Received: 13 March 2023 | Accepted: 13 December 2023

DOI: 10.1111/1365-2745.14258

Journal of Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Revisiting the bucket model: Long-term effects of rainfall variability and nitrogen enrichment on net primary production in a desert grassland

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Funding information
National Science Foundation, Grant/Award Number: DEB-1655499 and DEB-1856383

Handling Editor: Yoann Le Bagousse-Pinguet

Abstract

1. The predicted intensification of the North American Monsoon is expected to alter growing season rainfall patterns in the southwestern United States. These patterns, which have historically been characterized by frequent small rain events, are anticipated to shift towards a more extreme precipitation regime consisting of fewer, but larger rain events. Furthermore, human activities are contributing to increased atmospheric nitrogen deposition throughout this dryland region.
2. Alterations in rainfall size and frequency, along with changes in nitrogen availability, are likely to have significant consequences for above-ground net primary production (ANPP) and plant community dynamics in drylands. The conceptual bucket model predicts that a shift towards fewer, but larger rain events could promote greater rates of ANPP in these regions by maintaining soil moisture availability above drought stress thresholds for longer periods during the growing season. However, only a few short-term studies have tested this hypothesis, and none have explored the interaction between altered rainfall patterns and nitrogen enrichment.
3. To address this knowledge gap, we conducted a 14-year rainfall addition and nitrogen fertilization experiment in a northern Chihuahuan Desert grassland to explore the long-term impacts of changes in monsoon rainfall size and frequency, along with chronic nitrogen enrichment, on ANPP (measured as peak biomass) and plant community dynamics.
4. Contrary to bucket model predictions, small frequent rain events promoted comparable rates of ANPP to large infrequent rain events in the absence of nitrogen enrichment. It was only when nitrogen limitation was alleviated that large infrequent rain events resulted in the greatest ANPP. Furthermore, we found that nitrogen enrichment had the greatest impact on plant community composition under the small frequent rainfall regime.
5. *Synthesis*. Our long-term field experiment highlights limitations of the bucket model by demonstrating that water and nitrogen availability sequentially limit dryland ecological processes. Specifically, our findings suggest that while water availability is the primary limiting factor for above-ground net primary production

in these ecosystems, nitrogen limitation becomes increasingly important when water is not limiting. Moreover, our findings reveal that small frequent rain events play an important but underappreciated role in driving dryland ecosystem dynamics.

KEYWORDS
above-ground production, Chihuahuan Desert, global change ecology, monsoon season, nitrogen enrichment, precipitation variability, rainfall frequency, rainfall size

1 | INTRODUCTION

Precipitation patterns in the arid and semi-arid ecosystems (i.e. drylands) of the southwestern United States (US) have become increasingly variable within and between years over the past century (Maurer et al., 2020; Zhang et al., 2021). For example, growing season rain events driven by the North American Monsoon have become smaller and more numerous throughout the northern Chihuahuan Desert despite no overall change in total seasonal precipitation (Petrie et al., 2014). Yet, climate model projections for the southwestern US indicate an intensification of the hydrologic cycle, particularly during the summer monsoon (Diffenbaugh et al., 2008; Moustakis et al., 2021), which will increase the occurrence of extreme precipitation events (Donat et al., 2016; Easterling et al., 2000, 2017), punctuated by longer dry spells between events (Bradford et al., 2020; Cook et al., 2021). Changes in rainfall size and frequency have important implications for dryland ecosystem structure and functioning (Collins et al., 2014; Schwinning & Sala, 2004). While relatively small rain events can trigger microbially driven biogeochemical processes in surface soils (Austin et al., 2004; Belnap et al., 2005; Collins et al., 2008), larger rain events, which tend to infiltrate deeper into the soil profile where moisture persists longer, are typically necessary to initiate plant growth and production (Noy-Meir, 1973; Schwinning & Sala, 2004).

Grasslands are especially sensitive to changes in total growing season precipitation (Cleland et al., 2013; Hsu et al., 2012; Knapp & Smith, 2001), yet their responses to changes in the size and frequency of rain events during the growing season are less understood. However, given the strong response of drylands to interannual variation in total precipitation (Sala et al., 2012; Unger & Jongen, 2015; Wilcox et al., 2017), within-season changes in rainfall patterns are likely to also have significant consequences on dryland ecosystem structure and functioning, especially if rain events become larger and more sporadic. The conceptual bucket model (Knapp et al., 2008) predicts how terrestrial ecosystems will respond to a more extreme growing season precipitation regime characterized by fewer, but larger rain events. Inspired by soil hydrological models, the bucket model predicts that in drylands, infrequent large rain events would fill an empty 'bucket' represented by the uppermost soil layers where the maximum root biomass occurs, thereby maintaining soil moisture availability above drought stress thresholds for longer periods during the growing season. This contrasts with bucket model predictions for mesic ecosystems, in which extreme precipitation events would result in more frequent moisture deficits between rain events (e.g. Laseter et al., 2012). In other words, a shift to fewer, but larger rain events is predicted to benefit ecological processes in drylands and negatively impact them in mesic systems.

Few studies have explored how changes in rainfall size and frequency impact dryland ecological processes, such as above-ground net primary production (ANPP) or plant community composition, in the context of bucket model predictions (Liu et al., 2020; Unger & Jongen, 2015; Zeppel et al., 2014). Moreover, previous support for the model's predictions in drylands has come primarily from relatively short-duration field experiments (e.g. Heisler-White et al., 2008, 2009; Thomey et al., 2011). For example, in a 2-year study conducted in Chihuahuan Desert grassland, large infrequent rain events significantly increased soil moisture availability and ANPP of the dominant grass compared to small frequent rain events, although the magnitude of this response differed between years (Thomey et al., 2011). However, in mesic grasslands, fewer but larger rain events reduced ANPP, consistent with bucket model predictions (Heisler-White et al., 2009; Knapp et al., 2002), but had limited effects on plant community composition and structure (Jones et al., 2016). Nevertheless, short-term studies do not sufficiently capture the long-term impacts of altered rainfall regimes on ecosystem processes that might be expected from future climate scenarios (Beier et al., 2012).

