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RESEARCH ARTICLE

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As above, not so below: Long-term dynamics of net primary production across a dryland transition zone

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Abstract

Drylands are key contributors to interannual variation in the terrestrial carbon sink, which has been attributed primarily to broad-scale climatic anomalies that disproportionately affect net primary production (NPP) in these ecosystems. Current knowledge around the patterns and controls of NPP is based largely on measurements of aboveground net primary production (ANPP), particularly in the context of altered precipitation regimes. Limited evidence suggests belowground net primary production (BNPP), a major input to the terrestrial carbon pool, may respond differently than ANPP to precipitation, as well as other drivers of environmental change, such as nitrogen deposition and fire. Yet long-term measurements of BNPP are rare, contributing to uncertainty in carbon cycle assessments. Here, we used 16 years of annual NPP measurements to investigate responses of ANPP and BNPP to several environmental change drivers across a grassland–shrubland transition zone in the northern Chihuahuan Desert. ANPP was positively correlated with annual precipitation across this landscape; however, this relationship was weaker within sites. BNPP, on the other hand, was weakly correlated with precipitation only in Chihuahuan Desert shrubland. Although NPP generally exhibited similar trends among sites, temporal correlations between ANPP and BNPP within sites were weak. We found chronic nitrogen enrichment stimulated ANPP, whereas a one-time prescribed burn reduced ANPP for nearly a decade. Surprisingly, BNPP was largely unaffected by these factors. Together, our results suggest that BNPP is driven by a different set of controls than ANPP. Furthermore, our findings imply belowground production cannot be inferred from aboveground measurements in dryland ecosystems. Improving understanding around the patterns and controls of dryland NPP at interannual to decadal scales is fundamentally important because of their measurable impact on the global carbon cycle. This study underscores the need for more long-term measurements of BNPP to improve assessments of the terrestrial carbon sink, particularly in the context of ongoing environmental change.

KEYWORDS
aboveground production, belowground production, carbon cycle, Chihuahuan Desert, ecotone, fire, nitrogen enrichment, precipitation

1 | INTRODUCTION

Drylands, which currently occupy 45% of the terrestrial land surface and account for 40% of global net primary production (NPP), are undergoing accelerated expansion worldwide as a consequence of anthropogenic climate and land-use change (Burrell et al., 2020; Huang et al., 2016, 2017; Prăvălie et al., 2019). These characteristically water-limited ecosystems are disproportionately impacted by large-scale climatic anomalies, such as the El Niño–Southern Oscillation, that contribute strongly to patterns of interannual variation in the terrestrial carbon sink (Ahlström et al., 2015; Houghton, 2000; Poulter et al., 2014). While other perturbations facing drylands, such as increased nitrogen deposition (Fenn et al., 2003), altered fire regimes (Aslan et al., 2018), and shrub encroachment (D'Odorico et al., 2012), also contribute to regional variation in the terrestrial carbon cycle (Keenan & Williams, 2018), considerably less is known about the longer-term implications of such disturbances in dryland ecosystems.

Despite being a key regulator of the global carbon cycle, current knowledge around the patterns and controls of dryland NPP is based largely on measurements of aboveground production, particularly in the context of altered precipitation regimes. Indeed, several broad-scale analyses have found aboveground net primary production (ANPP) to be especially sensitive to changes in mean annual precipitation in water-limited ecosystems (Hsu et al., 2012; Huxman et al., 2004; Knapp & Smith, 2001; Maurer et al., 2020), although temporal relationships between ANPP and precipitation are often weaker than spatial relationships due to legacy effects as well as local-scale vegetation and soil characteristics (Sala et al., 2012; Ukkola et al., 2021). Yet, belowground net primary production (BNPP) is the main contributor to soil organic carbon (Sokol & Bradford, 2019), which represents the largest terrestrial carbon pool (Janzen, 2004; Scharlemann et al., 2014). Consequently, BNPP represents a significant proportion of total NPP in dryland ecosystems (Gherardi & Sala, 2020). While limited evidence provided by recent meta-analyses suggests ANPP and BNPP in water-limited ecosystems exhibit dissimilar responses to changes in precipitation (Wang et al., 2022; Wilcox et al., 2017; Wu et al., 2011; J. Zhang et al., 2021), and that soil properties may play a more important role than climate in driving BNPP responses (Sun et al., 2021), long-term empirical measurements of BNPP are exceedingly rare. Yet these data are essential for strengthening connections between dryland ecosystem dynamics and the global carbon cycle.

The predominantly arid and semiarid ecosystems of the southwestern United States (US) have been especially impacted by climate change in recent decades (Friedlingstein et al., 2022), with high temporal and spatial variation in carbon storage capacity (Biederman et al., 2017). Recent studies have revealed that precipitation patterns have become increasingly variable throughout this region (Maurer et al., 2020; F. Zhang et al., 2021), with climate models projecting greater intensification of the hydrologic cycle into the future (Diffenbaugh et al., 2008; Moustakis et al., 2021). However, precipitation alone cannot fully explain year-to-year variation in carbon cycle processes, particularly over local and regional scales (Lauenroth & Sala, 1992). Atmospheric nitrogen deposition, which is strongly correlated with growing season precipitation (Báez et al., 2007), is increasing in many dryland regions as a consequence of anthropogenic activities (Fenn et al., 2003). Although nitrogen is an important limiting resource for dryland ecosystem processes (Austin et al., 2004; Hooper & Johnson, 1999; Yahdjian et al., 2011), evidence from the Sonoran and Chihuahuan Deserts suggests nitrogen enrichment may only stimulate greater ANPP in years with above average precipitation (Hall et al., 2011; Ladwig et al., 2012). Conversely, findings from semiarid Inner Mongolian grasslands indicate that BNPP declines with nitrogen addition (Bai et al., 2015; Li et al., 2011; Wang et al., 2019).

Fire is also a key driver of vegetation change in dryland ecosystems (Andela et al., 2013; Aslan et al., 2018; Hély et al., 2019; Humphrey, 1974). In Chihuahuan Desert grasslands for example, ANPP tends to recover slowly following fire (Drewa & Havstad, 2001; Gosz & Gosz, 1996; Parmenter, 2008), whereas burning has limited effects on BNPP (Burnett et al., 2012). However, fire can counteract the early stages of woody shrub encroachment in desert grasslands (Li et al., 2022; Ravi et al., 2009; Sankey et al., 2012; White, 2011), which has significant implications for regional carbon cycle dynamics (Archer et al., 2017; Barger et al., 2011). Indeed, the reduction of fine fuel loads caused by intensive livestock grazing is thought to be a primary driver of rapid shrub encroachment that occurred throughout the southwestern US in the 20th century (Archer et al., 2017; Grover & Musick, 1990; Van Auken, 2000, 2009). Consequently, fire continues to be a common management practice for preserving pastoral economies in many dryland regions (Hanan et al., 2021).

Current understanding around the patterns and controls of dryland NPP at interannual to decadal scales is relatively poor, contributing to uncertainty in assessments of the terrestrial carbon sink (Friedlingstein et al., 2022; Keenan & Williams, 2018; Niu et al., 2017). To address this knowledge gap, we used 16 years of data to explore temporal patterns of ANPP and BNPP in response to several key drivers of environmental change across a grassland–shrubland transition zone in the northern Chihuahuan Desert. We asked: (1) How does precipitation affect temporal patterns of ANPP and BNPP *within* and *among* sites? (2) How well are ANPP and BNPP correlated *within* and *among* sites? (3) How do nitrogen enrichment and fire affect temporal patterns of ANPP and BNPP *within* a site?

2 | MATERIALS AND METHODS

2.1 | Study area

This study was conducted using 16 years of data (2005–2020) from three long-term research sites situated along a grassland–shrubland transition zone in the Sevilleta National Wildlife Refuge (NWR), central New Mexico, USA (Figures S1 and S2). Here, Great Plains grassland dominated by blue grama (*Bouteloua gracilis*) transitions into Chihuahuan Desert shrubland dominated by creosote bush

(*Larrea tridentata*) along a north-to-south gradient separated by a narrow ecotone of Chihuahuan Desert grassland dominated by black grama (*Bouteloua eriopoda*; Gosz, 1993; Gosz & Gosz, 1996). Dominant species account for up to 80% of total ANPP within each of these ecoregions (Muldavin et al., 2008; Peters & Yao, 2012), and there is considerable overlap of subordinate species among ecoregions (Hochstrasser & Peters, 2004; Kröel-Dulay et al., 2004).

This dynamic region provides an ideal location for studying ecosystem responses to environmental change. Rapid encroachment of native C_3 evergreen shrubs into native perennial C_4 grasslands began in the mid to late 1800s throughout central and southern New Mexico, coinciding with the influx of large-scale cattle ranching (Gross & Dick-Peddie, 1979; Grover & Musick, 1990; Van Auken, 2000, 2009). After more than a century of historically high stocking rates and extensive overgrazing, domestic livestock were permanently excluded from the Sevilleta NWR in 1973 (Parmenter, 2008; Rand-Caplan, 2006). Unencroached grasslands have since recovered (Collins & Xia, 2015), but are periodically subjected to lightning-caused wildfires or prescribed management burns (Parmenter, 2008).

Soils in this region of the Sevilleta NWR are classified as Typic Haplocalcids formed by calcareous aeolian and alluvial deposits (Soil Survey Staff, 2019). Soil texture in the top 30 cm, where the majority of root biomass occurs (Gibbens & Lenz, 2001; Jackson et al., 1996; Kurc & Small, 2007; McCulley et al., 2004), consists of 60%–68% sand, 22%–30% silt, and 10% clay, with 10%–15% as $CaCO_3$ (Kieft et al., 1998). A petrocalcic layer, ranging from 72–80 cm beneath the soil surface in Great Plains grassland to 26–29 cm in Chihuahuan Desert shrubland, further constrains moisture infiltration and rooting depth (Buxbaum & Vanderbilt, 2007; Gibbens & Lenz, 2001; Schenk & Jackson, 2002). Atmospheric nitrogen deposition occurs primarily through wet deposition at a rate of $0.2\,g\,m^{-2}\,year^{-1}$, with 57% deposited as NH_4 and 43% deposited as NO_3 (Báez et al., 2007). Low deposition rates combined with a low abundance of nitrogen fixers in biological soil crusts (Fernandes et al., 2018, 2022) contribute to nutrient-poor soils throughout the region (Brown et al., 2022; Zak et al., 1994).

