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Response of soil carbon dioxide efflux to temporal repackaging of rainfall into fewer, larger events in a semiarid grassland

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Changing rainfall patterns will alter soil water availability to plants and microbes and likely impact soil CO_2 efflux (F_s) in semiarid ecosystems. However, our understanding of the response of F_s to compound changes in rainfall event size and frequency remains relatively limited. To address this knowledge gap, we examined how compound changes in rainfall size and frequency impact F_s in a semiarid grassland by deploying automated soil chambers at a rainfall manipulation experiment. All plots within the experiment received equal total summer growing season precipitation that was temporally repackaged into regular events of inversely varied size and frequency, with event sizes ranging from 5 to 50 mm and dry intervals ranging from 3.5 to 21 days. We found that repackaging rainfall into few/large events with long dry intervals decreased seasonal cumulative F_s. Repackaging influenced key aspects of pulses including mean, maximum, and antecedent (day before irrigation) values of soil moisture and F_s and their rate of decline during drying intervals. Soil moisture explained substantial variation in F_s ($R^2 > 0.84$) for all treatments; however, the sensitivity of F_s to soil moisture decreased in the few/large regime compared to the reference and many/small regimes. Dynamics in plant phenology (quantified by plot greenness) and soil temperature interacted with soil moisture to influence the seasonal evolution of F_s pulses and cumulative efflux. Our findings demonstrate that soil moisture and vegetation responses to changes in rainfall size and frequency impact soil CO_2 efflux pulses and seasonal emissions in semiarid grasslands. These results, coupled with the knowledge that CO_2 efflux pulses play an outsized role in dryland carbon exchange, indicate the possibility of future climate-mediated shifts in the carbon cycling of semiarid ecosystems.

KEYWORDS

soil respiration, soil efflux, rainfall intensification, soil moisture, pulse, semiarid

Introduction

Intensification of precipitation driven by climate warming is changing the intensity, frequency, and length of time between storms (McCabe et al., 2010; Polade et al., 2014; Guerreiro et al., 2018; Fowler et al., 2021). In the southwest United States, widespread warming has been accompanied by increases in precipitation variability and the frequency of prolonged drought (Demaria et al., 2019; Zhang et al., 2021), and general circulation models predict further intensification of precipitation, with a shift toward larger, fewer events with longer dry intervals (Cook et al., 2020; Moustakis et al., 2021). Due to tight carbon-water coupling in globally-expansive arid and semiarid ecosystems (Noy-Meir, 1973; Huxman et al., 2004; Schwinning and Sala, 2004), precipitation changes that alter the amount and timing of soil moisture availability have implications for the terrestrial carbon sink (Poulter et al., 2014; Ahlström et al., 2015; Biederman et al., 2016).

Soil moisture regulates the metabolic activity of plants and soil organisms in arid and semiarid ecosystems (Jenerette et al., 2008) and therefore exerts strong control over soil CO_2 efflux (F_s). F_s, the soil-atmosphere flux of carbon dioxide, is the sum of heterotrophic respiration and belowground autotrophic (root) respiration. In arid and semiarid ecosystems, F_s has a pulsed response to rainfall driven by physical and microbial responses to soil wetting (Birch, 1958; Huxman et al., 2004; Schwinning and Sala, 2004). Understanding F_s responses to rainfall is important because F_s indicates rates of ecosystem metabolism and nutrient cycling (Orchard and Cook, 1983; Luo and Zhou, 2006) and often dominates ecosystem-scale carbon exchange immediately after rain events (Huxman et al., 2004; Sponseller, 2007; López-Ballesteros et al., 2016). Because the temporal pattern of rainfall is a key control on soil moisture and F_s dynamics (Porporato et al., 2002; Vargas et al., 2012; Leon et al., 2014), it is necessary to examine how F_s will respond to shifts in precipitation timing and intensity.

Although prior work has examined F_s responses to key precipitation metrics—including seasonal amount (Liu et al., 2009; Zhao et al., 2021), event size/timing (Thomey et al., 2011; Vargas et al., 2018; Post & Knapp, 2021), and interstorm duration (Sponseller, 2007)—it remains unclear how F_s will respond to compound changes in event size and frequency. Projected shifts in rainfall toward infrequent, larger events may enable larger post-wetting F_s pulses due to increased soil moisture relative to antecedent conditions (Austin et al., 2004; Cable et al., 2008; Niu et al., 2019) and substrate accumulation during long dry intervals (Franzluebbers et al., 2000; Sponseller, 2007); however, soil moisture stress during prolonged dry periods is known to reduce F_s (Knapp et al., 2008). In contrast, a rainfall regime with many small events would support smaller post-wetting F_s pulses but more frequent activation of metabolic activity in near-surface soils where soil organic carbon and microbial activity are concentrated (Garcia-Pichel & Belnap, 1996; Vargas et al., 2018). Moreover, it is likely that F_s responses to event size and frequency are modulated by changes in autotrophic respiration associated with plant responses to root-zone infiltration, such as rhizosphere priming and photosynthetic substrate supply (Ogle & Reynolds, 2004; Kuzyakov & Gavrichkova, 2010; Yan et al., 2011; Liu W et al., 2017; Wang et al., 2019). Interactions among these environmental and vegetative drivers of respiration processes challenge predictions of F_s responses to rainfall intensification (Barron-Gafford et al., 2011; Roby et al., 2019).

