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CHIHUAHUAN DESERT ANNUALS: IMPORTANCE OF WATER AND NITROGEN¹

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Abstract. We examined the effects of water supplementation and nitrogen amendment on biomass, cover, and density of annual plants on a termite-free and a termite-present area in the Chihuahuan Desert. Soil moisture was higher in the termite than in the termite-free plots, and in the watered than in the unwatered plots during the spring and summer. There were no differences in soil moisture among plots during the winter. Soil nitrogen was higher in the termite-free than in the termite plots. There were no differences in total plant biomass produced in termite and termite-free areas. There were significant differences in relative abundances of species among treatments. Natural rainfall was sufficient for maximum spring-annual biomass development on all plots except for the termite-free unfertilized, unwatered plots. These were the driest plots but had high soil nitrogen. Most of the herbaceous species responded to the water amendments by lengthening growing seasons, increasing density, or increasing biomass. When there was sufficient water for most of the spring annuals, high soil nitrogen levels favored increased densities and biomasses of *Descurainia pinnata* and *Lepidium lasiocarpum*. The absence of C₄ summer annuals in the high-nitrogen plots suggests that relatively high soil nitrogen adversely affected the summer annuals. Termite-free watered plots had higher soil moisture than the termite-unwatered plots, but summer annuals were relatively abundant on the latter. Water amendments had a greater effect on the species abundances in the termite-free area than in the one with termites. In the area with termites, nitrogen amendments had a greater effect on species abundances. Species diversity and richness were affected by site fertility as was species composition. This study demonstrates that we must understand patterns of soil nitrogen availability and processes affecting nitrogen availability in addition to water availability, in order to understand productivity and species composition of Chihuahuan Desert annual plants.

Key words: biomass production; Chihuahuan Desert; community composition; density; desert annual plants; irrigation; nitrogen fertilization; phenology; soil moisture; soil nitrogen; termites.

INTRODUCTION

Water is generally considered to be the main limiting factor for germination, growth, and productivity of herbaceous plants and shrubs in desert ecosystems (Went 1948, 1949, Went and Westergaard 1949, Juhren et al. 1956, Tevis 1958a, b, Beatley 1967, 1974, Noy-Meir 1974). Annuals occur as live plants only during short periods that are favorable for germination and growth. They survive as seeds during periods when soil moisture and temperature are not suitable for growth. Desert annual plants are classified as summer annuals if they germinate after summer or early autumn rains when ambient temperatures are above 20°C, and as winter annuals if they germinate in autumn or early winter rains at temperatures below 20° (Beatley 1974). Seasonal differences in temperature affect the growth rates of annual species. Summer annuals have a shorter life cycle and a greater overlap of phenological phases than winter annuals. However, most summer annuals

are C₄ species with a high photosynthetic efficiency at high temperatures when water is available (Mulroy and Rundel 1977).

If water is a limiting factor, then additional water should increase plant productivity in a desert ecosystem. In the Chihuahuan Desert, however, there is some evidence that productivity does not vary directly with water (Ludwig and Flavill 1979, Gutierrez and Whitford 1987). Nitrogen is generally considered to be limiting after water in North American deserts (West and Skujins 1978, Skujins 1981). Applications of nitrogen fertilizer had little effect on shrub production but greatly increased production of annual herbs in the northern Mojave Desert (Wallace et al. 1978). In the Chihuahuan Desert, nitrogen fertilization increased the biomass production of the shrub *Larrea tridentata* and the grass *Erioneuron pulchellum* (Ettershank et al. 1978). In the Mojave and Sonoran Deserts, growth of winter annuals appears to be so dependent upon nutrient availability that relatively nitrogen-rich "fertile islands" beneath shrubs support much larger plants with higher production efficiency than the nitrogen-poor soil in open areas (Mott and McComb 1974, Halvorson and Patten 1975, Patten 1978, Romney et al. 1978).

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Nevertheless, many subtle effects of both nitrogen and water have not been considered in the interaction of limiting factors in determining whether or not response to either will be obtained (Romney et al. 1978).

In the northern Chihuahuan Desert, several studies showed that subterranean termites affect soil properties (Parker et al. 1982, Brown 1983, and Elkins et al. 1986). Parker et al. (1982), in a study comparing annual plants on a series of plots from which termites had been eliminated with plots with termites present, found that although total annual-plant density and biomass were not different, dominant species on termite-free plots ranked considerably lower than where termites were present. Parker et al. (1982) attributed these changes in species importance to the increased nitrogen levels in soils from which termites had been eliminated. In a subsequent study Elkins et al. (1986) reported that water infiltration was significantly lower on plots where termites had been removed. Thus plots without termites are characterized by higher soil nitrogen and lower water availability.

These relationships led us to re-evaluate the findings of Parker et al. (1982). We hypothesized that the species composition and productivity of Chihuahuan Desert annual plant communities vary as a function of the interaction between water and nitrogen availability. We hypothesized that some species, such as *Descurainia pinnata* and *Lepidium lasiocarpum*, that increased in importance on termite-free plots (Parker et al. 1982) are nitrogen-limited species and that other species, such as *Astragalus tephrodes* are water-limited species. We hypothesized that productivity would be highest and species assemblages most similar on nitrogen-rich sites over a broad range of soil moisture availability based on the data in Gutierrez and Whitford (1987). By imposing irrigation and nitrogen fertilization on small plots on termite-free and termite-present areas, we were able to obtain a wide range of nitrogen and water contents in the plots to test these hypotheses. The results of these studies also provide an answer to the question of whether the primary indirect influence of termites on annual-plant communities is by their effects on nitrogen or on water.

STUDY AREA

The study area is located at the Jornada Long-Term Ecological Research Site on the New Mexico State University Experimental Ranch, 40 km north northeast of Las Cruces, Dona Ana County, New Mexico. This site is a desert watershed that empties into an ephemeral lake. The watershed varies in elevation from ≈ 1200 –2000 m. Our studies were conducted on the midslope area of the watershed where the vegetation is essentially monotypic, *Larrea tridentata* shrubs with other shrubs being limited to the margins of drainages. The plots were on *L. tridentata* uplands on soils where the caliche layer (calcium carbonate deposition layer) was between 0.8 and 1.0 m in depth. The 100-yr annual precipita-

tion ± 1 SD is 211 ± 77 mm, with most rainfall occurring during late summer from convective storms. Maximum summer temperatures reach 40°C and freezing temperatures are recorded from October to mid-March (Houghton 1972).

METHODS AND MATERIALS

Original study design and data

In October and November 1977, a factorial experiment was set up to study the effects of termite removal. The experimental design consisted of four blocks with five completely randomized 30×40 m treatment plots per block. Two plots in each block were treated with chlordane, at an application rate of 10.3 kg/ha, to eliminate termites. Chlordane is a recalcitrant chlorinated hydrocarbon that binds to clay particles in the soil, thereby losing its contact toxicity. Subterranean termites ingest soil and the chlordane apparently is released in their guts. The only soil animals that did not survive the chlordane treatment or recolonize the treated areas were subterranean termites. Chlordane treatment had no apparent effect on numbers of ant colonies. The densities of ants are very low on this creosotebush-dominated bajada (Whitford 1977). There were six ant colonies on the termite-free plot and five ant colonies on the termite plot at the time this experiment was conducted. The termite-free plot had two *Pogonomyrmex desertorum* colonies, two colonies of *Pheidole* spp., and one colony each of *Novemessor cockerelli* and *Myrmecocystus desertorum*. The other area had three *Pogonomyrmex desertorum* colonies and two *Pheidole* spp. colonies. No active microarthropods were found on or in treated soils to a depth of 20 cm through the spring of 1978, but in spring 1979 there were no detectable differences in soil microarthropods and nematodes in chlordane-treated and untreated soils. At the time of this study the populations of soil microarthropods were higher on termite-free plots (2300 individuals/m²) than on plots with termites present (1100 individuals/m²) (Silva et al. 1985). The taxonomic composition of the soil microarthropod assemblages was not different.

