UNIVERSITY OF CALIFORNIA, MERCED

Ecological influences on soil resistance in Sierra Nevada subalpine meadows

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

in

Environmental Systems

by

Joy Sarah Baccei

Committee in charge:

Professor Stephen C. Hart, Chair
Professor Asmeret Asefaw Berhe
Professor Mitchel P. McClaran

2014

The Thesis of Joy Sarah Baccei is approved, and it is acceptable in quality and form for publication on microfilm and electronically:

Asmeret Asefaw Berhe, Ph.D.

Mitchel P. McClaran, Ph.D.

Stephen C. Hart, Ph. D.
Committee Chair

University of California, Merced

2014

Table of Contents

INTRODUCTION 1
STUDY AREA & METHODS 3
Study Area 3
Study Design & Field Measurements 6
Laboratory Analyses 8
Statistical Analyses 9
RESULTS 10
Question 1: Does SR, and potential ecological influences on SR, significantly differ among meadow plant community types and meadow gradient classes? 10
Question 2: Can a few key ecological factors be used to best explain SR among dominant plant community types in Sierra Nevada meadows? 14
DISCUSSION 18
Question 1: Significant differences in SR, and ecological influences on SR, among meadow plant community types and meadow gradient classes 18
Question 2: Best explanatory factors of SR among plant community types 20
Management Implications 22
Climate Change Implications 24
CONCLUSION 25
REFERENCES 27
APPENDICES 33
Appendix I: Meadow biotic and biotic variable mean values and standard errors, significantly different by plant community type and meadow gradient class 33
Appendix II: Meadow biotic and biotic variable mean values and standard errors. 34
Appendix III: Soil Particle Size Distribution & Texture Class 36

List of Figures

Figure 1. Study area map, location and appearance of subalpine meadows used to evaluate ecological influences on soil resistance. 4
Figure 2. Hydrologic regimes (hydric, mesic, xeric) of study meadows based on aerial imagery classification.. 7
Figure 3. Diagram of stratified random sampling design in a meadow. 7
Figure 4. Stratified random sampling with 1 m^2 study plots (quadrats). 8
Figure 7. Relationships between soil resistance and gravimetric water content 16

List of Tables

Table 1. Meadow and location attributes (size, elevation, coordinates, hydrogeomorphic type, soil subgroup and texture, plant community types, meadow gradients, and average annual stock use reported). 5
Table 2. Wetland code delineation for target plant community types. 6
Table 3. Two-way ANOVA models displaying significant spatial and limited temporal heterogeneity among multiple biotic and abiotic variables by two grouping factors 13
Table 4. Tukey honest significant difference post-hoc test results for variables that significantly differed by plant community type 14
Table 5. Pearson's product moment correlation matrix displaying positive and negative linear correlations among biotic and abiotic variables. 15
Table 6. Significant correlations between SR and multiple explanatory variables using Pearson's product moment correlation analysis.. 16
Table 7. Top five best explanatory models of SR based on AIC and BIC information criterions used in linear mixed effects regression (LMER). 17
Table 8. . Mean values and standard errors for select biotic and abiotic variables that signifcantly differed by plant community type 33
Table 9. Mean values and standard errors for select biotic and abiotic variables that signifcantly differed by meadow gradient class 33
Table 10. Emeric Lake meadow gradient, soil texture classification, landscape positions, plant community types, abiotic and biotic variable mean values and standard errors. 34
Table 11. Middle Lyell Canyon meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors 34
Table 12. Snow Flat meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors. 35
Table 13. Tuolumne Meadows meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors. 35
Table 14. Upper Lyell Canyon meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors 36
Table 15. Particle size distribution and soil texture class by plant community types 36
Table 16. Particle size distribution and soil texture class by meadow 36

Preface

This thesis was made possible as part of the Meadow Opening Dates (MOD) pilot study done at Yosemite National Park (YNP) by Resources Management and Science staff and academic collaborators from the University of Arizona and University of California, Berkeley from 2012-2013. Collaboration was made possible through a Cooperative Ecosystem Studies Unit (CESU) task agreement to assist with study design and analysis. We conducted this two-year study to address the question of appropriate timing for pack stock in wilderness meadows to inform the upcoming Wilderness Stewardship Plan.

The project had three main objectives: 1) examine soil resistance in relation to subalpine meadow dry-down rates, vegetative cover, and plant phenology over the growing season; 2) evaluate potential relationships of soil resistance to climatic and synoptic variables, and/or front-country conditions, to facilitate forecasting of anticipated meadow opening dates; and 3) develop an on-site rapid assessment protocol to inform the determination of actual opening dates. Specifically, we examined abiotic and biotic factors that could explain seasonal variation in soil resistance to pack stock trampling as meadow dry-down occurs over the growing season among dominant plant community types.

Study goals included examination of whether existing meadow opening date approaches at Sequoia Kings Canyon National Park (based on snow melt-out date) could be fine-tuned to be more specific to Yosemite (meadows are smaller and higher in elevation) by determining whether site-specific relationships exist among Yosemite wilderness meadows. The study ultimately seeks to provide a defensible scientific basis for decision making frameworks to determine optimal timing and facilitation of forecasted meadow opening dates for pack stock users without causing significant ecological damage.

Acknowledgements

I would like to acknowledge everyone who helped make this master's thesis possible. First, I would like to thank Tim Kuhn, hydrologist with Resources Management & Science at YNP for commendable project leadership with the Meadow Opening Dates study. I would also like to thank Laura Jones (ecologist with Resources Management & Science) and Linda Mazzu (Division Chief of Resources Management & Science) for their continued support with my decision to continue my education while retaining my position at YNP. Cooperative Ecosystem Studies Unit (CESU) academic collaborators include; Dr. Mitch McClaran, Dr. Jamie Bartolome, and graduate student Felix Ratcliff, who were all instrumental in aiding with study design and statistical analysis of preliminary data for the park study. Valuable and very much appreciated academic mentorship is attributed to my graduate committee; Dr. Stephen C. Hart (advisor), Dr. Asmeret Asefaw Berhe (committee member), and Dr. Mitch McClaran (committee member). I would also like to thank my project field partner, Brina Mocsny, who worked long hours and hiked many miles to make this study happen. In addition, I would like to thank members of the Hart Lab for their help with lab analysis, statistical analysis, and morale. Finally, I would like to thank my husband Josh for his enduring support.

ABSTRACT

Title: Ecological influences on soil resistance in Sierra Nevada subalpine meadows
Student: Joy Sarah Baccei
Degree: Master of Science, Environmental Systems
School: University of California, Merced 2014
Committee Chair: Stephen C. Hart

Meadows in the Western U.S. are greatly valued for their ecological and socioeconomic functions. Yet, they are subject to multiple stressors, which can result in loss due to degradation. In the Sierra Nevada, seasonally wet meadows are vulnerable to potentially significant damage by recreational pack stock use, when soil water content is high and vegetation is developing. On federally managed lands, meadow degradation from pack stock use is of significant concern. My study provides an investigation of ecological influences on spatial variability in meadow vulnerability to disturbance, as measured by soil resistance (SR). I examined SR on both local and site scales, by plant community type and meadow gradients class. My research addressed two ecological questions: 1) Does SR, and potential ecological influences on SR, significantly differ among plant community types and meadow gradient classes?; and 2) Can a few key ecological factors best explain variation in SR among meadow plant community types? My findings suggest that SR is a robust indicator of vulnerability to disturbance by recreational pack stock use. When stratifying by plant community type and meadow gradient class, my findings suggest that SR, and ecological influences on SR, significantly differed on local and site scales. Among factors that most influenced SR, water content was identified as the key driver of variation. In addition to water content alone, a few key factors best explained spatial variation in SR among plant community types. These included bulk density, root mass, and coarse fragments. On a site-scale, soil texture and subsequent water availability (water holding capacity and water content) most significantly differed between meadow gradient classes. My results indicate that even in dry years, some plant community types, representative of Sierran meadow hydrologic regimes, cannot support pack stock use without incurring damage. This may be due to variation in water availability and other covariates of SR based on differences in meadow gradient class. My findings provide new information to help develop vulnerability indices and risk assessments that aim to inform science-based, best management practices for maintaining meadow function. This can inform determination of pack stock site suitability among seasonally wet meadows.

INTRODUCTION

Meadows in the Western U.S. are greatly valued for their ecological and socioeconomic functions as water storage and filtration systems, flood attenuators, hotspots for plant diversity, critical habitat for wildlife, and popular recreational destinations (Norton et. al. 2014, Roche et. al. 2012). In spite of their ecological importance, more than 90 percent of California's wetlands have been lost to land conversion over the last 200 years (Dahl, 1990; Russo et. al. 2012). In the Sierra Nevada, meadows occupy only 10% of the entire range (Ratliff 1985), yet they are subject to multiple stressors including: land conversion and fragmentation from development, altered fire regimes, invasive species, climate change, recreational use, and overgrazing (UC Davis 2007).

Despite their relatively small size on the greater landscape, typically ranging in size from less than a hectare to hundreds of hectares, Sierran subalpine meadows support a diverse array of plants. They are mainly typified by grasses (*Poaceae*), sedge (*Cyperaceae*), and rush (*Juncaceae*) families (Ratliff 1985), which are palatable to pack stock animals (horses and mules). These graminoid plants serve as a significant food source for pack stock used for remote access to mountainous wilderness areas. Subalpine wilderness meadows also provide recreational opportunities for pack stock users and backpackers alike due to their scenery and water proximity. This makes them susceptible to damage by recreational use (Cole et. al. 1987).

Sierran meadows are particularly vulnerable to potentially significant damage by pack stock use when soil water content is high and vegetation is developing (DeBenedetti and Parsons 1983). During the early part of the growing season, post-snowmelt, pack stock use in wet meadows can cause hoof punching and trampling, which breaks the soil sod layer. Trampling by pack stock can disrupt soil stability, and alter and degrade meadow condition (McClaran and Cole 1993, Cole et. al. 2004) through a series of chain events. In the short term, soil disaggregation & compaction can occur, leading to increased bare ground and decreased plant productivity. In the long-term, this can ultimately lead to altered hydrology & species composition shifts, which significantly alters meadow condition (DeBenedetti and Parsons1983, Olson-Rutz et. al. 1996, McClaran 2000, Cole et. al. 2004). Alteration in meadow condition can lead to degradation through loss of biotic and abiotic ecosystem stability (Benedict 1982) and loss of proper function (Prichard et. a. 1996).

On federally managed lands, degradation from pack stock use is of significant concern. In recent years, Sierra Nevada pack stock use in meadows has become a focal point of both ecological concern and contentious litigation (USDC 2008). Within designated wilderness areas in national parks, the Wilderness Act of 1968 and the Organic Act of 1916, require that meadows are protected and preserved in natural condition, while also providing for visitor enjoyment. Often, public land management agencies are subject to increased public and political pressures to implement strategies allowing for use of natural resources while simultaneously maintaining ecological integrity (Wohl et. al. 2007). Yosemite National Park provides a poignant example of the juxtaposition land managers face when balancing ecosystem preservation with recreational opportunity, and high visitor use. Yosemite typically receives over four million visitors annually. While meadows are popular destinations, they constitute only 3% of the entire park area (Keeler-Wolf et. al. 2012). Best management practices are needed to avoid potential degradation in these distinct ecosystems. This can be done through determination of appropriate timing, intensity, and spatial arrangement of pack stock use in seasonally wet meadows subject to dry-down. Studies on this topic are limited, therefore my study aims to provide new information for guiding risk assessments and pack stock best management practices in Sierran wilderness meadows.

Previous pack stock use studies have found that high soil water content covaries with negative impacts on plant communities and meadow condition (DeBenedetti and Parsons 1983, Neuman1997, Shryock 2010, Lee 2013). However, little is known about which factors drive spatial variation in wet meadow vulnerability to disturbance. Like other wetlands, Sierran meadows are characterized by spatial and temporal variability in hydrology, soil properties, and vegetation. Among these factors, water content is the key driver of variability in plant communities (Ratliff 1985). Climatic factors drive temporal variability in water content in these often seasonal wetlands. Snowmelt timing and duration of seasonally high water tables influence length of soil saturation and short growing seasons (Moore et. al. 2013, Loheide et. al. 2009). Multiple ecological factors that characterize meadow plant community variability in water content may also influence vulnerability to disturbance by pack stock use. Factors include soil structure, water table depth, soil redox potential, and organic matter (Castelli et. al. 2000; Dwire et. al. 2006; Rodriguez- Iturbe and Porporato 2004, Chambers et. al. 1999, Loheide et. al. 2009).

Including other factors that influence water content and soil susceptibility to disturbance in meadow plant community types might improve on our understanding of pack stock use effects. Soil resistance (SR), a measure of soil strength, is one way of quantifying vulnerability to hoof punching and trampling in varying soil moisture conditions. This measure of soil strength is often used in rangeland management, and refers to the ability of soil to resist deformation under applied pressure (Lull 1959, Herrick and Jones 2002, Herbin 2011). The SR indicator can be used to determine both appropriate timing and spatial arrangement of pack stock in seasonally wet meadows that undergo drying. Previous studies on SR in livestock grazing in grassland systems have found that soil damage is dependent on three major factors: grazing intensity, soil type, and soil water content (Drewry et al., 1999; Daniel et al., 2002; Piwowarczk et. al. 2011). However, results from livestock grassland studies may not be applicable to Sierran meadows that undergo pack stock use. Subalpine meadows differ from grasslands in elevation, hydrology, soils, and vegetation. Pack stock animals may also exhibit different grazing behavior patterns than livestock. In the Sierra Nevada, one known study focused on SR in relation to pack stock use in wilderness meadows (Neuman 1997). However, the author sampled only two plant community types in two wilderness meadows. Hence, further expansion of plant community and meadow types is needed to account for local and site scale spatial variation in SR among meadows.

Multiple-scale assessments are an invaluable tool for developing proactive, long-term approaches to ecosystem management (Wohl et. al. 2007). Few meadow studies in the Western U.S. have included site-scale spatial variation, such as landform type (Heikes-Knapton 2009, Norton et. al. 2011, 2014). Previous studies have established that local-scale variation in plant communities and landscape positions influence meadow response to grazing (Martin and Chambers, 2001; Dwire et. al.2006; Blank et. al. 2006, McIllroy 2012, Lee 2013). However, meadow landform type also can be used to account for site-scale spatial variation. Weixelman and others (2011) recently classified Sierra Nevada meadows by hydrogeomorphic functional types based on earlier work by Brinson (1993). This classification system is based on hydrology (i.e., surface, groundwater), geomorphology (i.e., gradient class, parent material) and plant species. Within this system, meadow gradient class (low, middle, high) provides a simple and efficient means for categorizing landform type. Quantification of SR by plant hydrologic regime and meadow landform type may be useful for detecting spatial variability on both local and site-scales. This is because factors that influence SR among plant community types may differ from factors that influence SR among meadows of differing landform types (i.e., low versus middle, and high gradient slopes). While soils on steep slopes are more prone to soil erosion, soils on gentler slopes have greater sediment deposition (Brady and Weil 2008, Therrel et. al. 2006). Therefore, meadows of differing gradients likely have differing hydrology, vegetation, and soils.

My study provides a novel investigation of ecological influences on spatial variability in SR among plant community types and meadow gradients representing both local and site scales. No studies to-date have addressed ecological influences on SR to determine both local and site scale vulnerability to disturbance in meadow wetland ecosystems subject to seasonal pack stock use. I studied five riparian, subalpine meadows of differing gradient classes, and dominant plant community types, representative of Sierran meadows located in Yosemite National Park (YNP). As part of a larger temporal study that addressed the question of appropriate timing, my study addressed the question of appropriate spatial arrangement of pack stock in wilderness meadows.

My research addressed two ecological questions: 1) Does SR, and potential ecological influences on SR, significantly differ among plant community types and meadow gradient classes?; and 2) Can a few key ecological factors best explain variation in SR among meadow plant community types? My assumptions, based on previous related literature, were that soil water content would be detected as the key driver of variation among plant community types and meadows. In addition to soil water content, I assumed that a combination of a few key factors would best explanation variation in SR on local and site-scales. To address my study questions, I conducted a stratified, random sampling design to measure the SR response variable, and ecological influences on SR, in dominant plant community types within subalpine meadows at YNP. I took in-situ measurements of SR, and potential explanatory factors of SR, within randomized plots, in plant community types of differing hydrologic regimes, among meadows of differing gradient classes. My findings provide new information for guiding meadow risk assessments, monitoring and management.