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) that include the Five Points station, located in the Chihuahuan Desert grassland and shrubland ecotone (34.3350° N, 106.7293° W, elevation 1613 m; Figure S1), and the Deep Well station, located in the Great Plains and Chihuahuan Desert grassland ecotone (34.3592° N, 106.6911° W, elevation 1600 m; Figure S1). From 1990 to 2020, mean annual water year precipitation (MAP) recorded by the Deep Well station was 233 ± 9.6 mm, with approximately 51% falling between July and September from localized convective storms driven by the North American Monsoon. Consequently, sporadic winter and spring precipitation together with monsoon rainfall create distinct spring and fall growing seasons in this region (Notaro et al., 2010). Mean annual temperature recorded over this same 31-year period was 13.7 ± 0.0°C, with monthly temperatures ranging from 25.4 ± 0.2°C in July to 1.3 ± 0.3°C in December.

2.1.1 | Plains grassland

In 1995, a long-term nitrogen fertilization experiment was established in Great Plains grassland (34.4012° N, 106.6765° W, elevation 1562 m; Figures S1 and S2a). This experiment consisted of twenty 5 × 10 m plots with 10 *fertilized* plots receiving $10\,g\,N\,m^{-2}\,year^{-1}$ applied as ammonium nitrate (NH_4NO_3) each June prior to the summer monsoon, and the remaining 10 *unfertilized* plots serving as ambient controls (Ladwig et al., 2012). In 2004, four permanently located $1\,m^2$ quadrats were established within each replicate plot, enabling nondestructive measurements of seasonal ANPP (Rudgers et al., 2019; see Section 2.2) in 80 quadrats at this site ($n_{ANPP} = 40$ per treatment) until fall 2019 when measurements were reduced to two quadrats per plot ($n_{ANPP} = 20$ per treatment). In fall 2004, root ingrowth donuts (Milchunas et al., 2005; see Section 2.3) were installed in 20 plots ($n_{BNPP} = 10$ per treatment), resulting in the first annual measurements of BNPP in 2005. Precipitation records for this site (hereafter referred to as plains grassland) were provided by the Deep Well meteorological station.

2.1.2 | Ecotone grassland

In June 2003, a prescribed fire burned approximately 1200 ha encompassing the ecotone where Great Plains and Chihuahuan Desert grasslands converge (Burnett et al., 2012). In 2004, seasonal measurements of ANPP began in 40 permanently located $1\,m^2$ quadrats in *burned* grassland (34.3583° N, 106.6878° W, elevation 1601 m; Figures S1 and S2b) as well as in *unburned* grassland located ~35 m to the west across a firebreak (34.3586° N, 106.6911° W, elevation 1601 m; Figure S1), serving as ambient controls ($n_{ANPP} = 40$ per treatment). In fall 2004, root ingrowth donuts were installed in the *burned* and *unburned* grasslands, respectively ($n_{BNPP} = 10$ per treatment), resulting in the first annual measurements of BNPP in 2005. In August 2009, a lightning-caused wildfire swept through the *unburned* grassland. Consequently, fall measurements of ANPP did not occur in these quadrats, which were later relocated to another area within the Great Plains and Chihuahuan Desert grassland ecotone that was unaffected by either the 2003 or 2009 fires (34.3363° N, 106.7019° W, elevation 1620 m; Figure S1). In spring 2010, seasonal measurements of ANPP were reduced ($n_{ANPP} = 30$ per treatment) and in spring 2017, ANPP measurements were not collected. In spring 2019, seasonal measurements of ANPP ceased in *burned* grassland. Precipitation records for this site (hereafter referred to as ecotone grassland) were provided by the Deep Well meteorological station.

2.1.3 | Desert shrubland

In Chihuahuan Desert shrubland (34.3331° N, 106.7350° W, elevation 1611 m; Figures S1 and S2c), seasonal measurements of ANPP began in 1999 in four permanently located $1\,m^2$ quadrats that were established within four $5\,m^2$ plots on the cardinal points along the

perimeter of five 200 m diameter small mammal trapping webs (Muldavin et al., 2008; Parmenter et al., 2003). In spring 2004, seasonal measurements of ANPP were reduced to two quadrats per plot in each of the five webs ($n_{ANPP}=40$). In fall 2004, root ingrowth donuts were installed between two of the trapping webs ($n_{BNPP}=10$), resulting in the first annual measurements of BNPP in 2005. Precipitation records for this site (hereafter referred to as desert shrubland) were provided by the Five Points meteorological station.

2.2 | Aboveground NPP

Aboveground NPP was determined using a nondestructive allometric scaling approach based on height and cover measurements of individual plants recorded in permanently located 1 m^2 quadrats in each of the three study sites during the spring (April–May) and fall (September–October) growing seasons (Muldavin et al., 2008). 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 from adjacent areas (Rudgers et al., 2019). Annual ANPP per quadrat was calculated as the sum of peak seasonal (spring or fall) ANPP for each species.

2.3 | Belowground NPP

Permanently located root ingrowth donuts (Milchunas et al., 2005) were used to estimate annual BNPP *within* each of the three sites from 0 to 30 cm in depth, where moisture infiltration is highest and most roots are concentrated (Gibbens & Lenz, 2001; Jackson et al., 1996; Kurc & Small, 2007; McCulley et al., 2004; Schenk & Jackson, 2002). All methods used to estimate BNPP have their biases, including the potential to underestimate production as well as the secondary effects of soil disturbance (Neill, 1992; Tierney & Fahey, 2007; Zhou et al., 2012). Nevertheless, root ingrowth donuts have been determined to provide conservative, but reliable and repeatable comparative estimates of BNPP with minimal soil disturbance (Milchunas, 2009). Root ingrowth donuts were 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, a 15.2 cm diameter by 30 cm tall polyvinyl chloride (PVC) cylinder was inserted into the center of the hole and filled with sandbags to hold it in place. Sieved soil (2 mm mesh) was then added to the space between the PVC cylinder and the plastic mesh, creating a donut-shaped cylinder of root-free soil into which roots can grow. At the conclusion of each successive fall growing season, this cylinder of soil was harvested, and a fresh batch of sieved root-free soil obtained from the surrounding area was used to reconstruct the root ingrowth donut for the next annual harvest. Following harvests, soils were passed through a 2 mm sieve and roots were floated in water for collection. Roots were subsequently dried at 60°C for 48 h and weighed. To calculate BNPP, root weights were divided by the area of the root ingrowth donut and scaled up to 1 m^2 to enable comparisons with ANPP (Diabate et al., 2018).

2.4 | Statistical analyses

In this study, we analyzed 16 years of data (2005–2020), reflecting the period during which both ANPP and BNPP data were collected from all three sites. To determine *within*-site responses of ANPP and BNPP to nitrogen enrichment and fire in the plains and ecotone grasslands, respectively, we constructed repeated measures linear mixed-effects models for each site using the *nlme* package in *R* (Pinheiro et al., 2020), where the interaction between year and treatment was a fixed effect and sampling location, which included an appropriate nesting structure to match the experimental design of each site, was a random effect. Models also included a continuous first-order autoregressive correlation structure to account for temporal autocorrelation. NPP data were natural log transformed to satisfy assumptions of normality (evaluated using Q–Q plots) and homoscedasticity (evaluated by plotting residuals against fitted values). Post-hoc Tukey's honest significant difference pairwise comparisons were used to assess differences in treatment effects over time, which were considered statistically significant when $p \leq .05$. Pearson correlations were used to investigate relationships between NPP and annual water year precipitation as well as between ANPP and BNPP *within* and *among* sites. All analyses were conducted using *R* version 3.6.3 (R Core Team, 2020).

3 | RESULTS

Mean annual NPP over our 16-year study was generally low but exhibited moderate to high interannual variation (Figure 1; Table 1). ANPP ranged from 97.3 ± 8.9 g m^{-2} in *burned* ecotone grassland to 142.6 ± 17.5 g m^{-2} in *fertilized* plains grassland, which also had the highest temporal variability in ANPP (Table 1). BNPP was lower than ANPP in most years, ranging from 70.1 ± 11.2 g m^{-2} in *burned* ecotone grassland to 86.1 ± 17.2 g m^{-2} in *unfertilized* plains grassland (Figures 1 and 4; Table S1). BNPP was also far less temporally and spatially consistent than ANPP. This was especially apparent in desert shrubland, where temporal variability in ANPP was relatively low (Figure 1c) but exhibited the highest temporal variability in BNPP compared to other sites (Figure 1f; Table 1).

3.1 | How does precipitation affect temporal patterns of NPP *within* and *among* sites?

