



# Carbon Stocks and Total Belowground Carbon Flux Respond to Weather and Grazing in Semiarid Montane Meadows

Brian M. Morra,<sup>1\*</sup> Will C. Richardson,<sup>2</sup> Tamzen K. Stringham,<sup>2</sup> and Benjamin W. Sullivan<sup>1,3</sup>

<sup>1</sup>Department of Natural Resources and Environmental Science, The University of Nevada, 1664 N. Virginia St. Mail Stop 186, Reno, Nevada 89557, USA; <sup>2</sup>Department of Agriculture, Veterinary, and Rangeland Sciences, The University of Nevada, 1664 N. Virginia St., Reno, Nevada 89557, USA; <sup>3</sup>The Global Water Center, The University of Nevada, 1664 N. Virginia St., Reno, Nevada 89557, USA

## ABSTRACT

Montane meadow ecosystems are regional carbon (C) hot spots relative to surrounding uplands and can be substantial C sinks or sources. In the semi-arid Great Basin region of the western United States, meadows are vital to hydrology, livestock production, and wildlife. To elucidate factors contributing to meadow C cycling in the Great Basin, we measured the impact of interannual weather, grazing, vegetation communities, and edaphic characteristics on carbon stocks and total belowground C flux (TBCF) in meadows. Meadow carbon stocks were three times larger than average ecosystem carbon stocks in surrounding uplands. Fluxes in the surface (0–15 cm) soil dominated TBCF. In years with above average precipitation, TBCF rates were among the highest we found in the literature. In years with below average precipitation, TBCF was near or below zero, likely indi-

cating soil C loss. Roots consistently contributed 40% of their biomass to soil C. Belowground carbon fluxes differed by plant community and benefited from grazing reduction during periods of below average precipitation, demonstrating the importance of matching grazing intensity to annual weather. Among fluxes (soil respiration, change in root C, change in soil C, and litter inputs), soil C change dominated TBCF. Measuring the gross C inputs to soils (TBCF) may be an effective way to assess the impact of management and interannual weather on meadow C stock before net changes in soil C are observed. Due to the large C stocks found in meadows, the impacts of grazing management and interannual weather should be considered in regional C inventories.

**Key words:** before-after-control-impact; ground-water-dependent; Great Basin; control points; root mass; soil carbon.

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\*Corresponding author; e-mail: bmorra@nevada.unr.edu

## HIGHLIGHTS

- Semiarid meadows are larger carbon (C) hot spots than meadows in more humid climates.

- Change in soil C was the largest flux contributing to total belowground C flux.
- Reductions in belowground C fluxes occurred in dry years under grazing.

## INTRODUCTION

Soils contain more carbon (C) than plants and the atmosphere combined (Hiederer and Köchy 2012), and soil C provides ecosystem services like soil stability, atmospheric carbon dioxide (CO<sub>2</sub>) sequestration, and storage of nutrients and water (Schmidt and others 2011). Soil C is unevenly distributed across Earth's surface primarily because of imbalances between autotrophic inputs and heterotrophic outputs. Fluxes of C in or out of soils have different climatic and edaphic drivers that can change with management. Because ecosystems with large C stocks and fluxes can have a disproportionate contribution to regional C budgets (Dutta and others 2006), understanding C fluxes in managed ecosystems with large C stocks is important for maintaining ecosystem services.

Per unit area, montane meadows contain disproportionate C stocks relative to surrounding upland ecosystems, making them hot spots (or more recently, control points (Bernhardt and others 2017)) in the landscape. For example, meadow soil C stocks in the Sierra Nevada in the states of California and Nevada, USA, exceed 20 kg m<sup>-2</sup>, more than 1.5 times the soil C contained in the surrounding upland (Norton and others 2014). Is the degree to which meadows contrast with their surrounding uplands consistent among climates? Climate might alter the degree to which meadow C stocks differ from their surrounding uplands by altering either upland C stocks or meadow C stocks. Total ecosystem C stocks in upland montane forests surrounding meadows in the Sierra Nevada mountains of California, USA, can be 32 kg C m<sup>-2</sup> (Mattson and Zhang 2019), while drier and warmer upland montane ecosystems found at similar elevations of the Great Basin, USA, have ecosystem C stocks as low as 4 kg C m<sup>-2</sup> (Rau and others 2011). Alternatively, climate may impact meadow C stocks themselves: Soil C stocks decreased with increasing mean annual temperature (MAT) and increased with mean annual precipitation (MAP) in grassland meadows of Yunnan Province, China (Balasubramanian and others 2020). As groundwater-dependent ecosystems, meadows exist in semiarid regions (regions receiving less than 50 cm of rain annually) because their hydrogeomorphic landscape position accumulates water from the

surrounding watershed, which is sensitive to climate. Therefore, relative to uplands, meadows in semiarid ecosystems may contrast with their surrounding ecosystems to a different degree than meadows found in more humid regions.

The accumulation of soil moisture in meadows from the surrounding watershed can result in extended periods of shallow groundwater. Spatial and temporal variation of groundwater depths influences the distribution of plants within meadows (Allen-Diaz 1991; Castelli and others 2000). Meadow plant distribution drives C cycling and storage by creating an imbalance between C inputs and outputs (Norton and others 2014; Reed and others 2021). Though meadow vegetation is diverse, it can be grouped into communities based on a tolerance of, or reliance on, shallow groundwater. Plant communities range from wetland-obligate herbaceous plants to upland shrubs (Castelli and others 2001; Stringham and others 2001; Darrouzet-Nardi and others 2006). These communities may differ in their annual productivity and proportion of C allocated belowground (De Deyn and others 2008; Norton and others 2011; Reed and others 2021). Meadows with more wetland-obligate or facultative plants experienced net C sequestration, whereas meadows with more upland plants experienced net C loss. These differences in soil C change may be attributed to different rates of plant inputs to soil, not respiratory losses of soil C (Reed and others 2021). Given this, the gross flux of C by plants to soil (total belowground carbon flux, or TBCF) may be an important ecological function in montane meadows.

