Revista Chilena de Historia Natural
66: 323-336, 1993

Litter decomposition in deserts: an overview with an example from coastal arid Chile

Descomposición del mantillo en desiertos: una visión general con un ejemplo de Chile árido costero

JORGE G. CEPEDA-PIZARRO

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

ABSTRACT

In the last two decades different native and introduced species of saltbushes (*Atriplex:* Chenopodiaceae) have been extensively used to increase food resources for domestic livestock in some desertified areas of arid and semiarid Chile. Much of the present knowledge on the environmental impact of such revegetation programs refer to domestic livestock, and little is known on the effects of saltbush litter on soil chemical properties, soil mesofauna, microflora and on decomposition processes. The aim of this paper is twofold: (1) to review some recent ideas regarding surface litter decomposition in desert areas and their applicability to understanding litter decomposition processes and desertification in north-central Chile and (2) to report the results of a study on surface litter decomposition of three *Atriplex* species (*A. repanda, A. semibaccata* and *A. nummularia*). The study was conducted in the coastal desert of north-central Chile (Coquimbo, IV Region, 30° S). After one year in the field, litter of *A. repanda* showed the highest mass losses (18%), followed by *A. nummularia* (16%) and by *A. semibaccata* (11%), differences were significant. For desert areas these mass losses are among the lowest reported in the literature. Reduction in organic matter was about 52% during the first year. Differences were not significant among the litter of the three species of *Atriplex*. The curves of decrement of organic matter followed a three step (phases) pattern. During the initial 150 d (dry season) the average percentage of organic matter losses was about 10%, then it increased to 35% in the nest 150-270 d (wet season), to decrease to about 7% during the final 270-330 d (dry season following year). This result was a function of the amount of rainfall of the respective phases (0, 119.5 and 2 mm, respectively). Total N content decreased gradually, while P decreased erratically. Other mineral constituents of the litter showed strong increments through time.

Key words: Litter decomposition, ecosystem reclamation, coastal deserts, aridlands, South American deserts.

RESUMEN

En la última década diferentes especies nativas, e introducidas de pasto salado (*Atriplex:* Chenopodiaceae), se han usado extensivamente para aumentar el recurso alimentario para el ganado doméstico en algunos sectores desertificados de la región árida y semiárida de Chile. Gran parte de la información disponible se refiere a sus efectos sobre el ganado y poco acerca de sus efectos sobre las propiedades químicas del suelo, su mesofauna, la microflora y sobre los procesos de descomposición del mantillo. Los propósitos de este artículo son: (1) revisar algunas ideas recientes sobre descomposición del mantillo superficial en áreas desérticas y su aplicación en la comprensión de los procesos de descomposición y desertificación de Chile septentrional, y (2) comunicar los resultados de un estudio sobre descomposición del mantillo superficial de tres especies de *Atriplex* (*A. repanda, A. semibaccata* y *A. nummularia*). El estudio se realizó en la región norte-centro del desierto costero de Chile (Coquimbo, IV Región, 30° S). Después de un año de exposición a las condiciones de campo, la hojarasca de *A. repanda* mostró las mayores pérdidas de masa (18%), seguida por *A. nummularia* (16%) y por *A. semibaccata* (11%). Estas diferencias fueron significativas. Estos porcentajes están entre los más bajos encontrados en la literatura de zonas desérticas. La reducción en materia orgánica fue cercana al 52% durante el primer año del estudio. Las diferencias encontradas entre los tipos hojarasca no fueron significativas. La disminución en materia orgánica siguió un patrón escalonado (fases): durante los primeros 150 d (la estación seca) el porcentaje promedio de pérdida fue cercano al 10%, luego incrementó al 35% en los siguientes 150-270 d (la estación húmeda) para finalmente decrecer a un aproximadamente 7% en el período restante (la siguiente estación seca). Este resultado es una función de la cantidad de lluvia caída en el período estudiado (0, 119,5 y 2 mm, respectivamente). El contenido de N total de la hojarasca disminuyó en forma gradual, mientras que el P lo hizo en forma errática. El contenido de los otros nutrientes minerales analizados incrementó marcadamente con el tiempo de exposición a las condiciones de campo.

Palabras claves: Descomposición del mantillo (hojarasca), recuperación del ecosistema, desiertos costeros, zonas áridas, desiertos sudamericanos.

INTRODUCTION

A widely accepted general model for ecosystem functioning proposes the existance of three distinct and complementary compartments: the plant, the herbivore, and the decomposer subsystems (Swift *et al.* 1979). The decomposer compartment plays two major roles: the mineralization of essential elements and the formation of soil organic matter. In

(Received 13 July 1992; accepted 28 June 1993.)

the decomposer subsystem, the plant material is broken down by the combined action of the decomposer community (biotic decomposition) and the physical and chemical action of environmental factors such as water, radiation and wind (abiotic decomposition). Decomposition is usually understood as a change of state of a food-resource (Swift *et al.* 1979, Seastedt 1984) and its simplest expression is a decrease in dry mass through time. A considerable variation in decay rates (on a per year basis) has been found among ecosystems (Swift *et al.* 1979). Different studies have demonstrated that local variations in climate, soil topography, soil physical and chemical characteristics, and plant cover can produce different rates of organic turnover, mineralization and soil organic matter accumulations (Frankland *et al.* 1963, Santos *et al.* 1978, Seastedt & Crossley 1980, Day 1982). However, most of the present knowledge on litter decomposition comes from research conducted on mesic environments (Swift *et al.* 1979) and much of the information from arid environments is novel and controversial (Schaefer *et al.* 1985, Whitford 1986, Strojan *et al.* 1987, Moorhead & Reynolds 1989a, Steinberger *et al.* 1990).

The importance of monitoring litter decomposition in terrestrial ecosystems is not only theoretical but also practical. It is related to global desertification (Schlesinger *et al.* 1990) and to ecosystem rehabilitation (Ovalle *et al.* 1993). In Chile desertification processes in different degrees of intensity affect the intervalley areas of a large part of Coquimbo, IV Region (30° S) (Etienne *et al.* 1986). Reclamation programs have depended upon introduction of different drought-resistant shrubs and trees species, among them different species of saltbushes (*Atriplex:* Chenopodiaceae) (CONAF 1990) that have become dominant plants on the local landscape. However very little is known about the basic ecological processes in these transformed rangeland ecosystems. In this paper I review some recent ideas regarding surface litter decomposition in desert areas and their applicability to understanding litter decomposition processes and desertification in northern Chile. Additionally I report the results of a study on surface litter decomposition of three *Atriplex* species: the native *A. repanda* Phil., and the introduced *A. nummularia* Lindl. and *A. semibaccata* R. Br.

A GENERAL PARADIGM ON SURFACE LITTER DECOMPOSITION IN DESERTS

Surface litter decomposition processes in deserts are regulated and shaped by the spatial and temporal variability of the driving variables controlling these processes (Horner *et al.* 1988, Moorehead & Reynolds 1989a, b, 1991). These driving variables are litter quality (*e.g.*, C/N), the decomposers (*e.g.*, termites) and a set of abiotic decomposing factors (*e.g.*, precipitation, sunlight and heat). The next paragraphs are addressed to examine them.

Litter quality

In deserts, age as well as the chemical constituents of the plant are important factors controlling litter quality (Nelson 1970, Pieper *et al.* 1978, Khalil *et al.* 1986, Watson *et al.* 1987, Silva Colomer & Passera 1990). For instance, in eight species of grasses of south-central New Mexico (Pieper *et al.* 1978) the protein and P content, and digestibility ("toughness") declined with age. While the content of some minerals decreased over the season (*e.g.*, K, Mg, Bo, Zn, Sr), others changed little (*e.g.*, Ca, P, Mn). Forbs from the same area were high in ash, protein and lipids, but relatively low in fiber and quite variable in lignin. Nelson *et al.* (1970) found that some forbs were low in lignin at all stages of development, but others showed high levels of lignin only at maturity. Compared to grasses, forbs were also high in Ca and in P.