Parker et al. (1982) sampled all termite-free and termite-present plots in their study of changes in nitrogen and annual plants following termite removal. Elkins et al. (1986) utilized plots on two of the original four blocks in their study of infiltration and sediment yield. Based on those studies, we were confident that differences in infiltration, soil water storage, and soil nitrogen were attributable to removal of termites. Although logistic limitation prevented utilization of more than one pair of plots, we were confident that our experiments would provide data allowing interpretation of the indirect effects of termites on annual plants. The utilization of a termite-free and termite-present plot on which smaller plots were irrigated and fertilized provided a wide range of soil moisture-available ni-

TABLE 1. Regressions between species' aboveground dry biomass (grams per square metre; Y) and volume (V) or area (A). R^2 = coefficient of determination.

Species	Equations	Conditions†	R^2
<i>Astragalus nuttallianus</i> DC.*	$Y = 0.0062 + 0.0028V$	(1)	0.998
<i>Baileya multiradiata</i> Harv. & Gray	$Y = 0.0145V^{0.553}$	(2)	0.918
<i>Cryptantha angustifolia</i> (Torr.) Greene	$Y = 0.0078V^{0.616}$	(2)	0.859
<i>Cryptantha micrantha</i> (Torr.) Johnston.	$Y = 0.0092V^{0.669}$	(1)	0.767
<i>Descurainia pinnata</i> (Walt.) Britton	$Y = 0.0034V^{0.728}$	(1)	0.934
<i>Dithyrea wislizeni</i> Engelm.	$Y = 0.0310V^{0.590}$	(1)	0.869
<i>Eriastrum diffusum</i> (Gray) Mason	$Y = 0.0044V^{1.061}$	(1)	0.931
<i>Eriogonum abertianum</i> Torr.	$Y = 0.0200V^{0.662}$	(1)	0.958
<i>Eriogonum rotundifolium</i> Benth.	$Y = 0.0130V^{0.628}$	(1)	0.895
<i>Eriogonum trichopes</i> Torr.	$Y = 0.0003V^{0.998}$	(1)	0.731
<i>Euphorbia micromera</i> Boiss.	$Y = 0.0116 + 0.0033A$	(3)	0.763
<i>Euphorbia serrula</i> Engelm.	$Y = 0.0083A^{0.896}$	(3)	0.804
<i>Lepidium lasiocarpum</i> Nutt.	$Y = 0.0052V^{0.758}$	(2)	0.898
<i>Mollugo cervina</i> (L.) Seringe	$Y = 0.0023V^{0.023}$	(1)	0.570
<i>Tidestromia lanuginosa</i> (Nutt.) Standl.	$Y = 0.1032 + 0.0026A$	(3)	0.885

* After Kearney and Peebles (1969).

† (1): $V = (3.14159/3) \times r^2 \times h$; (2): $V = (3.14159/3) \times 4 \times r \times h^2$; (3): $A = 3.14159 \times r^2$, where r = canopy radius, h = plant height.

trogen combinations that allowed us to examine the hypothesized water-nitrogen relationships of annual plants.

Experimental design

Twelve 3×3 m subplots were established on an area with termites and twelve on a nearby area with no termites. The plots were surrounded with chicken-wire fences to exclude rabbits. Six plots were sprinkler-irrigated with 13 mm H_2O every 15 d, and the other six received only natural rainfalls (unwatered plots). The plots were sprinkler-irrigated with well water that was stored in an open-surface concrete holding tank at the ranch headquarters. Water chemistry analysis showed that, in summer, NO_3-N (0.052 mg/L) and NH_4-N (0.036 mg/L) were lower than in winter (0.395 mg/L and 0.190 mg/L, respectively). In contrast, total N was greater in summer (1.63 mg/L) than in winter (0.75 mg/L). There were no seasonal differences in SO_4 , Cl, Na, K, Mg, Ca, and P.

Three of the watered and three of the unwatered plots

in termite and termite-free areas were fertilized with ammonium nitrate, active ingredient, at a rate of 2.4 g/m². Fertilizer was applied on 10 August 1982, 28 February 1983, and 16 August 1983. This provided eight treatments replicated three times. Wescor soil psychrometers were placed at 10 and 20 cm depth in each plot. These were read four to six times a month from September 1982 through October 1983. Effects of watering, termites, and the interactions between these on soil water potentials were examined by a factorial ANOVA, and means were compared by the LSD (Steel and Torrie 1980).

Soil and plant nitrogen measurements

In August and November 1982 and in February and September 1983, two soil samples at 0–10 cm depth were collected in each 3×3 m plot for analysis of total nitrogen, ammonium, nitrite, and nitrate. In May and October 1983 only one sample was collected from each plot. Total nitrogen was measured by microKjeldahl digestion (Bremner and Mulvaney 1982). Ammonium, nitrite, and nitrate were measured as described by Kee-ney and Nelson (1982).

In May 1983, one plant each of the following species, *Baileya multiradiata*, *Descurainia pinnata*, and *Eriastrum diffusum*, was collected from each plot. In addition, *Cryptantha angustifolia* was collected only in the termite plots and *Lepidium lasiocarpum* only in the termite-free plots. These species were chosen because they were the most abundant and therefore probably best reflected the treatment effects. After harvest, these plants were oven-dried at 60° for 72 h. After roots and reproductive parts were removed, leaves and stems were ground in a Wiley mill for nitrogen analysis by Kjeldahl digestion.

Plant measurements

Plants were sampled at regular intervals from 28 August 1982 through 15 October 1983. Four 50×40

TABLE 2. Factorial analysis of variance (ANOVA). Treatments, degree of freedom (df), and Error Mean Squares (EMS) used to determined the F values. Error a was used to test main effects, and error b was used to test interactions and changes through time.

Treatments*	df	F
T \times W \times N (replicates)	16	Error a
D	22	b
D \times T	22	b
D \times W	22	b
D \times N	22	b
D \times T \times W	22	b
D \times T \times N	22	b
D \times W \times N	22	b
D \times T \times W \times N	22	b
D \times T \times W \times N (replicates)	352	Error b

* T = termites, W = water, N = nitrogen, D = date.

cm permanent quadrats were located in each plot. The height and mean diameter of each plant were recorded on each sampling date. In October 1982 and June 1983, 15 plants of each species represented in the experimental plots were collected from outside the study area to obtain the data for establishing the relationship between plant size and biomass (Table 1). The quadrat data were used to estimate population densities and cover.

The data were analyzed by factorial ANOVA, and treatment comparisons were done by LSD (Steel and Torrie 1980). The treatments, associated degrees of freedom (df), and the Error Mean Squares (EMS) used to calculate *F* values are shown in Table 2.

RESULTS

Soil temperature and soil moisture

There were no significant differences in soil temperature among treatments at either 10 or 20 cm. There were marked differences in soil moisture among treatments at both 10 and 20 cm. At 10 cm the no-termite plots (pooling all data) were drier than the termite plots (Fig. 1). These differences were greater in November 1982 and May through September 1983 (summer season) ($F_{13,280} = 9.88, P < .001$). There were no differences in soil moisture from December 1982 to April 1983 (winter season) as a result of low temperatures and lower evaporation, and high precipitation during December 1982 (62.0 mm) and January 1983 (26.2 mm). For both termite and termite-free plots, irrigation increased the soil moisture, but the effect was greater in the termite plots ($F_{1,280} = 68.98, P < .001$), especially from May to October 1983 (Fig. 1).

Total soil nitrogen

The no-termite plots had more total surficial soil nitrogen than the termite plots ($P < .05$) both before and after nitrogen fertilization (Table 3). In February 1983 and September 1983, which corresponded to the end of the growing season for summer and spring ephemeral plants, respectively, watered plots had more nitrogen than the unwatered plots. The nitrogen fertilization did not produce significant changes in total soil nitrogen, probably because of the small quantities of added nitrogen.

