



# Power and limitation of soil properties as predictors of variation in peak plant biomass in a northern mixed-grass prairie



Kurt O. Reinhart\*, Lance Vermeire

United States Department of Agriculture- Agricultural Research Service, Fort Keogh Livestock & Range Research Laboratory, 243 Fort Keogh Road, Miles City, MT, 59301-4016 USA

## ARTICLE INFO

### Keywords:

Calcareous grassland  
Locally applicable indicators  
Plant-soil relationships  
Predictive indicators  
Predictive uncertainty  
Rangeland health  
Rangeland stewardship  
Soil health spatial variability

## ABSTRACT

Soil properties are thought to affect annual plant productivity in rangelands, and thus soil variables that are consistently correlated with plant biomass may be general indicators of rangeland health. Here we measured several soil properties (e.g. aggregate stability, organic carbon, total nitrogen) and tested each as a would-be predictor of local variation in peak aboveground grassland biomass. Individual properties explained a slight ( $\leq 10\%$ ) amount of variation in plant biomass. Plant biomass was mainly (negatively) associated with two soil properties, subsurface soil carbonate concentration and the stability of soil macroaggregates near the soil surface. Less important predictive variables included: elevation, plant community composition, surface soil organic carbon, and soil carbon:nitrogen. Plot-to-plot variation in plant biomass is seemingly difficult to predict based on soil properties, including popular indicators of soil and rangeland health and even root biomass. While protection of soil is critical to overall rangeland ecosystem function, our findings suggest that the relationship between soil properties and plant biomass in natural grasslands is complex. Thus, there may not be one or even several soil properties that consistently predict appreciable variation in peak grassland biomass, especially variation within an ecosystem independent of precipitation.

## 1. Introduction

Rangelands are the most common biome type in the world, occurring in vast regions (Ellis and Ramankutty, 2008). Many have relatively low productivity, yet the capacity of rangelands to annually produce plant biomass (and animal biomass) is a fundamental ecosystem function and measure of their sustainability (De Groot et al., 2002; Havstad et al., 2007). The accurate assessment of whether rangeland function is improving, stable, or degrading is of local to global importance (e.g. Baveye et al., 2016; Eldridge et al., 2016), especially since these regions are understudied relative to their geographic area (Martin et al., 2012). One approach is to indirectly monitor ecosystem function/health (e.g. Reeves and Baggett, 2014; Stephens et al., 2015) with, for example, ground-based data of various indicators of ecosystem function (Pellant et al., 2005; Tongway and Hindley, 2004). There are, however, innumerable putative indicators (e.g. animal, insect, plant, soil, spectral) of ecosystem function and health which ideally require objective (i.e. evidence-based) selection criteria (Andrews and Carroll, 2001; Ludwig et al., 2004; Rezaei et al., 2006). Robust indicators seemingly should be well-documented, highly correlated with ecosystem functions, and have minimal collinearity with other indicator

variables (Andrews and Carroll, 2001). Unfortunately, it may be slow, logistically and analytically difficult, and expensive to discern optimal indicators from a large pool of would-be indicators (Andrews and Carroll, 2001; Rezaei et al., 2006; Toledo et al., 2014) and to then determine the importance of each in separate rangeland types. To our knowledge, relatively few studies have attempted to determine the best minimum set of soil properties to predict local variation in plant biomass in natural grasslands (Reinhart et al., 2016; Rezaei et al., 2006).

Despite the popularity of measuring many putative indicators of ecosystem function by land managers and scientists (e.g. Herrick et al., 2010; <https://vimeo.com/channels/raythesoilguy>), few studies have actually quantified the predictive accuracy of an indicator or determined the best (and worst) predictors (Rezaei et al., 2006; Wang, 2010). One of the most relevant studies tested the importance of many biological, chemical, and physical soil properties on productivity of Iranian rangelands (i.e. total yield, herbaceous plant production, and utilizable forage) (Rezaei et al., 2006). Two of the most important predictor variables were a nutrient cycling index (*sensu stricto* Tongway and Hindley, 2004) and soil profile effective thickness. Some scientists are starting to acknowledge 1) that many putative soil (health

\* Corresponding author.

E-mail address: [kurt.reinhart@ars.usda.gov](mailto:kurt.reinhart@ars.usda.gov) (K.O. Reinhart).

or quality) indicators may not explain appreciable amounts of *actual* variation in ecosystem function (Baveye et al., 2016; Bennett et al., 2010; Letey, 1991; Oldfield et al., 2015; Reinhart et al., 2015) and 2) the importance of quantifying the predictive uncertainty of such indicators.

Here we tested (i.e. mensurative experiment) whether local variation in grassland peak (aboveground) biomass could be predicted by other plant, soil, and/or site properties. While moderately large amounts of year-to-year variation in plant biomass ( $r^2 \geq 0.74$ ) was explained by annual variation in precipitation (Wiles et al., 2011), the best predictive soil properties (i.e. soil physical, microbial, and chemical properties) have explained only slight amounts ( $0.15 \leq r^2 \leq 0.19$ ) of local (plot-to-plot) variation in plant biomass in the Northern Great Plains (Reinhart et al., 2016; Reinhart et al., 2015). In previous work, we were able to explain slight amounts of plot-to-plot variation in plant biomass by subsurface (5–15 cm) microbial biomass ( $r^2 = 0.18$ ), plant available nutrients (boron [ $r^2 = 0.19$ ], manganese [ $r^2 = 0.17$ ], and phosphorus [ $r^2 = 0.18$ ]; Reinhart et al., 2016), and soil water infiltration data ( $r^2 = 0.15$ , Reinhart and Vermeire, 2016). Additional research in northern mixed-grass prairie in North Dakota indicated that comparable amounts of variation in annual net primary productivity were explained by plant (i.e. plant community composition) and soil properties (i.e. bulk density, infiltration, mollic horizon depth, silt, and soil organic matter) (Wang, 2010). We tested whether putative predictors explained appreciable (local) variation in peak plant biomass. Based on prior studies (e.g. Pellant et al., 2005; Rezaei et al., 2006; Wang, 2010), we predicted peak aboveground plant biomass would be positively associated with soil organic carbon concentration, soil organic matter, total nitrogen concentration, and water-stable aggregates.

## 2. Methods

### 2.1. Study site and system

Research was conducted at the USDA-Agricultural Research Service's Fort Keogh Livestock and Range Research Laboratory (Fort Keogh, 21,214 ha) near Miles City, Montana, USA. Mean annual precipitation was 34 cm (1937–2011). Peak above-ground annual productivity for this system occurs in July and is dominated by perennial  $C_3$  graminoids (Vermeire et al., 2009). Fort Keogh is centrally located in the Northern Great Plains Steppe ecoregion where grasslands cover more than 22 million ha in five states in the USA and two Canadian provinces and are dominated by temperate and semiarid mixed-grass prairie (Martin et al., 1998). Average annual precipitation for this region ranges from less than 25–50 cm with most occurring during the growing season (May and June). The grasslands support an estimated 11 million animal unit months of livestock grazing.