STUDY AREA & METHODS

Study Area

My study area is located within the subalpine biotic zone, along the eastern portion of Yosemite National Park (YNP), in the central Sierra Nevada of California (Figure 1). Yosemite National Park experiences a Mediterranean-type climate with warm, dry summers and cool to cold, moist winters (Moore et. al. 2013). Mean minimum and maximum air temperatures at Tuolumne Meadows (one of the study sites; TM) are -12.7 °C and 21.3 °C for January and July, respectively (Table 1). The average annual precipitation in TM is 755 mm (Western Regional Climate Center 2011; Moore et. al. 2013). Typically, 80%–90% of annual precipitation in the subalpine zone (above 2,400 m) falls as snow. Seasonal snowpack accumulation occurs from October through April, and melts in a large pulse during May and June (Clow et al. 2010). Subalpine meadows in the park are often surrounded by large expanses of exposed bedrock and talus (Clow et. al. 2010), composed of granitic neo-glacial till, talus, and alluvium (Huber et. al. 1989). Areas within the subalpine zone are interspersed with coniferous forests and primarily herbaceous meadows.

Subalpine meadows selected for study (n=5) shared similar elevations and plant community types, based on spatial analysis of topographic and botanical data using ArcGIS software (ESRI, Redlands, CA). Some sites were located in designated wilderness, and frequented by pack stock over-night users (n=3), where average pack stock nights differed among sites for an 8-year reported period (Table 1). Other sites were non-wilderness and not used by stock (n=2), but were often frequented by day-use visitors (Fig. 1). Wilderness meadows used by pack stock included Emeric Lake, Middle Lyell Canyon, and Lyell Canyon-South, and non-wilderness, non-pack stock meadows included Snow Flat, and Tuolumne Meadows.

Field data were collected when plants were at peak standing biomass in July of 2013. This was done to measure plants at maturity, to control for temporal variation in above and below ground plant biomass (standing vegetation and roots), which may influence SR.

While meadows were similar in elevation, hydrogeomorphic type (i.e., riparian), soil subgroup, and dominant plant community types, they differed in gradient (2-4%), size (4-154 ha), stream type (ephemeral to perennial), and soil texture. Meadow soils were derived from granitic alluvium, were moderately acidic (mean pH = 5 for water solution), and ranged from coarse to fine textured (sandy loams to loams). Meadows were also subject to seasonal frost conditions and seasonal soil saturation (Table 1).

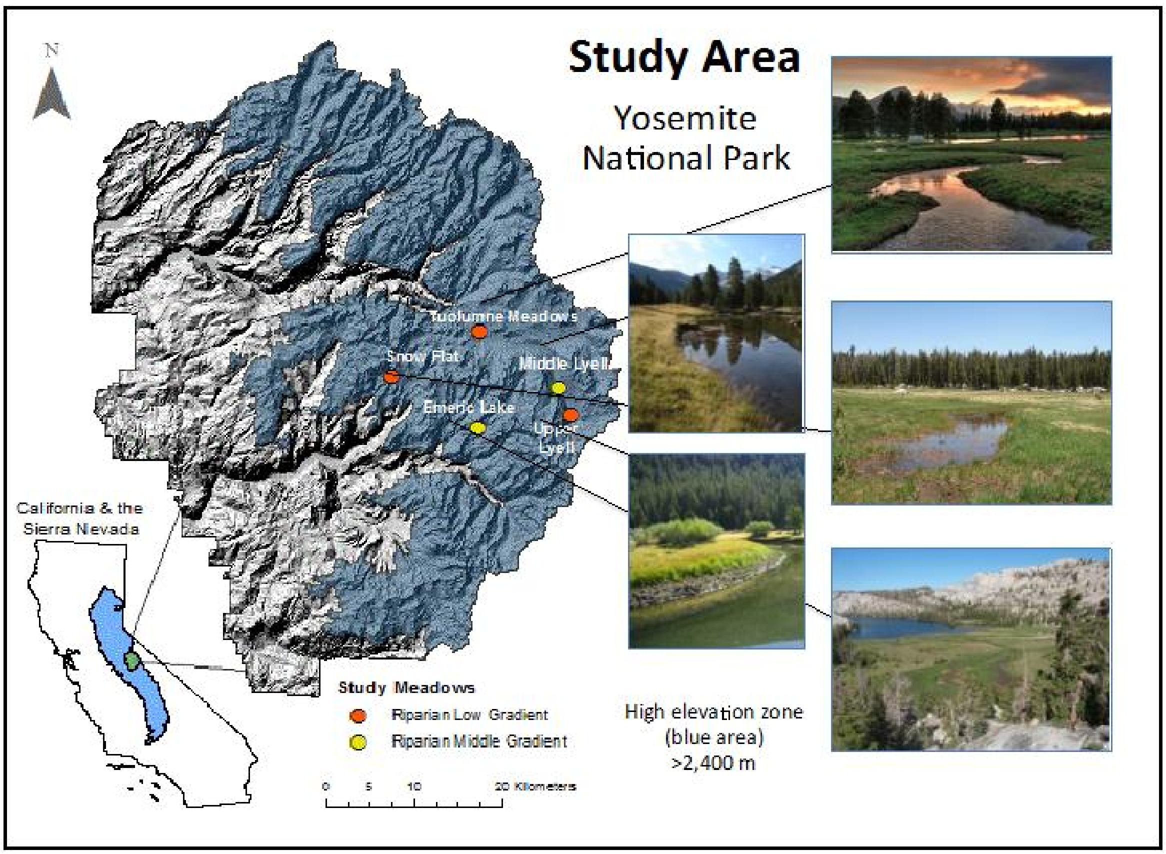

Figure 1. Location and appearance of subalpine meadows used to evaluate ecological influences on soil resistance. Study area map depicts high elevation zone (blue area, >2,400 m) in eastern portion of Yosemite National Park study area (left) within central Sierra Nevada of California (bottom left). Photographs (right) of individual study sites showing their location within the park and hydrogeomorphic type. Photographs (right) of individual study sites showing their location within the park and hydrogeomorphic type (riparian low gradient and riparian middle gradient).

Table 1. Meadow attributes (size, elevation, easting and northing coordinates (based on Universal Transverse Mercator (UTM), North American Datum (NAD) 83; Zone 11 projection), hydrogeomorphic type, soil subgroup, and plant type: *Calamagrostis breweri* (CB), *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK). Meadow gradients: low: <2%, middle: 2-4%. Average annual stock use reported for Lyell Canyon is not reported by meadow within the canyon, therefore estimated use per meadow is shown in parentheses. X denotes plant community type sampled, NA denotes meadows that did not receive pack stock use, and were therefore not applicable for reported average annual stock use from 2004-2011.

Location	Easting	Northing	Size (hectares)	Elevation (meters)	Meadow Gradient (%)	Hydrogeomorphic Type	Hydrologic Features	Soil Subgroup	Plant Community Types				Average reported annual stock use* (2004-2011)
									CB	CV	DC	PK	
Emeric Lake	290212	4184049	9.7	2,846	3	Lacustrine fringe and riparian middle gradient	Emeric Lake and ephemeral stream	Xeric Dystrocryepts	X			X	89
Snow Flat	280382	4190163	4	2,667	1	Riparian low gradient	Perennial stream	Xeric Dystrocryepts	X		X	X	NA
Middle Lyell Canyon	299604	4188795	6.1	2,708	3.7	Riparian middle gradient	Lyell Fork of the Tuolumne River	Oxyaquic Dystrocryepts and Xeric Dystrocryepts	X	X	X		0 (168)
Upper Lyell Canyon	300749	4186397	14	2,737	1.9	Riparian low gradient	Lyell Fork of the Tuolumne River	Oxyaquic Dystrocryepts and Xeric Dystrocryepts		X	X	X	336 (168)
Tuolumne Meadows	290104	4194858	153.8	2,621	2	Riparian low gradient	Tuolumne River	Oxyaquic Dystrocryepts and Xeric Dystrocryepts	X	X		X	NA

Dominant plant species targeted for study included those considered palatable to pack stock, and representative of hydrologic regimes (xeric, mesic, hydric) and wetland indicator types common within Sierra Nevada meadows. Plant community types represented four different hydrologic regimes based on wetland status as defined by US ACE (Table 2). This was done to detect whether SR, and multiple explanatory factors of SR, differed by plant type hydrologic regimes. Plant species, corresponding hydrologic regimes, and wetland indicator types included: *Carex vesicaria* (CV; hydric, obligate wetland), *Deschampsia cespitosa* (DC; hydric-mesic, facultative wetland), *Calamagrostis breweri* (CB; mesic; facultative), and *Ptilagrostis kingii* (PK; mesic-xeric, facultative upland). While CB is now considered a facultative wetland species (US ACE 2013), it is treated as facultative for the purposes of this study based on former classification (Reed et. al. 1998). The reason for this is that CB was intended to represent mesic conditions.

Combinations of plant species sampled among meadows differed depending on which species were most dominant among sites. Within each site, two to three of the four target plant community types were sampled. Target plant species sampled comprised the majority of study meadow areal extent (>75%), although some meadow areas were left unsampled because they were not comprised of target plant species. Ancillary data on plot landscape position were also collected because plant community types representing various hydrologic regimes were not always located in the same landscape positions (i.e., upland/meadow edge, water edge; stream, oxbow, pond, and mid-floodplain; classification based on Blank et. al. 2006).

Table 2. Wetland code delineation for target plant community types (based on US ACE 2013).

Plant Code	Plant Name	Wetland Code	Wetland Name	Likelihood to Occur in Wetland
CV	*Carex vesicaria*	OBL	Obligate	>99%
DC	*Deschampsia cespitosa*	FACW	Facultative-wetland	67-99%
CB	*Calamagrostis breweri*	FAC	Facultative	34-66%
PK	*Ptilagrostis kingii*	FACU	Faculative-upland	1-33%

Study Design & Field Measurements

I employed a stratified, random sampling design to measure soil resistance and multiple biotic and abiotic explanatory variables. ArcGIS 10.1 software was used to classify aerial imagery by hydrologic regime among study meadows (Figure 2). Study plots were randomly generated within dominant plant community types representing differing hydrologic regimes (Fig. 3) based on previously collected botanical survey spatial data (Ballenger et. al. 2008). Aerial imagery classification by hydrologic regime was done in ArcGIS using the IsoCluster imagery analysis tool of Normalized Difference Vegetation Index (NDVI) transformed National Agricultural Inventory Program (NAIP) aerial imagery. The NDVI transformation uses the normalized differences between red and near infrared bands to detect spatial differences in plant productivity and moisture (Jensen 2007). Classification was based on 2012 imagery, as 2013 imagery was not available. Both water years shared similar April 1st snow water equivalents (SWE), where 2012 SWE was 50% of average, and 2013 SWE was 53% of average (DWR, CDEC 2014).

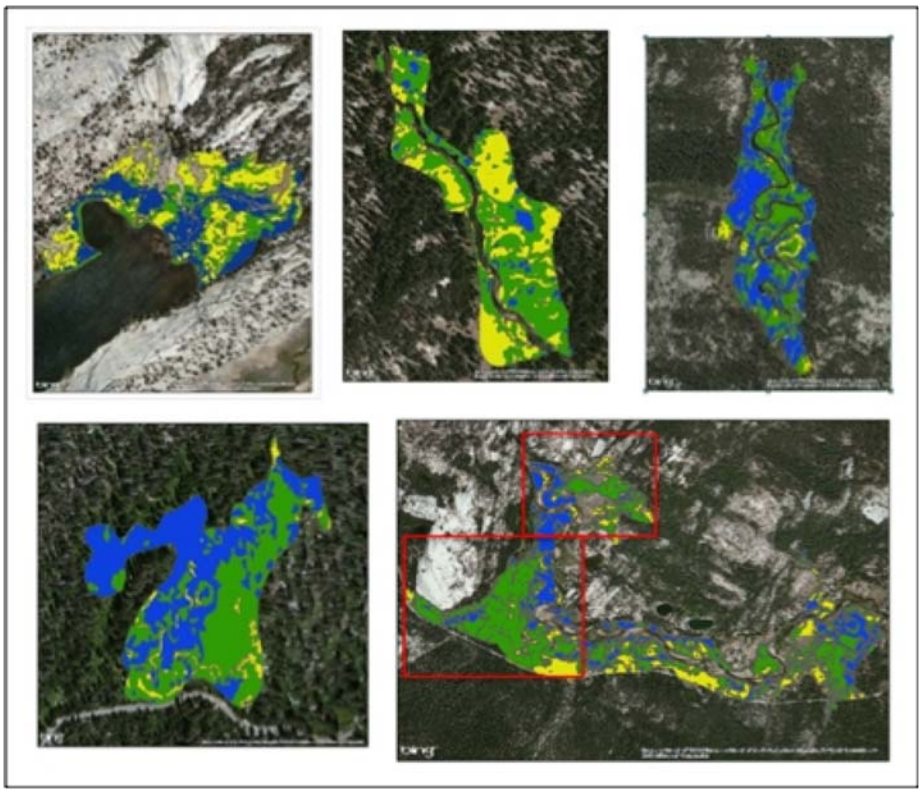

Figure 2. Hydrologic regimes (hydric, mesic, xeric) of study meadows based on aerial imagery classification. Imagery derived from National Agricultural Inventory Program (NAIP) for 2012, and transformed using Normalized Difference Vegetation Index (NDVI). Blue=hydric area, green=mesic area, yellow=xeric area. Upper left=Emeric Lake, upper middle=Middle Lyell, upper right=Upper Lyell, bottom left=Snow Flat, bottom right=Tuolumne Meadows (red boxes indicate approximate study area).

Study plot locations were selected within dominant plant community types (n=4) representative of varying hydrologic regimes (n=4) within study meadows (n=5). Meadows were classified as either low gradient (n=3) or middle gradient (n=2) based on hydro-geomorphic type (low gradient <2%, middle gradient 2-4%), as classified by Weixelman and others (2011). At each meadow, two to three of the four plant community types were sampled because not all plant community types occurred within each meadow. Plots were spaced at least 4 m apart to ensure spatial independence based on vegetation composition (Weixelman and Riegel 2012). Plot coordinates were uploaded onto Trimble Juno ST GPS devices for navigation to plot locations and collection of field data within plots. Weekly sampling of six plots per plant type was done to achieve a total of 18 replicate plots per plant type over a three-week period in July, 2013 (Fig. 3).

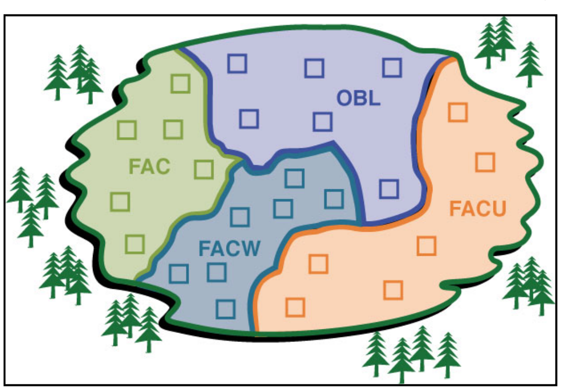

Figure 3. Diagram of stratified random sampling design in a meadow. Four dominant plant community types used represented four hydrologic regimes and wetland indicator statuses: obligate (OBL), facultative (FAC) facultative wetland (FACW), and facultative (FACU). Randomized one square meter plots depicted for one (n=6) of three study weeks (n= 18 plots total) within plant community types (figure not to scale).

Soil resistance was measured within study plots using a dynamic cone penetrometer (Synergy Resource Solutions Inc., Belgrade, MT; Herrick and Jones 2002). Plots were oriented North-South, and measurements were taken 30 cm from the southwest corner of plots (Figure 4). Explanatory variables of SR measured included volumetric water content and plant cover. Volumetric water content (0-12 cm depth) was determined using a HydroSense II Time Domain Reflectometer (Campbell Scientific, Logan, UT). Absolute foliar plant cover was determined based on ocular estimates by the same observer (Elzinga et. al. 1998) within 1 m^2 plots and nested 707 cm^2 plots located within a 5 cm radius from the center of penetrometer readings.

Intact soil cores (5 cm dia.by 15 cm depth) were taken using an AMS soil core sampler (AMS Inc., American Falls, ID) to assess additional soil properties that may covary with SR. The total number of soil cores extracted from each meadow varied depending on plant community types sampled, where one meadow had two plant community types, while others had three types. Two of the four target plant community types were sampled at Emeric Lake (soil cores extracted=36), while three of the four plant species were sampled among Middle and Upper Lyell Canyons, Snow Flat, and Tuolumne meadows (soil cores extracted=54). In total, 252 soil cores (one core per plot) were extracted from within a 5-cm radius of the center of penetrometer readings. Soil cores were capped and enclosed in 4-mm thick, polyethylene bags to prevent water loss. They were kept as cool as possible in the field (by keeping them in shaded areas) and during transport to the laboratory (by placing them in coolers with ice blocks). Once in the laboratory, soils were stored in a cold room at 4 °C prior to processing, which occurred over one month.

