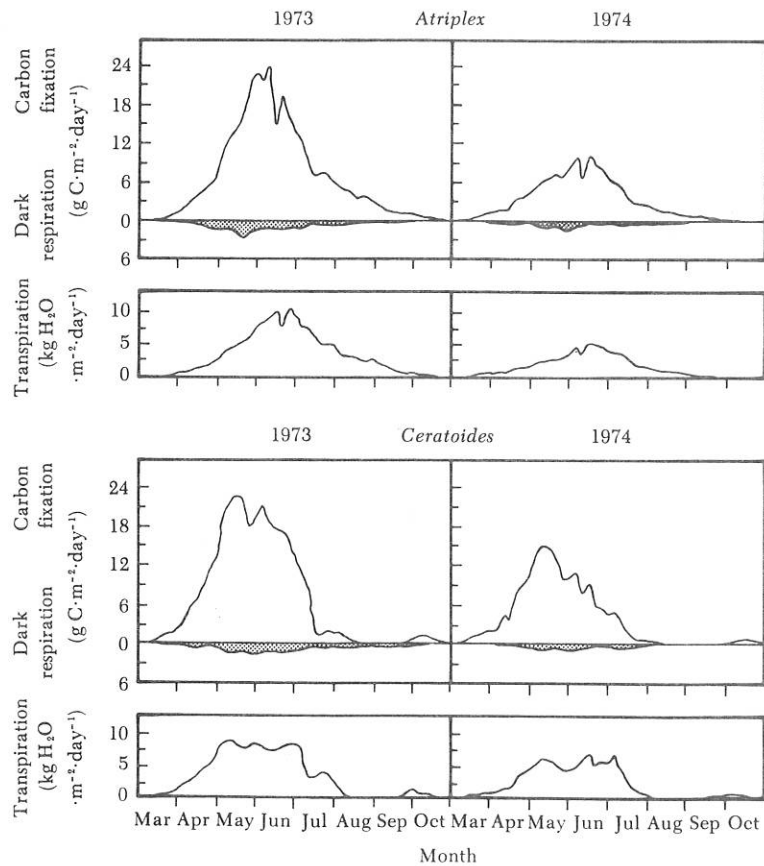


Figure 1. Seasonal progression of photosynthetic carbon fixation, dark respiration and transpiration for 1973 and 1974 for the *Atriplex* and *Ceratoides* communities. Gas exchange rates per foliage mass were derived from the model operating on the meteorological data for these two years. The seasonal progression of foliage mass per ground area in the two communities was derived from biweekly foliage:biomass ratio determinations, community biomass assessments and other information on community structure.