The N content for certain North American desert shrubs is low, leaves containing higher percentages than roots and stems (*e.g.*, *Larrea divaricata* has a 1.6% N in roots, 1.2% in stems and 2.2% in leaves) (García-Moya & McKell 1970). The green shoots of plants growing in saline soils tend to accumulate Na and Cl in addition to Ca and K. Bazilevich *et al.* (1981) report that this storage can reach values as high as 16% of dry weight in *Anabasis salsa*. They also indicate that Ca, K and S are the most abundant elements in litter in plant communities in non-saline soils.

Literature is rather scarce on research concerning the effects of plant chemistry on litter decomposition in deserts. Analyses of nine classes of defensive chemicals in plant species from Arizona and New Mexico suggest that young leaves of woody perennial may have three or more classes of toxins; whereas the annuals have two or less (Cates 1980). For carbon-based plant secondary metabolites, the relative concentration of lignin decreases from the lower to the higher end of the gradient of water availability, while that of tannin increases. According to Meentemeyer (1978), the relative control over annual decomposition rate by lignin increases along with actual evapotranspiration. Horner *et al.* (1988) state that the opposite occurs with terpenes, phenolic monomers and tannins.

The decomposers

Given the sensitivity of microflora populations to moisture constraints of the desert habitats, decomposition by macrodecomperses is thought to be the most important (Crawford 1981). In this regard, nematodes and social insects, for instance termites, are believed to have the greatest and most direct impact on the flow of energy and nutrient cycling in some deserts (Wood 1976, Whitford *et al.* 1982c, 1983, 1992, Freckman & Mankau 1977, Freckman *et al.* 1987, Freckman 1988). The feeding habits of termites make them particularly suitable for processing plant material. Decomposing litter, specially woody litter in various stages of decay is the principal source of food for many lower termites, and soil feeding behavior has been adopted as specialized habit by many species of higher termites. Plant material consumed by termites is sujected to physical and chemical transformations in the termite's gut and the minerals are returned to the ecosystem either as feces or assimilated forms either salivary excretions (carton), dead bodies or in their predators body and excreta. Predators of termites are important agents of nutrient cycling in this type of ecosystem (Fowler & Whitford 1980, Parker *et al.* 1982, Whitford *et al.* 1982b, c). In the Chihuahuan Desert, termites are the most common macroarthropods, with population densities ranging from 300,000 to 4,000,000 per hectare, depending on the soil characteristics. They can account for values of mass losses as high as 92% of creosotebush litter after one year in the field (Elkins *et al.* 1982). Their ecological importance in the nutrient and energy budgets in warm desert has been stressed in several related papers by Whitford and co-workers (Ettershank & Whitford 1980, Johnson & Whitford 1975, Parker *et al.* 1982, Whitford 1991, Whitford *et al.* 1982a, b, c, 1992a, b). Termites are very important for litter decomposition in Australian, African and Asian Deserts (WG Whitford, personal com-muniction 1992), but their importance is much lower in mediterranean climate regions than in tropical ecosystems, as the mediterranean climate becomes more isolated from tropical summer-rainfall influences (Di Castri & Di Castri 1981).

Taylor (1982), Taylor & Crawford (1982) and Crawford & Taylor (1984) have emphasized the possible role of symbiotic microorganisms inhabiting the gut of other than termites detritivores. They have shown that bacteria capable of breaking down cellulose are much more abundant in the gut of insects, such as a common gryllacridid (*Ammobaenetes* sp.) than in soil. Nevertheless, their quantitive role in nutrient cycling and the degree of commonness of this type of association is to be explored in more detail.

Along with termites, ants are the most ubiquitous group of soil macroarthropods in arid lands (Crawford 1981). Although many studies have investigated the social organization and autoecology of ants, few report on the quantitative assessments of the importance of ants in nutrient cycling and in the energy budget in deserts. It is believed that their most direct impact has to do with the conservation, localization and turnover of nutrients, especially food gathering and nutrient concentration by harvester ants (Crawford 1981). The only group that clearly affects litter decomposition in deserts belongs to the Attine group (genus *Atta* and *Trachymyrmex* in North America, WG Whitford personal communication 1992). *T. smithi,* a fungus-growing ant that occurs at low densities in northern Chihuahuan Desert, nests under *Proposis* and forages on mesquite litter (Schumacher & Whitford 1976, Wisdom & Whitford 1981). In the north-central coastal desert of Chile ants are rather scarce (Snelling & Hunt 1976) and their importance in litter dissapearance is unclear.

In the Chilean arid zone, some genera of Tenebrionidae (Coleoptera), *e.g.*, *Gyriosomus* (Cepeda-Pizarro 1989) and earthworms (Annelida) become quite active during wet years (author's observation). Tenebrionids have been recorded as feeding on aerial parts of geophytes as well as on dead standing annuals (author's observation); however, their role in this type of ecosystem needs to be evaluated.

Next to ants and termites, nematodes and microarthropods are thought to play a major role in decomposition and nutrient cycling. Microarthropod distribution and abundance in desert sites have been studied by Covarrubias *et al.* (1984), Franco *et al.* (1979), Wallwork (1972a), Wallwork (1972a, b), Steinberger and Whitford (1984), Santos *et al.* (1978), Wallwork *et al.* (1985), Cepeda-Pizarro & Whitford (1989a, b, c, 1990b). The ecology of soil microartrophods, particularly mites, has been reviewed by Seastedt (1984) and Wallwork *et al.* (1984). According to Seastedt (1984), the feeding activities of microarthropods affect mass losses much more than nutrient losses; the absolute amount of N in litter are either decreased or remain unchanged. This seems to be true in mesic habitats where oribatid mites dominate over prostigmatid mites; however, in deserts, prostigmatid mites are dominant over oribatid mites (Whitford & Parker 1989).

Several authors have stressed on the role of microartrophods as regulators of litter decomposition by affecting species composition and growth of litter microflora, standing crop of fungi, bacteria and bactivorous nematodes (Whitford & Parker 1989). Santos *et al.* (1981), Santos & Whitford (1981), Elkins & Whitford (1982), and Parker *et al.* (1984) have shown that the elimination of mites can cause significant reductions in litter decomposition and in rates of C-mineralization. Microarthropods achieve this regulation by grazing on fungi, bacteria and yeasts. These authors state that, depending upon population size, microarthropods may either stimulate mineralization rates, depress them or have no effect. Since microarthropods can be active in very dry soils (moisture potentials > –40 MPa), they tend to uncouple mineralization from abiotic constraints (Paker *et al.* 1984). This group of soil animals are also though to play a role on P-mineralization, which can be an important function since P is a limiting nutrient in some deserts (West 1981).

In deserts many processes are patchy. The ideas of island effect, the pulse paradigm and the autoecological hypothesis all concur with this view (Noy-Meir 1973, 1974, 79/80, 1981, 1984, 1987). Even though the density of microarthropods and nematodes is far below that found in soils of temperate forests, their distribution follow the general trend of patchiness. The amount of litter and soil organic matter being among the most important factors (Santos *et al.* 1978, Freckman & Mankau 1977). Manipulative experiments with simulated rainfall and litter quantity conducted by Steinberger *et al.* (1984) have shown that microflora, protozoans and microarthropods respond differentially to moisture availability and organic matter amendments. According to the same authors, water is less important than adequate organic matter for population growth of nematodes and microarthropods. No clear trends were found for bacteria, fungi and protozoans. Furthermore, after rainfall, the redistribution of moisture and concomitantly that of temperature follows the vagaries of topography, soil characteristics and other physical features of the soil surface. All of these factors can be responsible for the spatial variability in decomposition rates (Whitford *et al.* 1981b, Steinberger *et al.* 1984, Parker *et al.* 1984, Cepeda-Pizarro & Whitford 1990a).

The abiotic factors

Climate sets up the upper and the lower limits to potential decay rates, but the fine control at the local level is determined by resource quality and factors of the edaphic complex (Swift *et al.* 1979). The overall efect of macroclimate variables, mainly temperature and rainfall have been related to litter decomposition (Meentemeyer 1978, Seastedt *et al.* 1983). The effect of rainfall on decay rates is a controversial issue (Whitford *et al.* 1980, 1981a, 1982a, b, Santos *et al.* 1984, Strojan *et al.* 1987, Steinberger *et al.* 1990). Conventional wisdom holds that, in deserts, biological processes are triggered and maintained by rainfall (Noy-Meir 1984). Santos *et al.* (1984) observed that surface litter disappearance are more correlated with long term average rainfall than with actual precipitation. The opposite has been shown by Strojan *et al.* (1987).

