Title
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Permalink
https://escholarship.org/uc/item/8bx1m9dq

Journal
Journal of Geophysical Research: Biogeosciences, 122(12)

ISSN
2169-8953

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Publication Date
2017-12-01

DOI
10.1002/2017JG004146

Peer reviewed
Effects of drought manipulation on soil nitrogen cycling: A meta-analysis

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Key points:

1. A meta-analytical approach was used on 37 studies that reduced precipitation.
2. The supply of mineral N did not decrease under drought treatment; extractable \(\text{NH}_4^+\) increased 25%.
3. Microbial biomass and \(\text{N}_2\text{O}\) emissions declined and \(\text{NH}_4^+\) increased with increasing drought intensity.

Keywords:
Nitrogen cycling; drought stress; rainfall exclusion; soil moisture; meta-analysis; dry soil
Plain language summary:

Many regions on Earth are expected to become drier with climate change, which may impact N cycling rates and availability. We summarized the results of field experiments that reduced precipitation and measured the effects on N cycling. Because microbes are sensitive to changes in moisture and their activity decreases as soils dry, reducing precipitation could lower rates of N cycling. However, we found that reducing precipitation did not shut down the supply of mineral N to ecosystems and that microbial biomass increased at lower levels of proportional precipitation reduction while decreasing as water was withheld. Our results expand on early laboratory studies evaluating N dynamics in dry soils. While it is clear that microbial N transformations decrease in dry soils incubated in the laboratory, we show that under field conditions, some N cycling processes are less sensitive to precipitation reduction. Non-rainfall water inputs, such as the movement of atmospheric water vapor into soil, can stimulate drought-tolerant microbial processes in the field, and may maintain active microbial N processing despite low water content when soils are measured in bulk. Sustained N processing during drought could result in greater ecosystem N losses during subsequent wetting events.
Abstract

Many regions on Earth are expected to become drier with climate change, which may impact N cycling rates and availability. We used a meta-analytical approach on the results of field experiments that reduced precipitation and measured N supply (i.e., indices of N mineralization), soil microbial biomass, inorganic N pools [ammonium (NH$_4^+$) and nitrate (NO$_3^-$)], and N$_2$O emissions. We hypothesized that N supply and N$_2$O emissions would be relatively insensitive to precipitation reduction and that reducing precipitation would increase extractable NH$_4^+$ and NO$_3^-$ concentrations because microbial processes continue whereas plant N uptake diminishes with drought. In support of this hypothesis, extractable NH$_4^+$ increased by 25% overall with precipitation reduction; NH$_4^+$ also increased significantly with increasing magnitude of precipitation reduction. In contrast, N supply and extractable NO$_3^-$ did not change and N$_2$O emissions decreased with reduced precipitation. Across studies microbial biomass appeared unchanged, yet from the diversity of studies it was clear that proportionally smaller precipitation reductions increased microbial biomass, whereas larger proportional reductions in rainfall reduced microbial biomass; there was a positive intercept ($P = 0.005$) and a significant negative slope ($P = 0.0002$) for the regression of microbial biomass vs. % precipitation reduction ($\text{LnR} = -0.009 \times (% \text{ precipitation reduction}) + 0.4021$). Our analyses imply that relative to other N variables, N supply is less sensitive to reduced precipitation whereas processes producing N$_2$O decline. Drought intensity and duration, through sustained N supply, may control how much N becomes vulnerable to loss via hydrologic and gaseous pathways upon rewetting dry soils.
591. **Introduction**

Nitrogen (N) is an essential nutrient; it often constrains ecosystem productivity and can influence rates of decomposition and carbon (C) sequestration [LeBauer and Treseder, 2008; Melillo et al., 1982; Vitousek and Howarth, 1991]. Understanding which environmental factors govern N availability is, therefore, critical to predicting ecosystem C inputs and losses [e.g., Averill and Waring, In press; Terrer et al., 2016]. Climate models predict that many regions on Earth will become drier by 2100 [Feng and Fu, 2013; Huang et al., 2016; Maestre et al., 2016], potentially altering rates of soil N cycling and N availability. Drought can influence N cycling because water availability i) maintains hydration for the microbial processes that fix and transform N and ii) controls substrate advection, diffusion, and microbial and plant access to N [Farooq et al., 2009; Manzoni et al., 2012; Stark and Firestone, 1995]. These moisture effects suggest that arid conditions should limit soil N cycling rates as confirmed in laboratory studies [Campbell and Biederbeck, 1972; Pilbeam et al., 1993; Reichman et al., 1966]. However, under in-situ field conditions, N fluxes and pools can increase as soils dry [Jackson et al., 1988; Parker and Schimel, 2011; Sullivan et al., 2012].