Precipitation over our 16-year study generally tracked the longer-term regional climate record (Figure 2). MAP recorded within our study region was 229.4 ± 9.5 mm, or ~2% less than the long-term mean. *Within* sites, ANPP was significantly correlated with annual

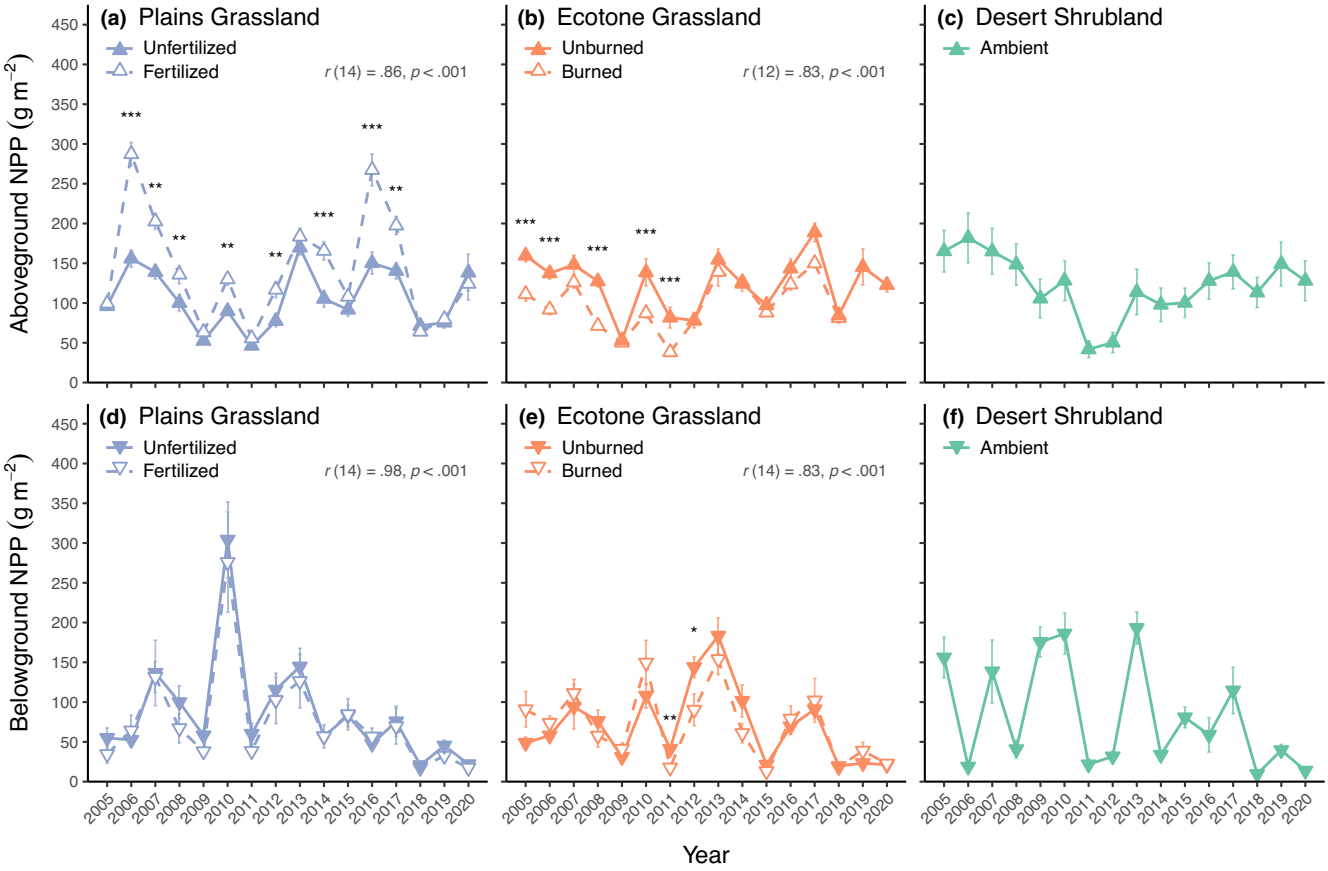

FIGURE 1 Sixteen years (2005–2020) of mean annual above- (a–c) and belowground (d–f) net primary production (NPP; g m^{-2}) in three long-term research sites situated along a grassland–shrubland transition zone, with plains grassland in blue, ecotone grassland in orange, and desert shrubland in green. Solid lines and filled points reflect NPP in the ambient controls *within* each of the three sites, whereas dashed lines and hollow points reflect NPP in the *fertilized* (10 g N m^{-2} year^{-1}) and *burned* (in 2003) treatments in the plains and ecotone grasslands, respectively. Error bars indicate standard errors of the means. Asterisks indicate significant *within*-site differences by year, where ***$p \leq .001$, **$p \leq .01$, *$p \leq .05$. Pearson's r(df) and p-values reflect the strength and significance of the overall temporal correlation between treatments *within* the two grassland sites. Additional summary statistics are provided in Table 1. [Colour figure can be viewed at wileyonlinelibrary.com]

precipitation in both *unburned* and *burned* ecotone grassland, but not in plains grassland (Figure 3a; Table 1; Table S1). ANPP in desert shrubland exhibited the strongest *within*-site temporal correlation with annual precipitation (Figure 3a; Table 1). Desert shrubland was also the only site across the transition zone where BNPP exhibited a weak, but significant correlation with annual precipitation (Figure 3b; Table 1). Across the landscape, ANPP was significantly, but weakly correlated with annual precipitation (Figure 3a); however, we found no equivalent correlation between BNPP and annual precipitation *among* sites (Figure 3b).

3.2 | How are above- and belowground NPP correlated *within* and *among* sites?

Overall, *within*-site temporal correlations between ANPP and BNPP were generally weak to nonexistent except in *burned* ecotone grassland (Figure 4; Table 2). Across the landscape, we found ANPP to be significantly correlated *among* ambient controls in all three sites (i.e., *unfertilized* plains grassland, *unburned* ecotone grassland, and desert shrubland; Figure 5). In other words, ANPP generally exhibited similar trends *among* sites each year, with the strongest correlations occurring between the two grasslands as well as between ecotone grassland and desert shrubland. BNPP *among* ambient controls was not as well correlated at the landscape scale, with only the two grassland sites and the plains grassland and desert shrubland exhibiting similar significant trends (Figure 5).

3.3 | How do nitrogen enrichment and fire affect temporal patterns of NPP *within* a site?

Annual nitrogen fertilization resulted in significantly greater ANPP in plains grassland in 8 of the 16 years (Figure 1a), with *fertilized* plains grassland exhibiting the greatest overall ANPP *among* all sites over our study period (Table 1). In contrast, BNPP was highly correlated between *unfertilized* and *fertilized* treatments in plains grassland and not significantly impacted by nitrogen fertilization

TABLE 1 Summary statistics of above- and belowground net primary production (NPP; $g\,m^{-2}\,year^{-1}$) *within* each site and treatment (also, see Figure 1). Means ± standard errors (SEs) reflect NPP over the 16-year study (2005–2020), whereas minimum (min) and maximum (max) values reflect the lowest and highest mean annual NPP observed over the study period. Coefficients of variation (CV; %) reflect *within*-treatment interannual variability in NPP. Pearson's *r* values indicate the strength and directionality of overall temporal correlations between NPP and water year precipitation, and R^2 values indicate the proportion of variance in NPP explained by precipitation (also, see Figure 3). Degrees of freedom (df) for Pearson's *r* was 14, except for aboveground NPP in *burned* ecotone grassland, where df was 12.

			Net primary production				Precipitation		
			Mean ± SE	Min ± SE	Max ± SE	CV			
	Site	Treatment	$g\,m^{-2}\,year^{-1}$	$g\,m^{-2}\,year^{-1}$	$g\,m^{-2}\,year^{-1}$	%	*r*	R^2	*p*-Value
Aboveground	Plains grassland	Unfertilized	106.2 ± 9.5	46.3 ± 4.9	169.8 ± 9.8	35.9	.47	.22	.067
		Fertilized	142.6 ± 17.5	55.7 ± 4.9	287.3 ± 14.5	49.1	.36	.13	.177
	Ecotone grassland	Unburned	124.1 ± 9.0	53.3 ± 3.6	189.0 ± 11.7	29.0	**.60**	**.36**	**≤.05**
		Burned	97.3 ± 8.9	38.1 ± 3.9	150.0 ± 5.4	34.1	**.68**	**.46**	**≤.01**
	Desert shrubland	Ambient	122.3 ± 9.6	41.9 ± 10.4	181.9 ± 31.2	31.4	**.82**	**.66**	**≤.001**
Belowground	Plains grassland	Unfertilized	86.1 ± 17.2	20.7 ± 4.8	304.2 ± 47.7	79.8	−.12	.01	.664
		Fertilized	75.9 ± 15.9	17.4 ± 4.4	276.0 ± 63.2	83.9	−.09	.01	.727
	Ecotone grassland	Unburned	70.7 ± 12.0	19.5 ± 3.6	183.3 ± 22.6	67.6	.17	.03	.541
		Burned	70.1 ± 11.2	13.1 ± 2.2	153.9 ± 19.2	63.8	.40	.16	.121
	Desert shrubland	Ambient	82.0 ± 16.8	9.6 ± 2.5	193.1 ± 20.4	82.2	**.49**	**.24**	**≤.05**

Note: Significant relationships ($p \leq .05$) are in bold font.

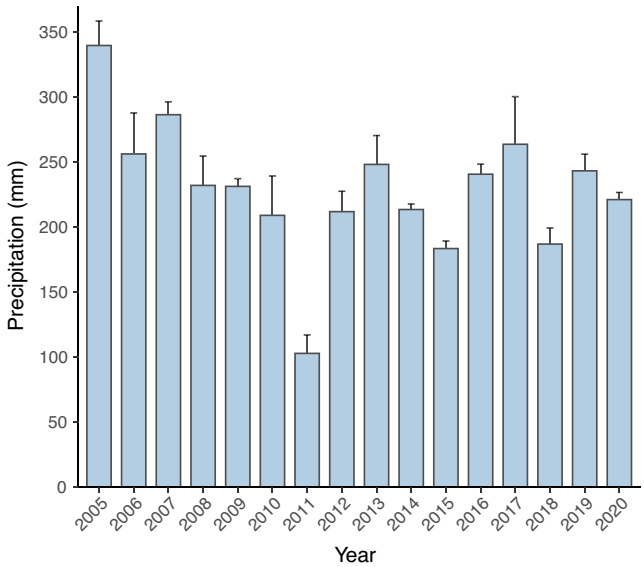

FIGURE 2 Mean annual precipitation (mm) per water year (October–September) recorded by both the Deep Well and Five Points meteorological stations during the 16-year study (2005–2020). Error bars indicate standard errors of the means. [Colour figure can be viewed at wileyonlinelibrary.com]

(Figure 1d). Overall, ANPP was lowest in *burned* ecotone grassland (Table 1) following a one-time prescribed management burn, taking 9 years to recover to unburned levels of production (Figure 1b). Like nitrogen fertilization in plains grassland, fire had little impact on BNPP in ecotone grassland. The only notable differences occurred 8–9 years following the prescribed burn, when BNPP was significantly lower in the *burned* treatment than in the *unburned* treatment (Figure 1e).

