

THESIS

RESTORING CARBON ACCUMULATING PROCESSES IN A DEGRADED WET
MEADOW

Submitted by

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Graduate Degree Program in Ecology

In partial fulfillment of the requirements

For the Degree of Master of Science

Colorado State University

Fort Collins, Colorado

Summer 2018

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ABSTRACT

RESTORING CARBON ACCUMULATING PROCESSES IN A DEGRADED WET MEADOW

Wet meadows throughout the Sierra Nevada range of western North America were historically disturbed and are thought to be losing soil water holding capacity and the ability to store carbon (C). I tested whether herbivore exclosures and the reestablishment of a sedge-dominated community at Tuolumne Meadows, a high elevation wet meadow in Yosemite National Park, can restore the C accumulating function of this ecosystem. In 2016, 20,000 *Carex scopulorum* (mountain sedge) were planted into the meadow. An empirical model of growing season carbon dynamics was created to determine if these treatments increase the meadow's C storage compared to controls. The second summer after planting, there was no difference in C storage capacity between treatment types and controls, and model estimates indicate that Tuolumne Meadows is a net source of carbon dioxide (CO₂) to the atmosphere. Significant relationships between net ecosystem exchange (NEE) and percent vascular cover indicate that increasing vegetation cover could revert the ecosystem to carbon storing. However, future warmer, drier climatic conditions could maintain the system's current state as a C source.

ACKNOWLEDGEMENTS

First, a huge thank you to Yosemite National Park staff and crews for their assistance and support with this project. Thank you to my committee member, Joe von Fischer, who was instrumental in developing gas sampling methodology and discussing carbon modelling options. A special thanks to David Steingraeber, my other committee member, for expanding my knowledge of botany and exciting me to learn more. Thank you to Dave Millar, without whose help I would still be fiddling around trying to figure out a model. At any opposition or obstacle, David Cooper, my advisor, proved to be a tremendous advocate and mentor, so thank you for your support on this project. Thank you to my amazing lab group; your feedback has been instrumental every step of the way. Lastly, thank you so much to Melissa Booher- you made work fun and I would have been lost on this project without your help.

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INTRODUCTION

Wetlands occupy only 5-8% of the earth's surface yet they store approximately 20-30% of the world's terrestrial carbon (C) as soil organic matter (SOM) (Mitsch and Gosselink, 2007; Waddington and Roulet, 2000; Bridgham et al., 2006). Soil organic matter accumulates in wetlands when rates of production exceed decomposition, typically in areas of poor drainage and anaerobic soil conditions (Whiting and Chanton, 2001). When sufficient oxygen (O₂) and soil water is available, soil microbes can decompose organic matter and release carbon dioxide (CO₂) through aerobic respiration. However, the anaerobic conditions of wetlands limit organic matter decomposition (Batzer and Sharitz, 2006). As a result, C may be sequestered within wetlands for centuries (Smith et al., 2004). If wet meadows dry out due to disturbances or climate change and O₂ becomes more available within the soil, the organic matter can decompose, shifting these wetlands from net sinks of C to net sources (Keddy et al, 2009).

Tuolumne Meadows in Yosemite National Park is a well-known Sierra Nevada wet meadow ecosystem. Wet meadows are characterized by a seasonally shallow water table, generally fine textured mineral soil with high organic matter content, and dense herbaceous vegetation (Ratliff, 1985). In the Sierra Nevada, these wetlands are vital for flood attenuation, habitat for endangered animals, as a cultural resource, and as C reservoirs (Ballenger et al., 2009). In Tuolumne Meadows, highly organic soil in the meadows indicates its long-term role as a C sink, yet the current sparse cover of vegetation with low biomass production and large areas of bare soil indicate that this ecosystem has potentially shifted into a C source to the atmosphere.

Legacy effects of intensive sheep grazing in the 1800's, reductions in water availability due to decreased annual precipitation, and land use changes are reported to be responsible for the

degraded state of Sierra Nevada meadows (Ratliff, 1985). Tuolumne Meadows has higher cover of bare ground and a higher ratio of forbs to graminoids compared to reference meadows in the central Sierra Nevada (Ballenger, 2009). We hypothesize that the wetland portions of Tuolumne Meadows were formerly dominated by wetland species such as *Carex scopulorum*, *Carex vesicaria*, and *Juncus mexicanus* but has been converted to *Oreostemma*-dominated vegetation due to intensive livestock grazing in the 19th century (Wolf and Cooper, 2016; Ballenger, 2009). The current dominant vegetation (*Oreostemma alpigenum*) in Tuolumne could not have produced the highly organic soil of the meadow (Cooper et al., 2006).

A high percentage of SOM enhances soil water retention, providing approximately 35 water stress-free days for herbaceous plants in the growing season in Tuolumne Meadows (Ankenbauer and Loheide, 2017). Increased soil moisture can facilitate wetland plant production (Veihmeyer and Hendrickson, 1927) and maintain anaerobic conditions that limits SOM decomposition (Batzer and Sharitz, 2006). The decomposition of SOM coupled with reduced organic matter production is reducing soil water holding capacity (Ankenbauer and Loheide, 2017). To maintain or enhance the soil water holding capacity of Tuolumne Meadows, it is essential to increase meadow net primary productivity, organic matter storage, and carbon sequestration (Ankenbauer and Loheide, 2017) (Figure 1).

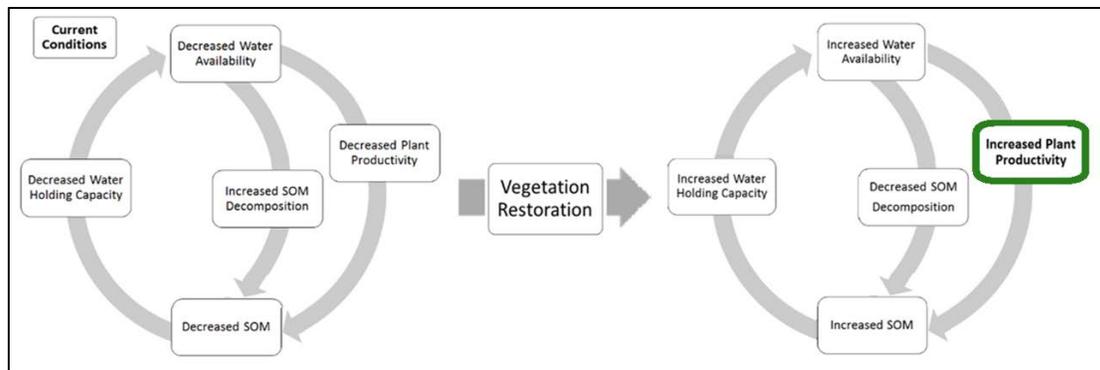


Figure 1. Water availability and SOM. Decreased water availability leads to both decreased plant productivity and increased rates of SOM decomposition which both lead to decreased amounts of SOM. Decreases in SOM result in decreased water holding capacity leading to lower water availability. The addition of new vegetation into the system will increase plant productivity which will lead to increases in SOM and thus water holding capacity. Increased water holding capacity should increase water availability which will decrease rates of SOM decomposition and further increase plant productivity.

