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Precipitation legacy effects on gross N mineralization and nitrification rates in a Pinyon-Juniper dryland under altered precipitation

Jamie C. Irby · Alexander H. Krichels · Marko J. Spasojevic · Darrel G. Jenerette · Erin J. Hanan · Peter M. Homyak

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Abstract Changes in precipitation patterns can influence soil nitrogen (N) cycling by altering the timing and extent of moisture availability. Arid conditions, associated with more frequent and severe droughts, can increase soil inorganic N concentrations when diffusion constraints decouple N sources and sinks, making this N susceptible to loss. Further, shifts in precipitation patterns in one season can "carry over" N into subsequent seasons, known as precipitation legacies. However, how these legacies increase soil N availability through changes in inorganic N production (i.e., gross N mineralization and nitrification) remain unclear. We manipulated the amount and timing of precipitation in a pinyon–juniper dryland by either adding or excluding precipitation during the winter or summer months and then measured the effects on inorganic N production using isotope pool dilutions. Excluding precipitation in the winter wet season—the most severe drought imposed—reduced average (±std. error) gross N mineralization by ~2.5 times to 0.3 ± 0.08 µg N g^{-1}_{soil} h^{-1} ($p = 0.0463$) and gross nitrification by ~9.5 times to 0.2 ± 0.05 µg N g^{-1}_{soil} h^{-1} ($p < 0.0001$) relative to ambient conditions, yet inorganic N production persisted under dry conditions. Because this mineralized N was not subsequently taken up by N sinks, inorganic N accumulated in the soil; soil N concentrations were ~6 times greater than ambient conditions (0.5 ± 0.2 µg NO_3^- -N g^{-1} soil) under experimental winter drought. This winter drought also produced a legacy effect the following summer, where gross N mineralization declined by ~2 times below ambient (*Winter*- $= 0.4 \pm 0.2$ µg N g^{-1}_{soil} h^{-1}) even though the drought had ended. Across seasons, precipitation legacy effects reduced gross N mineralization when

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J. C. Irby (✉) · A. H. Krichels · P. M. Homyak
Department of Environmental Sciences, University of California, Riverside, CA, USA
e-mail: jirby001@ucr.edu

A. H. Krichels
USDA Forest Service, Rocky Mountain Research Station, Albuquerque, NM, USA

M. J. Spasojevic
Department of Evolution, Ecology, and Organismal Biology, University of California, Riverside, CA, USA

M. J. Spasojevic
Environmental Dynamics and GeoEcology Institute, University of California Riverside, Riverside, CA 92521, USA

D. G. Jenerette
Center for Conservation Biology, Department of Botany and Plant Sciences, University of California, Riverside, CA, USA

E. J. Hanan
Department of Natural Resources & Environmental Science, University of Nevada, Reno, NV, USA

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organic N was depleted, but did not affect gross nitrification, favoring the accumulation of nitrate over ammonium, a more mobile anion susceptible to loss. Precipitation legacies also carried over ammonium from summer to winter, likely due to the buildup of ammonium from dry conditions in the previous summer. Our results highlight how the legacies of past precipitation can increase soil N availability, selecting N species that are vulnerable to loss when ecosystem N sources and sinks decouple. These legacies can favor N loss over retention, contributing to ecosystem N limitation and to overall declining N availability in regions experiencing increasing drought frequency.

Keywords Climate change · Drought · Gross N transformations · Isotope pool dilution · Soil inorganic N

Introduction

Climate change is altering global precipitation patterns, increasing the frequency and severity of droughts and extreme rainfall events (Cook & Seager 2013; Seager et al. 2007). These global changes in precipitation can, in turn, affect the plant and microbial processes that cycle nitrogen (N), an essential nutrient often limiting ecosystem productivity (Vitousek et al. 2022). N is largely cycled through microbial processes that depend on substrate diffusion, including: i) gross nitrification, the oxidation of ammonium (NH_4^+) to nitrate (NO_3^-) and ii) gross N mineralization, the transformation of organic N to inorganic N—i.e., production of NH_4^+ and further oxidation to NO_3^- via nitrification; hereafter, both processes are referred to as "inorganic N production" (Austin et al. 2004; Schwinning & Sala 2004). In water-limited ecosystems (e.g., drylands) diffusion restricts inorganic N production (Manzoni et al. 2012; Stark & Firestone 1995), yet N accumulates during dry periods (Parker & Schimel 2011), suggesting that microbial N production can persist at higher rates than the plant and microbial processes that take up N (i.e., N immobilization). The balance between N production and N immobilization can be restored when increased precipitation reestablishes diffusive transport of solutes and hydrologic connectivity in soil pore space (Austin et al. 2004). However, this may lead to increased potential for N loss, as the first wetting of dry soils can cause a pulse of N gas emissions (Eberwein et al. 2020; Firestone & Davidson 1989; Krichels et al. 2023c) and promote rapid leaching of N away from major sinks, such as plants and microbes (Walvoord et al. 2003). While the immediate effects of water limitation on inorganic N production are relatively well documented (Homyak et al. 2017; Manzoni et al. 2012; Reichman et al. 1966), the microorganisms that mineralize and nitrify N can respond to changes in water availability at different time scales (Schimel & Parton 1986), potentially establishing "precipitation legacy effects" where past precipitation controls current ecosystem process rates (Fig. 1; Reichmann et al., 2013a; Sala et al. 2012). This raises questions as to how precipitation legacies can influence inorganic N production, increase soil inorganic N pools when microbial activity should be low, and affect ecosystem N availability during dry periods.

Precipitation legacies alter ecosystem processes in ways that persist even after precipitation patterns revert to antecedent conditions. For example, increases in soil inorganic N concentrations during droughts have been observed to persist even after the drought ends (Krichels et al. 2023a), as past dry seasons can lower N immobilization rates and increase the fraction of soil N that carries over into the following season (i.e., the N carryover hypothesis; Krichels et al. 2023a; Sala et al. 2012; Shen et al. 2016). Similarly, less precipitation in one season can decrease microbial biomass the following season (Krichels et al. 2023a), limiting both inorganic N production and N immobilization. The microbial communities that process inorganic N may have distinct responses to water availability, such that N mineralization and nitrification may respond differently to drought (Manzoni et al. 2012). For example, dry conditions can constrain NH_4^+ diffusion, thereby increasing competition for NH_4^+ and inhibiting nitrification to a greater extent than N mineralization (Recous et al. 1990; Schimel et al. 1989; Stark & Firestone 1995). If this diffusion limitation hinders nitrifying microorganisms, then nitrification may take more time to recover even after diffusion is reestablished (Bernhardt & Likens 2002; Leptin et al. 2021). In other cases, microbial communities may be well adapted to drought (Leizeaga et al. 2021), limiting the effects of precipitation variability on N production.

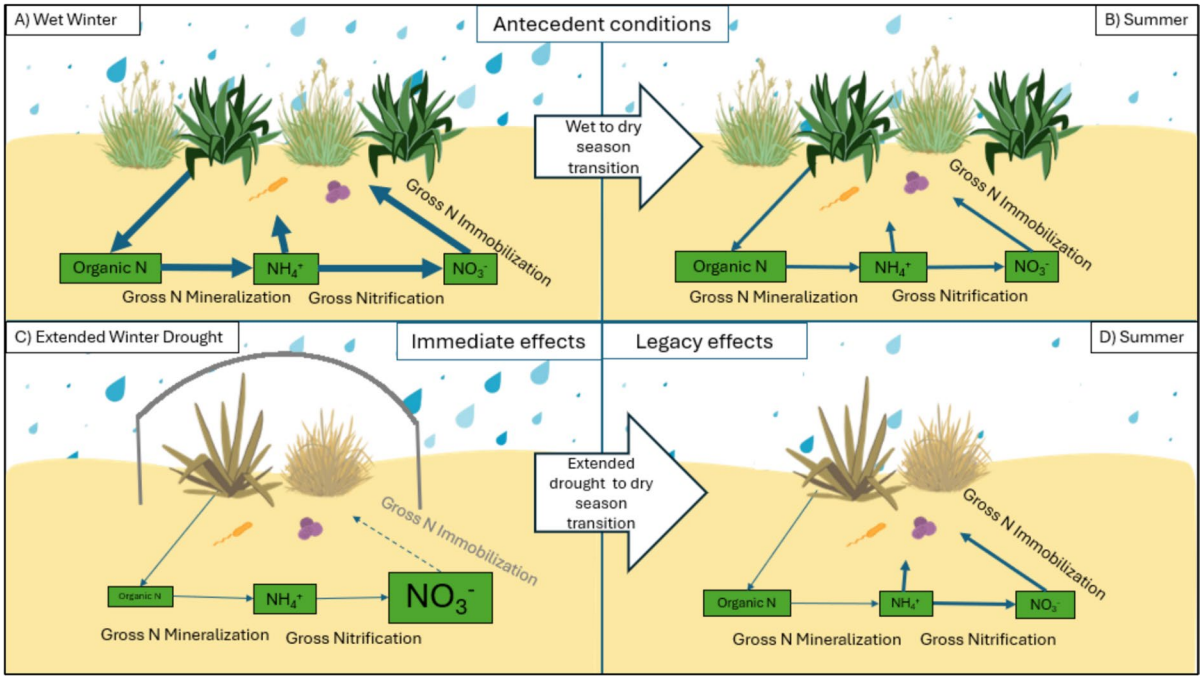


Fig. 1 Conceptual diagram illustrating how wet winter antecedent conditions **A** transition into the drier summer season **B**, and how the effects of imposing a winter drought, by excluding winter precipitation, induce both "immediate" effects during winter **C** and "legacy" effects the following summer **D** on soil N cycling. Green squares represent soil N pools and the size of the square indicates the relative size of the pool. Arrows indicate soil N transformations with their relative strength represented by arrow thickness. Dotted arrows represent no flux

