

## Effect of season, substrate quality, litter quality, and soil conditions on edaphic microarthropods in a coastal desert site of north-central Chile

Efecto de la estación, calidad del sustrato y del mantillo, y de las condiciones  
del suelo sobre microartrópodos edáficos en un ecosistema desértico-costero  
de la región norte-centro de Chile

JORGE G. CEPEDA-PIZARRO, MARCO A. ROJAS G., MARIA R.  
MALDONADO C., JAIME L. VILCHES and  
NELLY M. PEREIRA P.

Departamento de Biología. Universidad de La Serena. Casilla 599. La Serena, Chile.

### ABSTRACT

We tested the numerical responses of desert soil microarthropods to season, substrate quality, litter quality and soil conditions. The numerical changes were monitored with litterbags which enclosed 10.0 g of oven-dried leaf material collected from three *Atriplex* species. These species have been widely utilized on land reclamation programs in north-central Chile. In terms of numbers of microarthropods, *A. repanda*-litter apparently constituted a better habitat than *A. semibaccata* and *A. nummularia*, an introduced Australian species. Across the main taxa, we detected seasonal patterns of density which were apparently related to litter quality and soil conditions.

**Key words:** Deserts, soil microarthropods, mites, soil insects, seasonal changes, *Atriplex*-litter, litter quality.

### RESUMEN

Estudiamos las respuestas numéricas de los microartrópodos edáficos en un ecosistema desértico costero a los cambios en las estaciones del año, a la calidad del sustrato, a la calidad de la hojarasca y a las condiciones del suelo mineral subyacente. Las variaciones numéricas fueron monitoreadas con sacos de hojarasca que contuvieron 10,0 g de hojas secas (secadas a estufa) de tres especies de *Atriplex*. Estas especies han sido intensivamente usadas en programas de recuperación de áreas desertificadas de la región norte-centro de Chile. En relación al número de individuos registrados, la hojarasca de *A. repanda* parece constituir un mejor hábitat que la hojarasca de *A. semibaccata* y *A. nummularia*, una especie introducida desde Australia. Detectamos patrones estacionales de la densidad de microartrópodos, siendo estas respuestas aparentemente dependientes de la calidad de la hojarasca y de las condiciones del suelo mineral subyacente.

**Palabras claves:** Desiertos, microartrópodos del suelo, ácaros, insectos del suelo, cambios estacionales, *Atriplex*-hojarasca, hojarasca-calidad.

### INTRODUCTION

Because of desertification, climatic global changes, world hunger, geopolitical difficulties and lack of enough knowledge (Cloudsley-Thompson 1988, 1982, Safriel *et al.* 1989, Caviedes *et al.* 1989, Schlesinger *et al.* 1990), there is an ever increasing scientific interest in deserts.

North-central Chile is a transitional belt between the true desert (the Atacama) and the mediterranean zone. It suffers from severe desertification problems (CONUD 1977, Fuentes & Hajek 1978), these not only affect the regional landscape, but

also the life quality of local human settlements (Caviedes *et al.* 1989).

To prevent more land deterioration and poverty, some state and private land reclamation programs, based on desert adapted plant species, have been conducted since the 1970s. Some of these programs have heavily relied upon species of the genus *Atriplex* (Chenopodiaceae, salt-bushes) for their potential as forage crops for local domestic livestock (e.g., goats). As a result of those programs, some areas of north-central Chile are currently planted with both native and introduced species of *Atriplex*, mainly *A. nummularia* Lindl

(pasto salado, introduced from Australia) and *A. repanda* Phil (sereno, a native species) (CONAF 1984).

Planting pasto salado and sereno as agronomical crops has caused changes in the landscape of a formerly more heterogeneous rangeland. For this we suggest that the structure and dynamics of the ecosystem may also have changed. Consequently, we would expect in the future some changes in the structure and dynamics of invertebrate communities. In this work we paid attention to the numerical responses of the total soil microarthropod community. We attempted to answer the following questions: (1) is there a litter quality effect? (2) is there a substrate effect (litter vs mineral soil)?, (3) is there a microhabitat effect (litter and the underlying mineral soil combined), and (4) are the detected relationships time-dependent? Field experiments were designed to falsify the null hypothesis of no-treatment effects.

#### MATERIAL AND METHODS

##### Study site

The work was conducted in the Agronomical Experimental Station "Las Cardas", owned by Universidad de Chile and located in north-central Chile (30°13'S, 71°13'W). The climate is characterized as mediterranean arid (Di Castri & Hajek 1976). The annual rainfall average is between 100-150 mm, with most of the rains concentrated in winter (May through June). Inter-annual rainfall variability is high (CV close to 80%). The annual mean air temperature ranges between 11-19°C. But it increases to 26-27°C during summer—which is moderately hot and dry—, and then decreases to 7-8°C in winter—which is in turn moderately cold and wet. Because of the ocean proximity, cloudiness is high, with air relative humidity ranging between 65-80% for most part of the year.

