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ECOSYSTEMS

Differential Controls of Water Input on Litter Decomposition and Nitrogen Dynamics in the Patagonian Steppe

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ABSTRACT

Studies of the effects of precipitation on litter decomposition and nitrogen mineralization in arid and semiarid environments have demonstrated contradictory results. We conducted a manipulative experiment with rainout shelters in the semiarid Patagonian steppe, aimed at assessing the direct effects of water availability on litter decomposition and net nitrogen mineralization while isolating the indirect effects. We created four levels of precipitation input: control and three levels (30, 55 and 80%) of precipitation interception and we examined litter decomposition and nutrient release of a dominant grass species, *Stipa speciosa*, inorganic soil nitrogen, and in situ net nitrogen mineralization over two consecutive years. Litter decomposition rates (k, year^{-1}) varied significantly ($P < 0.001$) among precipitation interception treatments and were positively correlated with incoming annual precipitation (APPT, mm/year) ($k = 0.0007 \times \text{APPT} + 0.137$). In contrast, net N mineralization was not correlated with incoming precipitation. Soil NO_3^- significantly decreased with increasing precipitation input, whereas soil NH_4^+ concentration did not differ among precipitation interception treatments. Controls of water input on litter decomposition appear to be different from controls on N mineralization in the semiarid Patagonian steppe. We suggest that although water availability affects both the mineralization of C and N, it differentially affects the movement and fate of the inorganic products. A consequence of the accumulation of inorganic N during dry episodes is that periods of maximum water and soil nutrient availability may occur at different times. This asynchrony in the availability of N and water in the soil may explain the observed lags in the response of primary production to increases in water availability.

Key words: arid ecosystems; decomposition; net N mineralization; Patagonian steppe (Argentina); phosphorus and nitrogen release; rainfall interception; rainout shelter; soil NO_3^- and NH_4^+; *Stipa speciosa*; water manipulations.

INTRODUCTION

Decomposition of plant material is a crucial link for both carbon and nitrogen cycling as the bulk of nitrogen supply is derived from turnover of above and belowground detritus (Schlesinger 1997). Nitrogen mineralization provides a significant proportion of the nitrogen necessary for plant and microbial growth, and N availability is, after water availability, the most likely resource to determine plant productivity in water-limited ecosystems (West and Skujins 1978; Burke and others 1997). In addition, decomposition influences ecosystem

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carbon storage through the control of soil carbon turnover as decomposition of litter (including root litter) contributes about 70% to the total annual carbon flux (Raich and Schlesinger 1992). Due to the current interest in controlling rising atmospheric carbon dioxide concentrations, and the large extent of arid and semiarid ecosystems (Ajtay and others 1979), understanding the potential capacity of water-limited ecosystems to sequester carbon from the atmosphere has become crucial.

Controls on N cycling in arid and semiarid ecosystems are poorly understood, particularly the role of moisture as a control on microbial mineralization affecting soil inorganic N availability. Fisher and others (1987) showed that increased rainfall in the Jornada Basin increased net N mineralization but decreased extractable N, similarly, in the same ecosystem, several authors showed that soil extractable N accumulated during drought (Whitford and others 1995; Reynolds and others 1999). Also in the northeastern Patagonian steppe, Mazzarino and others (1998) found higher N mineralization during a wet year than during a previous dry year, but available N was lower in the wet year. In contrast, Fisher and Whitford (1995) reported that extractable N was greater during the wet season at the Jornada Basin, and was significantly reduced by drought, and Schimel and Parton (1986) showed in the shortgrass steppe that mineralization rates can be sustained in dry horizons and were not increased by frequent small rainfall events.

Evidence regarding the controls of decomposition in water-limited ecosystems is also contradictory. Traditional conceptual models maintain that deserts are water-limited systems and that their biological processes are triggered and maintained by rainfall (Noy-Meir 1973). These ideas are in agreement with evidence that primary production is generally highly correlated with annual rainfall at regional scales (Webb and others 1978; Lauenroth 1979; Sala and others 1988), and decomposition rates also correlate well with precipitation or with actual evapotranspiration (AET) (Meentemeyer 1978; Aerts 1997; Austin and Vitousek 2000), even in some arid ecosystems (Strojan and others 1987; Jacobson and Jacobson 1998). However, Santos and others (1984) found low correlation between actual rainfall and mass loss of litter in North American hot deserts, and Steinberger and others (1990) showed that there was no direct relationship between mass losses from decomposing litter and rainfall along a rainfall gradient in the Judean desert of Israel. Also, the addition of 300 mm/year of water had no effect on decomposition in the Northern Chihuahan Desert (Whitford and others 1986) and supplemental water during the wet season in the Negev desert of Israel had no effect on the mass loss of *Stipa capensis* (Steinberger and Whitford 1988). By contrast, induced drought reduced decomposition rates of roots, while irrigated plots had no effect on the rates of decomposition (Whitford and others 1995), and decomposition rates of leaves of shrubs under rainout shelters declined during the latter half of a long-term field study in the Northern Chihuahuan Desert (Kemp and others 2003).

Current correlative models relating precipitation or AET and decomposition rates (k) are based on data within the 300–5500 mm precipitation range, so they do not include the arid extreme (Meentemeyer 1978; Aerts 1997; Austin and Vitousek 2000). These traditional models cannot account for the rapid turnover of material observed in many arid systems (Vossbrinck and others 1979; Schaefer and others 1985; Montaña and others 1988; Moorhead and Reynolds 1989), or the lack of correlation of decomposition with rainfall in very arid environments (Steinberger and others 1990). In addition, current decomposition models are based on spatial data and therefore are likely to be inadequate to predict and describe temporal patterns. Lauenroth and Sala (1992) showed that the controls of precipitation on aboveground primary production through space and time are quite different and, similarly, Jobbágy and others (2002) showed that models relating temperature and primary production through space and time were different.