Previous work in Tuolumne Meadows tested the effects of herbivore exclusion on growth and carbon flux across a hydrological gradient (Wolf, 2017). Fencing treatments were designed to exclude small mammal herbivores in Tuolumne Meadows, including Belding’s ground squirrels (*Urocitellus belding*) and voles (*Microtus* spp.) (Smolen and Keller, 1987). After three years, fenced plots in wetter areas had the greatest change in plant biomass with significantly lower CO₂ efflux than unfenced control plots (Wolf, 2017). Fenced plots had higher overall biomass and higher cover of *Carex scopulorum*, a native sedge species that can produce high belowground biomass. Data from the pilot study indicated that fencing and planting *Carex scopulorum* seedlings may be a viable method for restoring carbon accumulation processes in Tuolumne Meadows, but did not specifically test adding plants and was on a scale too small to test practicable restoration projects (plots were 1 m²).

To clarify the effects of increasing vegetation cover and production and small mammal herbivory on the carbon dynamics of a degraded Sierra Nevada wet meadows on a larger scale, my research addresses the following three questions:

1. Does the planting of the native clonal, rhizomatous sedge, *Carex scopulorum*, increase carbon sequestration in a degraded wet meadow after two growing seasons?
2. Does herbivore exclusion increase the vegetation production and carbon sequestration of a degraded wet meadow?
3. How does carbon exchange vary along a soil moisture gradient in a degraded wet meadow?

STUDY AREA

Tuolumne Meadows (37.874°N, -119.377°W) is in the eastern portion of Yosemite National Park in the Sierra Nevada, California (Figure 2). At 2621 m elevation and with a total area of 5.3km², it is one of the largest high elevation meadows in the southern Sierra Nevada. The meadow is in a glacially carved valley and a layer of highly organic soil overlays alluvial gravel and sand (Loheide et al., 2008). The meadow vegetation is groundwater-dependent with inputs from spring snowmelt that recharge lateral moraine hillslopes (Loheide et al., 2008). In 2017, average daily air temperature during the growing season varied from -1.3 to 13.8 °C. Lodgepole pine (*Pinus contorta*) dominates dry upland slopes, bunch grasses (*Deschampsia cespitosa* and *Calamagrostis breweri*) and tundra aster (*Oreostemma alpigenum*) dominate more mesic areas, and sedges (*Carex scopulorum* or *Carex vesicaria*) and the rushes (*Juncus balticus* or *Juncus mexicanus*) occupy the wettest low-lying areas (all plant species nomenclature follows Botti and Sydoriak, 2001).



Figure 2. Study site location. Tuolumne Meadows in Yosemite National Park, California

METHODS

Experimental Design and Implementation

The effects of *Carex* seedling planting and herbivory were evaluated in a two by two factorial field experiment that tested two independent variables: small mammal exclusion (yes and no) and planting *Carex scopulorum* seedlings (4 plants/m² and no planting). Five study blocks each containing the four plot types were randomly generated in ArcGIS and located in lowland portions of western Tuolumne Meadows dominated by *Oreostemma alpigenum*. Each plot contained one of the four possible permutations of the two treatments (i.e. fencing and planting). Unplanted plots were 121 m² while planted plots were 283.5 m² (Figure 3). Two subplots were established within each plot for measuring greenhouse gas fluxes. Five reference subplots were established approximately 100 m west of experimental plots in a wetter area of the meadow with denser *Carex scopulorum* dominated vegetation.

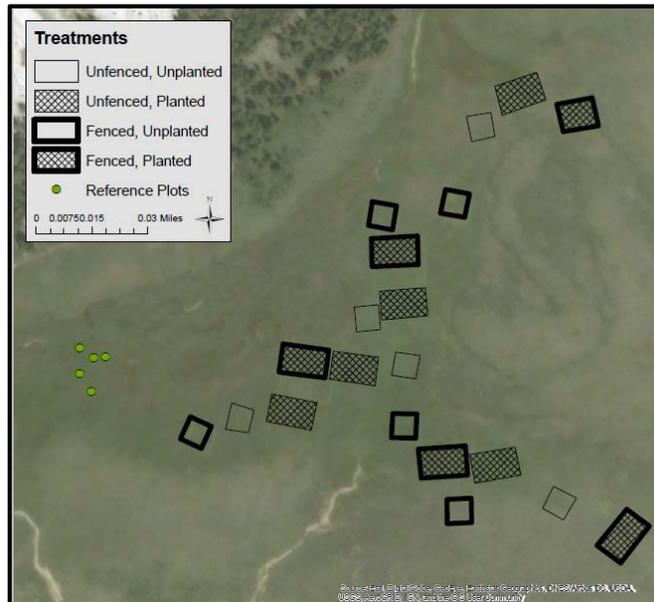


Figure 3. Experimental design. Plot locations and treatments in Tuolumne Meadows

Carex scopulorum seedlings were grown from seed collected within a 15-mile radius of Tuolumne Meadows by Cornflower Nurseries in Sacramento, CA. The plants were grown in 16.5 cm³ SC7 Stubby Ray Leach cone-tainers in a growing media of peat moss, vermiculite, and perlite at a rough ratio of 2:3:1 with added 15-5-10 fertilizer, Dolomite AG 6.5, zinc phosphate, and micro nutrients. Approximately 1,000 seedlings were installed in each planted plot in late June 2016 at a density of four plants/m² for a total of 9,555 planted seedlings.

To exclude small mammal herbivores, galvanized steel 0.64 cm hardware cloth was installed around the fenced plots creating a 31 cm tall fence with a 15 cm wide section flat on the ground to deter tunneling herbivores. Approximately 15 cm wide metal flashing was installed on the top of the fencing to deter small mammals from climbing over.