4 | DISCUSSION

We used 16 years of empirical data to explore spatiotemporal dynamics of ANPP and BNPP across a grassland–shrubland transition zone in the northern Chihuahuan Desert. Characteristic of dryland ecosystems, NPP varied through time and space, with BNPP exhibiting consistently higher variation than ANPP. Although ANPP was significantly correlated with annual precipitation at the landscape scale, this relationship was less consistent within sites. BNPP was generally unaffected by any of the environmental change drivers we explored here, other than exhibiting a significant response to annual precipitation in desert shrubland. Moreover, we found the temporal relationship between ANPP and BNPP to be extremely weak overall. Chronic nitrogen enrichment tended to stimulate aboveground production, resulting in significantly greater ANPP in plains grassland during half of the years in our study, as well as the greatest overall ANPP across the landscape. In contrast, fire had strong negative impacts on ANPP in ecotone grassland, which took 9 years to return to prefire levels of production following a one-time prescribed management burn.

We found ANPP to be significantly correlated with annual precipitation in ecotone grassland, regardless of burn status, as well as in desert shrubland. Our results complement earlier findings that ANPP in both Chihuahuan Desert grassland and shrubland was positively correlated with annual precipitation (Muldavin et al., 2008). NPP in desert shrubland exhibited the strongest overall relationship with precipitation, which in the context of predicted increases in precipitation variability, has been shown to promote production in desert shrubland at the expense of desert grassland (Gherardi & Sala, 2015). Although a strong spatial relationship exists between mean annual

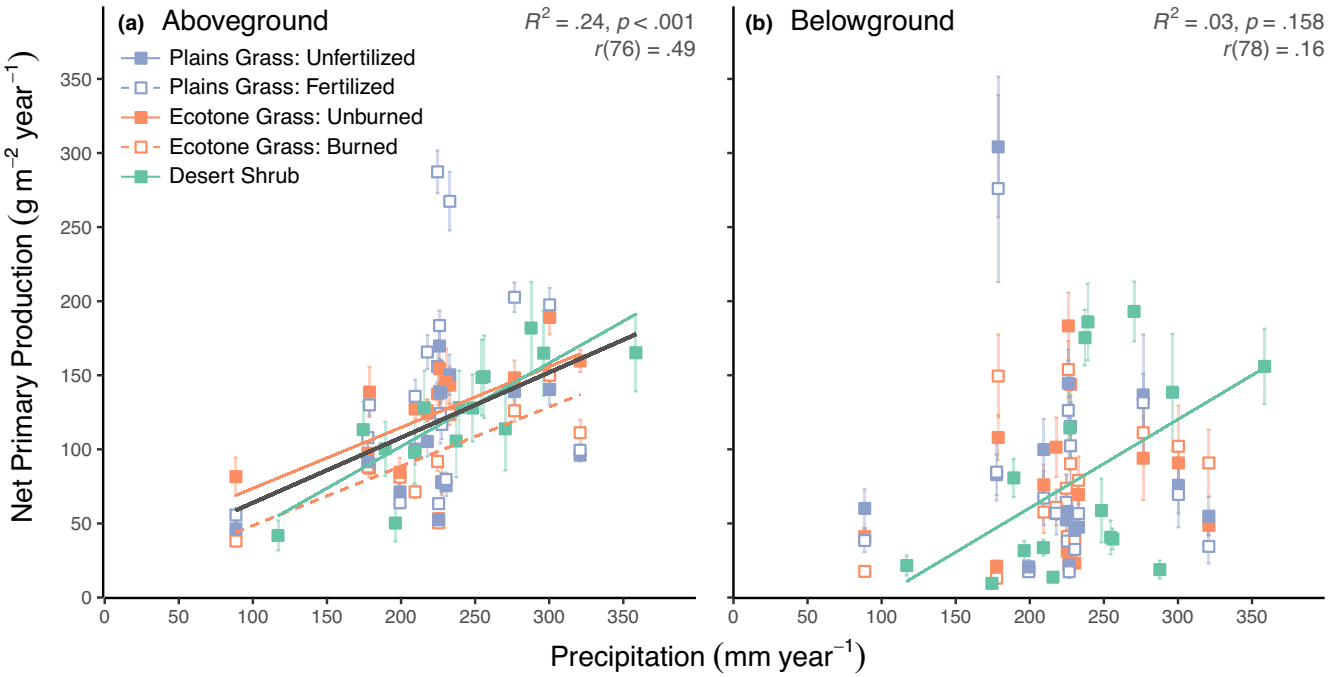

FIGURE 3 Relationships between (a) above- and (b) belowground net primary production (NPP; g m^{-2} year^{-1}) and water year precipitation (mm year^{-1}) across a grassland–shrubland transition zone over the 16-year study (2005–2020), with plains grassland in blue, ecotone grassland in orange, and desert shrubland in green. Filled points represent ambient controls in all three sites, whereas hollow points represent *fertilized* (10 g N m^{-2} year^{-1}) and *burned* (in 2003) treatments in the plains and ecotone grasslands, respectively. Error bars indicate standard errors of the means. Solid linear regression lines reflect significant temporal correlations between NPP and precipitation *within* ambient controls, whereas dashed linear regression lines reflect significant temporal correlations *within* the *fertilized* and *burned* treatments (refer to Table 1 for corresponding *within*-treatment statistics). R^2 values indicate the proportion of variance in NPP explained by precipitation *among* sites over time, with Pearson's r(df) and p-values indicating the strength and significance ($p \leq .05$) of these relationships. Solid gray regression lines reflect significant correlations *among* sites over time. [Colour figure can be viewed at wileyonlinelibrary.com]

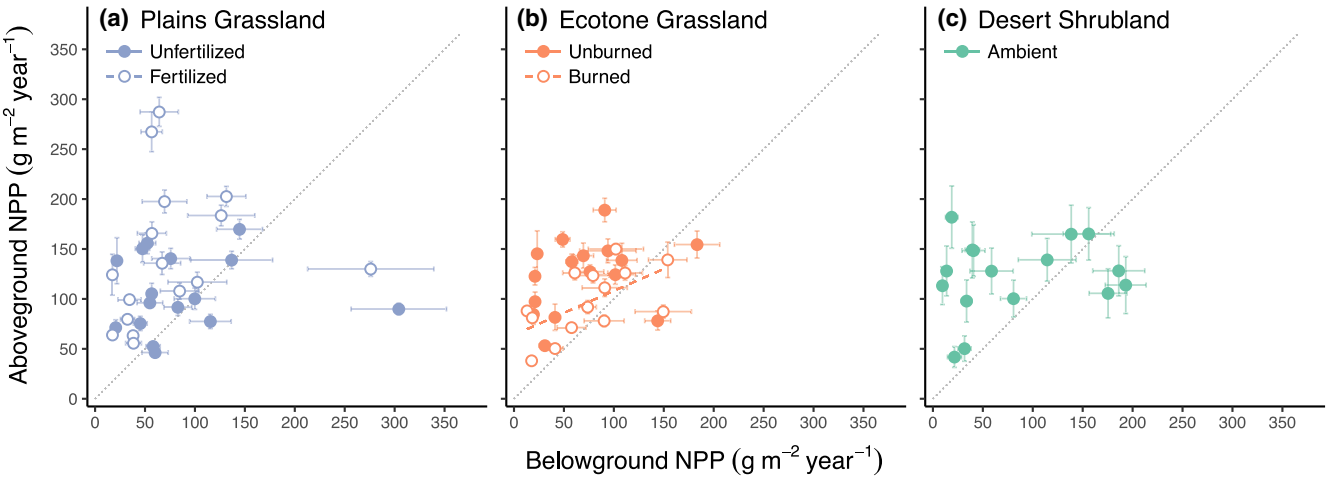

FIGURE 4 Relationships between above- and belowground net primary production (NPP; g m^{-2} year^{-1}) *within* sites across a grassland–shrubland transition zone over the 16-year study (2005–2020), with plains grassland in blue (a), ecotone grassland in orange (b), and desert shrubland in green (c). Filled points represent ambient controls in all three sites, whereas hollow points represent *fertilized* (10 g N m^{-2} year^{-1}) and *burned* (in 2003) treatments in the plains and ecotone grasslands, respectively. Error bars indicate standard errors of the means. Linear regression lines indicate significant ($p \leq .05$) *within*-site relationships (refer to Table 2 for corresponding summary statistics). Dotted gray lines indicate the 1:1 relationship between above- and belowground NPP *within* each site. [Colour figure can be viewed at wileyonlinelibrary.com]

ANPP and mean annual precipitation (Huxman et al., 2004; Knapp & Smith, 2001; Sala et al., 1988), temporal relationships between ANPP and precipitation at local and regional scales are often much weaker and less predictable (Lauenroth & Sala, 1992; Maurer et al., 2020; Sala et al., 2012; Ukkola et al., 2021) as we also found in this study. A previous analysis found no correlation between ANPP and mean

TABLE 2 Relationships between above- and belowground net primary production (NPP; $g\,m^{-2}\,year^{-1}$) over the 16-year study (2005–2020) *within* each site and treatment (also, see Figure 4). Pearson's *r* values indicate the strength and directionality of overall temporal correlations between above- and belowground NPP, and R^2 values indicate the proportion of variance in aboveground NPP explained by belowground NPP and vice versa. Degrees of freedom (df) for Pearson's *r* was 14, except for aboveground NPP in *burned* ecotone grassland, where df was 12.

Site	Treatment	*r*	R^2	*p*-Value
Plains grassland	Unfertilized	.05	.00	.845
	Fertilized	.20	.04	.452
Ecotone grassland	Unburned	.31	.10	.242
	Burned	**.60**	**.36**	**≤.05**
Desert shrubland	Ambient	.21	.04	.439

Note: Significant relationships ($p \leq .05$) are in bold font.