The study site ( $46^{\circ}18'20.8''N$ ,  $105^{\circ}58'42.8''W$ ) is a silty range site on an upland plain with a gentle slope ( $1.05^{\circ}$  slope) and fine loamy soil (Eapa loam, frigid Aridic Argiustolls). Carbonates in the B horizon indicate the site is a calcareous grassland. The study site (0.3 ha) was selected because it matched one of the most common grassland types (*Hesperostipa comata*, *Bouteloua gracilis*, and *Carex filifolia*) in the Northern Great Plains (e.g. Coupland, 1961; Martin et al., 1998) and allowed us to sample across local gradients (plot-to-plot) in peak plant productivity while controlling many abiotic factors.

### 2.2. Sampling design

Nearly one third (0.1 ha) of the sampled area was within a livestock enclosure established in 1999 (Fig. 1). The other two thirds were equally divided among two pastures that on average were grazed at light to moderate levels (based on USDA-NRCS recommendations) primarily from May through October. In terms of pasture area per cow, pasture "A" averaged 16 ha per cow (522 kg = 1150 lbs) during

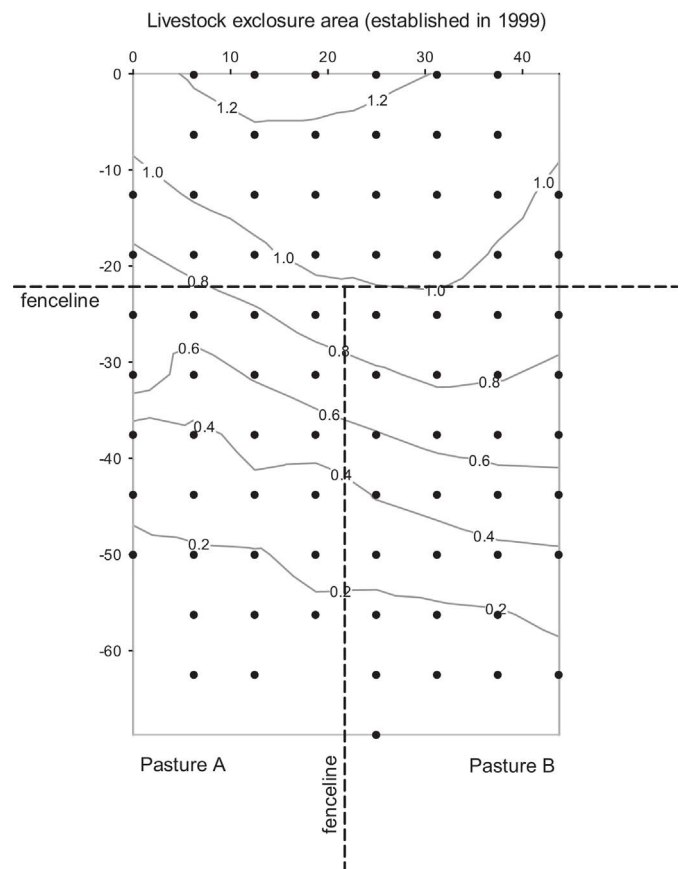


Fig. 1. Map of the sampling grid. Sampling was divided equally among three adjacent areas: a livestock enclosure and two adjacent pastures (A, B) grazed annually by cows. Systematic sampling points ( $n = 81$ ) are shown (●), axes' units are meters, and contour lines represent elevation gain (m) relative to the lowest point in the sampled area. Map redrawn from Reinhart and Vermeire (2016).

May and October while pasture "B" averaged 14 ha per cow [between 1991 and 2011 the lowest unit area per cow per month was 2.2 and 2.8 ha per cow, respectively]. We fenced off the remaining sampling area (i.e. portions of pastures "A" and "B" shown in Fig. 1) from livestock in 2011 to prevent removal of pin flags and confounding of plant biomass measures.

### 2.3. Plant aboveground biomass and composition

We sampled annual aboveground biomass and community composition at peak production for 81 quadrats ( $0.25\text{-m}^2$ ). Quadrats were placed 0.5 m to the east of each systematically placed point (Fig. 1) and clipped from July 5–12, 2011. The vegetation in the quadrat was clipped and separated by dominant species and functional groups. Dominant species included four graminoids (*Carex filifolia*, *Koeleria macrantha*, *Hesperostipa comata*, and *Pascopyrum smithii*) and one cactus (*Opuntia polyacantha*). Additional species were grouped as forbs, other grasses, or shrubs. Our intent was to measure variation in dominant plant species which are believed to be the main drivers of ecosystem function (Grime, 1998) and may affect soil properties (Derner et al., 2006; Gould et al., 2016; Schuman et al., 2009). Plant material was dried to constant weight, separated into current-year and older material, and weighed. Because *Opuntia* is difficult to dry, we used a correction calculation ( $0.2 \times$  fresh weight), derived by researchers at Fort Keogh, to estimate the dry weight of *Opuntia*.

### 2.4. Soil core analysis

We measured several soil properties including: root biomass, soil

organic carbon (SOC), soil organic matter (SOM), total nitrogen (N), and % water-stable aggregates. Soil cores were used to measure most soil properties, except water-stable aggregates. Soil was cored with an 87 mm diameter soil column cylinder auger, which was hammered to 65 cm deep into the soil (Sunvalley Solutions Inc./Eijkelpkamp, FL, USA) by a hand-held jackhammer powered with compressed air June 12–17, 2012. Surface vegetation was clipped prior to coring. Compaction of the soil column during the sampling procedure was corrected based on the measured length of the soil core and the hole depth (Don et al., 2007). Compaction was on average  $1.5\% \pm 2.1$  standard deviation. The soil cores were segregated into 0–10, 10–30, and 30–60 cm increments and placed in sealed plastic bags. We sampled 81 points 0.2 m to the west of fixed points (Fig. 1). The 81 cores resulted in a total of 243 samples that were brought back to the lab. In the lab, samples were broken up and weighed. A 5 g subsample was used to determine % water content of the entire sample. The sample was sealed in a plastic bag and frozen ( $-20^{\circ}\text{C}$ ) until processed further.

Because gathering fine root fragments is tedious, we used a subsampling routine and available sieving equipment to expedite quantification of root biomass. Samples were thawed and roots were extracted by hand from fresh samples as described by Reinhart and Vermeire (2016). The samples were sieved (2 mm) for 1 min on a mechanical sieve shaker (RO-TAP, RX-29, W.S. Tyler, Mentor, Ohio). Rocks ( $> 2$  mm) were collected by hand and weighed. A 10 g subsample of soil ( $< 2$  mm) was extracted and roots were removed by hand. From this, a 2 g soil sample was dried at  $50^{\circ}\text{C}$  and used to determine SOM with the loss on ignition test ( $550^{\circ}\text{C}$ , 16 h). A portion of the root biomass data (77 cores and only 0–30 cm depth increment) were previously published (Reinhart and Vermeire, 2016).

