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Livestock grazing in intermountain depressional wetlands—Effects on plant strategies, soil characteristics and biomass

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ABSTRACT

Prairie wetlands are considered valuable habitat for plants, birds, and wildlife. Livestock use of these wetlands can create conflicts with conservation issues. To achieve proper management, patterns and processes induced by grazing livestock need to be understood. In this study, we examined interactions of livestock use, soil and vegetation of depressional prairie wetlands in British Columbia, Canada. Plant community composition, biomass, and soil properties (bulk density, salinity, nitrogen and carbon content) were sampled on transects in marsh and wet meadow vegetation zones of wetlands along a grazing intensity gradient. Grime's CSR-strategies were used to calibrate strategy signatures, which indicate the importance of competition, stress and disturbance. Heavily grazed sites had higher salinity, less biomass, and proportionally less belowground biomass. Differences concerning strategies between vegetation zones were only apparent in un/lightly grazed sites, where stress was higher in marsh and competition higher in wet meadow zones. Livestock use and nitrogen were positively correlated with ruderal abundance and negatively correlated with competitors and stress-tolerators. Livestock use was identified to be most influential on plant strategies. Our results indicate that heavy livestock use significantly alters vegetation patterns and processes in prairie wetlands and may have negative impact on valuable habitat. Management decisions should consider reduced livestock access and incorporate conservation issues in grazing schemes.

1. Introduction

Prairie wetlands and their associated vegetation play important ecological and economic roles in large parts of North America (Mitsch and Gosselink, 2000). As islands within relatively dry regions, they are especially vital for providing several ecological services, such as water filtration and storage (Leibowitz, 2003) and carbon sequestration (Euliss et al., 2006). They are fundamental in offering breeding habitat and shelter to a variety of waterfowl (Batt et al., 1989; Johnson et al., 2005), other wetland associated birds (Weller and Spatcher, 1965), and amphibians (Piha et al., 2007). Besides also hosting a number of wetland plant species, they supply wildlife with water and forage, and are thus of great conservation concern (Leibowitz, 2003; Seabloom and van der Valk, 2003). The semiarid grasslands, where these wetland ecosystems can be found, are important forage pastures for livestock and agriculture industries. Many of these wetlands have thus either been converted to agricultural land (Galatowitsch, 1993), or are under high grazing pressure by livestock (van Ryswyk et al., 1992).

Grazing is known to have the potential to alter ecosystems and change their structure and function (Hobbs, 1996). The general effects of livestock use on vegetation and soil are well-studied; cattle remove aboveground biomass, reduce litter accumulation, compact and disturb the soil (Austin et al., 2007; Greenwood and Mackenzie, 2001; Schulz and Leininger, 1990; Wheeler et al., 2002), further promoting erosion through mechanical disturbance of the soil surface (Pietola et al., 2005). Additionally, several studies have observed changed nutrient conditions (Bakker et al., 2004; Golluscio et al., 2009; McNaughton et al., 1997; Reeder and Schuman, 2002) and an increase in soil salinity (Belsky et al., 1999; Lavado and Taboada, 1987; Srivastava and Jefferies, 1996) under grazing in several regions. Moreover, a number of studies have investigated the responses of wetland vegetation communities to livestock use, and have found reactions to be dependent on hydrological conditions, and the intensity and seasonal occurrence of grazing (Austin et al., 2007; Jones et al., 2011; Lucas et al., 2004; Schulz and Leininger, 1990). Consistent findings regarding changes in vegetation and community structure show a decrease in litter accumulation, and shifts in plant functional types including

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decreased abundance of tall and rhizomatous species, and an increase of species with an annual lifecycle and short canopy height. On the other hand, moderate levels of disturbance have been shown to diversify vegetation composition and structure (e.g. Grace and Jutila, 1999; Marty, 2005; Jones et al., 2011), according to the 'hump-backed model' of plant species richness (Grime, 1973), and thus diversify habitats for other species (van Wieren, 1995; Metera et al., 2010). However, studies rarely consider the interactions of soil characteristics and livestock use and their relative importance in shaping vegetation patterns in prairie wetland vegetation.

One attempt to describe responses of plant communities to different soil and site characteristics has been made with Grime's plant strategy theory (Grime, 1974, 1977, 2001). This theory makes predictions about the distribution of species according to their adaptations to stress and disturbance, as well as their competitive ability when those two factors are negligible. Herein, stress is defined as a limitation of plant growth, either due to a deficit in essential resources or the presence of a growth-limiting factor, and disturbance as the destruction or damage of living plant material. Wetland vegetation is naturally exposed to stress through excess levels of water causing anoxic conditions. Livestock use has the potential to add to the stress component, by reducing nutrient availability and increasing salinity. Grazing and trampling, however, act as a disturbance (Grime, 2001), further altering competitive interactions (Gough and Grace, 1998). Species that are either tolerant or adapted to grazing (e.g. low palatability, adapted growth form) can react with compensatory growth, compensating or even increasing productivity (McNaughton, 1983), and are thus favored (Grime, 2001). Besides affecting plant growth, heavy grazing and trampling also creates gaps and reduces litter accumulation. This changes the competition for light (Olff and Ritchie, 1998), promoting the establishment of low growing perennial forbs and ruderal, early successional species (e.g. Bullock et al., 2001; Evju et al., 2010; Milchunas et al., 1988; van der Valk, 1986).

