

REMOTE SENSING GRASSLAND PHENOLOGY IN THE GREATER
YELLOWSTONE ECOSYSTEM: BIOPHYSICAL CORRELATES,
LAND USE EFFECTS AND PATCH DYNAMICS

by

Nathan Brian Piekielek

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Dr. Andrew J. Hansen

Approved for the Department of Ecology

Dr. David W. Roberts

Approved for The Graduate School

Dr. Carl A. Fox

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ABSTRACT

Vegetation phenology refers to the seasonal timing of repeat biological events such as bud burst and primary-productivity and their relationship to climate. The spatial location and timing of phenology is relevant to a wide-variety of questions in ecology including the space use and population dynamics of migratory herbivores. Recent technological (remote sensing) and methodological (statistical smoothing algorithms and weighted-regression) advancement now allow for mapping spatial and temporal patterns of vegetation phenology across large spatial extents and at fine-temporal scales. It also allows for examination of vegetation response to climate. An understudied topic investigates how human activity (i.e. land use) modifies broad-scale patterns of phenology from their natural state. Land use effects on phenology is important in the context of parks and protected areas where human activity in surrounding areas can compromise biodiversity conservation goals. With this in mind, we posed the following research questions for a study-area within the Greater Yellowstone Ecosystem: 1) What are the biophysical correlates and likely drivers of landscape-scale grassland phenology under wildland conditions? 2) How do different types of land use modify grassland phenology from its wildland state? And, 3) Do spatial and temporal patterns of green forage patches produced with new tools and datasets display seasonal-dynamics that are consistent with current ecological understanding? To answer these questions we used the Normalized Difference Vegetation Index (NDVI) produced by the Moderate Resolution Imaging Spectroradiometer (MODIS) as input to the TIMESAT algorithm to produce estimates of grassland phenology. Our principle findings are that: 1) Seasonal variation in solar radiation, water availability, evaporative demand and temperature explained much of the variation in the timing of wildland grassland phenology; 2) All land use types extended the length of the growing season and agriculture increased two estimates of productivity; And, 3) New tools are capable of producing nearly-spatially and -temporally continuous maps of the pattern of green forage patches that are consistent with current ecological understanding. Results of the present study suggest that land use intensification in the Greater Yellowstone Ecosystem has the potential to alter landscape-scale ecosystem process with a variety of expected consequences for wildlife conservation and management.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

Vegetation phenology (hereafter “phenology”), refers to the annual timing of plant processes including budburst, flowering, productivity and leaf senescence (Keatley and Hudson 2010). Phenology provides an often powerful link between climate-drivers (i.e. biophysical setting) and biological response across trophic-levels and at different spatial and temporal scales. Knowledge of patterns of phenology has been useful to answer questions across a wide-range of topics in ecology (Pettorelli et al. 2011). Recent technological (remote sensing) and methodological (statistical smoothing algorithms and weighted-regression) advancement now allows mapping of phenology across large spatial extents and at fine temporal scales.

Investigations of how human activity modifies broad-scale patterns of wildland phenology is an underdeveloped research topic (Buyantuyev and Wu 2009) that is relevant to the management and conservation of parks and protected-areas (Tang et al. 2011). Human land use has been intensifying around parks (Gimmi et al. 2011) and this may compromise biodiversity preservation goals (Brashears et al. 2001).

The present dissertation investigates patterns and potential drivers of grassland phenology in the Greater Yellowstone Ecosystem (GYE). Grasslands in the GYE are underrepresented on public lands and have disproportionately been the subject of human development on private lands. Seasonal pulses of grassland productivity are an important

ecosystem process thought to explain (in part) the space use and population dynamics of migratory herbivores that are of high conservation and management concern. Future human modification of grasslands and herbivore space use could have a variety of ecological consequences that would likely present significant management and conservation challenges.

Organization of the Dissertation

After this brief introduction, the dissertation is organized into three chapters each of which represents a stand-alone paper with its own introduction and conclusions (conclusions are incorporated into discussion sections). Chapter 2 develops estimates of land surface phenology metrics for natural grasslands within the Upper Yellowstone River Basin study-area using the latest technology and methods. We hypothesized that at broad spatial scales phenological development of grasslands is controlled by seasonal changes in climate. Therefore, we used spatially-continuous maps of phenology and climate to identify correlates and potential drivers of phenology. Climate correlates were used to build statistical models. In addition to developing an understanding of vegetation-climate relationships, this step was undertaken to make predictions of wildland grassland phenology across the study-area, including for areas presently under human land use.

Predicted wildland grassland phenology was compared to actual phenology observed under present-day land use in Chapter 3. The difference between predicted wildland and present-day phenology was quantified and interpreted as the land use effect. Understanding of climate-drivers of grassland phenology developed in Chapter 3 along

with the magnitude and direction of observed modification to wildland phenology were then used to discuss the likely modes of change (i.e. human activity). The ecological consequences of likely future land use change were also discussed in Chapter 3 within the context of landscape-scale biodiversity management and conservation.

In Chapter 4 methods were presented to map the spatial and temporal dimensions of productive grasslands patches (i.e. forage patches) within the study-area. Patch-dynamics approaches to mapping habitat have historically been focused on natural disturbance and vegetation development and succession over the course of decades to centuries. As such, this chapter suggested a variation on traditional patch-dynamics approaches by highlighting how they are also applicable to the seasonal phenological development of forage patches.

A short conclusion followed the content chapters and outlined future research directions and conclusions.

This dissertation took the most recent remote sensing data and statistical methods and applied them to an intensive study of grassland phenology and land use effects in the GYE. In so doing, it highlighted potential future conservation and management challenges as a result of expected future land use change in this ecosystem.

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CHAPTER 2

BIOPHYSICAL CONTROLS ON LAND SURFACE PHENOLOGY OF
GRASSLANDS IN THE UPPER YELLOWSTONE RIVER BASINAbstract

Spatial and temporal variation in vegetation phenology and productivity is relevant to a wide-variety of questions in ecology. Recent technological and methodological advancements have revolutionized this research field. The study of land surface phenology uses dense time-series of satellite imagery to estimate the timing and magnitude of vegetation response to biophysical setting (i.e. climate, soils etc.) at moderate spatial scales. Estimates can be produced nearly-continuously across space and through time. In combination with other spatially-continuous datasets these data offer unprecedented opportunity to examine the relationship between biophysical setting and vegetation, as well as how this changes across environmental gradients. The objective of the present study was to identify the biophysical correlates and potential drivers of grassland phenology in the Upper Yellowstone River Basin including portions of Yellowstone National Park and surrounding private-lands. This was accomplished by using satellite data and well-established methods to produce land surface phenology results and analyzing these relative to seasonal changes in gridded continuous climate surfaces using regression-tree techniques. Results suggest that seasonal variation in solar radiation serves as the outer-envelope climate-control on phenology. Within this outer-envelope, early-season phenology appears to respond to variation in temperature, while

interactions between water-availability and evaporative demand are important to determining late-season phenology and productivity. Peak greenness and estimates of total annual above-ground productivity appear to be limited by water-availability at lower-elevations and by length of the growing season at higher-elevations. Results also suggest that climate-controls on vegetation phenology and productivity likely change across the study-area whereby snow-dynamics are important at higher-elevations, but not lower-elevations. Land surface phenology data and methods provide powerful tools for both monitoring and investigations of climate change impacts on ecosystems.

Introduction

Vegetation phenology (hereafter “phenology”), refers to the annual timing of plant processes including budburst, flowering, productivity and senescence (Keatley and Hudson 2010). Phenology provides an often powerful link between climate-drivers (i.e. biophysical setting) of ecosystem process and biological response across trophic-levels and at different spatial and temporal scales. Knowledge of patterns of phenology has been useful to answering questions across a wide-range of topics in ecology including: population dynamics and movements of herbivores (Boone et al. 2006; Cebrian et al. 2008; Mueller et al. 2008; Post and Forchhammer 2008; Hammel et al. 2009; Proffitt et al. 2010); spatial patterns of bird and other taxonomic species richness (Wright 1983; Phillips et al. 2008; Nightingale et al. 2008; Waring et al. 2006); fuel accumulation and drying as determinates of wildfire activity (Littell et al. 2009; Westerling 2006; Westerling et al. 2011); detection of forest insect outbreaks and subsequent recovery

(Neigh et al. 2008; DeBeurs and Townsend 2008; Spruce et al. 2011); nutrient cycling (Potter 2001; Risch and Frank 2010); biological response to climate change (Cleland et al. 2007; Myneni et al. 1997; Parmesan and Yohe 2003); and in integrated analyses with the hydrologic cycle (Cayan 2001; Sun et al. 2008). Petorelli et al. (2011) gives a particularly good overview of some of the more surprising ways in which recently developed estimates of phenology have been useful to answering a breadth of questions in the discipline of animal ecology. Recent technological innovation as well as interest in global and climate change studies has reinvigorated the phenology research field (Justice et al. 1998; Schwartz 2003).

