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ECOSYSTEMS

Size of Precipitation Pulses Controls Nitrogen Transformation and Losses in an Arid Patagonian Ecosystem

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ABSTRACT

Arid ecosystems receive precipitation pulses of different sizes that may differentially affect nitrogen (N) losses and N turnover during the growing season. We designed a rainfall manipulation experiment in the Patagonian steppe, southern Argentina, where we simulated different precipitation patterns by adding the same amount of water in evenly spaced three-small rainfall events or in one-single large rainfall event, three times during a growing season. We measured the effect of the size of rainfall pulses on N mineralization and N losses by denitrification, ammonia volatilization, and nitrate and ammonia leaching. Irrigation pulses stimulated N mineralization ($P < 0.05$), with small and frequent pulses showing higher responses than large pulses ($P < 0.10$). Irrigation effects were transient and did not result in changes in seasonal net N mineralization suggesting a long-term substrate limitation. Water pulses stimulated gaseous N losses by denitrification, with large pulses showing higher responses than small pulses ($P < 0.05$), but did not stimulate ammonia volatilization. Nitrate leaching also was higher after large than after small precipitation events ($P < 0.05$). Small events produced higher N transformations and lower N losses by denitrification and nitrate leaching than large events, which would produce higher N availability for plant growth. Climate change is expected to increase the frequency of extreme precipitation events and the proportion of large to small rainfall events. Our results suggest that these changes would result in reduced N availability and a competitive advantage for deep-rooted species that prefer nitrate over ammonia. Similarly, the ammonium:nitrate ratio might decrease because large events foster nitrate losses but not ammonium losses.

Key words: nitrogen–water interactions; precipitation pulses; net N mineralization; denitrification; ammonia volatilization; arid ecosystems; Patagonian steppe; soil inorganic N; nitrate leaching.

INTRODUCTION

Water availability has been identified as the main control of ecosystem functioning in arid and semiarid ecosystems (Noy-Meir 1973; Le Houérou and others 1988; Sala and others 1988). However, nitrogen (N) also has been shown to limit net primary production in desert ecosystems (West and Skujins 1978; Hooper and Johnson 1999;

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Krueger-Mangold and others 2004; Yahdjian and others 2010); and interactions between water and N availability were reported for several low precipitation ecosystems (Gutierrez and others 1992; Evans and Ehleringer 1994; Hooper and Johnson 1999). N is one of the most frequently limiting elements to plant growth in terrestrial ecosystems (Vitousek and Howarth 1991; LeBauer and Treseder 2008) and its availability is mainly controlled by internal cycling (Schlesinger 1997). Therefore, potential N losses from ecosystems have a long-lasting effect on nutrient availability and primary production. In addition, some N gaseous losses have greenhouse potential and leaching losses may negatively affect water quality and freshwater ecosystems (Howarth and others 1996).

Nitrogen gaseous losses and leaching in arid ecosystems are mainly controlled by precipitation pulses (Austin and others 2004; McCalley and Sparks 2008). As precipitation in arid ecosystems usually occurs as discrete rainfall events interspersed by dry periods, soils experience wet-dry cycles that have large biological consequences (Austin and others 2004). During inter-pulse periods, turnover of both C and N slows down, microbial death occurs, and plant uptake is reduced, leading to an increase in soil NO_3^- (Yahdjian and others 2006). When soils are rewetted, C and N mineralization is stimulated, increasing soil microbial biomass and reducing labile organic matter pools (Austin and others 2004). Also, potential loss of N may increase after a precipitation event due to increased nitrification, leaching, and denitrification (McCalley and Sparks 2009). In arid ecosystems, denitrification rates after precipitation pulses may be comparable to those in mesic environments (Peterjohn and Schlesinger 1991; Groffman and others 1993; Mummey and others 1994; Zaady and others 1996; McCalley and Sparks 2009), and precipitation events can stimulate ammonia volatilization in desert soils (Schlesinger and Peterjohn 1991; McCalley and Sparks 2008). In addition, nitrate leaching in arid ecosystems was considered negligible (Peterjohn and Schlesinger 1990), but Waldvoord and others (2003) found a large reservoir of bioavailable N in subsoil zones of arid regions that suggests important long-term leaching from desert soils.

The Patagonian steppe is an arid ecosystem dominated by grasses and shrubs with low vegetation cover (Golluscio and others 1982). Vegetation is distributed in patches and two contrasting microsites can be identified: dense vegetated patches formed by shrubs surrounded by a ring of grasses and scattered tussocks in a bare soil matrix (Soriano and others 1994). Precipitation is scarce and variable among years, with a clear seasonality with rainfall concentrated during fall and winter (Paruelo and others 1998). N availability is low (0.1 g N m^{-2}) (López and others 2003; Yahdjian and others 2006), which suggests that N may limit primary production at least during some periods of the year.

