

Copyright Notice

This electronic reprint is provided by the author(s) to be consulted by fellow scientists. It is not to be used for any purpose other than private study, scholarship, or research.

Further reproduction or distribution of this reprint is restricted by copyright laws. If in doubt about fair use of reprints for research purposes, the user should review the copyright notice contained in the original journal from which this electronic reprint was made.

The decomposition of litter in grasslands of northern Mexico: a comparison between arid and non-arid environments

Carlos Montaña*, Exequiel Ezcurra*, Antonio Carrillo* & J.P. Delhoume*†

Accepted 4 February 1987

The mass loss of grass litter was studied in two climatically contrasted zones: the Bolson de Mapimi (Chihuahuan Desert, annual rainfall 271 mm) and La Michilia (Western Sierra Madre pine-oak forest, annual rainfall 788 mm). Plastic grass litter bags were placed on the ground and collected periodically over 29 months, dried, weighed and analysed for carbon and nitrogen. The dry mass data were fitted to time, rainfall and temperature as independent variables, using differential equation models that assume constant or variable decomposition rates.

The overall velocity of decomposition was strongly correlated with the proportion of leaves and stems in the initial litter. In La Michilia, decomposition rates decreased as the litter disappeared. Weight loss was found to be associated more with temperature and rainfall than with time, and the C:N ratio decreased strongly as decomposition progressed. In Mapimi, on the other hand, decomposition rates did not decrease so strongly as litter disappeared; time was found to be an adequate predictor of mass loss, and the C:N ratio was more constant. It is concluded that abiotic factors (physical weathering) are responsible for a large portion of the mass loss of grass litter in arid environments.

Introduction

Surface litter goes through a series of transformations that include physical fragmentation, the elaboration and subsequent leaching of hydrosoluble compounds and the elimination of some products of mineralisation before it is incorporated into the soil profile. The dynamics of this stage in the disappearance of surface litter are little known, particularly in arid environments. Authors who have approached this question (e.g. Saito, 1957, 1965; Kendrick & Burges, 1962; Zlotin & Khodashova, 1980; Ludwig & Whitford, 1981; West, 1981; Noy Meir, 1985) have mentioned both biotic (micro-organisms, mesofauna) and abiotic factors (solar radiation, temperature, rainfall, composition of the lower layers of the atmosphere) as being important elements that influence this process. In this paper we report data that permit the relative importance of biotic and abiotic factors in the decomposition of grass surface litter in arid and semi-arid environments to be explored.

Methods

The study area

The study was performed simultaneously in the Biosphere Reserves of Mapimi (Chihuahuan Desert, 26° 40' N, 103° 40' W, altitude 1100 m, annual rainfall 271 mm, mean annual

* Instituto de Ecología, Apartado 18-845, 11800 Mexico, D.F., Mexico.

† ORSTOM, 213 rue Lafayette, 75010 Paris, France.

temperature 20°C) and La Michilia (Western Sierra Madre, 23° 30'N, 104° 20'W, altitude 2300 m, annual rainfall 788 mm, mean annual temperature 11.5°C). In Mapimi, where vegetation consists mainly of scrub-type communities and *playa* grasslands, the mass losses of *Hilaria mutica* (Buckl.) Benth. and *Sporobolus airoides* (Torr.) Torr. litter were followed on two sites dominated by each of the respective species and from which grazing had been excluded since 1981. In La Michilia, where the vegetation is formed of a mosaic of pine-oak forests and grasslands, the mass losses of *Elyonurus barbiculmis* Hack. and *Aristida schiedeana* Trin. et Rupr. were followed on a site dominated by these two species together with *Muhlenbergia rigida* (H.B.K.) Kunth. and where grazing had been excluded since 1982.

