

THESIS

ESTABLISHING CAREX SCOPLUORUM SEEDLINGS TO RESTORE THE VEGETATION OF TUOLUMNE
MEADOWS, YOSEMITE NATIONAL PARK, USA

Submitted by:

Melissa Booher

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

Master's Committee:

Advisor: David Cooper

Troy Ocheltree
Monique Rocca

Copyright by Melissa Booher 2018

All Rights Reserved

ABSTRACT

ESTABLISHING CAREX SCOPLUORUM SEEDLINGS TO RESTORE THE VEGETATION OF TUOLUMNE MEADOWS, YOSEMITE NATIONAL PARK, USA

Wet meadows are critically altered and at-risk ecosystems globally and in the Sierra Nevada of California. The low vegetation cover created by legacy disturbances is a restoration priority due to the importance of organic-rich soils for future plant establishment, carbon storage, and water retention. Wet meadows are characterized by seasonally saturated fine-textured mineral soils with significantly more organic matter than surrounding areas, shallow groundwater (< 1 m), and vegetation dominated by herbaceous plant species. This research focused on the establishment requirements of seedlings of the native sedge *Carex scopulorum* in Tuolumne Meadows, Yosemite National Park, USA. I provide critical information on biomass contribution of a key wet meadow species that could also be used in other restoration efforts in similarly degraded subalpine meadows. We tested the suitability of this species for use in future restoration work and assessed the growth of *C. scopulorum* seedlings in a fully factorial experiment with small mammal herbivore exclosures and planting density treatments. Seedlings were planted in June 2016 and survival was high, approximately 98%, living through the summer of 2016 and 71% surviving through the end of the 2017 summer. After two seasons of growth, planted seedlings more than doubled in area (horizontal tiller spread) and nearly doubled their longest leaf lengths. Total *C. scopulorum* seedling biomass increased more than six-fold from the delivered seedlings in 2016 to end of the 2017 growing season. *Carex*

scopulorum seedlings had greater mean biomass, $703.44 \text{ g/m}^2 \pm 246.54$, than all other species in our study plots and had more than twice the belowground biomass per unit area of other herbaceous species sampled. In addition, planted *C. scopulorum* seedlings allocated a greater portion of their biomass below-ground (higher mean ratio) than all herbaceous species (all comparisons $p = <0.05$) other than *Carex subnigricans* ($p = 0.051$). Our results indicate that *C. scopulorum* is an appropriate species for restoration in Tuolumne Meadows where increasing biomass inputs to the system is a priority and could be a valuable tool for revegetation and restoration of other degraded meadows in the Sierra Nevada.

ACKNOWLEDGEMENTS

Thank you first and foremost to my advisor David Cooper. I am grateful for the opportunity you provided me to work and develop my skills in an ecosystem and landscape I love. Many thanks to present and former Resource Management and Science employees of Yosemite National Park. The staff of the Vegetation and Ecological Restoration branch, including but not limited to Sue Beatty, Tim Kuhn, Athena Demetry, Victoria Hartman, Matt Jones, Linda Mazzu and Rick McNeil, was essential in making this project succeed. Evan Wolf took a lead role in setting up this study, mentoring me in the field, and was always happy to help over the past two years. I greatly appreciate the top-notch field assistance from Micheala Snow in 2017. Thanks to Lydia Baldwin for spending more time with me over the past two years than any other person. I am so fortunate to have had such a sharp and fun research partner. Thank you to the Cooper lab for answering all my questions and supporting my progress. My twin brother, Evan Booher, was my number one editor. Thank you to my committee members, Monique Rocca and Troy Ocheltree for joining in on the fun. Thank you to the Colorado State University Statistics Consulting Lab, specifically Ann Hess for analysis guidance. Thank you to Chris Lizza for graciously sharing his home with us during our 2017 field season. Thank you to all my friends and family for all the support and distractions through this entire process. Thank you to David Campbell for putting up with my move to Colorado and supporting me in my decision to pursue a graduate degree.

TABLE OF CONTENTS

ABSTRACT	ii
ACKNOWLEDGEMENTS	iv
LIST OF TABLES	vii
LIST OF FIGURES	viii
1. INTRODUCTION	1
2. METHODS.....	7
2.1 STUDY SITE	7
2.2 EXPERIMENTAL DESIGN.....	8
2.2.1 EXCLOSURE TREATMENT	8
2.2.2 COMMERCIALLY GROWN SEEDLINGS.....	9
2.2.3 PLANTING DENSITY TREATMENT.....	9
2.3 FIELD MEASUREMENTS	10
2.3.1 TREATMENT EFFECTS	10
2.3.2 ENVIRONMENTAL SITE CONDITIONS.....	11
2.3.3 SPECIES BIOMASS COMPARISONS.....	11
2.4 ANALYSIS.....	12
2.4.1 TREATMENT EFFECTS	12
2.4.2 ENVIRONMENTAL SITE CONDITIONS.....	13
2.4.3 SPECIES BIOMASS COMPARISONS.....	13
3. RESULTS	14
3.1 SITE HETEROGENEITY	14
3.2 SEEDLING SURVIVAL.....	15

3.3 SEEDLING GROWTH	15
3.4 SEEDLING BIOMASS ACCUMULATION	16
4. DISCUSSION.....	18
4.1 SEEDLING SURVIVAL.....	19
4.2 RATE OF CAREX GROWTH AND SPREAD	20
4.3 SEEDLING BIOMASS.....	21
5. CONCLUSION.....	24
TABLES AND FIGURES	25
LITERATURE CITED.....	38

LIST OF TABLES

TABLE 1: SURVIVAL AND GROWTH SUMMARY STATISTICS.....	33
TABLE 2: SEEDLING BIOMASS SUMMARY.....	36

LIST OF FIGURES

FIGURE 1: CONCEPTUAL ILLUSTRATION OF MEADOW.....	25
FIGURE 2: LOCATION OF STUDY SITE.....	26
FIGURE 3: EXCLOSURES.....	26
FIGURE 4: CAREX SCOPULORUM SEEDLINGS PLANTING.	27
FIGURE 5: SEEDLING AREA MEASUREMENT METHOD.	27
FIGURE 6: TILLER GROWTH MEASUREMENT METHOD.....	28
FIGURE 7: BIOMASS CLIPPING METHOD.....	29
FIGURE 8: ABSOLUTE COVER METHOD.....	29
FIGURE 9: BIOMASS CORES METHOD.....	30
FIGURE 10: ABSOLUTE COVER OF SUBSTRATES AND PLANT FUNCTIONAL GROUPS.....	31
FIGURE 11: GROWTH SUMMARY STATISTICS.....	32
FIGURE 12: LINEAR REGRESSION SURVIVAL AND SOIL SATURATION.....	34
FIGURE 13: TILLERING RATE, NEW TILLER NUMBER, AND VWC (%).	35
FIGURE 14: MEAN ABOVEGROUND AND BELOWGROUND TOTAL BIOMASS (G M-2)	36
FIGURE 15: MEAN BELOWGROUND:ABOVEGROUND BIOMASS RATIOS.....	37

1. INTRODUCTION

All ecosystems on Earth, including those in wilderness areas, have experienced pervasive human influence (Vitousek et al. 1997). The Wilderness Act of 1964 was established and now protects over 44 million ha of land in the U.S. from most human caused degradation. The paradox of maintaining untrammelled landscapes, while concurrently managing lands to restore or preserve ecosystems, complicates restoration planning and implementation (Cole 2000; Throop and Purdom 2006; Watson et al. 2015). Ecological value is a key component of the designation of wilderness. Wetlands provide a myriad of values, including biological productivity, water quality improvement, and carbon sequestration (Junk et al. 2013). Nonetheless, human-induced disturbance in wilderness wetlands exists and restoration is needed to enhance their ecological value for future generations.

Globally, wetlands comprise only 6% of terrestrial ecosystems (Junk et al. 2013), yet they provide critical ecosystem services, including flood attenuation, erosion control, water storage and filtration, habitat for threatened and endemic species, and carbon sequestration (Morton and Pereyra 2010; Ratliff 1985; Smith et al. 1995; Viers et al. 2013). Wet meadows are characterized by seasonally saturated fine-textured mineral soils with significantly more organic matter than surrounding areas (Pyrooz et al. 2015), shallow groundwater (< 1 m), and vegetation dominated by herbaceous plant species (Weixelman et al. 2011). Groundwater dynamics can determine an ecosystem's hydrologic functioning (Ratliff 1985; Weixelman et al. 2011), soil moisture (Loheide et al. 2009), and influence its vegetation composition (Allen-Diaz 1991; Hammersmark et al. 2009; Lowry et al. 2011; McIlroy and Allen-Diaz 2012).

Wet meadows are one of the most altered and at risk ecosystems, largely due to their extensive disturbance history, including grazing, ditching, mining, logging, and infrastructure development (Loheide et al. 2009; Viers et al. 2013). Present-day impacts are apparent over a range of spatial and temporal scales and include livestock and pack stock grazing (Cole et al. 2004; Ostoja et al. 2014; Walden-Schreiner et al. 2017), meadow fragmentation (Holmquist, Schmidt-Gengenbach, and Ballenger 2014), and climate change (Arnold, Ghezzehei, and Berhe 2014; Vale 1987).

Wet meadows comprise only approximately 3% of the landscape in the Sierra Nevada of California, and significant reductions in their functioning have been reported due to multiple factors, such as disturbance history and climate change (Fryjoff-Hung and Viers 2012). In many Sierra meadows, sparse cover of sedges and rushes (Norton et al. 2011) and high cover of bare soil indicates an extensive disturbance history (Cole et al. 2004; Cooper et al. 2006; Kuhn et al. 2015; Lee et al. 2017; Ostoja et al. 2014; Ratliff 1985). Climate change is a current stressor with potential for influencing the functioning and persistence of meadows. Air temperature has been steadily rising in California with each of the last three decades being warmer than all previous decades on record (WRCC 2018). Mean annual temperatures in California may be 1-2 °C warmer by 2060 (Hayhoe et al. 2004; Pierce et al. 2013), with increased uncertainty of extreme droughts (Diffenbaugh, Swain, and Touma 2015; Williams et al. 2015) and precipitation (Allen and Luptowitz 2017). High elevation wet meadows have increasingly higher mean annual air temperature and are experiencing earlier onset of snowmelt, signs of accelerated environmental change (Arnold, Ghezzehei, and Berhe 2014). During the drought years of 2012 and 2013, a 6% reduction in total meadow carbon stock was documented in one Sierra Nevada

meadow attributed to increased soil respiration during the prolonged dry summer (Arnold, Ghezzehei, and Berhe 2014). Actively increasing the vegetation cover of degraded meadows could be used to decrease soil carbon loss (Kayranli et al. 2010; Lawrence and Zedler 2013).

The restoration of meadow vegetation is being prioritized by land managers to preserve organic-rich soils for future meadow functioning and plant establishment (Ankenbauer and Loheide 2017; Norton et al. 2011, 2014). A long-term decline of vegetation cover can have cascading effects on plant establishment through changes in soil texture, water availability, and increased losses of organic matter in soils (Figure 1) (D’Odorico et al. 2013; Hobbs et al. 2006; Miller and Bestelmeyer 2016). Native sedge species with high biomass production are ideal for meadow restoration, because their productivity contributes to soil development, increased soil water retention, and increased vegetation cover (D’Odorico et al. 2013; Kayranli et al. 2010; Norton et al. 2011).

Carex scopulorum Holm var. *bracteosa* (L.H. Bailey) F.J. Herm. is a common plant species in high elevation meadows in the western USA (Baldwin and Goldman 2012). Its abundance in mountain landscapes makes *C. scopulorum* a useful species for restoration. It is used as an indicator species in wetland vegetation classifications (Arnold, Ghezzehei, and Berhe 2014; Bowman et al. 1993; Fisk, Schmidt, and Seastedt 1998; Knowles, Blanken, and Williams 2015; Ratliff 1985), and its dominance in stands has been considered an indicator of healthy meadow conditions (Cole 1981). Despite its abundance in subalpine and alpine wet meadows in the western US, there have been relatively few studies of *C. scopulorum* across a variety of natural conditions that influence its distribution, and growth.

