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Sensitivity of soil organic matter to climate and fire in a desert grassland

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Abstract Drylands contain a third of the organic carbon stored in global soils; however, the long-term dynamics of soil organic carbon in drylands remain poorly understood relative to dynamics of the vegetation carbon pool. We examined long-term patterns in soil organic matter (SOM) against both climate and prescribed fire in a Chihuahuan Desert grassland in central New Mexico, USA. SOM concentration was estimated by loss-on-ignition from soils at 0–20 cm depth each spring and fall for 25 years (1989–2014) in unburned desert grassland and from 2003 to 2014 following a prescribed fire. SOM concentration did not have a long-term trend but fluctuated seasonally at both burned and unburned sites, ranging from a minimum of 0.9% to a maximum of 3.3%. SOM

concentration declined nonlinearly in wet seasons and peaked in dry seasons. These long-term results contrast not only with the positive relationships between aboveground net primary production and precipitation for this region, but also with previous reports that wetter sites have more SOM across drylands globally, suggesting that space is not a good substitute for time in predicting dryland SOM dynamics. We suggest that declines in SOM in wet periods are caused by increased soil respiration, runoff, leaching, and/or soil erosion. In addition to tracking natural variability in climate, SOM concentration also decreased 14% following prescribed fire, a response that magnified over time and has persisted for nearly a decade due to the slow recovery of primary production. Our results document the surprisingly dynamic nature of soil organic matter and its high sensitivity to climate and fire in a dry grassland ecosystem characteristic of the southwestern USA.

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Introduction

Carbon storage in dryland ecosystems have important effects on the global carbon (C) cycle and future climate change (Lal 2019; Plaza et al. 2018b).

Drylands comprise one of the largest terrestrial biomes on Earth, currently covering $\sim 45\%$ of land surface and are projected to expand by 5–11% by the end of this century (Huang et al. 2016; Lal 2019; Právělie et al. 2019; Schimel 2010). Given the large area (~ 67 million km²), dryland soils store about 470 Pg organic C in the top meter of soil (Plaza et al. 2018b), which accounts for up to a third of the global soil organic carbon (SOC) pool in the top meter (Ciais et al. 2013; Friedlingstein et al. 2019; Jackson et al. 2017; Plaza et al. 2018b). This pool size is comparable to that of the atmosphere C pool before industrialization (589 Pg; Ciais et al. 2013). Recent studies suggest that ecosystem processes in drylands are highly dynamic (de Graaff et al. 2006; Li et al. 2015; Plaza et al. 2018a), and thus, they play a critical role in determining the trend and variability of the global C cycle (Ahlström et al. 2015; Poulter et al. 2014). However, most studies have focused on the dynamics of the relatively small vegetation C pool in drylands (65–170 Pg; Lal 2019), with much less attention paid to SOC or soil organic matter (SOM) (Lal 2019; Luo et al. 2017).

Our understanding of dryland carbon dynamics can be improved with better knowledge of long-term dynamics in SOM and its responsiveness to environmental factors, such as climate change and fire. Many studies have examined the sensitivity of the dryland C cycle (e.g., primary production and soil respiration) to climate (e.g., precipitation) (Ahlström et al. 2015; Biederman et al. 2017; Knapp and Smith 2001; Maurer et al. 2020; Poulter et al. 2014; Xu et al. 2004). These studies suggest that the dryland C cycle is accelerated by high precipitation and temperature but slowed by drought. Additional evidence suggests positive relationships between SOC and climate across drylands (Burke et al. 1989; Gaitán et al. 2019). Spatial relationships, however, may be poor predictors of SOC responses to climate within a site over time because spatial relationships confound climate with ecosystem state (e.g., vegetation type and soil physiochemical properties). Although vegetation change within a site can be relatively rapid in response to climate and fire (e.g., Collins et al. 2020), soil physical properties will not change appreciably within a site over the timescale of decades (Knapp et al. 2017). As a consequence, temporal patterns, which are strongly influenced by climate variability and vegetation change, but much less by changes in ecosystem state, should be more useful than spatial relationships for

predicting SOM storage and dynamics under future climate scenarios. (Knapp et al. 2017; Rudgers et al. 2018). However, temporal relationships between SOM and climate have rarely been explored in drylands, nor in many other terrestrial biomes, primarily due to a lack of long-term (i.e. decades or longer) observations.

During the past two decades, ecological processes, such as primary production, have been increasing recognized to respond not only to the climate mean but also to climate variance (Gherardi and Sala 2019; Haverd et al. 2017; Hsu et al. 2012; Knapp et al. 2017; Maurer et al. 2020; Rudgers et al. 2018; Vázquez et al. 2017). The effect of climate variance on an ecological variable can be predicted from the relationship with climate over time via “climate sensitivity functions” (Rudgers et al. 2018). A linear sensitivity function indicates a response of the ecological variable to a change in mean, whereas nonlinear functions indicate responsiveness to both mean and variance (Rudgers et al. 2018; Vázquez et al. 2017). This approach has been used to explore the effect of climate variability on primary production (Gherardi and Sala 2019; Rudgers et al. 2018) but has not yet been applied to long-term data on SOM pools. Given projected increase in climate variability in the future (IPCC 2012; Pendergrass et al. 2017), it is vital to explore whether and how future changes in climate variability will affect SOM in drylands.

Environmental change includes shifting disturbance regimes in addition to changes in climate (Collins et al. 2017; IPCC 2012). Fire is an increasingly important disturbance in dryland ecosystems because the probability of fire increases during periods of drought (Collins et al. 2017; van der Werf et al. 2017; Westerling et al. 2006). Burning releases on average 2.2 Pg C year⁻¹ from global terrestrial ecosystems (Pellegrini et al. 2018; van der Werf et al. 2017), offsetting two-thirds of the annual land C sink (i.e. 3.2 Pg year⁻¹; Friedlingstein et al. 2019). Fire consumes plant live biomass as well as litter and thus often decreases organic inputs to soils (Pellegrini et al. 2018). Postfire recovery of dominant species may take more than a decade in drylands (Ladwig et al. 2014; Parmenter 2008). Therefore, fire may have long-term effects on drylands SOC (Pellegrini et al. 2018), but the dynamics of SOC recovery following fire are not yet well understood (Alexis et al. 2012; Sawyer et al. 2018). In addition, previous studies suggest that

fire interacts with climate to influence plant community structure and primary production in drylands (Collins et al. 2017). Whether or not fire interacts with climate to affect long-term SOM dynamics in drylands, however, remains unknown.

