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## RESEARCH ARTICLE

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### Key Points:

- Legacy livestock grazing created persistent impacts leaving Tuolumne Meadows with few highly productive plant species and abundant bare soil
- The meadow soil has high organic carbon content but the current vegetation could not have formed and cannot maintain these soils
- We planted sedge seedlings to restore the degraded meadow vegetation, but after 4 years the meadow still had an annual net soil carbon loss

### Supporting Information:

Supporting Information may be found in the online version of this article.

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## Can the Carbon Storage Function of a Degraded Mountain Wet Meadow Be Restored?

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**Abstract** Sierra Nevada meadows experienced intense livestock grazing in the 19th century, resulting in a shift from deep-rooted highly productive perennial clonal sedges to short-lived and shallow-rooted plants. The current meadow vegetation contains >20% bare ground and <10% cover of highly productive clonal sedges and rushes. We hypothesized that the existing vegetation was insufficiently productive to have formed or to maintain the 2000-year-old carbon-rich meadow soils. We established a multiyear experiment (2016–2019) to determine if planting *Carex scopulorum* seedlings into Tuolumne Meadows in Yosemite National Park could reverse the impacts of legacy grazing and restore the soil carbon storage function. Planted *C. scopulorum* had a high 4-year survival rate (75.2%) with slow but significantly increasing belowground biomass production (1.34 g plant<sup>-1</sup> yr<sup>-1</sup>). Field-measured and gap-fill modeled carbon fluxes indicate an annual average ecosystem respiration (ER) of 0.96 kg C m<sup>-2</sup> yr<sup>-1</sup> and gross primary production (GPP) of 0.59 kg C m<sup>-2</sup> yr<sup>-1</sup>, resulting in a net ecosystem exchange loss of 0.37 kg C m<sup>-2</sup> yr<sup>-1</sup>. This represents an annual loss of 1.3% of the 29.4 kg C m<sup>-2</sup> of soil organic carbon (SOC). The transplanted sedges would need to increase meadow GPP by 63%, or ER decreases by 39%, to achieve a net annual storage of SOC to reestablish the processes that formed the organic rich soil. Active planting to increase the currently sparse high-productivity plant species is a good option to boost GPP, but climate change could accelerate ER and increase net ecosystem carbon loss.

**Plain Language Summary** Wet meadows in the Sierra Nevada are snowmelt supported groundwater dependent ecosystems. Historically, these wetlands produced soils rich in organic matter driven by the highly productive deep rooted vegetation dominated by long-lived clonal plants, and seasonally anaerobic soils that limited organic matter decomposition. Livestock production in the 19th century led to heavy grazing and initiated a vegetation change to less productive shallow rooted plants. Degraded meadows are in a state of ecological collapse with rapid loss of soil organic matter through decomposition. We initiated a restoration project in Tuolumne Meadows to determine if we could reverse legacy land-use impacts by reestablishing a highly productive sedge that would become the dominant species. The meadow was planted with native *Carex scopulorum* seedlings and ecosystem carbon dynamics were monitored over 3 years. Sedge plantings had high survival and a steady but slow increase in belowground biomass. Four years after planting, the meadow had not switched from an annual net loss to a net gain of soil organic carbon. Continued long-term research is needed to provide insights into meadow conditions that may limit native vegetation growth and the reestablishment of a functional wet meadow ecosystem.

## 1. Introduction

Wet meadows are groundwater dependent wetland ecosystems with seasonally or perennially shallow water tables (WTs) (Aldous & Bach, 2014; Loheide et al., 2009; Lowry et al., 2010; Pollock & Norman, 2025). They cover a small land area in mountain regions throughout the world where local or regional drainage patterns focus water flow. The WT is near the ground surface in the early months of the growing season and limits the establishment of most woody plant species (Allen-Diaz, 1991; Loheide et al., 2009); however, soils may dry by late summer. In the northern hemisphere, wet meadow vegetation is typically dominated by highly productive clonal species of sedges (Cyperaceae) (Cooper et al., 2012; Malanson et al., 2019) and seasonally anoxic soil facilitates carbon sequestration processes and the formation of highly organic soils (Chimner & Cooper, 2003a, 2011; Pollock & Norman, 2025). Soil organic matter (SOM) is essential to ecosystem function as it retains soil water

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(Ankenbauer & Loheide, 2016; Hudson, 1994; Saxton & Rawls, 2006), increases soil cation exchange capacity (Van Erp et al., 2001), and supports the microbial community (Drenovsky et al., 2004). Any process that reduces plant production, increases disturbance and bare ground, or lowers the WT during the growing season can result in the loss of SOM, creating feedbacks that increase soil respiration and emissions of greenhouse gasses such as CO<sub>2</sub> (Reed et al., 2021). Because wet meadows typically have higher annual productivity of herbaceous vegetation than adjacent upland forests or shrublands (Ratliff, 1985), they have been the focal area for human settlement and land use, particularly domestic livestock grazing (Norton et al., 2011, 2014).

In the 18th century, settlers from Mexico arrived in what today is California and began raising livestock in coastal areas and the central valley (Allen-Diaz, 1991; Dull, 1999). The 1849 California gold rush greatly increased demand for animal products leading to the summer pasturing of domestic livestock in the Sierra Nevada (Allen-Diaz, 1991; Ratliff, 1985), where wet meadows had the highest quality forage and became the preferred areas for herders (Dull, 1999; King, 1902; Ratliff, 1985; Reed et al., 2021; Vankat & Major, 1978). Well known conservationist John Muir accompanied a band of over 2,000 sheep into the Sierra Nevada in 1869 and noted that other bands of sheep preceded him (Muir et al., 1911). He described the vegetation of Tuolumne Meadows (TUM) as “the grass of the meadows is mostly fine and silky, with exceedingly slender leaves, making a close sod”, suggesting a continuous vegetation carpet. Likely Muir was on the meadow’s dryer margins that today are dominated by the fine and silky *Ptilagrostis kingii* and *Calamagrostis breweri*. Joseph Le Conte reported on 10 August 1870, “the Tuolumne Meadows are celebrated for their fine pasturage. Some twelve to fifteen thousand sheep are now pastured here. They are divided into flocks of about two thousand five hundred to three thousand” (Le, 1875). Muir also elaborated on the impacts caused by “sheepmen”, “Incredible numbers of sheep are driven to the mountain pastures every summer and their course is ever marked by desolation. The shrubs are stripped of leaves as if devoured by locusts, and the woods are burned” (Muir, 1877).

In 1864, the US government gifted the Yosemite Grant to the state of California. This was the first instance of the U.S. government protecting land as a public trust for enjoyment. A much larger Yosemite National Park, including the high mountain regions, was established in 1890. Even after the establishment of the National Park and the presence of the US Army to protect park resources, the superintendent reported that illegal livestock grazing continued until about 1905 (Holmes, 1979). In the 1940s, Yosemite National Park staff scientists noted that 19th century livestock grazing of meadows occurred during an era with little control over the use of federal land and no limits on the number of livestock or duration of use (Ernst, 1949). During this period, many native perennial plants were replaced by short lived plants due to intense grazing and sods were broken and replaced by bare mineral soil (Beesley, 1996; Kinney, 1996).

Livestock grazing was one of the first Caucasian lands uses in the Sierra Nevada, but the pre-settlement meadow vegetation composition was never described. Changes in species composition and decreased long-term vegetation production driven by livestock can create persistent effects on ecosystem functioning (Eldridge et al., 2016), including high greenhouse gas emissions that persist long after livestock use has ceased. Meadow vegetation changes during the 19th century in the Sierra Nevada were documented using pollen and macrofossil analysis (Davis & Moratto, 1988; Dull, 1999), comparisons with highly isolated meadows that may have had less livestock use (Cooper et al., 2006; Menke et al., 1996; Ratliff, 1985; US Department of Interior, 1963), and oral histories (Vankat & Major, 1978). Many have hypothesized where grazing was heaviest, complete vegetation type conversion occurred (Hunsaker et al., 2015; McKelvey et al., 1992; Ramstead et al., 2012; Vernon et al., 2022) from a dominance of long-lived clonal plants, particularly sedges, to short lived plants. However, the effects of this legacy grazing on Sierra Nevada meadow vegetation composition, biomass production, and SOM are still debated (Snyder, 2003).

TUM is the largest and best-known meadow complex in southern California. Its snowmelt-supported ground-water flow system maintains the meadow WT near the ground surface in early summer and it slowly declines throughout the summer (Loheide et al., 2009; Lowry et al., 2010). The hydrologic regime is suitable for the persistence of wet meadow vegetation (Lowry & Loheide, 2010). The soil is highly organic, suggesting that in the past it sustained productive vegetation and long duration growing season soil saturation (Ankenbauer & Loheide, 2016; Cooper et al., 2006). However, the current vegetation is dominated by species that produce little above or belowground biomass and bare ground exceeds 20%–30% in many areas (Cooper et al., 2006). Recent research has demonstrated that many meadows in the Sierra Nevada have an annual net loss of SOM (Blankinship & Hart, 2014; Reed et al., 2021; Wolf, 2017), and some may be losing more than 1% of their carbon stock per year

(Reed et al., 2021; Wolf, 2017). Ankenbauer and Loheide (2016) determined that a reduction in SOM from 17% to 5% can reduce plant available water in summer by 120% limiting plant growth and production. The loss of SOM is a critical issue that threatens the functioning and persistence of these wet meadows.

Physical disturbances such as ditching and channel incision can produce hydrologic changes that lower WTs and degrade meadows. These impacts can be restored by filling or blocking the ditches (Cooper et al., 1998; Schmelpfenig et al., 2014). However, hydrologically intact meadows may be degraded by the loss of vegetation or a composition shift to species with low biomass production. Increasing the canopy cover of native species that can produce high aboveground and belowground biomass could reverse the legacy effects of land use and increase meadow resistance and resilience to future climate changes. Most species of hydrophytic sedges do not naturally migrate to meadows from adjacent landscapes and active restoration is needed to re-establish their populations (Wang et al., 2019). Natural establishment of *Carex* may be limited by intense spring and fall frost action in bare ground that reduces seedling survival (Chimner, 2011) and subnival herbivory by species of *Microtus* (Howe et al., 2006). In addition, summer herbivory by Belding's ground squirrels and deer may also limit seedling survival.

*Carex scopulorum* Holm var. *bracteosa* (L.H. Bailey) F.J. Herm., hereafter *C. scopulorum*, is the native clonal dominant of many subalpine meadows in the central and southern Sierra Nevada (Potter, 2005) and we hypothesized it was the historic native dominant in TUM prior to the period of intensive grazing, yet its canopy cover now is <5% (Cooper et al., 2006; Wolf, 2017). McCabe Meadow located 14.5 km north of TUM, and not along the main valley trails in the region, may have sustained less historic livestock use and supports dense sods in *C. scopulorum* dominated wet meadows (Figure S4 in Supporting Information S1). We planted *C. scopulorum* seedlings in TUM and attempted to reduce small mammal herbivory using fences to determine if we could reassemble the meadow food web, reduce bare soil, increase aboveground and belowground biomass, and alter the meadow's carbon dynamics. Vegetation restoration by planting native species has been successful in many mountain regions of the western U.S. (Cooper et al., 2017; Schook et al., 2020; Wolf et al., 2019). In this manuscript, we tested whether planting *C. scopulorum* seedlings could initiate the restoration of the meadow's vegetation composition and influence carbon sequestration processes. To analyze these ideas, we addressed the following questions:

1. What is the current soil organic carbon (SOC) stock and SOC content of the meadow?
2. Is TUM currently characterized by plant species that could have formed the highly organic meadow soil?
3. What is the survival rate of planted *C. scopulorum* seedlings, and how did biomass increase over 4 years?
4. Did planting *C. scopulorum* seedlings alter meadow carbon dynamics and the vegetation composition?
5. Is TUM a carbon gaining or losing ecosystem?