Water availability affects decomposition directly and indirectly. Direct abiotic effects include litter fragmentation and leaching of labile compounds from the litter surface. In addition, soil water status directly affects the biotic activity of soil microorganisms responsible of litter decomposition (Freckman 1986). Although all soil microorganisms reduce their activity with decreasing water availability, functional groups show different thresholds and response patterns and consequently they stay active for variable periods of time between rainfall events (Treonis and others 2000; Schwinning and Sala 2004). Indirectly, soil water availability affects decomposition through changes in the species composition and abundance of plants and microorganisms (González and Seastedt 2001). Along precipitation gradients, plant species composition changes with mesic species replacing xeric species with consequent changes in litter quality (Aerts 1997). Those changes when analyzed along a precipitation gradient in the Central Grassland region of North America involved increased C/N ratio, percent lignin, and lignin/N ratio in litter with increasing precipitation (Murphy and others 2002), whereas when tropical and temperate regions are included in the gradient, litter N and P concentrations increases with AET and the lignin/N ratios decreases (Aerts 1997). Changes in litter quality also modify, in turn, the species composition of decomposer organisms (Swift and others 1979).

Part of the apparent contradictory nature of water availability-decomposition studies may be the result of many experiments confounding direct and indirect effects. In general, spatial studies include both direct and indirect effects and cannot disentangle the contribution of each effect unless they include in the design reciprocal transplanting or a common substrate. In contrast, temporal studies allow for the evaluation of direct effects of precipitation on the decomposition process in a site with variable precipitation inputs among years. However, as decomposition studies are intrinsically temporal studies, the design must carefully distinguish between changes during the decomposition process (in time) and changes among years with different precipitation inputs. A possible way to achieve this is to address questions related to the controls on decomposition using different, experimentally-achieved, precipitation levels. Our experimental design was aimed at disentangling the direct effects of precipitation on decomposition through an isolation of the indirect effects. Rainfall supplementation experiments provide some insight into how climate variation may affect ecosystem functioning. However, drought studies are essential to really understand ecosystems effects of climate variability because there is high uncertainty as to whether the response to drought would be symmetrical to the response to water additions (Whitford and others 1995; Knapp and Smith 2001).

The study described here was designed to assess the effect of precipitation on litter decomposition and net nitrogen mineralization independently of litter quality, floristic composition, and soil characteristics. Specifically, we wanted to address the following questions:

1. How does inter-annual variability in water availability affect decomposition and N mineralization in arid environments?
2. Are controls on carbon loss through litter decomposition different from controls on soil net N mineralization in arid environments?

To address these questions, we conducted an experiment in the Patagonian steppe, in southern Argentina, where we manipulated water input and examined litter decomposition and nutrient release of a dominant grass species, *Stipa speciosa* Trin et Ruprecht, soil NO_3^- and NH_4^+ content, and estimated in situ net N mineralization during two consecutive years. We used rainout shelters designed to create four levels of water input: ambient and three levels (30, 55 and 80%) of water interception (Yahdjian and Sala 2002).

METHODS

Study Site

This study was conducted in Río Mayo, Chubut, Patagonian region of Argentina (45°41′S, 70°16′W) from May 1999 to May 2001. Precipitation and other standard meteorological variables were recorded during the course of this experiment by an automatic weather station equipped with a datalogger Campbell SCI 21X. Mean monthly temperature ranged from 1°C in July to 15°C in January. Precipitation is mainly rainfall and its mean annual value, recorded over 20 years, was 168 mm and ranged between 90 and 275 mm. Rainfall is concentrated during fall and winter periods (March–September). The asynchrony of precipitation and temperature results in high potential evapotranspiration and low water availability from the middle of the spring to the end of the summer, while there is a recharge of the soil profile almost every year during fall and winter (Paruelo and Sala 1995). The topography is flat and the soils are coarse textured, with pebbles that account for 47% of its weight in the upper 0–45 cm soil layer and it has a cemented-calcareous layer at about 45 cm depth (Paruelo and others 1988). Organic matter in the upper soil layer in bare soil is 0.4% and pH is neutral (Paruelo and others 1988). The 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 and others 1989). Tussock grasses are represented principally by *Stipa speciosa*, *S. humilis* Cav., and *Poa ligularis* Nees ap. Steud. The dominant shrubs are *Mulinum spinosum* (Cav.) Pers., *Adesmia campestris* (Rendle) Rowlee, and *Senecio filaginoides* DC (Golluscio and others 1982).

Experimental Design

We selected forty individuals of *Mulinum spinosum* shrubs of similar size and established plots of 3.76 m^2 (2 × 1.88 m) around each shrub in a 2 ha grazing enclosure, which had been fenced 2 years before starting the experiment. Our treatments included three levels of rainfall interception (30, 55, and 80%) and an ambient control. We used fixed-location rainout-shelters for passively intercepting precipitation while minimally affecting other environmental variables (Yahdjian and Sala 2002). We randomly assigned the plots to one of three drought treatments or as a control, so each interception level was replicated ten times and we also had ten control plots without rainout shelters. Our response variables were litter decomposition and N and P release of *S. speciosa*, measured for a 20-month period, and soil inorganic nitrogen, and in situ net N mineralization, measured for two consecutive years.

Rainout Shelters

Each rainout-shelter type had a roof, made of bands of transparent acrylic without UV filter (acrilicopaolini®), which blocked different amounts of incoming rainfall. We tested the performance of the three kinds of shelters and we found that the amount of water intercepted by each rainout shelter type (30, 55, and 80% rainfall interception) was quite near the expected values (Yahdjian and Sala 2002). Soil water content was significantly lower under the rainout shelters in comparison with controls (Yahdjian and Sala 2002). The edge effect in sheltered plots was small but nevertheless we made all the measurements in the center of the plots. The effects of the shelters on micro environmental variables such as radiation, air temperature, and soil temperature were minimal. The maximum effect was observed under the shelter that intercepted the largest fraction of precipitation (80%) and still it was quite small, with average radiation reduction of less than 10% (Yahdjian and Sala 2002).