In this study, we examined patterns of SOM concentration and their relationship to climate and fire in a Chihuahuan Desert grassland, using a long-term dataset (1989–2014, prescribed fire occurred in 2003). Based on the known responses of primary production to climate at this site (Rudgers et al. 2018) and the previously reported positive relationship between SOC and precipitation across drylands (Burke et al. 1989; Gaitán et al. 2019), we hypothesized that SOM would track current season climate and therefore would be positively and nonlinearly related to precipitation and negatively nonlinearly related to aridity (Hypothesis Ia). Alternatively, we hypothesized that SOM would not track current season climate (Hypothesis Ib) due to the slow turnover of SOM and legacy effects of primary production (Friedlingstein et al. 2019; Luo et al. 2019; Sala et al. 2012). Second, we hypothesized that prescribed fire would decrease SOM and the effect size would increase with the level of drought (Hypothesis II), because postfire recovery of plant growth is slower in dry years than in wet years (Collins et al. 2017; Ladwig et al. 2014). Third, we hypothesized that effect size of prescribed fire on SOM would increase with time (Hypothesis III), because postfire declines in plant growth can last for more than a decade (Parmenter 2008). To test these hypotheses, we used long-term data from a Chihuahuan Desert grassland and climate sensitivity function theory to quantify long-term patterns in SOM dynamics in response to fire and climate variability.

Materials and methods

Study site

This study was conducted in a Chihuahuan Desert grassland in the Sevilleta National Wildlife Refuge (SNWR, latitude: 34° 20' N, longitude: 106° 43' W), located in Socorro County, central New Mexico, United States. The grassland had been grazed extensively for decades (Collins et al. 2017), but has been protected from grazing since the SNWR was

established in 1973. The grassland was co-dominated by *Bouteloua eriopoda* and *B. gracilis*. Other common species include shrubs or subshrubs (e.g., *Yucca glauca* and *Ephedra torreyana*) and a mixture of subdominant grasses (e.g., *Pleuraphis jamesii*) and forbs (e.g., *Cryptantha crassicaarpa*) (Mulhouse et al. 2017). Vegetation covers about 75% of the soil surface area. Soils are Typic Haplargids derived from piedmont alluvium, with 70% sand, 9% silt, and 21% clay in the upper 20 cm (Buxbaum and Vanderbilt 2007), where the largest root biomass occurs (Kurc and Small 2004).

The site has a mean annual precipitation of 234 mm, more than half of which (~ 150 mm) occurs during the convective storms of the summer monsoon (Anderson-Teixeira et al. 2011; Gosz et al. 1995). Mean annual temperature at the site is ~ 13 °C, with mean monthly maximum/minimum temperatures ranging from 36/15 °C in June to 11/– 9.5 °C in January during 1989–2013 (Collins et al. 2017).

Dataset description

The main data set used in this study includes long-term measurements of SOM concentration at 0–20 cm mineral depth in desert grassland, which together with the metadata are available as White and Moore (2016). SOM concentration was measured twice per year (May/June and September/October) in most years (37 times) in an unburned grassland starting in April 1989 through May 2014, and 23 times in an adjacent burned grassland from June 2003 through May 2014. In each measurement period, three to 12 (mostly 10) composite soil samples at 0–20 cm mineral depth were collected using a soil core (4 cm or 4.2 cm diameter by 20 cm long) from permanently located quadrats within three to five (depending on year) 30 × 30 m areas. In the burned grassland, soils were collected from two quadrats in each of five 30 × 30 m burned plots starting in June, 2003. In total, 613 composite soil samples were collected for measuring SOM concentration.

All composite soil samples were placed into an ice chest and transported to the University of New Mexico, where they were sieved (2 mm) to remove obvious live roots, then stored at 5 °C. Gravimetric soil moisture content of each fresh sample was determined by mass loss upon heating at 105 °C for 24 h. SOM concentration was determined by loss-on-

ignition (LOI) from oven-dried samples placed in a muffle furnace and brought to 500 °C for 2 h. Water holding capacity was determined by saturating ~ 50 g sieved soil in a funnel with deionized water for 30 min, and then allowing the sample to drain by gravity for 30 min. The drained soil was transferred to pre-weighed soil tins and dried in an oven at 105 °C for 24 h. The water lost upon drying was the water-holding capacity of the soil sample.

To explore whether temporal patterns in SOM tracked temporal patterns of primary production, we used long-term (2000–2014) observations of above-ground net primary production (ANPP) in nearby desert grassland (Rudgers et al. 2018) and another long-term (2004–2014) ANPP data set in burned and unburned grassland that was established to monitor grassland recovery following the prescribed fire in 2003. ANPP was recorded by species as peak biomass in each year (i.e. September) in 22–106 permanently located 1-m² plots. Biomass was calculated allometrically via linear regression models with intercepts through the origin (see Rudgers et al. 2019 for details). All data and R code are freely accessible via Rudgers et al. (2020).

Climate variables

To explore climate relationships with SOM and primary production, we used both precipitation and the Standardized Precipitation Evapotranspiration Index (SPEI), a metric that explicitly incorporates temperature via potential evapotranspiration (Vicente-Serrano et al. 2010). Positive SPEI values indicate much wetter (more humid) conditions. To pair with the SOM measurements, SPEI was calculated for spring (December–May) and fall (May–October) based on the prior 6 month period (Rudgers et al. 2018) with meteorological data measured at the site. Precipitation in spring and fall were calculated as the cumulative precipitation amount during February–May and June–October, respectively.

Statistical analyses

Before statistical analyses, we checked for possible outliers in the SOM dataset. We excluded one extremely high value (i.e. 5.8% vs. 0.5–4.2% of the rest) from further analyses. Long-term patterns in SOM and primary production and their relationships to

climate variables and responses to prescribed fire were examined via model selection procedures with linear mixed-effects models, generally according to Rudgers et al. (2018) and Zuur et al. (2009).

