

Effects of water, nitrogen and sulfur amendments on cover, density and size of Chihuahuan Desert ephemerals

John A. Ludwig*†, Walter G. Whitford* and Joe M. Cornelius*

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The generality of the water-limited–nitrogen-regulated plant growth hypothesis for desert ecosystems was tested by applying water, nitrogen and sulfur amendments in a complete factorial design to three Chihuahuan Desert ecosystems. Water was added every 2 weeks at a rate to about double the long-term annual precipitation average of 225 mm and nitrogen and sulfur were added once in May 1983 (10 g/m²). Living-canopy area of all herbaceous plants was measured monthly (from April 1983 to December 1984). Since plants can respond to water and nutrients either by establishing more, but smaller, plants or by growing fewer, but larger, plants, density and plant size were measured (once, in mid-April 1984). Only C₃ winter-ephemerals significantly changed in cover, density or plant size in response to the amendments; no significant responses were observed in C₄ summer-ephemerals or perennial grasses and forbs. Species that significantly increased in density did not significantly increase in size and vice versa. Water tended to limit the number (richness) and density of species, whereas nitrogen regulated plant growth (size). Sulfur generally reduced soil pH and species density. This study demonstrated that these general plant responses to increased water and nutrients were highly species and site specific.

Introduction

Previous studies examining the relative importance of water and soil nutrients on the growth of desert plant populations generated the hypothesis that the Chihuahuan Desert was a water-limited, nitrogen-regulated ecosystem (Ettershank *et al.*, 1978; Gutierrez & Whitford, 1987; Gutierrez *et al.*, 1988). In other words, adding supplemental water above natural rainfall would have little effect on plant growth unless nitrogen was available. Adding nitrogen under conditions of average to above-average rainfall greatly increased plant production and changed species composition. However, these earlier studies were all conducted within creosotebush communities of the Chihuahuan Desert and did not examine the effects of nutrients other than nitrogen.

The aim of this study was to test the generality of the water-limited–nitrogen-regulated hypothesis by applying water and nitrogen amendments to three different Chihuahuan Desert ecosystems: (1) a piedmont desert–grassland, (2) a creosotebush bajada, and (3) a basin yucca–grassland (see Study area section for a description of these ecosystems). The importance of other nutrients as ecosystem regulators was tested by adding elemental sulfur to these systems. Sulfur could have a direct effect or, more likely, an indirect effect

* Department of Biology, New Mexico State University, Las Cruces, New Mexico 88003, U.S.A.

† Present address and correspondence to: J. A. Ludwig, CSIRO Rangelands Research Centre, Deniliquin, New South Wales 2710, Australia.

by changing soil pH towards acidity, perhaps releasing essential phosphorus bound in the soil (e.g. calcium phosphates).

The previous studies cited above examined plant growth (e.g. biomass production) responses to water and nitrogen amendments. To examine growth responses of ephemeral plant populations through time, we measured live canopy cover monthly from the start of the study in April 1983 to its conclusion in December 1984. However, plant populations can respond to such amendments by either establishing many more plants (but each plant smaller), or by maintaining a small number of plants (but each plant growing larger). Thus, in this study, we made two additional populations measurements: (1) density and (2) plant size (diameter and height). These were measured in mid-April 1984 when most C₃ winter-ephemerals attained maximum development.

Study area

In 1982 a long-term ecological research (LTER) gradsect (gradient oriented transect) was established on the New Mexico State University Desert Experiment Station (College Ranch) located about 40 km north of Las Cruces in southern New Mexico. The research gradsect extended over a distance of 2700 m from the lower rocky slopes of the Dona Ana Mountains, down across piedmont slopes with desert-grassland (*Bouteloua eriopoda* and *Erioneuron pulchellum*), onto bajada slopes with creosotebush shrubland (*Larrea tridentata*), into a basin with yucca-grassland, (*Yucca elata* and *Aristida* spp.) down into a swale of mesquite (*Prosopis glandulosa*), and finally terminating in a dry-lake of vine-mesquite and tobosa grass (*Panicum obtusum* and *Hilaria mutica*, respectively). Details of soil and vegetation patterning along this LTER gradsect are provided by Wierenga *et al.* (1987), and for the area in general by Smith & Ludwig (1978) and Stein & Ludwig (1979). This area in the northern Chihuahuan Desert is characterized by summer precipitation (about 50% in July, August and September out of an annual average of about 225 mm).