Figure 4. Stratified random sampling with 1 m^2 study plots (quadrats). In-situ sampling done for following: soil resistance (using dynamic cone penetrometer; far left), soil moisture (using TDR; middle left), absolute aerial foliar cover (via ocular estimation; middle right), and soil sampling (using AMS corer; far right).

Laboratory Analyses

Soil properties analyzed in a laboratory included: root mass (within soil cores), percent coarse fragments (2-4 mm), gravimetric water content (105 °C), water holding capacity, particle size distribution (dry mass percent sand, silt, clay fractions), bulk density, pH, soil organic matter content, carbon and nitrogen concentration. Field-moist soil cores were removed from polycarbonate sleeves, sieved field-moist through a 4-mm mesh sieve, and roots (minimal plant litter was included) and coarse fragments were separated by hand with tweezers. Roots (mostly fine and less than 2mm in diameter) were oven-dried at 70 °C, weighed (g), and units were converted to g/m^2 and percentage of soil core. Coarse fragments were oven dried at 105 °C and weighed (g). Sieved soils were air-dried (20-25 °C) or oven-dried (105 °C) depending on analysis.

Gravimetric water content (GWC) was determined by weighing drying field-moist, sieved soils (5 g) at 105°C in a gravity convection oven for 48 hours. Particle size distribution (PSD) was determined using the hydrometer method (Bouyoucos 1962, Gee and Bauder 1986). Bulk density (BD) was calculated as the oven-dry mass of soil (< 2 mm fraction) per core volume. Soil pH was measured on a 1:1 (w/v) soil to deionized water soil suspension (10 g soil to 10 mL of water) using a Fisher Scientific Accumet Basic AB15 pH meter (Thermo Fisher Scientific, Waltham, MA) and Ross Sure Flow glass combination electrode (Sparks et. al. 1996).

Soil organic matter content was determined by Loss on Ignition (LOI; modified from Combs and Nathan 1998; Schulte and Hopkins 1996; and Storer 1984). Sieved, air dried soil (5-10 g, < 4 mm fraction) was oven-dried (105°C for 8 h), and then placed in a muffle furnace at 360 °C for 2 h. Carbon (C) and Nitrogen (N) concentrations were determined for a subset of soil samples to verify accuracy of the LOI method. Elemental analysis was done using a Costech ECS 4010 CHNSO elemental analyzer (Valencia, CA) on finely ground, oven-dried soils.

Soil water holding capacity was determined using modified methods from Haubensak et al. (2002). Ten to 15 g of sieved (<2 mm), air-dried soils were placed in weighed Buchner funnels containing wetted, Whatman No. 2 filter paper. Soils were wetted with deionized water repeatedly, and allowed to drain by gravity for 48 h at 100% humidity, in a closed environment. Suction (-33 kPa) was then applied to soils by attaching Buchner funnels to a sidearm flask connected to a vacuum line. When soil drainage ceased in response to the applied suction, Buchner funnels containing the soil was reweighed. Soil water holding capacity (%) was calculated as the ratio of the water mass retained (after accounting for the soil water content at air-dryness) to the oven-dry mass of the soil, multiplied by 100%. A separate soil subsample was used to estimate the oven-dry mass equivalent.

Statistical Analyses

A total of 252 observations were available for analysis for the following variables: soil resistance (SR), total and target vegetation cover for two plot sizes ($1m^2$, $707\ cm^2$), root mass (g/m^2), bulk density (BD; g/cm^3), volumetric water content (VWC %), gravimetric water content (GWC %), soil organic matter (SOM %), percent carbon and nitrogen (C and N), and percent roots and coarse fragments (>2mm, >4mm). Laboratory analysis was only done on a subset of soil cores for the following variables: pH, water holding capacity (WHC %), and particle size distribution. Therefore, a subset of the entire data set (n=252) was compiled for all statistical analyses to ensure equal numbers of observations among all variables (n=98, after accounting for some missing laboratory data). All percentage values were converted to whole numbers (by multiplying by 100). Summary statistics were generated to quantify means and standard errors of variables by: plant type (n=4), meadow (n=5), and meadow gradient class (n=2;Tables 8-15, Appendix I-II). All statistical analyses were done using the statistical program R, version 0.97.551 (R Core Team 2012). For statistical tests, an a priori α level of 0.05 was used to determine significance.

Explanatory variables of SR included multiple biotic and abiotic factors that may influence SR. Biotic variables included total vegetation cover for two plot sizes ($1\ m^2$, $707\ cm^2$), and root mass (g/m^2) and percentage. Abiotic variables included: bulk density (BD; g/cm^3), field-measured volumetric water content (VWC, %), laboratory-measured gravimetric water content (GWC %), soil organic matter (SOM, %), pH, water holding capacity (WHC, %), and particle size distribution data; percent sand, silt, clay, coarse fragments ((>2 mm, >4 mm). Ancillary data were also analyzed for descriptive purposes. These included: redoxymorphic feature depth (cm), and percent carbon and nitrogen, and carbon-to-nitrogen (C:N) mass ratios. Soil redoxymorphic features indicate oxidation and reduction patterns indicative of seasonal saturation and dry-down of meadow soils, which could potentially affect SR (Dwire et. al. 2006). Percent C, N, and corresponding C:N ratios are indicative of differing SOM decomposition rates among meadows. Normality was assessed for all variables using histograms, and transformations (i.e., log, sq. root).

To address my first research question, I employed a two-way ANOVA to detect whether SR, and potential ecological influences on SR, significantly differed among plant community types and meadow gradient classes. This was done to detect whether there was spatial variability in the SR response variable and potential explanatory variables of SR on local and site scales. To detect whether there was potential temporal variability in my dataset, interaction terms were also included between study variables and time (study weeks) by plant community type and meadow gradient class grouping variables. While temporal variability was not the study focus of my study, I chose to test whether temporal patterns were present in the data that may have confounded spatial variability detected, as these data were collected over a three week period. When ANOVA models were significant, I conducted Tukey-Kramer HSD post hoc tests to differentiate significant differences between plant community types (using the ‘multcomp’ package in R). Post-hoc tests were not needed for meadow gradient, since only two classes were used.

Soil resistance (SR) response values were compared to a threshold SR value of 500 kPa (McClaran et. al. 2014) using one-way analysis of variance (ANOVA). The threshold value represents the SR needed to support a horse with rider or mule with load with incurring disturbance to soils. In relation to my first research question, I conducted this analysis determine whether plant community types and meadow gradients significantly differed in ability to support pack stock use without incurring disturbance. The SR threshold was determined as a conservative estimate of the SR needed to support a horse with rider or mule with load based on previous work by Schofield and Hall (1986) and Kai et al. (2000). The threshold value was modified conservatively to account for variation in animal, rider, load weight, and measurement error (McClaran et. al. 2014). Mean SR values for plant community types among meadows were compared with the SR threshold. Post hoc tests were used when ANOVA models were significant.

To address my second research question, I used Pearson's product moment correlation analysis (using 'corrplot' package in R) and multiple linear mixed effects regression (LMER; using the'lme4' package in R). Pearson's correlation analysis was used to reveal which ecological factors were most correlated with SR, and which potential explanatory factors of SR were collinear (highly correlated at $r \geq 0.75$, Philippi 1993, Legendre and Legendre 1998; Graham 2003). The LMER approach was used to determine whether a few key ecological factors best explained variation in SR among meadow plant community types. This approach takes into account fixed variability among plant community types, while also accounting for random variability among sites (meadows). The LMER mixed, modeling approach also accounts for stratified study design, where plant community types were nested within study meadows that varied randomly. By accounting for stratified study design, this approach addressed autocorrelation and non-constant variance that arose when using a larger dataset (n=98), rather than carrying out regression on the means (n=14) by plant community type (Zuur et. al. 2007).

Best explanatory models of SR were selected using Akaike and Bayesian information criterions (AIC and BIC) based on results from backwards, stepwise regression (Bates et. al. 2012). The backwards stepwise approach was used to systematically remove non-significant variables from a full model of all non-collinear explanatory variables. Best model criterion used aim to identify model goodness-of-fit balanced with parsimony (Crawley 2007), although each criterion has differing model selection goals (Dziak et. al. 2012). The AIC provides an explanation of ecological complexity in a system, while the BIC penalizes complexity more heavily (Zuur et. al. 2007), which may aid in revealing the best, underlying true model. Hence, models with lowest AIC values were assumed to be best for explaining ecological complexity, while models with lowest BIC values were assumed to best for explaining key drivers of variability (or best, true model) in a system. Another approach is to use AIC and BIC together (Dziak et. al. 2012) to balance model goodness-of-fit balanced with parsimony.

Typically, an AIC difference of 2 between two models indicates significant improvement of one model over the other, although a larger difference provides stronger evidence of model improvement (Dziak et. al. 2012, Zuur et. al. 2007). In LMER, significant model improvement is denoted by significant p-values (<0.05) associated with maximum likelihood ratio tests and chi-squared (χ^2) values. Logistical likelihood and χ^2 values are derived from comparison of models that contain explanatory factors in question against the model without explanatory factors in question (the null model) based on Bates et. al. (2012). Chi-squared values indicate the reduction in deviance from the maximum likelihood criterion (smaller deviance indicates better fit) between candidate models being compared and the null model (Bates et. al. 2012). Hence, best explanatory models identified had lowest AIC or BIC values, also had smallest logistical likelihood, deviance, χ^2, and p-values. Best models were evaluated by examining scatterplots of predicted versus actual SR values, and residual plots Model assumptions (normality, linearity, independence, non-constant variance) were assessed.

RESULTS

Question 1: Does SR, and potential ecological influences on SR, significantly differ among meadow plant community types and meadow gradient classes?

Temporal variability was not a significant factor in any of the variables measured, regardless of grouping by plant community type or meadow gradient class. Exceptions included root mass and N among plant community types, SOM and C among meadow gradients, and coarse fragment percentage among plant community types and meadow gradients (Table 3). Root mass was expected to change due to plant root growth during peak growing season. Changes in SOM, C, and N may have been due to changes in litter inputs and decomposition states among plant community types. Changes in percent coarse fragments likely reflected spatial variability among plots sampled over time. Thus, sampling date (by week) did not appear to alter explanatory variables measured, which indicates that pooling data over a three week period is acceptable.

Soil resistance (SR) significantly differed among meadow plant community types (F=9.92, p<0.00) and meadow gradient classes (F=8.63, p<0.00; Table 3). Among plant community types, ecological influences on SR that most significantly differed included: total vegetation cover in 1 m^2 study plots (F=15.64, p<0.00), BD (F=10.83,p<0.00), GWC (F=7.03, p<0.00), and WHC (F=6.20, p<0.00). Among meadows of differing gradient classes, greatest significant differences included: WHC (F=13.22, p<0.00) and GWC (F=15.02, P<0.00), and particle size distribution (PSD): sand (F=30.64, p<0.00) silt (F=27.92, p<0.00), clay (F=16.86, p<0.00). See Tables 16 and 17 in Appendix III for details on means and standard errors.

The obligate wetland plant type (CV) most significantly differed in SR from facultative (CB) and facultative upland (PK) plant types , based on post-hoc tests (Table 4). *Calamagrostis breweri* had highest mean SR, whereas CV had lowest SR (Table 8, Appendix I). *Carex vesicaria* also had greater mean WHC, GWC, and SOM, and lower mean BD, in relation to all other plant types. Water holding capacity was greatest for CV (85%), followed by PK (65%), CB (54%) and DC (54%). Mean GWC was also highest for CV (114%), followed by DC (76%), CB (61%), and PK (55%). Plant community types shared similar mean BD (0.51 g/cm³), with the exception of CV which had much lower BD (0.41 g/cm³). Among meadows of differing gradient classes, low gradient meadows had significantly lower mean SR (452 kPa; p<0.00) than middle gradient meadows (709 kPa; Table 9, Appendix I).

Particle size distribution (PSD) showed greatest significant differences in silt and sand content between obligate (CV) and facultative upland (PK) plant types (p=0.05, Table 4). Mean silt content for CV was 40%, while mean sand content for PK was 59% (Table 15, Appendix III). Greater silt content in CV also corresponded to oxbow landscape positions for Tuolumne and Upper Lyell meadows (Tables 13,14 , Appendix 1I).

Among meadows, sand and silt content significantly differed by gradient class. Differences were greatest between EL (middle gradient; sand=69%, silt=21%) and TM and UL (low gradient; sand=45%, silt=41% for both). Mean clay content was higher for two low gradient meadows (TM and UL; 14% respectively) in comparison with other meadows. Middle gradient meadows also had coarser grained soil textures (sandy loams) in comparison with low gradient meadows, which had finer textured, soils classified as loams (Fig. 5, Table 9, Appendix I).

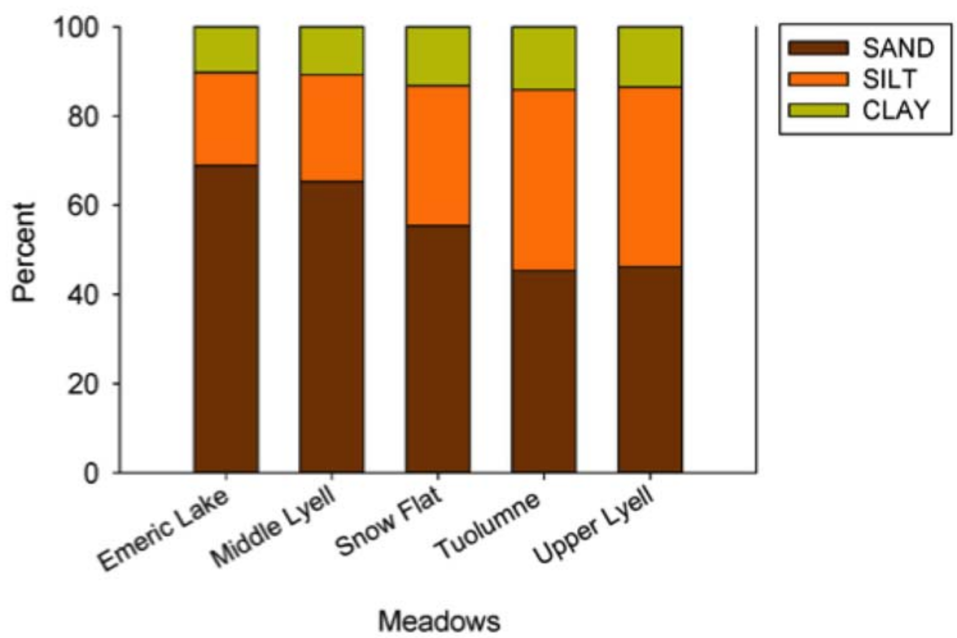

Figure 5. Particle size distribution (percent sand, silt, clay) among middle gradient meadows with sandy loam soil textures (left) and low gradient meadows of loam soil textures (right). Color scheme: sand=brown, silt=orange, clay=yellow.

Differences in SR threshold among plant community types and meadows

Soil resistance (SR) values significantly differed from the SR threshold value of 500 kPa, among plant community types ($F=27.32$, $p<0.00$) and meadow gradient classes ($F=25.58$, $p<0.00$). *Calamagrostis breweri* had consistently highest SR values across meadows (mean SR=890 kPa) that exceeded the 500 kPa SR threshold (Fig. 6) *Ptilagrostis kingii* soils exceeded the threshold at some meadows, but not others (mean SR=666 kPa). *Deschampsia cespitosa* and CV soils did not achieve the SR threshold (mean SR=232 and 270 kPa respectively). *Carex vesicaria* most significantly differed from all other plant community types ($p<0.00$) based on post-hoc tests (Table 4), in that it had lowest SR. *Calamagrostis breweri* was most different from CV ($p<0.00$), in that it had the highest SR values, followed by *Ptilagrostis kingii* ($p<0.00$; Fig. 6, Table 4).