Ecological responses to changes in rainfall size and frequency are also likely to be influenced by additional factors, such as nutrient availability (Brown et al., 2022; Jongen et al., 2014; Nielsen & Ball, 2015). Nitrogen is an important limiting resource for ANPP in grassland ecosystems globally (Austin et al., 2004; Borer & Stevens, 2022; Fay et al., 2015; Yahdjian et al., 2011). Yet it remains unclear how increases in atmospheric nitrogen deposition will impact ANPP in drylands, especially under more variable precipitation regimes. Although nitrogen enrichment has been found to increase ANPP in the Sonoran and Chihuahuan Deserts, this response may only occur in years with above-average precipitation (Hall et al., 2011; Ladwig et al., 2012). Furthermore, changes in resource availability could also result in shifts in dryland plant community structure, which could underlie variation in ecosystem responses to increased precipitation variability (Avolio et al., 2014; Isbell et al., 2013; Wheeler et al., 2021).

Given that current empirical knowledge of dryland ecosystem responses to altered precipitation regimes is based largely on short-term studies that potentially underestimate the ecological consequences of future directional changes in climate, it remains uncertain if bucket model predictions for drylands are valid at the decadal scale. To address this knowledge gap, we used a long-term (2007–2020) rainfall manipulation experiment to improve our understanding of how differences in monsoon rainfall size and frequency, along with chronic nitrogen enrichment, influence ANPP and plant community dynamics in a northern Chihuahuan Desert grassland. We hypothesized that: (1) Large infrequent rain events would consistently result in greater ANPP than small frequent rain events over time; and (2) chronic nitrogen enrichment coupled with large infrequent rain events would have the greatest impact on plant community composition and ANPP.

2 | MATERIALS AND METHODS

2.1 | Site description

This study was conducted over a 14-year period (2007–2020) in the Sevilleta National Wildlife Refuge (NWR), central New Mexico, USA, under annual permits granted by the US Fish and Wildlife Service to the Sevilleta Long-Term Ecological Research (LTER) program. Domestic livestock were permanently excluded from the Sevilleta NWR in 1973 following more than a century of extensive cattle grazing (Parmenter, 2008; Rand-Caplan, 2006). The abundance of dominant grasses such as *Bouteloua eriopoda* has since recovered (Collins et al., 2020; Collins & Xia, 2015; Ryerson & Parmenter, 2001); however, these grasslands are periodically subjected to lightning-caused wildfires (Parmenter, 2008). Precipitation in this region exhibits high intra- and interannual variability, with growing season rainfall originating primarily from localized convective thunderstorms driven by the North American Monsoon (Muldavin et al., 2008; Pennington & Collins, 2007). The summer monsoon, which spans July through September, is typically preceded by a 2-month period with high daytime temperatures and minimal precipitation (Notaro et al., 2010). Climate parameters in the Sevilleta NWR have been recorded continuously for over three decades by a spatially distributed network of automated meteorological stations (Moore, 2021). From 1990 to 2020, the mean annual temperature recorded by the Deep Well station (34.3592° N, 106.6911° W, elevation 1600 m) was 13.7 ± 0.2°C, with monthly temperatures ranging from 25.4 ± 0.2°C in July to 1.2 ± 0.3°C in December. The mean annual water year precipitation recorded over this same 31-year period was 233 ± 9.6 mm, with 118 ± 8.3 mm falling during the summer monsoon. Atmospheric nitrogen deposition occurs primarily through wet deposition at a rate of $0.2\,\mathrm{g\,N\,m^{-2}\,year^{-1}}$, with 57% deposited as NH_4 and 43% as deposited as NO_3 (Báez et al., 2007).

2.2 | Experimental design

The Monsoon Rainfall Manipulation Experiment (MRME; 34.3441° N, 106.7272° W, elevation 1604 m) was established in 2007 to investigate how changes in the size and frequency of monsoon rain events affect ecosystem structure and functioning in a northern Chihuahuan Desert grassland. Vegetation in MRME is dominated by black grama (*Bouteloua eriopoda*), a native shallow-rooted perennial C_4 grass (Gibbens & Lenz, 2001; Thomey et al., 2011). Other common grasses include *Muhlenbergia arenicola* and *Sporobolus* spp. Commonly observed forbs include *Salsola tragus*, *Chamaesyce* spp. and *Kallstroemia parviflora*. Broom snakeweed (*Gutierrezia sarothrae*), a C_3 sub-shrub, is the most abundant small woody species. Soils are classified as Typic Haplocalcids formed by calcareous aeolian and alluvial deposits (Soil Survey Staff, 2019). Soil bulk density is $1.51\,\mathrm{g\,cm^{-2}}$ and porosity is 43% (Thomey et al., 2011), with a texture distribution in the upper 20 cm consisting of 68% sand, 22% silt and 10% clay, with <10% as $CaCO_3$ (Kieft et al., 1998). Soils are underlain by a petrocalcic layer ~30 cm beneath the surface, which constrains moisture infiltration and rooting depth (Bryan-Ricketts, 2012; Buxbaum & Vanderbilt, 2007; Gibbens & Lenz, 2001). Low rates of atmospheric nitrogen deposition in this region, together with a low abundance of nitrogen fixers in biological soil crusts (Fernandes et al., 2022), contribute to nutrient-poor soils in this experiment (Brown et al., 2022).

MRME consists of 13 8 m × 13 m plots (Figure S1), with three plots serving as ambient controls, and the remaining 10 receiving one of two experimentally applied rainfall addition treatments ($n = 5$ per rainfall treatment) for 12 consecutive weeks during the summer monsoon each year. Specifically, 'small frequent' plots received a 5 mm rainfall addition once per week ($n = 12$), whereas 'large infrequent' plots received a 20 mm rainfall addition once per month ($n = 3$), resulting in all rainfall addition plots receiving the same total amount of supplemental rainfall (60 mm) by the end of each monsoon season. Rainfall treatments were applied via raindrop-quality overhead sprinkler systems using reverse-osmosis water that was stored in onsite tanks. Ambient precipitation, received by all plots throughout the duration of this study, was measured continuously by a tipping bucket rain gage (TE525MM; Campbell Scientific Inc., Logan, UT, USA), with any missing or suspect data gap-filled from the nearby Five Points meteorological station (34.3350° N, 106.7293° W, elevation 1613 m; Moore, 2021). In August 2009, an intense lightning-caused wildfire burned through the experiment, consuming all above-ground vegetation. Following the wildfire, soil moisture sensors (CS616; Campbell Scientific Inc., Logan, UT, USA) were installed within the rooting zone (0–16 cm) of a randomly selected black grama tussock in each plot to provide continuous depth-integrated measurements of soil volumetric water content (SVWC).

