Revista Chilena de Historia Natural
65: 83-90, 1992

The effects of water and macronutrients addition on aboveground biomass production of annual plants in an old field from a coastal desert site of north-central Chile

Los efectos de la adición de agua y macronutrientes en la producción de biomasa sobre el suelo de plantas anuales en un campo abandonado ubicado en un sitio costero desértico del Norte Chico de Chile

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ABSTRACT

We investigated the effects of water and macronutrient (N, P, K, Ca, and Mg) on the above-ground dry biomass production of annual plants in an old field from a coastal desert site in North-Central Chile. Field experiments were conducted in two 1-ha plots located on a marine terrace at 30°06'S. Experimental plots differed in soil characteristics (E.C., O.M., N, P, K, and Ca), in the depth of a calcareous hardpan layer ("tertel"), which varied between 30 cm (Plot 1) to > 1 m (Plot 2), and in species composition. In Plot 1, only two species out of five, *Erodium malacoides* and *Oxalis micrantha,* had higher biomass in the watered quadrats. In Plot 2, 7 out of 10 species, *Adesmia tenella, Calandrinia trifida, Cryptantha glomerata, Cryptantha glomerulifera, Oenothera coquimbensis, Oxalis micrantha,* and *Plantago hispidula* had higher biomass in watered quadrats. In Plot 1, except for *Erodium malacoides,* species had higher biomass in nitrogen amended quadrats. In Plot 2, 4 species, *Calandrinia trifida, Camissonia dentata, Cryptantha glomerulifera,* and *Schismus arabicus* had significantly higher biomass in nitrogen amended quadrats. In both plots, annual species did not responded to P, K, Ca, Mg and ground tertel addition. Whereas in Plot 1 no interaction effects of water and fertilizer were detected, in Plot 2 *Calandrinia trifida* and *Schismus arabicus* showed a significant combined effect of water and nitrogen. We suggest that species responses to water and nitrogen may be related to the depth of the tertel layer, since moisture stays longer at the surface in shallower soils. In contrast, infiltration reduces water availability for the plants in soils where tertel is deep. This could explain why more species responded to artificial irrigation in Plot 2 than in Plot 1. By stimulating plant growth, irrigation and rainfall have forced more species to encounter limiting nitrogen levels in Plot 1.

Key words: Chilean Desert, annual plants, water, nitrogen, nutrient limitation.

RESUMEN

Se investigó los efectos de la adición de agua y macronutrientes (N, P, Ka, Ca y Mg) en la producción de biomasa seca sobre el suelo de plantas anuales, en un campo abandonado ubicado en un sitio costero desértico del Norte Chico de Chile. Los experimentos de terreno se realizaron en dos parcelas de 1 há cada una, ubicadas en una terraza marina a los 30°06'S. Las parcelas experimentales diferían en las características del suelo (C.E., M.O., N, P, K y Ca), en la profundidad de una capa dura calcárea ("tertel") que se encuentra entre 30 cm (Parcela 1) y > 1 m (Parcela 2) y en la composición de especies. En la Parcela 1 sólo dos especies de cinco, *Erodium malacoides* y *Oxalis micrantha,* tenían más biomasa en cuadrantes regados que en cuadrantes sin regar. En la Parcela 2, 7 de 10 especies, *Adesmia tenella, Calandrinia trifida, Cryptantha glomerata, Cryptantha glomerulifera, Oenothera coquimbensis, Oxalis micrantha* y *Plantago hispidula* tenían más biomasa en cuadrantes regados. En la Parcela 1, con excepción de *Erodium malacoides,* todas las otras especies tenían más biomasa en cuadrantes fertilizados con nitrógeno que en cuadrantes sin fertilizar. En la Parcela 2, 4 especies, *Calandrinia trifida, Cryptantha glomerulifera, Camissonia dentata* y *Schismus arabicus* tenían más biomasa en los cuadrantes fertilizados con nitrógeno. En ambas parcelas la respuesta de las especies a la fertilización con P, K, Ca, Mg y tertel molido no fueron significativas. Mientras en la Parcela 1 no se detectó ningún efecto de la interacción entre agua y fertilizantes, en la Parcela 2 *Calandrinia trifida* y *Schismus arabicus* respondieron positivamente a la interacción de agua y nitrógeno. Sugerimos que la respuesta de las especies al agua y el nitrógeno puede estar relacionada a la profundidad de la capa de tertel en las parcelas. La humedad en suelos con tertel superficial permanece por largo tiempo en la superficie. En contraste, la mayor infiltración en suelos con tertel profundo reduce la disponibilidad de agua para las plantas. Esto explicaría porqué más especies respondieron al riego artificial en la Parcela 2 que en la Parcela 1. Al estimular el crecimiento de las plantas por el riego y la lluvia se habría forzado a que más especies encontraran niveles limitantes de nitrógeno en la Parcela 1.