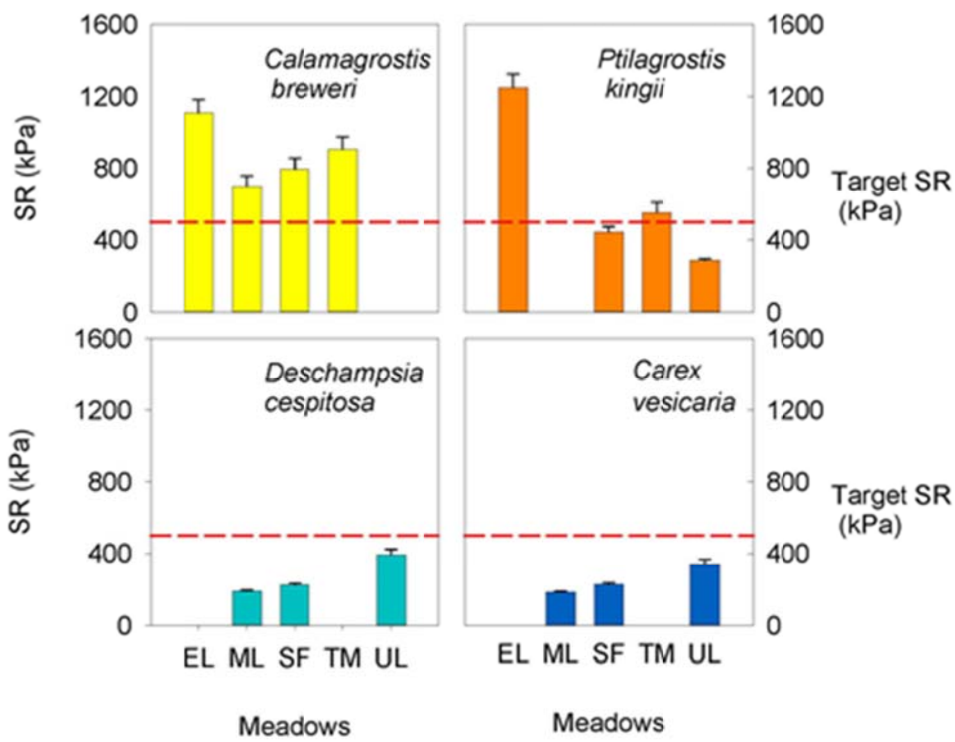

Figure 6. Soil resistance (SR) by plant type among meadows for the month of July, 2013. Dashed line indicates SR threshold value (500 kPa) needed to support a horse with rider or mule with load without incurring soil disturbance. Error bars represent standard error across plots, based on plant community types across meadows.

Among meadows of differing gradient classes, mean SR was below the SR threshold for low gradient meadows (452 kPa), and above the threshold for middle gradient meadows (709 kPa). However, variability was high among meadows, where mean SR for low gradient meadows ranged from 351-511 kPa (SE ±39-53), while mean SR for middle gradient meadows ranged from 346-1177 kPa (SE ±36-76). See Table 9, Appendix I for further details.

Table 3. Two-way ANOVA models displaying significant spatial and limited temporal heterogeneity among multiple biotic and abiotic variables by two grouping factors representing local-scales: plant types (n=4), site-scales: meadow gradient class (n=2) for 3 study weeks in July 2013 (n=98). Differences among weeks and interaction between week and grouping variables indicate significance of temporal variation or between week spatial variation. P-values (p) statistically significant at 95% confidence level (<.05). Bolded p and F-values (F) indicate greatest significance at a 99% confidence level of p < 0.004. The SR response variable was log transformed, and the following were square root transformed: GWC, WHC, SOM, C, N, C:N, roots, and clay. List of acronyms and abbreviations: Soil resistance (SR), bulk density (BD), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), tot. total vegetation cover (tot. veg. cover), coarse fragments (coarse frag.).

Grouping Factor	Plant Type						Meadow Gradient					
	Plant Type		Week		Plant Type * Week		Meadow Gradient		Week		Meadow Gradient*Week	
Variables	F	p	F	p	F	p	F	p	F	p	F	p
SR (kPA)	**9.92**	**0.000**	0.10	0.758	0.45	0.720	**8.63**	**0.004**	0.05	0.82	1.57	0.213
BD (g/cm³)	**10.83**	**0.000**	1.80	0.183	2.27	0.086	3.20	0.077	1.32	0.25	2.34	0.130
VWC (%)	4.27	**0.007**	0.16	0.692	0.18	0.907	**11.05**	**0.001**	0.08	0.78	2.35	0.128
GWC (%)	**7.03**	**0.000**	0.18	0.672	1.73	0.166	**15.02**	**0.000**	0.11	0.74	1.77	0.186
WHC (%)	**6.20**	**0.001**	0.98	0.325	0.53	0.664	**13.22**	**0.000**	1.22	0.27	2.99	0.087
pH	0.77	0.513	0.15	0.703	0.09	0.964	2.34	0.130	0.10	0.76	0.26	0.610
SOM (%)	0.95	0.419	0.49	0.486	2.40	0.073	6.64	0.012	0.60	0.44	5.31	0.023
C (%)	1.65	0.184	0.22	0.640	2.26	0.087	3.46	0.066	0.27	0.61	5.35	0.023
N (%)	3.18	0.028	0.50	0.482	2.89	0.040	7.51	0.007	0.58	0.45	1.12	0.294
C:N (%)	0.65	0.585	0.15	0.696	0.17	0.918	2.48	0.119	0.21	0.65	3.33	0.071
Sand (%)	2.38	0.075	0.05	0.821	0.59	0.621	**30.64**	**0.000**	0.16	0.69	0.56	0.455
Silt (%)	2.76	0.047	0.08	0.784	0.62	0.605	**27.92**	**0.000**	0.19	0.66	0.39	0.532
Clay (%)	0.77	0.517	0.02	0.892	0.56	0.645	**16.86**	**0.000**	0.00	0.98	0.44	0.507
Coarse frag. >2mm (%)	0.60	0.617	0.87	0.354	0.70	0.552	4.16	0.044	1.40	0.24	30.18	**0.000**
Coarse frag. >4mm (%)	1.02	0.390	0.77	0.382	3.18	0.028	**8.63**	**0.004**	0.86	0.36	7.99	0.006
Tot. Veg. Cover (1 m^2)	**15.64**	**0.000**	0.97	0.329	1.64	0.186	1.78	0.185	0.94	0.34	0.02	0.878
Tot. Veg. Cover (707 cm^2)	6.27	**0.001**	0.29	0.593	1.15	0.335	0.26	0.611	0.25	0.62	0.57	0.453
Roots (g/m^2)	0.94	0.424	3.79	0.055	2.15	0.099	0.47	0.494	3.30	0.07	0.50	0.480
Roots (%)	2.37	0.076	2.99	0.087	3.83	0.012	0.01	0.909	2.42	0.12	0.00	0.947

Table 4. Tukey honest significant difference post-hoc test results for variables that significantly differed by plant community type: SR, BD, WHC, GWC, VWC, SAND,SILT, and CLAY. Table displays statistically significant p-values at 95% confidence level). Bolded p-values indicate greatest statistical signifcance. List of acronyms and abbreviations: *Calamagrostis breweri* (CB), *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK), soil resistance (SR), bulk density (BD), tot. total vegetation cover (tot. veg. cover), water holding capacity (WHC), gravimetric water content (GWC), volumetric water content (VWC).

GROUPING VARIABLE	SR (kPa)	BD (g/cm^3)	TOT. VEG ($707\ cm^2$)	WHC (%)	GWC (%)	VWC (%)	SAND (%)	SILT (%)	CLAY (%)
CV-CB	**0.00**	**0.00**	0.07	**0.00**	**0.00**	0.09	0.16	0.08	1.00
DC-CB	0.25	0.35	0.93	1.00	0.95	0.89	1.00	1.00	0.77
PK-CB	1.00	1.00	0.23	0.98	0.87	0.60	0.98	1.00	0.69
DC-CV	**0.03**	**0.01**	**0.02**	0.01	**0.02**	0.41	0.18	0.17	0.72
PK-CV	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	**0.00**	0.07	**0.05**	0.64
PK-DC	0.26	0.44	0.64	0.95	0.60	0.24	0.99	0.98	1.00

Question 2: Can a few key ecological factors be used to best explain SR among dominant plant community types in Sierra Nevada meadows?

Correlations between SR and ecological influences on SR

When evaluated across all plots, some single variables correlated well with SR (Table 5). These included soil water content and bulk density. A total of nine variables had statistically significant correlations with SR based on p-values (Table 6). Many of these variables also correlated with GWC, which was significantly correlated with SR. This is because GWC and SR have a significantly negative correlation ($r= -0.33, p<0.001$). Other explanatory variables that most significantly negatively correlated with SR include: VWC ($r=-0.28, p<0.005$), WHC ($r=-0.27, p<0.008$), and silt ($r=-0.27, p<0.007$). Conversely, bulk density: BD ($r=0.31, p<0.002$) most significantly positively correlated with SR. While GWC and VWC are both measures of soil water content, GWC has a higher negative correlation with SR. Many of the explanatory variables also correlated with each other. Variables that strongly correlated with GWC include: WHC, BD, SOM and silt. Particle size distribution (sand, silt, and clay) was strongly correlated with WHC, where silt and clay positively correlated with WHC, while sand negatively correlated with WHC. Some components of particle size distribution (percent sand and silt) were also highly correlated ($r=0.80$). In addition, SOM was strongly negatively correlated with BD. Correlation results are valuable for determining the strength and direction of relationships among variables, but do not take into account plant community type or between-meadow variability, such as meadow gradient class. Scatterplots showed general trends between SR and most correlated explanatory variables (GWC and BD) by plant community type (Fig. 7). Multi-collinearity among some explanatory variables of SR was detected based on Pearson's correlations of 0.75 or greater ($r \geq 0.75$), as described by Graham (2003). Explanatory variables that highly correlated with each other were not combined in potential best models of SR using backwards, stepwise LMER techniques. Highly collinear variables included BD, GWC, VWC, and WHC ($r > 0.85$; Table 5).

Table 5. Pearson's product moment correlation matrix displaying positive and negative linear correlations among biotic and abiotic variables. The number 1 indicates a 1:1 relationship between the same variable. Bolded numbers to shown to two decimal places indicate strong relationships (r≥0.75, n=98 observations). List of acronyms and abbreviations: soil resistance (SR), bulk density (BD), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), tot. total vegetation cover (tot. veg. cover), coarse fragments (coarse frag.).

Variables	pH	SOM (%)	C (%)	N (%)	C.N (%)	GWC (%)	BD (g/cm³)	WHC (%)	Sand (%)	Silt (%)	Clay (%)	Coarse frag. >2mm	Coarse frag. >4mm	Roots (g/cm^2)	Roots (%)	VWC (%)	Total Veg. Cover	Target Veg. Cover	Tot. Veg. Cover (707cm^2)	SR (kPa)
pH	1	-0.15	-0.16	-0.12	-0.08	-0.03	-0.01	0.00	0.04	-0.03	-0.07	-0.06	-0.04	-0.14	-0.08	0.05	0.13	0.01	-0.07	-0.12
SOM (%)	-0.15	1	**0.95**	**0.77**	0.09	0.71	-0.72	0.68	-0.50	0.48	0.37	0.01	-0.41	0.03	0.36	0.44	0.00	0.07	-0.05	-0.18
C (%)	-0.16	**0.95**	1	**0.80**	0.12	**0.76**	**-0.77**	0.70	-0.47	0.47	0.29	0.03	-0.40	-0.01	0.32	0.50	-0.04	0.00	-0.10	-0.24
N (%)	-0.12	**0.77**	**0.80**	1	-0.37	0.69	-0.64	0.66	-0.47	0.47	0.30	-0.01	-0.26	-0.08	0.21	0.41	-0.08	-0.01	-0.09	-0.26
C.N (%)	-0.08	0.09	0.12	-0.37	1	-0.02	-0.07	-0.07	0.15	-0.16	-0.06	0.10	-0.09	0.15	0.18	0.00	-0.03	0.03	-0.04	0.03
GWC (%)	-0.03	0.71	**0.76**	0.69	-0.02	1	**-0.86**	**0.88**	-0.64	0.66	0.33	0.05	-0.35	-0.05	0.32	0.66	-0.15	0.09	-0.20	**-0.33**
BD (g/cm³)	-0.01	-0.72	**-0.77**	-0.64	-0.07	**-0.86**	1	-0.71	0.47	-0.50	-0.18	0.01	0.33	-0.11	-0.48	-0.60	0.07	-0.18	0.17	**0.31**
WHC (%)	0.00	0.68	0.70	0.66	-0.07	**0.88**	-0.71	1	-0.74	**0.75**	0.41	0.07	-0.36	-0.14	0.20	0.51	-0.18	0.02	-0.18	**-0.27**
Sand (%)	0.04	-0.50	-0.47	-0.47	0.15	-0.64	0.47	-0.74	1	**-0.98**	-0.71	-0.26	0.44	0.22	-0.03	-0.40	0.04	0.00	0.14	0.26
Silt (%)	-0.03	0.48	0.47	0.47	-0.16	0.66	-0.50	0.75	**-0.98**	1	0.57	0.24	-0.44	-0.21	0.06	0.40	-0.05	0.01	-0.14	**-0.27**
Clay (%)	-0.07	0.37	0.29	0.30	-0.06	0.33	-0.18	0.41	-0.71	0.57	1	0.22	-0.29	-0.18	-0.06	0.27	0.02	-0.03	-0.09	-0.14
Coarse frag. >2mm (%)	-0.06	0.01	0.03	-0.01	0.10	0.05	0.01	0.07	-0.26	0.24	0.22	1	-0.22	-0.16	-0.13	0.09	0.09	0.01	0.01	-0.08
Coarse frag. >4mm (%)	-0.04	-0.41	-0.40	-0.26	-0.09	-0.35	0.33	-0.36	0.44	-0.44	-0.29	-0.22	1	-0.09	-0.23	-0.41	-0.10	-0.07	-0.01	0.16
Roots (g/m2)	-0.14	0.03	-0.01	-0.08	0.15	-0.05	-0.11	-0.14	0.22	-0.21	-0.18	-0.16	-0.09	1	**0.87**	0.06	0.26	0.29	0.25	0.23
Roots (%)	-0.08	0.36	0.32	0.21	0.18	0.32	-0.48	0.20	-0.03	0.06	-0.06	-0.13	-0.23	**0.87**	1	0.29	0.15	0.31	0.10	0.01
VWC (%)	0.05	0.44	0.50	0.41	0.00	0.66	-0.60	0.51	-0.40	0.40	0.27	0.09	-0.41	0.06	0.29	1	0.07	0.10	-0.20	**-0.28**
Tot. Veg. Cover (1m2)	0.13	0.00	-0.04	-0.08	-0.03	-0.15	0.07	-0.18	0.04	-0.05	0.02	0.09	-0.10	0.26	0.15	0.07	1	0.41	0.57	0.05
Target Veg. Cover (1m2)	0.01	0.07	0.00	-0.01	0.03	0.09	-0.18	0.02	0.00	0.01	-0.03	0.01	-0.07	0.29	0.31	0.10	0.41	1	0.36	0.08
Tot. Veg. Cover (707cm2)	-0.07	-0.05	-0.10	-0.09	-0.04	-0.20	0.17	-0.18	0.14	-0.14	-0.09	0.01	-0.01	0.25	0.10	-0.20	0.57	0.36	1	0.12
SR (kPa)	-0.12	-0.18	-0.24	-0.26	0.03	-0.33	0.31	-0.27	0.26	-0.27	-0.14	-0.08	0.16	0.23	0.01	-0.28	0.05	0.08	0.12	1

Table 6. Significant correlations between SR and multiple explanatory variables using Pearson's product moment correlation analysis. List of acronyms and abbreviations: r (Pearson's correlation coefficient), p (p-values), gravimetric water content (GWC), bulk density (BD), volumetric water content (VWC), water holding capacity (WHC), nitrogen (N), carbon (C), soil organic matter (SOM). P-values indicate statistical significance at >95% confidence interval ($p<0.05$). Bolded p-values indicate greatest statistical significance, indicating largest Pearson's correlation coefficients (regardless of positive or negative relationship).

