SPATIOTEMPORAL VARIATION IN GRASSLAND BIOMASS AND QUALITY ACROSS THE UPPER YELLOWSTONE RIVER BASIN: VARIATION ACROSS PHENOLOGY AND LAND USE GRADIENTS AND VALIDATION OF REMOTE SENSING VEGETATION INDICES

By

Erica Lynn Garroutte

A thesis submitted in partial fulfillment
of the requirements for the degree

of

Master of Science

in

Biological Sciences

MONTANA STATE UNIVERSITY

Bozeman, Montana

May 2016

ACKNOWLEDGEMENTS

This project would not have been possible without the support from the University of Wyoming-National Park Service Research Center, the Montana Academy of Sciences, and the Montana EPSCoR. I would like to thank my advisor, Andrew Hansen, and my committee members, Scott Creel, Rick Lawrence, and Jim Robison-Cox, for their support and guidance throughout this process. I would also like to thank Tony Chang, Nathan Piekielek, and Katie Ireland for their advice and encouragement. In addition, I thank Christie Hendrix, Stacey Gunther, Dan Stahler, P.J. White, and Roy Renkin from Yellowstone National Park for their logistical support and advice; Karen Loveless, Kelly Proffitt, and Justin Gude from Montana Fish Wildlife and Parks for their support and for supplying elk GPS collar data; and Michel Kohl and Dan MacNulty from Utah State University for supplying elk GPS collar data. This study would not have been feasible without the field and laboratory help from Phil Merta, David McGuire, Tucker Porter, John Linsley, Jakob Woodland, Birch Malotky, Janel Schietzelt, Russell Spann, John Landsiedel, and numerous citizen science volunteers. I would like to thank the landowners of the Paradise Valley for their hospitality and dedication to the Greater Yellowstone Ecosystem. Most importantly, I thank my family and my fiancé, John Linsley, for their continued enthusiasm, encouragement, and unwavering support throughout this graduate program and thesis.

TABLE OF CONTENTS

TABLE OF CONTENTS – CONTINUED

TABLE OF CONTENTS - CONTINUED

LIST OF TABLES

Table Page

LIST OF FIGURES

Figure Page

LIST OF FIGURES-CONTINUED

Figure Page

ABSTRACT

Spatial and temporal heterogeneity in forage biomass and quality is known to play an integral role in the movement and population dynamics of migratory ungulates. Once limited by field-based forage assessments, the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) have gained considerable attention as proxies for landscape-scale forage biomass and quality at fine temporal scales. In the Greater Yellowstone Ecosystem (GYE), these indices have become especially important for understanding how potential advances in the timing of spring green-up due to climate change and human land use may be influencing the forage patterns available to migratory elk (*Cervus elaphus*). Given this concern, more information is needed on how the forage biomass and quality available to elk varies across elevation-related phenology and land use gradients and on the reliability of using NDVI and EVI to map forage patterns across the GYE. Using 250m^2 MODIS NDVI and EVI and field estimates of grassland biomass and quality, we examined how the rate and magnitude of seasonal variation in forage biomass and quality differed across elevation-related phenology and land use gradients, assessed how the accuracy of NDVI and EVI as proxies for forage biomass and quality differed across the landscape, and then mapped spatiotemporal variation in the abundance of high quality forage for elk across the Upper Yellowstone River Basin (UYRB). We found that: (1) Grasslands with late onset of growth and irrigated agriculture had a faster rate of growth and a greater seasonal magnitude of biomass and quality for elk than all other grasslands; (2) 250m^2 NDVI and EVI explained minimal variation in grassland biomass and quality across the UYRB; and (3) the accuracy of NDVI and EVI differed across elevation-related phenology and land use gradients in the UYRB. These results provide novel information on the rate and magnitude of seasonal variation in forage biomass and quality and on the reliability of using NDVI and EVI to map the forage patterns available to migratory elk

INTRODUCTION TO THESIS

Spatial and temporal heterogeneity in forage biomass and quality is known to play an integral role in the movement and population dynamics of migratory ungulates [1,2]. In seasonal environments, migratory ungulates are known to exploit spatiotemporal variation in forage biomass and quality to maximize their access to forage with high levels of protein and digestibility [3,4]. This increased access to high quality forage is recognized as a driving force in the evolution of migration and helps explain the traditionally higher reproductive rates, body mass, and population size of migratory ungulates compared to their residential counterparts [1,5–7]. Across temperate landscapes, heterogeneity in climate, soil, grazing patterns, fire, topography, the timing of growth, and human land use are all known to drive spatiotemporal variation in forage biomass and quality [5,8–10]. Among these well-established drivers, much recent attention has been given to understanding how potential advances in the timing of spring green-up due to climate warming and increasing human land use may be influencing the forage patterns for migratory ungulates [9,11,12]. Given this concern, understanding how forage biomass and quality varies spatially and temporally across temperate landscapes has become a key focus of research and management.

While numerous studies have documented how the timing of grassland growth varies across elevation and land use gradients in temperate landscapes [9,11,13–16], few studies have examined how the rate of growth and the magnitude of forage biomass and

quality differ across these gradients throughout the season [11,17]. Given that the same biophysical factors that drive the timing that grasslands start their seasonal growth (e.g., snowmelt, climate, topography, solar radiation) have also been shown to influence the rate of growth, the primary productivity, and the quality of forage [9–11,13], the rate and magnitude of seasonal variation in forage biomass and quality should differ across the elevation-related phenology gradient [17]. Furthermore, because agricultural practices (e.g., irrigation, fertilization, the seasonal harvest) are designed to both prolong vegetation growth and increase productivity [9,18], the rate of growth and the magnitude of forage biomass and quality should also differ by land use. Understanding how the rate and magnitude of seasonal variation in forage biomass and quality vary across elevation-related phenology and land use gradients is needed for a more comprehensive understanding of the patterns of forage available to migratory ungulates [11].

The remote sensing Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) have gained considerable attention in ecological research and management as proxies for the forage biomass and quality available to migratory ungulates at large spatial scales and frequent temporal scales [19–21]. NDVI and EVI are ratios that contain reflectance from red and near infrared (NIR) wavelengths that are thought to be correlated with the “greenness” of the vegetation canopy, which is a property of the photosynthetic activity, leaf area, and canopy structure of terrestrial

vegetation [22,23]. Based on these relationships, NDVI and EVI have been widely used as proxies for the aboveground biomass [24,25], chlorophyll content [26,27], primary productivity [28–30], phenology [31,32], and quality [14,33] of forage available to herbivores across a variety of ecosystems. Despite their popularity, however, NDVI and EVI are influenced by soil exposure, variable topography, senescent vegetation, and atmospheric contaminants [19,22,34]. While previous studies have documented the limitations of NDVI and EVI [35], a comprehensive understanding of how the accuracy of NDVI and EVI as proxies for forage biomass and quality differs across the elevation-related phenology and land use gradients used by migratory ungulates is needed. In addition, more information is needed to determine where and when accounting for curvilinear relationships, differences the soil and vegetation properties by site, and season may improve the accuracy of NDVI and EVI estimates of forage biomass and quality across temperate landscapes [36]. These results provide novel information on the reliability of using NDVI and EVI to map spatiotemporal patterns of forage available to migratory ungulates.

In the Greater Yellowstone Ecosystem (GYE), understanding how forage biomass and quality varies spatially and temporally across the landscape is especially important for the research and management of migratory elk (*Cervus elaphus*). Migratory elk in the GYE are known to follow variation in the timing of grassland growth from their low-elevation winter range to their high-elevation summer range to maximize their access to

an abundance of high quality forage [5,37]. Recent concern has grown, however, that advances in the timing of spring green-up due to climate change and shifts in human land use may be altering the forage patterns available to migratory elk [12]. Given this concern, understanding how forage biomass and quality varies across elevation-related phenology and land use gradients used by migratory elk has become a key focus of research and management. Thein et al. [13] and Piekielek [9], for example, used NDVI to map variation in grassland phenology and primary productivity across the elevation and land use gradients in the GYE. Also, Christianson and Creel [26] found a relationship between seasonal variation in NDVI and elk fecal chlorophyll. Middleton et al. [12] also used NDVI to link spatiotemporal variation in the timing of spring green-up to the reproductive rates of elk in the GYE. While much is known about how the timing of grassland growth varies across GYE [13,26], more information is needed on how the rate of growth and magnitude of forage biomass and quality differ across the elevation-related phenology and land use gradients in the GYE. In addition, while previous studies have documented the limitations of NDVI [35,38], more information is needed on the reliability of using NDVI and EVI as proxies for forage biomass and quality across the GYE and on when and where accounting for curvilinear relationships, site effects, and season is needed in NDVI and EVI models. This information will enhance our understanding of spatiotemporal patterns of forage biomass and quality available to migratory elk across the GYE.

In Chapter 1, we examined how the rate and magnitude of seasonal variation in forage biomass and quality varied across elevation-related phenology and land use gradients in the Upper Yellowstone River Basin (UYRB) of the GYE. To meet this goal, we used a previous NDVI phenology analysis [9] and elk GPS collar data to identify grassland plots that started growth at different times and had different land uses within the migratory range of elk in the UYRB. In each of these grassland plots, we collected field estimates of grassland biomass, crude protein, and digestibility throughout the growing season. Then, to assess the relevance of these seasonal forage patterns for elk, we used the nutritional requirements of captive elk [39] to examine how the abundance of forage of adequate quality for elk varied across the UYRB. Specifically, we addressed the following research questions: (1) How does the rate and magnitude of seasonal variation in grassland biomass and quality differ across elevation-related phenology and land use gradients in the UYRB? and (2) how does the abundance of forage of adequate quality for elk [39] differ across the elevation-related phenology and land use gradients?

In Chapter 2, we assessed the reliability of using NDVI and EVI to map spatiotemporal variation in the forage biomass and quality available to migratory elk across the UYRB. Specifically, we examined how the accuracy of NDVI and EVI differed across the landscape, determined if accounting for curvilinear relationships, site differences, and season improved these models, and then mapped spatiotemporal forage patterns across the UYRB. We collected satellite-derived NDVI and EVI and field estimates of grassland biomass, chlorophyll, crude protein, and digestibility in grasslands

that started growth at different times and land uses in the UYRB throughout the growing season. Field data were used to address the following research questions: (1) How does the accuracy of NDVI and EVI as proxies for forage biomass and quality differ in grasslands that start growth at different times and in different land uses throughout the growing season? (2) Does including polynomial functions and effects for phenology, land use, and season in NDVI and EVI models improve the accuracy of their forage biomass and quality estimates across the UYRB? and (3) how does the abundance of forage of adequate quality for elk [39] vary across the UYRB throughout the growing season?

SPATIOTEMPORAL VARIATION IN FORAGE BIOMASS AND QUALITY ACROSS THE UPPER YELLOWSTONE RIVER BASIN

Abstract

Spatial and temporal heterogeneity in the abundance of high quality forage is known to play an integral role in the movement and population dynamics of migratory ungulates. In the Greater Yellowstone Ecosystem (GYE), variation in climate, soil, grazing patterns, topography, fire, the timing of growth, and land use are all known to drive spatiotemporal variation in the forage biomass and quality available to migratory elk (*Cervus elaphus*). Among these well-established drivers, much recent attention has been given to understanding how potential advances in the timing of spring green-up due to climate warming and shifts in human land use may be altering the forage patterns available to migratory elk. Given this concern, more information is needed on how the biomass and quality vary across the migratory range of elk. Here, we (1) examined how the rate and magnitude of seasonal variation in grassland biomass and quality differed across elevation-related phenology and land use gradients and then (2) assessed how the abundance of forage of adequate quality for elk [39] varied across these gradients in the Upper Yellowstone River Basin (UYRB). We found that grasslands that started growth late in the season had a faster rate of growth, a more rapid decline in forage quality, and a greater seasonal magnitude of biomass and quality than grasslands that started growth early and mid season ($p<0.01$). Irrigated agriculture, however, had a faster rate of growth,

a slower decline in forage quality, and a greater seasonal magnitude of biomass than all other grasslands in the UYRB ($p<0.001$). The abundance of forage of adequate quality for elk was greater in high-elevation grasslands that started growth late in the season and in irrigated agriculture compared to all other grasslands in the UYRB, suggesting that these grasslands play an especially important role in the movement and fitness of migratory elk. Overall, these results indicated that the duration and magnitude of high quality forage available to elk varies across the elevation-related phenology and land use gradients in the UYRB throughout the growing season. These results provide novel information on the forage patterns available to migratory ungulates.

Introduction

Spatial and temporal heterogeneity in the abundance of high quality forage plays an integral role in the movement and population dynamics of migratory ungulates [1,2,40]. In seasonal environments, ungulates require a sufficient quantity of protein-rich, digestible forage to meet the physiological demands of winter survival, growth, and reproduction [6,39]. Because the protein content and digestibility of vegetation declines with seasonal growth as fibrous cell wall structures accumulate [6], ungulates are thought to preferentially graze on grasses and forbs (referred to as forage in this study) in early growth stages because they provide an optimal trade-off of forage biomass and quality [3,4,41]. Across temperate landscapes, heterogeneity in the biophysical environment and land use results in spatiotemporal variation in the timing that grasslands reach this

optimal level of biomass and quality [10,42,43]. Migration, therefore, confers a selective advantage for ungulates, because it allows them to exploit this spatiotemporal variation in the timing of growth to prolong their access to abundant forage with high levels of crude protein and digestibility [1,44,45]. This increased access to high quality forage is recognized as a major driving force in the evolution of migration and helps explain the traditionally higher fecundity and body mass of migratory ungulates compared to their residential counterparts [1,2,46]. Given this role in migratory ungulate ecology, understanding how forage biomass and quality varies spatiotemporally across temperate landscapes has become a key focus of research and management [19].

This is especially true in the Greater Yellowstone Ecosystem (GYE), where spatiotemporal variation in forage biomass and quality is known to play an important role in the movement and population dynamics of migratory elk (*Cervus elaphus*) [5,37,47]. In the GYE, variation in climate, edaphic properties, grazing intensity, topography, fire, the timing of growth, and land use have all been documented to drive spatiotemporal variation in grassland biomass and quality across the landscape [9,10,43,48,49]. Among these well-established drivers, much recent attention has been given to understanding how potential advances in the timing of spring green-up due to climate change and shifts in human land use may be influencing the forage patterns available to migratory elk [12,45,50]. Given this concern, much attention has been given to understanding how forage biomass and quality differs across elevation-related phenology and land use gradients throughout the growing season in the GYE.

Spatial and temporal heterogeneity in the timing that grasslands start their seasonal growth (referred to as phenology in this study) is known to influence the spatiotemporal patterns of forage biomass and quality across temperate landscapes [13,19,51]. In the GYE, the timing that grasslands start their growth is known to vary from low to high elevations throughout the growing season following seasonal and spatial variation in snowmelt (which is strongly dependent on elevation, aspect, slope and prevailing winds), temperature, and solar radiation [9,52]. Because biomass varies substantially with growth stage, this elevation-related variation in the timing that grasslands start their growth influences the timing and location that grasslands accumulate biomass, reach their seasonal peak in biomass, and transition into senescent stages with declining biomass [6,13]. In addition, because the crude protein and digestibility of forage declines with seasonal vegetation growth as fibrous cell wall structures accumulate [6], this elevation-related variation in the timing of the start of growth also influences the timing and location that high quality forage is available across the landscape. In the GYE, elevation-related variation in the timing of the start of growth results in a “green-wave” of accumulating high quality forage that proceeds from low elevations in spring to high elevations mid summer [5,9,13]. The movement of migratory elk in the GYE is tightly coupled with this elevation-related phenology gradient as they move from their low-elevation winter range to their high-elevation summer range [5,37].

Human land use is also known to influence spatiotemporal patterns of forage biomass and quality across temperate landscapes [53]. In the GYE, 32% of the area is composed of privately owned agriculture and exurban development found primarily in the low-elevation grasslands outside of Yellowstone National Park that compose the winter foraging habitat for migratory elk [9,54]. Agricultural practices (e.g., irrigation, fertilization, seasonal harvest) on these private lands have been shown to increase plant productivity and prolong the period that high quality forage is available throughout the season [9]. This increased productivity and prolonged availability of high quality forage has been shown to supplement the forage intake of elk and influence the benefits of migratory versus residential movement strategies of elk [44,50,53,55]. Middleton et al. [12], for example, suggested that access to high quality forage in irrigated agriculture was responsible for the high reproductive rates of residential elk in the GYE. Wilmers and Levi [56], additionally, documented that the Clark's fork elk herd in the GYE foraged on irrigated pastures, especially in drought years. Furthermore, Hebblewhite et al. [44] found that access to hay contributed to a shift in the ratio of migratory versus residential elk in the Canadian Rockies.

While a great deal has been learned about how the timing of grassland growth varies across the elevation and land use gradients in the GYE [9,13], few studies have examined how the rate and magnitude of seasonal variation in forage biomass and quality available to migratory elk differ across these gradients throughout the growing season.

Given that the same biophysical factors that drive the timing that grasslands start their growth (e.g., snowmelt, climate, solar radiation) have also been documented to influence the rate of growth, the productivity of grasslands, and the nutrient content of soils in the GYE [9–11,13], the rate and magnitude of seasonal variation in forage biomass and quality should differ across the elevation-related phenology gradient [17]. Additionally, because agricultural practices (e.g., irrigation, the seasonal harvest) are designed to prolong vegetation growth and increase the productivity of vegetation [9], the rate of growth and magnitude of forage biomass and quality should differ with land use in the GYE. Previous studies have documented that the primary productivity, the duration of growth, and the rate of spring green-up differs with topography, grazing intensity, edaphic properties, elevation, and land use in the GYE [9,10,13]. Few studies, however, have directly quantified how the rate of growth and magnitude of forage biomass and quality vary along the elevation-related phenology and land use gradients used by elk in the GYE. Because even small differences in the rate of growth and quality of forage can have substantial impacts on the fitness of ungulates [11,39,41], understanding how the rate and magnitude of forage biomass and quality varies across these gradients will help us understand how the duration and magnitude of high quality forage available to elk varies across the GYE. This information will help us better understand the drivers of elk migration, identify important foraging habitat for elk, and anticipate how shifts in forage patterns due to climate change and increasing human land use may influence the population dynamics and movement of migratory elk in the GYE.

In this study, we examined how the rate and magnitude of seasonal variation in forage biomass and quality differ across the elevation-related phenology and land use gradients in the Upper Yellowstone River Basin (UYRB). To meet this goal, we used the results of a prior phenology analysis [9] and elk GPS collar data (MacNulty and Kohl from Utah State University and FWP, pers comm.) to identify grassland plots that started growth at different times and had different land uses within the migratory range of elk in the UYRB. In each of these plots, we collected field estimates of grassland biomass, crude protein, and digestibility throughout the growing season to assess how forage biomass and quality varied across these gradients. Then, to assess the relevance of these forage patterns for elk, we used the nutritional requirements of captive elk from Cook et al. [39] to examine how the abundance of forage of adequate quality for elk varied across these gradients throughout the growing season. The specific objectives of this study were to: (1) determine how the rate and magnitude of seasonal variation in biomass, crude protein, and digestibility differed in grasslands that started growth early, mid, and late in the season; (2) examine how the rate and magnitude of seasonal variation in biomass, crude protein, and digestibility differed in irrigated agriculture, private grasslands, and public grasslands; and (3) assess how the abundance of forage of adequate quality for elk varied across the elevation-related phenology and land use gradients in the UYRB throughout the growing season.

Methods

Study Area

The 7,400 sq. km UYRB encompasses the low-elevation floodplains of the Yellowstone and Lamar Rivers and the high-elevation grassland plateaus in the northern range of Yellowstone National Park [9]. The 100,000ha of grasslands and shrub-grasslands in the UYRB form the primary grazing habitat for the migratory northern Yellowstone elk herd as well as populations of bison (*Bison bison*), pronghorn (*Antilocapra Americana*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis Canadensis*) [49]. Land uses in the UYRB consist of privately-owned irrigated agriculture and low-density rural development in the low-elevation grasslands in the Paradise Valley and public grasslands in the mid and high elevations of Yellowstone National Park and the Absaroka-Beartooth Wilderness [9,54]. The UYRB exhibits strong variation in climate and edaphic properties across its 1,524-2743m elevation gradient [9,51]. Average annual temperature ranges from 8^0C to -2^0C and average annual precipitation ranges from 300mm to 1500mm from low to high elevations [9]. Glacial erosion has resulted in rhyolite alluvium in low elevations, mixed colluviums in mid elevations, and andesitic soils in high elevations [9,54]. Plant species vary across these gradients, with mesic meadows, forbs, and sagebrush found primarily on the moisture-retaining, andesitic soils and grasses and shrubs found primarily on dry, rhyolite soils [5,8,9]. Low-elevation grasslands were dominated by bluebunch wheatgrass (*Pseudoroegnaria spicata*), Sandberg's bluegrass (*Poa secunda*) as well as non-native

crested wheatgrass (*Agropyron cristatum*), cheatgrass (*Bromus tectorum*), and annual wheatgrass (*Eremopyrum triticeum*) [8,51,58]. Mid elevations contained Idaho fescue (*Fetuca idahoensis*), big sagebrush (*Artemisia tridentate*), and bluebunch wheatgrass (*Pseudorogeneria spicata*) [8,51]. High elevations consisted of sheep fescue (*Fetuca ovina*), rushes (*Juncus*), and Rydberg's fleabane (*Erigeron rydbergii*) [59]. (Figure 1.1)

Identification and Classification of Grassland Plots

To represent grasslands along the elevation-related phenology and land use gradients in the UYRB, we selected grassland plots that started growth at different times (SOS classes) and had different land uses (land use classes) in the UYRB. A map of grasslands from Piekielek [9], which was derived from vector-delineated habitat types from Despain [8] and the National Land Cover Dataset (2011), was used to identify all 250m^2 grassland plots in the UYRB. To identify plots that start growth at different times, we used an analysis from Piekielek [9] that used the Normalized Difference Vegetation Index (NDVI) to estimate the average start of season date of all grassland plots in the UYRB (average date that grassland plots reached half of their seasonal NDVI amplitude from 2001-2009) to categorize grassland plots into early (Julian day 39-121), mid (Julian day 122-143), and late (Julian day 144-221) SOS classes (Figure 1.2). To identify grassland plots in different land use classes, we used the Montana cadastral data, the National Land Cover Dataset (2011), and field observations to classify grassland plots into irrigated agriculture, private grassland (all non-irrigated private lands), and public

grassland land use classes [9,60]. To be sure these grassland plots were relevant to migratory elk, we selected grassland plots within the migratory range of elk carrying GPS collars between 2007 and 2012 (MacNulty and Kohl from Utah State University and Montana Fish, Wildlife, and Parks, pers. comm). Finally, to maximize the number of plots that could efficiently be sampled, we selected plots less than 3km from roads and trails. While we recognize that this proximity to roads and trails may have deterred elk from these plots [61], we did not observe a difference in grasslands in these plots compared to other grasslands in the UYRB and did not see a difference in migratory elk use of these grasslands from the GPS collar data. From this final selection of grassland plots, we randomly selected four plots in early, mid, and late SOS classes and four plots in irrigated agriculture, private grasslands, and public grasslands. This selection of plots, however, did not constitute a full factorial design. Because irrigated agriculture and private grasslands were only present in the low-elevation grasslands with early onset of growth, our land use analysis was restricted to the early SOS class. Furthermore, because all mid and late SOS classes fell within public grasslands, the SOS analysis was restricted to public grasslands. These selected plots were mostly located in the southern portion of the UYRB because we had access to private lands in this area and were clustered in high elevations because we avoided bear management areas (Figure 1.1).