Wetland restoration is expensive and planting is often a predominant project cost (Zentner, Glaspy, and Schenk 2003). Experiments introducing *C. scopulorum* seedlings to degraded meadows at multiple planting densities can help land managers determine appropriate plant density for restoration projects. While responses to planting density treatments may operate on a time scale beyond the scope of this study (1.5 years) (Martin and Chambers 2002), they could become significant over time and therefore are important to implement for long-term monitoring. Direct seeding can be more cost effective than planting rooted seedlings, but wet meadow projects have seen greater success using seedlings because many species do not germinate well (Zentner, Glaspy, and Schenk 2003). Planting sedge species as seedlings increases the chances for survival (Roth et al. 1999). The genus *Carex* is known to have notoriously specific germination requirements (Kettenring, Gardner, and Galatowitsch 2006; Van Der Valk, Bremholm, and Gordon 1999).

Grazing by herbivores has been shown to limit the survival of planted seedlings (Fraser and Madson 2008; Gao et al. 2011; Howe et al. 2006; Hulme 2008; Huntly 1991; Wu et al. 2009), or impact plant growth, resulting in increased turnover rates and overall reduced production (Belsky 1986; de Masancourt, Loreau, and Abbadie 1998; Owen and Wiegert 2018). Grazing can also influence plant root to shoot ratios. Below-ground growth can be suppressed by premature defoliation by grazing, leading to reduced allocation of nonstructural carbohydrates to roots and rhizomes (Sarr and Park 2017). Understanding how herbivory influences plant growth is critical to creating successful restoration plans.

Restoration aims to create conditions and establish vegetation that facilitates recovery over time (McDonald et al. 2016). The main mode of reproduction for many plant species may

be changing in today's climate, which could inhibit a damaged ecosystem from recovering. For example, *C. scopulorum* appears to have shifted from a reliance on sexual propagation to clonal propagation in alpine populations studied on Colorado's Niwot Ridge (Forbis 2003; Linhart and Gehring 2003). Genetic analyses of *C. scopulorum* populations confirm genetic heterogeneity between tillers separated by 1-2 m, suggesting a past of significant cross-pollination and sexual reproduction (Linhart and Gehring 2003). Another seedling demography study conducted in the same location recorded a lack of *C. scopulorum* seedlings, indicating a reliance on clonal propagation (Forbis 2003). In degraded areas with large proportions of bare soil, planting seedlings can increase the number of genets from which clonal propagation can occur.

The goal of this research was to assess the fate and contribution of *C. scopulorum* seedlings planted in a portion of Tuolumne Meadows, Yosemite National Park, CA, USA with large areas of bare ground. The establishment requirements of three month old *C. scopulorum* seedlings were evaluated to identify if small mammal exclosures, designed for use in wilderness, significantly affect survival and growth of the seedlings. The revegetation approach involved a fully factorial experiment with minimally intrusive herbivore exclosures around two different *C. scopulorum* seedling planting densities. The establishment and growth of *C. scopulorum* seedlings were analyzed to address the following questions:

1. Do herbivore exclosures affect the survival and growth of *C. scopulorum* seedlings?
2. Does planting density affect the survival and growth of *C. scopulorum* seedlings?
3. How does *C. scopulorum* seedling survival and growth vary along environmental gradients of soil moisture, absolute plant cover, and annual site productivity (ANPP_{site})?

4. How does total *C. scopulorum* biomass production compare to other species in the meadow?
5. Does *C. scopulorum* below-ground biomass allocation compare to other species in the meadow?

2. METHODS

2.1 STUDY SITE

Tuolumne Meadows, at 2,600 m elevation in Yosemite National Park, USA (37°52'36", -119°23'32") (Figure 2) is one of the largest high elevation meadows in the southern Sierra Nevada. Precipitation in the Sierra Nevada is characterized by California's Mediterranean climate with wet winters and dry summers. Between November and March, precipitation above 1,500 m typically occurs as snow. California's snowpack contains about 70% as much water as stored in its reservoirs (Dettinger and Anderson 2015). Snowpack in this region is also critical for sustaining high elevation meadows because groundwater dynamics are mainly controlled by discharge derived from snowmelt (Lowry et al. 2010). Because little precipitation occurs during the summer in the Sierra Nevada, wetland plants rely on shallow ground-water and water held in soils with high organic content for survival during the dry growing season (Cooper et al. 2006; Loheide et al. 2009; Lowry et al. 2011; McIlroy and Allen-Diaz 2012; Ratliff 1985).

The western portion of Tuolumne Meadows is designated Wilderness and is characterized by high bare soil and low below ground plant biomass and production (Cooper et al. 2006). Wet-meadow species in the study area are dependent on groundwater flow, soil water-storage, and capillary rise from the water table to survive (Loheide et al. 2009). Vegetation in the western portion of the meadow is dominated by the herbaceous dicot, *Oreostemma alpigenum* var. *andersonii*, and a small perennial sedge, *Carex subnigricans*. All nomenclature is based on the Jepson Herbarium eFlora database of native and naturalized vascular plants of California (Baldwin and Goldman 2012). Soil analyses demonstrated the

presence of high organic content relative to other Sierra Nevada meadows (Ankenbauer and Loheide 2017; Cooper et al. 2006; Ratliff 1985). It is unlikely that the existing vegetation formed these soils due to the low below ground biomass production of the species present (Ankenbauer and Loheide 2017; Cooper et al. 2006).

Sheep grazing was prevalent in the Sierra Nevada from the mid-1800's into the early 1900's (Sharsmith 1959). A southern Sierra Nevada study used palynological evidence to attribute late 19th century meadow vegetation changes to intense livestock grazing (Dull 1999). Grazing ceased in Yosemite National Park in 1905 (Holmes 1979), but legacy effects of intensive grazing are suspected to be a driver of meadow degradation throughout the Sierra Nevada (Norton et al. 2011).

2.2 EXPERIMENTAL DESIGN

2.2.1 EXCLOSURE TREATMENT

Prior to implementing this experiment, five blocks were randomly located in the western portion of Tuolumne Meadows using ArcGIS to account for site heterogeneity (Figure 2). Groundwater modeling in Tuolumne Meadows has shown that vegetation patterning is likely related to topography of abandoned river meanders (Loheide et al. 2009). Our study locations span these depressions in the landscape, justifying our block design. Treatment plot locations were also randomly generated in each block in ArcGIS. In each block, a 22 m by 22 m enclosure treatment was implemented on half the replicates. Galvanized hardware cloth (0.635 cm mesh) was installed by park volunteers and staff on July 12-13, 2016. When installed, 15 cm of hardware cloth lay flush with the ground surface while 31 cm projected perpendicular upward (Figure 3). Rebar 61 cm long was fixed to the enclosure corners and sides to support the

enclosure. The hardware cloth was fastened to the rebar with zip ties and secured flush to the land surface with landscape staples. Small mammals were anecdotally observed breaching our enclosures during the 2016 season, highlighting a need for enclosure design improvements in 2017. Modifications were made to the enclosures between July 4, 2017 and July 10, 2017, by adding flashing material on the enclosure tops, at a 45-degree angle downward (Howe et al. 2006).

Reference populations of naturally occurring *C. scopulorum* stands were identified to the west of our experimental plots (Figure 2). These adjacent reference plots likely received similar impacts that effected degraded areas of Tuolumne Meadows, but were able to persist in greater densities. These reference plots of naturally occurring *C. scopulorum* were used to gauge the growth potential of our planted seedlings.

2.2.2 COMMERCIALY GROWN SEEDLINGS

Seedlings were grown from seed collected in wetlands near the Tioga Pass entrance station in Yosemite National Park, USA (37°55' N, 119°15' W). They were grown by a commercial nursery (Cornflower Farms, Elk Grove, CA) in 6.5 in3 SC7 Stubby Ray Leach containers. The potting medium was peat moss, vermiculite, and perlite at a 2:3:1 ratio, with 15-5-10 fertilizer of Dolomite AG 6.5, zinc phosphate, and micro nutrients. Prior to transplanting, plant leaves were trimmed to 3 cm height to reduce shading of neighboring seedling and reduce water loss through evapotranspiration.

2.2.3 PLANTING DENSITY TREATMENT

Carex scopulorum seedlings were transported to Tuolumne Meadows and planted from June 29, 2016 to July 11, 2016. Seedlings were planted in bare soil using planting dibbles (Figure

4). Two planting density treatments were implemented creating a 2-factor split plot design. These densities were used to test future cost efficiency assessments, as planting density can have significant influence on restoration costs (Zentner, Glaspy, and Schenk 2003). The high density (8 plants m^2) treatment and low density (4 plants m^2) treatment each contained approximately 1,000 plants per plot. All high density plots were 6.25 m by 20 m with a 1 m buffer along the edge. All low density planted areas were 12.5 m by 20 m with a 1 m buffer along the edge. High density and low density plots were planted with equal numbers of seedlings (~ 1000), resulting in different size planting areas. Plant spacing was determined using grid lines across entire planting areas (Figure 4). Park volunteers and staff planted 19,110 *C. scopulorum* seedlings in a 0.915 acre area.

2.3 FIELD MEASUREMENTS

2.3.1 TREATMENT EFFECTS

The response of *C. scopulorum* seedlings to the experimental treatments was assessed at peak standing living biomass in 2016 (August 7-15) and 2017 (August 14-18) for survival, longest leaf length, expansion area, and percent of leaf area lost to herbivory. Data were collected on planted seedlings in three 1-m radius (3.14 m^2) replicates in each treatment combination in each block (Figure 2). Two perpendicular linear measurements were made on each seedling between the farthest spread tillers (see Figure 5), then multiplied to calculate expansion area.

In 2017, individual growth rates of seedlings were summarized at the end of the season using weekly (July through September) and bi-weekly new tiller data (October) within 0.305 m radius (0.29 m^2) replicates. Each planted seedling in each replicate was marked in 2016 using

distinctly colored wire combinations, and the number of naturally occurring *C. scopulorum* in each replicate was recorded. During each additional assessment, new tillers were marked with uniquely colored wire and the shortest distance from planted seedling edge to new tiller edge was measured (Figure 6).

2.3.2 ENVIRONMENTAL SITE CONDITIONS

Annual above-ground net productivity ($ANPP_{site}$) and absolute cover was measured in each replicate. Above-ground biomass was clipped in 20 cm by 20 cm quadrats 1 m south of replicate centroids between August 31, 2017 and September 4, 2017, stored in paper bags, oven dried for 72 hours at 55°C, and weighed (Figure 7). Absolute cover of plants and substrate types were recorded at peak standing living biomass using continuous visual cover estimation by observer pairs to reduce error (Figure 8) (Vittoz and Guisan 2007), then divided into functional groups (e.g., graminoid, forb, bare ground). Soil moisture (VWC) was recorded using a Field Scout TDR 100 Soil Moisture Meter (Spectrum Technologies, Aurora, IL) at each replicate weekly. Percent saturation was calculated by dividing weekly VWC by fully saturated VWC (standing water) measurements.

Five replicates were excluded from analyses for one of these reasons: heavy site disturbance from human foot traffic, inability to distinguish planted seedlings from naturally occurring individuals, thick litter deposition limited plant survival, or plants could not be relocated.

2.3.3 SPECIES BIOMASS COMPARISONS

Carex scopulorum biomass production and the below ground/above ground biomass ratio was measured between September 23-25 in 2016 and between August 19-28 in 2017.

Thirty-three unplanted seedlings were dried and washed clean of soil and their above and below biomass analyzed. Three months post planting, 18 seedlings were excavated using hand trowels in approximately 100 cm² areas and to depths of approximately 150 cm. In 2017, 17 cores (15.24 cm diameter) were centered on planted *C. scopulorum* seedlings (treatment cores) near plot corners and six cores were centered on naturally occurring *C. scopulorum* (reference cores). Cores were excavated to a depth of 20 cm (Figure 9). Samples were washed to remove soil, and biomass was separated by species and placed into paper bags. Roots that could not be identified to species were omitted. Above and below ground biomass was separated, oven dried for 72 hours at 55 degrees C, and weighed.