While the effects of altered precipitation variability on soil N cycling are complex, especially in drylands where climate change is expected to have disproportionate effects on biogeochemical processes (Osborne et al. 2022), experimental approaches that: (i) simulate these changing conditions, (ii) integrate the intrinsic seasonality of drylands, and (iii) integrate indices of ecosystem N availability, like the isotopic composition of N in bulk soil (i.e., δ^{15}N enrichment), could help determine the extent to which changes in precipitation variability and the legacies of past precipitation shape inorganic N production. For instance, many drylands experience precipitation during cool wet winters with low evaporative losses that keep soils relatively moist as well as monsoonal precipitation during summers that interrupt otherwise hot and dry conditions (Ludwig et al. 1988; Osborne et al. 2022; Spasojevic et al. 2022). Thus, by experimentally excluding precipitation in the winter, followed by the typical drier summer, the soil microbial communities responsible for N production would be exposed to a prolonged or relatively "extreme drought." In contrast, imposing a summer drought may not induce substantial water stress on microbes already adapted to the high heat and low precipitation typical of summer (De Nijs et al. 2019), constituting a "moderate drought." Similarly, increasing precipitation during the already wet and cool winter would be expected to keep soils moist for a longer period relative to increasing precipitation in summer, suggesting a greater potential to extend biological activity from winter into the summer (Brown et al. 2022; Wu et al. 2022). These changes in precipitation, and the potential legacies they promote, would be expected to influence N retention, altering the isotopic composition of N in soil (Brunello et al. 2024; Mao et al. 2024; Robinson 2001; Von Sperber et al. 2017; Wang et al. 2014). While many factors affect bulk soil δ^{15}N values (e.g., vegetation, mycorrhizal associations, and atmospheric N deposition; Robinson 2001), there is growing evidence soil δ^{15}N increases with aridity because arid conditions stimulate fractionating N losses that enrich the residual soil N pool (Von Sperber et al. 2017; Wang et al. 2014). To understand how

precipitation variability affects soil N availability, we combine these approaches to ask: How does drought affect inorganic N production and the accumulation of N in soils? And, how do precipitation legacies affect gross N transformations and soil N pools?

To answer these questions, we manipulated the amount and timing of precipitation in a Pinyon-Juniper dryland in southern California where we either added or excluded precipitation during the winter or summer months (the experiment began at the end of summer 2018). We then measured gross N mineralization and nitrification rates in the laboratory using isotope pool dilution on soil samples collected during winter and summer in 2023. While these lab measurements cannot yield in situ gross N transformation rates for dry soils—the soils were wetted when the isotope label was added—they enabled comparisons among treatments and assessment of the relative sensitivity of both gross N mineralization and nitrification to the legacy effects of drought stress. We also measured bulk soil $\delta^{15}N$ values as an index of ecosystem N retention in response to shifts in precipitation during both winters and summers. We hypothesized that: (1) N accumulates in dry soils because both gross N mineralization and nitrification persist during drought when N sinks decouple (e.g., plants and microbes); and that (2) the effects of drought and increased precipitation on inorganic N production persist through seasons because of a lag in microbial response to ecosystem changes in precipitation between seasons (i.e., a precipitation legacy effect). Specifically, gross N mineralization is less sensitive to precipitation legacies than gross nitrification because nitrifier activity is more dependent on substrate diffusion than the heterotrophic microbes that mineralize N, resulting in more accumulation of NH_4^+ than NO_3^- when drought constrains gross nitrification.

Methods

Site description

We conducted our study in annual plant communities at the Pinyon Flats precipitation manipulation experiment in Southern California (33° 36 ′36.7″ N, 116° 27′ 01.1″ W), located in a pinyon-juniper dryland that is part of the University of California Philip L. Boyd Deep Canyon Desert Reserve (Spasojevic et al. 2022). The landscape at Pinyon Flats was historically dominated by *Juniperus californica* (Cupressaceae) and *Pinus monophyla* (Pinaceae), with a diversity of annual plants growing in the open spaces between these dominant species, including *Portulaca oleracea* (Portulacaceae) and *Erodium cicutarium* (Geraniaceae) (Spasojevic et al. 2022). Soils are gravelly fine sandy loams classified as loamy, mixed, superactive, nonacidic, mesic, shallow Typic Xerorthents and mapped in the in Omstott series. The soil pH is 7.6 measured in a 1:1 soil and water slurry, and the mean soil total C content (upper 10 cm) is 4.8 kg C per kg soil and 0.5 kg N per kg soil. The site receives annual mean precipitation of 235.7 mm which falls in two distinct seasons: (i) cool wet winters from November to May, characterized by average monthly low temperatures of 14.1 °C, average high temperatures of 25.9 °C, and average monthly precipitation of 24.1 mm, and (ii) monsoonal summers from June through October, characterized by average monthly low temperatures 24.7 °C, average high temperatures of 38.2 °C, and average monthly precipitation of 7.1 mm from 2000–2022 (https://deepcanyon.ucnrs.org/weather-data/). Air temperature and precipitation events between 2022 and 2023 are depicted in Fig. 2. The aridity index (i.e., the ratio of precipitation to potential evapotranspiration) for this site is estimated to be 0.22 (Zomer et al. 2022) and modeled total atmospheric N deposition is 3.6 kg N ha-1 y-1 (National Atmospheric Deposition Program, 2023).

Precipitation has been experimentally added or excluded in 24, 6.1-m × 8.5-m plots, during the winter and summer at Pinyon Flats since 2018 (Fig. 3; Spasojevic et al. 2022) according to the following treatments (listed from driest to wettest): *Winter-* received ambient summer precipitation while winter precipitation was excluded. On March 7th, 2023, approximately 25 mm of rain entered one of our *Winter-* plots, forcing us to exclude it from our analysis; therefore, $n = 3$ *Winter-* plots. *Summer-* ($n = 4$ plots) received ambient winter precipitation while summer precipitation was excluded. *Control* ($n = 8$ plots) received both ambient summer and winter precipitation. *Summer+* ($n = 4$ plots) received ambient winter precipitation and received additional water during the summer (Table S1). *Winter+* ($n = 4$ plots) received ambient summer precipitation and additional water

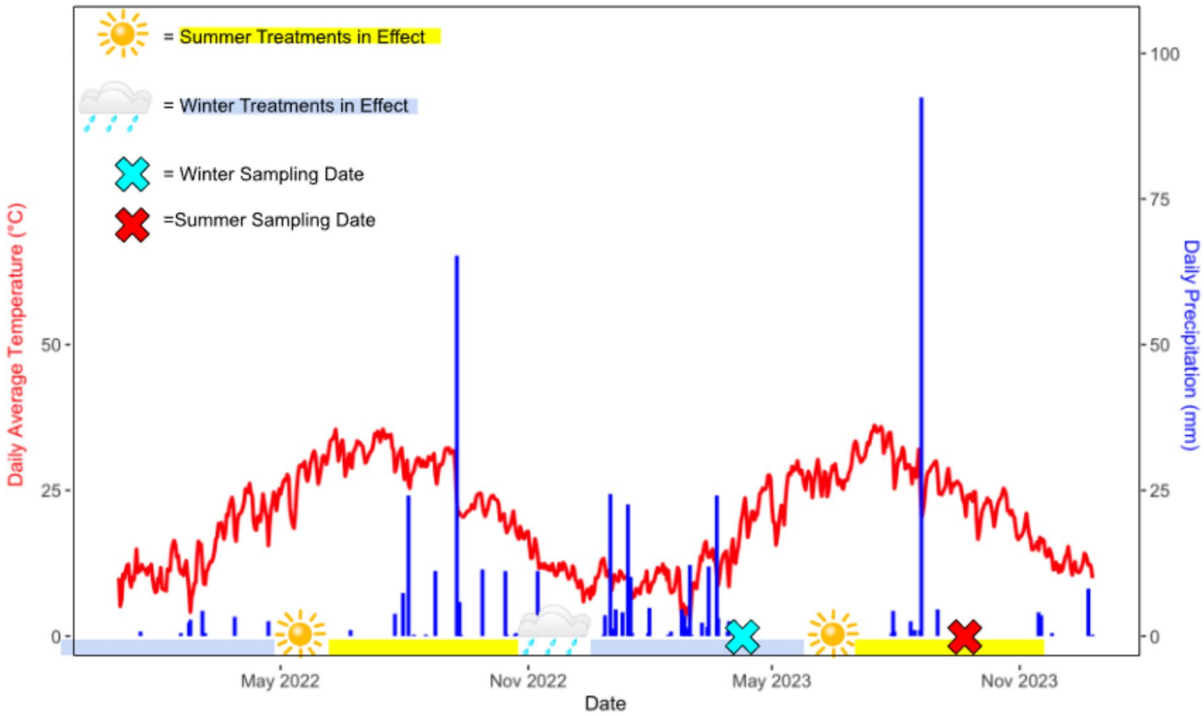


Fig. 2 Daily precipitation and air temperature at our experimental field site from 2022–2023. The cloud and blue bars represent when winter treatments (*Winter*- and *Winter*+) were in effect. The sun and yellow bars represent when summer treatments (*Summer*- and *Summer*+) were in effect. The "×" denotes when soil samples were collected in winter and summer 2023

during the winter (Table S1). Precipitation treatments were randomly assigned to the 24 plots across the experimental area.

