

# Non-linear dynamics of litter decomposition under different grazing management regimes

Natalia Banegas · Ada S. Albanesi · Raúl O. Pedraza · Daniel A. Dos Santos

Received: 28 November 2014 / Accepted: 6 April 2015  
© Springer International Publishing Switzerland 2015

## Abstract

**Aims** To understand and model the dynamics of litter decomposition in a climatically seasonal region subject to different modalities of land pasture management.

**Methods** Decomposition was quantified through the litterbag technique. Sampling was performed at monthly intervals on an annual basis with replications for 2008, 2009 and 2010. Treatments were native vegetation (NV) and grazed (G), grazed and N-fertilized (GF), hayed (H), hayed and N-fertilized (HF) plots. For each combination of treatment and year, a sigmoid model was fitted.

Parameters included remnant litter, steepness and inflection of decomposition curve.

**Results** The sigmoid model adjusted excellently well the data. In considering the overall effect on litter decomposition, treatments differ among them as follows symbolically: ((GF>G)>(HF>H)) >>NV. Results are consistent across the yearly replications.

**Conclusion** Pasture management (grazed versus hayed) is the primary factor controlling the rate of decomposition, whereas fertilization has a secondary role. The sigmoid model captures realistically the different phases of decomposition detected over a year, namely stationary at conditions of low temperature (later autumn and winter), accelerated at increasing temperature and humidity (transition from spring to summer) and decelerated when residual organic matter becomes less profitable and weather conditions more stringent (summer and earlier autumn).

Responsible Editor: Alfonso Escudero.

**Electronic supplementary material** The online version of this article (doi:10.1007/s11104-015-2472-y) contains supplementary material, which is available to authorized users.

N. Banegas  
Instituto de Investigación Animal del Chaco Semiárido,  
INTA, Chañar Pozo S/N (4113), Leales, Tucumán, Argentina

N. Banegas · A. S. Albanesi  
Facultad de Agronomía y Agroindustrias – Universidad  
Nacional de Santiago del Estero, Avenida Belgrano 1912  
(4200), Santiago del Estero, Argentina

N. Banegas · R. O. Pedraza  
Facultad de Agronomía y Zootecnia – Universidad Nacional  
de Tucumán, Avenida Kirchner 1900 (4000), San Miguel de  
Tucumán, Tucumán, Argentina

D. A. Dos Santos (✉)  
Instituto de Biodiversidad Neotropical, CONICET – UNT,  
Miguel Lillo 205 (4000), San Miguel de Tucumán, Tucumán,  
Argentina  
e-mail: dadossantos@csnat.unt.edu.ar

**Keywords** Chaco · Sigmoid model · Grazing · Cattle · Nitrogen · *Chloris gayana*

## Introduction

Litterfall represents the dominant pathway for the annual return of nutrients to the soil, being litter the principal source of bioelements and a remarkable reservoir of carbon in agroecosystems. The accretion of organic residues allows the formation of organic matter on the soil surface over which each ecosystem imposes its ecological signature. Notwithstanding, the role of litter

as deposit of elements that guarantees a permanent contribution of nutrients to the soil (Palma et al. 1998) is only attainable if we consider the occurrence of a decomposition process on it (Giese et al. 2009). This process is a microbial-mediated progressive breakdown of organic materials with final end products released into the ecosystem at both a local and a global scale (Kumar and Goh 2000).

There are many factors that regulate the decomposition of plant residues such as their quantity and quality, environmental conditions, soil fertility, microbial diversity, tissue components associated to different plant species, management and grazing (Semmartin et al. 2004; Torres et al. 2005; Noé and Abril 2008; Mahney 2010). Therefore, decomposition rate is characteristic of each ecosystem (Xu et al. 2010; Carranza et al. 2012). In natural ecosystems, decomposition is synchronized with plant growth and C and other nutrients are optimally used (Gregorich and Janzen 1998), but the anthropic disturbance may retard or accelerate the decomposition since functional compartments of the ecosystem are altered. Learning this process is necessary to guide the strategies of farm practices and produce effectively. Grazing is expected to alter the decomposition process mainly via effects on local environmental parameters, litter quality (Semmartin et al. 2004) and by altering features associated to litter deposition and its decomposition (Semmartin et al. 2008). There are contrasting views about how herbivores influence the productivity of ecosystems (Olofsson and Oksanen 2002). They may interfere either positively (McNaughton 1985; Holland et al. 1992; Zimov et al. 1995; Ritchie et al. 1998; Sirotiak and Huntly 2000) or negatively (Bryant et al. 1991; Pastor and Naiman 1992) with the course of nutrient cycling and associated rates of decomposition. Although the mechanisms behind these contradictory effects are not completely understood (Garibaldi et al. 2007), grazing is undoubtedly considered a regulator factor in the dynamics of litter processing as well as a good predictor of soil quality (Williams et al. 1995).

Besides cattle grazing, nitrogen (N) supply acts on the rate of litter decomposition through an influence on the composition and activity of microbial communities (Güsewell and Gessner 2009). In spite of being considered that the availability of nitrogen controls rates of litter decomposition, particularly in

the early stages of decay, experiments geared towards testing the hypothesis of N limitation for decomposition have been inconsistent (Prescott 1995). The controversy about the degree of influence exerted by agricultural litter quality and N availability still remains contentious (Grandy et al. 2013). Positive, negative or no effects of added inorganic N on decomposition and microbial activity have been reported (Cheshire and Chapman 1996; Knorr et al. 2005). One reason behind this inconsistency relies probably on the fact that fertilization alters the dynamics of litter decomposition at the same time that it increases litter C inputs (Grandy et al. 2013). In systems such as grass pastures, changes induced by N enrichment point to the structure of edaphic communities, enzymatic activities and rates of litter decomposition (Knorr et al. 2005; Garland et al. 2012), but the actual biological mechanisms underlying soil and litter C responses to N availability remain uncertain (Grandy et al. 2013).