Methods

Experimental plots for water, nitrogen and sulfur amendments were established within the piedmont desert-grassland, the bajada creosotebush shrubland, and the basin yucca-grassland zones of the LTER gradsect. Within each of these three zones, eight square 8 m × 8 m plots (Fig. 1) were fenced with mesh to exclude rabbits (livestock are excluded from the entire LTER area). Water was added by overhead sprinklers every 2 weeks from May

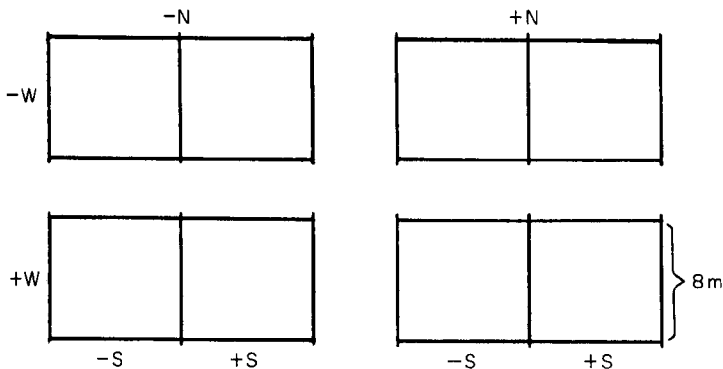


Figure 1. Factorial design for water, nitrogen and sulfur amendments applied to three different Chihuahuan Desert ecosystems.

1983 to December 1984 at a rate to about double the long-term average (i.e. about 10 mm every 2 weeks), which added about 250 mm to the natural rainfall regime. Nitrogen was added as a one-time application in May 1983 at a rate of 10 g/m² of NH₄NO₃. Elemental sulfur was also added in May 1983 at the same rate. Four of the eight plots received water, four received nitrogen and four sulfur in a complete factorial design (Fig. 1).

The growth dynamics of plant populations was monitored by photoquadrats (0.5 m × 0.5 m) monthly from early April 1983 (2 weeks before water and nutrients were added) to December 1984. The color negatives were digitized to obtain living canopy cover by species (field notes aided species identifications and phenological states). Four permanent quadrats were photographed within each factorial treatment each month. Repeated measures analysis of variance (ANOVA) was used to analyze these cover data to test for significant treatment (water, nitrogen, sulfur) effects and interactions.

Density of plant populations and individual plant sizes (diameter and height) were measured in mid-April 1984 (about 1 year after the initial nitrogen and sulfur amendments), and at a time when there was a peak response of the C₃ winter-ephemerals. Density was estimated using five quadrats (0.4 m × 0.4 m) within each factorial treatment. Plant diameter and heights were measured on each species within these same quadrats and a mean plant size (by species) was computed assuming a canopy shaped like an inverted cone (Ludwig *et al.*, 1975). A total canopy volume for each quadrat (by species) was also computed. The density and plant size data were analyzed by ANOVA for significant treatment effects and interactions.

Results

Growth dynamics

Of the numerous herbaceous plants on our LTER plots that could have shown a growth response to water, nitrogen or sulfur amendments, only three desert ephemerals exhibited significant ($p = 0.05$) changes (through time) in canopy cover; and this was only during the spring of 1984 (Fig. 2). *Lepidium lasiocarpum* significantly increased in cover in response to nitrogen plus water amendments, irrespective of the sulfur amendment, in the creosotebush and the yucca-grassland communities. Neither the water alone nor the nitrogen alone treatments produced a growth response different from the control (natural precipitation and nutrient levels).

Lesquerella gordonii also exhibited a significant increase in canopy cover in the spring of 1984 on the yucca-grassland plot in response to the combination of added nitrogen, water and sulfur and to nitrogen plus water and water alone—other treatment combinations were not significantly different from each other (Fig. 2). The only species to significantly change in cover on the desert-grassland plot was the mexican poppy, *Eschscholzia mexicana*. Again, the response was to the nitrogen plus water amendment (with and without sulfur) in the spring of 1984.