Above-ground NPP (ANPP) was measured as peak biomass during the fall growing season using a non-destructive allometric scaling approach based on height and cover measurements of individual plants (Muldavin et al., 2008). Peak biomass is a commonly used surrogate for ANPP in herbaceous ecosystems (Fahey & Knapp, 2007). Species-level ANPP was estimated using linear regression models of weight-to-volume ratios, where intercepts were forced through the origin, developed from reference specimens harvested over multiple years from adjacent areas (Rudgers et al., 2019). Measurements were recorded in two permanently located 1 m^2 quadrats within two 2 × 2 m subplots in each plot (Figure S1). One *fertilized* subplot received 5 g N m^2 $year^{-1}$, applied as ammonium nitrate (NH_4NO_3) pellets each June prior to the summer monsoon, while the other subplot served as an *unfertilized* control (Figure S1). Plant Root Simulator (PRS®) probes (Western Ag Innovations, Saskatoon, Saskatchewan, CA) were also buried within the rooting zone of a randomly selected black grama tussock in one *unfertilized* and one *fertilized* quadrat in each plot prior to the summer monsoon in most years (Collins, 2020). PRS® probes mimic plant uptake of nitrogen using ion-exchange resin membranes, providing a seasonally integrated estimate of plant available nitrogen. Following each summer monsoon, probes were retrieved, rinsed in deionized water and shipped to the manufacturer, where they were analysed for ammonium (NH_4^+-N) and nitrate (NO_3^--N).

2.3 | Statistical analyses

All data analyses were conducted using *R* version 4.3.1 (R Core Team, 2023). To assess the seasonal and overall effectiveness of rainfall treatments following the 2009 wildfire, repeated-measures analyses of variance (ANOVAs) were performed using the mean daily SVWC averaged across each rainfall treatment between July and September of each year. Seasonally integrated nitrogen supply rates measured by PRS® probes were analysed similarly using a linear mixed-effects model, where the rainfall and fertilization treatment combination was specified as a fixed effect and plot as a random effect.

To investigate treatment effects on ANPP over time, we constructed separate linear mixed-effects models for *unfertilized* and *fertilized* treatments, where the interaction between year and rainfall treatment was specified as a fixed effect. Additional linear mixed-effects models were constructed for the dominant grass (black grama), a widespread sub-shrub (broom snakeweed), and subdominant plant functional types (other grasses and forbs) found in MRME, where the interaction among year, rainfall treatment and fertilization treatment was specified as a fixed effect. Three rarely occurring evergreen species (*Ephedra torreyana*, *Opuntia phaeacantha* and *Sclerocactus papyracanthus*) were excluded from these analyses because ANPP could not be accurately estimated for these species. The quadrat nested within the subplot within the plot (see Figure S1) was specified as the random effect in all ANPP models.

Linear mixed-effects models were constructed using the *nlme* package in *R* (Pinheiro et al., 2023) and included a continuous first-order autoregressive correlation structure to account for temporal autocorrelation. Response variables were either natural log or square root transformed prior to model runs to satisfy assumptions of normality (evaluated using Q-Q plots) and homoscedasticity (evaluated by plotting residuals against fitted values). Post-hoc Tukey's Honestly Significant Difference (HSD) pairwise comparisons were conducted using the *emmeans* package in *R* (Lenth et al., 2023) to further investigate treatment effects on response variables, which were considered statistically significant when $p \leq 0.05$.

To visualize interactive treatment effects on plant community composition over time, we constructed a Bray–Curtis dissimilarity matrix from Wisconsin double standardized square root transformed species-level abundances in each plot, measured as ANPP, followed by a three-dimensional non-metric multidimensional scaling (NMDS) analysis using the *metaMDS* function in the *vegan* package in *R* (Oksanen et al., 2022). NMDS is considered the ordination method of choice for collapsing multidimensional ecological community data into reduced dimensional space, where species occurring in less than 10% of all observations were omitted prior to computing Bray–Curtis dissimilarities to reduce noise and improve interpretation (McCune & Grace, 2002). To determine if community composition differed significantly among the six treatment pairs, we conducted permutational multivariate analyses of variance (PERMANOVAs) using the *adonis2* function in *vegan*, with the plot specified as a random effect using the strata parameter, followed by pairwise comparisons using the *pairwise.adonis2* function in the *pairwiseAdonis* package in *R* (Martínez Arbizu, 2020). Permutational multivariate analysis of dispersion (PERMDISP) within treatments was calculated using the *betadisper* function in *vegan*, followed by ANOVA and Tukey's HSD pairwise comparisons. Finally, the degree of community divergence among treatments was calculated with the *usedist* package in *R* (Bittinger, 2020).

3 | RESULTS

3.1 | Soil moisture and nitrogen availability

Ambient monsoon rainfall over this 14-year study exhibited high interannual variation, ranging from 71.2 mm in 2019 to 222.2 mm in 2013, with a coefficient of variation (CV) of 40% (Figure 1). Although average monsoon rainfall received over the study period was ~7% lower than the longer-term regional mean, treatments increased ambient monsoon rainfall by ~61% on average. Mean seasonal post-fire SVWC differed significantly among all rainfall treatments, ranging from 11.0 ± 0.1% in ambient to 12.7 ± 0.1% in small frequent to 14.1 ± 0.1% in large infrequent, with rainfall addition, regardless of treatment size or frequency, resulting in significantly higher SVWC compared to ambient in nearly all post-fire years (Figure S2). Fertilization resulted in significantly higher mean seasonally integrated net inorganic nitrogen (NH_4^+-N + NO_3^--N) supply rates than unfertilized treatments, regardless of rainfall treatment. However, large infrequent rainfall consistently resulted in less plant available nitrogen over the study period, especially in the absence of nitrogen enrichment (Figure S3).

