

Do litter decomposition and nitrogen mineralization show the same trend in the response to dry and wet years in the Patagonian steppe?

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Abstract

In arid environments, dry and wet years have similar number of small rainfall events but wet years result from the occurrence of a few large rainfall events. What are the implications of these different precipitation patterns on ecosystem functioning? Here, we examined the differential response of soil processes to wet and dry years. Specifically, we assessed litter decomposition and soil N mineralization responses to precipitation excess in the Patagonian steppe, and compared with responses to drought conditions previously reported for this ecosystem.

Litter decomposition rates did not differ significantly between simulated wet year and control, while litter decomposition rates decreased under a drought of a similar absolute magnitude. We hypothesize that decomposition rate in this ecosystem may be driven more by number of rainfall events than by total precipitation amount. Net nitrification increased in the simulated wet year but only for a short period of time. Moreover, irrigation positive effects on nitrification were offset by negative effects on net ammonification. Consequently, net N mineralization was not affected by water availability. Our results suggest that the different microorganisms responsible of nitrification and ammonification have differential sensitivity to water availability and that the environmental controls might be overwhelmed by substrate availability in longer time scales.

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1. Introduction

One of the common features of precipitation patterns in arid-semiarid ecosystems is that the amount of precipitation fallen in small (less than 5 mm) events is similar in dry and wet years, while large (higher than 10 mm) precipitation events are more common in wet years. As a consequence, a wet year is characterized by

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the occurrence of a few large rainfall events. This pattern was described for the Patagonian steppe, an arid ecosystem in South of Argentina (Golluscio et al., 1998), and in the shortgrass steppe of Colorado (USA) (Sala et al., 1992), suggesting that this could be a general phenomenon in arid and semiarid regions. The consequences of wet and dry years may be different for organisms living on the soil surface, in the uppermost soil layers or for plants that integrate water availability in the entire soil profile.

Litter decomposition in arid environments has different dynamics from those in mesic regions and general models relating litter decomposition rates along ample precipitation gradients account for only a fraction of the variability of the process in arid regions (Elkins et al., 1982; Meentemeyer, 1978; Montaña et al., 1988; Schaefer et al., 1985; Steinberger et al., 1990; Whitford et al., 1981). Annual precipitation relates to decomposition rates even in arid environments (Jacobson and Jacobson, 1998; Steinberger et al., 1990; Strojan et al., 1987; Whitford et al., 1986). However, rainfall manipulation experiments in water-limited ecosystems showed variable results. Water additions generally showed no effects on litter decomposition process in arid ecosystems (MacKay et al., 1987; Steinberger and Whitford, 1988; Whitford et al., 1986) with the exception of supplemental water applied during the dry season (Steinberger and Whitford, 1988). On the contrary, precipitation interception experiments showed strong consequences on decomposition rates (Kemp et al., 2003; Salamanca et al., 2003; Yahdjian et al., 2006). In addition, Whitford et al. (1995) conducted a drought and rainfall augmentation experiment in a creosotebush-dominated ecosystem in the Chihuahuan desert and found that decomposition rates were affected by drought but were not affected by irrigation treatments. Apparently, responses of litter decomposition to dry and wet years are different, with reductions during dry years that are not mirrored by an augmentation during wet years.

N availability, which is actually estimated by net N mineralization, is highly variable in space and time in arid environments (Mazzarino et al., 1996; Schlesinger et al., 1996; West and Skujins, 1978). Variable precipitation is in part responsible for this pattern, along with spatial vegetation heterogeneity. Empirical correlation between annual precipitation and net N mineralization in water-limited ecosystems has been elusive (Barrett et al., 2002; Yahdjian et al., 2006). In addition, irrigation experiments did not always show a nitrogen mineralization pulse (for example, Fisher and Whitford, 1995; Fisher et al., 1987; Schimel and Parton, 1986). By contrast, increases in soil inorganic N content under drought conditions have been reported in several arid ecosystems (Reynolds et al., 1999; Whitford et al., 1995; Yahdjian et al., 2006).