Depressional wetlands in the intermountain west are situated in a matrix of semiarid grasslands, similar to those in the Prairie Pothole Region of North America. But unlike the prairies east of the Rocky Mountains, this region did not support large herds of herbivores before human settlement and the introduction of cattle and horses (Mack and Thompson, 1982). Cattle ranching is now a widespread land use practice and of great commercial importance (van Ryswyk et al., 1992) making wetlands prone to alterations in their form and function. For this reason, it is essential to understand the processes, especially those altered by livestock use, to develop sustainable management practices for these valuable ecosystems.

This study examined the effects of livestock use on soil properties and plant strategies in depressional wetlands of southern interior British Columbia in the summer of 2010. We hypothesized that (i) soil salinity would increase, but soil carbon content, along with biomass and the proportion of belowground biomass, would decrease with increasing livestock use. We further expected (ii) stress-tolerant species to be more abundant in the more frequently inundated parts of the wetlands, and competitors to dominate drier and less disturbed areas. Additionally, we hypothesized that (iii) higher levels of salinity and decreased levels of nitrogen would increase the importance of stress tolerance, whereas high degrees of disturbance would primarily alter the vegetation community to more ruderal species, and decrease the importance of competition.

2. Methods

2.1. Study area

The study was conducted on the Thompson plateau in south central British Columbia, Canada (Fig. 1). This region is characterized by a continental semiarid climate, with mean annual precipitation of approximately 380 mm, and mean July temperature exceeding 20 °C at altitudes of the study sites (Wikeem and Wikeem, 2004).

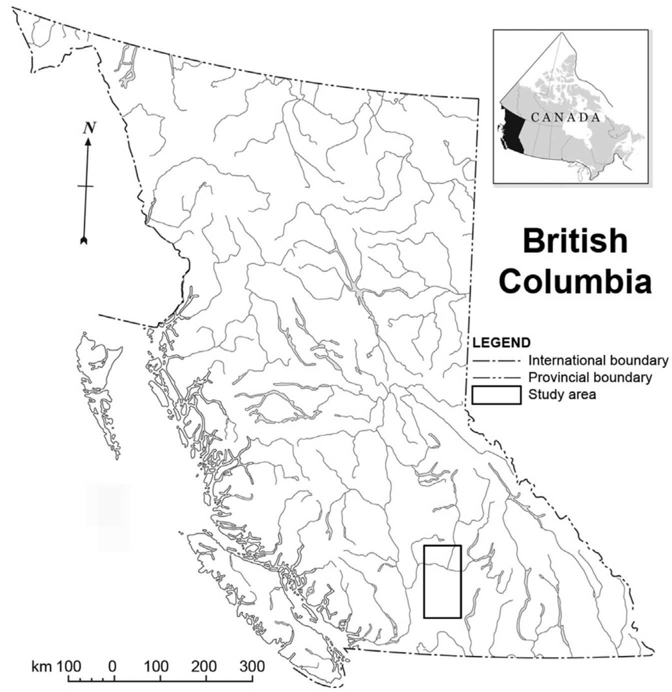

Fig. 1. Map of the study area.
Source: http://atlas.gc.ca.

Depressional wetlands in this area are similar in structure to those of the Prairie Pothole Region of North America (Kantrud, 1989), and are characterized by vegetation zones that form according to flooding height and duration (Jones et al., 2011). The marsh zone is defined by the open water and the height of the seasonal inundation, and is dominated by perennial graminoids such as *Scirpus acutus* and *Puccinellia nuttaliana.* The wet meadow zone does not experience regular flooding, and draws the line to the upland vegetation. It is dominated by *Juncus balticus*, *Hordeum jubatum* and *Poa pratensis*.

Eleven depressional wetlands at two locations representing a grazing intensity gradient were chosen for the study. Five were located at Hamilton Commonage southwest of Nicola Lake, and six were located in Lac du Bois Grasslands Provincial Park north of Kamloops. Three wetlands were fully fenced off, and two had partial fencing. The latter two and the remaining six wetlands were part of one or more pastures with stocking rates ranging from 0.8 to 2 cattle/ha. Wetland size ranged from 0.3 to 65 ha, and flooding was permanent to seasonal.