Measuring Phenology

Phenology was historically measured at small dispersed plots via clipping and handheld radiometers that offered a high level of confidence in their results, but lacked spatial and temporal coverage (Boelman et al. 2003; Buyantuyev and Wu 2009). Relatively recent technological and methodological breakthroughs now allow for the mapping of phenology across large spatial extents and fine temporal scales. New methods use remotely-sensed data (surface reflectance) and advanced statistical techniques (weighted-regression, higher-order smoothing splines and others). Numerous studies have demonstrated the relationship between spectral reflectance, rates of photosynthesis, and plant biomass and stoichiometry (Huete et al. 1999; Prince and Goward 1996; Reeves et al. 2006; Running et al. 1994; Thoma 2002; Tucker et al. 1985; Thein et al. 2009). These relationships are based on properties of leaf chlorophyll and other pigments involved in photosynthesis that absorb red portions of the electromagnetic spectrum and reflect near-

infrared portions. Transformations of reflectance (the Normalized Difference Vegetation Index, or NDVI), have been used to estimate phenology in what has become known as land surface phenology (LSP) in order to distinguish it from plot-based observations (Moody and Johnson 2001). NDVI is calculated by the following formula using near-infrared and red bands of satellite sensors:

Equation 2.1

$$NDVI = \frac{(NIR - RED)}{(NIR + RED)}$$

Where: NIR = near-infrared reflectance and;
RED = red band reflectance

LSP is measured by dense time-series of satellite images that depict seasonal and interannual changes in NDVI. NDVI observations are often obtained from the National Aeronautics and Space Administration (NASA), Moderate Resolution Imaging Spectroradiometer (MODIS). The MODIS sensor takes observations at different moderate spatial (250-meter or 1-kilometer) and fine temporal (daily at its finest) scales. Formal data products and quality assessments are produced by the MODIS program at 16-day intervals using a maximum compositing (MC) algorithm. MC techniques are based on observations that most sensor interference has a dampening effect on NDVI values (Huete et al. 1999). LSP methods fit smooth annual curves to discrete NDVI observations on a per-pixel basis. From these curves, phenologically significant points in time are identified as LSP metrics, (other techniques have been suggested; see White and Nemani 2006 for an alternative) (Bradley et al. 2007; Jönsson and Eklundh 2002, 2004;

DeBeurs and Henebry 2005; Eklund and Jönsson 2010; Reed 1994; Moody and Johnson 2001; White et al. 2009).

Annual LSP methods typically produce two metrics that estimate the timing of phenological events (start and end of the growing season), and two that estimate the magnitude (peak annual greenness and total annual productivity) of estimates of productivity (this reference to magnitude represents a somewhat expanded use of the term 'phenology' although one that is consistent with the LSP literature). The timing of the start of the growing season (SOS) and end of the growing season (EOS) is estimated as a Julian or Ordinal day of the year (DOY) where January 1st refers to day 1 and days count up consecutively to the last day of the year (365, or 366 in leap years). Peak annual greenness indicates the maximum annual NDVI (MAX) achieved and is generally related to a time during the growing season when biomass is high and growth is rapid. Finally, the integration under the growing season (SOS to EOS) NDVI curve (INDVI) refers to the annual area encompassed by growing season length in days on the x-axis and NDVI on the y-axis (see Figure 2.2 for a graphic of these metrics identified from an annual NDVI time-series from the present study-area). This last measure provides an estimate of total above-ground gross annual primary-productivity (Goward et al. 1985; Reed et al. 1994). NDVI values prior to SOS and following EOS are typically excluded from annual integrations used to generate INDVI because they are thought to represent background levels of surface reflection that have little to do with vegetation activity. Background values vary from observation to observation based on atmospheric interference and from pixel to pixel based on different surface properties. Therefore, background values

represents noise rather than vegetation signal. LSP metrics are generated for each pixel in a scene of interest although spatial-averaging across phenologically similar regions is also sometimes undertaken (White and Nemani 2006). LSP estimates do not correspond to the timing of a phenological event of a single species (i.e. flowering date for example), but rather they capture the aggregate greening, growth (i.e. biomass accumulation) and interception of photosynthetically-active-radiation by vegetation at moderate spatial scales (e.g. typically from about 250-meter resolution up to 8-kilometer resolution depending on the satellite sensor used to capture NDVI data).

Phenology as an Indicator of Vegetation Response to Climate

LSP holds great promise in tracking vegetation response to climate change (Fisher and Mustard 2007). As an integrated measure of multiple individuals and species, LSP methods overcome typical issues of scale and spatial mismatch when relating observations of phenology (usually plot-based) to observations of climate. Spatial mismatches arise when observations of climate (from distant weather stations for example) are only coarsely representative of areas where plot-based observations of phenology are taken. Despite holding great promise, quantifying the relationship between LSP and climate remains an outstanding research objective for many landscapes. This is perhaps in part due to challenges associated with the complex- and spatially-variable relationship between phenology and climate (Penuelas et al. 2004).

In general, three primary requirements for plant growth that relate directly to climate are recognized: solar radiation to drive photosynthesis; temperatures that are

amenable to biochemical reactions involved in photosynthesis; and water as a reactant in photosynthetic reactions (Chapin et al. 2002). In climate terms, these three requirements translate roughly to photoperiod and solar radiation; air and soil temperatures; and precipitation and soil-moisture. A fourth requirement, soil-nutrients, is indirectly related to climate and is also thought to play an important role in determining spatial-variation in plant-productivity (Hansen 2000; Nicholson and Farrar 1994).

Grassland Phenology and Climate in the Greater Yellowstone Ecosystem

In the Northern Rocky Mountains, U.S., grass and shrublands (hereafter referred to collectively as “grasslands”), are an important natural land cover that is underrepresented within protected-areas (Scott et al. 2001) and has disproportionately been the subject of land use change on private-lands (Piekielek and Hansen accepted). Seasonal pulses of grassland productivity in the Greater Yellowstone Ecosystem (GYE) are thought to play an important role in driving large-scale ecosystem process (Frank et al. 2002; White 2010). In this view, investigation of grassland phenology and its relationship to climate in the GYE is of high research interest and is important for conservation planning and management.

One prior research effort has generated LSP metrics for grassland meadows within Central and Northern Yellowstone National Park (YNP) (Thein et al. 2009), while another investigated the relationship between LSP and climate at SNOTEL stations within YNP for a single year (Hudson Dunn and Debeurs 2011). To the author’s knowledge, LSP has not been generated for grasslands on private-lands surrounding

YNP, nor have any prior studies investigated the relationship between grassland LSP and their biophysical correlates at landscape scales. We therefore expand previous work by focusing on a study-area (Figure 2.1) that spans the YNP boundary and identify the following research objectives:

1. Develop LSP (SOS, EOS, MAX and INDVI) metrics for natural grasslands of the Upper Yellowstone River Basin study-area (Figure 2.1).
2. Identify the biophysical correlates and potential drivers of grassland LSP in natural settings.
3. Develop and test regression models of natural grassland LSP that can be used to predict phenology as it might exist in the absence of human-activity for areas now under human land use.

With the above objectives in mind and based on our understanding of climate-vegetation relationships in the study-area, we present the following hypotheses:

Start of Season (SOS)

1. For portions of the study-area where all three requirements of plant growth are met prior to snowmelt, variation in the timing of snowmelt is the primary climate-driver of SOS (Despain 1990; Fagre et al. 2003; Pederson et al. 2011).
 - a. What variation in SOS is not explained by snowmelt can be explained by variation in accumulated growing degree days following snowmelt (Frank and Hofman 1989).

End of Season (EOS)

2. Water-deficit (demand that exceed availability) is primary climate-driver of EOS so that when critical thresholds are crossed, the growing season ends (Jolly et al. 2005; Osonubi and Davies 1980; Tenhunen 1982).