No	Explanatory Variables	r	p
1	GWC (%)	**-0.33**	**0.001**
2	BD (g/cm^3)	**0.31**	**0.002**
3	VWC (%)	**-0.28**	**0.005**
4	Silt (%)	-0.27	0.007
5	WHC (%)	-0.27	0.008
6	N (%)	-0.26	0.009
7	Sand (%)	0.26	0.009
8	C (%)	-0.24	0.016
9	Roots (g/m^2)	0.23	0.024

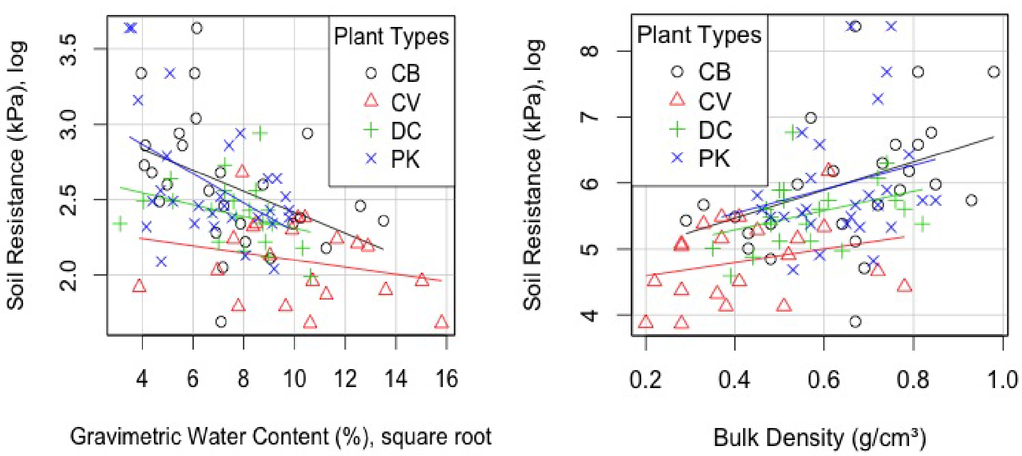

Figure 7. Relationships between soil resistance and gravimetric water content (left panel) and bulk density (right panel) for the different plant community types. Soil resistance negatively correlated (kPa) with gravimetric water content (percent) among plant types, and correlated with bulk density (g/cm^3). SR was log transformed and GWC was square root transformed to achieve normality. Plant type acronyms: *Calamagrostis breweri* (CB), *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK).

Developing the best model for explanation of SR

A few explanatory variables best explained spatial variation in SR based on lowest AIC and BIC values, which differed among the top five models selected using LMER. Best models had lowest AIC or BIC, and lowest χ^2 and p-values (as shown in Table 7). Model results are based on non-collinear, parsimonious combinations of explanatory variables, including interactions with plant community types. Grouping factors included plant community type as fixed effects and meadows as random effects. Main factors included: bulk density (g/cm^3), gravimetric water content (%), root mass (g/m^2), and coarse fragment percentage (> 4mm). Models interactions between main factors and plant community types included root mass and coarse fragments. When models were compared with the null model (plant community type and meadow grouping factors only), best models showed significant improvements over the null.

The model with lowest BIC included only gravimetric water content (GWC) as the best explanatory factor of SR (BIC=225; Table 7). This model had greatest parsimony. The model with lowest AIC included three main factors (bulk density, root mass, coarse fragments), which may have provided a better indication of ecological complexity. The model with lowest AIC provided better goodness-of-fit than the gravimetric water content model based on the lowest χ^2 value (1.46; Bates et. al. (2012). Among candidate models, the best explanatory model of SR (model 1) had a lower significantly lower AIC (AIC=196) than the model with lowest BIC (AIC=206), or the null model (AIC=227). When considering both AIC and BIC to balance parsimony with model goodness-of-fit (Dziak et. al. 2012) model 3 had lowest combined AIC and BIC values (AIC=202, BIC=230). These results indicate that the model with gravimetric water content alone (model 5) represents the best, true model for explaining spatial variation in SR. However, when aiming to identify complexity, the model with a few key variables (model 1; bulk density, root mass, coarse fragments) best explained complexity and spatial variation in SR. When aiming to balance goodness-of-fit and parsimony (based on lowest combined AIC and BIC), the model with two key factors (model 3; gravimetric water content and root mass) best explained variation in SR. When considering other selection parameters (logistical likelihood, deviance, χ^2). results show that model 1 provided the best explanation of SR (Table 7). Hence, model 1 was selected as the best explanatory model of SR based on a few key factors: bulk density, root mass, and coarse fragments, and their interactions with plant community type.

Table 7. Top five best explanatory models of SR based on AIC and BIC information criterions used in linear mixed effects regression (LMER). Additional model selection parameters included: logistical likelihood (logLik) and Chi-squared values (⍰2). Lowest AIC and BIC values, and p-values (p) <0.05 indicates statistically significant improvement from null model and other candidate models. Model grouping factors include plant community type as a fixed factor and meadow as a random effect factor. Model main factors include multiple, non-collinear explanatory variables. Interactions between plant community type and main factors include root mass and coarse fragments. The SR response variable was log transformed.

Models	No. Main Factors	Plant Type	Meadow	BD (g/cm^3)	GWC (%)	Root mass (g/m^2)	Coarse frag. >4mm (%)	Plant Type* Root mass	Plant Type* Coarse fragments	AIC	BIC	χ^2	p
Null	n/a	*x*	*x*							*227*	*243*	*n/a*	*n/a*
Model 1	**3**	**x**	**x**	**x**		**x**	**x**	**x**	**x**	**196**	235	1.46	0.00
Model 2	3				x	x	x	x	x	197	236	14.59	0.01
Model 3	2				x	x				202	230	19.48	0.00
Model 4	2			x		x		x		204	233	7.03	0.00
Model 5	1				**x**					206	**225**	22.79	0.00

DISCUSSION

Question 1: Significant differences in SR, and potential ecological influences on SR among meadow plant community types and meadow gradient classes

Soil resistance (SR) significantly differed among plant community types and meadow gradient classes. Strong spatial variability in the response variable (SR) and explanatory variables were detected on local scales (plant community types) and site scales (meadows gradient classes). My study findings are consistent with knowledge that wetland ecosystems show local-scale and site-scale spatial variability in soil properties (Inglett et. al. 2011, Lyons et al. 1998; Stolt et al. 2001; Bruland and Richardson 2004, Grunwald et al. 2006; Cohen et al. 2008; Nkheloane 2012).

On a local scale, my results suggest that wetter plant community types cannot support pack stock use, even in an extremely dry year. *Carex vesicaria* and *Deschampsia cespitosa* both had mean SR values below the SR threshold value (500 kPa) needed to support pack stock animals without incurring disturbance for the month of July in 2013. The year 2013 was one of the driest years on record for California (DWR, CDEC 2014). These results suggest that these wetter plant communities are likely unsuitable for use by pack stock (based on a limited sample size). Conversely, one of the drier plant community types may be more suitable for use by pack stock. *Calamagrostis breweri* (CB) was consistently above the SR threshold needed to support pack stock use without incurring damage to soils. However, the other dry plant community type sampled (*Ptilagrostis kingii*) showed considerable spatial variability in SR among meadows.

Variation in SR for *Ptilagrostis kingii* (PK) was likely due to differences in water content among meadows of differing gradient classes. One middle gradient meadow with PK (Emeric Lake) had significantly higher SR than low gradient meadows with PK (Upper Lyell and Snow Flat). Among low gradient meadows with PK, Tuolumne Meadows was the exception. This may have been due to higher SR and lower water content as a result of greater clay content. Clay is more susceptible to disturbance when saturated, but is stronger when dry (Lull 1959). This suggests that plants occurring in soils high in clay will have greater SR when dry. The majority of meadows surveyed were fairly low in clay content (<15%), but significantly differed in sand and silt content, SOM concentration, and resulting water content depending on meadow gradient.

Soil water availability is the main driver of differences in plant community types representing local-scale hydrologic regimes, which corresponds with SR based on my findings. The obligate plant type (*Carex vesicaria*) had greatest water content and SOM concentration, which corresponded with subsequently lowest BD and SR than other plant community types. Conversely, the facultative plant type (*Calamagrostis breweri*) by far had the highest BD and SR due to lower water content and SOM, in combination with coarser soils. These results suggest that abiotic factors associated with plant community hydrologic regime influence SR.

Meadow gradient is an important factor to consider when evaluating site-scale meadow suitability for pack stock use. Site-scale variation in meadow gradient may drive variability in sand and silt content, which may explain differences in WHC and resulting SR among plant community types. Low gradient meadows had significantly greater silt content and WHC, and resulting lower SR than middle gradient meadows. Low gradient meadows also had primarily hydric plant communities (CV, DC). Conversely, middle gradient meadows had primarily mesic to xeric plant communities (CB, PK). However, one middle gradient meadow (Middle Lyell) also had the *Carex vesicaria* hydric plant community type present within oxbow landscape positions. Presence of this hydric plant type may have resulted in lower SR at this middle gradient meadow. Hence, meadow gradient class influences plant community types present, which influences SR.

Water holding capacity and dominant plant community hydrologic regime differed among meadows of differing gradient classes. Low gradient meadows had significantly higher WHC than middle gradient meadows. This suggests that landform variability drives differences in soil texture and resulting SR. For example, low gradient meadows had significantly higher silt content and lower sand content than middle gradient meadows, and vice versa. Similarly, low gradient meadows had greater SOM concentration, and finer, loam textures, which may have resulted in significantly lower SR. Conversely, middle gradient meadows had significantly higher SR, coarser, sandy loam soil textures (dominated by sand) and lower SOM concentration. These results suggest that meadow gradient significantly influences meadow soil water availability and subsequent SR due to variation in particle size distribution, SOM, and other covariates of SR.

Among meadows of different gradient classes, depositional events may influence differences in silt and sand content by local-scale landscape positions. Fine grained sediments are typically deposited in low lying areas, such as oxbows within low gradient meadows. Conversely, deposition of coarse grained materials, are often related to steeper gradients (Therell et. al. 2006). Finer grained soils typically have greater WHC. Higher soil water availability supports hydric plant communities, which had lower SR. Within low gradient meadows, *Carex vesicaria* had lowest SR, greatest silt content, and greatest WHC. Conversely, PK had greatest sand content and coarse fragments, lower WHC, and greater SR. *Carex vesicaria* occurred in oxbow (O) low gradient, depositional landscape positions, which had higher silt content and SOM concentration (Tables 10-14, Appendix 1). Loheide and others (2009) reported similar findings, where they found that CV occurred in oxbow areas. This suggests that landscape position plays a role in soil texture and SOM variability, water availability and subsequent SR on local and site scales.

My research presents novel findings on spatial variation in SR by meadow gradient landform position and plant community type (indicative of hydrologic regime). While an earlier study by Heikes-Knapton (2009) found that water retention in subalpine wetlands differed based on landform variability, this study did not address soil susceptibility to grazing by pack stock. Heikes-Knapton (2009) detected differences in soil texture, SOM, and water availability among subalpine wetlands of differing landform positions in the Northern Rockies in Montana. Patterns in Sierra Nevada subalpine meadow wetlands may show differing spatial trends in water retention. My study builds upon this previous study, in that my research addressed spatial variability in Sierran subalpine meadow vulnerability to disturbance (as measured by SR) on local and site scales. My findings suggest that low gradient meadows have wetter plant community types, higher SOM, higher water availability, and resulting lower SR than middle gradient meadows in the Sierra. This is important for determining site suitability for pack stock use.

Question 2: Best explanatory factors of SR among plant community types

Numerous meadow studies in the Sierra Nevada have found that water content is the key driver of ecosystem response to stock animal disturbance (Shryock 2010, Lee 2013, McIllroy and Allen-Diaz 2012, Moore et. al. 2013, Norton et. al. 2011, Roche et al. 2012). Similarly, previous livestock studies on SR in grasslands have found that soil water content and bulk density are the two most significant factors influencing livestock impacts on soil conditions (Vaz and Hopmans 2001, Herbin et. al. 2011, Piwowarczk et. al. 2011). My results also suggest that gravimetric water content and bulk density alone best correlated with SR in meadows.

The novelty of my study is that I detected additional factors that most influence SR, in addition to water content and bulk density alone, by gradient class and plant community type in meadow ecosystems. My findings represent new information, where I found that a few explanatory factors significantly improved explanation of SR. Using mixed effects linear regression, I was able to detect ecological complexity associated with meadow hydrology, soils, and vegetation on local and site scales. While some plant community types were more resistant than others, meadow gradient played a significant role in soil water availability and resulting SR.

No other meadow studies to-date have used linear mixed effects regression (LMER), and both AIC and BIC criterions to identify meadow complexity and underlying key drivers of variability in SR. Use of mixed effects modeling for explaining both fixed and random variability on multiple scales has been gaining popularity in ecological studies (Gruebber et. al. 2011). When using the LMER approach, I detected which explanatory factors best explained SR by plant community type, among meadows that randomly varied. The novelty of this approach is that it makes the assumption that meadows were random selections from a larger population of Sierran subalpine meadows, which differ in numerous, yet unknown ways. Using two different model selection criterions, I answered differing ecological questions. The use of the BIC criterion was helpful in identifying the underlying true model of variability in SR. This criterion identified gravimetric water content as the single best predictor of spatial variability in SR. However, it is known that water content is the key driver of variability in wetland ecosystems. When using the AIC criterion to detect ecological complexity, a few key factors were identified as best explanatory factors of SR. These included bulk density (BD), root mass, and coarse fragments.

Explanatory factors of SR share a common theme of soil aggregation and macroporosity needed to achieve SR levels that support pack stock animals without incurring damage. Larger coarse fragments may provide greater macro-porosity for root development than small coarse fragments, which pack together more densely, creating smaller pores (which affects bulk density). These explanatory factors of SR likely increase soil aggregation and strength, in that all three best explanatory factors had a positive relationship with SR. Good soil aggregation provides large macropores. This aids in soil water drainage, which is needed to support pack stock without incurring damage. Highly aggregated meadow soils with greater BD (as an indirect result of lower GWC), combined with higher root mass, and coarse fragments, will have greater SR (Herbin et. al. 2011, Piwowarczk et. al. 2011). Conversely, meadow soils high in GWC are more likely to experience disaggregation, which leads to lower SR (Piwowarczk et. al. 2011). When soil water content levels are high, water forces will reduce soil strength and particle binding through disaggregation. Soil saturation can reduce soil strength due to destruction of soil aggregates (Inglett et. al. 2011). Water content determines the degree of soil structure loss, which is due to loss of macropores (Herbin et. al. 2011). When soil macropores are saturated with water, soils will flow around the hooves of animals, leaving defined hoof prints (Lull 1959).

Soils high in clay have greater cohesive strength when dry (Perumpral 1987). However, clay soils are more likely to experience disaggregation (than organic soils) when saturated, which increases soil susceptibility to trampling (Scholefield and Hall 1985). Highly organic soils often have water stable aggregates (clusters of air spaces and soil particles held together to provide soil structure), that are not easily destroyed by water saturation (Brady and Weil 2008). Soil aggregation will increase aeration, promote root growth and elongation (Therrell et. al. 2006), and improve water infiltration and drainage. While soil saturation can increase root penetration by wetland plants (Inglett et. al. 2011), seasonally saturated soils, high in water content, are more vulnerable to disturbance via hoofpunching and trampling. Conversely, in drier soils with air-filled (rather than water filled) macro-pores, compaction of the soil may occur with a loss of macroporosity, but little evidence of trampling (Lull 1959, Piwowarczk et. al. 2011). This indicates that increased soil strength can be a function of decreased water content, other biotic and abiotic factors such as particle size class and root mass, and increased soil compaction.

Soils have high strength due to both cohesive forces between soil particles, and frictional resistance met by particles forced to slide over each other from interlocked positions (Johnson et. al. 1987, Vaz and Hopmans 2001). Additionally, soils high in clay content typically have greater cohesive forces when dry (Brady and Weil 2008). My research suggests that meadow soils were low in clay content (<15%), indicating that frictional forces may be more important than cohesive forces for providing soil strength. However, high water content may reduce frictional forces that improve soil SR, depending on soil texture and SOM concentration. (Piwowarczk et. al. 2011).

My results suggest that soil organic matter concentration and soil texture, such as silt and sand content, strongly correlated with water availability. These combined ecological factors likely additively influence SR, depending on differences in meadow gradient. While low gradients meadows had loam soil textures, higher silt content, and greater SOM concentration, middle gradient meadows had sandy loam textures and higher in sand content, and less SOM. In low gradient meadows, this resulted in higher water availability, lower BD, and lower SR. The opposite was the case for middle gradient meadows. Hence, meadows of lower gradients likely had greater water content and lower SR due to deposition of finer soils, and SOM accumulation.

In addition to frictional forces, soil aggregation (as indicated by greater bulk density, root mass, and coarse fragments) is the main reason why soil strength is higher in some plant community types in comparison with others among study meadows. However, consideration of other factors that covary with explanatory factors of SR is important for understanding the mechanisms that drive spatial variability in SR among plant community types and meadows of differing gradients. While SOM had an indirect negative effect on SR, in that it lowered BD and influenced other covariates such as GWC, it also aided in improving soil aggregation. Similarly, root mass does not best explain SR alone, unless other factors are considered. These include interactions between plant growth form, hydrologic regime, and soil texture. These biotic and abiotic factors most significantly influence SR when combined, as shown by modeling results.