The most important physico-chemical factors operating in deserts are soil temperature, soil water potential, salinity, pH and leaching. Leaching, especially under heavy rainfall, can play an important function at the soil surface because many decomposition curves, based on the litterbag technique, show an initial mass loss that is much higher than subsequent ones. In turn, the most important topographic features seem to be those related to slope and water runoff (Cepeda-Pizarro & Whitford 1990a) and site microtopography (Santos *et al.* 1978, Steinberger & Whitford 1983, Whitford 1992). Water runoff and solar radiation are recognized as important factors in the final mass losses in some sites (*e.g.*, steep and rocky slopes, open microsites) (Moorehead & Reynolds 1989a, b, 1991, Cepeda-Pizarro & Whitford 1990a).

MODEL USED IN PREDICTING AND MODELLING SURFACE LITTER DECOMPOSITION

In deserts, the quantification of decomposition and its relationship to environmental factors have been approached by means of the AET/lignin model (Meentemeyer 1978) and/or by regression models (Wieder & Lang 1982). The Meentemeyer's model predicts litter decomposition as a function of the actual evapotranspiration (AET) and the lignin content of the substratum. The regression models, in turn, use differential equations to describe the behavior of the relative rate of decomposition (*e.g.*, the rate of decomposition per unit mass litter) as a function of environmental parameters (*e.g.*, soil temperature, rainfall) or time.

The AET/lignin model

Meentemeyer (1978) related lignin content and actual evapotranspiration to estimate annual decomposition of surface litter. AET was chosen as an climatic index, while lignin content was considered and index of litter quality. This method have been used to estimate litter dissappearance in some North American desert sites (*e.g.*, Chihuahuan Desert), in which the technique underestimates mass losses (Whithford *et al.* 1981a, Elkins *et al.* 1982, Schaefer *et al.* 1985, Moorhead & Reynolds 1989a). The AET model has not been used in deserts from other latitudes, therefore its generality remains to be tested.

Regression models

The predictors most frequently used by regression techniques are time, rainfall, and temperature. The methods are intensively discussed in Wieder & Lang (1982), Ezcurra & Becerra (1987) and in Montaña *et al.* (1988). Montaña *et al.* (1988) found that time describes better litter dissappearance for a site with 271 mm of mean annual rainfall (arid) than for a site with 788 mm (cloud forest).

Model fitting for surface mass losses over time of several types of litter set across different topographic levels on a northern Chihuahuan desert watershed has shown that the double exponential decay model is a satisfactory descriptor of mass losses in rainy years; but the single negative exponential and the asymptotic models may become also appropiate under other conditions (Wieder & Lang 1982, Cepeda-Pizarro 1986).

Even though information regarding decomposition processes from other deserts is beginning to be available (*e.g.*, Steinberger *et al.* 1990), most of the knowledge on litter decomposition processes in arid regions is from North American deserts, particularly northern Chihuahuan desert through the Jornada Long Term Ecological Research Program. Among other desert areas, coastal deserts such as those of northern Chile become suitable "arena" for hypotesis testing in this and other fields of desert ecology.

CURRENT RESEARCH ON SURFACE LITTER CHEMISTRY IN NORTH-CENTRAL CHILE

Since 1989, a team of researchers at Universidad de La Serena has been conducting studies on litter ecology of three *Atriplex* species (*A. repanda, A. semibaccata* and *A. nummularia*) (Cepeda-Pizarro *et al.* 1992a, b), which are grown in the arid region of north-central Chile (Coquimbo, IV Region, 30° S) as forage crops for goat and sheep feeding. In this section I report preliminary results on decomposition patterns linked to surface litter of these three *Atriplex* species.

Study site and Methods

The field work was conducted in Las Cardas Agronomical Experimental Station (30°13' S, 71°13' W). The climate of the site is arid Mediterranean, having an annual rainfall average of 100-150 mm, with most of the precipitation during the winter months (May through June). The interannual rainfall variability is high (CV ca. 80%), with severe and recurrent droughts. In 1989, the year of the study, total precipitation was ca. 122.0 mm seasonally distributed as follows: 19.5 mm (fall), 100.0 mm (winter) and 2.00 mm (spring). The mean annual air temperature ranges between 11-19° C, the maximum is 26-26° C and the minimum 7-8° C. Because of the ocean proximity, cloudiness is high, the air relative humidity is between 70-80% for a large part of the year. Soils are low in organic matter and sandy loam (Table 1).

TABLE 1

Physical and chemical conditions of soil surface in the Las Cardas Agronomical Experimental Station (30°13' S, 71°13' W)

Condiciones físicas y químicas del suelo superficial de la Estación Experimental Agronómica de Las Cardas (30°13' S, 71°13'O)

Parameters	Depth (cm)	
	4.5	16.50
Texture	Sandy loam	Sandy loam
Clay (%)	12.5	11.6
Silt (%)	19.7	17.9
Sand (%)	67.7	70.6
EC (mmhos/cm)	1.4	1.0
Active pH	7.1	7.6
Total N (%)	0.1	0.5
OM (%)	1.3	0.6
C (%)	0.6	0.3
C/N	6.1	6.0
Available P (ppm)	63.4	39.1
Available K (ppm)	370.0	280.0

The plant community is dominated by the shrub *Flourensia thurifera* (Mol.) DC. (Compositae), *Gutierrezia resinosa* H. et A: Blake (Compositae) and *Heeiotropium stenophyllum* H. et A. (Boraginaceae). Subdominant shrubs are *Senna cummingii* (H. et A.) Irw. et Barnaby (Caesalpinaceae), *Baccharis* sp. (Compositae), *Senecio* sp. (Compositae) and the tree *Lithraea caustica* (Mol.) H. et A. (Anacardiaceae). Experimental plots with different *Atriplex* species are also present.

The study on surface litter decompositon and litter chemistry was conducted in one of the experimental plots planted with *A. nummularia.* The shrubs were almost 12 years old at the beginning of the study. Sets of three litterbags (10 x 10 cm, 2 mm mesh size), each confining 10 g of oven-dried (50° C) freshly collected leaves of *A repanda, A. nummularia* and A. semibaccta, were pinned under the canopy of 45 individuals of *A. nummularia* and left in the field. Groups of 5 sets of litterbags randomly selected were bimonthly retrieved for more than one year and the litter chemically analized. Standard chemical analyses were done from 0 to 330 days in the field and included total OM N, K, Na, Ca, Mg, Fe, Cu, Mn, Zn, total ash, lignin, cellulose and total fiber. Nutrient contents of the decomposing litter are expressed as percentages of the original mass.

RESULTS

Resource quality of Atriplex litter

The results reported here are from litter collected at time 0. *A. repanda* was higher in organic matter than *A. semibaccata* and *A. nummularia. A. semibaccata,* in turn, was higher in total nitrogen than *A. repanda* and *A. nummularia.* The three litter species were not different regarding their acid detergent lignin and cellulose contents. Total ash content was lower in *A. repanda* than in *A. semibaccata* and in *A. nummularia.* The litter species also differed in their Na content, being lower in *A. repanda,* but not in the remaining nutrients (Table 2).