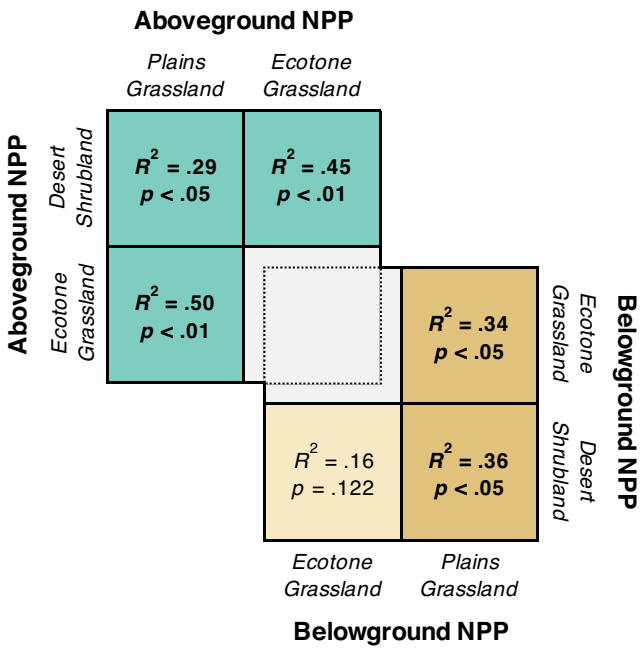

FIGURE 5 Relationships between above- (green) and belowground (brown) net primary production (NPP) *among* ambient controls in all three sites over the 16-year study (2005–2020). Pearson's *r*(df) and *p*-values indicate the strength and significance ($p \leq .05$) of these relationships, with significant relationships indicated by bold text and darker shading. [Colour figure can be viewed at wileyonlinelibrary.com]

annual precipitation in our study area between 1999 and 2008 (Sala et al., 2012), which suggests the importance of long-term studies, especially in drylands where interannual variability in precipitation tends to be high. Surprisingly, BNPP did not exhibit a significant or consistent relationship with precipitation across this transition zone, despite limited evidence from other terrestrial ecosystems showing otherwise (Wang et al., 2022; Wilcox et al., 2015, 2017; Wu et al., 2011). However, the spatial scale of our study was relatively limited in comparison.

We found little evidence that BNPP was temporally correlated with ANPP within a site, consistent with earlier findings in this region (Burnett et al., 2012; Ladwig et al., 2012). Across the landscape, we found temporal variability in ANPP was generally higher in grasslands compared to shrubland, supporting earlier findings (Knapp & Smith, 2001). In contrast, temporal variation of BNPP was quite high in all sites, especially in desert shrubland, which exhibited some of the highest temporal variability in BNPP across the landscape. Although ANPP exhibited similar trends across the landscape, the spatial relationship between plains grassland and desert shrubland was weaker and somewhat less significant than relationships among the other sites. Given that plains grassland and desert shrubland were located furthest away from each other suggests there may be a distance limitation at which the spatial correlation of ANPP breaks down across this grassland–shrubland transition zone. This may be attributed to high spatial variability in precipitation (Petrie et al., 2014). Although the strongest ANPP relationships occurred among sites situated closer to each other, this was not the case for BNPP, which was less temporally and spatially correlated overall. This may be due to differences in soil texture (Kieft et al., 1998) and depth to the petrocalcic layer (Buxbaum & Vanderbilt, 2007). Indeed, emerging evidence suggests that edaphic characteristics, such as soil texture and pH, may exert a stronger influence on BNPP in dryland ecosystems (Sun et al., 2021; Wang et al., 2021).

The positive effects of nitrogen enrichment on ANPP were not surprising given that nitrogen is second to water as the most important limiting resource for ecological processes in dryland ecosystems (Austin et al., 2004; Yahdjian et al., 2011). Although previous studies have found Chihuahuan Desert grassland to be steadily encroaching northward into Great Plains grassland (Collins et al., 2020; Collins & Xia, 2015; Peters & Yao, 2012), others have shown nitrogen enrichment tends to favor plains grassland over desert grassland (Báez et al., 2007; Collins et al., 2010; Ladwig et al., 2012). Our results suggest that Great Plains grassland may respond favorably to increased rates of atmospheric nitrogen deposition in the future, potentially counteracting encroachment trends in this region. BNPP, on the other hand, was generally unaffected by nitrogen enrichment, extending earlier findings that nitrogen enrichment does not impact BNPP in this system (Ladwig et al., 2012). Our results also complement a few other short-term studies conducted in cold semiarid grasslands of Inner Mongolia that found nitrogen enrichment had no impact on BNPP, even when water limitation was alleviated (Gao et al., 2011; Gong et al., 2015; Li et al., 2011).

It has been hypothesized that as water availability becomes less limiting to dryland ecological processes, ecosystem sensitivity to precipitation decreases, and the limitation of other resources increases (Huxman et al., 2004). However, plains grassland was the only site within our study area where ANPP was not significantly correlated with annual precipitation. Furthermore, we found no evidence to support the hypothesis that nitrogen limitation is alleviated only in years with above average precipitation (Ladwig et al., 2012). While outside the scope of this study, the timing and magnitude of rain events can play an important role with respect to nitrogen

limitation of NPP in desert grasslands. Although rain events have become smaller and more frequent in this region over the past century, infrequent large rain events during the growing season significantly influence total precipitation amounts (Petrie et al., 2014), and have been found to significantly reduce plant available nitrogen that would otherwise be stimulated by small frequent events (Brown et al., 2022). Moreover, small frequent and large infrequent growing season rain events have been found to result in comparable rates of ANPP, and it is only under nitrogen enrichment that large infrequent rains significantly increase ANPP over ambient conditions, albeit at the cost of reducing the abundance of the dominant species (Brown, 2022).

A prescribed fire negatively impacted ANPP, but not BNPP, for nearly a decade in ecotone grassland where Chihuahuan Desert and Great Plains grasslands converge. Although fire is a common management practice in semiarid grasslands, our results are consistent with earlier studies that found fire to have long-term detrimental impacts in Chihuahuan Desert grassland, which is an important source of forage grasses for wildlife in this region (Drewa & Havstad, 2001; Gosz & Gosz, 1996; Parmenter, 2008). Yet, whereas Chihuahuan Desert grassland is especially sensitive to fire, Great Plains grassland has been found to recover quickly (Collins et al., 2020; Ladwig et al., 2014; Parmenter, 2008). The susceptibility of this particular ecotone to fire has likely resulted in past fluctuations between grassland and shrubland states (Humphrey, 1974), influencing the carbon sequestration capacity of the dominant ecosystems in this region (Petrie et al., 2015). While many have written about the broad-scale implications of woody shrub encroachment (e.g., Archer et al., 2017; Barger et al., 2011; D'Odorico et al., 2012; Knapp et al., 2008), our study suggests that increased fire frequency, either from natural causes or as a management practice, could alternately shift this inherently dynamic region from Chihuahuan Desert grassland to Great Plains grassland. While fire has been found to reduce the establishment of young shrubs in this ecotone (Li et al., 2022), our results together with previous work suggest that prescribed fires are not an effective management strategy in natural arid and semiarid grasslands, particularly in the absence of grazing by domestic livestock (Liu et al., 2022).

Terrestrial ecosystems sequester nearly one-third of anthropogenic CO_2 emissions through NPP (Ahlström et al., 2015; Friedlingstein et al., 2022; Keenan & Williams, 2018). Given that dryland ecosystems are expected to comprise half of the terrestrial surface by the end of this century (Huang et al., 2016), improving understanding around the patterns and controls of NPP in these ecosystems is fundamentally important because of the measurable impact they have on the global carbon cycle. Our study uses the longest known dataset of empirical measurements of above- and belowground production in a dryland region to demonstrate that BNPP may be controlled by a different set of drivers than ANPP, such as edaphic characteristics, and that the effects of environmental change may differentially impact dryland grasslands and shrublands. Consequently, estimates of carbon storage cannot be inferred solely from ANPP measurements. We found that BNPP exhibits greater temporal and spatial variation than ANPP, which likely contributes substantially to variation in the terrestrial carbon sink. This study underscores the need for additional long-term empirical measurements, particularly of BNPP, given that it represents the main source of soil organic matter for carbon storage and sequestration (Sokol & Bradford, 2019). Given that BNPP represents a significant proportion of total NPP in dryland ecosystems, changes in BNPP would undoubtedly result in profound effects on the terrestrial carbon sink.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

All above- and belowground NPP data that support the findings of this study are openly available under a Creative Commons Attribution 4.0 International (CC BY 4.0) license from the Environmental Data Initiative Repository (EDI) at https://doi.org/10.6073/pasta/6359b205829aa232f9479ac2e27eb503 (Brown & Collins, 2022). Meteorological data used in this study are also openly available from EDI at https://doi.org/10.6073/pasta/1cbc37ae4d40b3844b5e4be9f6f18073 (Moore, 2021).

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REFERENCES

Ahlström, A., Raupach, M. R., Schurgers, G., Smith, B., Arneth, A., Jung, M., Reichstein, M., Canadell, J. G., Friedlingstein, P., Jain, A. K., Kato, E., Poulter, B., Sitch, S., Stocker, B. D., Viovy, N., Wang, Y. P., Wiltshire, A., Zaehle, S., & Zeng, N. (2015). The dominant role of semi-arid ecosystems in the trend and variability of the land CO_2 sink. *Science*, *348*(6237), 895–899. https://doi.org/10.1126/science.aaa1668

Andela, N., Liu, Y. Y., van Dijk, A. I. J. M., de Jeu, R. A. M., & McVicar, T. R. (2013). Global changes in dryland vegetation dynamics (1988-2008) assessed by satellite remote sensing: Comparing a new passive microwave vegetation density record with reflective greenness data. *Biogeosciences*, *10*(10), 6657–6676. https://doi.org/10.5194/bg-10-6657-2013

Archer, S. R., Andersen, E. M., Predick, K. I., Schwinning, S., Steidl, R. J., & Woods, S. R. (2017). Woody Plant encroachment: Causes and consequences. In D. D. Briske (Ed.), *Rangeland systems* (pp. 25–84). Springer International Publishing. https://doi.org/10.1007/978-3-319-46709-2_2

Aslan, C. E., Samberg, L., Dickson, B. G., & Gray, M. E. (2018). Management thresholds stemming from altered fire dynamics in present-day arid and semi-arid environments. *Journal of Environmental Management*, *227*, 87–94. https://doi.org/10.1016/j.jenvman.2018.08.079

Austin, A. T., Yahdjian, L., Stark, J. M., Belnap, J., Porporato, A., Norton, U., Ravetta, D. A., & Schaeffer, S. M. (2004). Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia*, *141*(2), 221–235. https://doi.org/10.1007/s00442-004-1519-1