Maximum Annual Greenness (MAX)

3. An interaction between soil-moisture and maximum temperature is the primary predictor of peak greenness (MAX) so that locations that experience optimal temperatures for peak growth at times of year when they still have sufficient soil-moisture, will exhibit the highest MAX values (Jenerette et al. 2010).

Estimated Total Annual Productivity (INDVI)

4. Total annual productivity (INDVI) is explained by water-availability, soil-nutrients and accumulations of temperature (Hansen et al. 2000).

Methods

Study Area

The 7,400 square kilometer study-area (Figure 2.1) encompasses the Upper Yellowstone River Basin, including headwater streams Slough, Soda Butte, Hellroaring and Tower Creeks, which form the Lamar and Gardiner Rivers inside the YNP boundary and eventually the Yellowstone River just north of YNP near the town of Gardiner, MT. Most of the study-area is within the Middle Rockies Ecoregion as defined by Omernik (1987). Within YNP, the study-area includes the high-elevation peaks and middle-elevation valleys of the Yellowstone Plateau. Continuing downstream and north into

Montana, the study-area includes the mostly privately-owned grasslands of the Paradise Valley. The Paradise Valley is a low-elevation floodplain valley (~1,500 meters) surrounded by the high peaks (up to ~3,000 meters) of the Gallatin and Absarorka mountain ranges. The northern-most portion of the study-area includes some of the Northern Great Plains Ecoregion (Omnernik 1987) including areas around the town of Livingston, MT (see Figure 2.1 for location).

Grasslands are interspersed throughout much of the study-area. Low-elevations are dominated by bluebunch wheatgrass (*Pseudoroegneria spicata*), Sandberg's bluegrass (*Poa secunda*) and a variety of nonnative species; middle-elevations by Idaho fescue (*Festuca idahoensis*), wheatgrass (*Elymus* spp.) and species of sagebrush (*Artemisia* spp.); and high-elevation tundra by sheep fescue (*Festuca ovina*), rushes (*Juncus* spp.) and cushion plants typical of alpine areas. Underlying parent materials are primarily andesitic and rhyolitic derived from volcanic activity of the Eocene era along with some sedimentary limestone, sand stone and shales deposited during the Paleozoic era. Intermittent glaciation eroded, mixed and redeposited parent materials so that today's soils vary from glacial outwash and mixed alluvium of often rhyolitic origin in low-elevation floodplains of the Lamar and Yellowstone River valleys, to mixed colluviums and glacial till at toeslope and broad middle-elevation plateaus of Yellowstone National Park and finally, shallow soils of andesitic origin and exposed rock at the highest-elevations. Rhyolite derived soils tend to retain only enough soil moisture for one month of plant growth, while those of andesitic origin can retain moisture to last the whole

growing season at higher elevations. Mesic meadows and sagebrush are associated with andesitic areas and dry grass and shrublands with sedimentary soils (Despain 1990).

Climate of the study-area varies dramatically across steep elevational gradients (Despain 1990; Piekielek and Hansen unpublished; Watson and Newman 2009). The northern and most low-elevation reaches of the study-area are the most mild with average annual temperatures near 8 degrees C, accumulated growing degree days (AGDD) (with 0 degree C base value), of ~3500 AGDD and average maximum annual temperatures above 35 degrees C. The areas of mild temperature also tend to be the driest, receiving approximately 300 millimeters (~12 inches), of precipitation per year on average. Plants in mild areas rely on rain to meet soil-moisture demands as they are typically under continuous snow-cover for only a couple of weeks per year. Climate conditions are most severe at the highest-elevations in the southeastern portion of the study-area in the Absaroka Mountains to the north and east of YNP. In these areas, average annual temperatures are nearly 6 degrees C below zero, average AGDD accumulates to only 750 AGDD and annual maximum temperatures average 24 degrees C. Annual precipitation increases with elevation and southward with areas in the southeastern portion of the study-area receiving up to 1,500 millimeters (~60 inches), per year on average. Most precipitation here comes as snow. The growing season is short at higher-elevations where snow-cover can be continuous and typically lasts at least 250 days per year on average for areas over 2,500 meters.

Developing Land Surface
Phenology for Natural Grasslands

Identifying Grasslands: A map of natural grasslands was created for the study-area at a 1-kilometer resolution using the following data and methods (all spatial resampling steps were matched to the MODIS 1-kilometer grid to be consistent with LSP input data). For areas within YNP, vector-delineated habitat types from Despain (1990) were reclassified as grassland and non-grassland and only 1-kilometer pixels that were completely covered by grassland polygons were identified as grassland pixels. On public-lands outside of YNP, the 30-meter resolution National Land Cover Dataset (NLCD) 2001 (Homer et al. 2004) was reclassified and only 1-kilometer pixels that were completely covered by grass- or shrub-land cover types were identified as grasslands. To identify undeveloped grasslands on private-lands, we downloaded vector-based information on private property parcels from the Montana Cadastral Mapping program during the summer of 2009. Montana cadastral data describes land use by parcel as recorded for property valuation and taxation purposes. Private parcels in grassland settings for which there was no record of current agricultural or residential use were identified as natural grasslands. This was necessary in order to ensure that the full-range of biophysical settings (including privately-owned valley-settings) were represented in the dataset even though it is likely that all grasslands on private-lands have been disturbed by human activity to some degree. Only private grasslands that covered an entire 1-kilometer pixel were used in the analysis. In total we identified 360 1-kilometer natural grassland sites in the study-area.

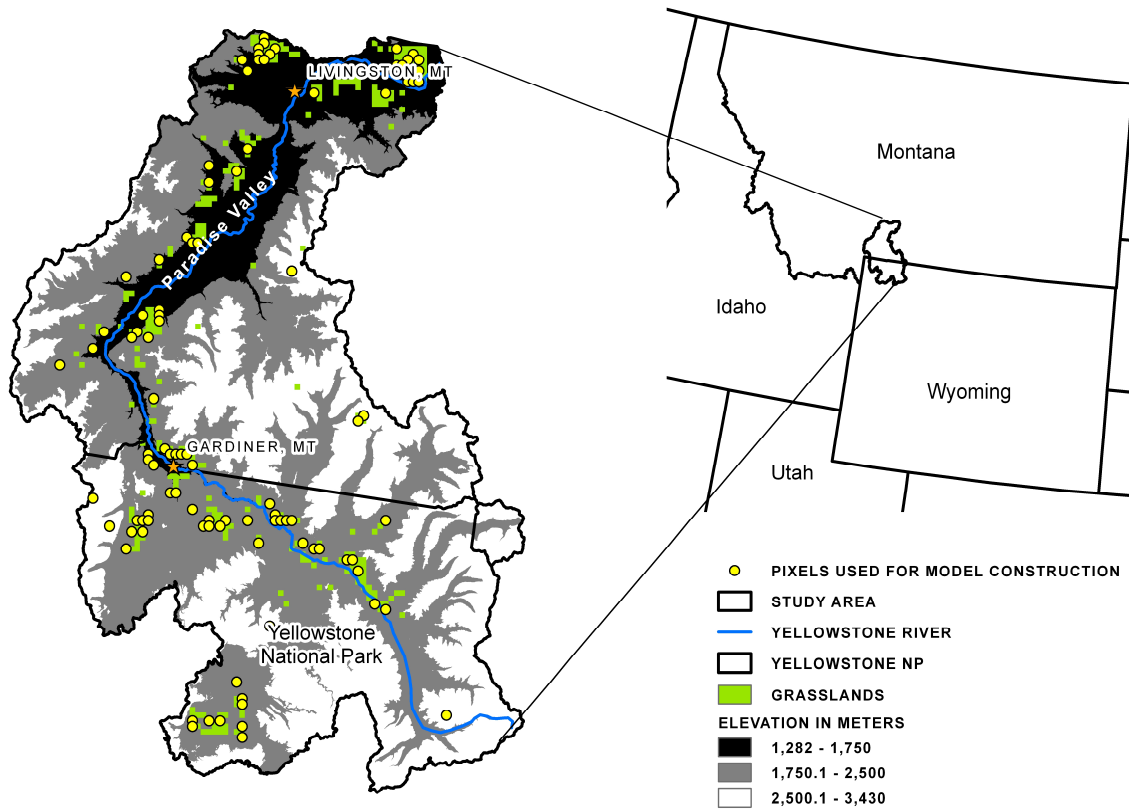


Figure 2.1. Study-area and grassland pixels used for modeling the relationship between land surface phenology (LSP) and their biophysical drivers in the Upper Yellowstone River Basin.