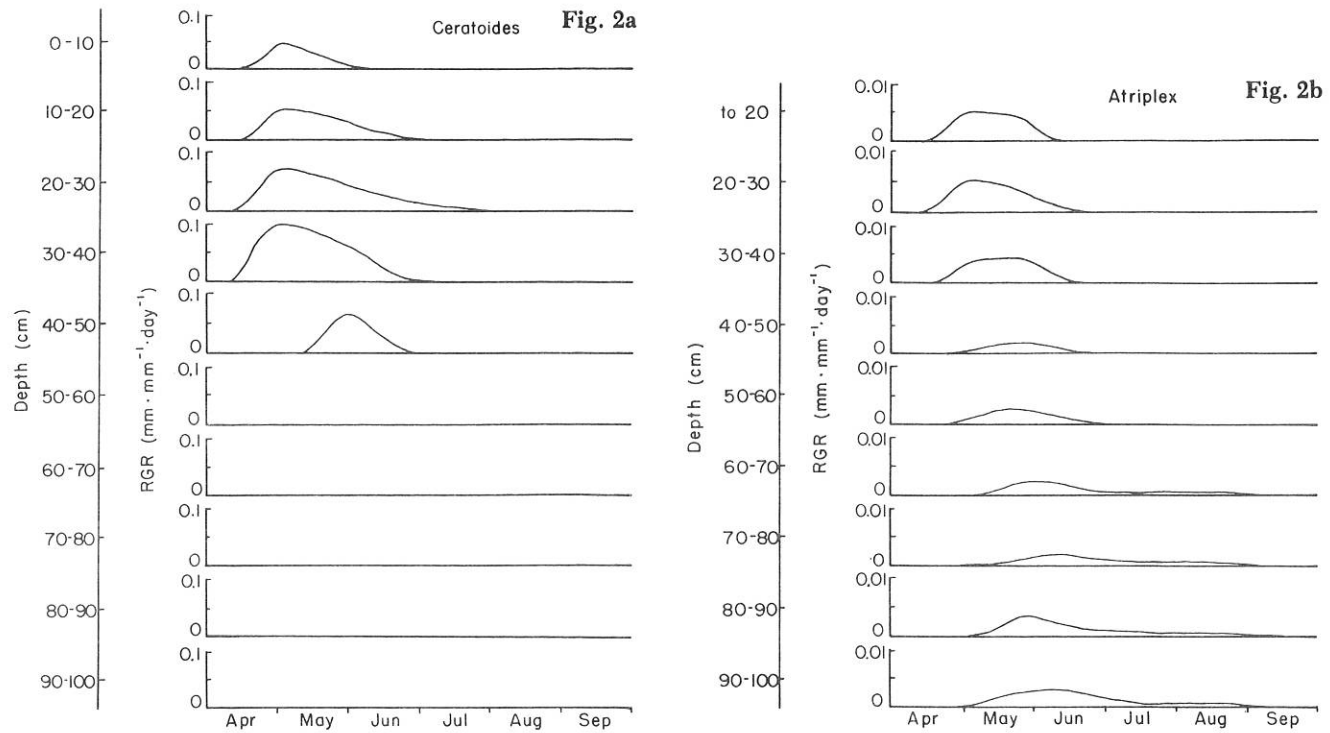


Figure 2. Relative root growth activity of *Ceratoides lanata* (a) and *Atriplex confertifolia* (b) growing in monospecific stands.

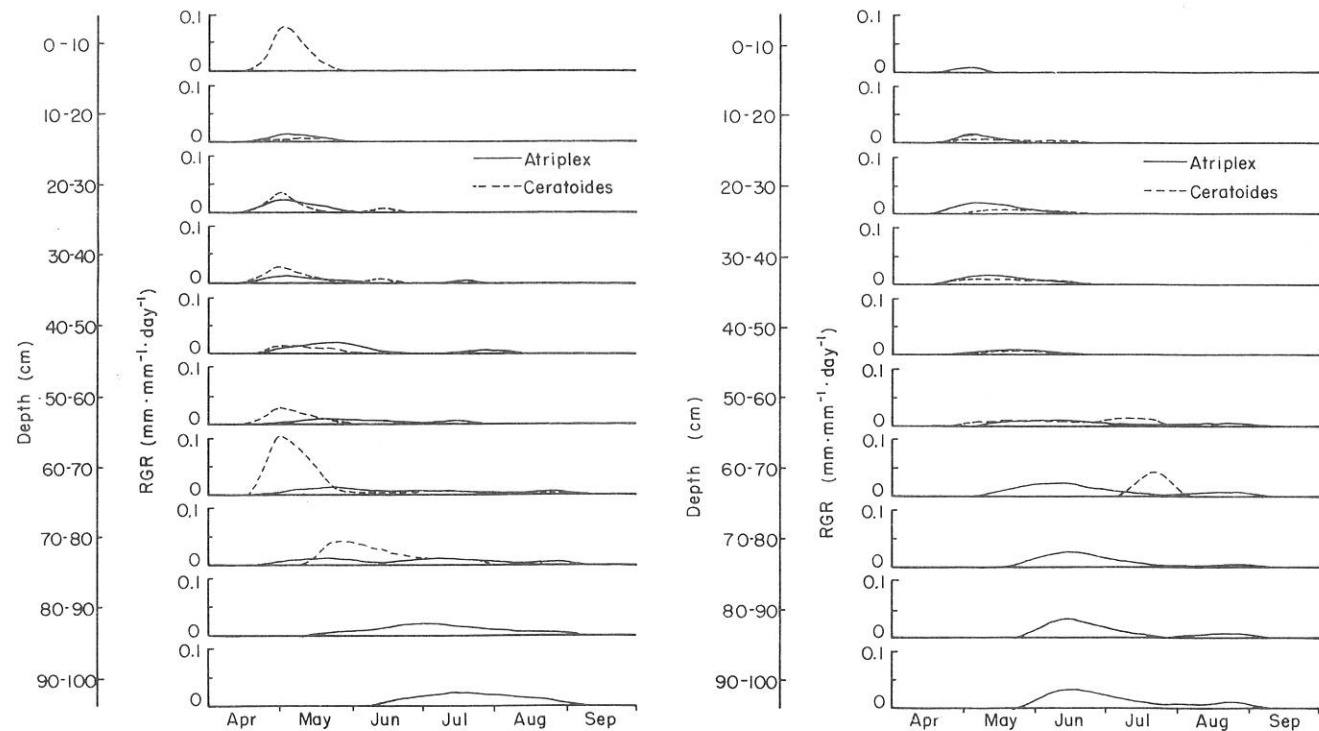


Figure 3. Relative root growth activity of *Atriplex confertifolia* and *Ceratoides lanata* growing in mixed communities; replicates from two different observation chambers.