Specifically, we first constructed a linear mixed-effects model where the fixed component contained all explanatory variables and as many interactions as possible, which yields the *beyond optimal* model (Zuur et al. 2009). To examine long-term pattern in SOM, sampling time was used as the only fixed variable. A linear model was used because we wanted to detect unidirectional trends (i.e. increase or decrease) in SOM over the studied period. To test Hypotheses Ia and Ib about the relationship between SOM and climate, climate factor (i.e., SPEI or precipitation) and its cubic form were used as the fixed component. To test Hypotheses II and III about the interactive control of climate (or time) and fire on SOM, a climate factor (or time) and its cubic form, site, as well as their interactions were used as the fixed components.

Second, we used the beyond optimal model to identify the optimal structure of the random component using the Akaike's Information Criterion for small sample sizes (*AICc*) in package “MuMIn” version 1.43.17 (Barton 2020) in R version 3.6.1 (R Core Team 2017). The optimal random component was a best combination of sampling location (quadrat nested in plot), sampling year, and first-order autoregressive correlation structure (i.e. with smallest *AICc*). Sampling location was used to account for the possible non-independence of repeated measurements within a quadrat in a plot. Sampling year was considered as a random factor to account for the possible non-independence of repeated measurements within a year (Rudgers et al. 2018). First-order autoregressive correlation was used to account for temporal autocorrelation in the repeated measurements (Rudgers et al. 2018; Zuur et al. 2009).

Once the optimal random structure was determined, we then determined the optimal fixed structure. We used the “dredge” function in R package “MuMIn” version 1.43.17 (Barton 2020) to generate all possible combinations of fixed variables from the global model. Among the combinations of fixed variables, we selected the combination of fixed variables with the minimum *AICc* value as our optimal fixed structure. Finally, we presented the optimal models using REML estimation (Zuur et al. 2009). All linear mixed model

analyses were performed with the R package “nlme” version 3.1.148 (Pinheiro et al. 2017). Fits of linear mixed models to observations were visualized using the R packages “visreg” version 2.7.0 (Breheny and Burchett 2017) and “lme4” version 1.1.23 (Bates et al. 2014).

We also examined differences in soil measurements between two adjacent sampling times and between the unburned and burned sites at each sampling time using the “emmeans” package (Lenth et al. 2018) in R. Relationships among climate variables, SOM, and soil water were explored using Pearson correlation. Finally, we examined the relationship between SOM (dependent variable) and the current or previous season’s ANPP (independent variable) via regression analyses applied to the mean values for each sampling time because vegetation and SOM data were not derived from the same quadrats. We compared model fit using the second order Akaike Information Criterion (AICc).

Results

Temporal patterns in climate

Annual precipitation varied between 107.3 mm and 348.7 mm (mean 232.0 mm). Precipitation varied between 2.2 mm and 86.6 mm (mean 37.2 mm) in spring and between 44.0 mm and 244.6 mm (mean 139.9 mm) in fall (Fig. 1a). Precipitation did not show a long-term trend on an annual scale ($P = 0.75$), in spring ($P = 0.39$), or in fall ($P = 0.87$) (Fig. 1a). Similar temporal patterns were observed for SPEI (Fig. 1a) due to the significant positive correlation between SPEI and precipitation ($r = 0.54$, $P < 0.001$; Fig. S1).

Temporal patterns in SOM and soil water measurements

SOM varied significantly across seasons from 1.0 to 3.3% (mean 1.7%) in the unburned grassland and from 0.9 to 2.0% (mean 1.6%) in the burned grassland (Fig. 1b; Table 1). However, there was no long term, unidirectional change in SOM either in the unburned grassland ($\phi = 0.16$, $P = 0.67$) or in the burned grassland ($\phi = 0.15$, $P = 0.10$) (Fig. 1b). In the unburned grassland, SOM was considerably greater

in July 1996 (i.e. 3.31%) than in other times (0.98–2.39%) (Fig. 1b; Table 1). However, after these high values were removed, there was still no temporal trend in SOM under unburned conditions ($P = 0.40$). Soil water holding capacity and water content also varied considerably with time (Fig. S2). Neither measure of soil water significantly correlated with SOM in either grassland (Fig. S1), except for a weakly positive correlation between SOM and water holding capacity in the burned grassland ($r = 0.25$, $P < 0.001$; Fig. S1).

Relationships between SOM, ANPP, and climate

In the unburned grassland, SOM declined nonlinearly in seasons with greater precipitation, with no apparent change when precipitation was less than ~ 160 mm but a sharp decrease when precipitation crossed this threshold (marginal $R^2 = 0.23$, $P < 0.001$, $AICc = 168.1$; Fig. 2a). This pattern was opposite to the positive relationship between ANPP and precipitation, which had a concave shape during dry periods and a convex shape during wet periods (marginal $R^2 = 0.25$, $P < 0.001$, $AICc = 10472.2$, Fig. 2c). In comparison to precipitation, SPEI explained slightly more of the variation in both SOM (marginal $R^2 = 0.27$, $AICc = 195.1$) and ANPP (marginal $R^2 = 0.30$, $AICc = 10364.4$) in the unburned grassland ($P < 0.001$; Fig. 2b, d), likely because of the additional effects of heat on soil moisture that are not captured by precipitation alone. SOM declined at greater SPEI values, with the most SOM during hot/dry periods, the least SOM during cool/wet periods, and little fluctuation in SOM during normal climate periods (Fig. 2b). In contrast, ANPP increased with cool/wet conditions at high values of SPEI, but additionally had a convex relationship with SPEI during dry periods, which is indicative of benefits to ANPP of increasing interannual variance in SPEI, and a concave shape during wet periods, which signals declines in ANPP under increasing interannual variance in SPEI (Fig. 2d).