Soil ammonium, nitrite, and nitrate

In May 1983, the soils on the watered plots had less ammonium ($0.007 \mu\text{g/g}$) than did those on the unwa-

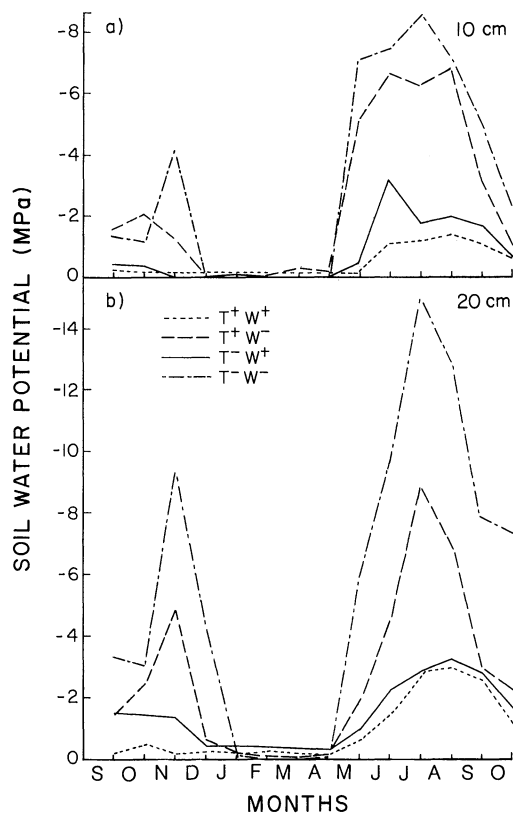


FIG. 1. Soil moisture at (a) 10 cm and (b) 20 cm depth in irrigated (W+) and natural-rainfall (W-) plots in the termite-present (T+) and termite-absent (T-) sites from September 1982 through October 1983.

tered plots ($2.92 \mu\text{g/g}$) ($F_{1,15} = 11.92, P < .01$). The soils on the nitrogen-fertilized plots had more ammonium ($2.55 \mu\text{g/g}$) than the control plots ($0.142 \mu\text{g/g}$) ($F_{1,15} = 8.16, P < .05$). Interactions between water and nitrogen treatments showed that the unwatered, nitrogen-fertilized plots had more ammonium ($5.10 \mu\text{g/g}$) than did the other water-nitrogen combinations ($0.0-0.5 \mu\text{g/g}$) ($F_{1,15} = 7.08, P < .05$). Soil nitrate-nitrite followed the same pattern.

Plant nitrogen

Baileya multiradiata, a species that has some perennial characteristics, accumulated more nitrogen per unit mass in the termite plots (16.98 mg/g) than in the no-termite plots (13.51 mg/g) ($F_{1,11} = 10.95, P < .01$). The other treatments (water, nitrogen, and water-nitrogen interactions) were not significant. *Eriastrum dif-*

TABLE 3. Average moisture and soil nitrogen in the treatment plots at the end of the 1983 growing season. T+, termites present; T-, termites absent; W+, irrigated; W-, natural rainfall; N+, fertilized; N-, unfertilized.

	Treatments							
	T+W+N+	T+W+N-	T+W-N+	T+W-N-	T-W+N+	T-W+N-	T-W-N+	T-W-N-
Soil moisture (MPa)	-0.5	-0.5	-4.5	-4.5	-1.5	-1.5	-6.0	-6.0
Soil nitrogen ($\mu\text{g/g}$)	484	504	458	466	578	526	464	562

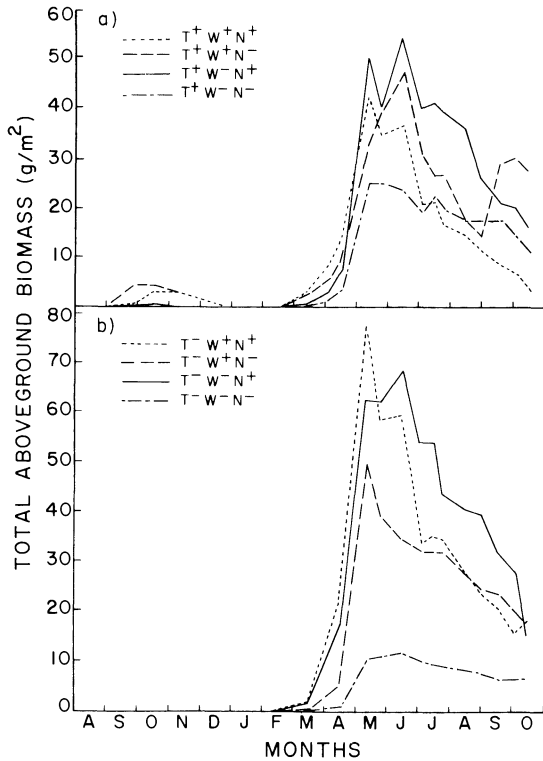


FIG. 2. Total dry aboveground biomass of all the annual species in the experimental plots from August 1982 through October 1983. W+, irrigated; W-, natural rainfall; N+, fertilized; N-, unfertilized. (a) T+, termites present; (b) T-, termites absent.

fusum, a relatively long-lived annual, accumulated more nitrogen in the termite (23.58 mg/g) ($F_{1,9} = 14.49$, $P < .01$) and watered plots (16.01 mg/g) ($F_{1,9} = 5.30$, $P < .05$) than in the termite-free (13.86 mg/g) and unwatered plots (13.87 mg/g). *Descurainia pinnata*, a short-life-span annual, accumulated less nitrogen in the no-termite, unwatered plots (3.76 mg/g) than in the other three termite-water combinations (7.05–8.54 mg/g) ($F_{1,10} = 10.16$, $P < .01$).

Cryptantha angustifolia, obtained only from the termite plots, did not show a significant response to water and nitrogen amendments. This species had a short growth period when compared with *B. multiradiata* and *E. diffusum*. Similar results were obtained with the short-lived *Lepidium lasiocarpum*, samples of which were taken only from the no-termite plots.

Vegetative biomass and cover

The pooled means of total aboveground biomass of annual plants for the different treatments were not significantly different. However, between 6 April and 14 June 1983, biomass was higher in the watered than in the unwatered plots ($F_{22,352} = 1.95$, $P < .01$), and from 11 May through 30 August 1983 the biomass was higher in the no-termite watered plots ($F_{22,352} = 2.32$, $P < .01$) than in the other three termite-water combina-

tions (Fig. 2). Watered plots had more plant cover than the unwatered ones ($F_{1,16} = 5.76$, $P < .05$). Plant cover paralleled plant biomass response, but cover was higher in the nitrogen-fertilized plots than in the unfertilized ones (Fig. 3).

When the cover data for termite and no-termite plots were analyzed separately, it was clear that the nitrogen effect through time was greater in the termite plots ($F_{22,176} = 3.76$, $P < .001$) than in the no-termite plots ($F_{22,176} = 1.47$, $P = .0881$). The opposite was true for water treatments where cover response was higher on the no-termite plots ($F_{22,176} = 4.27$, $P < .001$) than on the termite plots ($F_{22,176} = 3.42$, $P < .001$).

In the following sections we present the data on responses of the species of annual plants on a water-nitrogen gradient resulting from fertilization and irrigation of plots on areas with and without termites. As is shown in Fig. 1, irrigation produced moister soils on the termite area than on the no-termite area. However, even with nitrogen fertilization, the termite area generally had lower available nitrogen than the termite-free area (Table 3).