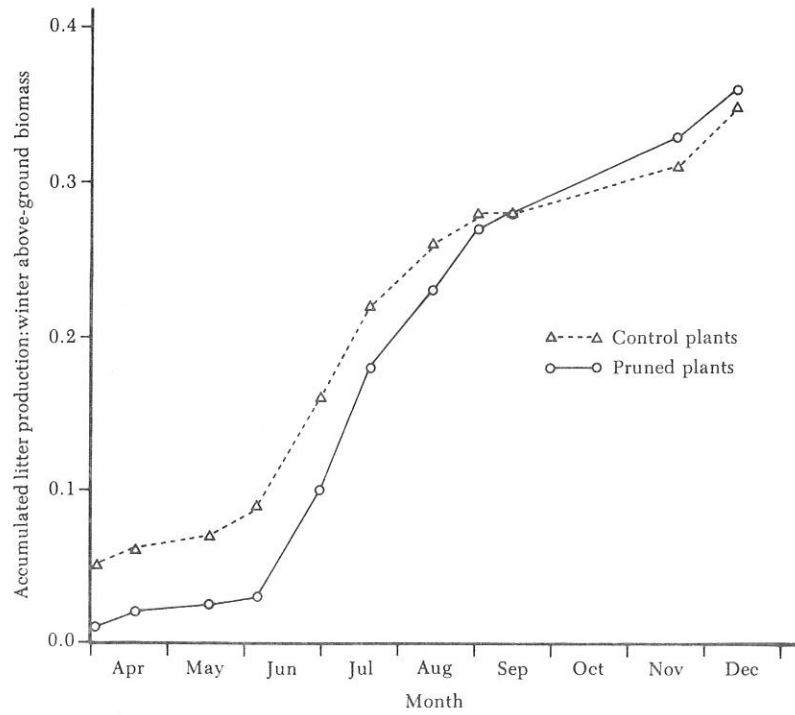


Figure 4. Accumulated litter production in 1976 for *Atriplex* plants which were clipped in 1975 and for unclipped plants. Litter production is represented as a fraction of the plant's above-ground winter biomass.

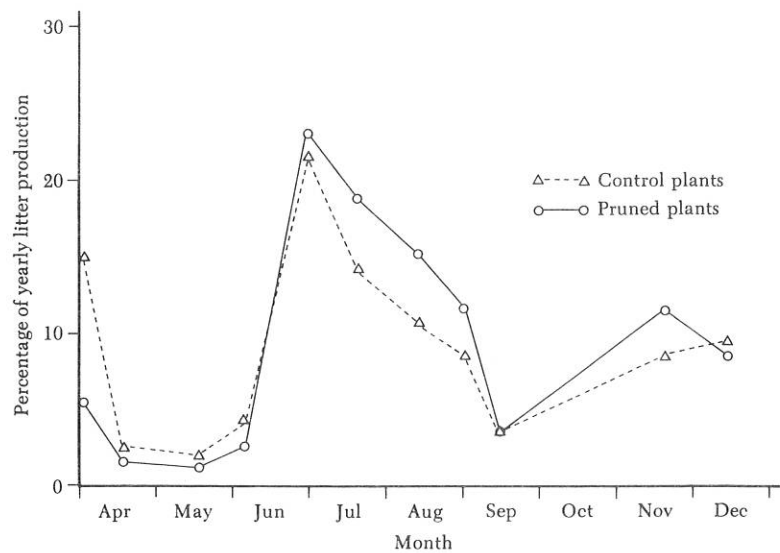


Figure 5. Seasonal distribution of litter production in 1976 for *Atriplex* plants which were clipped in 1975 and for unclipped plants.