## 2. Materials and Methods

### 2.1. Study Area

This research was conducted in TUM in Yosemite National Park, California, USA (37°52'36", −119°23'32") at 2,600 m elevation (Figure 1). It is one of the largest high elevation meadows in the southern Sierra Nevada. Glacial moraine deposits mantle many of the granite slopes immediately adjacent to the meadow, providing significant hillslope groundwater storage and discharge into the meadow (Loheide et al., 2009). The meadow surface is underlain by up to 28 m of alluvium deposited and reworked by the Tuolumne River within a granitic glacially carved basin (Ciruzzi & Lowry, 2017). The single-thread meandering Tuolumne River has left a sequence of abandoned meanders across the active floodplain that indicate a long history of channel migration (DeLong et al., 2021). The surface soil of TUM is approximately one m thick and composed of humic silt and sand loam developed over the past ~2,300 years with no evidence of beaver damming (Wood, 1975). The Mediterranean type climate of the Sierra Nevada produces wet winters and dry summers. From November to March, precipitation above 1,500 m elevation typically falls as snow and spring meltwater recharges hillslope aquifers that supply groundwater to the meadow during the summer (Lowry et al., 2010). Little precipitation occurs during the summer and plants rely on stored soil water and shallow groundwater (Cooper et al., 2006; Loheide et al., 2009; Lowry et al., 2010; McIlroy & Allen-Diaz, 2012; Ratliff, 1985).

We worked in the western portion of TUM where the wet meadow vegetation is currently dominated by the perennial herbaceous dicot *Oreostemma alpinum* var. *andersonii*, the annual grass *Muhlenbergia filiformis*, and

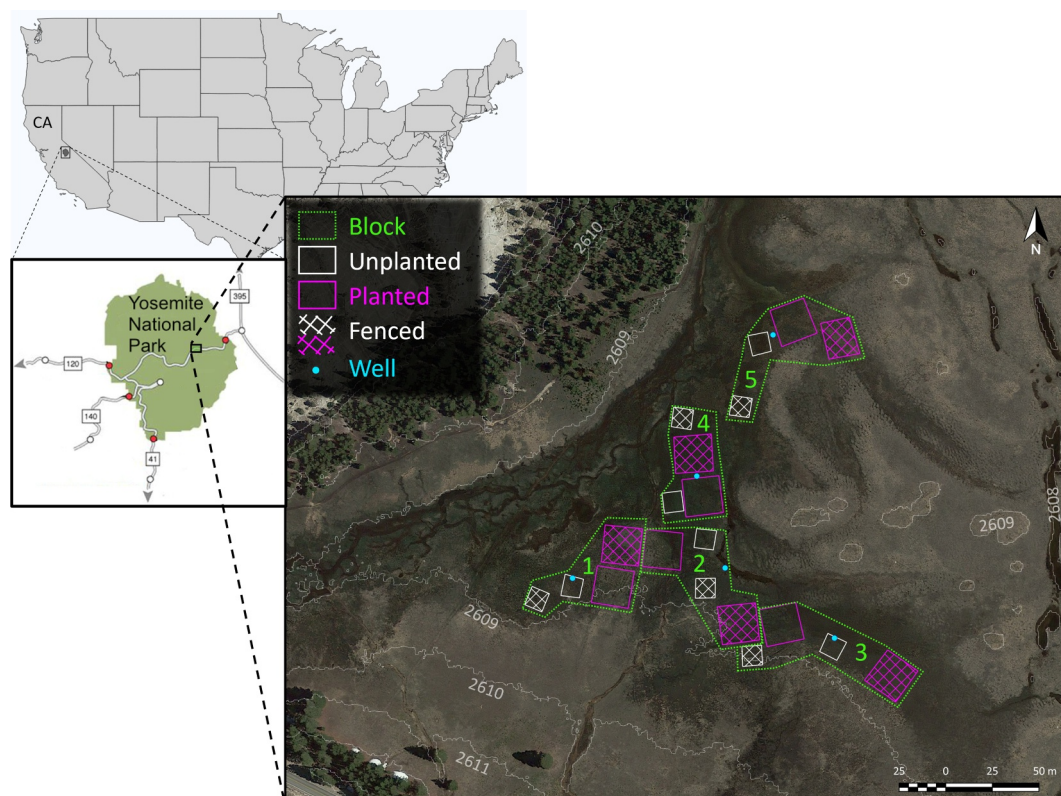


**Figure 1.** Aerial image and topography (1 m contour interval) showing the location of the study area in Yosemite National Park, CA, USA (inset) and the layout of the study design in 5 blocks (green), with unplanted controls (white), planted (pink) and fenced (hatched) treatments, and groundwater monitoring wells (blue).

the small perennial sedges *Eleocharis quinqueflora* and *Carex subnigricans*. Bare ground is abundant, although the meadow soil has high organic matter content (Ankenbauer & Loheide, 2016; Cooper et al., 2006). Plant species nomenclature follows the Jepson Herbarium eFlora database for California (Jepson Flora Project, 2026).

*Carex scopulorum* can dominate subalpine and alpine wet meadows and fens in the Sierra Nevada, Cascade Range, and southern Rocky Mountains. It is a long-lived clonal species that produces short tillers and high belowground biomass. A *C. scopulorum* dominated community is common in central and southern Sierra Nevada meadows above 2400 m elevation (Ferren et al., 1996; Major & Taylor, 1977; Potter, 2005; Sawyer & Keeler-Wolf, 1995) where its canopy cover can average >50%. In TUM, *C. scopulorum* occurs as small scattered clones.

## 2.2. Experimental Design

We used a full factorial experimental design with blocking to evaluate seedling survival and growth and its effect on carbon dynamics relative to unplanted controls. The study area was divided into 400 m<sup>2</sup> polygons within five blocks that span the range of hydrologic and vegetation variability within the wet meadow ecosystem. We randomly chose 20 polygons, four in each of the five blocks. One polygon per block was randomly assigned as control (C) with neither planting nor fencing, one was fenced and not planted (F), one was planted with no fence (P) and one had fences and plantings (Figure 1). Unplanted plots were shrunk to 100 m<sup>2</sup> to reduce perimeter fencing length while planted plots were kept at 400 m<sup>2</sup> to accommodate the full number of nursery-grown transplants. To try to exclude small mammals, galvanized 0.64 cm steel hardware cloth 45 cm tall with a 15 cm wide section flat on the ground was installed around fenced plots to deter small mammal herbivores. Fencing was secured to the rebar with zip ties and staples. Metal flashing 15 cm wide was installed on the top of the fencing to deter climbing mammals.

### 2.3. Plant Propagation

*Carex scopulorum* seed was collected in the fall prior to planting years from natural populations near the study area. Seed was tested for viability using tetrazolium chloride and was as high as 93% for some seed lots. Seeds were cold and moist stratified for 60 days, then germinated and grown in a commercial nursery in California for 3 months prior to planting. Plants were grown in 16.5 cm<sup>3</sup> SC7 Stubby Ray Leach cone-tainers in a growing media of peat moss, vermiculite, and perlite at a ratio of 2:3:1 with added 15-5-10 fertilizer, Dolomite AG 6.5, zinc phosphate, and micro-nutrients. In late June 2016, we planted 20,000 seedlings, with approximately 2,000 seedlings installed in each planted plot at two different densities: four and eight plants per m<sup>2</sup>. We used a dibble to create suitable sized holes and seedlings were removed from their cone-tainer, placed in the hole and hand packed to stabilize them. A second planting of 20,000 seedlings occurred in June 2018 outside our 5-block experiment in the same ecological setting. Survival and growth measurements were taken on the 2018 plantings, but no gas flux readings were made within the 2018 planting area.

### 2.4. Environmental Measurements

Depth to WT in each block was monitored in 2017, 2018, and 2019 in manually installed fully slotted PVC wells. Non-vented pressure transducers (Levellogger Junior Model 3001; Solinst, Georgetown, Ontario, Canada) installed near the well bottom recorded total pressure. A barologger (Barologger Gold Model 3001; Solinst, Georgetown, Ontario, Canada) installed in an adjacent wooded area provided barometric compensation and water level was calculated as total pressure minus barometric pressure. Monthly manual WT depth measurements were conducted during the growing season to confirm pressure transducer accuracy. A photosynthetically active radiation (PAR) smart sensor (Onset Computer Corporation, Bourne, MA, USA) was deployed on a post in the center of the field site. Soil temperature sensors (Apogee Instruments, Logan, Utah, USA) were buried at 12 cm depth in the center of each block. The PAR and temperature loggers recorded hourly data. Daily snow depth, snow water equivalent, air temperature, solar radiation, and daily precipitation were downloaded from the TUM micrometeorological station of the California Department of Water Resources Data Exchange Center (<https://cdce.c.water.ca.gov/cdecstations>), located approximately 3 km from our study site.

Data from the Sentinel-2 satellite, level 2A at 20 m resolution, was used to develop a chlorophyll index (CI) (Garisoin et al., 2024; Gitelson & Merzlyak, 1994). The red edge (680–780 nm) reflectance-related CI multiplied by PAR is strongly correlated with gross primary production (GPP) (Lin et al., 2022). We used CI to create a seasonal chlorophyll curve from snowmelt in spring to plant senescence in fall. The curve represents the mean CI for each date. We related plant cover in our flux plots to CI, so the mean cover of all plots was considered to be the mean of CI at peak growing season in late July.

### 2.5. Plant Measurements

Survival of the 2016 planted *C. scopulorum* seedlings was determined in 2016 and 2017 in three 1 m radius plots in each control and treatment of each block. In those years, we also measured the number of tillers and tiller internode length on each plant. In 2018 and 2019, to increase sample size, we analyzed seedling survival along 20 m long transects in each plot, with the transects following the rows of planted seedlings. For seedlings in all years we noted survival, and for living plants measured the longest leaf and the area of the clone.

We retained 20 *C. scopulorum* plants from the 2016 seedling cohort to quantify aboveground and belowground biomass at the time of planting. Planted individuals from this cohort were excavated at the end of the 2016, 2018 and 2019 growing seasons to quantify growth after one, three and four growing seasons. We excavated plants from the 2018 cohort at the end of the 2019 growing seasons and quantified the longest leaf, number of new tillers, total plant width, and tiller internode length. Plants were washed to remove sediment, separated into aboveground and belowground materials, dried to a constant mass, and weighed. Seedling aboveground and belowground biomass for 2016 and 2018 plantings were compared using ANOVA with Dunn's multiple comparison test.

We quantified vegetation canopy cover in the 60 gas flux plots using an ocular estimate of aerial cover. We quantified aboveground biomass of vegetation in 2018 and 2019 by clipping vegetation at the soil surface in 20 × 20 cm quadrats adjacent to each of the 60 gas flux plots. Samples were dried and weighed. We used a 6 cm inside diameter stainless steel gouge auger (AMS, Inc., American Falls, ID, USA) to collect 50 cm deep soil cores

adjacent to each of the gas flux plots in 2018. The cores were cut into 10 cm sections, washed, dried, and total root biomass was reported by depth. We also collected 27, 30 cm diameter and 20 cm deep cores in representative locations within each block in 2017, washed soil from roots, separated species, and dried and weighed the aboveground and belowground components to determine biomass per species.

## 2.6. Meadow Soil Carbon Stock

We collected six soil cores in 2018 that extended from the ground surface to the underlying cobble up to 90 cm deep, using a 6.4 cm diameter  $\times$  100 cm long open-faced stainless steel gouge auger (AMS, Inc., American Falls, ID, USA). Cores were collected from the center of each block. Intact cores were placed into 50 cm long PVC trays to prevent disturbance to core volume, wrapped with plastic film, transported to Colorado State University, and frozen. Partially thawed cores were cut with a serrated knife into 1 cm thick slices and dried in a convection oven at 65°C to a constant mass. Dry bulk density ( $\text{g cm}^{-3}$ ) was calculated by dividing the oven dried mass by the original sample volume determined from the cross-sectional area of the gauge auger multiplied by sample length. Organic matter content for each section was determined for  $\sim 1$  g subsamples by loss on ignition (LOI) at 550°C for 4 hr (Chambers et al., 2011). We used SOM (determined by LOI) and percent carbon (determined by elemental analysis) data from other wet meadows in the region to create a linear equation ( $\% \text{ carbon} = 0.5542 \times \% \text{ organic matter}$ ) ( $R^2 = 0.9994$ ;  $p < 0.01$ ) to calculate  $\% \text{ organic carbon (OC)}$  in each core section. Carbon density for each core section was calculated as the product of dry bulk density ( $\text{g cm}^{-3}$ ), sample length (cm), and  $\% \text{ OC}$ . Total belowground meadow carbon stock per unit area ( $\text{kg m}^{-2}$ ) was calculated for each core by summing the carbon density per unit area of all individual samples in the entire core.