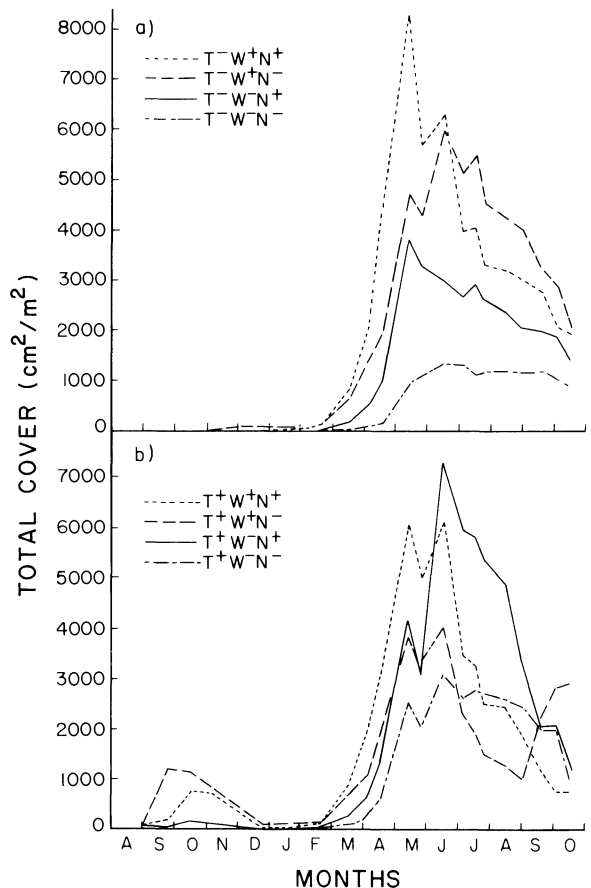


FIG. 3. Total cover of all the annual species in the experimental plots from August 1982 through October 1983. W+, irrigated; W-, natural rainfall; N+, fertilized; N-, unfertilized. (a) T-, termites absent; (b) T+, termites present.

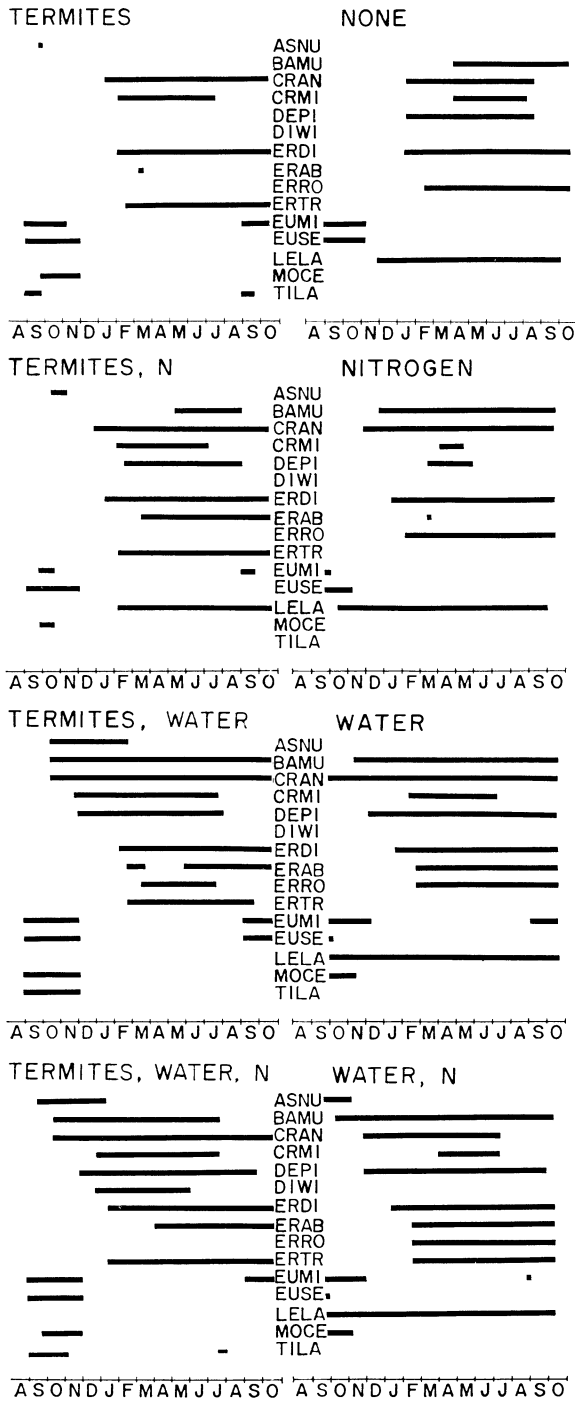


FIG. 4. Growing season of the annual-plant species in the experimental plots from August 1982 through October 1983. ASNU: *Astragalus nuttallianus*; BAMU: *Baileya multiradiata*; CRAN: *Cryptantha angustifolia*; CRMI: *Cryptantha micrantha*; DEPI: *Descurainia pinnata*; DIWI: *Dithyrea wislizeni*; ERDI: *Eriastrum diffusum*; ERAB: *Eriogonum abertianum*; ERRO: *Eriogonum rotundifolium*; ERTR: *Eriogonum trichopes*; EUMI: *Euphorbia micromera*; EUSE: *Euphorbia serrula*; LELA: *Lepidium lasiocarpum*; MOCE: *Mollugo cervina*; TILA: *Tidestromia lanuginosa*.

Species presence-absence and phenophase effects

Fifteen annual-plant species were present in at least one of the treatments (Fig. 4). The presence or absence of species in the various treatments and the period of time from germination to death varied among treatments. *Astragalus nuttallianus* occurred only on plots with higher moisture contents. *A. nuttallianus* was present in all of the termite plots that had wet soils but only in the water–nitrogen-fertilized plots on the termite-free area. The presence of *Eriogonum trichopes*, *Er. abertianum*, and *Mollugo cervina* was determined by water availability (Fig. 4). Water affected the phenophases of several species. *Cryptantha angustifolia*, *Cryptantha micrantha*, *Descurainia pinnata*, *Lepidium lasiocarpum*, and *Euphorbia micromera* appeared earlier on watered plots or on termite plots with water enhancement. Several of these species also survived for longer periods on watered plots (Fig. 4).

Species present only with enhanced nitrogen availability were *L. lasiocarpum* and *Eriogonum rotundifolium*. Higher nitrogen availability reduced the length of life of *C. micrantha* and *M. cervina*. The presence and phenophase of *Eriastrum diffusum* was unaffected by the water–nitrogen combinations.

Densities of individual species

Supplemental water had a positive effect on the densities of *A. nuttallianus*, *C. angustifolia*, *C. micrantha*, *Euphorbia micromera*, *B. multiradiata*, and *D. pinnata* (Fig. 5). *E. diffusum* occurred at lower densities in watered plots. Supplemental water plus nitrogen produced the highest densities among treatments in *Er. abertianum*, *D. pinnata*, and *L. lasiocarpum* (Fig. 5).

Enhanced nitrogen availability, regardless of water status of the soils, produced higher densities of *E. diffusum*, *Er. trichopes*, *Er. rotundifolium*, and *L. lasiocarpum*. *Tidestromia lanuginosa* density was lower on fertilized plots than on unfertilized plots ($P < .01$). Enhanced nitrogen resulted in lower densities of *B. multiradiata* and *A. nuttallianus* ($P < .01$). *Euphorbia serrula* densities were unaffected by the treatments ($P > .5$).

Biomass response of the individual species

Species that had higher biomass on watered plots than on unwatered plots regardless of soil nitrogen levels were *Er. abertianum* and *B. multiradiata*. Species that had highest biomass on watered termite plots and higher biomass on watered termite-free plots than on any unwatered plots were: *C. angustifolia*, *C. micrantha* (Fig. 6), *Euphorbia micromera*, and *Eu. serrula* ($P < .01$). The biomass of *E. diffusum* was highest on the unwatered plots (Fig. 6).

Annual plant species in which biomass production exhibited a positive response to higher nitrogen or combined nitrogen–water enhancement were *D. pinnata*, *Er. rotundifolium*, and *L. lasiocarpum*.