Sampling design

During May 1982, samples of recently dead material of each of the above species were collected, air dried and placed in plastic litter bags (17 × 17 cm, mesh size 2 mm, 10 g litter per bag). The bags were placed randomly in the different study sites and fixed to the soil surface with metallic pegs. Three randomly selected bags were harvested at irregular intervals over 29 months (Fig. 1). The material collected was washed with a 0.3 mm sieve to eliminate soil, oven dried at 65°C, weighed and then milled until the size of the particles was less than 0.25 mm. Percentage nitrogen and carbon were determined for some of the samples (Table 1). Rainfall and temperature were obtained from standard meteorological stations in both reserves.

Decomposition models

The quantitative aspects of the decomposition process and its relationship to environmental variables were approached through the fitting of a theoretical mathematical model

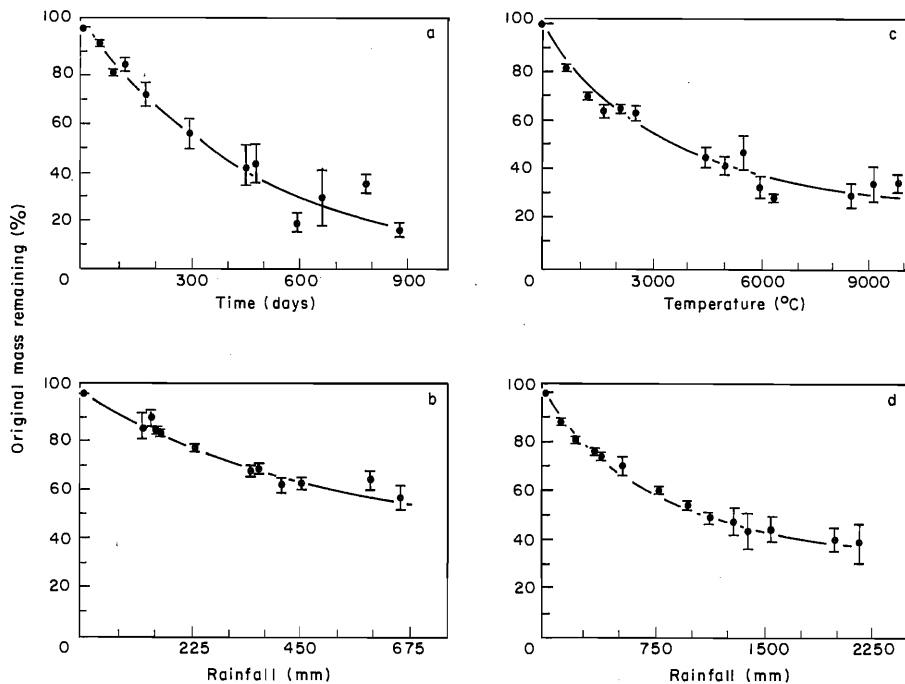


Figure 1. Litter mass loss for the four grass species (mean \pm 0.5 standard deviation), and curve for the best fitted model. (a) *Sporobolus airoides*; (b) *Hilaria mutica*; (c) *Elyonurus barbiculmis*; (d) *Aristida schiedeana*.

Table 1. Carbon and nitrogen contents (mean \pm standard deviation)

	June 1982			October 1984		
	C(%)	N(%)	C/N	C(%)	N(%)	C/N
<i>Sporobolus airoides</i>	51.5 \pm 1.6	0.7 \pm 0.0	71.5	42.6 \pm 1.1	0.7 \pm 0.0	59.1
<i>Hilaria mutica</i>	52.2 \pm 0.4	0.7 \pm 0.0	72.5	35.9 \pm 2.5	0.7 \pm 0.0	49.8
<i>Elyonurus barbiculmis</i>	49.3 \pm 0.6	0.5 \pm 0.0	104.8	36.0 \pm 0.3	1.0 \pm 0.1	37.1
<i>Aristida schiedeana</i>	50.8 \pm 0.8	0.4 \pm 0.0	115.4	38.2 \pm 1.5	0.7 \pm 0.0	53.0

simulating the mass loss of plant material (*see* Wieder & Lang, 1982; Ezcurra & Becerra, 1987). The basic assumption of this model is that the relative decomposition rate can be expressed as a nonlinear function of the remaining litter fraction:

$$\frac{1}{X} \frac{dX}{dt} = -k (X/X(0))^b$$

where $X(0)$ is the amount of litter at the beginning of the experiment ($t = 0$) and b is a shape coefficient. Three limiting cases can be visualised for this basic equation: (a) when $b = 0$ the relative rate is constant; (b) when $b = 1$ the relative rate decreases linearly with the remaining litter fraction; and (c) in all other cases the relative rate decreases exponentially with the remaining fraction.