Palabras claves: Desierto chileno, plantas anuales, agua, nitrógeno, limitación de nutrientes.

(Received 16 August 1990; accepted 3 November 1991.)

INTRODUCTION

Water is generally considered the main limiting factor for germination, growth, and productivity of herbaceous plants and shrubs in desert ecosystems (Went 1948, 1949, Went & Westergaard 1949, Juhren *et al.* 1956, Tevis 1958a, 1958b, Beatley 1967, 1974, Noy-Meir 1973). However, recent studies indicate that soil nutrients, such as nitrogen, can also be important limiting factors (West & Skujins 1978, Gutiérrez & Whitford 1987a). For instance, Gutiérrez & Whitford (1987a) have shown that available soil nitrogen can significantly affect the abundance, diversity and spatial distribution of annual plants in northern Chihuahuan Desert. Other studies suggest that, when water is abundant, nitrogen may become limiting (West & Skujins 1978). Thus, after two years of artificial irrigation in a Chihuahuan Desert site, Gutiérrez & Whitford (1987b) failed to find any relationship between water amendments and annual plant growth and they postulated that nitrogen limited growth in the second year of irrigation. In the Australian desert, plant and animal distributions declined because of phosphorus deficiency during the second of two consecutive years of high rainfall (West & Skujins 1978). Hence, the mechanisms controlling plant productivity in arid ecosystems are far more complex than is usually assumed, and plant responses to water may be linked to the availability of certain macronutrients, such as nitrogen and phosphorus.

Annual plant communities in North-Central Chile have high species-richness compared to other areas of the country (Arroyo *et al.* 1988), but the individual species often form distinctive patches. Soil samples taken in patches of five different annual species in Lagunillas (IV Región, Coquimbo) differed significantly with respect to nitrogen and phosphorus (Gutiérrez *et al.*, unpublished data).

Another soil factor influencing the structure of the vegetation in some areas of the Chilean coastal desert is the presence of a layer of calcium carbonate, locally called "tertel", at different depths. Tertel is formed by an ancient (ca. 500,000 years B.P.) deposition of molluskan shells (Paskoff 1970). Tertel forms an impermeable layer that greatly reduces water infiltration and restricts the availability of certain nutrients (especially phosphorus).

We propose that the structure of annual plant communities in the Chilean desert reflects differences in available water and soil nutrients. In this work, we report the results of a field experiment designed to investigate the combined effects of macronutrients, tertel and water on the aboveground biomass production of annual plants in a Chilean coastal desert site.

STUDY SITE AND METHODS

The study sites were located on a coastal marine terrace with soils derived from fossil dunes and/or colluvial deposits on top of a calcareous hardpan ("tertel" hereafter). The experiments were carried out in 1987 at Lagunillas (30°06'S, 71° 21'W), 15 km south of Coquimbo, IV Región, Chile. The site is in an old wheatfield abandoned about 25 years ago. Presently, the area is subjected to seasonal grazing by livestock (mainly goats and sheep). The 49-year annual rainfall average is 102.6 mm (Di Castri & Hajek 1976) with most of the precipitation occurring between June and August (Muñoz 1985). Summer maximum and winter minimum air-temperatures are 25 and 3°C (INE 1987).