2.4 ANALYSIS

The 2017 data were analyzed using the lmerTest package (Kuznetsova, Brockhoff, and B. 2017), and lsmeans package (Lenth 2016) in R (R Core Team 2016). Linear mixed-effects models were fit to the data using the lme4 package (Bates et al. 2015). Tukey adjusted pairwise comparisons were considered to determine the relative importance of different effects.

2.4.1 TREATMENT EFFECTS

A logistic model was fit using proportion survival at the plot level to calculate treatment effect on survival. In each growth model, the response variable was the measured metric (seedling area occupied, longest leaf length, herbivory, cumulative tiller count). Fixed predictor variables in each model were enclosure presence or absence and planting density, and covariates were scaled percent saturation, absolute plant cover, and ANPP_{site}. Percent saturation was scaled by dividing centered values by one standard deviation. Block and plot were treated as random effects. Block*enclosure was included to account for the split plot

design (with enclosure as the whole plot factor). To meet the assumptions of normality, linearity, and equal variance, seedling area data were square root transformed. Three replicates of treatments in each block were aggregated for use in analyses (n = 20). By design, all models met the assumption of independent observations because replicates were aggregated.

2.4.2 ENVIRONMENTAL SITE CONDITIONS

To analyze the influence of percent saturation as a predictor of seedling survival, we analyzed this relationship without regard to treatments. A logistic model was fit to seedling survival data at the replicate level with percent saturation to find the optimum average percent saturation and optimum overall change in percent saturation over the growing season (maximum saturation – minimum saturation).

2.4.3 SPECIES BIOMASS COMPARISONS

In each biomass model, the response variable was either the biomass ratio or total biomass, the predictor variables were plant species or core location, and all effects were fixed. To meet the assumptions of normality, linearity, and equal variance, the biomass ratio data were log transformed. Species with less than one occurrence were omitted from the analyses. A linear regression was fit to seedling biomass samples from three time points to approximate how long it will take to reach reference *C. scopulorum* biomass totals.

3. RESULTS

3.1 SITE HETEROGENEITY

Percent soil saturation decreased consistently through the summer in all plots (Figure 11). Mean summer percent of saturation was similar between excluded and non-excluded plots (excluded $88\% \pm 7$ in both densities, non-excluded $91\% \pm 3$ in low density, $92\% \pm 5$ in high density). Variation in percent saturation was slightly lower in non-excluded plots, with mean changes in percent saturation of 17% (± 5 low density, ± 6 high density). Excluded plots had mean changes (maximum saturation – minimum saturation) of 20% (± 9) and 22% (± 9) in low and high density treatments.

One to 10 vascular plant species occurred per 0.29 m^2 plot. Mosses were present in about half of the plots and included in absolute cover. Bare ground covered more of the study plots than any plant species, with means of 48% to 55% for treatment plots and 40% in reference plots (Figure 10). Litter had the second highest cover, with a mean of 9% to 17% in treatment plots, and 8% in reference plots. When divided into plant functional groups, the largest difference in cover was for graminoids (grasses, sedges, and rushes). Graminoid cover ranged from 14% to 17% in treatment plots and averaged 40% in reference plots. The forb (herbaceous dicot) cover ranged from 13% to 18% in treatment plots, and 11% in reference plots. The no-exclosure and high-density treatment type had the highest cover of subshrub (5%). Moss cover ranged from 0% to 2% in treatment plots but was $<1\%$ in reference plots. Site annual aboveground net productivity ($\text{ANPP}_{\text{site}}$) varied little between the treatments, with a mean of $268.48 \text{ g/cm}^2/\text{yr}$ for all treatment types.

3.2 SEEDLING SURVIVAL

Initial seedling survival was high, with approximately 98% of all planted seedlings living through the summer of 2016 (Figure 11). At the end of 2017, after two summers of growth and one winter, overall survivorship was 71%. In 2017, survival rates were 22% higher in plots without exclosures than plots with exclosures. Exclosure presence ($p = 0.044$, $\alpha = 0.05$) and the interaction between exclosure and planting density ($p = 0.010$, $\alpha = 0.05$) were statistically significant predictors of survival (Table 1). When survival was modeled at the plot level and included treatment effects, no significant differences in survivorship occurred along the soil moisture gradient. When assessed at the replicate level, the highest survival occurred in sites with the highest average percent saturation (94% of saturation) (Figure 11) and the site with the lowest variance in percent saturation (16% change).

3.3 SEEDLING GROWTH

Planted seedlings more than doubled in area (horizontal spread) and longest leaf length increased by 45% from August 2016 to August 2017 (Figure 10). In 2017, absolute plant cover ($p = 0.046$, $\alpha = 0.05$) and exclosure presence ($p = 0.019$, $\alpha = 0.05$) were significant predictors for differences in seedling area (Table 1). Mean seedling area was 11 cm^2 greater in non-exclosures plots, a statistically significant difference ($p = 0.019$, $\alpha = 0.05$). The modeled slope indicated that a $<1 \text{ cm}^2$ decrease in seedling area is predicted by a 1% increase in absolute cover. Soil moisture did not influence seedling area ($p = 0.484$, $\alpha = 0.05$).

Site annual aboveground net productivity ($\text{ANPP}_{\text{site}}$) was used to characterize naturally occurring differences between plots, and it was the only significant predictor for increased leaf length ($p = 0.021$, $\alpha = 0.05$). The modeled slope indicated that a 1 cm increase in leaf length is

predicted by a 6 g increase in AANP of a site. Percent saturation was nearly significant for longest leaf length ($p = 0.055$, $\alpha = 0.05$). Mean percent of seedling leaves affected by herbivory was low (<1%) across all plots, and no predictor variables were significant. Of the 79 seedlings monitored for new tiller production, 12 did not form a new tiller. However, on average, *C. scopulorum* seedlings added approximately 2 new tillers during the 2017 growing season (Figure 12). No predictor variables were significant for cumulative seedling tiller counts (Table 1).

3.4 SEEDLING BIOMASS ACCUMULATION

Carex scopulorum seedling biomass increased more than six-fold from the seedlings delivered in 2016 to plants in the field at the end of the 2017 growing season (Table 2). Mean biomass of seedlings delivered from the nursery in 2016 was nearly 2 g. Three months post planting, mean seedling biomass had increased to almost 3 g, and at the end of the 2017 summer mean biomass was nearly 13 g.

Carex scopulorum seedlings had greater mean biomass by area ($703.44 \text{ g/m}^2 \pm 246.54$), than all other species in cores centered on seedlings in our study plots. *C. scopulorum* seedlings had more than twice the belowground biomass per unit area of other herbaceous species in these cores (Figure 12). In addition, planted *C. scopulorum* seedlings contributed a greater portion of their biomass below-ground (higher mean ratio) than all other species from the cores (*Ranunculus californicus* $p = 0.042$, *Trichophorum clementis* $p = 0.040$, *Oreostemma alpigenum* $p = <0.001$, *Eleocharis quinqueflora* $p = <0.001$, *Muhlenbergia filiformis* $p = <0.001$, *Gentian* spp. $p = <0.001$) other than the woody plant *Vaccinium cespitosum* (Figure 13). All but *Carex*

subnigricans, had statistically different below/above ground biomass ratios than *C. scopulorum* ($p = 0.051$).

4. DISCUSSION

The biomass of planted *Carex scopulorum* seedlings increased nearly 700% during two summers of growth, indicating its value in the restoration of plant production and biomass in this subalpine wet meadow. Belowground total biomass was greater than that of other dominant species in the meadow and accounted for 43% of cumulative belowground biomass in cores centered on seedlings by the end of the 2017 growing season. Similar rapid increase in seedling growth has been found for restoration with other species of Cyperaceae. In Halstead Meadow, Sequoia National Park, *Scirpus microcarpus* seedlings grew to create a nearly complete cover in degraded wet meadows in just three years (Cooper unpublished data). In Mountain Village, Colorado *Carex utriculata* and *Carex aquatilis* reached maximum tiller densities after five years (Cooper et al. 2017).

The effects of exclosures were opposite of what we expected (Q1), with greater seedling survival and growth, longest leaf length, in unexclosed plots. We did not find an effect of planting density (Q2) on seedling survival and growth. Responses to the planting density treatments may operate on a time scale beyond the scope of this study (two summers), and could become significant over time (Martin and Chambers 2002). We observed significant effects of absolute vegetation cover and ANPP_{site} on seedling growth (Q3) including seedling area and longest leaf length. These relationships could be indicative of site-specific conditions conducive to plant growth. Planted *C. scopulorum* seedlings had more biomass (Q4) than other species in degraded areas of Tuolumne Meadows and allocated (Q5) more of their biomass belowground than other herbaceous species on site. It is important to acknowledge that

planting seedlings increased biomass in degraded areas of Tuolumne Meadows, but high survival and additional growth of seedlings are responsible for a larger proportion of seedling biomass over the study period.

4.1 SEEDLING SURVIVAL

Planting sedge species as seedlings instead of direct seeding increased the likelihood of establishment and survival (Roth et al. 1999). This is due to the notoriously specific germination requirements for species of *Carex* (Kettenring, Gardner, and Galatowitsch 2006; Van Der Valk, Bremholm, and Gordon 1999). Our mean survival rate of 71% for *C. scopulorum* seedlings after two summers is comparable to those of other sedge species used in meadow restoration efforts. An experiment in the southern Sierra Nevada reported survival rates of 30-100% for the clonal sedge *Carex utriculata* one year post planting (Sarr and Park 2017). In an Icelandic highlands grazing experiment, planted seedling of the clonal sedge *Carex bigelowii*'s had a survival rate from 76-87% (Jónsdóttir 1991).

Small mammal herbivory is a plausible mechanism to explain how exclosures might impact survival (Wolf 2017). However, we observed low rates of herbivory in 2017 and no significant differences in herbivory between treatments. The low level of herbivory in 2017 is distinct from previous observations in Tuolumne Meadows (Wolf 2017). We observed very few ground squirrels in our study area in 2017, and the large 2016-2017 snowpack and extensive spring flooding could have reduced local ground squirrel populations, greatly limiting herbivory. It does not appear that herbivory during 2017 influenced seedling survival or growth. We did not measure herbivory in 2016, and it is possible that herbivory from the 2016 summer influenced 2017 survival and growth. We changed our exclosure treatment in 2017 with the

addition of flashing, thus this exclosure treatment remains untested in its effectiveness to preventing herbivory. Given a lack of plausible mechanisms to account for differences between exclosed and unexclosed plots, our results may be an artifact of natural heterogeneity in random plot placement. Other factors, including soil texture, pH, nutrient limitations and bacterial and mycorrhizal associations, may have influenced our results (De Deyn, Cornelissen, and Bardgett 2008; Farrer and Suding 2016; Ratliff 1985). As the study continues, potential increases in herbivory could allow us to test the effectiveness of our exclosures at limiting herbivory. A six-year prairie grassland experiment that excluded meadow voles (*Microtus pennsylvanicus*) did not report drastic changes between exclosed and not exclosed plots until its third year of observations (Howe et al. 2006).

4.2 RATE OF CAREX GROWTH AND SPREAD

Carex scopulorum seedling growth rates in our study were lower than reported in other sedge restoration projects, but this may be due to differences between species and sites. After two growing seasons, *Carex utriculata* seedlings planted at 4 plants/m² in a golf course restoration project in Mountain Village, Colorado were at 30% of their peak tiller density (Cooper et al. 2017). By comparing our reference mean total biomass (1.3 g/m²) to our mean 13-month seedling biomass (0.3 g/m²) from our core samples, we estimate that our planted seedlings are at 21% of their anticipated size. It is important to note that this estimate does not consider the spaces between seedlings, since the cores were centered on planted seedlings.