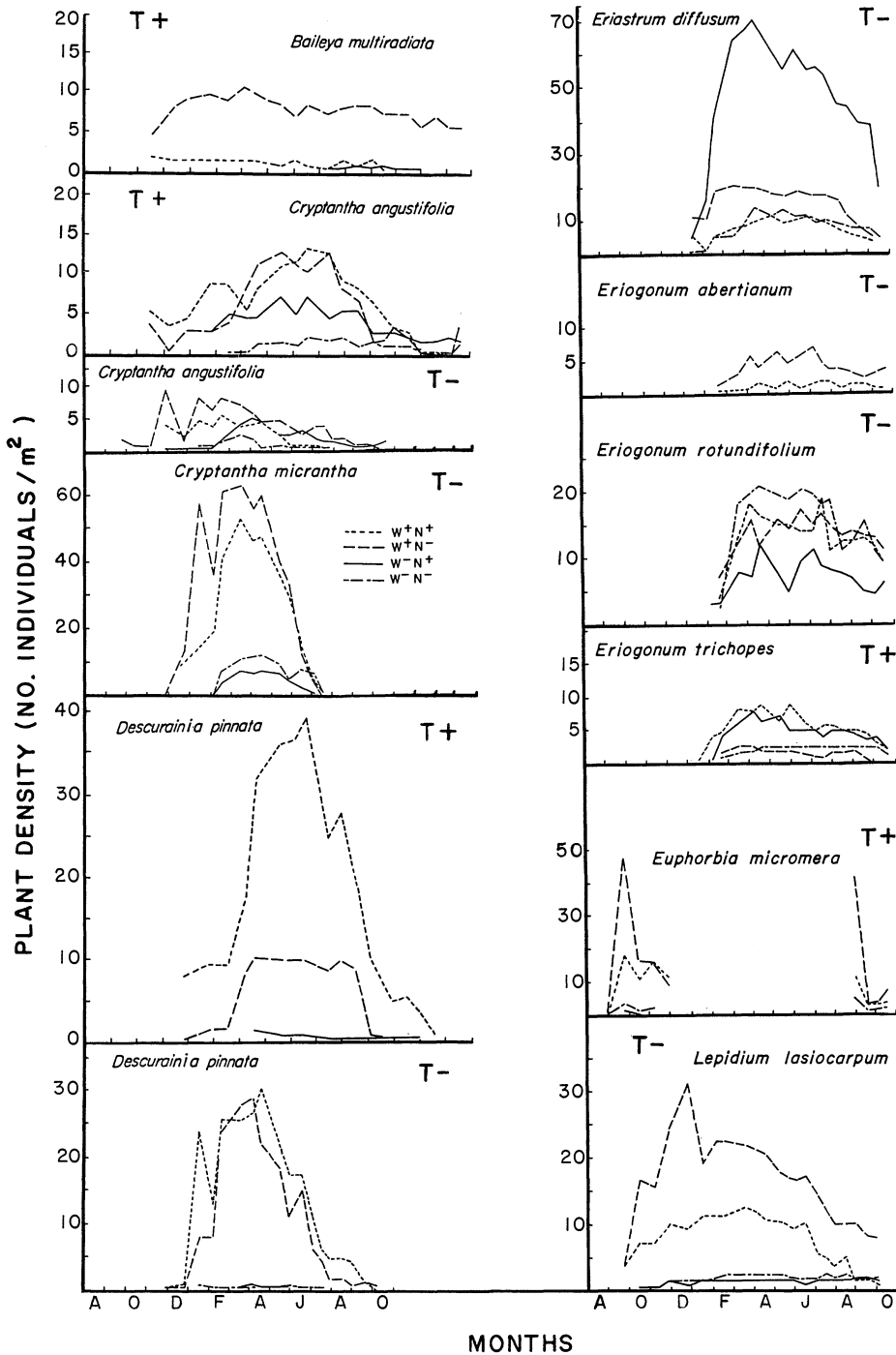


FIG. 5. Density response of annual-plant species to the treatments from August 1982 through October 1983. T+, termites present; T-, termites absent; W+, irrigated; W-, natural rainfall; N+, fertilized; N-, unfertilized.

Species assemblage relationships

There were significant differences in relative biomass of species among treatments. In the termite plots the dominant species in all the treatments was *E. diffusum*, however, biomass of this species decreased markedly in the watered plots where other species such as *B. multiradiata* and *C. angustifolia* shared the dominance.

In the termite-free plots, *L. lasiocarpum* was the dominant species except in the unwatered-fertilized plots, where *E. diffusum* was the most abundant species. These plots, despite fertilization, had lower amounts of soil nitrogen and showed the lowest diversity. Apparently, soil nitrogen is a determinant of the number of species present in this system, because the plots that had higher

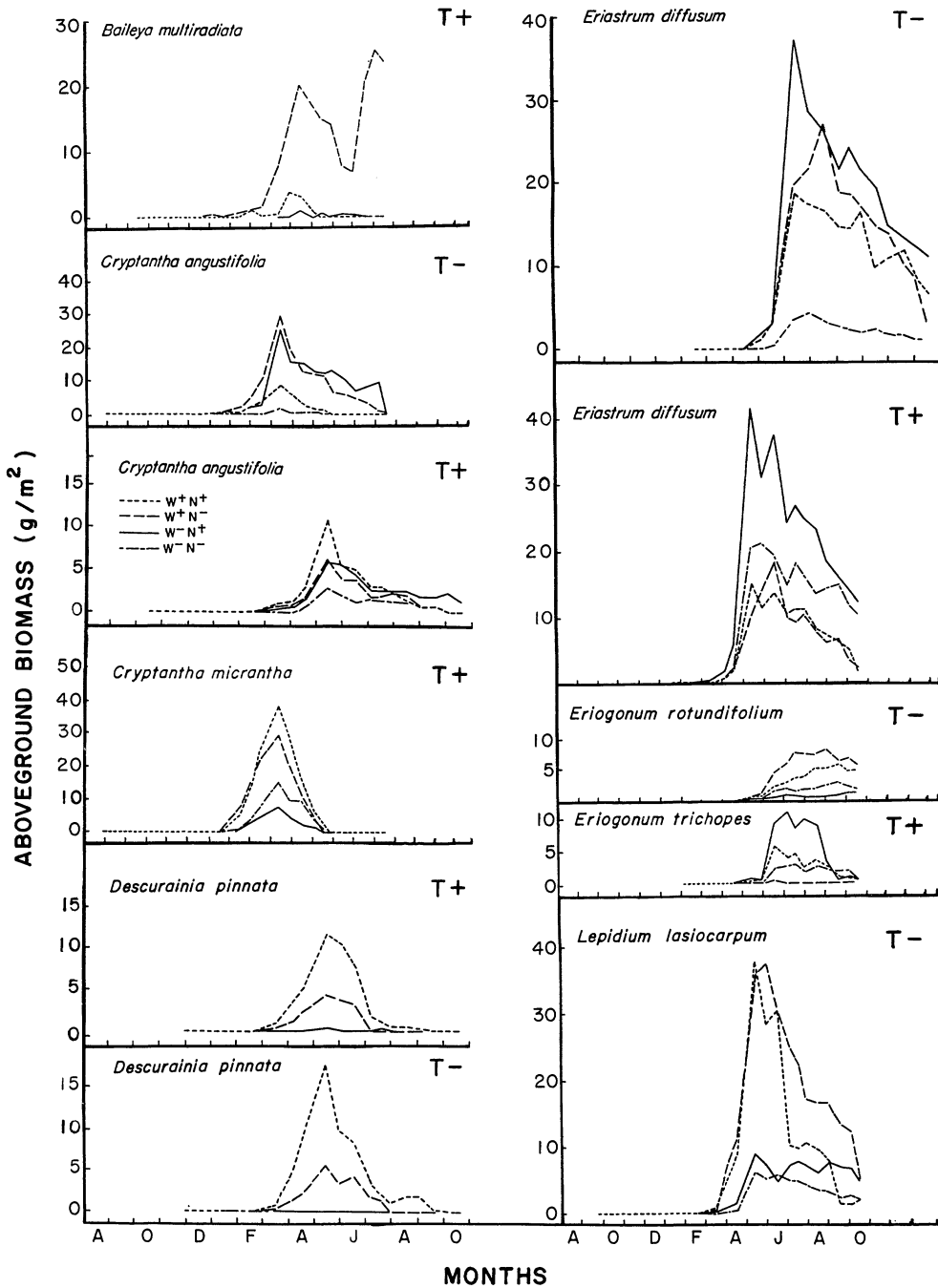


FIG. 6. Dry aboveground biomass response of annual-plant species to the treatments from August 1982 through October 1983. T+, termites present; T-, termites absent; W+, irrigated; W-, natural rainfall; N+, fertilized; N-, unfertilized.

diversities were those that had the highest soil nitrogen concentrations.

