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Small rainfall events increase belowground production in Chihuahuan Desert grassland

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Abstract

Dryland productivity is highly sensitive to precipitation variability, and models predict that rainfall variability will increase in the future. Numerous studies have documented the relationship between productivity and precipitation, but most focus on aboveground production (ANPP), while the effects on belowground production (BNPP) remain poorly understood. Furthermore, previous research suggests that ANPP and BNPP are uncoupled within ecosystems, but the degree to which rainfall variability affects the interplay between aboveground and belowground production is unknown. We conducted a long-term rainfall manipulation experiment in Chihuahuan Desert grassland to investigate how the size and frequency of growing season rain events affected BNPP and its relationship to ANPP. Experimental plots received either 12 small-frequent rain events or 3 large-infrequent events during the monsoon season for a total of 60 mm of added rainfall per treatment per year. All plots, including three controls, received ambient rainfall throughout the year. Total BNPP ranged from a low of 94.7 ± 38.2 g m^2 year^{-1} under ambient conditions to a high of 183.7 ± 44.6 g m^2 year^{-1} under the small-frequent rainfall treatment. Total BNPP was highest under small-frequent rain events, and there was no difference in BNPP between 0–15 and 15–30 cm soil depths in either rainfall treatment. ANPP and BNPP were uncorrelated within rainfall treatments, but weakly positively correlated across all plots and years. Our results contribute to a growing body of research on the importance of small rain events in drylands and provide further evidence regarding the weak coupling between aboveground and belowground processes.

KEYWORDS
aboveground production, belowground production, desert grassland, precipitation variability

INTRODUCTION

Net primary production (NPP) is the main source of carbon entering terrestrial ecosystems. The drivers of aboveground production are well studied and generally related to within- and between-season precipitation variability in water-limited systems, such as grasslands (Brown & Collins, 2024; Gherardi & Sala, 2018; Heisler-White et al., 2009; Maurer et al., 2020). Belowground production (BNPP), however, is estimated to account for 33%–78% of total NPP (Gherardi & Sala, 2020; Jackson et al., 1996; Schenk & Jackson, 2002;

Sun et al., 2021) and typically contributes more carbon to the soil carbon pool than aboveground production (ANPP) in herbaceous ecosystems (Jackson et al., 2017; Sokol & Bradford, 2019). Given that BNPP comprises a significant portion of total NPP in drylands, it is crucial to enhance our knowledge of the patterns and controls of BNPP, yet such studies lag well behind those of aboveground production (Sasaki et al., 2023; Wilcox et al., 2017; Wu et al., 2011). Consequently, our understanding of factors governing BNPP is rudimentary for most terrestrial ecosystems, hindering our ability to model soil carbon storage capacity (Niu et al., 2017; Wilcox et al., 2023), as well as the terrestrial carbon budget under climate change (Wang et al., 2023).

Drylands are described as pulse-driven ecosystems in which ecological processes are governed by the size and frequency of rain events during the growing season (Collins et al., 2014). Climate change is expected to alter the amount and variability of precipitation in the future (Cook et al., 2015; Moustakis et al., 2021), and evidence indicates that interannual climate variability is already increasing locally and globally (Maurer et al., 2020; Rudgers et al., 2018; Zhang, Biederman, et al., 2021; Zhang, Shen, et al., 2021). Furthermore, within-season precipitation regimes are also predicted to intensify in the future, characterized by larger events separated by longer dry periods during the growing season (Feldman et al., 2024; Gutzler & Robbins, 2011). The impacts of changes in the size and frequency of within-season rain events on ANPP are hypothesized to vary across gradients of mean annual precipitation. The bucket model predicts that ANPP will decline in mesic systems but increase in drylands under a precipitation regime characterized by fewer but larger rain events (Knapp et al., 2008), and short-term field experiments have supported aspects of this model (Goldstein & Suding, 2014; Heisler-White et al., 2009; O'Donnell et al., 2021; Thomey et al., 2011). In a modeling study, however, Ye et al. (2016) found that fewer, larger rain events reduced ANPP in mesic systems, consistent with bucket model predictions, but that responses in drylands were variable. For example, in a long-term rainfall manipulation experiment in a desert grassland, Brown and Collins (2024) found no difference in ANPP in treatments that manipulated the size and frequency of rainfall unless plots were fertilized with nitrogen, highlighting the importance of resource limitation on ecosystem responses to rainfall variability. Thus, the long-term impacts of within-season precipitation variability in drylands remain uncertain and require further study.