Density dependent effects are a plausible driver of growth and survival in populations. However, there was no difference in growth rates between our density treatments, and the seedling tillers did not overlap, suggesting that intraspecific competition was not a limiting

factor. Alternatively, our two summer study may be too short to detect significant effects of density treatments. A 3-year study that assessed the establishment requirements of *Carex stricta* seedlings determined that different planting densities of 9 plants/m² and 2 plants/m² were not significantly associated with survival or growth (Budelsky and Galatowitsch 2004). Due to niche differences, rare species have been observed to increase their populations at a higher rate than more common species, which supports overall community diversity (Levine and HilleRisLambers 2009). If our observed positive trend in seedling growth continues in future years, competition could become an important factor influencing *C. scopulorum* growth rates.

In the Sierra Nevada, *C. scopulorum* is abundant in wet meadow communities and its presence has been positively correlated with soil moisture (Lee et al. 2017). A near-record spring snowpack produced saturated soils during the 2017 field season. The 2017 April 1st snow water equivalent reading for the central Sierra Nevada was 173% of the long term average (California n.d.). Observed soil saturation rates stayed high, with the minimum soil percent of saturation for study plots ranging from 59-95% and average soil saturation ranging from 74-98%. A high water year created a lack of variation in soil moisture within our study area. Given minimal variation in this predictor variable, our inability to detect significant effects of soil saturation on our response variables, seedling survival and growth, was anticipated.

4.3 SEEDLING BIOMASS

Soil carbon dynamics studies in the Sierra Nevada highlight the need for a better understanding of greenhouse gas dynamics in meadows, because degraded meadows can act as sources of atmospheric carbon (Arnold, Ghezzehei, and Berhe 2014; Blackburn 2017; Blankinship and Hart 2014). Results from our study support previous efforts to document the

role of species specific biomass contributions using carbon sequestration modeling (Lawrence and Zedler 2013; Tripathee and Schäfer 2014). Above-ground plant production has been studied in many montane and subalpine meadows in the Sierra Nevada (Cole et al. 2004; Moore et al. 2000, 2013; Ostoja et al. 2014; Ratliff 1985; Stohlgren, DeBenedetti, and Parsons 1989), but the role of each plant species in belowground biomass production is a critical knowledge gap. Quantifying belowground biomass inputs of plants species solely from aboveground estimates can be misleading. For example, total biomass from three wetland communities along a hydrologic gradient in northeastern Oregon revealed similar aboveground biomass, but belowground to aboveground ratios were two to four times higher for the wet meadow than dry meadow communities (Dwire et al. 2004).

Storage of carbon, as soil organic matter, is a key component of the global carbon cycle (Amundson 2001; De Deyn, Cornelissen, and Bardgett 2008; Jobbagy and Jackson 2000), and belowground plant biomass contributes more carbon to soil organic matter than aboveground growth (Rasse, Rumpel, and Dignac 2005). Root-derived carbon has a longer mean residence time in soils due to chemical recalcitrance, physio-chemical protection, and physical protection from roots hairs (Rasse, Rumpel, and Dignac 2005). Our observed below/above ground biomass ratios for *C. scopulorum* seedlings (10.3) and reference *C. scopulorum* (15.2) are similar to the ratios for this species reported from alpine wet meadows on Niwot Ridge, Colorado. The Niwot Ridge ratios vary from approximately 4 (Bowman and Bilbrough 2001) to 7-13 (Bowman et al. 1993). Sierra Nevada meadows have higher overall biomass production and greater below-ground biomass allocation than those on Niwot Ridge (Rundel 2015), which is a higher elevation alpine tundra site with a more extreme climate. Our results provide evidence that after two

summers and one winter of growth, *C. scopulorum* seedlings are contributing more total biomass and have higher belowground allocation rates than other sampled species in this community type in Tuolumne Meadows. Overall production and allocation of biomass are critical factors that influence soil formation. The influence of certain plant species on soils demonstrates their potential importance in terrestrial ecosystem processes (Lawrence and Zedler 2013; Tripathee and Schäfer 2014).

5. CONCLUSION

Reestablishment of native, high production vegetation in degraded Sierra Nevada meadows is a high priority for scientists and land managers (Ankenbauer and Loheide 2017; Norton et al. 2011, 2014). We demonstrated that *C. scopulorum* is a suitable species for restoration in the Sierra Nevada. High biomass production of this species can contribute to meadow revegetation and important building of organic matter in soils.

Wetlands are a primary component of the global carbon budget (Meng et al. 2016) and loss of wetlands is influencing global carbon cycling and budgets (Junk et al. 2013). Because plant biomass is the primary contributor to soil carbon (De Deyn, Cornelissen, and Bardgett 2008), we need to conserve and restore the vegetation of these important ecosystems. Revegetating degraded wetlands is a key opportunity to provide some ecosystem resilience against large scale stochastic events that will become more common with human caused climate change. This research study adds to the growing body of research required for informing the restoration of vegetation and carbon sequestration processes in wetlands. We provide critical information on biomass contributions of a key wet meadow species and recommend their use in future restoration efforts in similarly degraded meadows. *Carex scopulorum* is an appropriate species for restoration in meadows where increasing biomass inputs to the system is a priority. We recommend the prioritization of revegetating degraded wetlands, which could provide some small but important contributions to ecosystem resiliency in globally endangered habitats.

TABLES AND FIGURES

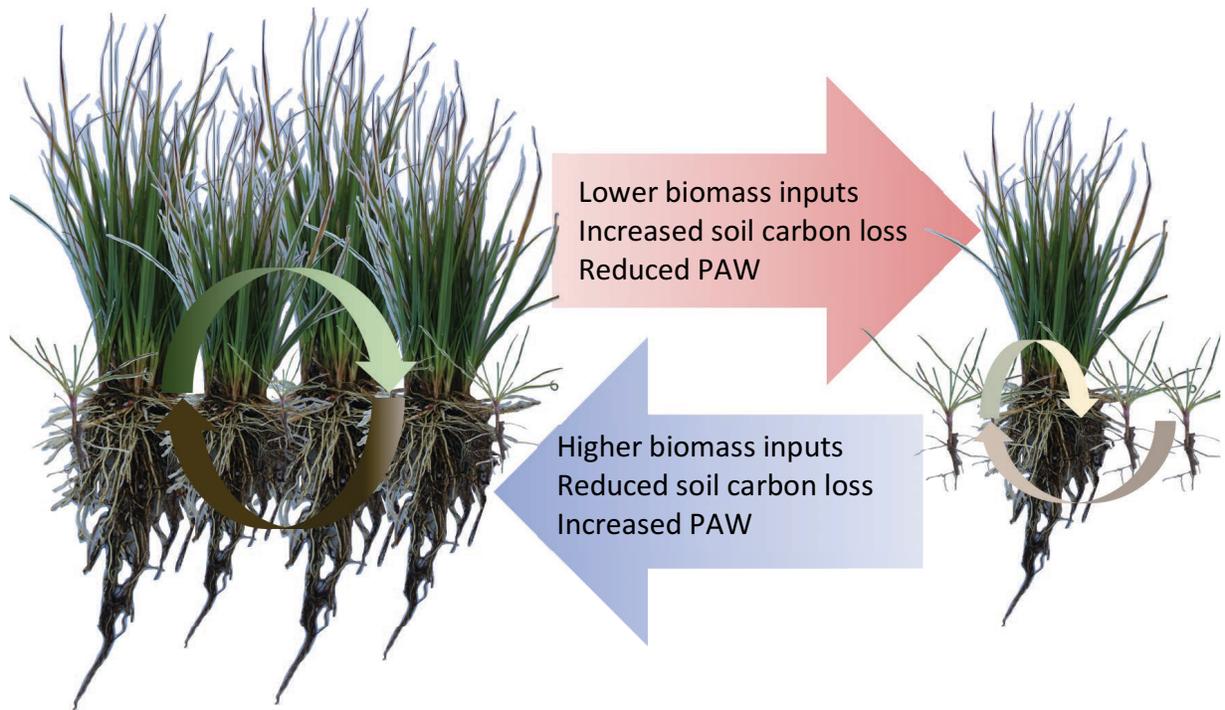


Figure 1: Conceptual illustration of differences in healthy (left) and degraded (right) wet meadow through changes in biomass inputs, soil carbon, and Plant Available Water (PAW). Negative feedback (red arrow) associated with vegetation cover loss leads to further degradation, while positive feedbacks (blue arrow) associated with increased vegetation cover leads to increased meadow health.

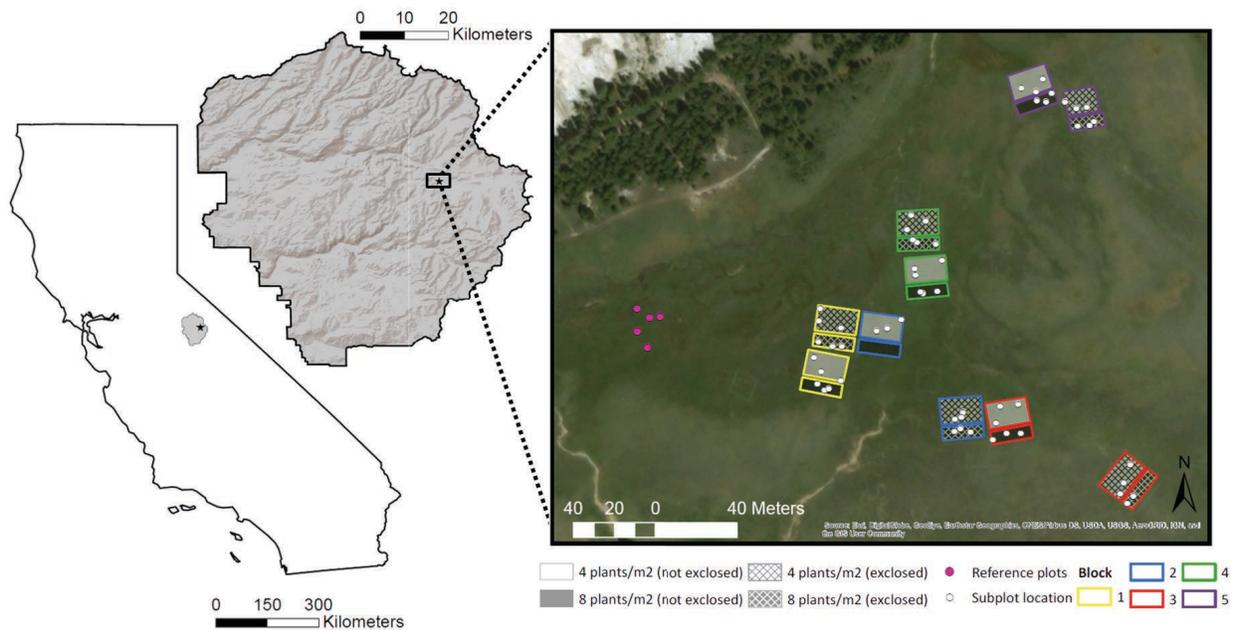


Figure 2: Location of study site in western portion of Tuolumne Meadow (right panel) in Yosemite National Park (center), California (left). Site map (right panel) shows block locations, plot locations, treatments, and subplot sampling locations. Tioga Pass road (bottom-left in right panel) runs adjacent to the meadow's southern edge.



Figure 3: Enclosures were installed in 2016 (left) using hardware cloth 31 cm vertical and 15 cm flush with the ground surface. In 2017, flashing was installed (right) at a 45-degree angle downward.



Figure 4: *Carex scopulorum* seedlings were planted using dibbles, specialized planting tools (left), and using a grid system (right) to obtain desired spacing for planting densities.

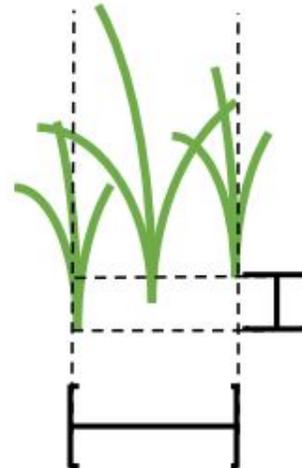


Figure 5: Seedling expansion area was measured as a combination of two perpendicular linear measurements between farthest spread tillers.