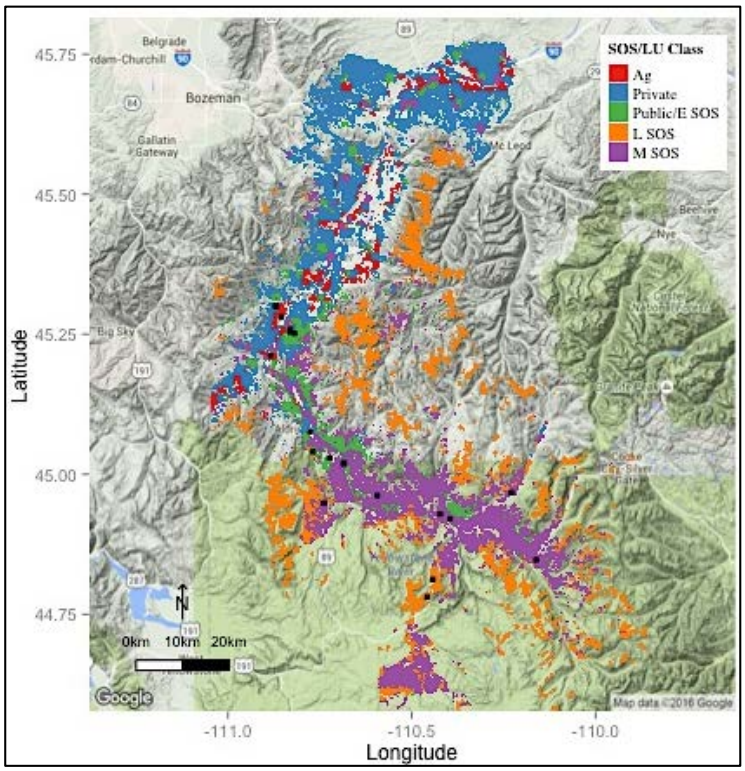


Figure 1.1 Study area map of grassland plots in the start of season (SOS) classes and the land use classes. Irrigated agriculture and private grasslands were only present in the low elevations in the early SOS class.

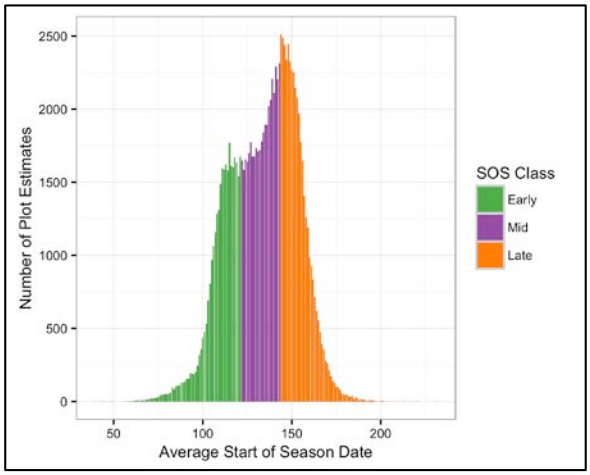


Figure 1.2 Histogram of the average start of season date (the average date that plots reached half of their seasonal amplitude [9]) of all grassland plots in the Upper Yellowstone River Basin used to classify plots into start of season (SOS) classes.

Field Estimation of Forage Biomass and Quality

To estimate the forage biomass and quality available to migratory elk in the UYRB, we estimated the aboveground biomass, crude protein (percent of degradable and rumen assimilated proteins), and *in vitro* dry matter digestibility (IVDMD) (percent of biomass digested *in vitro* with the rumen fluid of a cow) of each grassland plot throughout the growing season [6]. Crude protein was used as a measure of the available protein needed by ungulates for maintenance and growth and IVDMD was used as a measure of the fibrous, indigestible cell wall structures in grasses [6]. To collect these field estimates, we harvested all aboveground biomass (<1cm from soil) from ten, $0.25m^2$ quadrats in 2013 and twenty, $0.25m^2$ quadrats in 2014 randomly located across each grassland plot every ten days throughout the sampling period. Sampling in the early and mid SOS classes occurred from Julian day 119 to 275, and sampling in the late SOS class started after the snow melted on Julian day 155 and ended on Julian day 265. To avoid repeated sampling, quadrats were moved within a $5m^2$ area at each sampling period using a handheld GPS. Harvested vegetation was stored in paper bags, dried at 55ºC, weighed to the nearest 0.01g, ground over a 1mm screen, and pooled by pixel and sampling period [26]. To estimate the average aboveground biomass (g/m^2) of each plot, we averaged the dry biomass weight from all $0.25m^2$ quadrats within each plot and converted the estimates to the g/m^2 scale. To estimate the average crude protein (%) of each plot, we estimated the nitrogen content of four 0.12±0.01g samples from the pooled quadrats in

each plot with a LECO FP-228 Nitrogen Determinator Combustion tool [62], averaged the nitrogen estimates, and then multiplied them by 6.25 [63]. To estimate the average IVDMD (%) of each plot, we digested two 0.5±0.1g samples from the pooled quadrats in each plot in the rumen fluid of an inoculated cow (fed an alfalfa and hay diet) for 48 hours in an ANKOM Daisy II incubator and then calculated the average IVDMD [IVDMD=(total sample mass−undigested mass)/total sample mass]. In total, we analyzed 321 plot estimates of biomass, crude protein, and IVDMD.

Seasonal Variation in Forage Biomass and Quality

To identify the top models of forage biomass and quality, we compared multiple mixed effect models with different combinations of fixed effects, interactions, linear and polynomial functions, variance structures, and spatial and temporal autocorrelation structures [64] (Appendix A). Because all land use classes were not represented in all SOS classes (i.e. irrigated agriculture was only in the low-elevation grasslands in the early SOS class), we selected models separately for the SOS data (public grasslands only) and for the land use data (early SOS only). Models with a categorical effect for SOS or land use class were included to determine if forage differed by class, models with an effect for date were compared to assess how forage varied throughout the growing season, and models with an effect for year were included to assess if forage differed in 2013 and 2014. In each of these models, we included a random categorical effect for plot to account for variation between repeat plot estimates [64]. To examine how grassland biomass and quality varied throughout the season, we compared models with linear,

quadratic, cubic, and basis spline functions for date. Basis spline functions, which are piecewise polynomial functions, with two knots were included to determine if the shape of variation in forage biomass and quality differed before, during, and after the peak in biomass [64]. Models with an interaction between date and SOS/land use class were compared to determine if the shape of seasonal variation in forage biomass and quality differed by SOS or land use class. Because the classification of SOS classes was based on known differences in the timing of seasonal variation in biomass, models with an interaction between SOS class and date (SOS*date) were included in the biomass models. We compared models with variance structures to determine if variation in biomass and quality differed by class [64]. Finally, we compared models with temporal and spatial autocorrelation structures to determine if there was correlation between pixel estimates from sequential sampling periods and from similar locations [64,65]. The corrected Akaike Information Criterion (AIC_c) was used in forward-backward model selection to identify the top models of biomass and quality (>2 AIC_c units less than other models) and F-tests were used to compare models [66]. Maximum likelihood estimation was used to estimate the model parameters, residual plots were used to assess if model errors were normally distributed and had homogeneous variance, and the intra-class correlation (ICC) was used to estimate the correlation between plot estimates [64]. While AIC_c was used to select the top models of biomass and quality, we also reported the conditional coefficient of determination (R^2), the partial R^2 for each fixed effect (r_p^2), the F-statistics and the p-values to aid in interpretation [64]. The conditional R^2 was a measure of the variance

explained by both the fixed and random effects in the mixed effect models [67] and the partial R^2 is the variation explained by each fixed effect. Finally, to compare irrigated agriculture to all other grasslands, we compared the same models but replaced SOS and land use class with a "class" effect (Appendix A) [64].

Seasonal Variation in the Abundance of High Quality Forage for Elk

To assess the relevance of these findings for elk, we examined how the abundance of forage of adequate quality for elk [39] varied across the elevation-related phenology and land use gradients in the UYRB throughout the growing season. First, we used the nutritional thresholds for elk from Cook et al. [39], which were based on the minimum crude protein (≥8.2%) and digestibility (≥56.3%) levels that supported the summer weight gain of lactating elk, to classify the crude protein and IVDMD estimates from the top models into low and high forage quality classes (Crude protein: low<8.2% and high≥8.2%; IVDMD: low<56.3% and high≥56.3%). Then, we compared multiple mixed effects models to identify the top models of the abundance of forage of low and high crude protein and digestibility for elk. The same mixed effect models described above were included in model selection, but we also included models with a categorical effect for forage quality class (low and high) to assess how the abundance differed for low and high quality forage, an interaction between forage quality class and SOS/land use class to determine if the abundance of low and high quality forage differed with by SOS and land use class, and an interaction between forage quality class and date to assess how the abundance of forage of low and high quality for elk differed throughout the season. In all

models, the response variable was biomass (because we were modeling the abundance forage) and the explanatory variables were forage quality class (high/low), SOS or land use class, date, and year. Each model included a random categorical effect for plot to account for variability between plots[64]. We compared models with the same combinations of fixed effects, interactions, linear and polynomial functions, variance structures, and spatial and temporal autocorrelation structures described above.

Assumption about Herbivory Effects

Herbivores are known to influence the biomass and quality of vegetation by removing biomass, altering edaphic properties, and stimulating regrowth [10,68]. Because excluding herbivores from grassland plots was not feasible in this study, we made the assumption that the effects of herbivory were consistent across our plots [10]. To assess the validity of this assumption, we counted elk scat piles along four transects in each plot throughout the season and compared the number of scat between plots [10].

Results

Variation in the Timing of Grassland Growth

The timing that grasslands reached their seasonal peak in biomass corresponded to their SOS classification (i.e. grasslands in the early SOS class reached a peak in biomass earliest in the season) (Figure 1.3). Although the late SOS class was exposed and sampled for a shorter period of the season due to prolonged snow cover, biomass

increased to a peak and then declined in all SOS classes throughout their sampling periods. Biomass peaked on Julian day 180 in the early SOS class, on Julian day 187 in the mid SOS class, and on Julian day 200 in the late SOS class. Crude protein and IVDMD, conversely, peaked at the start of sampling and then declined in all SOS classes throughout the sampling period. Crude protein and IVDMD was greatest on Julian day 119 in the early and mid SOS classes and on Julian day 155 in the late SOS class.

Table 1.1 Description of the top models of biomass, crude protein, and IVDMD in all start of season (SOS) and land use classes.

Top SOS models
Biomass~bs(Date,df=5)+SOS+bs(Date,df=5)*SOS+varIdent(SOS)+random(plot)
Crude protein~Date+SOS+Date*SOS+varIdent(SOS)+random(plot)
IVDMD~Date+SOS+Year+varIdent(SOS)+random(plot)
Top land use models
Biomass~Date+land use+Year+$Date^2$+$Date^3$+$Date^3$*land use+varIdent(land use)+random(plot)
Crude protein~Date+land use+Year+Date*land use+varIdent(land use)+random(plot)
IVDMD~Date+land use+Year+varIdent(land use)+random(plot)

*Models included basis spline functions (bs), Date (Julian days), Year (2013 & 2014), variance structures (varIdent), and random plot effects.

Rate and Magnitude of Biomass and Quality Differed by SOS and Land Use Class

Grasslands in the late SOS class and irrigated agriculture had a faster rate of growth and a greater seasonal magnitude in biomass than all other grasslands in the UYRB (Figure 1.3 & Tables 1.1-1.2). Biomass varied non-linearly throughout the season in the different SOS and land use classes, differed by sampling year, and there was random variability between plot estimates (R^2=0.86 & 0.52) (Appendix B). The SOS and land use class effects explained most of the seasonal variation in biomass in these

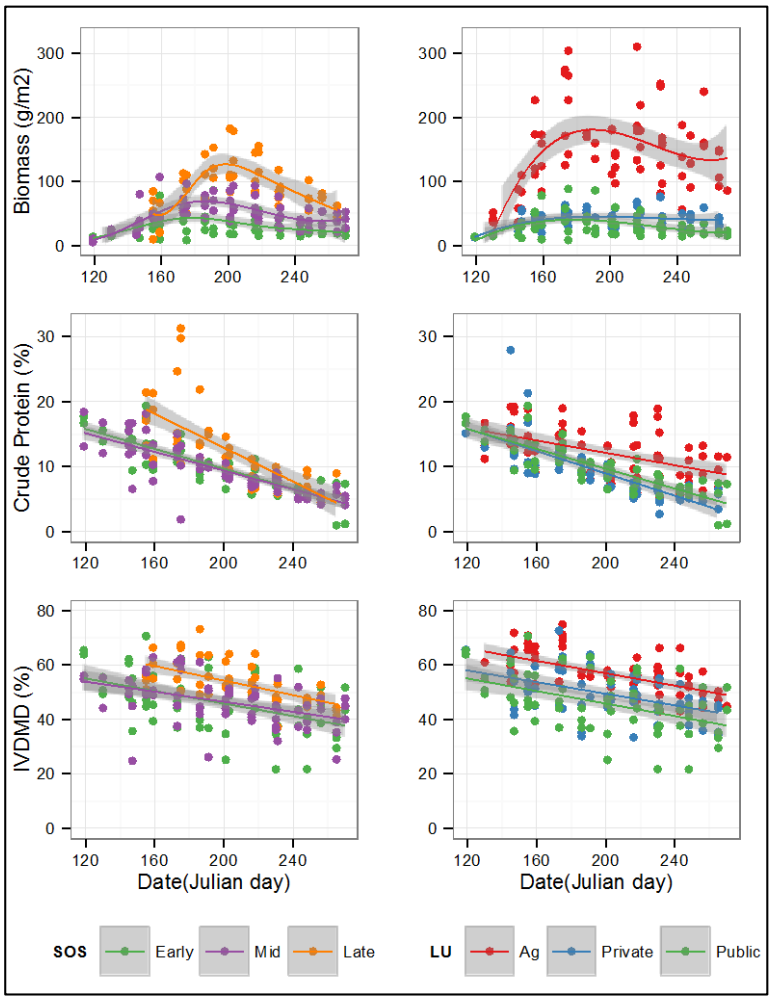


Figure 1.3 Seasonal variation in grassland biomass, crude protein, and IVDMD in the start of season (SOS) and land use classes. Gray represents 95% confidence intervals.

models, and there was some correlation between plot estimates (ICC=0.14 & 0.15). The residuals from these models were normally and homogeneously distributed. Between SOS classes, the late SOS class grew up to 1.2±0.55 g/m^2 (AVG±SE) per day faster and had up to 72.8±13.8 g/m^2 more biomass at their seasonal peak than the early and mid SOS classes ($p<0.001$). There were no detectable differences in the rate of growth

between the early and mid SOS classes, but the mid SOS class had up to 33.2±12.1 g/m^2 more biomass at its seasonal peak than the early SOS class ($p<0.006$). Between land use classes, irrigated agriculture grew up to 1.1±0.4 g/m^2 per day faster and had up to 113.9±9.9 g/m^2 more biomass at their seasonal peak than private and public grasslands ($p<0.001$). There was no detectable difference in the rate of growth or the magnitude of biomass in the private and public grasslands ($p=0.39$). Irrigated agriculture grew up to 1.1±0.4 g/m^2 per day faster and had up to 127.3±25.1 g/m^2 more biomass than all other grasslands throughout the sampling period ($p<0.001$) (Appendix C).

Crude protein was greater in the late SOS class and in irrigated agriculture than in all other grasslands in the UYRB throughout most of the sampling period (Figure 1.3 & Tables 1.1-1.2). Crude protein declined linearly throughout the sampling period in all SOS and land use classes, differed by sampling year, had a different variance in each SOS and land use class, and varied between plot estimates (R^2=0.75 & 0.52) (Appendix B). In these models, date explained most of the variation in crude protein and there was moderate correlation between plot estimates (ICC=0.19 & 0.16). The residuals from these models were normally and homogeneously distributed. Crude protein in the late SOS class was up to 3.51±0.62% greater at the start of the sampling period ($p<0.001$) and declined up to 0.08±0.01% per day faster than the early and mid SOS classes ($p<0.001$). We did not detect a difference in the seasonal magnitude or the rate of decline in crude protein between the mid and early SOS classes ($p=0.52$). Between land use classes, crude protein did not differ at the start of the sampling period ($p<0.05$), but declined

Table 1.2 Statistics from the top models of grassland biomass, crude protein, and IVDMD in the start of season (SOS) and land use classes.

Response variable	AIC_c	R^2	Fixed effects	r_p^2	df	F	p
Start of season classes							
Biomass (g/m^2)	1619.9	0.86	bs(Date)	0.24	5,160	22.13	<0.001
			SOS	0.37	2,160	12.85	<0.001
			bs(Date)*SOS	0.11	10,160	5.61	<0.001
Crude protein (%)	895.9	0.75	Date	0.51	1,172	364.99	<0.001
			SOS	0.09	2,172	10.79	<0.001
			Date*SOS	0.04	2,172	5.65	0.004
IVDMD (%)	1300.3	0.41	Date	0.18	1,173	67.33	<0.001
			SOS	0.14	2,173	17.54	<0.001
			Year	0.06	1,173	14.83	<0.001
Land use classes							
Biomass (g/m^2)	1807.9	0.52	$Date^3$	0.06	3,176	12.72	<0.001
			land use	0.36	2,11	69.56	<0.001
			Year	0.01	1,176	10.52	<0.001
			$Date^3$*land use	0.06	6,176	5.38	<0.001
Crude protein (%)	968.7	0.52	Date	0.44	1,182	282.77	<0.001
			land use	0.11	2,11	12.45	0.002
			Year	0.02	1,182	4.38	0.038
			Date*land use	0.03	2,182	4.91	0.008
IVDMD (%)	1376.9	0.56	Date	0.19	1,184	76.01	<0.001
			land use	0.22	2,11	44.22	<0.001
			Year	0.03	1,184	8.82	0.003

**Statistics included the corrected AIC, conditional R^2 (variation explained by fixed and random effects), the partial R^2 (r_p^2), F-statistics, and p-values. Basis spline functions had df=5.*

0.03±0.01% per day slower in irrigated agriculture than in private and public grasslands (p<0.001). This slow decline in irrigated agriculture caused it to have 4.48±2.65% greater crude protein than private and public grasslands at the end of the season (p<0.01). There was no detectable difference between the rate of decline in crude protein in private and public grasslands (p=0.37). Early in the season, crude protein was 3.51±0.62% greater in the late SOS class than in all other grasslands in the UYRB (p<0.001) (Appendix C). Late

in the season, crude protein was 4.5±2.6% greater in irrigated agriculture than in all other grasslands in the UYRB ($p<0.01$).

IVDMD was greater in the late SOS class and in irrigated agriculture than in all other grasslands in the UYRB throughout the sampling period (Figure 1.3 & Tables 1.1-1.2). IVDMD declined linearly at the same rate in all SOS classes and in all land use classes, differed by SOS and land use class, differed by sampling year, had a different variance in each SOS and land use class, and there was random variability between plot estimates (R^2=0.41 & 0.56) (Appendix B). In these models, the date and the SOS/land use class effects explained most of the variation in IVDMD and there was some correlation between plot estimates (ICC=0.16 & 0.05). The residuals from these models were normally and homogeneously distributed. IVDMD declined 0.12±0.01% per day in all SOS classes, but was up to 8.66±1.64% greater in the late SOS class than in the early and mid SOS classes throughout the sampling period ($p<0.001$). There was no detectable difference in IVDMD between the early and mid SOS classes throughout the sampling period ($p=0.59$). IVDMD declined 0.12±0.01% per day in all land use classes, but was up to 7.4±1.2% greater in irrigated agriculture than in private and public grasslands throughout the sampling period ($p<0.001$). There was no detectable difference in IVDMD between public and private grasslands throughout the season ($p=0.31$). Across the UYRB, IVDMD in irrigated agriculture was up to 10.9±1.4% greater than in all other grasslands throughout the sampling period ($p<0.001$) (Appendix C).

Spatiotemporal Variation in the
Abundance of High Quality Forage for Elk

In all SOS and land use classes throughout the sampling period, 64% of the estimates had adequate crude protein for elk (>8.2%) and 26% of the estimates had adequate IVDMD for elk (Figure 1.4 & 1.5). Throughout the sampling period, the abundance of forage of both low and high quality for elk increased to a peak and then declined in all SOS and land use classes (Figure 1.4). From the start of sampling to Julian day 200, the accumulating forage had adequate crude protein and IVDMD for elk. After Julian day 200, the declining forage had inadequate crude protein and IVDMD for elk.

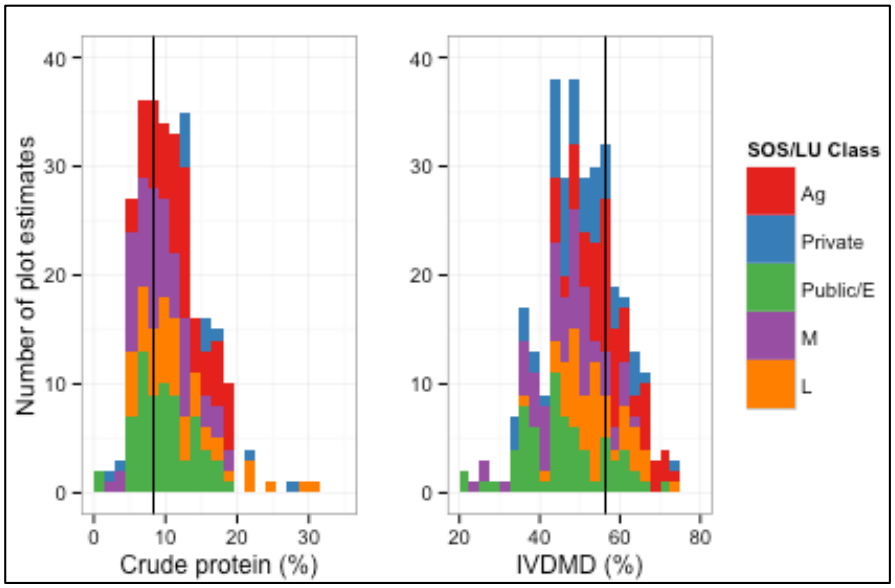


Figure 1.4 Histogram of the crude protein and IVDMD estimates from the start of season (SOS) and land use classes. Lines represent the levels required by elk [39] that were used to classify estimates into forage quality classes.