With the remaining fine soil subsamples ( $< 2$  mm root free soil), SOC concentration was determined after grinding 1.5 g of soil. SOC concentration of ground samples was determined by measuring total carbon concentration (measured with Flash 2000 Series Nitrogen and Carbon Analyzer, Thermo Scientific, MA, USA) subtracting the soil inorganic carbon (SIC) which represents the carbonate-C. SIC was determined by the modified pressure-calimeter method (Sherrod et al., 2002). N concentration was measured simultaneously with total carbon. Because of our soil coring method and dry soil conditions, we observed that many soil cores had soil particles migrate from the top of the core to the bottom. So reliable bulk density values could be estimated for only a small subset of cores ( $n = 26$ ), and bulk density (and soil carbon stocks) is not included in analyses. Both % SOC and % N were corrected for free water in the dried sample.

Soil aggregate stability data were collected 0.5 m to the south of all 81 points. We measured % water-stable (soil) aggregates following standard methods (Kemper and Rosenau, 1986) described in detail by Reinhart et al. (2015). In brief, the samples were first dry-sieved, and the percentage of water-stable aggregates was determined for three macroaggregate size classes (0.25–1, 1–2, and 2–4 mm) by wet-sieving. Data were previously published (Reinhart and Vermeire, 2016) and used to explain variation in biomass of three dominant graminoids and root biomass.

## 2.5. Analysis

Outliers (average = 0.8 per variable) were identified and removed based on the maximum normal residual method (Snedecor and Cochran, 1989) and  $P < 0.05$ . Subsequently, plots with missing data were omitted from analyses ( $n = 58$ ). Data summaries are provided (Table 1). Correlation coefficients among all plant and soil properties are also provided (Table 2).

Our aim was to identify appreciable associations between plant and soil properties. The data, however, were potentially spatially correlated, which would violate the assumption of sample independence for analyses (Legendre, 1993). Variables with spatial autocorrelation were subjected to additional tests to control for spatial autocorrelation. First,

**Table 1**

Study site properties [mean  $\pm$  normal-based 95% CI (minimum, maximum)] for three adjacent subsections (a grazing enclosure and two adjacent pastures [Fig. 1]) of a northern mixed-grass prairie site. Variation among the three areas can be interpreted by whether 95% CI overlap.

	depth (cm)	Area 1 (grazing enclosure, n = 21)	Area 2 (pasture A, n = 15)	Area 3 (pasture B, n = 22)
shoot biomass	–	2082 $\pm$ 185 (1460, 3092)	1784 $\pm$ 184 (1158, 2226)	1730 $\pm$ 194 (944, 2898)
root biomass	0–60	15348 $\pm$ 3144 (3869, 24986)	6854 $\pm$ 1544 (3168, 14376)	11047 $\pm$ 2640 (2901, 26768)
%N	0–10	1.12 $\pm$ 0.05 (0.90, 1.31)	1.23 $\pm$ 0.07 (1.00, 1.41)	1.18 $\pm$ 0.06 (1.00, 1.41)
	10–30	0.75 $\pm$ 0.03 (0.70, 0.91)	0.79 $\pm$ 0.05 (0.60, 0.91)	0.82 $\pm$ 0.04 (0.60, 1.00)
	30–60	0.70 $\pm$ 0.03 (0.60, 0.81)	0.82 $\pm$ 0.06 (0.60, 1.01)	0.80 $\pm$ 0.04 (0.60, 0.91)
	0–60	0.78 $\pm$ 0.02 (0.70, 0.85)	0.87 $\pm$ 0.04 (0.77, 1.00)	0.86 $\pm$ 0.03 (0.74, 0.97)
%SIC	0–10	0.15 $\pm$ 0.01 (0.10, 0.18)	0.16 $\pm$ 0.03 (0.06, 0.28)	0.16 $\pm$ 0.02 (0.04, 0.25)
	10–30	4.24 $\pm$ 1.39 (0, 10.59)	0.62 $\pm$ 0.58 (0.11, 3.39)	2.95 $\pm$ 1.81 (0.08, 10.49)
	30–60	15.04 $\pm$ 1.73 (1.03, 17.96)	8.38 $\pm$ 4.10 (0.26, 18.82)	12.66 $\pm$ 2.62 (0.24, 19.35)
%SOC	0–10	1.17 $\pm$ 0.07 (0.95, 1.43)	1.22 $\pm$ 0.10 (0.97, 1.62)	1.17 $\pm$ 0.07 (0.93, 1.55)
	10–30	0.70 $\pm$ 0.03 (0.61, 0.85)	0.69 $\pm$ 0.03 (0.60, 0.81)	0.70 $\pm$ 0.04 (0.52, 0.88)
	30–60	0.62 $\pm$ 0.02 (0.52, 0.74)	0.68 $\pm$ 0.05 (0.48, 0.88)	0.68 $\pm$ 0.04 (0.56, 0.88)
	0–60	0.73 $\pm$ 0.02 (0.65, 0.80)	0.76 $\pm$ 0.03 (0.69, 0.85)	0.76 $\pm$ 0.03 (0.66, 0.86)
%SOM	0–10	3.65 $\pm$ 0.22 (2.45, 4.88)	3.72 $\pm$ 0.24 (3.04, 4.43)	3.65 $\pm$ 0.13 (3.27, 4.21)
	10–30	3.53 $\pm$ 0.11 (3.10, 3.89)	3.38 $\pm$ 0.12 (3.10, 3.96)	3.41 $\pm$ 0.13 (2.96, 4.05)
	30–60	3.41 $\pm$ 0.09 (3.08, 3.85)	3.57 $\pm$ 0.20 (3.06, 4.30)	3.52 $\pm$ 0.12 (3.01, 4.18)
WSA1†	0–10	68.4 $\pm$ 3.8 (55.0, 86.1)	80.9 $\pm$ 4.9 (62.5, 95.2)	75.7 $\pm$ 5.1 (31.9, 91.0)
WSA2†	0–10	41.8 $\pm$ 4.7 (29.5, 70.2)	55.2 $\pm$ 5.7 (40.6, 74.4)	49.8 $\pm$ 3.7 (24.4, 66.9)
WSA3†	0–10	45.5 $\pm$ 5.9 (27.0, 77.0)	56.9 $\pm$ 6.9 (36.8, 81.2)	54.8 $\pm$ 4.5 (33.6, 71.7)

shoot biomass = peak (aboveground) plant biomass (kg per ha), root biomass = living and dead root biomass (kg per ha), %N = concentration of total nitrogen in root free soil  $< 2$  mm ( $\% \times 10^3$ ), %SIC = soil inorganic carbon (carbonates;  $\% \times 10^3$ ), % SOC = concentration of soil organic carbon in root free soil  $< 2$  mm ( $\% \times 10^2$ ), % SOM = soil organic matter (%), and WSA = % water-stable aggregates of three size classes of macroaggregates (1 = 0.25–1 mm, 2 = 1–2, and 3 = 2–4). † indicates most of these data were published by Reinhart and Vermeire (2016).