The first of these cases (Model 1) is obtained from the integrated equation when $b = 0$, and results in Olson's (1963) negative exponential decomposition model:

$$X(t) = X(0) \exp(-kt)$$

The other two limiting cases were developed by Ezcurra & Becerra (1987) and assume relative decomposition rates that vary with time. The first of these (Model 2) considers decomposition rate to be a linearly decreasing function of the remaining litter fraction ($b = 1$). The integrated equation now becomes:

$$X(t) = \frac{X(0)}{1 + kt}$$

Model 3, on the other hand, considers the relative decomposition rate to be a nonlinear function of the remaining litter fraction. Integrating the complete differential equation, the litter remaining at time t can be predicted as:

$$X(t) = \frac{X(0)}{(1 + bkt)^{1/b}}$$

Fitting the equations

The equations were fitted by means of a Hooke and Jeeves direct search algorithm (Himmelblau, 1972) which estimates numerically the least-squares values of the parameters. The statistical significance of a fitted model was calculated as the F ratio between the mean square of the regression error (given by the difference between the mean of every harvest and the values predicted by the model) and the mean square of the pure error (given by the

dispersion of the data points around the sample mean of their respective harvest). The null hypothesis for this test is that the regression error does not differ significantly from the pure error, which is a measure of the intrinsic variation in the data, i.e. the null hypothesis implies that the fit is adequate. Details of this procedure can be found in Draper & Smith (1981) and Ezcurra & Becerra (1987).

Results

Model 3 was fitted to the dry mass data (% original weight) of the four grass species, with three independent variables tried as predictors (t) of the decomposition process: time, accumulated rainfall, and accumulated mean daily temperature. A stepwise fitting procedure was used, in which the variables were tried one at a time and the best individual predictor was chosen. If the shape parameter (b) in Model 3 approached zero, then for reasons of parsimony it was assumed that the decomposition rate was nearly constant and the process was described using Model 1. Likewise, if b tended to 1 it was assumed that the decomposition rate decreased in a linear fashion, and Model 2 was used to describe the process.

Table 2 summarises the information on the fitted decomposition models for the four species. The corresponding curves are shown in Fig. 1. The *Michilia* species show better fits with rainfall and temperature, and with Models 2 and 3, while the *Mapimi* species show a better relation with time and Model 1 (*S. airoides*) and with rainfall and Model 2 (*H. mutica*).

Table 1 shows the percentages of carbon and nitrogen at the beginning and end of the experiment. It is clear from this table that the C:N ratio decreased more quickly in *La Michilia* than in *Mapimi*. Percentage nitrogen tended to increase substantially with decomposition in the more mesic environment of *La Michilia*, while it remained constant in the arid environment of *Mapimi*.

The half-life values estimated with Model 1 for the four species under study were 338 days for *E. barbiculmis*, 359 days for *S. airoides*, 502 days for *A. schiedeana*, and 909 days for *H. mutica*. The average proportions of stems in the initial masses were 14%, 26%, 54% and 66%, respectively. Taking three replicates per species, a significant quadratic regression was found between the initial proportion of stems in the samples and the half-life values ($r^2 = 0.94$, $p < 0.001$).