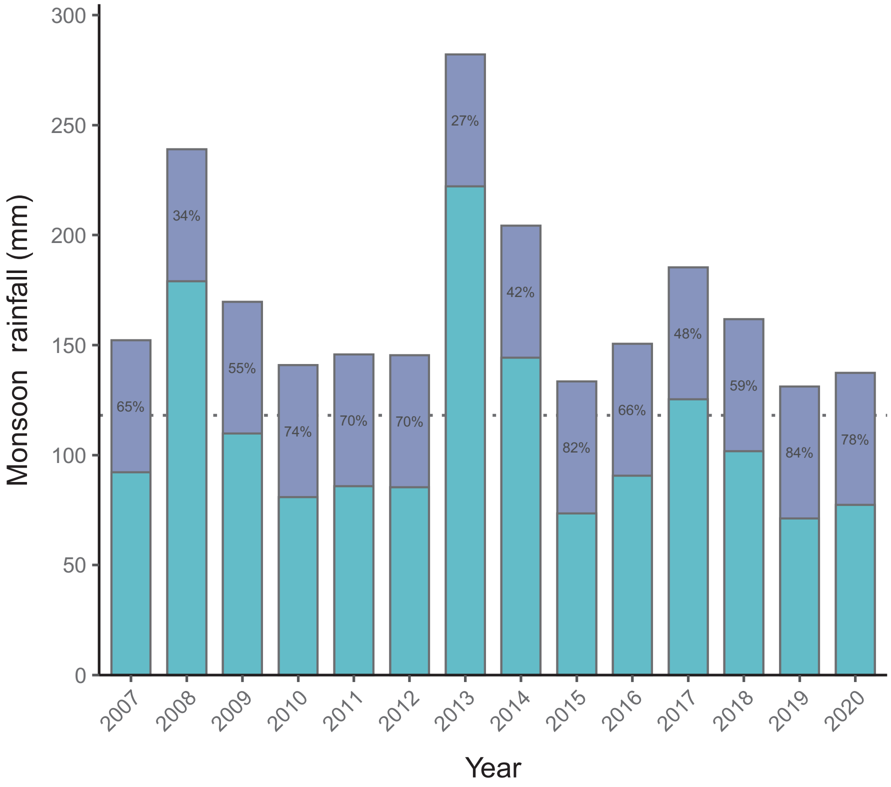


FIGURE 1 Total summer monsoon (July–September) rainfall (mm) received by the Monsoon Rainfall Manipulation Experiment (MRME) over the 14-year study (2007–2020). The lower (light blue) portions of each stacked bar represent ambient rainfall received by all plots, while the upper (purple) portions represent the 60 mm of supplemental rainfall added each summer through either small frequent (5 mm weekly; $n = 12$) or large infrequent (20 mm monthly; $n = 3$) events. Values within the upper portions reflect the annual percentage increase in total monsoon rainfall attributed to rainfall addition treatments. The dashed line reflects the mean long-term monsoon precipitation (i.e. 118 mm) recorded in the Sevilleta NWR between 1990 and 2020.

3.2 | Above-ground net primary production

ANPP exhibited high interannual variation across all treatments over the study period (CV = 49%), with means ranging from $63.1 \pm 9.5\,\mathrm{g\,m^{-2}\,year^{-1}}$ in the unfertilized ambient treatment to $147.3 \pm 16.3\,\mathrm{g\,m^{-2}\,year^{-1}}$ in the fertilized large infrequent treatment (Figure 2). In the absence of nitrogen enrichment, both rainfall addition treatments consistently increased ANPP over ambient conditions, especially during 2011–2016 (Figure 2A). Across the entire study period, these trends were quite strong ($p \leq 0.01$), with the small frequent rainfall treatment resulting in the greatest overall ANPP. Combining rainfall addition with fertilization treatments also increased ANPP over ambient conditions. However, in contrast to rainfall addition alone, fertilization generally only resulted in statistically significant increases in ANPP relative to ambient conditions under large infrequent rainfall. Moreover, the fertilized large infrequent treatment resulted in the greatest ANPP overall (Figure 2B; $p \leq 0.01$). We also found greater separation among ANPP responses to rainfall treatments in the presence of nitrogen enrichment; however, there were no statistically significant differences in ANPP between the small frequent and large infrequent treatments, regardless of fertilization.

The average proportion of ANPP attributed to the dominant species, black grama, ranged from 31% in the fertilized large infrequent treatment (Figure 3f) to 56% in the unfertilized large infrequent treatment (Figure 3e). Overall, rainfall addition alone did not have a notable impact on plant functional types, except for black grama, which exhibited significantly greater production under large infrequent rainfall (Figure 3e; $p \leq 0.05$) compared to ambient conditions (Figure 3a). However, rainfall addition combined with fertilization significantly reduced the proportion of ANPP attributed to black grama (Figure 3d,f). Forbs, on the other hand, were particularly responsive to nitrogen enrichment, exhibiting greater ANPP compared to unfertilized treatments, especially under small frequent rainfall (Figure 3b).

3.3 | Plant community composition

The interactive effects of rainfall and fertilization treatments resulted in significant differences in plant community composition over the study period ($R^2 = 0.10$, $p \leq 0.001$), which were driven solely by fertilization treatments within each rainfall treatment ($0.03_{\text{large infrequent}} \leq R^2 \leq 0.08_{\text{ambient}}$, $p \leq 0.001$). In other words, plant community composition did not differ significantly among rainfall treatments over the 14-year study.