Rainfall manipulation experiments are a useful tool to examine how interactive aspects of precipitation impact ecosystem processes (Knapp et al., 2015). Whereas many studies have investigated plant responses to rainfall manipulation (e.g., Heisler-White et al., 2008; Gherardi and Sala, 2015), comparatively few have examined the response of soil processes to simultaneous changes in event size and frequency (Griffin-Nolan et al., 2021; Rousk and Brangarí 2022). Although prior studies have provided useful information on ecosystem-scale respiration responses to repackaging (Liu Z et al., 2017), automated chamber systems can better capture transient F_s patterns during wetting-drydown cycles characteristic of semiarid regions (Huxman et al., 2004; Savage et al., 2009). Such an approach may increase our understanding of how soil and plant processes modulate F_s responses to rainfall intensification. To address this gap, we examined how compound changes in rainfall size and frequency impact F_s in a semiarid grassland by deploying automated soil chambers within a rainfall manipulation experiment. Our objective was to address the following questions: 1) How does temporal repackaging of rainfall impact F_s pulses and cumulative growing season F_s? and 2) How do changes in environmental and vegetative drivers under rainfall repackaging scenarios impact F_s rates and the seasonal evolution of F_s pulses?

Materials and methods

Site description

We conducted this experiment at the Rainfall Manipulation in the Santa Rita Experimental Range (RainManSR) site in southeast Arizona, United States (31.79° N, 110.90° W; elevation: 1,075 m). While the experiment was conducted in plots under rainout-exclusion shelters, the surrounding ecosystem is a semiarid grassland that has experienced significant increases in mesquite (Prosopis velutina) shrub cover in the 20th century. The ecosystem is composed mainly of perennial bunchgrasses, short trees/shrubs, and bare soil which can support annual grasses and forbs given adequate rainfall. Mean annual temperature is 18.6°C and mean annual precipitation (1922–2021) is 377 mm, roughly 50% of which occurs during the summer (July–September) monsoon season (https://cals.arizona.edu/SRER/data.html). Soils are well-drained sandy loams (78% sand, 8% clay, 14% silt). Plots within the experiment represent a mixture of C4 perennial bunchgrasses, C4 annual grasses, and C3 forbs. Because the ambient ecosystem has inherently heterogeneous cover, native perennial bunchgrass (*Digitaria californica*) seedlings were transplanted in November 2019 into all plots at a density of 20 plants m^{-2}. This was done to ensure a relatively consistent plant community at the start of the experiment and to better capture vegetation responses to rainfall manipulation and potential impacts on the plant-mediated component of F_s.

Experiment design and precipitation manipulation

To block all ambient precipitation, large rainout-exclusion shelters were covered with transparent film with each shelter covering 12 plots (1.2 by 1.5 m). To hydrologically isolate the plots, the perimeter of each plot was trenched to a depth of 80 cm and wrapped in polyethylene film. Plots were then lined with steel flashing which extended from a depth of 50 cm to 10 cm above the soil surface. We used a completely randomized design with two replicates of each irrigation treatment in each shelter ($n = 4$ plots per treatment). All plots received 205 mm of total summer irrigation (the long-term mean seasonal precipitation amount) and were hand-irrigated using a digital flow meter. Irrigation was applied to the area within soil collars when the automated chambers were in the open position. The experiment began on July 14 when 38 mm was applied to all plots. Thereafter, irrigation treatments were imposed with the following combinations of mean event size and dry intervals: many/small (9 mm; 3.5 days); reference (34 mm; 7 days, which is the climatic normal precipitation frequency at this site), and few/large (51 mm; 21 days). For more details about the experimental design of RainManSR, Zhang et al. (2022).

Soil CO_2 efflux measurements

We measured the net efflux of carbon dioxide (CO_2) at the soil-atmosphere interface (F_s; μmol CO_2 m^{-2} s^{-1}) hourly using automated chambers connected to a multiplexer and infrared gas analyzer (LI-8100, LI-COR, Nebraska, United States). One week before data collection began, we inserted 20 cm diameter soil collars into the ground with roughly 3 cm of the collar extending above the soil surface. Soil within the collars was weeded by hand weekly to exclude aboveground vegetation from the sampled volume. Data were collected continuously during day and night hours, and F_s was determined each hour by fitting an exponential curve to the change in CO_2 molar fraction during a 120 s observation period. We excluded F_s estimates when the fitted exponential curve had a coefficient of determination below 0.95 and/or when individual chambers malfunctioned (poor seals between chamber heads and baseplates, ruptured tubing, power loss, etc.). Overall, 11% of data was discarded and gaps in the hourly chamber data were filled with treatment means for missing hours.