For the exclusion treatments (*Winter*- and *Summer*-), precipitation was excluded using metal frames covered with polyethylene plastic (Tuff Lite IV; Berry Plastics, USA). *Summer*- roofs were placed in early June and moved to *Winter*- roofs in mid-October. During each season, precipitation was collected from the exclusion plots through a downslope PVC system filling four 1,500-gallon tanks. Water collected in the tanks was added to the water addition treatments (*Winter*+ in the winter and *Summer*+ in the summer) within roughly one week of each precipitation event by pumping water from the tanks through 17-mm drip tubing (Netafim Irrigation, Inc., Fresno, CA). We used a data logger (Campbell CR1000x) to collect hourly meteorological information including air temperature (Campbell 108-L Betatherm 100K6A1IA Thermistor), soil moisture (Campbell CS616 30 cm Water Content Reflectometer) and precipitation (Campbell TE525MM-L Metric Rain Gage). Air temperature and precipitation for the year leading up to (i.e., 2022) and containing our sampling (i.e., 2023) are presented in Fig. 2.

Soil collection and analysis

For the soils that we aimed to measure gross N transformation rates, we collected soil (A horizons; top 10 cm; ~ 500 g) from each of the 24 plots in both the winter (April; aimed at capturing peak plant activity) and summer of 2023 (September; aimed at capturing summer-dry soils before the onset of the wet season) approximately five years after we began manipulating precipitation at the site. Soils were collected using an aluminum corer (10 cm in length × 4 cm in diameter), sieved (2 mm), and a subsample was oven-dried at 104 °C for 24 h to determine soil gravimetric water content (GWC).

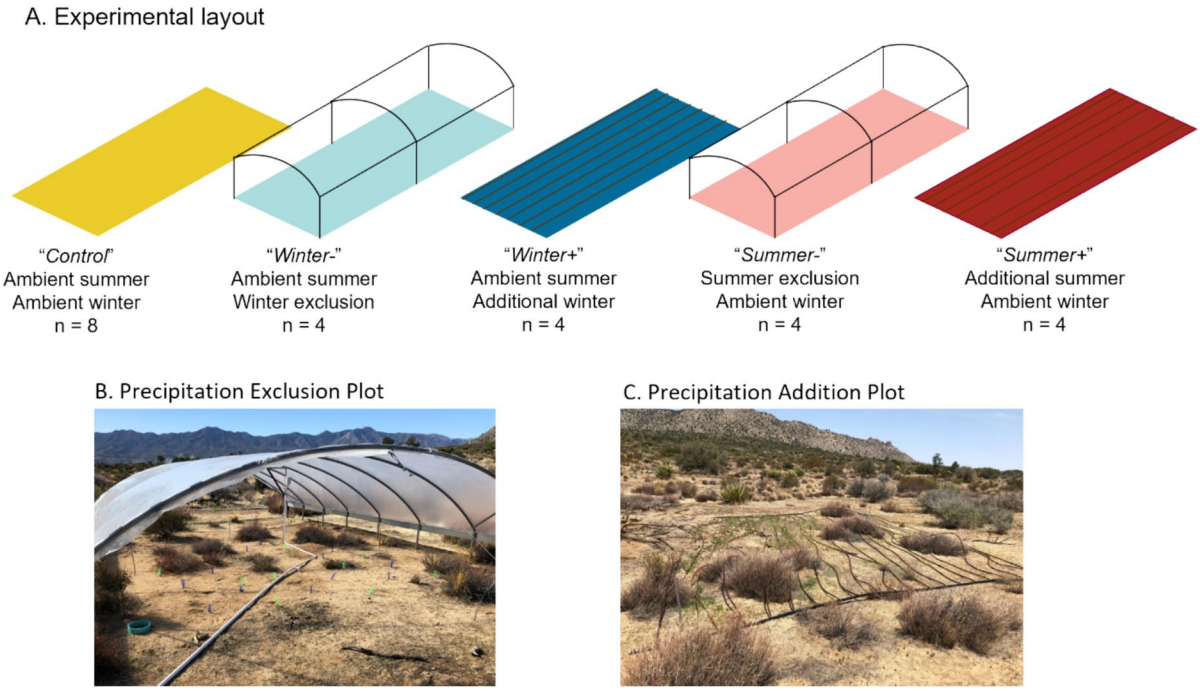


Fig. 3 **A** Field experimental layout of our research site with treatments represented by different colors. **B** Plastic roofing was used to exclude precipitation in *Winter-* and *Summer-* plots and **C** irrigation lines were used to supplement precipitation in *Winter+* and *Summer+* plots

Soil water holding capacity (WHC, g_{water}/g_{soil}) was measured as the water retained by water-saturated soils against gravity over an 8-h period (Franzluebbers 2020), where soils were allowed to drain inside an airtight container to minimize evaporative losses. Soil extractable NO_3^- and NH_4^+ concentrations were measured by extracting 3 g of soil in 30 mL of 2 M KCl, followed by shaking for 1 h and filtered filtering (Whatman 42 filter paper; 2.5 µm pore size). Colorimetric assays were used to measure extractable NO_3^- (SEAL cadmium-sulfanilamide method EPA-126-A, limit of quantitation (LOQ) = 0.03 mg L-1) and NH_4^+ (SEAL phenol-hypochlorite method EPA-129-A, LOQ = 0.05 mg L-1).

Soil microbial biomass C and N were measured using a chloroform slurry extraction (Vance et al. 1987). Briefly, 10 g of soil was extracted in 40 mL of 0.5 M K_2SO_4, with or without 0.5 mL of chloroform, and shaken for 4 h (Vance et al. 1987). The extractions were then filtered (Whatman 42 filter paper; 2.5 µm pore size) and analyzed for total organic C and N using a total organic C analyzer (TOC-L CPH, Shimadzu Scientific Instruments, LOQ = 4 µg L-1) connected to a nitrogen monoxide chemiluminescence analyzer (TNM-L, LOQ = 30 µg L-1). Microbial biomass C and N were calculated as the difference in total organic C or total organic N between the two extractions with or without chloroform. Our measurements represent a flush of C and N held in biomass rather than total microbial biomass, as we did not correct for extraction efficiency.

Short-term gross N transformation rates

To measure soil gross N mineralization and gross nitrification rates, we performed isotope pool dilutions (Davidson et al. 1991). To measure gross nitrification rates, we added $^{15}N\text{-}KNO_3^-$ to raise the isotopic composition of the NO_3^- pool to 10 atom% (our measurements show we achieved ~ 8.60 ± 0.95 atom% enrichment). Time 0 started when the label was added, which included wetting the soil samples to 60% WHC to stimulate a wetting without stimulating widespread anaerobic conditions and to allow for even distribution of the isotope label. While wetting soils stimulates microbial activity, we used the pool dilutions to assess

relative differences between treatments and infer how changes in antecedent moisture and soil N affected N dynamics. After adding the label the soils were mixed for approximately 3 min to ensure even distribution of the label. After both 15 min and 4 h, 50 g of soil from the jars were extracted in 150 mL of 2 M KCl for subsequent measurement of $NO_3^-$and NH_4^+ concentrations and isotopic composition (Davidson et al. 2003). We chose to measure gross N transformations up until 4 h post-wetting because previous research at the site demonstrated that much of the N-cycling activity occurs within 4 h of wetting (Krichels et al. 2023a, 2023b). To measure gross N mineralization rates, we used the same procedure outlined above but with 10 atom% $^{15}NH_4Cl$ (our measurements showed we achieved 7.85 ± 0.95 atom% enrichment). The ^{15}N enrichment of the NH_4^+ was determined using acid trap diffusion (Brooks et al. 1989), where NH_4^+ in the extract is volatilized to NH_3 by raising the pH with MgO, and the NH_3 is trapped onto a paper disk acidified with 2.5 M potassium bisulfate. The same method was used to measure the ^{15}N enrichment of NO_3^-pools with the addition of Devarda's alloy to first reduce NO_3^- to NH_3. The paper disks were dried for 24 h in a desiccator before analysis on an elemental analyzer (Costech) coupled to an isotope ratio mass spectrometer at the Facility for Isotope Ratio Mass Spectrometry at UC Riverside (FIRMS, https://ccb.ucr.edu/facilities/firms).