Two 1-ha experimental sites differing in soil parental material and in depth of the tertel layer were chosen. Plot 1 (shallow tertel) is characterized by soil derived from fossil dunes; tertel was found less than 30 cm below the surface, outcropping in some places. Plot 2 (deep tertel) was located on an alluvial fan or bajada. The soil was formed by colluvial deposits resulting from erosion of a nearby watershed and by air-borne sand particles. Tertel was found deeper than 1.2 m below the surface. Both plots were poor in organic matter (< 1%), nitrogen (< 15 ppm), and phosphorus (< 25 ppm) (Table 1). Plot 1

TABLE 1

Physical and chemical characteristics of soil samples taken in Plot 1 (surface tertel) and Plot 2 (deep tertel). Each value corresponds to the mean ($\bar{x}$) and one standard deviation (SD) of 42 samples. *: $P < 0.01$.

Características físico-químicas de muestras de suelo tomadas en el Plot 1 (tertel superficial) y Plot 2 (tertel profundo). Cada valor corresponde al promedio ($\bar{x}$) y una desviación estándar (SD) de 42 muestras. *: $P < 0{,}01$.

	pH	E.C.	O.M.	N	P	K	Ca	Mg
Plot 1 $\bar{x}$	6.78	0.74	0.96	14.0	19.5	213.5	791.8	86.0
SD	0.23	0.28	0.41	3.8	4.5	77.5	103.3	11.2
Plot 2 $\bar{x}$	6.81	0.31	0.60	11.5	22.2	364.5	455.3	85.4
SD	0.20	0.14	0.14	3.7	2.6	73.6	102.1	10.2
t values	0.64	8.90*	5.39*	3.01*	3.30*	9.15*	15.01*	0.26

had higher organic matter, nitrogen, and calcium contents than Plot 2. In contrast, Plot 2 had more phosphorus than Plot 1 (Table 1).

Both plots were wire-fenced to exclude livestock and hares. Within each plot, forty two 3 x 3 m quadrats were arranged into six blocks of seven quadrats each. Blocks were 10 m apart from each other and the distance between quadrats was 6 m. Each quadrat was bordered by a line of house bricks wrapped in polyethylene bags, buried 8 cm into the soil and forming a strip of 7 cm in height. The brick lines prevented water run-off from neighboring quadrats. Treatments included nitrogen (10 g/m^2), phosphorus (5 g/m^2), potassium (30 g/m^2), calcium (5 g/m^2), magnesium (8 g/m^2), and ground tertel (50 g/m^2) addition, plus a control (no fertilizer addition). N was added as $(NH_3)_2CO$, P as $CaHPO_4$, K as $KHSO_4$, Mg as Mg_2SO_4, and Ca as Ca_2CO_3. The six treatments and control were randomly assigned to the seven quadrats within each block. Fertilizers were hand broadcasted in May 1987, just before the onset of winter rains. Three out of six blocks of quadrats were watered monthly starting in May 1987. The irrigated blocks received a volume of well water equivalent to 5 mm of rain and the other three received only natural rainfall. Sprinkler heads were located at 1.5 m above the ground surface to mimic natural rainfall.

In September 1987, at the peak of the growing season, we randomly harvested 2-6 individuals per treatment of all species that were present in both the treatment and control quadrats. Plants, harvested at ground level, were oven-dried at 50°C for 72 h, and weighed to the nearest mg in a Sartorious scale.

Due to the unequal sample sizes (number of plants of one species in different treatment quadrats) and that some species were absent from some of the quadrats, we considered the individual plants for a given species as replicates within a water-nutrient combination. Because individuals were collected from three quadrats spread across the entire 1-ha plots for each treatment combination, rather than from a single large quadrat, the results are much more likely to reflect treatment effects than microsite differences. Data for each of the two 1-ha plots were analyzed separately and no statistical comparisons between plots were attempted because of the lack of replicates. All data were analyzed by unbalanced two-way ANOVA using the GLM procedure of SAS (SAS Institute Inc. 1988). Significant differences in mean plant biomass between fertilized and control quadrats were assessed using the Dunnett procedure (Steel & Torrie 1980).

