RESEARCH ARTICLE

Sensitivity of root production to long-term aridity under environmental perturbations in Chihuahuan Desert ecosystems

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Funding information
Division of Environmental Biology, Grant/Award Number: 1655499, 1748133 and 1856383

Handling Editor: Yoann Le Bagousse-Pinguet

Abstract

1. Root production influences carbon and nutrient cycles and subsidizes soil biodiversity. However, the long-term dynamics and drivers of belowground production are poorly understood for most ecosystems. In drylands, fire, eutrophication, and precipitation regimes could affect not only root production but also how roots track interannual variability in climate.

2. We manipulated the intra-annual precipitation regime, soil nitrogen, and fire in four common Chihuahuan Desert ecosystem types (three grasslands and one shrubland) in New Mexico, USA, where the 100-year record indicates both long-term drying and increasing interannual variability in aridity. First, we evaluated how root production tracked aridity over 10–17 years using climate sensitivity functions, which quantify long-term, nonlinear relationships between biological processes and climate. Next, we determined the degree to which perturbations by fire, nitrogen addition or intra-annual rainfall altered the sensitivity of root production to both mean and interannual variability in aridity.

3. All ecosystems had nonlinear climate sensitivities that predicted declines in production with increases in the interannual variance of aridity. However, root production was the most sensitive to aridity in Chihuahuan Desert shrubland, with reduced production under drier and more variable aridity.

4. Among the perturbations, only fire altered the sensitivity of root production to aridity. Root production was more than twice as sensitive to declines with aridity following prescribed fire than in unburned conditions. Neither the intra-annual seasonal rainfall regime nor chronic nitrogen fertilization altered the sensitivity of roots to aridity.

5. *Synthesis*. Our results yield new insight into how dryland plant roots respond to climate change. Our comparison of dryland ecosystems of the northern Chihuahuan Desert predicted that root production in shrublands would be more sensitive to future climates that are drier and more variable than root production in dry grasslands. Field manipulations revealed that fire could amplify the climate sensitivity of dry grassland root production, but in contrast, the climate sensitivity of root production was largely resistant to changes in the seasonal rainfall regime or increased soil fertilization.

1 | INTRODUCTION

Plant production belowground subsidizes soil biodiversity and drives belowground carbon and nutrient dynamics (Freschet et al., 2013; Jackson et al., 2002; Ravenek et al., 2014; Wardle, 2013; Yuan & Chen, 2010), but relatively few studies track how perturbations impact long-term dynamics in plant productivity belowground. As a consequence, we know little about the drivers of belowground primary production in many ecosystems, and it is the most uncertain component of the terrestrial carbon cycle (Gherardi & Sala, 2020). Yet, root production is estimated to constitute 33%–46% of global annual net primary productivity (Gherardi & Sala, 2020; Jackson et al., 1997), with the bulk of plant roots occupying the top 15–30 cm of the soil profile across a range of herbaceous-dominated ecosystems, such as grasslands (Gill et al., 1999; Kurc & Small, 2007; Weaver et al., 1935). Root production is an important long-term reservoir of carbon that fuels soil food webs and plant-microbe interactions (Crowther et al., 2016; Gill et al., 1999; Milchunas et al., 2005), and a majority of the carbon belowground derives from plant roots and their biotic associates (Carol Adair et al., 2009; Sokol & Bradford, 2019). Therefore, understanding drivers of belowground production can improve predictions on potential carbon sequestration in soils.

Environmental perturbations that disrupt root production include global warming, nitrogen deposition, fire and altered precipitation regimes, among others. The relative influence of these perturbations on root production and their importance in different ecosystem types remain largely unresolved (e.g. Deng et al., 2021). The impacts of environmental perturbations on plant roots can vary with soil depth and the composition of dominant vegetation, and effects on roots can even flip direction over time or with weather conditions. For example, anthropogenic nitrogen deposition has exceeded natural levels since the 1980s (Vitousek et al., 1997) and may double by 2050 in some regions (Phoenix et al., 2006), changes that can alter species composition and carbon sequestration (Van Houtven et al., 2019). Nitrogen fertilization increased root biomass in the organic soil horizon of a mixed hardwood forest over 25 years, although nitrogen reduced roots in deeper mineral soil (Carrara et al., 2018). Nitrogen addition to a semiarid California shrubland over 11 years initially increased, but ultimately reduced, root biomass and had the strongest effects during wet periods (Vourlitis et al., 2021), indicating the potential for this environmental perturbation to interact with the sensitivity of root production to climate. Long-term data on root production also demonstrate important influences of short-term warming, simulated grazing, plant diversity, and elevated CO_2 (Carrillo et al., 2014; Maier et al., 2022; Mueller et al., 2013; Xu et al., 2012). However, the degree to which these perturbations influence the sensitivity of root production to background climate,

and particularly climate *variability*, has not, to our knowledge, been examined. For example, fire, through the elimination of aboveground biomass, could amplify the sensitivity of belowground production to climate as plants recover. Similarly, nitrogen deposition could magnify increases in plant aboveground growth during wet years by reducing soil nutrient limitation and thereby amplifying the sensitivity of aboveground production to climate. In contrast, nitrogen addition may have the reverse effect on the sensitivity of roots to climate, for example, if fertilization reduces belowground production because fewer roots are required for nitrogen acquisition.

Determining how future changes in climate mean and variability will affect ecosystem carbon processes remains a key ecological challenge (Felton et al., 2021). Understanding how belowground plant production, the primary source of soil carbon, tracks climate when exposed to environmental perturbations can improve the accuracy of predictions on long-term soil carbon dynamics, nutrient cycling, and ecosystem function for terrestrial ecosystems (Wang, Gao, et al., 2019; Wilcox et al., 2015; Zhang et al., 2019). While long-term experiments provide platforms to detect whether environmental perturbations interact with climate variability to influence belowground plant production, such analyses hinge on the collection of consistent long-term data. Many experiments often lack the repeated measures necessary to evaluate the degree to which belowground production tracks climate and test whether or not such sensitivity to climate is altered by interaction with environmental perturbations.