Belowground C fluxes can be further altered by management activities such as grazing via direct impacts to plant communities or indirect effects on plants due to changes in hydrology—and grazing impacts may change with climate (Milchunas and others 1988; Trimble and Mendel 1995; Enriquez and others 2015). In some cases, grazing may cause a compensatory growth response and belowground C stocks are increased (Hafner and others 2012). The compensatory growth response can be decreased (Zhao and others 2008) or increased by low soil moisture (Van Staaldunin and Anten 2005). Grazing was associated with lower C stocks in drier portions of meadows than wetter ones (Norton and others 2011) and grazing reduced meadow soil C stocks in dry climates with fine textured soils (Mcsherry and Ritchie 2013; Enriquez and others 2015). In severe cases, grazing can contribute to the establishment of shrubs or annual plants (McIlroy and Allen-Diaz 2012) by altering hydrology through the formation of dominant flow paths,

leading to incised channels (Trimble and Mendel 1995; Darrouzet-Nardi and others 2006; Loheide and Gorelick 2007). Following incision, increased depth to groundwater allows shrubs to replace bank-stabilizing herbaceous vegetation, allowing for further erosion and continued channel incision (Debinski and others 2010). This shift in vegetation may convert meadows from net C sinks to net C sources. Although less impacted meadows can gain soil C at rates of 300–850 g C m<sup>-2</sup> y<sup>-1</sup>, hydrologically impacted meadows in the California Sierra Nevada, USA, were observed losing about 400 g C m<sup>-2</sup> annually and had greater depth to groundwater, less root biomass, more bare ground, and more xeric vegetation (Reed and others 2021). Understanding the interaction of management and plant communities on total belowground inputs may help indicate the direction and magnitude of changes in soil C on an annual basis.

It is likely meadows disproportionately contribute to the C cycle and forage production of semiarid regions. These areas remain productive long after upland areas experience annual water limitations and concentrate wild and domesticated herbivores due to dense communities of herbaceous vegetation. To understand how grazing interacts with moisture availability to impact soil C cycling in semiarid meadows, we designed this study to address the following questions:

- How do meadow C stocks in semiarid meadows differ from surrounding upland ecosystems and meadows in more humid climates?
- What are the gross rates of belowground C flux in semiarid meadows, and how do they differ among different meadow vegetation communities, grazing regimes, and years with different antecedent winter precipitation?
- How do the soil environment and annual weather change C fluxes in semiarid meadows?

## METHODS

### Site Description

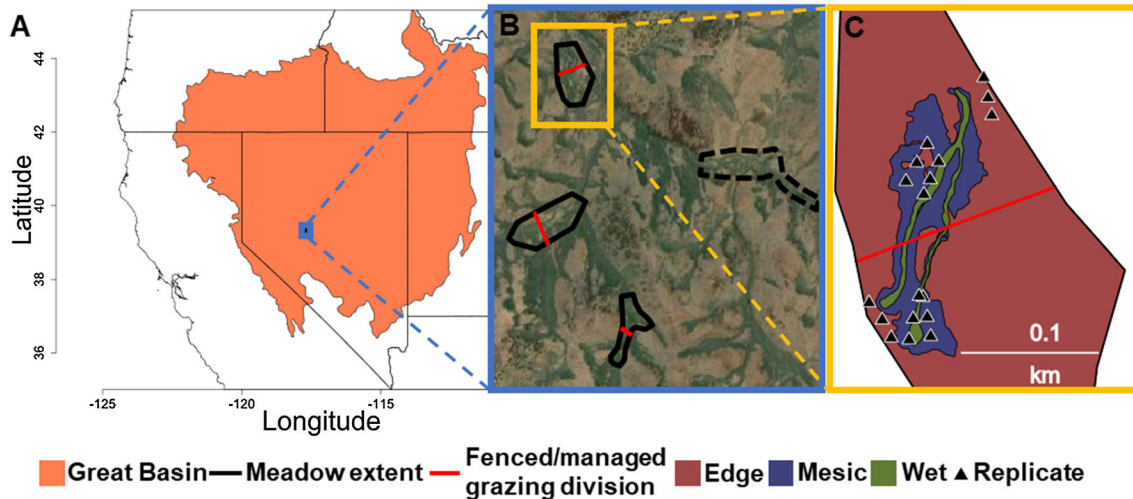
This research was conducted in four meadows in the Desatoya Mountains in central Nevada (Figure 1A), USA, a semiarid region of the Great Basin which has a mean annual precipitation of 315 mm, a mean annual temperature ranging from 4.6 to 7.6 °C, and a 30-year average of 5.8 °C (Prism Climate Group 2022). Our study meadows ranged in size from 0.2 ha to 1.4 ha (Figure 1B). Similar meadows can be found throughout the Great Basin (Germanoski and Miller 2004). Our study captured

the wettest (419 mm in 2019) and driest (175 mm in 2020) conditions in the last 30 years (Prism Climate Group 2022).

Data collection began in the spring of 2019 and captured one season of consistent grazing across the four meadows. Grazing by wild horses (*Equus ferus*) was uncontrolled while cattle (*Bos taurus*) grazed in late spring. In November 2019, fences were built to split three of the four meadows into grazing exclusion and managed grazing treatments (Figure 1C). Managed grazing excluded horses all year; cattle grazing began in mid-June and continued until forage species were consumed to a stubble height of 10 cm (Hall and Bryant 1995). The fourth meadow was left unfenced and maintained year-round use by wild horses and seasonal cattle grazing (unmanaged grazing). With two grazing levels across three meadows and one meadow with unmanaged grazing, we established a total of seven plots (Figure 1B). Within each of the seven plots, three plant communities were delineated by Richardson and others (2021) based on degree of dependence on shallow water tables. Defined here as wet, mesic, and edge plant communities, each community contained a set of three replicated subplots, creating a total of 63 subplots where data were collected to measure C fluxes (Figure 1C; Figure S1).