Precipitation, air temperature and relative humidity were recorded from a small weather station installed at the study site.

RESULTS

Climatic data

Total annual rainfall during 1987 was 170 mm, that is, 60 mm above the 49-year annual average for the area (Di Castri & Hajek 1976). Rains occurred in May (20 mm), July (145 mm) and August (5 mm). Mean monthly air-temperatures ranged from 20 (January and February) to 13°C (August). Maximum air-temperatures ranged from 24.5 (February) to 17°C (August), and minimum air-temperatures ranged from 17 (January) to 8°C (September). Relative air-humidity was permanently over 80%, and showed little fluctuation during the year.

Species responses to irrigation

Five species in Plot 1 and ten species in Plot 2 were present in all the treatments and were selected for the analysis (Table 2). To assess the effects of the irrigation treatment, we compared the mean above-ground dry-biomass per plant (biomass, hereafter) for each species in irrigated and non-irrigated quadrats pooled over all the nutrient treatments. More species responded to irrigation in Plot 2 than in Plot 1. In Plot 1 only *Erodium malacoides* and *Oxalis micrantha* showed significant increment in mean biomass in response to irrigation (Table 2). These species had 30% and 77% higher biomass, respectively, in the irrigated quadrats.

TABLE 2

Means ($\bar{x}$) and one standard deviation (SD) of above-ground dry biomass (g)/plant in irrigated (IQ) and non-irrigated (NIQ) quadrats pooled over nutrient treatments in Plot 1 (surface tertel) and Plot 2 (deep tertel). n: number of plants.

Promedios ($\bar{x}$) y una desviación estándar (SD) de biomasa seca sobre el suelo (g)/planta en cuadrantes irrigados (IQ) y no irrigados (NIQ) sin considerar los tratamientos de nutrientes en la Parcela 1 (tertel superficial) y Parcela 2 (tertel profundo). n: número de plantas.

Plot 1

	IQ			NIQ					
Species	n	$\bar{x}$	SD	n	$\bar{x}$	SD	F	df	p
Calandrinia sp.	35	0.128	0.089	34	0.134	0.126	0,07	1,55	< NS
*Erodium cicutarium**	33	0.343	0.300	29	0.305	0.227	0.48	1,48	NS
*Erodium malacoides**	39	0.258	0.151	36	0.198	0.095	4.17	1,61	< 0.05
*Erodium moschatum**	35	0.220	0.128	36	0.196	0.123	0.99	1,57	NS
Oxalis micrantha	37	0.053	0.051	31	0.030	0.018	7.49	1,54	< 0.005

Plot 2

	IQ			NIQ					
Species	n	$\bar{x}$	SD	n	$\bar{x}$	SD	F	df	p
Adesmia tenella	36	0.075	0.045	37	0.056	0.031	4.20	1,59	< 0.05
Calandrinia trifida	28	0.043	0.037	36	0.027	0.022	6.64	1,50	< 0.05
Camissonia dentata	37	0.040	0.038	26	0.036	0.027	0.28	1,49	NS
Cryptantha glomerata	40	0.407	0.439	35	0.217	0.188	5.87	1,61	< 0.05
Cryptantha glomerulifera	22	0.127	0.093	24	0.085	0.046	5.11	1,32	< 0.05
*Erodium malacoides**	35	0.184	0.193	37	0.122	0.144	2.40	1,58	NS
Oenothera coquimbensis	20	0.056	0.044	26	0.030	0.041	5.01	1,32	< 0.05
Oxalis micrantha	39	0.057	0.055	35	0.035	0.036	4.40	1,60	< 0.05
Plantago hispidula	39	0.123	0.077	35	0.060	0.033	21.05	1,60	< 0.005
*Schismus arabicus**	22	0.068	0.085	27	0.042	0.030	3.15	1,35	NS

* Introduced species.