Gross nitrification rates were calculated from the dilution of the enriched NO_3^-pool between 15 min and 4 h after adding the ^{15}N label (Kirkham & Bartholomew 1954). Gross N mineralization rates were calculated as the sum of the dilution of the enriched NH_4^+ pool between 15 min and 4 h after adding the ^{15}N label and gross nitrification rates. We used the timepoint at 15 min post label addition to account for the initial abiotic processing of ^{15}N commonly observed in pool dilution experiments (Davidson et al. 1991). Dissimilatory nitrate reduction to ammonium (DNRA) was also measured with this isotope pool dilution (see supplemental information S1).

Long-term field observations: Net N mineralization and net nitrification rates, soil extractable NH_4^+, NO_3^-, and organic N pools, and natural abundance soil $\delta^{15}N$

Since 2019, we have conducted quarterly assessments of in situ soil extractable NH_4^+ and NO_3^-, as well as in situ net N mineralization and net nitrification rates using 30-day incubations. At the start of each quarter (i.e., January for winter, April for spring, July for summer, and October for autumn), a 10-cm long by 4 cm diameter PVC core was installed in each plot. An initial soil sample from the upper 10 cm (A horizon) next to the PVC core was collected to determine initial concentrations of extractable NH_4^+ and NO_3^-. The PVC cores were capped with PVC lids with pre-drilled 3-mm diameter holes on the side to prevent N inputs from the atmosphere and N losses to leaching but allow gas exchange. After 30 days, the cores were retrieved for analysis of extractable NH_4^+ and NO_3. Net nitrification was calculated as the difference in the NO_3^- pool over the 30-day period and net N mineralization was determined as the difference in the inorganic nitrogen pool (sum of NH_4^+ and NO_3^-) over the same period. During summer 2023, wildlife disturbed the cores in multiple plots and are missing from our analysis, such that $n = 4$ in *Control*, $n = 2$ in *Summer-*, and $n = 3$ in *Winter-*, *Winter+*, and *Summer+*.

Natural abundance $\delta^{15}N$ for bulk soil was measured in finely ground samples combusted on an elemental analyzer (Costech Elemental Combustion System, LOQ = 1 µg) coupled to an isotope ratio mass spectrometer (Delta V Advantage IRMS, $\delta^{15}N$ precision = 0.06 ‰) at FIRMS. We estimated organic N concentrations as the difference between total bulk soil N and extractable inorganic N per treatment.

Statistical analyses

All statistical analyses were conducted in R version 4.4.0 (R Core Team, 2019). We compared gross N transformation rates and soil properties across seasons when we sampled and between precipitation treatments using one linear mixed effects model for the winter and summer sampling times. Treatment, season, and their interaction were evaluated as fixed effects, plot as a random effect, and gross N transformation rates and soil properties as response variables in separate models using the "nlme" package. When a significant interaction effect ($p < 0.05$) between season and treatment or, a significant main effect for treatment was detected, we applied post hoc pairwise comparisons using "emmeans" and applied the Tukey adjustment for multiple comparisons. To explore relationships among soil properties and gross N cycling rates across seasons and treatments, we used least squares linear regressions.

In our analysis, we defined "immediate" effects as a significant season×treatment interaction where the *Control* means differed from the precipitation treatment means in the same season. For example, if the *Control* in the winter season was significantly different than the *Winter-* or *Winter+*, we considered this an immediate effect and present the *p*-value from the post-hoc test related to that comparison. We defined "legacy" effects as a significant season×treatment interaction where the *Control* in either winter or summer differed from treatments that were not active in that season. For example, if the *Control* in the summer was significantly different than the *Winter-* or *Winter+*, that would be considered a precipitation legacy and we present the p-value from the post-hoc test related to that comparison. We used least squares linear regressions to explore relationships among soil properties and gross N cycling rates across seasons and treatments.

To understand the relationship between precipitation and soil $\delta^{15}N$, we plotted $\delta^{15}N$ for soils collected since 2019 against the cumulative precipitation of the water year per treatment at the time of sampling, including water added to precipitation addition treatments. We used a polynomial mixed effects model to model the interaction of season, treatment, and precipitation; a quadratic term for rainfall ($rain^2$) was included to account for the observed non-linear relationship between $\delta^{15}N$ and precipitation. To account for the repeated measures taken from the same plots over multiple years, random intercepts were included for both plot and sampling date. For all statistical tests, we evaluated model assumptions of normality using the Shapiro–Wilk test and homogenous variance using Q-Q plots and residual plots of the fitted model. When the model assumption of homoscedasticity was not met, we modeled heterogeneous variances using a variance structure from the nlme package to account for heteroscedasticity in our mixed effects model. We log-transformed summer soil extractable NO_3^-, summer soil moisture, summer DNRA rates, and summer and winter soil extractable NH_4^+ prior to analyses.

Results

Soil gravimetric water content (GWC)

Manipulating seasonal precipitation had immediate effects on soil GWC. Average soil GWC was nearly three times higher in winter than in summer and was sensitive to changes in precipitation imposed by our treatments (Fig. 4A-B, F4, 18 = 13.77, $p < 0.0001$): in the winter, excluding precipitation significantly lowered soil GWC (*Winter-* = 2.44 ± 0.45%) by nearly two times relative to the *Control* (4.4 ± 0.88%, $p = 0.0002$), and by nearly two times relative to treatments that received extra water (*Winter+;* 4.74 ± 0.97%, $p = 0.0013$; *Summer+* = 4.73 ± 0.24%, $p = 0.0067$). In the summer, excluding summer precipitation (*Summer-;* 0.33 ± 0.08%) significantly lowered soil GWC relative to all other treatments (Fig. 4B; $p = 0.0433$), whereas adding extra water (*Summer+;* 3.50 ± 1.26%) significantly increased GWC relative to all other treatments ($p = 0.0342$). The legacies of past precipitation, however, had no effect on soil GWC (i.e., manipulating precipitation during the prior season had no effect on soil moisture, $p = 0.82$).

Soil extractable NH_4^+ and NO_3^- concentrations

Manipulating seasonal precipitation had no immediate effects in the winter or summer on NH_4^+ concentrations. However, the legacies of past precipitation significantly affected soil extractable NH_4^+ concentrations (Fig. 4C-D, treatment by season interaction: $F_{4,\ 18} = 5.88$, $p = 0.0033$); excluding precipitation in the summer (*Summer-*) increased extractable NH_4^+ concentration the following winter by approximately two times over the control (*Summer-* = 1.7 ± 0.4 μg NH_4^+-N g^{-1} soil; *Control* = 0.8 ± 0.50 μg NH_4^+-N g^{-1} soil, $p = 0.0454$). In the summer, manipulating prior winter season precipitation had no effect on NH_4^+; *Winter-* and *Winter+* treatments were no different than the control (Fig. 4D, $p > 0.17$).

In contrast to the observed effects on NH_4^+, manipulating seasonal precipitation had immediate effects on soil extractable NO_3^- (Fig. 4E-F); treatment by season interaction: $F_{4,18} = 6.32$, $p = 0.0023$); excluding winter precipitation increased winter NO_3^- concentrations by nearly six times over the control (*Winter-* = 2.6 ± 0.3 μg NO_3^- -N g^{-1} soil; *Control* = 0.5 ± 0.2 μg NO_3^- -N g^{-1} soil, $p = 0.0015$; Fig. 4E). In contrast to the increase in NO_3^- from excluding winter precipitation, excluding summer precipitation lowered NO_3^- concentrations relative to the *Control* (Fig. 4F; *Summer-* = 0.6 ± 0.2 μg NO_3^- -N g-1 soil;