Measuring ecohydrological conditions and carbon flux

Volumetric water content (VWC) and soil temperature were measured weekly from July 5th to September 30th, 2017 at each plot with a Spectrum Technologies Field Scout TDR 100 Soil Moisture Meter and a Fisher Scientific Thermometer respectively (Hatfield et al., 2005). Three VWC measurements on the perimeter of the subplot at an averaged depth of 0-12 cm were averaged and compared to VWC measurements at soil saturation to calculate percent soil saturation (PSAT). A continuously logging photosynthetically active radiation (PAR) smart sensor (Hobo External Data Loggers, Onset Computer Corporation, Bourne, MA, USA) attached to the fence of a central plot and three soil temperature sensors (Apogee Instruments, Logan, Utah, USA) buried at a depth of 12 cm within plots at the three corners of the study area recorded hourly measurements of PAR and soil temperature. Visual estimates of bare ground, litter, rock, bryophyte, and vascular plant species cover were conducted for each plot at peak standing biomass from August 17th-24th, 2017.

Carbon dioxide fluxes were measured weekly at each subplot to calculate ecosystem respiration (ER) and gross primary production (GPP) from July 5th -September 30th, 2017. The first measurement was determined by the date of snowmelt and access to the meadow study area. Flux was measured using a clear acrylic chamber (61 cm tall by 61 cm diameter) and an EGM-4 portable infrared gas analyzer (PP Systems, Amesbury, MA, USA). The EGM-4 probe recorded PAR and air temperature for every flux measurement. Because the study was conducted in a federal wilderness area, the installation of permanent gas chamber bases (collars) was not permitted. Before each measurement, the chamber was tilted from the ground to allow the circulation of fresh air and then placed snugly against the flat. A 10 cm wide ring of 6 mm thick plastic sheeting was attached to the bottom edge of the chamber and weighed down with jack chain to create a seal between the chamber and ground. Because Tuolumne Meadows is fairly flat and conditions were saturated for most of the 2017 season, we were confident that this method effectively sealed the chamber.

Each flux measurement taken with the clear chamber represents the combination of ER and GPP, or net ecosystem exchange (NEE) (Wilson et al., 2016). Measurements with an opaque cover followed clear chamber measurements, representing only ER. The difference between ER and NEE was used to calculate GPP (Wilson et al., 2016; Waddington and Roulet, 2000).

Over the course of the 2017 season, shade cloths limiting incoming PAR by 70%, 40%, and 10% were used twice at each subplot to quantify the relationship between GPP and PAR. Measuring GPP at different levels of light was used to generate a light response curve to create a robust model of GPP (Munir et al., 2014). The shade cloths were used at all the subplots at peak standing biomass and either early or late in the growing season.

Data Analysis

Modeling carbon dioxide fluxes

We used models adapted from Millar et al. (2017) to estimate growing season GPP and ER at all plots. Gross primary production (GPP) ($\text{g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$) was modeled as a function of PAR, percent soil saturation (PSAT), percent vascular cover at peak biomass (VPC), and the running average of soil temperature (three weeks before and one week after the sampling date) (RAV) as a proxy of seasonality. A rectangular hyperbola models the response of GPP to incoming PAR while a Gaussian function describes the relationship between GPP and percent soil saturation. A Gaussian function is also used to model soil temperature as the seasonality term, allowing the GPP model to track changes in plant growth associated with the season. A sigmoidal function models the response of GPP to VPC.

$$1) \ GPP_i = \frac{A_{max} * \alpha * PAR_i}{A_{max} + \alpha * PAR_i} * e^{-0.5 \left(\frac{RAV_i - RAV_{optGPP}}{RAV_{devGPP}} \right)^2} * e^{-0.5 \left(\frac{PSAT_i - PSAT_{optGPP}}{PSAT_{devGPP}} \right)^2} * \left(1 - e^{-1 * \left(\frac{VPC}{Va} \right)^{Vb}} \right)$$

The parameter A_{max} ($\text{g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$) represents a theoretical maximum rate of GPP and α ($\text{g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$) represents the light use efficiency of the system. RAV_{optGPP} ($^{\circ}\text{C}$) represents the optimum value of RAV for GPP and RAV_{devGPP} represents the standard of deviation for the function. Similarly, $PSAT_{optGPP}$ (%) represents the optimum value of percent soil saturation for GPP and $PSAT_{devGPP}$ represents the standard of deviation for the function. The parameter Va controls the shape of the sigmoidal function relating vascular cover to GPP while parameter Vb influences the size or scale.

Ecosystem respiration (ER) ($\text{g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$) was modeled as a function of air temperature, percent soil saturation, and RAV as a proxy of seasonality. A modified Van't Hoff equation was used to model the exponential increase of respiration in response to changes in air

temperature. Gaussian functions were used to model the response of ER to both PSAT and soil temperature similar to the GPP model. A sigmoidal function models the response of ER to VPC.

$$ER_i = R_{10} * Q_{10}^{\left(\frac{ST_i - 10}{10}\right)} * e^{-0.5\left(\frac{PSAT_i - PSAT_{optER}}{PSAT_{devER}}\right)^2} * \left(1 - e^{-1 * \left(\frac{VPC}{Vc}\right)^{Vd}}\right)$$

The parameter R_{10} ($\text{g CO}_2\text{-C m}^{-2} \text{ hr}^{-1}$) represents the rate of ecosystem respiration with soil temperature at 10°C with all other factors being nonlimiting. The parameter Q_{10} represents the rate of change in ER per increase of 10°C in soil temperature. RAV_{optGPP} ($^\circ\text{C}$) represents the optimum value of RAV for respiration and RAV_{devER} represents the standard of deviation for the function. Similarly, $PSAT_{optER}$ (%) represents the optimum value of percent soil saturation for GPP and RAV_{devER} represents the standard of deviation for the function. The parameter Vc controls the shape of the function relating vascular cover to ER while parameter Vd influences the scale.