The NMDS ordination (Figure 4) revealed a distinct temporal shift beginning in 2014, following an above-average monsoon in 2013 (Figure 1). Therefore, we focused additional analyses on the last 7 years of the study (2014–2020), when plant community composition was most stable over time. Interactive treatment effects during this period similarly resulted in significant compositional differences ($R^2 = 0.14$, $p \leq 0.001$), still driven solely by the fertilization treatment ($0.04_{\text{large infrequent}} \leq R^2 \leq 0.14_{\text{ambient}}$, $p \leq 0.001$). The greatest difference in plant community composition during 2014–2020 occurred between the fertilization treatments under small frequent rainfall. Distances between fertilization treatment centroids ranged from 0.06 in ambient to 0.51 in the small frequent treatment. Plant

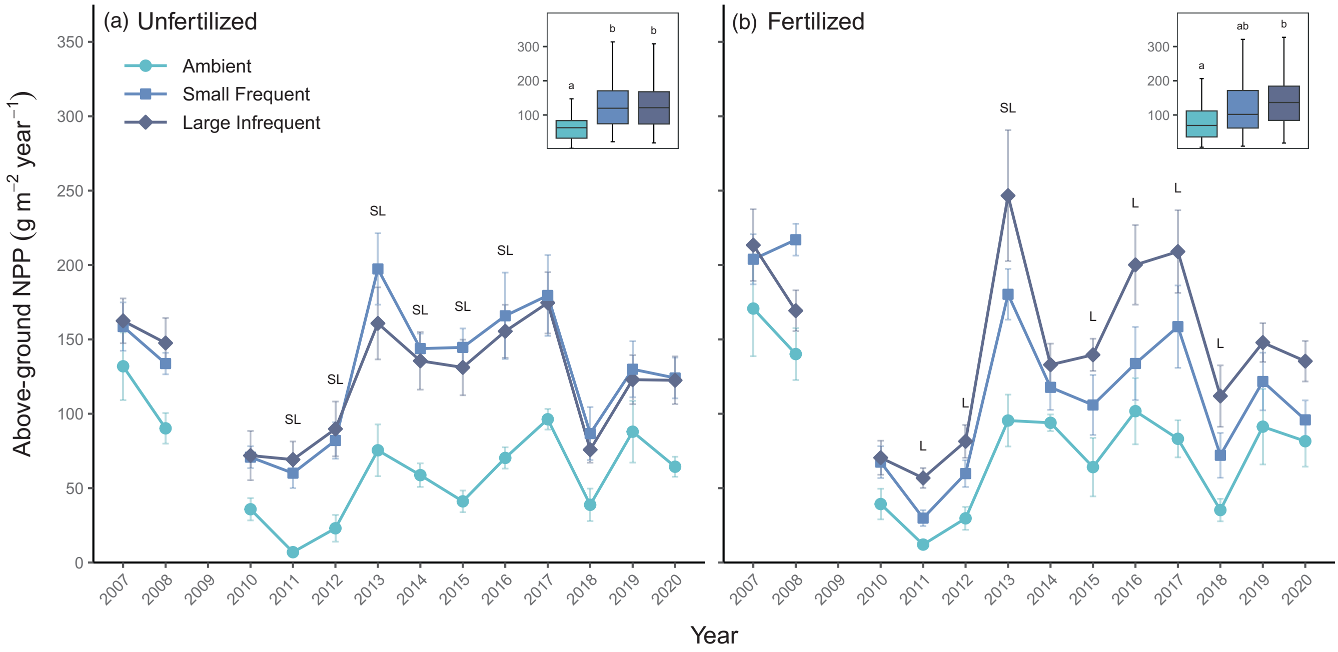


FIGURE 2 Mean fall season above-ground net primary production (ANPP; g m^{-2} year^{-1}) responses to rainfall and fertilization treatments over the 14-year study (2007–2020). Rainfall addition treatments include ambient controls (light blue; circular symbols), small frequent (5 mm weekly; medium blue; square symbols) and large infrequent (20 mm monthly; dark blue; diamond symbols). All plots received ambient rainfall year-round. Fertilization treatments included (a) unfertilized controls and (b) 5 g N m^2 year^{-1}. No ANPP measurements were made in 2009 due to a wildfire that burned through the experiment. Symbols represent the mean ANPP for each rainfall treatment by year, with error bars indicating standard errors of the means. Letters indicate significant within-year differences ($p \leq 0.05$) among rainfall treatments within each fertilization treatment, where 'S' indicates a significant difference between the ambient and small frequent treatments, 'L' between the ambient and large infrequent treatments and 'SL' between the ambient and both rainfall addition treatments. Box plot insets reflect the mean ANPP over the entire study, with different letters indicating significant differences ($p \leq 0.01$) among rainfall treatments within the respective fertilization treatment.

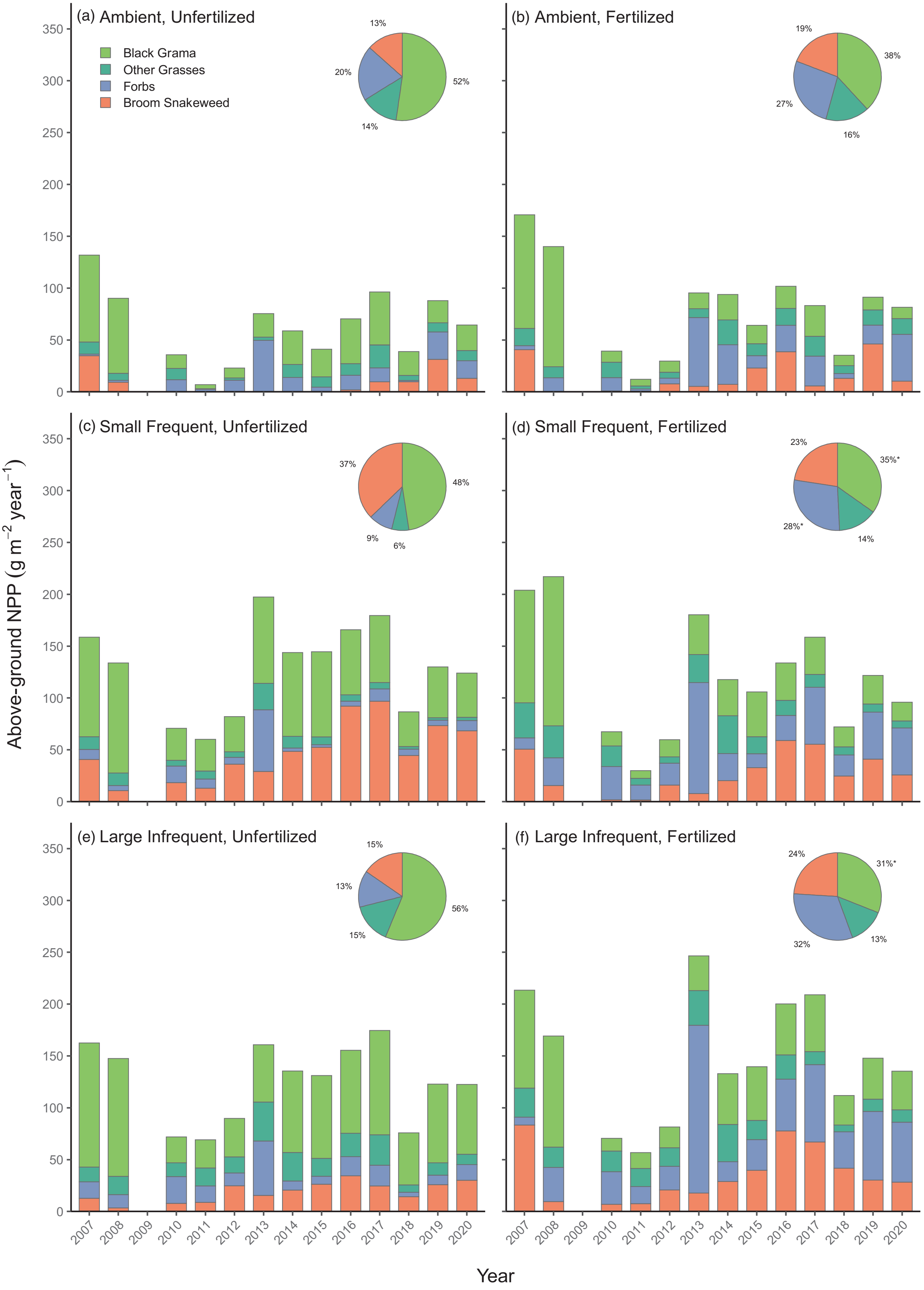
communities exhibited significant temporal dispersion around the centroids only under small frequent rainfall (Figure 4b, $p \leq 0.01$).