Decomposition Experiment

We carried out a decomposition experiment using the litterbag approach, a widely used method to study decomposition at soil surface, in which we confined recently-senesced leaves of *S. speciosa* in mesh bags, placed them on the ground, and collected them at periodic intervals (Singh and Gupta 1977). We anchored four litterbags of leaves in the field at each plot (ten plots per treatment). We collected litterbags at 3, 7, 15 and 20 months, randomly selecting one bag per plot at each date.

We used a 2 mm-mesh size, large enough to allow access to mesofauna and most macrofauna, yet small enough to avoid excessive loss of large litter fragments (Robertson and Paul 2000). We collected senescent leaves of *S. speciosa* in May 1999 from the Patagonian steppe, close to the area where the rainout shelters were installed, and we transported the leaves to the laboratory to select uniform material and to air dry it. Then, we oven dried (70°C for 24 h) subsamples of the leaves to calculate initial moisture content of the air dried leaves, and to determine initial values for ash-free dry mass (500°C for 4 h), total nitrogen, and phosphorus content using a Kjeldahl digest procedure. We placed 1.00 g of air-dried leaves of *S. speciosa* in 10 × 10 cm fiberglass litterbags. In October 1999, we anchored the litterbags in the field, on bare soil, and secured them with wire pins to prevent movement. 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, and so on.) and dried them at 70°C for 48 h for determination of dry mass. We determined ash-free dry mass on subsamples of ground material, and we analyzed subsamples for total nitrogen and phosphorus using a Kjeldahl digests procedure. Nutrient determinations were completed on an Alpkem® autoanalyzer (O-I Corporation, College Station, Texas, USA), which uses a colorimetric analysis of inorganic nitrogen and phosphorus in liquid extracts.

We fitted data for litter ash-free dry-mass remaining to a negative exponential model (Olson 1963):

$$x_t/x_o = e^{-kt}$$

Where x_o 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}. We performed the regressions of $\ln(x_t/x_o)$ over time separately for each set of litterbags in each plot to provide independent estimates of k in the various decomposition microenvironments ($n = 10$).

Soil Nitrogen Dynamics

We estimated *in situ* net N mineralization rates during each incubation period as the difference between initial and final content of ammonium and nitrate in tubes that prevented plant uptake (Raison and others 1987). In addition, as repeated samples taken through an annual cycle allow an estimate of annual net N mineralization (Pastor and others 1984), we calculated annual net N mineralization for the two experimental years. Net N mineralization measured with the tubes incubated in the field represents mineralization in excess of microbial immobilization, in the absence of plant uptake (Kaye and Hart 1997).

The PVC tubes were 5 cm diameter, and we placed them in bare soil to a depth of 7.5 cm, at least 15 cm from adult plants in each of the forty plots. Every 2–3 months, we collected soil from the cylinders and we replaced the tubes in a location 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 discarded soil samples containing roots because presence of freshly dead fine roots may alter the balance between N immobilization and N mineralization (Binkley and Vitousek 1989; Hook and Burke 1995). 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 (NH_4^+ and NO_3^-). We kept soil samples cold until return to the laboratory and filtered extracts as soon as possible.

In the laboratory, we placed a subsample of soil in a drying oven at 105°C for 48 h for determination of gravimetric soil water content. We simultaneously measured gravimetric soil water content inside and outside net N mineralization tubes. We corrected soil nitrogen concentrations for soil water content (Robertson and others 1999), and we converted these concentrations and the N mineralization rates to an aerial basis (mass of N per unit area of soil) using bulk density for the fine soil fraction from Paruelo and others (1988). We analyzed soil extracts using an Alpkem® autoanalyzer (O-I Corporation, College Station, Texas, USA), which uses a colorimetric analysis of inorganic nitrogen in liquid extracts.

Statistical Analyses

We subjected data for remaining litter mass and litter N and P content to a two-way analysis of variance, with drought and time as treatments (time was an independent factor because at any one sampling time a completely independent sample was collected). To test if the method used to estimate net N mineralization in the field produced changes in soil water content, we performed a paired *t*-test between gravimetric soil water content inside and outside net N mineralization tubes with all treatments and for all dates. Statistical analyses were performed using PROC GLM and PROC REG in the SAS version 6.12 package (SAS Institute, Cary, NC) and orthogonal single degrees of freedom contrasts. Unless otherwise stated, significance was assumed at $P < 0.05$. Data for N soil content were analyzed with repeated measures ANOVA with drought 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.

RESULTS

Precipitation and Experimental Water Inputs

Annual precipitation at Río Mayo was very similar during the 2 years of the rainfall manipulation experiment, with 140 mm the first year and 155 mm the second, a value quite similar to the 20-year mean of 168 mm. The seasonal distribution of rainfall was typical of the Patagonian steppe, with maximum precipitation occurring in fall and winter periods (March–September) (Figure 1). The precipitation of the year previous to the start of water manipulations was also near the mean of the site, 164 mm, so conditions prior to the experiment were normal.

The amount of water intercepted by the three kinds of shelters measured during a 4-month period was approximately similar to the expected value. For the 30% interception treatment, we measured a 29% interception; for the 55% interception treatment, we measured 47% interception, while for the 80% interception treatment, we observed a 71% interception, which was significantly lower than the expected value (Yahdjian and Sala 2002). We used observed percentages to calculate the amount of water input in each treatment plot by subtracting the percentage of intercepted water to the incoming rainfall in our study site.