TABLE 2

Average nutrient contents (%DM) of summer collected leaf-material of three species of saltbushes (*Atriplex* spp.) in a mediterranean arid ecosystem of northern Chile (Las Cardas Agronomical Experimental Station, 30°13' S, 71°13' W)

Contenido promedio de nutrientes (%MS) en material foliar colectado en verano de tres especies de pasto salado (*Atriplex* spp.) en un ecosistema mediterráneo árido del norte de Chile (Estación Experimental Agronómica de Las Cardas, 30°13' S, 71°13' O)

	Plant species			
Parameters	*A. repanda*	*A. semibaccata*	*A. nummularia*	$p < 0.05$
Organic mater	82.1 (1.3)	78.1 (0.9)	77.6 (0.5)	*
Total N	2.8 (0.4)	3.9 (0.6)	2.6 (0.2)	*
Acid detergent fiber	16.2 (0.9)	13.7 (1.1)	16.0 (0.9)	*
Acid detergent lignin	5.3 (1.0)	4.7 (1.0)	6.7 (1.2)	ns
Cellulose	10.9 (1.7)	9.0 (1.9)	9.3 (1.9)	ns
Total ash	17.9 (1.3)	21.9 (1.0)	22.4 (0.5)	*
Na	1.1 (0.4)	2.5 (1.1)	2.8 (0.4)	*
K	0.9 (0.3)	1.1 (0.4)	1.0 (0.2)	ns
Ca	0.7 (0.2)	0.6 (0.2)	0.5 (0.1)	ns
Mg	0.4 (0.1)	0.5 (0.1)	0.4 (0.1)	ns
Cu	8.4 (4.0)	11.0 (6.1)	7.2 (1.8)	ns
Zn	63.8 (11.5)	53.0 (11.0)	47.1 (8.6)	*
Fe	167.8 (101.6)	346.9 (194.5)	174.5 (24.9)	*
Mn	44.6 (13.6)	35.1 (20.6)	26.8 (3.8)	ns

Numbers in parenthesis correspond to ± t SE (95%).
Números en paréntesis corresponden a ± t EE (95%).

Surface litter decomposition

For many litter constituents losses are generally high during the first year followed by lower rates at longer periods. These changes are provoked by mechanical weathering, leaching, cellular decay or microbial inmobilization. In this study and after one year in the field, there were accumulations of inorganic constituents (*e.g.*, Na, K, Cu, Ca, Mg, Figs. 1-3). Zn initially accumulated (0-180 d) and then decreased (180-330 d), while P was erratic. In the absence of comparative data, these results must be interpreted with caution. Increases in the concentrations of inorganic nutrients indicate accumulations from the environment. Actual rainfall recorded during the year of the study was near to the lower end of annual

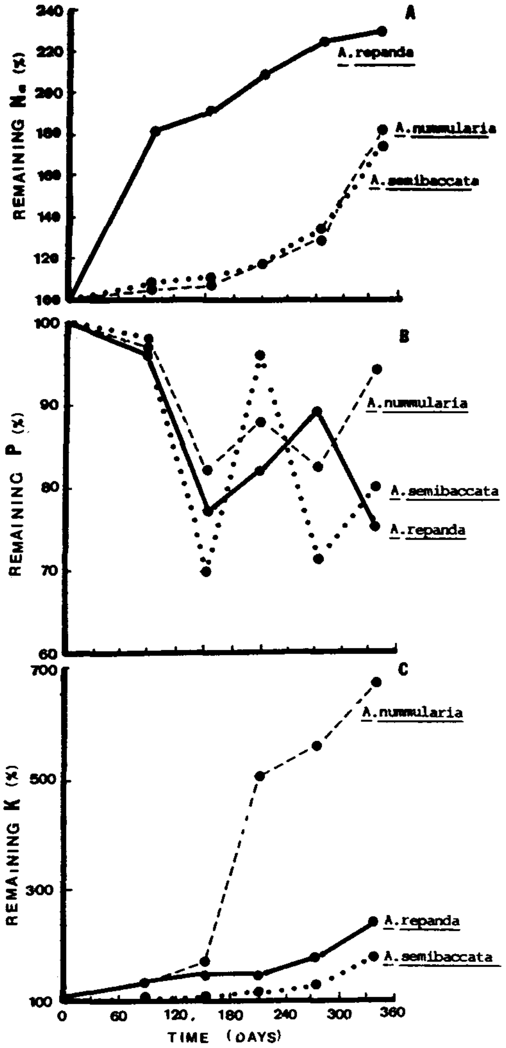

Fig. 1: Changes in litterbag contents of Na (A), P (B), and K (C) of *Atriplex repanda, A. semibaccata,* and *A. nummularia* installed in La Cardas Experimental Station (30° 13' S, 71° 13' W, Chile). Each value is the mean percentage of the initial litterbag content remaining at the end of each interval (n = 5 per date). The values were determined by multiplying the concentration of a constituent in a sample by the dry mass remaining and expressing the product as a percentage of the original content of litterbags placed in the field on 25 March 1988.

Cambios en el contenido de Na (A), P (B) y K (C) en sacos de hojarasca de *Atriplex repanda, A. semibaccata* y *A. nummularia* instalados en la Estación Experimental Las Cardas (30° 13' S, 71° 13' W, Chile). Cada valor es el promedio porcentual del contenido inicial del nutriente que permanece al término de cada intervalo (n = 5 sacos por fecha de muestreo). Estos valores se obtuvieron multiplicando la concentración de un constituyente dado en la muestra por la masa que permanece y luego expresando este producto como porcentaje del contenido original de los sacos instalados en el terreno el 25 de marzo de 1988.

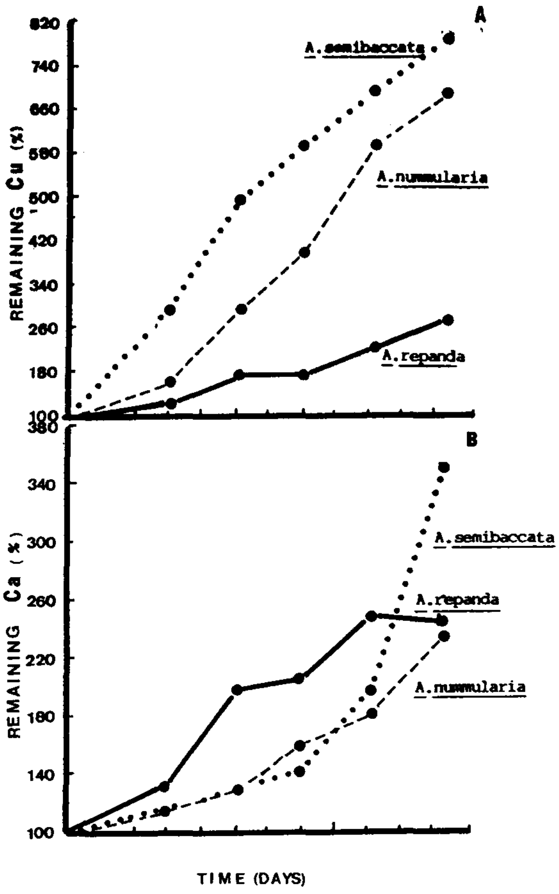

Fig. 2: Changes in litterbag contents of Cu (A) and Ca (B) of *Atriplex repanda, A. semibaccata,* and *A. nummularia* installed in La Cardas Experimental Station (30° 13' S, 71° 13' W, Chile). Values obtained as those in Fig. 1.

Cambios en el contenido de Cu (A) y Ca (B) en sacos de hojarasca de *Atriplex repanda, A. semibaccata* y *A. nummularia* instalados en la Estación Experimental Las Cardas (30° 13' S, 71° 13' W, Chile). Valores obtenidos como los de la Fig. 1.

mean, but neither the small rainy events nor the fog, which is abundant in the site for most of the year, seem to have provoked enough leaching as to reduce the inorganic content of the litter. The area is windy and dust deposition inside the litterbags could have occurred. Nevertheless, increases in nutrients as litter decomposes are also reported from less xeric environments (Baker & Attiwill 1985, Klemmedson 1992). Changes in organic constituents (*e.g.*, lignin and cellulose) were from nill to moderate. Species series from higher to lower losses of cellulose was *A.*