Although considerable research has investigated how ANPP responds to precipitation variability, the response of BNPP to within-season precipitation variability is virtually unknown. Recent studies have shown that responses of ANPP and BNPP to climate variability are generally decoupled in many ecosystems (Brown & Collins, 2023a; Keller et al., 2023; Sun et al., 2021; Wilcox et al., 2017; Yang et al., 2023). That is, there is little to no correlation between above- and belowground production within a site over time, suggesting that BNPP cannot be predicted from our understanding of the drivers of ANPP. For example, Gao et al. (2023) found a positive correlation between above- and belowground plant traits, but that these traits responded independently to altered biotic and abiotic conditions. In some water-limited systems, both ANPP and BNPP responded positively to increased precipitation (Fiala et al., 2009; Wang et al., 2023), whereas in annual grassland, the response of BNPP, but not ANPP, to rainfall variability was curvilinear (Zhu et al., 2016). In semiarid grasslands, BNPP and precipitation were generally uncorrelated (Brown & Collins, 2023a; Gao et al., 2011). Thus, additional long-term research is needed to decipher patterns and controls of BNPP.

Dryland ecosystem processes are particularly dependent on rainfall (Collins et al., 2008). In the northern Chihuahuan Desert, ANPP is primarily driven by precipitation during the North American Monsoon, which typically occurs from July to mid-September each year (Notaro et al., 2010). Over the past 100 years in this region, the number of monsoon rain events per day has increased, whereas the average size of rain events has decreased (Petrie et al., 2014). Together, these patterns result in a change in the size and frequency of rain events, with no net change in the total amount of seasonal precipitation. Despite these historical patterns, regional models predict a future regime characterized by less frequent but larger rain events (Feldman et al., 2024). Therefore, we used a long-term rainfall manipulation experiment in the northern Chihuahuan Desert to quantify how belowground net primary production responded to changes in the size and frequency of rain events and the degree to which ANPP and BNPP were coupled during the growing season under different rainfall regimes. Earlier work in this and other systems found that large-infrequent rain events resulted in deeper and longer lasting soil moisture pulses relative to smaller rain events (Brown et al., 2022; Vargas et al., 2012). Therefore, we hypothesized that (1) BNPP is positively correlated with precipitation, (2) BNPP is greatest under large-infrequent rain events, especially in deeper soil layers, but that (3) ANPP and BNPP are uncorrelated in response to altered rainfall regimes because of asymmetric responses to rainfall variability.

METHODS

Study site

Our long-term experiment (2012–2020) was conducted in the Sevilleta National Wildlife Refuge (SNWR), central New Mexico, USA. Annual precipitation is highly variable within and between years. From 1990 to 2020, mean annual water year precipitation was 230 ± 9.3 mm, with 118 ± 7.8 mm falling during the summer monsoon. Mean annual water year temperature at the study site was 13.7 ± 0.2°C, with an average monthly high temperature of 25.4 ± 0.2°C in July and an average low of 1.2 ± 0.3°C in December (Brown & Collins, 2024; Moore, 2021).

Experimental design

The Monsoon Rainfall Manipulation Experiment (MRME; 34.3441° N, 106.7272° W, elevation 1604 m) was established in 2007 to determine how the size and frequency of monsoon rain events affected ecosystem structure and functioning in a northern Chihuahuan Desert grassland (Appendix : Figure S1). The dominant species is black grama (*Bouteloua eriopoda*), a native shallow-rooted perennial C_4 grass (Brown & Collins, 2024; Gibbens & Lenz, 2001; Thomey et al., 2011). Common forbs and subshrubs include *Salsola tragus*, *Chamaesyce* spp., *Kallstroemia parviflora*, and *Gutierrezia sarothrae*. Soils are classified as Typic Haplocalcids formed by calcareous eolian and alluvial deposits (Soil Survey Staff 2019). Soil bulk density is 1.51 g cm^{-2} and porosity is 43% (Thomey et al., 2011) and soil texture in the upper 20 cm is 68% sand, 22% silt, and 10% clay, with <10% as $CaCO_3$ (Kieft et al., 1998). A petrocalcic layer occurs 30–50 cm beneath the soil surface, which constrains moisture infiltration and rooting depth of herbaceous plants (Buxbaum & Vanderbilt, 2007).