Developing the model

Models were fit to data from the 2017 growing seasons using Bayesian methods in R Statistical Software. Markov chain Monte Carlo (MCMC) analysis in the *rjags* package for R was used to estimate model parameters (Plummer, 2011). Four chains were used with 100,000 total iterations with burn-in after 30,000 iterations. Vague priors were used for all model parameters. Gamma with shape and rate parameters equal to 0.001 were used as priors for both A_{max} and α . Uniform distributions with limits from 0 to 30 were used as priors for both RAV_{optGPP} and RAV_{devGPP} and were used as priors with limits from 0 to 100 for both $PSAT_{optGPP}$ and $PSAT_{devGPP}$. Uniform distributions with limits from 0 to 100 were used as priors for both Va and Vb . Gamma distributions with shape and rate parameters equal to 0.001 were used as priors for R_{10} and Q_{10} . Uniform distributions with limits from 0 to 100 were used as priors for Vc and

Vd and for both $PSAT_{optER}$ and $PSAT_{devER}$. The Gelman-Rubin diagnostic was run on both models to confirm model convergence (Gelman and Rubin, 1992).

Table 1. Mean posterior estimated model parameters with standard of deviation and goodness of fit

Gross Primary Productivity		Ecosystem Respiration	
A_{max}	4.27 (0.93)	Q_{10}	2.58 (0.18)
α	0.0084 (0.0084)	R_{10}	0.42 (0.070)
Va	76.46 (16.58)	$Psat_{optER}$	80.67 (1.65)
Vb	0.63 (.044)	$Psat_{devER}$	22.14 (2.17)
RAV_{optGPP}	25.98 (2.60)	Vc	43.35 (28.55)
RAV_{devGPP}	8.78 (1.08)	Vd	0.37 (0.14)
$Psat_{optGPP}$	74.13 (9.75)		
$Psat_{devGPP}$	55.11 (17.49)		

Simulating growing season carbon dioxide fluxes

After model parameters were estimated, GPP and ER models were run for each plot for the period from July 11th to September 26th, 2017. Hourly air temperature, soil temperature, and PAR data were used to drive the model. Single measurements of VPC at peak biomass were used as model inputs for each plot. A cubic polynomial was fit to the weekly PSAT data to extrapolate hourly values of soil moisture at each plot for the GPP and ER models (all R^2 at least 0.70). Daily and growing season ER and GPP flux totals were calculated using MCMC with a total of 6000 iterations and burn in after 3000 iterations. NEE growing season estimates were calculated as the difference between estimated ER and GPP.

A factorial ANOVA accounting for random effects of block and plot location was used to determine if any statistically significant differences in growing season estimates of NEE, GPP, and ER exist between treatment and reference plots. Using the lme4 package in R (Bates, et al. 2015), we developed linear regression models to compare growing season flux estimates of ER, GPP, and NEE to average PSAT, average soil temperature, and percent vascular plant cover. All data analysis was conducted in R statistical software.

RESULTS

Ecohydrological conditions

In 2017, average daily soil and air temperature both increased through May and June, peaked at 16.4 °C and 19.1 °C respectively in early July, and then decreased through September (Figure 4). Peak daily PAR decreased from July until September (Figure 4) and varied from 836 $\mu\text{molm}^{-2}\text{sec}^{-2}$ to 2153 $\mu\text{molm}^{-2}\text{sec}^{-2}$ with variable cloud cover (Figure 4). Smoke from nearby wildfires during the 2017 season also potentially lowered PAR values at various times during the summer (Tang et al, 1996; Davies and Unam, 1999; Roderick et al., 2001). Soil moisture and the water table were highest in the early summer following snowmelt and decreased over the growing season. Both of these variables increased during and just after summer precipitation events. There were no significant differences in PSAT between treatment types over the 2017 growing season ($p > 0.05$); however, unfenced, planted plots had higher soil moisture than fenced, planted plots when considering the plots at just peak biomass (8/14/17-8/18/17) ($p = 0.0491$). VPC and percent *Carex scopulorum* cover varied between plots, but there were no significant differences between treatments (Figure 5). Reference plots had higher VPC and percent cover of *Carex scopulorum* than all treatment plots ($p < 0.05$). There was no significant correlation between average percent soil saturation content and vascular plant cover ($p = 0.65$).

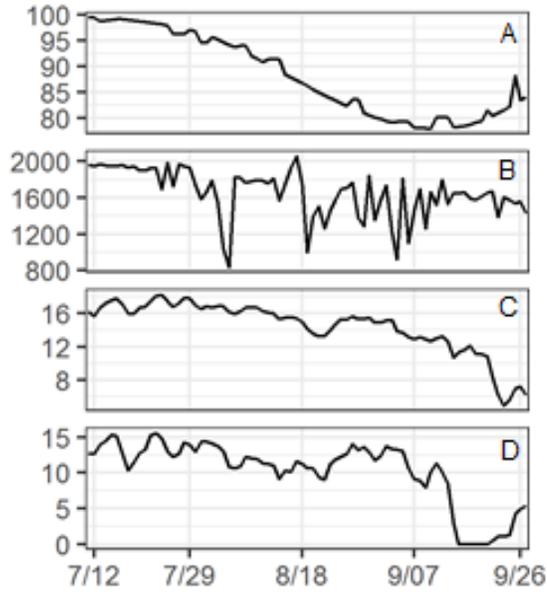


Figure 4. 2017 Ecohydrological conditions. Ecohydrological conditions in Tuolumne Meadows for the period of model estimates. A. Mean percent soil saturation (%); B. Daily peak photosynthetically active radiation (PAR) ($\mu\text{molm}^{-2}\text{sec}^{-2}$); C. Mean soil temperature ($^{\circ}\text{C}$); D. Air temperature ($^{\circ}\text{C}$).

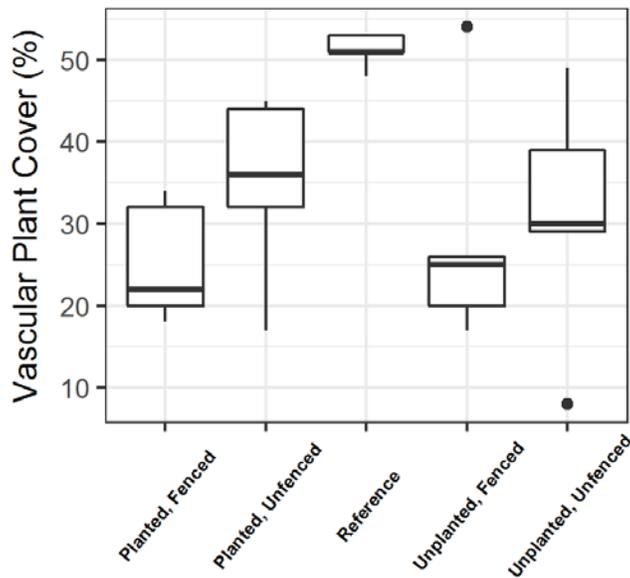


Figure 5. 2017 vascular plant cover. Mean vascular plant cover during peak biomass for each treatment. Dots represent outliers, the dark line inside a box represents the median. The top of the box is the 75% quantile and the bottom of the box is the 25% quantile. The end points of the lines are at a distance between the 25th and 75th percentiles.