Global climate change will involve changes in the size of precipitation events (Easterling and others 2000), which may affect nutrient cycling. Also, anthropogenic activity may reduce N availability within arid ecosystems due to grazing (Evans and Ehleringer 1993; Schlesinger and others 1996) or may increase availability due to N deposition (Galloway and others 2004; Báez and others 2007; Galloway and others 2008). Although arid ecosystems occupy 40% of the terrestrial surface (Reynolds and others 2007), information relating N cycling in these ecosystems and its relationship with the water cycle is still scarce. Our general objective was to examine the effects of size of precipitation pulses on N transformations and losses during the growing season in an arid ecosystem, the Patagonian steppe. The specific hypotheses that guided our study were: (1) small precipitation events will stimulate N mineralization more than large precipitation events; (2) small precipitation events will stimulate N gaseous losses more than large precipitation events; (3) large precipitation events will stimulate N leaching losses more than small events. The rationale for these hypotheses is based on the location in the soil profile of microbial activity and moisture resulting from small or large events. Sala and Lauenroth (1982), in an article focused on plant responses to small events, hypothesized that small events, which wet only the uppermost layers of the soil, will have a larger impact on N cycling than large events because substrate for N mineralization is concentrated on the upper horizons. Small events would enhance gaseous losses resulting from microbial activity in the top layers of the soil whereas large events, which penetrate deep into the soil profile, may result in infrequent but significant N leaching events.

To test these hypotheses, we designed a rainfall manipulation experiment in the Patagonian steppe, in Southern Argentina, where we simulated different precipitation patterns by adding the same amount of water in evenly spaced three-small rainfall events or in one-single large rainfall event. We repeated this irrigation pattern three times during the growing season, in October, December and, January. We also had control plots, without water addition. We evaluated the effect of the size of rainfall pulses on N mineralization and N losses during the growing season in vegetated and bare soil patches.

MATERIALS AND METHODS

Study Site

We conducted this research in the Río Mayo Experimental research site managed by the Instituto Nacional de Tecnología Agropecuaria (INTA), Chubut, Patagonian region of Argentina (45°41′ S, 70°16′ W, and elevation 500 m.a.s.l.). Climate at the site is arid/semiarid with rainfall concentrated during fall and winter (March–September). The mean annual rainfall recorded over 20 years was 168 mm, with a range between 90 and 275 mm. Long-term mean annual temperature of the site was 8.4°C, with mean monthly temperature ranging from 1°C in July to 15°C in January. The topography is flat; soils are coarse textured with pebbles, which account for 47% of its weight in the upper soil layer, and have a cemented-calcareous layer at a depth of about 45 cm (Paruelo and others 1988). The combination of flat topography and coarse textured soils determines minimum runoff and relatively high infiltration rates (Paruelo and Sala 1995). Volumetric water content at field capacity (soil water potential, SWP, −0.01 MPa) in the upper layer is 8% and the available water (-0.01 MPa $<$ SWP < -5.9 MPa) for the first 45 cm of the profile is 23 mm (Paruelo and others 1988). Organic matter in the upper soil layer in bare soil patches is 0.4% and pH is neutral (Paruelo and others 1988). Soil ammonium concentration at 0–5 cm depth varies during the year between 0.02 and 0.10 g m^{-2}, and soil nitrate concentration varies between 0.002 and 0.02 g m^{-2}, which accumulates during drought (Yahdjian and others 2006). 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* Trin. et Rupr., *S. humilis* Cav., and *Poa ligularis* Nees ap. Steud. The dominant shrubs are *Mulinum spinosum* (Cav.) Pers., *Adesmia volkmanni* Philippi (ex- *A. campestris*), and *Senecio filaginoides* DC (Golluscio and others 1982). We recorded rainfall and other standard meteorological variables during the course of this experiment using an automatic weather station equipped with a datalogger Campbell SCI 21X (Campbell Sci., Logan, UT, USA), located near the experimental area.

Experimental Design and Manipulations

We designed a manipulative experiment in the Patagonian steppe where we added water in two pulse sizes, small and large events (Sala and others 1992) while maintaining the total amount of water constant. In the Patagonian steppe, events smaller than 5 mm are almost constant among years and the interannual variability of total precipitation is mostly accounted for by the occurrence of a few large precipitation events, as pulses higher than 10 mm (Golluscio and others 1998). We added water in one large 15 mm event and in three separate small 5-mm events, 1 day a part. We had control plots, without water addition; and we repeated treatments three times during the growing season in October, December, and January, to evaluate if responses to water addition were consistent along the growing season. We established 30 plots of 9 m^2 each in May, 10 replicates per treatment, and we applied manipulations during the following growing season (October–January). We randomly assigned plots to treatments. Water pulses were applied with two water sprinklers at 50 cm height, located in the west side of the plots, the predominantly wind direction in our study site. Small pulses consisted of 5-mm pulses, where 45 l of water were uniformly scattered in each 9 m^2 plot, at a rate of 3 l/min. Large pulses consisted of a 15-mm event, achieved by adding 135 l/plot, at a rate of 4 l/min. The rate of water application was similar to the rate of absorption by the soil, to prevent water runoff from the plots. Small pulses were applied during 3 consecutive days, and the large pulse was applied the same day as the third small pulse. In this way, the response variables measured after precipitation pulse addition experienced the same time since the last pulse addition in the small- and large-pulse treatments. Water application was repeated three times during the growing season totaling an extra annual rainfall input of 45 mm/year in both, small- and large-pulse treatments. We extracted the irrigation water from a local well, and we analyzed water for nitrate and ammonium concentration, using an Alpkem® autoanalyzer (O-I Corporation, College Station, TX, USA), which uses a colorimetric analysis for inorganic N in liquid extracts. Ammonium and nitrate concentrations in the irrigation water were 0.012 ± 0.003 and 0.2 ± 0.02 ppm, respectively.