## 2.7. Meadow Carbon Dynamics

Carbon dynamics during the snow free season were measured in the field using the closed chamber method (Hutchinson & Mosier, 1981). An Infrared Gas Analyzer (IRGA; EGM-4; PP Systems, Amesbury, USA) connected to a custom-made clear acrylic chamber (diameter 60 cm  $\times$  height 60 cm) was used to measure  $\text{CO}_2$  fluxes. The chamber was equipped with two 10 cm diameter computer fans powered by an external battery, a vent to reduce atmospheric pressure gradients between the inside and outside of the chamber, and a PAR sensor (TRP-3 probe, PP Systems, Amesbury, USA). The IRGA and chamber created a closed path sampling system with a constant pump flow rate of approximately  $350 \text{ cm}^3 \text{ min}^{-1}$ . The chamber was flushed with ambient air by holding its open end up and then placed on the plot to begin each measurement. Because soil collars were not allowed in the study area, the plot locations were marked with pin flags to assure repeated measurements at the exact same location.

Two plots were installed in each control and four plots in each planting treatment for 12 plots per block and 60 plots across all five blocks. The plot locations were randomly assigned in each treatment. The chamber was sealed to the soil surface with an affixed 10 or 20 cm wide fabric skirt weighted with a stainless steel coil chain. A tight seal to the soil surface was confirmed by linear nonfluctuating  $\text{CO}_2$  readings. Measurements were made approximately every two weeks during the snow-free seasons of 2017–2019. Each flux measurement taken with the clear chamber represented net ecosystem exchange (NEE), the combination of ecosystem respiration (ER; plant and microbial respiration) and GPP. The chamber was then removed from the plot and allowed to air out. Next, ER was measured by returning the chamber to the plot with an opaque cover to block sunlight and prevent photosynthesis. Measured PAR within the chamber was monitored to confirm that it remained at zero during the measurement period. GPP was the difference between NEE and ER (Waddington & Roulet, 2000; Wilson et al., 2016).  $\text{CO}_2$  flux in the chamber ( $\Delta\text{C}/\Delta t$  in  $\mu\text{mol mol}^{-1} \text{ s}^{-1}$ ) was calculated from the slope of a quadratic fit of the  $\text{CO}_2$  concentration (ppm) curve over a sample period of 124 s with  $\text{CO}_2$  concentration recorded every 4.8 s. We used the ideal gas law incorporating air temperature, barometric pressure, molar mass of  $\text{CO}_2$ , and ratio of chamber volume to plot area to convert the  $\text{CO}_2$  flux from a volumetric to mass basis ( $\text{g CO}_2 \text{ m}^{-2} \text{ hr}^{-1}$ ) and then converted to carbon flux equivalents ( $\text{g C m}^{-2} \text{ hr}^{-1}$ ). We use the sign convention in which negative values signify ecosystem release of  $\text{CO}_2$ , and positive values signify ecosystem uptake of  $\text{CO}_2$ . During each gas flux measurement volumetric water content (VWC) was measured with a soil moisture probe with 12.2 cm long rods (FieldScout TDR 150; Spectrum Technologies, Inc, Aurora, IL, USA). Three different locations adjacent to the soil collar were measured to obtain an average VWC for each measurement.

Site access in the winter is extremely difficult as all roads are closed and a deep snowpack is usually present for many months. Winter carbon fluxes may contribute significantly to yearly carbon budgets because winter is the longest season (Knowles & Blanken, 2016). Abundant vole activity under the snow creates tunnels in the snowpack that may function as suitable pathways for gas movement. The presence of abundant small mammals under the snow indicates that CO<sub>2</sub> is not trapped near the soil surface, or the voles would suffocate. Furthermore, snow pack has been shown to not suppress gas diffusivity (Kim et al., 2019). To estimate winter CO<sub>2</sub> flux, 10 soil cores, each 10 cm in diameter and 40 cm deep, were collected from the study site in 2018 by pounding polyvinyl chloride (PVC) pipes into the soil with a rubber mallet and extracting the cores by digging. Two cores were collected from each of the five blocks (control and planted treatments). After collection, the bottom and top of each PVC pipe were immediately fitted with flexible rubber caps with steel clamps to prevent soil and water loss. Cores were immediately transported upright to limit soil horizon disturbance to Colorado State University and placed in a chest freezer in a dark environment simulating conditions under a deep snowpack. The freezer temperature was regulated with a digital temperature controller equipped with a thermocouple that was inserted into the center of one of the cores. This configuration allowed precise control of internal soil core temperatures. Cores were subjected to a range of temperatures and WT positions to represent winter conditions as determined from the soil temperature loggers and WT pressure transducers in TUM. Soil VWC was measured at four depths (0–10, 10–20, 20–30, 30–40 cm) by drilling small holes in the side of the PVC pipe to insert a soil moisture probe fitted with 7.6 cm long rods (FieldScout TDR 150; Spectrum Technologies, Inc, Aurora, IL, USA). Holes were sealed with waterproof tape after VWC measurements to prevent water loss. The soil core and field VWC readings at 0–10 cm at full saturation were similar, indicating that soil bulk density and porosity were not altered during core extraction and transport, which can affect microbial respiration processes. We created a custom closed chamber from an opaque 10 cm diameter PVC cap with a vent to reduce atmospheric pressure gradients. The chamber was fitted over the cores and CO<sub>2</sub> flux measurements and calculations followed the methods used for the field ER flux measurements.

Methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) fluxes were measured in the field using the static chamber technique (Hutchinson & Mosier, 1981; Sanchez et al., 2017). Chambers (60 cm diameter  $\times$  30 cm height) were constructed with PCV sheeting and wrapped with reflective tape to reflect sunlight and prevent temperature increases during deployment. Chambers were equipped with a 5 mm diameter by 20 cm long vent tube (to minimize pressure differentials), a sampling port with septa, and a 10 cm computer fan powered with an external battery pack. Chamber measurements were taken at the same plots used for CO<sub>2</sub> measurements. The chamber was sealed to the soil surface with an affixed 20 cm wide fabric skirt weighted with a stainless steel coil chain. Gas samples were taken from the chamber's port every 15 min over 60 min per plot using a 60 ml polypropylene syringe and needle. We flushed pre-evacuated glass vials (12 ml Exetainers; Labco Limited, United Kingdom) with 40 ml of sample and then injected the remaining 20 ml of sample in each vial to over-pressurize the vials. The syringe was flushed 2–3 times with ambient air before taking the next sample. During each day of the sampling campaign, ambient air was taken over the meadow to use for headspace corrections. The headspace correction was calculated to adjust CH<sub>4</sub> and N<sub>2</sub>O chamber gas concentrations to account for chamber gas dilution when the 60 ml gas sample was taken from the chamber, assuming the removed headspace gas was replaced via the vent tube with ambient air. We prepared field CH<sub>4</sub> and N<sub>2</sub>O standards at Colorado State University and transported them to TUM to test for vial leakage during sample storage and transport. We flushed and overpressurized four 10 ml exetainers with 10 ppm CH<sub>4</sub> standard and another four 10 ml exetainers with 100 ppm CH<sub>4</sub> standard. The 2018 field samples were analyzed for CH<sub>4</sub> and N<sub>2</sub>O with a mass chromatograph (Varian CP- 3800, Palo Alto, CA, USA) and the 2019 samples analyzed for CH<sub>4</sub> with a trace gas analyzer (Methane Analyzer, Los Gatos Research Inc., San Jose, CA, USA). Methane and N<sub>2</sub>O fluxes in the chamber ( $\Delta C/\Delta t$  in  $\mu\text{mol mol}^{-1}\text{m}^{-1}$ ) were calculated from the slope of a linear fit of the CH<sub>4</sub> and N<sub>2</sub>O concentration (ppm) curve over the sample period. We used the ideal gas law incorporating air temperature, barometric pressure, molar mass of CH<sub>4</sub> and N<sub>2</sub>O, and ratio of chamber volume to plot area to convert the CH<sub>4</sub> and N<sub>2</sub>O flux from a volumetric to mass basis (grams). Calibration curves were constructed from 0.1, 5, 10, 100 ppm for CH<sub>4</sub> and 0.01, 0.1, 1, and 10 ppm for N<sub>2</sub>O with 1% tolerance calibration gases. Methane and N<sub>2</sub>O fluxes with an  $R^2 < 0.75$  were removed from the data analysis (Davidson et al., 2024); however, fluxes with slopes approaching zero were retained despite low  $R^2$  because they represent low or zero flux events.

## 2.8. Modeling CO<sub>2</sub> Fluxes

We modified the models from Millar et al. (2016) to calculate annual meadow GPP and ER CO<sub>2</sub> fluxes. The 12 gas flux plots in each block, including a control and three treatments, were pooled and the means of all five blocks are represented by  $\mu\text{GPP}(j)$  ( $j$  = blocks 1–5) in Equation 1. Gross primary production ( $\text{gCO}_2\text{-Cm}^{-2}\text{hr}^{-1}$ ) was modeled as a function of PAR, depth to WT, CI, and soil temperature ( $\text{temp}$ ). A rectangular hyperbola model was used to create a relationship between GPP and incoming PAR. A Gaussian function describes the seasonal relationship between GPP and the meadow WT position in relation to the soil surface. Power functions were used to model the seasonal variation of GPP to CI and soil temperature at 10 cm depth. The satellite CI curve provides a seasonal term allowing the GPP model to track seasonal changes in vegetation growth.

$$\mu\text{GPP}(j) = a_j * \frac{A_{\max j} * \alpha_j * \text{PAR}}{A_{\max j} + \alpha_j * \text{PAR}} * e^{-0.5 \left( \frac{\text{wt} - \text{optwtgpp}}{\text{devwtgpp}} \right)^2} * \text{CI}^{p\text{CI}j} * \text{temp}^{p\text{temp}j} \quad (1)$$

The parameter  $A_{\max}$  ( $\text{g CO}_2\text{-C m}^{-2} \text{hr}^{-1}$ ) represents the theoretical maximum rate of GPP. The  $\alpha$  ( $\text{g CO}_2\text{-C m}^{-2} \text{hr}^{-1}$ ) term represents the light use efficiency of the system, which is calculated from the initial slope of the light response function. The parameter  $\text{optwtgpp}$  (cm) represents the optimum value of WT position for plant growth and  $\text{devwtgpp}$  represents the standard deviation for the function. The parameters  $p\text{CI}$  and  $p\text{temp}$  control the shape of the power functions relating seasonal changes in CI and soil temperature to GPP. The power function provided a steep rise in CI and soil temperature right after snow melt, reaching a maximum in July, and gradually tapering off until plant senescence in late fall. These patterns match the seasonal vegetation and soil properties occurring in our study area. Soil temperature controls vegetation metabolic processes and microbial processing of soil nutrients needed for photosynthetic activity and plant growth.

Ecosystem respiration ( $\text{g CO}_2\text{-C m}^{-2} \text{hr}^{-1}$ ) was modeled as a function of soil temperature ( $\text{temp}$ ), WT position ( $\text{wt}$ ), and CI. Similar to GPP, the 12 gas flux plots in each block were pooled and the means of all five blocks are represented by  $\mu\text{ER}(j)$ . A modified Van't Hoff equation was used to model the combined autotrophic and heterotrophic respiration as a function of soil temperature. Gaussian functions were used to model the response of ER to both WT position and CI.

$$\mu\text{ER}(j) = R_{10j} * Q_{10j}^{\frac{\text{temp} - 10}{10}} * e^{-0.5 \left( \frac{\text{wt} - \text{optwt}j}{\text{devwt}j} \right)^2} * e^{-0.5 \left( \frac{\text{CI} - \text{optci}j}{\text{devci}j} \right)^2} \quad (2)$$

The parameter  $R_{10}$  ( $\text{g CO}_2\text{-C m}^{-2} \text{hr}^{-1}$ ) models the flux of ER with soil temperature at 10°C, with all other parameters nonlimiting. The parameter  $Q_{10}$  represents the rate of change in ER per increase of 10°C in soil temperature. The parameters  $\text{optwt}j$  (cm) and  $\text{optci}j$  represent the optimum value of WT position and CI for ER and  $\text{devwt}j$  and  $\text{devci}j$  represent the standard deviations for each function. WT position has a strong effect on soil matrix potential, regulating the ability of microbial and plant communities to access soil water. The CI parameter provided a parameter to closely model plant respiration as well as the seasonal production of belowground plant exudates known to influence the rate of microbial processing of soil carbon substrates.