MRME consists of thirteen 8 m × 13 m plots. Five plots receive a rainfall addition treatment of 5 mm per week for 12 weeks (small-frequent) during the summer monsoon (July–mid-September). Five plots receive 20 mm per month for three months (large-infrequent) during this time, resulting in both treatments receiving the same total amount of added rainfall (60 mm) by the end of each monsoon season, but differing in size and frequency of added rain events. Three plots serve as ambient controls. The unbalanced design was initially implemented to assess differences between rainfall treatments more so than differences between added rainfall and ambient precipitation. Rainfall treatments were applied via raindrop-quality overhead sprinkler systems using reverse-osmosis water stored onsite. All plots receive ambient precipitation throughout the year. Precipitation at the site was measured continuously by a tipping bucket rain gauge. Soil moisture was recorded as soil volumetric water content (SVWC) within the rooting zone (0–16 cm depth) of a randomly selected black grama tussock in each plot using time domain reflectometry probes (CS616; Campbell Scientific Inc., Logan, UT, USA).

Starting in 2012, permanently located root ingrowth donuts (Milchunas et al., 2005) were used to estimate annual BNPP from 0 to 30 cm in depth where moisture infiltration is highest and most roots are concentrated (Gibbens & Lenz, 2001; Kurc & Small, 2007). Although most estimates of BNPP have biases (Neill, 1992; Zhou et al., 2012), root ingrowth donuts provide reliable long-term comparative estimates of BNPP (Milchunas, 2009). One root ingrowth donut per plot was created by excavating a 20.3 cm diameter by 30 cm deep hole and lining the outer wall with 2 × 2 mm plastic mesh. Next, two 15.2 cm diameter by 15 cm tall PVC cylinders were inserted, one on top of the other, into the center of the hole and filled with sandbags to hold them in place. Sieved soil (2 mm mesh) was then added to the space between the PVC cylinder and the plastic mesh lining the outer edge of the hole, creating a donut-shaped cylinder of root-free soil into which roots can grow (see Vojdani et al., 2024). In early November each year, the 0–15 cm and 15–30 cm depth soil cylinders were harvested. New, sieved root-free soil obtained from the surrounding area was used to reconstruct the root ingrowth donut for the next annual harvest. Harvested soils were passed through a 2-mm sieve and roots were floated in water for collection. Root material was dried at 60°C for 48 h and weighed. To calculate BNPP, root weights within each depth partition were divided by the area of the root ingrowth donut and scaled up to 1 m^2 to enable comparisons with ANPP. Total BNPP (0–30 cm) was the sum of BNPP from 0 to 15 and 15 to 30 cm depths.

Aboveground net primary production (ANPP) was measured during the fall growing season each year using a nondestructive allometric scaling approach based on height and cover measurements of individual plants. Measurements were recorded in two permanently located 1-m^2 quadrats in each plot (Appendix S1: Figure S1). Allometric size-biomass regression equations were developed by harvesting individual plants growing outside the experimental plots across a range of size classes over multiple years (Muldavin et al., 2008; Rudgers et al., 2019).

Statistical analyses

Hypothesis 1. *BNPP is positively correlated with precipitation*. To investigate the relationship between moisture availability and BNPP, we first examined the Pearson correlations between ambient precipitation and soil moisture both within and among rainfall treatments to understand how well precipitation can predict SVWC. We found a strong correlation between SVWC and precipitation (Appendix S1: Figure S2) indicating that precipitation is a good surrogate for soil water availability in this system. Therefore, subsequent analyses focused on the relationship between productivity and precipitation, because precipitation is much more frequently measured than soil moisture in rainfall manipulation experiments facilitating comparisons with other studies. Linear models were constructed for each depth partition (total, 0–15 cm, and 15–30 cm) and treatment combination, where BNPP was the response variable and precipitation was the predictor variable. We also ran linear models for all treatments combined in each depth partition.