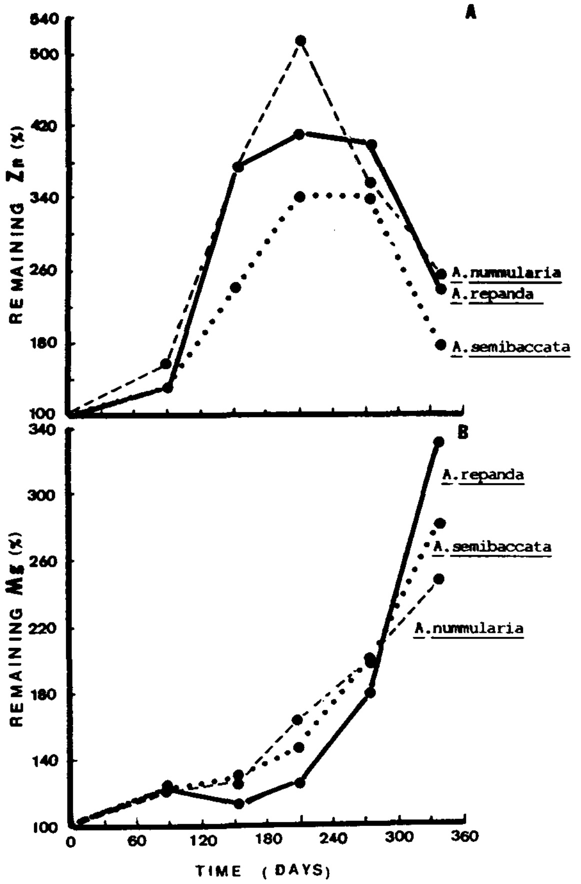

Fig. 3: Changes in litterbag contents of Zn (A) and Mg (B) of *Atriplex repanda, A. semibaccata,* and *A. nummularia* installed in La Cardas Experimental Station (30° 13' S, 71° 13' W, Chile). Values obtained as those in Fig. 1.

Cambios en el contenido de Zn (A) y Mg (B) en sacos de hojarasca de *Atriplex repanda, A. semibaccata* y *A. nummularia* instalados en la Estación Experimental Las Cardas (30° 13' S, 71° 13' W, Chile). Valores obtenidos como los de la Fig. 1.

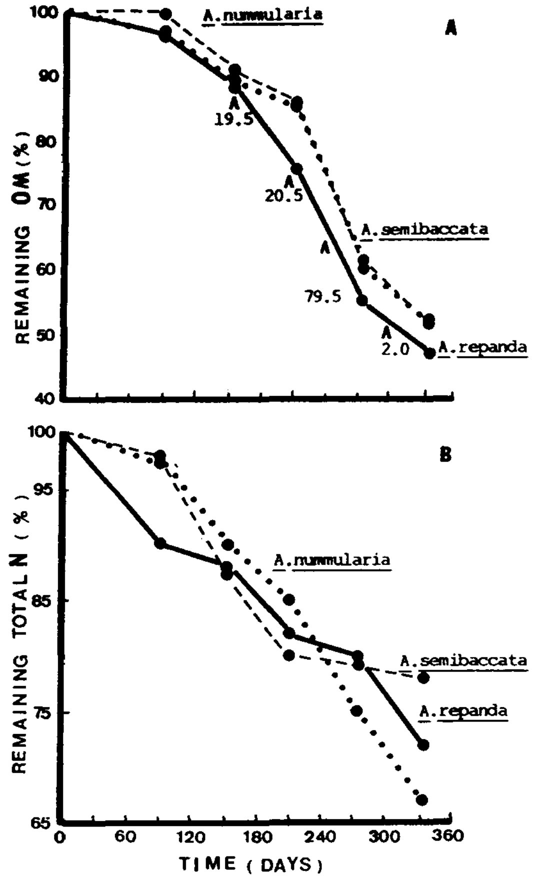

Fig. 4: Changes in litterbag contents of OM (A) and total N (B) of *Atriplex repanda, A. semibaccata,* and *A. nummularia* installed in La Cardas Experimental Station (30° 13' S, 71° 13' W, Chile). Values obtained as those in Fig. 1.

Cambios en el contenido de MO (A) y N total (B) en sacos de hojarasca de *Atriplex repanda, A. semibaccata* y *A. nummularia* instalados en la Estación Experimental Las Cardas (30° 13' S, 71° 13' W, Chile). Valores obtenidos como los de la Fig. 1.

repanda > *A. semibaccata* > *A. nummularia.* Lignin content decreased less than celullose, in this case the sequency was *A. semibaccata* > *A. repanda* and *A. nummularia* (Fig. 4).

The litter of the three species showed similar patterns of OM and total N losses. After 330 d, the average loss of OM was about 50% and total N was ca. 17% (Fig. 5A). Several authors (cited by Schlesinger & Hasey 1981) have reported accumulations of N in decomposing litter due to absorption from atmospheric precipitation, contaminating debris or import of nitrogen in fungal hyphae. In the absence of a significant atmospheric precipitation of N and contamination by organic debris, the results suggest very low fungal colonization and microbial activity in the litter bags. This, however, must be examined more closely. Total mass losses were higher in *A. repanda* than in *A. nummularia* and in *A. semibaccata* (Fig. 5); however, the range (11-18%) is among the lowest reported in the literature (Table 3). Similar values have also been found in decomposition studies using wheat straw and conducted in sites of the Judean Desert (Steinberger *et al.* 1990) with rainfall

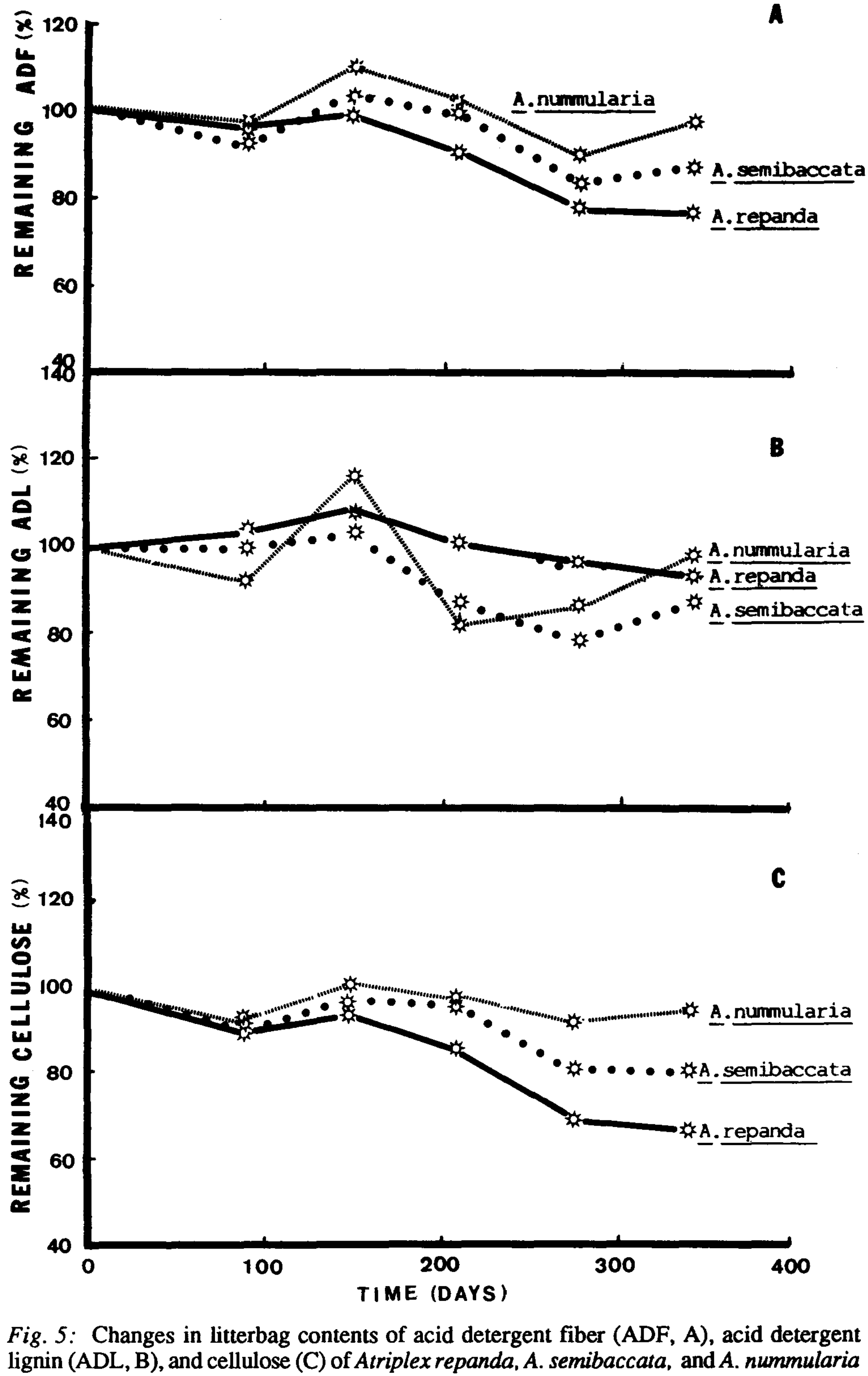

Fig. 5: Changes in litterbag contents of acid detergent fiber (ADF, A), acid detergent lignin (ADL, B), and cellulose (C) of *Atriplex repanda*, *A. semibaccata*, and *A. nummularia* installed in La Cardas Experimental Station (30° 13' S, 71° 13' W, Chile). Values obtained as those in Fig. 1.