Ecosystem respiration and GPP models were fitted to field data from snowmelt in spring to plant senescence in fall for 2017–2019 as well as the freezer core winter ER simulation laboratory experiment using Bayesian methods in R Statistical Software v. 4.5.2 (R Core Team, 2025). Markov chain Monte Carlo (MCMC) analysis in the rjags package v. 4.17 for R was used to estimate ER and GPP model parameters (Plummer, 2025). The following R packages were also used: cowplot v. 1.2.0 (Wilke, 2025), gridExtra v. 2.3 (Auguie, 2017), reshape2 v. 1.4.5 (Wickham, 2007), scales v. 1.4.0 (Wickham et al., 2025), tidyquant v. 1.0.11 (Dancho & Vaughan, 2025), tidyverse v. 2.0.0 (Wickham et al., 2019), tune v. 2.0.1 (Kuhn, 2025).

For the Bayesian MCMC implementation, 4 chains were used. Each chain was initialized with a burn-in of 20,000 iterations. Following burn-in, 20,000 further iterations were conducted per chain, resulting in 80,000 simulated values from the posterior distribution.

Vague priors were used for all model parameters. Gamma distributions with shape and rate parameters equal to 0.001 were used as priors for  $A_{max}$ ,  $a$ ,  $pci$ ,  $ptemp$ ,  $R_{10}$ ,  $Q_{10}$ ,  $devwtgpp$ ,  $devwter$ ,  $devcier$ . Normal Distributions with mean 0 and precision 0.001 were used as priors for  $optwtgpp$ ,  $optwter$ , and  $optcier$ . A Uniform distribution with limits from 0 to 0.1 was used as a prior for  $\alpha$ .

Growing season  $CO_2$  fluxes were simulated by running the GPP and ER models for each block for the period from January 1 to December 31 for years 2017–2019. GPP was set to zero from fall plant senescence to spring meadow snow melt off. Hourly soil temperature, WT, CI index, and PAR data were used to drive the model. Satellite CI data were linearly interpolated (Gitelson & Merzlyak, 1994) to extrapolate hourly values of CI at each plot for the GPP and ER models. Daily and growing season ER and GPP flux totals were calculated using MCMC with a total of 200,000 iterations and burn-in after 20,000 iterations. The NEE growing season estimates were calculated as the difference between the estimated ER and GPP. Positive values represent a loss of carbon from the meadow and negative values represent carbon uptake by the meadow.

### 3. Results

#### 3.1. Site Characteristics

Daily maximum air temperature averaged 19.5, 22.9 and 21.9°C in June, July and August 2017 through 2019 (Figure 2). Summer nights are cold, averaging 0.1, 4.2, and 2.6°C in June, July and August, and the clear skies and low humidity allow radiative cooling. PAR reached approximately 2000  $\mu\text{mol m}^{-2} \text{s}^{-1}$  each day except for the uncommon days with high cloud cover or when smoke from regional forest fires influenced the area.

Soil at 12 cm depth remained above 0°C during the winter (Figure 2) and rose rapidly after snow melted. Soil temperature exceeded 10°C from mid-July through August and reached its seasonal peak in late July. Diurnal variation during summer months was 2–3°C with a high near midnight and a low in early morning.

The April 1st snowpack snow water equivalent (SWE) has been measured at the TUM snow course since 1930. Over the 95-year record through 2025, the average April 1st SWE was 58.3 cm, with a maximum of 158.8 cm recorded in 2023 and a minimum of 0.0 cm in 2015. The April 1st SWE measurements during and immediately preceding this study were 54.6 cm in 2016, 123.2 cm in 2017, 34.3 cm in 2018, and 92.7 cm in 2019 (Figure 2). The date when snow melted from the meadow controlled the start of the growing season and occurred on 1 June 2017, 28 April 2018, and 29 May 2019.

The high SWE of 2017 and 2019 recharged hillslope groundwater systems that flowed into the meadow and supported a WT near the soil surface until early August and only dropped to about 50 cm deep in late August (Figure 2). In 2018, the WT decline began in June and was more than 100 cm deep by mid-July. Groundwater levels measured in the study area from 2006 to 2019 indicate that the WT is near the soil surface in early summer every year, but can drop to more than a meter deep in the fall before winter precipitation occurs (Figure S7 in Supporting Information S1).

Volumetric water content in the upper 10 cm of the soil across the 60 gas flux plots varied between study years. It remained higher through the summer of 2017 and 2019, with an average VWC of 59.1 (sd = 8.0)  $\text{cm cm}^{-3}$  and 56.1 (8.5)  $\text{cm cm}^{-3}$ , than in 2018 with an average of 45.3 (12.0)  $\text{cm cm}^{-3}$ . Volumetric water content declined throughout the summer. In 2017 and 2019, VWC was 65.4 (4.8)  $\text{cm cm}^{-3}$  and 62.4 (4.7)  $\text{cm cm}^{-3}$  in July, 60.1 (7.1)  $\text{cm cm}^{-3}$  and 56.2 (6.2)  $\text{cm cm}^{-3}$  in August, and 54.6 (7.8)  $\text{cm cm}^{-3}$  and 47.8 (7.1)  $\text{cm cm}^{-3}$  in September. Soil water content declined earlier in 2018 with a VWC of 49.1 (6.5)  $\text{cm cm}^{-3}$  in July, 30.5 (8.0)  $\text{cm cm}^{-3}$  in August, and 28.1 (7.4)  $\text{cm cm}^{-3}$  in September.

#### 3.2. Meadow Vegetation and Biomass

When viewed from an obtuse angle, TUM vegetation appears green and continuous (Figures S1 and S2 in Supporting Information S1). However, when viewed vertically, the cover is low and the most abundant species have small stature (Table 2, Figure S3 in Supporting Information S1). Over 20% of the ground is bare soil in mid summer (Table 1), likely due to subnival herbivory and soil disturbance by voles (*Microtus montanus* ssp. *montanus* Peale) and summer activity by Belding's ground squirrel (*Urocitellus beldingi* Merriam). The presence of subnival small mammal populations indicates that sufficient oxygen is present at the ground surface for their

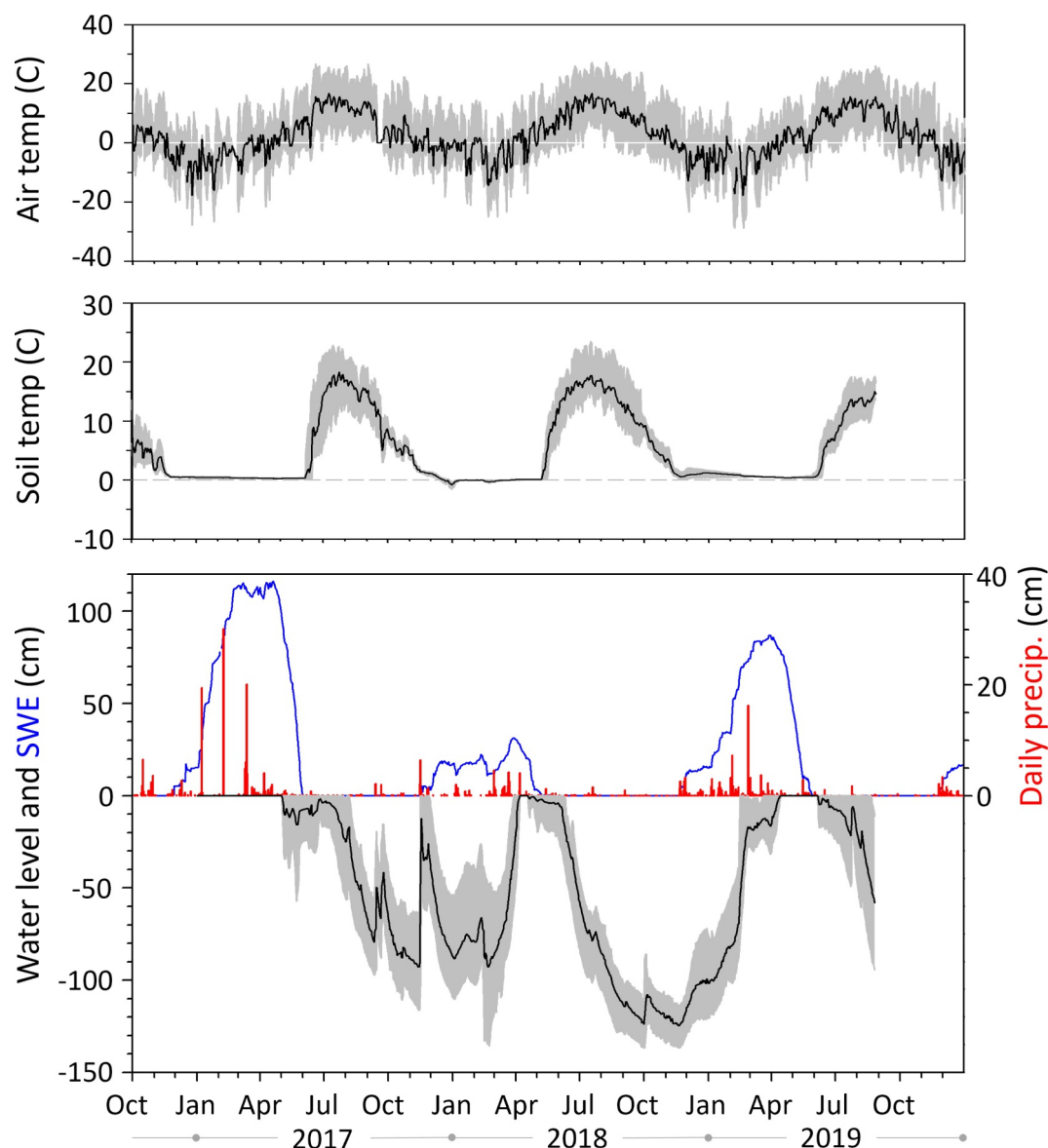


**Figure 2.** Onsite measurements of daily average (black line) and range (gray) of air temperature (top panel), soil temperature at 12 cm depth (middle panel), and water level relative to ground surface (black and gray, lower panel). Local weather station measurements of daily snowpack water equivalent (SWE, blue, left y-axis) and daily precipitation (red bars, right y-axis) are shown in the lower panel.

survival. Frost heaving of the bare soils in spring and fall creates another disturbance factor (Chimner, 2011). The native long-lived clonal species *Eleocharis quinqueflora*, *C. scopulorum*, *C. vessicaria*, *C. subnigricans*, and *Juncus balticus subsp. mexicanus* have a mean cover of 20.7%, 4.4%, 1.0%, 0.4%, and 0.8%, occupying small areas of the meadow. The vegetation composition is similar to what occurred in 2005–2008 (Ballenger & Acree, 2009; Cooper et al., 2006), indicating that it has not changed in the 10 years prior to the initiation of this research. The native *C. scopulorum/Oreostemma alpigenum* community described by Potter (2005) is common in subalpine wet meadows in the Sierra Nevada with a mean *C. scopulorum* cover of 53%, and a total canopy cover exceeding 200%, indicating tall overlapping vegetation that is not present in TUM.