Belowground primary production may respond not only to average climate conditions but also to variability in climate. Climate sensitivity functions use observational time series data to predict the relationships between ecological variables and both the mean and the variance in climate (Rudgers et al., 2018). A sensitivity function describes the complex relationship between a biological process (e.g. root production) and a climate variable (e.g. aridity, Figure 1). Sensitivity to *variance* in climate is characterized by the shape of the nonlinear function (Hsu & Adler, 2014) rather than by a conventionally used linear slope. When a sensitivity function is nonlinear, increases in the variance of the climate driver alone will affect the biological response, even if the mean climate does not change (Lawson et al., 2015; Vazquez et al., 2017) based on the mathematical principle of Jensen's Inequality. A concave function (Figure 1a) yields net negative effects of increasing variance because small values of the climate variable (e.g. dry conditions) cause large declines in the ecological response, while large values of the climate variable (e.g. wet conditions) cause only small increases; the net effect is a cost of increasing variance. In contrast, a convex function predicts that increasing climate variance is beneficial (Figure 1b) because increases in the ecological response during wet conditions outweigh losses under arid conditions. If the function changes concavity over
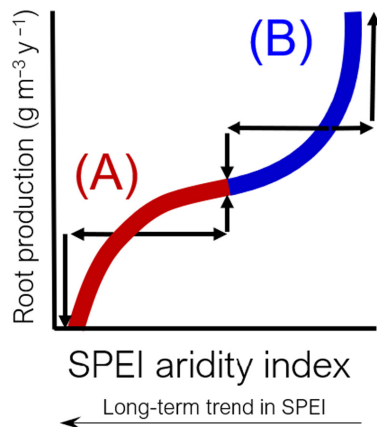
FIGURE 1 Climate sensitivity function theory for belowground root production. The predicted response of root production to variability in climate depends on the shape of the nonlinear relationship with climate. Here, the climate variable is the *SPEI* aridity index, which has become increasingly drier over the past 100 years (Rudgers et al., 2018). Large values of the index indicate relatively wet/cool conditions, while small values indicate relatively drier/hotter than average conditions. (A) The concave down (red) nonlinearity signals a cost of increasing variance in aridity because the increases in root production in wetter-than-average conditions are smaller than the decreases in root production in drier-than-average conditions, as indicated by the length of the vertical arrows. (B) In contrast, a convex up (blue) nonlinearity signals a benefit of increasing variance because increased root production during wetter-than-average conditions exceeds declines under drought. Variance effects can also depend on the mean climate variable: The full cubic curve (A + B) depicts a scenario in which increasing variability in interannual climate is predicted to be costly to root production under a dry mean climate but beneficial under a wet mean climate.

the observed range of climate conditions (Figure 1, full range of climate variable), then the variance in climate could have positive or negative effects depending on the climate mean because the mean and variance interact. Thus, the degree of nonlinearity in the climate sensitivity function predicts the *magnitude* of ecological sensitivity to variance in climate, and the shape of the nonlinearity predicts the *direction* of sensitivity to variance (benefit or cost). For example, Rudgers et al. (2018) documented differences among ecosystem types in the climate sensitivities of aboveground plant production by using observational data over a long period of interannual climate variability.

The sensitivity of root production to climate may be particularly large in drylands because of their strong water limitation and large year-to-year variability in climate (Maurer et al., 2020; Wardle, 2013). Understanding these dynamics is important because drylands cover >40% of the terrestrial land surface, support >35% of the human population, and continue to expand in extent (Huang et al., 2016; Plaza et al., 2018; Pravalie, 2016). Belowground plant production in drylands may present a range of sensitivities to climate that interact with environmental perturbations. Furthermore, how root production tracks precipitation may differ greatly between

ecosystems dominated by shrubs with deep roots versus grasslands with shallow-rooted grasses and forbs. Ecosystem models suggest that root production is either less responsive or slower to respond to abiotic conditions, such as drought, than aboveground production (Shi et al., 2014), but long-term, empirical datasets on root production are far sparser than aboveground data because they are harder to obtain (Deng et al., 2021; Song et al., 2019; Zhou et al., 2016).

We used single-factor long-term field manipulations of the intra-annual rainfall regime, nitrogen fertilization, and fire to evaluate their interactions with the sensitivity of root production to interannual climate (both mean and variance) in four ecosystem types in central New Mexico, USA. Prior work reported that, unlike aboveground production, mean root production was generally unrelated to precipitation and unaffected by fire and nitrogen addition, other than a weak but significant response to annual precipitation in desert shrubland (Brown & Collins, 2023). Moreover, variability in root production was greatest in shrublands relative to the grasslands. These results beg the question, if precipitation is not the main driver, what factors govern root production in these dryland ecosystems? Here, we used 17 years of root production data (2005–2021) to generate climate sensitivity functions between belowground plant production and the Standardized Precipitation Evapotranspiration Index (SPEI), a measure of aridity that integrates temperature and precipitation over annual time scales. In central New Mexico, the 100-year record of SPEI revealed both long-term drying trends during the summer growing season and significant increases in year-to-year variability in aridity since the 1980s (Maurer et al., 2020; Rudgers et al., 2018). Specifically, we addressed the following questions. (1) Do dry-land ecosystem types differ in the sensitivity of root production to the mean or interannual variance in aridity? We compared four common ecosystem types, three types of dryland C_4 grasslands and one shrubland, that together represent ~55 million ha of the southwestern US (Anderson-Teixeira et al., 2011). We predicted that desert shrubland, dominated by the long-lived roots of creosote bush (*Larrea tridentata*), would be the least sensitive to aridity relative to the grasslands because of its high variability and weak response to precipitation (Brown & Collins, 2023). Alternatively, we expected Plains grassland to be the most sensitive to aridity because we sampled this ecosystem at the southern edge of its geographic range, where conditions are among the most arid for this ecosystem type. We also evaluated whether and how environmental perturbations interacted with the sensitivity of root production to the mean and variability in observed climate aridity, by addressing (2) Does the intra-annual rainfall regime alter the sensitivity of root production to annual mean or interannual variance in aridity? We predicted that root production would be less sensitive to background aridity with additions of large, once-monthly rain events, relative to small weekly rain additions, because large events result in longer periods of soil moisture availability (Vargas et al., 2012). Next, we asked (3) Does chronic nitrogen fertilization alter the sensitivity of root production to mean or variance in aridity? Given the lack of difference in belowground production in fertilized and control plots (Brown & Collins, 2023), we expected no differences in the sensitivity of root

production to aridity, despite increased nutrient availability under chronic fertilization. However, fertilizer should increase inorganic nitrogen readily available to plants and reduce the need for large root systems in the low-nitrogen soils of our region, thereby reducing the sensitivity of root production to aridity (Kieft et al., 1998; White et al., 2004). Lastly, although aboveground plant production recovers slowly from fire (Parmenter, 2008), we asked, (4) Does fire alter the sensitivity of root production to mean or variance in aridity? Given that prior research suggested that fire has limited or no significant impacts belowground (Brown & Collins, 2023; Burnett et al., 2012), we predicted that fire would have limited effects on the sensitivity of root production to climate variability relative to the other environmental changes in these drylands. The novelty of this study is twofold: first, the detection of sensitivity of root production to *variance* in climate, and second, the evaluation of whether the sensitivity of root production to climate mean or variance *interacts* with other environmental perturbations, including the intra-annual rainfall regime, nitrogen fertilization or fire.