Cambios en el contenido de fibra detergente ácida (FDA, A), lignina detergente ácida (LDA, B) y celulosa (C) en sacos de hojarasca de *Atriplex repanda*, *A. semibaccata* y *A. nummularia* instalados en la Estación Experimental Las Cardas (30° 13' S, 71° 13' W, Chile). Valores obtenidos como los de la Fig. 1.

TABLE 3

Summary of data on initial surface mass losses from litterbags studies conducted in different desert sites

Resumen de la información sobre pérdidas iniciales de masa obtenidas de estudios con sacos de hojarasca en diferentes áreas desérticas

Desert site	Litter species	Days in the field	% mass loss	Reference
Mapimí (Southern Chihuahuan Desert)	*Sporobolus airoides*	359	50	Montaña *et al.* (1988)
Naaka Junction (Judean Desert)	Wheat straw	313	17	Steinberger *et al.* (1990)
Metzukei Dragot (Judean Desert)	Wheat straw	313	22	Steinberger *et al.* (1990)
Gruya (Judean Desert)	Wheat straw	313	16	Steinberger *et al.* (1990)
Carlsbad (Northern Chihuahuan Desert)	*Larrea tridentata*	365	93	Steinberger *et al.* (1990)
Carlsbad (Northern Chihuahuan Desert)	*Quercus harvardii*	365	20	Steinberger *et al.* (1990)
Carlsbad (Northern Chihuahuan Desert)	Mixed grasses (*B. eriopoda, S. brevifolia*)	365	21	Steinberger *et al.* (1990)
Rock Valley (Mojave Desert)	*Larrea tridentata*	378	43	Strojan *et al.* (1987)
Rock Valley (Mojave Desert)	*Ambrosia dumosa*	378	58	Strojan *et al.* (1987)
Rock Valley (Mojave Desert)	*Lycium pallidum*	378	63	Strojan *et al.* (1987)
Jornada (Northern Chihuahuan Desert)	*Yucca elata*	365	64	Schaefer *et al.* (1985)
Jornada (Northern Chihuahuan Desert)	*Chilopsis linearis*	365	77	Schaefer *et al.* (1985)
Jornada (Northern Chihuahuan Desert)	*Prosopis glandulosa*	365	31	Schaefer *et al.* (1985)
Jornada (Northern Chihuahuan Desert)	*Larrea tridentata*	365	35	Schaefer *et al.* (1985)
Jornada (Northern Chihuahuan Desert)	*Flourensia cernua*	365	41	Schaefer *et al.* (1985)
Jornada (Northern Chihuahuan Desert)	Annuals	365	62	Schaefer *et al.* (1985)
Jornada (Northern Chihuahuan Desert)	*Larrea tridentata*	350	45	Cepeda-Pizarro & Whitford (1989)
Jornada (Northern Chihuahuan Desert)	*Panicum obtusum*	360	40	Cepeda-Pizarro & Whitford (1989)
Jornada (Northern Chihuahuan Desert)	*Prosopis glandulosa*	350	43	Cepeda-Pizarro & Whitford (1989)
Jornada (Northern Chihuahuan Desert)	*Baileya multiradiata*	350	60	Cepeda-Pizarro & Whitford (1989)
Jornada (Northern Chihuahuan Desert)	*Erioneuron pulchellum*	350	58	Cepeda-Pizarro & Whitford (1989)
Jornada (Northern Chihuahuan Desert)	*Bouteloua eriopoda*	350	34	Cepeda-Pizarro & Whitford (1989)
Las Cardas (Sourthern Chilean Desert)	*Atriplex repanda*	330	18	This study
Las Cardas (Southern Chilean Desert)	*Atriplex semibaccata*	330	11	This study
Las Cardas (Southern Chilean Desert)	*Atriplex nummularia*	330	16	This study

comparable to our Chilean site. The lower values found in this study as compared to those reported from hot deserts (Table 3) for the may be due to the lower soil temperatures and UV radiation of the more temperate Chilean site.

CONCLUSIONS

From this and the other works mentioned in the former paragraphs, some generalizations, which may become working hypotheses in other desert sites, can be stated as follows: (1) owing to moisture limitation on microbial activity, detritivorous organisms, mainly arthropods, may play an important role in surface litter decomposition, (2) microbial decomposition of litter and wood at or near the soil surface must be restricted to periods of water availability, (3) a large proportion of nutrients is attached to the soil surface, (4) mass losses from surface litter display the seasonal influences of rainfall and related phenomena (*e.g.*, water runoff). In coastal deserts, because of frequent cloudy cover, abiotic decomposition (*e.g.*, due to high temperature and UV radiation) must be attenuated; initial mass losses from surface litter must be low, and litter accumulations under shrubs increases inorganic constituents as a consequence of dust deposition, reduced leaching of soluble constituents and low decomposition rates. Finally, whether or not decomposition rate is dependent on actual or long term mean annual rainfall is an open field for further research.

ACKNOWLEDGMENTS

This work has partially been supported by FONDECYT Nº 1214/88-89, DIULS 130.2.42, Fundación Andes and OAS scholarships to JG Cepeda-Pizarro and by research grant from the US National Science Foundation: the Jornada-LTER BSR 8114466 and BSR 821539 to WG Whitford. I would like to tank to J.R. Gutiérrez for his comments throughout the writing of this paper and two anonymous reviewers whose comments greatly improved the paper. The use of Las Cardas Agronomical Experimental Station has been possible due to the kind permission granted by the Centro de Estudios de Zonas Aridas (CEZA) of Universidad de Chile.

LITERATURE CITED

BAZILEVICH NI, BA BAYKOV, LJ KUROCHKINA (1981) Cycles of mineral elements. In: Goodall DW, RA Perry & KMW Howes (eds) Arid Land Ecosystems. Structure, Functioning and Management. IBP 17. Vol. 2: 183-188. Cambridge University Press, London.

BAKER TG & PM ATTIWILL (1985) Loss of organic matter and elements from decomposing litter of *Eucalyptus obliqua* L'Herit. and *Pinus radiata* D. Don. Australian Forestry Research 15: 309-319.

CATES RG (1980) Feeding patterns of monophagous and polyphagous insect herbivores. The effect of resource abundance and plant chemistry. Oecologia 46: 22-31.

CONAF (1990) Plantaciones CONAF y privados en la IV Región. Corporación Nacional Forestal. Departamento Técnico. Programa Control Forestal. IV Región.

CEPEDA-PIZARRO JG (1986) Spatial and temporal patterns of decomposition and microarthropod assemblages in decomposing surface leaf-litter on a Chihuahuan Desert watershed. Ph. D. Dissertation. New Mexico State University, Las Cruces, New Mexico, USA, 245 pp.

CEPEDA-PIZARRO JG, MA ROJAS, MB MALDONADO, J VILCHES & N PEREIRA (1992a) Effect of season, substrate quality, litter quality and soil conditions on edaphic microarthropods in a coastal desert site of north-central Chile. Revista Chilena de Historia Natural 65 (1): 65-74.