Mean aboveground biomass in 2018 and 2019 averaged  $153.4$  ( $n = 60$ ,  $sd = 87.7$ ) and  $127.8$   $\text{g m}^{-2}$  ( $n = 60$ ,  $sd = 54.8$ ). Aboveground biomass contributed by the most abundant species totaled  $68.3$   $\text{g m}^{-2}$ . Total root biomass in the upper 50 cm of soil averaged  $639.3$   $\text{g m}^{-2}$  ( $se = 45.8$ ) for the 60 cores, with an average of

**Table 1**

Mean Percent Canopy Cover by Species, Including Bare Ground, in the 60 Gas Flux Plots in Tuolumne Meadows and the Mean, Range, and Constancy of Cover From 10 Vegetation Plots in the *Carex scopulorum*/*Oreostemma alpigenum* (Formerly *Aster alpigenus*) Plant Association in the Central and Southern Sierra (Potter, 2005, p. 481–487)

| Cover type                                         | Tuolumne<br>Meadows<br>Mean<br>% Cover | <i>Carex scopulorum</i> / <i>Oreostemma alpigenum</i> ,<br>10 plots |                  |                |
|----------------------------------------------------|----------------------------------------|---------------------------------------------------------------------|------------------|----------------|
|                                                    |                                        | Mean<br>% Cover                                                     | Range<br>% Cover | Constancy<br>% |
| <i>Oreostemma alpigenum</i> var. <i>andersonii</i> | 29.5                                   | 26                                                                  | 3–63             | 70             |
| Bare ground                                        | 20.8                                   | 1                                                                   | 1–5              | 100            |
| <i>Eleocharis quinqueflora</i>                     | 20.7                                   | 9                                                                   | 3–15             | 20             |
| <i>Muhlenbergia filiformis</i>                     | 9.3                                    | 16                                                                  | 3–38             | 60             |
| <i>Deschampsia cespitosa</i>                       | 5.7                                    | 18                                                                  | 3–38             | 40             |
| <i>Carex scopulorum</i> , naturally occurring      | 4.4                                    | 53                                                                  | 38–88            | 100            |
| <i>Genetiana newberryi</i> var. <i>tiogana</i>     | 2.9                                    | –                                                                   | –                | –              |
| <i>Primula tetrandra</i>                           | 1.3                                    | 7                                                                   | 3–15             | 30             |
| <i>Carex vesicaria</i>                             | 1.0                                    | 15                                                                  | 15               | 20             |
| <i>Vaccinium cespitosum</i>                        | 0.9                                    | –                                                                   | –                | –              |
| <i>Calamagrostis muiriana</i>                      | 0.8                                    | –                                                                   | –                | –              |
| <i>Juncus balticus</i> subsp. <i>mexicanus</i>     | 0.8                                    | –                                                                   | –                | –              |
| <i>Gentianopsis holopetala</i>                     | 0.7                                    | 30                                                                  | 3–15             | 30             |
| <i>Carex subnigricans</i>                          | 0.4                                    | –                                                                   | –                | –              |
| <i>Calamagrostis brewerii</i>                      | 0.3                                    | 6                                                                   | 3–15             | 40             |
| <i>Trichophorum clementis</i>                      | 0.2                                    | –                                                                   | –                | –              |
| <i>Danthonia intermedia</i>                        | 0.1                                    | –                                                                   | –                | –              |
| <i>Potentilla grayi</i>                            | 0.1                                    | –                                                                   | –                | –              |
| <i>Bistorta bistortoides</i>                       | 0.1                                    | 17                                                                  | 3–38             | 60             |
| <i>Erythranthe primuloides</i>                     | 0.1                                    | 24                                                                  | 3–63             | 50             |

497.1 g m<sup>−2</sup> ( $n = 59$ ,  $se = 38.4$ ) or 77.8%, in the upper 10 cm, indicating the shallow rooting depth of plants and the low root biomass in soil layers below 10 cm (Figure 3).

Individual plants of *Oreostemma alpigenum* had mean above and below ground biomass of 1.55 and 7.16 g (Table 2). Other abundant plants, including *Eleocharis quinqueflora* and *Carex subnigricans* had above ground biomass <0.5 g, and below ground biomass of <2.0 g. *Muhlenbergia filiformis*, the most numerically abundant species, had individual plant above and below ground biomass of 0.12 and 0.55 g.

**Table 2**

Aboveground (A) and Belowground (B) Individual Plant Species Biomass (Mean and Standard Deviation (sd)) of the Most Abundant Plant Species in the Study Area From Core Samples in 2017

| Cover type                                         | A mean g/plant | sd   | B mean g/plant | sd   | B/A |
|----------------------------------------------------|----------------|------|----------------|------|-----|
| <i>Oreostemma alpigenum</i> var. <i>andersonii</i> | 1.55           | 0.81 | 7.16           | 5.12 | 4.6 |
| <i>Eleocharis quinqueflora</i>                     | 0.47           | 0.44 | 1.89           | 2.01 | 4.0 |
| <i>Carex subnigricans</i>                          | 0.34           | 0.22 | 1.73           | 1.37 | 5.2 |
| <i>Muhlenbergia filiformis</i>                     | 0.12           | 0.19 | 0.55           | 0.79 | 4.6 |
| <i>Genetiana newberryi</i> var. <i>tiogana</i>     | 0.03           | 0.06 | 0.02           | 0.06 | 0.7 |

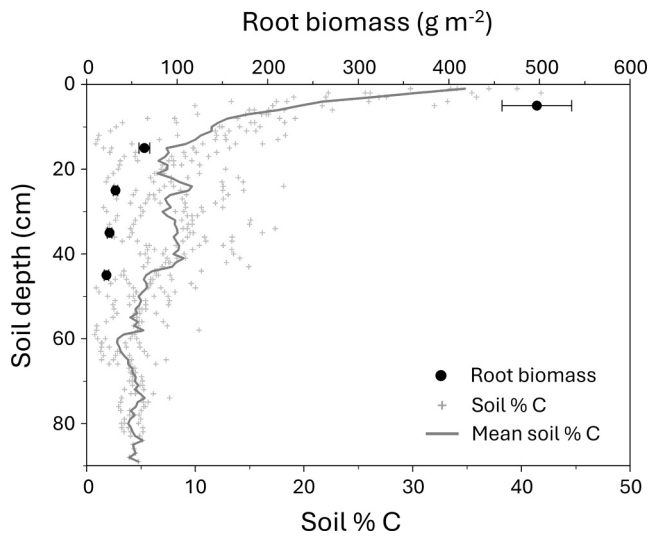


**Figure 3.** Root biomass (top x-axis) and percent soil organic carbon (bottom x-axis) by soil depth (y-axis) for soil cores from each of the five blocks. Black circles represent the live root biomass ( $\text{g m}^{-2}$ , mean  $\pm$  SE) centered on 10 cm depth increments. Gray crosses are individual soil % carbon measurements and the solid gray line is the mean (% C, by mass).

### 3.3. Planted Seedling Survival, Seedling Biomass and Size

*Carex scopulorum* seedlings planted in 2016 had 98.0% survival through the first summer (Table 3) and 75.0% survival through the fourth summer in 2019 ( $n = 773$ ). Seedlings planted in 2018 had 98.2% survival through the first year, and 84.9% survival through their second year. 2016 seedlings had a mean of 4.0 new tillers by the end of year 1, and more than 8 after three years. Seedling leaf length was variable and the longest leaves varied from 9.0 to over 16 cm and were similar to wild *C. scopulorum*. The area of each planted seedling was  $9.5 \text{ cm}^2$  in 2016, and over  $70 \text{ cm}^2$  after three years. The mean internode length between tillers was 3.97 cm, which was statistically similar to wild plants.

Planted seedlings had mean aboveground and belowground biomass of  $0.34 \text{ g}$  ( $n = 20$ ,  $\text{se} = 0.05$ ) and  $0.88 \text{ g}$  ( $n = 20$ ,  $\text{se} = 0.16$ ), respectively, with a belowground/aboveground biomass ratio of 2.56 (Figure 4). By the end of year 4 (2019), aboveground biomass was not significantly greater than the initial plantings ( $p = 0.125$ ). However, belowground biomass had increased more than 6-fold to an average of  $5.42 \text{ g}$  ( $n = 50$ ,  $\text{se} = 0.61$ ) (Figure S5 in Supporting Information S1). After four growing seasons, the belowground/aboveground biomass ratio was 7.69.

### 3.4. Meadow Soil Carbon Stock

Soil core depth in the blocks was limited by underlying gravel and cobbles and reached 50–89 cm deep (Figure S6 in Supporting Information S1). Mean total soil carbon stock was  $29.39 \text{ kg m}^{-2}$  (Table 4). The upper 10 cm soil layer had a mean SOC of 20.2%, and was lower below 10 cm. SOC was lowest in blocks 1–3 (mean = 5.5%) compared with blocks 4 and 5 (mean = 8.0%). SOC density averaged  $0.62 \text{ kg m}^{-2}$  for the upper 10 cm soil layer, while below 10 cm it was 0.59 and  $0.42 \text{ kg m}^{-2}$  for cores 1–3 and 4–5. SOC stock matched the distribution of belowground biomass (Figure 3) with 77% of live root biomass in the upper 10 cm. The meadow soil lacks the % OC and organic material thickness to be classified as an organic soil or histosol (Soil Survey Staff 2014), although some cores had layers 7–24 cm thick with >12% SOC. Bulk density in the upper 10 cm averaged  $0.36 \text{ g cm}^{-3}$ . Cores 1–3 located closer to the southern hillslopes had the highest bulk density variance below 10 cm (mean =  $0.76 \text{ g cm}^{-3}$ , range =  $1.72\text{--}0.28 \text{ g cm}^{-3}$ ), suggesting periodic mineral soil inputs. Cores 4 and 5, located farther from the mountain slopes, had a more even down-core soil bulk density profile (mean =  $0.55 \text{ g cm}^{-3}$ , range =  $0.86\text{--}0.24 \text{ g cm}^{-3}$ ).

### 3.5. Meadow Greenhouse Gas Fluxes

The 2017 water year snow cover was the deepest and most long lasting in many decades, not melting until June. This likely resulted in the death by starvation or drowning of the Beldings ground squirrel population in TUM

**Table 3**

Mean ( $\pm 1$  SD) for Number of Tillers, Longest Leaf Length (cm), Clone Cover Area ( $\text{cm}^2$ ), and Internode Length (cm) for *Carex scopulorum* Seedlings Planted in 2016 ( $n = 46$  Plots in 2016, 45 Plots in 2017, and 892 Plants Analyzed in 2018 and 773 Plants in 2019), and Native Wild Plants ( $n = 24$ )

| Year        | % survival | N tillers     | Longest leaf   | Clone area      | Internode length |
|-------------|------------|---------------|----------------|-----------------|------------------|
| 2016–yr 1   | 98.0       | 4.0 $\pm 1.8$ | 9.0 $\pm 2.0$  | 9.5 $\pm 2.5$   | 3.97 $\pm 1.8$   |
| 2016–yr 2   | 71.0       | 4.5 $\pm 2.1$ | 13.5 $\pm 2.0$ | 20.0 $\pm 10.5$ | 3.78 $\pm 2.1$   |
| 2016–yr 3   | 76.0       | 8.2 $\pm 2.1$ | 9.5 $\pm 5.3$  | 72.0 $\pm 2.9$  | nd               |
| 2016–yr 4   | 75.0       | nd            | 12.2 $\pm 3.7$ | 70.5 $\pm 78.3$ | nd               |
| 2018–yr 1   | 98.2       | nd            | 16.2 $\pm 9.0$ | nd              | nd               |
| 2018–yr 2   | 84.9       | 2.3 $\pm 1.9$ | 9.9 $\pm 3.7$  | 21.9 $\pm 22.8$ | hd               |
| Wild plants |            |               | 14.9 $\pm 3.9$ |                 | 4.09 $\pm 1.5$   |

Note. 2018 seedlings sample includes  $n = 662$  in year 1, and 695 plants in year 2. nd = no data collected.