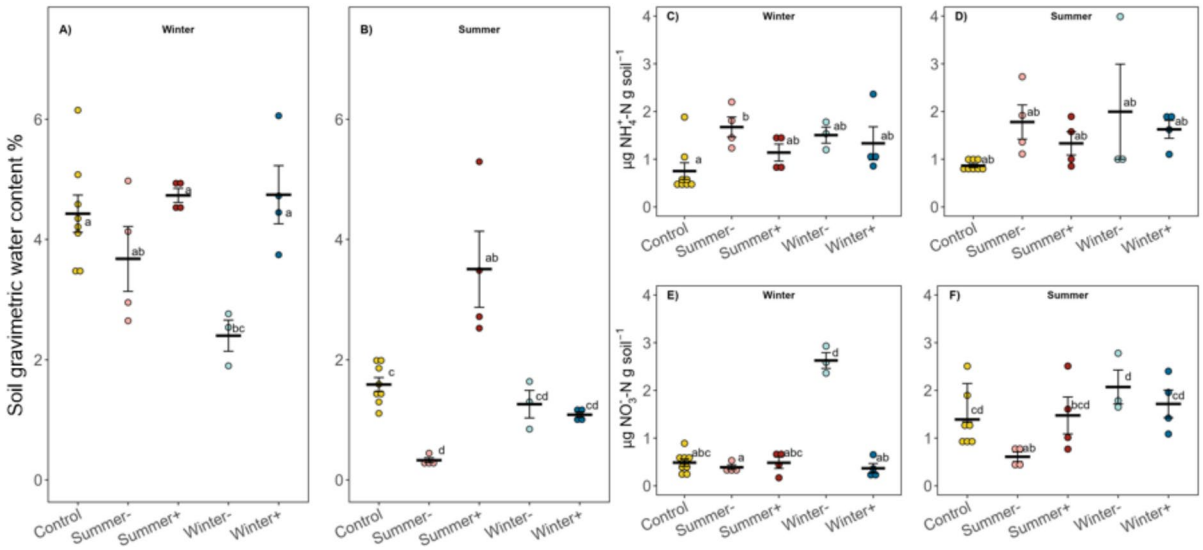


Fig. 4 Soil gravimetric water content (%; g_{water} g_{soil}^{-1}) for each rainfall manipulation treatment in the **A** winter and **B** summer of 2023. Soil extractable ammonium (NH_4^+, **C–D**) and nitrate ($NO_3.^-$, **E–F**) concentrations for each rainfall manipulation treatment during winter and summer 2023. For a description of treatments see Fig. 3. Different letters denote statistically significant differences between treatments among seasons (winter and summer) as determined by pairwise comparisons following a linear mixed effects model ($\alpha = 0.05$). Black horizontal lines represent the average of observations, dots are individual observations, and error bars represent standard errors ($n = 8$ for the *Control*, $n = 3$ for *Winter-*, and $n = 4$ for all other treatments)

Control = 1.7 ± 1.1 μg NO_3^- -N g-1 soil, $p = 0.0346$). We note, however, this contrasting result was measured in soils sampled approximately one week after a large storm (Fig. 2), and it is possible surface runoff could have entered our precipitation exclusion plots. The legacies of past precipitation did not affect soil extractable NO_3^- (Fig. 4E–F); *Summer+* and *Summer-* were no different than the *Control* in the winter ($p > 0.98$), and *Winter+* and *Winter-* were no different than the *Control* in the summer ($p > 0.99$).

Gross N mineralization rates

Manipulating precipitation had both immediate and legacy effects on gross N mineralization rates in the lab, as assessed by the significant interaction between treatment and season effects (Fig. 5A–B, F4, 18 = 4.17, $p = 0.0145$). Specifically, excluding precipitation the winter (*Winter-*) had immediate effects by lowering gross N mineralization rates ~ 2.5 times relative to the *Control* (Fig. 5A; $p = 0.04$; *Winter-* = 0.12 ± 0.03 μg N g^{-1} soil h^{-1}; *Control* = 0.30 ± 0.08 μg N g^{-1} soil h^{-1}, $p = 0.0463$). This drought stress induced in the winter then prompted a legacy effect the following summer by lowering gross N mineralization rates in the *Winter-* treatment by ~ 2 times relative to the *Control* (Fig. 5B; $p = 0.03$; *Winter-* = 0.19 ± 0.03 μg N g^{-1} soil h^{-1} and *Control* = 0.41 ± 0.19 μg N g^{-1} soil h^{-1}, p = 0.0289). Further, increasing precipitation in the summer (*Summer+* = 0.69 ± 0.21 μg N g^{-1} soil h^{-1}) significantly increased gross N mineralization rates compared to increasing precipitation in the winter (*Winter+* = 0.23 ± 0.07 μg N g^{-1} soil h^{-1}, $p = 0.0018$). Across our precipitation treatments, gross N mineralization in the wet winter had no relationship with soil GWC (Fig. S1A, p > 0.36). In contrast, gross N mineralization was positively correlated with soil GWC (Fig. S1B, p < 0.0001) in the summer, which also had lower soil GWC than in winter.

Gross nitrification rates

Similar to gross N mineralization, manipulating precipitation had immediate effects on gross nitrification (treatment by season interaction: $F_{4,\ 18} = 26.19$, $p < 0.0001$, Fig. 5C–D); excluding winter precipitation significantly lowered gross nitrification rates

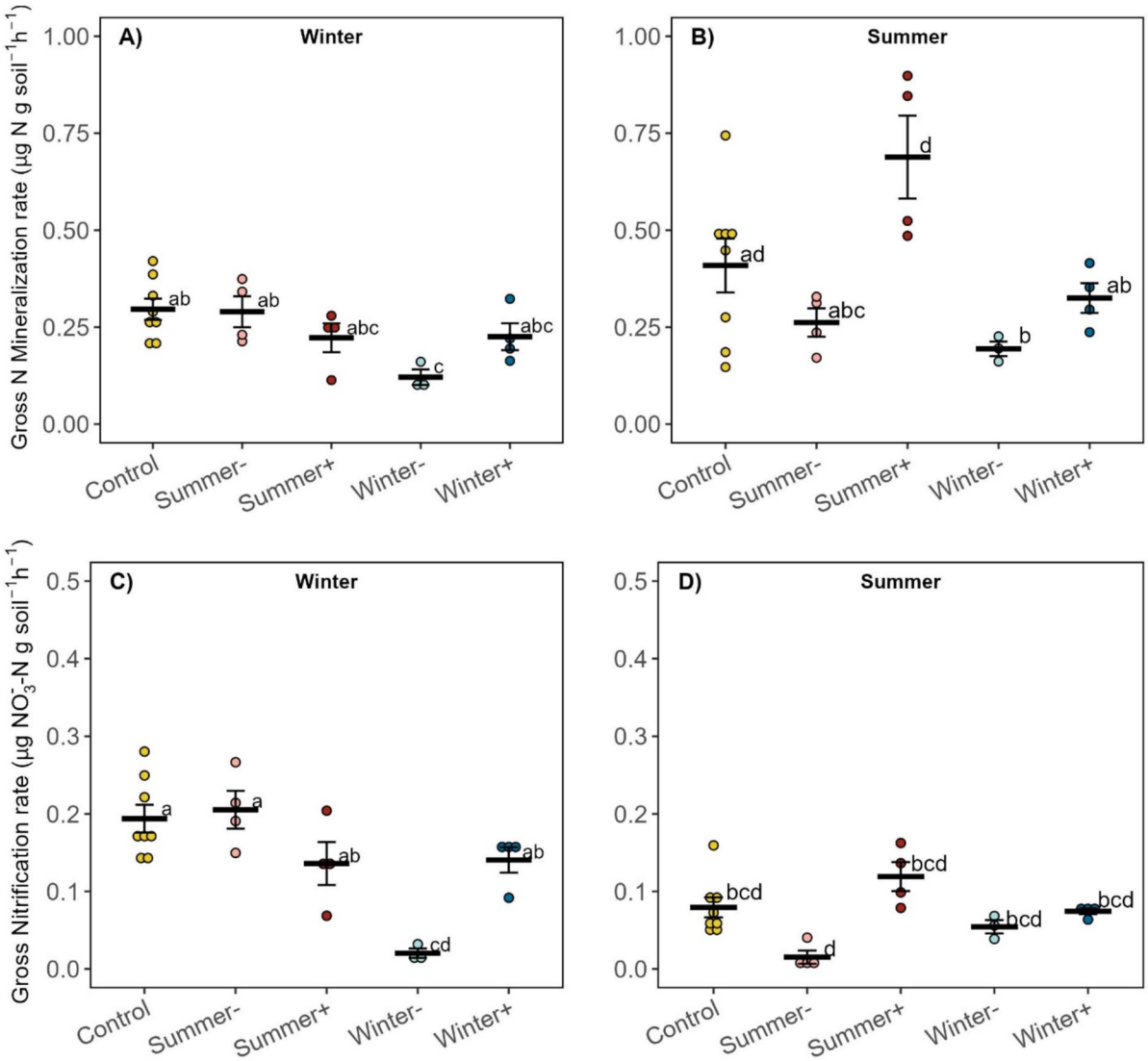


Fig. 5 Gross N mineralization **A**–**B** and gross nitrification **C**–**D** rates for each rainfall manipulation treatment measured from soils collected in winter and summer 2023. For a description of treatments see Fig. 3. Different letters denote statistically significant differences between treatments among seasons (winter and summer) as determined by pairwise comparisons following a linear mixed effects model ($\alpha = 0.05$). Black horizontal lines represent the average of observations, dots are individual observations, and error bars represent standard errors ($n = 8$ for the *Control*, $n = 3$ for *Winter-*, and $n = 4$ for all other treatments)

by ~ 9.5 times compared to the *Control* (Fig. 5C; *Winter-* = 0.02 ± 0.01 µg N g^{-1} soil h^{-1}; *Control* = 0.19 ± 0.05 µg N g^{-1} soil h^{-1}, $p < 0.0001$). In contrast to the winter season, manipulating summer precipitation had no immediate effect on gross nitrification rates when comparing treatments to control plots (Fig. 5D, $p > 0.20$), where on average, we measured lower gross nitrification rates than in the wetter winter (summer season = 0.07 ± 0.04 µg N g^{-1} soil h^{-1}; winter season = 0.15 ± 0.07 µg N g^{-1} soil h^{-1}, $p < 0.0001$). Moreover, gross nitrification rates in the *Summer-* plots during summer were ~ 13 times lower than in winter, emphasizing the sensitivity of gross nitrification to drought stress (Fig. 5D; 0.20 ± 0.05 µg N g^{-1} soil h^{-1} in winter compared to 0.02 ± 0.02 µg N g^{-1} soil h^{-1} in summer; $p < 0.0001$).