The site is on a slight slope. The soil is well drained, sandy, stony or partially covered by desert pavement. A calcareous hardpan layer on the soil surface or below it may be found in some areas.

The general ecosystem corresponds to an open shrubland with sparse succulents. The most abundant shrub species are *Flourensia thurifera* (Mol.) DC. (Compositae) (incienso), *Gutierrezia resinosa* (H. et A.) Black (Compositae) (pichanilla) and *Heliotropium stenophyllum* H. et A. (Boraginaceae). Secondary species are *Senna cummingii* (H. et A.) Irw et Barnaby (Caesalpiniaceae), *Baccharis* sp. (Compositae), *Senecio* sp. (Compositae) and *Lithrea caustica* (Mol.) H. et A. (Anacardiaceae). Herbs are mainly represented by *Erodium cicutarium* (L.) L'Herit, *E. moschatum* (L.) L'Herit (Geraniaceae) (alfilerillos), *Bromus berterianus* Colla (Gramineae) (pasto largo) and *Plantago hispidula* E et P var *tumida* (Link) Pilger (Plantaginaceae). Some areas have experimental stands—not older than 10 years at the time of the study— of *Atriplex repanda* Phil., *A. semibaccata* (R. Br.), and *A. nummularia* Lindl. The present study was conducted in one of the *A. repanda* stands.

##### Experimental design

We used fresh leaf-material collected from individuals of *Atriplex repanda*, *A. nummularia* and *A. semibaccata* grown in the area. The collected leaves were kept under sunlight for dehydration for a week, and then at 50°C in a mechanical convection oven for another week. Once dry, the leaves were cleaned up of strange material or thick petioles, and set in litter-bags (15x15 cm) made of plastic screen mesh (0.5 - 1.0 mm diam). We weighted 10.0 g of that plant material per litter-bag.

A total of 165 groups of litter bags—each group formed by one litter bag per litter type— was laid out under the canopy of individuals of *A. repanda*. The study was started at the end of the summer of 1988 (March) and ended in the middle of the summer of 1989 (February). Sampling was conducted every 90 d. During sampling, we randomly retrieved a subset of 10 groups of litter bags. Simultaneously, we collected a soil sample (5.0 x 10.0 cm, diam x depth) from under each one of the retrieved litter bags. Once in the laboratory, the bags were carefully opened, and the

contents installed in soil microarthropod extractors (a modified version of Berlesse funnels). Light bulbs (25 W) were turned on for 72 hrs. After that, the extracted specimens were retrieved from the surface of the collecting liquid (tap water). The specimens were set in microscope slides for counting purposes. A collection of reference is kept in the soil ecology laboratory at Universidad de La Serena (Chile).

Standard chemical analysis for soil conditions were performed at the end of the summer of 1988, the winter of 1988 and in the summer of 1989. Additionally, moisture, organic matter, total nitrogen and Na contents of the litter of the 3 *Atriplex* species were measured at time zero.

Series of analysis of variance (ANOVA, fixed model, completely randomized design) for hypothesis-testing were conducted. Previously to the analysis, the data were square root transformed. Pair-wise multiple comparisons were performed with protected-LSD ( $p < 0.05$ ).

## RESULTS AND DISCUSSION

During 1988 total rainfall was 34.7 mm, 76% lower than the 12-year mean (145.4 mm). The month with the largest amount of rain was June (23.2 mm), followed by August (8.3 mm) and September (3.2 mm). Fig. 1 shows the rainfall pattern for the study site as well as the precipitation recorded in 1988. We collected 2,730 soil microarthropods throughout the study. This number was made up of by Acari (65.3%) and by Insecta (34.7%). Over time, total microarthropods, Arachnida and Insect counts exhibited an unimodal pattern, with the peak of the curve in the winter. The patterns were similar both in litter and in the underlying mineral soil (Fig. 2A-D).

Acari was represented by Actinedida (63.3%), Oribatida (27.1%), Acaridida (7.2%), and Gamasida (2.4%). Among insects, the most important orders were Psocoptera, Collembola and Thysanoptera.