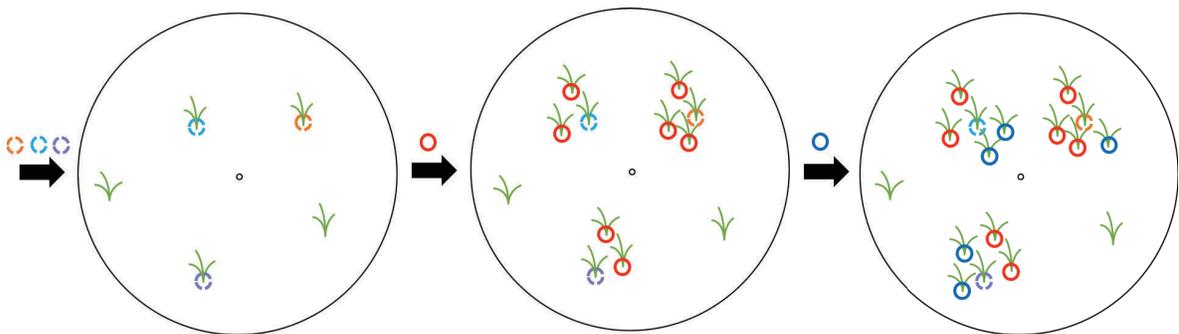


Figure 6: Colored wires were used to track seedling growth during the 2017 growing season (bottom). Entire planted seedlings were marked in 2016 (bottom-left, colored dashed circles) and new tillers were marked weekly in 2017 (bottom-center and bottom-right, colored solid circles). Final new tiller counts were made at the end of October (top).

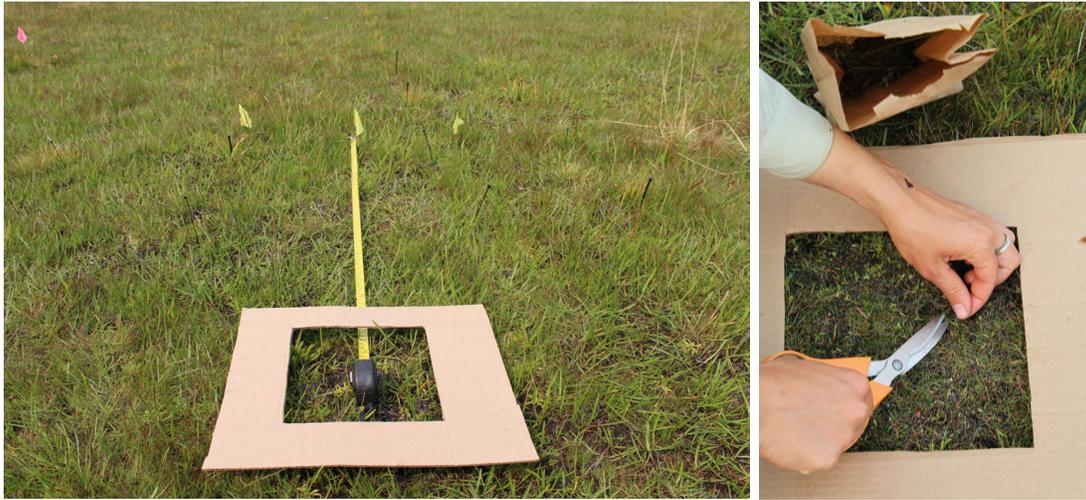


Figure 7: All above-ground biomass was clipped in 20 cm by 20 cm quadrats (right) 1 m south of replicate centroids (left) to estimate site annual above-ground net productivity ($ANPP_{site}$).



Figure 8: Absolute cover of plants and of surface types were recorded using continuous visual cover estimation by observer pairs to reduce error.



Figure 9: Cores were centered on planted *Carex scopulorum* seedlings (top-left) and excavated to a depth of 20 cm (top-right, blue line on corer). Intact cores (bottom-left) were rinsed (bottom-center) and separated by species (bottom-right, *Muhlenbergia filiformis*).

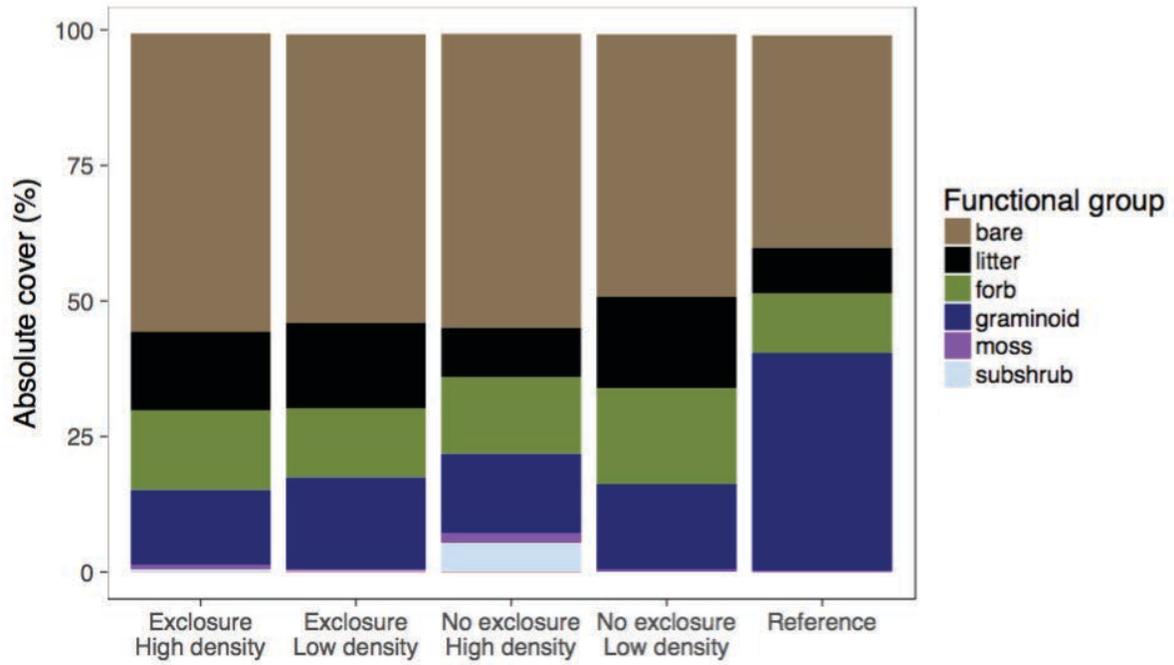


Figure 10: Mean absolute cover of substrates and plant functional groups for each treatment combination.

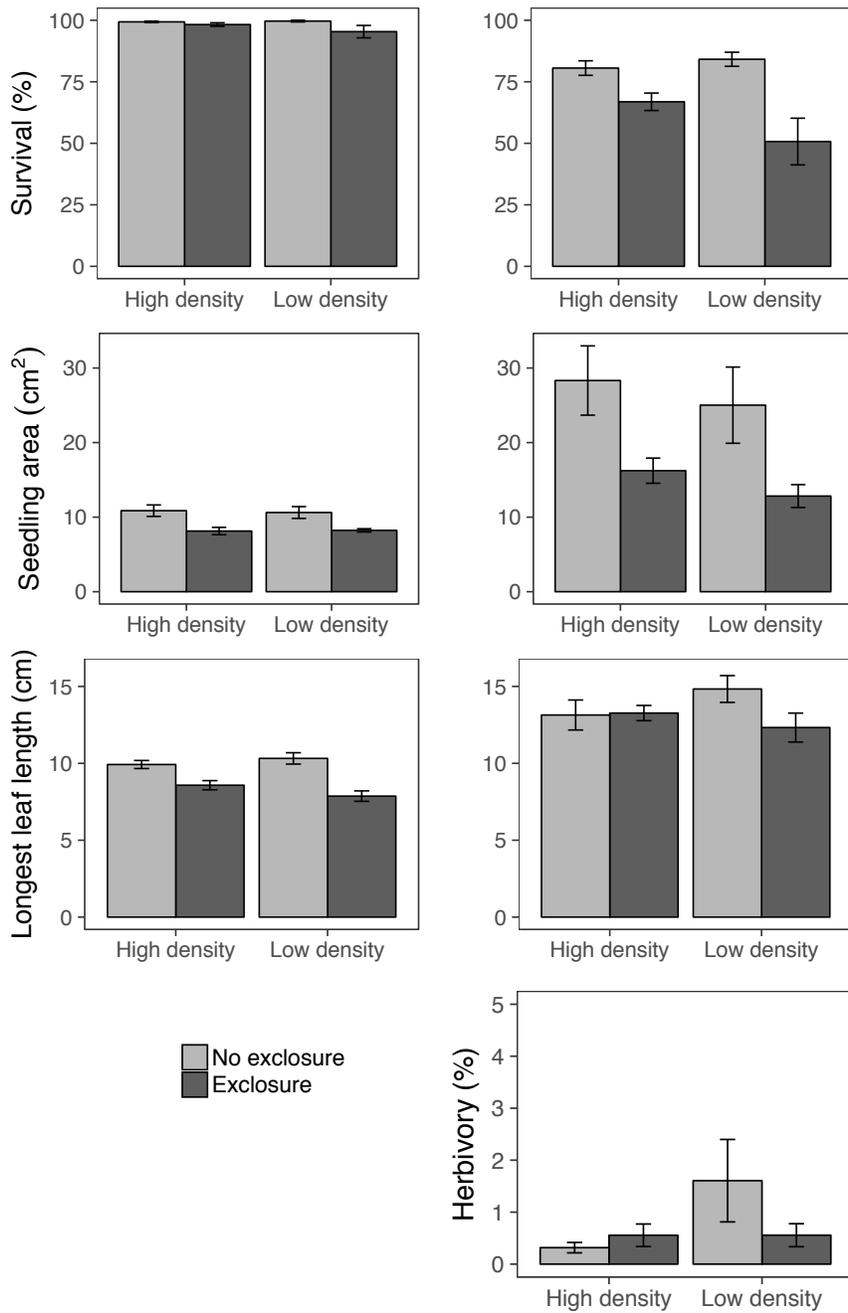


Figure 11: Summary statistics for seedling survival, area occupied, and longest leaf length for 2016 (left) and 2017 (right) show generally higher survival and growth rates in plots without exclosures. Note: For herbivory (measured in 2017) note the y-axis shows values from 0-5%.

Table 1: Mean (± 1 SD) seedling survival and growth metrics under treatment conditions in 2016 (one month post planting) and 2017 (thirteen months post planting). Seedling measurements were aggregated at the replicate level, then averaged across treatment type (N=20).

Treatment		Survival (%)		Seedling area (cm ²)		Longest leaf length (cm)		Herbivory (%)
<i>Exc</i>	<i>Den</i>	2016	2017	2016	2017	2016	2017	2017
+	L	95 (± 6)	50 (± 21)	8.0 (± 0.5)	13.0 (± 3.5)	8.0 (± 1.0)	12.5 (± 2.0)	1 (± 1)
+	H	98 (± 2)	67 (± 8)	8.0 (± 1.0)	16.0 (± 4.0)	8.5 (± 0.5)	13.5 (± 1.0)	1 (± 0)
-	L	100 (± 1)	84 (± 6)	10.5 (± 2.0)	25.0 (± 11.5)	10.5 (± 1.0)	15.0 (± 2.0)	2 (± 2)
-	H	99 (± 1)	81 (± 7)	11.0 (± 2.0)	28.5 (± 10.5)	10.0 (± 0.5)	13.0 (± 2.0)	<1 (± 0)
Mean		98 (± 4)	71 (± 45)	9.5 (± 2.5)	20.0 (± 10.5)	9 (± 2.0)	133.5 (± 2.0)	1 (± 0)

2017 ANOVA, Significance of F Value (p)

	Survival	Seedling area	Longest leaf length	Cumulative new tillers	Herbivory
Exclosure	0.044	0.019	0.389	0.093	0.354
Planting density	0.382	0.163	0.554	0.944	0.158
Soil saturation (%)	0.129	0.484	0.055	0.600	0.597
ANPP	0.773	0.544	0.021	0.117	0.124
Absolute cover	0.789	0.046	0.860	0.171	0.384
Exclosure:Planting density	0.010	0.860	0.113	0.213	0.121

Treatments: either exclosure or no exclosure (Exc +, Exc -); planting density low or high (Den L, Den H). Sqrt transformation was used on seedling area data. P-values ($\alpha=0.05$) are shown for predictor variables. Percent saturation was scaled for all tests and absolute cover was scaled for the cumulative tiller test.