Despite being considered of great importance in system productivity, the quantitative aspects related to decomposition rates in pastures of tropics and subtropics need further study, specially the changes linked to different modalities of management (Sánchez Cárdenas 2007). The Chacoan region constitutes a real case that illustrates these issues. It lies in the center of South America and covers about 650,000 km<sup>2</sup> encompassing parts of Argentina, Bolivia and Paraguay. The area is a low-lying plain subject to semi-arid climatic conditions under a monsoon regime (Bucher 1982). It is the warmest region of South America, with the highest absolute temperature (around 49 °C) recorded along the year. The southern Chaco becomes grassier and merges with the Pampas, whereas northward along the Paraguay River in the east it becomes warmer and wetter and merges into tropical forest (Demarchi and García Ministro 2008). The mean annual temperature exceeds 25 °C in the north, while in the southern area is 18 °C. The mean annual precipitation varies between 500 and 700 mm, mainly concentrated between November and April in the hottest semester. There is a marked dry season from late autumn to early spring. An important characteristic of this region is the high variability in the pluviometric regime. Over the last years, Semiarid Chaco experienced a great ecosystem transformation derived from agricultural expansion and

displacement towards Northwestern Argentina of livestock activity originally performed in the Pampean region which is now devoted to double cropping. With the increase in productivity through no-till practices and concomitant decrease in litter burial and soil disturbance, a substantial litter build-up in agroecosystems is expected to occur. However, little is known about the rates of litter decomposition in Chacoan grasslands, and even less their dynamics in systems consisting of tropical pastures under different management practices (Perez-Harguindeguy et al. 2000; Abril and Bucher 2001; Bucher et al. 2003).

Given the characteristics of Semiarid Chaco, livestock production has an enormous potential, and the introduction of tropical pastures emerges like a good option. With a view to find out the amount of residues needed to keep up the soil productivity and to ensure environmental protection, it is important to generate information of decomposition rate and analyze accurately its behavior when exposed to different types of management. With all these cautions in mind, the scope of this paper is to fit accurate statistical models to empirical data of litter degradation (monthly sampled along the year) and compare their performance within and between the years for different modalities of land pasture management as well as for the native surrounding vegetation. In other words, our work aims (1) to offer a unified statistical framework to characterize and compare the non-linear nature of litter decomposition across the year in Semiarid Chaco and (2) to assess the effect produced by different modalities of pasture

management including cattle grazing, haylage and N fertilization.

## Materials and methods

### Study area

This research was conducted at the Animal Research Institute of the Semiarid Chaco (IIACS) dependent of the National Institute of Agricultural Technology (INTA), located in Leales to the southeast of Tucumán province, Argentina (27°11' S, 65°17' W). This area corresponds to a depressed saline plain and has an altitude of 335 m above sea level. The mean annual precipitation is 880 mm and rainfalls are concentrated between November and April. The mean annual temperature reaches around 19 °C, ranging from 25 °C in January to 13 °C in July. The climate is subtropical sub-humid with a dry season, matching up the latter with the relatively colder period of year spanned from April to October. The soil type subsumes into the class Fluvacuentic Haplustoll following the US Soil Taxonomy System. Table 1 lists the soil characteristics of study area.

### Experimental design

The experiment was carried out in a 12 Ha pasture divided into 16 plots composed of *Chloris gayana* cv Finecut. The pasture showed no signal of degradation, the grass cover was around the 90 % and yielded a

**Table 1** Soil characteristics in *Chloris gayana* pasture and native vegetation at the Animal Research Institute of Semiarid Chaco (IIACS), Tucumán. References: Pasture: *Chloris gayana* cv

Finecut. OM Organic Matter (%). N Nitrogen (%). P Phosphorus (mg.Kg of soil<sup>-1</sup>). EC Electrical Conductivity (dS.m<sup>-1</sup>)

Site	Depth (cm)	Textural class	OM	N	P	pH	EC
Native vegetation	0–20	Loam	3.1	0.16	15	7.2	5.5
	21–40	Silt Loam	0.11			7.7	2.9
	41–60	Silt Loam				8.2	4.0
	61–80	Loam				9.0	4.2
	81–100	Silt Loam				9.5	4.2
Pasture	0–20	Silt Loam	2.8	0.11	9.7	5.3	4.7
	21–40	Silt Loam	0.18			7.1	2.3
	41–60	Silt Loam				7.5	2.5
	61–80	Loam				8.2	1.7
	81–100	Loam				8.5	1.5