2.2. Field sampling

We laid out three to six transects at each wetland, equally spaced around its edge. This resulted in a total of 46 transects that were 60–650 m apart. The number of transects per wetland depended on its accessibility and on the presence of partial fencing in which case we increased the sampling effort. Transects were oriented perpendicular to the hydrologic gradient, from the inundated marsh to the edge of the lower prairie vegetation. Each transect was classified as either 'un-/lightly grazed' or 'heavily grazed' prior to field sampling, mainly based on indications of use, like trampling and signs of grazing, as well as local factors, such as abundance and accessibility of wetlands, and stocking rates. However, stocking rates

Table 1
Recorded vegetation, soil, and site parameters, units of measure, and sampling sizes.

Parameter	Unit	Sampling size
Species cover	%	0.25 m × 0.5 m
Aboveground biomass	kg/m^2	0.25 m × 0.25 m
Root biomass	kg/m^2	Ø10 cm, 10 cm deep
Percent root biomass	%	
Cover of bare ground	% of quadrat corners	
Soil bulk density	g/cm^3	Ø10 cm, 10 cm deep
pH		Scatter sample
Conductivity	dS/m	Scatter sample
Total soil carbon	%	Scatter sample
Total soil nitrogen	%	Scatter sample
Inclination	%	
Lifestock use category	"Un-/lightly grazed" or "heavily grazed"	
Vegetation zone	"Marsh" or "wet meadow"	

of the adjacent upland areas by itself were found to be no good indication of livestock use intensity of the sampling sites. Actual intensity of wetlands through livestock depended on more than just this variable, and was found to be affected by factors such as water availability and quality, as well as abundance and accessibility of wetlands (LM Teuber, personal observation). For example, partly fenced wetlands in a lightly grazed area that only had a few access points were found to show signs of heavy grazing at the accessible sites. Transects on such sites were classified as heavily grazed in this study.

We estimated total vegetation cover, as well as cover of each species in ten 0.25 m × 0.5 m frames at equal distances along each transect. Bare ground was measured as the number of sampling quadrate corners intersecting bare ground (Jones et al., 2011), and was later transformed to range from 0 to 100. We additionally recorded mean slope for each transect. All data was combined for each zone at each transect, resulting in a total of 92 samples (46 marsh and wet meadow samples each).

We sampled biomass once in both vegetation zones of each transect, by clipping aboveground parts and taking soil cores with a sharpened PVC pipe for belowground biomass (Table 1). Soil was sampled for chemical analyses from five random spots in each vegetation zone, using a soil sampler (Ø 2.5 cm). Seven soil and belowground biomass samples could not be taken due to sampling difficulties. The remaining samples ($n = 85$) were used for statistical analysis. All field sampling was conducted in July 2010.

2.3. Laboratory analysis

Aboveground biomass was dried at 60 °C, soil cores at 105 °C, and weighed. Subsequently, roots, rhizomes and coarse soil fragments (>2 mm) were washed out of the soil cores, their volume was measured, and both were dried at 60 °C and weighed separately. We then calculated soil bulk density for the top 10 cm (Soil Survey Staff, 2009). We analyzed total soil nitrogen and carbon in the scatter samples using a C/N-Analyzer. Conductivity, as a measure for salinity, and pH were also analyzed for all field samples in soil solution according to Soil Survey Staff (2009).

2.4. CSR-strategies

In order to assess the response of strategy types to livestock use and soil parameters, we assigned plant species to Grime's CSR (competitor–stress-tolerators–ruderal) strategies. CSR-values of 48 species (53%) could be obtained from Grime et al. (2007). Following the dichotomous key and checklist provided by Grime (1984), we added values for missing species (for a detailed list of CSR values see supplementary material). We then used the strategies to calculate C-, S-, and R-signatures for both zones at each transect similar to the method described by Hill et al. (2002). Ten points were distributed between the three strategy types for each species, while for the site signatures species were weighted with their relative cover. This method creates a C-, S-, and R-index, and provides a way to assess the importance of each of the three factors, stress, disturbance, and competition in a numeric fashion.

2.5. Data analysis

Due to the partial fencing at some of the sites, the consequential ecological separation of the transects, and the spatial variability at the wetland-level, we chose un-/lightly and heavily used transects and not the wetlands as the sample units. We believe that because of the variable wetland size, the high distance and the lack of interconnectedness between transects even within the same use category, transects can be regarded as independent of one another.