Báez, S., Fargione, J., Moore, D. I., Collins, S. L., & Gosz, J. R. (2007). Atmospheric nitrogen deposition in the northern Chihuahuan Desert: Temporal trends and potential consequences. *Journal of Arid Environments*, *68*(4), 640–651. https://doi.org/10.1016/j.jaridenv.2006.06.011

Bai, W., Guo, D., Tian, Q., Liu, N., Cheng, W., Li, L., & Zhang, W.-H. (2015). Differential responses of grasses and forbs led to marked reduction in below-ground productivity in temperate steppe following chronic N deposition. *Journal of Ecology*, *103*(6), 1570–1579. https://doi.org/10.1111/1365-2745.12468

Barger, N. N., Archer, S. R., Campbell, J. L., Huang, C., Morton, J. A., & Knapp, A. K. (2011). Woody plant proliferation in north American drylands: A synthesis of impacts on ecosystem carbon balance. *Journal of Geophysical Research: Biogeosciences*, *116*(G4), G00K07. https://doi.org/10.1029/2010JG001506

Biederman, J. A., Scott, R. L., Bell, T. W., Bowling, D. R., Dore, S., Garatuza-Payan, J., Kolb, T. E., Krishnan, P., Krofcheck, D. J., Litvak, M. E., Maurer, G. E., Meyers, T. P., Oechel, W. C., Papuga, S. A., Ponce-Campos, G. E., Rodriguez, J. C., Smith, W. K., Vargas, R., Watts, C. J., … Goulden, M. L. (2017). CO2 exchange and evapotranspiration across dryland ecosystems of southwestern North America. *Global Change Biology*, *23*(10), 4204–4221. https://doi.org/10.1111/gcb.13686

Brown, R. F. (2022). *Above- and belowground responses to environmental change in the northern Chihuahuan Desert* (Publication No. 29398011) [Doctoral dissertation, University of New Mexico]. ProQuest Dissertations and Theses Global. https://www.proquest.com/docview/2780013042

Brown, R. F., & Collins, S. L. (2022). *Long-term above- and belowground net primary production (NPP) measurements from a grassland-shrubland transition zone in the Sevilleta National Wildlife Refuge, New Mexico, USA* [data set]. Environmental Data Initiative. https://doi.org/10.6073/PASTA/6359B205829AA232F9479AC2E27EB503

Brown, R. F., Sala, O. E., Sinsabaugh, R. L., & Collins, S. L. (2022). Temporal effects of monsoon rainfall pulses on plant available nitrogen in a Chihuahuan Desert grassland. *Journal of Geophysical Research: Biogeosciences*, *127*(6), e2022JG006938. https://doi.org/10.1029/2022JG006938

Burnett, S. A., Hattey, J. A., Johnson, J. E., Swann, A. L., Moore, D. I., & Collins, S. L. (2012). Effects of fire on belowground biomass in Chihuahuan desert grassland. *Ecosphere*, *3*(11), 107. https://doi.org/10.1890/ES12-00248.1

Burrell, A. L., Evans, J. P., & De Kauwe, M. G. (2020). Anthropogenic climate change has driven over 5 million km^2 of drylands towards desertification. *Nature Communications*, *11*(1), 3853. https://doi.org/10.1038/s41467-020-17710-7

Buxbaum, C. A. Z., & Vanderbilt, K. L. (2007). Soil heterogeneity and the distribution of desert and steppe plant species across a desert-grassland ecotone. *Journal of Arid Environments*, *69*(4), 617–632. https://doi.org/10.1016/j.jaridenv.2006.11.017

Collins, S. L., Chung, Y. A., Baur, L. E., Hallmark, A. J., Ohlert, T. J., & Rudgers, J. A. (2020). Press–pulse interactions and long-term community dynamics in a Chihuahuan Desert grassland. *Journal of Vegetation Science*, *31*(5), 722–732. https://doi.org/10.1111/jvs.12881

Collins, S. L., Fargione, J. E., Crenshaw, C. L., Nonaka, E., Elliott, J. R., Xia, Y., & Pockman, W. T. (2010). Rapid plant community responses during the summer monsoon to nighttime warming in a northern Chihuahuan Desert grassland. *Journal of Arid Environments*, *74*(5), 611–617. https://doi.org/10.1016/j.jaridenv.2009.10.005

Collins, S. L., & Xia, Y. (2015). Long-term dynamics and hotspots of change in a desert grassland plant community. *The American Naturalist*, *185*(2), E30–E43. https://doi.org/10.1086/679315

Diabate, B., Wang, X., Gao, Y., Yu, P., Wu, Z., Zhou, D., & Yang, H. (2018). Tillage and haymaking practices speed up belowground net productivity restoration in the degraded Songnen grassland. *Soil and Tillage Research*, *175*, 62–70. https://doi.org/10.1016/j.still.2017.08.003

Diffenbaugh, N. S., Giorgi, F., & Pal, J. S. (2008). Climate change hotspots in the United States. *Geophysical Research Letters*, *35*(16), L16709. https://doi.org/10.1029/2008gl035075

D'Odorico, P., Okin, G. S., & Bestelmeyer, B. T. (2012). A synthetic review of feedbacks and drivers of shrub encroachment in arid grasslands. *Ecohydrology*, *5*(5), 520–530. https://doi.org/10.1002/eco.259

Drewa, P. B., & Havstad, K. M. (2001). Effects of fire, grazing, and the presence of shrubs on Chihuahuan Desert grasslands. *Journal of Arid Environments*, *48*(4), 429–443. https://doi.org/10.1006/jare.2000.0769

Fenn, M. E., Haeuber, R., Tonnesen, G. S., Baron, J. S., Grossman-Clarke, S., Hope, D., Jaffe, D. A., Copeland, S., Geiser, L., Rueth, H. M., & Sickman, J. O. (2003). Nitrogen emissions, deposition, and monitoring in the western United States. *Bioscience*, *53*(4), 391–403. https://doi.org/10.1641/0006-3568(2003)053[0391:NEDAMI]2.0.CO;2

Fernandes, V. M. C., Machado de Lima, N. M., Roush, D., Rudgers, J. A., Collins, S. L., & Garcia-Pichel, F. (2018). Exposure to predicted precipitation patterns decreases population size and alters community structure of cyanobacteria in biological soil crusts from the Chihuahuan Desert. *Environmental Microbiology*, *20*(1), 259–269. https://doi.org/10.1111/1462-2920.13983

Fernandes, V. M. C., Rudgers, J. A., Collins, S. L., & Garcia-Pichel, F. (2022). Rainfall pulse regime drives biomass and community composition in biological soil crusts. *Ecology*, *103*(9), e3744. https://doi.org/10.1002/ecy.3744

Friedlingstein, P., Jones, M. W., O'Sullivan, M., Andrew, R. M., Bakker, D. C. E., Hauck, J., Le Quéré, C., Peters, G. P., Peters, W., Pongratz, J., Sitch, S., Canadell, J. G., Ciais, P., Jackson, R. B., Alin, S. R., Anthoni, P., Bates, N. R., Becker, M., Bellouin, N., … Zeng, J. (2022). Global carbon budget 2021. *Earth System Science Data*, *14*(4), 1917–2005. https://doi.org/10.5194/essd-14-1917-2022

Gao, Y. Z., Chen, Q., Lin, S., Giese, M., & Brueck, H. (2011). Resource manipulation effects on net primary production, biomass allocation and rain-use efficiency of two semiarid grassland sites in Inner Mongolia, China. *Oecologia*, *165*(4), 855–864. https://doi.org/10.1007/s00442-010-1890-z

Gherardi, L. A., & Sala, O. E. (2015). Enhanced precipitation variability decreases grass- and increases shrub-productivity. *Proceedings of the National Academy of Sciences of the United States of America*, *112*(41), 12735–12740. https://doi.org/10.1073/pnas.1506433112

Gherardi, L. A., & Sala, O. E. (2020). Global patterns and climatic controls of belowground net carbon fixation. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(33), 20038–20043. https://doi.org/10.1073/pnas.2006715117

Gibbens, R. P., & Lenz, J. M. (2001). Root systems of some Chihuahuan Desert plants. *Journal of Arid Environments*, *49*(2), 221–263. https://doi.org/10.1006/jare.2000.0784

Gong, X. Y., Fanselow, N., Dittert, K., Taube, F., & Lin, S. (2015). Response of primary production and biomass allocation to nitrogen and water supplementation along a grazing intensity gradient in semi-arid grassland. *European Journal of Agronomy*, *63*, 27–35. https://doi.org/10.1016/j.eja.2014.11.004

Gosz, J. R. (1993). Ecotone hierarchies. *Ecological Applications*, *3*(3), 369–376. https://doi.org/10.2307/1941905

Gosz, R. J., & Gosz, J. R. (1996). Species interactions on the biome transition zone in New Mexico: Response of blue grama (*Bouteloua gracilis*) and black grama (*Bouteloua eripoda*) to fire and herbivory. *Journal*

of Arid Environments, *34*(1), 101–114. https://doi.org/10.1006/jare.1996.0096

Gross, F. A., & Dick-Peddie, W. A. (1979). A map of primeval vegetation in New Mexico. *The Southwestern Naturalist*, *24*(1), 115. https://doi.org/10.2307/3670631

Grover, H. D., & Musick, H. B. (1990). Shrubland encroachment in southern New Mexico, U.S.A.: An analysis of desertification processes in the American southwest. *Climatic Change*, *17*(2), 305–330. https://doi.org/10.1007/BF00138373

Hall, S. J., Sponseller, R. A., Grimm, N. B., Huber, D., Kaye, J. P., Clark, C., & Collins, S. L. (2011). Ecosystem response to nutrient enrichment across an urban airshed in the Sonoran Desert. *Ecological Applications*, *21*(3), 640–660. https://doi.org/10.1890/10-0758.1

Hanan, N. P., Milne, E., Aynekulu, E., Yu, Q., & Anchang, J. (2021). A role for drylands in a carbon neutral world? *Frontiers in Environmental Science*, *9*. https://doi.org/10.3389/fenvs.2021.786087

Hély, C., Alleaume, S., & Runyan, C. W. (2019). Fire regimes in dryland landscapes. In P. D'Odorico, A. Porporato, & C. Wilkinson Runyan (Eds.), *Dryland Ecohydrology* (2nd ed., pp. 367–399). Springer International Publishing. https://doi.org/10.1007/978-3-030-23269-6_14