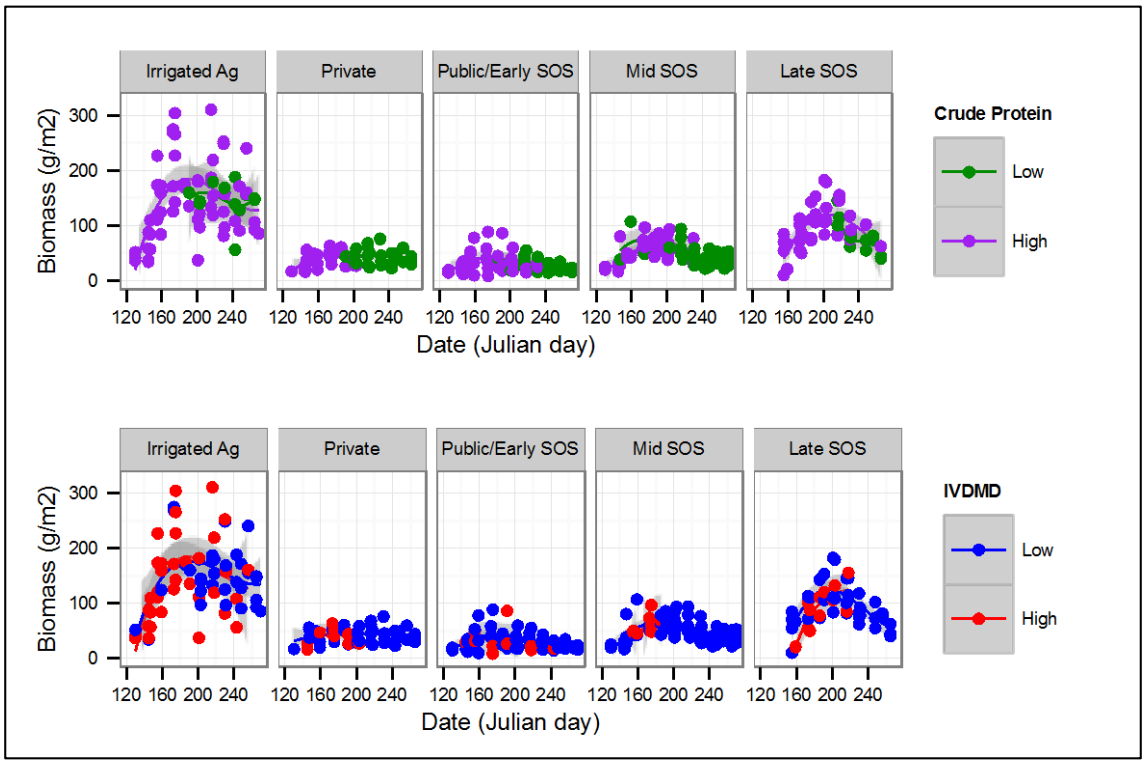


Figure 1.5 Seasonal variation in the abundance of forage with low and high crude protein and IVDMD for elk in the start of season (SOS) and land use classes.

Grasslands that started growth late in the season and irrigated agriculture had a greater abundance of forage of adequate quality for elk at their seasonal peak than all other grasslands in the UYRB (Figure 1.5 & Table 1.3). The abundance of forage with low and high crude protein for elk differed by SOS and land use class, varied non-linearly throughout the sampling period, differed by sampling year, varied differently in each SOS and land use class, and varied between plots (R^2=0.81 & 0.41) (Appendix D). The abundance of forage with low and high IVDMD differed by SOS and land use class, varied non-linearly throughout the sampling period, differed by sampling year, varied differently in each SOS and land use class, and varied randomly by plot (R^2=0.83 & 0.39)

(Appendix D). The residuals from these models were normally and homogeneously distributed and there was some correlation between plot estimates (ICC=0.51 & 0.49). At their seasonal peak, grasslands in the late SOS class had up to 57.1±11.6 g/m^2 more forage with adequate crude protein and IVDMD for elk than the early and mid SOS classes ($p<0.001$). There was no detectable difference in the abundance of forage with adequate quality for elk in the early and mid SOS classes throughout the season ($p<0.51$). Across the UYRB, irrigated agriculture had up to 115.8±12.6 g/m^2 more forage of adequate quality for elk than all other grasslands in the UYRB ($p<0.001$) (Appendix C).

Table 1.3 Statistics from the top models of the abundance of forage of low and high quality for elk in the start of season (SOS) and land use classes.

Response	**AIC$_c$**	**R^2**	**Fixed effects**	**r$_p^2$**	**df**	**F**	**p**
			SOS classes				
Biomass	1645.4	0.81	FQ-CP	0.04	1,16	11.77	<0.001
			SOS	0.44	2,16	15.05	<0.001
			bs(Date)	0.13	5,16	16.08	<0.001
Biomass	1644.8	0.83	FQ-IVDMD	0.01	1,16	0.18	0.67
			SOS	0.46	2,16	14.78	<0.001
			bs(Date)	0.15	5,16	18.61	<0.001
			Land use classes				
Biomass	1821.7	0.41	FQ-CP	0.03	1,17	6.59	0.01
			land use	0.16	2,11	59.16	<0.001
			Date^3	0.05	3,17	12.25	<0.001
			Year	0.01	1,17	11.71	0.008
			FQ-CP*land use	0.01	2,17	4.53	0.01
Biomass	1824.6	0.39	FQ-IVDMD	0.04	1,18	0.47	0.49
			land use	0.18	2,11	62.17	<0.001
			Date^3	0.05	3,18	13.11	<0.001
			Year	0.01	1,18	9.56	0.002

**Models included forage quality class (FQ-CP & FQ-IVDMD), start of season class (SOS), land use class, Date (Julian day), Year (2013 & 2014), and basis spline functions with df=5.*

Herbivory Assumption

The average number of elk scat piles counted was less than one in all SOS and land use classes in the UYRB throughout the sampling period. We found no detectable difference between the elk scat piles counted in the SOS and land use classes in the UYRB throughout the sampling period (Appendix F).

Discussion

We found that the rate and magnitude of seasonal variation in forage biomass and quality differed across elevation-related phenology and land use gradients in the UYRB throughout the growing season. The principal results from this study were that: (1) grasslands that started growth late in the season had a faster rate of growth, a faster decline in forage quality, and a greater seasonal magnitude in biomass and quality than grasslands that started growth early and mid season; (2) irrigated agriculture had a greater seasonal magnitude of biomass and a slower decline in forage quality than all other grasslands in the UYRB; and (3) the abundance of forage of adequate quality for elk was greatest in grasslands that started growth late in the season and in irrigated agriculture throughout the growing season. While previous studies have documented how the timing of grassland growth varies across elevation-related phenology and land use gradients [9,13], this study is one of the first to document that the rate and magnitude of seasonal variation in forage biomass and quality differ across these gradients throughout the

growing season. This variation in the rate and magnitude of forage biomass and quality may have important effects on the fitness and movement of migratory elk in the GYE.

Rate and Magnitude Differed across Phenology Gradient

Grasslands that started growth late in the season had a faster rate of growth and a more rapid decline in forage quality than grasslands that started growth early and mid season. Although sampling began 35 days later in the high-elevation grasslands due to their prolonged snow cover, they grew twice as fast at the start of their sampling period when the snow melted than grasslands that started growth earlier in the season at the start of their sampling periods. We speculate that the faster rate of growth was because the high moisture and nutrient content of soils in high elevations (due to the nitrogen deposition and increased moisture from prolonged snowmelt, high precipitation, and the high nutrient content of andesitic soils), combined with warm spring temperatures, promoted rapid vegetation growth [11]. In addition, this fast rate of growth was also likely a strategy that evolved for high-elevation grasslands to compensate for their short growing season [11,69]. Piekielek [9] similarly documented that the rate of spring green-up increased along the elevation gradient in the UYRB. Pettorelli et al. [11] also found that changes in the timing of spring green-up influenced the rate of grassland growth. Furthermore, we expect that the rapid decline in forage quality was likely because the fast accumulation of biomass in these high-elevation grasslands diluted the nitrogen content of grasses at a faster rate than in the slow-growing grasslands that started growth earlier in the season [70–72]. The rapid rate of decline in forage quality suggests that the

nitrogen available in high elevations was insufficient to maintain the nitrogen content of grasses during this fast accumulation of biomass at the start of the sampling period [71]. Doiron et al. [71] consistently found that advances in the timing of spring green-up, due to experimental warming, increased the rate of decline in forage quality throughout the growing season. For elk, this combination of the fast rate of growth and the rapid decline in forage quality in high-elevation grasslands likely reduced the period that high quality forage was available in these grasslands late in the season [11]. Overall, these results suggest that the duration of available high quality forage available to elk differs across the elevation-related phenology gradient throughout the growing season.

Grasslands that started growth late in the season had a greater magnitude of biomass, crude protein, and digestibility at their seasonal peak than grasslands that started growth early and mid season. We speculate that the greater magnitude of biomass and quality was due to the high moisture and nutrient content of soils, the cooler temperatures, the increased precipitation, and the observed greater forb cover in these high-elevation grasslands [8,73–76]. Specifically, we expect that the nitrogen deposition and high soil moisture from prolonged snow cover and the increased nutrient and moisture content of andesitic soils increased the productivity and nitrogen content of grasslands in high elevations [75–78]. In addition, the cool temperatures and the increased precipitation in high elevations reduced the evapotranspiration rates and water stress, and thus, increased the productivity of grasslands [8,79]. In addition, previous studies have shown that nitrogen content of grasses is greater in high-elevation grasslands

with cool temperatures, high precipitation, and shorter growing seasons, perhaps as a strategy that evolved for these grasslands to increase their photosynthesis rates in a short growing season [78]. Finally, because forbs have inherently higher crude protein and digestibility than grasses and shrubs [80], we expect that the greater forb cover observed in high elevations likely contributed to the greater magnitude of forage quality in high-elevation grasslands that started growth late in the season [8]. These results are consistent with the results from Thein et al. [13] and Piekielek [9] showing that primary productivity was greatest in the high-elevation grasslands of the GYE. Frank and Groffman [10] also documented that the nitrogen content of soils was greatest in the high-elevation grassland plateaus in the GYE. Previous studies also found that crude protein and digestibility increased across elevation gradients in Norway [7] and in the Canadian Rockies [44]. Overall, these results suggest that the magnitude of forage biomass and quality available to migratory elk differs across the elevation-related phenology gradient throughout the growing season.

These results suggest that there is a positive relationship between the timing of growth, the rate of growth, the rate of decline in forage quality, and the magnitude of grassland biomass and quality across the UYRB. Specifically, high-elevation grasslands with late onset of growth have a faster rate of growth, a more rapid decline in forage quality, and a greater magnitude in biomass and quality than grasslands that start growth earlier in the season in the UYRB. These relationships suggest that the same biophysical factors (e.g., snow cover, temperature, precipitation) that drive the timing that grasslands

start their growth also dictate the rate of growth, the rate of decline in forage quality, and the seasonal magnitude of biomass and quality [9,17]. Among these biophysical factors, we speculate that prolonged snow cover is primarily responsible for this correlation because it (1) delays the timing of growth and (2) increases the rate of growth and the magnitude of forage biomass and quality by increasing the nitrogen and moisture content of soils and protecting grasses from early season freeze events [11,17,81]. In an NDVI analysis, Piekielek [9] similarly documented that the primary productivity and rate of growth differed across the elevation gradient in the UYRB. Duparc et al. [17] similarly documented that more productive alpine communities reached their peak later in the season than less productive alpine communities in the French Alps. Pettorelli et al. [11] also documented a correlation between the timing of growth, the rate of growth, and the productivity of grasslands across temperate landscapes. Finally, Doiron et al. [71] found that experimental warming influenced the timing of growth, primary productivity, and the rate of decline in crude protein. Altogether, these relationships suggest that grasslands that start growth late in the season have a shorter period of available high quality forage, but a greater magnitude in biomass and quality during this short period late in the season.

Because forbs are known to have inherently greater biomass and quality than grasses and shrubs [70], we expected that the increased forb cover observed in high-elevation grasslands contributed to their greater magnitude of biomass and quality. To assess the legitimacy of this theory, we used photographs of quadrats to estimate the

percent cover of forbs in each plot and used weighted regression to determine if forb cover differed by SOS classes. Then, to assess if the percent forb cover contributed to the greater biomass and quality in high-elevation grasslands with late onset of growth, we compared the same mixed effects models used above but included models with an effect for forb cover (Appendix E). The results from this post-hoc analysis showed that the percent forb cover was greater in the late SOS class than the early and mid SOS classes ($F_{2,175}$=159.616, $p<0.001$) [80,82], but showed that the percent forb cover was not included in the top models of forage biomass and quality (Appendix E). More information is needed, therefore, to determine how forb cover influences forage biomass and quality across the elevation-related phenology gradient.

Rate and Magnitude Differed by Land Use Class

Irrigated agriculture had a faster rate of growth, a slower decline in forage quality, and greater seasonal magnitude in biomass than all other grasslands in the UYRB. This faster rate of growth and greater magnitude of biomass and quality was likely due to the high nutrient and moisture content of soils from irrigation and fertilization and the inherently greater biomass and quality of crop species [9,18]. The slower decline in crude protein was likely due to the prolonged growth from irrigation and the surge in forage quality after the seasonal harvest [9]. Previous studies have similarly documented that irrigated agriculture had a prolonged period of growth and the greater productivity of forage than non-irrigated grasslands [9,18,44,56].

Abundance of High Quality Forage across the UYRB

High-elevation grasslands that started growth late in the season had a greater abundance of forage with adequate levels of crude protein and IVDMD for elk than grasslands that started growth early and mid season in the UYRB. As described above, we speculate that this greater abundance of high quality forage for elk was due to the high nutrient and moisture content of soils and the reduced evapotranspiration in high elevations [8,73–76]. While previous studies have documented that forage quality varies across the elevation-related phenology gradient throughout the growing season [4,13], this study is one of the first to document that the abundance of forage of adequate quality for elk varies across the elevation-related phenology gradient throughout the season.

These results suggest that high-elevation grasslands that start growth late in the season may play a disproportionately important role in the fitness and movement of migratory elk in the UYRB. Specifically, these high-elevation grasslands may provide the bulk of the energy and nutrients for migratory elk in the critical foraging period late in the season [12,46]. In addition, these results may provide evidence that elk “jump” rather than “ride” the green-wave of vegetation phenology to increase their access to abundant high quality forage in the high-elevation grasslands late in the season [83]. Mysterud et al. [46] similarly documented that access to high quality forage across variable topographic and elevation gradients was linked to the elevated weight gain of migratory ungulates in Norway. Hebblewhite et al. [44] also found that migratory elk had greater

access to high quality forage across the elevation gradient compared to residential elk in low elevations in the Canadian Rockies. In the context of climate change, these results may suggest that advances in the timing of spring green-up in high-elevation grasslands may have critical impacts on the abundance of high quality forage available to elk late in the season [12,19]. Future research is needed to assess the role of abundant high quality forage in high-elevation grasslands on the movement and fitness of migratory elk.

The rapid rate of growth in the high-elevation grasslands that started growth late in the season may also have important implications on the population dynamics and movement of migratory elk. In a previous study, Pettorelli et al. [11] documented that a shift in the timing of growth and an increased rate of growth negatively influenced the fitness of juvenile ungulates because it reduced the period that high quality forage was available throughout the growing season. Together, the fast rate of growth and rapid decline in forage quality in high-elevation grasslands suggests that this abundant high quality forage is only available for a short period of time late in the season [11]. This short period of the season may be a critical time for elk to build up the energy and nutrient reserves needed to meet the physiological demands of winter survival, growth, and reproduction [6]. In the context of climate change, these results suggest that advances in the timing of growth in high-elevation grasslands may influence the duration that high quality forage is available to migratory elk in this critical period late in the season [11].

Irrigated agriculture had a greater abundance of forage of adequate quality for elk than all other grasslands in the UYRB throughout the growing season. While this is not

surprising [12,18,50,53], this study is one of the first to document that irrigated agriculture had up to twice as much forage with adequate levels of crude protein and digestibility for elk than non-irrigated grasslands throughout much of the growing season. These results provide evidence that the abundant high quality forage in irrigated agriculture may supplement the seasonal energy and nutrient intake of residential elk [12,44,50,53]. In addition, these results provide evidence that residential elk foraging on irrigated agriculture may have access to a greater abundance of high quality forage than migratory elk following the elevation-related phenology gradients [12,50,55], which may influence the benefits of migratory versus residential behavior in elk [7,12,44,50]. Shifts in the timing of growth due to climate change, may exacerbate the role of irrigated agriculture on the benefits of migratory versus residential behavior [12]. A shift from migratory to residential behavior in elk may have important consequences on disease transmission, human-wildlife conflict, and on the hunting industry [50]. Consideration for the abundant high quality forage available in irrigated agriculture, therefore, is critical for the conservation and management of migratory elk in the GYE.

Understanding how the rate and magnitude of forage biomass and quality differs across the landscape may be applicable to other herbivores that rely on seasonal variation in the duration and magnitude of forage across temperate environments. For example, variation in the magnitude of grassland biomass and the duration of abundant grasslands varies may be relevant to small mammal populations, ground-dwelling bird species, and

arthropod communities [19]. In addition, understanding these details may be useful for understanding soil carbon and nitrogen cycles, fire dynamics, and water cycles [19]. Overall, consideration for how the rate of growth and magnitude of forage biomass and quality differ across the landscape may be relevant to a variety of ecosystems.

Scope and Limitations

These results, however, must be considered in the context of the other factors known to influence the movement and population dynamics of migratory elk. While previous studies have shown that migratory elk select forage at the landscape scale [4,7,46], elk are also known to select forage at the plant, species, and community scale and may switch their diet throughout the season to maximize their nutrient and caloric intake [4,26,41,80]. In addition to forage, the movement and population dynamics of elk is also influenced by the direct and indirect effects of predation [84], winter severity [37,85], and hunting pressure [86]. Moreover, while crude protein and digestibility are commonly used estimates of forage quality, the mineral and tannin content of forage is also known to influence the palatability and quality of forage for elk [6,80]. While we believe that this study captured the general variation in forage biomass and quality throughout the growing season in the UYRB, we may have missed some of the critical foraging period for elk early in the spring before sampling began [37,85]. Finally, we made the assumption that the increased abundance of high quality forage in irrigated agriculture and high-elevation grasslands was important for elk, but more information is

needed on the quantity of high quality forage required by elk to assess if this is true or if other grasslands in the UYRB have sufficient quantities of high quality forage for elk.

The assumptions and limitations of this study should be considered when interpreting these results. We made the assumption that the effects of herbivory on forage biomass and quality was consistent across the landscape and minor compared to the differences across elevation-related phenology and land use gradients [10]. While we found that elk scat was consistent across the plots, we do expect that herbivory had an unaccounted for effect on forage biomass and quality (Appendix F). In addition, because of the logistical limitations of collecting field estimates, we expect that there was error in the field estimates of forage biomass and quality. Furthermore, because the aim of this study was to describe the patterns of forage biomass and quality, we can only speculate about which interacting biophysical and land use factors actually drove this variation in forage biomass and quality. Finally, future research should consider if the forage patterns observed in the UYRB are consistent across the GYE or in other temperate landscapes.

Because all land uses were not represented in all SOS classes, we were not able to compare the relative or interacting effects of the timing of growth and land use on the spatiotemporal patterns of forage biomass and quality in the UYRB. Because irrigated agriculture was only located in the low-elevation grasslands, our analysis of the effects of land use on forage biomass and quality was restricted to the early SOS class. And because the mid and late SOS classes were only present in the mid and high-elevation

grasslands in Yellowstone National Park, our analysis of the effects of the timing of growth on forage biomass and quality was restricted to the public grasslands. Because human land use is mostly located in low elevations in temperate landscapes, we think that these divisions are relevant for ungulates in most temperate landscapes. Future research, however, should consider the interacting effects of the timing of growth and land use on spatiotemporal variation in forage biomass and quality.

Conclusion

In summary, the results from this study suggested that the rate and magnitude of forage biomass and quality differed across the elevation-related phenology and land use gradients in the UYRB throughout the growing season. These results suggest that high-elevation grasslands with late onset of growth had a faster rate of growth, a faster decline in forage quality, and greater magnitude of biomass and quality than grasslands that started growth early and mid season. They also indicate that irrigated agriculture had a greater magnitude of forage biomass and quality than all other grasslands in the UYRB. For migratory elk, these results indicate that the duration and the magnitude of forage biomass and quality available to elk differs across the elevation-related phenology and land use gradients. Overall, this study shows that consideration for how the rate of growth and magnitude of forage biomass and quality differs across the landscape is critical for the research and management of migratory ungulates.

USING NDVI AND EVI TO MAP SPATIOTEMPORAL VARIATION IN THE BIOMASS AND QUALITY OF FORAGE AVAILABLE TO MIGRATORY ELK IN THE UPPER YELLOWSTONE RIVER BASIN

Abstract

The Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) have gained considerable attention in ecological research and management as proxies for landscape-scale vegetation biomass and quality. In the Greater Yellowstone Ecosystem (GYE), these indices have become especially important for understanding how variation in the timing of growth and human land use influence the forage patterns available to migratory elk (*Cervus elaphus*). Despite their popularity, however, few studies have assessed the reliability of using these indices across the migratory range of elk. Using satellite-derived NDVI and EVI and field estimates of grassland biomass, chlorophyll, crude protein, and digestibility, we: (1) examined how the accuracy of NDVI and EVI as proxies for forage biomass and quality differed across elevation-related phenology and land use gradients; (2) determined if accounting for curvilinear relationships, site differences, and season improved NDVI and EVI models; and then (3) used these models to map spatiotemporal variation in the abundance of forage of adequate quality for elk across the Upper Yellowstone River Basin (UYRB). We found that linear NDVI and EVI models explained minimal variation in grassland biomass (R^2=0.42-0.53), chlorophyll (R^2=0.03-0.04), crude protein (R^2=0.09-0.14), and

digestibility (R^2=0.11-0.18) across the UYRB. The accuracy of NDVI and EVI was lowest in grasslands that started growth late in the season, in irrigated agriculture, and after the peak in biomass. NDVI models with a polynomial function for NDVI explained 19-55% more variation in biomass and models with a date effect explained 14-69% more variation in forage quality than the linear NDVI and EVI models. Forage biomass and quality varied across the elevation-related phenology gradient throughout the growing season, but remained consistently high in irrigated agriculture. The abundance of forage of adequate quality for elk was greatest in grasslands with late onset of growth and in irrigated agriculture throughout the growing season, suggesting that these grasslands may play a disproportionately important role in the movement and fitness of migratory elk. Overall, these results show that understanding the limitations of NDVI and EVI is necessary when using these indices to map spatiotemporal variation in the forage biomass and quality available to migratory ungulates.

Introduction

Remote sensing vegetation indices have gained considerable attention in ecological research and management as proxies for landscape-scale vegetation biomass and quality [14,19,20]. Among the existing vegetation indices, the Normalized Difference Vegetation Index (NDVI) and the Enhanced Vegetation Index (EVI) are the most commonly used indices because of their simplicity, availability, and recognized utility in a variety of ecosystems [14,19,87]. NDVI and EVI are ratios containing red and near

infrared (NIR) reflectance bands that are thought to be correlated with the “greenness” of the vegetation canopy, which is a property of the photosynthetic activity, leaf area, and canopy structure of terrestrial vegetation [22,23]. Based on these relationships, NDVI and EVI have been used as proxies for the aboveground biomass [24,25], chlorophyll content [26,27], primary productivity [28–30], phenology [31,32], and forage quality [14,33] of vegetation in a variety of ecosystems. Once limited by field-based forage assessments, the availability of NDVI and EVI at large spatial scales and frequent temporal scales has made then particularly useful for understanding the role of forage patterns on the movement and population dynamics of herbivores [19]. This is especially important as climate warming and human land use increasingly alter the timing of growth and patterns of forage available to herbivores [12,54,88]. While previous studies have shown that NDVI and EVI vary by site, land use, and season, few have explored how variation in the accuracy of NDVI and EVI as proxies for forage biomass and quality may influence the utility of these indices in the research and management of migratory elk [3,5].

