



Rainfall amount and timing jointly regulate the responses of soil nitrogen transformation processes to rainfall increase in an arid desert ecosystem



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ABSTRACT

Climate models predict greater rainfall will occur in the arid and semiarid regions of Northwest China, where nitrogen (N) cycling is particularly sensitive to changes in rainfall regimes. Yet, how increasing rainfall regulates soil N transformation processes in these water-limited regions is still not well understood. We conducted a manipulative experiment in a desert ecosystem in Northwest China, whereby we simulated five different scenarios of future rain regimes (natural rains plus 0%, 25%, 50%, 75% and 100% of the local mean annual precipitation) each month from May to September in 2009. We examined *in situ* net N mineralization and soil N availability in both vegetated and bare soils, as well as leaf litter N release for the dominant shrub species *Nitraria tangutorum* monthly after each rain addition. We found that increased water availability via the simulated rain addition significantly decreased total net N mineralization rates over the growing season in both vegetated and bare soils. A larger amount of litter N was released after rain addition in vegetated soils, which could contribute to the higher concentrations of inorganic N in vegetated soils compared to bare soils. Furthermore, we found that the responses of soil N transformation processes to rain additions showed great seasonality, and thus both rainfall amount and timing jointly regulate the responses of soil N transformation processes to rainfall increase under future rainfall scenarios in this arid desert ecosystem. Over the growing season, rainfall addition reduced soil inorganic N concentrations but favored plant N uptake and microbial N immobilization. We suggest that the cycling of N will be greatly changed under future rainfall regimes, which may have consequences for ecosystem stability and functioning in this “N-conserving” desert ecosystem.

1. Introduction

Arid and semiarid ecosystems cover more than one-third of China's land surface, and they are constantly expanding due to climatic variability and land use change associated with unsustainable human activities (Huang et al., 2016; Li et al., 2015). Future climate scenarios predict that the precipitation regimes in the desert regions of Northwest China will likely change with an increasing amount of precipitation in the 21st century (Chen, 2013; Gao et al., 2012; IPCC, 2007; IPCC, 2013). For example, Gao et al. (2012) reported that an increase in annual precipitation of up to 25% and 50% is expected at the middle and end of the 21st century in Northwest China, respectively. In addition, a recent research by Wang et al. (2017) projected that some desert regions in Northwest China will experience an increase of more than 100% of mean annual precipitation at the end of the 21st century

compared with the end of the 20th century based on the RCP8.5 scenario. Furthermore, according to long-term precipitation data from the past 40 years, Liu et al. (2005) documented that the annual amount and frequency of precipitation in Northwest China increased at a rate of 3.9 mm/decade and 1.3 day/decade, respectively.

Conventional wisdom holds that most of the biological processes in arid and semiarid regions are controlled by soil water availability, which is generally triggered by rainfall events (Austin et al., 2004; Huxman et al., 2004a; Noy-Meir, 1973; Schwinnig and Sala, 2004). Therefore, an increase in the amount of precipitation in these water-limited regions of Northwest China under climate change may stimulate biological processes and increase primary productivity, potentially dampening future climate change (Knapp et al., 2008). However, the response of biological processes may be regulated by soil nitrogen (N) availability considering that N is the second most important controlling

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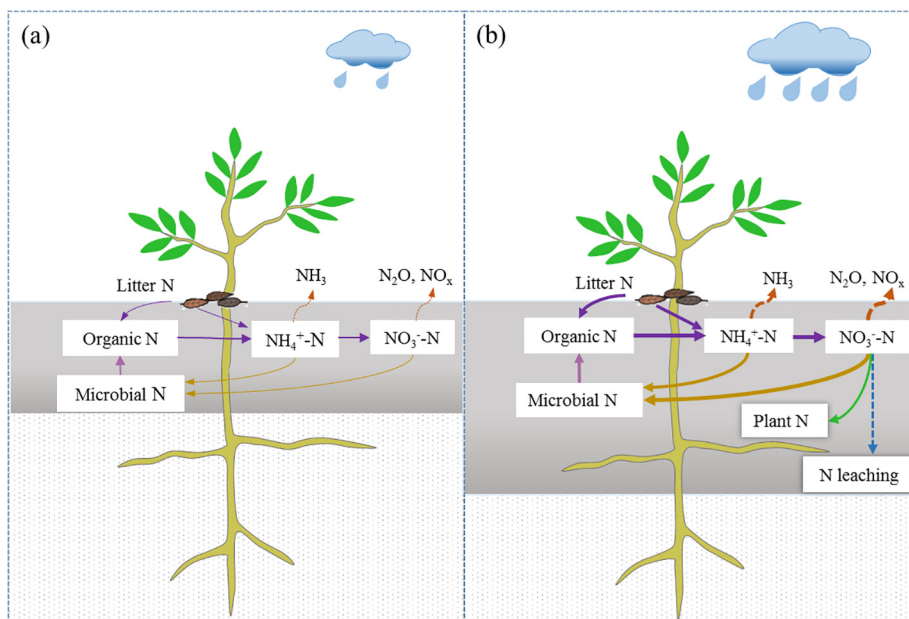


Fig. 1. Schematic diagrams to illustrate the main effects of a small rainfall event (a) and a large rainfall event (b) on the biogeochemical cycle of N in desert ecosystems without taking into account antecedent soil moisture conditions or seasonal effects. Width of the arrows indicates the relative importance of these processes in the two scenarios. Soil water content and depth is shown by shading in the soil box.

factor for plant growth and productivity in water-limited regions (Hooper and Johnson, 1999; Yandjian et al., 2011; Zaady, 2005). Thus, understanding how alterations in precipitation regimes under future climate scenarios will affect the N transformations in these water-limited regions of Northwest China is vital. Importantly, water and N availability usually interact with each other at various temporal and spatial scales to regulate ecosystem structure and function including vegetation composition, primary production and carbon cycling of desert ecosystems (Austin et al., 2004; Schwinning and Sala, 2004; Schwinning et al., 2004). To date, research evaluating the role of increasing precipitation and its seasonality in controlling *in situ* soil N cycling processes in these water-limited regions is still rare, and this represents a major gap in our knowledge of the soil N cycle under future precipitation scenario.

The episodic nature of soil water availability associated with rainfall events in arid and semiarid ecosystems has significant consequences on N cycling processes, which directly determine the amount, form and seasonality of N availability (Austin et al., 2004; Collins et al., 2008; Reichmann et al., 2013). In water-limited regions, after a small rainfall event (Fig. 1a), the water usually infiltrates into the surface soil layer without taking into account antecedent soil moisture conditions or seasonal effects. Increased water availability can activate microbial metabolic processes, such as organic matter mineralization and litter decomposition, thereby leading to an increase in N availability in surface soils (Collins et al., 2008). However, the increased N availability is often short-lived and N is often lost due to microbial immobilization and potential N gas losses (NH_3 , N_2O and NO_x) by nitrification, denitrification and volatilization (Fierer and Schimel, 2002; Groffman and Tiedje, 1988; Schlesinger and Peterjohn, 1991). In addition, such small rainfall events will have little or no impact on shrub growth because these plants usually have deep root systems which are not able to capitalize on the available N resource. After a large rainfall event (Fig. 1b), the water will infiltrate into the deep soil layers and can be accessed by shrub roots. Therefore, larger rainfall events can not only trigger a pulse of microbial metabolic processes but also lead to an increase in plant physiological activities and root N uptake (Collins et al., 2008; Huxman et al., 2004b). Besides, larger rainfall events can increase N gas losses because the concomitant decrease in the air-filled porosity reduced the oxygen concentrations and increased the activity of denitrifying enzymes (Guo et al., 2014; Homyak and Sickman, 2014; Vourlitis et al., 2015). A further complexity is that after large rainfall events the high soil water content can increase N losses to deeper soil

layers via leaching (Hentschel et al., 2007; Schlesinger and Peterjohn, 1991). Therefore, understanding the correlation between water and N availability in the context of projected changes in precipitation regimes is central for identifying the consequences for ecosystem structure and function of these water-limited regions.

