DISSERTATION

EFFECTS OF WATER AND NITROGEN STRESSES ON A SHORTGRASS PRAIRIE ECOSYSTEM

Submitted by

William K. Lauenroth

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WE HEREBY RECOMMEND THAT THE DISSERTATION PREPARED UNDER OUR SUPERVISION BY WILLIAM K. LAUENROTH ENTITLED EFFECTS OF WATER AND NITROGEN STRESSES ON A SHORTGRASS PRAIRIE ECOSYSTEM BE ACCEPTED AS FULFILLING IN PART REQUIREMENTS FOR THE DEGREE OF DOCTOR OF PHILOSOPHY.

Committee on Graduate Work

George Innis

CPP Reid

R M Hansen

Phillip L. Sims
Adviser

C. Wayne Cook
Head of Department

ABSTRACT OF DISSERTATION

EFFECTS OF WATER AND NITROGEN STRESSES ON A SHORTGRASS PRAIRIE ECOSYSTEM

Responses of a shortgrass prairie ecosystem to stresses created by excess inputs of water and nitrogen were studied during a two year period in northeastern Colorado. Nitrogen stress was created by maintaining soil mineral nitrogen at not less than 50 kg/ha greater than the control. Water stress was induced by maintaining soil water potential greater than -0.8 bars during the growing season.

Responses measured were net primary productivity, species composition and organization of primary producers, evapotranspiration, and small mammal densities.

Net primary productivity was more responsive to water and nitrogen in combination than to either individually. Aboveground contribution to net primary productivity was more sensitive to stresses than the belowground contribution. Ratios of above- to belowground productivity were increased by all stresses.

The major effect of stresses on species composition of primary producers was to reorder existing species relationships and increase the number of species coexisting on the treatments.

Primary producer organization (successional state) was assessed by diversity and dominance calculations. After two years of treatment the primary producers on the nitrogen treatment were at the highest level of

organization and those of the water plus nitrogen treatment at the lowest level.

Evapotranspiration of the treatments receiving additional water was close to the potential rate. The primary producers of the shortgrass prairie do not have the capacity to limit transpiration under conditions of high water availability.

Small mammal species demonstrated clear habitat preferences to the treatments. The prairie vole was caught almost exclusively on the water plus nitrogen treatment. The deer mouse was captured in approximately equal proportions on the water and the water plus nitrogen treatments and in much lower numbers on the remaining treatments. The grasshopper mouse and thirteen lined ground squirrel were caught in low numbers on the water treatments and in significantly higher numbers on the control and nitrogen treatments.

William K. Lauenroth
Range Science Department
Colorado State University
Fort Collins, Colorado 80521
August, 1973

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INTRODUCTION

Available soil water and mineral nitrogen are probably the most important nutrients limiting primary productivity in temperate terrestrial ecosystems. Certainly, they are the most frequently encountered limiting factors in the shortgrass region of the Great Plains of North America. The status of soil water and mineral nitrogen as important limiting factors gives them special value as variables to be manipulated in investigating shortgrass prairie ecosystems. Altering the quantities of these two variables within the range of variation normally encountered by the shortgrass ecosystem should produce responses identical to those that would be recorded by long term study of the ecosystem. Stress, defined as conditions caused by either a lack of or excess of inputs (Meier 1972), can be induced in the system by manipulating the levels of these two variables beyond the range normally encountered by the system. Such stresses should produce responses different from those recorded by long term study and should cause significant changes in the structural and functional attributes of the system. This type of experimental approach to the study of ecosystems should provide information about the system not obtainable by simply observing its normal dynamics.

Responses of ecosystems to stresses have been widely studied for aquatic ecosystems (Odum 1971) primarily because of the impetus provided by pollution. No such force has been present to stimulate interest in the response of terrestrial systems to stresses except in the case of biocides. Although the results of experiments involving stresses to terrestrial ecosystems caused by excess nutrient inputs are primarily of academic interest, they have the potential of providing much needed basic information about ecosystems. The only results of this nature available now are fertilizer and irrigation studies designed to investigate the effects of increased nutrients on the potential economic return from the land. This study was designed to investigate the effects of excess nitrogen and water on certain properties of the ecosystem.

The objective of this study was to examine the following hypotheses concerning a specific shortgrass prairie ecosystem subjected to water and nitrogen stresses (i.e., excess inputs).

I. Water and nitrogen stresses will increase net primary productivity.

II. Water and nitrogen stresses will differentially influence species group contribution to net primary productivity.

III. There is a positive interaction between water and nitrogen on net primary productivity.

IV. Net primary productivity is limited by the following: water on the control and the nitrogen treatments; nitrogen on the water treatment; phosphorous, light or CO_2 on the water plus nitrogen treatment.

V. Species composition of primary producers will change under the influence of water and nitrogen stresses.

VI. Water and nitrogen stresses will result in change in the successional state of the primary producers but not necessarily to any previous state of the system.

VII. Evapotranspiration from the treatments receiving supplemental water is limited more by internal plant resistances than by the availability of energy.

VIII. Small mammal species composition and biomass will be altered by water and nitrogen stresses.

EXPERIMENTAL DESIGN AND TREATMENTS

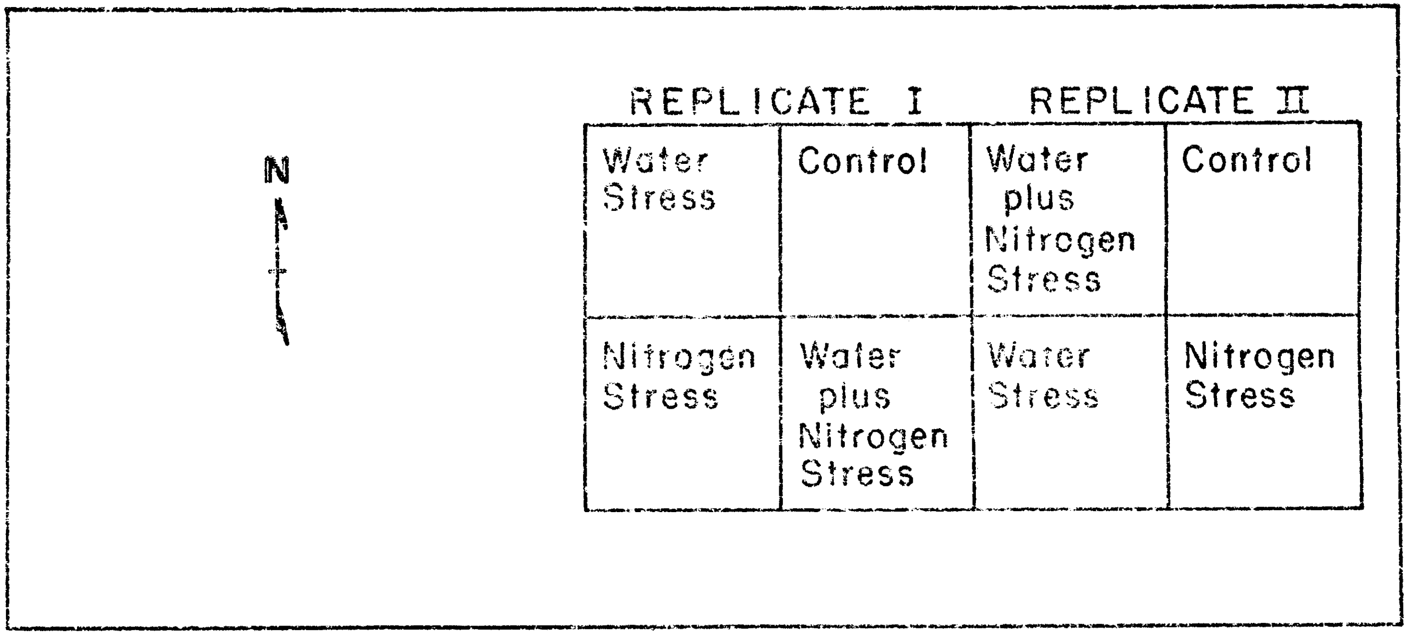
The experimental design consisted of two replications of four treatments (Figure 1). Each treatment replicate was located on a one hectare plot. The stress treatments were as follows: control; water; nitrogen; water plus nitrogen.

The nitrogen stress treatment consisted of maintaining a difference of at least 50 kg/ha of mineral nitrogen (NH_4 + NO_3) between the nitrogen stress and control treatments. This was accomplished initially by an application of 150 kg/ha of nitrogen as ammonium nitrate in the spring of 1970. In the spring of 1972 an additional 150 kg/ha of nitrogen was applied to the water and nitrogen stress treatments. The major criterion for choosing this as the nitrogen stress was to insure that the treatment was beyond the normal range of variation in soil mineral nitrogen normally encountered by the shortgrass prairie. This is also true of the water stress treatment.

The water stress treatment was initiated in 1971 and involved maintaining soil water potential above -0.8 bars at a depth of approximately 10 cm. The choice of -0.8 bars as the lower limit for soil water potential corresponds to the lower limit measurable with tensiometers. Soil water potential rarely got below -0.6 bars before watering was started. As implied above soil water potential was monitored by tensiometers and these were checked daily. The majority of the supplemental water was applied at night to minimize conflicts with sample collection activities. Water was applied by an individually controllable sprinkler

Figure 1. Exclosure and layout of stress treatments on a shortgrass prairie in northeastern Colorado.

ECOSYSTEM STRESS AREA



system on each one hectare plot. The sprinkler system was designed to have a uniformity coefficient of 80% (Zimmerman 1966.

STUDY AREA

The study area is located in Weld County, northeastern Colorado on the Pawnee Site of the U. S. IBP Grassland Biome. A detailed description of the Pawnee Site is given by Jameson (1969). The eight experimental plots (Figure 1) are located within an exclosure on an Ascalon sandy loam soil. The exclosure was built in 1969 to exclude large animals from the area. Previous to fencing the area had been lightly grazed by cattle for at least 10 years.

The Pawnee Site is near the western border of the Great Plains and the climate is predominantly continental. Approximately 70 percent of the 225 to 338 mm of annual precipitation falls during the April to September growing season. Long term seasonal distribution of precipitation as well as the distributions for the growing seasons in 1971 and 1972 are shown in Figure 2. Long term monthly average maximum and minimum air temperatures are shown in Figure 3.

The natural vegetation of the study plots is characteristic of a large portion of the shortgrass prairie and is basically a blue grama *(Bouteloua gracilis)* grassland with a mixed low shrub and half-shrub overstory. The major species are; blue grama, fringed sagewort *(Artemisia frigida)*, scarlet globemallow *(Sphaeralcea coccinea)*, plains prickly pear *(Opuntia polyacantha)*, broom snakeweed *(Gutierrezia sarothrae)*, and needleleaf sedge *(Carex eleocharis)*. A complete list of species encountered in the study is given in Table 24.

Figure 2. Long term average monthly precipitation and growing season precipitation for 1971 and 1972 for a shortgrass prairie in northeastern Colorado.

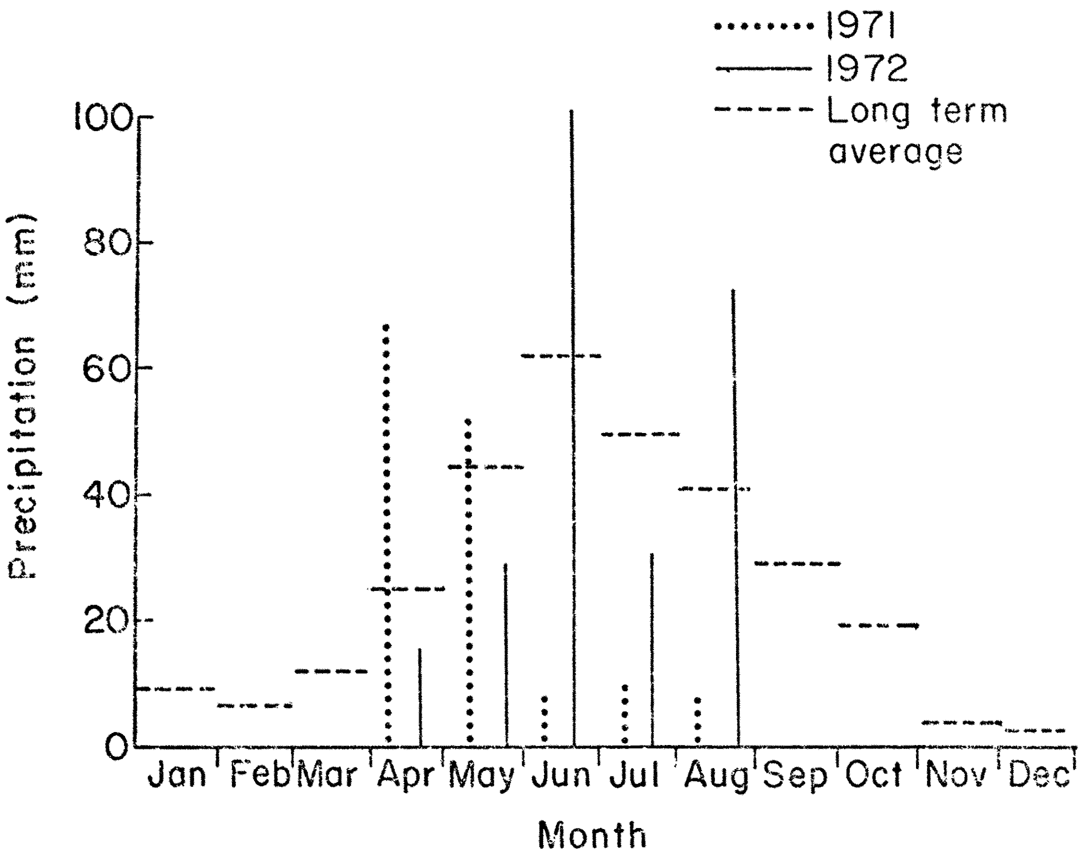
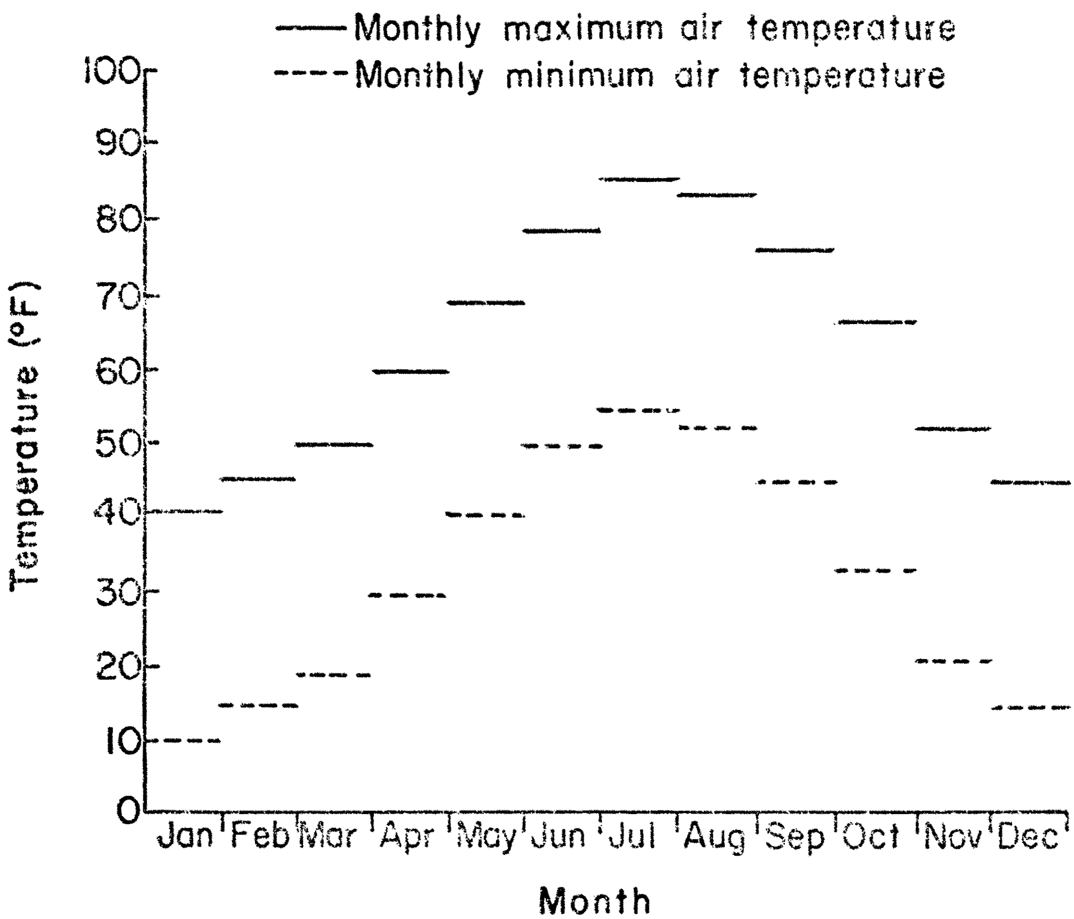

1971
1972
Long term average
Precipitation (mm)
100
80
60
40
20
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 3. Long term average monthly maximum and minimum air temperatures for a shortgrass prairie in northeastern Colorado.



Monthly maximum air temperature
Monthly minimum air temperature
Temperature (°F)
100
90
80
70
60
50
40
30
20
10
0
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

METHODS

Field Methods

Precipitation and Soil Water

Precipitation and water applied by the sprinkler system were measured by three rain gauges located in each watered plot and one rain gauge on each control plot. Soil water potential was monitored for each watered plot by three tensiometers. The rain gauges and tensiometers were checked daily during the growing season.

Soil water was measured by neutron moisture probe readings at 7 increments to a depth of 120 cm. Three access tubes per replicate or 6 tubes per treatment were sampled at approximately weekly intervals during the growing seasons of 1971 and 1972.

Biomass

Above- and belowground primary producer standing crop was sampled on all stress treatments during 1972, on nine dates beginning on April 4 and ending November 11. Samples were collected at approximately three week intervals from May 1 to September 4 and monthly intervals otherwise.