CEPEDA-PIZARRO JG, MA ROJAS, MB MALDONADO, J VILCHES & N PEREIRA (1992b) A litter-bag study of mite densities (Actinedida and Oribatida) in *Atriplex* litter and soil of a desert site in northern Chile. Journal of Arid Environments 23: 177-188.

CEPEDA-PIZARRO JG & WG WHITFORD (1990a) Decomposition patterns of surface leaf-litter of six plant species along a transect in a northern Chihuahuan Desert watershed. Americal Midland Naturalist 123: 319-330.

CEPEDA-PIZARRO JG & WG WHITFORD (1990b) Microartrópodos edáficos del Desierto Chihuahuense, al norte de México. Folia Entomológica Mexicana 78: 257-272.

CEPEDA-PIZARRO JG (1989) Actividad temporal de tenebriónidos epígeos y efectos de la manipulación de la vegetación arbustiva en un ecosistema árido-costero del norte de Chile. Revista Chilena de Historia Natural 62 (1): 115-128.

CEPEDA-PIZARRO JG & WG WHITFORD (1989a) The relationships between abiotic factors and the abundance patterns of soil microarthropods on a desert watershed. Pedobiología 33: 76-86.

CEPEDA-PIZARRO JG & WG WHITFORD (1989b) Spatial and temporal variability of higher microarthropod taxa along a transect in a northern Chihuahuan desert watershed. Pedobiología 33: 101-111.

CEPEDA-PIZARRO JG & WG WHITFORD (1989c) Species abundance distribution patterns of soil microarthropods in decomposing surface leaf-litter and mineral soil on a desert watershed. Pedobiología 33: 254-268.

COVARRUBIAS R, I RUBIO, F DI CASTRI (1964) Observaciones ecológico-cuantitativas sobre la fauna edáfica de zonas semiáridas del norte de Chile (Provincias de Coquimbo y Aconcagua). Boletín de Producción Animal. Serie A: Monografías sobre Ecología y Biogeografía de Chile Nº 2, Universidad de Chile, Santiago, Chile.

CRAWFORD CS & EC TAYLOR (1984) Decomposition in arid environments: role of detritivores gut. South African Journal Science 80 (4): 170-176.

CRAWFORD CS (1981) Biology of desert invertebrates. Springer-Verlag, New York.

DAY Jr F (1982) Litter decomposition rates in the seasonally flooded Great Dismal Swamp. Ecology 63 (3): 670-678.

DI CASTRI, F & V DI CASTRI (1981) Soil fauna of mediterranean climate regions. In: Di Castri F DW Goodall & RL Specht (eds.) Mediterranean-Type shrublands. Series Ecosystems of the World, Vol. 11: 445-478. Elvesier Scientific Publications Company, NY.

ELKINS NZ, Y STEINBERGER & WG WHITFORD (1982) Factors affecting the applicability of the AET model for decomposition in arid environments. Ecology 63 (2): 579-580.

ELKINS NZ & WG WHITFORD (1982) The role of microarthropods and nematodes in decomposition in a semiarid ecosystem. Oecologia, 55: 303-310.

ETTERSHANK G & WG WHITFORD (1980) Location of food resources by subterranean termites. Environmental Entomology 9: 645-248.

ETTIENE M, L FAUNDEZ & J VALDES (1986) Evaluación de la tasa de desertificación en la zona árida de Chile central. Ambiente y Desarrollo. Vol. II (2): 105-112.

EZCURRA E & J BECERRA (1987) Experimental decomposition of litter from the tamaulipan cloud forest: A comparison of four simple models. Biotropica 19 (4): 290-296.

FOWLER HG & WG WHITFORD (1980) Termites, microarthropods and the decomposition of senescent and fresh creosote bush (*Larrea tridentata*) leaf litter. Journal of Arid Environments 3: 63-68.

FRANCO PJ, EB EDNEY & JF McBRAYER (1979) The distribution and abundance of soil arthropods in the northern Mojave Desert. Journal of Arid Environments 2: 137-149.

FRANKLAND JC, JD OVINGTON & C MACRAE (1963) Spatial and seasonal variations in soil litter and ground vegetation in some lake district woodlands. Journal of Ecology, 5: 97-112.

FRECKMAN DW & R MANKAU (1977) Distribution and trophic structure of nematodes in desert soils. In: Lohm U & T Persson (eds) Soil Organisms as Components of Ecosystems. Ecological Bulletin 25: Proceedings IV International Soil Zoology Colloquium: 511-514. International Society Soil (ISSS), London.

FRECKMAN DW, WG WHITFORD & Y STEINBERGER (1987) Effect of irrigation on nematode population dynamics and activity in desert soil biology. Biology & Soil Fertility 3: 3-10.

FRECKMAN DW (1988) Bacterivorous nematodes and organic matter decomposition. Agriculture, Ecosystems and Environment 24: 195-217.

HORNER JD, JR GOSZ & RG GATES (1988) The role of carbon-based plant secondary metabolites in decomposition in terrestrial ecosystem. The American Naturalist 132 (3): 869-883.

JOHNSON KA & WG WHITFORD (1975) Foraging ecology and relative importance of subterranean termites in Chihuahuan Deset ecosystems. Environmental Entomology 4: 66-70.

KHALIL JK, WH SAWAYA & SZ HYDER (1986) Nutrient composition of *Atriplex* leaves grown in Saudi Arabia. Journal of Range Management 39: 104-108.

KLEMMEDSON JO (1992) Decomposition and nutrient release from mixtures of gambel oak and ponderosa pine leaf litter. Forest Ecology and Management 47: 349-361.

MEENTMEYER V (1978) Macroclimate and lignin content of litter decomposition rates. Ecology 59: 465-472.

MONTAÑA C, E EZCURRA, A CARRILLO & JP DELHOUME (1988) The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments. Journal of Arid Environments 14: 55-60.

MOORHEAD DL & JF REYNOLDS (1989a) Mechanisms of surface litter mass loss in the northern Chihuahuan Desert: a reinterpretation. Journal of Arid Environments 16: 157-163.

MOORHEAD DL & JF REYNOLDS (1989b) The contribution of abiotic processes to buried litter decomposition in the northern Chihuahuan Desert. Oecologia 79: 133-135.

MOORHEAD DL & JF REYNOLDS (1991) A general model of litter decomposition in the northern Chihuahuan Desert. Ecological Modelling 56: 197-219.

NELSON AB, CH HERBEL & HM JACKSON (1970) Chemical composition of forage species grazed by cattle on an arid New Mexico range. Agricultural Experimental Station Bulletin 561. New Mexico State University, Las Cruces NM, USA.

NOY-MEIR I (1973) Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics 4: 25-51.

NOY-MEIR I (1974) Desert ecosystems: higher trophic levels. Annual Review of Ecology and Systematics 5: 195-214.

NOY-MEIR I (1979/80) Structure and function of desert ecosystems. Israel Journal of Botany 28: 1-19.

NOY-MEIR I (1981) Spatial effects in modelling of arid ecosystems. In: Goodall DW, RA Perry and KMW Howes (eds) Arid Land Ecosystems. Structure, Functioning and Management. IBP 17. Vol. 2: 411-432. Cambridge University Press, London.

NOY-MEIR I (1984) Desert ecosystem structure and function. In: Goodall DW (ed) Hot deserts and arid shrublands. Ecosystems of the world (Vols. 12A, B) (Ch. 7): 93-103. Elvesier Scientifc Pub., New York.

OVALLE C, J ARONSON, J AVENDAÑO, R MENESES & R MORENO (1993) Rehabilitation of degraded ecosystems in central Chile and its relevance to the arid "Norte Chico". Revista Chilena de Historia Natural.

PARKER LW, HG FOWLER G ETTERSHANK & WG WHITFORD (1982) The effects of subterranean termite removal on desert nitrogen and ephemeral flora. Journal of Arid Environments 5: 53-59.

PARKER LW, DW FRECKMAN, Y STEINBERGER, L DRIGGERS & GW WHITFORD (1984) Effects of simulated rainfall on desert soil biota: soil respiration, microflora and protozoa. Pedobiologia 27: 185-195.