NDVI is widely used in ecological research and management as a proxy for the forage biomass and quality available to herbivores [19]. A ratio of reflectance from red wavelengths absorbed by photosynthetic pigments (e.g., chlorophyll) and NIR wavelengths scattered by leaf mesophyll cells, NDVI [NDVI=(NIR-red)/(NIR+red)] is thought to be directly and causally related to the quantity of photosynthetically active vegetation on terrestrial surfaces [22,26,90]. Because of this link, NDVI has been used to map spatiotemporal variation in the biomass, phenology, chlorophyll content, and

primary productivity of vegetation available to herbivores in a variety of ecosystems [11,19,26]. Furthermore, because the crude protein and digestibility of vegetation declines with seasonal growth as fibrous cell wall structures accumulate [6], NDVI has also been shown to be correlated with the quality of forage available for herbivores early in the season [14,26,91]. Because of these relationships, NDVI has been used in numerous studies to assess the role of spatiotemporal patterns of forage biomass and quality on the movement and population dynamics of herbivores [12,14,19].

The accuracy of NDVI as a proxy for forage biomass and quality, however, is known to be affected by soil exposure, topography, senescent vegetation, atmospheric contaminants, and dense biomass [20,22]. In sparsely vegetated areas, variation in the moisture and brightness of exposed soil is known to increase the irradiance of the NIR band and, thus, bias NDVI estimates [92,93]. Across topographically-diverse landscapes, variation in the viewing geometry, surface albedo, and sun elevation angle are known to degrade NDVI [22,94,95]. NDVI is also sensitive to scattering and elevated NIR irradiance from heterogeneous plant structures, senescent biomass, and atmospheric contaminants [22,94–98]. Lastly, because the red band reaches an asymptote before the NIR band, NDVI has been shown to saturate in dense vegetation [5]. Because of these limitations, the accuracy of NDVI as a proxy for vegetation biomass and quality differs by site, land use, and season [22,101–103]. Garonna et al. [104], for example, found that atmospheric contaminants were more likely to bias NDVI estimates in wet climates and

seasons than in dry climates and seasons. Additionally, Tittebrand et al. [101] documented that the accuracy of NDVI differed with land cover type. Also, Porter et al. [102] found that NDVI explained more variation in biomass in early growth stages than in senescent stages. To account for these limitations, previous studies have found that including polynomial functions for NDVI in biomass models improved their performance by accounting for the curvilinear relationship between NDVI and biomass in dense vegetation [34,36]. In addition, previous studies have found that accounting for differences in the soil background and vegetation structure by site and season improved the performance of NDVI models [21,35]. However, while the limitations of NDVI have been well documented [19,35,38], more information is needed on how the accuracy of NDVI as a proxy for forage biomass and quality differs across heterogeneous habitats, land uses, and seasons. In addition, more information is needed on when and where including polynomial NDVI, site, and date effects is needed to improve the accuracy of forage biomass and quality estimates.

EVI has been proposed as a more robust proxy for forage biomass and quality than NDVI because of its improved resilience to saturation and resistance to soil and atmospheric contamination [90,95,105]. Like NDVI, EVI [$EVI=2.5\times(NIR-Red)/(NIR+C_1\times Red-C_2\times Blue+L)$] is a ratio of red and NIR reflectance, but also includes an adjustment factor to account for the non-linear distortion from soil (L=1), a blue band to reduce the contamination of the red band, and aerosol resistance coefficients (C_1= 6,C_2=7.5) [22,106]. These adjustments are designed to make EVI more robust in areas

with high soil exposure and in dense vegetation [22,89]. These adjustments, however, have also been shown to make EVI more sensitive than NDVI to contamination from heterogeneous terrain [89,94,95]. Sesnie et al. [94], for example, found that EVI was more likely to be affected by variation in the sun elevation angle than NDVI in the topographically-diverse habitat of bighorn sheep (*Ovis canadensis*). Matsushita et al. [95] additionally found that the soil adjustment factor made EVI more sensitive than NDVI to contamination from variable topography. While the limitations of EVI and NDVI have been documented, more information is needed on how the accuracy of EVI versus NDVI as proxies for forage biomass and quality differs by site, land use, and season.

In the Greater Yellowstone Ecosystem (GYE), using NDVI and EVI as proxies for forage biomass and quality has become especially important for the research and management of migratory elk (*Cervus elaphus*). Throughout the growing season, migratory elk in the GYE are known to follow variation in the timing of grassland growth from their low-elevation winter range to their high-elevation summer range to maximize their access to forage with high levels of crude protein and digestibility [5,37]. Recent concern has grown, however, that advances in the timing of spring green-up due to climate warming and shifts in human land use may be altering the forage patterns available to migratory elk [12,54]. Given this concern, vegetation indices have become an important tool for mapping spatiotemporal variation in the forage biomass and quality available to migratory elk in the GYE [9,13]. Thein et al. [13] and Piekielek [9], for example, used NDVI to document that grassland phenology and primary productivity

differs across the elevation and land use gradients in the GYE. Christianson and Creel [26] also found a link between seasonal variation in NDVI and elk fecal chlorophyll. Middleton et al. [12] also used NDVI as a proxy for vegetation phenology to link advances in the timing of spring green-up to the reproductive rates of elk in the GYE. While the limitations of using NDVI in the GYE have been documented [13,35,38], few studies have directly quantified how the accuracy of NDVI and EVI as proxies for forage biomass and quality differs across the elevation-related phenology and land use gradients used by migratory elk [35]. Furthermore, few studies have assessed whether including polynomial NDVI and EVI, site, and date effects in NDVI and EVI models improve their estimates of biomass and quality across the GYE. This information is needed for a more comprehensive understanding of the utility and biological significance of using NDVI and EVI to map spatiotemporal variation in the forage biomass and quality available to migratory elk in the GYE.

The aim of this study was to assess the reliability of using NDVI and EVI as proxies for forage biomass and quality across the elevation-related phenology and land use gradients used by migratory elk in the Upper Yellowstone River Basin (UYRB). To meet this goal, we used the results from a previous phenology analysis in the UYRB [9] and elk GPS collar data (MacNulty and Kohl from Utah State University and FWP, pers comm.) to identify grassland pixels that started growth at different times and had different land uses within the migratory range of elk in the UYRB. Within these pixels, we collected NDVI and EVI estimates from the Moderate Resolution Imaging

Spectroradiometer (MODIS) and field estimates of grassland biomass, chlorophyll, crude protein, and digestibility throughout the summer growing season to validate NDVI and EVI models and to identify the top models of forage biomass and quality. Then, we used the nutritional requirements of elk from Cook et al. [39] to map spatiotemporal variation in the abundance of forage of adequate quality for elk across the UYRB. The specific objectives of this study were to: (1) examine how the accuracy of NDVI and EVI as proxies for grassland biomass and quality differed across elevation-related phenology and land use gradients throughout the growing season; (2) determine if including polynomial NDVI/EVI, site, and season effects in NDVI and EVI models improved their estimates of biomass and quality; and (3) then use these models to map spatiotemporal variation in the forage biomass and quality available to migratory elk across the UYRB.

Methods

Study Area

The 7,400 sq. km UYRB encompasses the low-elevation floodplains of the Yellowstone and Lamar Rivers and the high-elevation grassland plateaus in the northern range of Yellowstone National Park [9] (Figure 2.1). The 100,000ha of grasslands and shrub-grasslands in the UYRB form the primary grazing habitat for the northern Yellowstone elk herd as well as populations of bison (*Bison bison*), pronghorn (*Antilocapra Americana*), mule deer (*Odocoileus hemionus*), and bighorn sheep (*Ovis canadensis*) [49]. Human land uses in the UYRB consist of privately-owned irrigated

agriculture and low-density rural development primarily located in the low-elevation Paradise Valley and public grasslands in the mid and high elevations of Yellowstone National Park and the Absaroka-Beartooth Wilderness [54]. The UYRB exhibits strong variation in climate and edaphic properties across its 1,524-2,743m elevation gradient [51]. Average annual temperature ranges from 8^0C to -2^0C and average annual precipitation ranges from 300mm to 1500mm from low to high elevations [9]. Glacial erosion has resulted in a mixture of rhyolite alluvium in low elevations, mixed colluviums in mid elevations, and shallow andesitic soils in high elevations [54]. Plant species vary across these gradients, with mesic meadows and sagebrush found primarily in the moisture-retaining, andesitic soils and grasses and shrubs found mainly on dry, rhyolitic soils [8]. Low-elevation grasslands were dominated by bluebunch wheatgrass (*Pseudoroegnaria spicata*), Sandberg's bluegrass (*Poa secunda*) as well as non-native crested wheatgrass (*Agropyron cristatum*), cheatgrass (*Bromus tectorum*), and annual wheatgrass (*Eremopyrum triticeum*) [8,51,58]. Mid elevations contained Idaho fescue (*Fetuca idahoensis*), big sagebrush (*Artemisia tridentate*), and bluebunch wheatgrass (*Pseudoroegneria spicata*) [8,51]. High elevations consisted of sheep fescue (*Fetuca ovina*), rushes (*Juncus*), and Rydberg's fleabane (*Erigeron rydbergii*) [59].

Identification and Classification of Grassland Pixels

To represent the elevation-related phenology and land use gradients used by migratory elk [19,22], we selected grassland pixels that started growth at different times (SOS class) and had different land uses (land use class) in the UYRB. A map of

grasslands from Piekielek [9], which was derived from the vector-delineated habitat types from Despain [8] and the National Land Cover Dataset (2011), was used to identify all 250m^2 grassland pixels in the UYRB. To identify grasslands that start growth at different times, we used a previous NDVI analysis from Piekielek [9] of the average start of season date (average date that pixels reached half of their seasonal amplitude in NDVI from 2001-2009) to categorize grassland pixels into early (Julian day 39-121), mid (Julian

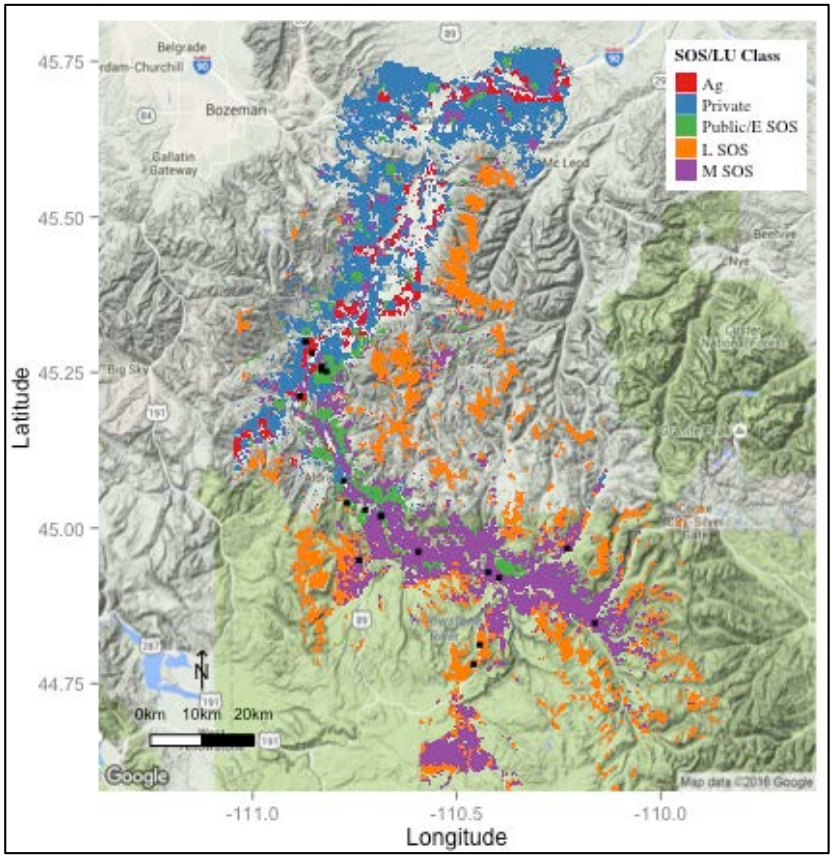


Figure 2.1 Study area map of grassland pixels in the start of season (SOS) and land use classes in the Upper Yellowstone River Basin. Irrigated agriculture and private grasslands were only present in the low-elevation grasslands in the early SOS class. Squares represent the pixels sampled in this study.

day 122-143), and late (Julian day 144-221) SOS classes [107] (Figure 2.2). To select pixels in different land uses, we used Montana cadastral data, the National Land Cover Dataset (2011), and field observations to classify grassland pixels into irrigated agriculture, private grassland (all non-irrigated private lands), and public grassland land use classes [9,60]. To be sure that these grasslands were relevant to elk, we selected pixels within the summer migratory range of elk carrying GPS collars between 2007 and 2012 (MacNulty and Kohl from Utah State University and Montana Fish, Wildlife, and Parks, pers. comm). Finally, to maximize the number of pixels that could logistically be sampled, we selected all grassland pixels less than 3km from roads and trails. While we acknowledge that this proximity to roads and trails may have deterred elk from these grassland pixels [61], we did not observe a difference in the vegetation or in the elk use of these pixels compared to other grasslands further away from roads and trails. From this final selection of grassland pixels, we randomly selected four pixels in early, mid, and late SOS classes and four pixels in irrigated agriculture, private grasslands, and public grasslands. This selection of pixels, however, did not constitute a full factorial design (i.e. not all land uses were represented in all SOS classes). Because irrigated agriculture and private grasslands were only present in grasslands with early onset of growth, the land use analysis was restricted to the early SOS class. Conversely, because the mid and late SOS classes were only present in the mid and high elevations in public grasslands, the SOS analysis was restricted to the public grasslands. These plots were mostly located in the southern portion of the UYRB because we only had access to

private lands in these areas and were clustered in high elevations because we avoided bear management areas and were limited by the distance to these grasslands plots.

Field Estimation of Grassland Biomass and Quality

To represent the forage biomass and quality available to migratory elk across the UYRB [3,6], we estimated the aboveground biomass, chlorophyll content (spectral density of 666nm wavelengths related to chlorophyll a), crude protein (percent of degradable and rumen assimilated proteins), and *in vitro* dry matter digestibility

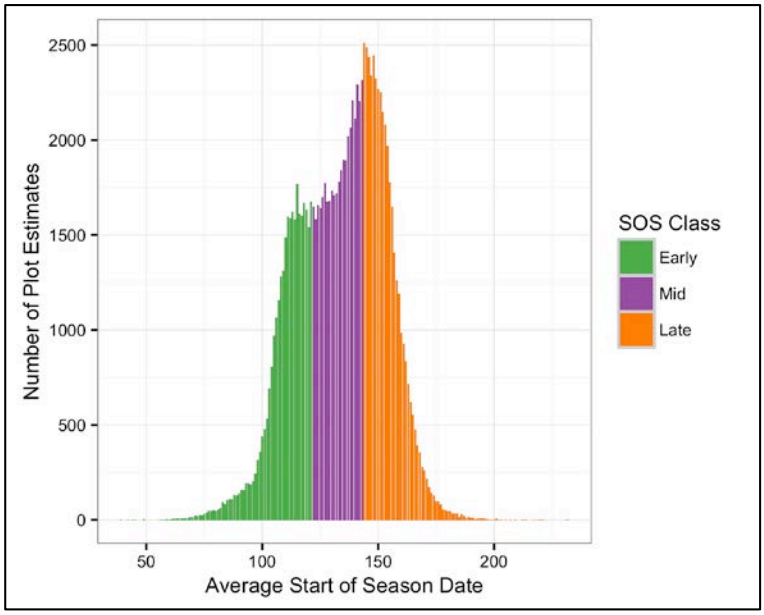


Figure 2.2 Histogram of the average start of season date (the average date that pixels reached half of their seasonal amplitude[9]) of all grasslands in the UYRB used to classify pixels into start of season (SOS) classes.

(IVDMD) (percent of biomass digested *in vitro* with the rumen fluid of a cow) of each grassland pixel throughout the growing season [6]. Crude protein was used as a measure

of the available protein needed by ungulates for maintenance and growth and IVDMD was used as a measure of the fibrous, indigestible cell wall structures available in grasslands [6]. To acquire these estimates, we harvested all aboveground biomass (<1cm from soil) from ten, 0.25m^2 quadrats in 2013 and twenty, 0.25m^2 quadrats in 2014 randomly located across each grassland pixel every ten days throughout the growing season. Sampling in the early and mid SOS classes occurred from Julian day 119 to 275, and sampling in the late SOS class started after the snow melted on Julian day 155 and ended on Julian day 265. To avoid repeat sampling, quadrats were moved within a 5m^2 area at each sampling period using a handheld GPS. Harvested biomass was stored in paper bags, dried at 55^oC, weighed to the nearest 0.01g, ground over a 1mm screen, and pooled by pixel and sampling period [26]. To estimate the average aboveground biomass of each pixel, we averaged the dry biomass weight from all 0.25m^2 quadrats within each pixel and converted the estimates to the g/m^2 scale. To estimate the chlorophyll content of each pixel, we used the methods outlined by Christianson and Creel [26] to extract the chlorophyll pigments, analyze the reflectance properties, and quantify the average chlorophyll content from four samples from the pooled quadrats in each pixel. To estimate the average crude protein of each pixel, we estimated the nitrogen content of four, 0.12±0.01g samples from the pooled quadrats in each pixel with a LECO FP-228 Nitrogen Determinator Combustion tool [62], averaged the nitrogen estimates, and then multiplied the average nitrogen estimates by 6.25 [63]. To estimate the IVDMD of each

pixel, we digested two 0.5±0.1g samples from the pooled quadrats in the rumen fluid of an inoculated cow (fed an alfalfa and hay diet) for 48 hours in an ANKOM Daisy II incubator and then used these estimates to calculate the average percent IVDMD [IVDMD=(total sample mass−undigested mass)/total sample mass] of each pixel. In total, we analyzed 321 pixel estimates of biomass, chlorophyll, crude protein, and IVDMD.

NDVI and EVI Data

NDVI and EVI estimates were derived from the daily, 250m^2 MODIS MOD09GQ images and from the daily, 500m^2 MOD09GA images on each field sampling date. MOD09GQ and MOD09GA images were downloaded from the USGS Land Processes Distributed Active Archive Center in their original sinusoidal projection, were resampled using the nearest neighbor method, and were reprojected to the Albers equal area projection to be consistent with Piekielek [9]. NDVI was calculated from the red (band 1:620-670nm) and NIR (band 2:841-876nm) reflectance bands from the daily, 250m^2 MOD09GQ images [NDVI=(band 2-band 1)/(band 2+band 1)] [98]. EVI was calculated from the red and NIR reflectance bands from the daily, 250m^2 MODIS MOD09GQ images and the blue (band 3:459-479nm) reflectance band from the daily, 500m^2 MOD09GA images [EVI=(band 2-band 1)/(band 2+(6×band 1)-(7.5×band 3)+1)] [98]. The blue band from the 500m^2 MOD09GA images was used to calculate EVI because the 250m^2 MOD09GQ images did not include a blue band [23]. MODIS quality assurance data, which is a measure of the quality of pixel estimates based on their degree of contamination, were used to estimate the quality of the pixel estimates [98]. When pixels

were of low quality, estimates from the next closest date were used. All NDVI and EVI estimates were acquired within five days of the field sampling dates.

Accuracy of NDVI and EVI across Phenology and Land Use Gradients

We analyzed how the accuracy of linear NDVI and EVI models of biomass, chlorophyll, crude protein, and IVDMD differed between SOS classes, land use classes, and before and after the peak in biomass. Because all land uses were not represented in all SOS classes (i.e. irrigated agriculture was only present in the low-elevation grasslands in the early SOS class), we fit separate linear NDVI and EVI models to the SOS data (public grassland land use only) and to the land use data (early SOS class only). First, we fit linear regression models with biomass, chlorophyll, crude protein, or IVDMD as the response variable and NDVI or EVI as the explanatory variable to the SOS data and to the land use data. The corrected Akaike Information Criterion (AIC_c), adjusted coefficient of determination (R^2), F-statistics, and p-values were used to assess the performance of these models across all SOS classes and across all land use classes. Residual plots were used to determine if the model errors were normally distributed and had homogeneous variation. Then, to examine how the predictive accuracy of the linear NDVI and EVI models differed across the landscape, we used repeat cross validation without replacement to estimate the average root mean squared error (RMSE) of the models in each SOS class, land use class, and before and after the peak in biomass. Specifically, we repeatedly fit (x1000) the linear NDVI and EVI models to a random 70% of the data within a specific class and then used the remaining 30% of data to

estimate the average RMSE of the models in each class. Weighted regression was used to analyze how the RMSE estimates differed between SOS classes, land use classes, and before and after the peak in biomass.

Top Models of Grassland Biomass and Quality

To determine if including polynomial NDVI, site, and season effects in NDVI and EVI models improved their estimates of forage biomass and quality, we compared multiple mixed effects models with different combinations of fixed effects, interactions, linear and polynomial NDVI/EVI effects, and correlation structures to identify the top models of forage biomass and quality (Appendix G). Again, because not all land uses were represented in all SOS classes, we selected separate top models for the SOS data (public grassland land use only) and for the land use data (early SOS class only). In these models, the response variable was biomass, chlorophyll, crude protein, or IVDMD and the explanatory variables included NDVI or EVI, SOS or land use class, and date. All models also included a random categorical effect for pixel to account for variability between pixel estimates [64]. To examine the shape of the relationship between NDVI/EVI and forage biomass and quality [36], we compared models with linear, quadratic, cubic, and basis spline functions for NDVI and EVI. Then, to assess how forage biomass and quality varied throughout the season, we compared models with linear, quadratic, cubic and basis spline functions for date. Basis spline functions (piecewise polynomial functions) with two knots were included to determine if the shape of the relationship differed before, during, and after the peak in biomass [64].

Furthermore, we compared models with an interaction between NDVI/EVI and SOS/land use class and an interaction between NDVI/EVI and date to determine if the shape of the relationship between NDVI/EVI and forage biomass and quality differed by class or throughout the season. In addition, models with a variance structure were compared to assess if the variation in forage biomass and quality differed by class [64]. Finally, we compared models with temporal and spatial autocorrelation structures to determine if there was correlation between pixel estimates from sequential sampling periods and from similar locations [64,65]. AIC_c was used in forward-backward model selection to identify the top models of biomass and quality (>2 AIC_c units less than other models) [66]. The intra-class correlation (ICC) was calculated to estimate the correlation between random pixel estimates [64], maximum likelihood estimation was used to estimate model parameters, and residual plots were used to determine if model errors were normally and homogeneously distributed. While AIC_c was used to select the top models, we also reported the marginal coefficient of determination (R^2), the partial R^2 for each fixed effect (r_p^2), the F-statistics, and the p-values to aid in interpretation [64]. The marginal R^2 is a measure of the variance explained by the fixed effects (See Nakagawa and Schielzeth [67]) and the partial R^2 is the variance explained by each fixed effect. Finally, we used the same repeat cross validation methods described above to compare the average RMSE in the different SOS classes, land use classes, and before and after the peak in biomass. To compare the top models to the linear NDVI and EVI models, we used F-tests to compare the performance of the models in all SOS and land use classes and used

weighted regression to compare the RMSEs from each model in each SOS class, land use class, and before and after the peak in biomass.