In water-limited regions, some studies have investigated how increases in rainfall regulate soil N cycling processes. However, most of these studies were conducted in a laboratory environment (Fisher et al., 1987; Mikha et al., 2005) or focused on inter-annual variations of natural precipitation (Ma et al., 2013; Yahdjian and Sala, 2008). For example, Reichmann et al. (2013) documented that wet years can result in more inorganic N loss than dry years in the desert grasslands of the Chihuahuan Desert. Generally, increasing precipitation affects soil N cycling processes in complex ways. First, the effects of increasing precipitation on soil N cycling processes are linked to the frequency and intensity of precipitation. Frequent drying and wetting of the soil profile may stimulate the mineralization of organic matter and increase the available inorganic N, but exacerbate N losses because of changes in the soil properties and soil oxic and anoxic periods (Birch, 1958; Canarini and Dijkstra, 2015). Second, the timing or seasonality of rainfall events may play a fundamental role in determining intra-annual variations in N cycling processes because of the complex interactions between the seasonal dynamics of environmental factors and microbial and plant activities (Xiang et al., 2008; Yahdjian et al., 2006). Therefore, the ability of plants to utilize the available N that is triggered by episodic rain events is critical in these water-limited regions (Schaeffer and Evans, 2005). For example, an increase in inorganic N after a certain amount of rainfall in the early growing season stimulates the growth of grasses and shrubs (Rao and Allen, 2010; Yang et al., 2011). Finally, the landscape in desert ecosystems is frequently characterized by a mosaic of bare and vegetated patches. Any shift in the dominant vegetation cover type can affect soil N cycling processes and N pools (Talmon et al., 2011). Thus, to predict the responses of N cycling to increased rainfall under future climate scenarios, the responses of different vegetation cover must be considered, particularly in dry and heterogeneous ecosystems.

Due to the complexity of the responses of soil N cycling processes to increasing precipitation under future climate scenarios, manipulative *in situ* experiments are needed to reveal the intra-annual or seasonal dynamics of soil N cycle processes. However, to the best of our knowledge, no studies have been performed to distinguish the nature of the responses of soil N cycle processes to increasing precipitation under

future precipitation scenarios in arid and semiarid regions, such as those of Northwest China. In this study, we focused on the effects of different levels of simulated rain addition on *in situ* soil N cycling processes in a desert ecosystem of Northwest China. We hypothesized that (1) rain addition treatments would increase soil inorganic N concentrations as a result of enhanced microbial decomposition; (2) soil N transformations in vegetated soils would be more strongly affected by changes in rainfall than that in bare soils because the presence of vegetation would provide additional biological effects on soil N transformations, and (3) temporal variations in soil N transformations would be high under larger rain addition treatments because of the larger changes in soil water content and greater responses of microbial and plant activity.

We conducted a field manipulative experiment in a desert ecosystem in Northwest China dominated by the shrub species *Nitraria tangutorum*. Five scenarios simulating future rain regimes (0%, 25%, 50%, 75% and 100% increases over the local long-term mean annual precipitation (115 mm)) were applied each month during the growing season (May–September) from 2008 to 2012. The levels of precipitation increase were chosen according to the predictions for the desert regions of Northwest China in the middle and end of the 21st century by many simulation models with different future scenarios (Chen, 2013; Gao et al., 2012; IPCC, 2007; Wang et al., 2017). To test the first and second hypotheses, we examined the soil nitrate (NO_3^- -N) and ammonium (NH_4^+ -N) concentrations and *in situ* net N mineralization rates monthly in vegetated and bare soils during the growing season of 2009. To test the third hypothesis, we measured soil water content, temperature, leaf litter decomposition, net primary production and microbial biomass during the growing season.

2. Materials and methods

2.1. Study site

This study was conducted in a desert region (102° 58' E, 38° 34' N), located in the transitional zone between the Badain Jaran Desert and Tengger Desert in Minqin County, Gansu province, China (see Fig. S1a for a picture of the region). The climate is arid temperate continental, with an average annual temperature of 7.8 °C and a mean annual precipitation of 115 mm. The dominant soil type is aeolian sandy soil (Entisols in the USDA soil taxonomy system) with a pH of 8.6. The only dominant species in this region is *Nitraria tangutorum* Bobr, a deciduous shrub with strong ability to resist drought, wind and dust.

The terrain of this region was generally flat and covered with small sand dunes which averaged 0.9 m in height and 14.2 m² in size. The sand dunes were northwest-southeast oriented and bear two distinct types of vegetation cover. The southeast slopes of the sand dunes were covered by bare soil, whereas the northwest flanks were covered by *N. tangutorum* plants occupying approximately 35% of the dune area.

2.2. Experimental design

To simulate future rainfall scenarios in this region, we established five rain addition treatments: 0% (control. CK), 25% (+25%PPT), 50% (+50%PPT), 75% (+75%PPT) and 100% (+100%PPT) increase in mean annual precipitation (115 mm) based on the long-term precipitation data (1978–2008) at the study site. The experiment used a randomized block design with four replicate blocks, and each block consisted of five 113 m² plots (treatments), separated by 10-m walkways. The rain addition treatments were applied with 16 field rain enrichment systems on the 10th day of each month from May to September using one-fifth of the intended annual rainfall increase; thus, the amounts of additional rain were 0, 5.8, 11.5, 17.3 and 23.0 mm each time for the five addition treatments. The land area irrigated by each rain enrichment system was estimated at 113 m², and the total land area receiving the same rain addition treatment was about 450 m².

This field rain manipulative experiment lasted four years, from 2008 to 2012. More detailed information on the experimental design and the irrigation system can be found in our previous studies (Song et al., 2012).

The irrigation water was pumped from a well (100 m deep) near the plots and the amount of water application in each treatment was controlled by a rain enrichment system composed of a water-pump, water meter and spraying arms. Chemical properties of the deep well water used to supplement rainfall were measured at the beginning of the experiment. The deep well water had a pH of 8.7, which was higher than that of the natural rainfall (pH = 7.7). The inorganic N in deep well water had a low content with nitrate and ammonium N were 0.01 mg/L and 0.15 mg/L, respectively. Thus, the total amount of added N by irrigation water was 0, 4.64, 9.28, 13.92 and 18.56 mg/m² for the five rain addition treatments, respectively, during the growing season. The salinity of the deep well water was 0.35 mg/L. In addition, when analysing the pulse-response of microbial respiration to natural rain and deep well water in bare soils, we did not find any significant difference in the response between the two water forms (Song et al., 2012). Thus, we believe that the addition of well water used in this study can simulate natural rainfall. We ran the simulated rain additions only in the morning when the wind speed and air temperature were relatively low (see Fig. S1b).

2.3. Measurements of soil water content and temperature

Soil temperature (Ts) was measured at a depth of 10 cm using a thermocouple soil temperature probe (LI-COR 6000-09TC, LI-COR, Lincoln, NE, USA). Soil gravimetric water content (SWC) of the 0–10 cm soil layer was measured using the oven drying method. The measurements were conducted only in the morning between 09:00 and 11:00 local time. We conducted the Ts and SWC measurements on the day before the rain addition treatments and every two days afterward during each month.