biomass accumulation of 8,000 Kg DM Ha<sup>-1</sup> year<sup>-1</sup>. Braford steers were allocated to the grazed plots with an initial live weight that varied from 150 to 160 Kg steer<sup>-1</sup>. The following treatments were applied to the experimental sites: 1) Grazed plots without fertilization (G). Each plot was rotationally used (10±3 days of grazing and 35±6 days of rest concurring with the growth time interval) and when grazed exposed to a stocking rate of 3 steers Ha<sup>-1</sup> year<sup>-1</sup>; in winters, deferred forage was used along 38±11 days in each plot. The dietary supplementation was both energetic and proteic in winter (1.4 % body weight), whereas it was only energetic in summer (0.8 % body weight). During the winter periods the diet also included hay of *Chloris gayana* cv Finecut (1.5 Kg steer<sup>-1</sup> day<sup>-1</sup>). 2) Grazed plots with nitrogen fertilization (GF). Fertilizer was administered in November after the first grazing instance through a dose adjusted to 100 Kg N Ha<sup>-1</sup>. 3) Hayed plots without fertilization (H). The animals had no access to these paddocks and the pasture was trimmed at the height of 15 cm above the ground three times during the rainy season. 4) Hayed plots with nitrogen fertilization (HF), applying 100 Kg N Ha<sup>-1</sup> in November after the cleaning cut. 5) A baseline or reference treatment corresponding to an area with native vegetation (NV) previously overexploited for forestry and livestock production. It represents an instance of a secondary ecological succession characterized by the presence of different autochthonous trees (e.g., *Zizyphus mistol*, *Geoffroea decorticans*, *Sideroxylon obtusifolium*, *Ruprechtia laxiflora*) and paucity in the herbaceous cover.

### Quantitative assessment of litter decomposition

Decomposition was evaluated through the litterbag technique (Bocock et al. 1960). We consider litter the dead plant material deposited on the surface of the soil no longer attached to the plant (Rezende et al. 1999). We directly collected existing litter from each treatment in April 2008, 2009 and 2010, dried and cleaned from adhering soil particles. All the existing litter collected was sieved through 2 mm mesh, removing all the material highly decomposed. We put 40 g of litter within each meshed Nylon bag (2 mm mesh size) and then we transfer the bags to the soil surface. For each treatment, four samples (i.e., 4 litterbags) were randomly picked out adopting a monthly sampling schedule. Samples

were later dried (>72 h. at 55 °C) until constant weight for estimating the amount of remaining material.

### Statistical modeling and analysis

We fit data to a four-parameter sigmoid or logistic model using the function *nls* available in the R software (R Core Team 2014) for statistical nonlinear regression. We use the next equation:

$$S(x) = \frac{b}{1 + e^{\frac{x - \text{infl}}{a}}} + c \quad (1)$$

where  $S(x)$  denotes the amount of remnant litter in grams at time  $x$  with months as time unit (April is 1, May is 2 and so on),  $c$  accounts for the remnant litter in the experiment (minimum asymptote),  $b$  is a measure of gross decomposition activity (difference between minimum and maximum asymptotes) and parameter  $a$  refers to the steepness of the curve (as  $a$  decreases the curve is more stretched or compressed along the time axis). The parameter *infl* corresponds to the time value where the curve achieves its inflection point (at which the curvature or concavity changes). Each combination of year per treatment was used as experimental unit and confidence intervals were inferred for each coefficient. We performed pairwise comparisons for parameter differences between those units, being the  $\alpha$ -level of significance (here 0.05) adjusted by the FDR procedure (false discovery rate, Benjamini and Hochberg 1995) which is encouraged when several simultaneous tests are carried out.

Besides the four parameters governing the shape of the curve, we also calculated the average residence time  $\tau$  (tau) of litter in the time domain used to fit the curve (that is, the window time spanning monthly from April to April of the next year). This value was adopted as a synthetic measure of the overall behavior of the curve and corresponds to the area under it whenever the y-axis is scaled to the unit interval:

$$\tau = \int_1^{13} \frac{S(x)}{(b+c)} dx \quad (2)$$

Finally, differences in  $\tau$  between the treatments were statistically assessed via classical one-way ANOVA. All graphics and statistical analyses were performed with the R platform.

## Results

All experimental units (treatment x year) were excellently adjusted with the sigmoid model of Eq. 1. Figure 1 shows the fitted curves with regard to each one of the experimental units. The corresponding best-fit parameters and their standard errors are detailed in the Table 2. In order to capture visually the relative size of the different parameter estimates, we have drawn a parallel coordinate's plot (Fig. 2). In this plot, all axes are scaled to the common interval [0, 1] being thus the values of distinct parameters linearly normalized to their ranges. The Online Resource retrieves the results of pairwise comparisons between experimental units across the four logistic parameters. It is clear from here that there is no effect of the factor year within treatments, whereas robust statistically significant differences between treatments can be tracked.

Table 3 expresses, in terms of the model parameters, the differences among treatments across the years. Thus, it summarizes the information content of the Online Resource. Consistently, the reference level (NV) differs significantly from the two categories of grazing (G and GF) at the four model parameters. With the exception of time at which the point of inflection occurs, both treatments of grazing (G and GF) can also be distinguished from those of haylage (H and HF). The decomposition curves for grazing levels (G and GF) are themselves almost equivalent, but the categories of haylage (H and HF) differentiate each other in the global amount of decomposed litter as indicated by parameters b and c. Finally, except the steepness of decomposition curve, all the remaining parameters measured under natural

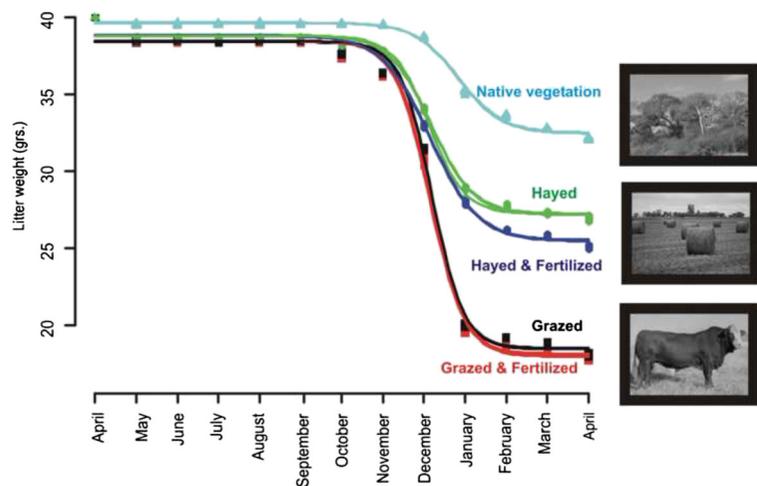
conditions (NV) depart significantly from those of H and HF levels.