4 | DISCUSSION

The conceptual bucket model proposed by Knapp et al. (2008) predicts that under a more extreme precipitation regime consisting of fewer, but larger rain events, dryland ecosystems will experience reduced drought stress due to deeper infiltration and longer persistence of soil moisture, consequently resulting in greater rates of ANPP. However, our first hypothesis that large infrequent rain events would result in greater ANPP compared to small frequent events was only partially supported. Surprisingly, in the absence of nitrogen fertilization, we found that small frequent and large infrequent rainfall regimes promoted similar rates of ANPP over our 14-year study. Only when nitrogen limitation was alleviated did we find that large infrequent rain events resulted in the greatest average ANPP, suggesting that northern Chihuahuan Desert grasslands are primarily water limited, with nitrogen acting as a secondary limiting resource. While nitrogen fertilization significantly increased ANPP under large infrequent rainfall, supporting our second hypothesis, this treatment combination did not influence plant community composition as expected. Instead, compositional changes were driven solely by nitrogen fertilization, with the greatest community divergence occurring under small frequent rainfall.

Our findings contrast with the few short-term empirical studies (Heisler-White et al., 2008; Knapp et al., 2002; Thomey et al., 2011) and modelling analyses (Hou et al., 2021) that have explicitly investigated bucket model predictions in dryland ecosystems. All these studies consistently reported higher rates of ANPP under rainfall regimes characterized by fewer, but larger rain events. Yet, previous

FIGURE 3 Mean fall season above-ground net primary production (ANPP; g m^{-2} year^{-1}) measured over the 14-year study (2007–2020), with rows representing rainfall treatments (ambient, small frequent and large infrequent) and columns representing fertilization treatments (unfertilized and fertilized). Different colours reflect the proportion of ANPP contributed by the dominant grass (black grama [*Bouteloua eriopoda*], light green), a widespread sub-shrub (broom snakeweed [*Gutierrezia sarothrae*], orange), along with other plant functional types (other grasses, dark green; forbs, blue) found in the site. No ANPP measurements were made in 2009 due to a wildfire that burned through the experiment. Pie chart insets reflect the average proportion of ANPP contributed by each functional group over the entire study, with asterisks indicating significant differences ($p \leq 0.05$) between fertilized and unfertilized treatments within each rainfall treatment.


(a) Ambient, Unfertilized
Black Grama
Other Grasses
Forbs
Broom Snakeweed
13%
20%
52%
14%
(b) Ambient, Fertilized
19%
38%
27%
16%
(c) Small Frequent, Unfertilized
37%
48%
9%
6%
(d) Small Frequent, Fertilized
23%
35%*
28%*
14%
(e) Large Infrequent, Unfertilized
15%
13%
56%
15%
(f) Large Infrequent, Fertilized
24%
31%*
32%
13%
Above-ground NPP (g m^{-2} year^{-1})
0
50
100
150
200
250
300
350
2007
2008
2009
2010
2011
2012
2013
2014
2015
2016
2017
2018
2019
2020
Year