Fire effects on SOM along temporal and climate gradients

Fire reduced SOM by 14% on average, but fire effects varied from -15 to 46% relative to unburned conditions over time (Fig. 3; Table 1). However, fire effects on SOM increased over time, as indicated by a

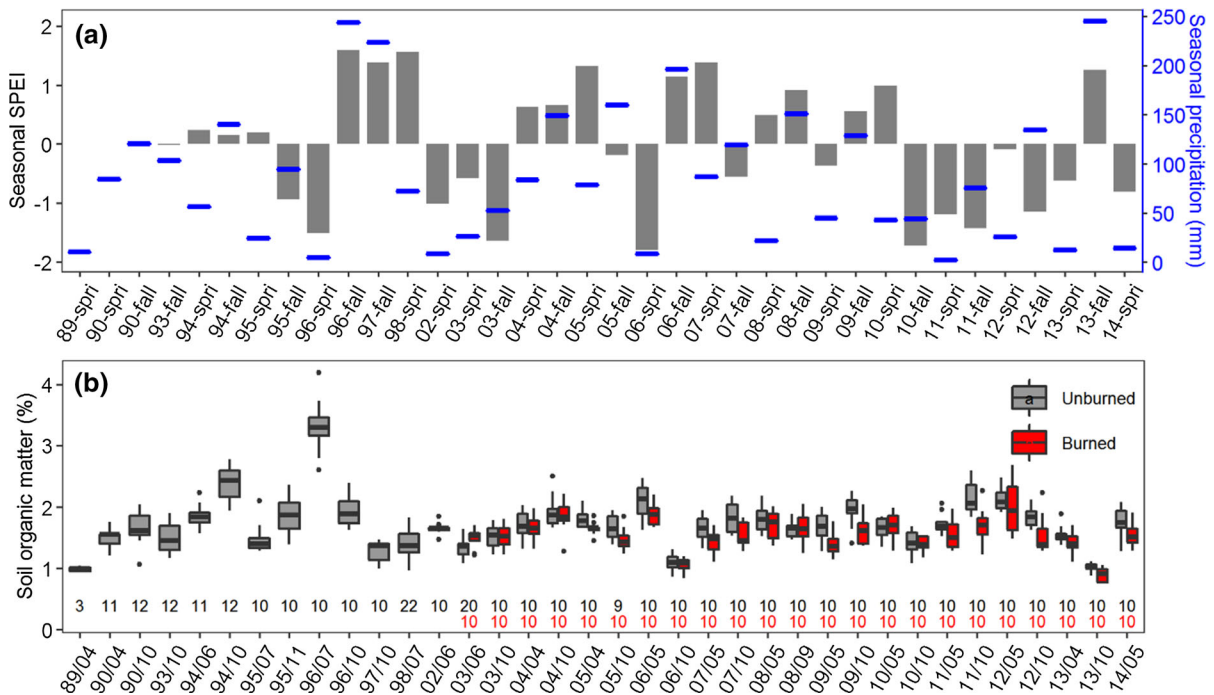


Fig. 1 Long-term patterns of climate and soil organic matter concentration in a desert grassland. **a** Long-term patterns of the Standardized Precipitation Evapotranspiration Index (SPEI, gray bar) and precipitation (blue line) in spring and fall. **b** Long-term pattern of soil organic matter concentration as affected by a prescribed fire on 19 June 2003. In **(b)** soil sampling time is shown on X axis in the format of 2-digit

year/month. For each sampling time, the thick horizontal line represents the median of the distribution, the box includes 50% of the data, and the whiskers reach the highest and lowest value within 95% of the distribution. Points represent single values outside 95% of the distribution. Number under box indicates sample size at sampling time

significant interaction between the prescribed fire and time (Figs. 1b and 4a). Fire also significantly reduced ANPP, but in contrast to SOM trends, the effect size for ANPP declined significantly with time as ANPP recovered to unburned levels 9 years after the prescribed fire (Fig. 4b). SOM was negatively correlated with ANPP (Unburned: $r = -0.78$, $P = 0.013$; Burned: $r = -0.81$, $P = 0.004$; Fig. 5). SOM did not significantly relate to the previous year's ANPP ($P > 0.05$, Fig. S3) or any other lag period (not shown), indicating no legacy effects of primary production on SOM. Despite strong effects of fire on SOM, the prescribed burn did not alter the relationships between SOM and climate variables, as there were no significant interactions between the prescribed fire and the climate factors (Fig. 3).

Discussion

With a unique long-term dataset of SOM, we revealed dynamic change in SOM and provided new insights into how climate and prescribed fire influence SOM in dry grasslands. SOM did not have a long-term trend but fluctuated significantly with seasons and years, capturing the dynamic nature of SOM in this Chihuahuan Desert grassland ecosystem. Surprisingly, SOM was negatively and nonlinearly related to precipitation and the SPEI aridity index, and the climate sensitivities of SOM did not track those of aboveground primary production. As expected, SOM was reduced by the prescribed fire, especially in the long-term (i.e., a decade). The dynamic nature of SOM together with its low concentration and a variable climate foretells the possibility of dramatic responses of SOM to future climate change in desert grasslands.

Table 1 Comparison of soil organic matter concentration between sampling times and sites