2 | MATERIALS AND METHODS

2.1 | Study sites

We used sites at the Sevilleta National Wildlife Refuge (SNWR) in central New Mexico, USA (Table 1) that are part of the Sevilleta Long-Term Ecological Research program (SEV LTER). Mean annual temperature is 13.7°C, and the mean annual precipitation is 233 ± 9.6 mm, of which ~50% falls during the summer monsoon (July–September). The five sites included the creosote bush-dominated Desert Shrubland Core Site (Muldavin et al., 2008; Rudgers et al., 2018), the Desert Grassland site of the Monsoon Rainfall Manipulation Experiment (Brown et al., 2022), the Plains Grassland location of the Nitrogen Fertilization Experiment (Ladwig et al., 2012), and two Mixed Grassland sites, near a location known as Deep Well, which

included a burned and unburned area resulting from a 2003 management fire (Table 1, Burnett et al., 2012). Each ecosystem was dominated by different plant species (Table 1). Soils are typic haplargids derived from piedmont alluvium, often underlain by a shallow calcic layer. Soil texture in the upper 20 cm, where most herbaceous roots occur (Kurc & Small, 2007), is approximately 68% sand, 22% silt, and 10% clay, with 2% calcium carbonate (Kieft et al., 1998).

2.2 | Root 'donut' estimation method for belowground production

To estimate annual root production, we created belowground root 'donuts' (Milchunas et al., 2005) made of recycled schedule 40 PVC pipes that were 15.24 cm in diameter and 30 cm deep (Figure S1). Root donuts are composed of two cut PVC pipe sections, each 15 cm long with an outer cylindrical shell of #7 plastic canvas cross-stitch mesh (7 strands per 2.5 cm) in 30.5 cm × 45 cm sheets (Darice, Strongsville, OH). First, we used a custom-made soil auger to excavate a ~20 cm diameter by ~30 cm deep hole within each plot or study location. We removed debris and rocks from the walls of the hole and levelled the base. Then, we inserted the cross-stitch mesh along the walls of the hole with the top of the mesh flush with the soil surface (Figure S1). Next, we stacked the two PVC sections in the centre of the hole and anchored them in place using plastic bags filled with sand to fill the inner space of the PVC sections. We sifted out the initial root biomass from the excavated soil in the field using coarse 1.5 mm wire mesh in a wooden frame. Then, we transferred the sifted, root-free soil to fill the space between the outer PVC pipe and the mesh walls of the hole, effectively creating a soil 'donut' into which roots grew during each year of monitoring.

Each November, we removed the soil from the donut area, cutting the internal soil adjacent to the cross-stitch mesh with a sharp knife, and collecting the soil and root materials. We refilled each donut with fresh soil from nearby, after sieving it through 1.5 mm

TABLE 1 List of ecosystems with long-term production monitoring as part of the Sevilleta Long-Term Ecological Research Program (SEV LTER), including GPS coordinates, the year of root donut installation, total number (*N*) of root donuts monitored yearly at each location, identity of the nearest meteorological station, and the species identity of the dominant plant(s).

Ecosystem/experiment	Latitude	Longitude	Year of instal	Root donut (*N*)	Met station	Dominant plant(s)
Creosotebush Desert Shrubland Core Site	34.334	−106.736	2004	10	Five Points	*Larrea tridentata*
Desert Grassland Monsoon Rainfall Manipulation Experiment	34.344	−106.727	2011	13	Five Points	*Bouteloua eriopoda*
Mixed Grassland Historically Unburned	34.358	−106.691	2004	10	Deep Well	*B. eriopoda* & *B. gracilis*
Mixed Grassland 2009 Wildfire Burned	34.358	−106.688	2004	10	Deep Well	*B. eriopoda* & *B. gracilis*
Plains Grassland Nitrogen Fertilization Experiment	34.401	−106.677	2004	20	Deep Well	*Pleuraphis jamesii* & *B. gracilis* (until 2011) then *B. eriopoda* (2011–present)

wire mesh inside a wooden frame sieve to remove preexisting roots and rocks. We took the soil and roots collected from the donuts to the laboratory and sieved the collection through stacked 4 and 1 mm sieves (USA Standard Testing Sieve) to separate the roots. We rinsed the roots to remove any remaining soil. We then dried roots at 60°C for 48 h and weighed dry mass to the nearest 0.001 g. Using the dimensions of the root donut, we calculated dry root biomass as g m^{-3} (Collins, 2024).

Estimating belowground production is challenging, and all methods have biases (Neill, 1992). The root donut method, however, has several advantages over alternative methods to estimate belowground production (Milchunas, 2009). Root donuts were designed for destructive harvests from long-term experiments that have limited sampling area and to maximize representation of areas under and between plants compared to randomly placed, one-point-in-space soil core methods. The donut method is especially reliable for long time series because the sampling location is fixed in place. Donut and other root ingrowth methods reduce labour costs compared to sequential soil coring methods or mini-rhizotrons, and installation does not require specialized machinery, making it less expensive and time-consuming than many alternatives (Milchunas, 2009). However, potential issues include possible overestimation of root production if installation reduces plant competition or if yearly soil sieving enhances N-mineralization or soil microbial activity, and underestimation if harvests act like chronic herbivory. Re-packing soil into donuts after yearly harvests may alter soil bulk density or the soil profile. These factors are common to many methods of estimating root production and could bias estimates of absolute root production in either direction (Milchunas, 2009). Nevertheless, root donuts are likely to have little effect on relative differences among treatments or years with different weather conditions. Thus, the root donut method is well suited to compare relative root production among long-term field treatments (Milchunas et al., 2005).

2.3 | Aridity: The Standardized Precipitation Evapotranspiration Index

Seasonal precipitation is a poor predictor of belowground production in part because precipitation alone does not override the strong effect of temperature on water availability in drylands (Williams et al., 2013). Metrics like the SPEI (Standardized Precipitation Evapotranspiration Index) have been useful predictors of climate sensitivity in drylands (Rudgers et al., 2018) because they explicitly incorporate temperature effects on aridity via potential evapotranspiration integrated over relevant time periods (Vicente-Serrano et al., 2010, 2015, 2020). We calculated SPEI with the Thornthwaite method (Beguería et al., 2014) for each water year (October–September) to match the timescale of root production (once yearly harvest in October/early November) and for each ecosystem. Negative values of SPEI indicate more arid conditions (hot/dry), and positive values indicate relatively cooler/wetter conditions. To determine SPEI, we used precipitation and air temperature data from

two long-term meteorological stations, matched to our experiments (Table 1). We gap-filled sparse missing daily data using data from the geographically nearest station within the SNWR. We then calculated potential evapotranspiration using the Thornthwaite method, and determined 12-month integrated SPEI ending on 30 September (the end of the water year) using the R package <SPEI> (R Core Team, 2023; Vicente-Serrano et al., 2010).