Maximum species densities and biomasses varied on the soil moisture–soil nitrogen gradient analyzed in this system (Fig. 7). Most of the species reached the maximum densities and biomasses at high soil moisture and low soil nitrogen conditions. *D. pinnata* and *L. lasiocarpum* produced the highest densities and biomasses with high soil moisture and high soil nitrogen.

Er. trichopes and *E. diffusum* reached maximum densities and biomasses at the dry end of the soil moisture gradient and in the lower portion of the nitrogen gradient.

Species composition on the experimental plots was compared by cluster analysis of biomasses of the species using the chord distance–flexible method (Legendre and Legendre 1983). This analysis revealed three groups of related treatment plots (Fig. 8). The first group was the

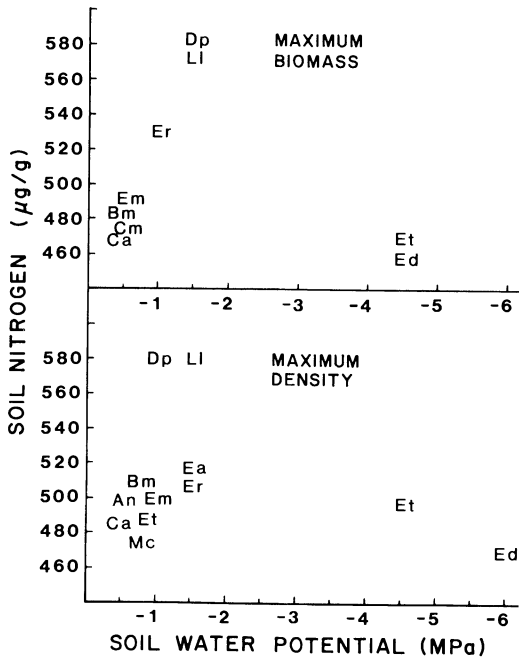


FIG. 7. Relative position of the species with respect to maximum density and biomass along a soil moisture–soil nitrogen gradient. An: *Astragalus nuttallianus*; Bm: *Baileya multiradiata*; Ca: *Cryptantha angustifolia*; Cm: *Cryptantha micrantha*; Dp: *Descurainia pinnata*; Ea: *Eriogonum aber-tianum*; Ed: *Eriastrum diffusum*; Er: *Eriogonum rotundifolium*; Et: *Eriogonum trichopes*; Em: *Euphorbia micromera*; Ll: *Lepidium lasiocarpum*; Mc: *Mollugo cervina*.

termite–watered plots regardless of the nitrogen treatment. The second group was the termite–unwatered plots (both fertilized and unfertilized plots) plus the unwatered, fertilized, termite-free plots. Plots in this group did not differ in the soil nitrogen concentration (Table 3). The third group was composed of the termite-free plots, which had the higher soil nitrogen concentrations. Since similarities among experimental plots were closely tied to the soil nitrogen concentrations this analysis suggests that nitrogen was the primary factor affecting species composition.

DISCUSSION

This study demonstrates that the productivity, length of life, and species assemblages of Chihuahuan Desert annual plants are functions of interactions between soil nitrogen and water availability. The changes in annual-plant communities resulting from termite removal (Parker et al. 1982) resulted from both increased nitrogen and decreased soil moisture on the termite-free plots. The most nitrogen-responsive species were *Lepidium lasiocarpum* and *Descurainia pinnata*, and the most water-responsive species was *Astragalus tephrodes*. Differences in densities and biomass of these species appeared to affect resources available to other species, thus markedly affecting species composition on the plots.

The positive response of ephemeral plant cover to nitrogen amendments provides further evidence that, in the Chihuahuan Desert, soil nitrogen is limiting. Annual plant responses to fertilizer nitrogen were greater in plots with termites than in the termite-free plots, indicating that the increased soil nitrogen in the termite-free plots was sufficient to affect growth of annuals, hence the additional nitrogen supplied by fertilization did not affect plant biomass production. Water amendments elicited a greater plant growth response in the termite-free plots than in the termite plots, reflecting the differences in infiltration of those soils (Elkins et al. 1986). Activities of subterranean termites modify the distribution and quantity of soil moisture and soil nitrogen (Parker et al. 1982, Elkins et al. 1986) thereby affecting biomass production of a variety of plant species. The differences in plant biomass response to water and nitrogen amendments in the termite and termite-free plots may in part be due to differences in plant species composition. Water-limited plant species should do better on sites where termites are present and nitrogen-limited plant species should do better where termites are absent. Our data allow classification of Chihuahuan Desert annuals into nitrogen-responsive and water-responsive species.

Watering decreased the ammonium, nitrite, and nitrate amounts available in the soil. Several processes can contribute to that result: (1) ephemeral plant biomass production was higher in the watered plots, therefore more mineralized nitrogen was extracted from those soils; (2) the irrigation could have stimulated ammonium volatilization (Klubek et al. 1978); (3) nitrogen could have been leached to deeper soil layers. The net result, after one growing season, was less mineralized nitrogen available for the plants in the watered plots. Gutierrez and Whitford (1987) failed to find any relation between water amendments and ephemeral plant biomass production during the 2nd yr of rainfall supplementation. They hypothesized that nitrogen was the factor limiting ephemeral plant production in the 2nd yr. In an Australian desert, in the second of two consecutive years of high rainfall, plant and animal production declined because of phosphorus deficiency (West and Skujins 1978). The data from this study showed that in the 2nd yr of irrigation, biomass production was lower than in the first growing season. It may be, that in the second of two successive wet years, nutrient deficiencies reduce primary productivity. This is a hypothesis that deserves further testing. The facts that unwatered, nitrogen-fertilized plots had more mineralized nitrogen than the watered, nitrogen-fertilized plots and that no differences in plant biomass between these treatments were detected, suggest that irrigation of sandy soils that have high infiltration capacities (12 mm/h: Elkins et al. 1986) leaches mineralized nitrogen from the surficial soil layers.

Nitrogen uptake by the plants in this system appears to be related to the growing season of the species being

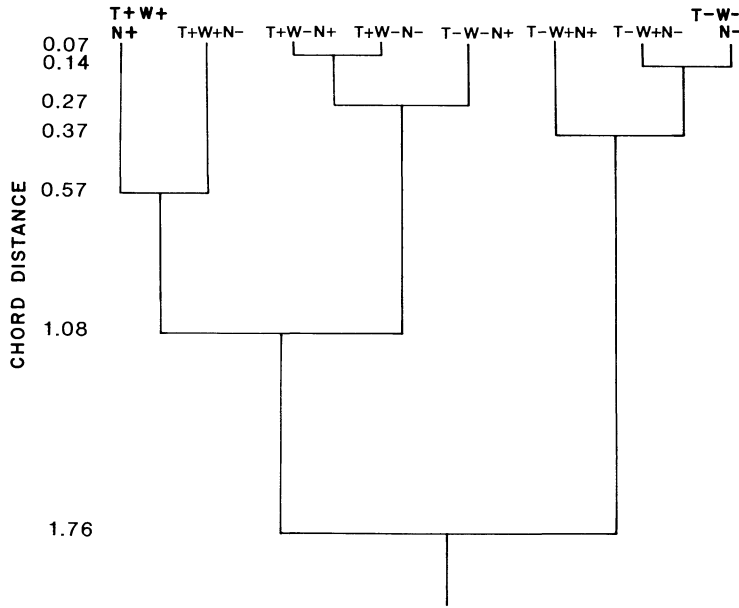


FIG. 8. Cluster dendrogram of the treatment plots. Biomasses of the species in the treatments. The chord distance-flexible method was used to construct the dendrogram. T+, termites present; T-, termites absent; W+, irrigated; W-, natural rainfall; N+, fertilized; N-, unfertilized.