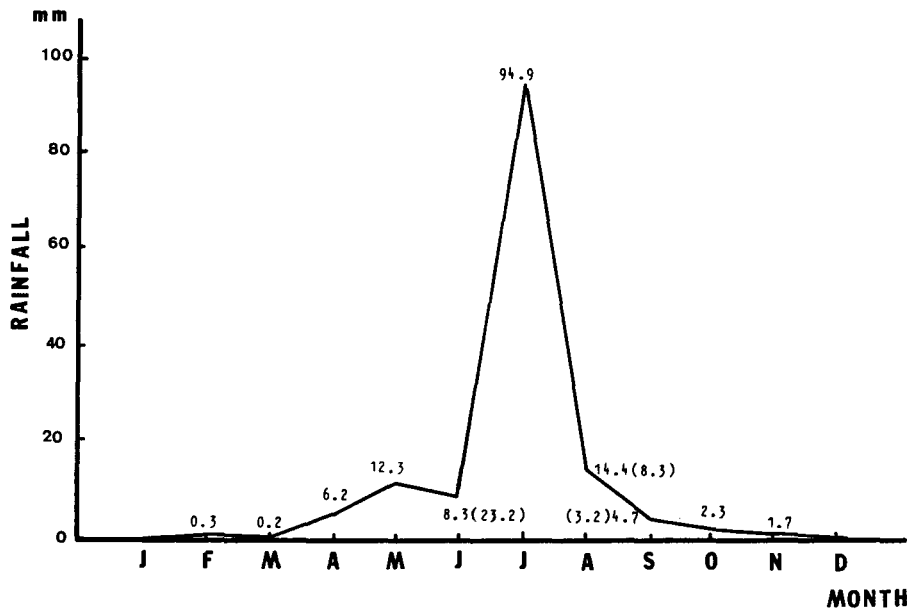


Fig. 1: Monthly rainfall pattern for "Las Cardas" Agronomical Experimental Station (30°13'S, 71°13'W). Annual mean for the last 12 years: 145.4 mm (CV: 80% ca), (recorded amount in 1988).

Patrón de precipitación mensual para el sector de la Estación Experimental Agronómica "Las Cardas" (30°13'S, 71°13'W). Promedio anual para el período de los últimos 12 años: 145.4 mm (CV: 80% ca), (agua caída en 1988).