Microbes respond to lower water potentials through changes in physiology and community structure [Schimel et al., 2007], both of which can alter rates of N cycling and availability [Fierer and Schimel, 2002; Fuchslueger et al., 2014b]. For instance, nitrifier activity decreases with decreasing water potential [Reichman et al., 1966; Wetselaar, 1968] along with fluxes of nitrogen gas (N\(_2\)) and nitrous oxide (N\(_2\)O) from denitrification [Soper et al., 2016a; Soper et al., 2016b]. Yet in the field N mineralization can continue as soils dry [Fisher et al., 2019; Homyak et al., 2016; Parker and Schimel, 2011; Reichmann et al., 2013]. Potential
Denitrification enzyme activity can increase [Parker and Schimel, 2011], and extractable ammonium (NH₄⁺) builds up [Homyak et al., 2014; Parker and Schimel, 2011], perhaps because some microbes are drought-tolerant or because low water potentials can kill microbes and can limit plant N uptake, thereby reducing competition against surviving microbes for N [Smith et al., 1997; Zhong et al., 2014].

In support of these field observations, Sullivan et al. [2012] measured either higher or comparable nitrification potentials (an index of the size of the nitrifying community) in dry relative to wet soils across a chronosequence in Arizona, with similar observations reported from other dry lands [Fisher et al., 1987; Homyak et al., 2014; Parker and Schimel, 2011]. In synthesizing these observations, Sullivan et al. [2012] proposed that microbial processes and rates of N cycling must be tolerant of dry conditions, and that the size of the microbial biomass pool can increase as soils dry. Although a number of field studies from Mediterranean regions support the hypothesis that soil microbial biomass can increase as soils dry [Boot et al., 2013; Homyak et al., 2014; Jackson et al., 1988; Parker and Schimel, 2011; Schaeffer et al., 2017], it is unclear whether this response is exclusive to Mediterranean climates, where seasonal drought may select for microbes adapted to low water potentials [e.g., Fuchslueger et al., 2014b; Schimel et al., 2007; Yuste et al., 2011]. It is also unclear whether increasing microbial biomass can sustain N fluxes as soils dry in-situ, or whether N fluxes decline in drying soils across ecosystems.

Ecosystem rainfall manipulations provide a powerful approach for understanding how drought affects N dynamics under in-situ field conditions. However, individual precipitation manipulations report conflicting responses of N fluxes and soil N pools [e.g., Borken and Matzner, 2009; Shi et al., 2012; Yahdjian et al., 2006]. Therefore, we addressed the following
104questions using data synthesis techniques: i) Are soil N processes and pools sensitive to drought  
105across different biomes? and ii) How does reducing precipitation affect the size of the microbial  
106biomass pool across ecosystems?

107 We used random-effects categorical and continuous meta-analyses to answer these  
108questions across biomes with field studies that used rain-out shelters to reduce or exclude  
109precipitation from plots. We identified studies that measured rates of N supply (i.e., indices of N  
110mineralization), soil microbial biomass, inorganic N pools (NH$_4^+$ and nitrate (NO$_3^-$)), or N$_2$O  
111emissions in response to precipitation reduction. We hypothesized that i) rates of N supply and  
112N$_2$O emissions would be relatively less sensitive to precipitation reduction in the field due to  
113greater microbial biomass (Fig. 1A) and higher NO$_3^-$ concentrations that stimulate denitrification,  
114and ii) field soil NH$_4^+$ and NO$_3^-$ concentrations should increase under precipitation reduction due  
115to ongoing microbial activity along with reduced plant growth and N uptake [Fig. 1A; Shi et al.,  
1162014; Wu et al., 2011; Zhong et al., 2014].

1172. Methods

1182.1. Data selection

119 We performed meta-analyses on field studies that used rain-out shelters (structures that  
120intercept precipitation) to reduce precipitation and lower soil moisture. We identified candidate  
121studies by searching ISI Web of Science (Thomson Reuters, New York, NY, USA) and Google  
122Scholar (Google, Mountain View, CA, USA) for published literature using a list of key words  
123and wildcards (Table S1) and identified additional studies by cross-referencing. Studies were  
124included if i) the authors measured soil microbial biomass, indices of N mineralization (net,  
125gross, anaerobic and potential N mineralization), soil extractable NH$_4^+$ and NO$_3^-$, or nitrous oxide
(N₂O) emissions; ii) the variables of interest were measured under reduced precipitation treatment and compared to a control; iii) experimental plots were not manipulated beyond precipitation reductions; and iv) means, standard deviations, and sample size were reported or could be determined. We were focused on understanding how drought influences rates of N cycling under field conditions, and we excluded greenhouse and laboratory studies. Published studies were collected for analysis until 1 January 2017. Overall, we found 37 studies that met our criteria, representing an “intermediate” sample size for meta-analysis [37 studies; Hedges et al., 1999] and allowing us to analyze the best available data from ecosystem precipitation manipulations.