### Measurements of Soils, Plants, and Soil Respiration

We collected soil cores in the spring of 2019, 2020 and 2021 and the fall of 2020 and 2021 to assess soil and root C stocks. We cored 0–45 cm soil in each of the subplots with a five-cm-diameter slide hammer (AMS Equipment Corp, American Falls, Idaho) in stratified 15-cm-deep increments (see SI Methods for more detail). Following sample collection, bulk density was calculated using the rock-free, root-free mass of dry soils that passed through a 2 mm sieve. Soil C stock (g C cm<sup>-2</sup>) was the product of the measurement depth, bulk density and soil percent C measured using a Costech 4010 Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA). To minimize uncertainty associated with changes in bulk density and soil moisture, we applied the mean subplot-level bulk densities from the Fall 2020 and Fall 2021 sampling events, when soils were driest, to all seasonal C stock estimates. Comparing the average fall bulk density to the bulk density, we measured at each time point gave a mean square error of 0.01, giving us confidence that annual changes in bulk density due to sampling events were minimal.



**Figure 1.** Hierarchy of the experimental design. **A** We collected samples from four meadows in the semiarid Great Basin, Nevada, USA. **B** In the late fall of 2019, after our first year of sampling, three of the meadows had fences installed that surrounded the meadows (solid black lines). Fences split the three meadows (red line) into grazing exclusion (no cattle or horse entry) or managed grazing (fenced, cattle entry controlled; horses excluded) pairs. A fourth meadow was left unfenced (dashed black line) and experienced unmanaged grazing—cattle and horses permitted throughout the growing season—which served as our reference meadow. **C** Within each grazing treatment, three plant communities were delineated, which we term edge, mesic, and wet. Each plant community contained three replicated subplots where measurements were taken (equaling 63 subplots total; Supplementary Figure 1).

Each year, we collected aboveground herbaceous plant biomass at peak biomass and at the end of the growing season at each subplot where a soil core was taken using 25-cm-diameter hoops. Herbaceous plant biomass was oven-dried at 60 °C, and a subset of three aboveground tissue samples and three root samples from each of the three plant groups were ground using a Wiley Mill (Thomas Scientific, Philadelphia, PA, USA) and analyzed for C concentration with elemental analysis. We used percent C measurements to convert grams of herbaceous biomass (aboveground tissues and roots) to grams C.

To characterize C respired from soils of semiarid meadows, we measured CO<sub>2</sub> and methane (CH<sub>4</sub>) fluxes approximately every three weeks during the growing season in 2019, 2020, and 2021 for a total of 18 soil respiration sampling events. We measured soil gas fluxes using the same static chamber and gas chromatography methods described in Reed and others (2018); see SI Methods for more detail. Soil CO<sub>2</sub> efflux was comprised of autotrophic and heterotrophic respiration while soil CH<sub>4</sub> flux included production and uptake by methanogens and methanotrophs, respectively. During gas sampling, we measured soil moisture and temperature using two methods: time-domain reflectometry (TDR) and analog thermometers for high spatial resolution ( $n = 63$  per sampling event) and soil

moisture and temperature probes deployed at the plant community level ( $n = 21$ ) for high temporal resolution. See SI Methods for instrumentation details. We used the high-temporal-resolution data to interpolate daily values between monthly measurements taken at high spatial resolution as explained in SI Methods.

We used C gas fluxes, root C, soil C, and aboveground herbaceous C to calculate total belowground C flux (TBCF; Eq. 1). Total belowground C flux is a mass balance approach which uses the sum of gaseous losses of C from soils (CO<sub>2</sub> and CH<sub>4</sub>) (respired soil C) and changes in C stored in roots ( $\Delta$  Root C) and soils ( $\Delta$  Soil C) to estimate the gross flux of C to soils from plants (Raich and Nadelhoffer 1989; Giardina and Ryan 2002)

$$\text{TBCF} = \frac{\Delta \text{soil C} + \Delta \text{Root C} + \text{respired soil C} - \Delta \text{litter C}}{\text{time}} \quad (1)$$

We estimated TBCF for the three growing seasons of 2019, 2020, and 2021. The growing season lengths were based on site access due to snowpack in spring and when soil respiration decreased by at least 50% (below 2  $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) and remained low for three consecutive samplings (SI Figure S2). Growing seasons lasted 115, 116, and 138 days for 2019, 2020, and 2021, respectively. For 2019, the change in soil C stock and root C stock was calcu-

lated as the difference between stocks measured in spring 2019 and spring 2020, while changes in soil C stock for 2020 and 2021 were calculated as the difference between spring and fall soil C stocks. We justify the difference in pretreatment sampling and posttreatment sampling with the assumption that there would be very little difference between soil C stocks (root and soil C) measured in late October of 2019 and at the start of the 2020 growing season in early May of 2020, and the impact of grazing was likely minimal over the winter months. Following the implementation of different grazing treatments, we increased the temporal resolution of our sampling to capture soil and root C stocks leading up to and following annual grazing. Because the standing stock of herbaceous biomass at the end of the growing season is the source of aboveground litter inputs in meadow ecosystems, we assumed end of season standing biomass was equal to the change in litter C. This likely overestimates actual litter C input to soil, as photooxidation is important in grasslands (Brandt and others 2010) and may reduce the actual amount of C that gets incorporated into soil. We ignored aboveground litter inputs from woody plants (*Artemisia* spp.) because their contribution to litter in our subplots was minimal.