Measured carbon dioxide exchange

In 2017, rates of GPP and ER both increased throughout July, peaked at -2.02 and 1.03 g CO₂-C m⁻² hr⁻¹, during the week of August 14th when plants were at maximum standing biomass, and declined to 0 g CO₂-C m⁻² hr⁻¹ by the end of September. NEE decreased during the beginning of the season, reached its lowest rate of -1.25 g CO₂-C m⁻² hr⁻¹ in early August and increased to 0 g CO₂-C m⁻² hr⁻¹ by the end of September. Rates of ER, GPP, and NEE all significantly increased with increasing soil temperature ($p < 0.0001$). Rates of GPP and NEE significantly increased with increasing PSAT ($p < 0.0001$). Rates of GPP and NEE both increased with increasing PAR.

Simulated carbon dioxide exchange

Modeled GPP values matched measured values with an R² of 0.65 (Figure 6) and the ER model had an R² of 0.47 (Figure 7). All plots were net C sources during the 2017 growing season (Table 2). The models of ER and GPP both tended to overestimate flux values at the beginning and end of the growing season, while underestimating flux values during peak biomass (Figures 9 and 10).

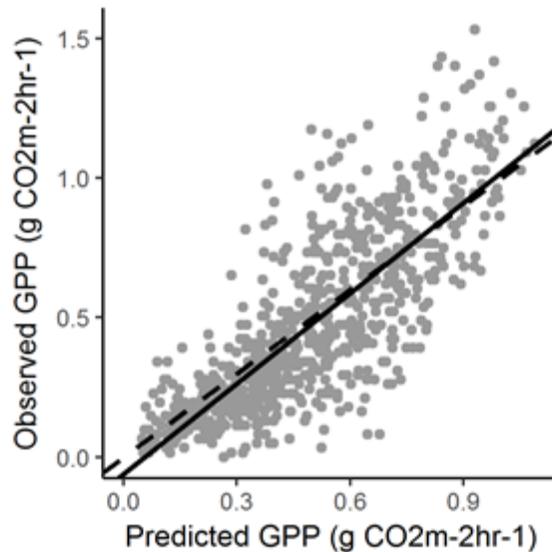


Figure 6. Observed vs. predicted values of GPP. Observed values of Gross Primary Productivity vs. values predicted from the GPP model for the 2017 season. Best fit line is solid: $y = 1.08x - 0.060$ and $R^2=0.64$. Dashed 1:1 line

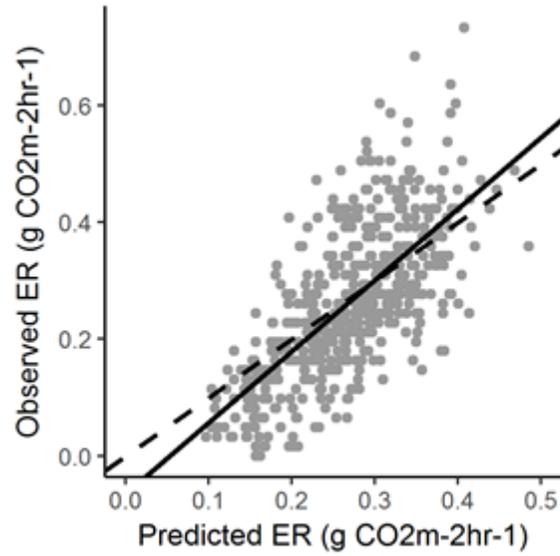


Figure 7. Observed vs. predicted values of ER. Observed values of Ecosystem Respiration for the 2017 growing season vs. values predicted from the GPP model. Best fit line is solid; $y = 1.22x - 0.065$ and $R^2 = .47$. Dashed 1:1 line

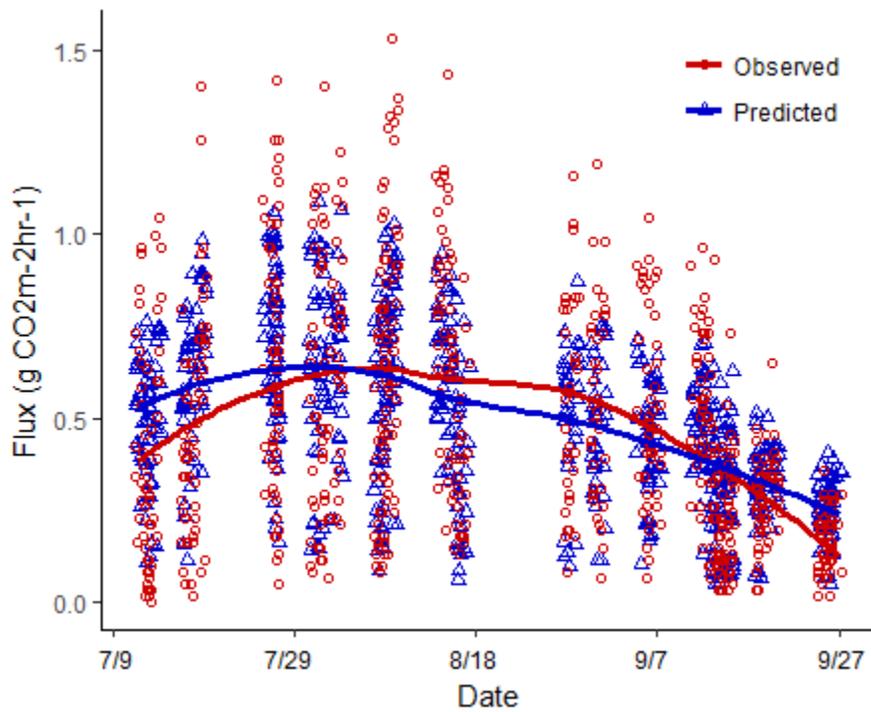


Figure 8. Observed and predicted flux data points of GPP over the growing season. Lines represent a locally weighted regression to clarify the difference between observed and predicted values over time.