2.4. Sampling and net N mineralization analysis

We conducted the *in situ* N mineralization experiment during the growing season of 2009. Because most mineralization occurs in the top 2.5–5 cm of soil (Norton et al., 2004; Schimel and Parton, 1986), we focused on net N mineralization rates in the top 10 cm soil layer in this study. Net N mineralization rates were determined using the *in situ* soil core incubation method (Raison et al., 1987). Prior to the rain addition treatments, we inserted two PVC tubes (5 cm in diameter and 12 cm in length) into the vegetated and bare soils to a depth of 10 cm in each plot. One PVC core was taken back to the laboratory to determine the initial concentrations of inorganic N. After the rain addition treatments, we quickly covered the top of the other PVC core with a plastic film that prevented water penetration and allowed for gas exchange; then, we incubated the core in the field for approximately 30 days. Five sampling periods were run during the growing season (May to September).

Soil samples before and after incubation were extracted with 2 M KCl. The concentrations of inorganic N (NH_4^+ -N and NO_3^- -N) in the filtered extracts (Whatman No. 1 filter paper) were determined using a flow injection autoanalyser (FIAstar 5000 Analyzer, Foss Tecator, Denmark). The expression of soil inorganic N concentrations is based on dry soil.

The net rates of ammonification, nitrification and mineralization were calculated by comparing the incubated inorganic N concentrations to the initial inorganic N concentrations over a given incubation period. The cumulative net ammonification, nitrification and mineralization values during the growing season were calculated as the sum of the net rates of ammonification, nitrification and mineralization, respectively, over the entire experimental period. Net rates of ammonification, nitrification and mineralization were calculated using the following equations:

For a time interval $\Delta t = t_{i+1} - t_i$

$$A_{\text{amm}} = c[\text{NH}_4^+ - \text{N}]_{i+1} - c[\text{NH}_4^+ - \text{N}]_i \quad (1)$$

$$A_{\text{nit}} = c[\text{NO}_3^- - \text{N}]_{i+1} - c[\text{NO}_3^- - \text{N}]_i \quad (2)$$

$$A_{\text{min}} = A_{\text{amm}} + A_{\text{nit}} \quad (3)$$

$$R_{\text{amm}} = A_{\text{amm}}/\Delta t \quad (4)$$

$$R_{\text{nit}} = A_{\text{nit}}/\Delta t \quad (5)$$

$R_{\text{min}} = A_{\text{amm}}/\Delta t$ (6) where t_i and t_{i+1} are initial and final incubation dates, respectively; $c[\text{NH}_4^+ - \text{N}]_i$ and $c[\text{NH}_4^+ - \text{N}]_{i+1}$ are the mean $\text{NH}_4^+ - \text{N}$ concentrations of the initial and incubated soil samples, respectively; $c[\text{NO}_3^- - \text{N}]_i$ and $c[\text{NO}_3^- - \text{N}]_{i+1}$ are the mean $\text{NO}_3^- - \text{N}$ concentrations of the initial and incubated samples, respectively; A_{amm} , A_{nit} and A_{min} are the accumulations of $\text{NH}_4^+ - \text{N}$, $\text{NO}_3^- - \text{N}$, and the total inorganic N ($\text{NH}_4^+ - \text{N}$ and $\text{NO}_3^- - \text{N}$), respectively; R_{amm} , R_{nit} and R_{min} are the net ammonification rates, net nitrification rates and net mineralization rates, respectively.

2.5. Leaf litter decomposition experiment

We conducted a decomposition experiment using the litterbag approach, which is a widely used method for studying decomposition at the soil surface. In late September 2008, we collected senescent leaves of *N. tangutorum*, the dominant species present in this desert region, near the area where the rain addition treatments were conducted in 2009. We transported the leaves to the laboratory for uniform material selection and air drying. We placed 6.00 g of the air-dried leaves in 2 mm-mesh nylon bags measuring 20 × 20 cm. On November 10, 2008, we anchored the litterbags in the field under the shrubs and secured them with wire pins to prevent movement. Ten litterbags were deployed on each plot (four replicate plots per treatment). We collected the litterbags on the 9th of each month, which was before the day of the rain addition treatments and during the rain addition experimental period from May to September 2009. We randomly selected one bag per plot each time. During transportation to and from the field site, we placed each litterbag in a paper bag to minimize the loss of plant material. We hand-sorted the litter to remove extraneous matter, such as in-growth plant material, and dried it at 70 °C for 48 h to determine the dry mass and N content.

2.6. Measurements of biotic factors

At the end of the experiment, we collected all the plant material within a 1 m × 1 m quadrat from the vegetation covered area of each plot to determine the biomass of plants (leaves, roots, stems). All of the plant samples were oven-dried at 70 °C for 48 h and then weighed. Leaf N concentration was measured by the Auto-Kjeldahl method (Kjektec system 1026 Distilling Unit, Sweden). We also sampled soils (0–10 cm) in both vegetated and bare areas to determine soil microbial biomass nitrogen (MBN) by the chloroform-fumigation-extraction method. More detailed information can be found in Song et al. (2012).

2.7. Statistical analyses

We applied four-way repeated-measures ANOVA (RMANOVAs) to examine the main and interactive effects of block, rain addition amount, vegetation cover type and sampling time on soil water content, soil temperature, inorganic N concentrations and net N mineralization rates. Rain addition treatment and vegetation cover type were treated as fixed effects, and block was treated as a random effect. Our preliminary analysis showed that the effect of block and the interactive effects of block and other factors were not statistically significant ($P > 0.05$), those RMANOVAs results were not presented so as to simplify the presentation. When the interaction was significant, several two-way ANOVAs were performed on these measured variables for each level of the third factor. If the two-factor interaction was significant, a follow-up simple main effect analysis was conducted using post hoc multiple comparison tests. Growing season mean values were averaged

by the monthly values and by plots in vegetated soil and bare soil, respectively. Two-way ANOVA was used to examine the effect of rain addition amount, vegetation cover type and their interaction on seasonal mean soil water content, temperature, inorganic N concentrations and cumulative N mineralization rates during the growing season. The statistical results were shown in Table S1. One-way ANOVA was performed to examine differences in decomposition rates among the rain addition treatments during the growing season and the statistical results were shown in Table S2. To test whether the method used to estimate net N mineralization in the field affected SWC, we performed a paired *t*-test between the gravimetric soil water content inside and outside the PVC tubes for all treatments and all dates. All ANOVAs were followed by Tukey HSD post-hoc tests with α value set at 0.05. The data were transformed as needed to meet normality and homogeneity of variance assumptions. Regression analysis was used to evaluate a possible relationship between inorganic N concentration, net N mineralization rate, litter N release, leaf N content, microbial biomass N and soil water content as well as soil temperature. All statistical analyses were performed using SPSS 16.0 (SPSS for Windows, Version 16.0, Chicago, IL, USA).

3. Results

3.1. Changes in soil water content and soil temperature

During the growing season, the total precipitation was 80.6 mm from May to September, and the maximum rainfall event (25.8 mm) occurred on August 18 of 2009 (Fig. 2a). The amount and seasonal distribution of rainfall during the growing season (May to September) was similar to the long-term (30 years) rainfall record (Fig. S2). The mean air temperature during the growing season was 20.5 °C, and the highest daily mean temperature was 29.0 °C on July 18, and the lowest mean temperature was 9.6 °C on September 20.

The soil water content of 0–10 cm layer (SWC) significantly changed in the vegetated (Fig. 2b) and bare (Fig. 2c) soils after the rain addition treatments each month. The change in magnitude and duration of elevated SWC in both vegetated and bare soils depended on the amount of rain added, with a larger rain addition amount resulting in a larger response magnitude and a longer duration (Fig. S3a). During the growing season, there was no significant difference in mean SWC between vegetated and bare soils (Table S1). The time course of soil temperature (Ts) at 10 cm depth showed similar trends to air temperature (Ta) in both vegetation cover types (Fig. 2d and e). Rain addition treatments had no significant effect on Ts in both vegetation cover types (Fig. S3b). There was no significant difference in Ts between the vegetated and bare soils under a given rain addition treatment, and no significant interaction was detected between vegetation cover type and rain addition amount during the entire experimental period (Table S1).