Decomposition

Decomposition rates varied significantly ($P < 0.001$) among rainfall interception treatments. Litter under the 80% interception treatment decomposed more slowly ($k = 0.152 \pm 0.019$ y^{-1}, mean ± SE, $n = 10$) than the litter from either 55% interception ($k = 0.180 \pm 0.018$ y^{-1}) or 30% interception ($k = 0.201 \pm 0.013$ y^{-1}), which did not differ significantly between them (Tukey test, $P > 0.05$). Finally, mean litter decay rate in control plots was the highest ($k = 0.236 \pm 0.009$ y^{-1}) (Figure 2). All exponential regressions used to describe mass loss through time were significant (average $r^2 = 0.85$).

After 20 months of decomposition, on average 31% of the initial litter was lost in control plots, an amount significantly different ($P < 0.001$) from the 20% mass lost from litter bags placed under the 80% rainfall-interception treatment (Figure 2). As

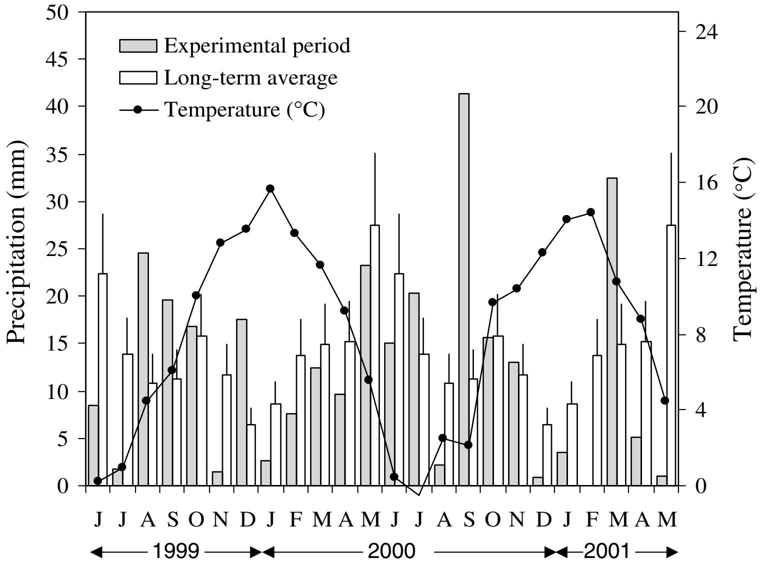

Figure 1. Monthly precipitation and monthly average temperature at the Río Mayo experimental study site in the Patagonian steppe during the manipulation period (June 1999–May 2001) and the long-term average monthly precipitation (mean + SE).

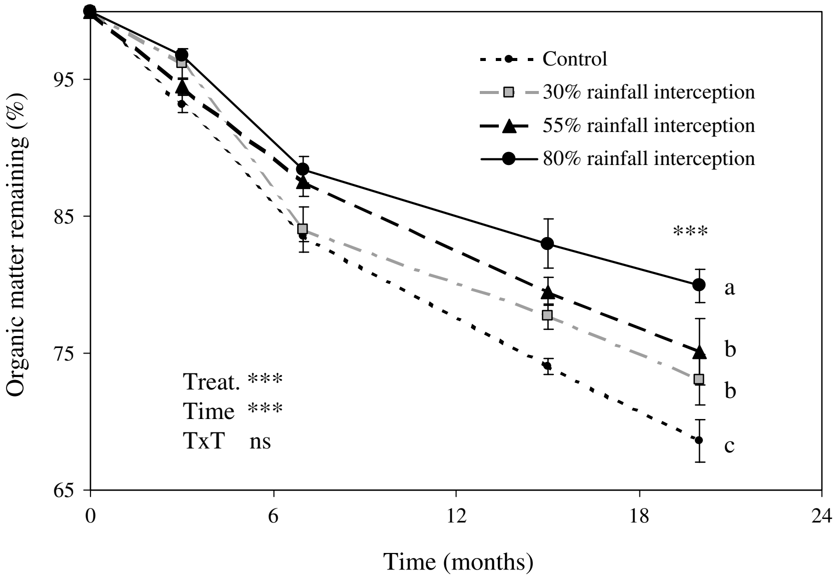

Figure 2. Mass loss through time of a common substrate, leaf litter of the grass *Stipa speciosa*, for different experimental rainfall interception treatments. The rainfall interception levels were 0% (control), 30, 55, and 80% of incoming rainfall and total precipitation during the 20-month (October 1999–May 2001) period was 571 mm. Mean values of mass remaining are on an ash-free basis (± SE) for $n = 10$. Significance of main effects of treatment (Treat.) and time (Time) are noted as $^{***}P < 0.001$; *ns* not significant. The ANOVA of the last date was significant ($P < 0.001$), and groups with different letters were significantly ($P < 0.001$) different.

expected, under the intermediate rainfall exclusion treatments, percent of mass loss was intermediate, 27 and 25% under the 30 and 55% interception rainfall respectively (Figure 2).

The initial N content of *S. speciosa* was 0.37 ± 0.015%, (mean ± SE, $n = 7$), and the P content was 0.04 ± 0.0018%. The remaining nitrogen content (expressed as percentage of initial amount calculated as = $\%N_{t1} \times mass_{t1}/\%N_{t0} \times mass_{t0}$) of decomposing litter changed over time, with different dynamics for the different treatments (Figure 3A). In plots that received more rainfall (control and 30% interception treatments), litter first immobilized N, and then shifted to releasing N after 7 months. Under the other two treatments, however, no N immobilization was recorded and the amount of the N released was related to the incoming water, being less in the 80%-water interception treatment than in the 55%-water interception, although the differences were not statistically significant (Figure 3A). Phosphorus dynamics followed a different pattern than nitrogen, with no immobilization occurring in any treatment. There were steady declines in phosphorus content over the period analyzed, the effect of precipitation on P released was significant ($P <$ 0.05) and the amount of P lost from litter increased with increasing rainfall input (Figure 3B).