We examined how the spatiotemporal patterns of forage biomass and quality across the UYRB differed by model. First, we used the linear NDVI, linear EVI, and top models to generate spatially explicit maps of biomass, chlorophyll, crude protein, and IVDMD across the UYRB throughout the sampling period. NDVI and EVI rasters, derived from red and NIR bands from $250m^2$ MOD09GQ images and the downscaled blue bands from $500m^2$ MOD09GA images, were used to interpolate biomass and quality across the UYRB. Because models were selected separately for SOS and land use data, we extracted all pixels within each SOS and land use class, used the appropriate model to estimate biomass and quality in those pixels, and then merged the pixels together into one image. To examine how these patterns varied throughout the season, we created maps on Julian day 128 to represent a date before grasslands reached their seasonal peak in biomass, on Julian day 187 to represent a date when most grasslands were at their seasonal peak in biomass, and on Julian day 263 to represent the date when biomass was declining across the UYRB [9]. Weighted regression models were used to analyze how biomass and quality differed by model.

Variation in the Abundance of High Quality Forage

To explore the relevance of these maps for elk, we used the nutritional requirements of elk from Cook et al. [39] to map spatiotemporal variation in the abundance of forage of adequate quality for elk across the UYRB. First, we used the

nutritional thresholds for elk [39], which were the minimum crude protein (≥8.2%) and digestibility (≥56.3%) levels that supported the weight gain of captive lactating elk, to identify crude protein and IVDMD estimates from the top models above these thresholds. Then, we used the top models of biomass to generate spatially explicit maps of the abundance of forage of adequate quality for elk across the UYRB. Weighted regression models were used to assess how the abundance of forage varied across the UYRB.

Results

NDVI and EVI Explained Minimal Variation in Biomass and Quality

The linear NDVI and EVI models explained minimal variation in biomass (R^2=0.17-0.53), chlorophyll (R^2=0.01-0.04), crude protein (R^2=0.05-0.14), and IVDMD (R^2=0.06-0.18) across the UYRB throughout the sampling period (Figure 2.3 & Tables 2.1-2.3). The residuals from these models were normally distributed, but had heterogeneous variation. The RMSEs from the linear NDVI and EVI models were greater in the late SOS class than in the early and mid SOS classes ($p<0.001$), greater in irrigated agriculture than in private and public grasslands ($p<0.001$), and greater after the peak in biomass than before ($p<0.03$). There was no detectable difference in the RMSEs in the early and mid SOS classes ($p=0.52$ & 0.62) or between the private and public grasslands ($p=0.62$ & 0.21).

The linear NDVI models explained 18-36% more variation in biomass, 2-3% more variation in chlorophyll, 4-9% more variation in crude protein, and 3-12% more

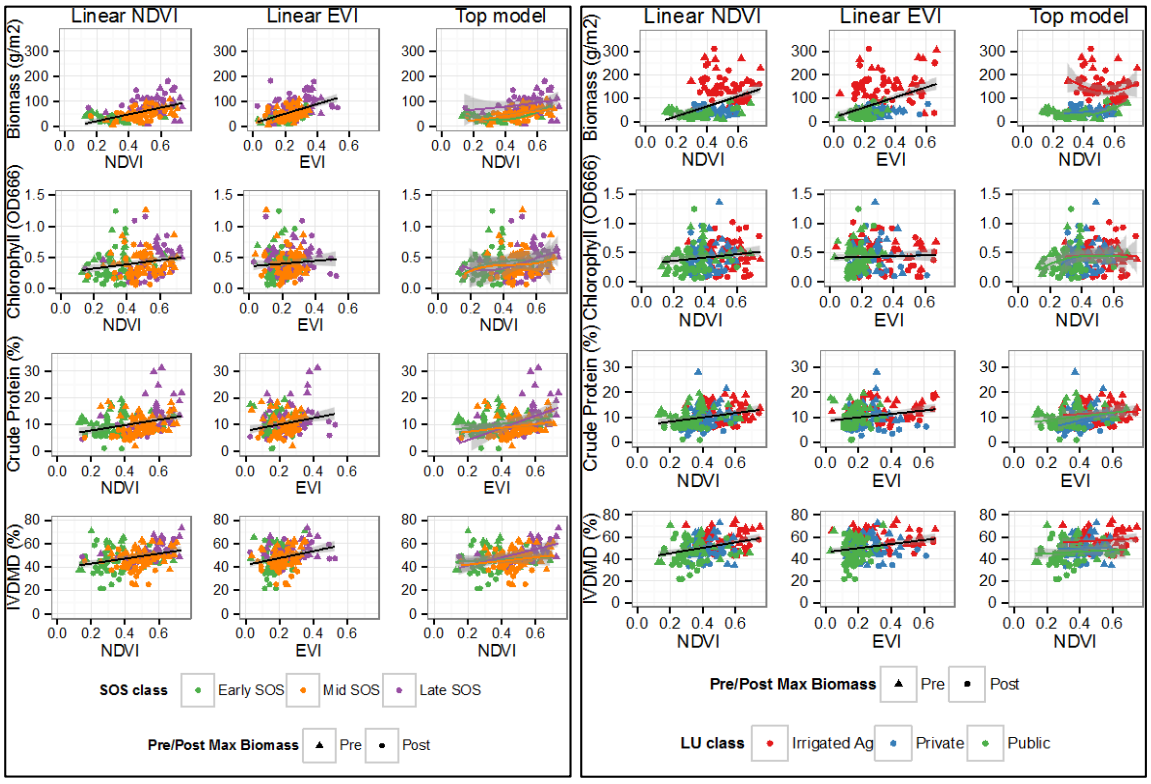


Figure 2.3 Linear NDVI, linear EVI, and top models of biomass, chlorophyll, crude protein, and IVDMD in the start of season (SOS) and land use classes. Shapes represent estimates from before and after the peak in biomass and grey shading represents 95% CI.

Table 2.1 Description of the top models of aboveground biomass, chlorophyll, crude protein, and IVDMD in the start of season (SOS) and land use classes.

Top SOS models
Biomass~bs(NDVI,df=5)+SOS+bs(NDVI,df=5)*SOS+varIdent(SOS)+random(pixel)
Chlorophyll~NDVI+Date+random(pixel)
Crude protein~bs(EVI,df=5)+SOS+Date+varIdent(SOS)+random(pixel)
IVDMD~NDVI+SOS+Date+NDVI*Date+varIdent(SOS)+random(pixel)
Top land use models
Biomass~NDVI+land use+Date+$NDVI^2$+$NDVI^2$*Date+varIdent(land use)+random(pixel)
Chlorophyll~NDVI+Date+random(pixel)
Crude protein~bs(EVI,df=5)+land use+Date+varIdent(land use)+random(pixel)
IVDMD~NDVI+land use+Date+$NDVI^2$+varIdent(land use)+random(pixel)

*Models included start of season class (SOS), land use class, Date (Julian day), variance structures, basis spline functions (bs, df=5), and a random effect for pixel.

Table 2.2 Description of the linear NDVI, linear EVI, and top models of biomass, chlorophyll, crude protein, and IVDMD in the start of season (SOS) and land use classes.

	Start of Season Classes							Land Use Classes					
	AIC_c	**R^2**	**Fixed effects**	**r_p^2**	**df**	**F***		**AIC_c**	**R^2**	**Fixed effects**	**r_p^2**	**df**	**F***
Aboveground Biomass (g/m^2)													
NDVI	1782.7	0.42	NDVI	0.42	1,187	134.1*	*NDVI*	2113.8	0.53	NDVI	0.53	1,198	226.7*
EVI	1834.9	0.24	EVI	0.24	1,187	57.2*	*EVI*	2228.9	0.17	EVI	0.17	1,198	40.8*
Top	1662.5	0.76	bs(NDVI)	0.59	5,160	13.1*	*Top*	1826.7	0.72	$NDVI^2$	0.62	2,181	53.8*
			SOS	0.08	2,160	12.9*				land use	0.07	2,11	30.5*
			bs(NDVI)*SOS	0.09	10,160	3.7*				Date	0.01	1,181	0.6
										$NDVI^2$*Date	0.02	2,181	14.4*
Chlorophyll (OD666)													
NDVI	-22.9	0.04	NDVI	0.04	1,187	8.6*	*NDVI*	-7.8	0.03	NDVI	0.03	1,198	6.4*
EVI	-15.8	0.01	EVI	0.01	1,187	1.3	*EVI*	-1.7	0.01	EVI	0.01	1,198	0.2
Top	-54.8	0.21	NDVI	0.06	1,175	10.3*	*Top*	-34.3	0.17	NDVI	0.06	1,184	7.4*
			Date	0.15	1,175	39.1*				Date	0.11	1,184	32.7*
Crude Protein (%)													
NDVI	1098.5	0.09	NDVI	0.09	1,187	18.9*	*NDVI*	1114.9	0.14	NDVI	0.14	1,198	31.4*
EVI	1106.4	0.05	EVI	0.05	1,187	10.4*	*EVI*	1132.8	0.05	EVI	0.05	1,198	11.7*
Top	896.9	0.74	bs(EVI)	0.16	5,169	15.3*	*Top*	971.7	0.51	bs(EVI)	0.14	5,180	18.8*
			SOS	0.04	2,169	3.3*				land use	0.06	2,11	5.9*
			Date	0.54	1,169	328.9*				Date	0.31	1,180	236.1*
IVDMD (%)													
NDVI	1369.7	0.11	NDVI	0.11	1,187	22.2*	*NDVI*	1453.9	0.18	NDVI	0.18	1,198	44.6*
EVI	1375.9	0.08	EVI	0.08	1,187	15.5*	*EVI*	1481.6	0.06	EVI	0.06	1,198	13.3*
Top	1307.5	0.37	NDVI	0.12	1,172	31.7*	*Top*	1383.2	0.56	$NDVI^2$	0.22	2,183	34.8*
			SOS	0.05	2,172	4.1*				land use	0.06	2,11	7.4*
			Date	0.18	1,172	60.2*				Date	0.28	1,183	82.2*
			NDVI*Date	0.02	1,172	7.7*							

**indicates p<0.05. Models include start of season class (SOS), land use class, Date (Julian day), and basis spline functions (df=5). Statistics include the corrected AIC (AIC_c), conditional R^2, partial R^2 (r_p^2), F-statistics, and p-values.*

variation in IVDMD than the linear EVI models across the UYRB (Figure 2.3 & Tables 2.1-2.3). The AIC_c estimates from the linear NDVI models were >2 units less than the linear EVI models. The RMSEs from the linear NDVI models of biomass, crude protein, and IVDMD were lower than the linear EVI models in all SOS ($p<0.04$) and land use ($p<0.001$) classes, but did not differ before and after the peak in biomass ($p=0.21$). There

Table 2.3 Average root mean squared errors (RMSE) from the linear NDVI, linear EVI, and top models in the start of season (SOS) and land use classes in the Upper Yellowstone River Basin. *Italics* represent the lowest RMSE.

	SOS classes					Land use classes				
Model	**Early**	**Mid**	**Late**	**Pre-max**	**Post-max**	**Ag**	**Private**	**Public**	**Pre-max**	**Post-max**
RMSE										
Aboveground biomass (g/m^2)										
NDVI	3.88±2.61	4.63±3.38	7.89±3.41	3.41±2.76	6.44±3.91	18.61±9.58	7.66±5.33	5.59±4.16	7.05±5.68	9.07±6.24
EVI	4.09±2.61	4.52±2.71	9.17±4.51	4.35±3.28	6.79±2.99	16.85±3.45	8.42±5.35	6.86±3.67	9.14±8.31	12.41±9.14
Top	*2.43±2.11*	*3.22±2.77*	*5.46±3.36*	*2.65±2.24*	*5.02±6.56*	*12.17±9.92*	*2.36±1.89*	*2.69±2.02*	*4.31±4.63*	*6.22±5.09*
Chlorophyll (OD666)										
NDVI	0.03±0.04	0.04±0.03	0.05±0.03	0.03±0.02	0.03±0.03	0.05±0.03	0.03±0.02	0.03±0.02	0.03±0.02	0.03±0.03
EVI	0.03±0.04	0.04±0.03	0.05±0.03	0.04±0.02	0.04±0.03	0.05±0.03	0.03±0.03	0.03±0.03	0.03±0.02	0.06±0.03
Top	*0.02±0.04*	*0.02±0.03*	*0.03±0.03*	*0.02±0.03*	*0.03±0.03*	*0.03±0.03*	*0.02±0.03*	*0.02±0.03*	*0.02±0.02*	*0.03±0.03*
Crude Protein (%)										
NDVI	0.68±0.53	0.73±0.47	1.02±0.97	0.73±0.41	0.99±1.01	0.87±0.49	0.76±0.58	0.67±0.54	0.47±0.44	0.67±0.56
EVI	0.68±0.53	0.76±0.51	1.03±0.98	0.79±0.46	0.87±1.05	0.87±0.49	0.73±0.63	0.71±0.45	0.44±0.46	0.55±0.53
Top	*0.38±0.32*	*0.32±0.38*	*0.77±0.79*	*0.32±0.29*	*0.53±0.84*	*0.71±0.58*	*0.41±0.45*	*0.35±0.29*	*0.38±0.42*	*0.45±0.33*
IVDMD (%)										
NDVI	1.41±1.17	1.51±1.25	1.98±1.44	1.41±0.91	1.53±1.78	2.01±1.45	1.54±1.06	1.71±1.32	1.36±1.39	1.45±1.42
EVI	1.56±1.17	1.59±1.27	2.01±1.44	1.47±0.94	2.06±1.81	2.13±1.46	1.71±1.31	1.85±1.35	1.48±1.24	2.05±1.26
Top	*1.08±0.83*	*1.31±1.11*	*1.77±1.36*	*1.24±0.95*	*1.74±1.35*	*1.85±1.26*	*1.11±1.15*	*1.52±0.91*	*1.07±1.06*	*1.46±1.36*

was no detectable difference in the RMSEs from the linear NDVI and EVI models of chlorophyll by SOS class, land use class, or before and after the peak in biomass ($p>0.05$).

Polynomial NDVI and Date Effects Improved Models

Models with a polynomial function for NDVI explained 19-55 g/m^2 more variation in biomass than the linear NDVI and EVI models in all SOS ($p<0.001$) and land use ($p<0.001$) classes in the UYRB (Figure 2.3 & Tables 2.1-2.3). In the SOS classes, a model that accounted for a different curvilinear relationship between NDVI and biomass

in each SOS class, differences in biomass by SOS class, different variation by SOS class, and variability between pixels explained 76% of the variation in biomass (Appendix H). In the land use classes, a model that accounted for a curvilinear relationship between NDVI and biomass throughout the season, differences in biomass by land use class, different variation by land use class, and variability between pixels explained 72% of the variation in biomass (Appendix H). In these models, the polynomial NDVI function was responsible for most of the explained variation in biomass (R_p^2=0.59 & 0.62) and there was moderate correlation between pixel estimates (ICC=0.41 & 0.14). The residuals from these models were normally and homogeneously distributed. The RMSEs were greater in the late SOS class than in the early and mid SOS classes ($p<0.001$), greater in irrigated agriculture than in private and public grasslands ($p<0.001$), and greater after the peak in biomass than before ($p<0.04$). There was no detectable difference between the RMSEs from the early and mid SOS classes ($p=0.21$) and from private and public grasslands ($p=0.31$). Between models, the RMSEs from the top models were lower than the linear NDVI and EVI models in the SOS classes ($p<0.01$), land use classes ($p<0.02$), and before and after the peak in biomass ($p<0.01$).

Models with a linear function for date explained more variation in forage quality across the UYRB than the linear NDVI and EVI models (Figure 2.3 & Tables 2.1-2.3). A model that accounted for a linear relationship between NDVI and chlorophyll, a seasonal decline in chlorophyll, and variability between pixels explained 14-20% more variation in chlorophyll than the linear NDVI and EVI models in all SOS ($p<0.001$) and land use

($p<0.001$) classes (Appendix H). In these models, the linear date function was responsible for most of this explained variation in chlorophyll (r_p^2=0.11 & 0.15) and there was minimal correlation between pixels (ICC=0.02 & 0.01). For crude protein, a model that accounted for a curvilinear relationship between EVI and crude protein, differences in crude protein by SOS or land use class, a seasonal decline in crude protein, different variation by SOS and land use class, and variability between pixels explained 37-69% more variation in crude protein than the linear NDVI and EVI models in all SOS ($p<0.001$) and land use ($p<0.001$) classes (Appendix H). In these models, the linear function for date was responsible for most of explained variation in crude protein (r_p^2=0.54 & 0.31) and there was some correlation between pixels (ICC=0.17 & 0.18). For IVDMD, a model that accounted for a linear relationship between NDVI and IVDMD throughout the season, differences in IVDMD by SOS class, different variation in IVDMD by SOS class, and variability in pixels explained 26% more variation in IVDMD than the linear NDVI and EVI models in all SOS classes ($p<0.001$) (Appendix H). A model that accounted for a curvilinear relationship between NDVI and IVDMD, differences in IVDMD by land use class, a seasonal decline in IVDMD, variation by land use class, and variability between pixels explained 50% more variation in IVDMD than the linear NDVI and EVI models in all land use classes ($p<0.001$) (Appendix H). In these models, the linear date function explained most of this variation in IVDMD (r_p^2=0.18 & 0.28) and there was some correlation between pixels (ICC=0.19 & 0.01). The residuals from these models were normally and homogeneously distributed. The RMSEs were greater in the late SOS class than in the early and mid SOS classes ($p<0.01$), greater in

irrigated agriculture than in private and public grasslands ($p<0.01$), and greater after the peak in biomass than before ($p<0.03$). There was no detectable difference in the RMSEs from the early and mid SOS classes ($p=0.21$) and from private and public grasslands ($p=0.12$). Between models, the RMSEs from the top models were lower than the linear NDVI and EVI models in all SOS classes ($p<0.03$), land use classes ($p<0.01$), and before and after the peak in biomass ($p<0.04$).

Spatiotemporal Variation in Grassland Biomass and Quality

Models including polynomial NDVI, date, and random pixel effects showed greater spatiotemporal heterogeneity in grassland biomass and quality across the UYRB than the linear NDVI and EVI models (Figures 2.4-2.7). While all models projected that biomass increased from low to high elevations throughout the sampling period, the top models projected a 38.1-99.1 g/m^2 greater range in biomass across the elevation gradient ($p<0.05$). Specifically, the top models estimated that biomass was 20.1 ± 2.2 g/m^2 greater in the high-elevation grasslands and $72.9\pm0.73 g/m^2$ greater in irrigated agriculture than the linear NDVI and EVI models ($p<0.05$). While all models projected that forage quality peaked early in the season and then declined across the UYRB, the top models estimated that the range in chlorophyll was 0.47-0.51 greater, the range in crude protein was 8.6-15.1% greater, and the range in IVDMD was 3.5-10.1% greater throughout the sampling period than the linear NDVI and EVI models ($p<0.05$). Across the UYRB, the top models projected that chlorophyll was 0.12 ± 0.01 greater early in the season, 0.03 ± 0.01

greater mid season, and 0.21±0.01 lower late in the season than the linear NDVI and EVI models ($p<0.01$). The top models projected that crude protein was 2.9±0.02% greater early in the season, 0.29±0.01% greater mid season, and 2.1±0.1% lower late in the season across the landscape than the linear NDVI and EVI models ($p<0.01$). The top models projected that IVDMD was 12.9±0.1% greater early in the season, 5.1±0.03% greater mid season, and 22.8±0.1% lower late in the season than the linear NDVI and EVI models ($p<0.01$).

Grassland biomass and quality varied across the elevation-related phenology and land use gradients in the UYRB throughout the sampling period (Figure 2.4-2.7). From low to high elevations, biomass varied from 50.6±0.1-6.3±0.6 g/m^2 early in the season, from 53.1±36.1-82.4±18.4 g/m^2 mid season, and from 53.8±16.2-86.1±33.6 g/m^2 late in the season ($p<0.01$). Chlorophyll varied from 0.54±0.14-0.49±0.21 early in the season, was an average of 0.46±0.31 mid season, and was an average of 0.28±0.11 late in the season across the elevation gradient ($p<0.01$). Crude protein varied from 14.5±0.7-7.3±0.9% early in the season, was an average of 11.1±2.4% mid season, and varied from 5.6±1.6-10.8±2.1% late in the season across the elevation gradient ($p<0.05$). IVDMD ranged from 52.9±0.1-63.5±1.6% early in the season, from 50.8±0.1-54.5±2.1% mid season, and from 38.6±0.1-47.1±2.1% late in the season from low to high elevations ($p<0.05$). At their seasonal peak, high-elevation grasslands that started growth late in the season had up to 45.7±5.3 g/m^2 more biomass, 0.2±0.1% greater crude protein, and 7.4±0.1% greater IVDMD than grasslands that started growth early and mid season

($p<0.01$). Across the UYRB, irrigated agriculture had up to 102.3±0.4 g/m^2 more biomass, 2.4±0.1% greater crude protein, and 11.2±0.1% greater IVDMD than all other grasslands throughout the sampling period ($p<0.01$). (See Appendix I for upper and lower confidence interval estimates from the linear NDVI, linear EVI, and top models of biomass, chlorophyll, crude protein, and IVDMD).

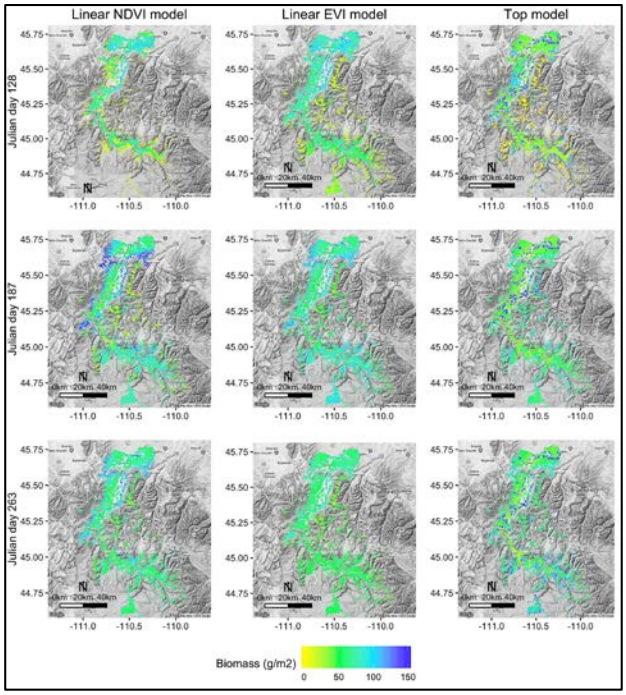


Figure 2.4 Spatiotemporal variation in grassland biomass across the Upper Yellowstone River Basin from the linear NDVI, linear EVI, and top models.