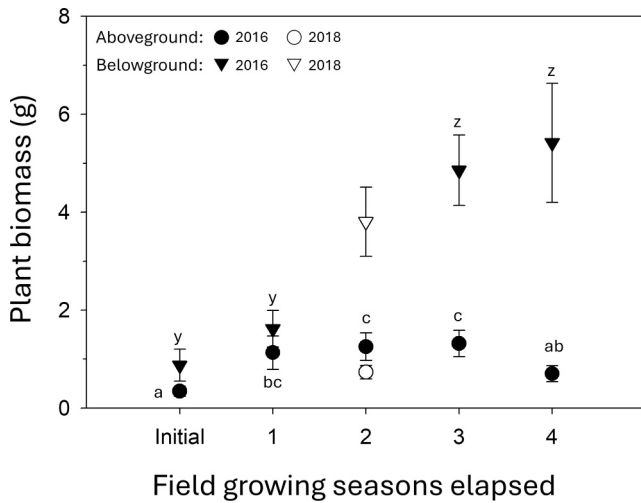


**Figure 4.** Aboveground (circles) and belowground (triangles) dry biomass (grams, mean  $\pm$  2SE) of individual *Carex scopulorum* seedlings as provided by the nursery initially and after 1, 2, 3, and 4 growing seasons for 2016 seedlings (black-filled symbols). Biomass of seedlings planted in spring 2018 (white-filled symbols) was assessed after 2 growing seasons, in late summer 2019. Letters indicate statistically different groups within aboveground (a, b, c) and belowground (y, z) biomass measurements for the 2016 plantings.

and although they were abundant in 2016, we saw no squirrels in 2017, 2018 or 2019. Since these mammals were the main herbivore that the fences were meant to exclude, and the fences could be breached by the ground squirrels, the fence treatment effect could not be assessed. The treatment effects of planting and fencing provided no improvement when compared to controls with our Bayesian model, and we concluded that over the first 4 years of this experiment there were no treatment effects on GPP or ER fluxes. Therefore, we aggregated the plots into a grouped average of twelve plots for each block.

Our Bayesian model fit the field data well, with observed to predicted ER having an  $R^2 = 0.73$  and GPP having an  $R^2 = 0.67$  (Figure 5). GPP had strong diurnal and seasonal trends, with maximum rates in mid summer (Figure 6). Annual GPP ranged from  $-0.43$  to  $-0.73$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  for our 5 blocks, while ER ranged from  $0.79$  to  $1.09$   $\text{kg C m}^{-2} \text{ yr}^{-1}$ , for a net loss of  $0.18$ – $0.47$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  and a mean average net loss of  $0.37$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  for the three study years (Table 3). Winter ER rates were low, measured in our freezer experiment, but the snow covered season is long and contributed an average of  $0.16$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  to the annual fluxes (Figure 6). The three study years had different cumulative ER, GPP and NEE totals; however, all years had net SOC losses, with the greatest loss in the dry year 2018 of  $0.53$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  and losses of  $0.33$  and  $0.27$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  for 2017 and 2019 (Figure 6). The large SOC loss is due to high ER totals of  $0.97$ ,  $1.12$  and  $0.80$   $\text{kg C m}^{-2} \text{ yr}^{-1}$  for 2017, 2018 and 2019 (Figure 7).

Mean daytime  $\text{CH}_4$  emissions across the five blocks for 2018 was  $3.9$   $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  ( $n = 58$ ,  $\text{sd} = 4.6$ ) for July 5 and  $1.6$   $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  ( $n = 32$ ,  $\text{sd} = 2.7$ ) for August 10 and for 2019 were  $0.3$   $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  ( $n = 38$ ,  $\text{sd} = 0.4$ ) for June 11,  $2.1$   $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  ( $n = 61$ ,  $\text{sd} = 4.7$ ) for June 27,  $6.7$   $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  ( $n = 61$ ,  $\text{sd} = 12.4$ ) for July 18, and  $0.0002$   $\text{mg CH}_4 \text{ m}^{-2} \text{ day}^{-1}$  ( $n = 21$ ,  $\text{sd} = 0.0003$ ) for September 12. Mean  $\text{N}_2\text{O}$

**Table 4**

Mean Soil Bulk Density ( $D_b$ ,  $\text{g cm}^{-3}$ ), Percent Organic Carbon (C %), and Carbon Density ( $D_c$ ,  $\text{kg C m}^{-2}$ ) at 0–10 and 10 cm to the Bottom of Each Core for Blocks 1–5

|                                                | Experimental blocks |                 |                 |                 |                 | Mean            |
|------------------------------------------------|---------------------|-----------------|-----------------|-----------------|-----------------|-----------------|
|                                                | B1                  | B2              | B3              | B4              | B5              |                 |
| Core depth (cm)                                | 89                  | 66              | 82              | 50              | 83              | 74              |
| Soil properties (0–10 cm)                      |                     |                 |                 |                 |                 |                 |
| $D_b$ ( $\text{g cm}^{-3}$ )                   | $0.40 \pm 0.05$     | $0.45 \pm 0.09$ | $0.34 \pm 0.03$ | $0.35 \pm 0.02$ | $0.29 \pm 0.03$ | $0.36 \pm 0.02$ |
| C (%)                                          | $18.8 \pm 2.9$      | $23.3 \pm 4.9$  | $18.6 \pm 2.2$  | $19.0 \pm 1.4$  | $21.1 \pm 2.8$  | $20.2 \pm 1.3$  |
| $D_c$ ( $\text{kg C m}^{-2}$ )                 | $0.65 \pm 0.05$     | $0.68 \pm 0.08$ | $0.59 \pm 0.05$ | $0.65 \pm 0.05$ | $0.54 \pm 0.03$ | $0.62 \pm 0.02$ |
| Soil properties (10 cm-core base)              |                     |                 |                 |                 |                 |                 |
| $D_b$ ( $\text{g cm}^{-3}$ )                   | $0.86 \pm 0.03$     | $0.63 \pm 0.04$ | $0.75 \pm 0.03$ | $0.48 \pm 0.02$ | $0.59 \pm 0.01$ | $0.69 \pm 0.01$ |
| C (%)                                          | $3.9 \pm 0.2$       | $8.1 \pm 0.7$   | $5.1 \pm 0.3$   | $9.8 \pm 0.5$   | $7.1 \pm 0.3$   | $6.4 \pm 0.2$   |
| $D_c$ ( $\text{kg C m}^{-2}$ )                 | $0.29 \pm 0.01$     | $0.39 \pm 0.02$ | $0.33 \pm 0.01$ | $0.44 \pm 0.01$ | $0.40 \pm 0.01$ | $0.36 \pm 0.01$ |
| Total soil C stock ( $\text{kg C m}^{-2}$ )    | 29.71               | 28.69           | 29.51           | 24.13           | 34.91           | $29.39 \pm 1.7$ |
| Mean C fluxes (years 2017–2019)                |                     |                 |                 |                 |                 |                 |
| ER ( $\text{kg C m}^{-2} \text{ year}^{-1}$ )  | 1.07                | 1.09            | 1.01            | 0.79            | 0.86            | 0.96            |
| GPP ( $\text{kg C m}^{-2} \text{ year}^{-1}$ ) | −0.63               | −0.73           | −0.54           | −0.60           | −0.43           | −0.59           |
| NEE ( $\text{kg C m}^{-2} \text{ year}^{-1}$ ) | 0.44                | 0.36            | 0.47            | 0.18            | 0.42            | 0.37            |
| Percent (%) soil C loss $\text{year}^{-1}$     | 1.47                | 1.26            | 1.58            | 0.76            | 1.21            | 1.27            |

Note. C fluxes ( $\text{kg C m}^{-2} \text{ year}^{-1}$ ) are the means for 2017, 2018 and 2019 for ER, GPP, and NEE by block. Percent soil C loss is the mean C loss based on NEE as a proportion of total C stock.

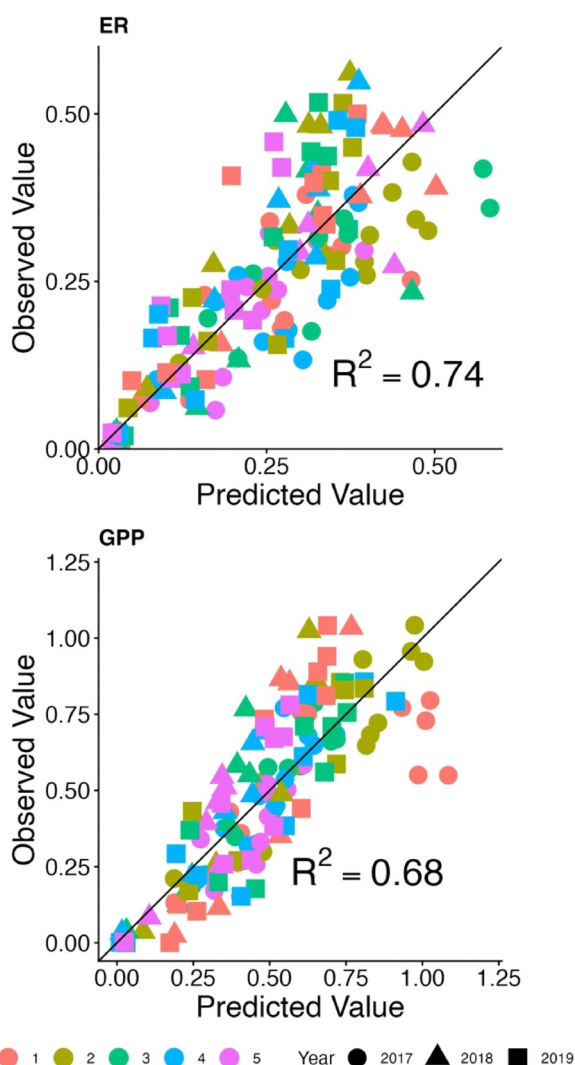


**Figure 5.** Observed and predicted ecosystem respiration (ER) (top panel,  $n = 169$ ) and gross primary production (GPP) (bottom panel,  $n = 129$ ) in  $\text{gC m}^{-2} \text{hr}^{-1}$  for five blocks in the three study years. The black line is the 1:1 line. The observed and predicted ER and GPP have a nonsignificant ( $p = 0.19$  and  $0.77$ ) relationship between observed and mean-predicted for the test intercept = 0 and slope = 0 (i.e.  $y = x$ ), indicating that the  $y = x$  relationship cannot be rejected.

emissions across the five blocks for 2018 were  $0.12 \text{ mg N}_2\text{O m}^{-2} \text{day}^{-1}$  ( $n = 54$ ,  $\text{sd} = 0.25$ ) for July 5 and  $0.08 \text{ mg N}_2\text{O m}^{-2} \text{day}^{-1}$  ( $n = 29$ ,  $\text{sd} = 0.21$ ) for August 10.

## 4. Discussion

### 4.1. Meadow Conservation and Loss

Yosemite National Park is one of the world's premier conservation areas and is visited by more than 4 million people each year, many of whom also visit TUM. The surrounding mountains are stunning and the meadow appears green in early summer, giving the impression it is pristine (Figures S1 and S2 in Supporting Information S1). However, the lack of cover by clonal sedges that dominate the vegetation and carbon dynamics of natural wet meadows and fens throughout the northern hemisphere (Chimner et al., 2002; Cooper et al., 2012) is striking, as is the current dominance of annual and short lived taprooted perennial plants and abundant bare ground (Table 2, Figure S3 in Supporting Information S1). Long-term precipitation records (Williams et al., 2021) and tree ring indices (King, 2006) indicate no drying trends that could have degraded the meadow vegetation over the past 150 years. Even during the severe drought of 2012–2015, the WT was near the ground surface in early summer, sustaining meadow soil saturation (Figure S7 in Supporting Information S1).

Grazing in the high elevation Sierra Nevada meadows occurred during what has been termed an “era of tacit consent” when the Federal Government made no attempt to control domestic livestock grazing on public lands. Ernst (1949) reported that the “character of the ground and nature of the vegetation able to survive or re-invade are slow in showing signs of ultimate recovery in the 1940s from the excessive impacts they sustained”. The floristic composition of TUM and other meadows in the Sierra Nevada prior to 1849 is unknown; however, using pollen analysis, Dull (1999) identified significant vegetation changes in southern Sierra Nevada meadows in the middle to late 1800s, likely driven by overgrazing. Davis and Moratto (1988) found that Cyperaceae (sedges) were the most abundant macrofossils in Exchequer and Dinkey Meadow soils, approximately 90 km south of TUM. In the remote McCabe Meadow, 14.5 km north of TUM, *Carex scopulorum* dominates the wet meadow zone (Figure S4 in Supporting Information S1). This species also occurs on lake and pond margins in the Tuolumne River watershed and based on this evidence, we hypothesized that prior to the livestock disturbances of the late 1800s the vegetation of TUM was dominated by *C. scopulorum*.