Hypothesis 2. *BNPP is greatest under large-infrequent rain events, especially in deeper soil layers*. We used linear mixed-effects models to investigate rainfall treatment effects on total, 0–15 cm, and 15–30 cm depth BNPP over time, where the interaction between year and rainfall treatment was a fixed effect and plot was a random effect. 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. BNPP was natural log 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 $p \leq 0.05$.

Hypothesis 3. *ANPP and BNPP are uncorrelated*. We performed simple linear regressions for each rainfall treatment and depth partition where BNPP was the response variable and ANPP was the predictor variable. We also used a linear regression comparing ANPP and BNPP across all treatments combined within each depth partition.

All data analyses were conducted using R version 4.3.1 (R Core Team, 2023).

RESULTS

Ambient monsoon rainfall over this 9-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 44% (Appendix S1: Figure S2). Average monsoon rainfall received over the study period was 7% lower than the long-term regional mean, with treatments increasing ambient monsoon rainfall by ~62% on average. ANPP ranged from a low of 61.8 ± 8.0 g m^{-2} year^{-1} under ambient conditions to 139.3 ± 13.0 g m^{-2} year^{-1} under the small-frequent treatment. Temporal variability of ANPP ranged from 24.8% under the large-infrequent rainfall treatment to 38.9% under ambient conditions (Brown & Collins, 2024). Total BNPP ranged from a low of 94.7 ± 38.2 g m^2 year^{-1} under ambient conditions to a high of 183.7 ± 44.6 g m^2 year^{-1} under the small-frequent rainfall treatment. Temporal variability of BNPP ranged from 64.0% under large-infrequent rainfall to 121.0% under ambient conditions.

Hypothesis 1. *BNPP is positively correlated with monsoon rainfall. Our first hypothesis was supported*. Unlike ANPP, total BNPP was positively correlated with monsoon precipitation in all three rainfall treatments with one exception (Figure 1; Appendix S1: Table S1, Table S2), and in all cases the strongest correlation occurred in plots receiving ambient precipitation. Total BNPP was also correlated with soil moisture but in all cases, *r* values were similar to that of precipitation. Surprisingly, correlations between monsoon precipitation and BNPP in treatments with added rainfall were somewhat lower than those observed in ambient plots. Correlations between BNPP and precipitation for each depth partition largely followed patterns for those of total BNPP, although correlations are weaker for 15–30 cm depth compared to 0–15 cm depth in water addition treatments (Appendix S1: Table S1).

Hypothesis 2. *BNPP is greatest under large-infrequent rain events, especially in deeper soil layers*. Our second hypothesis was not supported. BNPP varied over time by both rainfall treatment and depth partition (Figure 2, Appendix S1: Table S3). Total BNPP was highest as was BNPP from 0 to 15 cm in 2013, a year with exceptionally high monsoon rainfall, and then generally declined over time. Across all years, total BNPP was significantly higher in plots receiving small-frequent rain events relative to ambient conditions. Total BNPP under the large-infrequent treatment differed significantly from controls in only two years (2019, 2020) and from the small-frequent treatment only in 2012, the first year of measurement. The same patterns generally emerged for BNPP responses at both 0–15 cm and 15–30 cm depths. That is, average production was significantly higher at both depths under the small-frequent rainfall treatment relative to ambient conditions, whereas BNPP did not differ significantly at either depth (and total) between small-frequent and large-infrequent treatments, except for 0–15 cm depth in 2012 (Appendix S1: Table S3). Overall, BNPP was greatest under the small-frequent treatment compared to ambient regardless of depth.