we tested for the presence of spatial autocorrelations with Moran's I tests using the "ape" package (Paradis et al., 2004). We measured spatial autocorrelation using an inverse distance weighted residual error matrix. We also visually assessed spatial autocorrelation with spatial variograms. If spatial autocorrelation was present then we conducted regression analyses using generalized least squares (GLS) which can account for spatial autocorrelation in model residuals (Beale et al., 2010; Dormann et al., 2007). This was done for best multiple regression models (see next paragraph). For the GLS models, we tested six ways of fitting a parametric correlation function (uncorrelated errors, exponential, Gaussian, linear, rational quadratic, spherical) to the residual co-variance matrix, which were fit by maximizing the restricted log-likelihood. We selected the model (i.e. uncorrelated errors) with the lowest Akaike information criterion (AIC) score for each predictor variable. All tests were performed in R (R Development Core Team, 2011), and GLS was conducted with the "nlme" package. Only ordinary least squares regression results are presented because AIC scores for the GLS models with uncorrelated errors were consis-

**Table 2**

Pearson product-moment correlations ( $r$ ) for plant, site, and soil properties in a northern mixed-grass prairie ( $n = 58$ ). In bold are correlation coefficients with significant ( $\alpha = 0.05$ )  $p$ -values (\*  $< 0.05$ , \*\*  $< 0.01$ , \*\*\*  $< 0.001$ ).

	biomass	PC1	PC2	PC3	roots10	roots30	roots60	roots0.60	elevdiff
PC1	0								
PC2	-0.05	0.03							
PC3	0.16	-0.05	-0.06						
roots10	0.04	<b>-0.33*</b>	0.13	-0.01					
roots30	-0.1	<b>-0.48***</b>	<b>0.29*</b>	-0.22	<b>0.69***</b>				
roots60	-0.12	<b>-0.47***</b>	<b>0.40**</b>	-0.12	<b>0.35**</b>	<b>0.58***</b>			
roots0.60	-0.04	<b>-0.47***</b>	<b>0.27*</b>	-0.1	<b>0.92***</b>	<b>0.89***</b>	<b>0.64***</b>		
elevdiff	0.04	<b>-0.62***</b>	<b>0.32*</b>	-0.14	<b>0.38**</b>	<b>0.56***</b>	<b>0.57***</b>	<b>0.55***</b>	
CN.10	0.14	<b>-0.30*</b>	-0.16	-0.02	<b>0.51***</b>	<b>0.41**</b>	<b>0.30*</b>	<b>0.52***</b>	<b>0.35**</b>
CN.30	0.05	<b>-0.43***</b>	0.03	0.03	0.26	<b>0.45***</b>	<b>0.37**</b>	<b>0.39**</b>	<b>0.54***</b>
CN.60	-0.02	-0.18	0.26	-0.1	<b>0.34**</b>	<b>0.38**</b>	<b>0.47***</b>	<b>0.44***</b>	<b>0.42***</b>
CN0.60	0.06	<b>-0.38**</b>	0.12	-0.07	<b>0.49***</b>	<b>0.58***</b>	<b>0.56***</b>	<b>0.62***</b>	<b>0.60***</b>
N10	0.12	0.24	-0.19	<b>0.31*</b>	-0.02	<b>-0.35**</b>	<b>-0.28*</b>	-0.19	<b>-0.43***</b>
N30	-0.06	<b>0.29*</b>	0.13	0.01	0	-0.14	-0.05	-0.06	-0.15
N60	0.03	<b>0.48***</b>	<b>-0.28*</b>	0.21	<b>-0.29*</b>	<b>-0.63***</b>	<b>-0.59***</b>	<b>-0.52***</b>	<b>-0.63***</b>
N0.60	0.02	<b>0.51***</b>	-0.2	0.23	-0.21	<b>-0.60***</b>	<b>-0.51***</b>	<b>-0.45***</b>	<b>-0.62***</b>
SIC10	-0.2	0.21	-0.09	-0.14	-0.16	0.03	-0.16	-0.08	-0.17
SIC30	-0.18	<b>-0.37**</b>	<b>0.49***</b>	-0.21	<b>0.26*</b>	<b>0.57***</b>	<b>0.65***</b>	<b>0.50***</b>	<b>0.59***</b>
SIC60	<b>-0.32*</b>	<b>-0.53***</b>	0.17	-0.07	<b>0.39**</b>	<b>0.49***</b>	<b>0.47***</b>	<b>0.51***</b>	<b>0.67***</b>
SOC10	0.16	0.04	-0.24	0.24	0.24	-0.08	-0.08	0.1	-0.18
SOC30	-0.02	0.02	0.17	0.04	0.18	0.15	0.2	0.21	0.2
SOC60	0.03	<b>0.45***</b>	-0.16	0.17	-0.14	<b>-0.50***</b>	<b>-0.42***</b>	<b>-0.34**</b>	<b>-0.48***</b>
SOC0.60	0.07	<b>0.35**</b>	-0.15	0.24	0.09	<b>-0.31*</b>	-0.23	-0.1	<b>-0.32*</b>
SOM10	0.03	0.04	-0.08	0.16	0.17	-0.07	0.16	0.12	-0.1
SOM30	0.01	-0.19	0.15	0.08	0.06	0.25	0.25	0.18	<b>0.35**</b>
SOM60	-0.18	0.09	<b>-0.35**</b>	<b>0.33*</b>	-0.11	<b>-0.33*</b>	<b>-0.31*</b>	-0.25	-0.21
WSA1	-0.05	<b>0.29*</b>	-0.02	0.18	-0.22	<b>-0.31*</b>	-0.18	<b>-0.27*</b>	<b>-0.41**</b>
WSA2	-0.25	0.17	<b>-0.26*</b>	-0.01	-0.08	<b>-0.30*</b>	-0.08	-0.17	<b>-0.35**</b>
WSA3	<b>-0.26*</b>	0.11	<b>-0.33*</b>	-0.05	-0.07	<b>-0.27*</b>	-0.03	-0.14	<b>-0.27*</b>

Abbreviations: biomass (peak annual aboveground plant biomass in 2011), PC (principle component [1–3] for plant community composition), roots (living and dead root biomass [10 = 0–10 cm depth, 30 = 10–30, 60 = 30–60, or 0.60 = 0–60]), elevdiff (elevation difference), CN (ratio of soil organic carbon to total nitrogen [0–10, 10–30, 30–60, or 0–60 cm]), N (concentration of total nitrogen in root free soil < 2 mm [0–10, 10–30, 30–60, or 0–60 cm]), sic (soil inorganic [carbonate] concentration [0–10, 10–30, or 30–60 cm]), SOC (concentration of soil organic carbon in root free soil < 2 mm [0–10, 10–30, 30–60, or 0–60 cm]), SOM (% soil organic matter [0–10, 10–30, or 30–60 cm]), and WSA (% water-stable aggregates of three size classes of macroaggregates [1 = 0.25–1 mm, 2 = 1–2, and 3 = 2–4]).

tently smaller than other models.