The general objectives of the present study were: (1) to examine litter decomposition and N mineralization responses to precipitation excess in the arid Patagonian steppe and (2) to compare responses to excess against responses observed under drought conditions reported previously for this ecosystem (Yahdjian et al., 2006). The specific questions that guided our work were: (1) Do litter decomposition and net N mineralization show the same trend in the response to precipitation deficit and excess? (2) Are litter decomposition rates and net N mineralization related to annual precipitation input in the Patagonian steppe? (3) Does soil nutrient concentration change with precipitation input? To address these specific questions, we designed a field manipulative experiment where we irrigated plots of natural vegetation and measured litter decomposition of a dominant grass species, *Stipa speciosa*, during a 20-month period and in situ N mineralization during a year.

2. Methods

2.1. Study site

This study was conducted in Río Mayo, Chubut, Patagonia, Argentina (45°41'S, 70°16'W). Mean monthly temperature of the site ranged from 1 °C in July to 15 °C in January. Mean annual precipitation recorded over 20 years was 168 mm and ranged between 90 and 275 mm. Precipitation is concentrated during fall and winter periods (March–September), which results in high-potential evapotranspiration and low water availability from the middle of the spring to the end of the summer. Vegetation is a mixture of tussock grasses and shrubs that have a basal cover of 32% and 15%, respectively, the rest being bare soil (Sala et al., 1989). Tussock grasses are represented mainly by *S. speciosa*, *S. humilis* Cav., and *Poa ligularis* Nees ap. Steud. The dominant shrubs are *Mulinum spinosum* (Cav.) Pers., *Adesmia volckmanni* Philippi, and *Senecio filaginoides* DC (Golluscio et al., 1982). Topography is flat and soils are coarse textured with pebbles, which account for 47% of its weight in the upper 0–45 cm soil layer (Paruelo et al., 1988). A cemented-calcareous layer occurs at about

45 cm depth. Organic matter in the upper soil layer in bare soil patches is 0.4% and pH is neutral (Paruelo et al., 1988). Standard meteorological variables were recorded during the course of this experiment by an automatic weather station equipped with a datalogger Campbell SCI 21X. Data used in the present study included rainfall recorded with a weighting bucket rain gauge with a 0.1 mm limit of rainfall detection.

2.2. Experimental design and water manipulations

Our experimental design included experimental irrigation and controls with five replicates. In a 2 ha grazing enclosure, we selected 10 individuals of the shrub *M. spinosum* of similar size and established plots of 3.76 m² (2 × 1.88 m) around each shrub, which were randomly assigned to one of the two treatments. We irrigated plots during the growing season, in November and January, to simulate a wet year. Each event consisted of 80 l of water uniformly scattered in each plot with a sprinkler, to simulate a natural rainfall event of 21 mm (Yahdjian and Sala, 2006). The rate of water application was similar to the rate of absorption by the soil, to prevent water from pooling on the soil surface. The irrigation water was extracted from a local well, and water was analyzed for nitrates and ammonium concentration, using an AlpKem[®] autoanalyzer (O–I Corporation, College Station, TX, USA), which uses a colorimetric analysis of inorganic nitrogen in liquid extracts (Yahdjian and Sala, 2006).

2.3. Response variables

Our response variables were litter decomposition of the dominant grass species, *S. speciosa*, soil inorganic nitrogen content, and in situ net N mineralization and net nitrification. We carried out a decomposition experiment using the litterbag approach which consisted in confining 1 g of recently senesced leaves of *S. speciosa* in mesh bags, placing them on the ground, and collecting them at periodic intervals. Four litterbags of leaves were anchored in the field, on bare soil, at each plot (five plots per treatment). Litterbags were collected at 3, 7, 12, and 20 months, randomly selecting one bag per plot at each date. The 10 cm side litterbags were built using a 2 mm mesh size, the same mesh employed in a decomposition experiment performed under rainout shelters in this experimental site (Yahdjian et al., 2006). During transportation to and from the field, we placed each litterbag in a paper bag to minimize the loss of plant material. After collection, we returned each bag to the laboratory, we hand-sorted foreign materials from the litter (soil particles, floral parts, etc.) and dried them at 70 °C for 48 h for determination of dry mass. Ash-free dry mass was determined on subsamples of ground material.