Recalling that the average residence time  $\tau$  in Eq. 2 was adopted as a surrogate for the global performance of different treatments, we found a highly significant impact of them on litter decomposition across the annual replicates of experiments ( $F_{4, 10}=10977, p \ll 0.001$ ). Moreover, values of  $\tau$ 's were narrowly bounded at each treatment and no overlap was recorded between their ranges (Table 4). This finding suggests a clear arrangement of treatments in terms of their overall effect on litter decomposition that can be symbolically denoted as follows: ((GF>G)>(H>HF))>>NV.

## Discussion

Soil microorganisms are among the main biological drivers of organic matter decomposition. Their activities are subordinated to environmental factors such as proper conditions of moisture and temperature. Therefore, climate is expected to exert a relevant role in the decomposition process, making a footprint on the respective curve. For instance, Noé and Abril (2008) indicate that the moisture regime affects the rate of decomposition of plant residues in environments affected by low rainfall. In our work, first and foremost, climatic seasonality can be tracked. In fact, the stationary phase in the decomposition curve matches largely the cold and dry period of the region; whereas phases of active changes occur during the hot and rainy period. A second feature of adjusted curves concerns to their sigmoidal nature with the existence of an inflection

**Fig. 1** Sigmoid models adjusted to the different experimental units studied. April is the open/closed month of the experiments. Decomposition activity recorded at the very onset of the experiment (transition April–May) explains the gap between the initial weight of litterbags (40 g) and the fitted upper horizontal asymptote. The rainy season spans from November to April. Grazing is the primary factor influencing the intensity of decomposition whereas fertilization plays a secondary role



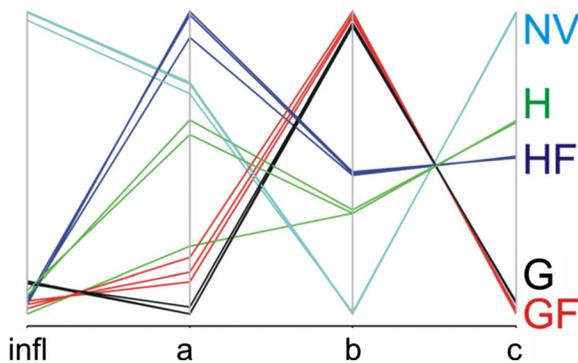
**Table 2** Parameters estimated for different combinations of treatments and years. Standard errors between parentheses. Treatments correspond to native vegetation (NV), grazed (G), grazed and fertilized (GF), hayed (H), hayed and fertilized (HF). Parameters

mean the following:  $a$ =steepness of the curve,  $b$ =amount of decomposed material,  $c$ =amount of remnant litter and  $infl$ =time at which the curve achieves its inflection point

Treatment	Year	Parameters			
		<i>infl</i>	<i>a</i>	<i>b</i>	<i>c</i>
GF	2010	9.14 (0.03)	0.42 (0.03)	20.50 (0.25)	17.95 (0.21)
	2009	9.15 (0.03)	0.41 (0.03)	20.35 (0.25)	18.08 (0.21)
	2008	9.16 (0.03)	0.40 (0.03)	20.24 (0.25)	18.16 (0.21)
G	2010	9.20 (0.03)	0.39 (0.03)	20.03 (0.25)	18.43 (0.21)
	2009	9.20 (0.03)	0.38 (0.03)	19.99 (0.25)	18.44 (0.21)
	2008	9.20 (0.03)	0.38 (0.03)	19.87 (0.25)	18.51 (0.21)
HF	2010	9.15 (0.03)	0.58 (0.03)	13.41 (0.17)	25.43 (0.14)
	2009	9.16 (0.04)	0.58 (0.03)	13.32 (0.18)	25.51 (0.15)
	2008	9.16 (0.04)	0.57 (0.03)	13.27 (0.17)	25.53 (0.14)
H	2010	9.18 (0.04)	0.50 (0.03)	11.56 (0.16)	27.26 (0.13)
	2009	9.17 (0.03)	0.51 (0.03)	11.72 (0.15)	27.15 (0.13)
	2008	9.13 (0.03)	0.43 (0.03)	11.56 (0.16)	27.24 (0.13)
NV	2010	9.85 (0.03)	0.53 (0.03)	7.13 (0.10)	32.51 (0.09)
	2009	9.83 (0.04)	0.53 (0.03)	7.20 (0.10)	32.45 (0.09)
	2008	9.85 (0.04)	0.54 (0.03)	7.17 (0.11)	32.49 (0.10)

point in the rates of decomposition. That point likely corresponds to an optimum response of soil microflora to temperature and moisture in the field. In a similar fashion, Coûteaux et al. (1995) considered this optimum response as largely dependent on the local climate. Kononova (1975) found that the maximum intensity of

decomposition of organic material is observed when the temperature reaches a moderate level (about 30 °C) and the moisture is about 60–80 % of the maximum water holding capacity of the soil. Interestingly, we detect inflections when the system enters into the summer months, that is to say when the average temperature rises the optimum value (so, enzyme activity falls) and soil moisture approaches to saturation (anaerobic conditions arise), as we can infer from published climographs for the region (Karlin 2012).