We first used principal component analysis (PCA) for a graphical analysis of soil properties and biomass parameters. Correlations of parameters with principal components were assessed with the Spearman rank correlation coefficient. We examined differences in soil properties and biomass between heavily and un-/lightly grazed sites in the two vegetation zones using two-way ANOVAs. The livestock use categories and vegetation zones were added as binary variables to test for effects of the single factors or their interaction. Inspection of residual distribution and homogeneity of variances was done graphically. Further, Spearman rank correlation coefficients were calculated for environmental, soil and biomass parameters in order to identify effects of site characteristics. p-Values were corrected for multiple tests according to the Bonferroni–Holm method.

Both, bare ground and soil bulk density, were recorded as livestock use indicators, and since the two factors showed only little redundancy (Spearman's $\rho = 0.48$), we used both to compute an index of livestock use. This was done by PCA of both variables, of which we used site scores of the first axis (eigenvalue = 1.48) as the new livestock use index (LU). PCA is commonly used to condense several variables into new ones that effectively summarize the original information and can be used for subsequent analysis (Quinn and Keough, 2003).

We first examined the responses of CSR-strategies to livestock use and soil parameters graphically by means of indirect ordination. Non-metric multidimensional scaling (NMDS) was conducted based on the Bray–Curtis dissimilarity matrix of the strategy signatures, using several random starts and a rotation so that most variance occurs on the first axis (function metaMDS of the 'vegan' package; Oksanen et al., 2011). The number of dimension used in this analysis was assessed by a screen diagram (stress vs. number of dimensions), and set to 2. We then analyzed effects of livestock use and soil properties on strategy signatures with multiple linear regression. Subsequent to the graphical assessment of the NMDS plot, we added LU and soil nitrogen as independent variables, and conductivity as a covariable to LU of all models. Final models were determined using backward model selection based on the lowest value of Akaike's information criterion (*R* function 'step'). Errors and variance of residuals were checked graphically, and assumptions of linear regression were met. These analyses were done separately for marsh and wet meadow, to assess differences in the extent of the effects between vegetation zones. We analyzed differences between vegetation zones in the two livestock use categories by means of two-way ANOVA.

The statistical software of choice for all data analysis was the R statistical package (R Development Core Team, 2010).

Table 2
Mean values and standard deviation of soil and biomass variables in the marsh and wet meadow of un-/lightly and heavily grazed sites. Differences of parameters between livestock use categories (use), vegetation zones (zone), or their interaction (use × zone) and their significance based on two-way ANOVAs are indicated by asterisks.

	Un-/lightly grazed		Heavily grazed		Difference in categories		
	Marsh ($n = 22$)	Wet meadow ($n = 22$)	Marsh ($n = 21$)	Wet meadow ($n = 20$)	Use	Zone	Use × zone
Aboveground biomass	1.04 ± 0.44	0.76 ± 0.22	0.38 ± 0.37	0.37 ± 0.28	***	**	
Belowground biomass	2.73 ± 1.98	2.56 ± 1.09	0.78 ± 0.99	1.00 ± 0.91	***		
% Roots	66.32 ± 15.88	74.95 ± 9.27	57.26 ± 23.19	67.23 ± 15.79			
Soil bulk density	0.40 ± 0.18	0.47 ± 0.19	0.62 ± 0.23	0.73 ± 0.29	**		
Bare ground	17.60 ± 13.32	4.26 ± 7.71	55.67 ± 24.85	58.49 ± 12.19	***	**	*
Conductivity	1.80 ± 1.22	1.50 ± 1.38	4.25 ± 2.77	2.67 ± 1.40	***		
pH	8.56 ± 0.34	8.50 ± 0.26	8.67 ± 0.33	8.57 ± 0.34			
C	11.21 ± 3.64	9.92 ± 3.07	12.24 ± 4.19	10.82 ± 4.38			
N	0.99 ± 0.33	0.88 ± 0.30	0.96 ± 0.40	0.85 ± 0.37			

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

3. Results

3.1. Soil properties and biomass

Soil pH ranged from moderately to strongly alkaline (pH 8.0–9.0), and samples showed no to moderate salinity (0.3–10.4 dS/m). Total carbon (C) and nitrogen (N) contents ranged from 4.2 to 23.6% and 0.33 to 1.85%, respectively. Topography of the sites, as measured by inclination, differed between livestock use categories (*t*-test: $p < 0.001$), heavily used sites being steeper (10.7 vs. 5.7%). Inclination showed correlations of moderate degree with bare ground (Spearman's $\rho = -0.43$, adj. $p < 0.01$), above- and belowground biomass ($\rho = 0.43$, adj. $p < 0.01$ and $\rho = 0.46$, adj. $p < 0.001$, respectively), N ($\rho = -0.37$, adj. $p < 0.05$), and C ($\rho = -0.49$, adj. $p < 0.001$). However, conductivity was not correlated with inclination ($\rho = -0.28$, adj. $p > 0.05$). Percent carbon was strongly correlated with nitrogen (Spearman's $\rho = 0.88$, adj. $p < 0.001$).