On each sample date the vegetation in 6 quadrats, 0.5 m^2 in area, was clipped at the soil surface and separated by species. After the quadrats were clipped, soil cores, 7.5 cm in diameter and 10 cm deep were collected for belowground primary producer standing crop. The number of 7.5 cm cores collected was either 2 or 3 per quadrat depending upon the sample date. On alternate sample dates a core 5 cm in diameter and approximately 60 cm deep was collected in place of one of the 7.5 cm diameter cores. Plant bases (crowns) were included with the belowground material.

All clipped material was placed in paper bags, oven dried to a constant weight, and weighed. All belowground samples were washed with water (Swift and French 1972), oven dried to a constant weight, weighed, ashed and then reweighed.

Botanical Composition

Primary producer density and basal cover were sampled in June of 1971 and 1972. Numbers of individuals of all species except blue grama, needleleaf sedge, six-week fescue and plains prickly pear were counted in 100 quadrats, 0.25 m^2 in area, per treatment. Plains prickly pear density represents the occurrence of live pads in the sample quadrats rather than the number of individuals. The remaining three species were not included in the density data, either because of the difficulty in distinguishing an individual or the excessive time required to count all of the individuals. All three species were included in the basal cover sampling. Basal cover was estimated using an inclined ten point frame and 1000 points per treatment were sampled. Basal hits were recorded by species and for a combined category of bareground and litter. The locations of the quadrats and the point frames were systematic to insure uniform coverage of the treatments.

Small Mammals

Live trap sampling was initiated in late July of 1971 and three trapping periods were completed during 1971. In 1972 sampling was begun in the spring and 5 trapping periods were completed. Each trapping period consisted of 5 nights.

The trap grid consisted of 42 traps on each plot making a total of 84 traps per treatment. Trapping and marking procedures followed Swift and French (1972).

Analytical Methods

Primary Productivity

Aboveground net primary productivity (ANPP) in g/m^2 was estimated using biomass data for species groups. The groups used were; warm season grasses, cool season grasses, warm season forbs and shrubs. Groups instead of individual species were used because of the variation in the estimates of standing crop for individual species. This was also the reason that succulents were excluded from the calculation. ANPP was estimated by summing the peak standing crop of the various groups. It was assumed that at the time of peak standing crop that all of the previous year's dead material had been incorporated into the litter. There are several major sources of errors for this method of calculating ANPP. The most important source involves the assumption about the previous year's dead material. If it in fact has not all been incorporated into the litter, ANPP will be overestimated. The second source of error is concerned with the fact that perennial parts of the shrubs were included in the estimate of ANPP again causing an overestimation of the true value. The remaining sources of errors are that some of the current season's production becomes part of the litter before the peak standing crop is reached and there is some productivity after the peak is reached. Both of these latter two errors tend to make the estimates of ANPP less than the true value.

Belowground net primary productivity (BNPP) in g/m^2 was estimated by summing the positive increments in root weight over the growing season. For ease of interpretation smooth curves were fitted to the data by polynomial regression, regressing root weight on sample date. Polynomials of sixth and seventh order were found to yield reasonable fits. Root weight refers to the dry weight of belowground organic material retained by the washing method including plant bases.

Herbivory was not accounted for in the estimates of either ANPP or BNPP. However large herbivores were excluded from the experimental area.

Diversity and Dominance

Diversity (H) was calculated using Shannon's formula

$$\bar{H} = - \Sigma \frac{n_i}{N} \ln \frac{n_i}{N}$$

and was used as an assessment of the level of organization of the primary producers (Margalef 1968). The value of n_i was the density for the i^{th} species for a treatment and N was the sum of the densities of all species for the treatment. In order to include blue grama in the calculations, since it was not included in the density data, and also to give it a weight in relation to its influence on the other species it was assigned a density in proportion to its biomass contribution on the date that the density data was collected. Fringed sagewort density was adjusted by the same method. Several methods were tried to arrive at weighted densities for blue grama and fringed sagewort including shoot densities. After several attempts it became evident that once n_i/N was greater than 0.30 further increases had very little effect on the index.

The range of n_i/N for blue grama and fringed sagewort densities adjusted by the biomass data was 0.04 to 0.51.

McNaughton's community dominance index was used to assess the degree to which the primary producers were dominated by the two most numerous species (McNaughton and Wolf 1970). The community dominance index was calculated for each treatment by the formula

$$D.I. = \left(\frac{n_1 + n_2}{N}\right) \times 100$$

where n_1 and n_2 were the densities of the two most numerous species and N was the sum of the densities of all species.

Evapotranspiration

Evapotranspiration was estimated by the water balance method. Rose (1966) gives the following formula for water balance

$$P = S + \Delta D + \Delta M + U + \int E\, dt$$

where P = precipitation, S = net surface runoff, ΔD = increase in surface detention, ΔM = change in soil water storage, U = increase in underground or subsurface storage in layers below that for which ΔM is calculated and $\int E\, dt$ = the total evapotranspiration over the period considered. Rose (1966) states that for most conditions ΔD is negligible and under the conditions of the shortgrass prairie, both watered and unwatered, it was assumed that S and U were also negligible. Because of two exceptionally heavy rains in 1972 there were reasons to believe that there was movement of water below the depths for which ΔD was measured but no estimate of the amount was available. The simplified water balance formula is

$$P = \Delta M + \int E\, dt$$

values of P and ΔM were known and the equation was solved for $\int E\, dt$.

Small Mammal Populations

Small mammal population estimates were based on the total number of individuals captured per treatment not including recaptures. Grant (1972) has shown that population estimates for these treatments based on the modified Zippin regression estimation techniques are essentially the same as total captures. Biomass estimates were arrived at by multiplying animal numbers times a mean biomass estimate per animal (Grant 1972).

Statistical Analyses

Treatment means were tested by an analysis of variance followed by a Duncans New Multiple Range test to test all possible differences between treatment means (Li 1964). An example of the Analysis of Variance table is shown in Table 1. All means were tested at the 5% level ($\alpha = .05$) and all differences referred to as significant are at this level.

TABLE 1. Example of analysis of variance table used to test differences among treatment means for the stress treatments on a shortgrass prairie in northeastern Colorado.

Source of variation	Degrees of freedom
Treatment	3
Error	4
Total	7

RESULTS

Net Primary Productivity

Aboveground Net Primary Productivity

Aboveground net primary productivity (ANPP) in 1972 ranged from a low of 205 $g/m^2/y$ for the control to a high of 1161 $g/m^2/y$ for the water plus nitrogen treatment (Table 2). ANPP for the water plus nitrogen treatment was significantly greater than all of the other treatments. The water treatment had a significantly greater ANPP than the control and it was greater, but not significantly, than the nitrogen treatment. The nitrogen treatment ANPP was larger, but not significantly larger than the control.

The contributions of the various species groups to ANPP are given in Tables 3, 19-22 and Figures 4-7. The contribution of warm season grasses to ANPP showed the largest treatment response of any of the species groups. Warm season grasses contributed approximately the same amount to ANPP on the control and the nitrogen treatments. Their contribution was increased four times by the water treatment and almost ten times by the water plus nitrogen treatment. The contributions ranged from 48 $g/m^2/y$ for the nitrogen treatment to 465 $g/m^2/y$ for the water plus nitrogen treatment.

The peak standing crop of cool season grasses ranged from 16 g/m^2 to 53 g/m^2 for the control and water plus nitrogen treatments respectively. The contribution to ANPP by the cool season grass group was the same for

TABLE 2. Total (TNPP), aboveground (ANPP) and belowground (BNPP) net primary productivity ($g/m^2/y$) for the stress treatments on a shortgrass prairie in northeastern Colorado in 1972.

	Treatment			
	Control	Water Stress	Nitrogen Stress	Water plus Nitrogen Stress
ANPP	205a[1/]	446b	290ab	1161c
BNPP	604d	618d	384d	688d
TNPP	809e	1064e	674e	1849f

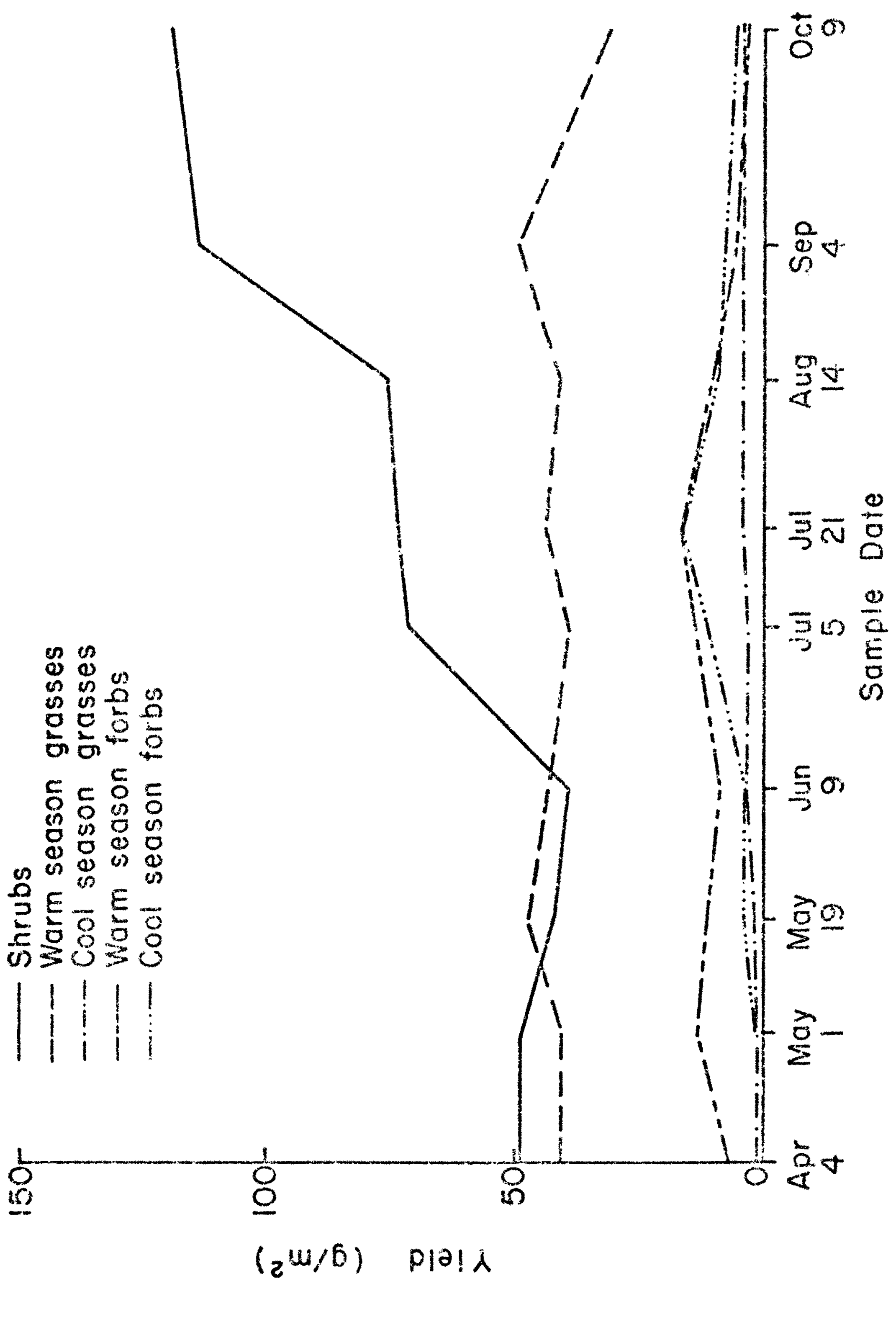
1/ Means in a row followed by the same letter are not different at the 5% level.

TABLE 3. Contributions of the species groups to ANPP ($g/m^2/y$) for the stress treatments on a shortgrass prairie in northeastern Colorado in 1972.

	Treatments							
	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	Contribution to ANPP		Contribution to ANPP		Contribution to ANPP		Contribution to ANPP	
	(g)	(%)	(g)	(%)	(g)	(%)	(g)	(%)
Warm Season Grasses	49a[1/]	24	176b	39	48a	17	465c	40
Cool Season Grasses	16a	8	22a	5	52a	18	53a	5
Warm Season Forbs	4a	2	39a	9	30a	10	65b	6
Cool Season Forbs	16a	8	18a	4	54a	19	20a	2
Shrubs	120a	58	191a	43	106a	37	558b	48
Total	205		446		290		1161	

1/ Means in a row followed by the same letter are not different at the 5% level.

Figure 4. Seasonal dynamics of aboveground standing crop for four species groups for the control treatment on a shortgrass prairie in northeastern Colorado in 1972.



Shrubs
Warm season grasses
Cool season grasses
Warm season forbs
Cool season forbs
Yield (g/m²)
150
100
50
0
Apr 4
May 1
May 19
Jun 9
Jul 5
Jul 21
Aug 14
Sep 4
Oct 9
Sample Date

Figure 5. Seasonal dynamics of aboveground standing crop for four species groups for the water treatment on a shortgrass prairie in northeastern Colorado in 1972.

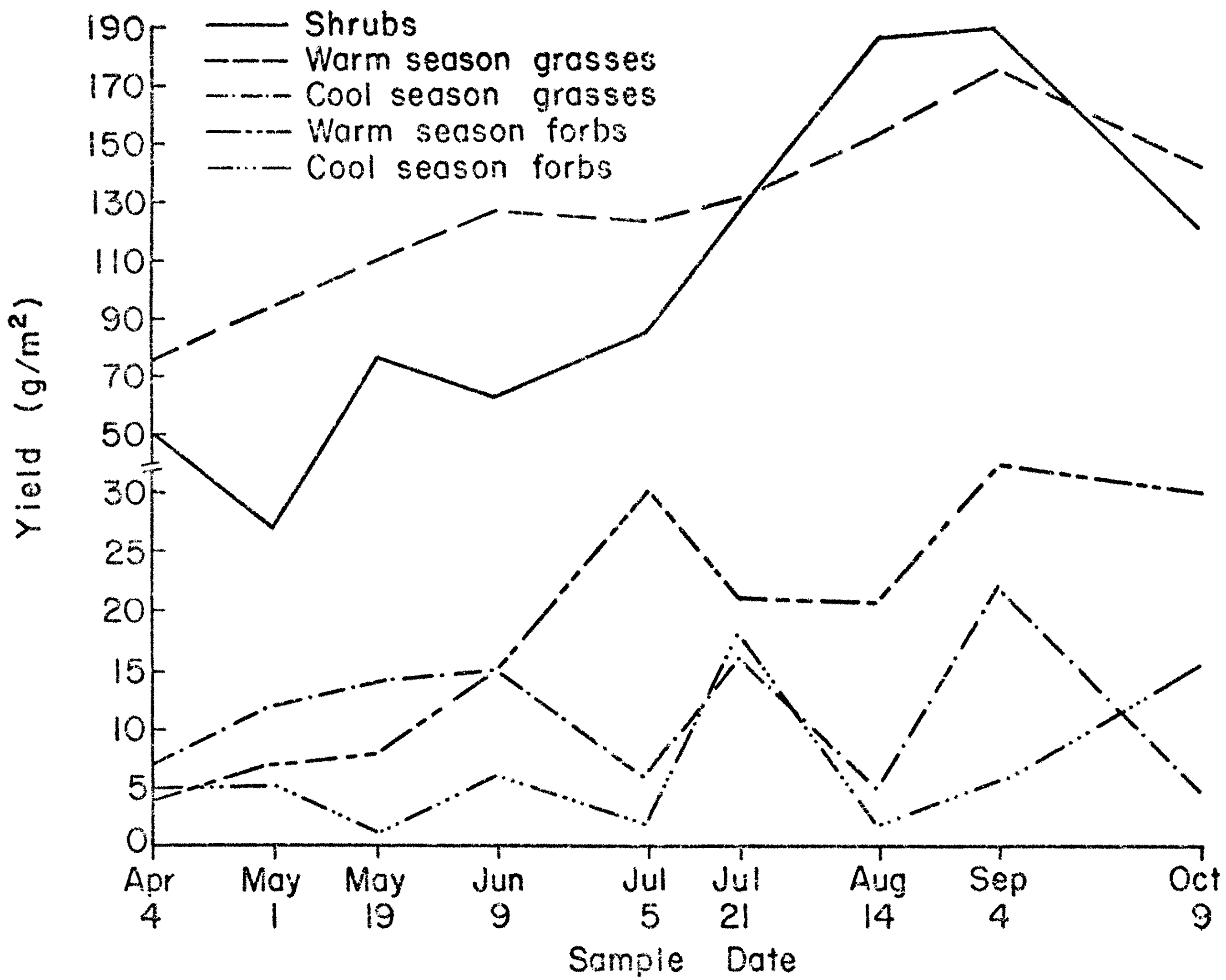

Shrubs
Warm season grasses
Cool season grasses
Warm season forbs
Cool season forbs
Yield (g/m²)
190
170
150
130
110
90
70
50
30
25
20
15
10
5
0
Apr 4
May 1
May 19
Jun 9
Jul 5
Jul 21
Aug 14
Sep 4
Oct 9
Sample Date

Figure 6. Seasonal dynamics of aboveground standing crop for four species groups for the nitrogen treatment on a shortgrass prairie in northeastern Colorado in 1972.