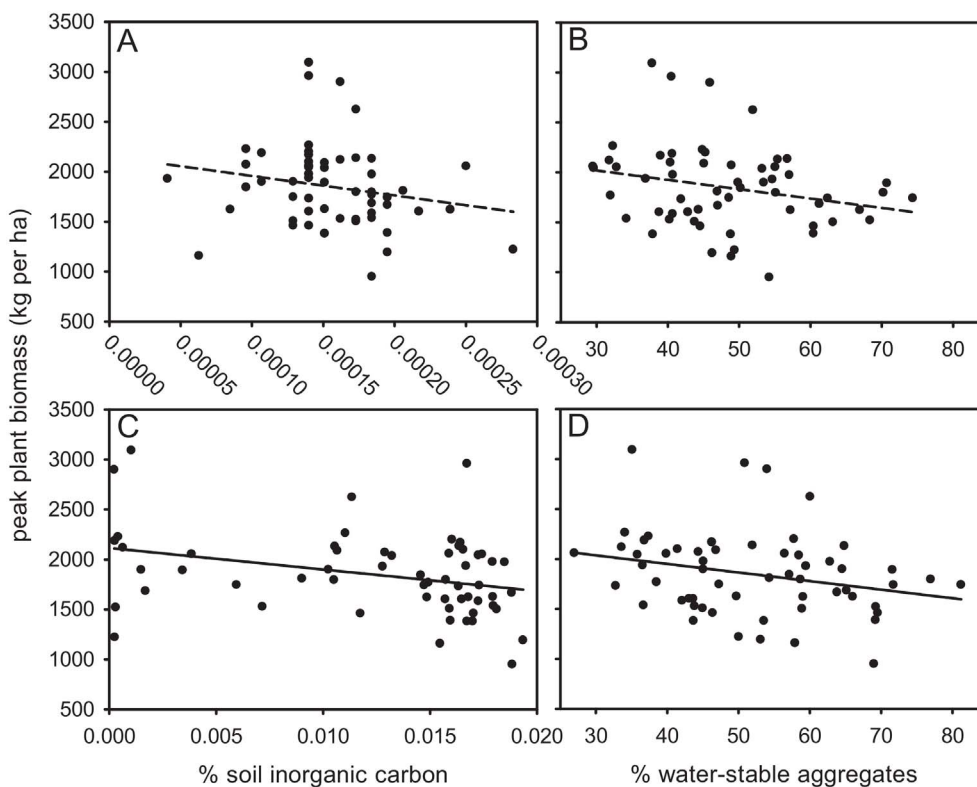
To identify the best minimum dataset for predicting peak aboveground plant biomass, we performed multiple linear regression analyses using plant, site, and soil properties. First, we performed a principal component analysis (PCA) of plant community composition data using the vegan package (Oksanen et al., 2015) in R. Plant abundance data were transformed with the command decostand(hellinger) in vegan, and total inertia was 0.24. Then, PCA scores with eigenvalues greater than the mean (i.e. PC1, PC2, and PC3) were incorporated into multiple linear regression (MLR) models. MLR predictor variables included: plant community composition data (PCA scores), carbonates, carbon:nitrogen ratio, elevation, N, root biomass, SOC, SOM, and water-stable aggregates. We used the regsubsets function in the leaps package (Lumley and Miller, 2009) in R with the exhaustive search method to determine the five best models per level of parameters. Leaps uses an efficient branch-and-bound algorithm to rapidly determine the best models. We then used Schwarz's Bayesian information criterion to identify the five best models. We report traditional parametric statistics for models. Residual analyses included visual confirmation that the assumptions of normality and homoscedasticity of residuals were not violated. We assessed multicollinearity among parameters in selected models with variance inflation factors. We also conducted an outlier analysis using Cook's distance (Cook and Weisberg, 1982) to see whether the model results changed, if the sample(s) with the highest influence on the particular model outcomes were excluded from the best MLR model. We calculated Cook's distance and excluded all samples with a Cook's distance greater than one while rerunning the particular model without them. This had no effect on significance levels.

### 3. Results

Plant and soil properties were quantified in three adjoining areas (grazing enclosure and two adjacent pastures). Areas varied appreciably in soil nitrogen, soil inorganic carbon, total roots, and water-stable aggregates, but not peak plant biomass, soil organic carbon, and soil organic matter (Table 1). [Differences between areas should not be interpreted as treatment effects because treatments (e.g. livestock enclosure) were not replicated.]

Several plant, soil, and site properties were correlated. Though elevation across the site varied by only one meter (Fig. 1), elevation was correlated with most plant and soil properties (Table 2). Several plant properties (i.e. biomass, principle components indicating variation in plant community composition, root biomass) were associated with variation in site (elevation) and/or soil properties (i.e. soil carbon:nitrogen, carbonates, total nitrogen concentration, soil organic carbon concentration, and water-stable aggregates) (Table 2). For example, total peak aboveground biomass was negatively correlated with subsurface carbonates and the stability of soil macroaggregates (2–4 mm aggregate size class) (Fig. 2). Many plant and most soil properties exhibited spatial autocorrelation (Moran's I test,  $P \leq 0.04$ ).

Modest amounts of variation in peak plant biomass ( $\leq 26\%$ ) were explained by relatively simple and equally parsimonious models (Table 3). The five best models explained 22–26% of the variation in peak plant biomass. Among the five best models, two predictor variables (subsurface soil carbonate concentration and elevation) were common. Others such as plant community composition (PC3), soil carbon:nitrogen (0–10 cm sample depth), soil organic carbon (0–10 cm), and water-stable aggregates (0–10 cm, 1–2 mm aggregate size class) were infrequently included as predictor variables.



**Fig. 2.** Relationship between peak plant biomass and four of the best soil predictor variables (A–D). Panels differentiate inorganic carbon data for the soil surface (0–10 cm soil depth, A) and subsurface (30–60 cm, C) and two size classes of macroaggregates (1–2 mm, B; 2–4 mm, D). Selection of best soil property predictors was based on results reported in Table 2. Best-fit lines (based on ordinary least squares) are solid when regressions were significant ( $\alpha = 0.05$ ) or dashed when non-significant.