considered. Short-lived species such as *L. lasiocarpum*, *C. angustifolia*, and *D. pinnata* did not exhibit differences in tissue nitrogen content among treatments. However, long-lived species (relative to the other species in the system) such as *B. multiradiata* and *E. diffusum* accumulated more nitrogen in the termite and watered plots, respectively, than in the no-termite and watered plots. In the more persistent species, tissue nitrogen accumulation was not related to nitrogen amendments, but probably to nitrogen accessibility to the root systems, i.e., watered plots and soil with good water infiltration (termite plots). Wallace et al. (1978) reported that in the Mojave Desert, tissue nitrogen concentration in winter annuals was generally lower than in perennial shrubs. Perennials seem to achieve higher levels of tissue nitrogen by exploiting a large soil volume and by highly effective internal conservation of nitrogen. Mojave winter annuals appear to have little organ replacement during their short lives, minimizing internal recycling (Williams and Bell 1981); and their small root systems are often crowded in the upper 10–20 cm of the soil (Bell et al. 1979), leaving only the resources of a small soil mass available to each individual. Williams and Bell (1981) hypothesize that the necessity for conserving nitrogen between generations ought to be great for nitrogen-limited desert annuals. Thus, reproductive and photosynthetic organs might compete for the small pool of nitrogen available within the plant. However, our results show that nitrogen fertilization affects ephemeral biomass production but not the nitrogen concentration in the vegetative tissue. These results are interesting from an evolutionary viewpoint, since tissue nitrogen accumulation by the species present in the

Chihuahuan Desert appears to be related to their life histories. Short-lived species appear to invest nitrogen in building up biomass rapidly to ensure seed production, and consequently increase the fitness of the species. Relief of nitrogen stress in desert annual plants appears to lead to increased vegetative development that ultimately produces greater biomass of both vegetative and reproductive structures (Williams and Bell 1981). However, long-lived species apparently store some of the nutrients available (in this case nitrogen) in order to overcome future stress. In this sense, *B. multiradiata* and *E. diffusum*, in the *r-K* continuum (Gadgil and Solbrig 1972), would be more *K*-selected than *L. lasiocarpum*, *C. angustifolia*, and *D. pinnata*. Additional data are necessary to confirm these suggested relationships.

Termite galleries increase soil water infiltration (Adams 1943, Robinson 1958, Elkins 1982) to deeper soil layers and provide better plant root aeration (Lee and Woods 1971). Soils devoid of termites are more compacted (Maldague 1964), and this should affect the presence of deep-rooted species. As expected, plant species compositions on termite and termite-free plots were different, and these differences were similar to those reported by Parker et al. (1982). For example, in 1979 *L. lasiocarpum* biomass and density were higher on the no-termite than in the termite plots, and in the present study *L. lasiocarpum* was practically absent on the termite plots and was the dominant species in the termite-free plots.

Most of the species that responded positively to the nitrogen amendments (e.g., *D. pinnata*, *E. diffusum*, *Er. trichopes*, *L. lasiocarpum*) are generally restricted

to sites under *Larrea tridentata* canopy (Parker et al. 1982). Several investigators have pointed out that in desert conditions the scattered occurrence of vegetation results in "islands of fertility" (Garcia-Moya and McKell 1970, West and Klemmenson 1978), or mosaics of nitrogen accumulation (Charley and McGarity 1964, Nishita and Haug 1973, Charley and West 1975, Skujins 1981) and nitrogen availability (Tiedemann and Klemmenson 1973) coinciding with the pattern of vegetation. Parker et al. (1982) and Brown (1983) analyzed the horizontal distribution of soil nitrogen in the Chihuahuan Desert and found the highest nitrogen concentrations were centered under *La. tridentata* canopy decreasing toward the canopy periphery. The lowest total soil nitrogen was in the intershrub space, and concentrations of soil nitrogen were higher in the upper soil profiles. This distribution pattern of soil nitrogen in the Chihuahuan Desert generates a fertility gradient that may be occupied by species with different nitrogen requirements. Spatial distributions of annual plants in the Chihuahuan Desert reflect such a gradient. This soil nitrogen variability provides conditions for species with different nitrogen requirements to coexist in this landscape.

Consistently, the summer annuals (e.g., *Euphorbia micromera*, *Eu. serrula*, *Mollugo cervina*, *Tidestromia lanuginosa*) did not respond to nitrogen amendments, and in some cases biomass or density of these species was lower in the nitrogen-fertilized plots, suggesting that additional nitrogen may have been toxic for them. All of these species use the C_4 photosynthetic pathway and therefore require high optimum temperature for growth and photosynthesis (Tieszen 1970, Bjorkman 1971); that is probably the reason that they are more abundant in the intershrub spaces (J. R. Gutierrez and W. G. Whitford, *personal observation*). Similar results have been reported for summer annuals in the Sonoran Desert (Thames [1975] as cited by McMahan and Schimpf [1981]). C_4 plants have been reported to be highly efficient in nitrogen-use compared with C_3 plants, particularly under conditions of low soil nitrogen supply (Wilson and Haydock 1971, Christie 1981). This efficiency apparently results from the lower investment in photosynthetic carboxylating enzymes compared with C_3 plants (Brown 1978). Most of the C_4 summer annuals increased biomass and density with water and had higher densities and biomasses in the termite plots that had soils with higher water content. An analysis of the long-term weather records for the Jornada Experimental Range shows that there is a relatively high probability of two successive "wet" years with "wet" summers and dry winters ($P = .45$) but a probability of only 16% of two wet winters in succession. Thus in the northern Chihuahuan Desert, summer annuals are regularly exposed to low nitrogen levels characteristic of the second successive wet year. Spring annuals germinate in late October and November and overwinter as a rosette. Because of low evapotranspiration, there

is deep soil water storage in a wet winter. As a result of this deeper soil water, roots of spring annuals may grow to depths of up to 1 m and, therefore, are able to obtain nitrogen from a larger soil volume than is available to shallow-rooted summer annuals (J. R. Gutierrez and W. G. Whitford, *personal observation*). These differences in rooting patterns and soil water availability are important factors in the differences in responses of spring and summer annuals in this study.

Plant biomass response to water supplementation was mainly during the spring and summer season, i.e., when water became a limiting factor (Romney et al. 1978). Irrigation is of relatively little value if it is supplied at a time when the soil has enough water or during a phenological stage of plant development when no response can be expected. Romney et al. (1978) reported that the extension of growth period is usually the most important effect of water addition. Our results show that, in the Chihuahuan Desert, most of the species in the irrigated plots extended their growing season and emerged earlier than the plants in the unwatered plots. During that period most of the species also increased their biomass production.

Unlike the soil nitrogen that is distributed in persistent patches, rainfall in the Chihuahuan Desert is highly variable throughout time (Houghton 1972, Ludwig and Whitford 1981). It would be expected, therefore, that plant species' responses to water amendments should be less variable than those to nitrogen supplementation. Most species responded to irrigation by increased growth and higher densities, which suggests that there are no major differences in water requirements of these species. The absence of some species in the no-termite plots could be a function of a root system that extracts water from the deeper soils.