PIEPER RD, AB NELSON, G STANLEY SMITH, EP PARKER, EJA BOGGINO & CF HATCH (1978) Chemical composition and digestibility of important range grass species in south-central New Mexico. Agricultural Experimental Station Bulletin 15. New Mexico State University, Las Cruces NM, USA.

SANTOS PF, E DEPREE, WG WHITFORD (1978) Spatial distribution of litter and microarthropods in a Chihuahuan Desert ecosystem. Journal of Arid Environments 1: 41-48.

SANTOS PF, J PHILIPS, WG WHITFORD (1981) The role of mites and nematodes in early stages of buried litter decomposition in a desert. Ecology 62 (3): 664-669.

SANTOS PF & WG WHITFORD (1981) The effects of microarthropods on litter decomposition in a Chihuahuan Desert ecosystem. Ecology 62 (3): 654-663.

SANTOS PF, NZ ELKINS, Y STEINBERGER & WG WHITFORD (1984) A comparison of surface and buried *Larrea tridentata* leaf litter decomposition in North American deserts. Ecology 65 (1): 278-284.

SCHAEFER D, Y STEINBERGER & WG WHITFORD (1985) The failure of nitrogen and lignin control of decomposition in a North American desert. Oecologia 65: 382-386.

SCHLESINGER WH & MM HASEY (1981) Decomposition of chaparral shrub foliage: losses of organic and inorganic constituents from deciduous and evergreen leaves. Ecology 62 (3): 62-774.

SCHLESINGER WH, JF REYNOLDS, GL CUNNINGHAM, LF HUENNEKE, WM JARREL, RA VIRGINIA & WG WHITFORD (1990) Biological feedbacks in global desertification. Science 247: 1043-1048.

SCHUMACHER A & WG WHITFORD (1976) Spatial and temporal variation in Chichuahuan Desert and faunas. Southwestern Naturalist 21: 1-8.

SEASTEDT TR (1984) The role of microarthropods in decomposition and mineralization processes. Annual Review of Entomology 29: 25-46.

SEASTEDT TR & DA CROSSLEY JR (1980) Effects of microarthropods on the seasonal dynamics of nutrients in forest litter. Soil Biology & Biochemistry 12: 337-42.

SEASTEDT TR, DA CROSSLEY JR, V MEENTMEYER & JB WAIDE (1983) A two-year study of leaf litter decomposition as related to microclimatic factors and microarthropods abundance in the southern appalachians. Holartic Ecology 6: 11-16.

SILVA COLOMER J & CB PASSERA (1990) The nutritional value of *Atriplex* spp. as fodder for arid regions. Journal of Arid Environments 19: 289-295.

SNELLING, RR & JH HUNT (1975) The ants of Chile (Hymenoptera: Formicidae). Revista Chilena de Entomología 9: 63-129.

STEINBERGER Y & WG WHITFORD (1983) The contribution of rodents to decomposition processes in a desert ecosystem. Journal of Arid Environments 6: 177-181.

STEINBERGER Y, DW FRECKMAN, LW PARKER & WG WHITFORD (1984) Effects of simulated rainfall and litter decomposition quantities on desert biota: nematodes and microarthropods. Pedobiologia 26: 267-274.

STEINBERGER Y & WG WHITFORD (1984) Spatial and temporal relationships of soil microarthropods on a watershed. Pedobiologia 26: 275-284.

STEINBERGER Y, A. SHMIDA & WG WHITFORD (1990) Decomposition along a rainfall gradient in the Judean desert, Israel. Oecologia 82: 322-324.

STROJAN CL, DC RANDALL & FB TURNER (1987) Relationships of leaf litter decomposition rates to rainfall in the Mojave Desert. Ecology 68 (3): 741-744.

SWIFT MJ, OW HEAL, JM ANDERSON (1979) Decomposition in terrestrial ecosystems. Oxford Blackwell Scientific. London.

TAYLOR EC (1982) Role of microbially acquired enzymes in digestion of cellulose by desert millipeds. Applied Environmental Microbiology 44: 281-291.

TAYLOR EC & CS CRAWFORD (1982) Microbial gut symbionts and desert detritivores. Science Review Arid Zone Research 1: 37-52.

WALLWORK JA (1972a) Mites and other microarthropods from the Joshua Tree National Monument, California. Journal of Zoology 168: 91-105.

WALLWORK JA (1972b) Distribution patterns and population dynamics of microarthropods of a desert soil in southern California. Animal Ecology 41: 291-310.

WALLWORK JA, BW KAMILL & WHITFORD (1984) Life styles of desert soil microarthropods: A Re-appraisal. South African Journal of Science 80: 163-169.

WALLWORK JA, BW KAMILL & WG WHITFORD (1985) Distribution and diversity patterns of soil mites and other microarthropods in a Chihuahuan Desert site. Journal of Arid Environments 9: 215-231.

WATSON MC, JW O'LEARLY & ED GLENN (1987) Evaluation of *Atriplex lentiformis* (Torr.) S: Wats. and *A. nummularia* Lindl. as irrigated forage crops. Journal of Arid Environments 13: 293-303.

WEST NE (1981) Nutrient cycling in desert ecosystems. In: Goodall DW, RA Perry & KMW Howes (eds) Arid Land Ecosystems: Structure, Functioning and Management. IBP 17. Vol. 2: 301-324. Cambridge University Press. London.

WHITFORD WG, M BRYANT, G ETTERSHANK, J ETTERSHANK & PF SANTOS (1980) Surface litter breakdown in a Chihuahuan Desert ecosystem. Pedobiologia 4: 243-245.

WHITFORD WG, V MEETEMEYER, TR SEASTEDT, K CROMACK JR, DA CROSSLEY JR, PF SANTOS, RL TODD & JB WAID (1981a) Exceptions to the AET model: deserts and clear-cut forests. Ecology 62: 275-277.

WHITFORD WG, DG FRECKMAN, NZ ELKINS, LW PARKER, R PARMALEE, J PHILLIPS & S TUCKER (1981b) Diurnal migration and response to simulated rainfall in desert biota microarthropods and nematodes. Soil Biology & Biochemistry 13: 417-425.

WHITFORD WG, R REPASS, LW PARKER, NZ ELKINS (1982a) Effects of initial litter accumulations and climate on litter dissappearance in a desert ecosystem. The American Midland Naturalist 108 (1): 105-110.

WHITFORD GW, R PASS, LW PARKER, NZ ELKINS (1982b) Litter dissapearance in a desert ecosystem. The American Midland Naturalist 108 (1): 105-110.

WHITFORD WG, Y STEINBERGER & G ETTERSHANK (1982c) Contributions of subterranean termites to the economy of Chihuahuan Desert ecosystems. Oecologia, 55: 298-302.

WHITFORD WG (1986) Decomposition and nutrient cycling in deserts. In: Whitford WG (ed) Pattern and Process in Desert Ecosystems (Ch. 5): 93-117. University of New Mexico, NM, USA.

WHITFORD WG, DW FRECKMAN, LW PARKER, D SCHAEFER, PF SANTOS (1983) The contributions of soil fauna to nutrient cycles in desert systems. Proceeding of the VIII International Colloquium of Soil Zoology.

WHITFORD WG & LW PARKER (1989) Contributions of soil fauna to decomposition and mineralization processes in semiarid and arid ecosystems. Arid Soil Research and Rehabilitation 3: 199-215.

WHITFORD WG, JA LUDWIG, JC NOBLE (1992) The importance of termites in semiarid ecosystems in south-eastern Australia. Journal of Arid Environments 22: 87-91.

WHITFORD WG (1993) Animal feedbacks in desertification: an overview. Revista Chilena de Historia Natural.

WISDOM WA & WG WHITFORD (1981) Effects of vegetation change on ant community of arid rangeland. Environmental Entomology 10 (6): 893-897.

WIEDER RK & GE LANG (1982) A critique of the analytical methods used in examining decomposition data obtained from litter bags. Ecology 63 (6): 1636-1642.

WOOD TG (1976) The role of termites (Isoptera) in decomposition processes. In: Anderson JM & A MacFadyen (eds) The role of terrestrial and aquatic organisms in decomposition processes. The 17th Symposium British Ecology Society (1975). Oxford Blackwell Scientific, London.