Response Variables

We evaluated soil N transformation and losses from the upper soil in vegetated patches of shrub surrounded by a ring of grasses and in bare soil patches with scattered tussocks during a growing season (October–January). The mean cover of vegetated and bare soil patches in the experimental plots was evaluated using the line-intercept method (Canfield 1941) (Table A1, Appendix A in Supplementary material). As we did not find significant differences in the proportion of patches in the experimental plots, and N fluxes between patch types did not differ either, we averaged fluxes taking into account the mean relative cover of both types of patches to estimate fluxes per square meter of steppe. Complementary, we measured the effect of water manipulations on soil inorganic N content and soil water content in vegetated patches and in bare soil (Figures A1 and A2, Appendix A in Supplementary material).

Net N mineralization was estimated in situ for the 30 experimental plots in vegetated and bare soil patches, in samples taken with PVC tubes of 5 cm diameter and 10 cm depth (Raison and others 1987) that were incubated during a 5-day period. An initial soil sample was collected when the tubes were established, the day before pulse application started, and the final soil samples were collected the day after the manipulations were completely applied. In addition, we evaluated net N mineralization along treatments for the whole period, from October to January, taking repeated samples through the season. Net N mineralization was calculated as the difference in nitrate and ammonium content between incubated and initial soil samples, and related to incubation periods. Net nitrification and net ammonification were calculated in the same way but relating only soil nitrates or soil ammonium, respectively.

Inorganic N leaching was evaluated for the same short periods relating to the rainfall manipulation, with ionic resin bags located at 10 cm depth (Lajtha 1988). Each resin bag contained 2 g of cation-exchange (AG® 50 W-X8 Resin Bio-Rad) and 2 g of anion-exchange resins (AG® 1-X8 Resin Bio-Rad). Initial and incubated soil samples, and resin bags were analyzed for nitrate and ammonium concentrations by extractions with 2 N KCl solution. Nitrate and ammonium concentrations in KCl solutions were determined using the laboratory autoanalyzer (O-I Analytical), and soil N concentrations were corrected for water content, which was estimated by drying 10-g sub-samples at 90°C for 48 h.

Denitrification was analyzed in soil samples of 0–10 cm depth extracted from vegetated and bare soil patches after water manipulations in each sampling date. Open top PVC tubes of 5 cm diameter were incubated in hermetic 1.000 cm^3 plastic jars with 10% v/v acetylene for 48 h to inhibit the last denitrification path (Ryden and others 1979; Mummey and others 1994). Gas extracts were analyzed for N_2O concentration with a gas chromatograph (GC 6890N, Agilent Technologies, San Francisco, USA), and the concentrations were related to dry soil mass and incubation period, after subtracting the blanks.

To estimate ammonia volatilization in each experimental plot, we pounded PVC tubes 20 cm diameter and 30 cm height into bare soil patches up to half their height, and we waited 3 months for equilibration. In each sampling date, 1 day after water manipulations, we collected NH_3 emitted in each tube for 24 h using 10 ml of 4% H_2SO_4 in a small open vial (Schlesinger and Peterjohn 1991). During the collection, we covered the tubes with aluminum foil held with a rubber band. We used silicon grease to ensure a tight seal between the tube and the foil covering (Schlesinger and Peterjohn 1991). We analyzed acid samples collected after 24 h for NH_4^+ concentration, determined colorimetrically with a laboratory autoanalyzer (O-I Analytical). We used differences between samples and blanks to calculate flux rates on an aerial basis, which was converted to a gravimetric basis using soil bulk density (Table A1, Appendix A in Supplementary material). After samples for N_2O flux and NH_3 volatilization were collected, a 10-cm-deep by 5-cm diameter soil core was extracted from bare soil and vegetated patches in each plot for analysis of gravimetric soil moisture and inorganic N ($NH_4^+ + NO_3^-$) content. We determined soil moisture by drying 10-g sub-samples at 90°C for 48 h and used these values to correct estimates of inorganic N for differences in water content. Inorganic N was estimated by extracting 5-g sub-samples in 25 ml of 2 N KCl for 24 h and by determining extracts colorimetrically using an autoanalyzer (O-I Analytical). We found higher soil inorganic N content in vegetated patches than in bare soil for the three dates (Figure A2, Appendix A in Supplementary material).