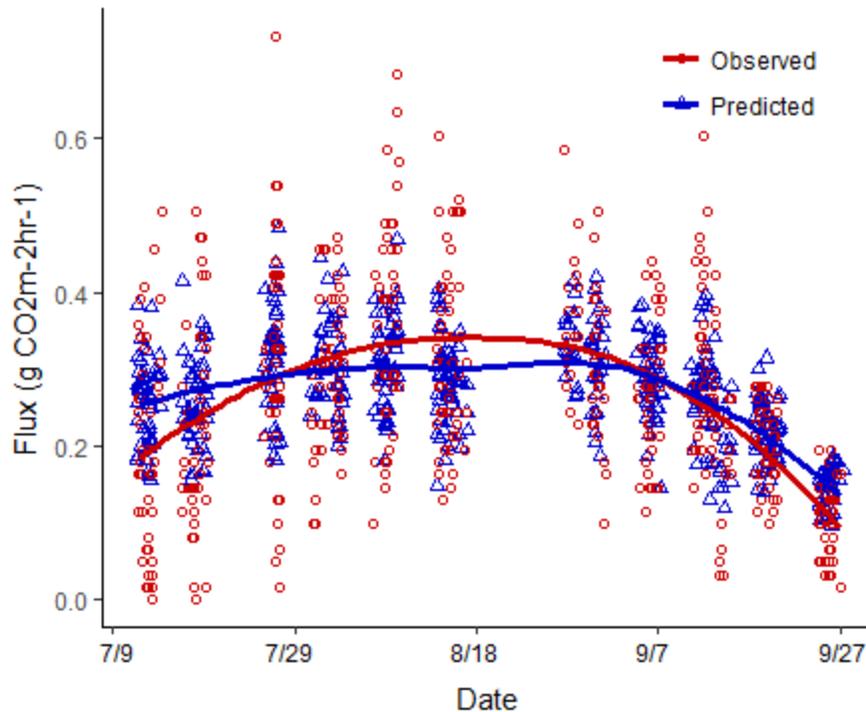


Figure 9. Observed and predicted flux data points of ER over the growing season. Lines represent a locally weighted regression to clarify the difference between observed and predicted values over time.

There were no statistically significant differences in growing season flux estimates of GPP, ER, or NEE between treatment types (Figure 10). Although fencing and planting had no effect on carbon flux during the second summer of this experiment, percent vascular plant cover at peak biomass (VPC) was positively correlated to estimates of ER ($p = 0.00013$) and GPP ($p = 7.51e^{-15}$) and negatively correlated to NEE ($p = 0.012$) (Figure 11). This relationship between VPC and flux rates indicated that if total vegetation cover increases due to growth of the planted seedlings, there would be concomitant increases in carbon sequestration. Average growing season PSAT was positively correlated to estimates of ER and NEE ($p = 0.036, 0.012$) indicating that carbon exchange varies along a water availability gradient (Figure 12). More carbon is lost through ER in drier areas and net losses of carbon (NEE) are less in wetter areas.

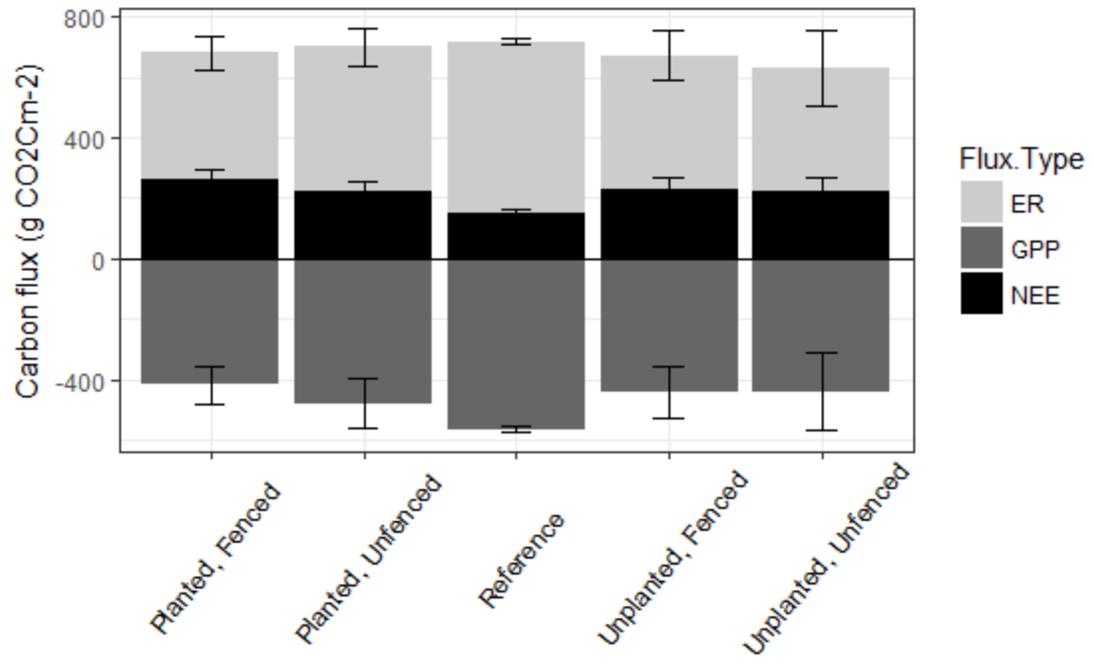


Figure 10. Average growing season flux estimates. Standard error included for each treatment

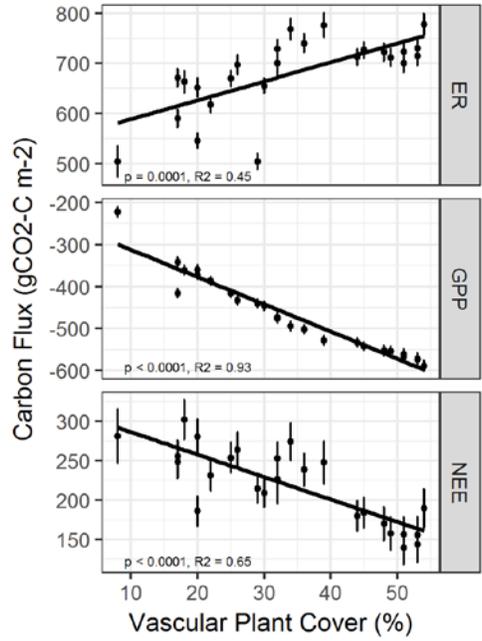


Figure 11. Flux estimates and percent vascular plant cover. Growing season carbon flux estimates versus percent vascular plant cover at peak growing biomass for each plot. Each point represents the carbon flux estimate for a plot for the growing season and the vascular cover at peak biomass