Environmental variables

We measured half-hourly volumetric water content (soil moisture, θ; m^3 m^{-3}) and soil temperature (T_s; °C) using Campbell Scientific CS655 probes inserted into the soil at 30° from vertical to integrate the measurement across the upper 10 cm of soil. Hourly means were calculated from half-hourly data to match the temporal resolution of soil chamber data. We also monitored plot-level phenology using nadir-oriented RGB images taken half-hourly from 09:00 to 16:00 local time with a Raspberry Pi Camera Module V2 (Raspberry Pi Foundation, Cambridge, United Kingdom). For each plot, half-hourly RGB images for the entire plot area were used to calculate a spatially-averaged, daily timeseries of the green chromatic coordinate (GCC) using the *phenopix* R package (Filippa et al., 2016). Daily GCC was calculated as the 90th percentile of all half-hourly values to minimize diurnal changes in illumination.

Data analysis

To quantify the effects of rainfall repackaging on F_s, T_s, θ, and GCC we used the R package *lme4* to build linear mixed-effects models with irrigation treatment, time, and their interaction as fixed effects and plot ID as a random effect to account for the repeated measurements (Bates et al., 2014). Variables were log-transformed when necessary to meet assumptions of normality. Cumulative F_s was calculated as the sum of daily mean F_s. To compare total seasonal F_s among repackaging treatments, we first used Levene's test for homogeneity of variance and found that the many/small regime had outsize variance compared to the other repackaging treatments ($F = 6.72$, $p < 0.05$; compare the variance in seasonal total F_s reported in Table 2). To account for unequal variance, we tried log-transforming the data and using the Kruskal-Wallis test, but did not find strong evidence of a difference in total seasonal F_s (ΣF_s) when including the many/small treatment. Therefore, to reduce the chance of type II error we conducted one-way analysis of variance (ANOVA) on total seasonal F_s values for the reference and few/large regimes. We used linear regression to quantify the relationship between daily F_s and θ as well as F_s

TABLE 1 Linear mixed-effects model results for daily mean soil CO_2 efflux (F_s), soil moisture (θ), soil temperature (T_s), and green chromatic coordinate (GCC) normalized anomalies.

Term	F_s		θ			T_s			GCC		
	df	***F***	***p***	**df**	***F***	***p***	**df**	***F***	***p***	**df**	***F***	***p***
Treatment	2	2.42	0.14	2	0.34	0.72	2	3.22	0.08	2	0.17	0.85
DOY	91	123.27	<0.001	90	297.06	<0.001	90	1441.20	<0.001	91	26.06	<0.001
Treatment × DOY	182	16.96	<0.001	180	76.19	<0.001	180	34.66	<0.001	182	5.49	<0.001

and GCC. We compared the slope of the $F_g - \theta$ relationship among rainfall repackaging treatments using analysis of covariance (ANCOVA) with the *aoctool* in MATLAB (MathWorks, Massachusetts, United States). For each treatment group, ANCOVA fits a separate line to the continuous variables F_s and θ; differences in slopes among treatments were assessed using Tukey's honestly significant difference for pairwise comparisons. To focus on temporal dynamics in greenness, we report normalized anomalies of GCC. We quantified the rapid increase in post-wetting $F_s(\Delta)$ and the rate of decay of F_s during interstorm periods (τ) by fitting a pulse model based on Kurc and Small (2004):

$$F_s(t) = \Delta e^{-\frac{t}{\tau}} + F_{ant}$$

where Δ (μmol CO_2 m^{-2} s^{-1}) is the difference between maximum post-wetting F_s and antecedent F_s (day before irrigation), t is time in days since irrigation, and τ (days) is the exponential time constant, also known as the e-folding time during which the initial pulse magnitude, Δ, has diminished by a factor of 1/e = 0.37. The model was fit and coefficient estimates for τ were obtained using the *fitnlm* function in MATLAB.

Results

Dynamics in soil CO_2 efflux and drivers under rainfall repackaging

The effects of rainfall repackaging on F_s, T_s, θ, and GCC were strongly time-dependent ($p < 0.01$; Table 1), which resulted in pronounced temporal dynamics in F_s and environmental drivers (Figure 1). At the beginning of the growing season, all plots exhibited low F_s and low GCC associated with low θ and high T_s. A uniform 38 mm irrigation event applied on 14 July resulted in similar increases in θ and F_s, and similar declines in T_s among treatments. After this uniform initial event, changes in irrigation event size and frequency caused patterns of F_s and environmental drivers to vary among treatments. As expected, plots irrigated with many/small events had smaller F_s pulses and reduced θ extremes, whereas plots irrigated with few/large events had larger F_s pulses separated by prolonged dry intervals with low F_s. We also observed differences in pulse patterns of T_s and seasonal dynamics in GCC under rainfall repackaging scenarios. Immediately after irrigation, T_s in the few/large regime decreased relative to the many/small regime; however, this difference reversed during prolonged dry intervals. Repackaging rainfall into few/large events delayed the timing of peak GCC relative to the many/small regime and decreased the duration of wet soil moisture conditions for much of the growing season (Supplementary Figure S1).

Temporal rainfall repackaging alters cumulative soil CO_2 efflux

Differences in pulse dynamics compounded to influence seasonal cumulative F_s (Figure 2; Table 2). Repackaging equal summer rainfall (205 mm) into fewer, larger events with long dry intervals decreased seasonal cumulative F_s by 8.3% relative to the reference regime ($p < 0.05$). Although seasonal cumulative F_s was greatest for the many/small regime, substantial variability among replicates for this treatment precluded the detection of significant differences among the many/small repackaging scenario and the other treatments. Differences in cumulative F_s were established during the first month of the experiment, after which a cumulative sum of 100 mm of water had been applied to all plots. The reduction in cumulative F_s for the few/large regime was thereafter maintained through the end of the growing season, which indicates that the size and timing of a few storms can drive divergent responses in seasonal carbon losses.