Spatial variation in biotic explanatory factors of SR, such as root mass, were only detected on local scales, among plant community types, but not on site scales (meadow gradient). Root mass positively correlated with SR for the obligate (CV) and facultative upland (PK) plant community types, but not the facultative wetland (DC) and facultative (CB) plant community types. This is likely due to variation in plant growth forms and associated soil aggregation.

The main reason that *Deschampsia cespitosa* (DC) had lower root mass and mean SR may be due to its' bunch grass growth form, which leaves open spaces between grass clumps that can be easily trampled. The smaller stature grass (CB) had lowest root mass, but by far highest

SR among all plant community types, which may be due to greater bulk density and coarser soils. *Carex vesicaria* (CV) had the second highest root mass, but lowest SR, which is likely due to greater silt and GWC content. My results for root mass are somewhat confirmed by other studies, which found that rhizomatous sedges have two to six times the rooting density and biomass of DC (Manning et al. 1989, Dunaway et al. 1994; Merrill 2012). *Ptilagrostis kingii*, by far had the highest root mass (resulting in higher SR), which is likely due to greater BD and lower GWC.

Management Implications

The SR indicator of ecosystem resistance provides an effective management tool for determining meadow vulnerability to recreational disturbance on both temporal and spatial scales. Explanatory models identified can help guide risk assessments for meadow monitoring and management programs. In national parks, SR explanatory models may be valuable for determining ways to preserve and protect natural resources, while providing for recreational visitor enjoyment. For example, an understanding of which factors most influence soil strength can inform site suitability assessments. While some plant community types are more resistant than others based on hydrologic regime and other covariates, meadow gradient plays a large role in soil water availability, which will influence meadow dry-down rates over time.

My study suggests that some hydric plant community types cannot support pack stock use, even in an extremely dry year. *Carex vesicaria* and *Deschampsia cespitosa* had high GWC, and low SR values, below the SR threshold needed to support pack stock use. These two plant communities are representative of Sierran subalpine meadows. This suggests that Sierran meadows dominated by these species are likely unsuitable for pack stock grazing. These results are based on one of the driest water years on record for California (DWR, CDEC 2014), indicating that these plant types may never support pack stock use without incurring damage.

The obligate plant type (*Carex vesicaria*) may be best for the development of a risk assessment of areas unsuitable for pack stock use. The facultative wetland plant type (*Deschampsia cespitosa*) is a preferred forage species for pack stock, which has important implications for developing best management grazing practices in meadows dominated by the type (Olson-Rutz et. al. 1996, Cole et. al. 2004, Ballenger et. al. 2008). The facultative plant type (*Calamagrostis breweri*) was most resistant to disturbance, indicating that meadows dominated by this plant type may be most suitable for use by pack stock. The facultative upland plant type (*Ptilagrostis kingii*) had the greatest variability in water content of all types sampled. However, plant growth form for PK may aid in greater rooting strength, and subsequently greater soil resistance in comparison with other plants. Conversely, *Deschampsia cespitosa* had greatest variability in SR, depending on soil water content, as influenced by meadow gradient and texture. These results indicate that some meadows may be unsuitable for use by pack stock based on wetter plant community types present, suggesting the importance of local and site assessments.

Multiple-scale analyses provide necessary spatial and temporal information for adequately understanding ecological form and function (Wohl et. al. 2007). Meadow gradient class (indicative of landform position) is important for assessing meadow function related to water availability. My results suggest that low gradient meadows tend to hold more water than middle gradient meadows, which results in lower SR, and lower suitability for pack stock use.

The development of a risk assessment identifying at-risk wet meadow sites that are unsuitable for pack stock use may be useful for avoiding potential soil disturbance. However, this may require quantification of soils data to that of meadow aerial extent. Vulnerable plant community types and meadow types at risk of potential disturbance can be identified via aerial imagery or remote sensing classification to quantify areas at risk, such as hydric areas. However, spatial classification of hydric areas will vary temporally depending on seasonal and inter-annual variability in soil moisture. This technique also provides coarser estimates of hydrologic regime than field measurements. Therefore, field measurement of soil moisture and other ecological covariates is critical for accuracy assessment. Classification of meadows based on hydrogeomorphic type can also help managers better understand variation in meadow function. My results suggest that low gradient meadows are more vulnerable to disturbance by pack stock use (via trampling) due to finer grained soils with greater water availability, often hydric plant communities, and lower SR.

Monitoring of meadow vulnerability to disturbance by recreational pack stock use should incorporate considerations on ecological influences on SR on both local scales and site scales. One way of performing ecological assessments that adequately capture spatial variability is through implementation of a rapid assessment. While meadow gradient can be easily quantified using remote sensing techniques, such as digital elevation models, gradient can also be quickly measured in the field by measuring slope. Soil texture classification can be used to estimate relative water holding capacity (WHC). My study results suggest that loams have greater WHC than sandy loams. Soil texture is easily measured in the field using the hand-feel method (Brady and Weil 2008). The laboratory methods I used also provide a rapid approach for quantifying root mass based on soil processing via hand-sorting, oven-drying, and weighing. This fairly coarse method provides an effective means for quantifying root mass for perennial graminoid species. The soil sample size, core type, and explanatory variables I used also appeared to be sufficient for detecting correlations in ecological factors that drive spatial variability in SR.

My findings suggest that GWC better correlated with SR, as opposed to VWC. While measurement of GWC requires laboratory analysis, it is a more accurate estimate of soil water content, (based on soil water lost during oven drying) than VWC. However, VWC can be measured more rapidly in the field using a TDR (time domain reflectometer), when laboratory access is not possible, and this field method allows for measurement of intact soils. Highly organic soils should be calibrated for absolute values, but they still should be good covariates with SR. The main shortcoming of TDR use is that soil water content can only be measured up to 53% if un-calibrated in highly organic soils. This is because soils only have about 50% porosity, which serves as the upper limit (Brady and Weil 2008). While GWC was identified as explaining greater variation in SR compared to that of VWC, the two were well-correlated based on regression of log transformed variables (for both variables) for the entire dataset (R^2=0.98, n=243). This suggests that GWC values can be extrapolated from VWC values, based on my study dataset. Drivers of variability in GWC, VWC, and SR would also need to be quantified among meadow gradients. By taking into account site-scale variation in water availability and SR, such as meadow gradient class, vulnerability to disturbance may be more easily quantified for informing risk assessments.

To fully understand ecosystem vulnerability to disturbance, an assessment of resilience also needs to be addressed. Meadows that are both vulnerable and at-risk to disturbance must be susceptible to, and unable to cope with, injury, damage or harm for a given area and reference period (DeLange 2010). For my study, this refers to areas with high spatial and temporal variability in sol water content, which influences SR. Ecosystem resilience is a measure of resistance to disturbance and the speed of return to an equilibrium state (DeLange 2010).

While low gradient meadows may be more vulnerable to disturbance by recreational pack stock use, they may also be more resilient based on greater SOM concentration, which could mitigate the effects of trampling. Wheeler and others (2002) suggest that meadow areas with hydric plant community types (high in GWC and SOM concentration) may recover more quickly from disturbance. They found that soil infiltration rates and BD returned to pre-disturbed values within 1 year after livestock grazing events in a montane riparian meadow in the Colorado Rockies. Full hydrologic recovery in these meadows may have been due to frequent freeze-thaw events and high SOM. These findings merit future research for at-risk Sierran meadows.

Upper Lyell Canyon (UL) represents a low gradient meadow that may be at greatest risk to potential disturbance by recreational pack stock use. This low gradient meadow contains fine grained soils, high water holding capacity, and hydric plant community types, which are indicative of high water content and saturated soil conditions (CV and DC). This meadow also receives the highest amount of recreational pack stock use of any meadow in YNP (Table 1). Not all areas within UL are classified as hydric, where xeric plant community types such as PK also occur. Therefore, to adequately quantify risk in this meadow, spatial quantification of areas at risk (hydric area extent) will need to be done based on remote sensing and field measurements.

Limitations to my study include the need for adequate up-scaling of meadow plant community data to that of a true meadow scale based on aerial extent. Entire meadow area was not captured by my study design because only dominant meadow plant communities were sampled. While dominant plant community types comprised the majority of meadows, the likelihood that meadow areas remained un-sampled is high among study sites. Hence, plant community type data were not weighted by aerial extent, which is important for future work.

Climate Change Implications

Meadow hydrologic conditions, which drive spatial variation in SR on both local and site-scales, are strongly influenced by climatic variables. These include snow pack (as measured by snow water equivalent; SWE), snow melt timing, temperature, precipitation, and slope and aspect. These combined climatic variables influence water depth and soil water holding capacity based on soil particle size distribution, soil structure, and SOM concentration. Changing climatic conditions can dramatically affect local and site scale variability in hydrologic conditions on differing time scales, such as throughout the growing season and among water differing years. Examination of climatic variables that influence variability within and among meadows with respect to SR would also be valuable for predicting changes to meadow condition and function in the face of a changing climate. For example, low gradient meadows may dry-down more quickly in drier water years, resulting in higher SR. Conversely, middle gradient meadows may remain saturated with water for longer in years with greater snow pack, which would lower SR.

My study represents data from one of the driest water years on record for the Sierra Nevada range and the state of California during peak growing season in summer (July 2013). Snow water equivalent (SWE) data for the April 1st snow pack in 2013 showed that SWE was 53% of average. However, in the previous year (2012), April 1st SWE was 50%, and in the subsequent year (2014), April 1st SWE was only 40%. Some climate California has been in an extreme drought for the past three years (indicating decreased precipitation in the form of snow in the Sierra Nevada and increased temperatures). Climate forecasting models have predicted continued decreases in snowpack for the state of California.

Most climate forecasting model scenarios estimate a 36% to 70% reduction of Sierra snow pack by 2050 (Dettinger et al. 2004). Under these scenarios, some fraction of winter precipitation would be converted from snow to rain, along with increased evaporative demand. This could convert some mesic and hydric mountain meadows to drier systems (Merrill 2012). Studies have shown that peak snow-melt is occurring at increasingly earlier dates (Peterson et al. 2008). These forecasts have important implications for water content and resulting changes in SR.

While drier meadows conditions would result in greater SR, ecological function would likely be altered. Warming temperatures and earlier snow melt could increase meadow dry-down rates, resulting in earlier meadow opening dates for seasonally wet meadows used by pack stock. However, combined stress from climate change and continued pack stock could dramatically alter meadow condition. This is because subalpine meadows are more vulnerable to increased solar radiation due to higher elevation. Increased evaporation and meadow dry-down rates during short growing seasons could lead to increased soil decomposition due to aerobic conditions. Loss of water holding capacity, a critical ecosystem function, could occur. Low gradient, highly organic meadows normally capable of storing large amounts of carbon (Norton 2011, Drexler et. al. 2013), could become sources of greenhouse gas emissions. Loss of carbon storage, coupled with soil disturbance from recreational pack stock use, could reduced water store capacity in meadows. Hence, consideration of climate change effects on meadow function is of utmost importance.

CONCLUSION

My findings provide new information to help develop vulnerability indices and risk assessments that aim to inform science-based, best management practices for maintaining meadow function. My findings can inform strategies to determine appropriate timing and spatial arrangement of pack stock use in seasonally wet meadows that are subject to dry-down. This can be done by evaluating when and where meadows may be unsuitable for pack stock, based on identifying which meadows have low gradient landform positions, dominated by wetter plant communities.

The novelty of my study is that I was able to identify which factors, in addition to water content, most influence meadow vulnerability to disturbance (as measured by soil resistance), by both plant community type and meadow gradient, which represent both local and site-scales. My results suggest that soil resistance can be explained by site-scale landform variability (meadow gradient) and local-scale variation in plant community hydrologic regime. In addition, factors that most influence SR on a local-scale differ from those factors that most influence SR on site-scales. On a local scale, combined factors that most influence SR, also influence soil aggregation, which is important for minimizing soil disturbance. On a site-scale, factors that most influence SR also influence water availability, which is an important for maintaining ecological function.

Some plant communities may be more resistant than others based on hydrologic regime, where meadow gradient may play a large role in soil water availability. My results suggest that soil texture strongly influences water holding capacity, which will affect meadow dry-down rates. Fine grained soils correlated with low gradient meadows and oxbow landscape positions, which had higher water availability. These conditions can prolong saturated soil conditions, and provide ideal conditions for hydric (facultative to obligate wetland) plant communities to persist. My findings suggest that wetter plant community types are at higher risk to disturbance, making them unsuitable for use by pack stock in Sierran subalpine meadows. Conversely, drier plant community types may be more resistant to potential disturbance. However, plant community types, and meadows of differing gradients may vary inter-annually in water content and SR.

Future studies should address inter-annual variability in soil resistance to disturbance, while increasing meadow sample size to better understand both temporal and spatial variability. McIllroy and Allen-Diaz (2012) found that studying a larger number of meadows was necessary for understanding spatial and temporal variation in meadow plant communities, hydrology, and grazing pressure among sites. However, similar to my study, McIllroy and Allen-Diaz sampled only five meadows. Future studies on a larger number of meadows may be beneficial for detecting greater variability in meadow plant community types and meadow gradients representative of hydrologic regime. Classification of meadows based on hydrogeomorphic type can also aid in furthering our understanding of variation in meadow function.

My investigation of soil resistance in Sierran subalpine meadows suggests that SR is a robust indicator of vulnerability to disturbance by recreational pack stock use. When stratifying by plant hydrologic regime and meadow gradient class, my research findings suggest significant spatial differences in SR, and ecological influences on SR, on both local and site scales. In addition to water content alone, explanation of SR was substantially improved by including additional key factors that influence variation among plant community types and meadow gradient classes. My results indicate that even in dry years, some plant community types, representative of Sierran meadows, cannot support pack stock use without incurring damage. This may be due to variation in water availability and other covariates, based on differences in meadow gradient landform position.

REFERENCES

Ballenger, E, J Baccei, L Acree (2010) 2008 Pack stock use assessment in subalpine meadows of the Tuolumne River watershed. DOI, NPS:Resource Management Report. El Portal, CA, USA. http://www.nps.gov/yose/parkmgmt/upload/MRP_Meadows_Report_20120424.pdf Accessed March 9th, 2013

Bates, DM and M Maechler, B Bolker (2012). lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-0

Benedict, NB (1982). Mountain meadows: stability and change. Madrono 29 (3):148-153

Blank, R, T Svejcar, G Riegel (2006) Soil attributes in a Sierra Nevada riparian meadow as influenced by grazing. Rangeland Ecol Manage, 59 (3): 321-329

Brady, NC and RR Weil (2008) The Nature and Properties of Soil. -14th ed. Pearson Higher Edu. (Prentice Hall)

Brinson, MM (1993) A hydrogeomorphic classification for wetlands. U.S. Army Corps of Engineers Waterways Experiment Station, Vicksburg, MS, USA. WRP-DE–4, NTIS No. AD A270 053

Bouyoucos, GJ (1962) Hydrometer method improved for making particle size analysis of soils. Agronomy Journal 54:464-465

Castelli RM, JC Chambers, RJ Tausch (2000) Soil–plant relations along a soil–water gradient in Great Basin riparian meadows. Wetlands 20:251–266

Chambers, J and D Martin (2002) Restoration of riparian meadows degraded by livestock grazing: above- and belowground responses. Plant Ecol, 163 (1): 77-91

Chambers, J, RR Blank, DC Zamudio, RJ Tausch (1999) Central Nevada riparian areas: physical and chemical properties of meadow soils. J. Range Manage. 52:92–99

Clow, DW, L Nanus, B Huggett (2010) Use of regression-based models to map sensitivity of aquatic resources to atmospheric deposition in Yosemite National Park, Water Resources Research, 46

Cole, DN, JW van Wagtendonk, MP McClaran, PE Moore, NK McDougald (2004) Response of mountain meadows to grazing by recreational pack stock. J Range Manage 57(2): 153-160

Cole, DN, M Petersen, R Lucas (1987) Managing wilderness recreation use: common problems and potential solutions. Gen. Tech. Report INT□230, USDA Forest Service, Intermountain Research Station: Ogden, UT. (http://www.wilderness.net/pubs/169.pdf). Accessed March 12, 2014

Cole, DN (1985) Research on soil and vegetation in wilderness: a state-of-knowledge review. Proceedings--National Wilderness Research Conference: issues, state-of-knowledge, future directions; 1985 July 23-26; Fort Collins, CO. Gen. Tech. Rep. INT-220. Ogden, UT: USDA For. Serv., Intermountain Research Station 135-177pp

Combs, SM, MV Nathan (1998) Soil organic matter. In Recommended chemical soil test procedures for the North Central Region. Missouri Agricultural Experiment Station SB 1001

Crawley, MJ (2007) The R Book. John Wiley & Sons Ltd., West Sussex, UK. Accessed Apr. 30, 2014. http://ia700206.us.archive.org/13/items/TheRBook/The_R_Book-Crawley.pdf

DeBenedetti, S.H. and D.J. Parsons (1983). Protecting mountain meadows: a grazing management plan. Park Science. 3 (3): 3-4.