## Upland C Stocks

To contextualize the importance of meadow C in the Great Basin region relative to vegetation C stocks present in a variety of Great Basin ecosystems, we conducted a literature review of C stocks in ecosystems characterized by dominant species common to semiarid regions of the Great Basin: *Artemisia* spp., *Bromus tectorum*, and *Pinus monophylla*. We used five data sets that contained 11 mean values to represent an average soil C stock, four data sets containing nine mean values to represent an average root C stock, and four data sets containing nine mean values to represent an average aboveground biomass C stock in regional upland vegetation. A full list of studies and mean values can be found in Table S1.

## Statistics

All statistical tests were performed using R (R Core Team 2021) treating individual subplots as replicates. In the effort to prioritize effect sizes, we report *p* values associated with the results and allow the reader to determine the strength of the evidence against null hypotheses.

To assess differences among meadow C stocks and compare meadow C stocks to those measured in upland ecosystems reported in our literature

review, subplot-level measurements were averaged across all five sample dates. We used analysis of variance (ANOVA) and Tukey's honest significant difference test (Tukey's HSD) to measure differences among C pools.

Our TBCF approach is based upon a before-after-control-impact (BACI) study design. In a similar low replication, complex BACI design, Ellison and others (2010) recommended presenting the slope of the line of the response variable (TBCF) as a function of time as the effect size to integrate change following the implementation of a treatment. We fit linear mixed models to subplot-level data (plant-level data nested within grazing intensity) that included a random intercept for the individual subplot as a way of accounting for dependence among repeatedly sampled subplots. We present the slopes of the mixed linear models as the effect size associated with the subplot-level data. We then compared the slopes among linear models using an analysis of covariance (ANCOVA) (Gotelli and Ellison 2004). The results of the ANCOVA were used to show the main effects (plant community, grazing treatment, and time) as well as the interactions among grazing intensity, plant community, and time. We used *t*-tests to determine the probability of TBCF and change in soil C stock being different than zero (positive) for a given plant community experiencing a particular grazing intensity.

We wanted to quantify the importance of properties within the soil environment as drivers of TBCF. We selected eight variables associated with the soil environment to analyze for their importance in explaining TBCF: peak biomass, days of vegetative growth, average volumetric water content (VWC) for the growing season, average soil temperature for the growing season, soil drought days, soil drying rate, max VWC, and average soil temperature for the first month of observation. The calculation of these values is explained in the supplementary materials. We focused this analysis on shallow soils (0–15 cm) because soil temperature and moisture measurements were confined to shallow soil depths. These nine variables were evaluated using backward stepwise linear regression and ranked based on their Akaike information criterion (AIC) score. To explore the role of roots in TBCF, we used linear models to explore the relationships between antecedent root mass and soil C stocks.

## RESULTS

### Meadow C Stocks

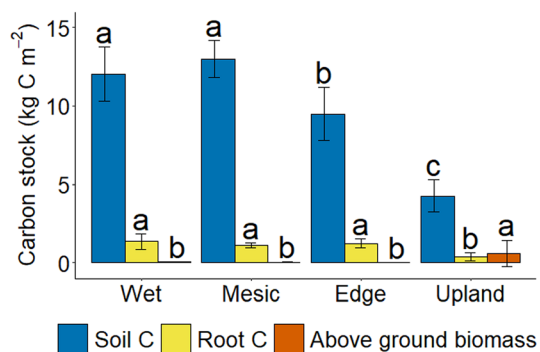
Soil C in the 0–45 cm depth was consistently the largest component of ecosystem C stocks, followed

by root C and aboveground C (Figure 2). Soil C stocks were different among the three plant communities ( $p < 0.001$ ): Mesic and wet plant communities had similar soil C stocks ( $13.00 \pm 0.18$  and  $12.03 \pm 0.24 \text{ kg C m}^{-2}$ , respectively), but the edge plant community had smaller soil C stocks ( $9.50 \pm 0.21 \text{ kg C m}^{-2}$ ) (Figure 2). In each vegetation group, soils contained nearly six times the C found in the other pools combined. Root C and aboveground C stocks were similar among the three meadow plant communities.

Per unit area, these meadows had larger C stocks than literature-derived estimates for typical surrounding upland Great Basin ecosystems dominated by *Artemisia* spp., *Bromus tectorum*, and *Pinus monophylla* (Figure 2). Compared to upland Great Basin ecosystems, meadows hold proportionally more of the total C stock in soil and roots than aboveground vegetation. These meadow soil C stocks were three times greater; root C stocks were two times greater, and aboveground C stocks were between six and 14 times lower than in upland Great Basin ecosystems.

### Components of TBCF

Comparing the fluxes contributing to TBCF, the largest individual flux that contributed to TBCF was change in soil C stock, followed by soil respiration



**Figure 2.** Belowground carbon stocks found in three meadow plant communities (wet, mesic, and edge) compared to literature-derived C stock estimates measured in non-meadow Great Basin ecosystems (upland). Values are the mean  $\pm$  the standard error. Meadow C stocks are the mean value over the three growing seasons of this study for unmanaged, managed grazing, and fenced meadows. Letters indicate differences in the sizes of C stocks (aboveground, root, soil) among plant communities (Tukey's HSD  $p < 0.05$ ); for example, comparing soil C among wet, mesic, edge, and upland plant communities, soil C stock was lowest in uplands, followed by edge plant communities; wet and mesic communities had similar large C stocks.