We measured volumetric soil-water content (SWC) in vegetated and bare soil patches after water manipulations in the 30 plots at 0–20 cm depth with the time domain reflectometry (TDR) technique (Reeves and Smith 1992), employing a Tektronix 1502C (Beaverton, OR, USA). At the initiation of the study, we inserted two pairs of TDR probes, one on vegetated patches and one on bare soil, in each plot, and we left the probes in place to monitor this variable after each manipulation event. SWC of plots corresponding to the treatment with small pulses was evaluated after each small pulse, while plots of the large-pulse treatment were measured once, after the irrigation event. We always measured SWC at the same time of the day (mid-morning), and only made comparisons among treatments within each date.

Statistics

Effects of irrigation pulses on soil water content and N transformations and losses were analyzed by a repeated-measure one-way analysis of variance (ANOVA RM) with three levels of irrigation pulses, and three dates (October, December, and January). Differences in soil inorganic N between microsites were also evaluated with an ANOVA RM with two levels of patches (shrubs surrounded by grasses and scattered tussocks in bare soil matrix) and for the same dates. Assumptions of ANOVA were evaluated using the Shapiro–Wilk test for normality and Levene's test for homogeneity of variance. When these assumptions were violated, data were log transformed. Following ANOVA, linear contrasts were used to analyze a priori comparisons of net N mineralization, denitrification, leaching, and ammonia volatilization among precipitation pulse treatments. Data were analyzed with PROC GLM in the SAS version 6.12 packages (SAS Institute, Cary, NC, USA). Unless otherwise stated, significance was assumed at $P < 0.05$.

RESULTS

Precipitation Patterns and Pulse Manipulation Effects on Soil Water Content

Annual precipitation during the year of the experiment was 141 mm and the amount received during the growing season (October–January) was 44.2 mm (Figure 1A). The addition of 45 mm by irrigation pulses applied three times during the growing season represented a 100% water excess during the growing season, and 26% excess during the year, in relation to control plots, totaling almost 200 mm (Figure 1A). The probability of the occurrence of a year with 200 mm annual precipitations was 0.30, based on the 20-year rainfall record (Rasevich 2008).

Water pulses caused consistent changes in SWC after the experimental rain events in the three dates, October, December, and January (Figure 1B). After small consecutive pulse additions, volumetric SWC at 0–20 cm depth increased daily, and was augmented by 25% on average after the end of the manipulation period in water addition treatments in relation to control (Figure 1B). After the third experimental pulse, precipitation pulses applied as three small pulses of 5 mm each did not cause significantly different volumetric SWC at 0–20 cm depth from precipitation applied as one single 15 mm pulse (Figure 1B). SWC was higher in bare soil than under vegetation patches in all treatments (Figure A1, Appendix A in Supplementary material). Estimated water infiltration in the coarse textured soil of the Patagonian steppe is approximately 5 cm depth for a 5 mm pulse and 15 cm for a 15 mm event when the soil is dry (Pablo Cipriotti, Personal Communication).

Nitrogen Transformations and Losses

Net N mineralization was significantly ($P < 0.001$) higher in irrigated than in control plots in the three manipulation dates, October, December, and January (Figure 2). Both, net ammonification and net nitrification were stimulated by irrigation ($P < 0.05$), and small pulses caused higher mineralization rates than large pulses, but differences were only marginally significant ($P < 0.10$) (Figure 2). Interactions between treatments and time were not statistically significant ($P > 0.05$). Nitrification rates did not change significantly during the growing season, while seasonal differences for ammonification rates were marginally significant (ANOVA RM terms for ammonification: irrigation pulses $F_{2,177} = 6.22$, $P = 0.002$; time $F_{2,177} = 2.73$, $P = 0.08$; for nitrification: irrigation pulses $F_{2,177} = 3.56$, $P = 0.03$; time $F_{2,177} = 0.77$, $P = 0.3$). On average for the three sampling dates, net nitrification was 30% higher under small pulses in relation to control, whereas net nitrification was 19% higher than control under large pulses. Net ammonification was 18 and 15% higher in irrigated plots with small and large pulses, respectively, relative to controls. Interactions between irrigation pulses and time were not statistically significant ($P > 0.05$). Differences in net N mineralization among treatments disappeared when the whole period, from October to January, was considered (control: -0.059 ± 0.08; small pulses: -0.067 ± 0.06; large pulses: -0.08 ± 0.04, μg $N\text{–}NO_3^- + NH_4^+$ g^{-1} dry soil day^{-1} ± SE for $n = 10$).