To maximize the likelihood of measuring a treatment effect, and meet the assumption of sample independence [Gurevitch and Hedges, 1999], we restricted our analyses to the final sampling date in studies that reported time series for the variables of interest—a standard meta-analytical approach that also minimized the likelihood of measuring disturbance effects associated with erecting shelters. We also refrained from using time series because small sample sizes limited our ability to test hypotheses concerning temporal trends and may have introduced biases by over-weighting studies with longer records. Moreover, if more than one paper reported data from the same field plots, we used the most recent or most comprehensive paper. For the two studies reporting data from both O and A soil horizons, we used A horizons to maintain consistency across studies and best represent processes occurring in the solum rather than in litter under various stages of decomposition. When studies reported on more than one mineral horizon, we used the uppermost horizon. For studies testing several levels of precipitation reduction, we focused on the most extreme reduction to maximize our ability to detect a rainfall exclusion effect. When a study included more than one site, we included as many sites as could reasonably
be considered independent based on geographical position, ecosystem type, or plant cover

*Treseder, 2008.*

### 2.2 Data collection

We extracted means, standard deviations (SD), and sample sizes (n) for each variable of interest. Data presented in figures were digitized using Plot Digitizer 2.6.6 (http://plotdigitizer.sourceforge.net). We grouped studies into agricultural, forest, grassland, meadow, shrubland, or tropical categories. The meadow biome was used for high-elevation studies at sites dominated by herbaceous plants (i.e., > 1,850 m a.s.l.) and the tropical biome for subtropical, montane, humid, and old-growth tropical forests. For each study, we recorded the mean annual precipitation (MAP), length of the experimental manipulation (years), % precipitation reduction (100×rainfall excluded/annual precipitation), % soil moisture reduction [100×(soil moisture control-soil moisture treatment)/soil moisture control)], whether the climate was Mediterranean (i.e., consisting of hot dry summers and cool wet winters typical of Mediterranean regions), and the type of shelter used to reduce precipitation (i.e., exclusion vs. reduction). Exclusion shelters removed 100% of incoming precipitation, whereas reduction shelters reduced precipitation by some fraction (i.e., < 100%) typically through openings in the roof. Standard errors (SE) were converted to SDs [SD = SE (n^{½})].

The studies we included measured microbial biomass by chloroform (CHCl₃) fumigation [Brookes et al., 1985], phospholipid fatty acid (PLFA) extraction [Frostegard and Baath, 1996], or substrate induced respiration (SIR) [Anderson and Domsch, 1978]. There is a paucity of studies measuring indices of N mineralization (net, gross, anaerobic and potential N mineralization) in precipitation exclusion experiments. Because we were interested in understanding whether N supply would be sensitive to reduced precipitation—not in quantifying
the actual flux rates—we included studies measuring net N mineralization, gross N
mineralization, anaerobic N mineralization, and potential N mineralization measurements as an
index of N supply in control vs. rainfall exclusion plots. Only 9 studies measured nitrification,
and we were unable to include this process in our meta-analysis. Extractable \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) were
measured after extraction in salt solution (e.g., \( \text{K}_2\text{SO}_4 \) or KCl) or in deionized water. Soil \( \text{N}_2\text{O} \)
emissions were measured by chamber methodology [Parkin and Venterea, 2010].

2.3. Statistics

We used meta-analyses to determine the effect of reduced precipitation on soil microbial
biomass, N supply, extractable \( \text{NH}_4^+ \) and \( \text{NO}_3^- \), and \( \text{N}_2\text{O} \) emissions. For each study and response
variable we calculated the effect size as the natural logarithm of the response ratio (\( \text{LnR} \)) or as
Hedge’s \( d \). \( \text{LnR} \) was used in the analysis of microbial biomass and extractable \( \text{NH}_4^+ \) and \( \text{NO}_3^- \)
pools, and is defined as:

\[ \text{LnR} = \ln \left( \frac{X_T}{X_C} \right) \]

where \( X_T \) is the treatment mean and \( X_C \) the control mean. If reducing precipitation increases the
treatment mean over the control, then \( \text{LnR}>0 \). Alternatively, \( \text{LnR}<0 \) when reducing precipitation
reduces the treatment mean relative to the control; \( \text{LnR}=0 \) when there is no effect of reducing
precipitation.

\( \text{LnR} \) cannot be used for negative values—it is undefined—so we used Hedge’s \( d \) as the
response variable for both N supply and \( \text{N}_2\text{O} \) emissions, which both included negative means.

Hedge’s \( d \) is defined as:
\[ d = \frac{|X_T - X_C|}{S} J \]

where \( S \) is the pooled standard deviation and \( J \) corrects for small sample bias [Gurevitch et al., 2001]. As with LnR, \( d > 0 \) if reducing precipitation increases the treatment mean relative to the control, \( d < 0 \) if reducing precipitation reduces the treatment mean relative to the control, and \( d = 0 \) if reducing precipitation has no effect. Along with mean effect sizes, we also calculated the variance (\( V \)) for both LnR and Hedge’s \( d \) using the means, SDs, and sample sizes for treated and control plots [Gurevitch et al., 2001].