**Table 3**  
Five best multiple regression models, based on Schwarz Bayesian Criterion scores (BIC), to explain local variation in peak annual (aboveground) plant biomass.

models	independent variables	BIC	t-value	F	P	R <sup>2</sup>
1	elev	–	2.84	–	0.006	–
	SIC60	–	–3.89	–	< 0.001	–
	total	–2.01	–	7.63	0.001	0.22
2	CN10	–	2.42	–	0.019	–
	SIC60	–	–3.49	–	< 0.001	–
	WSA2	–	–2.64	–	0.011	–
3	total	–1.04	–	6.25	0.001	0.26
	elev	–	3.05	–	0.004	–
	PC3	–	1.54	–	0.13	–
4	SIC60	–	–3.99	–	< 0.001	–
	total	–0.46	–	6.01	0.001	0.25
	elev	–	2.46	–	0.017	–
5	CN10	–	1.44	–	0.15	–
	SIC60	–	–4.02	–	< 0.001	–
	total	–0.15	–	4.09	0.002	0.25
5	elev	–	2.99	–	0.004	–
	SIC60	–	–3.88	–	< 0.001	–
	SOC10	–	1.32	–	0.19	–
total	0.19	–	5.74	0.002	0.24	

total = properties of the full model, CN10 = ratio of soil organic carbon to total nitrogen from 0 to 10 cm, elev = elevational difference, PC3 = principle component three for plant community composition, SIC60 = soil carbonate concentration from 30 to 60 cm, SOC10 = soil organic carbon concentration from 0 to 10 cm, and WSA2 = % water-stable aggregates (1–2 mm sized macroaggregates) from 0 to 10 cm. Significance of linear model was tested with ANOVA. Numerator and denominator degrees of freedom, respectively, were 2,55 for model 1, and 3,54 for models 2 through 5.

#### 4. Discussion

##### 4.1. Predictors of plant biomass

The capacity of rangelands to produce plant (and subsequently

animal) biomass annually is an essential metric of rangeland function and sustainability (Havstad et al., 2007; Reeves and Baggett, 2014). A major challenge is to identify robust indicators of rangeland plant productivity, especially leading indicators of future degradation. Here we tested whether local variation (plot-to-plot) in peak aboveground plant biomass was explained by several soil properties including: root biomass, soil carbonates, soil organic carbon concentration, soil organic matter, total nitrogen concentration, and water-stable aggregates. Two predictor variables (i.e. subsurface carbonates and water-stable aggregates) were significant albeit weak ( $r^2 \leq 0.10$ ) individual predictors of plot-to-plot variation in plant biomass. Oddly, plant biomass aboveground was not appreciably associated with root biomass thereby suggesting spatial variation in biomass allocation strategies.

The five best multiple linear regression models identified several soil (carbon:nitrogen, organic carbon, inorganic carbon [i.e. carbonates], and water-stable aggregates), plant (principle component 3), and site (elevation) properties that explained variation in plant biomass in the focal calcareous grassland. The variables subsurface carbonates and elevation were present in nearly all of the best multiple linear regression models, an indication of their overall importance as predictor variables. Elevational change across the site, however, was relatively small (1 m) and individually was not related to plant biomass (Table 2). After controlling for the variation in plant biomass caused by the variable subsurface carbonates, some of the remaining variation in plant biomass was then explained by elevation. In other words, variation in soil carbonates seemingly masked the relationship between plant biomass and elevation.

We believe subsurface soil carbonates was a useful predictor of plant biomass in the focal calcareous grassland because this soil property is inversely related to some plant available nutrients and soil depth. Specifically, soil carbonates may limit plant available phosphorus (Cross and Schlesinger, 2001) which may subsequently limit plant productivity in this (Reinhart et al., 2016) and other ecosystems

(DeLuca et al., 1989; Fay et al., 2015). Furthermore, soil thickness is often positively associated with rangeland biomass (Rezaei et al., 2006; Wang, 2010). We interpret that areas with low levels of carbonates from 10 to 60 cm soil depths have deeper soils than areas where carbonates are prevalent from 10 to 60 cm. Spatial variation in subsurface carbonates is likely to develop over long periods in response to leaching, weathering, and rhizosphere acidification. Some of the variation in soil carbonates is likely driven by subtle differences in geomorphology and soil development over long periods. Shifts in rangeland management practices (e.g. timing and intensity of grazing) may not affect plant biomass by effects on soil carbonates. Elucidating other soil properties that are responsive to rangeland management practices and associated with appreciable variation in ecosystem function should remain a priority.

Contrary to our predictions, the surface soil properties measured in this study were not strong predictors of plant biomass. Many soil properties are routinely measured and some are positively correlated with variation in plant biomass over large gradients (Craine and Jackson, 2009; Sala et al., 1988; Sims and Nielsen, 1986). Most of the soil properties measured in this study did not explain appreciable variation in peak grassland biomass. Unfortunately, popular soil indicators of agricultural management may not explain appreciable variation in *actual* ecosystem function (Bennett et al., 2010; Letey, 1991; Oldfield et al., 2015), especially in rangelands (Pierson et al., 2014; Reinhart et al., 2015). In other words, many putative indicators may mainly describe a soil's *potential* and not *actual* ecosystem function (Karlen et al., 1997).

Here we briefly discuss some important underlying assumptions and potential caveats. We expected that the focal grassland site, spanning two adjacent pastures and a grazing enclosure for a single soil series, contained adequate variation in plant biomass, composition, and soil properties to identify meaningful predictors. We also expect that management effects will make some vegetation and soil property patches more common and others less common within a grassland. For example, grazing pressure is known to cause gradual and reversible change to vegetation in the Northern Great Plains (Porensky et al., 2016). So measurements across a site should capture meaningful variation (Table 1). Furthermore, many land managers and scientists desire ground-based (leading) indicators of future change (or subtle changes) because aerial-based data (i.e. remote sensing imagery) can often detect only large changes in rangeland productivity (e.g. Reeves and Baggett, 2014). A limitation to our study may relate to residual variation associated with soil samples having been collected adjacent to (and not beneath) areas where biomass was clipped. However, other studies at the focal research station had similar variation in plant biomass and sources of residual error but identified stronger predictors of peak plant biomass (Reinhart et al., 2016; Reinhart et al., 2015).