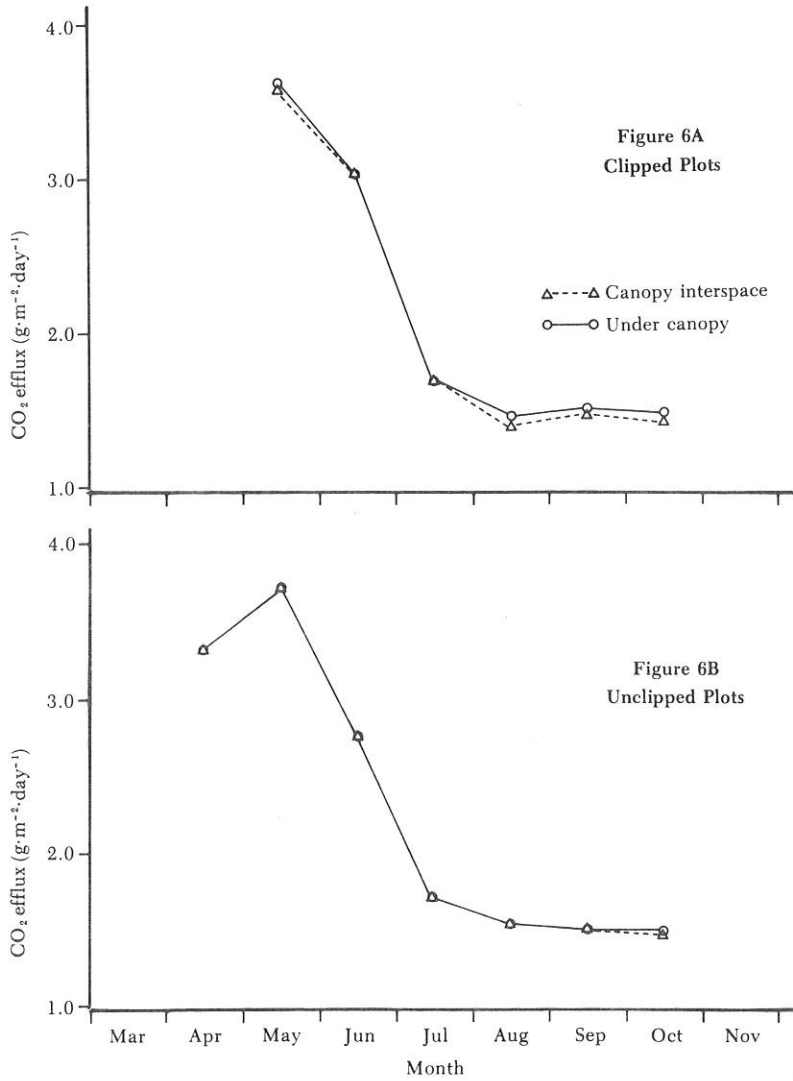
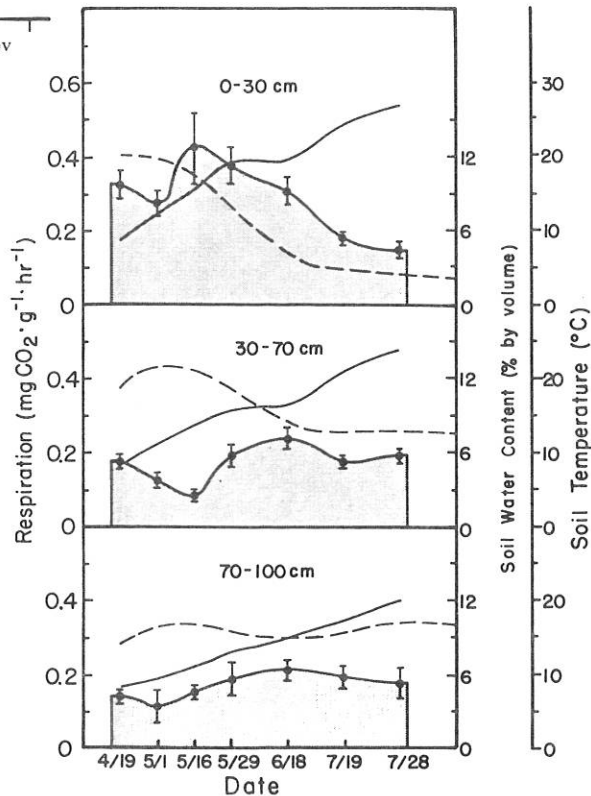


Figure 6. Carbon dioxide efflux at the soil surface during the 1975 season for *Atriplex confertifolia*-dominated communities: (A) plots subjected to foliage removal in June 1975; (B) control plot. Carbon dioxide was collected both in the canopy interspace and under the canopy of shrubs (A3UCB25).