Species showed great differences in their responses to nitrogen amendments. Soil nitrogen in the desert depends, to a great extent, on the litter produced by perennial shrubs, which are deep rooted and, therefore, less dependent on rainfall than are annual plants. In addition, litter decomposition (source of mineralized nitrogen) in the Chihuahuan Desert has been shown to be relatively independent of the precipitation (Santos et al. 1984, Whitford et al. 1986). In desert systems, nitrogen inputs from precipitation are probably not as important as nitrogen from organic matter cycling (West and Skujins 1978, Jornada Research Team, *personal communication*). Hence, nitrogen inputs in desert systems should be relatively constant and biomass production of the annual plant species largely restricted to the fertile islands under shrubs. Species occupying the intershrub spaces should be very close to their "biomass plateau"; i.e., in these nitrogen-limited areas, selective pressures have imposed restrictions on the maximum biomass that these species could accumulate. This proposition is fairly logical if we consider that the Chihuahuan Desert has persisted without too much change for at least 10 000 yr (Wells and Hunziker 1976),

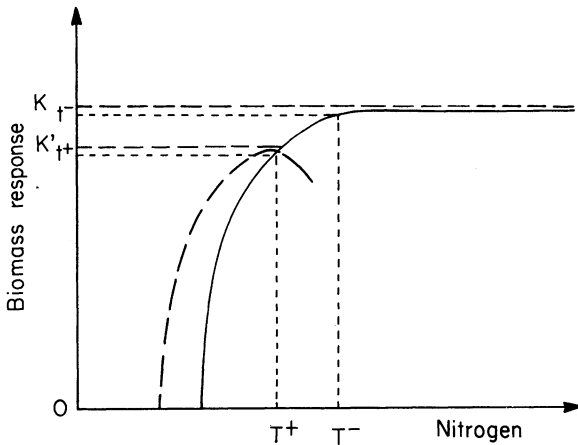


FIG. 9. Biomass response of annual plants to nitrogen amendments in the Chihuahuan Desert. $T+$ and $T-$ are the initial soil nitrogen levels in the termite and termite-free plots, respectively. K and K' represent the maximum physiological response to nitrogen amendments of spring and summer annual species, respectively. Biomass response of summer annuals species is represented by a broken curve. The distance between $t+$ or $t-$ and K represents the potential biomass response of spring annual species when nitrogen is added to the termite and termite-free plots, respectively. The distance between $t+$ and K' is the potential biomass response of summer annual species to nitrogen fertilization.

which is enough time to promote specific adaptations in annual plants (Stebbins 1950). Species responses to nitrogen amendment fit this model very well. Except for *D. pinnata* the other species that were present in the no-termite plots did not respond to nitrogen amendments, which suggests that the soil nitrogen on these plots was close to the maximum nitrogen threshold to elicit growth responses of the annuals. This was not the case on plots with termites present. It is also possible that in addition to soil nitrogen other nutrients could have become limiting.

A possible mechanism to describe biomass response to nitrogen amendments in the termite and no-termite plots has been schematized in Fig. 9. That figure shows that soil nitrogen in the no-termite plots is close to the amount that elicits maximum biomass response and, therefore, little or no plant response to nitrogen supplementations is found. Accordingly, the spatial distribution of the species in the Chihuahuan Desert (under- or intershrub sites) would be the upper limit (plateau) of biomass response to nitrogen amendments. In this sense, the C_4 species analyzed that are not restricted to under-shrub sites would reach their maximum physiological response to lower nitrogen amounts than the C_3 winter species. Apparently, soil nitrogen supply in the termite plots is close to the optimum for these species and this is one explanation of why some of these species responded negatively to nitrogen amendments and of the fact that they were practically absent in the no-termite plots. Behavior of the C_4 summer species in regard to nitrogen is represented with a broken line in Fig. 9.

Rainfall in the Chihuahuan Desert comes mainly from convectional storms. Heavy rains of >25 mm falling in a few hours are not rare in this desert (Ludwig and Whitford 1981). Hence, it would be expected that the plant potential to respond to water amendments would be higher in comparison with the potential to respond to nitrogen. Because of termite absence, plant response was greater in those plots; however, termite plots were also water-limited. A possible mechanism to describe biomass response to water amendments in the termite and no-termite plots has been schematized in Fig. 10. Note that the relative position of no-termite plots in regard to water is less than the termite plots, but both termite and no-termite plots are under the upper biomass plateau, and therefore additional water should elicit plant response.

Plant responses to water and nitrogen interactions were not so clear. *D. pinnata* was a species that consistently yielded more biomass in the watered, nitrogen-fertilized plots in both termite and no-termite plots. A similar response to water and nitrogen fertilization in this species was obtained by Romney et al. (1978) in the Mojave Desert. They proposed that water moved nitrogen down into the soil, making it accessible to *D. pinnata* root systems. Although Parker et al. (1982) reported *E. diffusum* to be the most abundant species, in our study *E. diffusum* reached peak abundance on the driest site at low soil nitrogen levels. *E. diffusum* is apparently unable to compete with *D. pinnata* and *L. lasiocarpum* at high soil nitrogen levels even when there is sufficient water for its development. *E. diffusum* may also be a poor competitor with other species as suggested by its lower biomass and density in the watered plots.

The high biomass response of *D. pinnata* in the termite, watered, nitrogen-fertilized plots could have af-

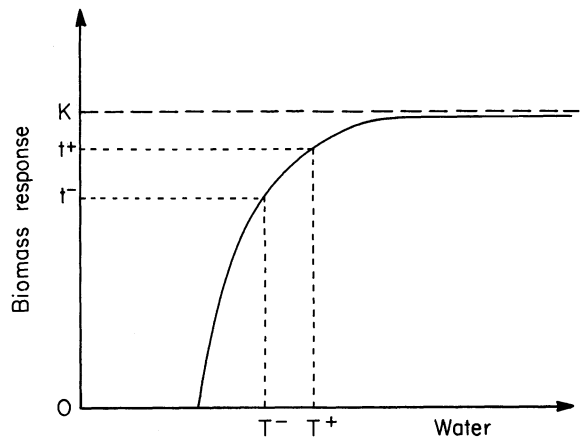


FIG. 10. Biomass response of annual plants to irrigation in the Chihuahuan Desert. $T-$ and $T+$ are the initial soil moisture in the termite-free and termite plots, respectively. K is the maximum physiological response to soil water supply in this system. The distance between $t-$ or $t+$ and K represents the potential biomass response of annual plants to irrigation in the termite-free and termite plots, respectively.

affected the abundance of *B. multiradiata* in those plots. Since *D. pinnata* has a faster growth rate than *B. multiradiata*, it might have diminished the resources to a level at which *B. multiradiata* biomass was severely depressed. This situation could be analogous to that described for *Erioneuron pulchellum* and *Larrea tridentata* in the Chihuahuan Desert (Ettershank et al. 1978). Our results suggest that location and morphology of the root systems of ephemeral plants are important if we are to understand the specific plant responses to the treatments. Without doubt, further research is needed to determine how species interactions affect plant responses to water and nitrogen treatments.

Recently Tilman (1982) proposed a model on resource competition and community structure that seems applicable to our results. He stated that numerous species can coexist, at equilibrium, in a spatially heterogeneous environment if the species differ in the proportion of the resources they require. In the Chihuahuan Desert, nutrient distribution is spatially heterogeneous, and plant species responses to nitrogen amendments have shown that these species differed in their nitrogen requirements. Hence, the spatial and temporal distributions of the ephemeral plants in the Chihuahuan Desert appear to be reflecting the spatial and temporal availability of resources. Data on soil nitrogen in the Chihuahuan Desert suggest that plants living relatively close to each other may experience significantly different rates of nitrogen supply.

Tilman (1982) points out that each species is a superior competitor for only a small range of resource supply ratios and that at a given level of resource richness, increased spatial heterogeneity should lead to increased species richness, with the most marked effects in resource-poor habitats. Ratio of resources would determine the dominant species in a community. Changes in the water/nitrogen ratios due to the absence of termites had a large effect on the species composition and on the species that became dominants, as predicted by Tilman's model. For instance, in the no-termite plots *L. lasiocarpum* was the dominant species with $\approx 30\%$ of the total biomass in those plots. This species was practically absent in the termite plots except for the unwatered, nitrogen-fertilized plots. In this example, the importance of termites in maintaining the water/nitrogen ratio effects on plant species composition in the Chihuahuan Desert is clear.

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