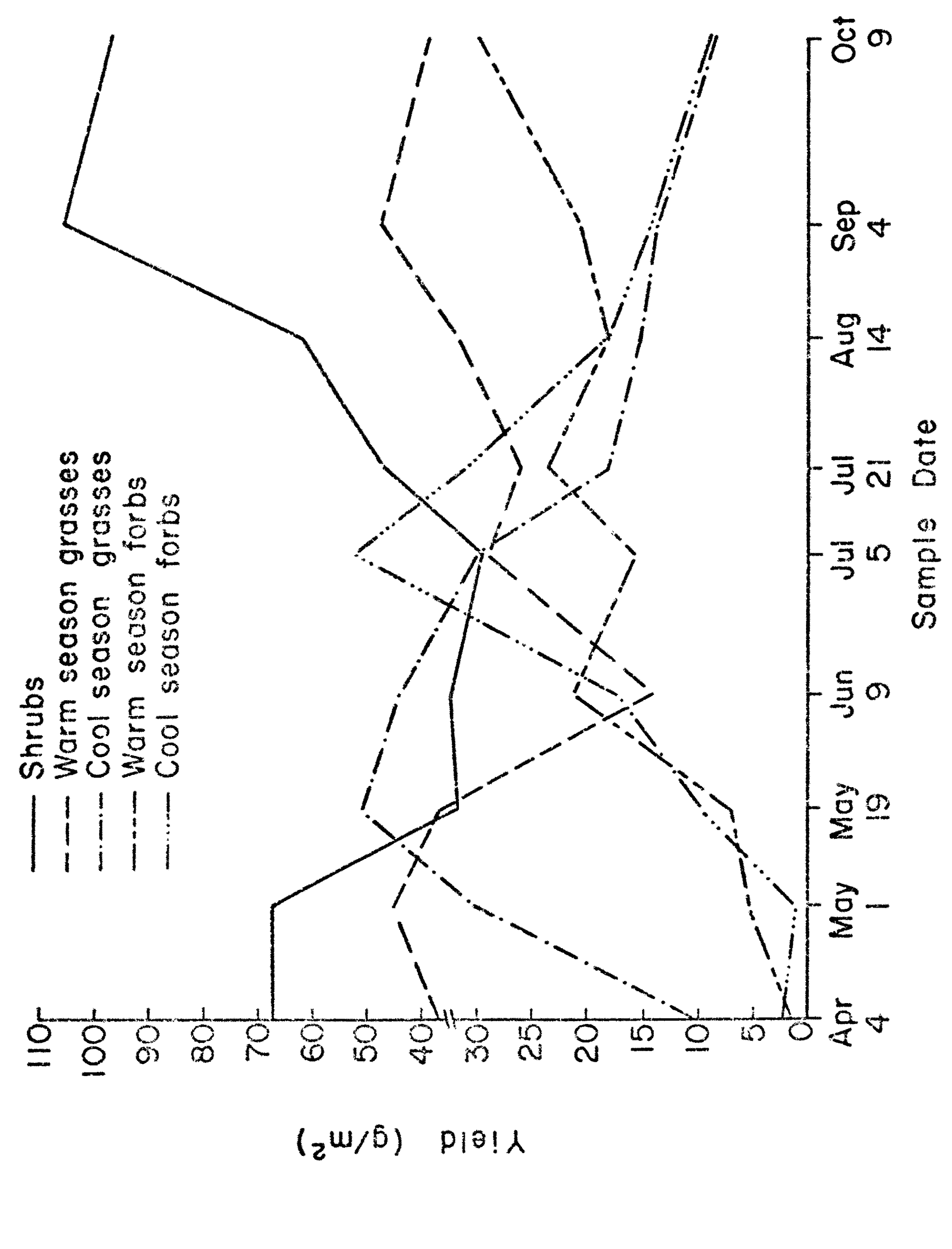
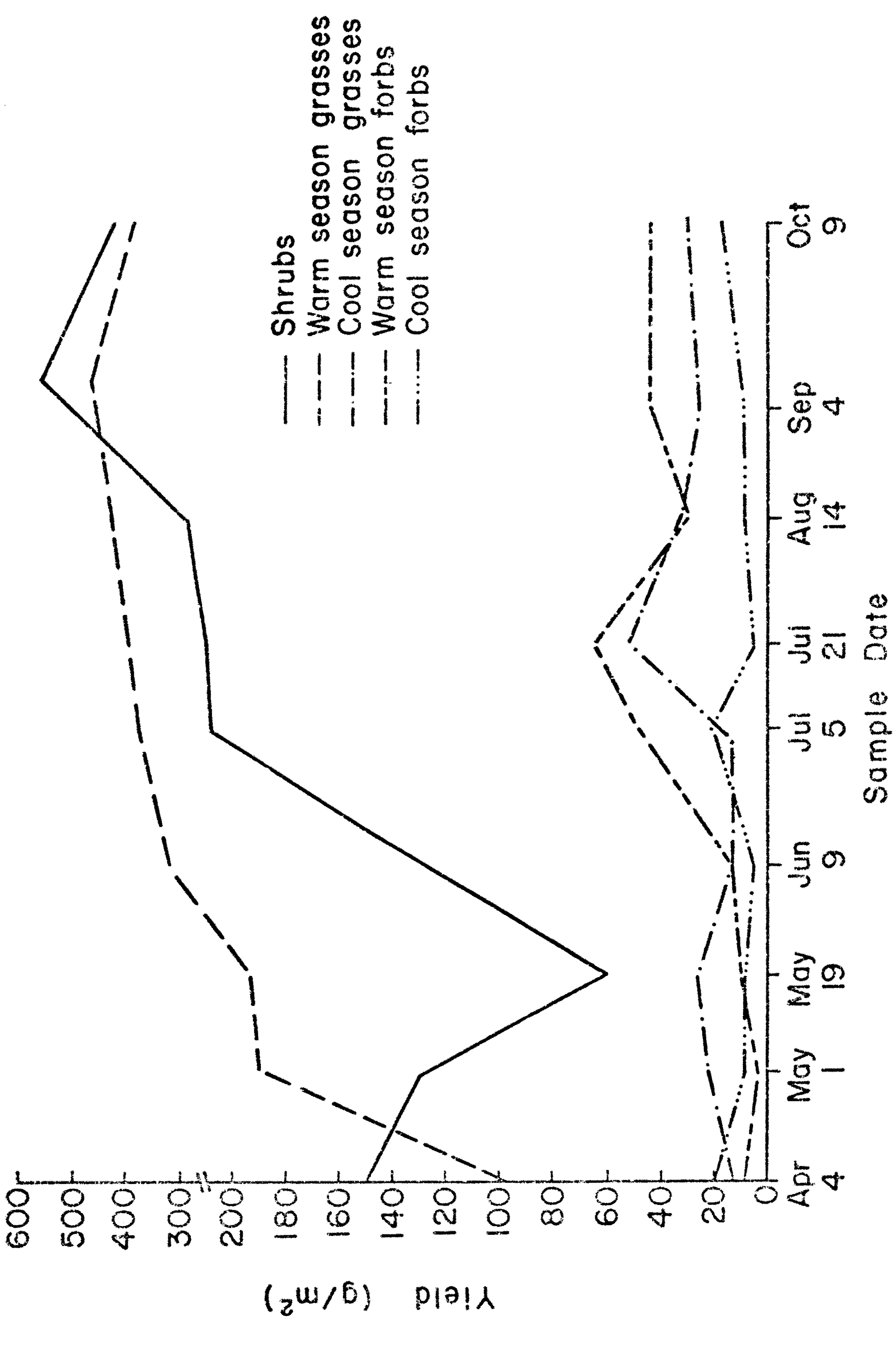

Shrubs
Warm season grasses
Cool season grasses
Warm season forbs
Cool season forbs
Yield (g/m2)
110
100
90
80
70
60
50
40
30
25
20
15
10
5
0
Apr 4
May 1
May 19
Jun 9
Jul 5
Jul 21
Aug 14
Sep 4
Oct 9
Sample Date

Figure 7. Seasonal dynamics of aboveground standing crop for four species groups for the water plus nitrogen treatment on a shortgrass prairie in northeastern Colorado in 1972.


Yield (g/m^2)
600
500
400
300
200
180
160
140
120
100
80
60
40
20
0
Apr 4
May 1
May 19
Jun 9
Jul 5
Jul 21
Aug 14
Sep 4
Oct 9
Sample Date
Shrubs
Warm season grasses
Cool season grasses
Warm season forbs
Cool season forbs

the control and water treatment and was approximately doubled by the nitrogen and water plus nitrogen treatments.

Warm season forbs contributed 4 $g/m^2/y$ to ANPP for the control and 65 $g/m^2/y$ for the water plus nitrogen treatment. The range in magnitude of the increases above the control was from seven times greater on the nitrogen treatment to 15 times for the water plus nitrogen treatment.

Cool season forbs showed the greatest treatment response to the nitrogen treatment and essentially no response to the other treatments. The contribution of cool season forbs to ANPP was 54 $g/m^2/y$ for the nitrogen treatment and approximately 18 $g/m^2/y$ for the remaining treatments.

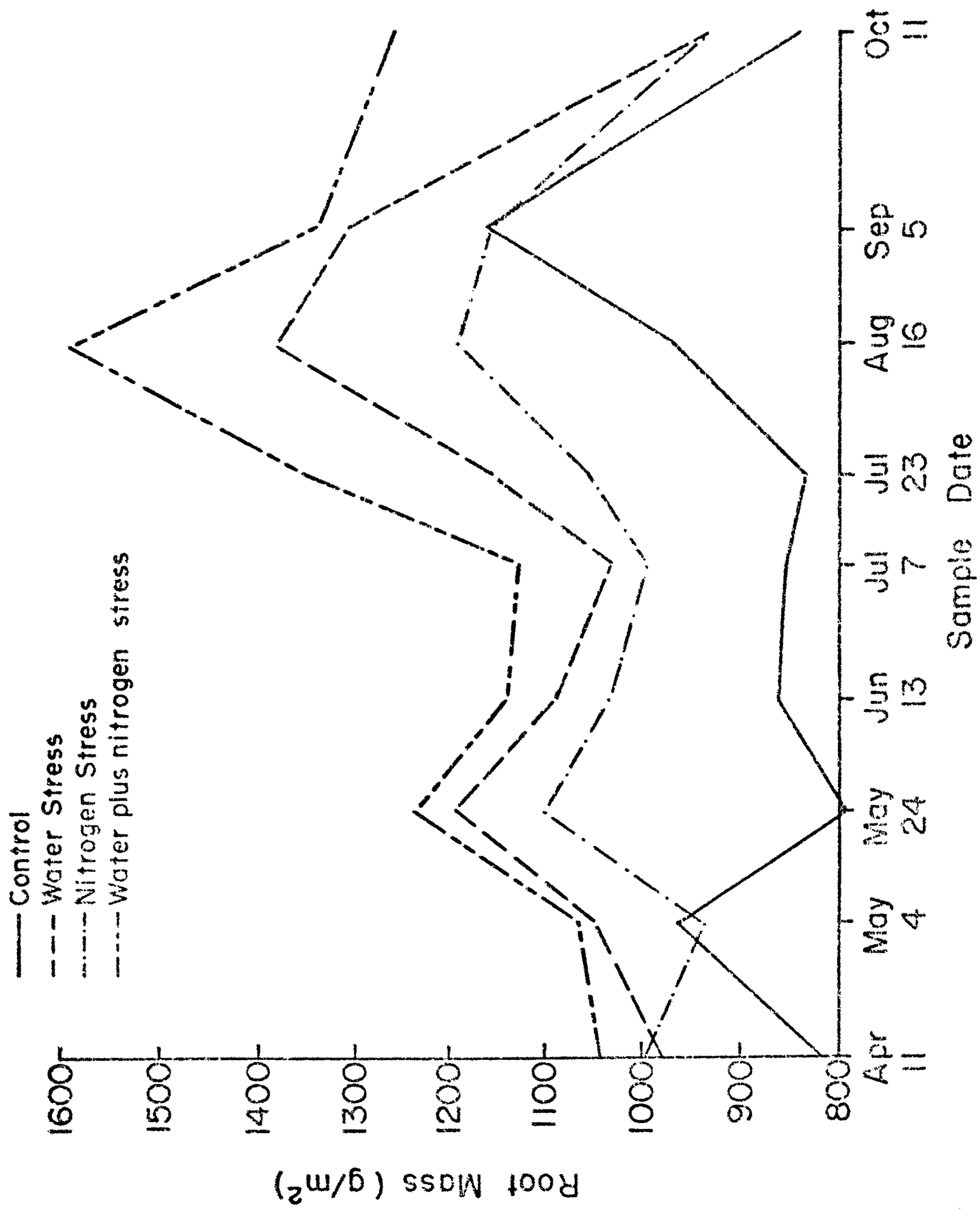
Shrubs had the largest contributions to ANPP of all of the species groups. The range of peak standing crop was from 106 $g/m^2/y$ for the control treatment to 558 $g/m^2/y$ for the water plus nitrogen treatment. The increase in standing crop of shrubs for the water plus nitrogen treatment was approximately five fold.

ANPP on all treatments was dominated by warm season grasses and shrubs. The percentage contribution to ANPP of warm season grasses and shrubs was greater than 80 percent on all treatments except the nitrogen treatment where it was still more than 50 percent. The decrease in percentage contribution of these two groups for the nitorgen treatment was attributable to an 8 percent decrease in warm season grasses and a 22 percent decrease in shrub production compared to the control.

Belowground Net Primary Productivity

Belowground net primary productivity (BNPP) ranged from a low of 384 $g/m^2/y$ for the nitrogen treatment to a high of 688 $g/m^2/y$ for the water plus nitrogen treatment (Tables 2 and 23, Figure 8). The

Figure 8. Seasonal dynamics of root weight for the stress treatments for a shortgrass prairie in northeastern Colorado in 1972.



Control
Water Stress
Nitrogen Stress
Water plus nitrogen stress
Root Mass (g/m²)
1600
1500
1400
1300
1200
1100
1000
900
800
Apr 11
May 4
May 24
Jun 13
Jul 7
Jul 23
Aug 16
Sep 5
Oct 11
Sample Date

variability in the root weight data was so large that no significant differences among any of the treatments could be detected. The water, nitrogen and water plus nitrogen treatments had bimodal curves for seasonal root weight dynamics in 1972 and the control treatment had a trimodal curve (Figure 8). It is important to remember that in these seasonal dynamics curves for root weight, the dependent variable is soil organic material plus plant bases.

The peaks and troughs of the bimodal root weight curves for the water, nitrogen and water plus nitrogen treatments occurred on the same sample dates. The initial peak occurred on May 24 with the subsequent trough occurring on July 7. The second and larger peak occurred on August 16. The three root weight peaks for the control treatment occurred on May 4, June 13 and September 5. The September 5 peak was the largest.

Total Net Primary Productivity

Total net primary productivity (TNPP) for 1972 was 809 for the control treatment, 1064 for the water treatment, 674 for the nitrogen treatment and 1849 $g/m^2/y$ for the water plus nitrogen treatment. TNPP for the water plus nitrogen treatment was significantly greater than the other treatments. There were no significant differences in TNPP among the other treatments.

The percentage contributions of ANPP and BNPP to TNPP for the four treatments were as follows: control 25 and 75%, water 42 and 58%, nitrogen 43 and 57%, and water plus nitrogen 63 and 37% respectively.

Botanical Composition of Primary Producers

Density

Total numbers of primary producers as well as species composition were altered by the stress treatments in 1971 and 1972. In 1971 total density of primary producers, including the weighted estimates for blue grama and fringed sagewort, ranged from a low of 20 individuals per 0.25 m^2 for the control treatment to 74 individuals per 0.25 m^2 for the water treatment (Table 6). Densities of primary producers for the water and water plus nitrogen treatments were significantly greater than the control. Density for the nitrogen treatment was not significantly different from any of the other treatments. In 1972 primary producer densities decreased on all treatments except the control. The lowest density, 32 individuals per 0.25 m^2 was found on the nitrogen treatment and the highest, 50 individuals per 0.25 m^2, was found on the water treatment. There were no significant differences in total density among any of the treatments in 1972.

Species composition of primary producers responded conspicuously to the stress treatments. In 1971 the most striking treatment effects were attributable to the response of several annual species (Table 4). The major species involved were prairie pepperweed *(Lepidium densiflorum)*, woolly indian wheat *(Plantago purshii)* and common six-weeks grass *(Festuca octoflora)*. Although common six-weeks grass appeared to contribute a large proportion to the annual aspect of the treatments in 1971 the only available assessment of its contribution was an estimate of basal cover. The other two species were included in the density counts and estimates of their densities are available for both 1971 and

TABLE 4. Mean density of primary producer species per 0.25 m^2 for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972.