3.2. Seasonal patterns of soil inorganic N concentrations under different rain addition treatments

During the growing season, soil $\text{NH}_4^+ - \text{N}$ concentrations showed a decreasing trend from May to September for all rain addition treatments in both vegetated and bare soils (Fig. 3a and b). Soil $\text{NO}_3^- - \text{N}$ concentrations varied greatly during the growing season, with the largest and smallest values occurred in August and September, respectively for both vegetation cover types (Fig. 3c and d). Total inorganic N concentrations showed similar patterns to those of soil $\text{NO}_3^- - \text{N}$ concentrations across all rain addition treatments (Fig. 3e and f).

We found that the amount of rain addition and sampling time had a significant interactive effect on soil $\text{NH}_4^+ - \text{N}$, $\text{NO}_3^- - \text{N}$ and total inorganic N concentrations during the experiment period (Table 1). In addition, rain addition treatment had also a significant interaction with vegetation cover type, such that the inorganic N pools in vegetated soils

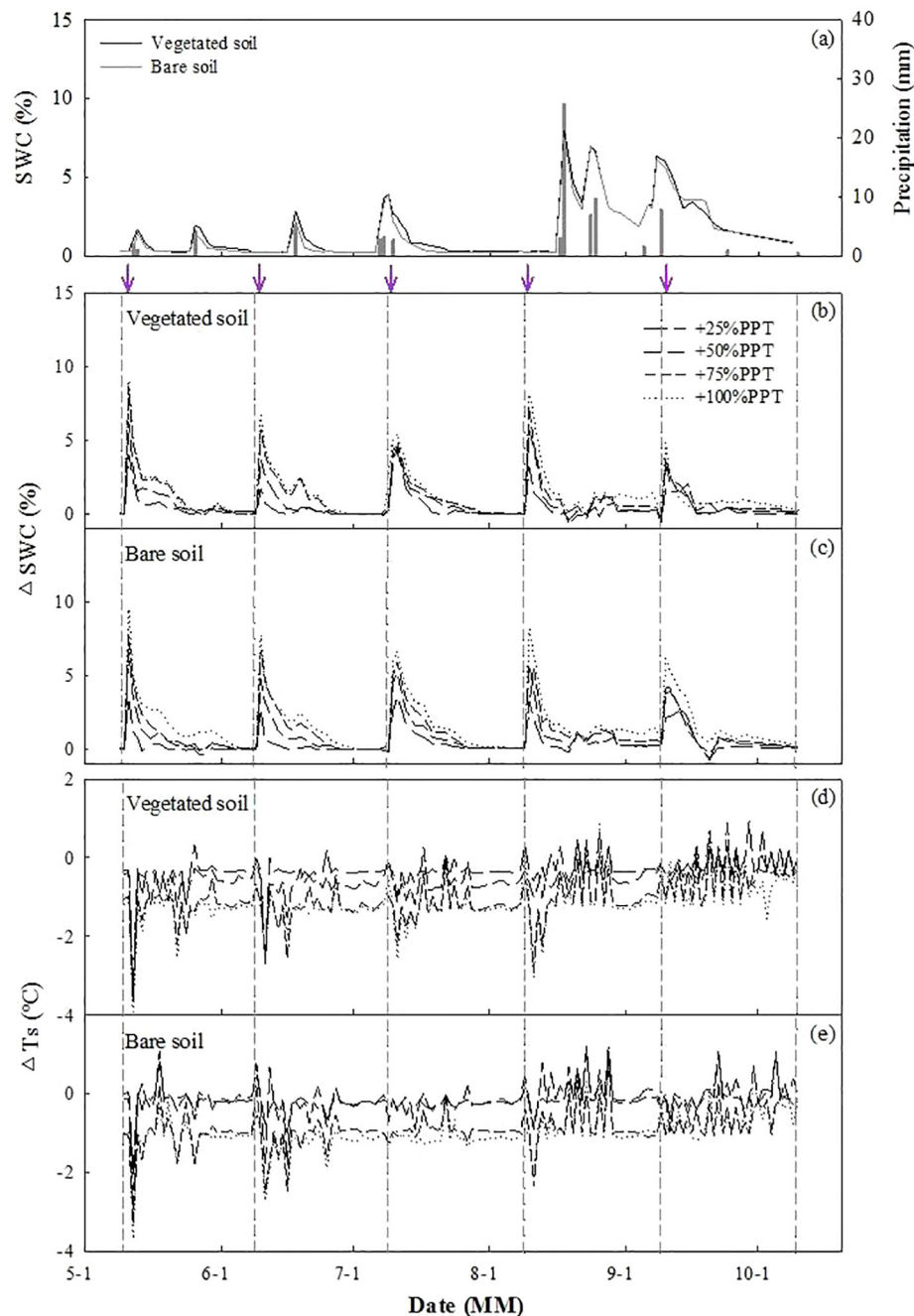


Fig. 2. Daily precipitation and temporal dynamic of soil water content (0–10 cm) in the control plots during the growing season (a), and treatment-induced changes in soil water content (b and c) and soil temperature (d and e) in response to different rain addition treatments. Solid arrows represent the timing of rain addition treatments.

had a larger response to rain addition treatment than that in bare soils (Table 1). Over the growing season, rain addition had no effect on seasonal mean $\text{NH}_4^+\text{-N}$ concentrations but significantly decreased $\text{NO}_3^-\text{-N}$ concentrations in both vegetated and bare soils (Fig. S4a and b). As a result, rain addition significantly reduced the seasonal mean concentrations of total inorganic N (Fig. S4c). In addition, we found that rain addition treatments differently affected the ratio of $\text{NO}_3^-\text{-N}$ to $\text{NH}_4^+\text{-N}$ of the two vegetation cover types. In the vegetated soils, the value of $\text{NO}_3^-\text{-N}:\text{NH}_4^+\text{-N}$ rose to a maximum in the + 50% PPT and then declined after larger rain addition treatments; while rain addition treatments had no effect on the ratio of $\text{NO}_3^-\text{-N}$ to $\text{NH}_4^+\text{-N}$ in bare soils (Fig. S5). The seasonal mean concentrations of the soil $\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$ and total inorganic N exhibited significant differences between

vegetated and bare soils, with vegetated soils having higher concentrations than bare soils (Table S1). We detected that there was a negative relationship between inorganic N concentration and soil moisture availability for both vegetation cover types (Fig. 4a and b), suggesting that increasing soil water content due to rain addition treatments favours the loss of inorganic N in this desert ecosystem. Furthermore, we found that there was a positive relationship between inorganic N concentration and soil temperature in both vegetated cover types (Fig. 5b).