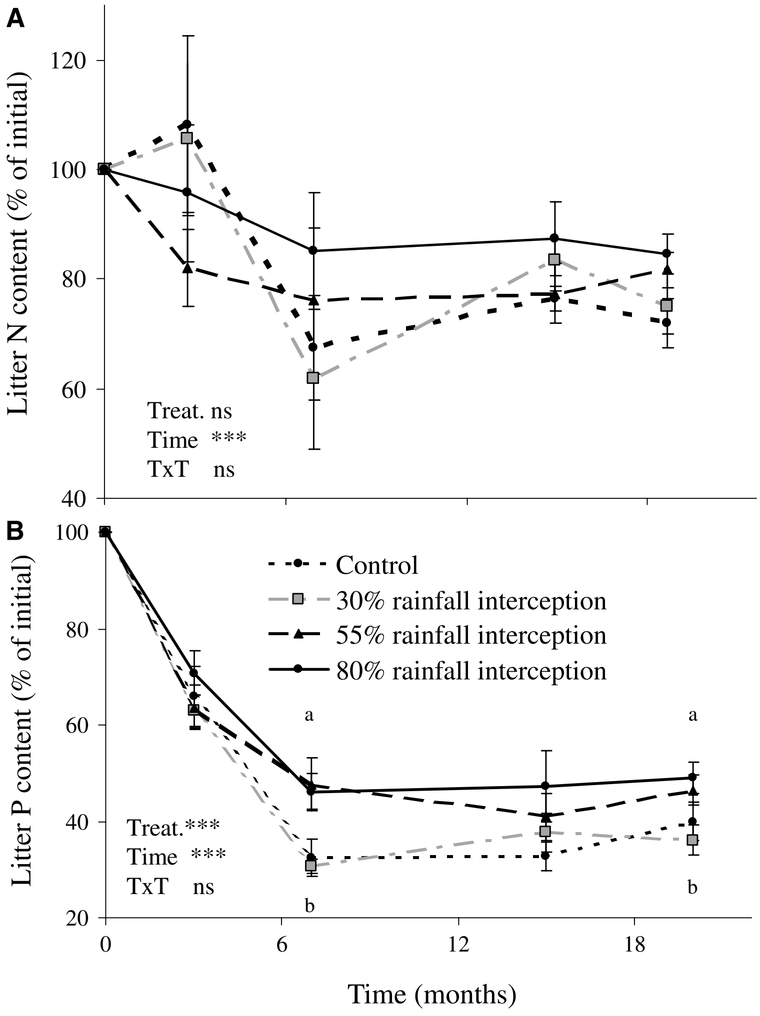

Figure 3. Nutrient release from litter during decomposition, expressed as percent of initial nutrient content, for (**A**) litter N content and (**B**) litter P content along the decay continuum of *Stipa speciosa* litter for different experimental rainfall-interception treatments. The rainfall-interception levels were 0% (control), 30, 55, and 80% of incoming rainfall and the amount of precipitation during the 20 months (October 1999–May 2001) period was 571 mm. Mean values (± SE) for $n = 10$. Significance of main effects of treatment (Treat.) and time are noted as $^{***}P < 0.001$; *ns* not significant. Different letters represent significant differences within a given date ($P < 0.05$).

Soil Nitrogen Dynamics

We found significant differences among treatments in soil NO_3^- concentration during the second year of rainfall manipulations with the general trend of higher NO_3^- concentration with decreasing rainfall input (Figure 4a). Soil nitrate seasonal fluctuations were similar along the 2 years and were characterized by higher concentrations during spring and summer (October–April) and minimal in autumn and winter (May–October). Nitrate concentrations in the upper soil layers varied between 0.002 and 0.02 g/m^2, and were similar to the amounts reported by Austin and Sala (2002) for the same site during the same time periods. This ecosystem has a higher fraction of inorganic N as nitrate when compared to adjacent systems with higher precipitation (Austin and Sala 2002). Soil ammonium concentration at 0–5 cm depth varied between 0.02 and 0.10 g/m^2, and we did not find significant treatment effects, in contrast with that observed for NO_3^- (Figure 4B). Soil ammonium content showed significant seasonal trends during the 2 years of the experiment, and the highest concentrations were found in January and the lowest in December and May.

Net nitrogen mineralization followed a clear seasonal pattern during the 2 years of the experiment, which followed the annual temperature changes at our study site, with high values in summer and low in winter periods (Table 1, see also Figure 1). Differences among dates were more important than differences among treatments of water input. Gravimetric soil water content did not differ inside and outside the net N mineralization tubes, (paired-*t* test with all dates and treatments: $t_{314} = 1.198$, $n = 315$, $P = 0.23$).

DISCUSSION

The effects of water input on litter decomposition appear to be different from the effects on net N