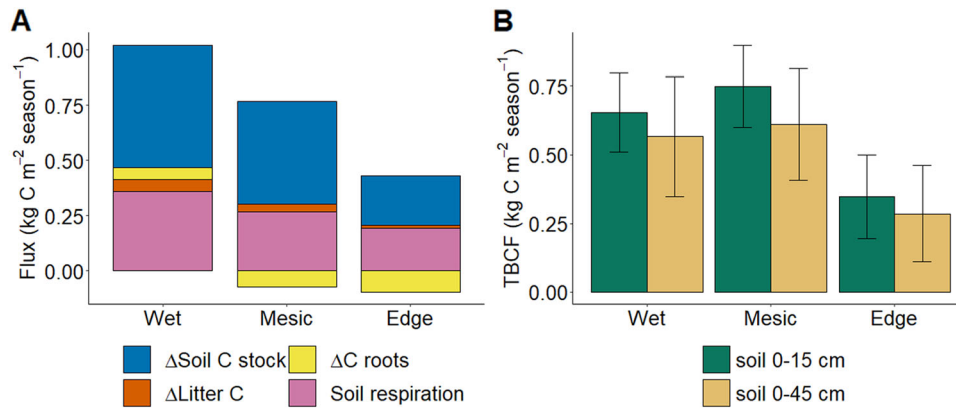
and root C change (Figure 3A). Soil respiration primarily consisted of  $\text{CO}_2$ ; the soil  $\text{CO}_2$  efflux was four orders of magnitude larger than soil  $\text{CH}_4$  flux (SI Table S3). End of season herbaceous biomass, which represents aboveground plant litter flux to meadow soil, was the smallest flux and was an order of magnitude smaller than changes in soil C stock (Figure 3A). When we averaged TBCF across growing seasons and grazing treatments, TBCF in the top 15 cm of soil accounted for over 75% of the TBCF measured in the 0–45 cm depth in all three vegetation communities (Figure 3B). We found that measurements of TBCF using soils 0–15 cm and 0–45 cm were not different in wet, mesic, and edge plant communities ( $p = 0.85$ ,  $0.66$ , and  $0.86$ , respectively). Therefore, we focus on shallow soil (0–15 cm) TBCF when exploring the impacts of vegetation community, grazing, and the physical environment on TBCF.

The largest component of TBCF, change in soil C, was highest during 2019, an abnormally wet year. We primarily saw annual gains in soil C stocks occurring in shallow soils (0–15 cm) during 2019; no plant community had mean soil C stock losses (Figure 4). By 2021, change in soil C stock was approximately zero across grazing intensities and plant communities.

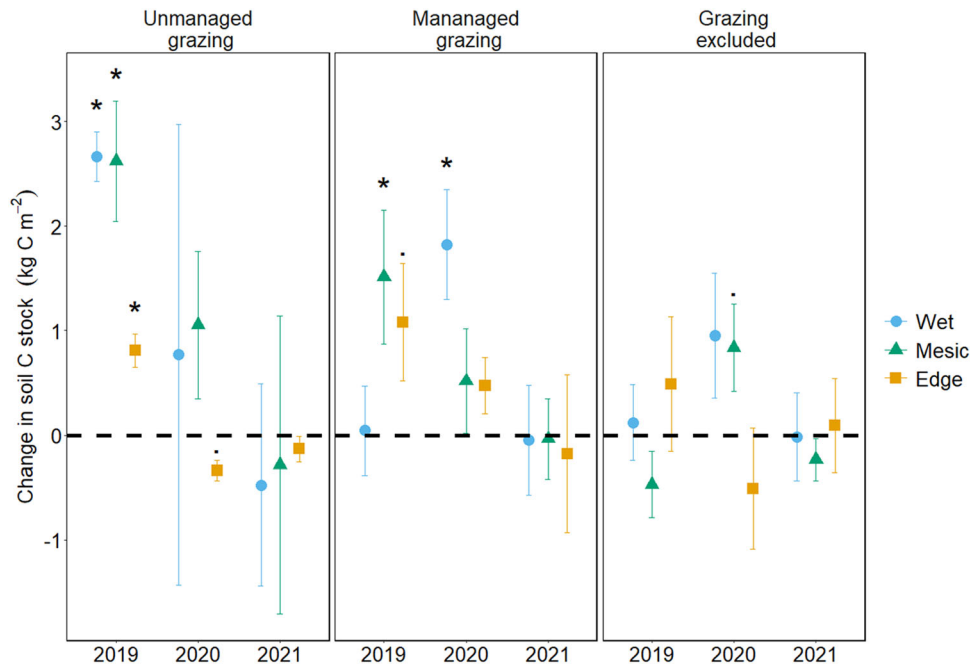
### Total Belowground C Flux Among Plant Communities and Grazing Regimes

Averaged across growing seasons, the edge, mesic, and wet plant communities had TBCF rates of  $0.35 \pm 0.03$ ,  $0.75 \pm 0.03$ , and  $0.65 \pm 0.03 \text{ kg C m}^{-2} \text{ y}^{-1}$ , respectively. In shallow soils (0–15 cm), TBCF was generally highest in 2019 and declined through 2021 (growing season main effect:  $p < 0.001$ ). Surface soil TBCF differed by grazing intensity (grazing main effect:  $p = 0.008$ ) and among plant communities (plant community main effect:  $p = 0.059$ ). There was greater evidence that the 2019–2021 interannual decline in TBCF differed with grazing intensity (grazing by growing season interaction:  $p = 0.063$ ) than by plant community (plant community by growing season interaction:  $p = 0.12$ ) or the interaction of grazing intensity and plant community (plant community by grazing by growing season interaction:  $p = 0.58$ ).

Shallow soil TBCF was positive in all three plant communities in 2019 (when all meadows were grazed prior to fencing, which occurred after the 2019 growing season) (Figure 5;  $p < 0.1$ ). In 2020, we measured positive TBCF in the wet plant community experiencing managed grazing ( $p = 0.04$ ).