2.4 | Core site long-term data

To compare dryland ecosystem types, we used data from the randomized control plots from three experiments described below. In addition, in 2004, we established 10 root 'donuts' in randomized locations along a transect within Chihuahuan Desert shrubland, dominated by creosote bush, and harvested yearly thereafter (Table 1).

2.5 | Monsoon rainfall manipulation experiment

Increased intra-annual variability in precipitation can alter the pulses of soil moisture that may drive primary production, community composition and ecosystem functioning. Therefore, we mimicked observed long-term change toward more, but smaller, monsoon rain events in our region (Petrie et al., 2014). The Monsoon Rainfall Manipulation Experiment (MRME) (Table 1) is dominated by black grama grass (*Bouteloua eriopoda*). Other prevalent grasses include *Sporobolus contractus*, *S. cryptandrus*, *S. flexuosus*, and *Muhlenbergia arenicola*.

2.5.1 | Experimental design

Since 2007, in addition to ambient precipitation, MRME has imposed the following treatments during the monsoon season (July to September) at the scale of 9 m × 14 m plots: Many-Small, a weekly addition of 5 mm rainfall ($n = 5$ plots); Few-Large: a monthly addition of 20 mm rainfall ($n = 5$ plots), or Control: only ambient precipitation ($n = 3$ plots) (additional information in Brown & Collins, 2024; Kwiecinski et al., 2020). Rainfall is added as reverse-osmosis water by an overhead system (5 m tall) fitted with sprinkler heads that produce rainfall-quality droplets. By the end of each summer, the Many-Small and Few-Large treatments received the same total amount of additional precipitation above ambient (60 mm), but delivered in different-sized events to alter the intra-annual rainfall regime. Root donuts were installed in 2011, and monitored yearly thereafter.

2.6 | Nitrogen fertilization experiment

Central New Mexico receives atmospheric deposition of ~0.2 g m^{-2} year^{-1} of nitrogen as approximately equal fractions of ammonium and nitrate (Baez et al., 2007). The long-term Nitrogen

Fertilization Experiment examines how chronic nitrogen fertilization that exceeds atmospheric deposition affects a plains grassland initially dominated by galleta grass (*Pleuraphis jamesii*) and blue grama grass (*Bouteloua gracilis*) with black grama grass (*B. eriopoda*) as a subdominant that began to dominate in 2011 (Table 1, additional details in Brown & Collins, 2023; Ladwig et al., 2012; Stursova et al., 2006).

2.6.1 | Experimental design

Twenty $10\,m \times 5\,m$ plots (10 control and 10 treatment) were established in 1995 in a fully randomized design to examine the impacts of N enrichment on above- and belowground processes (Johnson et al., 2003). Treatment plots receive $10\,g\,N\,m^{-2}\,year^{-1}$ as NH_4NO_3 each year prior to the summer monsoon and the remaining serve as ambient controls (Ladwig et al., 2012). Root donuts were installed in 2004 and monitored annually thereafter. All plots were burned in a prescribed fire in June 2003.

2.7 | Fire experiment

Fire is part of the natural regime in many dry grassland and shrubland ecosystems (Kozlowski & Ahlgren, 1974; Wright & Bailey, 1982) and is commonly used as a prescribed management tool (Parmenter, 2008; Wang, Li, et al., 2019). In 2004, following prescribed fire in June 2003, ten root donuts were installed at irregular intervals along a transect in a burned mixed grassland ecosystem co-dominated by *B. gracilis* and *B. eriopoda*, and 10 more were installed across a fire break in unburned mixed grassland ~35 m away. Root donuts were harvested yearly thereafter (Table 1) (see also Brown & Collins, 2023; Burnett et al., 2012). The unburned and burned mixed grasslands also support dropseed (*Sporobolus* spp.) and galleta grass (*Pleuraphis jamesii*). The fire treatment was not applied to the other perturbation experiments described above.

2.8 | Statistical analysis

All analyses used R (version 4.2.1, R Core Team, 2023). Mixed effects general linear models took the form of root biomass as a function of the SPEI aridity index, with the fixed effect of root depth (0–15 or 15–30 cm), and the repeatedly measured, random effect of root donut location. The two sampling depths were nested within the location of each unique root donut (root donut identity), such that each unique root biomass measurement was a repeated, random factor to enable models that assessed the structure of temporal autocorrelation in root biomass data. Statistical models were built using the lme function in package <nlme> to construct nonlinear models using the polynomial function, poly (Bates et al., 2015; Pinheiro et al., 2016). Analyses included the additional fixed factor of ecosystem type (Question 1) or experimental treatment (Questions 2–4). To evaluate Question 1, whether dryland ecosystems significantly differed

in the shape of their climate sensitivity functions (Figure 1), we used control plots from the experiments featured in questions 2–4. The general linear mixed effects model took the form of root biomass ~ soil depth × poly(SPEI) × ecosystem type (levels: shrubland, mixed grassland, plains grassland, or desert grassland) + the random effect of root donut identity. For questions 2–4, we constructed sensitivity functions that incorporated interactions among SPEI and the environmental change treatment (intra-annual rainfall, nitrogen fertilization or fire) by replacing ecosystem type with treatment in the general linear model. For each analysis, we used model selection procedures to evaluate a set of candidate climate sensitivity functions that included either a linear effect of aridity, a quadratic effect, or a cubic effect (e.g. full curve, Figure 1, Rudgers et al., 2018), using the 'poly' function to obtain standardized parameter estimates that are comparable across experiments and conditions. We fit models with maximum likelihood and selected the best model among linear, quadratic or cubic and alternative temporal autocorrelation structures, based on the second-order Akaike information criterion (*AICc*) obtained with package MuMIn (Bartoń, 2018) with a cut off of $\Delta AICc = 2$. To determine the appropriate variance–covariance matrix to account for temporal autocorrelation in the data, we selected models with no autocorrelation, autoregressive 1 or autoregressive 2 in lme. We obtained marginal R^2 values for the best model using the <rsquared> function in piecewiseSEM (Lefcheck, 2016). To decompose significant ($p < 0.05$) statistical interactions (e.g. soil depth × ecosystem type), we used post-hoc Tukey *HSD* contrasts of parameter estimates for SPEI with the <emtrends> or <emmeans> functions (Lenth et al., 2022 p. 202). For all analyses, we visualized results using graphics in ggplot2 (Wickham, 2016) and visreg (Breheny & Burchett, 2017). R scripts are provided as part of the publicly available scripts for this Sevilleta LTER study on GitHub (https://doi.org/10.5281/zenodo.10881402). In all analyses, root biomass per donut volume was transformed using *ln*(root biomass +10) and 6 of 1956 total observations were excluded due to extremely high values in order to meet assumptions of normality of residuals and homogeneity of variances that were evaluated with Q-Q plots, histograms and scatter plots of residuals against predicted values.