Coherent pulse responses of soil CO_2 efflux and soil moisture

We next focus on a complete wetting-drying cycle to examine how tradeoffs in event size and frequency

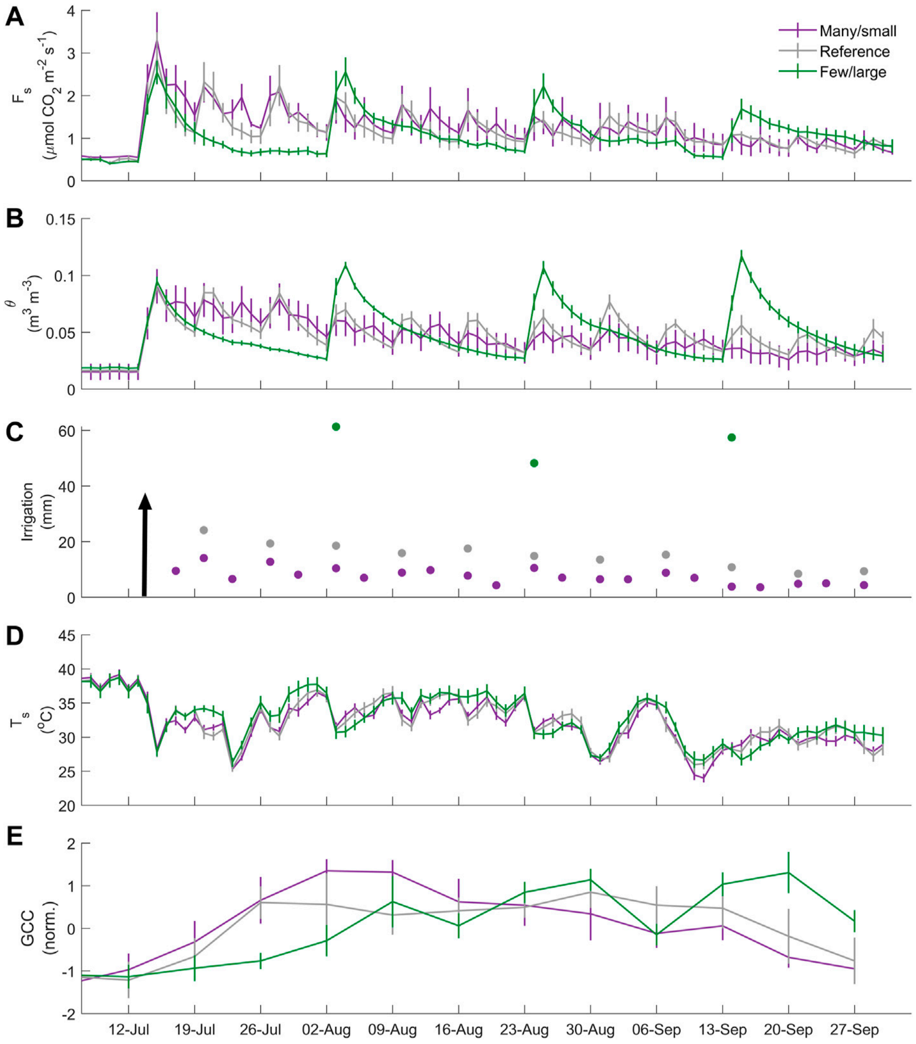

FIGURE 1
Growing season dynamics in **(A)** daily mean soil CO_2 efflux (F_s), **(B)** daily mean volumetric soil moisture (θ), 0–10 cm, **(C)** irrigation amount, **(D)** daily mean soil temperature (T_s, 0–10 cm), and **(E)** and weekly-average of daily mean green chromatic coordinate (GCC) normalized anomalies under three levels of rainfall repackaging. Arrow denotes uniform 38 mm irrigation event on 14 July. Vertical lines indicate standard deviation.

modulated pulse responses of F_s and θ (Figure 3A). Although plots with few/large events had larger post-wetting F_s pulses and increased F_s in the first week after irrigation, they experienced longer dry intervals with decreased F_s relative to plots with many/small events. During the few/large regime's prolonged interstorm periods, plots with reference and many/small treatments experienced additional events that kept F_s and θ relatively high. Averaged over the season, plots irrigated with few/large events had 38% and 67% higher maximum F_s and θ during pulses than plots in the many small/regime (Figures 3B,C). Average antecedent values (day before irrigation, which is also the last day of the previous dry-down cycle) of F_s and θ were 42% and 33% lower for few/large events than for many/small events.