N losses by denitrification were stimulated by precipitation pulses, with higher responses after large than after small pulses, except in October (ANOVA terms, pulses $F_{2,102} = 3.68$, $P = 0.03$; time $F_{2,102} = 20.4$, $P < 0.001$) (Figure 3A). Ammonia volatilization rates were not stimulated by irriga-

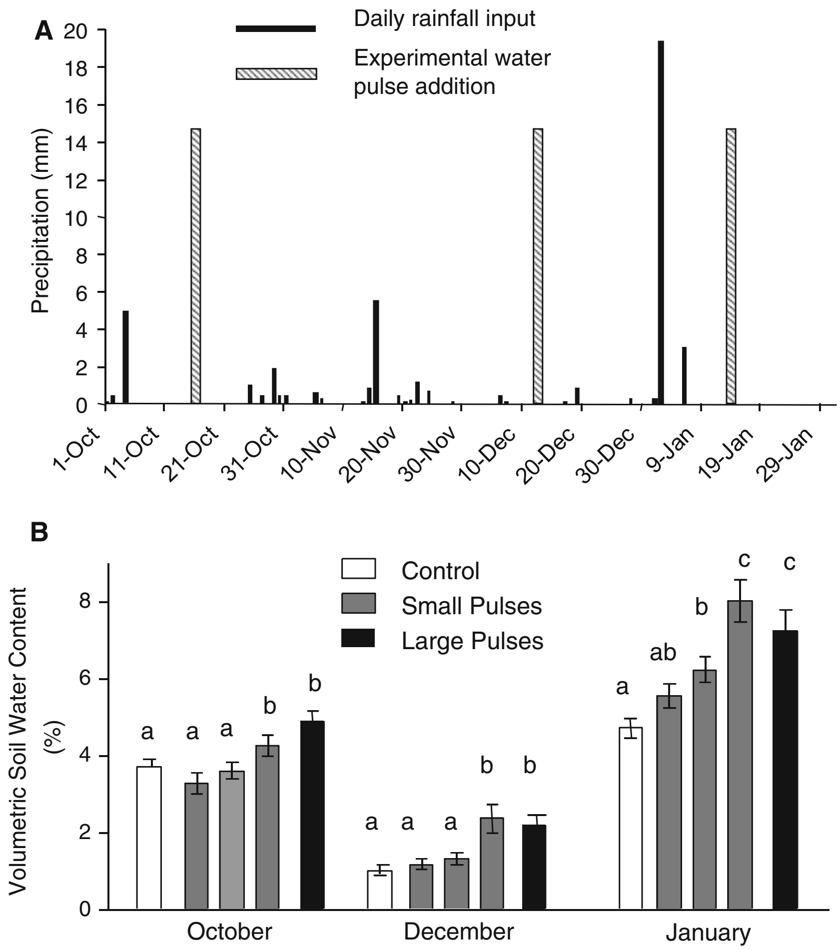

Figure 1. Effects of water-manipulation treatments on rainfall inputs (*upper panel*) and volumetric soil water content at 0–20 cm depth (*lower panel*) for the studied growing season October–January. **A** Daily rainfall inputs: *thin bars* correspond to rainfall events at the study site; *dashed bars* correspond to water irrigation in plots from the pulse treatments that received 15 mm experimental events, in October, December and January, in three small or one large-pulse event in each occasion. **B** Volumetric soil water content: *open bars* correspond to treatments receiving ambient rainfall quantities (*control*) and *solid bars* correspond to treatments with small (*gray*) or large (*black*) irrigation pulses, measured after pulse addition; *bars* represent mean values (±SE) with $n = 20$. *Different letters* show significant differences among treatments within each date at $P < 0.05$.

tion pulses and were similar to denitrification values (Figure 3B). Volatilization rates decreased during the growing season (ANOVA terms, irrigation pulses $F_{2,88} = 13.68$, $P = 0.53$; time $F_{2,88} = 20.4$, $P < 0.001$) (Figure 3B). Ammonia volatilization rates were not correlated with volumetric nor with gravimetric soil water content ($P > 0.05$).

Nitrate leaching from the first 10 cm soil was stimulated by precipitation pulses and was more stimulated under large than small pulses (Figure 4A). In a repeated-measure one-way ANOVA, irrigation pulse size had a significant effect on nitrate leaching, and nitrate leaching increased along the growing season, being maximum in January (ANOVA RM terms, irrigation pulses $F_{2,81} = 8.86$, $P = 0.001$; time $F_{2,81} = 12.27$, $P < 0.0001$). Interactions between pulse size and time were not statistically significant ($P > 0.05$). Ammonium leaching was not stimulated by irrigation pulses and decreased significantly along the growing season (Figure 4B) (ANOVA terms, pulses $F_{2,81} = 0.22$, $P = 0.8$; time $F_{1,81} = 23.4$, $P < 0.0001$).