### 4.2. Effects of Long Term Climate

Extended droughts and single year extreme climates are characteristic of the central and southern Sierra Nevada and have been well documented for the past 1200 years (Graumlich, 1993). The 20th and 21st centuries had two long and severe drought periods, 1915–1934 and 2012–2015, and a long period of high precipitation from 1937 to 1986, with extreme high precipitation years in 1997, 2017 and 2023. Approximately 85% of annual precipitation in the Sierra Nevada occurs during winter and no significant deviations from annual long term precipitation totals have been reported (Williams et al., 2021).

Natural or human caused fire regimes drive important ecological processes in Sierra Nevada forests, and fire scars have been cross dated in TUM (King, 2006). Most fire scars were from the 1700s and early 1800s, indicating that frequent patchy fires occurred in the area. The TUM forest margin has a well-defined line of 250–400 years old lodgepole pines, indicating the stability of the meadow edge. The removal of trees by fires could reduce

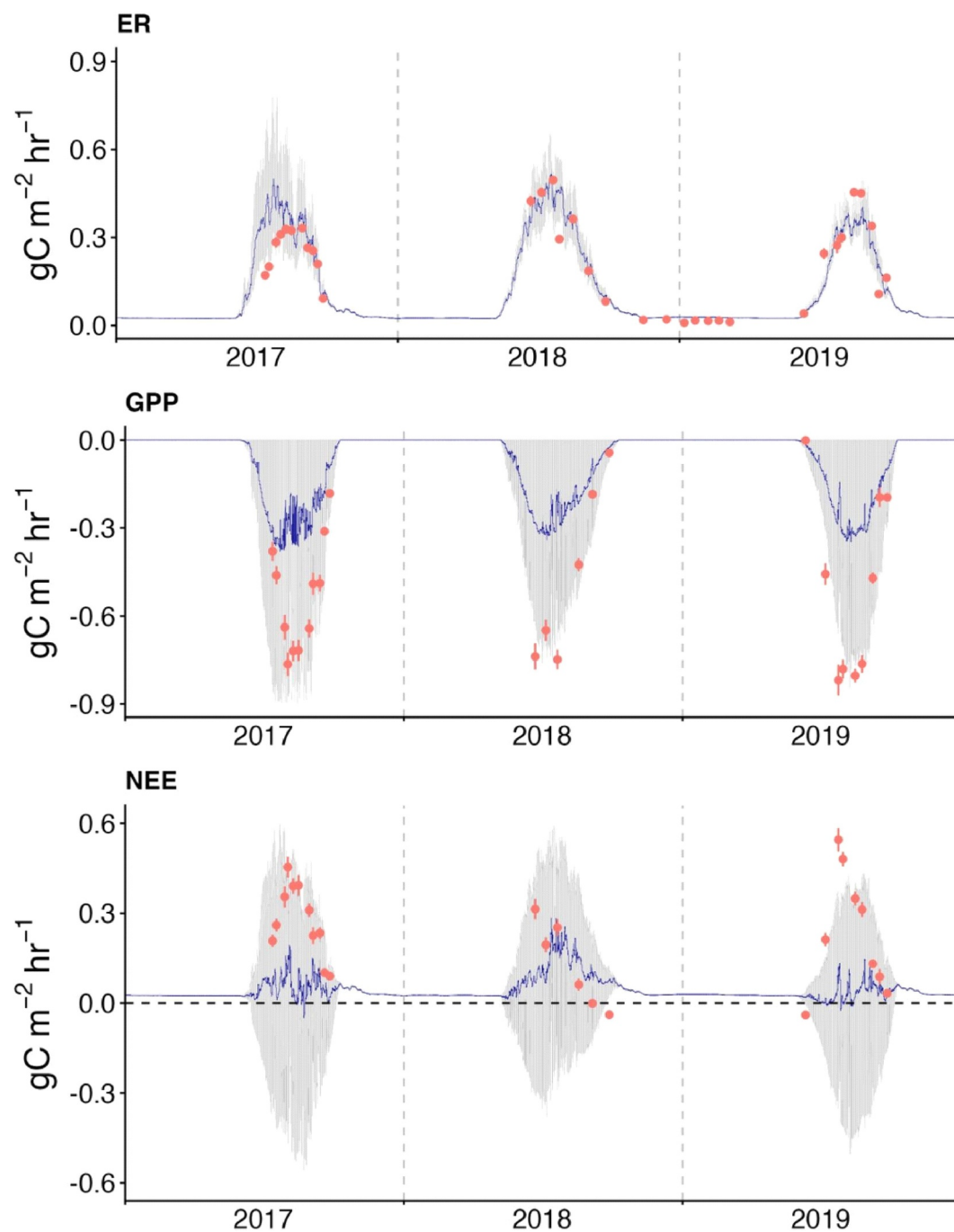


**Figure 6.** Ecosystem respiration (ER, top panel), gross primary production (GPP, middle panel) and net ecosystem exchange (NEE, lower panel) for the 3-year study period. Red dots are mean observed field values ( $\pm 1$  SE), the gray lines are hourly modeled values, and the blue lines are 24-hr moving averages of hourly modeled values.

evapotranspiration and potentially increase ground water availability. However, the hydrologic regime of TUM today is suitable for the persistence of wet meadow vegetation (Lowry et al., 2010).

Long term modeling forecasts a shift in Sierra Nevada winter precipitation from snow-dominated to rain-dominated as the climate warms (Beltran-Peña et al., 2025; Rhoades et al., 2018). Snow water equivalent could have increasing interannual variability and more consecutive snow drought years (Marshall et al., 2019).

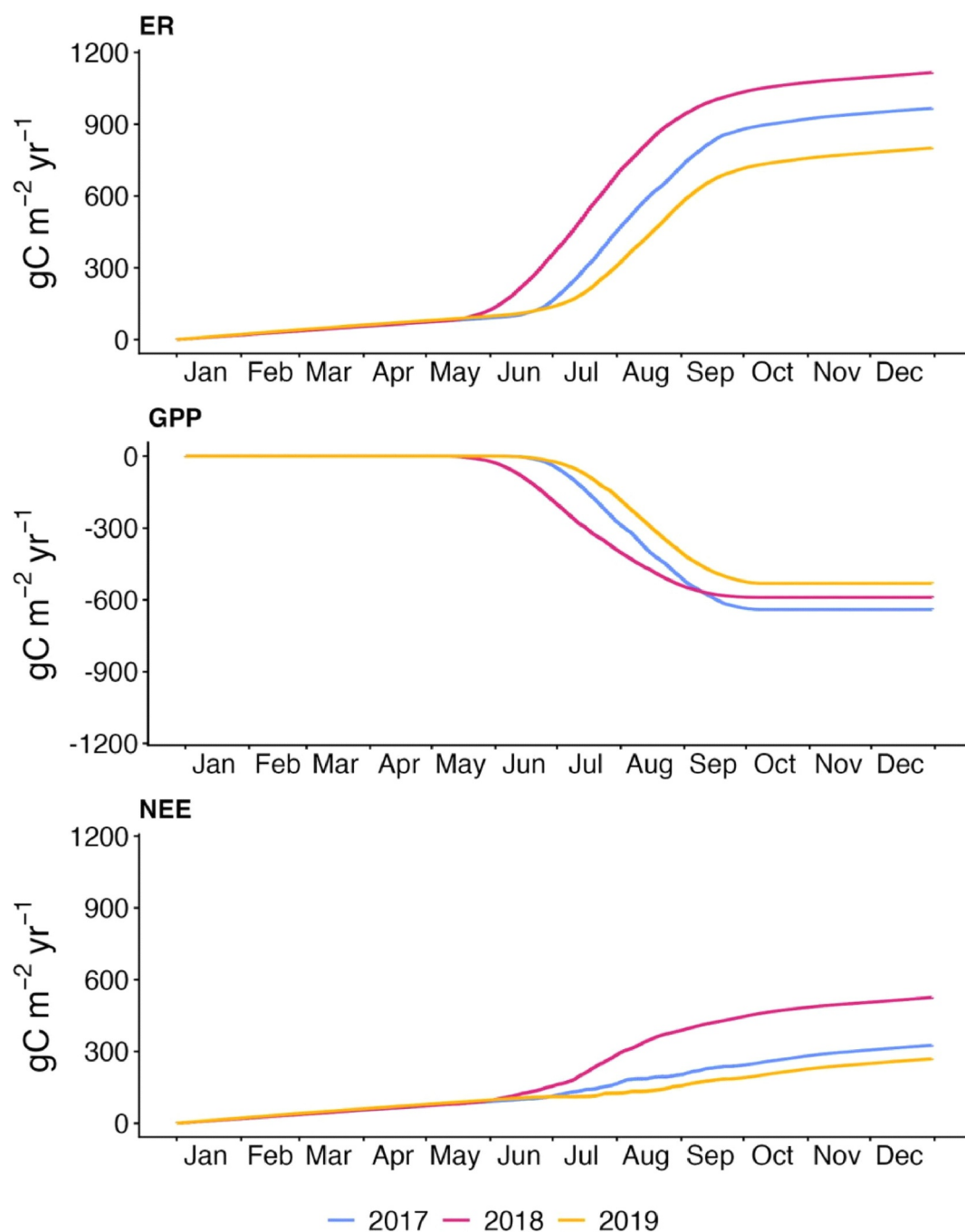


**Figure 7.** Cumulative total  $\text{gC m}^{-2} \text{yr}^{-1}$  for gross primary production, ecosystem respiration, and net ecosystem exchange in 2017, 2018 and 2019.

This could produce earlier onset snowmelt runoff, longer summers, and lower mid-summer soil water and deeper groundwater levels (Rhoades et al., 2018). These long term trends are critical to understand because years with lower SWE, such as 2018, had greater SOC loss than years with higher SWE, such as 2017 and 2019. Arnold et al. (2014) also found that low snowpack years produced higher  $\text{CO}_2$  fluxes from wet meadows in the TUM region. Increased soil drought and carbon loss could limit the success of reestablishing *C. scopulorum* and other native wetland plants.

### 4.3. Current Vegetation, Planting Success, Biomass and Soil Carbon Stock

Highly productive vegetation dominated by long lived plants is critical for belowground carbon storage in mountain meadows (Blackburn et al., 2021; Chimner & Cooper, 2003b). The seasonal fine root production of *C. scopulorum* can exceed  $350 \text{ g m}^{-2}$  (Fisk et al., 1998) and its deep rooting structure can allow it to be phreato-phytic, accessing groundwater in late summer and fall as the WT drops. However, only scattered shoots of native *C. scopulorum* occur in the study area with mean canopy cover less than 5% (Ballenger & Acree, 2009; Cooper et al., 2006; Wolf, 2017) (Table 1).

TUM wet meadow vegetation is dominated by *Oreostemma alpigenum* var. *andersonii*, *Eleocharis quinqueflora*, *Muhlenbergia filiformis*, and *Deschampsia cespitosa*, with total belowground live biomass averaging  $<700 \text{ g m}^{-2}$ . Bowman et al. (1993) reported belowground biomass in a *C. scopulorum*-dominated alpine wet meadow community of over  $3000 \text{ g m}^{-2}$  and Webber and May (1997) reported over  $4,000 \text{ g m}^{-2}$  from a similar community. Their Niwot Ridge, Colorado study site is at a higher elevation, occurs on a different bedrock type, experiences colder summer temperatures, has a shorter growing season, and receives less groundwater inputs due to its smaller watershed than TUM. Thus, we might expect the alpine sites to have lower below ground biomass than TUM. The Niwot Ridge sites provide an inference that belowground biomass in TUM is much lower than natural wet meadows, and in its undisturbed state productivity could have been higher. Our planted *C. scopulorum* seedlings had high survival over the study period, with steady belowground biomass increase over four summers (Figure 4). The near freezing temperature on most summer nights (Figure 2), cool soil temperatures, and deep late summer WT likely limit the growth of young plants. During our 4 year study the distributed individual transplants did not grow enough to alter the meadow carbon budget; however, it is likely the best long-term approach for meadow restoration. The closely related *Carex bigelowii* roots to at least 1 m deep (Hewitt et al., 2019) and if the planted seedlings can root to the late summer WT, it could greatly improve their growth and biomass accumulation.