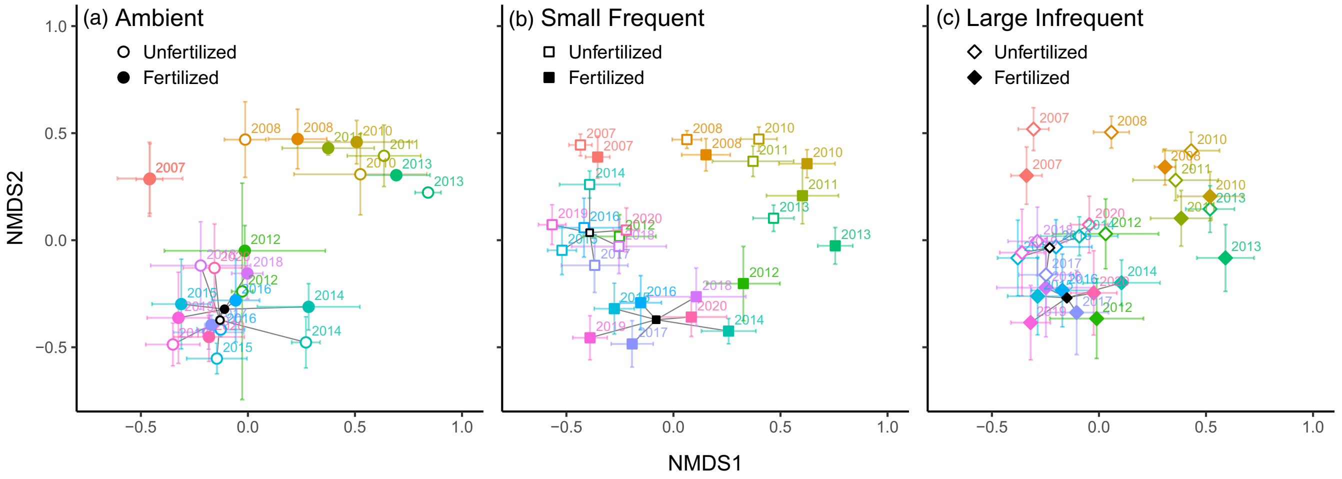


FIGURE 4 Non-metric multidimensional scaling (NMDS) ordination plots of a Bray–Curtis dissimilarity matrix visualized in two-dimensional space, where greater divergence in plant community composition is reflected by greater distances among points. Panels (a–c) reflect plant communities in unfertilized (open symbols) and fertilized ($5\,g\,N\,m^2\,year^{-1}$; filled symbols) treatments within each rainfall treatment (ambient, circles; small frequent, squares; large infrequent, diamonds). Coloured symbols represent mean NMDS scores within each treatment combination, labelled by year (2007–2020), with error bars indicating standard errors of the means. Smaller white (unfertilized) and black (fertilized) symbols represent the centroids, or mean NMDS scores over the last 7 years of the study (2014–2020; grey lines).

empirical tests of the bucket model in arid and semi-arid grasslands revealed that a shift from current rainfall patterns to fewer, but larger rain events led to considerable increases in soil moisture availability over the growing season (Heisler-White et al., 2008, 2009; Thomey et al., 2011). We also found large infrequent rain events result in increased moisture availability that also persists longer, particularly earlier in the summer monsoon when soils tend to be drier (Brown et al., 2022), in contrast to mesic grasslands (Heisler-White et al., 2009).

Ecological responses to large infrequent rain events were suggested by the bucket model to be contingent on ambient precipitation amounts. Thus, an important factor that could be causing different responses among previous studies and ours is that our design layered experimental rain events onto ambient rainfall each year, whereas ambient events were excluded by Heisler-White et al. (2008, 2009). Consequently, at the seasonal level, our two rainfall addition treatments resulted in a higher mean SVWC than observed by Heisler-White et al. (2009). In a revised bucket model framework, Thomey et al. (2011) proposed that the interannual variability of ambient precipitation likely influences the magnitude of production responses to these events, with greater responses expected in dry years compared to wet years. Consistent with this hypothesis, we observed that in nearly all post-fire years where ambient monsoon rainfall approached or exceeded the long-term regional average, soil moisture availability under rainfall addition treatments did not significantly differ from ambient conditions (i.e. 2013, 2014) or each other (i.e. 2018). This further demonstrates the modulating role of background climate variability on ANPP responses.

The bucket model assumes environmental conditions, such as soil texture, are similar across mesic and arid ecosystems, but as Knapp et al. (2008) noted, this is not necessarily a valid assumption. For example, the inverse texture hypothesis predicts that in drylands, coarse-textured sandy soils enhance ANPP compared to fine-textured soils by promoting infiltration, whereas the opposite is true in mesic systems (Noy-Meir, 1973; Sala et al., 1988). Despite clear differences in average soil moisture in our study, many small rain events resulted in similar amounts of ANPP relative to a few large events. This likely reflects the importance of soil texture as a regulator of soil moisture in this system, where sandy soils allow even small rain events to percolate into the rooting zone to drive ANPP. Indeed, a recent synthesis found that ANPP responses to altered precipitation patterns were positively correlated with sand content across grasslands globally, further highlighting the potential for edaphic factors like soil texture to mediate ecological responses in water-limited ecosystems (Su et al., 2023). Soil texture has also been found to play an important role in modulating ANPP across deserts in the southwestern US; however, this curiously did not hold true during the summer monsoon in the Chihuahuan Desert (Shepard et al., 2015). These collective insights underscore the need to not only consider but also improve understanding of how soil properties may regulate ANPP responses when applying the bucket model in different ecosystems.

Our findings suggest that small frequent rain events are equally important as large infrequent events for maintaining ANPP in northern Chihuahuan Desert grassland. Previous studies in this region have found that the dominant species, black grama, responds more strongly to large rather than small rain events (Báez et al., 2007; Stephens & Whitford, 1993; Thomey et al., 2014). Yet, numerous studies have demonstrated the importance of small rain events for a variety of ecological processes in arid and semi-arid grasslands, including nitrogen availability (Brown et al., 2022), diversity of biological soil crusts (Fernandes et al., 2022), lag effects on ANPP

(Petrie et al., 2015) and production of dominant grasses (Sala & Lauenroth, 1982). Although small rain events often do not percolate very deeply, persistent moisture availability in the top few centimetres of soil where roots are abundant (Gibbens & Lenz, 2001; Jackson et al., 1996; Kurc & Small, 2007; McCulley et al., 2004) can maintain plant production in this system where most rain events are small (Petrie et al., 2015). Thus, the occurrence of comparably high ANPP under small frequent and large infrequent rainfall regimes further highlights the ecological importance of small rain events in maintaining production in arid and semi-arid grasslands adapted to high rainfall frequency.

Compared to other studies, our results reveal more complex ANPP responses that depend on the interactive effects between altered rainfall and nutrient enrichment over time. Nitrogen enrichment may reconcile contrasting findings by alleviating secondary limitation under large infrequent rainfall. Indeed, we found greater divergence among ANPP responses when nitrogen was added. In the absence of nitrogen enrichment, the lack of significantly higher ANPP responses to large infrequent rainfall, in comparison to small frequent rainfall, can be attributed to the significantly reduced availability of soil nitrogen in the large infrequent rainfall regime. This aligns with findings from an earlier study conducted in the same experiment, where plant available nitrogen was highest under small frequent rainfall (Brown et al., 2022). That study also found that large rain events significantly reduced nitrate availability, whereas nitrogen-acquiring enzymatic activity and ammonium availability were stimulated by more frequent rain events. Therefore, projected increases in atmospheric nitrogen deposition coupled with a shift towards a more extreme rainfall regime may benefit ANPP in this system.