Date	Unburned grassland				Burned grassland				Difference
	Mean (%)	SD (%)	CV (%)	Season <i>P</i>	Mean (%)	SD (%)	CV (%)	Season <i>P</i>	<i>P</i> value
89/04	0.98	0.06	5.6	NA					
90/04	1.50	0.16	10.9	0.112					
90/10	1.65	0.26	15.9	1.000					
93/10	1.48	0.25	17.0	0.997					
94/06	1.85	0.18	9.9	0.030					
94/10	2.39	0.27	11.4	< 0.001					
95/07	1.48	0.25	16.8	< 0.001					
95/11	1.86	0.32	17.2	0.015					
96/07	3.31	0.45	13.5	< 0.001					
96/10	1.92	0.25	13.2	< 0.001					
97/10	1.29	0.17	13.1	< 0.001					
98/07	1.39	0.24	17.1	1.000					
02/06	1.65	0.10	5.8	0.181					
03/06	1.34	0.14	10.2	0.034	1.49	0.16	10.6	NA	0.046
03/10	1.53	0.20	12.8	0.945	1.52	0.19	12.3	1.000	0.941
04/04	1.71	0.25	14.4	0.993	1.66	0.19	11.2	1.000	0.760
04/10	1.93	0.27	13.8	0.887	1.84	0.25	13.5	0.991	0.487
05/04	1.81	0.16	8.7	1.000	1.65	0.11	6.5	0.979	0.141
05/10	1.67	0.20	12.2	1.000	1.47	0.18	12.5	0.990	0.050
06/05	2.10	0.28	13.3	0.005	1.88	0.17	9.2	0.004	0.037
06/10	1.10	0.13	11.8	< 0.001	1.06	0.11	10.3	< 0.001	0.807
07/05	1.66	0.19	11.5	< 0.001	1.44	0.19	13.1	0.012	0.040
07/10	1.83	0.25	13.8	0.997	1.55	0.21	13.6	1.000	0.006
08/05	1.81	0.22	12.0	1.000	1.71	0.24	14.3	0.998	0.363
08/09	1.65	0.14	8.8	0.997	1.66	0.24	14.6	1.000	0.789
09/05	1.68	0.22	13.3	1.000	1.42	0.21	14.6	0.736	0.010
09/10	1.95	0.26	13.4	0.528	1.61	0.22	13.7	0.974	0.001
10/05	1.65	0.17	10.5	0.275	1.70	0.22	12.9	1.000	0.544
10/10	1.43	0.20	14.1	0.853	1.40	0.12	8.6	0.282	0.928
11/05	1.73	0.17	9.9	0.248	1.56	0.24	15.4	0.999	0.120
11/10	2.15	0.26	12.2	0.002	1.68	0.31	18.3	1.000	< 0.001
12/05	2.12	0.18	8.5	1.000	2.00	0.45	22.3	0.134	0.287
12/10	1.85	0.17	9.4	0.419	1.55	0.31	20.2	< 0.001	0.004
13/04	1.55	0.15	9.7	0.228	1.42	0.17	11.8	1.000	0.274
13/10	1.02	0.07	6.5	< 0.001	0.89	0.12	13.3	< 0.001	0.216
14/05	1.76	0.24	13.5	< 0.001	1.55	0.19	12.3	< 0.001	0.043
Overall	1.71	0.46	26.9		1.55	0.31	20.0		0.007

Soil organic matter concentration at one sampling time was compared with the values at the last sampling time in each grassland, as indicated by Season *P* value. Difference between the unburned grassland and the burned grassland at each sampling time was tested, as indicated by the *P* value in the *Difference* column. *SD* indicates standard deviation and *CV* indicates coefficient of variance. Date are shown in the format of 2-digit year/month

NA indicates not available. *P* values < 0.05 are in bold

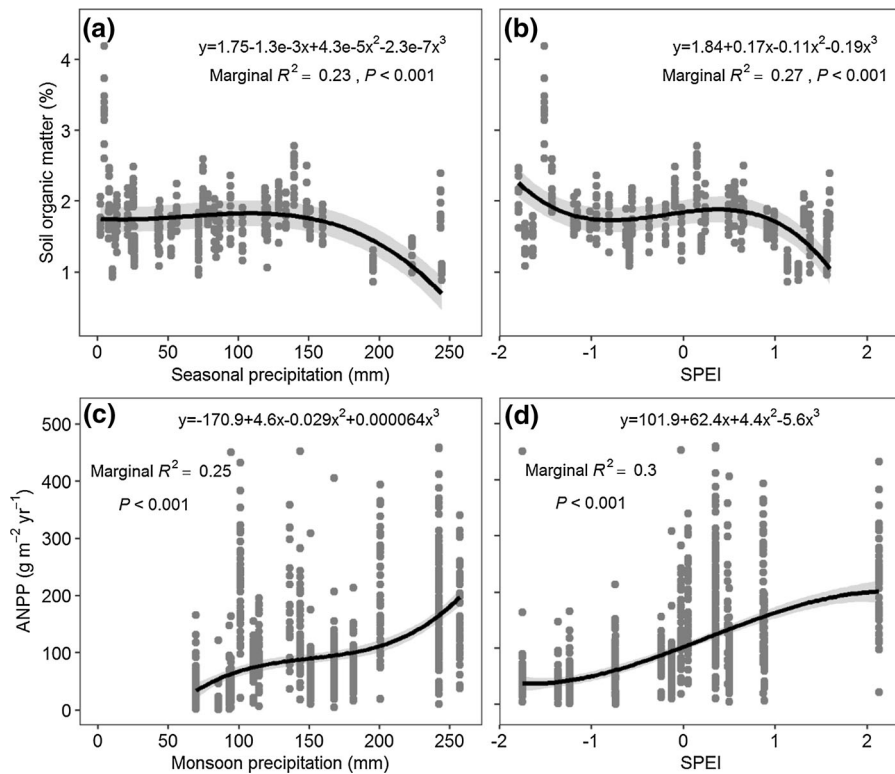


Fig. 2 Soil organic matter concentration and aboveground net primary production (ANPP) showed contrasting relationships with climate. **a** Soil organic matter concentration vs. seasonal precipitation ($AICc = 168.1$). **b** Soil organic matter concentration vs. standardized precipitation evapotranspiration index (SPEI) ($AICc = 195.1$). **c** ANPP vs. monsoon precipitation ($AICc = 10472.2$). **d** ANPP vs. SPEI ($AICc = 10364.4$). Each

point represents a single observation. Nonlinear models best fit the data and the prediction from the best model is shown with 95% confidence intervals in gray. **c** and **d** were redrawn from Rudgers et al. (2018) from a nearby site that used different meteorological data, therefore climate variable values in **c** and **d** were different from those in **a** and **b**