Figure 7. Soil temperature (—), soil water content (---) and excised root respiration assayed at 12 C (shaded curve) in three depth intervals during the 1976 growing season. Respiration values are shown plus or minus one standard error. Nonoverlapping error bars indicate significant differences between dates. Respiration data points represent means of 8 to 16 replicates.



DISCUSSION

The refined gas exchange model results for *A. confertifolia* and *C. lanata* (Fig. 1) for 1973 and 1974 yield values of total photosynthetic carbon fixation in these communities (240 and 223 g carbon·m⁻²·yr⁻¹, respectively), which appear to be very realistic when compared with other facets, which were determined independently, of the carbon balance of these communities. A manuscript describing the complete carbon balance of these communities has recently been submitted for publication. The mean annual transpiration for this two-year period was 11.7 and 12.3 cm for the *Atriplex* and *Ceratoides* communities, respectively (values taken from Fig. 1). Based on these values of community photosynthesis and transpiration over this two-year period, there is little indication that the *Atriplex* community either fixes significantly more carbon or transpires much less water in the course of this carbon fixation than the *Ceratoides* community. The annual transpiration of these communities, based on the gas exchange model determinations, suggests that only half of the annual precipitation was available for transpiration by the vegetation in these two sites. In order to provide an independent estimate of water transpired in these communities, annual water extraction from the profile was calculated from soil moisture content data of four years. These values are represented as the ratio of water extraction:annual precipitation for the four years in Figure 8. In the same figure, the ratios of annual transpiration:precipitation, based on the values of Figure 1, are presented. Although calculations of water extraction based on moisture content data necessarily involve assumptions on the fate of moisture in the uppermost layer of the profile, it appears that the proportion of annual precipitation ultimately transpired by the vegetation is about the same when determined by independent methods. Only approximately half of the annual precipitation (54%) during the six years represented is ultimately channeled through the transpiration stream of the vegetation, and the two communities appear to transpire equivalent amounts of water on an annual basis. Since there is essentially no overland flow in this nearly level basin nor loss of moisture to ground water or subsurface flow, over an extended period of time, moisture not transpired would necessarily be lost, either directly from the snowpack during the winter months or from soil surface evaporation. Direct measurements of these specific components of the hydrologic balance have not, however, been made.

Results from the two-year experiment involving partial foliage removal in an *A. confertifolia* community indicate that, even in the second year, effects of the spring 1975 foliage removal are still apparent. Differences in the accumulated litter deposition -- and particularly the timing of this litter deposition during the course of the season -- are apparent (Figs. 4 and 5). There is, however, no apparent difference in the CO₂ efflux from the soil surface for the two treatments during 1976 as was the case in 1975.

Since most of the productivity in these communities takes place below ground, the effects of foliage removal on

below-ground productivity may be of sizable quantitative importance. During the first year (Caldwell et al. 1976), there was no apparent difference in the below-ground turnover or productivity of the plots subject to foliage removal. This is contrary to classical reports with many horticultural shrubs. During 1976, the effects of the 1975 foliage removal became apparent in the below-ground system (Table 5). At all depths in the profile, the turnover coefficient of the control plots was consistently about twice as great as that of the plots subject to foliage removal in 1975. Although the biomass at the beginning of the year was essentially comparable in the two communities, the lower turnover coefficients of the pruned community were reflected in below-ground productivity, which was about half that of the control plots.

Patterns of root respiratory adjustment in 1976 (Fig. 7) generally tended to corroborate the observations made in 1975, but there was also strong evidence of year-to-year variation in root respiratory patterns. Variations from year to year could be partially dependent on precipitation patterns. Precipitation in 1975 was above normal, while the 1976 growing season was drier than normal.

From mid-April to late May in 1976, respiratory capacity of root segments from the 0-30 cm depth interval was significantly greater than respiratory capacity of root segments from greater depths. This relationship was maintained despite the fact that respiratory capacity of roots from all three depth intervals declined between mid-April and early June. This decrease could not be demonstrated statistically, but the observation of simultaneous decreases in respiration at all depths suggests that a reduction did occur. A decrease in respiratory capacity in early summer is difficult to explain from either a physiological or adaptive viewpoint, but it may be related to the expansion of new leaves on *A. confertifolia* in late April.

By May 16, respiratory capacity of root segments from the upper 30 cm of the soil profile had again increased and reached the maximum value observed during 1976. Respiratory capacity of root segments from below 30 cm showed little concurrent change, so the bulk of root zone activity was clearly located in the upper 30 cm of the soil profile at this time.