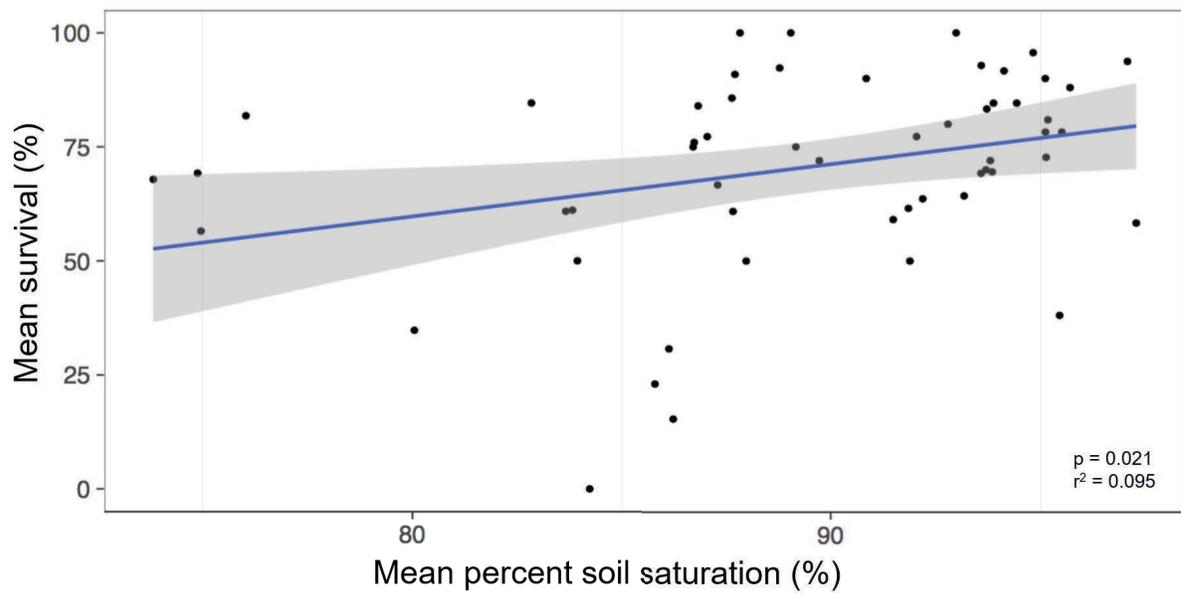


Figure 12: Linear regression of mean survival and mean percent soil saturation at the replicate level demonstrates the significant ($p = 0.095$) relationship between the two variables.

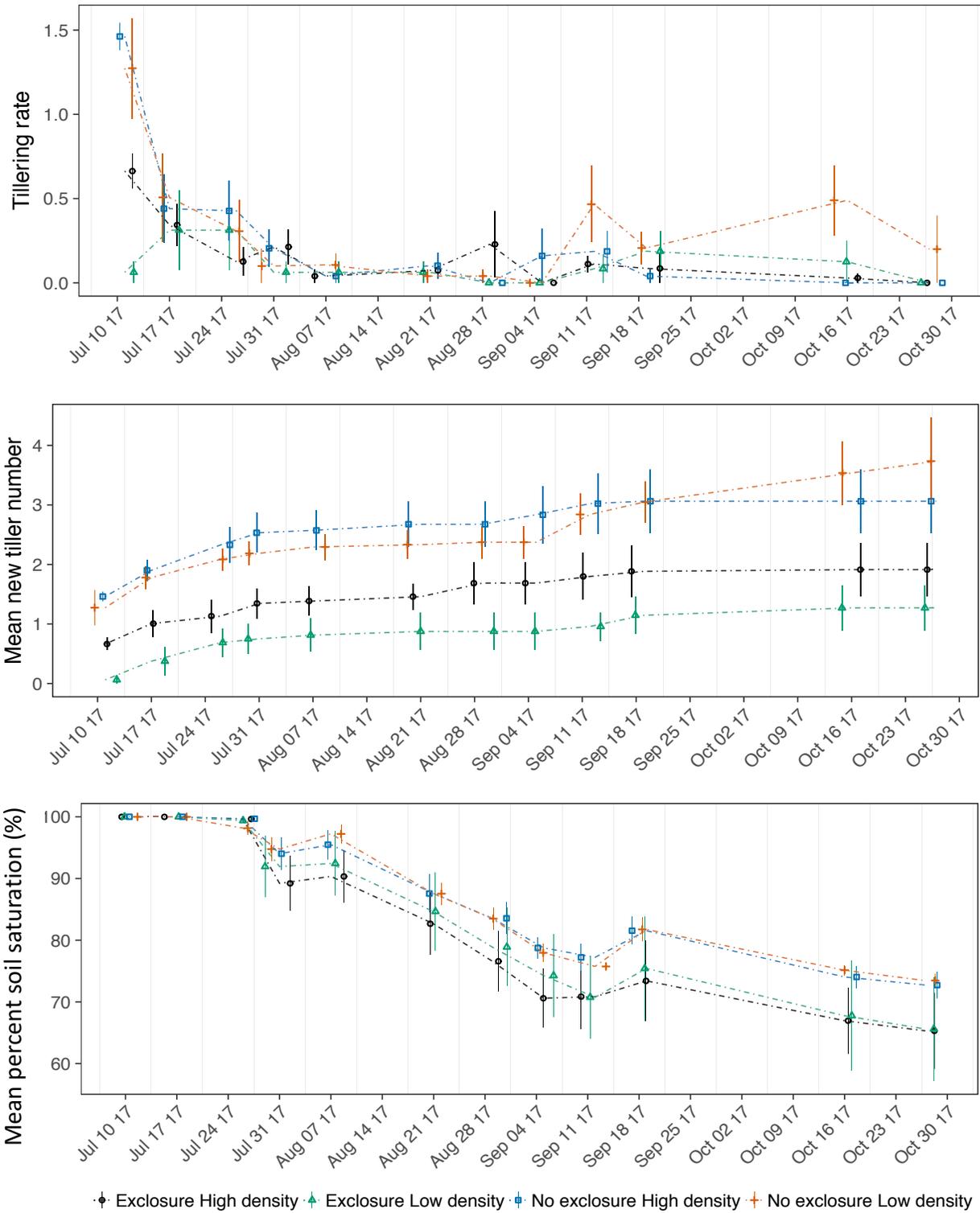


Figure 13: Mean tillering rate (top), new tiller number (middle), and mean percent soil saturation (%) (bottom) for *Carex scopulorum* seedlings per plant per plot averaged by treatment. N=20 plots for treatments.

Table 2: Average biomass (g) for *Carex scopulorum* seedlings increased within the 15-month study period.

<i>Carex scopulorum</i> seedling stage	n	mean biomass (g)	sd	SE
Seedlings delivered from nursery	33	1.87	1.45	0.25
3 months post planting	18	2.75	1.41	0.33
15 months post planting	17	12.83	4.50	1.09

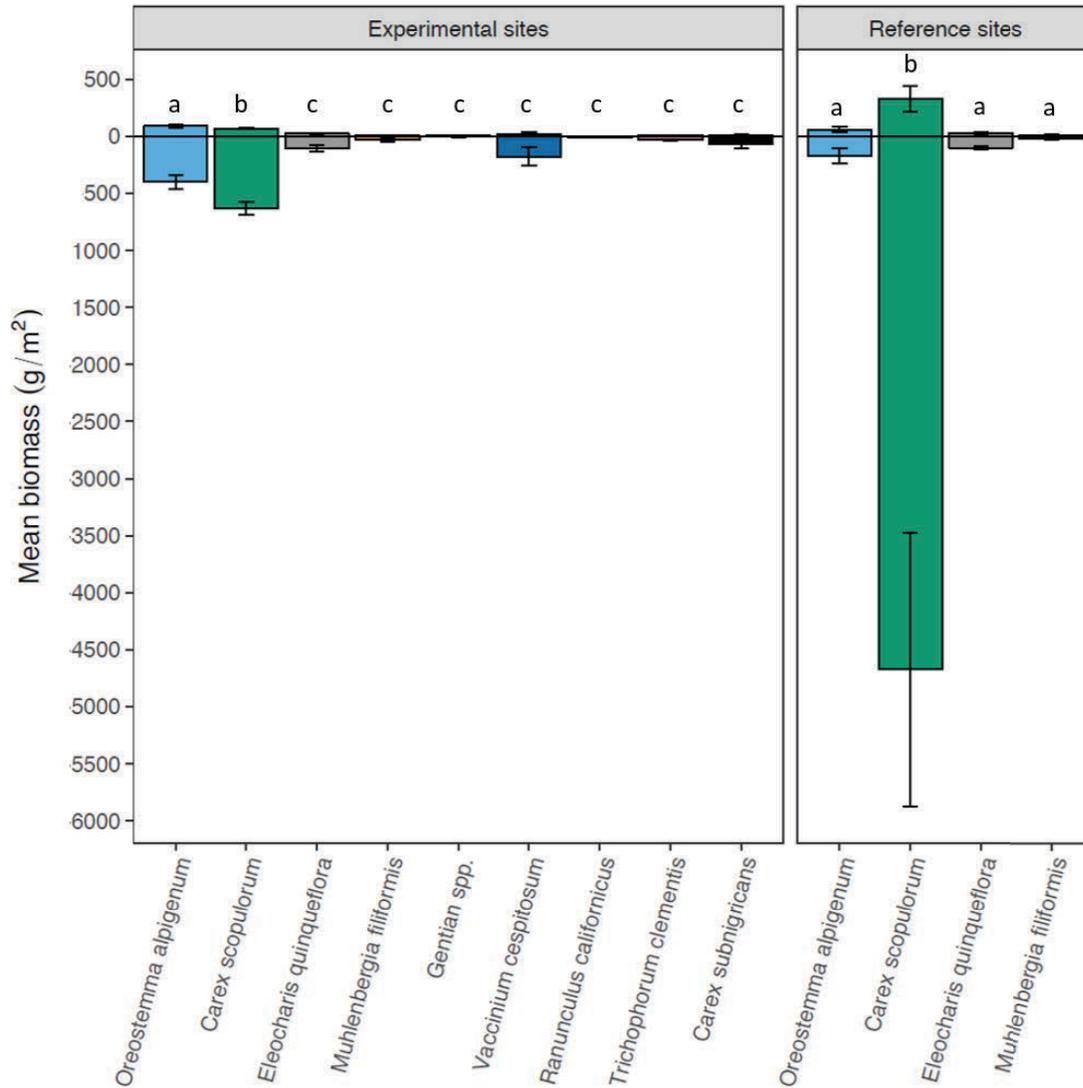


Figure 14: Mean total aboveground and belowground biomass (g m^{-2}) for planted *Carex scopulorum* seedlings and all species sampled in experimental (left) and reference (right) sites. Significance is denoted with letters above bars.