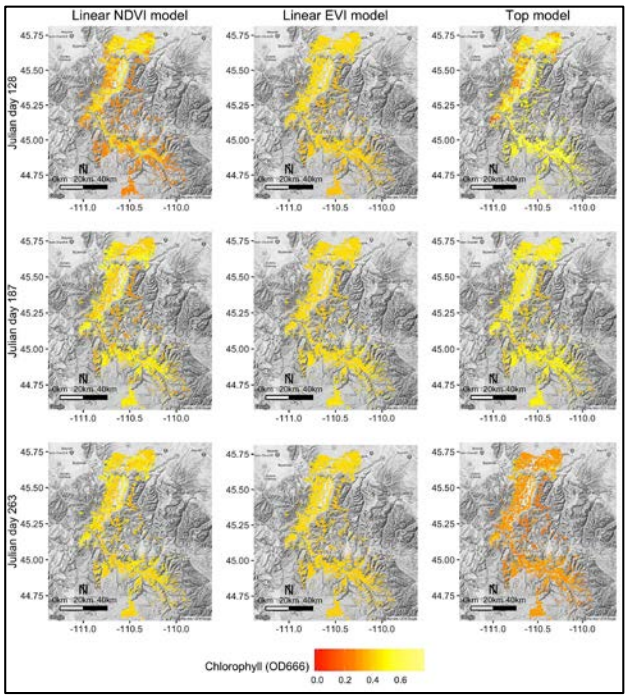


Figure 2.5 Spatiotemporal variation in chlorophyll across the Upper Yellowstone River Basin from the linear NDVI, linear EVI, and the top models.

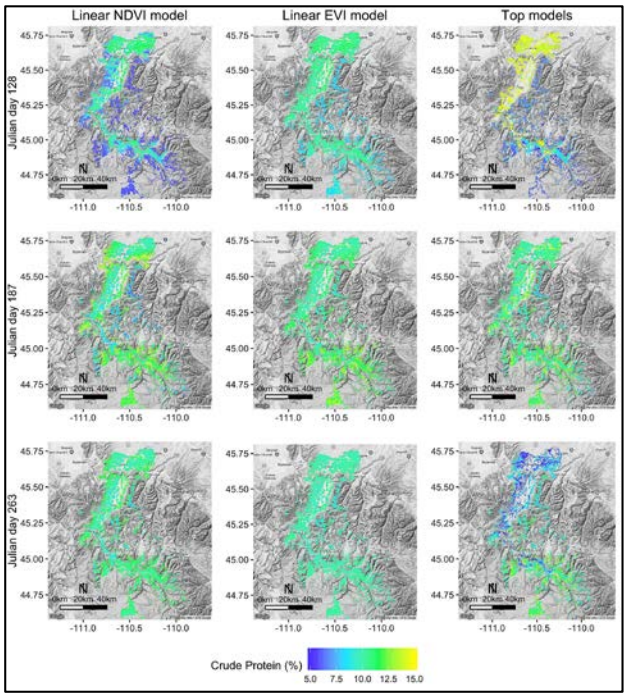


Figure 2.6 Spatiotemporal variation in crude protein across the Upper Yellowstone River Basin estimated from the linear NDVI, linear EVI, and the top models.

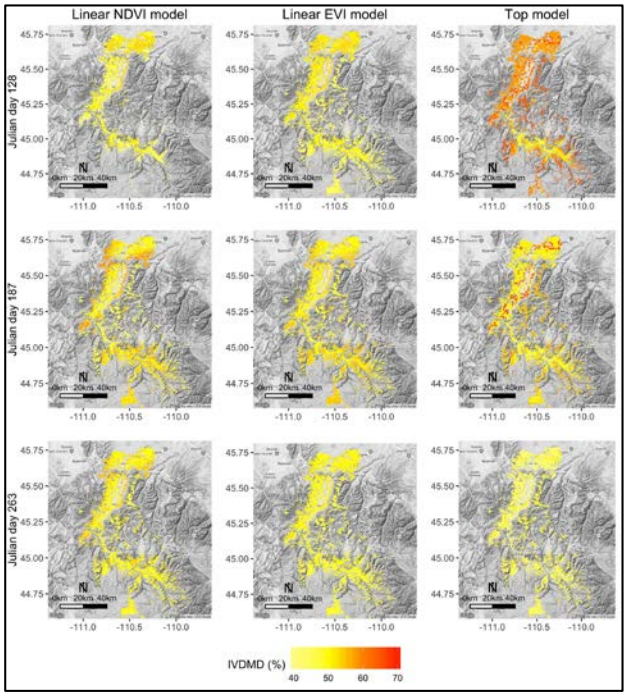


Figure 2.7 Spatiotemporal variation in IVDMD across the Upper Yellowstone River Basin estimated from the linear NDVI, linear EVI, and the top models.

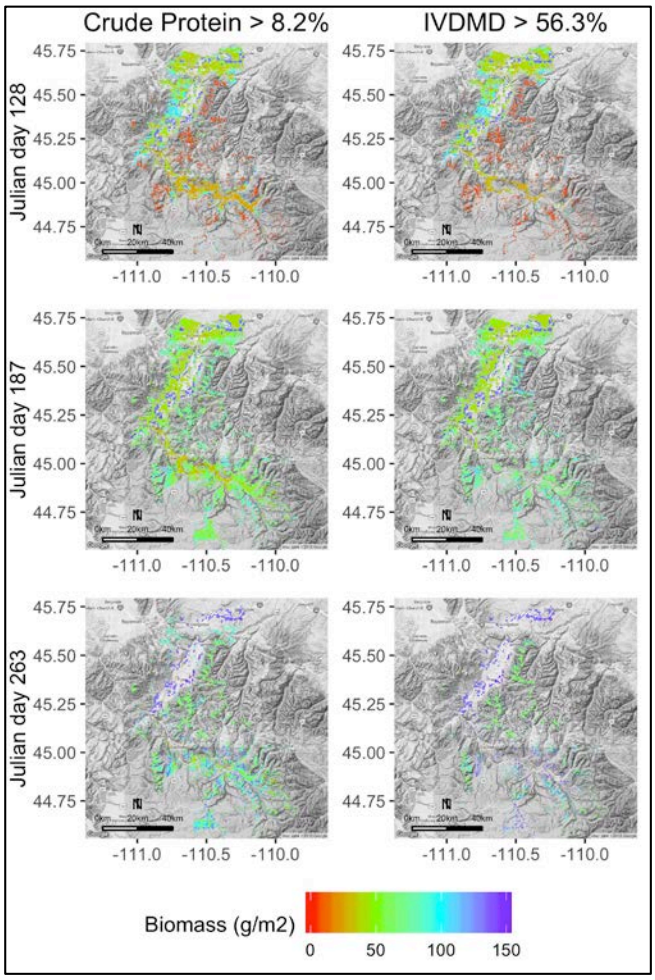


Figure 2.8 Spatiotemporal variation in the abundance of forage with adequate crude protein (>8.2%) and IVDMD *(*>56.3%) for elk in the Upper Yellowstone River Basin.

Spatiotemporal Variation in the Abundance of High Quality Forage for Elk

Crude protein and IVDMD estimates were above the thresholds required by elk [39] across the low and mid-elevation grasslands early in the season, across most of the grasslands in the UYRB mid season, and in small patches in high elevations late in the season (Figure 2.8). The abundance of forage of adequate quality for elk [39] differed

across the elevation-related phenology and land use gradients in the UYRB throughout the sampling period. Early in the season, the abundance of forage of adequate quality for elk ranged from 41.2±27.6-18.1±29.4 g/m^2 from low to high elevations, but was 54.8±42.7g/m^2 in irrigated agriculture ($p<0.01$). Mid season, the abundance of forage of adequate quality for elk ranged from 45.4±23.6-75.9±16.5 g/m^2 across the elevation gradient, and was 134.8±20.7 g/m^2 in irrigated agriculture ($p<0.01$). Late in the season, the abundance of forage of adequate quality for elk varied from 80.9±41.1-85.8±32.6 g/m^2 from low to high elevations, and was 144.6±14.6 g/m^2 in irrigated agriculture ($p<0.01$). At their peak, the abundance of forage of adequate quality for elk was 22.6±2.6 g/m^2 greater in grasslands with late onset of growth than in grasslands that started growth early and mid season ($p<0.01$). Across the UYRB, irrigated agriculture had up to 78.6±5.1 g/m^2 more forage of adequate quality for elk than all other grasslands ($p<0.01$).

Discussion

NDVI and EVI Explained Minimal Variation in Biomass and Quality

Linear NDVI and EVI models explained half of the variation in grassland biomass and minimal variation in forage quality across the UYRB throughout the sampling period. Overall, this poor relationship was likely due to the difference in spatial scale between the satellite estimates of NDVI and EVI and the field estimates of forage biomass and quality. In addition, the poor performance was also likely due to contamination from exposed soil, heterogeneous vegetation structure, and senescent

biomass [20,22,36,89,108]. The low accuracy of the linear EVI models of biomass was likely also due to contamination from variable terrain across the UYRB [95]. Furthermore, these results indicate that satellite-derived NDVI and EVI are not good proxies for forage quality and may be related to the quantity of high quality forage rather than the quality of forage [38,89]. The weak relationship between NDVI/EVI and chlorophyll is surprising because these indices are thought to be based on the absorption of red wavelengths by photosynthetic pigments (e.g., chlorophyll) [22], and may indicate that this relationship does not hold throughout the entire season. Previous studies, although conducted at smaller spatial scales, have similarly found that NDVI explained only 18-41% of the variation in biomass and 1% of the variation in crude protein in grasslands across Montana [35,38]. Overall, these results suggest that caution is needed when using satellite-derived NDVI and EVI as proxies for forage biomass and quality across the UYRB.

The accuracy of NDVI and EVI as proxies for forage biomass and quality was lower in grasslands that started growth late in the season than in grasslands that started growth early and mid season, lower in irrigated agriculture than in private and public grasslands, and lower after the peak in biomass than before. In grasslands with late onset of growth, this poor performance was likely due to contamination from the increased levels of atmospheric contaminants in these high-elevation grasslands and because the models did not account for the curvilinear relationship between NDVI and biomass in these grasslands' dense vegetation [76,94]. The low accuracy of the linear EVI models was likely due to contamination from the variable terrain in these high-elevation

grasslands [95]. The poor performance in irrigated agriculture was likely due to moisture contamination from irrigation and the curvilinear relationship between NDVI and biomass in dense crops [22,101,103]. Finally, the poor performance after the peak in biomass was likely due to the contamination from senescent biomass and exposed soil late season[102]. Previous studies have similarly found that the accuracy of NDVI differs by land cover type, land use, and throughout the season [21,35,38,102,108]. Consideration for how the accuracy of NDVI and EVI as proxies for forage biomass and quality differs across elevation-related phenology and land use gradients throughout the season is necessary when using these indices across the UYRB.

NDVI explained more variation in forage biomass and quality across the UYRB than EVI. This is likely because the adjustment factors made EVI more sensitive to contamination from the variable terrain across the UYRB than NDVI [94,95]. Previous studies have similarly found that NDVI outperformed EVI as a proxy for biomass in the Sonoran Desert [94] and for crude protein in Mongolia [89]. These results suggest that resilience to variable terrain may be more important than accounting for soil and atmospheric contamination when using these vegetation indices across the UYRB.

Polynomial NDVI and Date Effects Improved Models

Overall, the results from this study indicate that there is high variability in the relationship between NDVI/EVI and forage biomass and quality, but that accounting for curvilinear relationships, season, and variability between pixels may slightly improve the performance of models of forage biomass and quality across the UYRB. As previously

documented [34,36,109], the improved performance of biomass models with a polynomial function for NDVI was likely because the non-linear function explained more of the variability in forage biomass and quality than the linear functions. The improved performance of forage quality models with a function for date was likely because the season effect accounted for a decline in forage quality unexplained by NDVI and EVI due to the high variability in forage quality, the contamination from senescent vegetation, and the weak relationship between NDVI/EVI and forage quality late in the season [19,38,102]. Finally, the improved performance of models with random pixel effects is likely because these models accounted for local variation in biomass and quality that was unaccounted for by NDVI and EVI [64]. Overall, these results indicate that there is a high amount of variability in the relationship between NDVI/EVI and forage biomass and quality, but that including polynomial functions, season, and pixel effects helped explain some of this variation in forage biomass and quality [19,35,36,108].

Models that accounted for the curvilinear relationship between NDVI and biomass, seasonal variation in forage quality, and variability between pixels showed greater spatiotemporal heterogeneity in forage biomass and quality across the UYRB than the linear NDVI and EVI models. By accounting for the curvilinear relationship between NDVI and biomass, the top models had more accurate estimates of biomass in grasslands with dense biomass (e.g., high-elevation grasslands and irrigated agriculture) compared to the linear NDVI and EVI models. By accounting for season, the top models projected that forage quality was higher across the UYRB early in the season and lower across the landscape late in the season. While all models showed the same general trends in forage

biomass and quality, these results suggest that NDVI and EVI may underestimate biomass in areas with dense vegetation, underestimate forage quality early in the season, and overestimate forage quality late in the season. Given that even small differences in the quality of forage can have profound effects on the fitness of elk [39], the error associated with using NDVI and EVI may influence whether forage is projected to be of adequate or inadequate quality for elk. Overall, these results suggest that researchers and managers should consider the error associated with using satellite-derived NDVI and EVI before using it as a proxy for forage biomass and quality.

Spatiotemporal Variation in Grassland Biomass and Quality

As previously documented [9,13], the top models projected that grassland biomass and quality increased along the elevation-related phenology gradient in the UYRB, but remained consistently high in irrigated agriculture throughout the growing season. This study, however, is one of the first to show that the magnitude of biomass and quality differed across these gradients throughout the season. At their seasonal peak, high-elevation grasslands with late onset of growth had up to 50% more biomass, 5% greater crude protein, and 20% greater IVDMD than grasslands that started growth early and mid season. This was likely due to the high nutrient and moisture content of soils (from nitrogen deposition and moisture from prolonged snowmelt), the increased precipitation, and the reduced evapotranspiration in these high-elevation grasslands [8,9,75]. Across the UYRB, however, irrigated agriculture had 200% more biomass and 10% greater IVDMD than all other grasslands due to prolonged growth from irrigation,

the inherently higher biomass and quality of crop species, and the surge in quality after the seasonal harvest [9,54]. These results are consistent with the previous NDVI analyses from Piekielek [9] and Thein at al. [13] showing that primary productivity varied across the elevation gradient in the GYE. Duparc et al. [17] similarly found that more productive vegetation communities reached their peak in biomass later in the season than less productive alpine communities in the French Alps. Also, Albon and Langvatn [7] found that forage quality varied across an elevation gradient in Norway. Overall, these results suggest that the magnitude of biomass and quality differs across the elevation-related phenology and land use gradients in the UYRB throughout the growing season.

Variation in the Abundance of High Quality Forage

The abundance of forage with adequate crude protein and digestibility for elk [39] increased along the elevation-related phenology gradient in the UYRB throughout the growing season. Early and mid season, there was a relatively moderate abundance of forage of adequate quality for elk available across most of the low and mid-elevation grasslands in the UYRB. Late in the season, there was a high abundance of forage of adequate quality for elk in small patches in high elevations. While previous studies have documented that high quality forage varies along the elevation-related phenology gradient in the GYE [13], this study provides evidence that the abundance of forage with adequate levels of crude protein and IVDMD for elk varies across this gradient. For elk, these results suggest that forage selection may be especially important late in the season when forage of adequate quality is limited to small patches in high elevations.

High-elevation grasslands that started growth late in the season had up to 50% more forage of adequate quality for elk at their seasonal peak than grasslands that started growth early and mid season. This is likely because the increased nitrogen and moisture content of soils and the reduced evapotranspiration rates in these high-elevation grasslands promoted grassland biomass and quality [8,10,13,75]. For migratory elk, these results suggest that high-elevation grasslands provide the bulk of the energy and nutrients for elk in the critical foraging period late in the season [6,12,41]. Mysterud et al. [46] similarly found that access to forage across an elevation gradient was responsible for the increased weight gain of migratory ungulates in Norway. In addition, these results provide evidence that migratory elk may “jump” rather than “ride” the green wave of phenology to increase their access to abundant high quality forage in high elevations [83]. In the context of climate change, these results may indicate that shifts in the timing of growth in high-elevation grasslands may have especially negative impacts on migratory elk [12]. Future research should assess the role of this abundant high quality forage in high-elevation grasslands on the fitness and movement of migratory elk.

While irrigated agriculture is known to have high forage biomass and quality, this study is one of the first to document that irrigated agriculture had up to 200% more forage of adequate quality for elk than all other grasslands in the UYRB throughout the growing season. These results provide evidence that irrigated agriculture may supplement the nutrient and energy gain of residential elk throughout the season, and therefore, may influence the benefits of migratory versus residential strategies in elk [7,12,50]. Middleton et al. [12], for example, suggested that the elevated abundance and quality of

forage in irrigated agriculture was responsible for the high reproductive rates of residential elk in the GYE. Hebblewhite et al. [55], similarly, suggested tat access to hay was partially responsible for a shift in the ratio of residential versus migratory behavior in elk.

Scope and Limitations

These results should be considered with the limitations of this study in mind. Because the aim of this study was to assess the utility of NDVI and EVI as proxies for grassland biomass and quality across the UYRB, we did not directly control or assess which factors (e.g., senescent biomass, soil exposure, topography, etc.) affected the accuracy of these models across the landscape [22,93]. Future research is needed, therefore, to identify the specific factors that influenced the accuracy of these models across the UYRB. Moreover, while MODIS data is corrected for atmospheric, geo-referencing, and image processing errors, we expect that there may have still been some residual error in the NDVI and EVI estimates due to cloud cover and atmospheric contaminants [35]. Because of the limitations of collecting field estimates of biomass and quality at large spatiotemporal scales, we expect that there was error associated with the field estimates of forage. Finally, more information is needed to determine if these results are consistent across the GYE and in other temperate landscapes.

Because not all land uses were represented in all start of season classes in the UYRB (i.e. irrigated agriculture was only located in the low-elevation grasslands in the early SOS class), we were not able to compare the relative or interacting effects of the

timing of growth and land use on the accuracy of NDVI and EVI models in this study. Because irrigated agriculture was only located in the low-elevation grasslands, our analysis of how the accuracy of NDVI and EVI models vary by land use was restricted to the early SOS class. In addition, because the mid and late SOS classes were only present in the mid and high-elevation grasslands in Yellowstone National Park, our analysis of how the accuracy of NDVI and EVI varies across the elevation-related phenology gradient was restricted to public grasslands. Future research should consider how the effects of land use and phenology interact to influence the accuracy of NDVI and EVI.

Future research should consider if other vegetation indices (i.e. SAVI, TSAVI, etc.) or models with multiple individual bands may improve the estimates of biomass and quality across the UYRB [35,108]. Previous studies have documented that vegetation indices with adjustments for variable soil and atmosphere provided improved estimates of biomass [108]. Previous studies have also shown that models with multiple individual bands explained more variation in biomass because it allows for separate coefficients for each band and includes bands other than red and NIR bands [35,108].

Conclusion

The results from this study indicate that consideration for the limitations of NDVI and EVI as proxies for forage biomass and quality is crucial when mapping forage patterns available to migratory ungulates. The principal findings from this study were that: (1) satellite-derived NDVI and EVI explained minimal variation in grassland biomass and quality across the UYRB throughout the growing season; (2) the accuracy of

NDVI and EVI differed across elevation-related phenology and land use gradients throughout the season; (3) while there is substantial variation in the relationship between NDVI/EVI and forage biomass and quality, accounting for curvilinear relationships, seasonal variation in forage quality, and variability between pixels in NDVI and EVI models improved estimates of biomass and quality; and (4) grasslands that started growth late in the season and irrigated agriculture had a greater abundance of high quality forage for elk than all other grasslands in the UYRB. These results indicate that there is substantial variability in the relationship between satellite NDVI/EVI and forage biomass and quality, but models that account for curvilinear relationships and season show general patterns of forage biomass [35]. For migratory elk, these patterns suggest that grasslands with late onset of growth and irrigated agriculture may play an especially important role in the movement and population dynamics of migratory elk. Overall, this study provides novel information on the utility of using NDVI and EVI to map spatiotemporal variation in forage biomass and quality for migratory ungulates.

REFERENCES

1. Fryxell, J. M.; Greever, J.; Sinclair, A. R. E. Why are Migratory Ungulates So Abundant? *Am. Nat.* 1988, *131*, 781.

2. McNaughton, S. J. Ecology of a Grazing Ecosystem: The Serengeti. *Ecol. Monogr.* 1985, *55*, 260–294.

3. Fryxell, J. M. Forage Quality and Aggregation by Large Herbivores. *Am. Nat.* 1991, *138*, 478.

4. Hebblewhite, M.; Merrill, E.; McDermid, G. A Multi-Scale Test Of The Forage Maturation Hypothesis In A Partially Migratory Ungulate Population. *Ecol. Monogr.* 2008, *78*, 141–166.

5. Frank, D. A.; McNaughton, S. J.; Tracy, B. F. The Ecology of the Earth's Grazing Ecosystems. *Bioscience* 1998, *48*, 513–521.

6. Van Soest, P. J. *Nutritional Ecology of the Ruminant*; 2nd .; Cornstock Publishing Associates: Ithaca,NY, 1982.

7. Albon, S. . D.; Langvatn, R. Plant phenology and the benefits of migration in a temperate ungulate. *Oikos* 2009, *65*, 502–513.

8. Despain, D. *Yellowstone Vegetation: Consequences of Environment and History in a Natural Setting*; Boulder: Roberts Rinehart, 1990.

9. Piekielek, N. B. Remote Sensing Grassland Phenology in the Greater Yellowstone Ecosystem: Biophysical Correlates, Land Use Effects and Patch Dynamics, 2012.

10. Frank, D. A.; Groffman, P. M. Ungulate vs. landscape control of soil C and N processes in grasslands of Yellowstone National Park. *Ecology* 1998, *79*, 2229–2241.

11. Pettorelli, N.; Pelletier, F.; Von Hardenberg, A.; Festa-Bianchet, M.; Côté, S. D. Early onset of vegetation growth vs. rapid green-up: Impacts on juvenile mountain ungulates. *Ecology* 2007, *88*, 381–390.

12. Middleton, A. D.; Kauffman, M. J.; Mcwhirter, D. E.; Cook, J. G.; Cook, R. C.; Nelson, A. A.; Jimenez, M. D.; Klaver, R. W. Animal migration amid shifting patterns of phenology and predation: Lessons from a Yellowstone elk herd. *Ecology* 2013, *94*, 1245–1256.

13. Thein, T. R.; Watson, F. G. R.; Cornish, S. S.; Anderson, T. N.; Newman, W. B.; Lockwood, R. E. Chapter 7 Vegetation Dynamics of Yellowstone's Grazing System. *Terr. Ecol.* 2008, *3*, 113–133.