Data for litter ash-free dry-mass remaining were fitted to a negative exponential model (Olson, 1963):

$$\frac{x_t}{x_0} = e^{-kt},$$

where x_0 is the initial litter mass, x_t is the residual litter mass at time t , and k is the annual decay constant expressed in year⁻¹. The regressions of $\ln(x_t/x_0)$ over time were performed separately for each set of litterbags in each plot to provide independent estimates of k in the two decomposition microenvironments ($n = 5$).

We estimated in situ net N mineralization, net nitrification, and net ammonification rates during variable incubation periods as the difference between initial and final content of ammonium and nitrate or only nitrate or ammonium in tubes that prevented plant uptake (Binkley and Vitousek, 1989; Raison et al., 1987; Stark, 2000). We buried, to a depth of 7.5 cm, PVC tubes of 5 cm diameter in bare soil patches, which in all cases were at least 15 cm from adult plants. Every 2–3 months, we collected soil from the cylinders and we buried the tubes in a patch adjacent to the previous sample. When collected, we carefully lifted the cylinders and transferred the remaining soil that was enclosed by the cylinder into a plastic bag for transport to the laboratory. We sieved fresh soils to pass a 2 mm mesh, and we extracted a subsample of 10 g of soil in 50 ml 2N KCl for determination of inorganic nitrogen (NH₄⁺ and NO₃⁻). Soil nitrogen concentrations were corrected for soil water content (Robertson et al., 1999) by placing a subsample of soil in a drying oven at 105 °C for 48 h for determination of gravimetric soil water content. Nitrogen concentrations and the net N mineralization rates were converted to an aerial basis (mass of N per unit area of soil) using bulk density for the fine soil fraction

(Paruelo et al., 1988). Soil extracts were analyzed using an AlpKem[®] autoanalyzer (O–I Corporation, College Station, TX, USA), which uses a colorimetric analysis of inorganic nitrogen in liquid extracts.

2.4. Statistical analyses

We subjected data for remaining litter mass to a two-way analysis of variance, with supplemental water and time as treatments (time was an independent factor since at any one sampling time a completely independent sample was collected). We performed statistical analyses using PROC GLM and PROC REG in the SAS version 6.12 package (SAS Institute, Cary, NC). Unless otherwise stated, significance was assumed at $P < 0.05$. We performed regressions of decomposition rates and net N mineralization vs. precipitation with all the data and tested for the goodness of fit to the linear model with the class module of the PROC GLM of the same SAS version. For the sake of clarity, we plotted the mean values with their standard errors. Data for soil N content were analyzed with repeated measure ANOVA with water treatments as the main effect using PROC GLM in the same SAS version. Appropriate transformations of the primary data were used when needed to meet the assumptions of the analysis of variance.

3. Results

Litter decomposition dynamics did not differ between control and irrigation treatments ($P > 0.05$) (Fig. 1). The addition of two rainfall events during the growing season, which represented a 27% annual rainfall increase did not stimulate litter decomposition of the dominant grass species *S. speciosa*. After 20 months of decomposition, on average 37.7% and 36.3% of the initial litter mass was lost under irrigation and control treatments, respectively. With decomposition rates measured during a rainfall interception experiment in a previous study, and decomposition measured in the irrigation experiment reported in the present study, we constructed an experimental 40–220 mm/yr precipitation gradient, along which we found that litter decomposition rates (k , yr^{-1}) were positively correlated with incoming annual precipitation (APPT, mm/yr) ($k = 0.0007 \times \text{APPT} + 0.14$; $r^2 = 0.40$; $P < 0.01$) (Fig. 2). However, this regression is mainly explained by the relationship between annual precipitation and decomposition rates in the dry side of the range (40–160 mm/yr), while in the wet side of the range (160–220 mm/yr) we observed a lack of response of decomposition rates to annual precipitation. All exponential regressions used to describe mass loss through time were significant (average $r^2 = 0.90$).