To determine whether reducing precipitation affected soil microbial biomass, N supply, extractable \( \text{NH}_4^+ \) and \( \text{NO}_3^- \) pools, and \( \text{N}_2\text{O} \) emissions, we used a random effects model in the MetaWin software [Rosenberg et al., 2000] with a 95% confidence interval (CI) to assess significant effects; CIs not overlapping with 0 indicated significant responses at \( \alpha < 0.05 \). We used random effects categorical models to assess whether the effects of reducing precipitation on the variables of interest varied by manipulation type (i.e., precipitation exclusion vs. reduction) or biome (i.e., agricultural, forest, grassland, meadow, shrubland, and tropical) or whether the effect of reducing precipitation on microbial biomass was exclusive to a Mediterranean climate.

We used a continuous random effects model between the mean effect size and MAP (a proxy of overall site wetness) to test \( (\alpha = 0.05) \) whether wetter sites responded differently to reduced precipitation than drier sites. Lastly, we also used continuous random effects models to test for significant \( (\alpha = 0.05) \) relationships between the mean effect size and manipulation length, % precipitation reduction, and % soil moisture reduction.
Because we used random-effects meta-analyses, we did not test for total heterogeneity among studies (Q_T), as substantial variation among the population of studies included in our analyses is assumed and is already accounted for in random-effects models [Rosenberg, 2013]. For categorical meta-analyses, however, we partitioned Q_T into the amount of heterogeneity explained by the model structure (Q_M; between-class heterogeneity) and the amount of heterogeneity left unexplained after considering the model—the residual error heterogeneity (Q_E; within-class heterogeneity). The significance of both Q_M and Q_E was tested (α = 0.05) against a χ^2 distribution to determine whether the structural models could explain the total heterogeneity—i.e., a significant Q_M—and whether substantial heterogeneity was left unaccounted for by the models—i.e., a significant Q_E even if Q_M is significant [Rosenberg, 2013]. Lastly, we tested for publication bias (i.e., the likelihood of a study with high effect sizes being published over one with lower effect sizes) using Kendall’s tau and Spearman rank correlation tests [Holden and Treseder, 2013].

3. Results

We identified 37 published studies that used rain-out shelters to reduce or exclude precipitation across 6 biomes (agricultural, forest, grassland, meadow, shrubland, and tropical), from which we extracted 106 independent observations—27 observations of soil microbial biomass (19 CHCl_3 fumigation, 4 PLFA extraction, and 4 SIR), 24 of extractable NH_4^+, 24 of extractable NO_3^-, 16 of N supply (7 net N mineralization, 4 gross N mineralization, 3 potential N mineralization, and 2 anaerobic N mineralization), and 15 of N_2O emissions (Table S3). Mean effect sizes were not related to % soil moisture reduction (P > 0.2; Figs. S1-S5) and did not vary as a function of overall site wetness (P > 0.08; Fig. S6).
3.1. Soil microbial biomass

Opposite to our predictions, reducing precipitation had no overall effect on the size of the soil microbial biomass pool (Fig. 2; LnR = -0.03 ± 0.17 95% CI), but the microbial biomass pool decreased as a function of % precipitation reduction (Fig. 2; LnR = -0.009 × (% precipitation reduction) + 0.4021; P = 0.0002). Reducing precipitation by relatively small fractions significantly increased the size of the microbial biomass pool (LnR intercept = 0.4021; P = 0.005), whereas reducing precipitation by larger fractions reduced microbial biomass to levels lower than the experimental controls for each study (Fig. 2). There was no relationship between microbial biomass and manipulation length (Fig. S1; P = 0.3).

Based on categorical models, the response of microbial biomass to precipitation reduction did not depend on shelter type or Mediterranean climate (P ≥ 0.75; Table 1), but the effect of biome was marginally significant (P = 0.065). Extraction type accounted for a large fraction of the total heterogeneity among studies (Q_M P = 0.0003) but there were no statistically significant differences in effect size between the extraction methods (P > 0.05; Table 1)—i.e., extraction type did not influence the response of microbial biomass to reduced precipitation.

3.2. N supply

Consistent with our hypothesis, N supply was not affected by precipitation reduction (Fig. 3; Hedge’s d = 0.03 ± 0.46 95% CI) and was not related to manipulation length or % precipitation reduction (Fig. S2; P > 0.3). Accounting for shelter type in categorical models did not explain much of the heterogeneity among studies (Table 1; Q_M P > 0.4) whereas accounting for biome did (Table 1; Q_M P = 0.035); however, differences in the effect size of N supply among biomes were not significant (Table 1)—i.e., differences in biomes did not influence the response of N supply to reduced precipitation.
Kendall’s tau and Spearman rank correlation tests for publication bias suggest that, across experiments, reduced rates of N supply were more likely to be published than increased rates (Table S2).