The sensitivity of gross nitrification to drought stress gave rise to a positive correlation between gross nitrification rates and soil GWC in the summer (Fig. S1D, $R^2=0.453$, $p<0.0001$), but not in the winter when wetter soils would have minimized drought stress (Fig. S1C, $R^2=0.113$, $p=0.117$). Consistent with this understanding, we found that soil GWC was not correlated with gross nitrification rates in the plots receiving extra water to limit drought stress (*Winter+* and *Summer+*); instead, they were positively correlated with substrate availability (i.e., soil extractable NH_4^+; Fig. S2A, C; $R^2=0.687$, $p=0.011$). In contrast, the opposite was true in the drier summer season where gross nitrification was not correlated with substrate availability (NH_4^+), but it was correlated with soil GWC (Fig. S2B, D; $R^2=0.748$, $p<0.0001$). Unlike the patterns observed with gross N mineralization, gross nitrification rates were not affected by the legacies of past precipitation (Fig. 5C–D, $p>0.05$); rates in *Summer-* and *Summer+* treatments were no different than the *Control* in the winter (Fig. 5C, $p>0.32$) and *Winter-* and *Winter+* rates were no different than the *Control* in the summer (Fig. 5D, $p>0.99$).

In situ net N mineralization and nitrification rates

Manipulating seasonal precipitation had no immediate effects on net N mineralization (Fig. 6A–B, $F_{4,18}=2.63$, $p>0.06$) or net nitrification (Fig. 6C–D, $F_{4,18}=1.31$, $p>0.30$) when compared to *Control* plots. However, inducing extreme drought in the winter (*Winter-* plots) significantly increased net nitrification rates by ~8× (Fig. 6C; *Winter-* = 0.06 ± 0.04 µg N g-1 soil) when compared to *Summer-* treatments (0.007 ± 0.006 µg N g-1 soil, $p=0.0301$), opposite to the decrease in gross nitrification rates we observed in the lab (Fig. 5C). The legacies of past precipitation did not significantly affect either in situ net N mineralization (Fig. 6A–B) nor net nitrification rates (Fig. 6C–D); *Summer-* and *Summer+* rates were no different than the *Control* in the winter ($p>0.53$) and *Winter-* and *Winter+* rates were no different than the *Control* in the summer ($p>0.14$).

Soil organic N and total C content

Manipulating precipitation produced both legacy and immediate effects on soil organic N (Fig. S4, $F_{4,18}=4.27$, $p=0.0402$). Excluding winter precipitation produced a legacy effect the following summer by lowering soil organic N ($p=0.0421$); summer organic N in the *Winter-* treatments (13 ± 3 µg N g-1 soil) was ~2× lower than the Control (23 ± 6 µg N g-1 soil). Besides legacy effects, excluding precipitation in the winter significantly reduced organic N by ~2.5× compared to the *Control* (*Winter-* = 12 ± 2 µg N g-1 soil; *Control* = 27 ± 8 µg N g-1 soil h-1, $p=0.0431$). In contrast, manipulating precipitation had no effect on total C ($F_{4,18}=1.29$, $p>0.31$).

Bulk soil δ^{15}N natural abundance

Manipulating seasonal precipitation did not affect bulk soil δ^{15}N values (Fig. 7A, $p>0.30$) and there was no significant relationship between bulk soil δ^{15}N and annual cumulative precipitation (measured as cumulative precipitation per water year; Fig. 7B, $p>0.50$).

Microbial biomass C & N pools

Average microbial biomass C was 146 ± 79 µg C g-1 soil in the winter and 118 ± 80 µg C g-1 soil in the summer (Fig. S3A–B). Average microbial biomass N was 9 ± 4 µg N g-1 soil in the winter and 13 ± 7 µg N g-1 soil in the summer (Fig. S3C–D). We did not detect significant differences between seasons or treatments for either microbial biomass C ($F_{4,18}=1.07$, $p>0.39$) or N ($F_{4,18}=2.05$, $p>0.13$).

Discussion

Changes in precipitation patterns can influence soil N cycling depending on how ecosystems respond to subsequent changes in soil moisture, as well as through the legacies these changes in moisture may establish. However, how these legacies control the production of soil inorganic N remains difficult to predict. To this end, we measured soil inorganic N production (i.e., both *gross* and *net* rates of soil N mineralization and nitrification) and soil extractable N pools after manipulating precipitation in a Pinyon–Juniper dryland. We hypothesized that: 1) N accumulates in dry soil because inorganic N production persists during drought; and 2) the effects of drought and increased precipitation on inorganic N