Samples showed a clear distinction between the two livestock use categories. This distinction occurred along the first principal component (PC1, Fig. 2). Both, soil bulk density and bare ground were positively correlated (Spearman's $\rho = 0.74$ and $\rho = 0.77$, adj. $p < 0.001$), below- and aboveground biomass were negatively correlated ($\rho = -0.73$ and $\rho = 72$, adj. $p < 0.001$) with PC1, and all seemed to determine the differences between the use categories. The second principal component (PC2) mainly comprised a carbon and nitrogen gradient ($\rho = 0.87$ and $\rho = 0.77$, adj. $p < 0.001$). Differences between marsh and wet meadow zones could not be observed by this method.

Differences between the livestock use categories of bare ground, soil bulk density, conductivity, and above- and belowground biomass were revealed by the two-way ANOVAs (Table 2). Both variables that were used as livestock use indicators, soil bulk density and bare ground, had higher values in the heavily grazed sites; soil bulk density being 1.5-times higher in both zones, and bare ground three- and 14-times higher in marsh and wet meadow, respectively. Bare ground was, however, higher in the marsh of lightly unused sites, but slightly higher in the wet meadow of heavily used sites. Likewise, conductivity, which was found to correlate with bare ground (Spearman's $\rho = 0.49$, $p < 0.001$), showed a similar positive response to high use. Aboveground biomass was twice as low in the wet meadow, and almost three times lower in the marsh of heavily grazed sites compared to un-/lightly grazed sites. Belowground biomass was found to be 2.5- and 3.5-fold lower in wet meadow and marsh, respectively, under heavy grazing. However, aboveground biomass was found to differ between vegetation zones.

3.2. Plant strategies

The NMDS showed an excellent goodness of it (stress = 0.0323), and the most important of the recorded factors in influencing the distribution of plant strategies seemed to be the livestock use index. This factor strongly followed the first axis in the NMDS plot (NMDS1, Fig. 3), and most variance of this factor (indicated by symbol size) occurs along this axis. Site hydrology, as signified by vegetation zones, along with conductivity seemed to determine variation along the second axis (NMDS2). However, this was only prevalent at low intensities of livestock use, where marsh and wet meadow sites were noticeably distinct.

The livestock use index and soil nitrogen mostly predicted strategy signatures, whereas livestock use always had a greater effect on signatures (Table 3). While the competition (C) and stress (S) indices were negatively affected by increasing livestock use and soil nitrogen in the marsh zone, the ruderal signature (R) showed an increase with both variables. Effects were similar in the wet

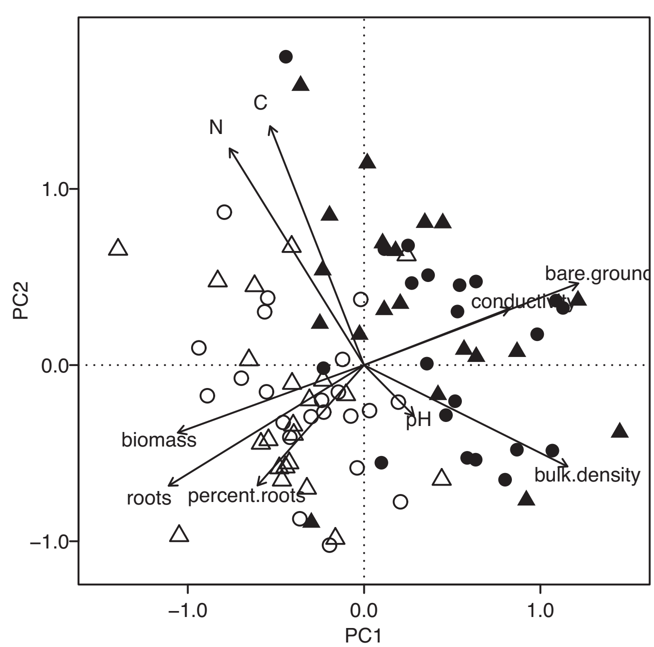

Fig. 2. Plot of principal components analysis of soil and biomass variables in marsh (○) and wet meadow (△) of un/lightly (open symbols) and heavily grazed (solid symbols) sites. Vectors are fitted for all variables and include above- and belowground (root-) biomass, percentage of belowground biomass (percent.roots), soil bulk density, cover of bare ground (bare.ground), conductivity, pH, as well as total soil carbon (C) and nitrogen (N). Vector length indicates correlation strength with principal components.