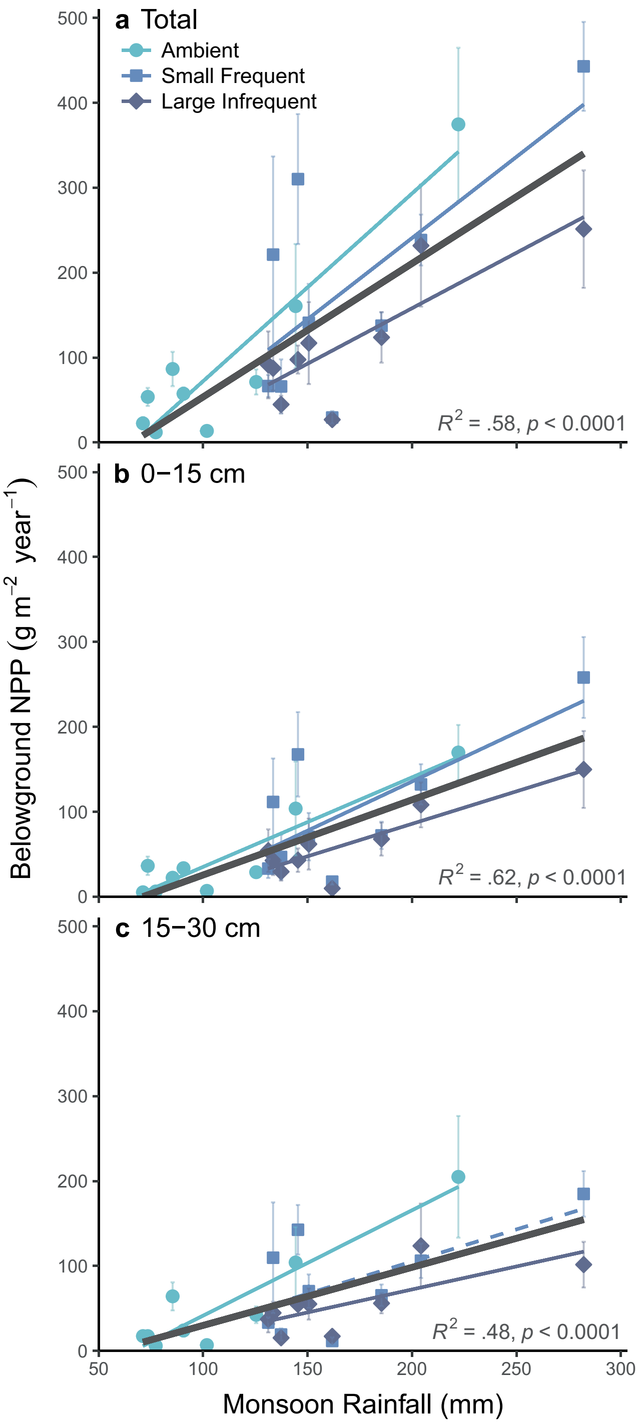

FIGURE 1 The relationship between monsoon rainfall and belowground net primary production from (a) 0–30 cm (total), (b) 0–15 cm, and (c) 15–30 cm depth measured annually from 2012 to 2020 using permanently located root ingrowth donuts. Rainfall treatments include ambient precipitation ($n = 3$), ambient precipitation plus twelve 5-mm rain events (small-frequent, $n = 5$), and ambient plus three 20-mm rain events (large-infrequent, $n = 5$) during the monsoon season (July through early- to mid-September) each year. Colored lines represent linear regressions for each treatment at each depth, with solid lines indicating statistically significant relationships ($p \leq 0.05$) and dashed lines indicating marginally significant relationships ($0.05 < p \leq 0.1$). Black lines, along with corresponding R^2 and p values, represent statistically significant regressions across all treatments within each depth. Full model statistics are provided in Appendix S1: Table S2.

Hypothesis 3. *ANPP and BNPP are uncorrelated*. Our third hypothesis was partially supported. Within treatments, although the trend was positive, we found no correlation between ANPP and BNPP in any of the individual rainfall treatments (Figure 3). Across all treatments, however, ANPP and BNPP were weakly but significantly positively correlated ($F = 5.25$, df $= 1$, 25; $r = 0.43$; $R^2 = 0.18$; $p < 0.027$). Thus, at best ANPP is a relatively weak predictor of overall variation in BNPP, but this variation is not affected by within-season rainfall variability.