**Fig. 2** Parallel coordinates plot of parameters used in sigmoid models. There are three lines per treatment that correspond to the different years (2008, 2009 and 2010) at which the experiences have been carried out. Treatments correspond to native vegetation (NV), grazed (G), grazed and fertilized (GF), hayed (H), hayed and fertilized (HF). Parameters mean the following:  $a$ =steepness of the curve,  $b$ =amount of decomposed material,  $c$ =amount of remnant litter and  $infl$ =time at which the curve achieves its inflection point

**Table 3** Synthetic comparative output between treatments derived from Online Resource 1. Letters account for the most frequent profile of differences in the parameter setting of best-fit models ( $i$ =time at inflection point,  $a$ =steepness of sigmoid curve,  $b$ =amplitude of sigmoid curve,  $c$ =amount of remaining matter in the litterbags). The upper triangular matrix is only informed. Empty cells denote absence of significant differences

	GF	G	HF	H	NV
GF	–		<i>abc</i>	<i>abc</i>	<i>iabc</i>
G	–	–	<i>abc</i>	<i>abc</i>	<i>iabc</i>
HF	–	–	–	<i>bc</i>	<i>ibc</i>
H	–	–	–	–	<i>ibc</i>
NV	–	–	–	–	–

**Table 4** Average residence time of litter in the experimental bags under one year time-window of integration. Note that none pair of treatment overlaps

Treatment	Tau ( $\tau$ ) range
GF	9.94–9.97
G	10.02–10.03
HF	10.67–10.69
H	10.84–10.86
NV	11.42–11.43

Decomposition was slowed in the area covered by native vegetation (shrub savanna in Semiarid Chaco), leading to longer residence time by comparison with pastoral systems (Fig. 1; Table 4). Additionally, the inflection point was achieved at a later time. We consider that the difference between natural and anthropic systems relies mainly on the susceptibility to degradation of the plant residues. While the material deposited on the ground of wild substrate is woody, the material of grazing systems is herbaceous with much lower lignin content. Actual data supporting this last statement (including reports about C:N ratio) will be published elsewhere. Similar results were obtained by Castro et al. (2010) when comparing decomposition of woody and grass residues.

Grazing can alter litter decomposition, either accelerating or decreasing the rate of decomposition, and consequently the nutrient cycling in these systems (Haynes and Williams 1993; McNaughton et al. 1997; Schuman et al. 1999; Johnson and Matchett 2001; Franzluebbers and Stuedemann 2009). The percentage of material loss was about 17 % in the shrubland, 52–50 % in grazed areas and 33–29 % for hayed plots, corresponding to fertilized scenarios of pasture systems the higher observed percentages. Succinctly, in our study area we found that pasture management (grazed versus hayed) is the primary factor behind the steepness, celerity and effective mineralization of litter. Fertilization acts a secondary modulator factor with slight impact in grazed systems and more marked for the hayed ones (Fig. 1). Garibaldi et al. (2007) observed similar trends in C3 and C4 floodplain pastures in Argentina, highlighting also the incidence of livestock in promoting decomposition. Semmartin et al. (2008) found that decomposition and nutrient cycling is faster in grazed sites than in ungrazed ones, linking this with the greater availability of N in the soil. Our contrasting results between hayed and grazed treatments rely probably on the joint mechanic action (cattle trampling) and promoting microbial activity (cattle dung and urine)

present at the latter system. Grazing animals have a dominant effect on the movement of nutrients and the fertility of pasture soils because they use only a small proportion of the ingested nutrients. A high fraction of the ingested nutrients, ranging from 60 to 99 %, is returned to the soil in the form of patches of dung and urine (Haynes and Williams 1993). Nutrients can be recycled back to the pasture through animal excreta which represent an important source of N, P and K for forage crops (Silveira et al. 2013) as well as decomposing microorganisms. Consequently, cattle grazing promotes indirectly the microbial activity (organic matter decomposition and transformation) in increasing the availability of inputs for decomposers.

After reading the pertinent literature, we found no consensus about the consequences of N directly injected into the system. While some authors pointed out a positive effect of extra-N addition on decomposition, others show either none or even negative effects (Aerts et al. 2003; Knorr et al. 2005; Knops et al. 2007; Hobbie 2008; Semmartin et al. 2008; Liu et al. 2010). We did detect slight differences between treatments with and without fertilization, being the former ones (i.e., GF and HF) characterized by a higher rate of decomposition when compared against the respective unfertilized treatments (i.e., G and H). The addition of N-fertilizer may influence the rate of decomposition by the combination of two processes: (i) overall increasing of directly available N in the soil and (ii) augmented amount of N in the topsoil (Liu et al. 2010). However, we must stress here that the addition of N-fertilizer did not significantly change the chemical composition of mulch between treatments (unpublished results), explaining thus its secondary role for tuning the dynamics of decomposition. Probably, the pragmatic procedure by which the N-fertilizer is scattered across the field (broadcast) offers reduced chances to detect large differences between fertilized and non-fertilized treatments. Studies in forest and pasture ecosystems clearly show that the addition of N can stimulate or inhibit microbial activity and community structure, depending on the amount of N applied and differences in litter quality (Waldrop et al. 2004; Craine et al. 2007; Keeler et al. 2009). In our experimental units, the greater availability of N in soil appears to have played a moderate effect on microbial activity.