Normalized Difference Vegetation Index Data: NDVI time-series were generated using MODIS MOD13A2 (1-kilometer spatial resolution), data for the time-period January 2000 to December 2010 at 16-day intervals. Data were downloaded from the USGS Land Processes Distributed Active Archive (LPDAAC) in their native Sinusoidal projection and Hierarchical Data Format for Earth Observing Systems. Reliability grids identified NDVI values as being of ‘good’ or ‘marginal’ quality, or that an NDVI observation could not be taken because the target was under ‘snow-cover’ or ‘obscured

by clouds'. NDVI and pixel reliability grids were reprojected to Albers-Equal-Area projection using the MODIS Reprojection Tool (MRT). Further preprocessing included scaling NDVI values to place them on the more commonly used range of -1 to 1. Within this range, negative values are typical of areas under water or partial snow-cover (Huete et al. 1999). Resulting grids portrayed NDVI and estimated data quality for every 16-day period from January 2000 to December 2010.

The generation of LSP metrics is based on a presumed smooth change from annual background values which represent no-growth conditions, to peak greenness and back again in a given year (Jönsson and Eklundh 2002, 2004). Technical challenges inherent to this task include the following: First, atmospheric interference and sparse cloud- or snow-cover can introduce noise into NDVI datasets including an increase in springtime NDVI associated with snow-melt and not with any known change in vegetation activity (Hudson-Dunn and DeBeurs 2011). Second, snow and cloud cover can obscure the target from the sensor and create long periods when no observations are taken (i.e. data gaps). Smoothing algorithms project existing trends into no-data space until another observation is encountered. Over the course of long data gaps, or data gaps at the margins of a time-series, this can lead to smoothed NDVI values that are outside of the valid data range (Eklundh and Jönsson 2010). The aforementioned challenges are overcome by the use of smoothing and gap-filling techniques. These techniques estimate smooth continuous annual NDVI curves, capturing the dominant NDVI signal and minimizing the effects of noise (Jönsson and Eklundh 2002, 2004). With smoothing and gap-filling methods there remain a number of practical decisions that need to be made the

user including: How to handle NDVI observations that are identified as being of ‘marginal-quality’; and whether to smooth towards an assumed background value of ‘0’ or a background value estimated with empirical observations. Portions of the present study-area are under snow-cover for up to 250 days of the year on average. For this reason, and to minimize the confounding effects of snowmelt on annual NDVI curves, we chose to fill snow-cover data gaps with empirical estimates of background values on a pixel-by-pixel basis. The present project estimated background values as the lowest NDVI value observed during the ten-year period of record that was identified as being of high-quality. These background values were used when and where pixels were under snow-cover (observations obscured by cloud-cover remained as data-gaps). With this approach, data gaps are infrequent and of short-duration. Also, springtime increases in NDVI associated with snowmelt are minimized.

Land Surface Phenology (Response Data): Jönsson and Eklundh (2002, 2004), have developed what has become one of the most widely used tools (TIMESAT) with which to generate LSP metrics using satellite observations (e.g. MODIS NDVI). Their method requires six-months of data prior to and following the time-period of interest. Smoothing and gap-filling is accomplished by using local polynomial least-squares functions that are fit to the upper-envelope of observed values (noise in the NDVI time-series is negatively biased; Huete et al. 1999), with an adaptive Savitzky-Golay filter (Eklundh and Jönsson 2010). Another useful aspect of their tool is that it can accommodate the incorporation of quality information associated with NDVI data in a weighted-regression framework where observations of marginal-quality contribute to

final polynomial fits less than do observations of high-quality. The two most common methods to identify the timing of SOS and EOS is to record the Julian DOY when a smoothed NDVI curve crosses a static threshold, or alternatively when it crosses a percentage of the annual amplitude of the present year. Extensive validation and intercomparison tests suggest that estimating SOS as the Julian DOY that NDVI crosses half of its annual amplitude best matches field and multi-scale and – instrument observations (White et al. 2009).

The present study used NDVI data from 2000 – 2010 as input to identify LSP metrics for the study-period 2001 – 2009. Marginal-quality observations contributed half the weight of high-quality observations to final polynomial fits. Background estimates also contributed only half the weight of high-quality observations. Finally, we identified half of the seasonal amplitude as being the start and end of the growing season consistent with the work of others (White et al. 2009).

Final LSP maps depicted SOS, EOS, MAX and INDVI for 360 1-kilometer pixels for the time-period 2001 – 2009 (years 2000 and 2010 contributed the necessary 6 months pre and post time-period of interest).

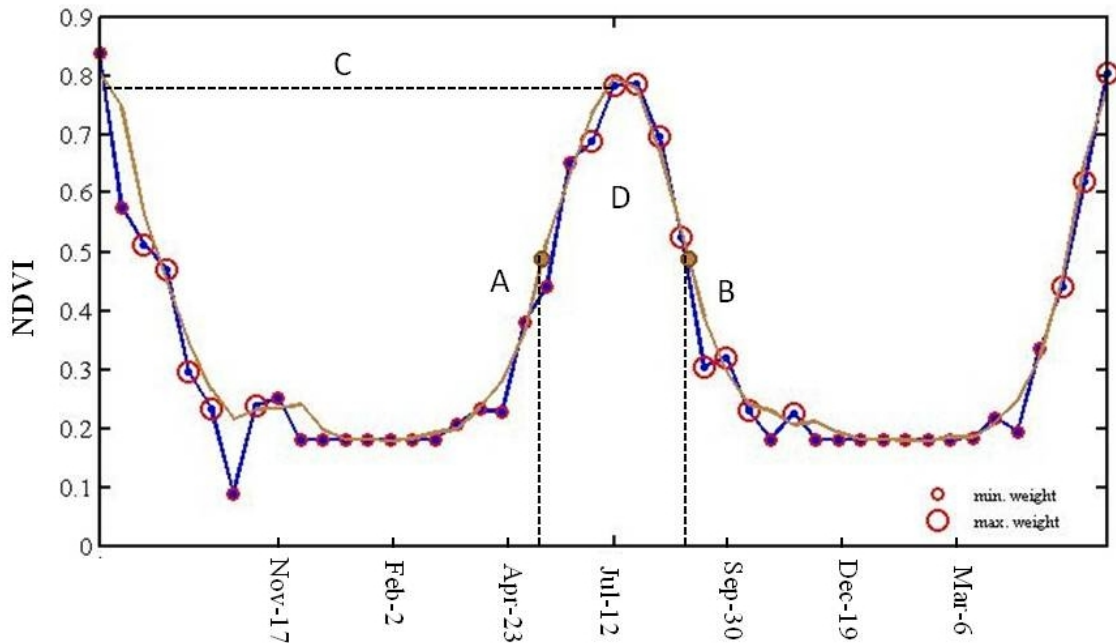


Figure 2.2. NDVI time-series and LSP metrics for an example grassland pixel for year 2005. Blue dots are raw NDVI observations, red-circles indicate the quality (small circles low, large circles high) of observations and hence weight that is assigned for Savitsky-Golay fits in TIMESAT software (Jönsson and Eklundh 2002, 2004). The brown line shows the Savitsky-Golay fitted continuous curve. A) Start of season (SOS) is identified by a brown dot and corresponds to the day of year when NDVI surpasses half of its annual amplitude. B) End of season (EOS) is identified by a brown dot and corresponds to the day of year when NDVI drops below half of its annual amplitude. C) Peak greenness (MAX) refers to the maximum annual NDVI value fit by Savitsky-Golay. D) Total integrated annual NDVI (INDVI) refers to the area under the growing season curve bounded by SOS and EOS on the x-axis and NDVI on the y-axis.

Biophysical Setting (Predictor Data)

Predictor data for modeling exercises are listed in Table 2.1 and discussed in detail in the sections that follow.

Snow Dynamics: The MODIS MOD10 data product maps snow-cover at a 500-meter spatial resolution with daily coverage (Justice et al. 1998). Accuracy assessment of these data suggest very low error rates from less than 1% in Australia (Hall et al. 2002),

to 6% in the Upper Rio Grande river basin of Colorado and New Mexico (Klein and Barnett 2003). There is general agreement that these data map snow-cover with around 93% accuracy in most conditions (Hall and Riggs 2007). Errors of omission are most common when snow depth is less than 4 centimeters (Hall and Riggs 2007).