After the first irrigation event, net nitrification was significantly higher ($P < 0.0001$) and net ammonification was lower in irrigated than in control plots, although the differences for ammonification rates were not

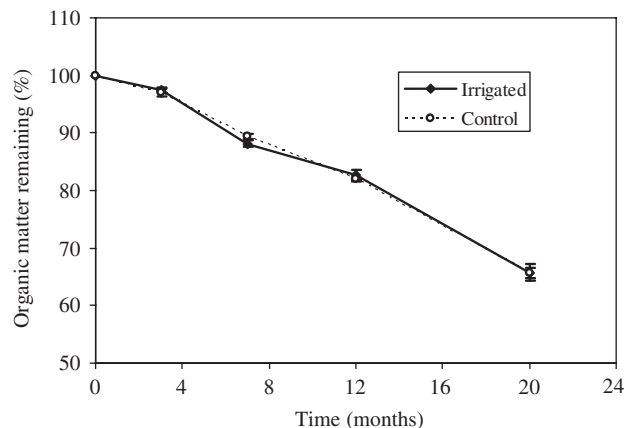


Fig. 1. Mass loss through time of a common substrate, leaf litter of the grass species *Stipa speciosa*, for experimental irrigation treatments. The irrigation treatments were addition of two pulse events of 21 mm each (27% rainfall addition) and control. Rainfall during the 20-month period was 262.5 mm. Mean values of organic mass remaining are on an ash-free basis (\pm S.E.) for $n = 5$. Significance of main effects of treatment (Treat.) and time (Time) are noted as ns not significant; *** $P < 0.001$.

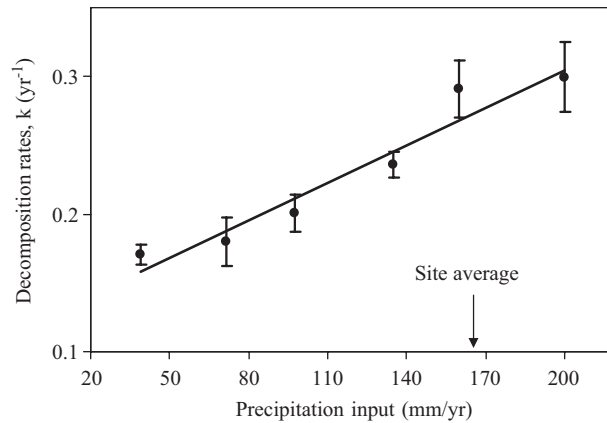


Fig. 2. Litter decomposition rates (k , yr^{-1}) vs. annual incoming precipitation (mm/yr) along an experimental precipitation gradient created with rainfall interception and irrigation experiments. The regression model is: $k = 0.0007 \times \text{APPT} + 0.14$; $r^2 = 0.40$, $P < 0.01$. Each symbol represents the mean litter decomposition rates per treatment (\pm S.E.) for $n = 10$ for rainfall interception period (40–160 mm/yr) from Yahdjian et al. (2006), and $n = 5$ for irrigation experiment (160–220 mm/yr).

Table 1

In situ net N mineralization, net nitrification, and net ammonification during seasons of the year during an irrigation experiment in the Patagonian steppe

	Pre-treatment (September 2001–November 2001)	1st irrigation event (November 2001–January 2002)	2nd irrigation event (January 2002–May 2002)
<i>Net N mineralization (mg/m²/d)</i>			
Irrigation	1.35 ± 0.24	0.76 ± 0.36	−0.47 ± 0.17
Control	1.85 ± 0.20	0.65 ± 0.25	−0.49 ± 0.11
<i>Net nitrification (mg/m²/d)</i>			
Irrigation	0.28 ± 0.03	0.27 ± 0.08 ^a	−0.110 ± 0.02 ^a
Control	0.35 ± 0.06	0.04 ± 0.05 ^b	−0.044 ± 0.04 ^b
<i>Net ammonification (mg/m²/d)</i>			
Irrigation	1.06 ± 0.24	0.48 ± 0.34	−0.40 ± 0.16
Control	1.39 ± 0.20	0.61 ± 0.22	−0.45 ± 0.08