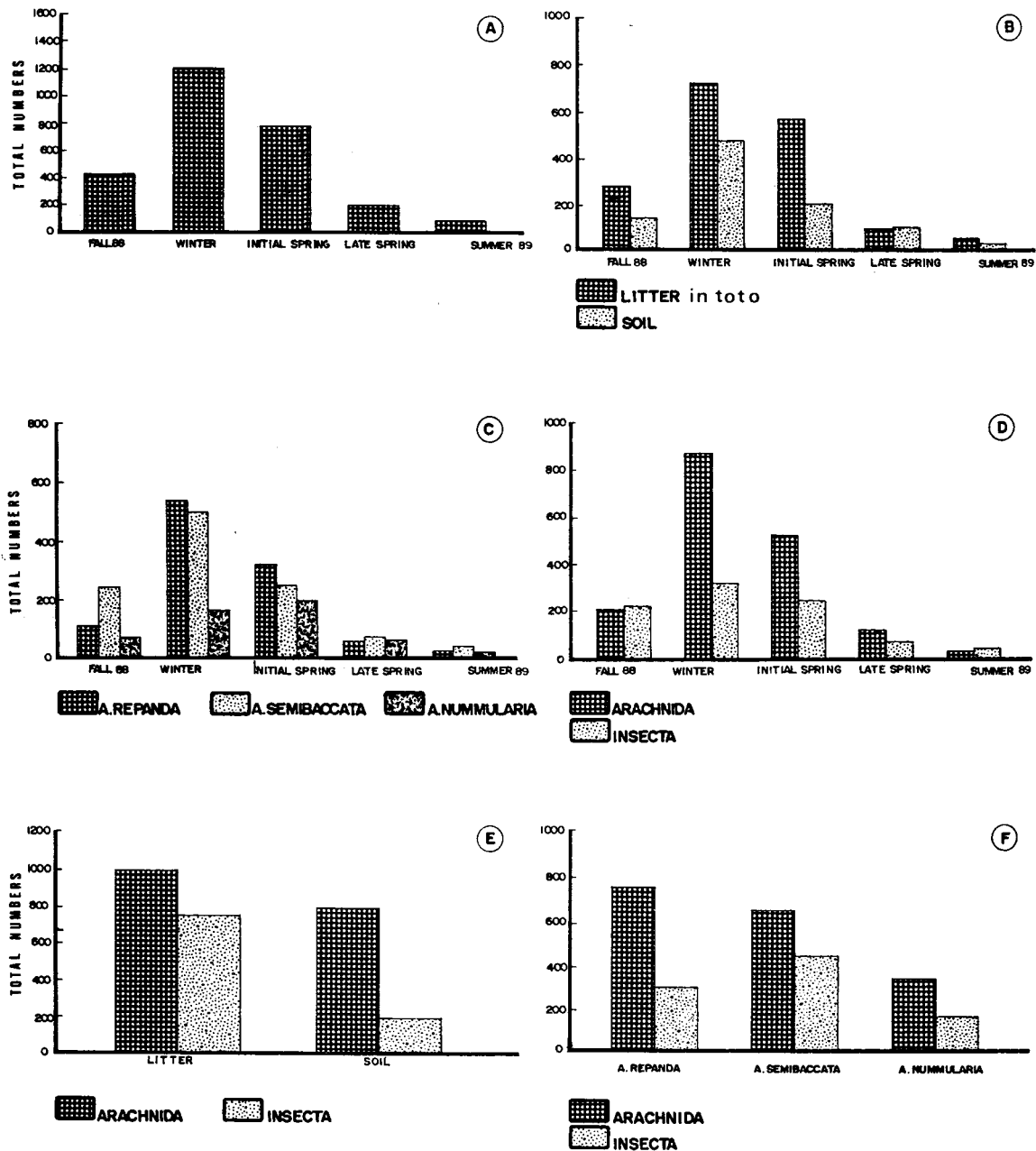


Fig. 2: Patterns of seasonal abundance of soil microarthropods in a saltbusch-dominated site. A: Overall pattern for total microarthropods. B: Effect of quality of substratum (*Atriplex*-litter vs the respective underlying mineral soil) on abundance pattern of total microarthropods. C: Effect of quality of *Atriplex*-litter on abundance pattern of total microarthropods. D: Seasonal pattern of abundance of Arachnida (Acari in toto) and Insecta (mainly Psocoptera). E: Effect of quality of substratum (*Atriplex*-litter vs the respective underlying mineral soil) on seasonal abundance of Arachnida (Acari) and Insecta (Psocoptera). F: Effect of quality of *Atriplex*-litter on seasonal abundance of Arachnida and Insecta.

Patrones de abundancia estacional de microartrópodos edáficos en un stand de pasto salado. A: Patrón general para el total de microartrópodos. B: Efecto de la calidad del sustrato (hojarasca de *Atriplex* vs. suelo mineral subyacente) sobre la abundancia estacional de microartrópodos totales. C: Efecto de la calidad de la hojarasca sobre la abundancia estacional de microartrópodos totales. D: Patrón de abundancia estacional de Arachnida (Acari) e Insecta (principalmente Psocoptera). E: Efecto de la calidad del sustrato (hojarasca de *Atriplex* vs. suelo mineral subyacente) en la abundancia estacional de Arachnida (Acari) e Insecta (principalmente Psocoptera). F: Efecto de la calidad de la hojarasca de *Atriplex* en la abundancia estacional de Arachnida e Insecta.

The numerical relations for both Acari and for Insecta across the studied factors are shown in Fig. 2E-F.

The temporal pattern was unimodal in the three subsystems —e.g., microhabitat, litter and soil conditions—, the sharpest one being that associated with mineral soil (Fig. 3A-C). The ANOVAs showed a significant time effect for microhabitat ( $F_{4,290} = 30.2$ ,  $p < 0.01$ ); for litter ( $F_{4,135} = 48.5$ ,  $p < 0.01$ ); and for soil conditions ( $F_{4,135} = 35.4$ ,  $p < 0.01$ ). Several multiple comparisons were significant as it is shown in Fig. 3 by the vertical bars (LSD, 95%).

Total number of microarthropods was higher in the decomposing *Atriplex* litter than in the underlying mineral soil ( $F_{1,290} = 27.4$ ,  $p < 0.01$ , a substrate quality effect). Globally, 63.7% was collected from litter and 36.7% from soil. Numbers of microarthropods collected from the combined strata (litter plus the respective underlying soil) were also significant different among litter types ( $F_{2,135} = 22.9$ ,  $p < 0.01$ , a microhabitat effect). Indeed, the number of microarthropods in *A. repanda* and in *A. semibaccata*-litter was higher than that in *A. nummularia*. A litter quality effect was also detected. As in the case of the microhabitat experiment, *A. repanda* and *A. semibaccata* provided higher numbers of microarthropods than *A. nummularia* ( $F_{2,290} = 12.9$ ,  $p < 0.01$ ). A significant effect of mineral soil condition was also detected ( $F_{2,135} = 4.0$ ,  $p < 0.01$ ).

Numerical responses of soil microarthropods to litter quality, to substrate quality, and to microhabitat conditions were time dependent, as it was shown by their highly significant interactions ( $F_{8,135} = 5.7$ ;  $F_{4,290} = 5.9$ ;  $F_{8,135} = 4.3$ , respectively,  $p < 0.01$ ). No significant interaction was found between time and mineral soil conditions ( $F_{8,135} = 1.7$ ,  $p < 0.1$ ). A graphical display of interaction trends is depicted in Fig. 4.