3.3. Extractable NH$_4^+$ and NO$_3^-$

As hypothesized, reducing precipitation increased extractable NH$_4^+$ concentrations by 25% across studies (Fig. 4; LnR = 0.22 ± 0.21 95% CI) and these concentrations increased with greater % precipitation reduction (Fig. 4; LnR = 0.0142 × (% precipitation reduction) - 0.4208; P = 0.0003). In contrast to microbial biomass, reducing precipitation by relatively small fractions significantly decreased the size of the extractable NH$_4^+$ pool (Fig. 4; LnR intercept = -0.4208; P = 0.03), whereas reducing precipitation by larger fractions increased NH$_4^+$. Extractable NH$_4^+$ concentrations were not related to manipulation length (Fig. S3; P = 0.2). Accounting for shelter type or biome in categorical models did not explain a significant fraction of heterogeneity among studies (Table 1; QM P > 0.7).

Unlike NH$_4^+$, and in contrast to our hypotheses, reducing precipitation had no effect on average extractable NO$_3^-$ concentrations (Fig. 3; LnR = 0.088 ± 0.16 95% CI) and NO$_3^-$ was not related to manipulation length or % precipitation reduction (Fig. S4; P > 0.2). Accounting for shelter type (QM P = 0.08) or biome (QM P = 0.4) in categorical models did not explain a significant proportion of the heterogeneity among studies (Table 1).

3.4. N$_2$O emissions

Opposite to our predictions, reducing precipitation significantly lowered N$_2$O emissions across studies (Fig. 3; Hedge’s $d = -0.76 ± 0.62$ 95% CI). N$_2$O was not related to manipulation
278length or % precipitation reduction (Fig. S5; $P > 0.1$). Based on categorical models, biome did
279not explain much of the heterogeneity among studies (Table 1; $Q_M P = 0.7$).

5. Discussion

We used meta-analysis to determine how experimental reductions in precipitation may
alter soil N cycling. Because microbes are sensitive to changes in moisture [Blankinship et al.,
Schimel et al., 2007; Skopp et al., 1990] and their activity decreases as soils dry [Fierer
and Schimel, 2002; Manzoni et al., 2012; Orchard and Cook, 1983], reducing precipitation could
lower rates of N cycling (Fig. 1A). However, we found that on average, only N$_2$O emissions
were lower under precipitation reduction in the field (Figs. 1B and 3) and that the effect of
reducing precipitation did not vary by biome for the variables of interest, except for tropical sites
where microbial biomass decreased (Table 1). Reducing precipitation had no effect on N supply
or NO$_3^-$ pools, and NH$_4^+$ pools increased on average. Microbial biomass pools demonstrated a
more dynamic relationship with rainfall manipulation—increasing at lower levels of proportional
precipitation reduction while decreasing as water was withheld—that was not exclusive to
Mediterranean regions (Table 1). Together, our results suggest that N supply is relatively less
sensitive to reduced precipitation, whereas other N cycling processes affecting the balance of
fluxes and magnitude of N stocks are more sensitive.

5.1. N supply

Consistent with our initial hypothesis, reducing precipitation did not have a significant
effect on N supply, suggesting that microbial processes regulating N supply may be drought
tolerant relative to other N cycling processes (Fig. 1). Sustained or higher rates of N
mineralization have been measured in Mediterranean regions where the dry season can last
several months [Homyak et al., 2016; Jackson et al., 1988; Parker and Schimel, 2011], and where microbial biomass N increases as soils dry [Homyak et al., 2014; Parker and Schimel, 2011; Schaeffer et al., 2017; Vourlitis et al., 2009], implying microbes maintain some level of N processing. N mineralization is carried out by a relatively “broad” range of organisms [Schimel and Schaeffer, 2012], so even if drought caused shifts in microbial community composition, N supply could be sustained.

We emphasize that small sample sizes prevent a conclusive test of the N supply response to drought. Net, gross, anaerobic, and potential N mineralization all measure different aspects of N supply, and there were insufficient studies to analyze these metrics individually. By combining these different metrics, we gain insight into the qualitative response of N supply to drought, but we cannot resolve the underlying mechanisms. For gross, anaerobic, and potential N mineralization, a lack of response to precipitation reduction suggests that the process is insensitive to drought. However, for net N mineralization, insensitivity to drought could also result from offsets in gross N mineralization and immobilization (e.g., a decrease in gross N mineralization coupled to an increase in N immobilization). Therefore, we cannot rule out the possibility that gross N mineralization was sensitive to drought in studies that only measured net N mineralization. Nevertheless, the lack of a response to precipitation reduction suggests that, relative to N immobilization, gross N mineralization may be less sensitive to drought—NH₄⁺ increased (Fig. 4) while microbial biomass decreased (Fig. 2) as precipitation was withheld. We also note there was significant publication bias in studies measuring N supply (Table S2), suggesting a negative response to precipitation reduction was more likely to be published than a positive response. That we still did not detect a significant effect of reduced precipitation on N
supply may suggest that our conclusion—that N supply is relatively tolerant of drought stress—could be conservative.