Environmental and vegetative controls on soil CO_2 efflux

To explain the strong coherence among pulse patterns of θ and F_s, we examined the response of F_s to soil moisture (Figure 4) and used analysis of covariance (ANCOVA) to test for differences in the slope of the $F_s - \theta$ relationship. F_s showed a strong linear relationship with θ ($p < 0.01$) and variation in θ explained 84%–86% of F_s variability. The slope coefficient was decreased for plots subject to few/large events compared to those with many/small events ($p < 0.01$) and the reference regime ($p < 0.01$), which indicates that rainfall repackaging influenced the sensitivity of F_s to θ. When comparing the many/small repackaging scenario to reference rainfall size and frequency,

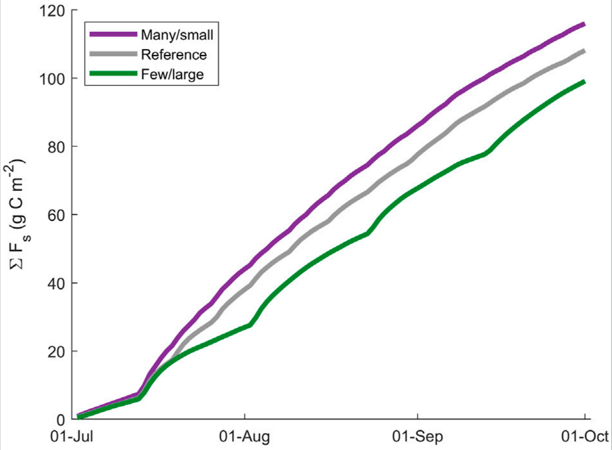

FIGURE 2
Cumulative daily soil CO_2 efflux (F_s) during the 2020 growing season.

TABLE 2 Mean and standard deviation (parentheses) of seasonal average daily mean soil CO_2 efflux (F_s), soil moisture (θ), soil temperature (T_s), and seasonal total F_s (ΣF_s) for the three levels of rainfall repackaging.

Treatment	F_s	ΣF_s	θ	T_s
Many/small	1.24 (0.537)	112.13 (19.52)	0.0441 (0.0161)	32.0 (3.35)
Reference	1.16 (0.447)	104.32 (3.66)	0.0469 (0.0167)	32.5 (3.30)
Few/large	1.06 (0.481)	95.99 (3.99)	0.0475 (0.0234)	32.8 (3.35)

we did not find strong evidence for a significant difference in the slopes ($p > 0.05$). We also investigated the response of F_s to soil temperature (T_s). Although the relationship between F_s and T_s was unclear at the daily scale, hourly F_s increased with T_s when θ was non-limiting (Supplementary Figure S2). Moreover, decreased T_s late in the season appeared to contribute to the reduction in the sensitivity of F_s to θ for the few/large plots (Supplementary Figure S3).

We next examined the relationship between F_s and green chromatic coordinate (GCC), a measure of plot-scale canopy greenness, which is correlated with vegetation gross productivity in open-canopy ecosystems (Yan et al., 2019; Zhang et al., 2022). This decision was based on prior work in this system, which found that vegetation productivity (quantified using ecosystem-scale photosynthesis) is a driver of F_s (Roby et al., 2019), and our observation that peak GCC timing varied among treatments (Figure 1E; see also Zhang et al., 2022). Whereas the relationship between daily F_s and GCC was unclear when θ was high, a positive relationship emerged during drier conditions ($\theta < 0.06$), during which GCC explained 34%–47% of F_s (Figure 5).

Seasonal evolution of soil CO_2 efflux pulses

We next examined the seasonal evolution of F_s and environmental drivers during pulse events (Figure 6). Average F_s and θ during pulses decreased seasonally for the many/small and reference treatments, but were relatively constant for the few/large treatment (Figures 6A,D). As the summer growing season progressed, we observed broadly decreasing trends in both pulse magnitude (Δ) and T_s for all treatments (Figures 6B,E). Whereas the rate of decay of pulses (τ) for the many/small and reference treatments was relatively constant during the experiment, τ and GCC for the few/large plots increased as the growing season progressed (Figures 6C,F).

Discussion

Repackaging equal total rainfall into fewer, larger events decreased summer growing season cumulative F_s relative to reference event size and frequency (Figure 2; Table 2), due to suppressed F_s during prolonged dry intervals (Figure 3) and a reduction in the sensitivity of F_s to soil moisture (Figure 4). These results demonstrate that the effects of rainfall repackaging on F_s varied over time and were modulated by soil moisture responses to interactions between event size and frequency (Table 1; Figure 1). Repackaging rainfall into fewer, larger events caused large fluctuations in θ that increased post-wetting F_s magnitude but suppressed F_s during prolonged dry intervals (Figures 1, 3). Long dry intervals result in dry antecedent conditions which stimulate large post-wetting F_s pulses (Birch, 1958; Xu et al., 2004; Cable et al., 2008; Yan et al., 2014) due to mineralization of microbial-derived carbon and physical displacement of CO_2 by infiltrating water (Fierer and Schimel, 2003; Luo and Zhou, 2006; Unger et al., 2010). Decreased F_s during longer dry intervals indicates a reduction in substrate diffusion and microbial activity associated with water stress (Orchard & Cook, 1983; Davidson et al., 1998; Moyano et al., 2013). Therefore, microbial responses to water stress during long dry intervals likely combined with reductions in oxygen availability during brief periods of saturation immediately after large irrigation events to decrease the sensitivity of F_s to θ in the few/large regime (Figure 4). In contrast, repackaging rainfall into many small events resulted in smaller F_s pulses but maintained higher F_s rates during brief interstorm periods (Figures 1, 3). Frequent wetting supported F_s activation likely by maintaining favorable soil moisture conditions in surface soils where microbes are concentrated (Garcia-Pichel and Belnap, 1996; Moyano et al., 2013). Ultimately, frequent wetting compensated for smaller pulses and increased the sensitivity of F_s to θ