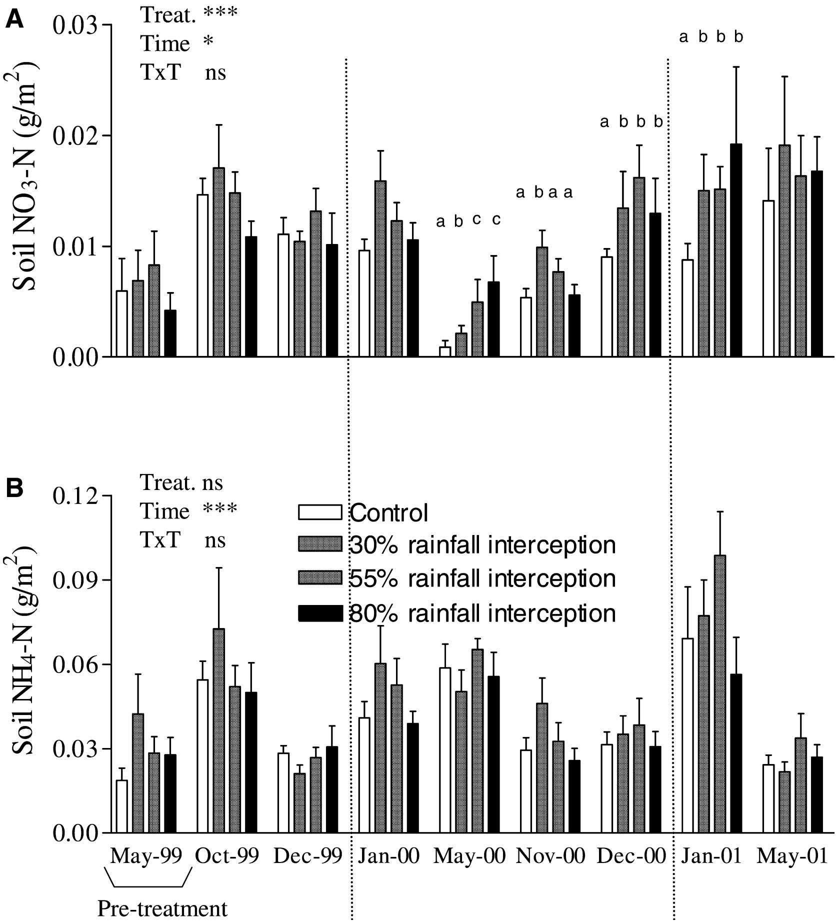

Figure 4. Soil nitrate (**A**) and ammonium (**B**) concentrations for different experimental rainfall interception treatments. The rainfall interception levels were 0% (control), 30, 55, and 80% of incoming rainfall. *Each bar* represents mean (+SE) for $n = 10$. Significance of main effects of treatment (Treat.) and Time are noted as $*P < 0.03$; $***P < 0.0001$; *ns* not significant. Different letters represent significant differences for a given date ($P < 0.05$).

Table 1. *In situ* Net N Mineralization under the Rainfall Interception Treatments

	Control mg/m^2	30% rainfall interception mg/m^2	55% rainfall interception mg/m^2	80% rainfall interception mg/m^2
Year 1				
Winter	0.14 (0.04)	0.02 (0.06)	0.13 (0.02)	0.23 (0.04)
Spring	−0.27 (0.09)	0.13 (0.33)	−0.20 (0.12)	0.00 (0.12)
Summer	0.83 (0.05)	1.07 (0.16)	1.01 (0.26)	1.08 (0.11)
Autumn	0.15 (0.09)	0.03 (0.09)	0.13 (0.04)	0.23 (0.08)
Year 2				
Winter	−0.09 (0.01)	−0.07 (0.01)	−0.15 (0.09)	−0.14 (0.04)
Spring	0.46 (0.04)	0.07 (0.12)	0.77 (0.04)	1.15 (0.09)
Summer	1.36 (0.16)	1.50 (0.04)	2.65 (0.12)	2.01 (0.16)
Autumn	−0.37 (0.08)	−0.27 (0.16)	−0.54 (0.07)	−0.37 (0.12)

In situ *net N mineralization for different seasons under the rainfall interception treatments during the two-year manipulation experiment (mean values for n = 10, 1 SE in parentheses). The rainfall interception levels were 0% (control), 30, 55, and 80% of incoming rainfall. The effect of treatment was not significant, whereas the effect of time was significant at P < 0.001.*

mineralization in the semiarid Patagonian steppe. With our rainfall manipulation experiment, we constructed an experimental rainfall gradient in a single site and found that litter decomposition was linearly related to water input (Figure 5). Decomposition constants (k, y^{-1}) were positively correlated with the annual incoming precipitation (APPT, mm/year), with:

$$k = 0.0007 * \mathrm{APPT} + 0.137, r^2 = 0.31, P = 0.0002$$

In contrast, *in situ* net N mineralization was not correlated with incoming rainfall for the same

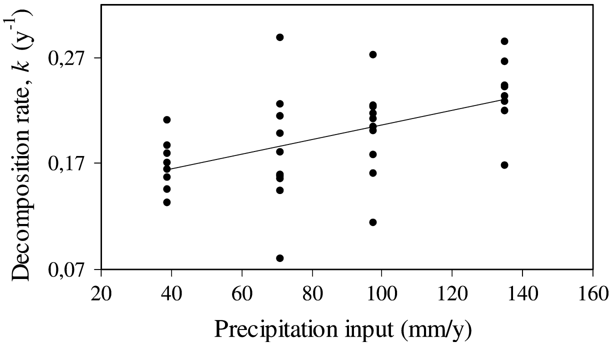

Figure 5. Relationships between annual incoming precipitation (APPT, mm/year) and decomposition rates (k, year^{-1}) of litter of *Stipa speciosa* measured in rainfall interception plots. *Each symbol* represents the k value in one plot, which was estimated by five litterbag collections. The x axis represents the precipitation during the decomposition process in the four treatments expressed on an annual basis (see Figure 2 for rainfall interception treatments). The regression equation is $k = 0.0007*\mathrm{APPT} + 0.137$, $r^2 = 0.31$, $P = 0.0002$.

rainfall gradient, as net N mineralization did not differ among treatments in any of the dates analyzed (Table 1). On an annual basis, we also did not find a significant relationship between annual net N mineralization and annual water input (Figure 6). This result is in agreement with seasonal studies in the semiarid short grass steppe (MAP 321 mm) where increased soil water content did not result in significant increases in net N mineralization (Hook and Burke 2000). Similarly, Barrett and others (2002) showed that there was no relationship between in situ net N mineralization and mean annual precipitation along a spatial precipitation gradient in the Central US grasslands, in spite of the modeled predictions that suggested a linear increase in net N mineralization with increasing rainfall (Burke and others 1997).