DISCUSSION

Net N mineralization was stimulated by precipitation pulses; and several small and frequent pulses produced slightly higher rates than a single large pulse with the same amount of water. We also showed that precipitation input stimulated nitrate

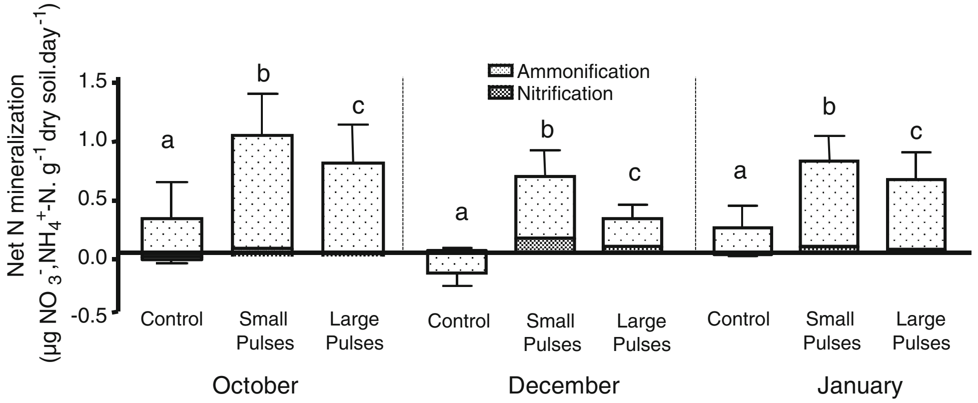

Figure 2. Net nitrification, net ammonification, and net nitrogen mineralization in irrigation treatments and control at 0–10 cm depth, measured in situ during 5-day periods when manipulations were applied. *Bars* represent mean values (+SE) for $n = 20$. *Different letters* show significant differences among treatments within each date at $P < 0.10$.

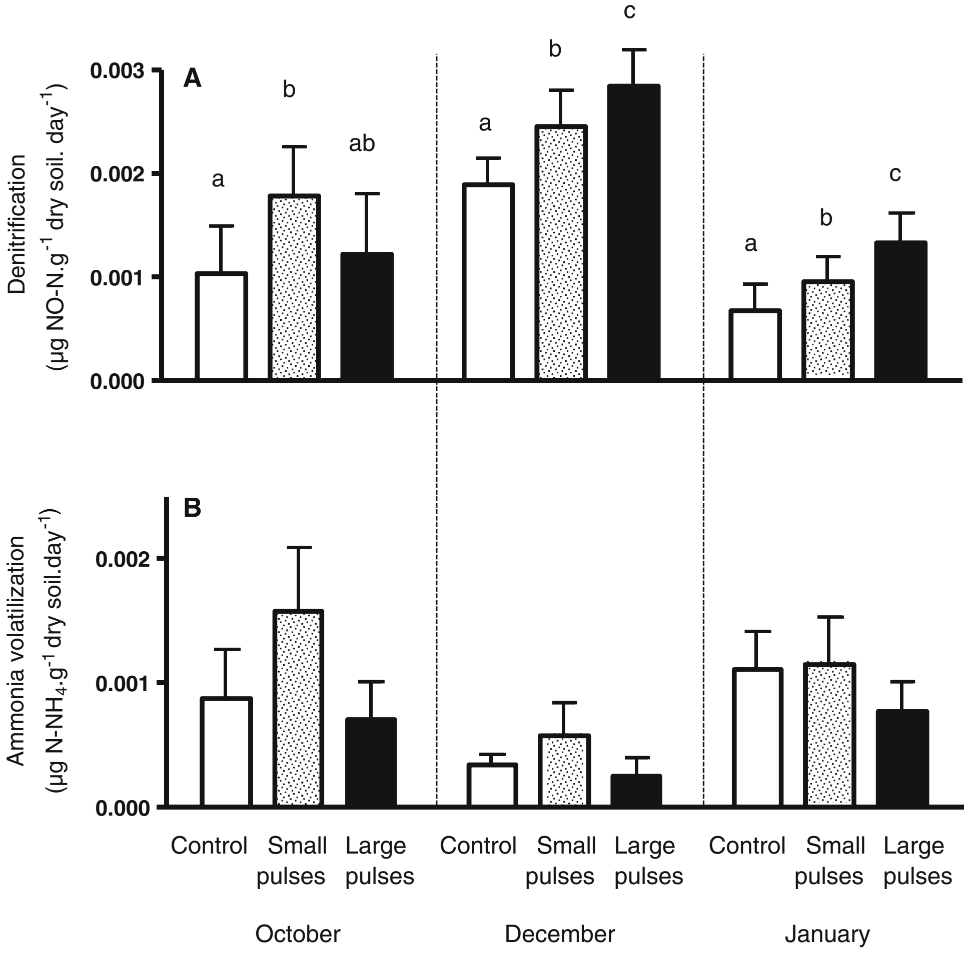

Figure 3. Nitrogen losses from the upper soil in irrigation treatments and control. **A** Denitrification; **B** ammonia volatilization. *Bars* represent mean values (+SE) for $n = 12$ for denitrification and $n = 10$ for volatilization rates. Irrigation treatments produced significant differences ($P < 0.05$) in denitrification rates but not in ammonia volatilization. *Different letters* show significant differences among treatments within each date at $P < 0.05$.

leaching and denitrification, with large pulses showing higher losses than small pulses. By contrast, water pulses did not stimulate ammonia leaching or ammonia volatilization.