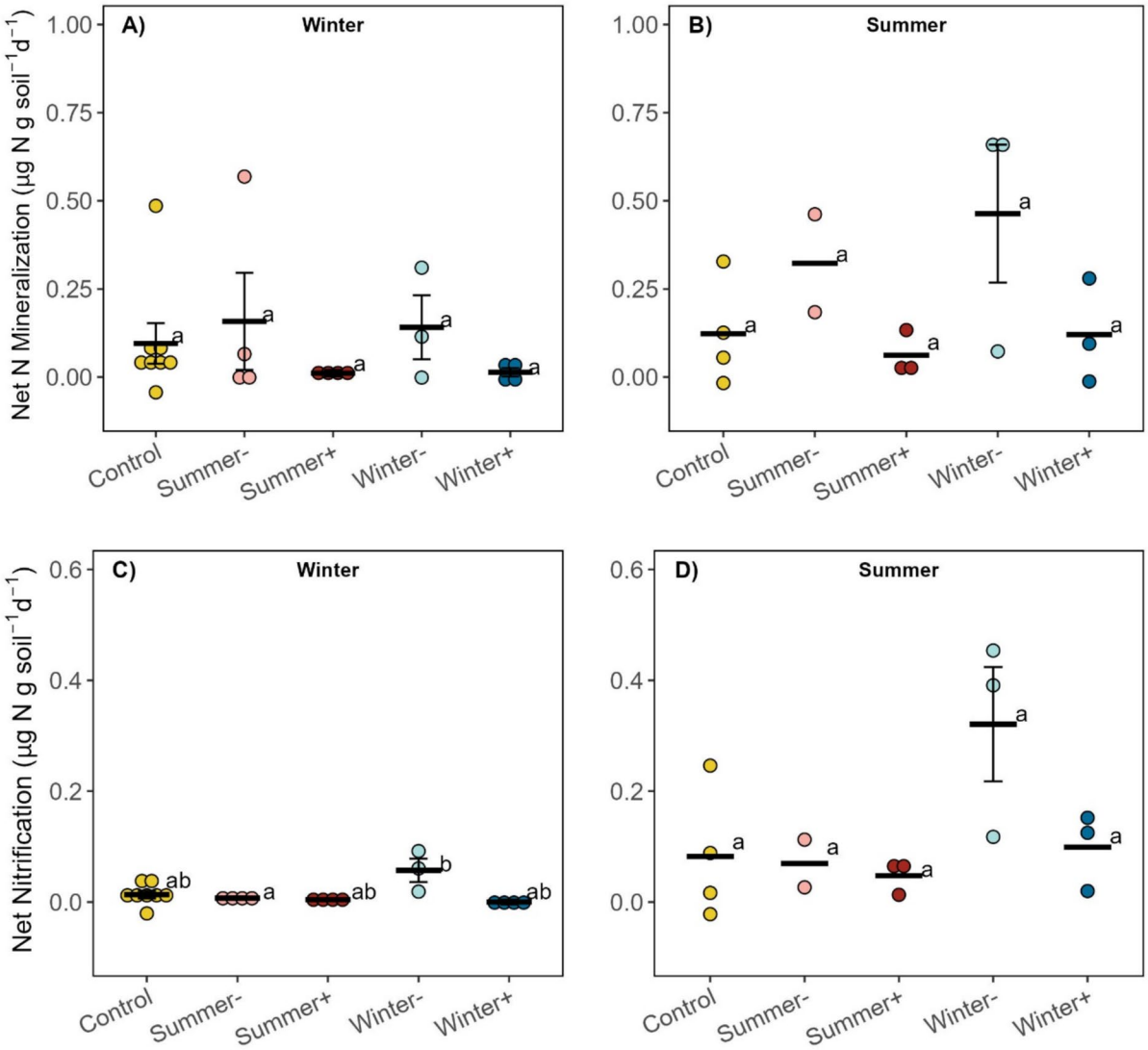


Fig. 6 Soil net N mineralization **A**, **B** and net nitrification **C**, **D** rates for each rainfall manipulation treatment from 30-day in situ incubations in winter (April) and summer (September) of 2023. For a description of treatments see Fig. 3. Different letters denote statistically significant differences between treatments among seasons (winter and summer) as determined by pairwise comparisons following a linear mixed effects model ($\alpha = 0.05$). Black horizontal lines represent the average of observations, dots are individual observations, and error bars represent standard errors (Winter: $n = 8$ for the *Control*, $n = 3$ for *Winter-*, and $n = 4$ for all other treatments; Summer: $n = 3$ for *Control*, *Summer+*, *Winter+*, and *Winter-*, $n = 2$ for *Summer-*)

production persist through seasons because of a lag in the response of microbes to changes in precipitation between seasons (i.e., a precipitation legacy effect). Specifically, we expected gross nitrification would be more sensitive to precipitation legacies than gross N mineralization because nitrifier activity depends more on substrate diffusion than the heterotrophic microbes that mineralize N, favoring the accumulation of NH_4^+ over NO_3^- when drought constrains nitrification.

In support of our first hypothesis, we found that wintertime drought—the most extreme drought we imposed—lowered both gross N mineralization and nitrification rates, though both rates must have remained above zero to account for the inorganic N

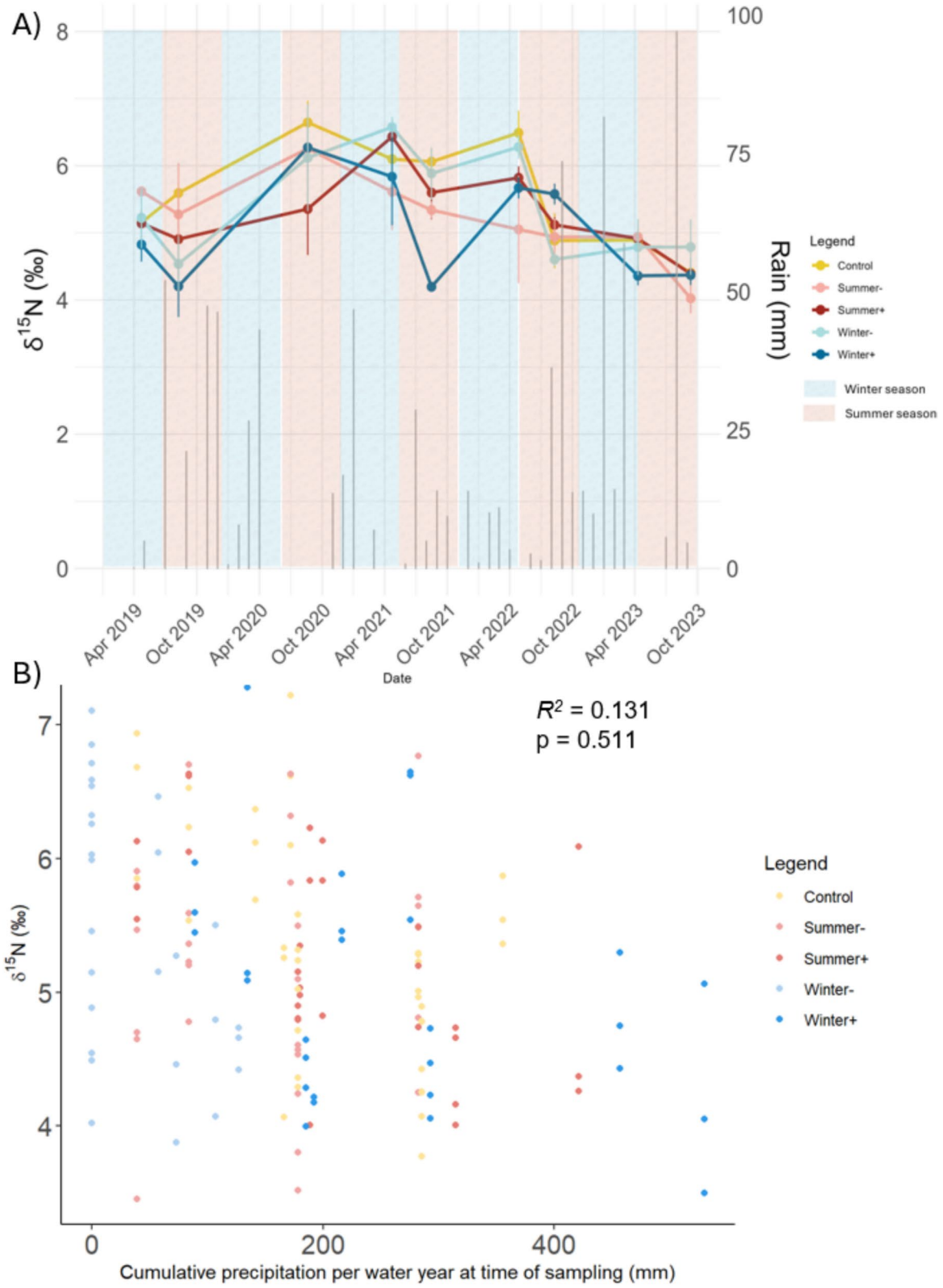
that accumulated in soil (Fig. 1C). We also found the wintertime drought we imposed established precipitation legacies that reduced gross N mineralization in following seasons when soil organic N was reduced, but contrary to our second hypothesis, did not affect gross nitrification (Fig. 1D). Further, we observed higher soil inorganic N concentrations consistent with precipitation legacies when the wintertime drought increased NO_3^- above ambient conditions (Fig. 4E). This implies the consumption of N (i.e., N immobilization rates) must have been lower than the rate of inorganic N production for the N to accumulate. Together, both immediate effects (i.e., significant treatment effects in the same season) and legacy effects (i.e., significant treatment effects detected the following season) induced by shifts in precipitation help explain the mechanisms interacting to carry N over between seasons (i.e., the N carryover hypothesis;Krichels et al. 2023a; Sala et al. 2012; Shen et al. 2016) That is, drought stress did not completely shut down inorganic N production, which together with constrained N immobilization rates, allowed inorganic N concentrations to increase in soil and carry over into the following seasons.

Immediate effects induced by shifts in precipitation: inorganic N production above N immobilization increased soil inorganic N concentrations

We found that sustained rates of inorganic N production, coupled with reduced N immobilization, were key to explaining the increase in soil inorganic N concentrations we measured under the most extreme drought we imposed (*Winter-* in the winter season). While this extreme drought lowered both gross N mineralization and nitrification rates below the control, the rates remained above zero (Fig. 5), contributing to the NO_3^- that accumulated (Fig. 4E). However, for this NO_3^- to have accumulated when inorganic N production decreased below the control, a simultaneous decrease in N immobilization must have occurred. As evidence for this, we observed positive in situ *net* N mineralization and *net* nitrification under extreme drought (*Winter-* treatment in the winter; Fig. 6A, C), which can only occur if the rate of *gross* inorganic N production exceeds *gross* N immobilization. Since gross inorganic N production rates persisted under dry conditions (Fig. 5), N immobilization must have had to decrease below inorganic N production to explain the positive in situ net N production we measured. These interpretations are consistent with dry soils restricting N diffusion and constraining plant and microbial N immobilization as observed elsewhere and at our site (Dijkstra et al. 2015; Homyak et al. 2016). For example, gross nitrification was low in dry soil but increased when we increased soil moisture in the summer (Fig. S2B), implying low diffusion and/or N mineralization were constraining these rates prior to increasing soil moisture, which is also consistent with the decrease in plant biomass under the extreme winter drought measured at our site (Spasojevic et al. 2022). Overall, our results indicate that inorganic N production can persist during dry conditions and, when not balanced by N immobilization, soil inorganic N concentrations can increase.