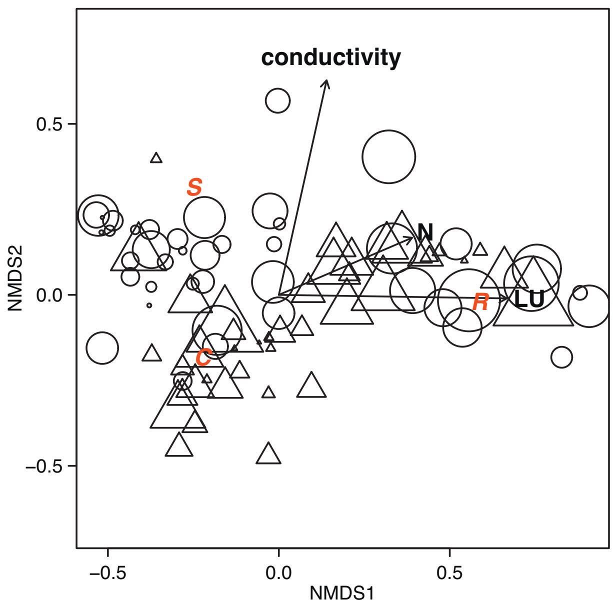

Fig. 3. Nonmetric multidimensional scaling results of CSR-signatures in marsh (◯) and wet meadow (△). Vectors are fitted for the livestock use index (LU), conductivity and soil nitrogen (N), vector length signifies strength of the gradient. Symbol size represents degree of livestock use intensity, with larger symbols indicating higher LU-values. The orientation of competitors, stress-tolerators, and ruderals in the ordination space are indicated by letters (C, S, and R). Final stress = 0.0323.

meadow, although nitrogen had no effect on the R signature and the S signature was only affected by the livestock use-conductivity interaction term. The adjusted R^2 was only reasonably high for C and S models. Effects of livestock use were generally higher in the wet meadow and those of nitrogen higher in the marsh zone.

The spatial variation of strategies among the vegetation zones, as well as differences between livestock use intensity categories were revealed by two-way ANOVA (Fig. 4). Differences in strategy-index values were not always apparent between vegetation zones; however values always differed between use categories, at least in one of the zones. The competition signature was highest in the wet meadow of un-/lightly grazed sites. It was also higher in this category than in heavily grazed sites, and was found to be the dominating strategy in wet meadows of un-/lightly grazed sites. Similarly, the stress signature differed only among zones in un-/lightly grazed transects. Whereas high grazing intensities decreased S in the marsh zone, it did not change levels in the wet meadow zone. The ruderal signature showed higher values under heavy grazing, but differences between vegetation zones could not be observed (Fig. 4).

4. Discussion

This study revealed the influence of livestock use on plant strategies, biomass, and selected physical and chemical soil properties in depressional prairie wetlands.

Most importantly, this study found a change in patterns of wetland vegetation caused by livestock grazing. The NMDS ordination showed that most variation in CSR-strategies occurred along the livestock use gradient. Differences between vegetation zones (i.e. hydrology and salinity) however, were only apparent at low grazing intensity. The position of C- and S-signatures in the ordination space indicate their association with wet meadow and marsh, respectively, when grazing is low. Spatial patterns of CSR-strategies were revealed by the comparison of vegetation zones and livestock use categories, and for the most part supported hypothesis (ii). Differences caused by livestock use were apparent for all indices, though stress did not differ in the wet meadow. Yet, only un-/lightly grazed sites displayed differences between the vegetation zones for C- and S- signatures. In the marsh zone, increased salinity as well as stress through frequent flooding cause stress tolerant species to be more abundant. Competition however was greatest in wet meadows of un-/lightly grazed sites. Here, flooding did not seem to cause great stress, yet water supply was still sufficient, and salinity was low compared to the more frequently inundated marsh zone. Vegetation cover and productivity in the wet meadow was high, causing competitive species to dominate, when not disturbed. The patterns found in un-/lightly grazed sites reflect the species' competitive performance and their ability to establish under different flooding regimes and levels of salinity (Engels et al., 2011; Fraser and Miletti, 2008; van der Valk and Welling, 1988).

Overall trends in plant strategies under livestock grazing showed a shift from competitors to ruderal strategists under increasing grazing intensity, only partly confirming the assumptions made in hypothesis (iii). Livestock use was identified as the most important factor in influencing plant community composition. The disturbance caused by trampling and grazing favored ruderal strategists. Ruderals often have an annual or short lived perennial lifecycle and mainly invest resources in rapid growth and seed production (Grime, 2001). By producing most of their biomass aboveground, and by depending on seeds for reproduction, ruderal species have adapted to disturbances such as trampling. Their short lifecycles and dispersal by seed further allows these species to invade bare ground gaps in the vegetation (Bullock et al., 2001), which were abundant on heavily grazed sites. In addition, ruderals rely on ample nutrient supply for their rapid growth and seed production (Grime, 2001). In this study, soil nitrogen availability was coupled with increased abundance of ruderal strategists, and decreased abundance of competitors and stress-tolerators. Salinity, which generally inhibits plant growth, showed no overall effect on plant strategies, since it

Table 3
Multiple linear regression results for CSR-signature models in marsh (m) and wet meadow (w). Degrees of freedom (df) and adjusted R^2 (R^2_{adj}) are listed along with *t*-values for livestock use intensity (LU), soil nitrogen (N), conductivity and the livestock use-conductivity interaction term (LU × conductivity). Only variables that were included in final models after backward selection are shown.