**Figure 3.** **A** Components of total belowground C flux (TBCF) in soils 0–15 cm in wet, mesic, and edge vegetation communities within Great Basin meadows demonstrate that  $\Delta$  Soil C stock was a major component of TBCF. In mesic and edge plant communities, there was a net decrease in root C. **B** Comparison of TBCF measured in shallow soils (0–15 cm) to TBCF measured to the full soil depth (0–45 cm) in each of the three vegetation communities. There was no difference in TBCF between 0–15 cm and 0–45 cm soil in all plant communities (T-test;  $p > 0.05$ ). In both panels, values are the subplot-level means observed across 2019–2021; Panel 3B includes the standard error among subplots and years.

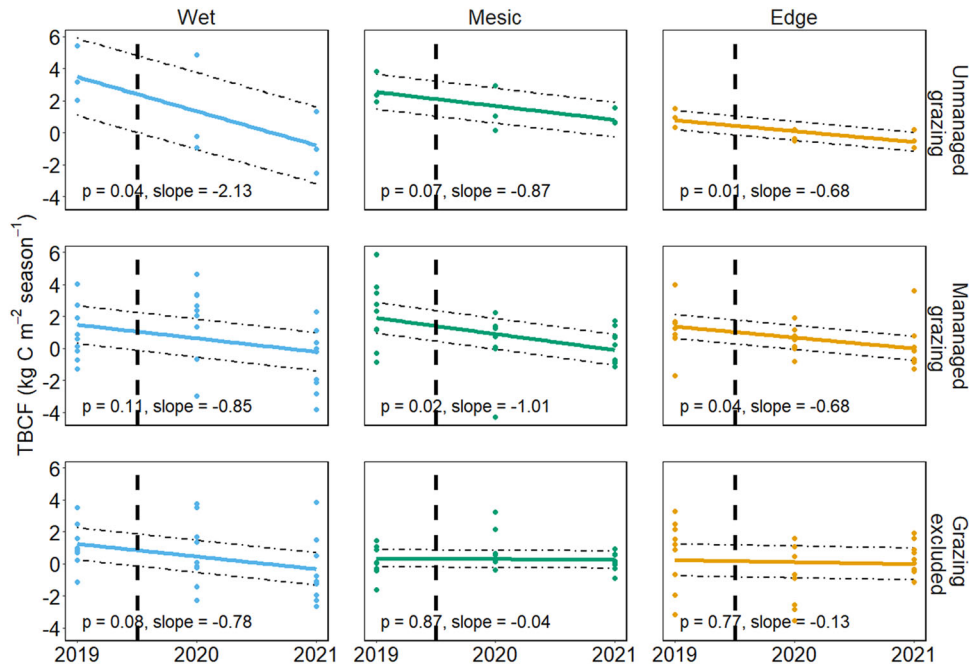


**Figure 4.** Changes in soil C stock in soils 0–15 cm in edge, mesic, and wet plant communities under unmanaged grazing, managed grazing, and grazing exclusion. Positive values indicate gains in soil C while negative values indicate soil C loss. Error bars show the standard error of the mean. Symbols are used to indicate the probability of changes in soil C stock being different than zero. An asterisk indicates  $p < 0.05$ , and a period indicates  $p < 0.1$ .

By 2021, TBCF was not different from zero under any grazing treatment or plant community ( $p$  values ranged from 0.26 to 0.96).

Linear models estimated a minimal decline in TBCF of  $0.31 \text{ kg C m}^{-2} \text{ y}^{-1}$  from 2019 to 2021 where grazing was excluded in 2020 and 2021, averaged across all plant communities (Figure 5;  $p = 0.14$ ). Relative to grazing exclusion, the aver-

age decline in TBCF between 2019 and 2021 was two times higher under managed grazing ( $0.84 \text{ kg C m}^{-2} \text{ y}^{-1}$ ;  $p < 0.001$ ) and almost four times higher under unmanaged grazing ( $1.2 \text{ kg C m}^{-2} \text{ y}^{-1}$ ; Figure 5;  $p = 0.003$ ). Under unmanaged grazing, the wet vegetation community had the largest decrease in TBCF between 2019 and 2021, decreasing by  $2.13 \text{ kg C m}^{-2} \text{ y}^{-1}$  (Fig-



**Figure 5.** Changes in total belowground carbon flux (TBCF) for soils (0–15 cm) in wet, mesic, and edge plant communities under unmanaged grazing, managed grazing, and grazing exclusion. The dashed line separates pretreatment data from measurements taken after the installation of fences and separates the above average precipitation year from the two subsequent below average precipitation years. Slopes and p-values are derived from linear models measuring the impact of subplot-level data on TBCF with respect to time. Dashed lines are the 95% confidence interval of the plant communities within the treatment.

ure 5;  $p = 0.04$ ). This interannual decrease in TBCF was twice as large as the next largest decrease which occurred in the mesic plant community of managed grazing ( $1.01 \text{ kg C m}^{-2} \text{ y}^{-1}$ ;  $p = 0.02$ ).

### Mechanisms Controlling TBCF

By sampling soil C and root biomass five times between 2019 and 2021, we could correlate soil C stocks and antecedent root mass at four time points during this study (Table 1). At a meadow level ( $n = 4$ ) in shallow soils (0–15 cm), we found positive correlations (Table 1) between C stock and antecedent root mass during three out of the four sampling dates. Where correlations existed, soil C stocks consistently changed, positively or negatively, by about 40% of antecedent root mass. When we combined wet and mesic plant communities (and excluded the edge community), only spring soil C stock was correlated with antecedent root mass ( $p = 0.08$  and  $0.04$ ) (Table 1). In the edge community, antecedent root mass predicted soil C stocks in one spring sampling and one fall sampling.

Stepwise linear model selection showed different environmental controls on TBCF among plant communities. However, the most parsimonious

models for each plant community only explained a fraction of the variation in TBCF ( $r^2$  values between 0.07 and 0.20; Table S4). Peak aboveground herbaceous biomass was the most important variable for predicting changes in belowground C fluxes in edge and wet plant communities. Additionally, the best models for wet and edge plant communities omitted soil drying rate and percent drought days. In the mesic plant community, the models with the lowest AIC were those related to water availability, including max VWC, number of growing days, and soil drying rate.