Lastly, the excellent adjustment of empirical data (despite the heterogeneity of treatments) to the sigmoid model deserves a separate bulk of considerations. Since the highly influential work of Olson (1963), the

common practice with litter decomposition data has been to fit an exponential decay function with a constant intrinsic decomposition rate. However, this model is completely unsatisfactory for real data whenever we face (i) weather seasonality and (ii) changes in the nutrient content or chemical profile of the remnant substrates. Similarly, Freschet et al. (2012) warn about the widespread assumption of exponential decay and encourage revising more critically its adequacy. Published results other than ours (e.g., Carnevale and Lewis 2001) support our assertion: data are fit with an exponential negative function but raw data subsume into a clear sigmoid pattern of decomposition. This last example is particularly interesting because focuses also on the Chacoan region and sigmoid empirical curve delivers an inflection time point near to the one estimated by us. The sigmoid model accounts better for the different phases of decomposition detected, namely stationary at low temperature (later autumn and winter), accelerated at increasing temperature and humidity (transition from spring to summer) and decelerated when residual organic matter becomes less profitable and weather conditions more stringent (summer and earlier autumn). Keeping the sigmoid model in mind, we can think about the decomposition process in terms of three main parameters: 1) curvature (to track the changes in acceleration along the process), 2) amplitude or difference between horizontal asymptotes (to assess the overall amount of decomposed material), and 3) inflection point (to find the time at which a change in the direction of curvature occurs). The uttermost importance of this last point consists of identifying when the process undergoes a phase transition (here, concave-convex transition). An open inquiry is why long-term decomposition experiments at field like ours fall into a sigmoid model, or equivalently which is the underlying mechanism for the phase transition between increasing and decreasing rate decays. The clue could be the succession of decomposing microbial consortia driven by changes in local environment and nutrient content with time. Fontaine et al. (2003) postulated a conceptual model centered at the notion of nutritional competition to account for some aspects of the dynamics of soil organic matter decomposition. These authors split the microbial community into two main compartments,  $r$  (grow quickly) and  $K$  (grow slowly) strategists, that experience a turnover as the

decomposition process progresses. After the incorporation of fresh organic matter to soils, many  $r$  microorganisms proliferate and attack only this resource. As the fresh material becomes limiting, the  $K$  organisms begin to prevail since they are best placed to acquire energy and nutrient from polymerized soil organic matter. If this mechanism truly operates on the studied systems, we would expect a significant change in the structure of the microbial consortia synchronized with inflection point of the curves. Certainly, this appealing prediction calls for a future research aimed to corroborate or refuse it.

## Conclusions

In this work we evaluated the dynamics of litter decomposition under different management systems in Semiarid Chaco of Argentina. Grazing systems have proved to be the most effective in the short-term, being the livestock activity responsible of such intense decomposition recorded. We finally argue that the typology of management in addition to climatic conditions (seasonal regimes of humidity and temperature) and intrinsic characteristics of the plant material (chemical composition) are shaping factors of the observed decomposition process.

The sigmoid model accounts accurately for the distinct instances detected along the decomposition process in Semiarid Chaco. So, it enables us to do proper comparisons among the different management systems in this region. Keeping in mind the sigmoid model, we can think about the decomposition process in terms of three main features: 1) curvature (to track the changes in acceleration along the process), 2) amplitude or difference between horizontal asymptotes (to assess the overall amount of decomposed material), and 3) inflection point (to find the time at which a change in the direction of curvature occurs).

**Acknowledgments** We are grateful to INTA, UNT and CONICET for facilitating our research. José Nasca and Pedro Pérez read an early version of our manuscript and made very useful comments. We would particularly like to thank one of the anonymous reviewers for the insightful comments on the paper. Fundings come from CIUNT project 2008–2009, INTA-AUDEAS-CONADEV 2009–20012 and ANPCyT project 2012–1910.