14. Hamel, S.; Garel, M.; Festa-Bianchet, M.; Gaillard, J. M.; Côté, S. D. Spring Normalized Difference Vegetation Index (NDVI) predicts annual variation in timing of peak faecal crude protein in mountain ungulates. *J. Appl. Ecol.* 2009, *46*, 582–589.

15. Klein, D. R. Variation in quality of caribou and reindeer forage plants associated with season, plant part, and phenology. *Rangifer* 1990, 123–130.

16. Perez, C. A.; Frangi, J. L. Grassland biomass dynamics along an altitudinal gradient in the Pampa. *J. Range Manag.* 2000, *53*, 518–528.

17. Duparc, A.; Redjadj, C.; Viard-Crétat, F.; Lavorel, S.; Austrheim, G.; Loison, A. Co-variation between plant above-ground biomass and phenology in sub-alpine grasslands. *Appl. Veg. Sci.* 2013, *16*, 305–316.

18. Buyantuyev, A.; Wu, J. Urbanization alters spatiotemporal patterns of ecosystem primary production: A case study of the Phoenix metropolitan region, USA. *J. Arid Environ.* 2009, *73*, 512–520.

19. Pettorelli, N.; Ryan, S.; Mueller, T.; Bunnefeld, N.; Jedrzejewska, B.; Lima, M.; Kausrud, K. The Normalized Difference Vegetation Index (NDVI): Unforeseen successes in animal ecology. *Clim. Res.* 2011, *46*, 15–27.

20. Myneni, R. B.; Hall, F. G.; Sellers, P. J.; Marshak, A. L. Interpretation of spectral vegetation indexes. *IEEE Trans. Geosci. Remote Sens.* 1995, *33*, 481–486.

21. Borowik, T.; Pettorelli, N.; Sönnichsen, L.; Jedrzejewska, B. Normalized difference vegetation index (NDVI) as a predictor of forage availability for ungulates in forest and field habitats. *Eur. J. Wildl. Res.* 2013, *59*, 675–682.

22. Huete, A.; Didan, K.; Miura, T.; Rodriguez, E. P.; Gao, X.; Ferreira, L. G. Overview of the radiometric and biophysical performance of the MODIS vegetation indices. *Remote Sens. Environ.* 2002, *83*, 195–213.

23. Jiang, Z.; Huete, A. R.; Didan, K.; Miura, T. Development of a two-band enhanced vegetation index without a blue band. *Remote Sens. Environ.* 2008, *112*, 3833–3845.

24. Tucker, C. J.; Vanpraet, C. L.; Sharman, M. J.; Van Ittersum, G. Satellite remote sensing of total herbaceous biomass production in the Senegalese Sahel - 1980-1984. *Remote Sens. Environ.* 1985, *17*, 233–249.

25. Cabrera-Bosquet, L.; Molero, G.; Stellacci, A. M.; Bort, J.; Nogués, S.; Araus, J. L. NDVI as a potential tool for predicting biomass, plant nitrogen content and growth in wheat genotypes subjected to different water and nitrogen conditions. *Cereal Res. Commun.* 2011, *39*, 147–159.

26. Christianson, D.; Creel, S. Fecal chlorophyll describes the link between primary production and consumption in a terrestrial herbivore. *Ecol. Appl.* 2009, *19*, 1323–1335.

27. Jones, C. L.; Weckler, P. R.; Maness, N. O.; Jayasekara, R.; Stone, M. L.; Chrz, D. Remote Sensing to Estimate Chlorophyll Concentration in Spinach Using Multi-spectral Plant Reflectance. *Am. Soc. Agric. Biol. Eng.* 2007, *50*, 2267–2273.

28. Paruelo, J. M.; Epstein, H. E.; Lauenroth, W. K.; Burke, I. C. ANPP estimates from NDVI for the central grassland region of the United States. *Ecology* 1997, *78*, 953–958.

29. Seaquist, J. W.; Olsson, L.; Ardö, J. A remote sensing-based primary production model for grassland biomes. *Ecol. Modell.* 2003, *169*, 131–155.

30. Tucker, C. J.; Sellers, P. J. Satellite remote sensing of primary production. *Int. J. Remote Sens.* 1986, *7*, 1395–1416.

31. Zhang, X.; Friedl, M. A.; Schaaf, C. B.; Strahler, A. H.; Hodges, J. C. F.; Gao, F.; Reed, B. C.; Huete, A. Monitoring vegetation phenology using MODIS. *Remote Sens. Environ.* 2003, *84*, 471–475.

32. Reed, B. C.; Schwartz, M. D.; Xiao, X. Remote sensing phenology. In *Phenology of Ecosystem Processes*; 2009; pp. 231–246.

33. Doiron, M.; Legagneux, P.; Gauthier, G.; Lévesque, E. Broad-scale satellite Normalized Difference Vegetation Index data predict plant biomass and peak date of nitrogen concentration in Arctic tundra vegetation. *Appl. Veg. Sci.* 2013, *16*, 343–351.

34. Tucker, C. J. Asymptotic nature of grass canopy spectral reflectance. *Appl. Opt.* 1977, *16*, 1151–6.

35. Maynard, C.; Lawrence, R.; Nielsen, G.; Decker, G. Modeling Vegetation Amount Using Bandwise Regression and Ecological Site Descriptions as an Alternative to Vegetation Indices. *GIScience Remote Sens.* 2007, *44*, 68–81.

36. Santin-Janin, H.; Garel, M.; Chapuis, J. L.; Pontier, D. Assessing the performance of NDVI as a proxy for plant biomass using non-linear models: A case study on the kerguelen archipelago. *Polar Biol.* 2009, *32*, 861–871.

37. Houston, D. *The Northern Yellowstone Elk:Ecology and Management*; 1st ed.; Collier Macmillan, 1982.

38. Thoma, D. P.; Bailey, D. W.; Long, D. S.; Nielsen, G. A.; Henry, M. P.; Breneman, M. C.; Montagne, C. Short-term monitoring of rangeland forage conditions with AVHRR imagery. *J. Range Manag.* 2002, *55*, 383–389.

39. Cook, J. .; Johnson, B. .; Cook, R. .; Riggs, R. .; Delcurto, T.; Bryant, L. .; Irwin, L. . Effects of summer-autumn nutrition and parturition date on reproduction and survival of elk. *Wildl. Monogr.* 2004, *155*, 1–61.

40. Levin, S. Population dynamic models in heterogeneous environments. *Annu. Rev. Ecol. Syst.* 1976, *7*, 287–310.

41. White, R. G. Foraging Patterns and Their Multiplier Effects on Productivity of Northern Ungulates. *Oikos* 1983, *40*, 377–384.

42. Chapin, F. S.; Matson, P. A.; Mooney, H. A. *Principles of Terrestrial Ecosystem Ecology*; 2002; Vol. 21.

43. Hansen, A. J.; Rotella, J. J.; Kraska, M. P. V; Brown, D. Spatial patterns of primary productivity in the Greater Yellowstone Ecosystem. *Landsc. Ecol.* 2000, *15*, 505–522.

44. Hebblewhite, M.; Merrill, E. H. Trade-offs between predation risk and forage differ between migrant strategies in a migratory ungulate. *Ecology* 2009, *90*, 3445–3454.

45. Berger, J. The last mile: How to sustain long-distance migration in mammals. *Conserv. Biol.* 2004, *18*, 320–331.

46. Mysterud, A.; Langvatn, R.; Yoccoz, N. G.; Stenseth, N. C. Plant phenology, migration and geographical variation in body weight of a large herbivore: The effect of a variable topography. *J. Anim. Ecol.* 2001, *70*, 915–923.

47. Brazda, A. R. Elk migration patterns, and some of the factors affecting movements in the Gallatin River drainage, Montana. *J. Wildl. Manage.* 1953, *17*, 9–23.

48. Frank, D. A.; Depriest, T.; Mclauchlan, K.; Risch, A. C. Topographic and ungulate regulation of soil C turnover in a temperate grassland ecosystem. *Glob. Chang. Biol.* 2011, *17*, 495–504.

49. Romme, W. H.; Boyce, M. S.; Gresswell, R.; Merrill, E. H.; Minshall, G. W.; Whitlock, C.; Turner, M. G. Twenty Years After the 1988 Yellowstone Fires: Lessons About Disturbance and Ecosystems. *Ecosystems* 2011, *14*, 1196–1215.

50. Haggerty, J. H.; Travis, W. R. Out of administrative control: Absentee owners, resident elk and the shifting nature of wildlife management in southwestern Montana. *Geoforum* 2006, *37*, 816–830.

51. Frank, D. A.; McNaughton, S. J. The ecology of plants, large mammalian herbivores, and drought in Yellowstone National Park. *Ecology* 1992, *73*, 2043–2058.

52. Post, E.; Stenseth, N. C. Climatic variability, plant phenology, and northern ungulates. *Ecology* 1999, *80*, 1322–1339.

53. Burcham, M.; Edge, W. D.; Marcum, C. Les Elk use of private land refuges. *Wildl. Soc. Bull.* 1999, *27*, 833–839.

54. Parmenter, A. W.; Hansen, A.; Kennedy, R. E.; Cohen, W.; Langner, U.; Lawrence, R.; Maxwell, B.; Gallant, A.; Aspinall, R. Land use and land cover change in the Greater Yellowstone Ecosystem: 1975-1995. *Ecol. Appl.* 2003, *13*, 687–703.

55. Hebblewhite, M.; Merrill, E. H.; Morgantini, L. E.; White, C. a.; Allen, J. R.; Bruns, E.; Thurston, L.; Hurd, T. E. Is the Migratory Behavior of Montane Elk Herds in Peril? The Case of Alberta's Ya Ha Tinda Elk Herd. *Wildl. Soc. Bull.* 2006, *34*, 1280–1294.

56. Wilmers, C. C.; Levi, T. Do irrigation and predator control reduce the productivity of migratory ungulate herds? *Ecology* 2013, *94*, 1264–1270.

57. Houston, D. B. Elk as winter-spring food for carnivores in Northern Yellowstone National Park. *J. Appl. Ecol.* 1978, *15*, 653–661.

58. Oliff, T.; Renkin, R.; McClure, C.; Miller, P.; Price, D.; Reinhart, D.; Whipple, J. Managing a complex exotic vegetation program in Yellowstone National Park. *West. North Am. Nat.* 2001, *61*, 347–358.

59. Aho, K.; Bala, J. Vascular Alpine Flora of Mount Washburn, Yellowstone National park, USA. *Madrono* 2012, *59*, 2–13.

60. Homer, C.; Fry, J.; Barnes, C. The National Land Cover Database. *US Geol. Surv. Fact Sheet* 2012, 1–4.

61. Montgomery, R. A.; Roloff, G. J.; Millspaugh, J. J. Variation in elk response to roads by season, sex, and road type. *J. Wildl. Manage.* 2013, *77*, 313–325.

62. Kowalenko, C. G. Assessment of Leco CNS-2000 analyzer for simultaneously measuring total carbon, nitrogen, and sulphur in soil. *Commun. Soil Sci. Plant Anal.* 2001, *32*, 2065–2078.

63. Webster, A. J. F. Nitrogen and energy nutrition of ruminants. *Br. Vet. J.* 1987, *143*, 285–286.

64. Zuur, A. F.; Ieno, E. N.; Walker, N. J.; Saveliev, A. A.; Smith, G. M.; Ebooks Corporation. *Mixed Effects Models and Extensions in Ecology with R*; 2009.

65. Box, G. E. P.; Jenkins, G. M. *Time Series Analysis: Forecasting and Control*; 1994; Vol. Third.

66. Hu, S. Akaike information criterion. *Cent. Res. Sci. Comput.* 2007.

67. Nakagawa, S.; Schielzeth, H. A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* 2013, *4*, 133–142.

68. Frank, D. A.; David Evans, R. Effects of native grazers on grassland N cycling in Yellowstone National Park. *Ecology* 1997, *78*, 2238–2248.

69. Walker, M. D.; Ingersoll, R. C.; Webber, P. J. Effects of interannual climate variation on phenology and growth of two alpine forbs. *Ecology* 1995, *76*, 1067–1083.

70. Baker, D. L.; Hobbs, N. T. Composition and quality of elk summer diets in Colorado. *J. Wildl. Manage.* 1982, *46*, 694–703.

71. Doiron, M.; Gauthier, G.; Levesque, E. Effects of experimental warming on nitrogen concentration and biomass of forage plants for an arctic herbivore. *J. Ecol.* 2014, *102*, 508–517.

72. Tolvanen, A.; Henry, G. H. R. Responses of carbon and nitrogen concentrations in high arctic plants to experimental warming. *Can. J. Bot.* 2001, *79*, 711–718.

73. Bowman, W. D.; Theodose, T. A.; Schardt, J. C.; Conant, R. T. Constraints of nutrient availability on primary production in two alpine tundra communities. *Ecology* 1993, *74*, 2085–2097.

74. Blumthaler, M.; Ambach, W.; Ellinger, R. Increase in solar UV radiation with altitude. *J. Photochem. Photobiol. B Biol.* 1997, *39*, 130–134.

75. Brooks, P. D.; Williams, M. W. Snowpack controls on nitrogen cycling and export in seasonally snow-covered catchments. *Hydrol. Process.* 1999, *13*, 2177–2190.

76. Baptist, F.; Yoccoz, N. G.; Choler, P. Direct and indirect control by snow cover over decomposition in alpine tundra along a snowmelt gradient. *Plant Soil* 2010, *328*, 397–410.

77. Borner, A. P.; Kielland, K.; Walker, M. D. Effects of Simulated Climate Change on Plant Phenology and Nitrogen Mineralization in Alaskan Arctic Tundra. *Arctic, Antarct. Alp. Res.* 2008, *40*, 27–38.

78. Kudo, G.; Nordenhall, U.; Molau, U. Effects of snowmelt timing on leaf traits, leaf production, and shoot growth of alpine plants: Comparisons along a snowmelt gradient in northern Sweden. *ECOSCIENCE* 1999, *6*, 439–450.

79. Zha, Y.; Gao, J.; Zhang, Y. Grassland productivity in an alpine environment in response to climate change. *Area* 2005, *37*, 332–340.

80. Alldredge, M. W.; Peek, J. M.; Wall, W. a Nutritional quality of forages used by elk in northern Idaho. *J. Range Manag.* 2002, *55*, 253–259.

81. Inouye, D. W. Effects of climate change on phenology, frost damage, and floral abundance of montane wildflowers. *Ecology* 2008, *89*, 353–362.

82. Baker, D. L.; Hobbs, N. T. Composition and quality of elk (Cervus elaphus nelsoni) summer diets in Colorado, USA. *J. Wildl. Manag.* 1982, *46*, 694–703.

83. Bischof, R.; Loe, L. E.; Meisingset, E. L.; Zimmermann, B.; Van Moorter, B.; Mysterud, A. A Migratory Northern Ungulate in the Pursuit of Spring: Jumping or Surfing the Green Wave? *Am. Nat.* 2012, *180*, 407–424.

84. Creel, S.; Winnie, J.; Maxwell, B.; Hamlin, K.; Creel, M. Elk alter habitat selection as an antipredator response to wolves. *Ecology* 2005, *86*, 3387–3397.

85. Christianson, D.; Klaver, R. W.; Middleton, A.; Kauffman, M. Confounded winter and spring phenoclimatology on large herbivore ranges. *Landsc. Ecol.* 2013, *28*, 427–437.

86. Proffitt, K. M.; Grigg, J. L.; Garrott, R. a.; Hamlin, K. L.; Cunningham, J.; Gude, J. a.; Jourdonnais, C. Changes in Elk Resource Selection and Distributions Associated With a Late-Season Elk Hunt. *J. Wildl. Manage.* 2010, *74*, 210–218.

87. Kerr, J. T.; Ostrovsky, M. From space to species: ecological applications for remote sensing. *Trends Ecol. Evol.* 2003, *18*, 299–305.

88. Parmesan, C.; Parmesan, C.; Yohe, G.; Yohe, G. A globally coherent fingerprint of climate change impacts across natural systems. *Nature* 2003, *421*, 37–42.

89. Kawamura, K.; Akiyama, T.; Yokota, H.; Tsutsumi, M.; Yasuda, T.; Watanabe, O.; Wang, S. Comparing MODIS vegetation indices with AVHRR NDVI for monitoring the forage quantity and quality in Inner. *Grassl. Sci.* 2005, *51*, 33–40.

90. Weier, J.; Herring, D. Measuring Vegetation (NDVI & EVI) http://earthobservatory.nasa.gov/Features/MeasuringVegetation/measuring_vegetation_1.php.

91. Ryan, S. J.; Knechtel, C. U.; Getz, W. M. Range and habitat selection of African buffalo in South Africa. *J. Wildl. Manage.* 2006, *70*, 764–776.

92. Gao, X.; Huete, A. R.; Ni, W.; Miura, T. Optical-biophysical relationships of vegetation spectra without background contamination. *Remote Sens. Environ.* 2000, *74*, 609–620.

93. Huete, A. R.; Jackson, R. D.; Post, D. F. Spectral response of a plant canopy with different soil backgrounds. *Remote Sens. Environ.* 1985, *17*, 37–53.

94. Sesnie, S. E.; Dickson, B. G.; Rosenstock, S. S.; Rundall, J. M. A comparison of Landsat TM and MODIS vegetation indices for estimating forage phenology in desert bighorn sheep (Ovis canadensis nelsoni) habitat in the Sonoran Desert, USA. *Int. J. Remote Sens.* 2011, *33*, 276–286.

95. Matsushita, B.; Yang, W.; Chen, J.; Onda, Y.; Qiu, G. Sensitivity of the Enhanced Vegetation Index (EVI) and Normalized Difference Vegetation Index (NDVI) to Topographic Effects: A Case Study in High-density Cypress Forest. *Sensors* 2007, *7*, 2636–2651.

96. Shen, M.; Chen, J.; Zhu, X.; Tang, Y.; Chen, X. Do flowers affect biomass estimate accuracy from NDVI and EVI? *Int. J. Remote Sens.* 2010, *31*, 2139–2149.

97. Li, Z.; Li, X.; Wei, D.; Xu, X.; Wang, H. An assessment of correlation on MODIS-NDVI and EVI with natural vegetation coverage in Northern Hebei Province, China. *Procedia Environ. Sci.* 2010, *2*, 964–969.

98. Justice, C. O.; Townshend, J. R. G.; Vermote, E. F.; Masuoka, E.; Wolfe, R. E.; Saleous, N.; Roy, D. P.; Morisette, J. T. An overview of MODIS Land data processing and product status. *Remote Sens. Environ.* 2002, *83*, 3–15.

99. Tanre, D.; Holben, B. N.; Kaufman, Y. J. Atmospheric correction algorithm for NOAA-AVHRR products: Theory and application. *IEEE Trans. Geosci. Remote Sens.* 1992, *30*, 231–248.

100. Tucker, C. J. A critical review of remote sensing and other methods for non-destructive estimation of standing crop biomass. *Grass Forage Sci.* 1980, *35*, 177–182.

101. Tittebrand, A.; Spank, U.; Bernhofer, C. H. Comparison of satellite- and ground-based NDVI above different land-use types. *Theor. Appl. Climatol.* 2009, *98*, 171–186.

102. Porter, T. F.; Chen, C.; Long, J. A.; Lawrence, R. L.; Sowell, B. F. Estimating biomass on CRP pastureland: A comparison of remote sensing techniques. *Biomass and Bioenergy* 2014, *66*, 268–274.

103. Guerschman, J. P.; Paruelo, J. M.; Burke, I. C. Land use impacts on the normalized difference vegetation index in temperate Argentina. *Ecol. Appl.* 2003, *13*, 616–628.

104. Garonna, I.; Fazey, I.; Brown, M. E.; Pettorelli, N. Rapid primary productivity changes in one of the last coastal rainforests: the case of Kahua, Solomon Islands. *Environ. Conserv.* 2009, *36*, 253–260.

105. Sims, D. A.; Rahman, A. F.; Cordova, V. D.; El-Masri, B. Z.; Baldocchi, D. D.; Flanagan, L. B.; Goldstein, A. H.; Hollinger, D. Y.; Misson, L.; Monson, R. K.; Oechel, W. C.; Schmid, H. P.; Wofsy, S. C.; Xu, L. On the use of MODIS EVI to assess gross primary productivity of North American ecosystems. *J. Geophys. Res. Biogeosciences* 2006, *111*.

106. Liu, H. Q.; Huete, A. A feedback based modification of the NDVI to minimize canopy background and atmospheric noise. *IEEE Trans. Geosci. Remote Sens.* 1995, *33*, 457–465.

107. White, M. A.; de Beurs, K. M.; Didan, K.; Inouye, D. W.; Richardson, A. D.; Jensen, O. P.; O'Keefe, J.; Zhang, G.; Nemani, R. R.; van Leeuwen, W. J. D.; Brown, J. F.; de Wit, A.; Schaepman, M.; Lin, X.; Dettinger, M.; Bailey, A. S.; Kimball, J.; Schwartz, M. D.; Baldocchi, D. D.; Lee, J. T.; Lauenroth, W. K. Intercomparison, interpretation, and assessment of spring phenology in North America estimated from remote sensing for 1982-2006. *Glob. Chang. Biol.* 2009, *15*, 2335–2359.

108. Lawrence, R. L.; Ripple, W. J. Comparisons among vegetation indices and bandwise regression in a highly disturbed, heterogeneous landscape: Mount St. Helens, Washington. *Remote Sens. Environ.* 1998, *64*, 91–102.

109. Ripple, W. J. Spectral reflectance relationships to leaf water stress. *Photogramm. Eng. Remote Sensing* 1986, *52*, 1669–1675.

APPENDICES

APPENDIX A

DESCRIPTION OF THE MODELS COMPARED TO IDENTIFY THE TOP MODELS OF FORAGE BIOMASS AND QUALITY

APPENDIX A. Description of the Models Compared to Identify the Top Models of Forage Biomass and Quality.

Model Description	**Variable Combinations[1]**
Date only	~Date+random(plot)
SOS/land use only	~SOS/land use+random(plot)
Year only	~Year+random(plot)
Date and SOS/land use	~Date+SOS/land use+random(plot)
SOS/land use class and Year	~SOS/land use+Year+random(plot)
Date and Year	~Date+Year+random(plot))
Date and SOS/land use interaction	~Date*SOS/land use+random(plot)
Date and SOS/land use interaction and Year	~Date*SOS/land use+Year+random(plot)
Models 1-8 with quadratic Date	“ ”+$Date^2$
Models 1-8 with cubic Date	“ ”+$Date^3$
Models1-8 with basis spline function for Date	“ ”+bs(Date)
All models with variance structure	“ ”+varIdent(SOS/land use)
All models with temporal autocorrelation	“ ”+corAR1(Date)
All models with spatial autocorrelation	“ ”+corSym(plot)
All models with variance structure and temporal autocorrelation	“ ”+varIdent(SOS/land use)+corAR1(Date)
All models with variance structure and spatial autocorrelation	“ ”+varIdent(SOS/land use)+corSym(site)

[1]*Models included start of season class (SOS), land use class, Date (Julian day), and Year (2013 & 2014), variance structures (varIdent), temporal autocorrelation structures (corAR1), and spatial autocorrelation structures (corSym). Basis spline*

APPENDIX B

DESCRIPTION OF THE TOP THREE MODELS OF FORAGE BIOMASS AND QUALITY

APPENDIX B. Description of the Top Three Models of Forage Biomass and Quality.