### DISCUSSION

Meadows are a hot spot of the C cycle in the semiarid Great Basin, containing dynamic gross soil C fluxes and large soil C stocks that may exceed total above and belowground C stocks in many upland Great Basin ecosystems. Total belowground C flux in meadows was largely made up of change in soil C stock resulting from root turnover. Along with changes in soil C and root mass, TBCF was driven by edaphic characteristics that varied among plant communities, reflecting different patterns in groundwater and root morphology within mead-



**Table 1.** Pearson Correlations Between Meadow Soil Carbon (C) Stocks and Root Mass From the Sampling Event Antecedent to the Soil C Measurement (Antecedent Root Mass) in Shallow (0-15 cm) Soils Across All Meadows

		Antecedent root mass among plants	Antecedent root mass edge	Antecedent root mass mesic	Antecedent root mass wet	Antecedent root mass wet + mesic
C stock Spring 2020	Slope	0.41	0.55	0.18	0.41	0.36
	p	<b>0.01</b>	<b>0.01</b>	0.60	0.15	<i>0.08</i>
	r	0.33	0.58	0.14	0.33	0.26
C stock Fall 2020	Slope	0.16	0.28	- 0.14	0.00	0.03
	p	0.17	0.19	0.48	0.98	0.76
	r	0.10	0.30	0.17	0.07	0.04
C stock Spring 2021	Slope	0.42	0.47	0.81	0.25	0.28
	p	<b>0.01</b>	0.22	<b>0.01</b>	0.21	<b>0.04</b>
	r	0.33	0.28	0.85	0.30	0.32
C stock Fall 2021	Slope	0.42	0.65	0.03	- 0.14	- 0.06
	p	<b>0.00</b>	<b>0.01</b>	0.91	0.48	0.70
	r	0.33	0.81	0.03	0.17	0.06

*Bold text indicates  $p < 0.05$  and italic text indicates  $p < 0.1$ .*

ows. Given management and weather, meadows in semiarid ecosystems are a potential atmospheric C sink.

### The Importance of Semiarid Meadows to the Regional C Cycle

Our meadow C stocks were only about 20% lower at equivalent depths to meadows in more humid montane regions (Reed and others 2021), but three times greater than surrounding semiarid upland ecosystem C stocks. Montane meadows in more humid regions contain only half the C stock of surrounding forests (32.30 kg C m<sup>-2</sup>; Mattson and Zhang 2019). Because meadow C is largely belowground, it is less vulnerable to fire, a common montane disturbance, than aboveground C.

Total belowground C fluxes from mesic and wet plant communities were three times larger than upland rates of gross primary productivity (GPP) measured in the Great Basin, which ranged from 0.38 to 0.51 kg C m<sup>-2</sup> y<sup>-1</sup> (Pandit and others 2019). Given TBCF must be smaller than GPP, TBCF in meadows vastly exceeds TBCF in regional upland ecosystems. Gross C fluxes to soils measured in these meadows are large and dynamic relative to measurements of TBCF found in more humid ecosystems. For example, from 2019

through 2021 we measured mean (across vegetation groups) annual meadow TBCF values of  $1.2 \pm 0.22$ ,  $0.61 \pm 0.23$ , and  $-0.11 \pm 0.18$  kg C m<sup>-2</sup> y<sup>-1</sup>, which are among the lowest and highest TBCF rates identified in a meta-analysis by Gill and Finzi (2016). Such high gross flux rates are supported by high net C flux rates in other meadows. Using different methodologies, Blackburn and others (2021) and Reed and others (2020) estimated net belowground C fluxes between  $-0.59$  and  $+0.85$  kg C m<sup>-2</sup> y<sup>-1</sup>, placing meadows among both the largest terrestrial net C sinks (Baldocchi 2008) and sources such as degraded peatlands (Kareksela and others 2015).

Given their large C stocks, high rates of belowground C flux, and unique hydrogeomorphic characteristics, semiarid meadows may be control points (Bernhardt and others 2017) of the C cycle regionally, despite their limited spatial extent. Within meadows, we measured high spatial and temporal variability, where anomalously high and low TBCF rates in individual subplots were observed (ranging between a minimum of  $-6.78$  kg C m<sup>-2</sup> y<sup>-1</sup> and a maximum of  $8.18$  kg C m<sup>-2</sup> y<sup>-1</sup> across all growing seasons, plant communities, and grazing treatments). These outlier values may not represent control points

within meadows, as these high flux rates were not maintained and were highly variable among similar subplots. Therefore, these values were not representative of the ecosystem, and we caution against the extrapolation of individual extreme values across other meadow ecosystems.

## Meadow TBCF in Context

We used the TBCF approach because, by definition, gross C fluxes are bigger than net fluxes, and a priori, we did not expect to be able to measure appreciable net fluxes over a short time span. The results here support previous findings that most of meadow GPP must be allocated belowground (Reed and others 2021). Because TBCF is a gross flux, TBCF should not be used for net C accounting in these meadows. In fact, the high degree of temporal and spatial variability of fluxes we observed speaks to the need for long-term data to establish net C fluxes over time in these ecosystems (for example, Reed and others 2021; Morra and others 2023).

Methodological approaches challenge comparisons between this and other studies of TBCF and its constituent fluxes. Most TBCF measurements have occurred in forests (Gill and Finzi 2016). In forest studies, changes in soil and root C have often been assumed to be negligible and are omitted, making TBCF equal to the difference between soil respiration and litterfall (Gill and Finzi 2016). In studies that have included change in soil C, it was the smallest component of TBCF, increasing by  $0.01 \text{ kg C m}^{-2} \text{ y}^{-1}$  in eucalyptus plantations (Giardina and Ryan 2002) and decreasing by  $0.01 \text{ kg C m}^{-2} \text{ y}^{-1}$  in temperate grasslands (Adair and others 2009).