Species	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	1971	1972	1971	1972	1971	1972	1971	1972
GRASSES:								
Agropyron smithii	0.14	--	0.08	0.08	0.90	1.34	--	0.55
Aristida longiseta	0.14	0.02	0.03	0.02	--	0.01	0.02	0.01
Sitanion hystrix	0.04	0.04	0.11	0.06	0.08	0.10	0.19	0.05
Sproobolus cryptandrus	0.01	0.19	0.16	0.07	--	--	0.08	0.05
Stipa comata	0.02	0.17	0.01	0.08	--	0.04	0.10	0.01
FORBS:								
Allium textile	--	--	--	--	0.01	--	0.01	0.01
Astragalus mollissimus	--	--	0.09	0.08	--	--	--	0.07
Aster tanacetifolius	0.01	0.48	0.03	0.02	--	0.74	0.19	0.01
Chenopodium leptophyllum	0.03	0.01	--	0.01	0.68	0.07	0.12	--
Cirsium undulatum	0.01	0.03	--	0.03	--	0.02	0.01	0.06
Conyza canadensis	--	--	--	0.03	--	--	0.22	0.23
Cryptantha jamesii	--	--	--	--	--	--	--	0.01
Cryptantha minima	0.16	0.31	0.07	0.02	0.20	0.54	0.42	0.02
Descurainia sophia	--	--	0.02	0.01	0.02	0.15	0.08	--
Echinocereus viridiflorus	--	0.09	--	0.09	--	0.21	--	0.03

TABLE 4. Continued

Species	Treatment							
	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	1971	1972	1971	1972	1971	1972	1971	1972
Erigeron bellidiastrum	--	--	--	0.02	--	--	--	0.01
Evolvulus nuttalianus	--	--	--	--	--	--	0.03	--
Gaura coccinea	--	0.07	0.13	0.14	0.05	0.09	0.24	0.13
Haplopappus spinulosus	0.19	0.03	0.04	0.09	--	0.02	0.03	0.02
Heterotheca villosa	--	0.01	0.04	0.15	--	0.03	0.01	0.10
Kochia scoparia	--	0.02	--	0.02	--	0.03	--	0.01
Lapula redowskii	0.21	0.33	0.02	--	0.36	0.12	0.80	0.01
Lepidium densiflorum	1.29a[1/]	2.93ab	4.34ab	0.59a	3.14a	5.21b	18.85b	0.09a
Leucocrinum montanum	0.02	--	--	--	--	--	0.01	--
Lithospermum incisum	0.02	--	--	0.02	--	--	--	0.02
Liatris punctata	--	--	--	0.02	0.05	--	--	0.04
Lomatium orientale	0.04	--	0.01	--	--	--	--	--
Lupinus pusillus	0.03	--	0.02	--	--	--	--	--
Mirabilis linearis	--	0.05	--	--	0.02	0.03	0.03	0.13
Oenothera albicaulis	0.04	0.07	0.22	0.04	--	0.18	0.32	0.02
Orobanche ludoviciana	--	--	0.03	0.33	--	--	0.04	0.19
Oxytrops lamberti	--	--	--	0.09	--	--	--	0.03
Penstemon albidus	--	--	--	0.01	0.01	--	0.02	--

TABLE 4. Continued

Species	Treatment							
	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	1971	1972	1971	1972	1971	1972	1971	1972
Penstemon angustifolius	--	--	--	--	--	--	0.01	--
Plantago purshii	0.93a	6.07a	15.50b	4.92a	1.51a	5.03a	6.95ab	0.49a
Ratibida columnaris	--	--	--	--	--	--	--	0.01
Salsola kali	0.11	--	0.23	--	0.25	--	0.15	0.10
Sisymbrium altissimum	--	--	--	--	--	0.01	0.04	--
Sophora sericea	0.03	0.11	0.07	0.33	0.01	0.07	0.03	0.34
Sphaeralcea coccinea	2.84a	2.54a	2.77a	3.41a	2.15a	3.47a	3.29a	5.17a
Taraxacum officinale	--	--	--	--	--	--	--	0.03
Thelesperma trifidum	0.07	0.15	0.20	1.01	0.02	0.75	0.71	0.39
Townsendia grandiflora	--	--	0.01	0.09	--	0.01	--	--
Tragopogon dubius	--	--	--	0.01	--	--	--	0.07
Tradescantia occidentalus	--	--	--	--	--	--	--	0.01
SUCCULENTS:								
Mammillaria vivipara	0.11	0.01	0.07	--	0.10	0.02	0.01	0.02
Opuntia polyacantha	1.57a	1.67a	1.65a	1.70a	2.41a	4.01a	3.20a	2.34a

TABLE 4. Continued

Species	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	1971	1972	1971	1972	1971	1972	1971	1972
SHRUBS:								
Artemisia frigida	1.68a	3.52a	2.78a	5.97a	1.22a	3.90a	6.86b	6.56a
Chrysothamnus nauseosus	0.02	0.06	0.07	0.01	0.03	0.11	0.09	--
Eriogonum effusum	0.01	0.11	0.05	0.01	--	0.02	0.04	0.02
Gutierrezia sarothrae	0.21	0.23	0.14	0.33	0.18	0.20	0.15	0.24
Psoralea tenuiflora	0.05	0.11	0.11	0.18	0.13	0.11	0.08	0.22
Yucca glauca	--	0.02	--	--	--	--	--	--

1/ Only the species with letters after their means were statistically tested and those within a year followed by the same letter are not different at the 5% level.

1972. The densities of all annuals on the water treatment and the nitrogen treatment were increased ten times over the control in 1971. Density of annuals on the water plus nitrogen treatment was increased 20 times above the control level in 1971.

The density of prairie pepperweed was 1.29 for the control, 4.34 for the water, 3.14 for the nitrogen and 18.85 individuals per 0.25 m^2 for the water plus nitrogen stress treatment. Woolly indian wheat responded in a similar manner except that its highest density was found on the water stress treatment.

In 1972 the annual species decreased greatly from their 1971 levels with the treatments receiving supplemental water having the largest decreases. Prairie pepperweed density in 1972 on the water treatment was 0.59 and on the water plus nitrogen treatment was 0.09 individuals per 0.25 m^2. Woolly indian wheat had decreased to 4.92 individuals per 0.25 m^2 on the water treatment and to 0.49 individuals per 0.25 m^2.

Most of the perennial species with the exception of fringed sagewort had only limited responses to the stress treatments when the 1971 samples were collected. Fringed sagewort density was altered by all stress treatments in 1971. The greatest increase, approximately 400%, occurred on the water plus nitrogen treatment and a decrease of 30% occurred on the nitrogen treatment. The higher density for the water plus nitrogen treatment was significantly different from all other treatments. In 1972 the density of fringed sagewort increased on all treatments except the water plus nitrogen treatment which still had the largest density. There were no significant differences in fringed sagewort density among any of the treatments in 1972.

Density of scarlet globemallow, the most abundant perennial forb on the study plots, was not significantly altered by the stress treatments in either 1971 or 1972. In 1971 and 1972 the largest densities of this species were recorded for the water plus nitrogen treatment. In 1971 there were essentially no differences in scarlet globemallow density among the remaining treatments. In 1972 the water and the nitrogen treatments had higher densities of scarlet globemallow than the control.

The response of plains prickly pear to the stress treatments was similar to scarlet globemallow in that there were no significant differences in its density among any of the treatments for both years. The largest densities for this species were found on the water plus nitrogen treatment in 1971 and on the nitrogen treatment in 1972. Plains prickly pear density increased from 1971 to 1972 on all treatments except the water plus nitrogen.

Basal Cover

Blue grama was the only primary producer species with a measurable basal cover for all treatments in both years (Table 5). Blue grama basal cover in 1971 ranged from 7.5% for the control to 10.4% for the water plus nitrogen treatment. There were no significant differences in blue grama basal cover in 1971. In 1972 the water plus nitrogen treatment had 21.4% basal cover of blue grama which was significantly greater than all other treatments. The lowest basal cover of blue grama in 1972 was 3.9% for the nitrogen treatment. This represented a 58% decrease from its 1971 value.

Cover of bareground and litter was relatively uniform in 1971 ranging from 87.9% for the water plus nitrogen treatment to 91.8% for the

TABLE 5. Basal cover (%) by species for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972.

Species	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	1971	1972	1971	1972	1971	1972	1971	1972
Bouteloua gracilis	7.5a[1/]	6.3a	9.2a	10.2b	9.4a	3.9a	10.4a	21.4c
Buchloe dactyloides	--	--	0.2	0.3	--	--	0.1	0.2
Carex heliophila	--	0.5	--	0.3	--	0.1	--	--
Festuca octoglora	--	--	1.0	--	1.0	0.5	1.5	--
Mammillaria vivipara	--	--	--	--	0.1	--	0.1	--
Opuntia polyacantha	0.5	--	0.2	--	--	--	--	--
Bare ground and litter	91.8	93.0	89.4	88.8	89.5	94.8	87.9	78.0

1/ Means within a year followed by the same letter are not different at the 5% level. Means not followed by a letter were not tested.

control. In 1972 the differences were greater with a low of 78% for the water plus nitrogen treatment and a high of 94.8% for the nitrogen treatment.

Organization of Primary Producers

Diversity

Diversities for 1971 were not influenced greatly by the stress treatments (Table 6). The highest diversity was found for the control treatment and the lowest for the water treatment. The range of diversity in 1971 was from 2.0 to 1.7. In 1972 the range of diversity widened and varied from 2.3 for the nitrogen treatment to 1.6 for the water plus nitrogen treatment. Diversity decreased from 1971 to 1972 on the water plus nitrogen treatment.

The number of species recorded for the treatments in 1971 ranged from a low of 25 for the nitrogen treatment to a high of 38 species for the water plus nitrogen treatment. The number of species increased for all treatments from 1971 to 1972 except for the control. The largest number of species recorded in 1972 was 42 for the water plus nitrogen treatment.

Dominance

The dominance indices for 1971 were similar to the diversity calculations in that there were no large responses to the treatments (Table 6). The dominance index ranged from 58% for the control to 64% for the nitrogen treatment. In 1972 dominance was more variable with the lowest degree of dominance 36% found for the nitrogen treatment and the highest, 75%, found for the water plus nitrogen treatment.

TABLE 6. Number of species (S), total density (N), diversity ($\overline{H}$) and community dominance index (DI) for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972.

	1971				1972			
Treatment	S	N	$\overline{H}$	DI (%)	S	N	$\overline{H}$	DI (%)
Control	30	20a[1/]	2.0	58	30	44a	1.8	64
Water Stress	33	74b	1.7	63	38	50a	1.7	72
Nitrogen Stress	25	35ab	1.9	64	32	32a	2.3	36
Water plus Nitrogen Stress	38	72b	1.8	63	42	46a	1.6	75

1/ Means within a column followed by the same letter are not significantly different at the 5% level. Means not followed by a letter were not tested.

Treatment Water Relations

Soil Water

Soil water in centimeters for the four treatments in 1971 and 1972 are presented in Figures 9-12. Figures 9 and 11 show total soil water to a depth of 20 cm for both years and the horizontal lines at 3.8 cm correspond to the amounts of water that would be held in the soil at a matric potential of -0.3 bars. The same is true for the lines at 6.5 cm in Figures 10 and 12. The -0.3 bar values, determined using a pressure membrane apparatus, were taken from Van Haveren and Galbraith (1971).

In 1971 soil water for all treatments at both the 0 - 20 and the 20 - 45 cm depth increment was less than in 1972. This was more pronounced for the 0 - 20 cm increment. The shape of the soil water curves at both depths for the control and nitrogen treatments in 1971 indicated a steady depletion during the growing season. In contrast to this the 1972 data shows several major additions to soil water during the growing season.

The treatments receiving additional water showed substantially more soil water than the other two treatments in both 1971 and 1972. The lower levels of soil water maintained in 1971 were indicative of the very dry conditions during this year. The rapid decline in soil water of both the water and water plus nitrogen treatments after August 16, 1971 resulted from a cessation of watering because of problems with the well. It was assumed that the influence of the premature ending of the water treatment on the 1972 data were minimal since the majority of the species had begun to senesce by this time.

Figure 9. Total soil water in the 0-20 cm depth for the 1971 season for a shortgrass prairie in northeastern Colorado with a horizontal line at the equivalent of -0.3 bars soil water potential.

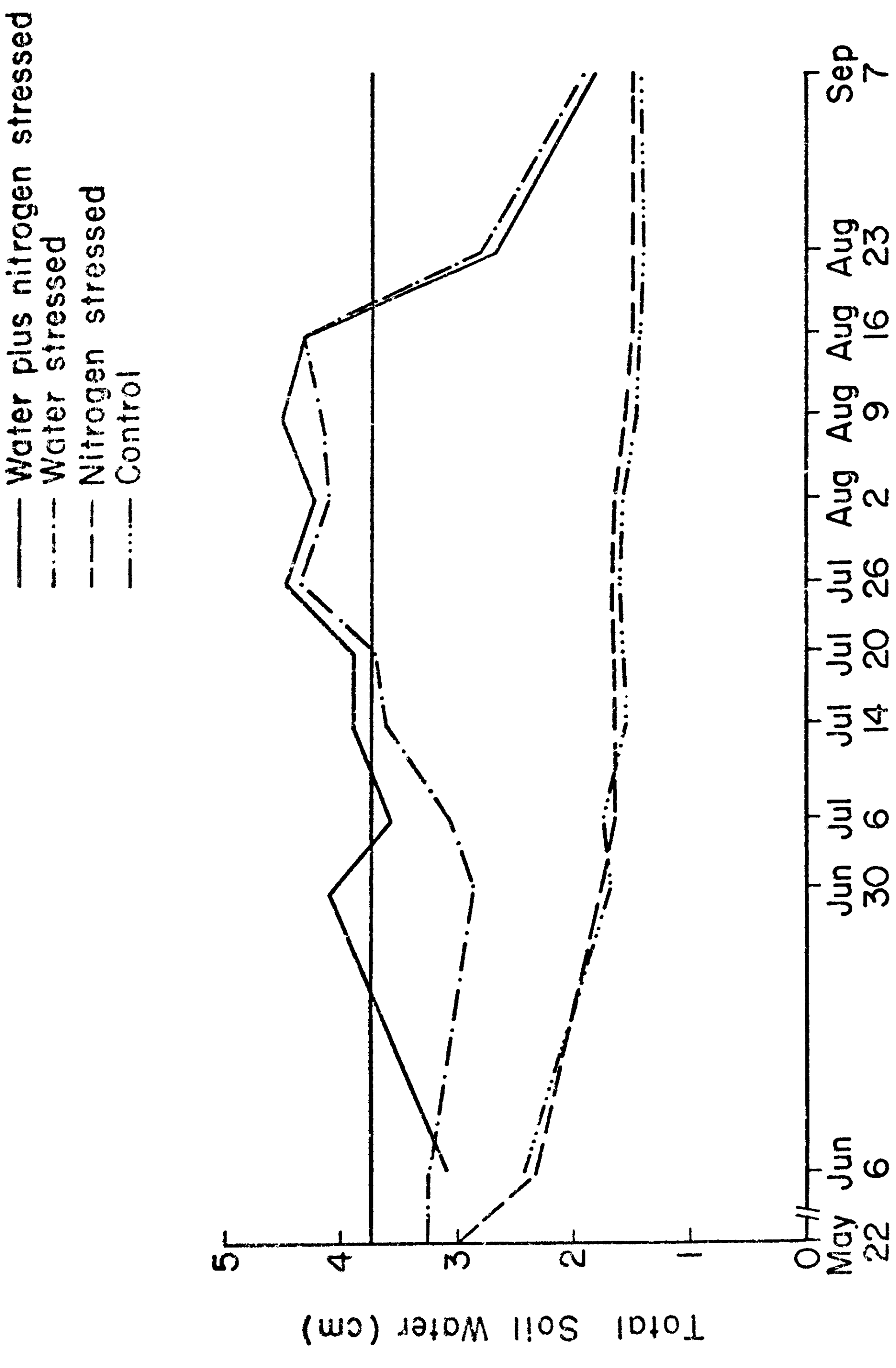

Water plus nitrogen stressed
Water stressed
Nitrogen stressed
Control
Total Soil Water (cm)
0
1
2
3
4
5
May 22
Jun 6
Jun 30
Jul 6
Jul 14
Jul 20
Jul 26
Aug 2
Aug 9
Aug 16
Aug 23
Sep 7
Sample Date

Figure 10. Total soil water in the 20-45 cm depth for the 1971 season for a shortgrass prairie in northeastern Colorado with a horizontal line at the equivalent of -0.3 bars soil water potential.