Precipitation manipulation effects on the carryover of N between seasons

Changes in precipitation from the previous season established precipitation legacy effects on soil inorganic N production rates and NH_4^+ concentrations the following season. Specifically, the legacy effect of establishing winter drought (i.e., *Winter-* plots) reduced gross N mineralization rates the following summer (Fig. 5B). We anticipated measuring lower gross N mineralization rates in *Winter-* plots since drought stress often lowers microbial biomass (Moyano et al. 2013; Reichman et al. 1966; Shen et al. 2016; Stark & Firestone 1995). However, microbial biomass was not sensitive to drought legacy effects (Fig. S3), similar to other studies where microbial biomass did not change or even increased under drought stress (Manzoni et al. 2012; Parker & Schimel 2011; Schaeffer et al. 2017). This suggests other factors besides microbial biomass, like substrate availability (i.e., organic N), may have controlled the legacy effect on gross N mineralization. Indeed, soil organic N concentrations decreased in the *Winter-* treatment in both summer and winter (Fig. S4), consistent with a reduction in organic N inputs that would have been expected from the loss of plants in *Winter-* plots (Spasojevic et al. 2022). Thus, droughts extreme enough to limit microbial access to soil organic N can constrain gross N mineralization, limiting the carryover of N into the next season; this was observed when NH_4^+ did not increase in *Winter-* plots from winter to


A)
δ15N (‰)
Rain (mm)
Date
Apr 2019
Oct 2019
Apr 2020
Oct 2020
Apr 2021
Oct 2021
Apr 2022
Oct 2022
Apr 2023
Oct 2023
Legend
Control
Summer-
Summer+
Winter-
Winter+
Winter season
Summer season
B)
R2 = 0.131
p = 0.511
δ15N (‰)
Cumulative precipitation per water year at time of sampling (mm)
Legend
Control
Summer-
Summer+
Winter-
Winter+

◂**Fig. 7** **A** Bulk soil $\delta^{15}N$ natural abundance (permil; ‰) and average monthly precipitation (mm) from April 2019 until September 2023. The blue background represents the wet winter seasons and the red background the drier summer seasons. Circles represent the average of observations and error bars represent standard errors ($n=8$ for the *Control*, and $n=4$ for all other treatments). For a description of treatments, see Fig. 3. **B** Change in bulk soil $\delta^{15}N$ (permil; ‰) as a function of cumulative precipitation for the water year at the time the soil sample was collected from each treatment (mm). A linear model was used to assess a relationship between bulk soil $\delta^{15}N$ and cumulative precipitation

summer (Fig. 4C–D). In contrast, droughts that may be more moderate to not deplete organic N pools may sustain gross N mineralization and carry over NH_4^+ into the next season; this was observed when NH_4^+ increased in winter after excluding summer precipitation (Fig. 4C). Overall, gross N mineralization was sensitive to changes in soil organic N availability, with relatively extreme droughts limiting the carryover of NH_4^+ into the following season, but relatively moderate droughts favoring the carryover of NH_4^+.

Unlike gross N mineralization, gross nitrification was not sensitive to the legacies of past precipitation as we had hypothesized. When we increased precipitation to favor substrate diffusion in the winter (i.e., *Winter+*), gross nitrification increased with NH_4^+ concentrations (Fig. S2C), implying substrate availability (i.e., NH_4^+) limits nitrification when diffusion is not limiting (Davidson et al. 1990; Stark & Firestone 1995). This is consistent with substrate availability (i.e., NH_4^+) and microbial access to NH_4^+ via diffusion operating as key controls over nitrification (Deng et al. 2021; Stark & Firestone 1995), and suggests that the carryover of both NH_4^+ and soil moisture into the following season is necessary to establish a precipitation legacy for nitrification (Shen et al. 2016). While soil moisture did not carry over from winter to summer (Fig. 4A-B), likely due to fast evaporative losses at our site (Reichmann et al. 2013; Shen et al. 2016), NH_4^+ was carried over from a moderate drought imposed the previous summer into the winter (Fig. 4C). We expected this NH_4^+ would carry over into winter to establish a precipitation legacy effect on gross nitrification, but it did not (Fig. 5C), suggesting other factors besides water and substrate availability were important. It is possible the wet conditions of winter may have increased NH_4^+ uptake by plants and microbes, outcompeting nitrifiers for N (Liang et al. 2024; Recous et al. 1990; Schimel et al. 1989). Further, because nitrification is more sensitive to drought than N mineralization (Slessarev et al. 2021; Stark & Firestone 1995), excluding summer precipitation may have adversely affected nitrifying communities, thereby preventing the establishment of precipitation legacies on gross nitrification even under high substrate availability. This underscores the sensitivity of nitrifying communities to in situ soil moisture that may supersede precipitation legacy effects.

Ecosystem implications

Links between the carryover of N between seasons, increased soil N availability, and subsequent loss of this N via gaseous pathways have been established at our research site (Krichels et al., 2023a; Zhao et al. 2025) suggesting precipitation legacies can alter the fate of soil N, particularly when N sources and sinks decouple (Eberwein et al. 2020; Homyak et al. 2016). Further, since winter legacies can decrease summer gross N mineralization without affecting summer gross nitrification, such conditions may favor accumulation of NO_3^- over NH_4^+, a more mobile anion that may be leached beyond plant and microbial reach (Ren et al. 2024) or stimulate emission of the powerful greenhouse gas, nitrous oxide, as measured at our site (Zhao et al. 2025). Thus, precipitation legacies may "open" the N cycle (i.e., favoring N loss over retention), contributing to ecosystem N limitation and to overall declining N availability across terrestrial ecosystems (e.g., Mason et al. 2022), especially if N limitation lowers primary productivity further promoting N loss (Ren et al. 2024).

To assess the potential for the legacies of past precipitation to open the N cycle and alter the carryover of N between seasons, we measured bulk soil $\delta^{15}N$ values as an index of ecosystem N availability (Brunello et al. 2024; Robinson 2001; Von Sperber et al. 2017). We expected that manipulating precipitation over the course of five years would have increased bulk soil $\delta^{15}N$ in *Winter-* and *Summer-* plots exposed to more arid conditions; aridity can stimulate fractionating N losses that enrich the soil residual substrate (Brunello et al. 2024; Mao et al. 2024; Von Sperber et al. 2017; Wang et al. 2014). However, even imposing our most extreme drought (i.e., *Winter-*) for five years did not affect bulk soil $\delta^{15}N$ (Fig. 7). It is possible our treatments did not alter aridity significantly or long enough to produce a response,

though the dramatic decline in plant biomass measured in *Winter*- plots suggests otherwise (Spasojevic et al. 2022). It is also possible that since dissimilatory nitrate reduction to ammonium rates were similar in magnitude to those of inorganic N production (Fig. S7; though these rates were highly variable), N recycling constrained N loss, minimizing effects on bulk soil $\delta^{15}N$. Alternatively, the drought we imposed may have been extreme enough to favor abiotic gaseous N loss pathways that are less fractionating than those driven by biology (Vitousek et al. 2022; Von Sperber et al. 2017), reversing the enrichment of bulk soil $\delta^{15}N$ as observed in other arid sites (Von Sperber et al. 2017; Wang et al. 2014). Specifically, dry conditions combined with the relatively high pH of dryland soils could have stimulated ammonia emissions (Krichels et al. 2023b; but see Slessarev et al. 2016 for cases in which dryland soils may have low pH). While the slightly alkaline soils at our site may be well equipped to support ammonia volatilization as observed in other nearby drylands (Krichels et al. 2023b), higher pH may be necessary for this to be a major N loss pathway. New studies that evaluate N fractionating processes in response to seasonal changes in precipitation relative to those experienced over multiple years are needed to understand bulk soil $\delta^{15}N$ dynamics in response to changes in precipitation.

Conclusions

Our results show that prolonged drought can reduce the rate of inorganic N production in soils, as both gross N mineralization and nitrification rates decreased under dry conditions, but neither were completely shut down. Under this persistent, albeit slow rate of inorganic N production that outpaced N immobilization, we found that N carried over between seasons, as influenced by both immediate (i.e., significant treatment effects measured the same season) and legacy effects (i.e., significant treatment effects measured the following season) of changing precipitation patterns. For droughts extreme enough to lower soil organic N pools, gross N mineralization decreased the following season, whereas for droughts that may be more moderate to not deplete organic N pools, gross N mineralization persisted and carried over NH_4^+ into the next season. Moreover, since gross nitrification was not sensitive to legacy effects, such conditions may favor accumulation of NO_3^- over NH_4^+, a more mobile anion that may favor ecosystem N loss. Overall, with precipitation increasing in variability, our results highlight how the legacies of past precipitation can increase soil N availability, making this N vulnerable to loss when ecosystem N sources and sinks decouple.

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Author contributions Field design and maintenance was performed by Jamie Irby, Alex Krichels, Marko Spasojevic, Darrel Jenerette, and Peter Homyak. Material preparation, data collection and analysis was performed by Jamie Irby, Alex Krichels, and Peter Homyak. The first draft of the manuscript was written by Jamie Irby and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Data availability Data is provided as private-for-peer review via the following link: http://datadryad.org/share/36NgBdQn9eS-CYpAd6E9CEjMjr-mKbOiJX7IPnF6cH8. Data will be made publicly available upon publication. Code used to process the data is available at the following link: https://github.com/jirby001/GrossNRates.

Declarations

Competing interests The authors declare no conflict of interest.

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