Our results support our hypothesis 1; small and frequent precipitation events stimulated net N mineralization more than large and less frequent precipitation events. Averaged along the growing

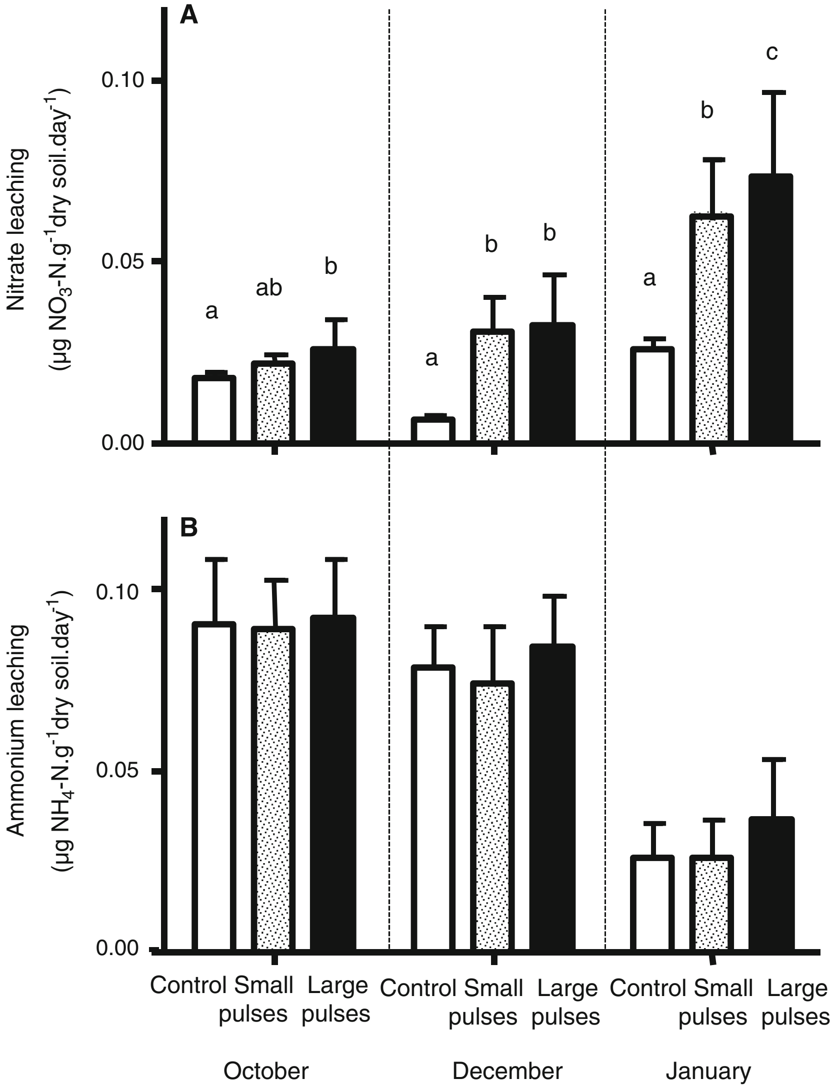

Figure 4. Nitrogen leaching from the upper soil in irrigation treatments and control. **A** Nitrate leaching; **B** ammonium leaching. *Bars* represent mean values (+SE) for $n = 20$. Irrigation treatments produced significant differences ($P < 0.05$) in nitrate leaching but not in ammonium leaching. *Different letters* show significant differences among treatments within each date at $P < 0.05$.

season, net N mineralization was 21% higher than control for the small-pulse treatment, whereas it was 16% higher than control for large pulses. Our explanation for this result is that small and more frequent rainfall events wet the soil layers where mineralization substrate and nitrifier organisms are concentrated. By contrast, large rainfall events penetrate deeper into soil layers where organic N and microbial activity are lower, and wet the shallow soil layers less frequently.