Population density and plant size

Based on ANOVAs of the mid-April 1984 population density and plant size data, a number of species significantly responded to the various amendment treatments (Table 1). From this analysis, some interesting patterns emerge. First, the response of a species differs with the ecosystem in which it occurs. For example, *Lepidium lasiocarpum* exhibited no significant change in density on the desert-grassland site but significantly increased in density with added water and nitrogen on the yucca-grassland site. On the creosotebush bajada *Lepidium* increased in density in response to water plus sulfur amendments but, interestingly, not nitrogen. *Eschscholzia mexicana* also differed in density on the desert-

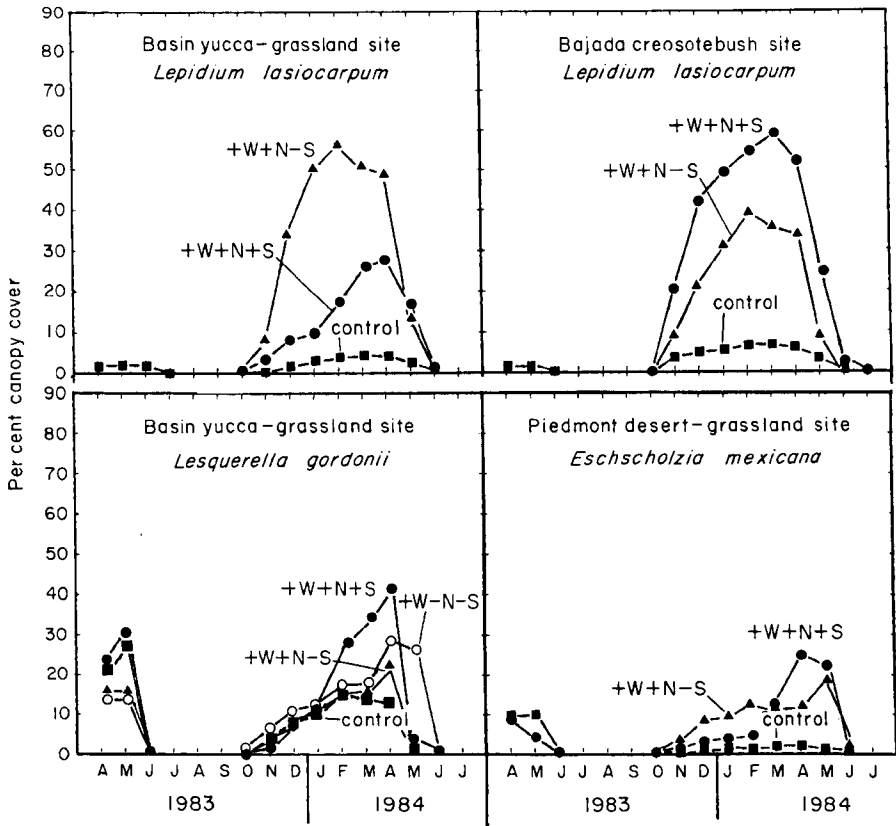


Figure 2. Canopy cover for Chihuahuan Desert ephemerals having significant responses to added water (+W), nitrogen (+N) and sulfur (+S) from the start of the amendment study (April 1983) to July 1984. Responses to amendment combinations not significantly different from the control (squares) are not shown.

grassland and yucca-grassland sites, with no significant change on the former but a significant increase in density with water on the latter. *Eriastrum diffusum* also responded differently on these two sites (Table 1).

A second interesting pattern emerging from our analysis of these data was that, in many cases, species with no significant change in density greatly increased in plant size. For example, on the desert-grassland site, *Eschscholzia* did not significantly change in density, but greatly increased in average plant size (i.e. volume on an individual and quadrat basis) in response to added water and nitrogen. The same response was evident for *Lepidium* on this site. The converse response was found in other species. For example, *Descurainia pinnata* and *Cryptantha micrantha* significantly increased in density but not in plant size on the desert-grassland site (with added water) and *Eriastrum* responded similarly on the yucca-grassland site. Some species increased both in density and plant size with added water and nitrogen and/or sulfur (e.g. *Eschscholzia* and *Lepidium* on the yucca-grassland site; Table 1).