3 | RESULTS

3.1 | Do dryland ecosystem types differ in the sensitivity of root production to the mean or interannual variance in aridity?

Of the four dryland ecosystems, we expected root production in the Chihuahuan Desert shrubland, dominated by long-lived, woody roots of creosote bush, to be the least sensitive to aridity because of the low climate sensitivity of aboveground plant production. Unexpectedly, root production in Desert shrubland was the *most* sensitive to aridity among the ecosystems (Figure 2; Tables S1 and S2), and was significantly more sensitive than either the Plains or Mixed grasslands (Table S1: SPEI × Ecosystem, $p < 0.0001$). For
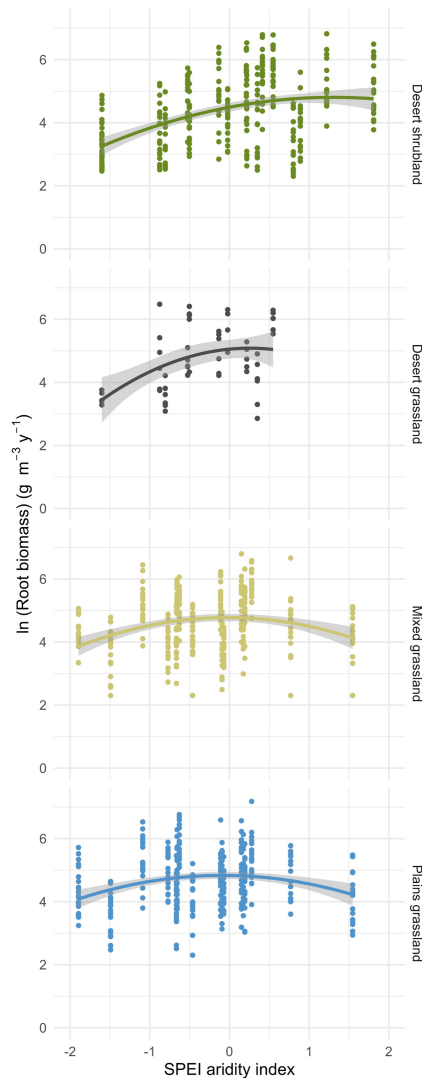
FIGURE 2 Climate sensitivity functions for root biomass (*ln*-transformed) in each of four dryland ecosystem types show data from unmanipulated control root donuts at two soil depths (0–15 and 15–30 cm). Positive values of the SPEI aridity index, integrated over the prior 12 month time period, indicate relatively wet/cool years, whereas negative values indicate relatively dry/hot years. Each point represents a single root donut depth in a single year. The shaded grey region bounds the 95% confidence interval around the nonlinear function estimated by a general linear mixed effects model.

Desert shrubland, the concave, monotonic nonlinear relationship with the SPEI aridity index resulted in two main predictions. First, root production should increase in years with cooler/wetter climates by 68 ($\pm$9 SE) g m^{-3} per unit SPEI (Figure 2, linear parameter estimates in text were back-transformed from *ln*-scale presented in Table S2), with a peak in maximal root production at SPEI value of ~0.5 (Figure 2), slightly above the average over the time series. Second, the significantly concave shape (quadratic term, Table S2) predicted that increasing year-to-year variability in aridity will be costly for root production in Desert shrubland and also in the other ecosystem types (Figure 2; Table S1: SPEI^2, $p = 0.0348$; SPEI$^2 \times$ Ecosystem, n.s.), because larger declines in root biomass

occurred in drier-than-average years than in wetter-than average years. Therefore, increases in year-to-year variability in aridity (which increases probabilities of wetter and drier extreme years equally) will have the net effect of reducing root production in all of the focal ecosystems.

In the Desert grassland, dominated by black grama grass at >80% vegetation cover, the climate sensitivity function predicted high sensitivity to both mean and variance in aridity (Table S2), with cooler/wetter climates predicted to increase root biomass by 59 ($\pm$38 SE) g m^{-3} per unit SPEI, which was not significantly different from the Desert shrubland due to the large uncertainty in the linear parameter estimate (Table S2), perhaps a function of the shorter time series for this ecosystem relative to the others. Coincident with their stronger sensitivity to mean aridity and the ongoing shift to a more arid climate, both desert ecosystems had significant long-term declines in root production over the time series (Table S3; Figures S2 and S3), although an uptick in root biomass during the most recent year of observation suggests potential for ongoing change and the need for continued monitoring.

In contrast to the two Desert ecosystems mentioned above, both Plains and Mixed grasslands had similar climate sensitivity functions (Figure 2) that predicted weaker sensitivities of root production to aridity, as indicated by linear terms that were less than half the magnitude of those in the shrubland (Table S2). The climate sensitivity functions signalled that cooler/wetter climates should not increase root production in the Plains grassland (slope of 10 ($\pm$9 SE) g m^{-3} per unit SPEI) and only increase roots in the Mixed grassland by 21 g m^{-3} per unit SPEI and with high uncertainty ($\pm$10 SE). Neither Plains nor Mixed grasslands had a significant temporal trend in root production (Table S3; Figure S2). However, the monotonic, concave relationship with SPEI in all of the grassland ecosystem types indicated a threshold effect similar to the Desert shrubland, in which negative SPEI values were associated with larger declines in root biomass than positive values were associated with increases in root biomass (Table S2, quadratic parameter estimates).

Beyond sensitivity to aridity, root production varied with depth differently among the ecosystem types (Table S1, Ecosystem × Depth, $p = 0.001$), and had significant temporal autocorrelation (autoregressive 2 variance–covariance matrix was the best fit; SPEI had no temporal autocorrelation Figure S3). Desert shrubland and Desert grassland both had ~130% more root production at the deeper (15–30 cm) depth than at 0–15 cm. In contrast, the Plains grassland had just 37% more roots at deeper depth, and the mixed grassland ecosystem had 12% *less* root production at deeper depth.

3.2 | Does the intra-annual rainfall regime alter sensitivity of root production to mean or variance in aridity?