Although there were no differences in net N mineralization among treatments, we did find that under high water-interception treatments, soil nitrate concentrations were significantly, and up to 50% higher, than nitrate concentrations in control plots (Figure 4). Plants of the dominant species of the Patagonian steppe preferentially absorb NO_3^- than NH_4^+ (Austin and others in press), such that even small differences in nitrate concentrations might have important consequences on primary productivity for this site. Other studies have shown an accumulation of inorganic N with drought in deserts (Fisher and others 1987; Reynolds and others 1999) and in seasonally dry tropical forests (Garcia-Méndez and others 1991; Davidson and others 1993). Accumulation of inorganic N near sites of mineralization can occur because movement of ions is restricted in thin water films of dry soil and because sinks of inorganic N are limited by reduced microbial growth and plant uptake (Stark and Firestone 1995). Another possible explanation for the difference in soil nitrate between water interception treatments and control plots is the differential leaching in plots that received different amounts of rainfall. Nitrogen loss from the soil by leaching was generally assumed to be negligible in deserts ecosystems (West and Skujins 1978; Peterjohn and Schlesinger 1990), however recently Walvoord and others (2003) found a large reservoir of bioavailable nitrogen in subsoil zones of arid regions that suggests important long-term leaching from desert soils.

When we analyzed the percent N remaining in litter (as a proportion of the initial N content) as a function of the mass remaining, we observed that carbon and nitrogen are being lost from litter in a proportional way (Figure 7A), which was different from the dynamics of the P loss from decomposing litter (Figure 7B). The percent mass remaining and percent N remaining for all of our treatments fall approximately on the 1:1 line indicating that C and N are being lost simultaneously.

The temporal synchrony between C and N loss in the litter layer and their relationship with incoming rainfall contrasts with the lack of response to net N mineralization occurring in the soil. And so, the question remains: why are there such large differences in the response to changes in rainfall input for litter decomposition, nutrient release, net N mineralization, and soil nitrate? We suggest that although water availability equally affects the mineralization of C and N, it differentially affects the movement and fate of their inorganic products. Carbon inorganic products mostly evolve as CO_2 whereas N inorganic products (NH_4^+ and NO_3^-) mostly dissolve and move downward into the soil solution even in arid regions (Peterjohn and Schlesinger 1990; Schlesinger and others 1996; Walvoord and others 2003). Water availability would control in similar ways the first stage of C and N mineralization but would affect differentially the fate of the inorganic products. C loss is affected by water availability only as it directly affects the conversion of organic matter to CO_2. On the contrary, water input affects the mineralization per se, and also affects the movement of inorganic N products. Increasing water availability would increase decomposer activity and gross N mineralization but also would increase the leaching of inorganic products. Because nitrate is relatively

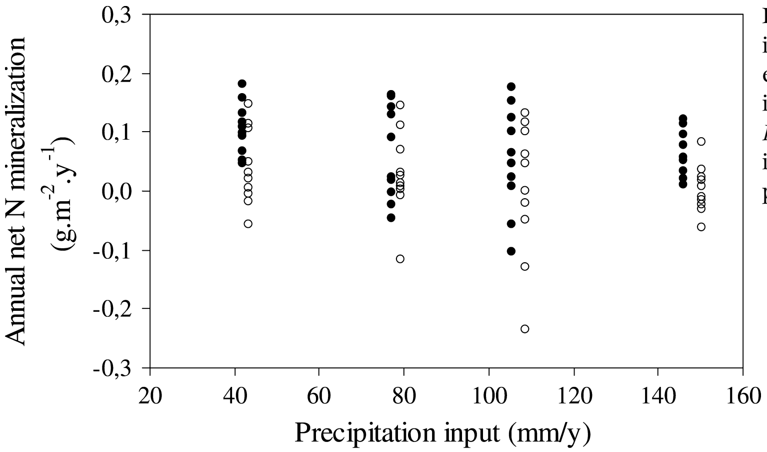

Figure 6. Relationships between annual incoming precipitation (APPT) and annual net N mineralization measured in situ in rainfall interception plots for two consecutive years. *Each symbol* represents the annual net N mineralization in one plot, which was estimated by repeated samples taken through an annual cycle.

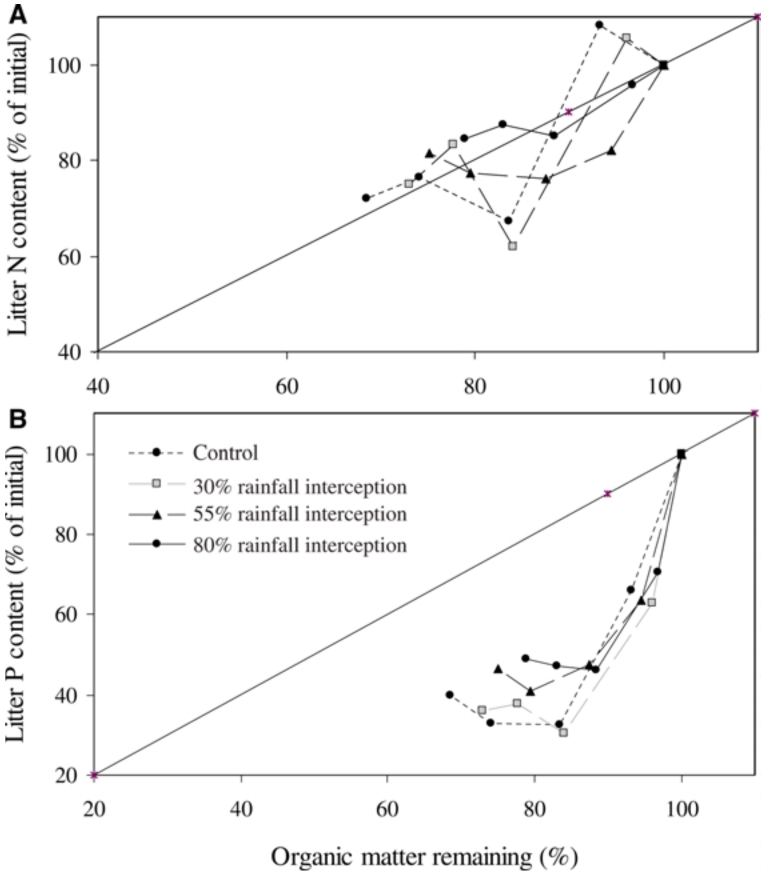

Figure 7. Relationships between the percent organic matter remaining of *Stipa speciosa* and the percent of initial (**A**) litter N content and (**B**) litter P content, at the 3, 7, 15, and 20 months incubation. The rainfall interception levels were 0% (control), 30, 55, and 80% of incoming rainfall. *Each point* represents mean values for $n = 10$.