## References

- Abril A, Bucher EH (2001) Overgrazing and soil carbon dynamics in the western Chaco of Argentina. *Appl Soil Ecol* 16:243–249
- Aerts R, de Caluwe H, Beltman B (2003) Plant community mediated vs. nutritional controls on litter decomposition rates in grasslands. *Ecology* 84:3198–3208. doi:10.1890/02-0712
- Benjamini Y, Hochberg Y (1995) Controlling the false discovery rate: a practical and powerful approach to multiple testing. *J R Stat Soc Ser B (Methodol)* 289–300
- Bocock KL, Gilbert O, Capstick CK, Twinn DC, Ward JS, Woodman MJ (1960) Change in leaf litter when placed on the surface of soils with contrasting humus types. Losses in dry weight of oak and ash leaf litter. *J Soil Sci* 11:1–9. doi:10.1111/j.1365-2389.1960.tb02196.x
- Bryant JP, Provenza FD, Pastor J, Reichardt PB, Clausen TB, du Toit JT (1991) Interactions between woody plants and browsing mammals mediated by secondary metabolites. *Annu Rev Ecol Syst* 22:431–446
- Bucher E (1982) Chaco and Caatinga-South American arid savannas. Woodlands and thickets. In: Huntley BJ, Walker BH (eds) *Ecology of tropical savannas*. Springer, Berlin, pp 48–79
- Bucher EH, Torres PA, Abril A (2003) Litter quality and litter removal by the native fauna in the Chaco woodland of Argentina. *J Trop Ecol* 19:337–341
- Carnevale NJ, Lewis JP (2001) Litterfall and organic matter decomposition in a seasonal forest of the eastern Chaco (Argentina). *Rev Biol Trop* 49:203–212
- Carranza C, Noe L, Merlo C, Ledesma M, Abril A (2012) Effect of forest clearing type on the decomposition of native and introduced pastures in the Arid Chaco, Argentina. *RIA* 38: 97–107
- Castro H, Fortunel C, Freitas H (2010) Effects of land abandonment on plant litter decomposition in a Montado system: relation to litter chemistry and community functional parameters. *Plant Soil* 333:181–190. doi:10.1007/s11104-010-0333-2
- Cheshire MV, Chapman SJ (1996) Influence of the N and P status of plant material and of added N and P on the mineralization of C from <sup>14</sup>C-labelled ryegrass in soil. *Biol Fertil Soils* 21: 166–170
- Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and litter quality. *Trends Ecol Evol* 10:63–66
- Craine JM, Morriw C, Fierer N (2007) Microbial nitrogen limitation increases decomposition. *Ecology* 88:2105–2113. doi:10.1890/06-1847.1
- Demarchi DA, García Ministro A (2008) Genetic structure of native populations from the Gran Chaco region, South America. *Int J Hum Genet* 8:131–141
- Fontaine S, Mariotti A, Abbadié L (2003) The priming effect of organic matter: a question of microbial competition? *Soil Biol Biochem* 35:837–843. doi:10.1016/S0038-0717(03)00123-8
- Franzluëbbers AJ, Stuedemann JA (2009) Soil-profile organic carbon and total nitrogen during 12 years of pasture management in the Southern Piedmont USA. *Agric Ecosyst Environ* 129:28–36. doi:10.1016/j.agee.2008.06.013
- Freschet GT, Weedon JT, Aerts R, van Hal JR, Cornelissen JHC (2012) Interspecific differences in wood decay rates: insights from a new short-term method to study long-term wood decomposition. *J Ecol* 100:161–170. doi:10.1111/j.1365-2745.2011.01896.x
- Garibaldi LA, Semmartin M, Chanton EJ (2007) Grazing-induced changes in plant composition affect litter quality and nutrient cycling in flooding Pampa grasslands. *Oecologia* 151:650–662. doi:10.1007/s00442-006-0615-9
- Garland JL, Zabaloy MC, Birmele M, Mackowiak CL, Lehman RM, Frey SD (2012) Examining N-limited soil microbial activity using community-level physiological profiling based on O<sub>2</sub> consumption. *Soil Biol Biochem* 47:46–52
- Giese M, Gao YZ, Zhao Y, Pan Q, Lin S, Peth S, Brueck H (2009) Effects of grazing and rainfall variability on root and shoot decomposition in a semi-arid grassland. *Appl Soil Ecol* 41:8–18. doi:10.1016/j.apsoil.2008.08.002
- Grandy AS, Salam DS, Wickings K, McDaniel MD, Culman SW, Snapp SS (2013) Soil respiration and litter decomposition responses to nitrogen fertilization rate in no-till corn systems. *Agric Ecosyst Environ* 179:35–40. doi:10.1016/j.agee.2013.04.020
- Gregorich EG, Janzen HH (1998) Microbially mediated processes: decomposition. In: Summer M (ed) *Handbook of soil science*. CRC Press, Boca Raton, pp 106–119
- Güsewell S, Gessner MO (2009) N : P ratios influence litter decomposition and colonization by fungi and bacteria in microcosms. *Funct Ecol* 23:211–219. doi:10.1111/j.1365-2435.2008.01478.x
- Haynes RJ, Williams PH (1993) Nutrient cycling and soil fertility in the grazed pasture ecosystem. *Adv Agron* 49:119–199
- Hobbie SE (2008) Nitrogen effects on decomposition: a five-year experiment in eight temperate sites. *Ecology* 89:2633–2644. doi:10.1890/07-1119.1
- Holland E, Parton WJ, Detling JK, Coppock DL (1992) Physiological responses of plant populations to herbivory and their consequences for ecosystem nutrient flow. *Am Nat* 140:685–706
- Johnson LC, Matchett JR (2001) Fire and grazing regulate below-ground processes in tall grass prairie. *Ecology* 82:3377–3389. doi:10.1890/0012-9658(2001)082[3377:FAGRBP]2.0.CO;2
- Karlin MS (2012) Cambios temporales del clima en la subregión del Chaco Árido. *Multequina* 21–36
- Keeler BL, Hobbie SE, Kellogg LE (2009) Effects of long-term nitrogen addition on microbial enzyme activity in eight forested and grassland sites: implications for litter and soil organic matter decomposition. *Ecosystems* 12:1–15. doi:10.1007/s10021-008-9199-z
- Knops JMH, Naeem S, Reich PB (2007) The impact of elevated CO<sub>2</sub>, increased nitrogen availability and biodiversity on plant tissue quality and decomposition. *Glob Chang Biol* 13:1960–1971. doi:10.1111/j.1365-2486.2007.01405.x
- Knorr M, Frey SD, Curtis PS (2005) Nitrogen additions and litter decomposition: a meta-analysis. *Ecology* 86:3252–3257. doi:10.1890/05-0150
- Kononova MM (1975) Humus of virgin and cultivated soils. In: Gieseking JE (ed) *Soil components I. Organic components*. Springer, New York, pp 475–526
- Kumar K, Goh KM (2000) Crop residues and management practices: effects on soil quality, soil nitrogen dynamics, crop yield, and nitrogen recovery. *Adv Agron* 68:197–319
- Liu P, Huang J, Jianxin Sun O, Han X (2010) Litter decomposition and nutrient release as affected by soil nitrogen availability