Strategy	Zone	df	R^2_{adj}	Lifestock use (LU)	N	Conductivity	LU × conductivity
C	m	2,37	0.42	−4.769***	−3.968***		
	w	2,35	0.63	−8.071***	−2.902**		
S	m	2,37	0.21	−2.676*	−2.966**		
	w	3,38	0.11	−2.004		−0.385	2.806**
R	m	2,37	0.44	4.740***	4.441***		
	w	2,35	0.55	6.796***	1.586		

* $p < 0.05$.
** $p < 0.01$.
*** $p < 0.001$.

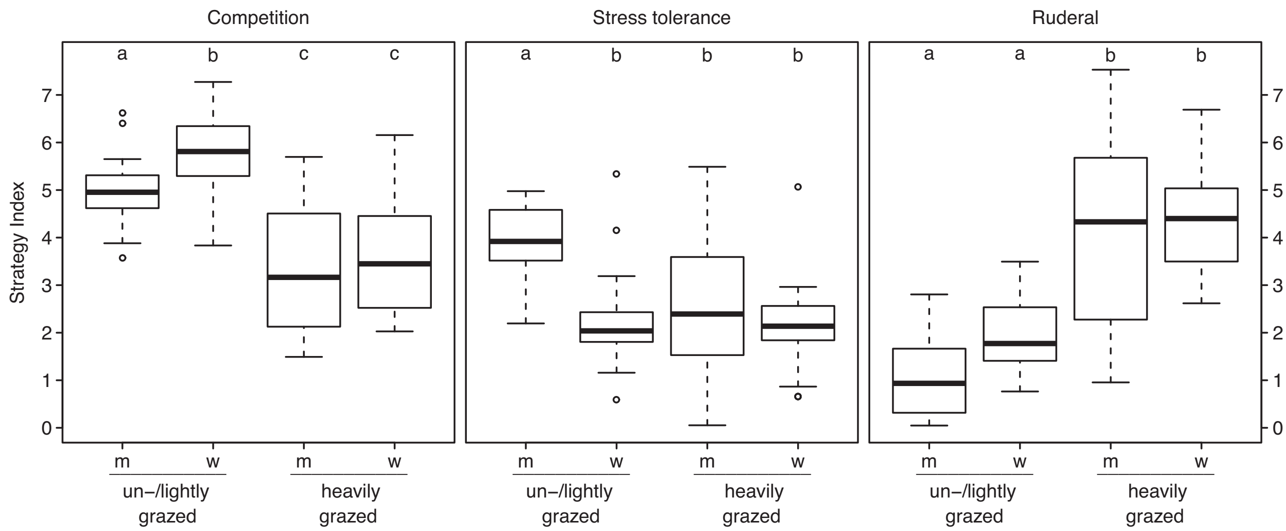

Fig. 4. Boxplots of competition, stress tolerance and ruderal strategy indices in marsh (m) and wet meadow (w) of the un-/lightly and heavily grazed sites. The strategy index is a calibrated measure of the relative abundance of competitors, stress-tolerators and ruderals, ranging from 0 to 10. Differences between categories based on ANOVA and a Tukey-HSD test ($p < 0.05$) are indicated by different letters.

was eliminated from most linear models by the backward selection procedure. However, salinity did increase the stress index when looked at with livestock use intensity as a covariate in the wet meadow zones. This indicates that under no or little grazing, salinity increases the abundance of stress tolerant species in the wet meadow zone. These results indicate that the influence of natural processes in determining plant community composition in depressional wetland vegetation is greatly reduced through the presence of heavy grazing. The disturbance caused by grazing livestock lead to drastic changes in the effects of hydrology and salinity on vegetation communities in both marsh and wet meadow. Only sites that are under low grazing pressure showed differences in plant strategies between the two vegetation zones, which are characterized by different flooding regimes and different levels of salinity. The importance of stress-tolerance and competitive ability in marsh and wet meadow, respectively, was significantly reduced, and adaptations to disturbance were favored. The lack of zonation of strategy types at heavily used sites could have been caused by the gentler slopes at these transects. However, we always found a zonation of species to be present in the field, which allowed us to make a visual separation of marsh and wet meadow.

Soil density and bare ground showed differences between the two livestock use categories in this study (Table 2) and have also been found to be good indicators of livestock use in other studies (e.g. Greenwood and Mackenzie, 2001). These results supported the use of their combined information as the livestock use index. Stocking rates, as mentioned before, were regarded as unsuitable indicators for this study.