In Plot 2, seven species had significantly higher biomass in irrigated quadrats. Biomass increased 34% in *Adesmia tenella*, 59% in *Calandrinia trifida*, 88% in *Cryptantha glomerata*, 49% in *Cryptantha glomerulifera*, 87% in *Oenothera coquimbensis*, 63% in *Oxalis micrantha*, and 105% in *Plantago hispidula*. Because of the large variances, differences for *Erodium malacoides* (51%) and *Schismus arabicus* (62%) were not statistically significant.

Species responses to fertilization

To assess the effect of nutrient addition to the soil, we compared the mean biomass of plants in fertilized and control quadrats pooled for each of the two water treatments. Similar numbers of species responded significantly to nutrient addition in both 1 ha-plots. In Plot 1, all the species had higher biomass in the nitrogen amended quadrats than in the control ones, but only four of these differences were significant (Table 3). Biomass increments were 91% in *Calandrinia* sp., 51% in *Erodium cicutarium*, 115% in *Erodium moschatum*, and 128% in *Oxalis micrantha*. Plants of *E. cicutarium* fertilized with P, Mg, and tertel showed significantly lower biomass than those growing in control quadrats.

In Plot 2, three species had significantly higher biomass in nitrogen amended quadrats (Table 3). Biomass increments were 67% in *Calandrinia trifida*, 226% in *Cryptantha glomerulifera*, and 142% in *Schismus arabicus*. Biomass of *Camissonia dentata* did not differ between the control and nitrogen amended quadrats, but it was significantly higher than in any of the other nutrient treatments.

Although we did not find significant effects of the addition of tertel on the average plant biomass (except for *E cicutarium* in Plot 1), 13 out of 15 species

TABLE 3

Means ($\bar{x}$) and one standard deviation (SD) of aboveground-dry blomass (g) plant in fertilized quadrats pooled over water treatment in Plot 1 (surface tertel) and Plot 2 (deep tertel).
Means in a row followed by an asterisk are significantly different from the control plants for an $\alpha = 0.05$. n: number of plants.

Promedios ($\bar{x}$) y una desviación estándar (SD) de biomasa seca sobre el suelo (g)/planta en cuadrantes fertilizados sin considerar el tratamiento de riego en la Parcela 1 (tertel superficial) y Parcela 2 (tertel profundo).
Promedios en una fila seguidos por un asterisco son significativamente diferentes de las plantas controles para un $q/\alpha = 0.05$. n: número de plantas.

Plot 1

Species		N	P	K	Ca	Mg	Tertel	Control	F	df	P
Calandrinia sp.	n	8	10	10	12	12	5	12			
	$\bar{x}$	0.201*	0.099	0.066	0.159	0.197*	0.051	0.105	3.36	6,55	<0.01
	SD	0.145	0.056	0.027	0.602	0.153	0.040	0.061			
Erodium cicutarium	n	10	8	8	10	10	9	7			
	$\bar{x}$	0.677*	0.173*	0.258	0.264	0.238*	0.202*	0.448	6.49	6,48	< 0.005
	SD	0.387	0.099	0.128	0.195	0.129	0.097	0.268			
Erodium malacoides	n	7	12	8	12	12	12	12			
	$\bar{x}$	0.304	0.224	0.260	0.213	0.241	0.184	0.222	0.69	6,61	NS
	SD	0.202	0.187	0.151	0.099	0.068	0.083	0.118			
Erodium moschatum	n	10	8	10	11	12	10	10			
	$\bar{x}$	0.374*	0.165	0.211	0.164	0.211	0.150	0.174	5.63	6,57	< 0.001
	SD	0.193	0.044	0.075	0.111	0.099	0.069	0.088			
Oxalis micrantha	n	5	12	8	10	9	12	12			
	$\bar{x}$	0.091*	0.030	0.035	0.067*	0.038	0.025	0.040	3.14	6,55	< 0.05
	SD	0.088	0.015	0.025	0.063	0.019	0.017	0.025			