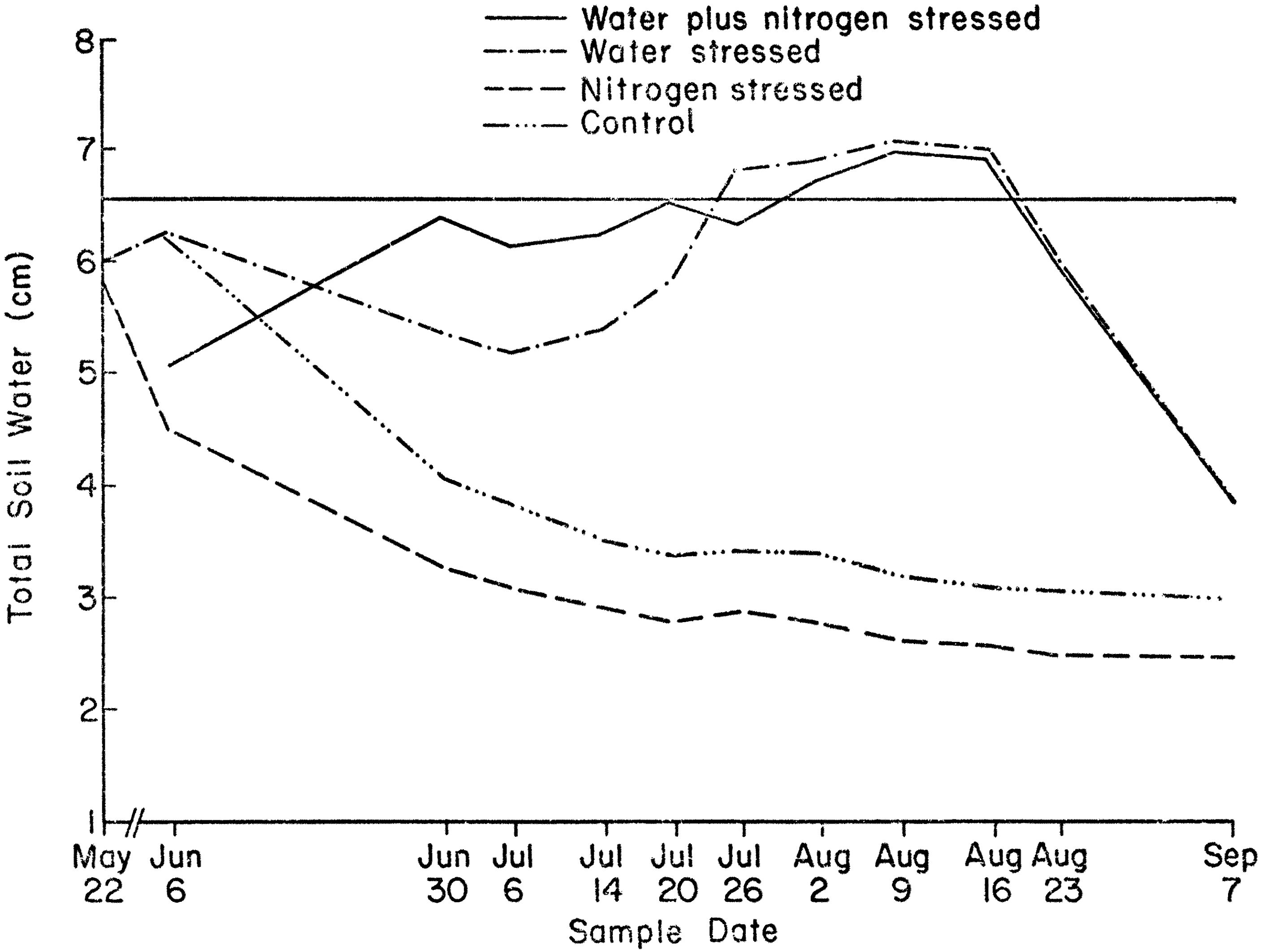
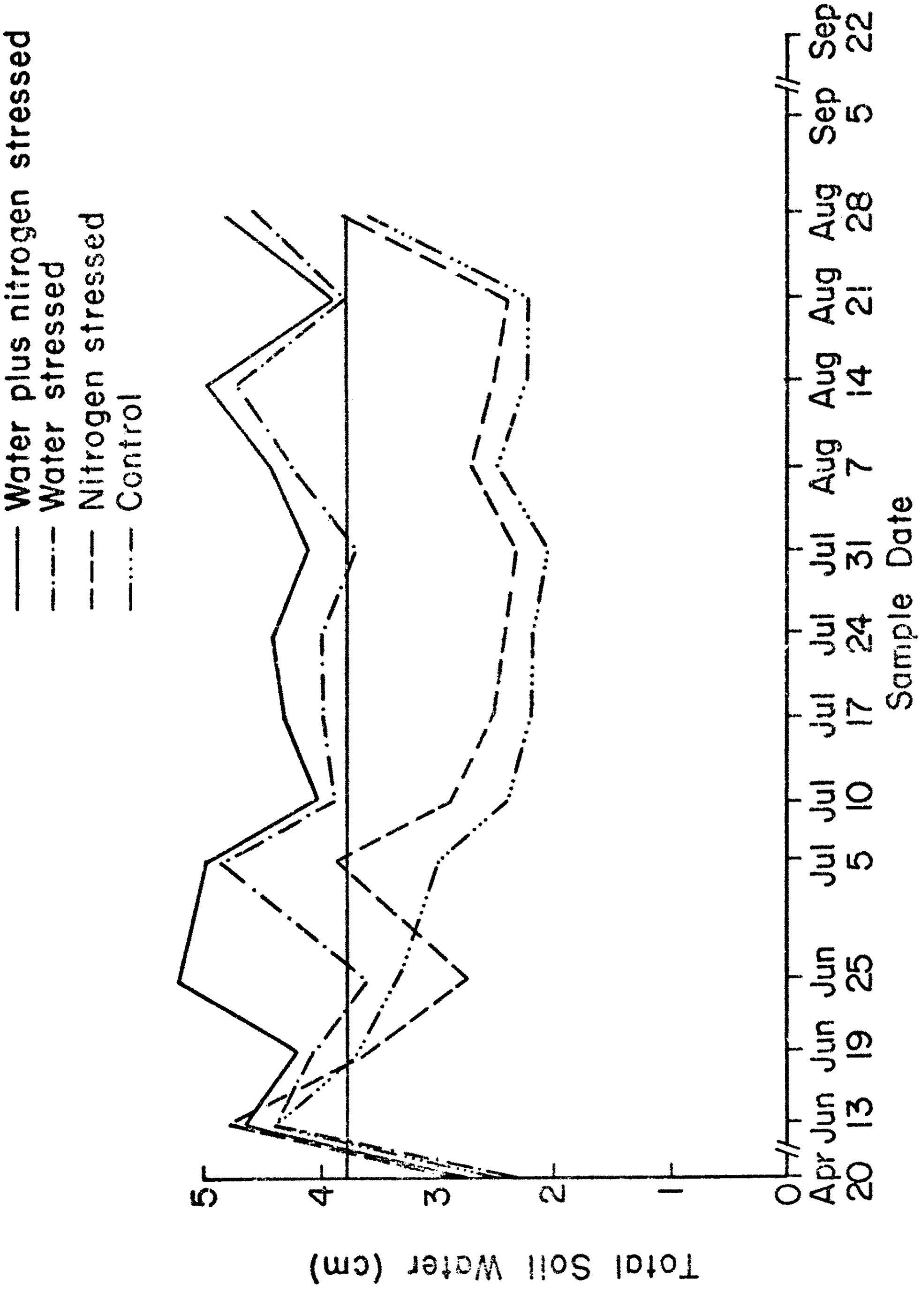
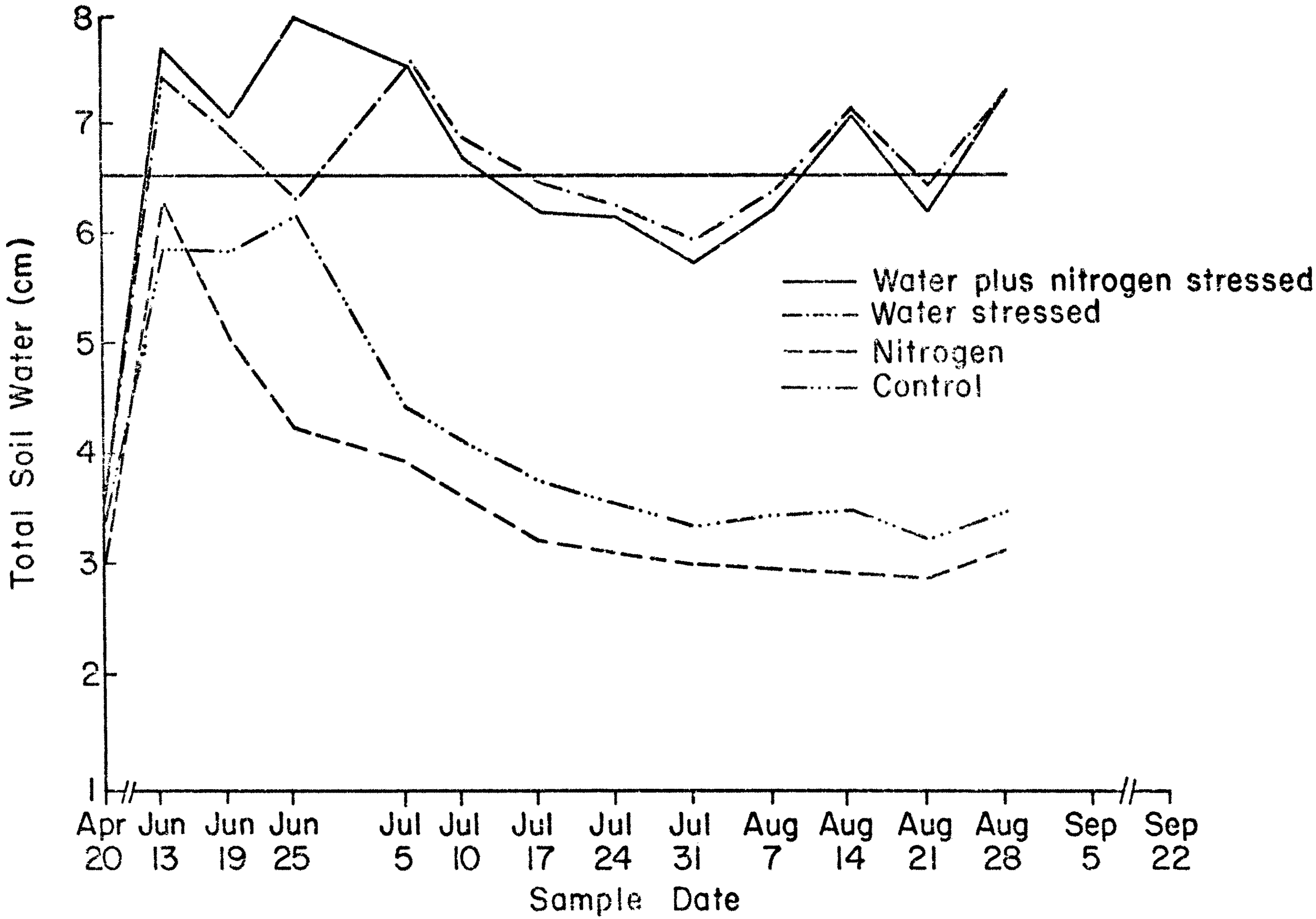

Water plus nitrogen stressed
Water stressed
Nitrogen stressed
Control
8
7
6
5
4
3
2
1
Total Soil Water (cm)
May 22
Jun 6
Jun 30
Jul 6
Jul 14
Jul 20
Jul 26
Aug 2
Aug 9
Aug 16
Aug 23
Sep 7
Sample Date

Figure 11. Total soil water in the 0-15 cm depth for the 1972 season for a shortgrass prairie in northeastern Colorado with a horizontal line at the equivalent of -0.3 bars soil water potential.



Water plus nitrogen stressed
Water stressed
Nitrogen stressed
Control
Total Soil Water (cm)
0
1
2
3
4
5
Apr 20
Jun 13
Jun 19
Jun 25
Jul 5
Jul 10
Jul 17
Jul 24
Jul 31
Aug 7
Aug 14
Aug 21
Aug 28
Sep 5
Sep 22
Sample Date

Figure 12. Total soil water in the 20-45 cm depth for the 1972 season for a shortgrass prairie in northeastern Colorado with a horizontal line at the equivalent of -0.3 bars soil water potential.



Total Soil Water (cm)
8
7
6
5
4
3
2
1
Water plus nitrogen stressed
Water stressed
Nitrogen
Control
Apr 20
Jun 13
Jun 19
Jun 25
Jul 5
Jul 10
Jul 17
Jul 24
Jul 31
Aug 7
Aug 14
Aug 21
Aug 28
Sep 5
Sep 22
Sample Date

Growing season precipitation (April 20 to September 4) was approximately 123 mm in 1971 and 240 mm in 1972. The long term average for this period is 220 mm.

Evapotranspiration

The water balance for the treatments in 1971 is given in Tables 7-10. Data were collected for the period May 15 to September 7 and evapotranspiration ranged from a low of 126 mm for the nitrogen treatment to a high of 577 mm for the water plus nitrogen treatment. The difference between the water and the water plus nitrogen treatment in 1971 was not significant. The control had a significantly higher amount of evapotranspiration than the nitrogen treatment. The majority of water utilized by the primary producers on the control and the nitrogen treatment was stored in the soil at the beginning of the soil water measurements.

The water balance for the treatments in 1972 is given in Tables 11-14. Evapotranspiration for the period April 4 to September 4 ranged from 197 mm for the nitrogen treatment to 545 mm for the water plus nitrogen treatment. Nitrogen at the levels maintained in this study did not increase the amount of water that the plants could extract from the soil. The estimate of evapotranspiration for the nitrogen treatment was not significantly greater than the control treatment. Nitrogen in combination with water significantly increase evapotranspiration over the water treatment. The data from the control and nitrogen treatments indicated that at the beginning of the growing season in 1972 the soil was drier than at the end and all of the soil water for plant growth was derived from current season precipitation. There was no soil water storage from the previous fall or winter.

TABLE 7. Water balance (mm) for the 1971 growing season for the control treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
Nay 15 - Jun 07	24	19.30	296.10	192.72	-122.68	5.11
Jun 08 - Jun 30	23	6.60	192.72	151.71	-47.61	2.07
Jul 01 - Jul 06	6	0.00	151.71	145.67	-6.04	1.01
Jul 07 - Jul 14	8	0.00	145.67	134.78	-10.89	1.36
Jul 15 - Jul 20	6	3.43	134.78	132.25	-5.96	0.99
Jul 21 - Jul 26	6	4.32	132.25	134.12	-2.45	0.41
Jul 27 - Aug 02	7	2.66	134.12	131.25	-5.53	0.79
Aug 03 - Aug 09	7	0.00	131.25	123.70	-7.55	1.08
Aug 10 - Aug 16	7	2.54	123.70	120.82	-5.42	0.77
Aug 17 - Aug 23	7	0.00	120.82	118.13	-2.69	0.38
Aug 24 - Sep 07	15	4.57	118.13	117.24	-5.46	0.36
Total		43.42			-222.28	

TABLE 8. Water balance (mm) for the 1971 growing season for the water treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
May 15 - Jun 07	24	78.56	296.10	277.80	-96.86	4.04
Jun 08 - Jun 30	23	117.65	277.80	242.93	-152.52	6.63
Jul 01 - Jul 06	6	22.39	242.93	249.97	-15.35	2.56
Jul 07 - Jul 14	8	43.22	249.97	240.15	-53.04	6.63
Jul 15 - Jul 20	6	30.78	240.15	256.93	-14.00	2.33
Jul 21 - Jul 26	6	41.30	256.93	282.81	-15.42	2.57
Jul 27 - Aug 02	7	35.90	282.81	291.78	-26.93	3.85
Aug 03 - Aug 09	7	42.38	291.78	302.70	-31.46	4.49
Aug 10 - Aug 16	7	41.66	302.70	307.94	-36.42	5.20
Aug 17 - Aug 23	7	0.00	307.94	275.65	-32.29	4.61
Aug 24 - Sep 07	15	4.57	275.65	229.86	-50.36	3.35
Total		458.41			-525.65	

TABLE 9. Water balance (mm) for the 1971 growing season for the nitrogen treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
May 15 - Jun 07	24	19.30	196.00	168.30	-47.00	1.96
Jun 08 - Jun 30	23	6.60	168.30	142.78	-32.12	1.41
Jul 01 - Jul 06	6	0.00	142.78	139.09	-3.69	0.62
Jul 07 - Jul 14	8	0.00	139.09	131.22	-7.86	0.98
Jul 15 - Jul 20	6	3.43	131.22	129.63	-5.02	0.83
Jul 21 - Jul 26	6	4.32	129.63	131.22	-2.73	0.46
Jul 27 - Aug 02	7	2.66	131.22	126.23	-7.65	1.09
Aug 03 - Aug 09	7	0.00	126.23	120.77	-5.46	0.78
Aug 10 - Aug 16	7	2.54	120.77	117.74	-5.57	0.80
Aug 17 - Aug 23	7	0.00	117.74	114.91	-2.83	0.40
Aug 24 - Sep 07	15	4.57	114.91	113.74	-5.74	0.38
Total		43.42			-125.67	

TABLE 10. Water balance (mm) for the 1971 growing season for the water plus nitrogen treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
May 15 - Jun 07	24	73.51	196.00	185.29	-84.22	3.51
Jun 08 - Jun 30	23	177.22	185.29	204.79	-157.72	6.86
Jul 01 - Jul 06	6	24.26	204.79	207.93	-21.12	3.52
Jul 07 - Jul 14	8	54.82	207.93	206.82	-55.83	6.98
Jul 15 - Jul 20	6	46.10	206.82	217.13	-35.79	5.96
Jul 21 - Jul 26	6	42.12	217.13	234.12	-25.13	4.19
Jul 27 - Aug 02	7	36.96	234.12	240.83	-30.25	4.32
Aug 03 - Aug 09	7	49.08	240.83	259.73	-30.18	4.31
Aug 10 - Aug 16	7	44.80	259.73	262.79	-41.74	5.96
Aug 17 - Aug 23	7	0.00	262.79	226.63	-36.16	5.16
Aug 24 - Sep 07	15	4.57	226.63	172.24	-58.96	3.93
Total		553.44			-577.10	

TABLE 11. Water balance (mm) for the 1972 growing season for the control treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil		Water Balance	Daily ET
			Beginning	End		
Apr 20 - Jun 13	54	117.22	120.86	203.31	-53.08	0.98
Jun 14 - Jun 19	6	3.68	203.31	183.71	-4.97	0.83
Jun 20 - Jun 25	6	0.00	183.71	159.58	-24.13	4.02
Jun 26 - Jul 05	10	19.55	159.58	161.83	-17.30	1.73
Jul 06 - Jul 10	5	0.00	161.83	149.60	-12.23	2.45
Jul 11 - Jul 17	7	7.50	149.60	144.87	-12.23	1.75
Jul 18 - Jul 24	7	3.18	144.87	139.21	-8.84	1.26
Jul 25 - Jul 31	7	1.92	139.21	136.12	-5.01	0.72
Aug 01 - Aug 07	7	25.28	136.12	142.36	-19.04	2.72
Aug 08 - Aug 14	7	3.56	142.36	139.25	-6.67	0.95
Aug 15 - Aug 21	7	3.56	139.25	134.09	-8.72	1.25
Aug 22 - Aug 28	7	38.10	134.09	151.63	-20.56	2.94

TABLE 11. Continued.