Chemical analysis of the litter at time 0 showed certain significant differences among litter types for both macronutrients and for micronutrients (Table 1); but we could not correlate these differences with

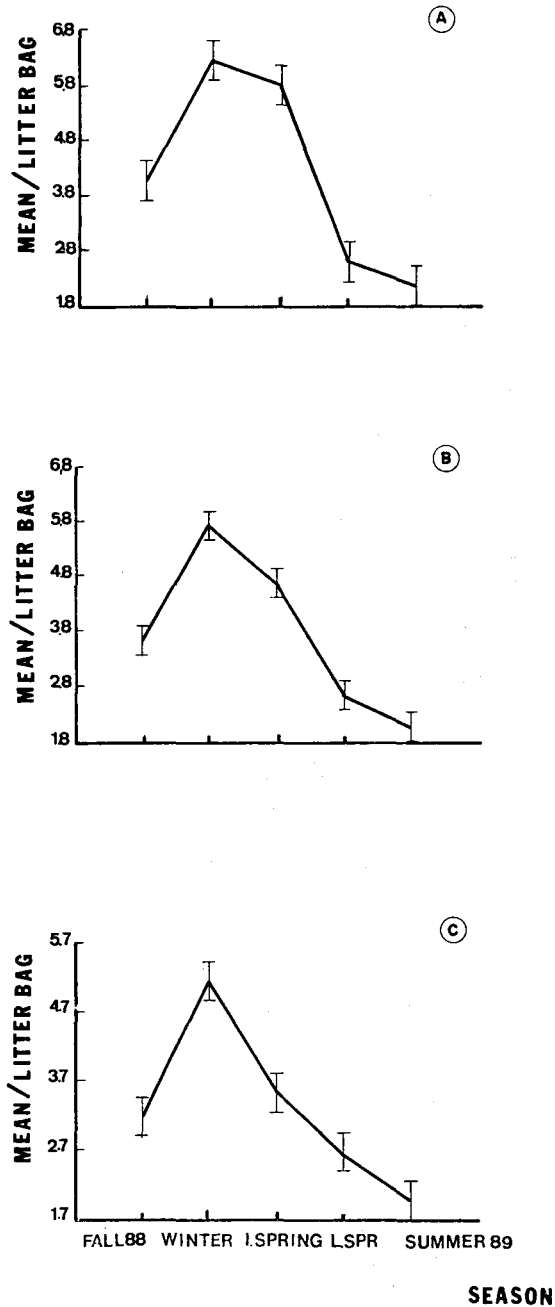


Fig. 3: *A posteriori* LSD comparisons (95%) for effect of time. A: Litter plus underlying mineral soil (microhabitat effect). B: Litter (litter quality effect). C: Mineral soil (soil condition effect). Vertical bars:  $\pm$  LSD (= least significant difference, 95%).

Comparaciones múltiples *a posteriori* (DMS, 95%) para el efecto del tiempo. A: Hojarasca y suelo mineral (efecto de microhabitat). B: Hojarasca (efecto calidad de la hojarasca). C: Suelo mineral (efecto de las condiciones del suelo). Barras verticales:  $\pm$  DMS (= diferencia mínima significativa, 95%).

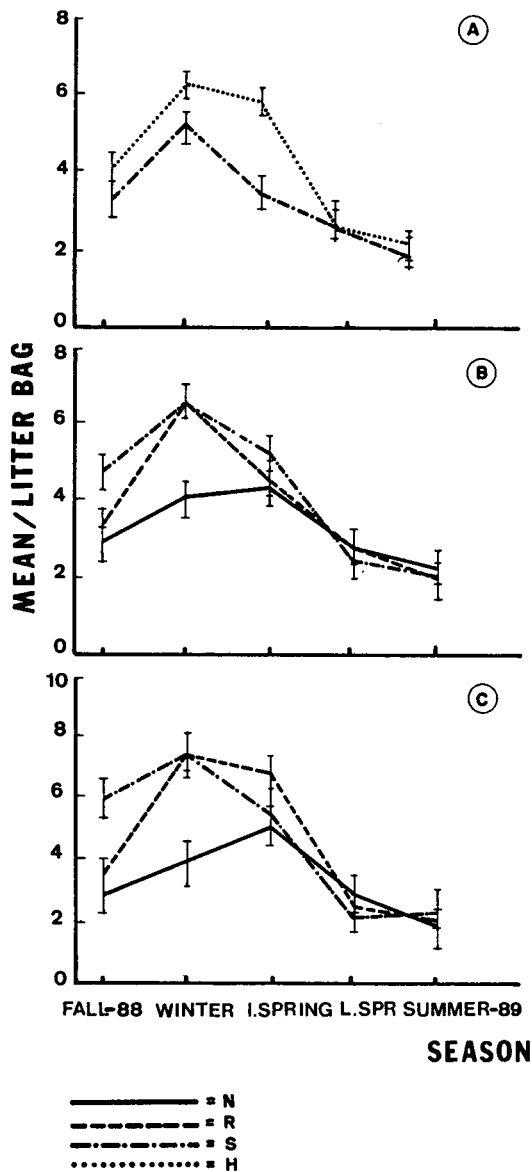


Fig. 4: Time interactions for abundance patterns of soil microarthropods. A: Effect of quality of substratum (*Atriplex*-litter vs underlying mineral soil). B: Effect of quality of *Atriplex*-litter. C: Effect of soil conditions (underlying mineral soil). Meaning of vertical bars as in Fig. 3. N: *A. nummularia*-litter. R: *A. repanda*-litter. S: Mineral soil (A) or *A. semibaccata*-litter (B, C). H: Litter.