	K	AIC	ΔAIC	w_i
Start of Season classes				
Biomass~bs(Date)*SOS+random(plot)+varIdent(SOS)	22	1619.8	0	0.45
Biomass~Date^3*SOS+random(plot)+varIdent(SOS)	16	1622.2	2.39	0.14
Biomass~bs(Date)*SOS+random(plot)+varIdent(SOS)+corAR1(Date)	23	1622.4	2.58	0.12
Crude protein~Date*SOS+random(plot)+varIdent(SOS)	10	895.9	0	0.29
Crude protein~Date*SOS+year+random(plot)+varIdent(SOS)	11	896.5	0.6	0.22
Crude protein~Date*SOS+random(plot)+varIdent(SOS)+corAR1(Date)	11	898.2	2.26	0.10
IVDMD~Date+SOS+random(plot)+varIdent(SOS)	9	1300.3	0	0.33
IVDMD~bs(Date)+SOS+year+random(plot)+varIdent(SOS)	13	1302.2	1.91	0.13
IVDMD~Date^2+SOS+Year+random(plot)+varIdent(SOS)	10	1302.2	1.92	0.13
Land Use classes				
Biomass~Date^3*land use+Year+random(plot)+varIdent(land	19	1804.6	0	0.74
Biomass~Date^3*land use+Year+random(plot)+varIdent(land use)	17	1807.9	3.24	0.15
Biomass~Date^3*land use+Year+random(plot)+varIdent(land use)+corAR1(Date)	18	1809.8	5.23	0.05
Crude protein~Date*land use+Year+random(plot)+varIdent (land use)	11	968.6	0	0.28
Crude protein~Date*land use+random(plot)+varIdent(land use)+corAR1(Date)	12	970.3	1.66	0.12
Crude protein~Date*land use+random(plot)+varIdent(land use)	10	970.7	2.03	0.10
IVDMD~Date+land use+random(plot)+varIdent(land use)	9	1376.9	0	0.43
IVDMD~Date^2+land use+Year+random(plot)+varIdent(land use)	10	1379.1	2.19	0.14
IVDMD~Date+land use+Year+random(plot)+varIdent(land use)+corAR1(Date)	10	1379.1	2.21	0.14
Start of Season and Land use classes				
Biomass~Date^3*class+Year+random(plot)+varIdent(class)	27	2902.3	0	0.35
Biomass~bs(Date)*class+Year+random(plot)+varIdent(class)	36	2904.1	1.85	0.14
Biomass~bs(Date)*class+Year+random(plot)+varIdent(class)	38	2904.4	2.09	0.12
Crude protein~Date*class+Year+random(plot)+varIdent(class)	17	1567.4	0	0.57
Crude protein~Date*class+Year+random(plot)+varIdent(class)+corAR1(Date)	18	1568.9	1.56	0.26
Crude protein~Date*class+random(plot)+varIdent(class)+corSym(plot)	19	1571.9	4.51	0.06
IVDMD~Date+class+Year+random(plot)+varIdent(class)	13	2180.8	0	0.33
IVDMD~Date^2+class+Year+random(plot)+varIdent(class)	14	2181.8	0.99	0.21
IVDMD~bs(Date)+class+Year+random(plot)+varIdent(class)	17	2182.9	2.1	0.12

**Statistics include the number of parameters (K), corrected AIC (AIC_c), delta AIC (ΔAIC), and Akaike weights (w_i). All basis spline functions had df=5.*

APPENDIX C

DESCRIPTION OF THE TOP MODELS OF FORAGE BIOMASS, FORAGE QUALITY, AND THE ABUNDANCE OF HIGH QUALITY FORAGE

APPENDIX C. Description of the Top Models of Forage Biomass, Forage Quality, and the Abundance of High Quality Forage.

Top models in all SOS and land use classes							
Biomass (g/m^2)	2902.3	0.93	$Date^3$	0.08	3,280	32.14	<0.001
			class	0.55	4,280	29.72	<0.001
			Year	0.01	1,280	5.45	0.02
			$Date^3$*class	0.07	12,280	6.76	<0.001
Crude protein (%)	1567.4	0.75	Date	0.44	1,290	473.40	<0.001
			class	0.11	4,290	9.91	<0.001
			Year	0.01	1,290	8.75	0.003
			Date*class	0.04	4,290	5.78	0.001
IVDMD (%)	2180.8	0.44	Date	0.19	1,294	123.21	<0.001
			class	0.22	4,294	29.04	<0.001
			Year	0.03	1,294	16.62	<0.001
Top models of abundance of low and high quality forage for elk							
Biomass	2948.09	0.89	FQ-CP	0.04	1,285	8.78	0.003
			class	0.54	4,285	26.94	<0.001
			bs(Date)	0.08	5,285	16.89	<0.001
			Year	0.00	1,285	5.27	0.02
			FQ-CP*class	0.00	4,284	1.86	0.12
Biomass	2943.81	0.91	FQ-IVDMD	0.03	1,289	0.02	0.89
			class	0.54	4,289	28.26	<0.001
			bs(Date)	0.08	5,289	18.79	<0.001
			Year	0.00	1,289	3.55	0.04

[1]*Models included start of season and land use class (class), Date (Julian day), and Year (2013 & 2014). Basis spline functions had df=5.*

APPENDIX D

STATISTICS FROM THE TOP MODELS OF THE ABUNDANCE OF FORAGE OF HIGH AND LOW QUALITY FOR ELK

APPENDIX D. Statistics from the Top Models of the Abundance of Forage of High and Low Quality for Elk.

Start of season classes	K	AIC_c	ΔAIC_c	w_i
Biomass~FQ-CP+SOS+bs(Date)+varIdent(SOS)	13	1645.5	0	0.33
Biomass~FQ-CP+SOS+bs(Date)+Year+varIdent(SOS)	14	1646.1	0.59	0.25
Biomass~FQ-CP+SOS+bs(Date)+varIdent(SOS)+corAR1(Date)	14	1647.8	2.3	0.11
Biomass~FQ-IVDMD+SOS+bs(Date)+varIdent(SOS)	13	1644.8	0	0.28
Biomass~FQ-IVDMD+SOS+bs(Date)+Year+varIdent(SOS)	14	1645.8	0.98	0.17
Biomass~FQ-IVDMD+SOS+bs(Date)+varIdent(SOS)+corAR1(Date)	14	1646.9	2.2	0.09
Land use classes				
Biomass~FQ-CP*LU+$Date^3$+Year+varIdent(LU)	14	1821.7	0	0.27
Biomass~FQ-CP*LU+bs(Date)+Year+varIdent(LU)	16	1822.9	1.13	0.15
Biomass~FQ-CP*LU+$Date^2$+Year+varIdent(LU)	15	1823.5	1.73	0.11
Biomass~FQ-IVDMD+LU+$Date^3$+Year+varIdent(LU)	12	1824.7	0	0.13
Biomass~FQ-IVDMD*LU+$Date^3$+Year+varIdent(LU)	14	1824.7	0.05	0.13
Biomass~FQ-IVDMD*LU+bs(Date)+Year+varIdent(LU)	16	1825.1	0.46	0.11
All start of season and land use classes				
Biomass~FQ-CP*SOS/LU+FQ-CP*bs(Date)+Year+varIdent(SOS/LU)	27	2943.2	0	0.23
Biomass~SOS/LU+FQ-CP*bs(Date)+Year+varIdent(SOS/LU)	23	2943.6	0.33	0.19
Biomass~SOS/LU+FQ-CP*bs(Date)+Year+varIdent(SOS/LU)	24	2944.6	1.32	0.12
Biomass~FQ-IVDMD+SOS/LU+Date+varIdent(SOS/LU)	18	2943.8	0	0.18
Biomass~FQ-IVDMD+SOS/LU+Date+varIdent(SOS/LU)+corAR1(Date)	19	2943.9	0.06	0.17
Biomass~FQ-IVDMD+SOS/LU+varIdent(SOS/LU)	17	2944.8	0.98	0.11

** Statistics include the number of parameters (K), the corrected AIC (AIC_c), the delta AIC (ΔAIC), and the Akaike weights. Basis spline functions had df=5.*

APPENDIX E

TOP MODELS FROM THE POST-HOC ANALYSIS EXAMINING THE ROLE OF FORB COVER IN MODELS OF FORAGE BIOMASS AND QUALITY

APPENDIX E. Top Models from the Post-Hoc Analysis Examining the Role of Forb Cover in Models of Forage Biomass and Quality.

Model	**K**	**AIC_c**	**ΔAIC_c**	**w_i**
Biomass~bs(Date)*SOS+varIdent(SOS)+random(plot)	22	1619.87	0	0.37
Crude protein~Date*SOS+varIdent(SOS)+random(plot)	11	893.82	0	0.33
IVDMD~Date+SOS+Year+varIdent(SOS)+random(plot)	12	1299.42	0	0.18

APPENDIX F

ESTIMATED DIFFERENCES IN THE NUMBER OF ELK SCAT PILES BETWEEN START OF SEASON (SOS) AND LAND USE CLASSES

APPENDIX F. Estimated Differences in the Number of Elk Scat Piles Between Start of Season (SOS) and Land Use Classes.

SOS and LU class	Estimate	Lower CI	Upper CI
Late SOS vs. Early SOS	-0.32	-0.69	0.05
Mid SOS vs. Early SOS	-0.37	-0.71	0.02
Irrigated agriculture vs. Early SOS	-0.46	-0.81	0.23
Private grassland vs. Early SOS	-0.51	-0.86	0.14
Mid SOS vs. Late SOS	-0.05	-0.42	0.32
Irrigated agriculture vs. Late SOS	-0.14	-0.51	0.22
Private grassland vs. Late SOS	-0.18	-0.57	0.19
Irrigated agriculture vs. Mid SOS	-0.09	-0.43	0.25
Private grassland vs. Mid SOS	-0.13	-0.49	0.22
Private grassland vs. Irrigated agriculture	-0.04	-0.39	0.31

APPENDIX G

MODELS COMPARED TO SELECT THE TOP MODELS OF BIOMASS, CHLOROPHYLL, CRUDE PROTEIN, AND IVDMD

APPENDIX G. Models Compared to Select the Top NDVI and EVI Models of Biomass, Chlorophyll, Crude Protein, and IVDMD.

Model description	Variable combinations[1]
Linear NDVI/EVI only	NDVI/EVI+random(pixel)
Linear NDVI/EVI with SOS/land use	NDVI/EVI+SOS/land use+random(pixel)
Linear NDVI/EVI with Date	NDVI/EVI+Date+random(pixel)
Linear NDVI/EVI with SOS/land use and Date	NDVI/EVI+SOS/land use+Date+random(pixel)
Linear NDVI/EVI with an interaction between NDVI/EVI and SOS/land use	NDVI/EVI*SOS/land use+random(pixel)
Linear NDVI/EVI with an interaction between NDVI/EVI and Date	NDVI/EVI*Date+random(pixel)
Linear NDVI/EVI with NDVI/EVI*SOS/land use interaction and Date	NDVI/EVI*SOS/land use+Date+random(pixel)
Linear NDVI/EVI with NDVI/EVI*Date interaction and SOS/land use	NDVI/EVI*Date+SOS/land use+random(pixel)
Models 1-8 with quadratic NDVI/EVI effect	$(NDVI/EVI)^2$+“ ”
Models 1-8 with cubic NDVI/EVI effect	$(NDVI/EVI)^3$ +“ ”
Models 1-8 with basis spline NDVI/EVI effect	bs(NDVI/EVI)+“ ”
All previous models with variance structure	“ ”+varIdent(SOS/land use)
All previous models with temporal autocorrelation	“ ”+corAR1(Date)
All previous models with spatial autocorrelation	“ ”+corExp(site)
All previous models with variance structure and temporal autocorrelation	“ ” +varIdent(SOS/land use)+corAR1(Date)
All previous models with variance structure and spatial autocorrelation	“ ”+varIdent(SOS/land use)+corSym(Site)

[1]*Models include NDVI, EVI, start of season (SOS) or land use class, Date (Julian day), variance structures (VarIdent), temporal autocorrelation structures (corAR1), and spatial autocorrelation structures (corSym). Basis spline functions had df=5.*

APPENDIX H

THE TOP NDVI AND EVI MODELS OF BIOMASS, CHLOROPHYLL, CRUDE PROTEIN, AND IVDMD

APPENDIX H. The Top NDVI and EVI Models of Biomass, Chlorophyll, Crude Protein, and IVDMD in the Start of Season (SOS) and Land Use Classes

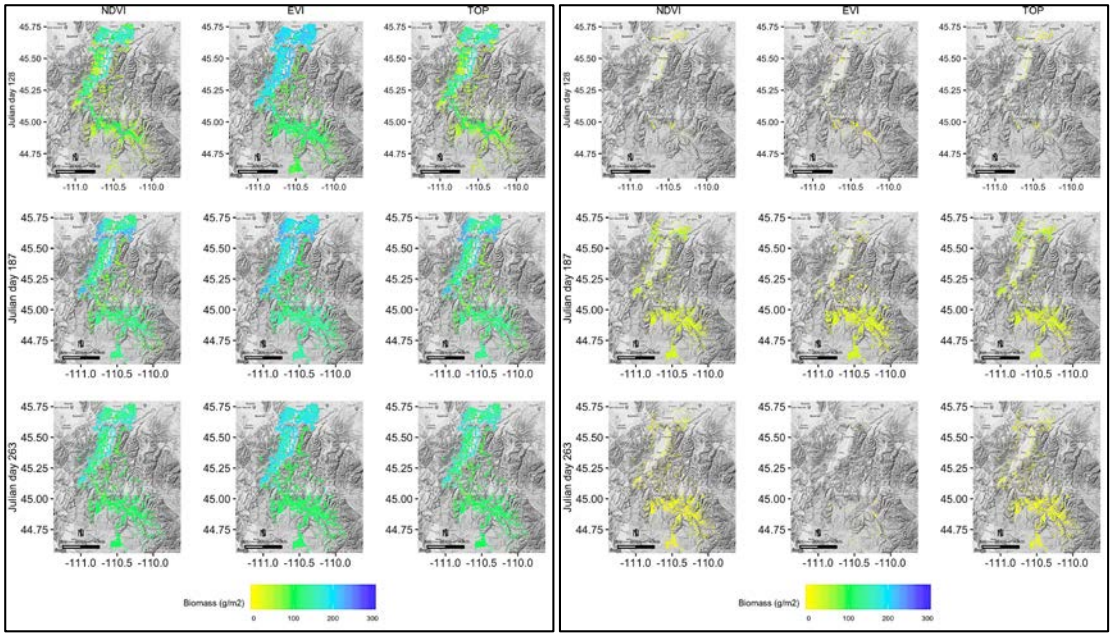
Model	K	AICc	ΔAICc	w_i
Biomass by SOS class				
~bs(NDVI)*SOS+random(pixel)+varIdent(SOS)	22	1662.47	0	0.43
~bs(NDVI)*Date+SOS+random(pixel)+varIdent(SOS)	18	1663.17	0.71	0.30
~bs(NDVI)*SOS+Date+random(pixel)+varIdent(SOS)	23	1665.05	2.59	0.12
Biomass by land use class				
~$NDVI^2$*Date+land use+random(pixel)+varIdent(land use)	12	1826.71	0	0.47
~$NDVI^2$*Date+land use+random(pixel)+varIdent(land use)+corSym(site)	14	1828.77	2.06	0.17
~$NDVI^2$*Date+land use+random(pixel)+varIdent(land use)+corAR1(Date)	13	1828.94	2.23	0.15
Chlorophyll by SOS class				
~NDVI+Date+random(pixel)	5	-54.81	0	0.12
~NDVI+Date+random(pixel)	6	-54.01	0.8	0.08
~NDVI*Date+random(pixel)	6	-53.82	0.98	0.07
Chlorophyll by land use class				
~NDVI+Date+random(pixel)	5	-34.34	0	0.19
~EVI+land use+Date+random(pixel)	7	-32.89	1.45	0.09
~NDVI*Date+random(pixel)	6	-32.63	1.71	0.08
Crude Protein by SOS class				
~bs(EVI)+SOS+Date+random(pixel)+varIdent(SOS)	13	896.9	0	0.25
~EVI^2*Date+SOS+random(pixel)+varIdent(SOS)	12	897.6	0.73	0.17
~EVI^3*Date+SOS+random(pixel)+varIdent(SOS)	14	898.4	1.55	0.11
Crude Protein by land use class				
~bs(EVI)+land use+Date+random(pixel)+varIdent(land use)	13	971.74	0	0.17
~bs(EVI)+land use+Date+random(pixel)+varIdent(land use)+corExp(site)	14	972.38	0.64	0.29
~$NDVI^2$*Date+land use+random(pixel)+varIdent(land use)	10	972.65	0.91	0.10
IVDMD by SOS class				
~NDVI*Date+SOS+random(pixel)+varIdent(SOS)	10	1307.52	0	0.30
~$NDVI^2$+SOS+Date+random(pixel)+varIdent(SOS)	10	1308.31	0.79	0.20
~NDVI*Date+SOS+random(pixel)+varIdent(SOS)+corAR1(Date)	11	1309.76	2.23	0.09
IVDMD by land use class				
~$NDVI^2$+land use+Date+random(pixel)+varIdent(land use)	10	1383.17	0	0.29
~$NDVI^3$+land use+Date+random(pixel)+varIdent(land use)	11	1385.41	2.24	0.09
~$NDVI^2$+land use+Date+random(pixel)+varIdent(land use)+corSym(site)	11	1385.41	2.24	0.09

[1]*Models included start of season (SOS) class, land use class, Date (Julian day), variance structures (varIdent), temporal autocorrelation structures (corAR1), and spatial autocorrelation structures (corSym).*

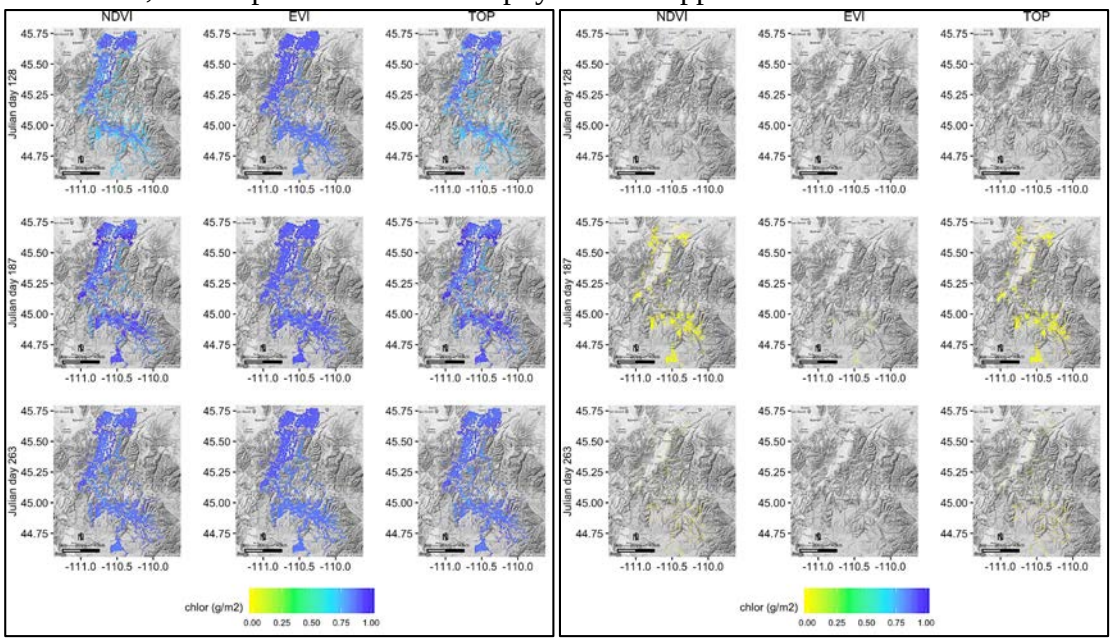
APPENDIX I

THE UPPER AND LOWER CONFIDENCE LIMITS FROM THE MODELS OF FORAGE BIOMASS AND QUALITY

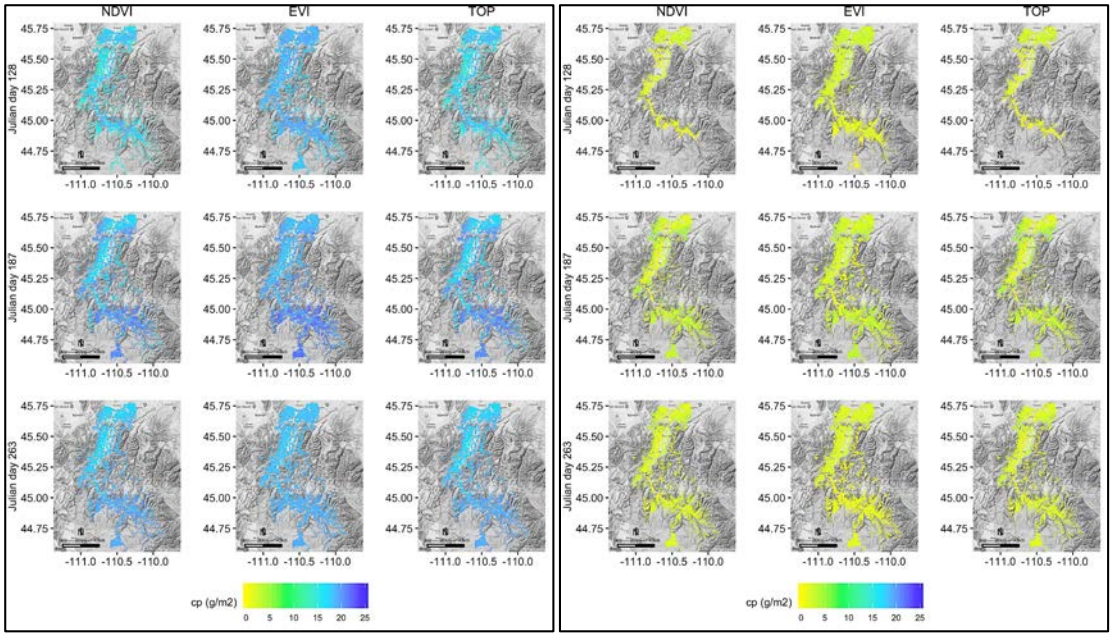
APPENDIX Ia: Upper and Lower Confidence Intervals for the Linear NDVI, Linear EVI, and Top Models of Forage Biomass and Quality in the Upper Yellowstone River Basin.



APPENDIX Ib: The Upper and Lower Confidence Intervals from the Linear NDVI, Linear EVI, and Top Models of Chlorophyll in the Upper Yellowstone River Basin.



APPENDIX Ic: The Upper and Lower Confidence Intervals from the Linear NDVI, Linear EVI, and Top Models of Crude Protein in the Upper Yellowstone River Basin.



APPENDIX Id: The Upper and Lower Confidence Intervals from the Linear NDVI, Linear EVI, and Top Models of IVDMD in the Upper Yellowstone River Basin.