We predicted infrequent but large-sized monsoon rainfall events would reduce the overall sensitivity of root production to

background aridity by increasing plant water availability in the Desert grassland ecosystem. However, 10 years of rainfall regime manipulations did not significantly influence the sensitivity of root production to background climate aridity (Figure 3a; Table S2; Treatment × SPEI $F = 1.2$, $p = 0.30$; Treatment × SPEI^2 $F = 0.9$, $p = 0.40$). Across rainfall treatments, root biomass significantly increased in wetter/cooler years (linear parameters, Table S2), with a consistently saturating concave relationship (quadratic parameters, Table S2), indicating net declines of root biomass under increasing variance in annual aridity regardless of the intra-annual rainfall treatment (e.g. Figure 1a). Root production declined non-significantly over time under all precipitation regimes (Table S3; Figure S2).

3.3 | Does nitrogen fertilization alter sensitivity of root production to mean or variance in aridity?

Similar to the 10-year intra-annual rainfall manipulation, chronic nitrogen addition in the Plains grassland did not significantly alter the sensitivity of root production to the mean or variance in background climate aridity (Figure 3b). Root biomass peaked at average aridity over the time series (SPEI ~0, Figure 3b) and was predicted to decline with greater variability in aridity (significantly concave, Table S2; SPEI^2 $F = 8.5$, $p = 0.004$) but without sensitivity to mean annual aridity (SPEI $F = 0.86$, $p = 0.35$). Root biomass tracked aridity in similar ways regardless of nitrogen fertilization (Treatment × SPEI $F = 0.39$, $p = 0.54$; Treatment × SPEI^2 $F = 0.09$, $p = 0.76$). In both fertilized and control plots, root biomass was 20% lower at 0–15 cm (mean [95% CL]: 102.9 g m^{-3} [86.3–122.4]) than at 15–30 cm (128.5 g m^{-3} [108.1–152.4]; Depth, $F = 5.84$, $p = 0.027$), and did not alter the lack of responsiveness of root biomass to fertilization (Depth × Nitrogen treatment, $F = 0.43$, $p = 0.52$). Rooting depth also did not alter the climate sensitivity of root production, as both deep and shallow root biomass were similarly sensitive to aridity (Depth × SPEI $F = 0.44$, $p = 0.50$; Depth × SPEI^2 $F = 0.02$, $p = 0.86$).

3.4 | Does fire alter the sensitivity of root production to mean or variance in aridity?

For 17 years following a prescribed burn in 2003, the chronic effects of fire increased the sensitivity of root production to mean annual aridity by more than twofold (Figure 3c; Table S2: Fire × SPEI $F = 11.0$, $p = 0.0009$). Fire did not, however, alter the sensitivity of root production to variance in aridity, as estimated by the similar quadratic terms of the burned and unburned climate sensitivity functions (Figure 3c; Table S2: Fire × SPEI^2 $F = 0.1$, $p = 0.82$). Fire also affected mean root production but in opposing directions depending on soil depth (Table S2: Fire × Depth $F = 6.2$, $p = 0.0021$). In 0–15 cm soils, fire increased root biomass by 21%, but in 15–30 cm soils, fire reduced root biomass by 17% relative to unburned areas. Root

biomass was highly variable from year to year in the Mixed grassland but did not significantly decline over time (Figure S3; Table S2, Year, $p = 0.78$).

4 | DISCUSSION

4.1 | Contrasting aboveground and belowground sensitivities to climate

Understanding differential sensitivities of aboveground and belowground production to climate can help to improve predictions on future nutrient and carbon dynamics. Previous studies have suggested that the responses of aboveground primary production to climate or other environmental factors rarely match the responses in belowground production (e.g. Brown & Collins, 2023; Hollister & Flaherty, 2010; Ladwig et al., 2012; Wang, Gao, et al., 2019). Across the focal sites in central New Mexico, aboveground plant biomas in Desert and Plains grasslands had cubic sensitivities to the SPEI aridity index (e.g. Figure 1, Rudgers et al., 2018), which signalled that effects of increasing variance in aridity on aboveground plant biomas will depend on the climate mean. However, aboveground plant biomas in Desert shrubland was weakly and only linearly related to aridity, indicating no sensitivity to variance in aridity (Rudgers et al., 2018). In contrast to these aboveground patterns, here we report the largest sensitivity of belowground primary production to aridity in the Desert shrubland, which was 40% more sensitive to mean aridity than in the Desert grassland, 350% more sensitive than in the Mixed grassland, and 730% more sensitive than in the Plains grassland (linear climate sensitivity function parameters, Table S2). In addition, climate sensitivities predicted that continued increases in year-to-year variance in aridity (Maurer et al., 2020; Rudgers et al., 2018) would cause net declines in belowground plant production in all four ecosystems (significant quadratic parameters, Table S2) due to the concave nonlinear relationships between annual root biomass and the annual aridity index (Figure 2).