Period	No. of Days	Water Received	Water in Soil		Water Balance	Daily ET
			Beginning	End		
Aug 29 - Sep 04	7	17.14	151.63	157.66	-11.11	1.59
Total		240.69			-203.89	

TABLE 12. Water balance (mm) for the 1972 growing season for the water treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
Apr 20 - Jun 13	54	251.72	191.61	338.61	-104.72	1.94
Jun 14 - Jun 19	6	14.14	338.61	336.57	-16.18	2.70
Jun 20 - Jun 25	6	16.51	336.57	319.28	-33.80	5.63
Jun 26 - Jul 05	10	72.06	319.28	350.65	-40.69	4.07
Jul 06 - Jul 10	5	0.00	350.65	334.03	-16.62	3.32
Jul 11 - Jul 17	7	41.32	334.03	325.64	-49.71	7.10
Jul 18 - Jul 24	7	25.03	325.64	319.25	-31.42	4.49
Jul 25 - Jul 31	7	25.94	319.25	307.66	-37.53	5.36
Aug 01 - Aug 07	7	39.90	307.66	317.42	-30.14	4.30
Aug 08 - Aug 14	7	47.42	317.42	332.59	-32.25	4.61
Aug 15 - Aug 21	7	4.26	332.59	310.18	-26.67	3.81
Aug 22 - Aug 28	7	57.19	310.18	345.19	-22.18	3.17

TABLE 12. Continued.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
Aug 29 - Sep 04	7	42.32	345.19	365.38	-22.13	3.16
Total		637.81			-464.04	

TABLE 13. Water balance (mm) for the 1972 growing season for the nitrogen treatment on a shortgtass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
Apr 20 - Jun 13	54	117.22	119.88	221.61	-15.49	0.29
Jun 14 - Jun 19	6	3.68	221.61	188.00	-37.29	6.22
Jun 20 - Jun 25	6	0.00	188.00	173.72	-14.28	2.38
Jun 26 - Jul 05	10	19.55	173.72	178.39	-14.88	1.49
Jul 06 - Jul 10	5	0.00	178.39	161.39	-17.00	3.40
Jul 11 - Jul 17	7	7.50	161.39	151.87	-17.02	2.43
Jul 18 - Jul 24	7	3.18	151.87	145.42	-9.63	1.38
Jul 25 - Jul 31	7	1.92	145.42	142.44	-4.90	0.70
Aug 01 - Aug 07	7	25.28	142.44	144.76	-22.96	3.28
Aug 08 - Aug 14	7	3.56	144.76	142.07	-6.25	0.89
Aug 15 - Aug 21	7	3.56	142.07	138.79	-6.84	0.98
Aug 22 - Aug 28	7	38.10	138.79	158.95	-17.94	2.56

TABLE 13. Continued.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
Aug 29 - Sep 04	7	17.14	158.95	163.87	-12.22	1.75
Total		240.69			-196.70	

TABLE 14. Water balance (mm) for the 1972 growing season for the water plus nitrogen treatment on a shortgrass prairie in northeastern Colorado.

Period	No. of Days	Water Received	Water in Soil Beginning	Water in Soil End	Water Balance	Daily ET
Apr 20 - Jun 13	54	270.67	151.25	317.19	-104.73	1.94
Jun 14 - Jun 19	6	15.75	317.19	293.74	-39.20	6.53
Jun 20 - Jun 25	6	17.94	293.74	312.16	-0.48	--
Jun 26 - Jul 05	10	76.72	312.16	289.15	-99.73	9.97
Jul 06 - Jul 10	5	0.00	289.15	270.37	-18.78	3.76
Jul 11 - Jul 17	7	47.04	270.37	260.19	-57.22	8.17
Jul 18 - Jul 24	7	32.80	260.19	253.53	-39.46	5.64
Jul 25 - Jul 31	7	31.66	253.53	238.64	-46.55	6.65
Aug 01 - Aug 07	7	37.92	238.64	237.49	-39.07	5.58
Aug 08 - Aug 14	7	58.51	237.49	259.20	-26.80	5.26
Aug 15 - Aug 21	7	4.70	259.20	239.39	-24.51	3.50
Aug 22 - Aug 28	7	55.27	239.39	273.39	-21.27	3.04

TABLE 14. Continued.

Period	No. of Days	Water Received	Water in Soil		Water Balance	Daily ET
			Beginning	End		
Aug 29 - Sep 04	7	47.50	273.39	303.05	-17.84	2.54
Total		695.77			-544.66	

Daily evapotranspiration provides a standardized comparison of evapotranspiration throughout the growing seasons for all treatments. The maximum rates observed were for the water plus nitrogen treatment in 1972 and the minimum rates were observed for the nitrogen treatment in 1971. The nitrogen treatment in 1971 had consistently lower values for daily evapotranspiration than any other treatment for either year.

Ratios of evapotranspiration to pan evaporation for 1971 and 1972 and ratios of total net primary productivity to evapotranspiration for 1972 are given in Table 15. Ratios of ET/Pan ranged from 0.087 for the nitrogen treatment in 1971 to 0.400 for the water plus nitrogen treatment in 1971. In all cases the ratios between years for the same treatment were within 0.06. The nitrogen treatment consistently had the lowest ratio and the water plus nitrogen treatment consistently had the highest.

Ratios of TNPP to ET indicate that the control treatment was most efficient in its water use and that the water stress treatment was the least efficient. The nitrogen and water and nitrogen treatments means were intermediate to the above two but closer to the control. None of the TNPP/ET ratios were significantly different from any of the others.

Small Mammals

Density

The total numbers of small mammals captured in 1971 and 1972 for the stress treatments as well as the numbers of individuals of each species captured are presented in Table 16. The total number of small mammals captured on the water plus nitrogen treatment in both 1971 and

TABLE 15. Evapotranspiration (ET) in millimeters, evapotranspiration/pan-evaporation ratios for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972 and TNPP/evapotranspiration ratios for 1972.

	Control		Water Stress		Nitrogen Stress		Water plus Nitrogen Stress	
	1971	1972	1971	1972	1971	1972	1971	1972
ET	222	204	526	464	126	197	577	545
ET/PAN	0.15	0.14	0.36	0.31	0.09	0.13	0.40	0.37
TNPP/ET	--	3.96	--	2.29	--	3.42	--	3.39

TABLE 16. Total number of small mammals captured[1/] on the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972.

	Species											
	Dipodomys ordii		*Microtus orchrogaster*		*Onychomys leucogaster*		*Peromyscus maniculatus*		*Spermophilus tridecemlineatus*		Total	
Treatment	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972
Control	0	1	0	0	18c[2/]	10b	8abd	4ab	6a	14b	32a	29a
Water Stress	0	0	1	2	2a	1a	16cd	15cd	2a	6a	21a	24a
Nitrogen Stress	1	0	0	0	18c	10b	1a	8ad	6a	16b	26a	34a
Water plus Nitrogen Stress	0	2	48	62	0a	0a	28e	13bcd	0a	1a	76b	78b

1/ Not including recaptures.

2/ Means for a species with the same letters are not different at the 5% level.

1972 was significantly different from all other treatments. There were no significant differences in total density among any of the other treatment totals.

The responses of the various species of small mammals to the stress treatments did not demonstrate the same trends as the totals of all species and there were many differences in species densities between treatments. The most striking difference among the treatments was attributable to the prairie vole *(Microtus orchrogaster)*. This species, not a normal inhabitant of upland prairie sites, was captured in large numbers and almost exclusively on the water plus nitrogen treatment. Three individuals were captured outside of the water plus nitrogen treatment and all of these were found on the water treatment.

The deer mouse *(Peromyscus maniculatus)* also seemed to prefer the water plus nitrogen treatment habitat, but not as markedly as the prairie vole. In 1971 there were significantly greater numbers of deer mice captured on the water plus nitrogen treatment than on any other treatment. There were also substantial numbers of individuals captured on the water treatment. In 1972 the number of deer mice captured on the water plus nitrogen treatment had declined, and was then only significantly different from the control. The number of deer mice captured on the water treatment was also significantly greater than the control. As a generalization it appears that both the prairie vole and the deer mouse prefer areas of heavy vegetative cover.

Onychomys leucogaster, the grasshopper mouse, and *Spermophilus tridecemlineatus*, the thirteen lined ground squirrel, responded just the opposite of the prairie vole and deer mouse. In both 1971 and 1972, there was a significant difference between the number of grasshopper mice captured on the treatments receiving additional water compared to those not receiving it. This was also true for the thirteen lined ground squirrel in 1972, but not in 1971. There was a decrease in the number of grasshopper mice from 1971 to 1972 on both the control and the nitrogen treatments, and for the same time period and treatments there was an increase in the number of thirteen lined ground squirrels.

Biomass

Small mammal biomass by species was proportional to the number of captures because of the method used to calculate biomass and hence the above discussion of numbers is also applicable here (Table 17). Total small mammal biomass per treatment was different from total captures because of the differences in average biomass for each species. Total biomass of small mammals was significantly different between the water and the water plus nitrogen stress treatments, but neither of these were significantly different from the other treatments in 1971. In 1972, the water treatment had a significantly smaller biomass of small mammals than any of the other treatments. There were no differences in small mammal biomass among the remaining treatments.

TABLE 17. Small mammal biomass (g/ha) by species for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972.

	Species											
	Dipodomys ordii		*Microtus orchrogaster*		*Onychomys leucogaster*		*Peromyscus maniculatus*		*Spermophilus tridecemlineatus*		Total	
Treatment	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972	1971	1972
Control	0	24	0	0	438	250	144	81	740	1788	1322 acd	2143 bcd[1/]
Water Stress	0	0	18	52	63	12	288	270	308	801	677a	1137a
Nitrogen Stress	24	0	0	0	451	263	18	135	678	1911	1171ac	2309b
Water plus Nitrogen Stress	0	73	1680	2188	0	0	513	234	0	62	2193bd	2557b

1/ Means followed by the same letter are not different at the 5% level. Means not followed by a letter were not tested.

DISCUSSION

Net Primary Productivity

Hypothesis I: Water and nitrogen stresses will increase net primary productivity.

Literature Review. Two types of experiments reported in the literature are relevant to Hypothesis I, although neither are directly comparable. The first involves the effect of stresses induced by non-nutrient chemicals on ecosystems and includes estimates of net primary productivity. The second are agronomic irrigation and nitrogen fertilization experiments on shortgrass and mixed grass prairie ecosystems and generally do not contain estimates of net primary productivity. In the latter case forage yields and root yields will be discussed.

Barrett (1968) investigated the effects of stress, induced by a single 2.25 kg/ha application of sevin, a carbamate insecticide, to a seeded millet *(Panicum ramosum)* ecosystem. He found no effect of the insecticide on net primary productivity. Malone (1969) applied 15.7 kg/ha of dazinon to an abandoned field in New Jersey and studied the effects for the following two years. He evaluated net primary productivity on both a treated and an untreated area and found a significant increase the first year and no difference the second year. The increase during the first year was attributed to a decrease in the activity of belowground arthropods.

Cosper and Thomas (1961) working in a mixed grass prairie in South Dakota found that the addition of 180 kg/ha of nitrogen doubled forage yield. Klages and Ryerson (1965) in a mixed grass prairie in eastern Montana determined that annual additions of 112 kg/ha of nitrogen over four years caused forage production to increase from 100% to 500% compared to the control. The addition of 608 mm of water during May, June and July increased forage production from 50 to 100%. The combination of water and nitrogen increased forage production three of the four years and the largest increase was ten times the control. They found nitrogen to be more effective than water in increasing yields.

Garwood (1967) investigated the effects of irrigation on the weight of grass roots under seeded pastures in England. He found a decrease in root weight by irrigation and postulated that it occurred because of faster decay of dead roots. He also investigated the effects of two levels of nitrogen, 273 and 546 kg/ha, with and without irrigation. He found that on non-irrigated pastures root weight decreased with increasing N and on irrigated pastures root weight was greatest for the 273 kg/ha treatment but still lower than the non-irrigated.

Cosper, Thomas and Alsayegh (1967) working with shortgrass prairie vegetation found that 180 kg/ha of nitrogen caused a significant increase in forage production of 786 kg/ha the year it was applied and a 449 kg/ha increase from the residual effects the following year.

Lehman, Bond and Eck (1968) investigated the capacity of a pure stand of blue grama to respond to nitrogen fertilization and irrigation. Seasonal precipitation plus irrigation averaged 900 mm for the three years of the study. Three levels of nitrogen, 225, 449, and 898 kg/ha were applied in the spring of the first year. No non-irrigated control was studied. Total forage production for the three years was increased about 90% for the 225 kg/ha treatment, almost 300% for the 449 kg/ha treatment and more than 400% for the 898 kg/ha treatment. They concluded that blue grama probably does not have a high yield potential compared to agricultural forage crops.

Discussion of Hypothesis I. The results of this experiment indicate that total net primary productivity of the shortgrass prairie is more sensitive to the addition of water and nitrogen in combination than to either nutrient separately. These results also provide evidence that water is more effective in altering net primary productivity than is nitrogen. These findings are contrary to those reported by Klages and Ryerson (1965) who found that nitrogen had a greater effect for increasing yields than water. The reason for the different findings between this study and Klages and Ryerson (1965) is probably attributable to the lower amount of evaporation in Montana compared to Colorado. This lower evaporation would increase the effectiveness of soil water for plant growth and lessen its importance in limiting productivity.

Although water altered total net primary productivity more than nitrogen, neither caused a significant deviation of TNPP from the control values in 1972. The reason that the water treatment did not cause a significant change in TNPP can be traced to the estimate of the belowground contribution to net primary productivity for this treatment. This was also a factor for the nitrogen treatment in addition to the carry over of effects from the extreme dry period in 1971.

The lack of a significant increase in BNPP by the stress treatments is in agreement with the findings of Garwood (1967). He postulated that this result was due to a faster rate of decay of dead roots under conditions of increased availability of water and nitrogen. Malone (1969) found that insecticide application increased the amount of belowground plant material and speculated that this was a result of a decrease in activity by decomposers. It seems reasonable to assume that although no differences could be detected in BNPP for this study that the values for the amended treatments represented a larger fraction of functional tissue than the control. The uncertainty of the response of the belowground portions of the primary producers was a large factor in the lack of a significant response of TNPP to the water treatment.

The postulated relationship between the drought period in 1971 and the decrease in primary productivity of the nitrogen treatment in 1972 is based entirely on indirect although plausable evidence. The dry period in 1971 began approximately the first of June and lasted through September. During this period 24 mm of rainfall were recorded compared to 140 mm for the same period in 1972 and 150 mm long term average. This dry period was preceeded by above average precipitation for April and May. Chemical analyses indicated that during May the nitrogen content of blue grama on the nitrogen treatment was 2.5% compared to 1.5% for the control treatment. The above data imply that during the spring of 1971 both water and nitrogen were available for rapid plant growth which under conditions of excess mineral nitrogen leads to rapid stem elongation and stem and leaf succulence. Both of these latter two conditions render plants particularly susceptable to drought injury (Treshow 1970). It is suggested that the interaction of rapid spring growth, high plant nitrogen and physiological water stress is enough to account for the decrease in primary producers observed on the nitrogen treatment from 1971 to 1972 (Tables 4, 5 and 6). It is also suggested that this decrease in the population of primary producers was a large factor in the lower net primary productivity observed for the nitrogen treatment in 1972. Widdowson et al. (1959) found that dry conditions following application of nitrogen fertilizer increased the amount of fertilizer "scorch" in cereal grasses.

Hypothesis II. Water and nitrogen stresses will differentially influence species group contributions to net primary productivity.

Literature Review. Cosper and Thomas (1961) found that the application of nitrogen to a mixed grass prairie site increased the proportion of non-grass over grass species. Klages and Ryerson (1965) reported that nitrogen, water and water plus nitrogen additions to a mixed grass prairie ecosystem decreased the proportions of grasses in total yields. Forbs and half shrubs were increased by nitrogen and water, but were only increased in two of the four years by water plus nitrogen. Blue grama decreased under 112 kg/ha of nitrogen, increased slightly with the addition of 608 mm of water during May, June and July and was increased two out of three years by water plus nitrogen.

Cosper, Thomas and Alsayegh (1967) determined that a single application of 180 kg/ha of nitrogen had no significant effect on the composition of yield. Goetz (1969) investigated the response of the vegetation on four range sites in North Dakota to 112 kg/ha of nitrogen. Midgrasses, shortgrasses, and perennial forbs increased on all sites. Annual forbs increased their proportion of yield on three of the four sites.

Choriki, Ryerson and Dubbs (1969) found that in Montana high rates of nitrogen eliminated some species, reduced the yield of blue grama and increased the yields of forbs and fringed sagewort. Ford and Siddoway (1971) also working in Montana determined that the yield of grasses and sedges increased five times and the yield of fringed sagewort and forbs was not changed by the application of 112 kg/ha of nitrogen. They also found that at very high rates of nitrogen, fringed sagewort was damaged by osmotic effects.

Discussion of Hypothesis II. The results of testing Hypothesis II are presented in Table 7. This hypothesis was qualitatively supported by all of the treatments but statistical analyses indicated that there were no significant changes in the composition of ANPP due to the nitrogen stress treatment. The water plus nitrogen treatment had the largest number of significant changes in species group contributions to ANPP. Three of the five groups were significantly greater than the control. The water treatment caused a significant change in only one of the five groups.

The species group with the largest response to the treatments was the warm season grasses. It was significantly increased on both the water and the water plus nitrogen treatments. As can be seen from Table 7 this group increased both its absolute and relative contribution to net primary productivity. This indicates that this group, which was primarily composed of blue grama, had the capacity to respond to additions of water and water plus nitrogen at the expense of other species groups. For both treatments this increase was at the expense of all groups except the warm season forbs.

The contributions of warm season forbs and shrubs to ANPP were significantly increased by the water plus nitrogen treatment. Cool season forb and cool season grass contributions to ANPP were not significantly changed by any of the stress treatments although both sustained large non-significant increases on the nitrogen treatment and the cool season grass peak standing crop was increased by the water plus nitrogen treatment.

The only indication of a fundamental change in the primary producer trophic level was the difference in the relative contributions of the species groups to ANPP for the nitrogen treatment compared to the other treatments. The control, water and water plus nitrogen treatments had basically the same patterns of relative contributions to ANPP. The two most important groups, shrubs and warm season grasses, contributed at least 82% and the remaining groups less than 10% each. The nitrogen treatment was different in that all five groups contributed 10% or more to ANPP. The largest contributor was shrubs with 37% and the smallest was warm season forbs with 10%. This appears to represent a basic alteration of the primary productivity relationships within this level of the ecosystem. The composition of ANPP for the other treatments appears to have been determined by the differential ability of the various species groups to compete for the added nutrients whereas for the nitrogen stress treatment the groups were exhibiting unequal capacities to withstand the nitrogen stress.

The two species groups that sustained the largest decrease because of the nitrogen treatment were the warm season grasses and shrubs. It appears that the reason they were injured and the other species groups were not was because of their opportunistic behavior. The data indicates that both of these groups respond markedly to increased availability of water and nitrogen. It seems probable that this response, previous to the dry period in 1971, was responsible for the decreases in both these species in 1972.

Hypothesis III. There is a positive interaction between water and nitrogen stress on net primary productivity.