De Lange, HJ, S Sala, M Vighi, JH Faber (2010) Ecological vulnerability in risk assessment, a review and perspectives. Sci Total Environ 408: 3871–3879.

Department of Water Resources, Data Exchange Center (DWR, CDEC) Snow water equivalents provided by California cooperative snow surveys. http://cdec.water.ca.gov/cdecapp/snowapp/sweq.action. Accessed May 1st 2014

Dettinger, MD, DR Cayan, MK Meryer, AE Jeton. 2004. Simulated hydrologic responses to climate variations and change in the Merced, Carson, and American rivers, Sierra Nevada, 1900–2099. Clim Chang 62: 283–317

Drexler, JZ, D Knifong, JL Tuil, LE Flint, AL Flint (2013). Fens as whole-ecosystem gauges of groundwater recharge under climate change. J Hydrology 481: 22–34

Dwire KA, Kauffman JB, Baham JE (2006) Plant species distribution in relation to water-table depth and soil redox potential in montane riparian wetlands. Wetlands 26:131–146

Dziak, JJ, DL Coffman, ST Lanza, R Li (2012). Sensitivity and specificity of information criteria. Technical Report No. 12-119. The Methodology Center, Pennsylvania State University, PA.

Elzinga, CL, DW Salzer, JW Willoughby (1998). Measuring and Monitoring Plant Populations. Bureau of Land Management. Denver, CO, BLM Technical Reference 1730-1

Gee, GW and JW Bauder (1986) Particle-size analysis. p. 383-411. In A Klute (ed.) Methods of Soil Analysis, Part 1. Physical and Mineralogical Methods. Agronomy Monograph No. 9 (2ed). American Society of Agronomy/Soil Science Society of America, Madison, WI

Graham, MH (2003) Confronting multicollinearity in ecological multiple regression. Ecology, 84(11), pp. 2809–2815

Gruebber, CE, S Nakagawa, RJ Laws, IG Jamieson (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol. 3(3): 699-711.

Haubensak, K, S Hart, J Stark (2002) Influences of chloroform exposure time and soil water content on C and N release in forest soils. Soil Biol Biochemi 34: 1549–1562

Heikes-Knapton, SM (2009). Subalpine wetlands: characterization, environmental drivers, and response to human perturbation and restoration. Master's thesis. Bozeman State University. Bozeman, MT.

Herbin, T, D Hennessey, KG Richards, A Piwowarczk, JJ Murphy, NM Holden (2011). The effects of dairy cow weight on selected soil physical properties indicative of compaction. Soil Use Manage, 27, 36–44

Herrick, J and T Jones (2002) A dynamic cone penetrometer for measuring soil penetration resistance. Soil Sci Soc Am J 66:1320-1324

Huber, NK, PC Bateman, C Wahrhaftig (1989) Geologic Map of Yosemite National Park and Vicinity, California, U.S. Geological Survey, Denver, Colorado

Inglett, PW, KR Reddy, WG Harris, EM D'Angelo (2011) Biogeochemistry of Wetlands, Chapter 20 In Huang, PM, Y Li, ME Sumner. Handbook of Soil Sciences. Resource Management and Environmental Impacts (2ed). Boca Raton, FL: CRC Press, pp. 830

Jensen, JR (2007) Remote Sensing of the Environment: An Earth Resource Perspective, 2nd Edition, Upper Saddle River: Prentice-Hall, 592 p

Kai, M, O Aoki, A Hiraga, H Oki, and M Tokuriki (2000) Use of an instrument sandwiched between the hoof and shoe to measure the vertical ground reaction forces and three- dimensional acceleration at the walk, trot and cantor in horses. Am J Vet Research 61:979-98

Keeler-Wolf, T, Moore, PE, Reyes, ET, Menke, JM, Johnson, DN, and Karavidas, DL (2012) Yosemite National Park vegetation classification and mapping project report. Fort Collins, Colorado: National Park Service, Natural Resource Technical Report NPS/ YOSE/NRTR–2012/598

Lee, SR (2013) Contemporary pack stock effects on subalpine meadow plant communities. Master's thesis, University of California, Merced, CA

Loheide, SP and EG Booth (2011) Effects of changing channel morphology on vegetation, groundwater, and soil moisture regimes in groundwater-dependent ecosystems. Geomorphology 126: 364–376

Loheide, SP, RS Deitchman, DJ Cooper, EC Wolf, CT Hammersmark, JD Lundquist (2009) A framework for understanding the hydroecology of impacted wet meadows in the Sierra Nevada and Cascade Ranges, California, USA." Hydrogeology Journal 17(1): 229-246

Lull, HW. Soil compaction of forest and range lands. Misc. Publ. 768. Washington, DC: U.S. Department of Agriculture; 1959. 33 p

Martin DW and JC Chambers (2001) Effects of water table, clipping, and species interactions on Carex nebrascensis and Poa pratensis in riparian meadows. Wetlands 21:422–430

McClaran, MP (2000) Improving livestock management in wilderness. In: Cole, David N.; McCool, Stephen F.; Borrie, William T.; O'Loughlin, Jennifer, comps (2000) Wilderness science in a time of change conference-Volume 5: Wilderness ecosystems, threats, and management; 1999 May 23–27; Missoula, MT. Proceedings RMRS-P-15-VOL-5. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. p. 49-63

McClaran, MP, F Ratcliff, JW Bartolome (2014) Soil resistance, vegetation cover, and soil moisture trends in Yosemite National Park subalpine meadows. Prepared for Yosemite National Park. Report in-review.

McIllroy, SK and DH Allen-Diaz (2012) Plant community distribution along water table and grazing gradients in montane meadows of the Sierra Nevada Range (California, USA). Wetlands Ecol Manage 20:287–296

Merrill, A (2012) A guide for restoring functionality to mountain meadows of the Sierra Nevada. Prepared by Stillwater Sciences, Berkeley, California for American Rivers, Nevada City, CA

Moore, PE, JW vanWagtendonk, JL Yee, MP McClaran, DN Cole, NK McDougald, ML Brooks (2013) Net primary productivity of subalpine meadows in Yosemite National Park in relation to climate variability. Western North American Naturalist 73(4):409-418

Nkheloane, T, Olaleye, AO, Mating, R (2008) Spatial heterogeneity of soil physico-chemical properties in contrasting wetland soils in two agroecological zones of Lesotho. Soil Research 1838: 675.

Neuman, MJ (1997) Packstock hoof print depth and soil strength relationships in wet meadow soils of Sequoia & Kings Canyon National Parks, California. Master of Science Thesis, University of Arizona, Tucson, AZ

Norton, JB, LJ Jungst, U Norton, HR Olsen, KW Tate, WR Horwath (2011) Soil carbon and nitrogen storage in upper montane riparian meadows. Ecosystems 14: 1217–1231

Norton, JB, HR Olsen, LJ Jungst, DE Legg, WR Horwath (2014) Soil carbon and nitrogen storage in alluvial wet meadows. J Soils Sediments 14:34–43 of the Southern Sierra Nevada Mountains, USA

Olson-Rutz, KM, CB Marlow, K Hansen, LC Gagnon, and RJ Rossi (1996) Pack stock grazing behavior and immediate impact on a timberline meadow. J Range Manage 49: 546-550

Peterson, DH, I Stewart, F Murphy. 2008. Hydrologic responses to climatic and geologic variability in the Sierra Nevada, California. San Francisco Estuary & Watershed Science. Feb Issue.

Perumpral, J.V. (1987). Cone Penetrometer Applications — A Review. Am Soc Agric Eng 30: 4.

Piwowarczk, GG and NM Holden (2011). Can soil moisture deficit be used to forecast when soils are at high risk of damage owing to grazing animals? Soil Use Manage, 27, 255–263

Prichard, D (1998) Riparian area management: process for assessing proper functioning condition. Denver (CO): Bureau of Land Management

Ratliff, RD (1985) Meadows in the Sierra Nevada of California: state of knowledge. Gen. Tech. Rep. PSW-GTR-84. USDA Forest Service, Pacific Southwest Research Station, Berkeley, CA

R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org

Reed, PB (1998) Revision of the National List of Plant Species that Occur in Wetlands. In cooperation with the National and Regional Interagency Review Panels, U.S. Fish and Wildlife Service, U.S. Army Corps of Engineers, U.S. Environmental Protection Agency, and Natural Resources Conservation Service. Washington, DC: U.S. Fish and Wildlife Service

Rillig, MC, SF Wright, VT Eviner (2002). The role of arbuscular mycorrhizal fungi and glomalin in soil aggregation: comparing effects of five plant species. Plant and Soil 238: 325–333

Roche, LM, B Allen-Diaz, DJ Eastburn, KW Tate (2012) Cattle grazing and Yosemite toad (Bufo canorus Camp) breeding habitat in Sierra Nevada meadows. Rangeland Ecol Manage 65:56-65

Rodríguez-Iturbe, I and A Porporato (2004) Ecohydrology of water-controlled ecosystems: soil moisture and plant dynamics. Cambridge University Press

Russo, T, A Fisher, J Roche (2012) Improving riparian wetland conditions based on infiltration and drainage behavior during and after controlled flooding. J Hydrology 432–433: 98–111

Shryock, DF (2010) Influence of hydrology and recreational pack stock grazing on subalpine meadows of the John Muir and Ansel Adams Wilderness Areas, California. Master's thesis, Humboldt State University, Arcata, CA

Schulte, EE and BG Hopkins (1996) Estimation of soil organic matter by weight-loss-on-ignition. In F.R. Magdoff et al. (eds.) Soil organic matter: analysis and interpretation. SSSA Spec. Publ. 46, Madison, WI.

Sparks, DL (1996) Soil pH & Soil Activity, pg. 487. In Methods of Soil Analysis, Part 3 Chemical Methods. American Society of Agronomy, Inc. Madison, WI, USA

Storer, DA (1984) A simple high volume ashing procedure for determining soil organic matter. Communications in Soil Science and Plant Analysis. 15:759-772

Svejcar, TJ and GM Riegel. 1998. Spatial pattern of gas exchange for montane moist meadow species. J Veg Sci 9: 85–94

Therrell, L, D Cole, V Claassen, C Ryan, MA Davies, (2006) Wilderness and backcountry site restoration guide. Tech. Rep. 0623-2815-MTDC. Missoula, MT: U.S. Department of Agriculture, Forest Service, Missoula Technology and Development Center. 394 p

UC Davis, Natural Heritage Institute, U.S. Forest Service, and California Department of Fish and Game (2007). final report: Sierra meadows: historical impact, current status and trends, and data gaps. Final Report to USEPA contract CD96911501. https://watershed.ucdavis.edu/pdf/SierraMeadows-2007.pdf Accessed May 2nd , 2013

US Army Corps of Engineers (2013) National list of vascular plant species that occur in wetlands. http://rsgisias.crrel.usace.army.mil/nwpl_static/data/docs/lists_2012/National/ERDC-CRREL_TR-12-11_NWPL_2012.pdf Accessed March 3rd, 2014

US Department of Agriculture, Natural Resources Conservation Service (2007) Soil survey of Yosemite National Park, California. http://soils.usda.gov/surve/printed_survey. Accessed May 3rd, 2013

US District Court for the Northern District of California (2008) Order for Injunctive Relief, High Sierra Hiker's Association vs. Randy Moore et al, National Forests Recreation Association. http://www.highsierrahikers.org/courtdocMay2008.pdf. Accessed February 5th, 2013

US Environmental Protection Agency 2008. USEPA risk assessment forum. Available online at: http://cfpub.epa.gov/ncea/raf/raf-purp.cfm. Accessed on May 10th, 2014

Vaz, CM and J Hopmans (2001) Simultaneous measurement of soil penetration resistance and water content with a combined penetrometer-TDR moisture probe. Soil Sci Soc Am J 65:4-12

Weixelman, DA, B Hill, B, DJ Cooper, EL Berlow, JH Viers, SE Purdy, AG Merrill, SE Gross (2011) A field key to meadow hydrogeomorphic types for the Sierra Nevada and Southern Cascade Ranges in California. General Technical Report. R5-TP-034. Vallejo, CA. U.S. Department of Agriculture, Forest Service, Pacific Southwest Region, 34 pp

Weixelman, DA and GM Riegel (2012) Measurement of spatial autocorrelation of vegetation in mountain meadows of the Sierra Nevada, California and Western Nevada. Madroño 59(3):143-149

Weixelman, DA, and DC Zamudio (2001) Determining Ecological Status of Sierra Nevada Mountain Meadows Using Plant Frequency and Soil Characteristics. In: Faber, P.M. (ed). 2003. California Riparian Systems: Processes and Floodplain Management, Ecology, and Restoration. 2001 Riparian Habitat and Floodplains Conference Proceedings, Riparian Habitat Joint Venture, Sacramento, CA. pp 463-470

Weixelman DA, Zamudio DC, Zamudio KA (1999) Eastern Sierra Nevada riparian field guide. intermountain region. USDA Forest Service, Toiyabe National Forest. Intermountain Region, R4-ECOL-99-01

Wheeler, MA, MJ Trlica, GW Frasier, JD Reeder (2002). Seasonal grazing affects soil physical properties of a montane riparian community. J Range Manage, 55 (1): 49-56.

Winters, DS, DJ Cooper, JD Hamerlink, N Lee, JR Maxwell, DP Peterson, NL Poff, FJ Rahel, DM Staley, EE Wohl (2004) Aquatic, riparian, and wetland ecosystem assessment, Bighorn National Forest, Wyoming. Unpublished report. USDA Forest Service http://www.fs.usda.gov/Internet/FSE_DOCUMENTS/fswdev3_009006.pdf Accessed March 15th, 2014

Wohl, E, D Cooper, L Poff, F Rahel, D Staley, D Winters (2007). Assessment of stream ecosystem function and sensitivity in the Bighorn National Forest, Wyoming. Environ Manage 40:284–302

Zuur, AF, EN Ieno, GM Smith (2007) Analyzing ecological data. Springer, New York, NY, USA.

APPENDICES

Appendix I: Meadow biotic and biotic variable mean values and standard errors, significantly different by plant community type and meadow gradient class.

Table 8. Mean values, standard errors, and p-values for select biotic and abiotic variables that significantly differed by plant community type. Table displays mean values and standard errors on left and significant p-values (p) on right, based on 95% confidence level; p<0.05). Bolded p-values indicate greatest statistically significant differences at 99% confidence level; p<0.007. List of acronyms and abbreviations: plant community type (PCT), soil resistance (SR), bulk density (BD), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), nitrogen (N), and total vegetation cover (tot. veg. cover). Plant community types: *Calamagrostis breweri* (CB), *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK).

Plant Community Type (PCT)	CB			CV			DC			PK			Significant differences by PCT
SR (kPA)	890.38	±	*65.37*	232.32	±	*35.09*	269.90	±	*18.14*	666.29	±	*55.68*	**0.000**
BD (g/cm³)	0.65	±	*0.01*	0.40	±	*0.01*	0.51	±	*0.01*	0.61	±	*0.01*	**0.000**
VWC (%)	32.58	±	*0.80*	44.96	±	*0.64*	36.77	±	*0.82*	29.72	±	*0.81*	**0.007**
GWC (%)	61.01	±	*2.30*	114.95	±	*3.10*	76.30	±	*2.73*	54.76	±	*1.68*	**0.000**
WHC (%)	53.80	±	*2.23*	85.17	±	*4.49*	54.23	±	*1.73*	50.95	±	*1.70*	**0.001**
N (%)	0.42	±	*0.02*	0.54	±	*0.03*	0.43	±	*0.02*	0.38	±	*0.02*	0.028
Silt (%)	29.99	±	*1.17*	40.25	±	*1.91*	31.00	±	*1.19*	29.29	±	*1.51*	0.047
Tot. Veg. Cover (1 m^2)	52.57	±	*0.70*	39.97	±	*0.50*	61.63	±	*0.75*	59.80	±	*0.68*	**0.000**
Tot. Veg. Cover (707	47.81	±	*0.68*	36.37	±	*0.76*	54.00	±	*1.00*	54.91	±	*0.75*	**0.001**

Table 9. Significantly different mean values, standard errors, and p-values by meadow gradient class (low versus middle) for select biotic and abiotic variables. Table displays mean values and standard errors on left and significant p-values (p) on right, based on 95% confidence level; p<0.05). Bolded p-values indicate greatest statistically significant differences at 99% confidence level; p<0.004. List of acronyms and abbreviations: soil resistance (SR), water holding capacity (WHC), gravimetric water content (GWC), volumetric water content (VWC),soil organic matter (SOM), carbon (C), nitrogen (N), coarse fragments (coarse frag.). Meadows: Snow Flat (SF) Tuolumne Meadows (TM), Upper Lyell (UL), Emeric Lake (EL), Middle Lyell (ML).