3.3. Responses of net N mineralization to the rain addition treatments

During the growing season, the monthly rates of soil net

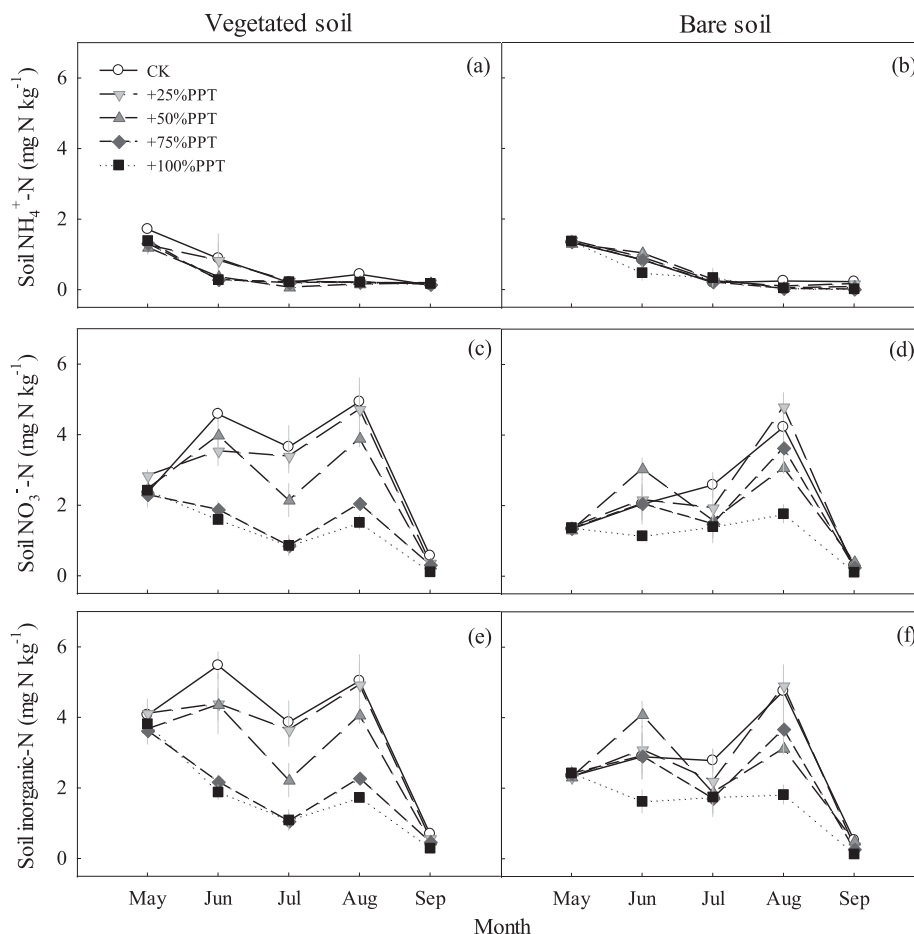


Fig. 3. Seasonal dynamics of soil $\text{NH}_4^+\text{-N}$ (a and b), $\text{NO}_3^-\text{-N}$ (c and d) and total inorganic N concentrations (e and f) during the growing season in vegetated and bare soils. Data are shown as mean \pm 1se (n = 4).

ammonification (R_{amm}) (Fig. 5a) and net nitrification (R_{nit}) (Fig. 4c and d) showed clear seasonal variations in both vegetated and bare soils. After the first rain addition treatment in May, negative R_{amm} but positive R_{nit} values were found in both vegetated and bare soils. In June and July, negative R_{amm} values were observed in all treatments, except for the CK plot for both vegetated and bare soils, whereas, positive R_{nit} values were observed in the CK and +25% PPT plot for the two vegetation cover types. In August, negative R_{amm} and R_{nit} values were observed in all treatments for both vegetated and bare soils, except for the CK and +25% PPT plot in bare soils. While, in September, positive R_{amm} and R_{nit} values were found for all treatments, except for the CK and +25% PPT plot in vegetated soils. Net N mineralization (R_{min}), which is the sum of R_{amm} and R_{nit} , also exhibited seasonal variations during the growing season in both vegetated and bare soils (Fig. 4e and f) similar to the seasonal dynamics of R_{nit} because of the higher absolute

values of R_{nit} .

The repeated measures ANOVA illustrated that there was a significant interactive effect between the amount of rain addition and sampling time on R_{amm} , R_{nit} and R_{min} (Table 1), indicating that the effect of rain addition treatments on these parameters was dependent upon the timing of sampling during the growing season. There were no significant interactions on R_{amm} , R_{nit} and R_{min} between the amount of rain addition and vegetation cover type. There were significant interactive effects between vegetation cover type and sampling time on R_{nit} and R_{min} but not on R_{amm} (Table 1). Over the growing season, rain addition significantly decreased the total cumulative R_{amm} , and the total cumulative R_{amm} showed a negative value for the five rain addition treatments in both vegetated and bare soils (Fig. 6a). Similarly, rain addition significantly decreased the total cumulative R_{nit} and R_{min} (Fig. 6b and c). Positive cumulative R_{nit} and R_{min} values were observed

Table 1

Results (*P*-values) of repeated-measures ANOVA on the effects of rain addition amount (Amount), vegetation cover type (Vegetation), block, sampling time (Time) and their interactions on soil water content (SWC), soil temperature (Ts), soil inorganic N concentrations ($\text{NH}_4^+\text{-N}$, $\text{NO}_3^-\text{-N}$, and total inorganic N) and monthly net ammonification (R_{amm}), nitrification (R_{nit}) and mineralization (R_{min}) during the growing season.

	SWC	Ts	$\text{NH}_4^+\text{-N}$	$\text{NO}_3^-\text{-N}$	Inorganic N	R_{amm}	R_{nit}	R_{min}
Amount	< 0.001	0.391	0.003	< 0.001	< 0.001	0.129	0.039	< 0.001
Vegetation	0.796	0.572	0.002	0.001	0.019	0.748	0.907	0.408
Time	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Amount \times Vegetation	0.267	0.993	0.023	0.009	0.014	0.711	0.987	0.613
Amount \times Time	< 0.001	0.002	0.070	0.028	0.013	< 0.001	0.012	< 0.001
Vegetation \times Time	0.007	0.860	0.033	0.035	0.705	0.274	< 0.001	0.030
Amount \times Vegetation \times Time	0.414	0.895	0.139	0.560	0.254	0.678	0.254	0.004