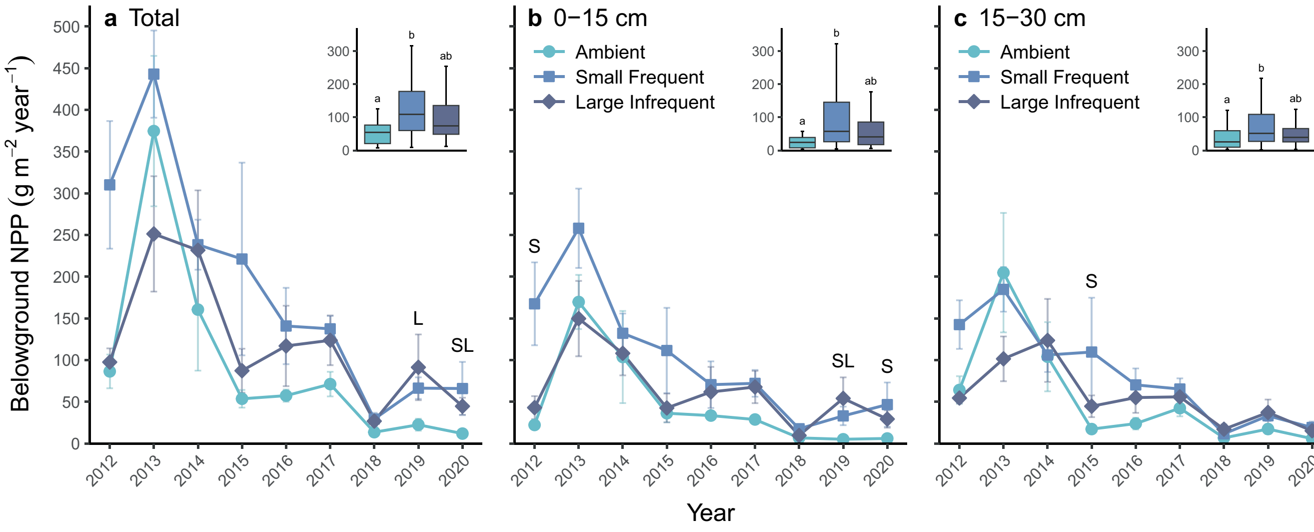

FIGURE 2 Belowground net primary production from (a) 0 to 15 cm, (b) 15 to 30 cm, and (c) 0 to 30 cm (total) combined measured annually from 2012 to 2020 using permanently located root ingrowth donuts. Rainfall treatments include ambient precipitation ($n = 3$), ambient precipitation plus twelve 5-mm rain events (small-frequent, $n = 5$), and ambient plus three 20-mm rain events (large-infrequent, $n = 5$) during the monsoon season (July through early- to mid-September) each year. Symbols indicate significant differences between small-frequent (S) and/or large-infrequent (L) rainfall treatments compared to ambient within each year based on linear mixed-effects models. Significant difference between small and large treatments occurred only in 2012. Full model statistics are provided in Appendix S1: Table S3. Insets show the 9-year mean belowground production by rainfall treatment.