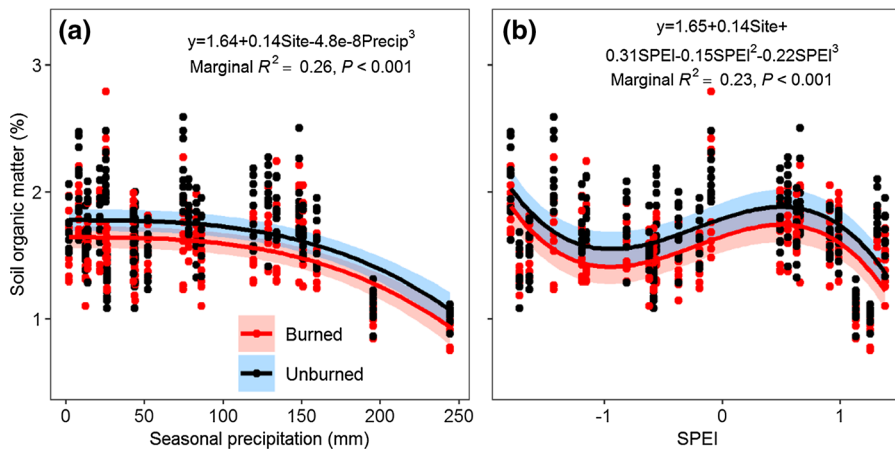


Fig. 3 Relationships between soil organic matter concentration and climate factors were similar between unburned and burned grasslands. Soil organic matter concentration vs. seasonal precipitation (**a**) and the standardized precipitation

evapotranspiration index (SPEI, **b**). Nonlinear models best fit the data and the prediction from the best model is shown with 95% confidence intervals in blue and red in the unburned and burned grasslands, respectively

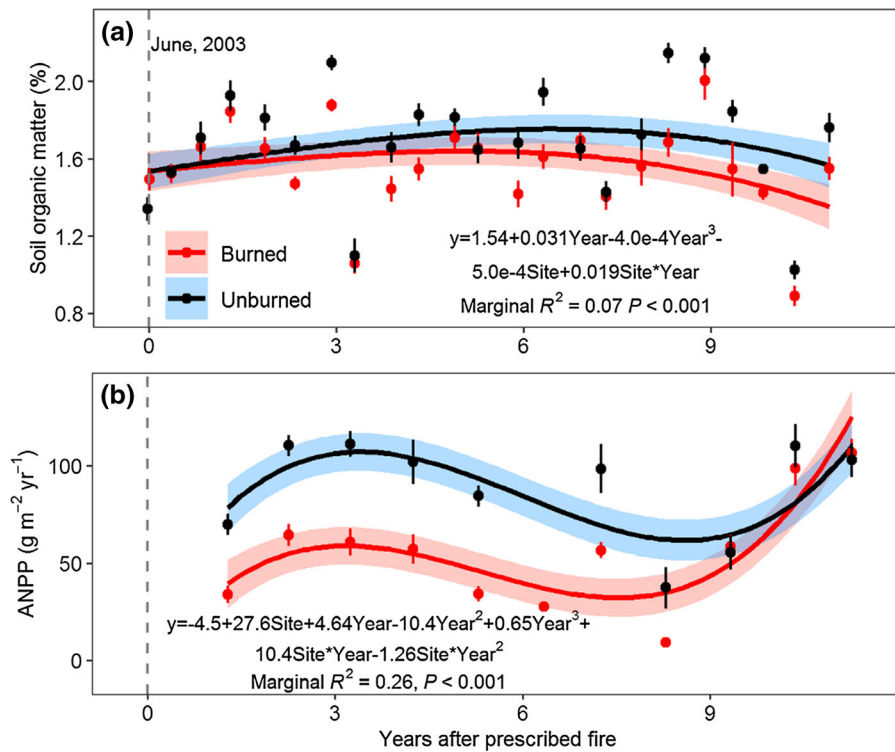


Fig. 4 Effects of prescribed fire on soil organic matter concentration and aboveground net primary production (ANPP) changed with time. **a** Effect of prescribed fire on soil organic

matter concentration increased significantly with time. **b** Effect of prescribed fire on ANPP decreased significantly with time. Points and error bars indicate means and standard errors

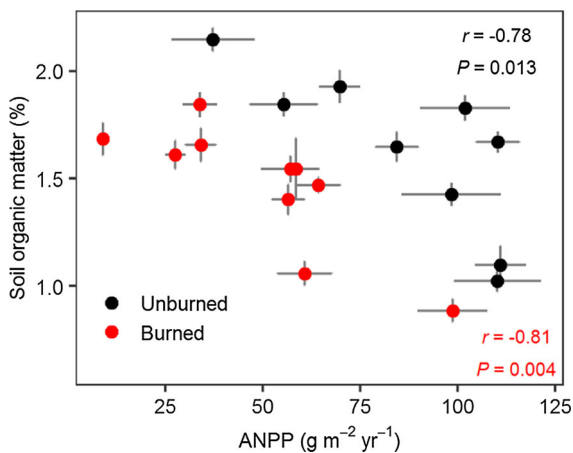


Fig. 5 Relationships between soil organic matter concentration and aboveground net primary production (ANPP). Vertical and horizontal error bars indicate the standard errors of soil organic matter concentration and ANPP, respectively

Temporal change in SOM

Temporal change in SOM is usually hard to detect in the field by repeated soil sampling due to slow turnover, large inherent spatial variability, and limited time spans (< 10 years) (Allen et al. 2010; Chen et al. 2015; Hoffmann et al. 2017; Schruppf et al. 2011; Smith 2004; Smith et al. 2020; Wuest 2014). These challenges were overcome in the present study with SOM measurements spanning 25 years, taken at high frequency (twice a year in most years), and measured with a considerable number of replicates (10 for most sampling times). With these efforts, a long-term trend in SOM, if present, should be detectable. As our analysis revealed no long-term trend in SOM, we suggest that SOM dynamics in this desert grassland were at a quasi-equilibrium state during the study period. This result is reasonable given that the site had been protected from extensive grazing since 1973 (Collins et al. 2020), with 16 years of recovery before the first soil sampling in our study, which began in 1989. Our results highlight the value of long-term data

for understanding temporal trends in SOM. Had our study spanned smaller time intervals, we would have reached very different conclusions, including that SOM was declining in the ecosystem from 3.31 to 1.34% (1996–2003), that SOM was increasing from 1.34 to 2.10% (2003–2006), or that SOM was stable (1.65–1.95%; 2007–2010) (Fig. 1b; Table 1).