Hochstrasser, T., & Peters, D. P. C. (2004). Subdominant species distribution in microsites around two life forms at a desert grassland-shrubland transition zone. *Journal of Vegetation Science*, *15*(5), 615–622. https://doi.org/10.1111/j.1654-1103.2004.tb02303.x

Hooper, D. U., & Johnson, L. (1999). Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation. *Biogeochemistry*, *46*(1), 247–293. https://doi.org/10.1007/BF01007582

Houghton, R. A. (2000). Interannual variability in the global carbon cycle. *Journal of Geophysical Research: Atmospheres*, *105*(D15), 20121–20130. https://doi.org/10.1029/2000JD900041

Hsu, J. S., Powell, J., & Adler, P. B. (2012). Sensitivity of mean annual primary production to precipitation. *Global Change Biology*, *18*(7), 2246–2255. https://doi.org/10.1111/j.1365-2486.2012.02687.x

Huang, J., Li, Y., Fu, C., Chen, F., Fu, Q., Dai, A., Shinoda, M., Ma, Z., Guo, W., Li, Z., Zhang, L., Liu, Y., Yu, H., He, Y., Xie, Y., Guan, X., Ji, M., Lin, L., Wang, S., … Wang, G. (2017). Dryland climate change: Recent progress and challenges. *Reviews of Geophysics*, *55*(3), 719–778. https://doi.org/10.1002/2016rg000550

Huang, J., Yu, H., Guan, X., Wang, G., & Guo, R. (2016). Accelerated dryland expansion under climate change. *Nature Climate Change*, *6*(2), 166–171. https://doi.org/10.1038/nclimate2837

Humphrey, R. R. (1974). Fire in the deserts and desert grassland of North America. In T. T. Kozlowski & C. E. Ahlgren (Eds.), *Fire and ecosystems* (pp. 365–400). Academic Press. https://doi.org/10.1016/B978-0-12-424255-5.50016-X

Huxman, T. E., Smith, M. D., Fay, P. A., Knapp, A. K., Shaw, M. R., Loik, M. E., Smith, S. D., Tissue, D. T., Zak, J. C., Weltzin, J. F., Pockman, W. T., Sala, O. E., Haddad, B. M., Harte, J., Koch, G. W., Schwinning, S., Small, E. E., & Williams, D. G. (2004). Convergence across biomes to a common rain-use efficiency. *Nature*, *429*(6992), 651–654. https://doi.org/10.1038/nature02561

Jackson, R. B., Canadell, J. G., Ehleringer, J. R., Mooney, H. A., Sala, O. E., & Schulze, E.-D. (1996). A global analysis of root distributions for terrestrial biomes. *Oecologia*, *108*(3), 389–411. https://doi.org/10.1007/BF00333714

Janzen, H. H. (2004). Carbon cycling in earth systems—A soil science perspective. *Agriculture, Ecosystems & Environment*, *104*(3), 399–417. https://doi.org/10.1016/j.agee.2004.01.040

Keenan, T. F., & Williams, C. A. (2018). The terrestrial carbon sink. *Annual Review of Environment and Resources*, *43*(1), 219–243. https://doi.org/10.1146/annurev-environ-102017-030204

Kieft, T. L., White, C. S., Loftin, S. R., Aguilar, R., Craig, J. A., & Skaar, D. A. (1998). Temporal dynamics in soil carbon and nitrogen resources at a grassland–shrubland ecotone. *Ecology*, *79*(2), 671–683. https://doi.org/10.1890/0012-9658(1998)079[0671:tdisca]2.0.co;2

Knapp, A. K., Briggs, J. M., Collins, S. L., Archer, S. R., Bret-Harte, M. S., Ewers, B. E., Peters, D. P., Young, D. R., Shaver, G. R., Pendall, E., & Cleary, M. B. (2008). Shrub encroachment in north American grasslands: Shifts in growth form dominance rapidly alters control of ecosystem carbon inputs. *Global Change Biology*, *14*(3), 615–623. https://doi.org/10.1111/j.1365-2486.2007.01512.x

Knapp, A. K., & Smith, M. D. (2001). Variation among biomes in temporal dynamics of aboveground primary production. *Science*, *291*(5503), 481–484. https://doi.org/10.1126/science.291.5503.481

Kröel-Dulay, G., Ódor, P., Peters, D. P. C., & Hochstrasser, T. (2004). Distribution of plant species at a biome transition zone in New Mexico. *Journal of Vegetation Science*, *15*(4), 531–538. https://doi.org/10.1111/j.1654-1103.2004.tb02292.x

Kurc, S. A., & Small, E. E. (2007). Soil moisture variations and ecosystem-scale fluxes of water and carbon in semiarid grassland and shrubland. *Water Resources Research*, *43*(6), W06416. https://doi.org/10.1029/2006WR005011

Ladwig, L. M., Collins, S. L., Ford, P. L., & White, L. B. (2014). Chihuahuan Desert grassland responds similarly to fall, spring, and summer fires during prolonged drought. *Rangeland Ecology & Management*, *67*(6), 621–628. https://doi.org/10.2111/REM-D-13-00133.1

Ladwig, L. M., Collins, S. L., Swann, A. L., Xia, Y., Allen, M. F., & Allen, E. B. (2012). Above- and belowground responses to nitrogen addition in a Chihuahuan Desert grassland. *Oecologia*, *169*(1), 177–185. https://doi.org/10.1007/s00442-011-2173-z

Lauenroth, W. K., & Sala, O. E. (1992). Long-term forage production of North American shortgrass steppe. *Ecological Applications*, *2*(4), 397–403. https://doi.org/10.2307/1941874

Li, J., Lin, S., Taube, F., Pan, Q., & Dittert, K. (2011). Above and belowground net primary productivity of grassland influenced by supplemental water and nitrogen in Inner Mongolia. *Plant and Soil*, *340*(1), 253–264. https://doi.org/10.1007/s11104-010-0612-y

Li, J., Ravi, S., Wang, G., Van Pelt, R. S., Gill, T. E., & Sankey, J. B. (2022). Woody plant encroachment of grassland and the reversibility of shrub dominance: Erosion, fire, and feedback processes. *Ecosphere*, *13*(3), e3949. https://doi.org/10.1002/ecs2.3949

Liu, Z., Liu, K., Shi, X., Ryan Lock, T., Kallenbach, R. L., & Yuan, Z. (2022). Changes in grassland phenology and growth rate, rather than diversity, drive biomass production after fire. *Agricultural and Forest Meteorology*, *322*, 109028. https://doi.org/10.1016/j.agrformet.2022.109028

Maurer, G. E., Hallmark, A. J., Brown, R. F., Sala, O. E., & Collins, S. L. (2020). Sensitivity of primary production to precipitation across the United States. *Ecology Letters*, *23*(3), 527–536. https://doi.org/10.1111/ele.13455

McCulley, R. L., Jobbágy, E. G., Pockman, W. T., & Jackson, R. B. (2004). Nutrient uptake as a contributing explanation for deep rooting in arid and semi-arid ecosystems. *Oecologia*, *141*(4), 620–628. https://doi.org/10.1007/s00442-004-1687-z

Milchunas, D. G. (2009). Estimating root production: Comparison of 11 methods in shortgrass steppe and review of biases. *Ecosystems*, *12*(8), 1381–1402. https://doi.org/10.1007/s10021-009-9295-8

Milchunas, D. G., Mosier, A. R., Morgan, J. A., LeCain, D. R., King, J. Y., & Nelson, J. A. (2005). Root production and tissue quality in a shortgrass steppe exposed to elevated CO_2: Using a new ingrowth method. *Plant and Soil*, *268*(1), 111–122. https://doi.org/10.1007/s11104-004-0230-7

Moore, D. I. (2021). *Meteorology data from the Sevilleta National Wildlife Refuge, New Mexico*. Environmental Data Initiative. https://doi.org/10.6073/pasta/1cbc37ae4d40b3844b5e4be9f6f18073

Moustakis, Y., Papalexiou, S. M., Onof, C. J., & Paschalis, A. (2021). Seasonality, intensity, and duration of rainfall extremes change in a warmer climate. *Earth's Futures*, *9*(3), e2020EF001824. https://doi.org/10.1029/2020ef001824

Muldavin, E. H., Moore, D. I., Collins, S. L., Wetherill, K. R., & Lightfoot, D. C. (2008). Aboveground net primary production dynamics in a

northern Chihuahuan Desert ecosystem. *Oecologia*, *155*(1), 123–132. https://doi.org/10.1007/s00442-007-0880-2

Neill, C. (1992). Comparison of soil coring and ingrowth methods for measuring belowground production. *Ecology*, *73*(5), 1918–1921. https://doi.org/10.2307/1940044

Niu, S., Fu, Z., Luo, Y., Stoy, P. C., Keenan, T. F., Poulter, B., Zhang, L., Piao, S., Zhou, X., Zheng, H., Han, J., Wang, Q., & Yu, G. (2017). Interannual variability of ecosystem carbon exchange: From observation to prediction. *Global Ecology and Biogeography*, *26*(11), 1225–1237. https://doi.org/10.1111/geb.12633

Notaro, M., Liu, Z., Gallimore, R. G., Williams, J. W., Gutzler, D. S., & Collins, S. L. (2010). Complex seasonal cycle of ecohydrology in the Southwest United States. *Journal of Geophysical Research: Biogeosciences*, *115*(G4), G04034. https://doi.org/10.1029/2010jg001382

Parmenter, R. R. (2008). Long-term effects of a summer fire on desert grassland plant demographics in New Mexico. *Rangeland Ecology & Management*, *61*(2), 156–168. https://doi.org/10.2111/07-010.1

Parmenter, R. R., Yates, T. L., Anderson, D. R., Burnham, K. P., Dunnum, J. L., Franklin, A. B., Friggens, M. T., Lubow, B. C., Miller, M., Olson, G. S., Parmenter, C. A., Pollard, J., Rexstad, E., Shenk, T. M., Stanley, T. R., & White, G. C. (2003). Small-mammal density estimation: A field comparison of grid-based vs. web-based density estimators. *Ecological Monographs*, *73*(1), 1–26. https://doi.org/10.1890/0012-9615(2003)073[0001:SMDEAF]2.0.CO;2