- and litter quality in a semiarid grassland ecosystem. *Oecologia* 162:771–780. doi:10.1007/s00442-009-1506-7
- Mahney WM (2010) Plant control on decomposition rate: the benefits of restoring abandoned agriculture land with native prairie grasses. *Plant Soil* 330:91–101. doi:10.1007/s11104-009-0178-8
- McNaughton SJ (1985) Ecology of a grazing ecosystem: the Serengeti. *Ecol Monogr* 55:260–294
- McNaughton SJ, Banyikwa FF, McNaughton MM (1997) Promotion of the cycling of diet-enhancing nutrients by African grazers. *Nature* 278:1798–1800
- Noé L, Abril A (2008) Interacción entre calidad de restos vegetales, descomposición y fertilidad del suelo en el desierto del Monte de Argentina. *Ecología Aust* 18:181–193
- Olofsson J, Oksanen L (2002) Role of litter decomposition for the increased primary production in areas heavily grazed by reindeer: a litterbag experiment. *Oikos* 96:507–515. doi:10.1034/j.1600-0706.2002.960312.x
- Olson JS (1963) Energy storage and the balance of producers and decomposers in ecological systems. *Ecology* 44:322–331
- Palma RM, Prause J, Fontanive AV, Jimenez MP (1998) Litter fall and litter decomposition in a forest of the Parque Chaqueño Argentino. *For Ecol Manag* 106:205–210. doi:10.1016/j.apsoil.2008.08.002
- Pastor J, Naiman RJ (1992) Selective foraging and ecosystem processes in boreal forests. *Am Nat* 139:690–705
- Perez-Harguindeguy N, Diaz S, Cornelissen JH, Vendramini F, Cabido M, Castellanos A (2000) Chemistry and toughness predict leaf litter decomposition rates over a wide spectrum of functional types and taxa in central Argentina. *Plant Soil* 218: 21–30
- Prescott CE (1995) Does nitrogen availability control rates of litter decomposition in forests? *Plant Soil* 168–169:83–88
- R Core Team (2014) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>
- Rezende CP, Cantarutti RB, Braga JM, Gomide JA, Pereira JM, Ferreira E, Tarré R, Macedo R, Alves BJR, Urquiaga S, Cadisch G, Giller KE, Boddey RM (1999) Litter deposition and disappearance in *Brachiaria* pastures in the Atlantic forest region of the South of Bahia, Brazil. *Nutr Cycl Agroecosyst* 54:99–112
- Ritchie M, Tilman D, Knops JMH (1998) herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology* 79:165–177. doi:10.1890/0012-9658(1998)079[0165:HEOPAN]2.0.CO;2
- Sánchez Cárdenas S (2007) Acumulación y descomposición de la hojarasca en un pastizal de *Panicum maximum* Jacq. y en un sistema silvopastoril de *P. maximum* y *Leucaena leucocephala* (Lam.) de Wit. Dissertation, La Habana
- Schuman GE, Reeder JD, Manley JT, Hart RH, Manley WA (1999) Impact of grazing management on the carbon and nitrogen balance of a mixedgrass rangeland. *Ecol Appl* 19: 65–71. doi:10.1890/1051-0761(1999)009[0065:IOGMOT]2.0.CO;2
- Semmartin M, Aguiar MR, Distel RA, Moretto AS, Ghersa CS (2004) Litter quality and nutrient cycling affected by grazing-induced species replacements along a precipitation gradient. *Oikos* 107:148–160. doi:10.1111/j.0030-1299.2004.13153.x
- Semmartin M, Garibaldi ALA, Chaneton EJ (2008) Grazing history effects on above- and below-ground litter decomposition and nutrient cycling in two co-occurring grasses. *Plant Soil* 303:177–189. doi:10.1007/s11104-007-9497-9
- Silveira ML, Rouquette FMJ, Haby VA, Smith GR (2013) Impacts of 37 years of stocking on soil phosphorus distribution in bermudagrass pastures. *Agron J* 150:999–1004. doi:10.2134/agronj2013.0009
- Sirotnak JM, Huntly NJ (2000) Direct and indirect effects of herbivores on nitrogen dynamics: voles in riparian areas. *Ecology* 81:78–87. doi:10.1890/0012-9658(2000)081[0078:DAIEOH]2.0.CO;2
- Torres PA, Abril AB, Bucher EH (2005) Microbial succession in Litter decomposition in Semiarid-Chaco woodlands. *Soil Biol Biochem* 37:49–54. doi:10.1016/j.soilbio.2004.04.042
- Waldrop MP, Zak DR, Sinsabaugh RL, Gallo M, Lauber C (2004) Nitrogen decomposition modifies soil carbon storage through changes in microbial enzymatic activity. *Ecol Appl* 14:1172–1177
- Williams TO, Powell JM, Fernandez Rivera S (1995) Soil fertility maintenance and food crop production in semiarid West Africa: is reliance on manure a sustainable strategy? *Outlook Agric* 24:43–47
- Xu G, Hu Y, Wang S, Zhang Z, Chang J, Luo C, Chao Z, Su A, Lin Q, Li Y, Du M (2010) Effects of litter quality and climate change along an elevation gradient on litter mass loss in an alpine meadow ecosystems on a Tibetan plateau. *Plant Ecol* 209:257–268. doi:10.1007/s11258-009-9714-0
- Zimov SA, Chuprynin VI, Oreshko AP, Chapin FS, Reynolds JF, Chapin MC (1995) Steppe-tundra transition: a herbivore driven biome shift at the end of the quaternary. *Am Nat* 146:765–793