The N mineralization stimulation by precipitation reported here contrasts with previous studies that did not find a relationship between annual precipitation and net N mineralization along an experimental precipitation gradient in this same ecosystem (Yahdjian and others 2006). Similarly, in North American grasslands, Barrett and others (2002) found no relationship between annual precipitation and annual N mineralization. We suggest that the difference between this and previous studies is based on the window used to estimate N mineralization and how constraints (water versus substrate limitation) change with the length of the incubation period. Whereas in the present study, we measured net N mineralization in short periods of time, encompassing the time between the beginning and end of water manipulations (5 days), previous studies integrated longer periods of time (1–3 months). Indeed, when we estimated net N mineralization in this study from October to January, relating initial with final N contents, we did not detect significant ($P > 0.05$) differences among treatments with different water availability. Net N mineralization responses to precipitation pulses in the Patagonian steppe were short lived and increased mineral N in soils lasted for short periods of time (at least shorter than 3 months) after precipitation pulses. In addition, net N mineralization rates did not differ between vegetation patches, although soil N concentration was higher under shrubs surrounded by a ring of grasses than in bare soil patches. The differences in inorganic N content between microsites may be a consequence of long-term differences in N inputs. We suggest that at a seasonal scale N mineralization may be limited by substrate availability (Yahdjian and Sala 2008). Ephemeral release of N upon wetting of dry soil was also observed in other field studies in arid ecosystems (see, for example, Cui and Caldwell 1997; Mummey and others 1994), although they did not compare water pulses of different size. The capacity of plants to use short pulses of N availability may define the competition balance between plants and microbes, and may determine the amount of N conserved in the ecosystem relative to losses (Austin and others 2004; Schwinning and Sala 2004).

Small and frequent precipitation events, in general, did not produce a relatively higher effect on N gaseous losses by denitrification and ammonia volatilization than large precipitation events, rejecting our second hypothesis. After a large precipitation pulse in January, denitrification increased up to a 50%. N losses by denitrification measured in plots receiving ambient rainfall quantities in the present study were particularly lower than rates reported in other water-limited ecosystems, like the Great Basin (Table 1), where losses by denitrification were almost 65% of N inputs (West and Skujins 1977). Also, denitrification rates in the Patagonian steppe were lower than nitrate leaching. The low denitrification rates in relation to those estimated in other arid ecosystems combined with the important values of nitrate leaching may be accounted for by the coarse soil texture characteristic of Patagonian soils. Denitrification pulses after water input (Mummey and others 1994; McCalley and Sparks 2008, 2009) or during wet periods (Peterjohn 1991) were reported in several arid and semiarid ecosystems, which would be expected because low soil oxygen concentration conditions that occur after a rainfall event may stimulate this process (Tiedje and others 1984; Groffman and Tiedje 1988). Gaseous N losses by ammonia volatilization from our control plots were similar to values reported for arid ecosystems of North America (Table 1). Indeed, ammonia volatilization rates, an abiotic pathway, are of the same order of magnitude among arid ecosystems, whereas denitrification rates, a biological flux of N loss, changes in a diverse way among the arid ecosystems compared (Table 1). However, precipitation pulses did not stimulate ammonia volatilization, which was different from results reported by Schlesinger and Peterjohn (1991) for the Chihuahuan Desert, and McCalley and Sparks (2009) for the Mojave Desert, where they found that water additions stimulated volatilization in experimental plots. As NH_3 is highly soluble in water, volatilization from moist soil is minimal in general. Indeed, Sharpe and Harper (1995) reported high volatilization rates in response to N addition, but rates were reduced with irrigation.

Large precipitation events had a relatively higher effect on N losses by nitrate leaching than small precipitation events, as we predicted in the third hypothesis. However, precipitation pulses showed a different effect on the two inorganic N species, nitrate and ammonium. Whereas water input stimulated nitrate leaching, ammonia losses were not affected by water input. Neither ammonia losses by volatilization nor leaching were stimulated by precipitation pulses. This will ultimately influence the ammonia:nitrate relationship after each precipitation event, and may help explain ammonia dominance in the budget of soil inorganic N in this ecosystem. Similarly, the ammonium:nitrate ratio may fluctuate from wet to dry periods with higher values after a rainfall event and declining throughout the drying cycle. This in turn may affect the competitive balance of different plant species of the Patagonian steppe that show a clear preference for ammonium or nitrate as the main N source (Gherardi and others, unpublished). Nitrate leaching from the upper soil might increase nitrate availability for shrubs, which have their roots

Table 1. Denitrification and Ammonia Volatilization Rates in Different Arid Ecosystems

Nitrogen fluxes	Chihuahuan Desert[1]	Mojave Desert[2]	Great Basin[3]	Patagonian steppe[4]
Denitrification (μg N_2O–N m^{-2} day^{-1})	1068	0.11	5200	150
Ammonia volatilization (μg NH_3–N m^{-2} day^{-1})	15–95	173	274	128

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[1] *Schlesinger and others 1990; Schlesinger and Peterjohn 1991; Peterjohn and Schlesinger 1991.*
[2] *Schaeffer and others 2003.*
[3] *West and Skujins 1977.*
[4] *Present study.*

concentrated in the lower soil layer (Sala and others 1989).

Precipitation pulses of different sizes differentially affect nutrient cycling, modifying the balance between nutrient transformations and losses. Climate change is expected to increase the frequency of extreme precipitation events (Groisman and others 1999; Easterling and others 2000; Huntington 2006) altering the proportion of large to small precipitation events in favor of the former. Hypothetically, these changes in climate may lead to reduced N mineralization in the upper soil layers and increased N losses via leaching, which will probably favor deep-rooted and nitrate-loving plant species.

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