A third response pattern evident was an apparent negative response in some ephemerals to added sulfur. For example, *Lesquerella gordonii* significantly increased in density, but only on those yucca-grassland plots without sulfur added. The same occurred with *Eriastrum* on the desert-grassland site (as long as nitrogen was also not added). The total

Table 1. Mean densities ($D = \text{No./m}^2$), plant size ($PS = \text{cm}^3$) and quadrat volume ($QV = \text{cm}^3/\text{m}^2$) for species with significant responses to a complete factorial of water (W), nitrogen (N) and sulfur (S) amendments

Site/species	-W				+W				
	-N		+N		-N		+N		
	-S	+S	-S	+S	-S	+S	-S	+S	
DG ESME	D	5	6	26	9	36	16	18	8
	PS	4	35	28	1	8	160	3215*	2372*
	QV	31	505	268	19	334	3602	53,482*	23,494*
DEPI	D	0	1	0	0	28*	14*	2	0
	PS	0	1	0	0	40	5947	256	0
	QV	0	4	0	0	1618	40,785	2822	0
LELA	D	21	9	24	19	28	8	6	8
	PS	30	218	6	224	148	2607*	677*	2168*
	QV	855	1808	149	3150	5459	16,452*	12,138*	14,928*
CRMI	D	1	0	8	0	60*	10	11*	1
	PS	<1	0	<1	0	18	16	232	<1
	QV	2	0	6	0	611	388	6390	4
ERDI	D	20*	1	10	0	18*	5	0	0
	PS	4	2	<1	0	10	10	0	0
	QV	116*	10	8	0	220*	102*	0	0
DIWI	D	0	0	1	1	0	0	0	10*
	PS	0	0	3	164*	0	0	0	1399*
	QV	0	0	18	1026*	0	0	0	14,620*
TOTAL	D	60*	44	85*	36	204*	79	51*	38
	QV	1025	2566	451	4195	8290	63,992*	74,842*	53,512*
CB LELA	D	36	18	82	39	66	266*	88	199*
	PS	<1	<1	1	4	8	1	305*	163*
	QV	5	1	80	146	676	314	24,499*	20,500*
YG ESME	D	2	0	0	0	29*	32*	14*	58*
	PS	<1	0	0	0	<1	59*	38*	22*
	QV	1	0	0	0	10	2644*	748*	831*
LELA	D	2	8	1	2	24	29	111*	76*
	PS	1	8	1	<1	<1	51*	32*	88*
	QV	9	145	3	4	13	1582	3708*	6135*
ERDI	D	0	0	2	0	13*	5*	34*	12*
	PS	0	0	<1	0	48	34	<1	3
	QV	0	0	<1	0	1175	861	22	61
LEGO	D	282*	140	160*	101	158*	21	201*	65
	PS	<1	9	2	6	1	19	86	451
	QV	145	615	139	154	109	675	11,408*	35,022*
TOTAL	D	295*	149	174*	105	271*	126	392*	275
	QV	155	760	142	158	1306	5762	15,885*	42,050*

Sites: DG, desert-grassland; CB, creosotebush bajada; YG, yucca-grassland.
 Species: ESME, *Eschscholzia mexicana*; DEPI, *Descurainia pinnata*; LELA, *Lepidium lasiocarpum*; CRMI, *Cryptantha micrantha*; ERDI, *Eriastrum diffusum*; DIWI, *Dithyrea wislizenii*; LEGO, *Lesquerella gordonii*.

* Significantly greater than the other factorial treatment mean(s); see text.

Table 2. Mean and range in species richness on three Chihuahuan Desert sites (DG, desert-grassland; CB, creosotebush bajada; YG, yucca-grassland) in response to a complete factorial of water (W), nitrogen (N) and sulfur (S) amendments

Site		-W				+W			
		-N		+N		-N		+N	
		-S	+S	-S	+S	-S	+S	-S	+S
DG	Mean	3.6	3.2	5.6	2.8	5.8	4.2	3.2	3.8
	Range	2-5	2-4	3-7	1-5	4-9	2-7	2-4	3-5
CB	Mean	2.0	0.8	2.6	1.2	5.0	3.8	2.1	1.4
	Range	0-4	0-2	2-4	1-3	3-6	3-5	1-3	1-3
YG	Mean	2.0	1.6	2.0	1.2	8.2	5.8	5.4	5.2
	Range	1-4	1-2	1-3	1-2	3-13	3-7	4-7	3-8

density of all ephemerals on the desert-grassland site also exhibited this negative-sulfur response pattern.

A fourth pattern was how different the same species could be in plant size on different sites in response to the same treatments. For example, *Eschscholzia* was much larger on the desert-grassland site than on the yucca-grassland site (in response to added water and nitrogen). Also, while *Lepidium* was significantly larger with water and nitrogen on all three sites, it was far larger on the creosotebush bajada than on the desert-grassland site, where plants were larger than on the yucca-grassland site.