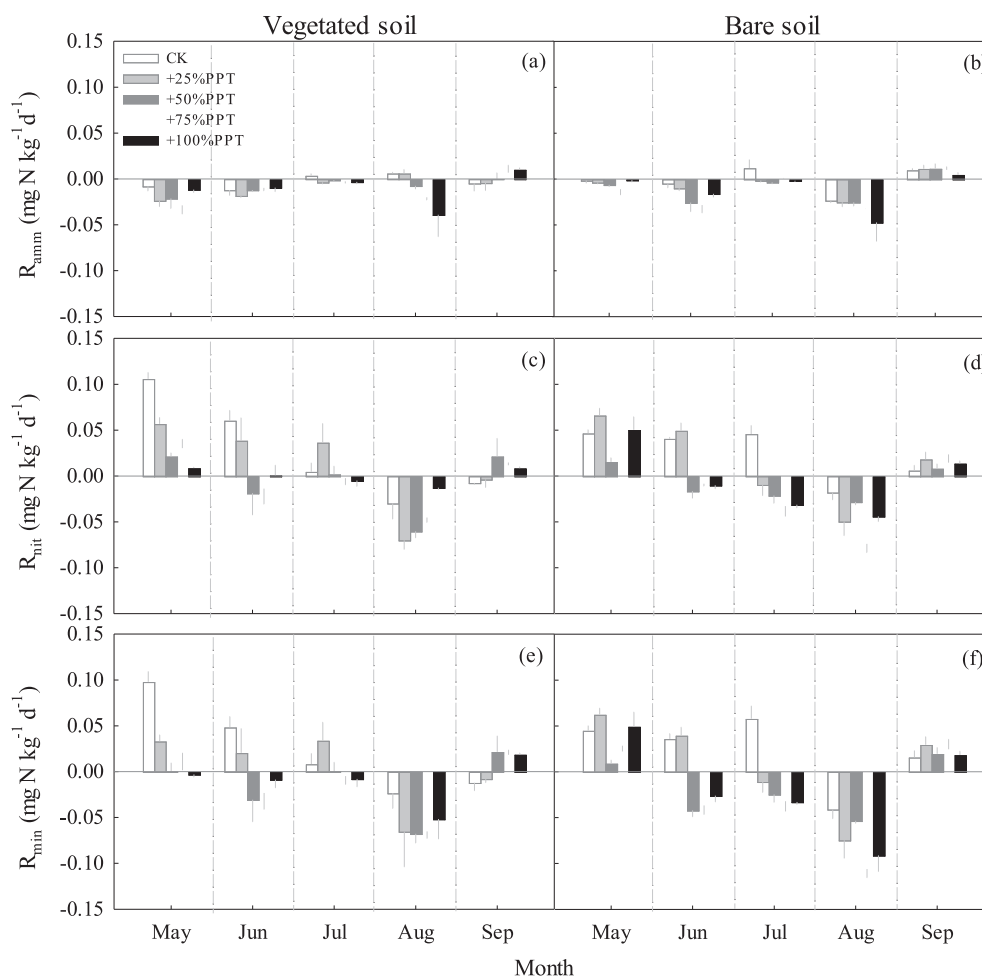


Fig. 4. Effects of simulated rain addition on monthly soil net ammonification (R_{amm} , a and b), net nitrification (R_{nit} , c and d) and net N mineralization (R_{min} , e and f) in vegetated and bare soils during the growing season. Data are shown as mean \pm 1se ($n = 4$).

only in the CK and +25% PPT plots in the vegetated and bare soils, whereas negative values were found in the +50% PPT, +75% PPT and +100% PPT plots. In addition, we found that there was a negative relationship between monthly R_{min} and monthly mean soil water content (Fig. 5c), but no relationship between monthly R_{min} and monthly mean soil temperature for both vegetation cover types (Fig. 5d).

3.4. Responses of litter decomposition and N release to the rain addition treatments

After one year of decomposition, an average of 81.3–84.6% of the initial litter mass was lost under the five rain addition treatments (Fig. 7a). We found that there were significant differences in litter mass remaining among the five rain addition treatments in the first three months (May, June and July) of the growing season, while no difference was found in August and September. Over the whole growing season, rain addition significantly enhanced the decomposition rate of litter of the dominant shrub species *N. tangutorum* (Table S2). After one year of decomposition, an average of 20.2–25.3% of the initial N content remained throughout the five rain addition treatments (Fig. 7b).

4. Discussion

4.1. Responses of soil inorganic N dynamics to rain additions

In contrast to our first hypothesis, simulated rain additions of 25–100% of mean annual precipitation (24–115 mm) during the

growing season (May to September) significantly decreased total inorganic N concentrations of the vegetated and bare soils in this desert ecosystem, where soils typically have low concentrations of inorganic N. In addition, we detected a negative correlation between inorganic N concentrations and soil water availability for both vegetation cover types, implying that increased rainfall under projected climate change in this region could lead to depression of soil inorganic N. Similar results have also been found in other arid and semiarid ecosystems (Cregger et al., 2014; Fisher et al., 1987; Reichmann et al., 2013).

Soil microorganisms can survive and adapt to the drying-rewetting cycles in water-limited regions and rapidly recover their activity in response to increases in the soil moisture associated with rainfall events (Fierer and Schimel, 2002; Iovieno and Baath, 2008; Xiang et al., 2008). Thus, after a rainfall event, a pulse in substrate supply associated with physical processes (such as aggregate disruption, organic matter redistribution, and desorption) can favor microbial activity and lead to a large increase in microbial biomass and N mineralization (Austin et al., 2004; Schimel et al., 2007; Xiang et al., 2008). However, the pulse response is often short-lived due to substrate limitations. As the soil dries, microbes must accumulate high concentrations of metabolites (osmolytes) to retain water inside the cell and prevent dehydration, and the amount of inorganic N allocated to microbial synthesis is potentially large relative to net N mineralization (Fierer and Schimel, 2002). Furthermore, increased soil water availability increased the growth of *N. tangutorum* plants in this study (Song et al., 2012). The higher plant physiological activity in the rain addition treatments implied a larger uptake of inorganic N by the shrubs (Fig. 8a). Furthermore, previous

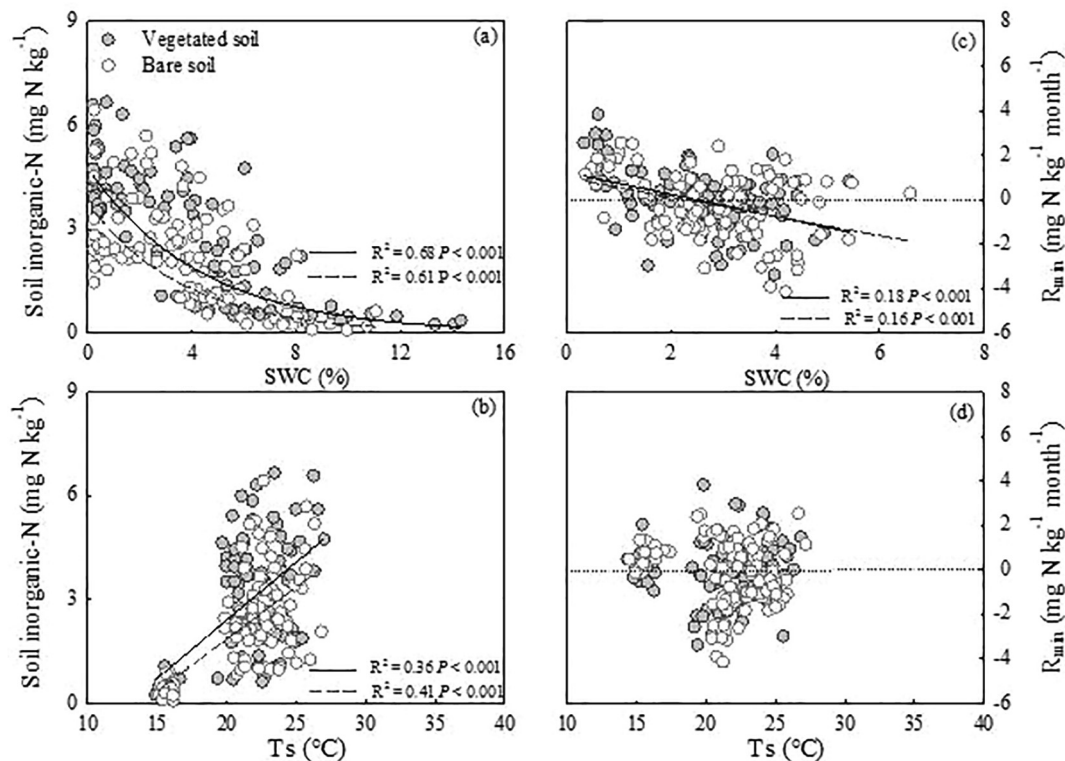


Fig. 5. Effects of rain addition on cumulative net ammonification (a), net nitrification (b), net N mineralization (c) during the growing season. Data are shown as mean \pm 1se (n = 4). Different letters under a given vegetation cover type denote significant differences among rain addition treatments ($P < 0.05$).

studies have been shown that N losses by volatilization and leaching are important processes in water-limited ecosystems, and soil rewetting can favor N gas losses by increasing the activity of denitrifying enzymes (Billings et al., 2002; Groffman and Tiedje, 1988; Schlesinger and Peterjohn, 1991; Vourlitis et al., 2015), and can promote leaching loss of inorganic N, particularly NO_3^- -N because of its high mobility and the coarse soil texture of this desert ecosystem (Austin et al., 2004; Borken and Matzner, 2009; Peterjohn and Schlesinger, 1990).