The present study used daily MODIS MOD10A1 data for the time-period January 1, 2000 to December 31, 2009. Data were downloaded from the LPDAAC in their native Sinusoidal projection and Hierarchical Data Format for Earth Observing Systems and reprojected to Albers-Equal-Area projection using the MRT. Because portions of the study-area can experience snow any month of the year and intermittent snow-cover is unlikely to be important to annual phenology, we generated a predictor variable (SNOW) that describes the timing of the arrival and departure of seasonally-continuous snow-cover. The SNOW variable identifies the last day in the spring that exhibited at least seven consecutive days of snow-cover and first day in the fall that exhibits seven consecutive days of snow-cover. In cases where the target was obscured from the sensor by cloud-cover, these 'no data' observations did not count for or against running tallies of continuous snow-cover. The resulting 500-meter resolution grids were spatially-averaged in order to produce a 1-kilometer predictor dataset.

Temperature and Precipitation: Spatially-continuous datasets were required for exploring the relationship between LSP and climate across the study-area. Continuous climate grids have been in development and used by researchers for some time (Daly et al. 1994; Thornton et al. 1997; and others). The generation of continuous climate grids uses point-based observations of weather and interpolates their values across space based

primarily on topography. Extensive accuracy assessment and validation of these datasets document impressive rates of error for temperature (~1 degree C for mean annual maximum and minimum temperatures), even as modeled over large spatial domains and across steep environmental gradients (Daly et al. 2000, 2002; Thornton et al. 1997, 1999, 2000). Errors in temperature estimates are typically lowest during the summer months and highest in winter. Errors in precipitation estimates are more modest and have been reported to be ~19% of total annual amounts, with an 83% success rate of identifying daily precipitation occurrence (Thornton et al. 1997). The DAYMET algorithm of Thornton et al. (1997) interpolates daily observations of temperature and precipitation to a gridded surface that is corrected for elevation based on a running average of empirical temperature lapse rates across elevations. Datasets produced by DAYMET have been used in ecological modeling exercises to explore spatial-variation of climate effects on ecosystems (Fagre et al. 2003; White et al. 1997).

Gridded temperature data was generated by the NASA Ecological Forecasting Laboratory (<http://ecocast.arc.nasa.gov/>) in 2009 following the methods of Thornton et al. (1997) and Jolly et al. (2005). Output grids included daily maximum temperature (TMAX), minimum temperature (TMIN) and precipitation (PRECIP). The present study also generated an accumulated growing degree day temperature predictor (AGDD), using a base-value of zero degrees C, assuming that sub-zero temperatures are not meaningful to plant growth (Frank and Hoffman 1989). AGDD was calculated using the following formula where superscript numbers refer to day one and day two (etc.) and only positive daily temperature values are summed:

Equation 2.2

$$AGDD = \left[\frac{TMAX^1 + TMIN^1}{2} \right] + \left[\frac{TMAX^2 + TMIN^2}{2} \right] \dots$$

Water Availability and Demand: Spatially-continuous estimates of soil-moisture (SOILW) and vapor-pressure deficit (VPD) were generated by the NASA Ecological Forecasting Laboratory using the methods of White and Nemani (2004) and Jolly et al. (2005). These methods run the Terrestrial Observation and Prediction System (TOPS)-BGC model in diagnostic mode to generate a suite of climate- and biology-based estimates of environmental parameters (Nemani et al. 2009). TOPS uses a “bucket model” based on an assumption of soil water-holding capacity, precipitation and estimates of leaf-area index (White and Nemani 2004) to estimate SOILW. VPD is based on an assumption that TMIN is a reasonable estimate of dew-point temperature during the growing season, the Murray (1967) formulation of vapor-pressure deficit and adjustments made to VPD across topographic gradients (Thornton et al. 2000).

Solar Radiation: Estimates of solar radiation (SRAD) were generated by the NASA Ecological Forecasting Laboratory using the methods of Thornton et al. (2000). Daily SRAD is estimated based on earth-sun geometry and day-length, atmospheric moisture and its ability to absorb radiation, and elevation, or the affect of decreasing optical airmass through which radiation must pass before reaching the earth’s surface with increasing elevation (Thornton et al. 2000). When applied to complex terrain in Austria, these methods were found to produce mean absolute errors of $\sim 2.5 \text{ MJ m}^{-2}$ (Thornton et al. 2000).

Climate predictor data (with the exception of those representing snow-dynamics) were summarized across the 16-day intervals that matched the timing of native NDVI data. For SOS, EOS and MAX response models, TMIN and TMAX predictors are presented as an average over the 16-day period. For INDVI models, predictors are summarized for the entire growing season (SOS to EOS) and presented as either an average (TMAX and TMIN) or accumulation (AGDD, PRECIP, SOILW and VPD).

Parent Material: A data layer mapping the spatial-coverage of underlying parent material (PMAT) in the study-area was created by Parmenter et al. (2003) using the Natural Resource Conservation Service (NRCS) 1:250 000 soils coverage and NRCS interactive soils website to identify a parent material associated with each soil type. This layer was resampled to a 1-kilometer spatial resolution using a nearest neighbor resampling routine in ArcGIS (ESRI 2006).

Summary of Modeling Steps: Two main modeling steps were undertaken with different objectives. First, models of LSP with biophysical predictor variables were constructed for the purposes of interpretation and identifying the main correlates and potential drivers of grassland phenology. Prediction was not an objective in this first step and because models constructed with the entire dataset exhibited errors that were clearly spatially-dependent and performed more poorly than models constructed with subsets of the complete dataset; we used a conservative subsample that preserved instances of most or all biophysical settings in which grasslands are found in the study-area. Models constructed with this subsample did not exhibit errors that were spatially-dependent and

we therefore had confidence that the main biophysical correlates identified were not biased by the size and location of grasslands (i.e. expansive grasslands contributed more to models than did smaller grasslands). The second objective involved constructing models with which to make predictions across the study-area for an average year. The tools in this modeling step were less sensitive to spatial-dependence and correlated predictor variables and we used all points and all variables to construct these models in order to produce the best predictions possible. The following two sections provide further details of these two modeling steps.

Identifying the Biophysical

Correlates of Land Surface Phenology: Identifying the main biophysical drivers of

LSP required a multi-step process in order to overcome several challenges. First, grasslands are patchily distributed across the study-area and of varying size meaning that some grasslands contained many MODIS pixels while others contained only one or a few. Because we employed common statistical methods (regression trees) that require independent observations as input, it was necessary to take a spatially-independent subsample of the complete dataset. The danger in keeping too many pixels was that the LSP-biophysical relationship described by models could have been biased towards the large contiguous grasslands of YNP at the expense of missing the relationship exhibited by lower-elevations where natural grasslands were small and dispersed. Second, for MAX and INDVI, which estimate a magnitude of response rather than timing we assume that it is the seasonal variation in climate that elicits a phenological response and therefore use the timing (rather than magnitude) of these LSP events in order to identify

their biophysical drivers. Third, although we recognized the likely importance of time-lags to predicting LSP (Wang et al. 2003), these complex relationships likely varied across the steep environmental gradients of the present study-area. This is because snow-dynamics (which varied across the study-area) mediated the relationship between surface climate and the physical environment as experienced by vegetation. For example, accumulated growing degree days prior to snowmelt should not influence phenology (Jonas 2008). Given the extent of the study-area, discovering spatially-variable time-lags was deemed of secondary importance to the main study objectives. As such, to generate the predictor dataset we averaged (or accumulated) climate across the 16-day periods that matched native NDVI data and used climate observations for only the period that intersected the timing of LSP events. This approach ignored accumulations of climate across multiple 16-day periods. However, it did capture the climatic conditions that were likely of greatest importance as phenology triggers. Further details of each step are outlined in the following paragraphs.