While change in soil C was the largest flux involved in meadow TBCF, at a meadow level the consistent correlations showing 40% of root mass contributing to soil C stock help explain dynamic meadow soil C stocks. This proportional contribution of biomass to soils has also been observed by Parsons and others (1983), who found that 42% of GPP was recovered as dead tissue in perennial ryegrass pastures. Differences in the timing of root contributions to soil C among plant communities show the different patterns in C allocation among functional groups. In the herbaceous-dominated communities, roots at the end of the previous growing season were responsible for changes in soil C stock in the subsequent year, rather than the roots present in the current spring. Similar fall season contributions of roots to soil C have been reported by Hooker and Stark (2012), who found root litter from perennial grasses in semiarid re-

gions was the dominant flux to stable soil C pools. They proposed this was due to the higher moisture content of the recently abscised root tissue relative to the surrounding soil. By contrast, in the shrub-dominated edge plant community, root mass may have a more consistent contribution to soil C stock throughout the growing season, as there were no consistent seasonal patterns between antecedent root mass and soil C stocks. The differences in the role of roots for changing soil C among plant communities are likely due to differing root morphologies of shrubs found in the edge plant community (characterized by woody coarse roots) and the herbaceous-dominated wet and mesic plant communities containing short-lived fine roots (Zhang and Wang 2015).

The bulk of meadow TBCF variability can be explained by roots changing the soil C stock. However, the plant communities we measured have different reliance on groundwater and other ecosystem characteristics. These characteristics differed by plant community and explained a portion of the variability (< 15%) in meadow C flux. Max VWC was the only variable common among the most parsimonious models for wet, mesic, and edge plant communities, and TBCF was higher with wetter soil, highlighting available moisture early in the growing season as an overall driver of TBCF among meadow plant communities. The most parsimonious models for the wet and edge plant communities both included aboveground biomass despite different water availabilities in each community. Wet and edge plant communities may have similar controls on TBCF because they experience longer periods of consistent depth to groundwater—either shallow (wet) or deep (edge). However, the mesic plant community might experience a wider range of rooting depths as wet conditions limit rooting depth for a portion of the growing season, followed by periods of drying where downward root growth must keep pace with increasing depth to groundwater (Darrouzet-Nardi and others 2006). The differing drivers of TBCF among plant communities are likely due to groundwater effects similar to those described by Castelli and others (2001), who found that the distribution of plants in semiarid meadows was the result of integrative variables that incorporated the number of days groundwater spent at less than 30 cm and less than 70 cm, as well as the number of days that roots were subject to anaerobic conditions.

## TBCF Variation Among Years, Plant Communities, and Grazing Intensities

This study occurred during the wettest year in over 30 years followed by two years of below average precipitation, allowing us to observe the impact of sustained year-over-year soil drying on TBCF under different grazing intensities. As the stepwise model selection results indicated, total belowground C flux was highest when meadows received above average precipitation and decreased during the following two years of below average precipitation. After the second year of below average precipitation, TBCF hovered near or below zero. A negligible or negative gross flux means these meadows were almost certainly net sources of CO<sub>2</sub> during these dry years. Meadows in other regions can be large net C sources to the atmosphere (Reed and others 2021), though it is surprising that we observed such a large change in a gross flux over only three years.

In some meadow ecosystems, light grazing induces higher belowground C fluxes, commonly referred to as a compensatory growth response (Hafner and others 2012). Here, we saw little evidence for the compensatory growth response. Compensatory growth responses decreased with increasing aridity in a global synthesis (Mcsherry and Ritchie 2013) and within a given location may be muted by reduced precipitation (Guo and others 2021). Our results show a negative relationship between grazing intensity and TBCF during this period, suggesting that matching grazing intensity to annual precipitation may prevent soil C loss, which can occur more rapidly than its replenishment (Sanderman and Baldock 2010). Important feedbacks may be involved between soil water and soil C loss. Soil C loss can decrease water retention of soils through increases in soil bulk density—in some cases shortening the growing season by as much as 35 days (Ankenbauer and Loheide 2017).

To better understand the mechanisms by which grazing impacted TBCF, we recommend that future studies control for the timing of grazing with respect to the availability of water and plant phenology. Here, grazing occurred across plant communities with different moisture availability and phenological timing (both among plant communities and years, (Richardson and others 2021)). The timing of grazing can alter how plants respond to biomass removal by altering their allocation of C (Luo and others 2015; Guo and others 2021). Differences in plant C allocation may result in changes in root biomass (Veen and others 2014), soil water content via evapotranspiration (Lu and

others 2011), and physical properties of soils (Sun and others 2017) that impact TBCF and soil C.

## CONCLUSIONS

In addition to being C hot spots, meadows serve other important ecosystem functions, such as water and nutrient cycling. Quantifying the response of meadows to land use and climate is critical for identifying conservation strategies. Here, we show the importance of available moisture in ground-water-dependent ecosystems within semiarid ecosystems, evidenced by large decreases in TBCF following years with below average precipitation. These decreases were highest in meadows experiencing unmanaged grazing and likely resulted in the loss of soil C. The importance of moisture in semiarid ecosystems has prompted the implementation of landscape treatments such as removal of pinion juniper woodlands to increase water availability to meadows and riparian ecosystems (Huxman and others 2005). However, increases in water availability will not offset moisture deficits created by years with low precipitation and higher temperatures (Carroll and others 2017). As annual weather becomes less reflective of historical climate, it may become increasingly important to match grazing intensity to annual precipitation as an important step to mitigate losses of soil C and associated benefits of healthy soils.

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