Our findings demonstrated that the effect of rain addition on soil total inorganic N and the two inorganic N species differed significantly over different months, indicating that the effect of rain addition treatments on inorganic N concentrations was dependent upon the timing of soil sampling. In addition, the two inorganic N species exhibited differential response patterns to rain addition, with a significant decrease in nitrate concentrations and no changes in ammonium concentrations during the growing season in both vegetated and bare soils, thereby changing the ratio of nitrate to ammonium. The changed ratio of inorganic N forms under different rain addition treatments could be associated with the differential movement of nitrate over ammonium under different wet conditions and differential plant preference for inorganic N forms, as well as differential moisture sensitivity of nitrifying over ammonifier bacteria (Reichmann et al., 2013). For example, it has been proposed that nitrification is more sensitive to moisture than ammonification, and wet conditions often inhibited nitrification processes in arid regions (Schimel and Parton, 1986). Therefore, we suggest that the different changes in inorganic N forms under future rainfall scenarios may have substantial consequences for the nutrient acquisition balance of plant species in this arid desert ecosystem considering that different plant species usually have a unique preference for inorganic N sources (Britto and Kronzucker, 2013; Wang and Macko, 2011).

4.2. Responses of net N mineralization to simulated rain additions

Increased water availability via the simulated rain addition significantly changed total net N mineralization rates over the growing season, resulting in lower or negative values in both vegetated and bare soils. These findings represent strong evidence that soil water availability controls the N balance in this desert ecosystem. However, the results are inconsistent with previous studies that found a positive relationship, or no relationship between wetting intensity and net N mineralization in water-limited ecosystems (Yahdjian et al., 2006), although they are consistent with findings from other desert regions (Fisher et al., 1987; Reichmann et al., 2013).

Why did rain addition result in a negative net N mineralization response in this desert ecosystem? Previous studies demonstrated that various net N mineralization responses to rain addition are associated with differences in soil organic matter content, experimental method and incubation period (Borken and Matzner, 2009; Wang et al., 2006). In this study, we measured *in situ* net N mineralization for one month, which encompassed the rain addition treatment and the subsequent soil drying periods. We speculate that the rain addition could have favored a higher microbial activity, therefore significantly increasing soil N immobilization. The increased microbial biomass N content in vegetated and bare soils (Fig. 8b) in this study partially supports this notion. While, because we did not measure gross N mineralization in this study, microbial immobilization of inorganic N within the core over the incubation period could not be determined. Therefore, we suggest that using net N mineralization rather than gross N mineralization rates may lead to some underestimation of available N from the mineralization processes, because a large part of the mineralized mineral N can be quickly utilized by microorganisms and converted into organic N (Davidson et al., 1992; Gelfand et al., 2012). While, by comparison, previous laboratory experiments that investigated the effect of soil rewetting often reported an increased rate of net N mineralization (Fisher et al., 1987; Mikha et al., 2005). The contradictory results might be

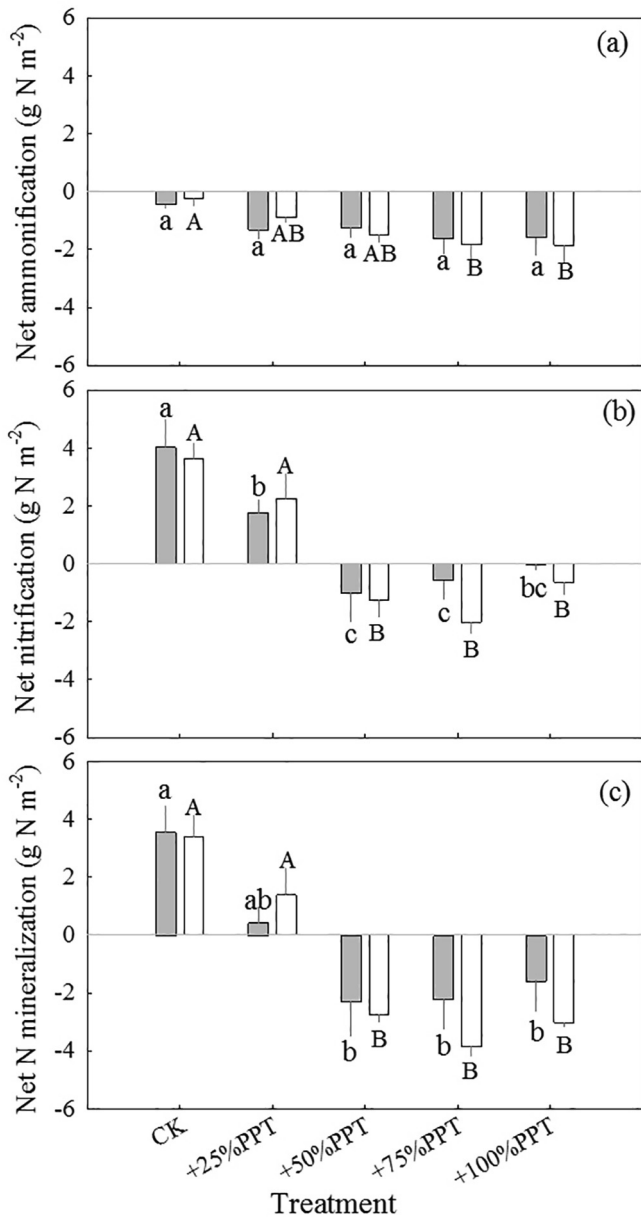


Fig. 6. Relationships between soil inorganic N concentration and soil water content (SWC, a) as well as soil temperature (Ts, b); and relationships between monthly net N mineralization (R_{min}) and monthly mean SWC (c) as well as monthly mean Ts (d) in both vegetated cover types.

related to the difference in soil and environmental conditions between the two methods because these laboratory experiments were mostly conducted with sieved mineral soils, which could supply pulses of substrate to the microbes due to physical changes in soil structure that occur during sieving (Mikha et al., 2005). In addition, given the coarse texture of these soils in this desert ecosystem, an alternative explanation for this phenomenon is that dissolved organic N was lost as gases or by leaching in the plots with high simulated rainfall; therefore, the amount of N directly available for mineralization at the beginning of the incubations was limited (Dodd et al., 2000; Reichmann et al., 2013) and led to a negative response of net N mineralization in this desert ecosystem.

We detected a significant interactive effect between the amount of rain addition and sampling time, which suggested that the effect of increased rainfall on net N mineralization changed over seasons under the future rainfall scenarios in this arid ecosystem. Previous studies

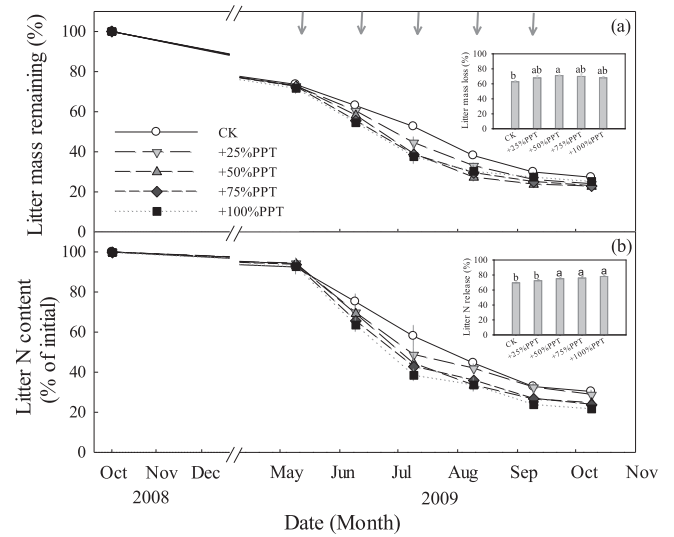


Fig. 7. Effects of simulated rain addition on leaf litter mass loss (a) and litter N remaining (b) of the shrubs *Nitaria tangutorum* during the growing season. The insets show the total changes of litter mass and N release during the whole growing season under different rain addition treatments. Different letters denote significant differences among rain addition treatments ($P < 0.05$). Data are shown as mean \pm 1se ($n = 4$).