In accordance with previous studies, heavy grazing greatly increased soil bulk density and bare ground, and decreased both above- and belowground biomass. The latter decrease can be largely explained by a change in species composition. As reported by Jones et al. (2011), and also found in this study (data not shown), grazing reduced rhizomatous and stoloniferous species, and favors annuals, or ruderal species in wetlands of the study region. Annuals invest most resources in the production of stem and leaf tissue, less in underground organs (Grime, 2001), thus the decline of belowground biomass.

The data further revealed higher salinity in heavily grazed wetlands, as has been previously described for semiarid regions (Belsky et al., 1999; Lavado and Taboada, 1987). The soil salinization is triggered by altered hydrological conditions of the topsoil through the removal of biomass and the exposure of bare ground, which causes total transpiration from plants to decrease, soil water to be raised by capillary action, and increased evaporation. This way, evaporating soil water transports and deposits salts in the topsoil increasing salinity. Moreover, water infiltration is reduced by the compaction of the soil (e.g. Hiernaux et al., 1999; Naeth et al., 1991), preventing rain water to leach salts back into deeper soil horizons. Inundation and thus soil water availability in the studied wetlands are however influenced by topography; more shallow depressions will be inundated over larger areas than steeper ones. The slope of depressions in this study was steeper in the un-/lightly grazed category, making this factor a possible explanatory variable for the differences in soil salinity. Topography has been shown to influence ecosystem processes in arid rangelands (Popp et al., 2009). Nonetheless, salinity and inclination showed no correlation, which allows us to infer that heavy grazing does indeed affect soil salinity in these ecosystems. These findings partly confirm the assumptions of hypothesis (i). However, Cook and Hauer (2007) find wetland salinity to depend on hydrologic connectivity through soil- or groundwater. This aspect has not been assessed in this study and needs further research regarding interactions with changes caused by grazing livestock.

The correlation of soil carbon and nitrogen possibly reflects the origin of both elements mostly from organic matter. Both factors were not affected by heavy grazing, as reported in previous studies (Biondini et al., 1998). These results suggests that effects of opposing processes described in the literature lead to no net effect of grazing on soil C and N. Bakker et al. (2004) and Golluscio et al. (2009) found that the removal of biomass by livestock decreases both nitrogen and carbon levels. On the contrary, McNaughton et al. (1997) and Reeder and Schuman (2002) argued that under heavy grazing less N and C is fixed in litter and belowground biomass increasing levels in the soil. Additionally, increased mineralization rates in the soil were thought to increase nutrient levels. The processes that increase C and N levels most likely compensated the loss through biomass removal in this study. However, only total soil carbon and nitrogen were measured, and effects might differ for organic carbon, or plant available nitrogen.

5. Conclusions

Heavy grazing was found to strongly affect soils as well as vegetation in the studied wetlands. Natural processes in soils and vegetation communities were greatly disrupted by heavy livestock use. Soil salinity increased, and the disturbance by livestock predominantly influenced plant strategies.

Grazing in the study area has greatly increased since the introduction of cattle and horses, given that large herds of wild ungulates are believed to have been absent from this region west of the Rocky Mountains (Mack and Thompson, 1982). For this reason, an understanding of natural processes and of those altered and caused by grazing livestock is essential to making sustainable management decisions for those ecosystems. The effects of grazing on both soil properties and vegetation properties emphasize the importance for sound management, whether managing for livestock or wildlife. The increased salinity of grazed wetlands reduces their quality as water sources for grazing livestock. Water supply for livestock might be a management goal for livestock owners, especially in some of the more remote rangelands. The alteration of water quality and wetland vegetation in grazed wetlands might also be a handicap to wildlife conservation. As reported by Jones et al. (2011), grazing negatively affects waterfowl populations in the study area. Corresponding to the 'intermediate disturbance hypothesis' (Grime, 1973), however, moderate levels of disturbance have been shown to diversify vegetation composition and structure (e.g. Grace and Jutila, 1999; Marty, 2005) and thus diversify habitats for other species (van Wieren, 1995; Metera et al., 2010). On the other hand, Jones et al. (2011) found native as well as exotic plant species richness to be highest at moderate grazing intensities in the study area, consistent with the 'intermediate disturbance hypothesis'.

All these issues need to be addressed when making decisions on stocking density, fencing of wetlands, and water supply. Partial fencing of wetlands retains some areas from grazing impacts, and maintains natural vegetation and soil structure and processes in those parts. Although access sites of partially fenced wetlands always showed impacts of heavy livestock use in this study, the changes did not seem to influence the fenced-off areas to any considerable extent.

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.agee.2013.04.017.

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