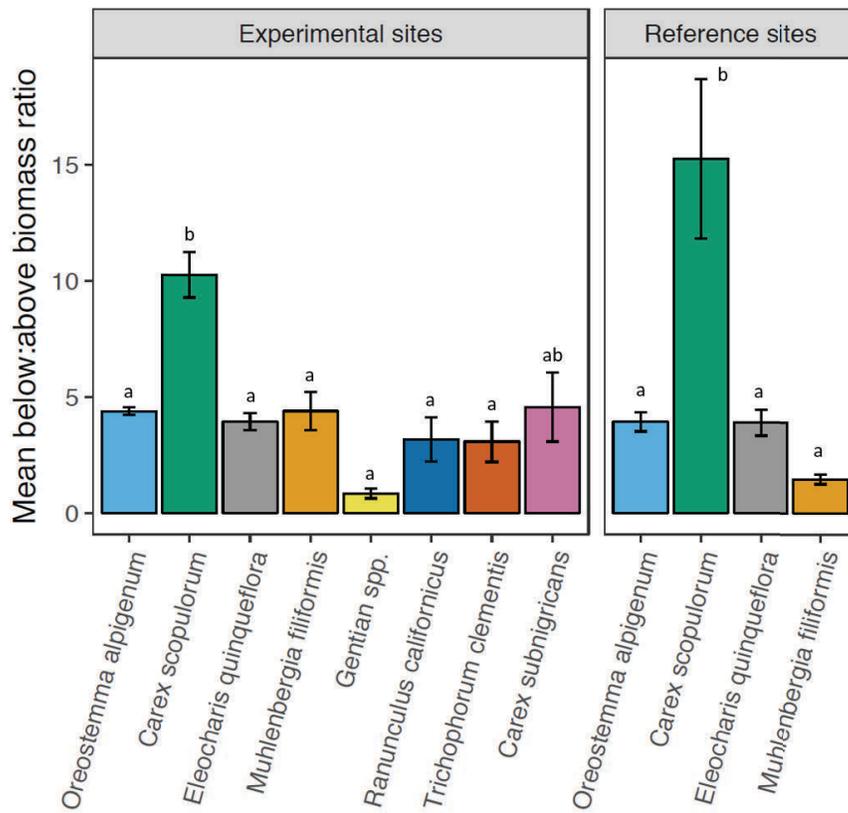


Figure 15: Mean belowground:aboveground biomass ratios for planted *Carex scopulorum* seedlings and all sampled herbaceous species in experimental (left) and reference (right) sites. Significance on the log scale is denoted with letters above bars.

LITERATURE CITED

- Allen-Diaz, Barbara H . 1991. "Water Table and Plant Species Relationships in Sierra Nevada Meadows." *The American Midland Naturalist* 126(1): 30–43.
- Allen, Robert J., and Rainer Luptowitz. 2017. "El Niño-like Teleconnection Increases California Precipitation in Response to Warming." *Nature Communications* 8(May): 1–15.
- Amundson, Ronald. 2001. "The Carbon Budget in Soils." *Annual Review of Earth and Planetary Sciences* 29(1): 535–62.
<http://www.annualreviews.org/doi/10.1146/annurev.earth.29.1.535>.
- Ankenbauer, Kyle J., and Steven P. Loheide. 2017. "The Effects of Soil Organic Matter on Soil Water Retention and Plant Water Use in a Meadow of the Sierra Nevada, CA." *Hydrological Processes* 31(4): 891–901.
- Arnold, Chelsea, Teamrat A. Ghezzehei, and Asmeret Asefaw Berhe. 2014. "Early Spring, Severe Frost Events, And Drought Induce Rapid Carbon Loss in High Elevation Meadows." *PLoS ONE* 9(9): 1–11.
- Baldwin, B. G., and D. H. Goldman. 2012. *The Jepson Manual: Vascular Plants of California*. Univ of California Press.
- Bates, Douglas, Martin Maechler, Ben Bolker, and Steve Walker. 2015. "Fitting Linear Mixed-Effects Models Using lme4." : 1–48. doi:10.18637/jss.v067.i01.
- Belsky, A. J. 1986. "Does Herbivory Benefit Plants? A Review of the Evidence." *The American Naturalist* 127(6): 870–92.
- Blackburn, Darren Alden. 2017. "Investigation of Carbon and Water Flux in a Sierra Nevada

- Meadow." San Francisco State University.
- Blankinship, Joseph C., and Stephen C. Hart. 2014. "Hydrological Control of Greenhouse Gas Fluxes in a Sierra Nevada Subalpine Meadow." *Arctic, Antarctic, and Alpine Research* 46(2): 355–64. <http://www.bioone.org/doi/abs/10.1657/1938-4246-46.2.355>.
- Bowman, William D., and Carol J. Bilbrough. 2001. "Influence of a Pulsed Nitrogen Supply on Growth and Nitrogen Uptake in Alpine Graminoids." *Plant and Soil* 233(2): 283–90.
- Bowman, William D., Theresa A. Theodose, James C. Schardt, and Richard T. Conant. 1993. "Constraints of Nutrient Availability on Primary Production in Two Alpine Tundra Communities." *Ecology* 74(7): 2085–97.
- Budelsky, Rachel A, and Susan M Galatowitsch. 2004. "Establishment of *Carex stricta* Lam . Seedlings in Experimental Wetlands with Implications for Restoration Author (S): Rachel A . Budelsky and Susan M . Galatowitsch Published by : Springer Stable URL : <http://www.jstor.org/stable/20146674> Accessed : 09-." 175(1): 91–105.
- California. "Department of Water Resources: California Data Exchange Center." 2018. <http://cdec.water.ca.gov/snowapp/sweq.action>.
- Cole, David N. 1981. "Vegetational Changes Associated with Recreational Use and Fire Suppression in the Eagle Cap Wilderness, Oregon: Some Management Implications." *Biological Conservation* 20(4): 247–70.
- . 2000. "Paradox of the Primeval: Ecological Restoration in Wilderness." *Ecological Restoration* 18(2): 77–86.
- . 2004. "Response of Mountain Meadows to Grazing by Recreational Pack Stock." *Journal of Range Management* 57(2): 153. <http://www.jstor.org/stable/4003913?origin=crossref>.

Cooper, David J. et al. 2006. "Effects of the Tioga Road on Hydrologic Processes and Lodgepole Pine Invasion into Tuolumne Meadows, Yosemite National Park, Report Prepared for Yosemite National Park." *Report to Yosemite National Park* (December): 146.

<http://faculty.washington.edu/jdlund/home/FINAL.pdf>.

———. 2017. "Mountain Wetland Restoration: The Role of Hydrologic Regime and Plant Introductions after 15 Years in the Colorado Rocky Mountains, U.S.A." *Ecological Engineering* 101: 46–59. <http://dx.doi.org/10.1016/j.ecoleng.2017.01.017>.

D’Odorico, Paolo et al. 2013. "Global Desertification: Drivers and Feedbacks." *Advances in Water Resources* 51: 326–44. <http://dx.doi.org/10.1016/j.advwatres.2012.01.013>.

Dettinger, Michael D., and Michael L. Anderson. 2015. "Storage in California’s Reservoirs and Snowpack in This Time of Drought." *San Francisco Estuary and Watershed Science* 13(2): 0–5. <http://escholarship.org/uc/item/8m26d692>.

De Deyn, Gerlinde B., Johannes H C Cornelissen, and Richard D. Bardgett. 2008. "Plant Functional Traits and Soil Carbon Sequestration in Contrasting Biomes." *Ecology Letters* 11(5): 516–31.

Diffenbaugh, Noah S., Daniel L. Swain, and Danielle Touma. 2015. "Anthropogenic Warming Has Increased Drought Risk in California." *Proceedings of the National Academy of Sciences* 112(13): 3931–36. <http://www.pnas.org/lookup/doi/10.1073/pnas.1422385112>.

Dull, R A. 1999. "Palynological Evidence for 19th Century Grazing-Induced Vegetation Change in the Southern" *Journal of Biogeography* 26(4): 899–912.
<http://www.jstor.org/stable/2656187%5Cnpapers://b09af06a-8ed4-446b-9067-dcd1aa2f4579/Paper/p1495>.

- Dwire, Kathleen A., J. Boone Kauffman, E. N. Jack Brookshire, and John E. Baham. 2004. "Plant Biomass and Species Composition along an Environmental Gradient in Montane Riparian Meadows." *Oecologia* 139(2): 309–17.
- Farrer, Emily C., and Katharine N. Suding. 2016. "Teasing Apart Plant Community Responses to N Enrichment: The Roles of Resource Limitation, Competition and Soil Microbes." *Ecology letters* 19(10): 1287–96.
- Fisk, Melanie C., Steven K. Schmidt, and Timothy R. Seastedt. 1998. "Topographic Patterns of above- and Belowground Production and Nitrogen Cycling in Alpine Tundra." *Ecology* 79(7): 2253–66.
- Forbis, Tara A. 2003. "Seedling Demography in an Alpine Ecosystem." *American Journal of Botany* 90(8): 1197–1206.
- Fraser, L. H., and E. B. Madson. 2008. "The Interacting Effects of Herbivore Exlosures and Seed Addition in a Wet Meadow." *Oikos* 117(7): 1057–63.
- Fryjoff-Hung, A, and Joshua H. Viers. 2012. "Sierra Nevada Multi-Source Meadow Polygons Compilation (v 1.0)." (December): 1–11.
- Gao, Yongheng, Xiaoyang Zeng, Martin Schumann, and Huai Chen. 2011. "Effectiveness of Exlosures on Restoration of Degraded Alpine Meadow in the Eastern Tibetan Plateau." *Arid Land Research and Management* 25(2): 164–75.
- Hammersmark, Christopher T, Mark C Rains, Allison C Wickland, and Jeffrey F Mount. 2009. "Vegetation and Water-Table Relationships in a Hydrologically Restored Riparian Meadow." *Wetlands* 29(3): 785–97. <http://www.springerlink.com/index/10.1672/08-15.1>.
- Hayhoe, K. et al. 2004. "Emissions Pathways, Climate Change, and Impacts on California."

Proceedings of the National Academy of Sciences 101(34): 12422–27.

<http://www.pnas.org/cgi/doi/10.1073/pnas.0404500101>.

Hobbs, Richard J. et al. 2006. “Novel Ecosystems: Theoretical and Management Aspects of the New Ecological World Order.” *Global Ecology and Biogeography* 15(1): 1–7.

Holmes, D. O. 1979. *Cultural Influences on Subalpine and Alpine Meadow Vegetation in Yosemite National Park. In First Conference on Scientific Research in the National Parks, Edited by RM Linn .*

Holmquist, Jeffrey G., Jutta Schmidt-Gengenbach, and Elizabeth A. Ballenger. 2014. “Patch-Scale Effects of Equine Disturbance on Arthropod Assemblages and Vegetation Structure in Subalpine Wetlands.” *Environmental Management* 53(6): 1109–18.

Howe, Henry F., Barbara Zorn-Arnold, Amy Sullivan, and Joel S. Brown. 2006. “Massive and Distinctive Effects of Meadow Voles on Grassland Vegetation.” *Ecology* 87(12): 3007–13.

Hulme, Philip E. 2008. “Herbivores and the Performance of Grassland Plants : A Comparison of Arthropod , Mollusc and Rodent Herbivory Author (S): Philip E . Hulme Source : The Journal of Ecology , Vol . 84 , No . 1 , (Feb . , 1996) , Pp . 43-51 Published by : British Ecologica.” 84(1): 43–51.

Huntly, Nancy. 1991. “Of Communities and Ecosystems.” *Annual Review of Ecology and Systematics* 22: 477–503.

Jobbagy, Esteban G., and Robert B. Jackson. 2000. “The Vertical Distribution of Soil Organic Carbon and Its Relation to Climate and Vegetation.” 10(2): 423–36.