Plot 2

Species		N	P	K	Ca	Mg	Tertel	Control	F	df	P
Adesmia tenella	n	7	12	12	12	11	9	10			
	x̄	0.081	0.062	0.069	0.068	0.060	0.075	0.049	0.59	6.59	NS
	SD	0.032	0.034	0.049	0.033	0.034	0.059	0.029			
Calandrinia trifida	n	9	12	6	12	10	7	8			
	x̄	0.065*	0.033	0.024	0.023	0.029	0.026	0.039	3.09	6,50	< 0.05
	SD	0.049	0.032	0.018	0.016	0.023	0.027	0.021			
Camissonia dentata	n	7	12	8	8	10	8	10			
	x̄	0.063	0.025*	0.031*	0.022*	0.019*	0.038*	0.077	6.20	6,49	< 0.005
	SD	0.035	0.013	0.023	0.016	0.006	0.027	0.050			
Cryptantha glomerata	n	10	12	10	10	12	10	11			
	x̄	0.485	0.185	0.419	0.211	0.225	0.237	0.495	1.88	6,61	NS
	SD	0.462	0.141	0.401	0.093	0.152	0.204	0.623			
Cryptantha glomerulifera	n	5	9	6	6	7	8	5			
	x̄	0.235*	0.084	0.090	0.120	0.108	0.067	0.072	3.97	6,32	< 0.005
	SD	0.155	0.045	0.036	0.043	0.044	0.016	0.022			
Erodium malacoides	n	9	9	8	11	12	11	12			
	x̄	0.183	0.150	0.276	0.111	0.123	0.174	0.096	1.25	6,58	NS
	SD	0.137	0.124	0.322	0.052	0.080	0.269	0.074			
Oenothera coquimbensis	n	6	5	7	5	9	9	5			
	x̄	0.041	0.052	0.018	0.019	0.028	0.054	0.088	2.17	6,32	NS
	SD	0.035	0.044	0.008	0.011	0.011	0.054	0.083			
Oxalis micrantha	n	12	9	12	10	12	9	10			
	x̄	0.061	0.030	0.031	0.036	0.059	0.028	0.074	1.76	6,60	NS
	SD	0.061	0.018	0.024	0.019	0.056	0.017	0.078			
Plantago hispidula	n	9	9	11	12	12	10	11			
	x̄	0.108	0.069	0.113	0.108	0.062	0.081	0.112	1.63	6,60	NS
	SD	0.081	0.032	0.050	0.051	0.036	0.050	0.125			
Schismus arabicus	n	10	4	8	5	4	9	9			
	x̄	0.116*	0.034	0.036	0.044	0.047	0.023	0.048	3.87	6,35	< 0.05
	SD	0.105	0.030	0.018	0.037	0.021	0.013	0.048			

had lower biomass in the tertel amended quadrats than in the control quadrats (Table 3), suggesting a possible detrimental effect of tertel on plant growth.

Species responses to water and nutrient interaction

In Plot 1, no significant effects of the interaction of water and fertilizer treatments on the biomass of the species studied were detected. In Plot 2, the interaction of water and fertilizer had significant effects on *Calandrinia trifida* ($F_{(635)} = 3.11; P < 0.05$) and *Schismus arabicus* ($F_{(6,50)} = 2.80$; $P < 0.05$). For both species, plant biomass was higher in the watered-nitrogen amended quadrats than in the control quadrats.