During late May and early June, respiratory capacity of root segments from the upper 30 cm decreased, while the capacity of root segments from below 30 cm increased. By June 18, root segments from the 30-70 cm depth interval attained their maximum observed respiratory capacity for the 1976 season, while respiratory capacity of root segments from the upper 30 cm had declined significantly. Respiration values of segments from the 70-100 cm depth interval appeared to increase during this period, but the change was not statistically significant. This pattern of simultaneous respiratory adjustments proceeding in opposite directions for different portions of the root system was similar to the pattern observed during July of 1975. However, in 1976, the respiratory capacity of root segments

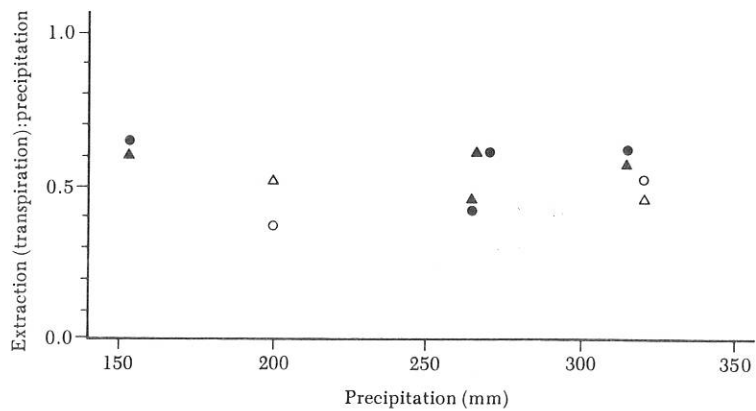


Figure 8. Annual water extraction from the soil profile in the *Atriplex* (\blacktriangle) and *Ceratoides* (\bullet) communities calculated from water content data of four years and represented as a fraction of the annual precipitation for the water year (October through September). Annual transpiration water loss derived from the gas exchange model for the two years depicted in Figure 1 is also represented as a fraction of the annual precipitation during the water year for the *Atriplex* (\triangle) and *Ceratoides* (\circ) communities.

from below 30 cm was never observed to exceed the capacity of segments from the upper 30 cm, as had been the case in 1975.

Respiration at 12 C of root segments from the upper 30 cm continued to decline throughout late June and July, while there were no significant changes in respiratory capacity of root segments from below 30 cm during this same period. As a result, the respiratory capacities of roots from all three depth intervals were virtually identical throughout the month of July. Thus, patterns of root respiratory activity in 1976 were similar to those observed in 1975, but the peaks of activity occurred earlier in the growing season in 1976 and the maximum respiration values were lower in 1976 than they had been in 1975. These differences in root respiratory activity between years may be associated with the more rapid depletion of soil moisture in 1976, as compared to 1975.

The overall pattern of respiratory adjustment of *A. confertifolia* roots appears to allow root function when conditions are favorable for uptake processes, and to reduce carbon usage to a minimum rate when soil conditions are unfavorable. It should be noted, however, that the apparent relationship between water extraction and respiratory capacity varies with depth in the soil profile. This occurs because roots from the top 30 cm in the soil profile reach their maximum seasonal respiratory capacity several weeks before roots from greater depths reach maximal capacity, while water extraction proceeds nearly synchronously throughout the soil profile. As a result, roots in the upper 30 cm reach maximum respiratory capacity just as water extraction begins to proceed rapidly. Respiratory capacity then declines quickly as soil water in the top 30 cm is depleted. In contrast, at depths below 30 cm in the profile, high rates of water extraction are observed while roots are still at moderate levels of respiratory capacity. The

respiratory capacity of these roots then slowly increases as water extraction proceeds. Maximum respiratory capacity is reached just shortly before the rate of water extraction declines, and then the respiratory capacity of roots below 30 cm also begins to decrease.

This progression of root respiratory activity, from upper to lower soil horizons during the growing season, is similar to the seasonal progression of root growth observed in *A. confertifolia*. Consequently, neither the growth activity nor the respiratory activity of the root system seems to be clearly related to changes in soil water. However, the delay observed in root system activity at greater depths in the soil may fulfill a function which is not so obviously related to water extraction. Since nutrient uptake is an active process which can be accelerated by both root metabolism and root growth, we might speculate that the seasonal progression of root zone activity is more closely linked to nutrient uptake than it is to water extraction. The delay in root zone activity at depths below 30 cm might then be interpreted as a strategy for prolonging the period of nutrient uptake past the time when the most readily available moisture and nutrients have already been extracted from the soil.

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