mobile in soil solution, it readily moves to plant roots or leaches with water percolation. In a study of inorganic nitrogen distribution with depth in the soil profile in the Patagonian steppe, NO_3^- concentration declined from 0.4 µg/g at the soil surface to 0.1 µg/g at 15 cm depth, and continuously decreased until 0.03 µg/g at 100 cm depth, both in the peak of the growing season and in autumn (Sala and others unpublished). With increasing rainfall, increased gross mineralization must have been offset by increasing NO_3^- leaching, especially in the absence of plant uptake, and yielded no differences in net N mineralization. Under reduced water-input treatments, leaching may be less important and that may be the reason for higher soil NO_3^- content in these plots than in controls. Another possible explanation for the observed differences in the rainfall control on decomposition and net N mineralization is the different substrate, litter in the former and soil in the latter. Those two substrates under a similar rainfall regime may have different water potential, and consequently different microbial activity.

Our results on the relationship between water input and decomposition differed from other decomposition studies in sites of different rainfall in arid and semiarid environments. Whitford and others (1981) and Santos and others (1984), who worked in four deserts in North America found no correlation between rainfall and decomposition. Steinberger and others (1990) who studied decomposition along a broad rainfall gradient of 100–500 mm and Hamadi and others (2000) on a 120–620 mm gradient, both in the Judean desert of Israel, found that there was no significant correlation between rainfall and mass loss, although higher rainfall sites did show faster decomposition.

In contrast, our results are supported by the findings of Strojan and others (1987) who showed that rates of surface litter decomposition of leaves of three species of Mojave Desert shrubs were strongly correlated with actual rainfall and by Jacobson and Jacobson (1998) who found that rainfall regulated decomposition of buried cellulose in the Namib desert. Also Schaefer and others (1985) found a strong positive relationship between mass loss of buried litter of six different litter types and AET in a North American desert, although they found no relationship between AET and decomposition from surface litterbags. Comparable decomposition rates for leaf litter in arid environments have been reported in desert of North America, Argentine grasslands, and through the US Great Plains (Gholz and others 2000; Epstein and others 2002; Moretto and Distel 2003).

Direct and indirect effects of precipitation on decomposition differ and may overshadow each other along spatially-defined precipitation gradients. Direct effects of precipitation result in an increase in decomposition through changes in leaching and on decomposer activity. Indirect effects of precipitation on decomposition occur via changes in floristic composition and the associated changes in litter quality and microbial species composition. Litter quality has been shown to decrease with increasing precipitation, which may reduce decomposition (Austin and Vitousek 2000; Murphy and others 2002), whereas changes in abundance and species composition of microorganisms may increase decomposition (González and Seastedt 2001). If the direct effects of precipitation on decomposition were constant and our model of direct effects valid across ecosystems, we speculate that the difference between spatial models and our model would be an estimate of the indirect effects of precipitation on decomposition. Several studies along spatial rainfall gradients confounded direct and indirect effects of precipitation through changes in both litter quality and rainfall gradient; (Dyer and others 1990; Aerts 1997) whereas many fewer studies separated direct and indirect effects (Vitousek and others 1994; Austin and Vitousek 2000; Hamadi and others 2000). Our results in this paper along with results of Lauenroth and Sala (1992) and Burke and others (1997) relating temporal and spatial patterns of rainfall and net primary production indicate that we cannot induce temporal controls of climate on ecosystem processes from spatial gradients. The study presented here allowed us to disentangle direct and indirect effects of precipitation on litter decomposition. If the changes in water inputs in this site were continuous, however, long-term consequences could include changes in ecosystem structure, species composition, and primary production, as well as changes in litterfall quantity or litter quality (indirect effects). These long-term responses to precipitation changes may resemble the responses observed in spatial gradients of precipitation.

A consequence of the accumulation of inorganic N during dry episodes is that periods of maximum water and soil nutrient availability may occur at different times, with moments when inorganic nutrient concentrations are high, but plants are either senescent or unable to respond to nutrient pulses (Jackson and others 1988; Austin and Vitousek 1998). Annual primary production in years following dry years was lower than expected based on the incoming rainfall and this low production lasted for 2 or 3 years after a severe drought (Lauenroth and Sala 1992; Jobbágy and Sala 2000). Our results suggest a mechanism for the observed lags in production and a test to the hypothesis of the biogeochemical constraints on primary production. During dry years, net N mineralization is less inhibited than plant and microbial immobilization, resulting in increased soil nitrate that is vulnerable to loss via leaching (Austin and others 2004). The first rainfall events following a dry year would result in large N leaching losses from the system. Consequently, primary production could be limited by N availability during years following a drought. N losses during the first rainfall could be large not only because of the abundance of vulnerable soil nitrate but also because of the reduced uptake capacity of plants constrained in their growth potential during the previous drought. This asynchrony in the availability of N and water in the soil may explain the observed lags in the response of primary production to increases in water availability (Lauenroth and Sala 1992) and the persistence of low N availability in arid and semiarid ecosystems.

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