Jónsdóttir, Ingibjörg S . 1991. “Effects of Grazing on Tiller Size and Population Dynamics in a Clonal Sedge (*Carex Bigelowii*) Author (S): Published by : Wiley on Behalf of Nordic

- Society Oikos Stable URL : <http://www.jstor.org/stable/354>." *Nordic Society Oikos* 62(2): 177–88.
- Junk, Wolfgang J. et al. 2013. "Current State of Knowledge Regarding the World's Wetlands and Their Future under Global Climate Change: A Synthesis." *Aquatic Sciences* 75(1): 151–67.
- Kayranli, Birol, Miklas Scholz, Atif Mustafa, and Åsa Hedmark. 2010. "Carbon Storage and Fluxes within Freshwater Wetlands: A Critical Review." *Wetlands* 30(1): 111–24.
- Kettenring, Karin M., Gary Gardner, and Susan M. Galatowitsch. 2006. "Effect of Light on Seed Germination of Eight Wetland Carex Species." *Annals of Botany* 98(4): 869–74.
- Knowles, John F., Peter D. Blanken, and Mark W. Williams. 2015. "Soil Respiration Variability across a Soil Moisture and Vegetation Community Gradient within a Snow-Scoured Alpine Meadow." *Biogeochemistry* 125(2): 185–202.
- Kuhn, Tim, Liz Ballenger, Rick Scherer, and John N. Williams. 2015. "Data Analysis and Assessment of High Elevation Wilderness Meadows Surveyed from 2008 to 2011, Yosemite National Park Resources Management and Science." : 98.
- Kuznetsova, A., P. B. Brockhoff, and Christensen R. H. B. 2017. "lmerTest Package: Tests in Linear Mixed Effects Models." : 1–26. doi: 10.18637/jss.v082.i13 (URL:[%0Ahttp://doi.org/10.18637/jss.v082.i13](http://doi.org/10.18637/jss.v082.i13)).
- Lawrence, Beth A., and Joy B. Zedler. 2013. "Carbon Storage by Carex Stricta Tussocks: A Restorable Ecosystem Service?" *Wetlands* 33(3): 483–93.
- Lee, Steven R. et al. 2017. "A Multi-Scale Evaluation of Pack Stock Effects on Subalpine Meadow Plant Communities in the Sierra Nevada." *PLoS ONE* 12(6): 1–20.
- Lenth, Russel V. 2016. "Least-Squares Means: The R Package Lsmeans." : 1–33.

- Levine, Jonathan M., and Janneke HilleRisLambers. 2009. "The Importance of Niches for the Maintenance of Species Diversity." *Nature* 461(7261): 254–57.
<http://dx.doi.org/10.1038/nature08251>.
- Linhart, Y B, and J L Gehring. 2003. "Genetic Variability and Its Ecological Implications in the Clonal Plant *Carex Scopulorum* Holm. in Colorado Tundra." *Arctic, Antarctic, and Alpine Research* 35(4): 429–33. <https://www.scopus.com/inward/record.uri?eid=2-s2.0-1242277752%7B&%7DpartnerID=40%7B&%7Dmd5=c5c0bf9e1310bf15ec86da631761ea93>.
- Loheide, Steven P. et al. 2009. "A Framework for Understanding the Hydroecology of Impacted Wet Meadows in the Sierra Nevada and Cascade Ranges, California, USA." *Hydrogeology Journal* 17(1): 229–46.
- Lowry, Christopher S., Jeffrey S. Deems, Steven P. Loheide, and Jessica D. Lundquist. 2010. "Linking Snowmelt-Derived Fluxes and Groundwater Flow in a High Elevation Meadow System, Sierra Nevada Mountains, California." *Hydrological Processes* 24(20): 2821–33.
- Lowry, Christopher S., Steven P. Loheide, Courtney E. Moore, and Jessica D. Lundquist. 2011. "Groundwater Controls on Vegetation Composition and Patterning in Mountain Meadows." *Water Resources Research* 47(9): 1–16.
- Martin, David, and Jeanne Chambers. 2002. "Restoration of Riparian Meadows Degraded by Livestock Grazing: Above-and Belowground Responses." *Plant Ecology* 163(1): 77–91.
- de Masancourt, Claire, Michel Loreau, and Luc Abbadie. 1998. "Grazing Optimization and Nutrient Cycling : When Do Herbivores Enhance Plant Production?" *Ecology* 79(7): 2242–52.
- Mcdonald, Tein, George D Gann, Justin Jonson, and Kingsley W Dixon. 2016. "International

- Standards for the Practice of Ecological Restoration – Including Principles and Key Concepts.” (First edition: December 2016): 48.
- McIlroy, S. K., and B. H. Allen-Diaz. 2012. “Plant Community Distribution along Water Table and Grazing Gradients in Montane Meadows of the Sierra Nevada Range (California, USA).” *Wetlands Ecology and Management* 20(4): 287–96.
- Meng, Lei et al. 2016. “Focus on the Impact of Climate Change on Wetland Ecosystems and Carbon Dynamics.” *Environmental Research Letters* 11(10): 1–4.
<http://dx.doi.org/10.1088/1748-9326/11/10/100201>.
- Miller, James R., and Brandon T. Bestelmeyer. 2016. “What’s Wrong with Novel Ecosystems, Really?” *Restoration Ecology* 24(5): 577–82.
- Moore, Peggy E. et al. 2000. “Meadow Response to Pack Stock Grazing in the Yosemite Wilderness: Integrating Research and Management.” *USDA Forest Service Proceedings RMRS-P-15-VOL-5*: 160–64.
http://www.fs.fed.us/rm/pubs/rmrs_p015_5/rmrs_p015_5_160_164.pdf.
- . 2013. “Net Primary Productivity of Subalpine Meadows in Yosemite National Park in Relation To Climate Variability.” 73(4): 409–18.
- Morton, Martin L., and Maria E. Pereyra. 2010. “Habitat Use by Yosemite Toads: Life History Traits and Implications for Conservation.” *Herpetological Conservation and Biology* 5(3): 388–94.
- Norton, Jay B. et al. 2011. “Soil Carbon and Nitrogen Storage in Upper Montane Riparian Meadows.” *Ecosystems* 14(8): 1217–31.
- . 2014. “Soil Carbon and Nitrogen Storage in Alluvial Wet Meadows of the Southern

- Sierra Nevada Mountains, USA." *Journal of Soils and Sediments* 14(1): 34–43.
- Ostoja, Steven M. et al. 2014. "Potential Environmental Effects of Pack Stock on Meadow Ecosystems of the Sierra Nevada, USA." *Rangeland Journal* 36(5): 411–27.
- Owen, Author D F, and R G Wiegert. 2018. "Nordic Society Oikos Do Consumers Maximize Plant Fitness ? Published by : Wiley on Behalf of Nordic Society Oikos Stable URL : <http://www.jstor.org/stable/3543467> REFERENCES Linked References Are Available on JSTOR for This Article : You May Need to Log I." 27(3): 488–92.
- Pierce, David W. et al. 2013. "Probabilistic Estimates of Future Changes in California Temperature and Precipitation Using Statistical and Dynamical Downscaling." *Climate Dynamics* 40(3–4): 839–56.
- Pyrooz, N.N et al. 2015. "Wet Meadow and Fen Mapping of Sequoia and Kings Canyon National Parks."
- R Core Team. 2016. "R: A Language and Environment for Statistical Computing." <https://www.r-project.org/>.
- Rasse, Daniel P., Cornelia Rumpel, and Marie France Dignac. 2005. "Is Soil Carbon Mostly Root Carbon? Mechanisms for a Specific Stabilisation." *Plant and Soil* 269(1–2): 341–56.
- Ratliff, Raymond D. 1985. "Meadows in the Sierra Nevada of California: State of Knowledge." *General Technical Report PSW-84*: 52.
http://www.fs.fed.us/psw/publications/documents/psw_gtr084/.
- Roth, S. et al. 1999. "Establishment of Helophytes in the Course of Fen Restoration Source : Applied Vegetation Science , Vol . 2 , No . 1 , From Basic to Applied Ecology : Vegetation Science for Nature Conservation (May , 1999), Pp . 131-136 Published by : Wiley Stable

URL :” *Applied Vegetation Science* 2(1): 131–36.

Rundel, Philip W. 2015. “Biomass, Productivity, and Nutrient Allocation in Subalpine Shrublands and Meadows of the Emerald Lake Basin , Sequoia National Park, California.” *Arctic, Antarctic, and Alpine Research* 47(1): 115–23.

Sarr, Daniel A, and Klamath Network-national Park. 2017. “Survival and Restoration Potential of Beaked Sedge (*Carex Utriculata*) in Grazed Riparian Meadows of the Southern Sierra Nevada (California) Author (S): Daniel A . Sarr and Tom L . Dudley Published by : University of Wisconsin Press Stable URL : Http.” 26(3): 186–88.

Sharsmith, C. 1959. *A Report on the Status, Changes, and Ecology of Back Country Meadows in Sequoia and Kings Canyon National Parks.*

Smith, Daniel R., Allan Ammann, Candy Bartoldus, and Mark M. Brinson. 1995. “An Approach for Assessing Wetland Functions Using Hydrogeomorphic Classification, Reference Wetlands, and Functional Indices.” *Wetlands Research Program Technical Report WRP-DE-9* (October): 90.

Stohlgren, T J, S H DeBenedetti, and D J Parsons. 1989. “Effects of Herbage Removal on Productivity of Selected High-Sierra Meadow Community Types.” *Environmental Management* 13(4): 485–91.

<http://www.springerlink.com/index/P102U71688020110.pdf%5Cnpapers://b09af06a-8ed4-446b-9067-dcd1aa2f4579/Paper/p322>.

Throop, William, and Rebecca Purdom. 2006. “Wilderness Restoration: The Paradox of Public Participation.” *Restoration Ecology* 14(4): 493–99.

Tripathee, R., and K. V R Schäfer. 2014. “Above- and Belowground Biomass Allocation in Four

- Dominant Salt Marsh Species of the Eastern United States." *Wetlands* 35(1): 21–30.
- Vale, Thomas R. 1987. "Vegetation Change and Park Purposes in the High Elevation of Yosemite National Park, California." *Annals of the Association of American Geographers* 77(1): 1–18.
- Van Der Valk, Arnold G., Tony L. Bremholm, and Elizabeth Gordon. 1999. "The Restoration of Sedge Meadows: Seed Viability, Seed Germination Requirements, and Seedling Growth of Carex Species." *Wetlands* 19(4): 756–64.
- Viers, Joshua H et al. 2013. "Montane Meadows in the Sierra Nevada: Changing Hydroclimatic Conditions and Concepts for Vulnerability Assessment." *General Technical Report* (January): 63.
- Vitousek, Peter M, Harold a Mooney, Jane Lubchenco, and Jerry M Melillo. 1997. "Human Domination of Earth' S Ecosystems." *Science* 277(5325): 494–99.
- Vittoz, Pascal, and Antoine Guisan. 2007. "How Reliable Is the Monitoring of Permanent Vegetation Plots? A Test with Multiple Observers." *Journal of Vegetation Science* 18(3): 413–22. <http://doi.wiley.com/10.1111/j.1654-1103.2007.tb02553.x>.
- Walden-Schreiner, Chelsey et al. 2017. "Environmental and Managerial Factors Associated with Pack Stock Distribution in High Elevation Meadows: Case Study from Yosemite National Park." *Journal of Environmental Management* 193: 52–63.
<http://dx.doi.org/10.1016/j.jenvman.2017.01.076>.
- Watson, Alan et al. 2015. "The Relationship Between Perceptions of Wilderness Character and Attitudes Toward Management Intervention to Adapt Biophysical Resources to a Changing Climate and Nature Restoration at Sequoia and Kings Canyon National Parks." *Environmental Management* 56(3): 653–63.

- Weixelman, Dave A. et al. 2011. "A Field Key to Meadow Hydrogeomorphic Types for the Sierra Nevada and Southern Cascade Ranges in California." *General Technical Report R5-TP-034*: 34.
- Williams, a. P. et al. 2015. "To California Drought during 2012 – 2014." *Geophysical Research Letters*: 1–10.
- Wolf, Evan Carl. 2017. "Ecosystem Function , Degradation , and Restoration in Wetlands of the Sierra Nevada , California."
- WRCC. 2018. "Western Regional Climate Center: California Climate Tracker."
<https://wrcc.dri.edu/monitor/cal-mon/index.html>.
- Wu, Gao Lin, Guo Zhen Du, Zhen Heng Liu, and Simon Thirgood. 2009. "Effect of Fencing and Grazing on a Kobresia-Dominated Meadow in the Qinghai-Tibetan Plateau." *Plant and Soil* 319(1–2): 115–26.
- Zentner, John, Jeff Glaspy, and Devin Schenk. 2003. "Wetland and Riparian Woodland Restoration Costs." *Ecological Restoration* 21(3): 166–73.