Net rates are reported for irrigation and control treatments during the manipulation experiment and pre-treatment conditions (mean values \pm 1 S.E. for $n = 5$). The irrigation levels were 0% (control) and 27% water addition relative to incoming rainfall. Different letters show significant differences among treatments in a given date at $P < 0.0001$.

statistically significant (Table 1). These patterns, in turn, determined significantly higher soil nitrate concentration and lower soil ammonium concentration in plots of the irrigation treatment than in control plots (Table 2). Net N mineralization, which is the sum of nitrification and ammonification, was not stimulated by irrigation because the irrigation effect on nitrification was compensated by the opposite effect on ammonification.

We calculated annual net N mineralization integrating season values along a year from May of one year to May of the following year, and we found no irrigation effect on annual net N mineralization (0.11 ± 0.01 vs. 0.06 ± 0.02 g/m²/yr for control and irrigation treatments, respectively). Annual values of net N mineralization estimated in the present study were similar to those estimated for this experimental site with the same soil sampling protocol during a rainfall interception experiment performed previously (Yahdjian et al., 2006). Indeed, annual net N mineralization was not correlated with annual precipitation input along the 40–220 mm/yr precipitation gradient (Fig. 3).

Table 2
Soil nitrate, soil ammonium, and total inorganic N concentrations in irrigation and control treatments

	November 01	January 02	May 02
<i>Nitrate</i> ($mg NO_3^- - N/m^2$)			
Irrigation	5.3 ± 0.7	13.3 ± 2.9 ^a	2.7 ± 0.6
Control	8.7 ± 1.1	8.4 ± 2.5 ^b	5.5 ± 1.2
<i>Ammonium</i> ($mg NH_4^+ - N/m^2$)			
Irrigation	74.8 ± 20.0	87.2 ± 14.4 ^a	66.5 ± 11.0
Control	91.0 ± 23.3	116.9 ± 18.7 ^b	80.8 ± 11.8
<i>Total inorganic N</i> ($mg NO_3^- + NH_4^+ - N/m^2$)			
Irrigation	80.1 ± 21.0	100.5 ± 16.4 ^a	69.2 ± 10.7
Control	99.7 ± 22.5	125.3 ± 12.3 ^b	86.3 ± 12.3

Soil concentrations are reported for irrigation and control treatments in different sampling dates during the manipulation experiment (mean values ± 1 S.E. for $n = 5$). Values in November and January correspond to conditions previous to irrigation in that date. The irrigation levels were 0% (control) and 27% addition relative to incoming rainfall. Different letters represent significant differences among treatments in a given date at $P < 0.05$.

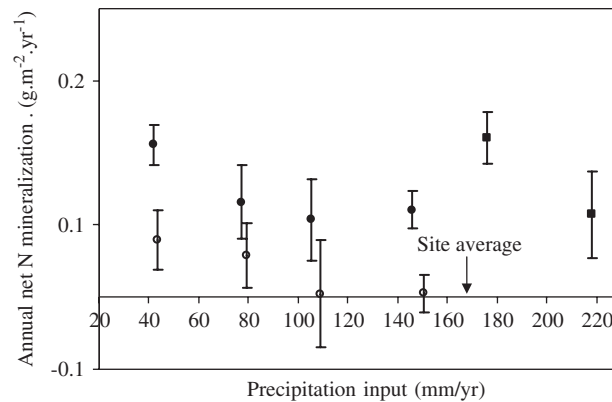


Fig. 3. Annual net N mineralization vs. annual incoming precipitation along an experimental precipitation gradient created with rainfall interception and irrigation experiments. Annual net N mineralization was measured in situ for 2 consecutive years in a rainfall interception experiment (from Yahdjian et al., 2006) and for 1 year in the irrigation experiment. Each symbol represents the mean annual net N mineralization per treatment (\pm S.E.), which was estimated by repeated samples taken through an annual cycle (open and filled circles represent rates measured during the two consecutive rainfall interception periods, $n = 10$ (40–160 mm/yr), and squares are for the irrigation experiment, $n = 5$ (160–220 mm/yr)).