The high sensitivity of belowground production in creosote bush-dominated Desert shrubland was surprising given the limited sensitivity of aboveground production to interannual climate for this ecosystem (Rudgers et al., 2018). Creosote bush is a very long-lived shrub common throughout the North American warm deserts. In a 5-year-long drought experiment that reduced growing season precipitation by 50%, aboveground production of creosote bush was more or less unchanged while associated grasses declined more than 60% (Baez et al., 2013). In contrast, Brown and Collins (2023) found that shallow root production (0–30 cm) in creosote bush shrubland was far more temporally variable than in adjacent Plains or Desert grasslands. Creosote bush develops both shallow and deep root systems (Gibbens & Lenz, 2001), and therefore has access to soil water sources that are unavailable to grasses, which typically have root systems restricted to the top 30 cm of soil (Kurc & Small, 2007). Our climate sensitivity functions newly suggest that shallow root
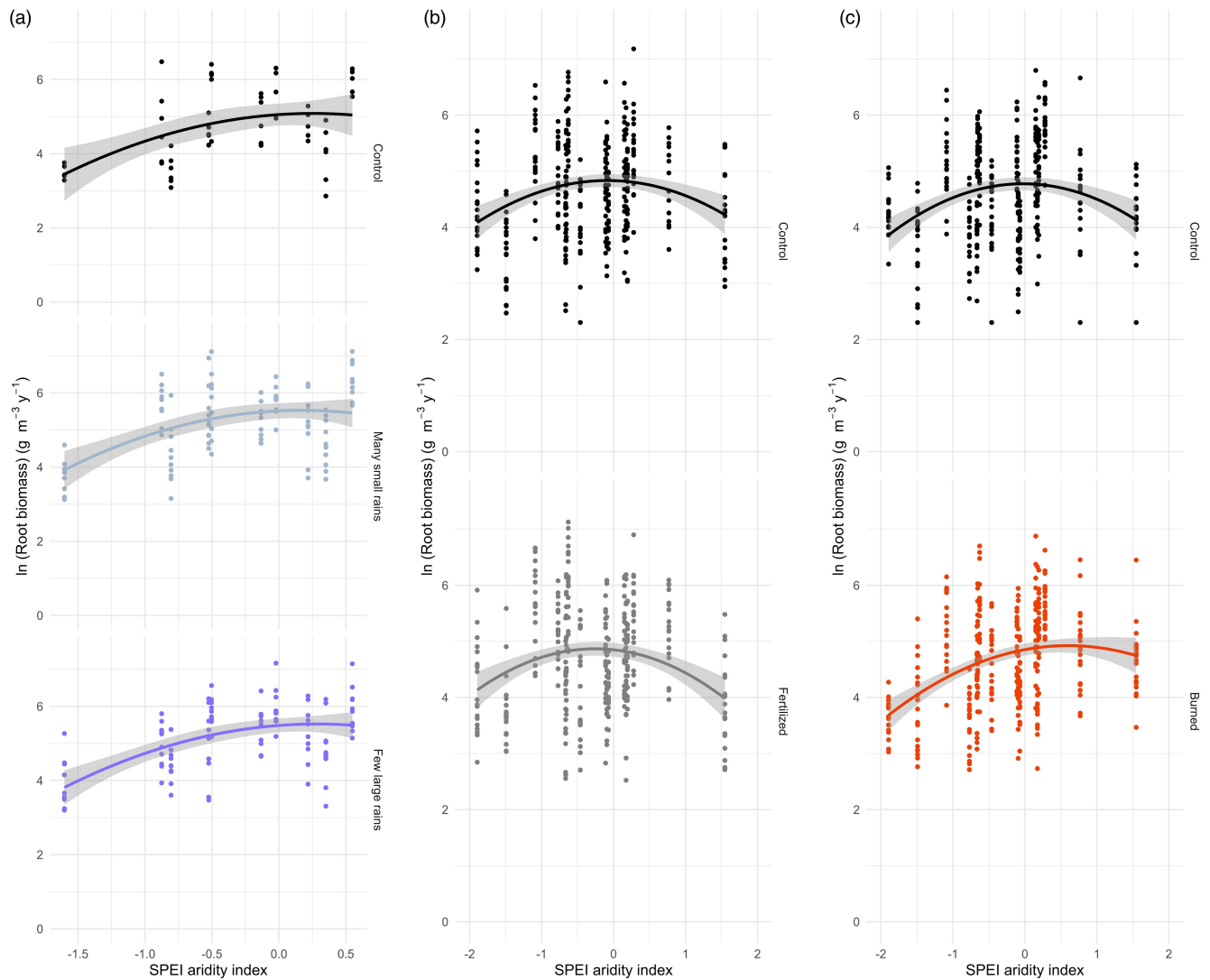
FIGURE 3 Root biomass (*ln*-transformed) increased in wetter years, but climate sensitivity functions did not differ among manipulations of the (a) intra-annual precipitation regime, including no water addition (Control), or with 20 mm additional rain per month (July to September) either as Few, large rains or Many, small rains. Root biomass was significantly greater ($p = 0.04$), on average, under few, large rains than in controls with no water addition. Climate sensitivity functions did not shift with (b) chronic nitrogen fertilization. However, root biomass was more than twice as sensitive to annual aridity in burned than unburned areas (c), although the quadratic sensitivity to variance in aridity was similar for burned and unburned areas (Table S2). Each point represents a single root donut depth sample in a single year. Lines show fitted regressions that account for temporal autocorrelation. Shaded areas show the 95% confidence intervals.

production in creosote bush Desert shrubland tracks interannual variability in aridity.

4.2 | The relative importance of environmental perturbations to climate sensitivities of root production

Only the perturbation of fire altered the sensitivity of root production to climate aridity. A single prescribed burn imposed in 2003 magnified the long-term sensitivity of belowground plant production to aridity, a result that has important implications for future fire

management in dry grassland ecosystems (White & Loftin, 2000). In contrast to the influence of fire, 10 years of rainfall regime manipulations had no significant effect on the sensitivity of root production to background climate aridity, a result consistent with previous work that showed dry grasslands were relatively insensitive to the size and frequency of rainfall events (Wilcox et al., 2015) instead responding primarily to total seasonal rainfall (R. F. Brown & S. L. Collins, unpublished data). Zhang et al. (2021) also reported no differences in belowground sensitivity to increases or decreases in precipitation. However, despite the lack of influence on the climate sensitivity of root production, rainfall additions, regardless of the few-large or many-small event regime, generally increased average root biomass

(S. L. Collins, unpublished data). This result was consistent with the pattern of greater root biomass in cooler/wetter years in the desert grassland (Figure 2), where the rainfall regime experiment occurred.

We originally predicted that nitrogen addition would reduce the sensitivity of root production to aridity by making inorganic soil resources readily available to plants and reducing the need for large root systems in low-nitrogen dryland soils (Kieft et al., 1998; White et al., 2004). Previous evidence from the Plains grassland ecosystem suggested that nitrogen becomes the limiting factor to plant growth following a wet season (Ladwig et al., 2012). However, like rainfall additions, nitrogen fertilizer additions had no influence on the sensitivity of root production to aridity, which was consistently smaller under both the wettest/coolest and driest/hottest conditions. In contrast to prior results, we did not detect significant long-term effects of nitrogen fertilization on root biomass at any soil depth (Carrara et al., 2018) or impacts that flipped in direction over time (Vourlitis et al., 2021). However, our results were generally consistent with Ma et al. (2023), who reported that nitrogen fertilization increased the temporal stability of root production in an alpine meadow.

We used long-term manipulations of the single environmental perturbations of fire, intra-annual rainfall regime or nitrogen to evaluate their potential to interact with background climate; however, future research ought to consider factorial environmental perturbations because many environmental changes are occurring simultaneously (Crain et al., 2008; Rillig et al., 2019). Factorial manipulations provide unique windows on the non-additive impacts of multiple environmental perturbations, impacts that cannot be uncovered using single-factor experiments (Folt et al., 1999), such as those reported here. Study of the interactive effects of multiple aspects of global environmental change could strongly alter future predictions for root production and represents an important area for future research (Komatsu et al., 2019).