5.2. Soil microbial biomass

While it is clear that some microbial activities decline as soils dry [Allison and Treseder, 2008; Manzoni et al., 2012; Ren et al., 2017], microbes can tolerate drought stress [Canarini et al., 2016; Lennon et al., 2012; Schimel et al., 2007], and even increase in biomass [Fig. 2A; Boot et al., 2013; Homyak et al., 2014; Jackson et al., 1988; Parker and Schimel, 2011; Ren et al., 2017; Schaeffer et al., 2017]. Indeed, a recent meta-analysis suggests that microbial biomass is less likely to decrease in response to reducing precipitation in dry (MAP ≤ 600 mm) relative to wet ecosystems [Ren et al., 2017]. Across the studies included in our analysis that reduced precipitation by relatively small proportions, a shift in the frequency of precipitation pulses could have increased microbial growth due to greater numbers of wet-dry cycles [Fierer and Schimel, 2002; Xiang et al., 2008]. Such a response could occur if deploying rain-out shelters for relatively short periods alters the frequency of precipitation pulses [Huxman et al., 2004] while having relatively little effect on total precipitation. In addition, microbes might survive in hydrologically disconnected microsites formed as soils dry despite bulk soils having negligible diffusivity at the macro scale [Manzoni and Katul, 2014]. Microbes surviving in these microsites may gain protection from predators and/or viruses, and reduced mortality rather than increased activity may explain the increased biomass [Parker and Schimel, 2011; Ranjard and Richaume, 2001]. Changes in community structure or dormancy may also explain shifts in the size of the microbial biomass pool in drying soils [Fuchslueger et al., 2014a; Fuchslueger et al., 2016; Lennon and Jones, 2011]. Sullivan et al. [2012] noted that archaea may fare better than bacteria at low water potential [but see Fuchslueger et al., 2014b], whereas other studies suggest drought
tolerant fungi may continue to produce biomass \cite{Treseder et al., 2010; Yuste et al., 2011}. One or more of these dynamics may explain why the size of the microbial biomass pool increased with small reductions in precipitation and, therefore, why microbial processes continued to mineralize N.

In contrast to the increase in microbial biomass when precipitation was reduced by small fractions, microbial biomass decreased as precipitation reduction approached 100 \% (Fig. 2A). Reducing precipitation by large percentages (i.e., deploying rain-out shelters for extended periods) reduced average soil moisture as well as the frequency of precipitation pulses. These persistently dry conditions could have desiccated soils beyond thresholds of microbial drought tolerance—about -14 MPa for mineral soils and -36 MPa for litter \cite{Manzoni et al., 2012}. This relationship was partly driven by responses to drought in the tropics, where microbial biomass declined particularly strongly at 100\% precipitation reduction (Table 1). If we exclude tropical studies from the continuous meta-analysis of microbial biomass versus \% precipitation reduction, a significant relationship is no longer observed ($P = 0.5$ without tropical studies). Although more studies would be required to draw firm conclusions about cross-biome variation, microbes adapted to moist tropical environments could be more sensitive to drought stress than microbes from more variable environments \cite{Hawkes and Keitt, 2015}.

5.3. Extractable NH$_4^+$

We observed that extractable NH$_4^+$ increased with greater precipitation reduction (Fig. 4A). Because microbial biomass decreased as precipitation reduction approached 100 \%, microbial death might have contributed to the increase in NH$_4^+$ and sustained N supply. However, since N supply did not significantly increase, other mechanisms probably contributed to the increase in NH$_4^+$. In particular, low water availability can limit plant growth \cite{Shi et al., 2014; Wu
et al., 2011], plant NH₄⁺ uptake [Zhong et al., 2014], and nitrification rates [Stark and Firestone, 1995; Wetselaar, 1968]. The balance of minor changes in these potential mechanisms, along with our observations, suggest that extractable NH₄⁺ increases with drought treatment due to reduced NH₄⁺ consumption (Fig. 1B).

372.4. Extractable NO₃⁻

The pool of extractable NO₃⁻ did not change with reduced precipitation (Fig. 3), even though other drivers of NO₃⁻ concentrations were likely affected (e.g., NH₄⁺ concentrations, nitrification, plant N uptake, and denitrification). Nitrification declines under low osmotic potentials [Stark and Firestone, 1995], and in drying soils a larger fraction of nitrified N can escape as NO [Fig. 1B; Davidson et al., 2008; Homyak et al., 2016; Homyak et al., 2017], which together imply NO₃⁻ production could have declined. Similarly, the processes consuming NO₃⁻ probably also declined; plant NO₃⁻ uptake declines under drought stress [Dijkstra et al., 2015; Meng et al., 2016] as do N₂O emissions (Fig. 3). Thus, NO₃⁻ concentrations may not have changed because reductions in production and consumption of NO₃⁻ offset one another (Fig. 1B).