Peters, D. P. C., & Yao, J. (2012). Long-term experimental loss of foundation species: Consequences for dynamics at ecotones across heterogeneous landscapes. *Ecosphere*, *3*(3), art27. https://doi.org/10.1890/ES11-00273.1

Petrie, M. D., Collins, S. L., Gutzler, D. S., & Moore, D. I. (2014). Regional trends and local variability in monsoon precipitation in the northern Chihuahuan Desert, USA. *Journal of Arid Environments*, *103*(1), 63–70. https://doi.org/10.1016/j.jaridenv.2014.01.005

Petrie, M. D., Collins, S. L., Swann, A. L., Ford, P. L., & Litvak, M. E. (2015). Grassland to shrubland state transitions enhance carbon sequestration in the northern Chihuahuan Desert. *Global Change Biology*, *21*(3), 1226–1235. https://doi.org/10.1111/gcb.12743

Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., & R Core Team. (2020). *nlme: Linear and nonlinear mixed effects models* [R package version 3.1-144]. https://cran.r-project.org/package=nlme

Poulter, B., Frank, D., Ciais, P., Myneni, R. B., Andela, N., Bi, J., Broquet, G., Canadell, J. G., Chevallier, F., Liu, Y. Y., Running, S. W., Sitch, S., & van der Werf, G. R. (2014). Contribution of semi-arid ecosystems to interannual variability of the global carbon cycle. *Nature*, *509*(7502), 600–603. https://doi.org/10.1038/nature13376

Prăvălie, R., Bandoc, G., Patriche, C., & Sternberg, T. (2019). Recent changes in global drylands: Evidences from two major aridity databases. *Catena*, *178*, 209–231. https://doi.org/10.1016/j.catena.2019.03.016

R Core Team. (2020). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. https://cran.r-project.org/

Rand-Caplan, R. L. (2006). *The history of the Sevilleta land grant and in the first person: Oral histories from La Joya de Sevilleta "the Jewel of the Sevilleta"* (Publication No. 89) [Masters thesis, University of New Mexico]. UNM Digital Repository. https://digitalrepository.unm.edu/hist_etds/89

Ravi, S., D'Odorico, P., Wang, L., White, C. S., Okin, G. S., Macko, S. A., & Collins, S. L. (2009). Post-fire resource redistribution in desert grasslands: A possible negative feedback on land degradation. *Ecosystems*, *12*(3), 434–444. https://doi.org/10.1007/s10021-009-9233-9

Rudgers, J. A., Hallmark, A., Baker, S. R., Baur, L., Hall, K. M., Litvak, M. E., Muldavin, E. H., Pockman, W. T., & Whitney, K. D. (2019). Sensitivity of dryland plant allometry to climate. *Functional Ecology*, *33*(12), 2290–2303. https://doi.org/10.1111/1365-2435.13463

Sala, O. E., Gherardi, L. A., Reichmann, L., Jobbágy, E., & Peters, D. (2012). Legacies of precipitation fluctuations on primary production: Theory and data synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *367*(1606), 3135–3144. https://doi.org/10.1098/rstb.2011.0347

Sala, O. E., Parton, W. J., Joyce, L. A., & Lauenroth, W. K. (1988). Primary production of the central grassland region of the United States. *Ecology*, *69*(1), 40–45. https://doi.org/10.2307/1943158

Sankey, J. B., Ravi, S., Wallace, C. S. A., Webb, R. H., & Huxman, T. E. (2012). Quantifying soil surface change in degraded drylands: Shrub encroachment and effects of fire and vegetation removal in a desert grassland. *Journal of Geophysical Research: Biogeosciences*, *117*(G2), G02025. https://doi.org/10.1029/2012JG002002

Scharlemann, J. P., Tanner, E. V., Hiederer, R., & Kapos, V. (2014). Global soil carbon: Understanding and managing the largest terrestrial carbon pool. *Carbon Management*, *5*(1), 81–91. https://doi.org/10.4155/cmt.13.77

Schenk, H. J., & Jackson, R. B. (2002). Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems. *Journal of Ecology*, *90*(3), 480–494. https://doi.org/10.1046/j.1365-2745.2002.00682.x

Soil Survey Staff. (2019). *Web soil survey*. Natural Resources Conservation Service, United States Department of Agriculture. https://websoilsurvey.sc.egov.usda.gov/

Sokol, N. W., & Bradford, M. A. (2019). Microbial formation of stable soil carbon is more efficient from belowground than aboveground input. *Nature Geoscience*, *12*(1), 46–53. https://doi.org/10.1038/s41561-018-0258-6

Sun, Y., Feng, Y., Wang, Y., Zhao, X., Yang, Y., Tang, Z., Wang, S., Su, H., Zhu, J., Chang, J., & Fang, J. (2021). Field-based estimation of net primary productivity and its above- and belowground partitioning in global grasslands. *Journal of Geophysical Research: Biogeosciences*, *126*(11), e2021JG006472. https://doi.org/10.1029/2021JG006472

Tierney, G. L., & Fahey, T. J. (2007). Estimating belowground primary productivity. In T. J. Fahey & A. K. Knapp (Eds.), *Principles and standards for measuring primary production*. Oxford University Press. https://doi.org/10.1093/acprof:oso/9780195168662.003.0008

Ukkola, A. M., De Kauwe, M. G., Roderick, M. L., Burrell, A., Lehmann, P., & Pitman, A. J. (2021). Annual precipitation explains variability in dryland vegetation greenness globally but not locally. *Global Change Biology*, *27*(18), 4367–4380. https://doi.org/10.1111/gcb.15729

Van Auken, O. W. (2000). Shrub invasions of north American semiarid grasslands. *Annual Review of Ecology and Systematics*, *31*(1), 197–215. https://doi.org/10.1146/annurev.ecolsys.31.1.197

Van Auken, O. W. (2009). Causes and consequences of woody plant encroachment into western north American grasslands. *Journal of Environmental Management*, *90*(10), 2931–2942. https://doi.org/10.1016/j.jenvman.2009.04.023

Wang, C., Sun, Y., Chen, H. Y. H., Yang, J., & Ruan, H. (2021). Meta-analysis shows non-uniform responses of above- and belowground productivity to drought. *Science of the Total Environment*, *782*, 146901. https://doi.org/10.1016/j.scitotenv.2021.146901

Wang, C., Vera-Vélez, R., Lamb, E. G., Wu, J., & Ren, F. (2022). Global pattern and associated drivers of grassland productivity sensitivity to precipitation change. *Science of the Total Environment*, *806*(3), 151224. https://doi.org/10.1016/j.scitotenv.2021.151224

Wang, J., Gao, Y., Zhang, Y., Yang, J., Smith, M. D., Knapp, A. K., Eissenstat, D. M., & Han, X. (2019). Asymmetry in above- and belowground productivity responses to N addition in a semi-arid temperate steppe. *Global Change Biology*, *25*(9), 2958–2969. https://doi.org/10.1111/gcb.14719

White, C. S. (2011). Homogenization of the soil surface following fire in semiarid grasslands. *Rangeland Ecology & Management*, *64*(4), 414–418. https://doi.org/10.2111/REM-D-11-00003.1

Wilcox, K. R., Shi, Z., Gherardi, L. A., Lemoine, N. P., Koerner, S. E., Hoover, D. L., Bork, E., Byrne, K. M., Cahill, J., Jr., Collins, S. L., Evans, S., Gilgen, A. K., Holub, P., Jiang, L., Knapp, A. K., LeCain, D., Liang, J., Garcia-Palacios, P., Peñuelas, J., … Luo, Y. (2017). Asymmetric responses of primary productivity to precipitation extremes: A synthesis of grassland precipitation manipulation experiments. *Global Change Biology*, *23*(10), 4376–4385. https://doi.org/10.1111/gcb.13706

Wilcox, K. R., von Fischer, J. C., Muscha, J. M., Petersen, M. K., & Knapp, A. K. (2015). Contrasting above- and belowground sensitivity of

three Great Plains grasslands to altered rainfall regimes. *Global Change Biology*, *21*(1), 335–344. https://doi.org/10.1111/gcb.12673

Wu, Z., Dijkstra, P., Koch, G. W., Peñuelas, J., & Hungate, B. A. (2011). Responses of terrestrial ecosystems to temperature and precipitation change: A meta-analysis of experimental manipulation. *Global Change Biology*, *17*(2), 927–942. https://doi.org/10.1111/j.1365-2486.2010.02302.x

Yahdjian, L., Gherardi, L. A., & Sala, O. E. (2011). Nitrogen limitation in arid-subhumid ecosystems: A meta-analysis of fertilization studies. *Journal of Arid Environments*, *75*(8), 675–680. https://doi.org/10.1016/j.jaridenv.2011.03.003

Zak, D. R., Tilman, D., Parmenter, R. R., Rice, C. W., Fisher, F. M., Vose, J., Milchunas, D., & Martin, C. W. (1994). Plant production and soil microorganisms in late-successional ecosystems: A continental-scale study. *Ecology*, *75*(8), 2333–2347. https://doi.org/10.2307/1940888

Zhang, F., Biederman, J. A., Dannenberg, M. P., Yan, D., Reed, S. C., & Smith, W. K. (2021). Five decades of observed daily precipitation reveal longer and more variable drought events across much of the western United States. *Geophysical Research Letters*, *48*(7), e2020GL092293. https://doi.org/10.1029/2020gl092293

Zhang, J., Li, J., Xiao, R., Zhang, J., Wang, D., Miao, R., Song, H., Liu, Y., Yang, Z., & Liu, M. (2021). The response of productivity and its sensitivity to changes in precipitation: A meta-analysis of field manipulation experiments. *Journal of Vegetation Science*, *32*(1), e12954. https://doi.org/10.1111/jvs.12954

Zhou, X., Fei, S., Sherry, R., & Luo, Y. (2012). Root biomass dynamics under experimental warming and doubled precipitation in a tallgrass prairie. *Ecosystems*, *15*(4), 542–554. https://doi.org/10.1007/s10021-012-9525-3

SUPPORTING INFORMATION

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

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