### 4.4. Meadow Carbon Dynamics

Soil organic matter is the largest terrestrial carbon pool, and understanding fluxes to and from that pool is essential for modeling local and global carbon cycles (Scharlemann et al., 2014). The main source of soil carbon in wetland ecosystems is from plant roots and rhizomes (Chimner & Cooper, 2003a) as their organic matter persists longer than leaf and culm derived matter (Rasse et al., 2005; Reed et al., 2021). Higher belowground-to-aboveground plant biomass ratios (B:A) are more likely to contribute to long term soil carbon storage (De Deyn et al., 2008) and *C. scopulorum* dominated wet meadows have been shown to have ratios greater than 10:1 (Bowman et al., 1993). Any process that alters total plant production or B:A allocation can affect the soil carbon pool.

A significant net loss of SOC occurs from TUM in years with high (2017), low (2018) and near average (2019) snow water equivalent. Our five blocks lost an average of  $0.31 \text{ kg C m}^{-2} \text{ yr}^{-1}$  and varied from a loss of  $0.14 \text{ kg C m}^{-2} \text{ yr}^{-1}$  in block 2 to  $0.41 \text{ kg C m}^{-2} \text{ yr}^{-1}$  in block 3. This loss represents an average of 1.07% of the carbon stock of our study area (Table 4) and may represent the long-term net carbon loss over many decades, and perhaps even a century or longer. Other studies in the region have also shown a net loss of carbon from wet meadows. Reed et al. (2021) found carbon loss from 10 of the 13 meadows studied elsewhere in the Sierra Nevada. They reported that four of their study meadows lost approximately 3% of their C stock in the 1 year of study, largely because the calculated GPP was low. Blankinship and Hart (2014) measured fluxes of  $\text{CO}_2$ ,  $\text{CH}_4$  and  $\text{N}_2\text{O}$  from Gaylor Meadow, just north of TUM and found that mid-summer fluxes were not explained by soil water content, and  $\text{CO}_2$  flux did not vary across their studied hydrologic gradient. However, it contributed 98.5% of the greenhouse gas emission totals. We estimated that TUM annual  $\text{CO}_2$  flux contributes more than 95% of its total greenhouse gas emissions due to extremely low fluxes of  $\text{CH}_4$  and  $\text{N}_2\text{O}$ . Arnold et al. (2014) assessed the variance in soil carbon gas fluxes and net primary production (NPP, determined by late season clipping and weighting of plant biomass) in Dana Meadows, east of TUM, showing greater soil respiration and lower NPP in low snowpack years compared with higher snowpack years. Annual NPP varied from approximately  $0.30\text{--}0.50 \text{ kg C m}^{-2} \text{ yr}^{-1}$ , while soil C flux averaged  $0.60\text{--}1.20 \text{ kg C m}^{-2} \text{ yr}^{-1}$ , suggesting an annual net loss of carbon.

The long-term loss of organic matter through decomposition has reduced TUM SOM and increased soil bulk density. Ankenbauer and Loheide (2016) demonstrated that the loss of organic matter from TUM soils can significantly reduce soil water available for plant transpiration and increase late summer water stress. *C.*

*scopulorum* plants in healthy conditions can acquire soil water and groundwater in early summer, but mainly groundwater in late summer. The ongoing decomposition of organic matter and persistent soil drought can result in root embolism and root dieback, limiting the ability of plants to acquire deeper groundwater (Rodríguez-Calcerrada et al., 2017). The loss of soil water holding capacity and concurrent reduction in soil matric potential due to the loss of SOC is a critical issue for the growth and survival of *Carex* plants.

Grazing disturbances in wet meadow vegetation on the Tibetan plateau created higher ER rates when compared with similar undisturbed areas (Ma et al., 2018). The disturbance also created bare soil that led to higher surface soil temperatures and reduced shading by vegetation that also contributed to higher ER rates. Reed et al. (2021) also found higher rates of ER in heavily disturbed meadows with low peak vegetation biomass and higher % bare ground, due to the loss of belowground carbon inputs and storage. The role of WT depth and soil saturation on carbon fluxes varies by study, with some showing little effect (Reed et al., 2021), and others indicating its importance for CO<sub>2</sub> (Chimner & Cooper, 2003a; Millar et al., 2016), CH<sub>4</sub> fluxes (Ma et al., 2018) or NPP (Arnold et al., 2014). On a global scale WT depth exerts greater control than climate and ecosystem related variables (Li et al., 2022).

#### 4.5. Synthesis: Past, Present and Future Meadow State and Carbon Dynamics

The high organic content soil in TUM could not have formed with the low GPP vegetation that exists today. The hydrologic regime of the meadow is intact without significant physical or climate driven changes (Cooper et al., 2006; Lowry et al., 2010). A plant community with a much higher GPP would have been present in the past to support long-term meadow carbon storage (Chimner & Cooper, 2003a; Hinzke et al., 2021; Reed et al., 2021). While short-term grazing may have minimal effects on plants (Volesky et al., 2011), long-term herbivory in wet meadows can reduce photosynthetic capacity and belowground biomass, trigger changes in vegetation composition, and increase soil temperature, all of which increase CO<sub>2</sub> efflux from soils (Chavez et al., 2025; Klumpp et al., 2009). Although the intensive use of TUM and other high elevation meadows in the Sierra Nevada occurred more than 120 years ago, the legacy effects persist (Figure 8). Loss of the dominant clonal plants, as well as the presence of large areas of bare ground, and annual net SOM loss have pushed the former stable wet meadow with a dominance of highly productive deep rooted sedges into a highly degraded alternative meadow state with less productive shallow rooted vegetation that appears to be stable (Figure 8). The ongoing loss of SOM and water holding capacity (Ankenbauer & Loheide, 2016) has created an artificially drought prone ecosystem, and the persistent grazing effects of mountain voles and Belding's ground squirrels have been sufficient to maintain the bare ground, and a disturbance regime that limits vegetation recovery, as shown in previous work with mammal exclosures (Wolf, 2017). While small patches of *C. scopulorum* are present in TUM they do not appear to be expanding on the time scale of decades to a century, yet this species would fill the important niche as a clonal sedge with high below ground biomass production.

#### 4.6. Management and Restoration Recommendations

The key to restoring organic soil in TUM is to restore the meadow vegetation composition and its biomass production. We found high survival of planted *C. scopulorum* seedlings through four summers and steady belowground biomass accumulation. Although this did not lead to differences in plot or block level carbon fluxes, the consistent growth suggests that restoring the clonal sedge-dominant vegetation through planting has great promise. Even though the 20th century was one of the wettest periods of the past 1,000 years (Graumlich, 1993), the loss of SOM and water holding capacity may be limiting natural *Carex* seedling establishment and growth. Two other small sedge species *Eleocharis quinqueflora* and *Carex subnigricans* are present, but their biomass production potential is low. *Juncus balticus*, a clonal rush species, is also present and can dominate low elevation fens (Millar et al., 2016) but is uncommon in TUM. *Carex vesicaria*, a large sedge species, is present in low lying depressions with long duration standing water, but these are rare in the landscape. No other clonal plant species with high biomass production occurred in the study area.

Future climate changes in the Sierra Nevada are predicted to reduce annual stream flow (Null et al., 2010), winter snowpack water content and groundwater recharge, and lengthen the summer (Cristea et al., 2013; Kapnick & Hall, 2010) leading to drier meadow conditions. Higher summer temperatures are also predicted (Liang et al., 2017; Stewart et al., 2017) that could increase evapotranspiration (Maher et al., 2017) and allow continued lodgepole pine invasion into dry and wet meadows by the end of the 21st century (Lubetkin et al., 2017). This

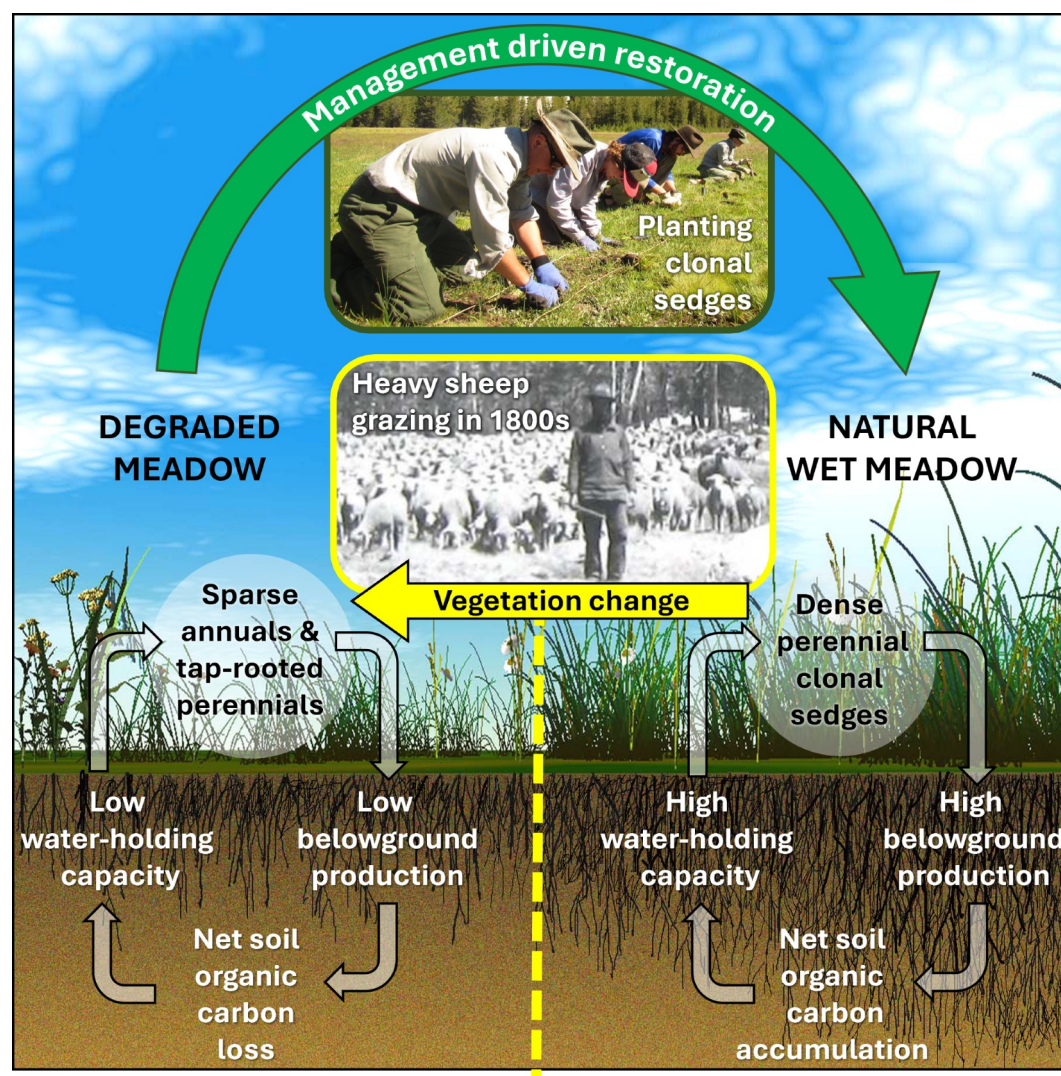


**Figure 8.** Conceptual model of the ecological feedbacks that stabilize (gray arrows) and the human management actions that shift (yellow and green arrows) the Tuolumne Meadows ecosystem between the natural wet meadow (right) and the degraded meadow (left). Background graphic used with permission of Dave Weixelman.

could create persistent conditions such as 2018, which had higher SOC losses than in 2017 or 2019 and could increase the long-term rate of SOM loss from the meadow. Many national parks, including Yosemite, were established long after significant landscape alterations had already occurred, and even though they are now protected, they are not immune to ecosystem changes and collapse (Bergstrom et al., 2021; Cooper et al., 2025). It is critical to restore the degraded meadow state and recreate a functional carbon accumulating wet meadow ecosystem to support the goals of Yosemite National Park.

### Conflict of Interest

The authors declare no conflicts of interest relevant to this study.

### Availability Statement

Sentinel-2 satellite data, level 2A at 20 m resolution, was used to develop the CI (<https://eos.com/find-satellite/sentinel-2/>). Tuolumne Meadows micrometeorological station of the California Department of Water Resources Data Exchange Center (<https://cdec.water.ca.gov/cdecstations>). DRYAD Data set: Cooper et al. (2026).

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