#### 4.2. Putative indicator of rangeland health

Soil aggregate stability is often used to interpret rangeland health (Herrick et al., 2010; Pellant et al., 2005; Tongway and Hindley, 2004) and is thought to be an indicator of carbon sequestration (Six and Paustian, 2014). Prior research at the focal research station and region, however, indicates that measures of aggregate stability are not reliable predictors of some ecosystem functions in natural grasslands (Reinhart et al., 2015; Reinhart and Vermeire, 2016; Wang, 2010). We found no appreciable (positive) relationship between aggregate stability and grassland (aboveground and belowground) biomass. In fact, all associations between measures of plant biomass and soil aggregate stability were negative (Table 2). This was consistent with other regional studies (Reinhart et al., 2015; Reinhart and Vermeire, 2016; Wang, 2010) but contrary to a rangeland health assessment which predicts aggregate stability is positively related to all major indices of rangeland health (Pyke et al., 2002). We suspect the failure to validate aggregate stability as an important indicator may relate to the confounding effects of

various plant (e.g. plant community composition, root biomass) (Gould et al., 2016; Reinhart and Vermeire, 2016) and soil properties (e.g. stability of 0.25–1 mm macroaggregates was negatively associated [ $r^2 = 0.18$ ] with subsurface soil carbonates [see Supplementary Information Table S1]). These results add to the growing certainty that aggregate stability is not a consistent predictor of ecosystem function and rangeland health in the Northern Great Plains. Other soil physical (i.e. infiltration) and chemical properties (e.g. plant available phosphorus) have explained larger amounts ( $0.15 \leq r^2 \leq 0.19$ ) of local (plot-to-plot) variation in plant biomass in the Northern Great Plains (Reinhart et al., 2016; Reinhart et al., 2015). Our findings call attention to the need to quantify predictive uncertainty (i.e. %... truth explained) for any ecosystem health assessment to ensure it accurately predicts *actual* (not potential) ecosystem function.

#### Acknowledgements

We thank C. Murphy, C. Parsons, B. Garber, K. Jeffers, J. Muscha, D. Strong, and E. Mott for assistance in the field and laboratory. We also thank A. Don and M. Liebig for sharing their expertise on SOC. Mention of trade names or commercial products in this publication is solely for the purpose of providing specific information and does not imply recommendation or endorsement by the U.S. Department of Agriculture.

#### 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.ecolind.2017.05.041>.

#### References

- Andrews, S.S., Carroll, C.R., 2001. Designing a soil quality assessment tool for sustainable agroecosystem management. *Ecol. Appl.* 11, 1573–1585.
- Baveye, P.C., Baveye, J., Gowdy, J., 2016. Soil ecosystem services and natural capital: critical appraisal of research on uncertain ground. *Front. Environ. Sci.* 4.
- Beale, C.M., Lennon, J.J., Yearsley, J.M., Brewer, M.J., Elston, D.A., 2010. Regression analysis of spatial data. *Ecol. Lett.* 13, 246–264.
- Bennett, L.T., Mele, P.M., Annett, S., Kasel, S., 2010. Examining links between soil management, soil health, and public benefits in agricultural landscapes: an Australian perspective. *Agric. Ecosyst. Environ.* 139, 1–12.
- Cook, R.D., Weisberg, S., 1982. *Residuals and Influence in Regression*. Chapman and Hall, New York, USA.
- Coupland, R.T., 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. *J. Ecol.* 49, 135–167.
- Craine, J.M., Jackson, R.D., 2009. Plant nitrogen and phosphorus limitation in 98 North American grassland soils. *Plant Soil* 334, 73–84.
- Cross, A.F., Schlesinger, W.H., 2001. Biological and geochemical controls on phosphorus fractions in semiarid soils. *Biogeochemistry* 52, 155–172.
- De Groot, R.S., Wilson, M.A., Boumans, R.M., 2002. A typology for the classification, description and valuation of ecosystem functions goods and services. *Ecol. Econ.* 41, 393–408.
- DeLuca, T.H., Skogley, E.O., Engel, R.E., 1989. Band-applied elemental sulfur to enhance the phytoavailability of phosphorus in alkaline calcareous soils. *Biol. Fertil. Soils* 7, 346–350.
- Derner, J.D., Boutton, T.W., Briske, D.D., 2006. Grazing and ecosystem carbon storage in the North American Great Plains. *Plant Soil* 280, 77–90.
- Don, A., Schumacher, J., Scherer-Lorenzen, M., Scholten, T., Schulze, E.D., 2007. Spatial and vertical variation of soil carbon at two grassland sites – Implications for measuring soil carbon stocks. *Geoderma* 141, 272–282.
- Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hitzel, A., Jetz, W., Kissling, W.D., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.
- Eldridge, D.J., Poore, A.G.B., Ruiz-Colmenero, M., Letnic, M., Soliveres, S., 2016. Ecosystem structure, function, and composition in rangelands are negatively affected by livestock grazing. *Ecol. Appl.* 26, 1273–1283.
- Ellis, E.C., Ramankutty, N., 2008. Putting people in the map: anthropogenic biomes of the world. *Front. Ecol. Environ.* 6, 439–447.
- Fay, P.A., Prober, S.M., Harpole, W.S., Knops, J.M.H., Bakker, J.D., Borer, E.T., Lind, E.M., MacDougall, A.S., Seabloom, E.W., Wrang, P.D., Adler, P.B., Blumenthal, D.M., Buckley, Y.M., Chu, C., Cleland, E.E., Collins, S.L., Davies, K.F., Du, G., Feng, X., Firm, J., Gruner, D.S., Hagenah, N., Hautier, Y., Heckman, R.W., Jin, V.L., Kirkman, K.P., Klein, J., Ludwig, L.M., Li, Q., McCulley, R.L., Melbourne, B.A., Mitchell, C.E., Moore, J.L., Morgan, J.W., Risch, A.C., Schütz, M., Stevens, C.J., Wedin, D.A., Yang, L.H.,