Literature Review. Adequate water is extremely important in the nitrogen nutrition of plants. It is required for the movement of nitrogen in the soil to plant roots, uptake from the soil by the roots and its metabolism once it is inside the plant. In many areas of grasslands in the United States the response to added nitrogen is nullified by the lack of adequate moisture (Vallentine 1971).

Klages and Ryerson (1965) found a statistically significant interaction between water and nitrogen on the yield of a mixed grass prairie grassland in Montana. Garwood (1967) working with the effects of water and nitrogen on grass roots also found a significant interaction between water and nitrogen.

D'aoust and Tayler (1968) investigated the interaction of water and nitrogen on the growth of seeded grass pastures. They found the interaction closely related to the effect of irrigation on the soil water availability in the top few centimeters of soil. They also suggested that irrigation increases the uptake of nitrogen out of proportion to total yield.

Viets (1967) reviewed nutrient availability in relation to soil water for agricultural situations and stated that interactions of nitrogen with water are more common than the lack of interaction. He suggested three reasons for this: nitrogen deficiency is very common; most nitrogen is absorbed in the highly mobile NO_3 form; and the nitrogen requirements of plants are high.

Discussion of Hypothesis III. The results of testing Hypothesis III are presented in Table 2. These results indicated that while there was not a significant change in TNPP for either the water or the nitrogen treatment, there was a significant interaction of water and nitrogen. This interaction apparently was caused by the very tight balance between water and nitrogen and the scarcity of both under natural conditions. This will be discussed in detail in the discussion of Hypothesis IV.

Another indication of the interaction between these two nutrients is provided by the ratios of TNPP/ET in Table 15. The ratios are not comparable between the watered and unwatered treatments because a proportion of the water treatments were applied after the species groups reached their peak standing crop. The difference between the ratios for the water treatment and the water plus nitrogen treatment reflects the importance of nitrogen once water is freely available and hence the interaction of water and nitrogen.

Hypothesis IV. Net primary productivity is limited by the following: water on the control and nitrogen treatment; nitrogen on the water treatment; phosphorous, light or CO_2 on the water plus nitrogen treatment.

Literature Review. Limiting, in Hypothesis IV is intended in the sense of Liebig's law of the minimum. This states that out of all the factors required for, in this case net primary productivity, the one that is closest to approaching the critical minimum needed will be the limiting factor (Odum 1971).

The fact that experiments in range fertilization and irrigation are being done on Great Plains grasslands indicates that these scientists hypothesized that one or the other or both are limiting forage production under natural conditions (Cosper and Thomas 1961, Klages and Ryerson 1965, Smika, Haas and Power 1965, Cosper, Thomas and Alsayegh 1967, Burzlaff, Fick and Ritterhouse 1968, Lehman, Bond and Eck 1968, Rauzi, Lang and Painter 1968, Goetz 1969, Whitman 1969).

Striffler (1969) in a review of the hydrologic cycle in grasslands emphasized the extreme importance of water as a limiting factor to productivity. Porter (1969) in a similar paper concerned with nitrogen in grassland ecosystems stressed the importance of both nitrogen and water in determining grassland productivity.

Discussion of Hypothesis IV. The discussion of this hypothesis will consider only factors other than the treatments as limiting factors. The effect of excess nitrogen on net productivity was discussed previously. It is recognized that the design of this experiment does not permit testing this hypothesis and much of the following discussion is speculative.

Net primary productivity on the control treatment in 1972 was limited by the availability of water as evidenced by the data in Table 2. TNPP was increased by the addition of water but not by adding nitrogen. As mentioned previously the warm season grasses had the greatest response to additional water.

Water was also the critical factor bounding TNPP in the nitrogen treatment. This was supported by the large increase in TNPP sustained by the water plus nitrogen treatment. If, as stated above, water is the factor limiting net primary production under natural conditions, the addition of large amounts of mineral nitrogen without the addition of water would serve to magnify the importance of water. This was demonstrated by the effects of the nitrogen treatment during the drought period in 1971.

The results from the water treatment support the hypothesis that water is the limiting factor to net primary productivity for the shortgrass prairie and also point out the important effects of nitrogen once water is in adequate supply. The water treatment increased TNPP 25% whereas the water plus nitrogen treatment increased it more than 100%. The effects on ANPP were more pronounced with water accounting for a doubling of ANPP and water plus nitrogen increasing it five times. It appears from this data that the availability of mineral nitrogen rapidly becomes the limiting factor to net primary production once the limiting effects of water are removed.

Water is so important in determining net primary productivity of the shortgrass prairie and since it is in short supply a large proportion of the year the growing season for this vegetation type might better be defined on the basis of temperature and soil water rather than on temperature alone. A similar suggestion was made by Lewis (1969). This approach would remove water from any discussion of limiting factors and put it in the same category as temperature. This would elevate soil mineral nitrogen to the status of the limiting factor to TNPP. The design of this study does not lend itself to a more detailed examination of nitrogen since it is likely that different responses would have been attained with additions of nitrogen less than 150 kg/ha.

The response of the primary producers to the water and nitrogen treatment substantiate and emphasize the importance of water and nitrogen to primary productivity of the shortgrass prairie (Table 2). The question of what becomes the limiting factor after water and nitrogen are in sufficient supply has not been examined but the most likely factors seem to be phosphorous, light or carbon dioxide. Vern Cole (Personal communication, Colorado State University) determined that during the 1972 growing season aboveground plant phosphorous for the water plus nitrogen treatment was not unusually low, which may be an indication that phosphorous was not limiting TNPP.

Dye, Brown and Trlica (1972) examined carbon dioxide exchange of blue grama on the stress treatments and found that its photosynthetic activity was not light saturated even at 1.3 langleys/min. They concluded that under conditions of adequate soil water, production would increase if more light energy were available.

Although no work has been done on the stress treatments with carbon dioxide concentrations, Zelitch (1971) reported that net photosynthesis of both C_3 and C_4 plants was enhanced by increasing carbon dioxide concentrations to near the saturation point. It seems quite likely that with the amount of vegetation present on the water plus nitrogen treatment any of the above factors may have been limiting net primary production.

Botanical Composition of Primary Producers

Hypothesis V. Species composition of primary producers will be altered by water and nitrogen stresses.

Literature Review: The majority of the experiments involving the addition of water, nitrogen or both to native prairies have included botanical composition data but most is reported on a species group rather than a species basis.

Goetz (1969) reported changes in species composition caused by the addition of 112 kg/ha of nitrogen to several mixed grass prairie sites. The major effect of the treatment was an increase in western wheatgrass *(Agropyron smithii)*, threadleaf sedge *(Carex filifolia)* and fringed sagewort and a decrease in blue grama.

Lorenz (1970) also working with mixed prairie vegetation, found that western wheatgrass density increased with nitrogen fertilization and blue grama basal cover decreased. Density of western wheatgrass increased from 13 per 0.37 m^2 for the control to 163 when 180 kg/ha of nitrogen was applied. Basal cover of blue grama decreased from 37 to 4%.

Discussion of Hypothesis V. The most interesting responses of botanical composition caused by the stress treatments were attributable to the following species: blue grama, fringed sagewort, plains prickly pear, scarlet globemallow, plains pepperweed *(Lepidium densiflorum)* and woolly indian wheat *(Plantago purshii)*. The response of the above species will be discussed in terms of density except for blue grama for which basal cover will be used.

There were no significant differences in blue grama cover among any of the treatments in 1971. In 1972 blue grama basal cover for the water plus nitrogen treatment was significantly greater than all other treatments and the water treatment was significantly greater than the nitrogen or control treatment. The decrease of blue grama basal cover on the control and nitrogen treatments was probably a response to the drought conditions in 1971 as has been discussed previously. Both Goetz (1969) and Lorenz (1970) found decreases in blue grama basal cover with nitrogen fertilization. Basal cover of blue grama subjected to the water treatment apparently was not increased and the reason that it was significantly greater than the control in 1972 seems to have been primarily due to the decrease of basal cover on the control treatment. The water plus nitrogen treatment in 1972 had more than three times as much basal cover of blue grama as the control. Here blue grama was demonstrating its dominance potential under what it was apparently finding as very favorable growing conditions. The data of Table 10 indicate that this additional area occupied by blue grama in 1972 was previously bareground or litter.

The density of live pads of plains prickly pear was not significantly altered by the stress treatment in either 1971 or 1972. The highest density of live pads was recorded for the nitrogen treatment in 1972 which indicated that this species was not as sensitive to the effects of high levels of nitrogen during drought periods as were blue grama and fringed sagewort. This was not unexpected since this species does not appear to have the rapid growth rate capability of either blue grama or fringed sagewort and therefore would be less susceptable to this type of injury. Another advantage of plains prickly pear is that its stomata remain closed during the daytime thus minimizing water loss.

Scarlet globemallow was the most abundant perennial forb on the study area. Density of this species was not significantly modified by the stress treatments in either year of the study. This species also was not adversely effected by the nitrogen treatment. It is likely that the reason this species was not altered by the stress treatments and particularly by the nitrogen treatment was due to its very extensive rhizome system and large storage of carbohydrate reserves (Personal communication, John Menke, Colorado State University).

Plains pepperweed and woolly indian wheat were the most abundant annual forbs encountered on the study plots and both responded markedly to the stress treatments. Plains pepperweed densities in 1971 ranged from a low of 1.29 for the control treatment to a high of 18.85 for the water plus nitrogen treatment. The most interesting response of this species to the treatments was illustrated by its densities for the water and the water plus nitrogen treatments. Density of plains pepperweed for the water treatment in 1972 was 0.59, a decrease of 3.75 from 1971. Density of this species for the water plus nitrogen treatment was 0.09 a decline of 18.76 from 1971. Over the same period the control and the nitrogen treatments had increases in plains pepperweed density. It appears that the decrease in plains pepperweed density was related to the water treatment and that the effect was magnified by nitrogen. Similar but not quite as drastic effects were recorded for the density of woolly indian wheat. Its density in 1971 responded markedly to the water treatment and somewhat less to the water plus nitrogen treatment. In 1972 woolly indian wheat density decreased 10.58 on the water treatment and 6.46 on the water plus nitrogen treatment.

The response of these two species provide an interesting contrast. Plains pepperweed responded most positively to the water plus nitrogen treatment whereas woolly indian wheat responded most to the water treatment. These two species are found in approximately the same quantities in some years under natural conditions yet they have such different responses to the two most important limiting factors in their environment.

The question of why these two species declined so drastically in 1972 on the treatments that they had previously found very favorable is a matter for speculation at this time. Both species produced large quantities of seeds in 1971. The most reasonable explanation for the decline in 1972 appears to be involved with two factors, the large accumulation of litter at the end of 1971 and the shading effect of the standing dead plant material at the end of 1971 and early in the growing season of 1972. The heavy litter layer would prevent seeds of these species from reaching the soil surface. A combination of a heavy litter layer and a large amount of standing dead vegetation would prevent the seedlings from receiving adequate light.

Organization of Primary Producers

Hypothesis VI. Water and nitrogen stresses will result in a change in successional state of the primary producers but not necessarily to any previous state of the system.

Review of Literature. Margalef (1968) characterized trends in ecosystem properties during succession as follows: there is a trend toward increase in biomass, stratification, complexity and diversity; and a decrease in dominance. Many authors have used diversity to either characterize or compare successional states of ecosystems or communities.

One of the most popular indices of diversity used by ecologists is the Shannon index proposed by Margalef (1968)

$$\bar{H} = - \Sigma\, p_i \ln p_i$$

where p_i is the proportion of the i^{th} species in the collection. The basic property that makes this function useful as a descriptor of diversity is that it is a minimum when all individuals belong to the same species and a maximum when all individuals belong to different species.

Monk (1967) found that tree species diversity in forests from north central Florida was partially a function of the successional status of the community. Auclair and Goff (1971) stated that diversity in forest communities of the western Great Lakes region was strongly related to structural organization. They also found an increase in diversity during succession up to the climax stage then a decrease. Loucks (1970) also found that diversity increased as succession proceeded toward the climax with a decrease occurring at climax.

Discussion of Hypothesis VI. Two important statements must be made before beginning the discussion of Hypothesis VI. One concerns the basic assumption of the discussion and the other delimits the scope of the results. The basic assumption of this discussion and the important conclusion from the literature review is that diversity and succession are related and by measuring appropriate variables for calculating diversity, inferences can be made about the relative successional state of a group of ecosystems. The second statement is made to indicate that there is no intent to generalize these results to the entire shortgrass prairie.

In 1971 there were indications that Hypothesis VI would be supported by the data although the changes were not large. The impact of the treatments on diversity of the primary producers was greatest on the water treatment. It had the lowest diversity of all the treatments and approximately the same degree of dominance as the nitrogen and the water plus nitrogen treatments. Both the nitrogen and the water plus nitrogen treatments had lower diversities than the control. Although the result of stresses on the primary producers was the same for all treatments, a decrease in the level of organization, the manner in which they changed was not. The water and the water plus nitrogen treatments were at a lower organizational level in 1971 primarily as a result of the ability of blue grama and fringed sagewort to respond rapidly to the increased nutrients and become very abundant. This response masked the fact that the number of species encountered on both treatments increased. The reason the nitrogen treatment changed successionally was attributable to an increase in fringed sagewort influence and a decrease in the number of species encountered.

In 1972 the depression in the successional state of the water and the water plus nitrogen treatments continued but the nitrogen treatment rebounded to a higher level than the control. The nitrogen treatment appears to have experienced the most disruptive influence on the level of organization of any of the treatments. In 1972, diversity on this treatment was 23% higher than the control and the degree of dominance almost 50% less. The major reason for this response was the severe nitrogen-drought interaction in 1971 causing a large reduction in the dominance of both blue grama and fringed sagewort. The effect of this was to even out the distribution of density among the species of primary producers.

The treatment resulting in the largest decrease in successional state was the water plus nitrogen. In 1972 it had 40% more species than the control treatment, approximately the same total density and a 17% increase in dominance. The primary reason for this decrease in organization was that four species contributed 92% of the density compared to 84% for the four most abundant species on the control treatment.

The influence of the water treatment on the level of organization of the primary producers paralleled the water plus nitrogen treatment but was not as severe. The major response again was the concentration of total density in a few species.

Treatment Water Relations

Hypothesis VII. Evapotranspiration from the treatments receiving supplemental water is limited more by internal plant resistances than by the availability of energy.

Literature Review. Hypothesis VII was proposed because it was felt that plants that have evolved under conditions of limited water availability would have adaptations for conservative use of water. This premise is contrary to evapotranspiration theory.

The theory states that potential evapotranspiration is "the amount of water transpired in unit time by a short green crop, completely shading the ground, of uniform height and never short of water " (Penman 1956). Furthermore it has been demonstrated that if the above conditions are met that evapotranspiration is dependent upon the availability of energy regardless of the species of plants present (Chang 1968).

Denmead and Shaw (1962) found that under conditions of high evaporative demand of the atmosphere actual evaporation of well watered corn plants departed from the potential rate at a soil water potential of -0.3 bars. Under moderate and low evaporative conditions these departures occurred at -2 and -12 bars respectively. These data suggest plant control of transpiration even under condition of high availability of water.

Several authors (Smika, Haas and Power 1965, Lehman, Bond and Eck 1968 and White and Brown 1972) have shown effects of additions of nitrogen on evapotranspiration. Smika, Haas and Power (1965) found that seasonal evapotranspiration was increased by nitrogen when additional water was supplied but not under natural precipitation conditions. Lehman, Bond and Eck (1968) and White and Brown (1972) found no effects of nitrogen on total evapotranspiration although it did increase water use efficiency.

Discussion of Hypothesis VII. Hypothesis VII was not supported by the data and it was concluded that this hypothesis should be rejected. There was no evidence that the primary producers of the shortgrass prairie ecosystem had the ability to use water conservatively.

Three empirical estimates of potential evapotranspiration were available to compare with the data. They were as follows: 363 mm for 1971, 405 mm for 1972, calculated by the Hamon method from the results of Keiser (1970); 610 mm as a general annual estimate for eastern Colorado by Thornthwaite's method (Striffler 1969); 750 mm as a general annual estimate for the entire shortgrass prairie (Personal communication, Freeman Smith, Colorado State University).

Estimates of evapotranspiration by the water balance method for 1971 and 1972 were; 525 and 464 mm for the water treatment; and 577 and 544 mm for the water plus nitrogen treatment. The water plus nitrogen treatment best met the criteria for potential evapotranspiration although both treatments exceeded the estimates by the Hamon method. It also seems likely that both would exceed the annual estimate of 610 mm by Thornwaite's method if the treatments could be continued for an entire year. The estimate of 750 mm per year appears to be the most reasonable estimate of potential evapotranspiration.

Nunn (1973) working on a shortgrass prairie site within two miles of the location of this study suggested that canopy resistances were important in restricting transpiration regardless of soil water condition. This result is in contrast to the results for the stress treatments.

There are two explanations for the differences between the observed evapotranspiration and the calculated potential evapotranspiration. The first is that with the quantities of water maintained in the soil, plant resistance had no effect on transpiration. The large amount of evidence that there are resistances within plants that restrict water flow (Kramer 1969, pp. 258-346) casts a certain amount of doubt on this explanation. The remaining explanation is that the estimates of potential evapotranspiration are actually quite conservative and while they do not include values for resistance to water movement within the plant, their conservativeness actually allows for it.

Small Mammals

Hypothesis VIII. Small mammal species composition and biomass will be altered by water and nitrogen stresses.

Literature Review. Barrett (1968) investigated the effects of insecticide stress on stocked populations of three species of small mammals within an enclosed grassland ecosystem. Three different responses were obtained from the three species. The cotton rat *(Sigmodon hispidus)* was directly effected by the treatment and its reproductive rate was altered. The house mouse *(Mus musculus)* responded to the decrease in competition from the cotton rat by increasing its population density to a point of compensating for the decrease in the cotton rat. The old-field mouse *(Peromysicus polionotus)* appeared to be unaffected by the treatments.