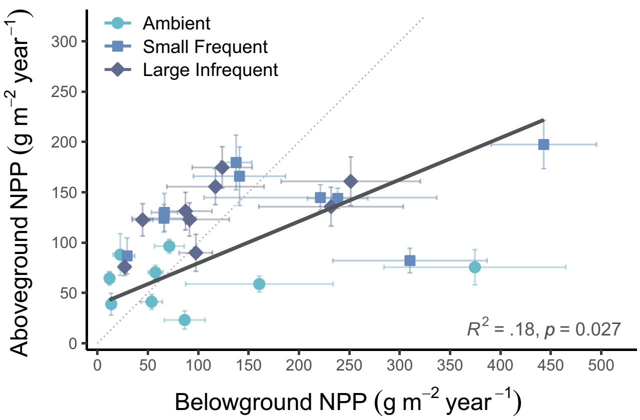

FIGURE 3 Relationship between aboveground and total belowground production under ambient precipitation ($n = 3$), ambient precipitation plus twelve 5-mm rain events (small-frequent, $n = 5$), and ambient plus three 20-mm rain events (large-infrequent, $n = 5$) rainfall treatments during the monsoon season (July through early- to mid-September) each year. Within individual treatments, relationships were weak and not statistically significant. For the ambient treatment, slope = 0.03, 95% CI (−0.15, 0.22), $t(7) = 0.42$, $p = 0.6891$, $R^2 = 0.02$, $F(1, 7) = 0.17$; for the small-frequent treatment, slope = 0.11, 95% CI (−0.13, 0.35), $t(7) = 1.12$, $p = 0.2980$, $R^2 = 0.15$, $F(1, 7) = 1.26$; and for the large-infrequent treatment, slope = 0.25, 95% CI (−0.06, 0.55), $t(7) = 1.90$, $p = 0.0995$, $R^2 = 0.34$, $F(1, 7) = 3.60$. Across all treatments, a weak but statistically significant positive relationship emerged, where slope = 1.03, 95% CI (0.13, 1.92), $t(25) = 2.35$, $p = 0.0270$, $R^2 = 0.18$, $F(1, 25) = 5.52$, as indicated by the solid black line.

DISCUSSION

We used a long-term rainfall manipulation experiment to determine the response of BNPP to within-season precipitation variability, as well as its relationship to ANPP under altered precipitation regimes. Contrary to our hypotheses, we found that total BNPP was highest, on average, in the small-frequent rainfall treatments, whereas BNPP under the large-infrequent regime rarely differed from ambient conditions. Additionally, we found few differences within years in BNPP (total, 0–15, and 15–30 cm depths) under any rainfall regime, and most differences reflected added rainfall versus ambient conditions. Furthermore, BNPP was positively correlated with ambient precipitation, but added rainfall weakened this relationship. Finally, we found a positive correlation between ANPP and BNPP across all rainfall treatments and years, but not within individual rainfall treatments. Together, our results highlight the importance of small-frequent rain events for BNPP, and that monsoon rainfall is an important driver of BNPP, but that ANPP and BNPP are weakly coupled, at best, under ambient and altered rainfall regimes.

Previous research has shown that grassland ANPP is strongly positively correlated to precipitation across sites but weakly correlated within sites over time (Huxman et al., 2004; Maurer et al., 2020 and Sala et al., 2012). Furthermore, field studies and modeling efforts suggest that increased within-season precipitation variability reduces ANPP in mesic systems and increases or has no effect on ANPP at low MAP (Brown & Collins, 2023a; Heisler-White et al., 2009; Zhang et al., 2013). Yet, few studies have investigated the long-term impacts of within-season rainfall variability on BNPP. Wilcox et al. (2015), for example, reported that the response of BNPP in C_3- and C_4-dominated systems to within-season precipitation variability was highly inconsistent among sites along a latitudinal gradient. In our study, we found that BNPP was highest, on average, in plots that received small-frequent rain events even though large events infiltrate deeper into the soil and moisture lasts longer than after small events (Bhark & Small, 2004; Brown et al., 2022; Vargas et al., 2012). Furthermore, small rain events are historically common in these dryland systems. Our results add to a growing body of work showing the positive effects of small rain events on ecophysiology (Sala & Lauenroth, 1982), primary production (Petrie et al., 2015), community composition (Brown & Collins, 2024), and diversity of biocrust communities (Fernandes et al., 2022) in drylands. Indeed, large rain events can reduce nitrogen availability in dryland soils that are already low in plant available nitrogen (Brown et al., 2022; Zhang, Biederman, et al., 2021; Zhang, Shen, et al., 2021). Therefore, altered precipitation regimes characterized by fewer, larger events under climate change may have negative consequences (lower resource availability) for ecological processes, such as primary production, despite increased soil moisture conditions in nutrient-poor dryland ecosystems.

We found that BNPP in ambient rainfall plots was positively correlated with seasonal precipitation, but that the relationship was weakened under both rainfall addition treatments. Previous studies have found variable responses of BNPP to precipitation. Across sites, BNPP decreases with mean annual precipitation in grasslands (Gherardi & Sala, 2020), but relationships within sites over time are less predictable (Brown & Collins, 2023a). For example, Hui and Jackson (2005) found no consistent response between mean annual precipitation and the belowground biomass fraction of total production across sites. Irrigation had no effect on BNPP in moderately and heavily grazed semiarid grasslands in China, whereas Fiala et al. (2009) found a positive correlation between root increment growth and precipitation in two Central European grasslands. In a fertilization experiment, BNPP saturated at lower levels of N addition than ANPP (Yang et al., 2023). Together, these results suggest a generally positive response of BNPP to precipitation, perhaps contingent upon belowground site-specific conditions including nutrient availability and soil texture.