382.5. N₂O emissions

Reducing precipitation significantly lowered N₂O emissions across studies (Fig. 3), perhaps suggesting that denitrification is more sensitive to drought than processes controlling N supply. Because shifts in the ratio of oxidant (e.g., NO₃⁻) to reductant (organic C) can influence whether N₂O or N₂ is produced during denitrification [Del Grosso et al., 2000], lower N₂O fluxes may reflect shifts in the ratio of N₂O:N₂ produced, not lower denitrification rates. The effect of reduced precipitation on denitrification is likely contingent upon ecosystem-specific factors that can both lower and even increase N₂O emissions as precipitation is withheld [Wieder et al., 2011]. For instance, potential denitrification enzyme activity [Parker and Schimel, 2011] and
both NO$_3^-$ and water-extractable organic C concentrations [Schaeffer et al., 2017] can increase as soils dry, presumably influencing N$_2$O emission rates during drying and/or upon rewetting soils. Nevertheless, our finding is consistent with greater denitrification under wet, anaerobic environments [Robertson and Groffman, 2007], because these conditions would have been less common under precipitation reduction. Compared to microbes that mineralize N, denitrifiers are more narrowly distributed phylogenetically [Schimel and Schaeffer, 2012] and require wetter conditions to maintain metabolic activity [e.g., Lennon et al., 2012]. Our results are consistent with studies reporting low N$_2$O emissions in drylands except during short periods following precipitation pulses when soils wet up [Soper et al., 2016a; Soper et al., 2016b] or when fast chemical reactions may occur [Heil et al., 2015].

5.6. Implications for N cycling under drought

Our results expand on previous laboratory studies evaluating N dynamics in dry soils. While it is clear that microbial N transformations decrease at low water potentials [Campbell and Biederbeck, 1972; Pilbeam et al., 1993; Reichman et al., 1966; Stark and Firestone, 1995], we show that under in-situ field conditions, processes that control N supply are less sensitive to precipitation reduction. Differences between field and laboratory studies likely stem from the artificial effects on water infiltration and oxygen diffusion generated by disrupting soil aggregates in microcosms, as well as by microbial interactions with soil physical and biological factors not well represented in the laboratory. For instance, interactions between plants and microbes shape soil aggregates [Blankinship et al., 2016], where microbes can remain hydrated in microsites despite low bulk soil water potential [Manzoni and Katul, 2014; Parker and Schimel, 2011]. Moreover, non-rainfall water inputs, such as the movement of atmospheric water vapor into soil, can stimulate drought-tolerant microbial processes in the field [McHugh et al.,]
and may maintain active microbial N processing despite low soil water content. Together, these microbial interactions with physical and biological factors, along with the relative tolerance of N mineralization to drought stress [Booth et al., 2005; Fisher et al., 1987; Pilbeam et al., Robinson, 1957], are consistent with the findings of our meta-analysis and may explain discrepancies between field and laboratory studies.

Our meta-analysis is constrained by the number of precipitation reduction studies available to assess effects on soil N cycling, particularly for N supply. Assuming both a small sample size and high variation between treatment and control plots within studies, using the last observation in a time-series to calculate an effect size—a standard meta-analytical approach—may bias interpretations. For instance, Davidson et al. [2008] reported lower N$_2$O emissions in rainfall exclusion plots than in control plots at the end of the experimental manipulation, but had the experiment ended about two years earlier, we would have calculated the opposite effect size, albeit small. Because we synthesized field studies, we expected high variation between and within sites, especially since soils under precipitation reduction treatment could have moisture levels similar to control soils if the % reduction in precipitation was small. To assess how manipulation length may have influenced our conclusions, we show with continuous meta-analyses that, across all studies and variables of interest, manipulation length did not significantly influence effect size ($P \geq 0.2$).

At the ecosystem scale, our analyses help inform predictions about N cycling in regions where drought magnitude and duration may increase [e.g., Delgado-Baquerizo et al., 2013]. Drought magnitude and duration should influence whether ecosystems operate as net N sinks or sources. A relatively mild drought would be expected to produce a small pool of bioavailable N [Fig. 4A; Hartmann et al., 2013], since ecosystem N sinks (e.g., microbial and plant N uptake
and soil organic matter) may persist or recover quickly from drought [e.g., de Vries et al., 2012; Fry et al., 2014; Homyak et al., 2014; Mauritz et al., 2014]. As drought severity increases, however, a larger mineral N pool, together with drought-stressed ecosystem N sinks may generate responses similar to those following ecosystem disturbance, favoring larger N losses via N gas evasion and leaching upon rewetting [e.g., Evans and Burke, 2013; Hanan et al., 2016; Homyak et al., 2016; Homyak et al., 2017; Homyak et al., 2014]. The temporal sequence of these different magnitudes of dry conditions may control the long-term changes in ecosystem N cycling transformations, fluxes, and stocks.