To address issues related to spatial-dependence without losing information (i.e. without losing spatial coverage) we took a spatially-balanced sub-sample of the total dataset using Generalized Random Tessellation (GRTS) sampling methods (Stevens and Olsen 2004; Diaz-Ramos et al. 1996). One of the most useful aspects of a GRTS sample is that all subsamples regardless of size are spatially-balanced. We iteratively took GRTS subsamples of increasing size, constructed models and examined both model performance (r-squared and similar values as well as predictive ability) and variograms and maps of model errors in order to evaluate spatial-dependence. The optimal sub-

sample was considered to be the one used to build models that exhibited the best performance across all four phenology metrics (SOS, EOS, MAX and INDVI) that did not display spatial-dependence in its error structure. The resulting subsample included 100 points whose spatial arrangement did not exhibit the gridded pattern of underlying data (Figure 2.1). All models discussed throughout the remainder of this chapter were constructed using a spatially-balanced random sample of 100 pixels. Considerable model experimentation confirmed that although modest gains in performance could have been achieved for individual LSP metrics using subsamples of increasing size; models built with 100 pixels represented the optimal subsample size when considering the performance of all four LSP models.

Although observations in close spatial proximity were clearly not independent, we interpreted observations from the same point through time (nine years of study) as being independent. The rationale behind this recognized that the relationship between phenology and climate likely changes across space in different ways than it does through time (Jonas et al. 2008). Covariance between LSP and climate on an interannual basis represented an important relationship that we hoped to capture with models. It was therefore necessary to keep observations from each year of study.

We undertook the following steps to identify the main biophysical correlates of SOS, EOS and MAX: First, we split the dataset into the first eleven 16-day periods (out of 22 per year) in the spring (SOS), the middle eleven 16-day periods in the summer (MAX) and last eleven 16-day periods in the fall (EOS). Second, we used the observed timing (DOY) of each LSP event to create a binary response variable that identified the

time-periods prior to the LSP event of interest as ‘0’ and time-periods following the event as ‘1’. In doing so, the response variable differentiated between for example, spring conditions that preceded and followed the start of the growing season (SOS). In the case of MAX only one time-period per year was identified with a ‘1’ because it represented a discrete event in time. For INDVI, we identified time-periods prior to SOS as ‘0’, during the growing season as ‘1’ and following EOS as ‘2’. Models of INDVI represent the timing of the growing season (SOS and EOS simultaneously) in contrast to non-growing portions of the year. Modeling the timing of INDVI was undertaken for comparison to the results of SOS and EOS models. In each case, SNOW predictors were also converted to binary variables differentiating between snow-cover and snow-free conditions. The final biophysical driver dataset described conditions for 100 study-points, each 16-day period (22 per year) over the nine years of study and had 19, 800 total rows of observations.

Regression-tree models were used to identify the main biophysical correlates and potential drivers of LSP. A tree-based approach was chosen because of its usefulness for interpretation (Iverson et al. 2008) and flexibility in representing hierarchical, nonlinear and interacting relationships (Breiman et al. 1984). Regression-trees as discussed in Breiman et al. (1984) and others, create binary partitions of a dataset at non-terminal nodes based on values of a single predictor variable so that variation in the response variable that is explained by each data split is maximized. In this way, collinear predictors do not share explanatory power for each data split, but rather the “best” single predictor is used. Partitions continue until the variation explained by each split accounts

for at least as much of the variation in the response as is specified by the user in setting a “complexity parameter” (cp) value. Because we were only interested in the main correlates of LSP and to avoid over-fitting, we set the cp value to 0.02. This means that if a data split did not explain at least 2% of the variation in the response then it was not included in the model. The choice of cp value was strictly pragmatic and chosen in order to generate relatively simple and interpretable models. The contribution of individual predictor variables was calculated as the deviance explained by each variable divided by the total model deviance. Regression-tree modeling steps were performed using the `rpart` package (Breiman et al. 1984) in R-statistical (R Development Core Team 2009).

Building and Testing Predictive

Models for an Average Year: Datasets used to identify the potential biophysical

drivers of SOS and EOS were averaged (by year) in order to make predictions across the study-area for an average year. However, for MAX and INDVI an additional step was necessary. Because we interpreted differences in the magnitude of MAX and INDVI as being a result of differences in climatic conditions during the time of MAX and INDVI; it was therefore necessary to first predict the timing of MAX and INDVI (as described in the above section) and then sample climate during that time-period in order to predict the magnitude of response to those conditions across the study-area.

We used Random Forests (RFs) (Breiman 2001) to build predictive models of LSP. RFs are a variation of regression-trees that is often used in ecology (Cutler et al. 2007) because of its ability to predict response even into novel parameter space (Prasad et al.

2006). Some strengths of RFs are that they can handle colinear predictor variables and offer reliable estimates of model performance without need for withholding validation data (Brieman 2001; Prasad et al. 2006). RFs build large ensembles of unpruned trees (1000 were used for the current study) based on random samples of predictors (often the square-root or one third of the number of predictors depending on whether classification or regression is being performed) at each data split. For prediction, each tree in the “forest” is allowed to vote towards an average predicted response. “Out-of-bag” estimates of model performance (based on a bootstrap sample of one-third of the data for each tree) provide reliable estimates of model prediction error. Finally, measures of variable importance are generated by iteratively randomizing variable values for out-of-bag cases and calculating the increase in model mean-squared error of models as compared to when true values are used. We report only the top two most important predictor variables for each model for comparison to regression tree results. All RFs were built using the `randomForest` package in R-statistical (R Development Core Team 2009).

Table 2.1. Biophysical predictors of LSP, their definitions and ecological relevance of hypothesized relationships.

Explanatory Variable	Climate Predictor	Definition	Relevance
Snow dynamics	SNOW	Last week-long period in spring that displays continuous snow-cover and first week-long period in the fall that displays continuous snow-cover	Snow dynamics mediate the relationship between plant growth and other climate factors, representing an indirect effect on LSP
Temperature	AGDD	Growing degrees, base value 0 degrees C, accumulated across 16-day periods or the growing season	Temperatures that are not amenable to photosynthesis (below base values) are not biologically meaningful. Temperature conditions have to accumulate through time prior to observing a plant growth response
	TMAX	Average maximum daily temperature for 16-day periods or growing season	Maximum temperatures determine rates of photosynthesis during daytime growth
	TMIN	Average minimum daily temperature for 16-day periods or growing season	Minimum temperatures depict early morning or late evening conditions that can limit rates of plant growth and/or damage plant tissues
Water	PRECIP	Cumulative precipitation across 16-day periods or growing season	Precipitation estimates water that is available for plant growth
	SOILW	Average daily soil-moisture across the 16-day periods or cumulative across the growing season	A “bucket model” estimates soil-moisture that is available for plant growth, via inputs, outflow and plant uptake
	VPD	Average daily vapor-pressure deficit across 16-day periods or cumulative across the growing season	Vapor-pressure deficit estimates evaporative-demand and water limitations on plant growth
Energy	SRAD	Average daily solar radiation for 16-day periods or cumulative across the growing season	Solar radiation estimates energy that is available for photosynthesis via estimates of photoperiod, aspect, elevation and atmospheric moisture
Substrate	PMAT	16 category classification of underlying parent material	Soil properties describe spatial-variation in nutrients available for plant growth

We reported two measures of RF model performance. RF models reported the predicted timing of SOS and EOS as a 16-day period (one period out of 22 possible) while actual observations represented a specific DOY. To calculate model error, we assumed that model predictions referred to the middle day of the predicted 16-day period and report the root-mean-squared-error (RMSE) in number of days between predicted timing and observed timing as model performance in Table 2.2. Because models were built on only 100 of 360 study-pixels and we were interested in predictive power across the study-area; we also apply models to the withheld portion of the dataset, calculate RMSE and report on the full distribution of errors (i.e. 95% confidence interval). Quantiles were estimated using a method that provided approximately median-unbiased estimates (Hyndam and Fan 1996). For MAX and INDVI models that predicted a continuous response (in contrast to classification of binary response in the case of SOS and EOS), pseudo-R-squared values generated by `randomForest` are also reported as a measure of goodness of fit.

Finding suitable low-elevation sites on private lands with which to model natural grassland phenology was a primary challenge of model construction. Many undeveloped grasslands on private lands have been disturbed and some harbor invasive species with different phenologies than native plants. Cheatgrass (*Bromus tectorum*) was the primary species of concern since it can have significantly earlier than natural phenology and has the ability to respond strongly to episodic rainfall events throughout the year. As such, a final model validation step used cheatgrass occurrence data to look for patterns in LSP consistent with cheatgrass contamination in low-elevation settings. A trend towards

earlier SOS as well as bimodal growth (rapid response to intermittent rainfall) would have been consistent with cheatgrass contamination of natural grassland LSP (Clinton et al. 2005).