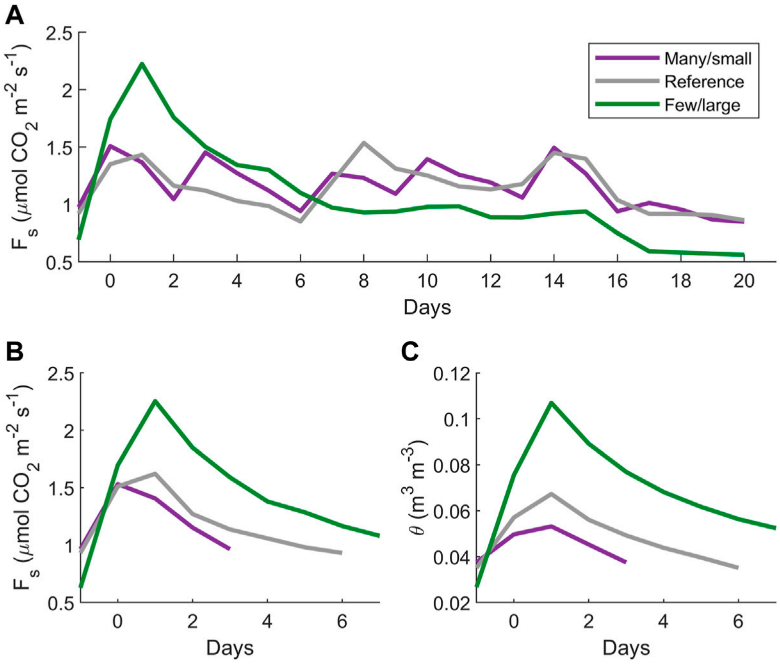

FIGURE 3
(A) Representative mid-growing season period showing soil CO_2 efflux (F_s) responses to irrigation events observed 23 August–13 September 2020 with x-axis showing days since 23 August. Lower panels show the first 7 days of the mean pulse response of **(B)** F_s and **(C)** 0–10 cm volumetric soil moisture (θ) for the three levels of rainfall repackaging averaged across all irrigation events for the entire duration of the experiment. In **(B)** and **(C)** the x-axis indicates days since irrigation event.

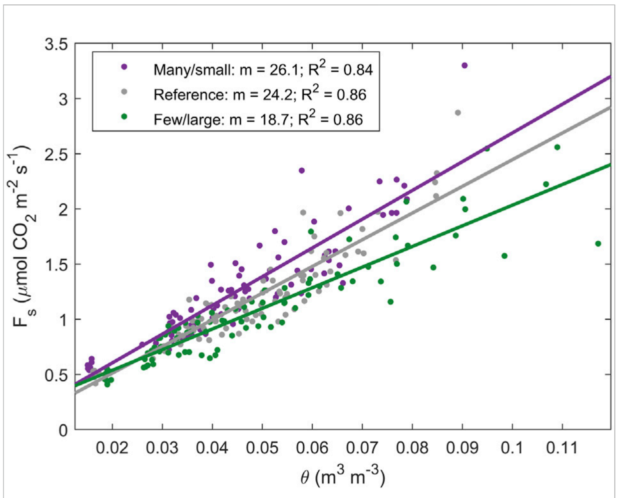

FIGURE 4
Response of daily mean soil CO_2 efflux (F_s) to soil moisture (θ) colored by rainfall repackaging treatment. Note *m* is the slope of the regression line for each treatment.

(Figure 4), resulting in increased seasonal cumulative emissions (Figure 2). Because all plots received equal total water, these findings suggest that the influence of rainfall frequency on the moisture sensitivity of F_s plays a key role in regulating soil CO_2 emissions in semiarid ecosystems.

Plot greenness (GCC) and soil temperature (T_s) were additional controls on F_s that interacted with θ to influence the seasonal evolution of pulses. We found a positive relationship between F_s and GCC during periods of low soil moisture (Figure 5), which likely indicates that measurements of plot greenness can capture the stimulatory effect of plant activity on F_s associated with root respiration and decomposition of recent plant-derived carbon in the rhizosphere (Ogle and Reynolds, 2004; Kuzyakov and Gavrichkova, 2010; Wang et al., 2019). Whereas F_s and GCC were decoupled immediately after irrigation events, a strong positive relationship emerged during drydowns ($\theta <$ 0.06; Figure 5). Because microbial respiration responds more rapidly to soil wetting than plant-mediated respiration (Carbone et al., 2011), our finding that the F_s-GCC relationship is conditional on θ suggests that microbial responses to wetting dominate F_s immediately after rainfall, whereas plant activity modulates F_s during interstorm periods by regulating substrate availability. Prior work in this system has shown that repackaging rainfall into larger, fewer events delays peak plant productivity (Zhang et al., 2022). In this study, we observed a delayed increase in GCC for the few/large regime that was accompanied by an increase in pulse duration