Table 2. Summary of fitted decomposition models for the four grass species (the exponential parameter for *A. schiedeana* fitted by Model 3 was $b = 1.52$)

Site	Species	Best predictor	Best model	r^2	Initial decomposition rate	Underlying assumption
Mapimi	<i>Sporobolus airoides</i>	Time*	1	0.89	$0.0019 \text{ g g}^{-1} \text{ d}^{-1}$	Rate constant
	<i>Hilaria mutica</i>	Rainfall†	2	0.87	$0.0012 \text{ g g}^{-1} \text{ mm}^{-1}$	Rate decreases linearly
La Michilia	<i>Elyonurus barbiculmis</i>	Temperature‡	2	0.90	$0.28 \text{ g g}^{-1} \text{ °C}^{-1}$	Rate decreases linearly
	<i>Aristida schiedeana</i>	Rainfall§	3	0.87	$0.0011 \text{ g g}^{-1} \text{ mm}^{-1}$	Rate decreases exponentially

* $p = 0.67$; † $p = 0.90$; ‡ $p = 0.37$; § $p = 0.99$.

Discussion and conclusions

The decomposition of litter is a complex process that depends basically on two sets of variables, biotic and abiotic, either of which can predominate under different environmental conditions. Biotic decomposition is performed by micro- and meso-organisms, and is characterised by a series of simple and distinctive traits: (a) decomposition rates should decrease as the more refractory fractions become concentrated in the litter (Wieder & Lang, 1982; Ezcurra & Becerra, 1987); (b) the process should depend more on temperature and available water as predictive variables than on time itself; and (c) the C:N ratio should decrease as the micro-organisms use part of the compounds, liberating carbon dioxide to the atmosphere and at the same time concentrating the available nitrogen in their cells and in refractory compounds. Abiotic disintegration of organic matter should show, on the other hand, contrasting traits: (a) a relatively constant decomposition rate, as physical breakdown does not distinguish so clearly between labile and recalcitrant compounds; (b) a dependence on time *per se* as the main driving variable; and (c) a relatively constant C:N ratio.

The *Michilia* species consistently show a better fit to models that assume a decreasing decomposition rate, and also show a greater decrease in the C:N ratio of the litter over time. Additionally, it is clear that time in itself is not as good a predictor of the disintegration of litter in this environment as are the more biologically related variables, rainfall and temperature. These facts indicate that decomposition in the temperate pine-oak forest is basically of a biological nature. In contrast, both grass species in Mapimi showed less change in the C:N ratio over time. The decomposition of one of these species (*S. airoides*) was best predicted by time using Model 1 (constant decomposition rate), while the other (*H. mutica*) showed a better fit to Model 2 (linearly decreasing rate) using rainfall. The lower variation in the C:N ratio of both desert species, and the constancy in the decomposition rate of *S. airoides*, independent of the remaining litter fraction, temperature and/or rainfall, suggest a predominance of abiotic factors in the fragmentation of litter in arid environments. The difference in decomposition between the two grass species is possibly due to the more favourable environmental conditions of the *Hilaria* grassland, which receives more runoff and is less saline than the *Sporobolus* site.

There seems to be an aridity gradient in the decomposition of litter, with biotic processes dominating at one end and abiotic processes at the other. It is possible to hypothesise that, as aridity increases, unfavourable environmental conditions and the absence of a continuous layer of litter hinder the development of a community of surface decomposers. Under arid conditions surface litter undergoes a process of weathering, physical fragmentation and mineralisation before it is incorporated into the soil profile, or it accumulates in patches on the soil surface where decomposing organisms can act more effectively. In relation to this, Santos & Whitford (1981, cited in Steinberg & Whitford, 1983) and Santos, Elkins *et al.* (1984) found that buried litter in the Chihuahuan Desert disappeared more quickly than surface litter, while Whitford, Bryant *et al.* (1980) and Whitford, Repass *et al.* (1982) reported that small quantities of litter on the soil surface of the same desert decomposed more slowly than larger accumulations.