2015. Grassland productivity limited by multiple nutrients. *Nat. Plants* 1, 15080.
- Gould, I.J., Quinton, J.N., Weigelt, A., De Deyn, G.B., Bardgett, R.D., 2016. Plant diversity and root traits benefit physical properties key to soil function in grasslands. *Ecol. Lett.* 19, 1140–1149.
- Grime, J.P., 1998. Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *J. Ecol.* 86, 902–910.
- Havstad, K.M., Peters, D.P.C., Skaggs, R., Brown, J., Bestelmeyer, B., Fredrickson, E., Herrick, J., Wright, J., 2007. Ecological services to and from rangelands of the United States. *Ecol. Econ.* 64, 261–268.
- Herrick, J.E., Lessard, V.C., Spaeth, K.E., Shaver, P.L., Dayton, R.S., Pyke, D.A., Jolley, L., Goebel, J.J., 2010. National ecosystem assessments supported by scientific and local knowledge. *Front. Ecol. Environ.* 8, 403–408.
- Karlen, D.L., Mausbach, M.J., Doran, J.W., Cline, R.G., Harris, R.F., Schuman, G.E., 1997. Soil quality: a concept, definition, and framework for evaluation. *Soil Sci. Soc. Am. J.* 61, 4–10.
- Kemper, W.D., Rosenau, R.C., 1986. Aggregate stability and size distribution. In: Page, A.L., Miller, R.H., Keeney, D.R. (Eds.), *Methods of Soil Analysis Part 1. Physical and Mineralogical Methods*, 2nd ed. American Society of Agronomy Inc., Soil Science Society of America Inc., Madison, WI, pp. 425–442.
- Legendre, P., 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* 74, 1659–1673.
- Letey, J., 1991. The study of soil structure – science or art. *Aust. J. Soil Res.* 29, 699–707.
- Ludwig, J.A., Tongway, D.J., Bastin, G.N., James, C.D., 2004. Monitoring ecological indicators of rangeland functional integrity and their relation to biodiversity at local to regional scales. *Austral Ecol.* 29, 108–120.
- Lumley, T., Miller, A., 2009. *Leaps: regression subset selection, R package version 2.9* ed. Martin, B.S., Cooper, S., Heidele, B., Hildebrand, T., Jones, G., Lenz, D., Lesica, P., 1998. *Natural Community Inventory Within Landscapes in the Northern Great Plains Steppe Ecoregion of the United States. A Report to the Natural Resource Conservation Service. Northern Plains Regional Office, Helena, MT*, pp. 1–211.
- Martin, L.J., Blossey, B., Ellis, E., 2012. Mapping where ecologists work: biases in the global distribution of terrestrial ecological observations. *Front. Ecol. Environ.* 10, 195–201.
- Oksanen, J., Blanchet, F.G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., Wagner, H., 2015. *Vegan: Community Ecology Package, R package version 2.2-1* ed.
- Oldfield, E.E., Wood, S.A., Palm, C.A., Bradford, M.A., 2015. How much SOM is needed for sustainable agriculture? *Front. Ecol. Environ.* 10, 527.
- Paradis, E., Claude, J., Strimmer, K., 2004. APE: analyses of phylogenetics and evolution in R language. *Bioinformatics* 20, 289–290.
- Pellant, M., Shaver, P., Pyke, D.A., Herrick, J.E., 2005. Interpreting Indicators of Rangeland Health. U.S. Department of the Interior, Bureau of Land Management, National Science and Technology Center, Denver, CO, pp. 1–122.
- Pierson, F.B., Williams, C.J., Kormos, P.R., Al-Hamdan, O.Z., 2014. Short-term effects of tree removal on infiltration, runoff, and erosion in woodland-encroached sagebrush steppe. *Rangeland Ecol. Manage.* 67, 522–538.
- Porensky, L.M., Mueller, K.E., Augustine, D.J., Derner, J.D., 2016. Thresholds and gradients in a semi-arid grassland: long-term grazing treatments induce slow, continuous and reversible vegetation change. *J. Appl. Ecol.* 53, 1013–1022.
- Pyke, D.A., Herrick, J.E., Shaver, P., Pellant, M., 2002. Rangeland health attributes and indicators for qualitative assessment. *J. Range Manage.* 55, 584–597.
- R Development Core Team, 2011. *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Reeves, M.C., Baggett, L.S., 2014. A remote sensing protocol for identifying rangelands with degraded productive capacity. *Ecol. Indic.* 43, 172–182.
- Reinhart, K.O., Vermeire, L.T., 2016. Soil aggregate stability and grassland productivity associations in a Northern mixed-grass prairie. *PLoS One* 11, e0160262.
- Reinhart, K.O., Nichols, K.A., Petersen, M., Vermeire, L.T., 2015. Soil aggregate stability was an uncertain predictor of ecosystem functioning in a temperate and semiarid grassland. *Ecosphere* 6, art238.
- Reinhart, K.O., Dang, S.R., Vermeire, L.T., 2016. The effect of fire intensity, nutrients, soil microbes, and spatial distance on grassland productivity. *Plant Soil* 409, 203–216.
- Rezaei, S.A., Gilkes, R.J., Andrews, S.S., 2006. A minimum data set for assessing soil quality in rangelands. *Geoderma* 136, 229–234.
- Sala, O.E., Parton, W.J., Joyce, L.A., Lauenroth, W.K., 1988. Primary production of the central grassland region of the United States. *Ecology* 69, 40–45.
- Schuman, G.E., Ingram, L.J., Stahl, P.D., Derner, J.D., Vance, G.F., Morgan, J.A., 2009. 2nd ed. *Influence of Management on Soil Organic Carbon Dynamics in Northern Mixed-grass Rangeland, Soil Carbon Sequestration and the Greenhouse Effect*, vol. 57. SSSA Special Publication, Madison, WI, USA, pp. 169–179.
- Sherrod, L.A., Dunn, G., Peterson, G.A., Kolberg, R.L., 2002. Inorganic carbon analysis by modified pressure-calimeter method. *Soil Sci. Soc. Am. J.* 66, 299–305.
- Sims, Z.R., Nielsen, G.A., 1986. Organic carbon in Montana soils as related to clay content and climate. *Soil Sci. Soc. Am. J.* 50.
- Six, J., Paustian, K., 2014. Aggregate-associated soil organic matter as an ecosystem property and a measurement tool. *Soil Biol. Biochem.* 68, A4–A9.
- Snedecor, G.W., Cochran, W.G., 1989. *Failures in the Assumptions, Statistical Method*, 8th ed. Iowa State University Press, Ames, Iowa, pp. 273–296.
- Stephens, P.A., Pettorelli, N., Barlow, J., Whittingham, M.J., Cadotte, M.W., 2015. *Management by proxy? The use of indices in applied ecology*. *J. Appl. Ecol.* 52, 1–6.
- Toledo, D., Sanderson, M., Johnson, H., Reeves, J.L., Derner, J.D., Vermeire, L., Hendrickson, J., 2014. Evaluating plant biodiversity measurements and exotic species detection in National Resources Inventory Sampling protocols using examples from the Northern Great Plains of the USA. *Ecol. Indic.* 46, 149–155.
- Tongway, D., Hindley, N., 2004. Landscape function analysis: a system for monitoring rangeland function. *Afr. J. Range Forage Sci.* 21, 109–113.
- Vermeire, L.T., Heitschmidt, R.K., Rinella, M.J., 2009. Primary productivity and precipitation-use efficiency in mixed-grass prairie: a comparison of northern and southern US sites. *Rangeland Ecol. Manage.* 62, 230–239.
- Wang, G., 2010. *Grazing Management Effects on the Plant Community, Soil Health, and Plant-soil System in Mixed-grass Prairie Within the Missouri Coteau Region*. North Dakota State University. 1–186.
- Wiles, L.J., Dunn, G., Printz, J., Patton, B., Nyren, A., 2011. Spring precipitation as a predictor for peak standing crop of mixed-grass prairie. *Rangeland Ecol. Manage.* 64, 215–222.