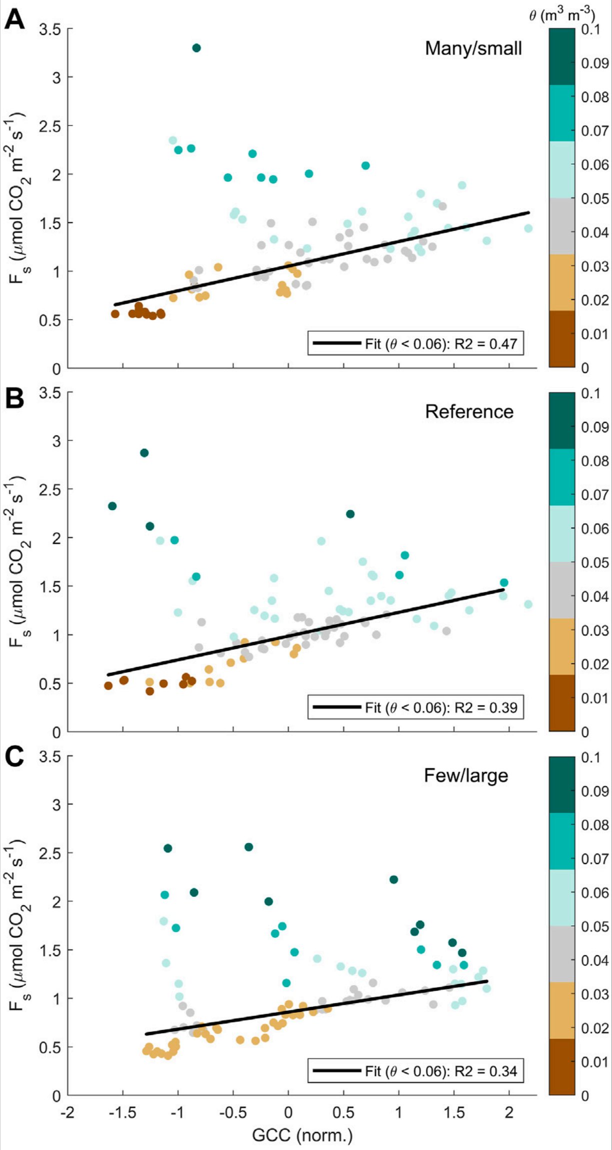

FIGURE 5
Response of daily mean soil CO_2 efflux (F_s) to normalized anomalies in green chromatic coordinate (GCC) colored by soil moisture (θ) for the three levels of rainfall repackaging. The regression line is only fit to low soil moisture values (θ < 0.06).

(quantified as τ) and a decrease in pulse magnitude (Δ; Figure 6). Pulse-average F_s was relatively steady for the few/large treatment, which suggests that increasing autotrophic respiration linked to plant growth led to more sustained pulses late in the season that offset the reduction in pulse magnitude. If we interpret GCC as a proxy for active plant biomass, the linear response (Figure 5) could be caused by the relationship between plant biomass/growth and autotrophic respiration, and through the influence of plant biomass on substrate quantity or quality used for heterotrophic respiration. Thus, the ability of GCC to capture how seasonality in plant growth shapes key aspects of F_s pulses indicates that greenness data may be a useful tool for examining plant and microbial contributions to F_s in future work.

Although F_s had no clear dependency on temperature at the daily scale, hourly F_s increased with T_s when θ was non-limiting (Supplementary Figure S2). These results provide additional evidence that water availability regulates the temperature response of F_s in arid and semiarid ecosystems (Conant et al., 2004; Roby et al., 2019; Wang B. et al., 2014; Chatterjee and Jenerette, 2011). We also observed seasonal reductions in pulse magnitude associated with decreasing T_s (Figure 6) and evidence that reduced T_s late in the season contributed to the decreased sensitivity of F_s to θ in the few/large treatment (Figure 1, Supplementary Figure S3).

Together, these results indicate that changes in environmental and vegetative drivers influenced the seasonal pattern of cumulative soil CO_2 emissions. The observed difference in cumulative F_s was established early in the season when higher F_s in the many/small and reference plots was supported by abundant moisture, warm temperatures, and increased substrate supply associated with an expanding plant canopy. The difference was maintained through the end of the season as decreasing temperatures decreased pulse magnitude and reduced the sensitivity of F_s to θ in the few/large plots. These findings build on studies of generalized pulse responses to rainfall (Knapp et al., 2008; Cable et al., 2013; Vargas et al., 2018; Roby et al., 2019) by demonstrating how soil and plant responses to event size and frequency modulate F_s in semiarid grasslands. The dependence of pulse responses on antecedent θ, T_s, and plant-mediated substrate supply indicates that seasonal changes in the timing of water inputs can influence F_s independent of changes in rainfall amount. Our results demonstrate that water stress effects on F_s during prolonged dry intervals may explain reported reductions in ecosystem-scale respiration to growing season rainfall repackaging in semiarid regions (Liu W. et al., 2017). Because a few individual events drove differences in cumulative F_s, this research indicates the potential for increased variability in the carbon cycling of water-limited regions in response to ongoing changes in precipitation (Sloat et al., 2018; Zhang et al., 2021).