Despite the lack of long-term trend, SOM fluctuated significantly among seasons and years. This finding may be unexpected, if we view change in SOM as a very slow process, as suggested by many previous studies (Friedlingstein et al. 2019; Li et al. 2015; Lu et al. 2018; Luo et al. 2019). The finding is, however, reasonable for drylands with low baseline levels of SOM ($\sim 1.5\%$), given the large variability in both climate and primary production across seasons (Fig. 1; Rudgers et al. 2018). In addition, our result is consistent with the finding of a synthesis study, in which yearly variation in SOM was considerable and exceeded the long-term change in SOM by far in eight widely distributed terrestrial ecosystems (Schrumpf et al. 2011). Similarly, a recent synthesis suggested that year effects on ecological dynamics (e.g. plant community composition) are pervasive and could be profound (Werner et al. 2020).

Significant changes in SOM or SOC within seasons and years were also reported in some other studies (Burke et al. 2019; Pandher et al. 2019; Turner et al. 2015; Wuest 2014). For example, Burke et al. (2019) reported that SOC content at 0–15 cm depth increased significantly from 6 Mg/ha in spring to 17 Mg/ha in summer and reduced back to 6 Mg/ha in the next spring over 1 year in a semi-arid cropland with sandy soils. Turner et al. (2015) observed a significant increase in SOC concentration at 0–10 cm depth from 4.0% in the dry season to 4.7% in the wet season over 1 year in a lowland tropical rain forest. Together, our results and these prior studies suggest that SOM can be dynamic in some ecosystems, which is contrary to the paradigm that SOM changes little within seasons or among years (Schmidt et al. 2011; Torn et al. 1997). Indeed, SOM turnover time can vary > 100 fold across ecosystems and even > 10 fold across biomes in both topsoils (0.3–111 years in 0–20 cm soils; Chen et al. 2013) and subsoils (from < 10 years to more than 6000 years in 30–100 cm soils; Luo et al. 2019). SOM turnover rate in the biome of our study site (i.e. desert grassland) appears to have the shortest SOM

turnover among global biomes documented so far (Chen et al. 2013; Lu et al. 2018; Luo et al. 2019).

Like most repeated soil sampling studies (Chen et al. 2015; Hoffmann et al. 2017), repeated sampling in our study may be spatially biased. One sign of the spatial bias may be the significantly greater SOM in July 1996 than at other sampling times (Fig. 1b). To minimize spatial bias in statistical analyses, we used mixed-effect models that accounted for the lack of independence associated with the location of each plot and quadrat and with the random effect of sampling year.

Sensitivity of SOM to climate

In contrast to our original hypotheses (Ia–b), SOM decreased significantly and nonlinearly with precipitation and the aridity index (SPEI). Given the opposite responses of SOM and ANPP to precipitation, SOM was negatively, rather than positively, correlated to ANPP (Fig. 5). These findings are novel and suggest the possibility of incorrect predictions on SOM under future climate scenarios if positive relationships between SOM and precipitation are assumed (e.g., Gaitán et al. 2019) or if positive correlations between SOM and ANPP are assumed (Luo et al. 2017). SOM depends on both the rate of organic inputs (mainly via litter input and rhizodeposition) and rates of removal caused by decomposition, runoff, leaching, and erosion, all of which are sensitive to climate (Lal 2019; Li et al. 2015; Plaza et al. 2018a; Turner et al. 2015; Vicca et al. 2014). Possible explanations for the negative relationship between SOM and precipitation found here include (i) a decrease in organic matter input (ii) an increase in the rate of soil organic matter decomposition (i.e. soil heterotrophic respiration), (iii) increases in losses of SOM via runoff, leaching, or erosion, and (iv) methodological problems of the SOM measurements. We therefore examined support for each mechanism.

Organic inputs into soil via rhizodeposition are expected to increase rather than decrease with more precipitation, because of the positive relationship between primary production and precipitation (Fig. 2c; Pausch and Kuzyakov 2018). However, stimulation of primary production by high precipitation may only boost litter input in the next season(s) rather than in the same season, a phenomenon known as a “legacy-effect” (Sala et al. 2012; Shen

et al. 2016). We detected no evidence for legacy effects of ANPP on SOM (Fig. S3). Therefore, possible lag effects of organic inputs across seasons were unlikely to account for the decrease in SOM in very wet seasons. However, we have not incorporated data on belowground plant biomass or photodegradation of litter (Austin and Vivanco 2006; Brandt et al. 2010); if this were decoupled from the dynamics of plants aboveground, then a decrease in organic matter input may contribute to our results.

Rain-enhanced soil respiration likely accounted for at least part of the observed decrease in SOM in very wet seasons. Soil respiration in drylands is limited by soil water availability and thus can be stimulated by large rains (Vargas et al. 2012), especially after a drought period, due to the accumulation of labile carbon and nitrogen during drought (Kieft et al. 1998; Noy-Meir 1973; White et al. 2004; Xu and Baldocchi 2004). For example, Xu and Baldocchi (2004) reported that the peak rate of ecosystem respiration (largely comprised of soil respiration) after big rains were 60–80 times greater than baseline ecosystem respiration rates in a dry grassland in California, USA. Ecosystem respiration after a rain of 61 mm can be up to 70 g C m^{-2} , equivalent to almost 10% of annual gross primary production (Xu and Baldocchi 2004). These results support soil respiration as a mechanism underlying the climate sensitivity function for SOM in our study.

Large rains may also reduce SOM via runoff and leaching of dissolved SOM (Plaza et al. 2018a), given the low vegetation cover ($\sim 75\%$) and the coarse-textured topsoils at our site (Buxbaum and Vanderbilt 2007). Some of the dissolved organic matter in topsoils may also transfer to the subsoils via water infiltration and be retained there, given that subsoils have higher clay contents than topsoils in our ecosystem (Buxbaum and Vanderbilt 2007). Future work to sample subsoils, which were not included in our study, would help to address this potential mechanism. Moreover, large rains may reduce SOM by disrupting soil aggregates and thus accelerating soil erosion either alone or together with winds (Brazier et al. 2014; Plaza et al. 2018a). Short-term studies of runoff that captured SOM losses suggested that SOM loss by water erosion in this region is important and is driven mainly by large rain events during wet periods (Brazier et al. 2014; Cunliffe et al. 2016; Turnbull et al. 2010).