4.3 | Belowground dynamics at ecosystem state transitions

The focal dryland ecosystems, while geographically proximal, are undergoing state transitions over time (Zinnert et al., 2021). Under future climates, we expect the Chihuahuan Desert shrubland to expand to replace Chihuahuan Desert grassland (Caracciolo et al., 2016; D'Odorico et al., 2010; Drees et al., 2023), and Desert grassland to overtake Plains grassland (Chung et al., 2019; Collins et al., 2020). For example, even during the course of this study, black grama grass overtook blue grama grass in the Plains grassland Nitrogen Fertilization experiment, effectively converting this ecosystem toward Desert grassland (S. Collins, unpublished data). If these state transitions continue to progress, then our results suggest that belowground plant production will become increasingly more sensitive to climate aridity, with increasingly greater declines occurring in hot/dry years. Because most soil organic carbon is derived from belowground plant production (Sokol & Bradford, 2019), amplified

sensitivity could translate to altered soil carbon dynamics that feed back to cause more flashy CO_2 emissions, already a hallmark of dryland ecosystems (Ahlstrom et al., 2015; Fawcett et al., 2022; Poulter et al., 2014). Although the regional climate is becoming increasingly more variable in aridity over time (Gutzler & Robbins, 2011; Maurer et al., 2020), we did not detect patterns that indicate that ecosystem state transitions would alter the sensitivity of root production to increasing climate *variance* because in all cases, the nonlinear aspect of climate sensitivity (Table S2) was consistent across ecosystem types and environmental perturbation treatments. Clearly, additional experiments to consider multiple environmental perturbations and larger spatial scales than our local-scale work are needed to refine such predictions.

4.4 | Limitations and future directions

Our study has some limitations. First, we used the large natural variability in climate in our region as a stand-in for direct climate manipulations, which are difficult and expensive to achieve on large scales and over long timeframes (Breshears et al., 2009). Thus, the long-term climate sensitivities determined in this study are correlations and can only suggest predictions about the influence of future increases in the mean and variance of aridity. Importantly, inference on outlier climate conditions (very arid or wet years) is limited to the range of observed climate; thus, continued long-term monitoring is critical to detect such rare extreme events. Second, our experiments, while long-term, may still be too short to detect significant differences among ecosystems or treatments in the sensitivity of root production to variance in aridity because large datasets are required to accurately estimate nonlinear relationships (Peters et al., 2004; Ridolfi et al., 2011). For example, the Desert grassland, which had the shortest time series, also had the most uncertainty in the climate sensitivity parameter estimates, which suggests that continued monitoring will increase our resolution on climate sensitivity. Our study also confounded treatments with ecosystem types: we applied fertilizer to the Plains grassland, manipulated the rainfall regime in the Desert grassland, and studied the effects of prescribed fire in the Mixed grassland at the ecotone between these grassland types. More robust conclusions could be derived with fully factorial replication of treatments across ecosystem types. Future studies might also glean new insight through separate estimates of root biomass for individual plant species, particularly dominants that cover large surface areas. Estimates of changes in belowground root architecture and morphology, including climate sensitivity in allometric relationships with biomass (e.g. Rudgers et al., 2019), could complement recent global databases that provide new insights on how root morphology varies geographically, coincident with climate (Tumber-Dávila et al., 2022). In addition, seasonal dynamics may be important. For example, in a prior study following the same 2003 prescribed burn, root production in the burned area was greater than in the unburned area early in the spring season, but by summer monsoon (August), root growth increased rapidly in unburned

conditions, exceeding that of burned (Burnett et al., 2012). Finally, because our focal ecosystems represent ~55 million ha of the south-western US, our results have potentially large-scale implications. However, root production data are needed from replicate sites across the geographic range of these ecosystems to confirm general-izability to the region. Thus, future studies could combine long-term empirical measurements of aboveground production, belowground production, and net ecosystem exchange across ecosystems (e.g. Anderson-Teixeira et al., 2011) to develop integrated assessments of carbon dynamics and ecosystem sensitivity to changes in seasonal and annual variability in climate.

5 | CONCLUSIONS

In summary, we found that belowground production significantly and nonlinearly tracked interannual variation in climate variability as measured by the aridity index, SPEI. However, among three common dryland environmental disturbances—altered rainfall regime, chronic nitrogen fertilization and fire—fire had the largest influence on the sensitivity of belowground production to climate aridity, amplifying the sensitivity of root production to climate relative to unburned controls. Across four common dryland ecosystem types, the Desert shrubland, dominated by creosote bush, had the greatest sensitivity of root production to aridity, but all ecosystems had patterns that signalled declines in root production caused by increasing interan-nual variability in aridity. Ongoing transitions among ecosystems, as Desert grassland replaces Plains grassland and Desert shrubland replaces Desert grassland, may ultimately amplify the sensitivity of belowground carbon inputs to future climate variability. Our results yield new insight into how environmental changes will interact with climate variability to alter belowground carbon inputs in widespread, dryland ecosystems.

CONFLICT OF INTEREST STATEMENT

The authors have no relevant financial or non-financial interests to disclose.

PEER REVIEW

The peer review history for this article is available at https://www.webofscience.com/api/gateway/wos/peer-review/10.1111/1365-2745.14319.

DATA AVAILABILITY STATEMENT

Our manuscript was derived from data as part of a long-term ecological research programme conducted on federal land. We share the results of our work with federal land managers and any other interested parties. Analysis scripts and data used in this study are available on Zenodo: https://doi.org/10.5281/zenodo.10881402 (Rudgers, 2024). The latest datasets are archived in the Environmental Data Initiative repository: https://doi.org/10.6073/pasta/4cc7f6b387744efd525f15c71dcb9315 (Collins, 2024).

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SUPPORTING INFORMATION

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

Figure S1: Diagram of a root donut.

Figure S2: Temporal patterns of root biomass ($g\,m^{-3}\,year^{-1}$), in four dryland ecosystem types in central New Mexico at the SNWR.

Figure S3: Temporal patterns of the Standardized Precipitation Evapotranspiration Index for four dryland ecosystem types in central New Mexico at the SNWR, represented by climate data from two meteorological stations, one situated at the interface of desert grassland and shrubland, the other between mixed grassland and plains grassland.

Table S1: Statistical results for the comparison of climate sensitivity functions in annual root biomass among four dryland ecosystem, showing results from the best model based on *AICc* model selection procedures.

Table S2: Parameter estimates including linear, quadratic and/or cubic estimates for climate sensitivity functions relating annual root biomass to the annual Standardized Precipitation Evapotranspiration Index (SPEI aridity index) with 95% confidence limits (CL).

Table S3: Results of time series analysis for change in *In* root biomass ($g\,m^{-3}\,year^{-1}$) over time, 2005 to 2021, across four dryland ecosystem types in central New Mexico at the SNWR.