Results

Land Surface Phenology

Results highlighted the spatially- and interannually-variable nature of the study-area's grassland growing season. In general, SOS in northern portions of the study-area and lower-elevation settings (areas below 1,750 meters and those adjacent to the Lamar and Gardiner Rivers within YNP) started in March and April (Figure 2.3). For most middle-elevations (1,750 – 2,500 meters) SOS began in May, and at the highest elevations (above 2,500 meters) the growing season began in June. Spatial patterns of SOS were coherent and exhibited an upslope migration, or green-wave, as spring progressed; although consistent with the work of others, this pattern was not perfectly stepwise upslope (Thein et al. 2009). For each pixel over the nine years of study SOS date varied by more than one month on average from earliest observed date to latest observed date (Figure 2.3). The most inter-annually variable SOS locations were at low-elevations while the most stable were in middle- and some low-elevations in the northern portion of the study-area. At least moderate inter-annual variability occurred across all settings. The delay between snowmelt date and SOS decreased with increasing elevation as has been noted for other areas (Jonas et al. 2008). For low-elevations SOS occurred an average of 94 days after snowmelt (study-period range of 79 to 110 days); for middle-

elevation sites an average of 36 days after snowmelt (study-period range of 19 to 52 days); and for the highest-elevations an average of 18 days after snowmelt (study-period range of 6 to 26 days).

EOS occurred earliest (July and August) on average in northern portions of the study-area and some low- and middle-elevations (Figure 2.4). EOS occurred somewhat

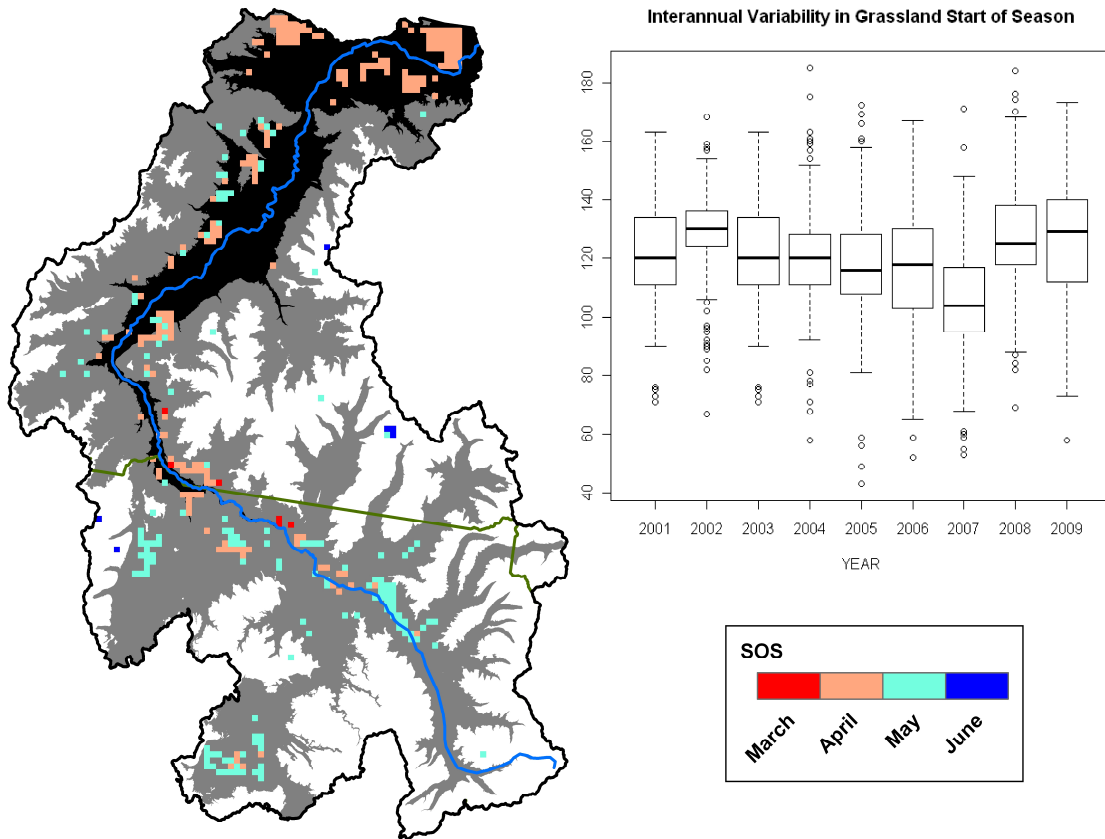


Figure 2.3. Average spatial and inter-annual patterns in the start of the grassland growing season (SOS) in the Upper Yellowstone River, 2001 – 2009. Boxplot shows data for 360 grassland pixels. (See Figure 2.1 for elevation ranges of shaded-relief).

later (September) in toeslope and north-facing areas of the Paradise Valley as well as some middle- and high-elevations. EOS occurred latest (October and November) in middle- and some high-elevations. Inter-annual variation in EOS was dramatic, over two months between earliest and latest observed date over the nine years of study (Figure 2.4). The most variable EOS occurred mostly in low-elevations although also in dispersed

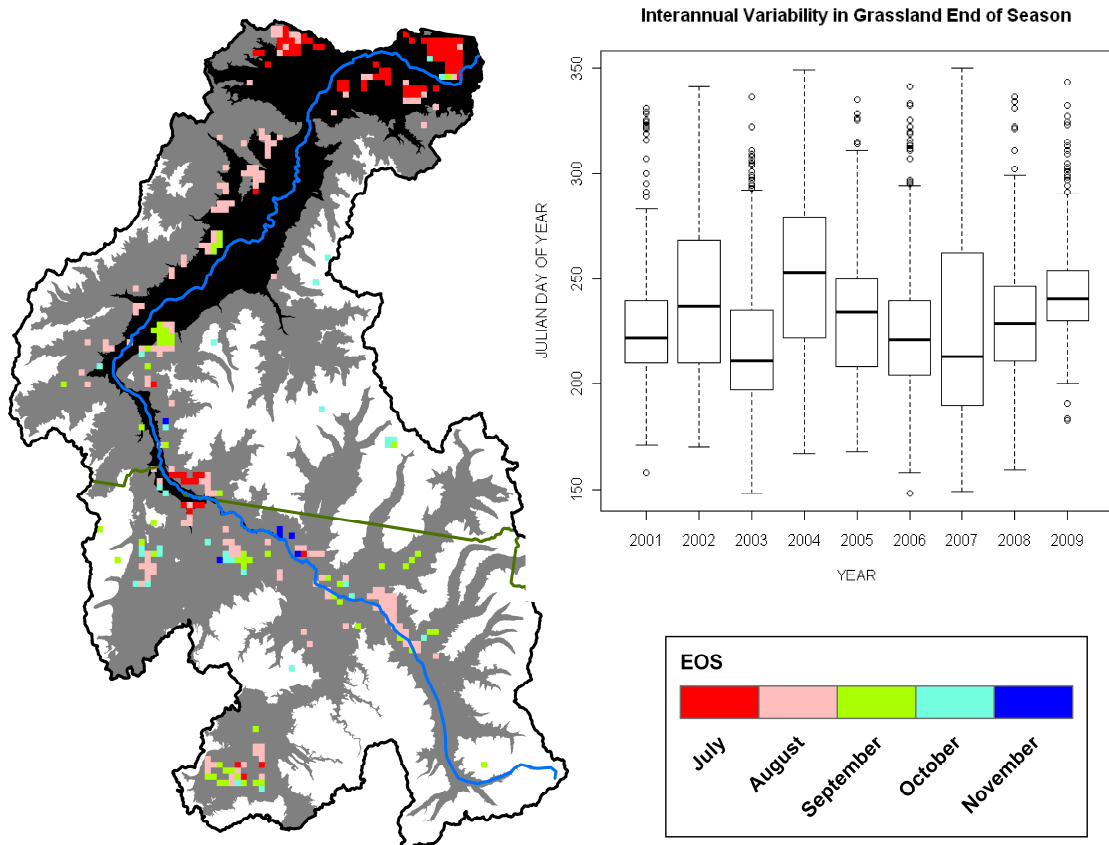


Figure 2.4. Average spatial and inter-annual patterns of the end of the grassland growing season (EOS) in the Upper Yellowstone River, 2001 – 2009. Boxplot shows data for 360 grassland pixels. (See Figure 2.1 for elevation ranges of shaded-relief).

locations across the study-area. The most stable EOS dates occurred in middle-elevations and northern portions of the study-area.