6. Conclusions

We did not detect significant changes in the rate of N supply in response to precipitation reduction, apparently as a result of microbes enduring through dry conditions. Because of the relatively low number of drought manipulation experiments, it is critical for ongoing and future studies to include N transformation measurements, as these data are urgently needed for calculating thresholds of microbial drought tolerance and N processing. We also emphasize reporting soil bulk density to facilitate calculation of water-filled pore space and allow comparisons of soil water content across sites varying in soil texture. Our analyses imply differences in drought sensitivity among N cycling processes, with processes controlling the rate of N supply appearing less sensitive to drought conditions than processes controlling N₂O emissions. Microbial biomass declines and NH₄⁺ accumulates as drought intensity increases, consistent with reduced plant and microbial uptake from mineral N pools. One implication of this finding is that increasing drought magnitude and duration, through sustained N supply, could control ecosystem N losses during subsequent wet-up periods.
Acknowledgments

We are thankful to Lara Reichman and Ellen Fry for helping us include their published data in our analyses and to JC Blankinship, LA Cat, CI Looby, M Gorris, AL Romero-Olivares, and three anonymous reviewers for their suggestions on earlier versions of this manuscript. This research was funded by an NSF Ecosystem Studies grant to SDA and KKT and Center for Environmental Biology funds associated with a gift from Mr. Donald Bren and the Irvine Company Foundation. The data used are listed in Table S3 in supplements.
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occur? Biogeochemistry 13, 87-115

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Plant and Soil 29, 9-17

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Global Change Biology 17, 3195-3207


Zhong, Y.Q.W., Yan, W.M., Chen, J., Shangguan, Z.P., 2014. Net ammonium and nitrate fluxes in wheat roots under different environmental conditions as assessed by scanning ion-selective electrode technique. Scientific Reports 4
### Table 1. Results of statistical comparisons among and within groups (MB = microbial biomass; †only groups with two or more studies were included in comparisons)

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Figure legends

Fig. 1. Conceptual model for N cycling in dry soils. **A** The hypothesized effects of dry conditions on soil N cycling, versus **B** the results of our meta-analyses. Pools of soil organic matter (SOM), microbial biomass (MB), ammonium (NH₄⁺), and nitrate (NO₃⁻) are represented by boxes. Fluxes are represented by arrows including N supply, nitric oxide (NO), and nitrous oxide (N₂O). Dotted arrows represent fluxes most sensitive to diffusion constraints as drought severity increases. An increase in the size of the pool or flux is represented by +, a decrease by -, and no change by =. *Plant growth and N uptake decrease in response to reducing precipitation (Zhong et al., 2014; Shi et al., 2014; Wu et al., 2011) whereas NO emissions increase because of tradeoffs between biotic and abiotic processes (Homyak et al., 2016).

Fig. 2. Natural logarithm of the response ratio (LnR) of soil microbial biomass as a function of precipitation reduction (% of mean annual precipitation; LnR = -0.009 × (% precipitation reduction) + 0.4021; P = 0.0002; intercept P = 0.005). Symbols represent LnR of individual studies ± the variance of LnR. The gray square is the grand mean effect size across all studies ± 95% confidence interval.

Fig. 3. Mean effect size ± 95% confidence intervals for the effects of precipitation reduction on N supply (Hedge’s d), N₂O emissions (Hedge’s d), and extractable NO₃⁻ (LnR). LnR = natural logarithm of the response ratio.

Fig. 4. Natural logarithm of the response ratio (LnR) of soil extractable NH₄⁺ as a function of precipitation reduction (% of mean annual precipitation; LnR = 0.0142 × (% precipitation reduction) - 0.4208; P = 0.0003; intercept P = 0.03). Symbols represent the LnR of individual
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Fig. 1. Conceptual model for N cycling in dry soils. **A)** The hypothesized effects of dry conditions on soil N cycling, versus **B)** the results of our meta-analyses. Pools of soil organic matter (SOM), microbial biomass (MB), ammonium ($\text{NH}_4^+$), and nitrate ($\text{NO}_3^-$) are represented by boxes. Fluxes are represented by arrows including N supply, nitric oxide (NO), and nitrous oxide ($\text{N}_2\text{O}$). Dotted arrows represent fluxes most sensitive to diffusion constraints as drought severity increases. An increase in the size of the pool or flux is represented by +, a decrease by −, and no change by =. *Plant growth and N uptake decrease in response to reducing precipitation.
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Fig. 3. Mean effect size ± 95% confidence intervals for the effects of precipitation reduction on N supply (Hedge’s $d$), $N_2O$ emissions (Hedge’s $d$), and extractable NO$_3^-$ (LnR). LnR = natural logarithm of the response ratio. N supply represents the combined response of net, gross, anaerobic, and potential N mineralization to reduced precipitation (see section 2.2).
Fig. 4. Natural logarithm of the response ratio (LnR) of soil extractable \(\text{NH}_4^+\) as a function of precipitation reduction (% of mean annual precipitation; \(\text{LnR} = 0.0142 \times (\% \text{ precipitation reduction}) - 0.4208; P = 0.0003; \text{intercept } P = 0.03\)). Symbols represent the LnR of individual studies ± the variance of the LnR. The gray square is the grand mean effect size across all studies ± 95% confidence interval.