We found that ANPP and BNPP were uncorrelated under all three rainfall regimes, but positively correlated when all treatments were combined. These results are consistent with other studies that find that ANPP and BNPP are often weakly coupled, at best (e.g., Brown & Collins, 2023a; Gao et al., 2023; Sun et al., 2021; Wang et al., 2019). In general, both carbon allocation belowground and ANPP decline with drought in grasslands (Knapp et al., 2015; Meng et al., 2022; Wu et al., 2011). Furthermore, a meta-analysis found that the response of ANPP to interannual precipitation variability was asymmetric in that ANPP increased more in wet years than it declined in dry years (Wilcox et al., 2017), whereas the response of BNPP was symmetrical (equal increases and decreases). These different responses reduce the correlation between ANPP and BNPP, which leads to a weak coupling of these processes in response to precipitation variability (Wilcox et al., 2017; Zhang, Biederman, et al., 2021; Zhang, Shen, et al., 2021). Indeed, Sun et al. (2021) suggested that aboveground production is driven more by climate whereas belowground production is more a function of vegetation and soil properties, factors that likely contribute to a weak correlation between these important carbon cycle processes.

In conclusion, based on our long-term rainfall variability experiment, we found that belowground production was highest, on average, under a small-frequent rainfall regime, even though large-infrequent rain events resulted in deeper and more persistent soil moisture (Brown et al., 2022; Vargas et al., 2012). This pattern is inconsistent with the response predicted for aboveground production based on the bucket model (Knapp et al., 2008), as well as empirical and modeling tests of that model (e.g., Heisler-White et al., 2009; Hou et al., 2021; Zhang et al., 2013; Zhang, Biederman, et al., 2021; Zhang, Shen, et al., 2021). We found that belowground production was positively related to seasonal precipitation, but despite that relationship, above- and belowground production was uncorrelated within any rainfall treatment. To our knowledge, this is the first long-term experimental test of within-season rainfall variability effects on belowground production. Our results suggest that predicted increases in extreme, but less frequent rain events will have limited effects on belowground production unless such a rainfall regime leads to a decline in seasonal soil moisture. Furthermore, the bucket model may not be applicable to belowground production in dryland systems because different factors may influence above- versus belowground responses. Clearly, further study in other systems is warranted.

Overall, our results have important implications for understanding the contributions of belowground production to the soil carbon pool. Belowground production is estimated to comprise over 50% of total NPP in grasslands (Sun et al., 2021), and it is the principal source of carbon sequestered in soils. Drylands, in particular, contribute the most to interannual variability in the global carbon budget (Ahlstrom et al., 2015; Poulter et al., 2014), but how climate change will affect the contribution of belowground production to that variability is poorly understood. Generally, belowground production is highly variable from year to year, often in response to forces in addition to precipitation. This variability confounds our ability to understand the key drivers of belowground production, especially efforts to incorporate the role of belowground production in carbon cycle models. Nevertheless, our results demonstrate that, like aboveground production, belowground production is positively correlated with seasonal precipitation, especially under a rainfall regime characterized by frequent but small rain events.

AUTHOR CONTRIBUTIONS

Scott L. Collins designed the experiment. Scott L. Collins and Renée F Brown conceived the analyses. Renée F Brown analyzed the data and produced the figures. Scott L. Collins drafted the first version of the manuscript, and both authors repeatedly edited and rewrote the text.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data are available through the Environmental Data Initiative in Collins (2021) at https://doi.org/10.6073/pasta/e38868ae3c3e11845128d2539c27520b and in Brown and Collins (2023b) at https://doi.org/10.6073/pasta/71dd9cc9409eb880fb7928faf6da80ed.

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SUPPORTING INFORMATION

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

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