Whitaker (1967) in a habitat study of small mammals in Indiana that included two species that occurred in this experiment, found definite habitat preferences of the species studied. *Microtus ochrogaster* and *Peromyscus maniculatus* were found to prefer grass and weed fields with *M. ochrogaster* preferring slightly heavier vegetative cover than *P. maniculatus*.

Rosenzweig (1973) conducted an experiment involving habitat modification and found that two coexisting rodents responded markedly. Merriam's kangaroo rat *(Dipodomys merriami)* and the desert pocket mouse *(Perognathos penicillatus)* showed definite habitat preferences upon encountering the modified areas.

Discussion of Hypothesis VIII. The responses of small mammal populations to the stress treatments were very similar in both 1971 and 1972. There were only a few cases of large changes in the numbers of a species caught on a particular treatment between years. In all instances where there was a change it did not alter the species-treatment relationship. The control, water and nitrogen treatments each supported three species in moderate abundance and one or two more in very low numbers. The water plus nitrogen treatment supported only two species of small mammals in abundance and two species in low numbers.

Table 18 presents the small mammal density data in terms of treatment effects. This data indicates that the prairie vole and the deer mouse were associated with some effect of water and that the grasshopper mouse and the thirteen lined groundsquirrel were associated with the treatments not receiving additional water. Closer examination of the table reveals that there were actually three categories. The prairie voles were associated with the interaction of water and nitrogen almost exclusively while the deer mouse was found in similar proportions on both the water and water plus nitrogen treatments. The last catecgry included the grasshopper mouse and the thirteen lined ground squirrel, both of which preferred the dryland situations. Neither of these latter two species showed any preference for one of the non-watered treatments over the other.

TABLE 18. Small mammal species densities for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972 by treatment effects.

Treatment Effect	Species				
	Dipodomys ordii	*Microtus orchrogaster*	*Onychomys leucogaster*	*Peromyscus maniculatus*	*Spermophilus tridecemlineatus*
Water	2	113	3	72	9
No Water	2	1	56	21	42
Nitrogen	3	110	28	50	23
No Nitrogen	1	4	31	43	28

The prairie vole as mentioned previously is not a normal component of the upland prairies in eastern Colorado but is more characteristic of streambanks and irrigated agriculture (Armstrong 1972). There are two possible sources from which the present population of voles could have dispersed. One is a permanent pond 4.8 kilometers away and the other is a small stream approximately 1.6 kilometers away. The stream site seems the most probable source since there are almost continuous roadside ditches between the experimental plots and the stream. The major obstacle is a state highway on the western boundary of the exclosure. Even so it is interesting that this species was able to locate this two hectare unit of favorable habitat the first year that it existed.

The deer mouse is a widely distributed species in Colorado occurring in habitats ranging from deserts to alpine meadows (Armstrong 1972). This species is a common inhabitant of the shortgrass prairie and its response to water stress may be proportional to the increase in food supply. Grant (1972) determined from stomach analyses that 62% of deer mouse diets were arthropods and 33% were plant parts in 1971, although he did not find a positive correlation between deer mice densities and arthropod densities. It may well be that because of the ubiquitous nature of this species that certain elements of the population found the treatments with heavier vegetation favorable and at least in the case of the water treatment free from competition.

The grasshopper mouse and the thirteen lined groundsquirrel did not alter their habitat preference under the influence of the stress treatments. They were captured in larger numbers on both the control and the nitrogen treatments than they were on light and heavy grazed pastures in the same area (Grant 1972). It is likely that the fact that they have access to the treatments with substantially more standing vegetation than the native prairie may account for this increase. The treatments are certainly providing a sanctuary for both arthropods and mammals.

CONCLUSIONS

Hypothesis I, concerning the influence of water and nitrogen stress on net primary productivity, was tested statistically and, in null hypothesis form, could not be categorically rejected in 1972. Total net primary productivity was significantly increased only by the water plus nitrogen treatment. The lack of a significant change in total net primary productivity, under the influence of water and nitrogen stresses individually, was due in part to the lack of a good technique for assessing changes in root weights.

Root weights were not as responsive to the effects of water and nitrogen stresses as were top weights. Two factors accounted for this difference. The large amounts of belowground organic material (primarily dead roots) had a buffering effect on seasonal root weight dynamics. Although there were essentially no differences among the treatments in belowground net primary productivity, except possibly for the nitrogen treatment, this was deceptive in that the proportions of live and dead roots was likely different for the various treatments. The second probable explanation for the lack of a significant response by the roots was that the necessity for an extensive root system is decreased when the major factors limiting growth are freely available.

Recommendations for further testing of this hypothesis include: increasing the number of replications of the treatments; increasing both sample size and numbers; and development of a technique to estimate either the amount of photosynthate translocated belowground or the seasonal dynamics of live roots and rhizomes.

Hypothesis II also proved to be testable statistically and again could not be categorically rejected in 1972. Stresses induced by making growing conditions more favorable did not alter the relationships among the proportions contributed to aboveground net primary productivity by the various species groups. However, in many cases the absolute amount was changed. In contrast to this, conditions less favorable for plant growth, created by excess mineral nitrogen, did alter primary producer relationships and had the effect of evening out the contributions of the various groups to net primary productivity. The explanation of this is involved with the strategies of the different species. The dominants, warm season grasses and shrubs, were primarily composed of species that are opportunists. These species have the ability to respond rapidly to favorable conditions, but this also makes them vulnerable to abrupt unfavorable conditions. Both warm season grasses and shrubs were injured in 1971 when growth was initiated under conditions of high mineral nitrogen and favorable soil moisture, but by June 1, soil moisture was depleted and no major recharge occurred for the remainder of the growing season. The subordinate species had a more conservative strategy that prevented them from taking rapid advantage of favorable conditions, but also protected them from unfavorable conditions. The subordinate species groups increased their contribution to net primary productivity following the 1971 drought.

Hypothesis II in its present form probably does not warrant further testing. Because of the variation in responses of the species groups to the treatments, a more useful approach would be to state hypotheses about the behavior of each group and how its contribution to net primary productivity will be altered by the treatments. Increasing the number of treatment replications, and sample size and number would also aid in testing a new set of hypotheses.

Hypothesis III was the only hypothesis of the set examined in this study that could be clearly rejected. There was a significant positive interaction between water and nitrogen on net primary productivity in 1972. This was evidence that although water was clearly the primary limiting factor there was a very close relationship between water and nitrogen in determining primary productivity. As water becomes available nitrogen rapidly limits primary productivity.

Hypothesis IV concerning factors limiting net primary productivity was not testable statistically and would require a much more extensive experiment to provide testable data. A conclusion that can be drawn about this hypothesis is that water is by far the most important factor limiting net primary productivity of the shortgrass prairie in northeastern Colorado.

Hypothesis V proved to be testable statistically but far too general to be useful. Several important species experienced large changes in the relative contribution to total density and others showed no apparent effects.

The major responses of the botanical composition of the treatments to the stresses were of two types. The first response involved a reordering of the relationships among existing species. Blue grama has the capacity to utilize additional nitrogen when accompanied by adequate water. Nitrogen alone decreased its basal cover and water alone increased it only slightly. Fringed sagewort has the capacity to utilize additional water or nitrogen or water plus nitrogen. It responded most rapidly to water plus nitrogen and was damaged during dry periods under the influence of nitrogen alone.

The second kind of response was the addition of new species with enhanced growing conditions. In only one case was a species found in both years on the control treatment not found on one of the stress treatments. Water and water plus nitrogen over a two year period substantially increased the number of species coexisting on the areas.

The successional states of the primary producers were altered by both one and two years of stress treatments. Hypothesis VI was not testable statistically because of the indirect nature of the criteria for assessing the successional states of the treatments. The evidence from the diversity and dominance data combined with the species composition results indicated in all cases that the treatments were remaining shortgrass prairie types. After two years of treatment there has been no substantial increase in species characteristic of either the mixed or mid grass prairies. It seems reasonable to assume that due to the anomalous conditions created by the treatments (very wet soil and very dry air) and the small area of the treatments that they will remain simply a magnified shortgrass prairie type.

Recommendations for further testing of this hypothesis would involve increasing the size of the treated areas and increasing the criteria for judging the states of the systems.

Hypothesis VII was not tested statistically because of the lack of data for estimating potential evapotranspiration from the stress treatments. Comparison of the estimates of evapotranspiration from the watered treatments with estimates of evapotranspiration from the literature provided evidence that even without a statistical test this hypothesis should be categorically rejected. There was no indication that the species on a shortgrass prairie in northeastern Colorado had the capacity to restrict water loss when water was freely available in the soil. It was suggested that estimates of potential evapotranspiration may be conservative enough to include the effects of plant resistances on transpiration.

Further testing of this and related hypotheses would require adequate micrometerological measurement on the stress treatments to evaluate potential evapotranspiration.

Small mammals living in and near the shortgrass prairie vegetation of the experimental plots not only had habitat preferences, but one in particular, the prairie vole, had the ability to seek out areas of preferable habitat over relatively long distances. The prairie vole preferred the habitat of the water plus nitrogen treatment exclusively. The deer mouse preferred the treatments receiving supplemental water and the grasshopper mouse and thirteen lined ground squirrel preferred the conditions of the native prairie. Conclusions about Hypothesis VIII, even though it was tested statistically, are tenuous at best and limited by the size of the experimental areas. This hypothesis would be more useful if stated more specifically and if the experimental areas were square kilometers instead of hectares.

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APPENDIX

TABLE 19. Aboveground standing crop (g/m^2) by the species groups in 1972 for the control treatment and aboveground net primary productivity (ANPP) on a shortgrass prairie in northeastern Colorado.

	Apr 4	May 1	May 19	Jun 9	Jul 5	Jul 21	Aug 14	Sep 4	Oct 9	Contribution to ANPP
Warm Season Grasses	40	40	47	43	39	44	41	49	31	49
Cool Season Grasses	7	13	11	8	14	16	10	5	3	16
Warm Season Forbs	1	1	2	3	3	4	4	4	4	4
Cool Season Forbs	1	1	3	3	12	16	9	8	5	16
Shrubs	48	48	42	39	72	74	76	114	120	120
Total	102	105	108	101	144	146	144	178	164	
									Total	205

TABLE 20. Aboveground standing crop (g/m^2) by the species groups for 1972 for the water stress treatment and aboveground net primary productivity (ANPP) on a shortgrass prairie in northeastern Colorado.

	Apr 4	May 1	May 19	Jun 9	Jul 5	Jul 21	Aug 14	Sep 4	Oct 9	Contribution to ANPP
Warm Season Grasses	76	94	110	127	123	131	153	176	143	176
Cool Season Grasses	7	12	14	15	6	16	5	22	5	22
Warm Season Forbs	4	7	8	15	31	21	21	39	30	39
Cool Season Forbs	5	5	1	6	2	18	1	6	15	18
Shrubs	50	27	76	64	85	129	188	191	121	191
Total	145	147	213	228	250	318	375	436	317	
										Total 446

TABLE 21. Aboveground yield (g/m^2) by the species groups for the nitrogen stress treatments in 1972 and aboveground net primary productivity (ANPP) on a shortgrass prairie in northeastern Colorado.

	Apr 4	May 1	May 19	Jun 9	Jul 5	Jul 21	Aug 14	Sep 4	Oct 9	Contribution to ANPP
Warm Season Grasses	37	45	37	14	29	26	34	48	39	48
Cool Season Grasses	10	30	52	45	30	18	16	14	8	52
Warm Season Forbs	2	5	7	21	16	24	18	20	30	30
Cool Season Forbs	2	1	10	17	54	32	18	14	9	54
Shrubs	67	67	34	35	29	48	62	106	97	106
Total	121	151	144	136	162	151	152	208	187	
										Total 290

TABLE 22. Aboveground standing crop (g/m^2) by the species groups for the water plus nitrogen stress treatment for 1972 and aboveground net primary productivity (ANPP) on a shortgrass prairie in northeastern Colorado.

	Apr 4	May 1	May 19	Jun 9	Jul 5	Jul 21	Aug 14	Sep 4	Oct 9	Contribution to ANPP
Warm Season Grasses	96	190	194	319	378	394	430	465	386	465
Cool Season Grasses	13	21	26	13	14	53	32	25	30	53
Warm Season Forbs	8	3	9	13	49	65	30	45	44	65
Cool Season Forbs	20	8	8	5	20	5	8	8	17	20
Shrubs	149	129	60	128	240	250	286	558	420	558
Total	286	352	297	478	701	767	785	1101	898	
										Total 1161

TABLE 23. Root weight (g/m^2) for the stress treatments on a shortgrass prairie in northeastern Colorado for 1972.

Treatment	Apr 11	May 4	May 24	Jun 13	Jul 7	Jul 23	Aug 16	Sep 5	Oct 11
Control	820	974	797	874	872	844	980	1170	846
Water Stress	984	1050	1195	1090	1028	1172	1390	1306	939
Nitrogen Stress	996	934	1100	1066	998	1060	1198	1165	932
Water plus Nitrogen Stress	1048	1069	1243	1144	1132	1357	1592	1345	1268

TABLE 24. Scientific names, common names and four-letter codes for species encountered for the stress treatments on a shortgrass prairie in northeastern Colorado in 1971 and 1972.

Code	Scientific Name	Common Name
AGSM	*Agropyron smithii* Rydb.	Western wheatgrass
ALTE	*Allium textile* Nels. + Macbr.	Textile onion
ARFR	*Artemisia frigida* Willd.	Fringed sagewort
ARLO	*Aristida longiseta* Steud.	Red three-awn
ASMO	*Astragalus mollissimus* Torr.	Woolly loco
ASTA	*Aster tanacetifolius* H.B.K.	Tansy-leaf aster
BOGR	*Bouteloua gracilis* (H.B.K.) Lag.	Blue grama
BUDA	*Buchloe dactyloides* (Nutt.) Engelm.	Buffalo grass
CAHE	*Carex heliophila* Mackenz.	Sun sedge
CHLE	*Chenopodium leptophyllum* Nutt.	Narrow-leaf goosefoot
CHNA	*Chrysothamnus nauseosus* (Pall.) Gritt.	Rubber rabbitbrush
CIUN	*Cirsium undulatum* (Nutt.) Spreng.	Wavy-leaf thistle
COCA	*Conyza canadensis* (L.) Cronquist	Canada horseweed
CRJA	*Cryptantha jamesii* (Torr.) Payson	James cryptantha
CRMI	*Cryptantha minima* Rydb.	Cryptantha
DESO	*Descurainia sophia* (L.) Webb Ex Prantl.	Flixweed tansymustard
ECVI	*Echinocereus vicidiflorus* Engelm.	Hedgehog cactus
ERBE	*Erigeron bellidiastrum* Nutt.	Fleabane
EREF	*Eriogonum effusum* Nutt.	Spreading wildbuck-wheat

TABLE 24. Continued.

Code	Scientific Name	Common Name
EVNU	*Evolvulus nuttalianus* Roem. + Schult.	Nuttal evolvulus
FEOC	*Festuca octoflora* Walt.	Common six-weeks grass
GACO	*Gaura coccinea* Nutt. Ex Pursh.	Scarlet gaura
GUSA	*Gutierrezia sarothrae* (Pursh.) Britt. + Rusby	Broom snakeweed
HASP	*Haplopappus spinulosus* (Pursh.) DC.	Iron-plant goldenweed
HEVI	*Heterotheca villosa* (Pursh.) Skinners	Hairy goldenstar
KOSC	*Kochia scoparia* (L.) Schrad.	Belvedere summer cypress
LARE	*Lapula redowskii* (Hornem.) Greene	Bluebur stickseed
LEDE	*Lepidium densiflorum* Schrad.	Prairie pepperweed
LEMO	*Leucocrinum montanum* Nutt.	Common starlily
LIIN	*Lithospermun incisum* Lehm.	Yellow gromwell
LIPU	*Liatris punctata* Hook.	Dotted gayfeather
LOOR	*Lomatium orientale* Coult. + Rose	Bisquitroot
LUPU	*Lupinus pusillus* Pursh.	Rusty lupine
MAVI	*Mammillaria vivipara* Nutt.	Purple mammilaria
MILI	*Mirabilis linearis* (Pursh.) Heimrl.	Four-o'clock
OEAL	*Oenothera albicaulis* Pursh.	Prairie evening primrose
OPPO	*Opuntia polyacantha* Haw.	Plains pricklypear
ORLU	*Orobanche ludoviciana* Nutt.	Louisiana broomrape
OXLA	*Oxytrops lamberti* Pursh.	Lambert crazyweed

TABLE 24. Continued.

Code	Scientific Name	Common Name
PEAL	*Penstemon albidus* Nutt.	White penstemon
PEAN	*Penstemon angustifolius* Nutt.	Narrow-leaf penstemon
PLPU	*Plantago purshii* Roem. + Schult.	Woolly Indianwheat
PSTE	*Psoralea tenuiflora* Pursh.	Slimflower scurfpea
RACO	*Ratibida columnaris* (Sims.) D. Don.	Upright prairiecone-flower
SAKA	*Salsola kali* Tausch.	Common Russian thistle
SIAL	*Sisymbrium altissimum* L.	Tumbling hedge mustard
SIHY	*Sitanion hystrix* (Nutt.) J. G. Smith	Bottlebrush squirrel-tail
SOSE	*Sophora sericea* Nutt.	Silky sophora
SPCO	*Sphaeralcea coccinea* (Pursh.) Rydb.	Scarlet globemallow
SPCR	*Sporobolus cryptandrus* (Torr.) A. Gray	Sand dropseed
STCO	*Stipa comata* Trin. + Rupr.	Needleandthread
TAOF	*Taraxacum officinale* Wiggars	Common dandelion
THTR	*Thelesperma trifidum* (Poir.) Britt.	Greenthread
TOGR	*Townsendia grandiflora* Nutt.	Townsendia
TRDU	*Tragopogon dubius* Scop.	Yellow salsify
TROC	*Tradescantia occidentalus* (Britt.) Smith	Prairie spiderwort
YUGL	*Yucca glauca* Nutt.	Small soapweed