4. Discussion

Litter decomposition in the Patagonian steppe showed a different trend in the response to wet years simulated by irrigation and to dry years achieved with rainout shelters. We found no response to irrigation treatments compared to control, while a litter decomposition experiment, which was previously reported using litter of the same grass species, *S. speciosa*, showed significantly reduced decomposition rates in a drought treatment than in control plots (Yahdjian et al., 2006). Although a 27% increase in precipitation had no effect on decomposition, a decrease in precipitation of similar absolute magnitude (30%) significantly reduced decomposition rates in this ecosystem (Yahdjian et al., 2006), indicating an asymmetrical response of litter decomposition to wet and dry years. The comparison between the experiments simulating dry and wet years was possible because we employed the same method to assess litter decomposition in the previous and in the present study, and because we used similar levels of rainfall interception and addition. Also, the rainout shelter employed in the previous experiment to simulate a dry year minimized other microenvironmental changes as,

for example, soil temperature (Yahdjian and Sala, 2002). The 16% reduction in decomposition due to a 30% decrease in precipitation was not mirrored by an increase resulting from a 30% increase in precipitation. Whitford et al. (1995) who conducted a drought and rainfall augmentation experiment in a creosotebush-dominated ecosystem in the Chihuahuan desert found the same different responses of decomposition to drought and irrigation treatments. We suggest that dry years may affect decomposition, whereas wet years may not, because the latter are represented by few large events that modify the total amount of water available for plants but minimally affect soil water conditions on the soil surface. In the Patagonian steppe, the occurrence of a few large rainfall events is sufficient to generate a wet year (Golluscio et al., 1998), which seems to be a general phenomenon in arid and semiarid regions (Sala et al., 1992). Large events penetrate deeper into the soil than small events but they do not differ largely on the period that the surface soil remains wet because the amount of water stored in shallow layers is the same after large and small events.

In an irrigation experiment in the Chihuahuan desert performed to study litter decomposition, Whitford et al. (1986) added the same amount of rainfall using two different numbers of events. Water was added in one single pulse of 25 mm, and in evenly spaced 6-mm events. Although decomposition rates of *Larrea tridentata* did not differ among treatments, the authors found higher mass losses in the 6 mm/week treatment than in the 25 mm/month on some sampling dates. Also, in the Negev desert of Israel, supplemental water did not stimulate litter decomposition when it was added during the wet season but significant litter decomposition of *Stipa capensis*, an annual grass, was recorded when four events of 30 mm each were added weekly during the dry season (Steinberger and Whitford, 1988).

The observed opposite response of nitrification and ammonification to irrigation suggests a differential sensitivity to water availability of the microorganisms responsible of these two soil transformations. Our results are in accordance with the high soil–water sensitivity reported for nitrifying bacteria (Stark and Firestone, 1995). In longer incubations, the enhance nitrification may not be sustained because of substrate limitation. Then, nitrification stimulation with irrigation may be just a transient phenomenon. Indeed, net annual N mineralization showed no response to rainfall as previously reported using an experimental gradient created during a rainfall interception experiment (Yahdjian et al., 2006). Consistently with our results, in a sandy soil in the Jornada desert, Fisher et al. (1987) found that N mineralization rates were not stimulated after water addition during a long incubation period of 192 days. However, pulses of net N mineralization were usually observed when incubation periods were short (Austin et al., 2004; Cui and Caldwell, 1997; Smart et al., 1999).

Our experiment showed that different soil processes from decomposition to nitrification and ammonification respond differently to precipitation pulses. Moreover, responses vary depending on the window of observation. So, short-term responses, such as those observed in nitrification, may be reversed in longer time scales. Ability to use pulses of nitrate availability may depend on the rapidity with which plants and microbes shift from a resistant to an active metabolic state. It is uncertain whether microbes or plants take advantages of high nutrient availability pulses (Schwinning and Sala, 2004). Microbial populations respond more rapidly than plant populations to increased resource availability, suggesting an advantage at using transient resource pulses. On the other hand, plants with their deep rooting systems are able to stay active throughout periods of drought and be ready to utilize transient pulses of N, which occur in upper soil layers.

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