Interacciones temporales de los patrones de abundancia de microartrópodos edáficos. A: Efecto de la calidad del sustrato (hojarasca de *Atriplex* vs. suelo mineral subyacente). B: Efecto de la calidad de la hojarasca de *Atriplex*. C: Efecto de las condiciones del suelo (suelo mineral subyacente). Significado de las barras verticales como en la Fig. 3. N: Hojarasca de *A. nummularia*. R: Hojarasca de *A. repanda*. S: Suelo mineral (A) u hojarasca de *A. semibaccata* (B, C). H: Hojarasca.

the differences in numbers of microarthropods. Neither clear trends emerged from the chemical analysis of the underlying mineral soil as litter decomposed (Table 2).

The number of microarthropods reported in this study is of the same order of magnitude as those reported by Covarrubias *et al.* (1964) and Di Castri & Di Castri (1971, 1981) for arid Chile; but much smaller than the densities communicated from works conducted in North-American and Australian deserts (Wood 1971, Wallwork 1972a, 1972b, Santos *et al.* 1978, Franco *et al.* 1979, Steinberger & Whitford 1984, 1985, Cepeda-Pizarro & Whitford 1989a). Among the microarthropod groups we recorded, Acarina and Insecta were dominant, being the first taxon dominant over the second one. Actinedid mites were the commonest among Acarina. Similar findings have been communicated by Covarrubias *et al.* (1964), Santos *et al.* 1978, Santos & Whitford (1983), Elkins & Whitford (1984), Cepeda-Pizarro & Whitford (1989b). Actinedida is a heterogeneous group both in size – it includes some of the smallest to the largest soil mites – and in ecological requirements (Kethley 1982), and there is no apparent reason for its dominance in xeric soils. However, some families –e.g., Nachorchestidae– seem to be well adapted to severe environments (Santos & Whitford 1983, Elkins & Whitford 1984). In our site and probably for more abundant food resources, soil microarthropods tended to concentrate in the surface litter rather than in the mineral soil. This result suggests us that some habitat separation occurred. Over time total density was clearly seasonal, being more marked in soil than in litter. While the maximum was observed in winter, the minimum was noticed in summer. This pattern –high density in winter, low in summer– has also been reported from other desert sites with a Mediterranean climate (for ref., see Di Castri & Di Castri 1981). Wallwork *et al.* (1984, 1986), working with oribatids, postulate that soil desert microarthropods may have evolved phenological patterns linked to the predictable season of rains. The advantages of coupling reproduction with the most

TABLE 1

Some chemical characteristics of *Atriplex* leaf-litter.  
 Algunas características químicas de hojarasca de *Atriplex*.

Atriplex litter	%								ppm			
	water content*	OM	Total N	Na	K	Ca	Mg	Total ash	Cu	Zn	Fe	Mn
Repanda	1.15 (0.70)	82.1a (1.34)	2.8b (0.20)	1.1a (0.39)	0.9 (0.25)	0.7 (0.23)	0.4 (0.12)	17.9 (1.34)	8.4 (3.95)	63.8 (11.56)	1677a (25.94)	44.6a (13.56)
Semibaccata	2.87 (0.26)	78.2b (0.98)	3.9a (0.30)	2.6b (0.60)	1.2 (0.46)	0.6 (0.25)	0.5 (0.18)	21.9 (0.98)	11.1 (6.18)	53.0 (11.05)	349.9b (30.60)	35.1a (20.55)
Nummularia	2.67 (1.18)	77.6b (0.53)	2.6a (0.2)	2.8b (0.4)	1.0 (0.18)	0.5 (0.14)	0.4 (0.07)	22.4 (0.53)	7.2 (1.80)	47.1 (8.55)	74.5a (24.94)	26.8b (3.86)

Means are based on  $n = 5$ . In parenthesis: tSE (95% CI). Numbers in the column followed by the same letter are not significant different. \*Dry weight at 105°C. Chemical determinations are based on dry weight at 55°C.

Valores promedios basados en  $n = 5$ . En paréntesis: tES (95% IC). Los valores en la columna seguido por la misma letra no son estadísticamente diferentes. \*Peso seco a 105°C. Determinaciones químicas basadas en peso seco a 55°C.

TABLE 2

Surface soil (0-10 cm) chemical conditions under *Atriplex* litter.  
 Características químicas del suelo superficial (0-10 cm) bajo mantillo de *Atriplex* sp.