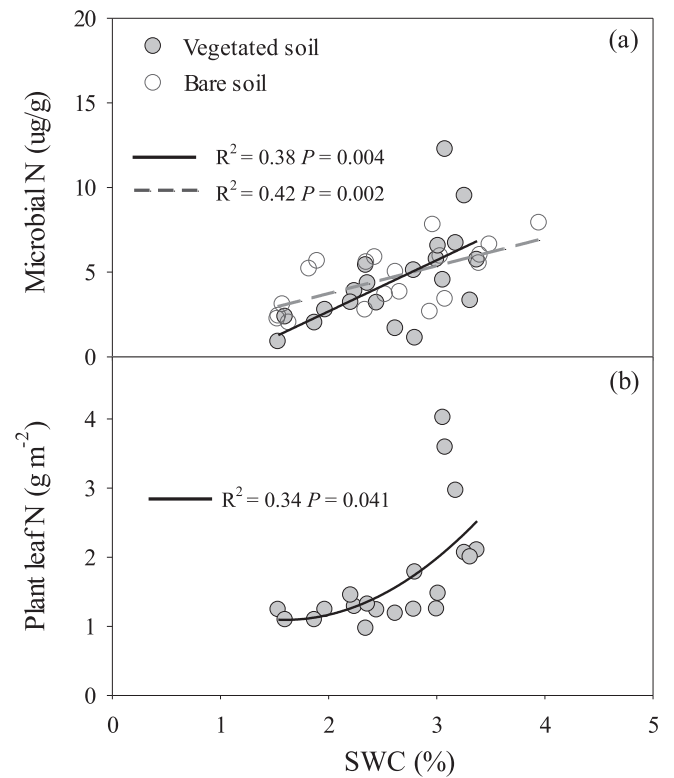


Fig. 8. Relationships between soil water content (SWC) and microbial N content (a) as well as plant leaf N content (b).

suggested that most mineralization occurs in the upper soil layers (Norton et al., 2004; Schimel and Parton, 1986), therefore the seasonal variations of net N mineralization under different rain addition treatments could have been triggered by the balance of direct and indirect effects of rainfall, seasonal changes in environmental factors, and in microbial activity, and the complex interactions among them (Xiang et al., 2008; Yahdjian et al., 2006). During the early- and peak-growing season (May to July), there were no large natural rainfall events. The

effect of a small rainfall event such as the +25% PPT treatment was often short-lived and the soil dried rapidly. Thus, we speculate that certain microbes might die because they could not tolerate the subsequent dry condition, and a large part of the biomass-derived osmolytes and metabolites with a low C/N ratio would be released, which could contribute to the positive values for net N mineralization for the CK plots and the +25% PPT treatment. However, the negative rates of net N mineralization under the high rain addition treatments could be attributed to the imbalance between increased gross mineralization and increased microbial N immobilization and potential N losses by gas emissions and/or leaching. It has been demonstrated that high soil moisture can favor N gas losses because the concomitant decrease in the air-filled porosity reduced the oxygen concentrations and increased the activity of denitrifying enzymes (Guo et al., 2014; Homyak and Sickman, 2014; Vourlitis et al., 2015). In addition, high soil moisture following large rainfall events can increase N losses to deeper soil layers via leaching (Hentschel et al., 2007; Schlesinger and Peterjohn, 1991). Accordingly, the negative net N mineralization rates in August for all the five rain addition treatments may have been related to the large natural rainfall events within this month. While, although the soil water content was high in all rain addition treatments, we found a positive net N mineralization rate in the late growing season (September), which could be related with the decreased soil temperature in this month. The low soil temperature could have not only inhibited microbial activity and N immobilization but also decreased N losses, thereby yielding an accumulation of soil inorganic N during this period in both vegetated and bare soils.

4.3. Responses of litter decomposition and N release to rain additions

In nutrient-limited desert ecosystems, the supply of nutrients released from decomposing litter is an important component for soil fertility, and it can potentially influence the structure and function of ecosystems (Austin et al., 2009; Parton et al., 2007). Previous studies have reported that litter decomposition is regulated by both biotic factors (e.g., litter quality, soil microbial activity) and abiotic factors (e.g., soil moisture and temperature) (Aerts, 1997; Garcia-Palacios et al., 2016; Zhou et al., 2008). In this study, the small and scattered natural rain events recorded between May and July were typical of the long-term quantity and pattern of the region. Rain addition treatments could have increased the activity of microbes and their access to litters, thereby increasing the litter decomposition processes (Jacobson and Jacobson, 1998; Steinberger and Whitford, 1988) and the loss of labile compounds (e.g., amino acids and sugar) in the litter due to their high sensitivity to soil moisture conditions (Gallardo and Merino, 1993; Yahdjian et al., 2006). However, in August and September, frequent natural rainfall events had wetted the litter layer soils, which might have weakened the role of rainfall treatment on the litter decomposition processes, leading to similar remaining litter masses among the five treatments at the end of the experiment.

During the growing season, the rain addition treatments significantly enhanced litter decomposition rates and litter N release, which would have the potential to change the dynamics of soil N cycling and alter the availability of N for plants and microbes in this N-limited ecosystem. After one year of decomposition, more than 80% of the litter mass was decomposed and a considerable proportion of litter N was released in all five rain addition treatments. In addition to the rain addition treatments, two other factors might also have contributed to the rapid decomposition rate that we observed. First, many studies have suggested that abiotic processes, such as photodegradation, exert a dominant control on aboveground litter decomposition in arid and semiarid ecosystems, and the decomposition rates triggered by photodegradation are relatively high compared to that mediated by microbial processes (Austin and Vivanco, 2006; Brandt et al., 2007; Marcy et al., 2009). Thus, the high levels of ultraviolet (UV) radiation in this region (Hu et al., 2007) might have promoted the physical and chemical

degradation of plant litter. Second, in this region, frequent and strong dust storms and winds may have disturbed the litter bags and decomposition processes (Zhang et al., 2003), which may have caused the litter debris to be released from the bags, thereby leading to high litter losses for all five rain addition treatments, particularly during the late growing season.

5. Conclusions

In arid and semiarid regions, water and N availability are the two major limiting factors controlling plant phenology, species composition, and net primary production (NPP) and thus regulating ecosystem structure and function (Bai et al., 2008; Burke et al., 1997). Using simulated rainfall experiments in an arid desert ecosystem of Northwest China, we demonstrated how rainfall amount and timing jointly regulate the responses of soil inorganic N and net N mineralization to rainfall increase in this arid desert ecosystem. We found that increasing rainfall decreased soil inorganic N but stimulated litter N release, plant N uptake and microbial N immobilization, which indicates that the N cycle will be accelerated under future scenarios of increased rainfall. In addition, the deficiency of inorganic N in the upper soil layers under increased rainfall conditions may have great consequences for nutrient acquisition from shallow-rooted plant species, potentially altering the community composition and related ecosystem functions of this desert ecosystem. Furthermore, our study provides new insights into the sensitivity of the soil N transformation processes to shifts in precipitation regimes in a desert ecosystem, which deserves further attention in studies considering long-term interactive effects of water and N on ecosystem functioning in the context of predicted climate change in these water-limited regions.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2020.114197>.

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