Our study also revealed that nitrogen enrichment, not differences in rainfall size and frequency, drove changes in plant community composition over time, with the greatest divergence occurring between the unfertilized and fertilized treatments under small frequent rainfall. Although black grama contributed a significantly greater proportion of ANPP under large infrequent rainfall compared to ambient conditions in the absence of nitrogen enrichment, the interaction between nitrogen fertilization and rainfall addition substantially reduced the proportion of ANPP attributed to this species. In contrast, forb production increased with fertilization, especially under small frequent rainfall. This contradicts many nitrogen enrichment studies, which have reported an increase in grass production following fertilization, with forb production either remaining unaffected or experiencing a decline (Borer & Stevens, 2022; Clark et al., 2019; Seabloom et al., 2021; You et al., 2017). However, our findings align with other studies where chronic nitrogen enrichment has been found to decrease the abundance of dominant native perennial C_4 grasses (Avolio et al., 2014; Isbell et al., 2013) while increasing the abundance of subdominant forbs (Avolio et al., 2014; Milchunas & Lauenroth, 1995) in both mesic and semi-arid grasslands. In some cases, compositional changes led to an eventual decrease in ANPP under nitrogen addition in these grasslands. However, ANPP in our system remained consistently higher than ambient conditions over the entire study period, as found in a wide array of grasslands globally (Seabloom et al., 2021).

This long-term field experiment provides important insights into how desert grasslands may respond to forecasted changes in seasonal rainfall patterns and increased nitrogen deposition. Our results reveal that fewer, but larger rain events may not stimulate ANPP to the extent predicted by the bucket model in nitrogen-limited drylands until secondary limitation is relieved. Overall, our long-term study demonstrates that ANPP and plant community composition responses in drylands are complex, as they are dependent on the interactive effects of altered rainfall patterns and nitrogen availability over time. These findings not only underscore the need to incorporate nitrogen dynamics into forecasts of dryland responses to altered precipitation regimes under global change, but also highlight the value of long-term field experiments for developing more accurate predictions of ecological responses to environmental change at decadal scales.

5 | CONCLUSIONS

The bucket model predicts that a more extreme rainfall regime consisting of fewer, but larger rain events will increase ANPP in dryland ecosystems (Knapp et al., 2008). Indeed, a few short-term field experiments and modelling studies have provided evidence to support these predictions (e.g. Heisler-White et al., 2008; Hou et al., 2021). Nevertheless, results from our 14-year rainfall manipulation experiment in Chihuahuan Desert grassland are not consistent with bucket model predictions. Instead, we found that ANPP was similar under large infrequent and small frequent rainfall regimes. In addition, ANPP tended to be greater under the large infrequent rainfall regime only when soil nitrogen limitation was alleviated. Furthermore, plant community composition between fertilized and unfertilized treatments diverged the most under the small frequent rainfall regime.

Regional climate models for the southwestern US predict a shift in growing season rainfall patterns, historically characterized by frequent small events, to a more extreme rainfall regime characterized by infrequent large events. Furthermore, as human populations continue to expand, atmospheric nitrogen deposition is predicted to increase, not only within the southwestern US (Báez et al., 2007; Fenn et al., 2003) but also globally (Gruber & Galloway, 2008). Long-term manipulative experiments on the interactive effects of these drivers can improve our ability to predict how dryland ecosystems will respond to changes in nutrient availability coupled with altered rain event size and frequency at decadal timescales. Our findings contribute further evidence that dryland ecological processes are sequentially resource limited and that small frequent rain events, which may be less common in the future, play an important ecological role in dryland ecosystem dynamics.

AUTHOR CONTRIBUTIONS

Renée F. Brown and Scott L. Collins both contributed to the conceptualization, investigation and validation of this study. Scott L. Collins secured funding, designed the experiment and provided project supervision. Renée F. Brown conducted all data analysis, visualization and curation and wrote the original draft of the manuscript. Both authors made critical contributions to manuscript revisions and approved the final version for publication.

ACKNOWLEDGEMENTS

We thank the Sevilleta Long-Term Ecological Research program and the US Fish and Wildlife Service at the Sevilleta National Wildlife Refuge for making this research possible. We also thank Jeb Barrett and two anonymous reviewers for their valuable feedback on earlier drafts of this manuscript. Their insightful comments and suggestions greatly improved the quality of our work. Funding was provided by several grants from the US National Science Foundation to the University of New Mexico for Long-Term Ecological Research, most recently under award number DEB-1655499, with additional support from DEB-1856383 for Long-Term Research in Environmental Biology.

CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

All above-ground net primary production and associated data presented in this study have been archived in the Environmental Data Initiative Repository (EDI) under a Creative Commons Attribution 4.0 International (CC BY 4.0) license and can be found at https://doi.org/10.6073/pasta/71dd9cc9409eb880fb7928faf6da80ed (Brown & Collins, 2023). Meteorological and PRS® data used in this study are also publicly available from EDI at https://doi.org/10.6073/pasta/1cbc37ae4d40b3844b5e4be9f6f18073 (Moore, 2021) and https://doi.org/10.6073/pasta/a17b125176a9c24dbb4caa760d2c9944 (Collins, 2020).

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Figure S1: Photo and site layout of the Monsoon Rainfall Manipulation Experiment (MRME), located in the Sevilleta National Wildlife Refuge, central New Mexico, USA.

Figure S2: Mean daily-averaged summer monsoon (July–September) soil volumetric water content (SVWC) recorded in each rainfall addition treatment each year following the 2009 wildfire.

Figure S3: Mean seasonally integrated net inorganic nitrogen ($NH4^{+}$-N + NO_3^{-}-N) supply rates ($\mu g\,N\,10\,cm^{-2}$) in unfertilized and fertilized ($5\,g\,N\,m^{2}\,year^{-1}$) treatments within each rainfall addition treatment averaged across the nine years in which usable PRS® data were generated.

How to cite this article: Brown, R. F., & Collins, S. L. (2024). Revisiting the bucket model: Long-term effects of rainfall variability and nitrogen enrichment on net primary production in a desert grassland. *Journal of Ecology*, *112*, 629–641. https://doi.org/10.1111/1365-2745.14258