DISCUSSION

Our results show that water and nitrogen are important limiting factors for the growth of herbaceous vegetation of the studied site. However, annual species exhibited different responses to water and nitrogen. Although we expect irrigation will have a greater effect on plant biomass in dry years, in 1987, a year of above average rainfall in the study area, two out of five species in Plot 1, and seven out of ten species in Plot 2 showed significant biomass increases in response to irrigation. *Oxalis micrantha* (in Plot 1) and *Plantago hispidula* (in Plot 2) exhibited the largest increases in biomass due to irrigation. *Adesmia tenella,* one of the species that showed a positive response to watering in Plot 2, is known to bear nitrogen-fixing bacteria associated with root nodules (F. Squeo, personnal communication). This may explain the positive response to water, but not to nitrogen. Fewer species responded to artificial irrigation in Plot 1 compared to Plot 2. In contrast, four out of five species in Plot 1, and four out of ten species in Plot 2 showed significant increases in biomass in response to nitrogen fertilization. In Plot 1, two out of the three Eurasian-introduced species of *Erodium* (Hunter *et al.* 1987) responded significantly to the addition of nitrogen. A similar response was observed in Plot 2 for *Schismus arabicus,* another Eurasian-introduced species (Hunter *et al.* 1987). Positive responses of aboveground biomass of weeds to the addition of nitrogen have also been reported for Chihuahuan Desert annuals (Gutiérrez *et al.* 1988).

The different responses of annual species to irrigation and nutrients may be related to differences in the depth of the tertel layer between plots. In Plot 1, water from rainfall and artificial irrigation should remain longer at the soil surface as the shallow tertel layer greatly reduces infiltration. As rains normally falls in winter, when air temperatures are lowest, the rate of water evaporation from the soil is reduced. Consequently, artificial irrigation may not elicit a differential growth response in many species, except for those having very high water requirements. In contrast, in Plot 2 where the tertel layer is found about 1 m deeper than in Plot 1, water infiltration is likely to be much faster. Soil moisture at 5 cm deep recorded weekly in Plot 2 was significantly lower than in Plot 1 (Gutiérrez, unpublished data). Reduced soil moisture availability for the plants may explain why a higher proportion of species responded to irrigation in Plot 2. We suggest that greater soil moisture availability in Plot 1 may have stimulated plant growth allowing more plants to encounter limiting nitrogen levels in control quadrats as shown by our results.

In general, annual plant biomass did not show significant responses to the addition of nutrients other than nitrogen. The lack of response to added P, K, Ca and Mg has been reported for grassland species of temperate regions in the northern hemisphere (Tilman 1984, 1987). The soils of the study site have high levels of K, Ca, and Mg, a common feature of soils in the Chilean arid zone (Carrasco *et al.* 1978). Consequently, the lack of response to some of the nutrient treatments is not surprising. However, the lack of response to phosphate was unexpected because of the low amount of soluble P reported for arid soils in Chile (Carrasco *et al.* 1978). Presently, we have no explanation for this result, however we postulate that the high concentration of calcium, due to presence of tertel, could have immobilized the added phosphate making it unavailable for plant uptake. In addition, many soils of arid regions worldwide, contain high levels of precipitated carbonates (Dregne 1976; Schlesinger 1982). Carbonates can control phosphorus levels in the soil solution through ion pairing with calcium, physical sorption onto $CaCO_3$, and the precipitation of secondary calcium phosphate minerals (Marion & Babcock 1977). The fixation of phosphorus by pedogenic carbonates has been implicated in the lowered crop responses to phosphorus fertilization in the US Southwest (McCaslin & Gledhill 1980). However more studies are needed to clarify this point.

This field experiment reveals that aboveground biomass of annual species in the studied area can be limited not only by water, but also by other resources, particularly nitrogen. Similar results have been reached for other arid systems (see West & Skujin 1978). Contrasting plant responses to water and nitrogen are apparently related to the different life-history, specific physiological and morphological characteristics of the species, and to the particular nature of the soils where these species occur (Chapin *et al.* 1987).

ACKNOWLEDGMENTS

We thank G. Arancio for identification of plants, and R. Gutiérrez, E. Tabilo and P. León for their help with the field work. We also thank E. Hajek and J.D. Molina for providing climatic data of the study site, and J. Cepeda and B. Milstead for critical review of an early version of the manuscript. We appreciate the collaboration of Gastón Villá for allowing the use of his property as the Universidad de La Serena Experimental Station. This research was supported by a Grant from the O.A.S. to J. R. Gutiérrez. This work is a contribution to the research program of the Unidad de Investigación de Zonas Aridas of the Universidad de La Serena.

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