Finally, the observed decrease in SOM in very wet seasons may result from problems with the LOI method in determining organic matter concentration of carbonate soils (Nelson and Sommers 1996; Westman et al. 2006). Carbonates, whose concentration in 0–20 cm soil is high at the study site (about 6% CaCO_3 equivalents; Kieft et al. 1998), were not removed before our determination of SOM using the LOI method. The majority of carbonates (e.g., calcite and dolomite) cannot be lost, but some soluble or volatile carbonates may be lost, on ignition at 500°C (Kasozzi et al. 2009; Nelson and Sommers 1996; Westman et al. 2006). If some carbonates were lost during these ignitions, our LOI measurements would reflect dynamics of organic matter plus some carbonates. Our observed decline in LOI in very wet seasons may then be partly because of carbonate losses driven by large rainfall events through runoff or infiltration into subsoils. Future work analyzing soils with and without carbonates removed are needed to assess this potential mechanism.

The concave relationship between SOM and precipitation suggests that SOM will respond negatively to increasing interannual variability in precipitation in the future. The result provides the first evidence, to our knowledge, that SOM can be influenced by precipitation variability. Moreover, the apparent decline in SOM at seasonal precipitation exceeding 160 mm supports the idea that slow variables in drylands possess thresholds that, if crossed, cause the system to move into a new state or condition (Knapp et al. 2017; Luo et al. 2017; Reynolds et al. 2007; Rudgers et al. 2018). The precipitation threshold created the nonlinear relationship that generated the prediction of sensitivity of SOM to variability in precipitation. In our region, changes in the precipitation regime include smaller, more frequent individual rain events (Petrie et al. 2014), a long-term decline in the SPEI during the monsoon season (i.e., fall 6-month SPEI), and a strong increase in the interannual variability in monsoon SPEI over the last century (Maurer et al. 2020; Rudgers et al. 2018).

In comparison to precipitation, SPEI explained slightly more of the variation in SOM because the highest levels of SOM occurred at the lowest values of SPEI, but not at the lowest values of precipitation. SOM increased during the hot/dry periods (i.e. low values of SPEI) perhaps because high temperatures exceeded optima for decomposer activity (Anderson-

Teixeira et al. 2011; Liu et al. 2018). An alternative mechanism is that organic inputs decreased (Fig. 2d; Rudgers et al. 2018) and photodegradation of litter continues (Austin & Vivanco 2006; Brandt et al. 2010) during the drought periods. Similar to precipitation, the nonlinear relationship between SOM and SPEI (Fig. 3) suggested consequences of increasing climate variability on SOM. However, for SPEI, increasing variability was predicted to have weak to positive effects on SOM under dry conditions but negative effects, similar to precipitation, under wet conditions. This result was supported by the cubic climate sensitivity function (Fig. 3), which signals an interaction between the mean climate and the variance in climate (Rudgers et al. 2018). If variability in SPEI increases under a hotter/drier climate, then the function predicts future increases in SOM.

Effect of prescribed fire on SOM

As hypothesized, the prescribed fire significantly decreased SOM, and the effect size increased significantly with time up to a decade (Fig. 4a). Fire usually does not directly consume SOM but affects SOM indirectly by changing organic inputs to soil, and postfire recovery of organic inputs could be slow (Collins et al. 2017; Parmenter 2008; Pellegrini et al. 2018). In this study, ANPP in the burned grassland did not recover to the level of the unburned grassland until 9 years after the fire (Fig. 4b), which was consistent with the finding of a previous study in the same ecosystem (Parmenter 2008). The long-lasting negative effect of fire on ANPP probably explained why the declines in SOM following fire expanded over time.

Since ANPP recovered a decade after the fire, we may expect a postfire recovery of SOM. The recovery may, however, take another decade or longer, unless the long-term (> 10 years) effect of fire on ANPP is positive. Fire did not affect belowground net primary production at the study site (Burnett et al. 2012) but may affect soil microbial activity and nutrient availability (Butler et al. 2018; Neary et al. 1999; Pellegrini et al. 2018), which are less well studied but could be important in mediating fire effects on SOM and postfire recovery of SOM. Moreover, fire can reduce SOM and retard postfire recovery of SOM by accelerating wind erosion (Dukes et al. 2018). Furthermore, fire may interact with climate to influence SOM via their interactive effects on plant community structure

and soil erosion (Collins et al. 2017; D'Odorico et al. 2013; Dukes et al. 2018). Although the interaction between fire and climate on SOM was not statistically significant in the present study, it could be ecologically significant in the future given projected climate change and increases in fire intensity and frequency (IPCC 2012; Pendergrass et al. 2017). Overall, our results suggest that fire has a significant and long-lasting effect on SOM in this desert grassland.

Conclusion

Long-term soil sampling in a northern Chihuahuan Desert grassland detected no long-term trend in SOM but uncovered strong seasonal and yearly fluctuations that tracked both precipitation and dryness. Unexpectedly, SOM declined nonlinearly with greater seasonal precipitation or reduced aridity (SPEI). These relationships contrast with the increases in ANPP under greater precipitation or less aridity, and challenge the common assumption that SOM increases with wetness globally. As predicted, fire reduced SOM, but long-term monitoring revealed increasingly amplified reductions in SOM up to a decade following the fire, probably due to the slow recovery of primary production. Together, our results demonstrate that SOM in desert grassland can be very sensitive to climate, climate variance and fire, which has important implications for predicting soil organic C storage in desert grasslands under future increases in precipitation variability, temperature, and fire risk.

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Author contributions CSW, DIM, JAR, and SLC designed the study. CSW and DIM collected soil samples and performed soil analyses. SLC and JAR provided ANPP data. EH and JAR performed the statistical analyses. EH wrote the first draft with significant contributions from all authors.

Data and code availability Data and code associated with this study are available at Environmental Data Initiative Data Portal: <https://doi.org/10.6073/pasta/d2d7344c94a67d2ce5dd3b53a2dea839>.

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