Litter	Season	pH	OM*	N	C:N	P	K
<i>A. repanda</i>	summer-88	7.4 (0.13)	1.4 (0.21)	0.3 (0.07)	2.0 (0.45)	49.7 (11.89)	539.8 (88.62)
	winter-88	6.9 (0.14)	0.9 (0.6)	0.09 (0.04)	4.29 (1.60)	67.87 (8.45)	417.76 (90.99)
	summer-89	7.67 (0.38)	1.72 (0.60)	0.16 (0.05)	4.81 (0.74)	99.68 (48.54)	590.60 (186.65)
<i>A. semibaccata</i>	summer-88	7.4 (0.13)	1.4 (0.21)	0.3 (0.07)	2.0 (0.45)	49.7 (11.89)	539.8 (88.62)
	winter-88	6.68 (0.16)	2.31 (0.92)	0.16 (0.04)	6.25 (0.86)	58.99 (3.40)	577.5 (92.05)
	summer-89	7.50 (0.20)	1.19 (0.42)	0.12 (0.02)	4.25 (1.07)	92.60 (11.02)	583.8 (67.62)
<i>A. nummularia</i>	summer-88	7.4 (0.13)	1.4 (0.21)	0.3 (0.07)	2.01 (0.45)	49.7 (11.89)	539.8 (88.62)
	winter-88	6.66 (0.44)	1.02 (0.34)	0.10 (0.02)	4.73 (0.75)	63.34 (11.06)	382.74 (95.09)
	summer-89	7.62 (0.26)	1.32 (0.46)	0.12 (0.03)	4.78 (0.65)	94.85 (23.21)	593.5 (88.35)

\* Organic matter (OM) and N content are given in %; P and K in ppm. Mean  $\pm$  tSE (in parenthesis, 95%).

probable moist period may be related to quantity and quality of food resources.

In coastal deserts, studies on the effects of litter quality on soil microarthropods are inexistent, and we had a practical interest on the subject. Given the potentiality of *Atriplex* species for forage crop production in arid lands, several state programs based on these species have been conducted since the 1970s. It is well known that many *Atriplex* species concentrate salts in their leaves (Osmond *et al.* 1980), and thus may provoke a patchy distribution of salts in the soil environment. Because of this, the litter and the soil may become unsuitable for many biological processes related to soil fertility and plant production. We found certain significant differences in chemical quality among the three litter types. These differences were referred to both macronutrients and micronutrients. The smaller numbers of microarthropods that were recorded from *A. nummularia* litter as compared to those recorded from *A. repanda* and from *A. semibaccata* may be related to these chemical differences or to unmeasured properties, e.g., leaves of *A. nummularia* range high in oxalate and fluoride contents (Watson *et al.* 1987). Unfortunately, we were unable to detect any chemical differences in the underlying soil as litter decomposed. This result may be related to the low litter decomposition rate as it has been estimated from a current study (unpublished data).

In deserts, the soil microarthropod community is rather simple: but it may become complex in mesic patches, where more suitable conditions may favor colonization and further settlement (Wallwork 1982). These facts provide one of the characteristic aspects of biota of desert soils: their spatial and temporal heterogeneity. With this study we provided information on the effect of time (season), litter, and substrate quality on the numerical responses of soil microarthropods inhabiting patches provided by replanted or introduced saltbushes in an attempt to prevent landscape deterioration and productivity.

#### ACKNOWLEDGMENTS

We thank J.R. Gutiérrez and two anonymous reviewers for their comments on the manuscript and to R. Narbona for reviewing the English grammar. The research is a contribution to the Arid Lands Research Program of Universidad de La Serena and was funded by FONDECYT 1214/88 and by Dirección de Investigación de la Universidad de La Serena, DIULS 130.2.42 to J.G. Cepeda-Pizarro.