Gradient Class	Low			Middle			Significant differences by gradient class
Meadow	SF, TM, UL			EL, ML			p
SR (kPA)	454.94	±	*45.94*	761.54	±	*55.75*	**0.004**
WHC (%)	66.17	±	*6.68*	48.67	±	*4.92*	**0.000**
GWC (%)	80.66	±	*2.85*	62.59	±	*2.54*	**0.000**
VWC (%)	37.87	±	*0.91*	31.27	±	*0.91*	**0.001**
SOM (%)	13.41	±	*0.35*	11.81	±	*0.40*	0.012
N (%)	0.46	±	*0.01*	0.40	±	*0.01*	0.007
SAND (%)	48.97	±	*4.95*	67.10	±	*6.78*	**0.000**
SILT (%)	37.46	±	*3.78*	22.42	±	*2.26*	**0.000**
CLAY (%)	13.58	±	*1.17*	10.49	±	*1.06*	**0.000**
COARSE FRAG. >2 MM (%)	7.19	±	*0.42*	6.12	±	*0.36*	0.044
COARSE FRAG. > 4MM (%)	3.46	±	*0.30*	4.79	±	*0.36*	**0.004**

Appendix II: Meadow biotic and biotic variable mean values and standard errors.

Table 10. Emeric Lake meadow gradient, soil texture classification, landscape positions, plant community types, abiotic and biotic variable mean values and standard errors. List of acronyms and abbreviations: soil resistance (SR), bulk density (BD), tot. total vegetation cover (tot_veg), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), coarse fragments (coarse frag.), redoxymorphic feature depth (redox depth). Plant types: *Calamagrostis breweri* (CB), *Ptilagrostis kingii* (PK).

Meadow gradient class	Middle					
Soiil texture	Sandy loam					
Landscape position	Mid-floodplain			Meadow's edge		
Plant community type	CB			PK		
SR (kPa)	1108.31	±	*73.00*	1248.98	±	*75.82*
BD (g/cm3)	0.54	±	*0.01*	0.60	±	*0.01*
TOT_VEG (%)	51.92	±	*0.45*	64.10	±	*0.58*
VWC (%)	39.05	±	*0.66*	27.34	±	*0.97*
GWC(%)	82.77	±	*3.28*	47.11	±	*1.88*
WHC(%)	64.19	±	*3.44*	37.41	±	*1.43*
SOM(%)	17.22	±	*0.54*	10.48	±	*0.28*
pH	4.70	±	*0.02*	4.80	±	*0.01*
C(%)	10.03	±	*0.31*	5.79	±	*0.14*
N(%)	0.58	±	*0.02*	0.35	±	*0.01*
C:N	16.92	±	*0.06*	16.18	±	*0.07*
SAND(%)	62.88	±	*1.37*	74.89	±	*1.04*
SILT(%)	25.83	±	*1.09*	15.90	±	*0.69*
CLAY(%)	11.29	±	*0.30*	9.21	±	*0.46*
COARSE FRAG. % (>2MM)	30.38	±	*0.65*	25.38	±	*0.30*
COARSE FRAG.% (>4MM)	4.06	±	*0.32*	7.86	±	*0.56*
ROOTS (%)	5.72	±	*0.16*	9.09	±	*0.35*
ROOTS (g/m2)	28.90	±	*1.13*	45.11	±	*1.92*
REDOX DEPTH (cm)	10.45	±	*0.20*	11.30	±	*0.26*

Table 11. Middle Lyell Canyon meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors (variable code and units shown on left). List of acronyms and abbreviations: soil resistance (SR), bulk density (BD), tot. total vegetation cover (tot_veg), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), coarse fragments (coarse frag.), redoxymorphic feature depth (redox depth). Plant types: *Calamagrostis breweri* (CB), *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC).

Meadow gradient class	Middle								
Soiil texture	Sandy Loam			Loam			Sandy loam		
Landscape position	Meadow's edge			Oxbow			Mid-floodplain		
Plant community type	CB			CV			DC		
SR (kPa)	661.18	±	*56.40*	153.44	±	*8.05*	186.40	±	*6.34*
BD (g/cm3)	0.87	±	*0.02*	0.45	±	*0.01*	0.60	±	*0.01*
TOT_VEG (%)	52.00	±	*0.91*	38.45	±	*0.65*	58.91	±	*1.03*
VWC (%)	20.47	±	*0.64*	42.50	±	*0.73*	24.65	±	*0.85*
GWC(%)	36.45	±	*1.35*	89.37	±	*1.96*	46.48	±	*1.69*
WHC(%)	39.29	±	*0.79*	60.19	±	*1.37*	40.13	±	*0.96*
SOM(%)	6.70	±	*0.12*	13.97	±	*0.42*	8.70	±	*0.21*
pH	5.75	±	*0.02*	5.01	±	*0.01*	5.13	±	*0.02*
C(%)	3.90	±	*0.08*	7.74	±	*0.21*	4.99	±	*0.11*
N(%)	0.26	±	*0.00*	0.43	±	*0.01*	0.31	±	*0.01*
C:N	15.02	±	*0.14*	18.42	±	*0.25*	15.82	±	*0.12*
SAND(%)	62.90	±	*0.57*	62.95	±	*1.39*	70.08	±	*0.78*
SILT(%)	25.91	±	*0.50*	25.24	±	*1.18*	20.76	±	*0.76*
CLAY(%)	11.19	±	*0.15*	11.81	±	*0.49*	9.16	±	*0.08*
COARSE FRAG. % (>2MM)	36.79	±	*0.41*	31.10	±	*0.80*	31.01	±	*0.32*
COARSE FRAG.% (>4MM)	3.12	±	*0.21*	2.88	±	*0.23*	4.08	±	*0.32*
ROOTS (%)	2.43	±	*0.09*	6.61	±	*0.46*	4.84	±	*0.28*
ROOTS (g/m2)	24.27	±	*1.43*	34.34	±	*1.91*	20.04	±	*0.70*
REDOX DEPTH (cm)	11.64	±	*0.31*	9.83	±	*0.41*	13.47	±	*0.39*

Table 12. Snow Flat meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors. List of acronyms and abbreviations: soil resistance (SR), bulk density (BD), tot. total vegetation cover (tot_veg), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), coarse fragments (coarse frag.), redoxymorphic feature depth (redox depth). Plant types: *Calamagrostis breweri* (CB), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK).

Meadow gradient class	Low								
Soiil texture	Loam								
Landscape position	Mid-floodplain						Water's edge		
Plant community type	CB			DC			PK		
SR (kPa)	1381.65	±	*69.38*	230.13	±	*8.17*	665.22	±	*29.78*
BD (g/cm3)	0.55	±	*0.01*	0.42	±	*0.01*	0.52	±	*0.01*
TOT_VEG (%)	50.42	±	*0.58*	60.33	±	*0.86*	56.41	±	*0.72*
VWC (%)	42.91	±	*0.48*	46.63	±	*0.47*	37.79	±	*0.61*
GWC(%)	73.13	±	*1.48*	111.01	±	*3.42*	78.28	±	*1.73*
WHC(%)	57.11	±	*1.66*	57.77	±	*2.02*	59.68	±	*1.31*
SOM(%)	14.73	±	*0.38*	17.32	±	*0.44*	13.48	±	*0.21*
pH	4.69	±	*0.01*	4.89	±	*0.02*	4.72	±	*0.01*
C(%)	8.03	±	*0.22*	9.40	±	*0.23*	7.37	±	*0.10*
N(%)	0.48	±	*0.01*	0.58	±	*0.01*	0.44	±	*0.01*
C:N	16.55	±	*0.08*	16.16	±	*0.04*	16.90	±	*0.05*
SAND(%)	47.18	±	*1.72*	59.49	±	*0.88*	57.97	±	*1.01*
SILT(%)	36.93	±	*0.85*	28.66	±	*0.67*	29.74	±	*0.92*
CLAY(%)	15.88	±	*0.88*	11.84	±	*0.31*	12.29	±	*0.24*
COARSE FRAG. % (>2MM)	30.30	±	*0.34*	30.28	±	*0.72*	37.15	±	*0.65*
COARSE FRAG.% (>4MM)	1.39	±	*0.12*	3.51	±	*0.34*	3.39	±	*0.19*
ROOTS (%)	6.53	±	*0.33*	9.91	±	*0.56*	6.48	±	*0.38*
ROOTS (g/m2)	52.677	±	*2.00*	33.5	±	*0.99*	36.9		*1.59*
REDOX DEPTH (cm)	12.00	±	*0.00*	13.33	±	*0.14*	10.66	±	*0.50*

Table 13. Tuolumne Meadows meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors. List of acronyms and abbreviations: soil resistance (SR), bulk density (BD), tot. total vegetation cover (tot_veg), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), coarse fragments (coarse frag.), redoxymorphic feature depth (redox depth). Plant types: *Calamagrostis breweri* (CB), *Carex vesicaria* (CV), *Ptilagrostis kingii* (PK).

Meadow gradient class	Low								
Soiil texture	Silt loam			Loam					
Landscape position	Mid-floodplain			Oxbow			Mid-floodplain		
Plant community type	CB			CV			PK		
SR (kPa)	1249.50	±	*63.37*	156.49	±	*11.45*	505.65	±	*57.93*
BD (g/cm3)	0.66	±	*0.01*	0.38	±	*0.01*	0.63	±	*0.01*
TOT_VEG (%)	55.59	±	*0.68*	40.85	±	*0.77*	54.05	±	*0.60*
VWC (%)	29.03	±	*0.69*	44.95	±	*0.48*	26.04	±	*0.75*
GWC(%)	50.43	±	*1.57*	122.80	±	*3.20*	50.97	±	*0.97*
WHC(%)	55.09	±	*1.68*	104.14	±	*5.76*	61.52	±	*1.85*
SOM(%)	9.60	±	*0.26*	15.66	±	*0.37*	11.13	±	*0.15*
pH	4.88	±	*0.01*	4.87	±	*0.02*	4.82	±	*0.01*
C(%)	5.46	±	*0.14*	8.55	±	*0.20*	6.16	±	*0.07*
N(%)	0.36	±	*0.01*	0.56	±	*0.01*	0.42	±	*0.01*
C:N	15.36	±	*0.13*	15.93	±	*0.20*	16.36	±	*0.20*
SAND(%)	53.50	±	*1.94*	37.47	±	*2.35*	45.03	±	*1.96*
SILT(%)	32.29	±	*1.71*	48.59	±	*2.11*	40.91	±	*1.91*
CLAY(%)	14.21	±	*0.30*	13.94	±	*0.34*	14.05	±	*0.22*
COARSE FRAG. % (>2MM)	34.54	±	*0.40*	26.94	±	*1.03*	31.14	±	*0.55*
COARSE FRAG.% (>4MM)	4.09	±	*0.30*	10.03	±	*0.54*	5.49	±	*0.41*
ROOTS (%)	3.74	±	*0.13*	6.10	±	*0.30*	4.55	±	*0.12*
ROOTS (g/m2)	25.85	±	*0.93*	27.94		*1.52*	31.54	±	*0.83*
REDOX DEPTH (cm)	13.38	±	*0.65*	12.83	±	*0.16*	10.70	±	*0.22*

Table 14. Upper Lyell Canyon meadow gradient, soil texture classification, landscape positions, plant community types, and abiotic and biotic variable mean values and standard errors. List of acronyms and abbreviations: soil resistance (SR), bulk density (BD), tot. total vegetation cover (tot_veg), volumetric water content (VWC), gravimetric water content (GWC), water holding capacity (WHC), soil organic matter (SOM), carbon (C), nitrogen (N), carbon-to-nitrogen ratio (C:N), coarse fragments (coarse frag.), redoxymorphic feature depth (redox depth). Plant types: *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK).

Soiil texture	Loam			Silt loam			Loam		
Soiil texture	Loam			Silt loam			Loam		
Landscape position	Oxbow			Mid-floodplain					
Plant community type	CV			DC			PK		
SR (kPa)	314.00	±	*59.62*	340.74	±	*28.95*	287.13	±	*8.56*
BD (g/cm3)	0.38	±	*0.01*	0.52	±	*0.01*	0.69	±	*0.01*
TOT_VEG (%)	40.71	±	*0.83*	65.76	±	*1.10*	64.81	±	*1.01*
VWC (%)	47.54	±	*0.66*	39.61	±	*0.48*	27.34	±	*0.71*
GWC(%)	129.50	±	*3.71*	71.40	±	*1.09*	41.58	±	*1.20*
WHC(%)	91.17	±	*4.47*	64.78	±	*1.05*	43.93	±	*0.96*
SOM(%)	17.73	±	*0.53*	12.11	±	*0.16*	9.11	±	*0.16*
pH	5.10	±	*0.02*	5.22	±	*0.01*	5.14	±	*0.01*
C(%)	9.64	±	*0.26*	6.61	±	*0.07*	5.17	±	*0.08*
N(%)	0.63	±	*0.02*	0.42	±	*0.00*	0.30	±	*0.01*
C:N	16.34	±	*0.22*	15.79	±	*0.05*	17.65	±	*0.25*
SAND(%)	39.26	±	*1.75*	42.31	±	*0.75*	56.95	±	*1.44*
SILT(%)	46.92	±	*1.50*	43.56	±	*0.74*	30.54	±	*1.30*
CLAY(%)	13.82	±	*0.29*	14.13	±	*0.20*	12.51	±	*0.28*
COARSE FRAG. % (>2MM)	30.15	±	*0.80*	33.90	±	*0.59*	33.61	±	*0.34*
COARSE FRAG.% (>4MM)	4.53	±	*0.56*	1.06	±	*0.07*	2.45	±	*0.19*
ROOTS (%)	8.77	±	*0.58*	5.29	±	*0.29*	4.30	±	*0.12*
ROOTS (g/m2)	36.29	±	*1.68*	25.47	±	*1.09*	29.41		*0.99*
REDOX DEPTH (cm)	10.21	±	*0.20*	11.83	±	*0.21*	11.33	±	*0.06*

Appendix III: Soil Particle Size Distribution & Texture Class

Table 15. Particle size distribution (percentage sand, silt, clay) and soil texture class by plant community types: *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK).

Plant Type	Sand %	Silt %	Clay %	Texture Class
CB	57	30	13	sandy loam
CV	47	40	13	loam
DC	58	31	12	sandy loam
PK	59	29	12	sandy loam

Table 16. Particle size distribution (percentage sand, silt, clay) and soil texture class by meadow and plant community types: *Carex vesicaria* (CV), *Deschampsia cespitosa* (DC), *Ptilagrostis kingii* (PK). Meadows: Snow Flat (SF) Tuolumne Meadows (TM), Upper Lyell (UL), Emeric Lake (EL), Middle Lyell (ML).

Meadow	Plant Type	Sand %	Silt %	Clay %	Texture Class
Emeric Lake		**69**	**21**	**10**	**sandy loam**
	CB	63	26	11	sandy loam
	PK	75	16	9	sandy loam
Middle Lyell Canyon		**65**	**24**	**11**	**sandy loam**
	CB	63	26	11	sandy loam
	CV	63	25	12	sandy loam
	DC	70	21	9	sandy loam
Snow Flat		55	31	13	**loam**
	CB	48	36	15	loam
	DC	60	28	12	sandy loam
	PK	57	30	12	sandy loam
Tuolumne Meadows		**45**	**41**	**14**	**loam**
	CB	53	32	14	loam
	CV	37	49	14	loam
	PK	45	41	14	loam
Upper Lyell Canyon		**46**	**40**	**13**	**loam**
	CV	39	47	14	loam
	DC	42	44	14	loam
	PK	57	31	13	sandy loam