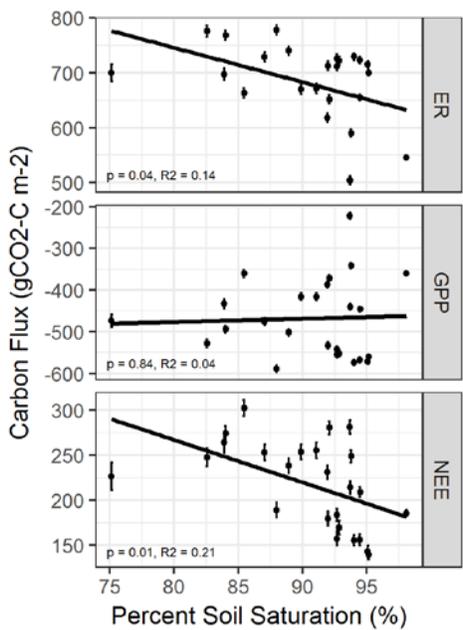


Figure 12. Flux estimates and soil saturation. Growing season carbon flux estimates versus growing season average percent soil saturation for each plot. Each point represents the carbon flux estimate for a plot for the growing season and the average PSAT for that plot. Estimates of ER and NEE decrease with increasing PSAT

Table 2. Growing season estimates of ER, GPP, NEE, and PSAT (± 1 standard of deviation). Peak VPC are included

Plot	Treatment	ER (gCO ₂ -Cm ⁻²)	GPP (gCO ₂ -Cm ⁻²)	NEE (gCO ₂ -Cm ⁻²)	Vascular Plant Cover (%)	PSAT (%)
11	Fenced, Unplanted	545 \pm 15.2	-359 \pm 11.1	186 \pm 18.8	20	98.1 \pm 3.16
12	Fenced, Unplanted	778 \pm 21.2	-588 \pm 12.6	189 \pm 24.8	54	87.9 \pm 8.48
13	Fenced, Unplanted	697 \pm 19.9	-433 \pm 10.2	264 \pm 22.3	26	83.9 \pm 11.2
14	Fenced, Unplanted	671 \pm 17.3	-415 \pm 9.9	256 \pm 20.1	17	91.1 \pm 8.85
15	Fenced, Unplanted	669 \pm 16.9	-416 \pm 10.2	254 \pm 19.6	25	89.9 \pm 8.2
21	Unfenced, Unplanted	655 \pm 15.0	-445 \pm 10.1	209 \pm 17.8	30	94.5 \pm 5.58
22	Unfenced, Unplanted	711 \pm 17.8	-554 \pm 11.7	157 \pm 21.2	49	92.7 \pm 7.95
23	Unfenced, Unplanted	776 \pm 24.5	-528 \pm 11.6	248 \pm 27.3	39	82.6 \pm 10.0
24	Unfenced, Unplanted	503 \pm 15.0	-440 \pm 9.9	214 \pm 18.0	29	93.7 \pm 7.01
25	Unfenced, Unplanted	503 \pm 31.8	-222 \pm 12.9	281 \pm 34.5	8	93.7 \pm 7.73
41	Unfenced, Planted	712 \pm 16.4	-532 \pm 10.5	180 \pm 19.5	44	91.9 \pm 7.98
42	Unfenced, Planted	590 \pm 17.5	-341 \pm 11.0	249 \pm 20.9	17	93.8 \pm 6.69
43	Unfenced, Planted	729 \pm 18.3	-476 \pm 9.8	253 \pm 20.7	32	87.0 \pm 8.81
44	Unfenced, Planted	726 \pm 16.7	-542 \pm 10.6	184 \pm 19.7	45	92.7 \pm 6.95
45	Unfenced, Planted	740 \pm 17.9	-501 \pm 9.8	239 \pm 20.5	36	88.9 \pm 8.22
61	Fenced, Planted	651 \pm 19.4	-371 \pm 10.9	280 \pm 22.4	20	92.1 \pm 7.32
62	Fenced, Planted	700 \pm 28.8	-473 \pm 12.8	227 \pm 31.5	32	75.1 \pm 15.3
63	Fenced, Planted	768 \pm 21.0	-494 \pm 10.7	274 \pm 23.5	34	84.0 \pm 8.54
64	Fenced, Planted	617 \pm 16.3	-386 \pm 10.3	231 \pm 19.2	22	91.9 \pm 7.71
65	Fenced, Planted	663 \pm 22.1	-360 \pm 11.3	302 \pm 24.9	18	85.5 \pm 8.87
90	Reference	723 \pm 19.3	-567 \pm 11.5	156 \pm 22.4	51	94.5 \pm 6.5
91	Reference	700 \pm 18.1	-560 \pm 12.1	139 \pm 21.7	51	95.1 \pm 5.2
92	Reference	729 \pm 19.1	-574 \pm 12.5	156 \pm 22.9	53	94.0 \pm 6.09
93	Reference	715 \pm 19.0	-571 \pm 12.3	143 \pm 22.7	53	95.1 \pm 6.42
94	Reference	722 \pm 17.6	-552 \pm 11.2	170 \pm 20.9	48	92.9 \pm 7.78

DISCUSSION

Carbon flux responses to planting and fencing

Our results indicate that Tuolumne Meadows was a net source of CO₂ to the atmosphere throughout the 2017 growing season. Modeled fluxes were similar to those observed in an unrestored cutover peatland in Alberta (Strack et al., 2014), a low elevation fen in Wyoming (Millar et al., 2017), and a rewetted temperate fen in north-eastern Germany (Gunther et al., 2014).

Fencing and planting have not yet had a significant effect on total plant cover or percent cover of *C. scopulorum* in the second summer after implementing the treatments. The 2016-2017 winter was particularly long with very deep snow that likely negatively impacted small mammal herbivore populations (Michener and Michener, 1977; Sherman and Morton, 1984). Many ground squirrels were observed in the area in the summer of 2016, but only one ground squirrel was observed in 2017. Their potential population decline could have precluded differences in plant productivity or survival between fenced and unfenced plots. Furthermore, plant growth in Tuolumne Meadows is limited by the short growing season which has cold nights and cool day time temperatures, harsh winters, and persistent cold soils. It will likely take several more years for the planted *C. scopulorum* seedlings to significantly affect total plant cover, in contrast with lower elevation fens and wet meadows in the Rocky Mountains where plant cover peaked within 4 years (Cooper et al., 2017). The Tuolumne sites should continue to be monitored to evaluate long-term restoration progress.