Species richness

The addition of water without nitrogen or sulfur consistently resulted in the establishment of more species of ephemerals than any other treatment or the control (Table 2). Species richness was highest in the yucca-grassland site and lowest in the creosotebush bajada site.

Discussion

The hypothesis that desert ecosystems are water limited but nutrient regulated was confirmed by the results of this set of water, nitrogen and sulfur amendment experiments; however, only certain plant species responded to these system inputs. In three different Chihuahuan Desert ecosystems, these species were always C₃ winter-annuals; no C₄ summer-annuals, perennial forbs or grasses significantly changed in cover, density or plant size.

The results of this study confirm the importance of both water and nitrogen as factors affecting the production of ephemeral plants and the species composition of Chihuahuan Desert communities. In addition, the data show that added sulfur and resulting pH changes (MacKay *et al.*, 1987) affect the densities of some species, generally by reducing the numbers.

This study extends the conclusions of Gutierrez *et al.* (1988) and Gutierrez & Whitford (1987) that productivity of winter-annuals in creosotebush areas of the Chihuahuan Desert is nitrogen limited when compared with other ecosystems (e.g. grasslands). In most of the ephemeral species, added nitrogen resulted in larger plants with no effect on the density of the species. However, the rapid growth of these nitrogen-responsive species apparently

resulted in a competitive effect that reduced the species richness of the nitrogen amendment plots. This result is consistent with the resource-ratio hypothesis of Tilman (1982), who attributed higher species richness at low nutrient levels to reduced competition; as nutrient resources are increased, species with optimal growth at higher nutrient levels grow rapidly and out-compete other species. Nitrogen fertilization provides conditions for rapid growth of plants that germinate early and, under these conditions, established plants can deplete the available soil nitrogen, thereby affecting the establishment of species that germinate later (Rathcke & Lacey, 1985). The species that responded to nitrogen fertilization in our study are species that typically germinate early (in autumn) and overwinter as rosettes (Kemp, 1983). Species that occurred in the watered plots but not in the water plus nitrogen plots were primarily species that germinate later (in late winter-early spring). Thus, our data are consistent with the conclusions of Rathcke & Lacey (1985).

Sufficient water is obviously necessary for the establishment of desert ephemerals, where increased water availability increases the number and density of species. However, this study demonstrates that responses to increased water and nutrients is highly species and site specific and one cannot predict the species composition and productivity of desert ecosystems from rainfall alone.

Site specificity has also been reported for the Mojave Desert, where Williams & Bell (1981) found as much as a seven-fold increase in biomass from fertilizing with nitrogen ($10 \text{ g/m}^2 \text{ NH}_4\text{NO}_3$) on a sandy entisol site over the same treatment applied to an alluvial aridisol. Our sites are all on alluvial aridisols (Wierenga *et al.*, 1987) and addition of $10 \text{ g/m}^2 \text{ NH}_4\text{NO}_3$ produced significant responses in the winter-ephemerals on all of our sites. The apparent differences in the results of the two studies probably resulted from the soil characteristics with respect to water storage and rates of nitrogen mineralization and not from the origin of the soil. In our study the soils with the higher infiltration and water-holding capacity and nitrogen mineralization had the highest species richness and highest production when watered but not fertilized (e.g. yucca-grassland). However, production on all our sites was increased by nitrogen fertilization. This suggests that on the alluvial aridisols studied by Williams & Bell (1981) nitrogen mineralization rates were sufficient to provide adequate nitrogen for their nitrogen-responsive species.

The sulfur effects are the most difficult to interpret. Adding elemental sulfur significantly reduced soil pH between 0.1 and 0.4 units on most of our plots (MacKay *et al.*, 1987), which should have increased nutrient availability on these calcareous soils. The effect of added sulfur was generally a reduced density of certain species, which could have resulted from interference from other species favored by increased nutrient availability or a toxic effect of increased sulfur compounds in the soil. Our data are insufficient to resolve this issue.

Although water was added on a regular basis, nitrogen and sulfur were added once, in May 1983 (end of spring), too late for a response from the 1982-3 C₃ winter-ephemerals which were just completing their life-cycle. What is puzzling is why there was no significant response from the C₄ summer-ephemerals, as additional nutrients should have been available; perhaps mineralization rates during the summer precipitation period were sufficient to provide adequate nutrients. Of course, there may be some long-term nutrient effects currently not evident.

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