Dryland ecosystems have high spatial heterogeneity in soil properties and vegetation distribution, which presents challenges for understanding ecosystem responses to changes in climate, including rainfall size and frequency (Osborne et al., 2022). Because we observed large variability in seasonal total F_s for the many/small regime (Table 2), future research should examine how spatial heterogeneity and co-limitation of multiple resources (e.g., water, carbon, nutrients) mediate carbon cycling responses to rainfall repackaging (Choi et al., 2022; Osborne et al., 2022). There is also a

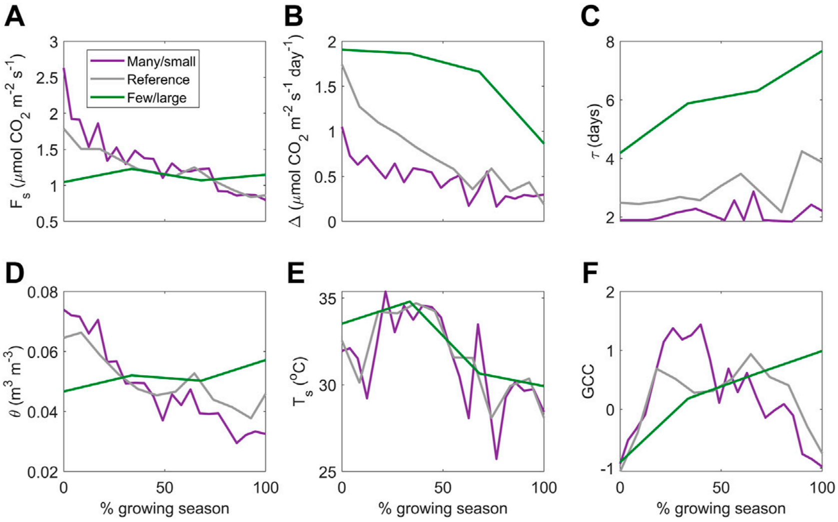

FIGURE 6
Seasonal evolution of the **(A)** average daily rate, **(B)** magnitude of pulse increase (Δ) and **(C)** exponential time decay constant (τ) of soil CO$_2$ efflux (F$_s$) during pulse events. Bottom row shows average daily **(D)** soil moisture (θ), **(E)** soil temperature (T$_s$), and **(F)** normalized anomalies of green chromatic coordinate (GCC) during pulse events. Colors denote the three levels of rainfall repackaging.

need to better understand how soil texture shapes F$_s$ responses to rainfall repackaging. Soil texture is a key determinant of F$_s$ pulse responses (Cable et al., 2008) and although high infiltration capacity of the sandy soils precluded extended periods of saturation in this study, F$_s$ may exhibit different responses to rainfall repackaging in soils with greater clay content. For example, increased clay content may cause oxygen limitation after large events that decrease F$_s$, whereas increased water holding capacity during interstorm periods may increase F$_s$ associated with moisture-dependent microbial and plant processes (Franzluebbers et al., 2000; Yan et al., 2018).

Climate models project continued changes in rainfall toward extreme events separated by longer dry intervals (Ficklin et al., 2022). Our results show that such changes in rainfall patterns may result in reductions in F$_s$ from semiarid regions. Given the widespread nature of pulse behavior, these results have broad relevance for how changing rainfall patterns influence carbon cycling in water-limited ecosystems (Feldman et al., 2018). Our results also highlight the need for models that can account for how changes in plant-mediated substrate and soil temperature interact with water availability to drive seasonality in F$_s$ pulses (Zhang et al., 2014). Future plot-scale work should examine the response of net ecosystem carbon exchange to contrasting compound extremes (Hoover et al., 2022); for example, to test if the observed reductions in F$_s$ with larger, less-frequent events offset losses in productivity caused by plant responses to stress (e.g., high atmospheric demand) during prolonged interstorm periods (Roby et al., 2020).

In conclusion, our findings suggest that projected changes in rainfall size and timing will likely have important effects on carbon losses from semiarid grasslands. Here we show that holding total amount constant, repackaging rainfall into fewer, larger events imposed more water stress that decreased cumulative seasonal soil CO$_2$ efflux in a semiarid grassland. We also found evidence that temporal rainfall repackaging affects the seasonality of F$_s$ pulses and likely alters plant and microbial contributions to soil CO$_2$ emissions. Due to the high spatial heterogeneity characteristic of dryland ecosystems, future studies should further examine how spatial variability in co-limiting resources mediates soil CO$_2$ efflux responses to changes in rainfall distribution. Our study advances understanding on how changes in rainfall timing and frequency alter environmental and vegetative factors that control respiratory losses of CO$_2$ from soil. Because pulses exert strong influence on dryland carbon exchanges, our study indicates the potential for future climate-mediated shifts in the carbon cycling of water-limited regions.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

MR analyzed the data and wrote the manuscript with input from all coauthors. JB and WS designed the rainfall manipulation experiment and identified the repackaging treatments. MR, RS, JB, WS, and DM designed the soil chamber experiment. MR installed and maintained soil chamber systems with assistance from JB and WS.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.940943/full#supplementary-material

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