By including reference plots that had greater canopy cover of *C. scopulorum* it was possible to examine the relationship between CO₂ fluxes and plant cover. Daily and growing

season estimates of GPP and ER increased with increasing vascular plant cover at peak biomass (VPC) (Figure 11).

Carbon flux and water availability

There was no significant relationship between growing season GPP estimates and average PSAT in 2017. This may be due to the fact that the record high snowpack of 2017 sustained a shallow water table throughout the summer with average PSAT being approximately 50% higher than 2016. In future years, average or below average snowpack and snowmelt could cause the spatial variability of PSAT to increase across Tuolumne Meadows during the growing season so that the relationship between GPP and PSAT becomes significant. Water level drawdown significantly decreased GPP in a Finnish fen (Riutta et al., 2007), suggesting that drier years could lead to lower productivity in Tuolumne Meadows.

Growing season estimates of ER decreased with increasing average soil PSAT in 2017. Similarly, drainage of peatlands in northern Finland and northern Alberta led to increased ecosystem respiration and CO₂ emissions in both systems (Martikainen et al., 1995; Munir et al., 2014). In future drier years the effect of PSAT on ER could be exacerbated resulting in much higher rates of ER and CO₂-C efflux. Although there was no discernible response of GPP to soil PSAT, the strong decline in ER due to increases in PSAT resulted in lower net CO₂-C efflux. This is similar to results for a Colorado subalpine fen where lower water tables were correlated with decreasing rates of NEE or higher net CO₂-C effluxes (Chimner and Cooper, 2003).

Effects of a changing climate on carbon flux

Climate change is predicted to severely impact wetland ecosystems and their carbon storage functions through changes in temperature and water availability (Erwin, 2008; Davidson and Jansen, 2006). In the Sierra Nevada, temperatures are predicted to rise between 3.9 and

5.6°C and snow cover for the month of April is projected to decrease by 48% by 2100 (Walton et al., 2017). Our results indicate that increased temperature can increase rates of ER and GPP, while reduced PSAT increases the rate of ER and decreases GPP, resulting in higher overall rates of NEE flux to the atmosphere.

Experimental warming of High Arctic tundra led to increased rates of ER and GPP with the rate of ER increase exceeding that of GPP (Welker et al., 2004) and, in fens in northern Canada, modeled flux rates under various climate change scenarios suggested that the wetlands became carbon sources with higher temperatures (Cai et al., 2010). Over the 2017 growing season, point measurements of ER and GPP increased with increasing soil and air temperature. Estimates of growing season GPP increased with average soil temperature while there was no relationship between ER estimates and average soil temperature. NEE decreased with increasing temperature indicating that the response of GPP to changes in temperature outweighs the response of ER. However, it is possible that warming due to climate change would push the temperature to a point where ER has a stronger response to the temperature changes.

Rising air temperatures affect soil water availability due to increased evapotranspiration rates (Barnett et al., 2005; Blankinship and Hart, 2014) and earlier snowmelt (Walton et al., 2017; Mote, 2006). Reduced annual precipitation will further reduce soil water availability especially in the Sierra Nevada where summer rainfall is unpredictable and rainless periods of many weeks can occur during the summer (Seager et al., 2007; Walton et al., 2017). Our results are consistent with other studies that have demonstrated the dependence of NEE on water table depth or soil volumetric water content (Riutta et al., 2007; Martikainen et al., 1995; Altor and Mitsch, 2016). Future drier growing seasons could lead to lower GPP and increased rates of ER, leading to increased decomposition of SOM and overall greater effluxes of CO₂-C. Severe

climate change could even push pristine wetlands into net carbon losing systems (Chivers et al., 2009; Welker et al., 2004), therefore it is vital to preserve and restore these potential carbon sources.

Potential improvements and model limitations

Although our GPP model produced flux estimates within a reasonable range, it could be improved in future work by replacing the running average of soil temperature by a term that more directly tracks seasonality and plant cover such as NDVI or greenness area (Riutta et al., 2007). NDVI was not used for the 2017 model due to wildfire smoke interfering with satellite imagery. This issue could be avoided in future years by using a camera to monitor site greenness throughout the growing season. Although the measurement of percent vascular cover at peak biomass was correlated with rates of GPP and ER at each time step, weekly measurements would improve both the GPP and ER model. Future ER modeling would be made more robust by measuring gas fluxes at night and collecting and including data on pH and soil texture. Soil pH can influence ER due to its effect on soil microbial activity and could be measured to account for variability across the landscape (Luo et al., 2006). Soil type or texture can also influence rates of ER (Cable et al., 2008; Lohila et al., 2002; Augustin and Cihacek, 2016). Most importantly, continued *in situ* gas flux measurements are necessary to continue informing and calibrating the model as site conditions change over time, to accurately inform future management decisions associated with restoration activities.

Our model calculates flux estimates for the growing season yet is not fully representative of annual carbon budget estimates. In some cases, winter C emissions have been reported to be low (Koch et al., 2008) and not a significant contributor to the overall carbon budget of an ecosystem (Oertel et al., 2016). Others have reported that although winter time ecosystem C

fluxes may be small, they still have meaningful impacts on annual budgets (Aurela et al., 2002; Sommerfeld et al., 1993; McDowell et al., 2000; Goulden et al., 1996). Additional CO₂ sampling outside of the growing season would be necessary to develop an annual budget of CO₂ flux from Tuolumne Meadows.

CONCLUSIONS

Tuolumne Meadows has not recovered from legacy disturbance impacts and the soil is continuing to lose carbon and act as a C source to the atmosphere. The clear relationship between vascular plant cover and C sequestration suggests that planting is a critical restoration method for restoring soil organic C and reverting the meadows to a C sequestering system. The Meadows are functioning as a C source in the second summer after planting. It is likely that our vegetation-based restoration method may take several years to affect the overall C balance in Tuolumne. However, decreased water availability and increased temperatures may limit the future potential for plant growth and C sequestration in Sierra Nevada meadows. It is also possible that these ecosystems may have already passed an ecological tipping point and are not restorable. More data from years with differing ecohydrological conditions and increased vegetation cover will help calibrate the model and enable its use as a predictive tool to determine the potential success of planting *C. scopulorum* as a restoration method.

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