The spatial pattern of vegetation at Mapimi demonstrates clumping at two different levels. At a small scale (0.5–1.0 m) grass tufts are separated by areas of bare soil, while at a larger scale (10–100 m) there is a mosaic of dense and sparse patches of vegetation. Soil organic matter content varies strongly within and between individual tufts (in an *Hilaria* grassland, from 2% to 0.7%) or within and between patches (averaging 2.6% within and 0.8% between densely vegetated patches). The data presented in this paper, although bags were placed randomly in the field, correspond in most cases to areas of bare soil (between tufts). It is possible that the decomposition rates are higher within tufts. The influence of spatial heterogeneity on the process of decomposition in arid environments is an aspect that needs further research.

This research was financed by the Regional Program for Scientific and Technological Development of the Organization of American States (PRDCYT-OEA) and the Consejo Nacional de Ciencia y Tecnología (CONACYT), Mexico. We thank Judith Becerra and Antoine Cornet for helpful discussions.

References

- Draper, N. R. & Smith, H. (1981). *Applied Regression Analysis* (2nd Edn). New York: Wiley. 709 pp.
- Ezcurra, E. & Becerra, J. (1987). Experimental decomposition of litter from the Tamaulipan cloud forest. A comparison of four simple models. *Biotropica* (in press).
- Himmelblau, M. D. (1972). *Applied Nonlinear Programming*. New York: McGraw Hill. 532 pp.
- Kendrick, W. B. & Burges, A. (1962). Biological aspects of the decay of *Pinus sylvestris* leaf litter. *Nova Hedwigia*, **4**: 313–342.
- Ludwig, J. A. & Whitford, W. G. (1981). Short-term water and energy flow in arid ecosystems. In: Goodall, D. W., Perry, R. A. & Howes, K. M. W. (Eds), *Arid Land Ecosystems: Structure, functioning and management, Vol. 2*. pp. 271–300. Cambridge: Cambridge University Press. 605 pp.
- Noy Meir, I. (1985). Desert ecosystem structure and function. In: Evenari, M., Noy Meir, I. & Goodall, D. F. (Eds), *Hot Deserts and Arid Shrublands, Vol. A*. pp. 93–103. Leiden: Elsevier. 361 pp.
- Olson, J. S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, **44**: 322–331.
- Saito, T. (1957). Chemical changes in beech litter under microbiological decomposition. *Ecological Reviews, Japan*, **14**: 209–216.
- Saito, T. (1965). Microbiological decomposition of beech litter. *Ecological Reviews, Japan*, **14**: 141–147.
- Santos, P.F. & Whitford, W. G. (1981). The effects of microarthropods on litter decomposition in a Chihuahuan desert ecosystem. *Ecology*, **62**: 654–663.
- Santos, P. F., Elkins, N. E., Steinberger, Y. & Whitford, W. G. (1984). A comparison of surface and buried *Larrea tridentata* leaf litter decomposition in North American hot deserts. *Ecology*, **65**: 278–284.
- Steinberg, Y. & Whitford, W. G. (1983). The contribution of rodents to decomposition processes in a desert ecosystem. *Journal of Arid Environments*, **6**: 177–181.
- West, N. E. (1981). Nutrient cycling in desert ecosystems. In: Goodall, D. W., Perry, R. A. & Howes, K. M. W. (Eds), *Arid Land Ecosystems: Structure, functioning and management, Vol. 2*. pp. 301–324. Cambridge: Cambridge University Press. 605 pp.
- Whitford, W. G., Bryant, M., Ettershank, G., Ettershank, J. & Santos, P. F. (1980). Surface breakdown in a Chihuahuan desert ecosystem. *Pedobiologia*, **4**: 243–245.
- Whitford, W. G., Repass, R., Parker, L. W. & Elkins, N. Z. (1982). Effects of initial litter accumulation and climate on litter disappearance in a desert ecosystem. *American Midland Naturalist*, **108**: 105–110.
- Wieder, R. & Lang, G. (1982). A critique of the analytical methods used in examining decomposition data obtained from litter bags. *Ecology*, **63**: 1636–1642.
- Zlotin, R. I. & Khodashova, K. S. (1980). *The Role of Animals in Biological Cycling of Forest-Steppe Ecosystems*. Stroudsburg, PA: Dowden, Hutchison and Ross. 221 pp.