#### LITERATURE CITED

- CAVIEDES E, R INFANTE, JM D'HERBES, J GALVEZ, G COVARRUBIAS & R CLERC (1989) Establecimiento de una zona piloto para un programa de manejo racional. Comunidad Agrícola Yerba Loca IV Región, Chile. Taller Interregional: Bases ecológicas para el desarrollo rural integrado y la lucha contra la desertificación en zonas áridas y semiáridas de Africa y América Latina. Coquimbo (Chile): Abril 9-14.
- CEPEDA-PIZARRO JG & WG WHITFORD (1989a) Spatial and temporal variability of higher microarthropod taxa along a transect in a northern Chihuahuan Desert watershed. *Pedobiologia* 33: 101-111.
- CEPEDA-PIZARRO JG & WG WHITFORD (1989b) Species abundance patterns of soil microarthropods in decomposing surface leaf-litter and mineral soil on a desert watershed. *Pedobiologia* 33: 254-268.
- CLOUDSLEY-THOMPSON JL (1982) Stressing desertification. *Environmental Conservation* 9 (3): 177-179.
- CLOUDSLEY-THOMPSON JL (1988) Desertification or sustainable yields from arid environments. *Environmental Conservation* 15 (3): 197-204.
- CONAF (1984) Contribución de CONAF (Corporación Nacional Forestal) al desarrollo de las zonas áridas. Corporación Nacional Forestal. Chile. IV Región-Coquimbo. Mimeografiado. 11 pp.
- CONUD (1977) Estudio de caso sobre la desertificación. Región de Combarbalá. Chile. Conferencia de las Naciones Unidas sobre la Desertificación. Nairobi.
- COVARRUBIAS R, I RUBIO & F DI CASTRI (1964) Observaciones ecológico-cuantitativas sobre la fauna edáfica de zonas semiáridas del norte de Chile (Prov. de Coquimbo y Aconcagua). Monografías de Ecología y Biogeografía de Chile. Sección A Nº 2.
- DI CASTRI F & V VITALI-DI CASTRI (1971) Colonización por organismos edáficos de territorios desérticos sometidos a riego (Estancia Castilla. Provincia de Atacama, Chile). *Boletín del Museo Nacional de Historia Natural de Chile*: 17-40.
- DI CASTRI F & ER HAJEK (1976) Bioclimatología de Chile. Vicerrectoría Académica de la Universidad Católica de Chile. Santiago, 123 pp.
- DI CASTRI F & V VITALI-DI CASTRI (1981) Soil fauna of mediterranean climate regions. In: Mediterranean type shrublands. F Di Castri, DW Goodall & RL Specht (eds.). Series Ecosystems of the world. Vol II. Elsevier Scientific Pub Co., New York.
- ELKINS NZ & WG WHITFORD (1984) The effects of high salt concentration on desert soil microarthropod density and diversity. *The Southwestern Naturalist* 29 (2): 239-241.



- FRANCO PJ, EB EDNEY & JF McBRAYER (1979) The distribution and abundance of soil microarthropods in the northern Mojave Desert. *Journal of Arid Environments* 2: 137-149.
- FUENTES ER & ER HAJEK (1978) Interacciones hombre-clima en la desertificación del Norte Chico chileno. *Ciencia e Investigación Agraria* 5 (3): 137-142.
- KETHLEY J (1982) Acariformis in: *Synopsis and classification of living organisms*. Vol. 2. SP Parker (ed.), McGraw-Hill, Book Co., New York.
- OSMOND CB, O BJORKMAN & D ANDERSON (1980) *Physiological Processes in Plant Ecology. Towards a synthesis with Atriplex*, Springer-Verlag, Berlin.
- SAFRIEL UN, Y AYAL, BP KOTLER, Y LUBIN, L OLSVIG-WHITTAKER & B PINSHOW (1989) What's special about desert ecology? *Journal of Arid Environments* 17: 125-130.
- SANTOS PF, E DE PREE & WG WHITFORD (1978) Spatial distribution of litter and microarthropods in a Chihuahuan Desert Ecosystem. *Journal of Arid Environments* 1: 41-48.
- SANTOS PF & WG WHITFORD (1983) Seasonal and spatial variation in the soil microarthropod fauna of the White Sands National Monuments. *The Southwestern Naturalist* 28 (4): 417-421.
- SCHLESINGER WH, J REYNOLDS GL CUNNINGHAM, LF HUENNEKE, WM JARREL, RA VIRGINIA & WG WHITFORD (1990) Biological feedbacks in global desertification. *Science* 247: 1043-1048.
- STEINBERGER Y & WG WHITFORD (1984) Spatial and temporal relations of soil microarthropods on a desert watershed. *Pedobiologia* 26: 275-284.
- STEINBERGER Y & WG WHITFORD (1985) Microarthropods of a desert tabosa grass (*Hilaria mutica*) swale. *American Midland Naturalist* 114 (2): 225-234.
- WALLWORK JA (1972a) Distribution patterns and population dynamics of microarthropods on a desert soil in southern California. *Journal of Animal Ecology* 41: 291-310.
- WALLWORK JA (1972b) Mites and other microarthropods from the Joshua Tree National Monument, California. *Journal of Zoology (London)* 168: 91-105.
- WALLWORK JA (1982) *Desert soil fauna*. Praeger Publishers, New York.
- WALLWORK JA, BW KAMILL & WG WHITFORD (1984) Life styles of desert microarthropods: A re-appraisal. *South African Journal of Science* 80: 163-169.
- WALLWORK JA, M MACQUITTY, S SILVA & WG WHITFORD (1986) Seasonality of some Chihuahuan Desert soil oribatid mites (Acari: Cryptostigmata). *Journal of Zoology London (A)* 208: 403-416.
- WATSON MC, JW O'LEARY & EP GLENN (1987) Evaluation of *Atriplex lentiformis* (Torr) S. Wats and *A. nummularia* Lindl as irrigated forage crops. *Journal of Arid Environments* 13: 293-303.
- WOOD TG (1971) The distribution and abundance of *Folsomides deserticola* Wood (Collembola: Isotomidae) and other microarthropods in arid and semiarid soils in southern Australia, with a note on nematode populations. *Pedobiologia* 11: 446-468.