In general, the highest MAX (between 0.60 and 0.80) was observed in middle-elevations, areas adjacent to the Lamar River within YNP and some high-elevations (Figure 2.5). The lowest MAX (0.20 – 0.50) was located almost exclusively in low-elevations. Intermediate MAX (0.50 – 0.60) was observed in some low-elevation settings

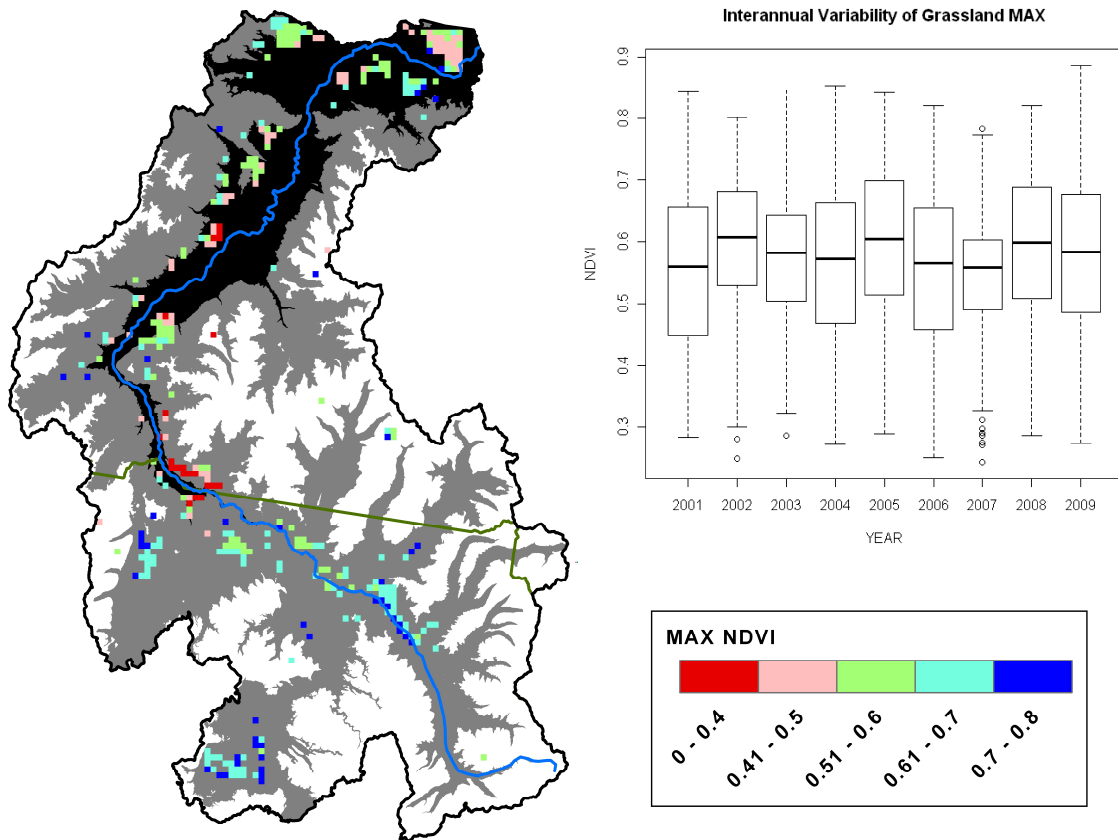


Figure 2.5. Average spatial and inter-annual temporal patterns of MAX in the Upper Yellowstone River, 2001 – 2009. Boxplot shows data for 360 grassland pixels. (See Figure 2.1 for elevation ranges of shaded-relief).

and northern portions of the study-area. Inter-annual variability in MAX was modest, averaging less than a 25% change between highest and lowest over the nine years of study (Figure 2.5). Portions of the Hayden Valley within YNP (southwestern portion of the study-area) exhibited the most inter-annually variable MAX, while other middle-elevations and northern portions of the study-area exhibited moderate inter-annual variability. Low-elevations exhibit low inter-annual variability.

The highest INDVI (3.00 – 8.00) occurred in some middle-elevation settings, the Hayden Valley and areas along the Lamar River in YNP (Figure 2.6). Intermediate INDVI (2.00 – 3.00) occurred in North-facing areas in the Paradise Valley, Northern portions of the study-area, and some middle- and high-elevations. The lowest INDVI (0 – 2.00) was observed almost exclusively in low-elevations. Inter-annual variability in INDVI averaged 50% between highest and lowest values observed over the nine years of study (Figure 2.6). The most variable locations occurred mostly in low-elevation settings and there was little spatial pattern to areas of intermediate and high inter-annual variability in INDVI.

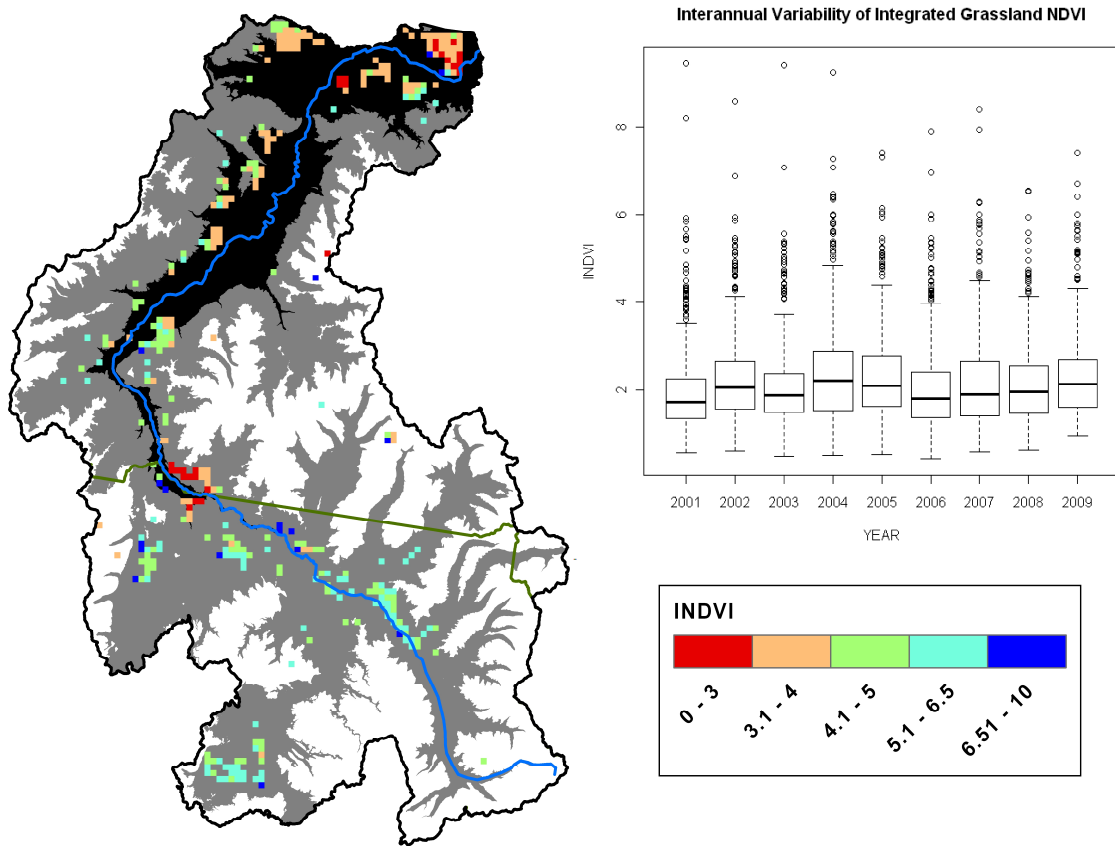


Figure 2.6. Average spatial and inter-annual temporal patterns of INDVI in the Upper Yellowstone River, 2001 – 2009. Boxplot shows data for 360 grassland pixels. (See Figure 2.1 for elevation ranges of shaded-relief)

Biophysical Correlates

Across space (study-area) and through time (2001 – 2009), climate predictors explained a substantial proportion of the variation in the timing of LSP (Table 2.2). Predictors explained the most variation in the timing of SOS (78%), followed by EOS (70%), MAX (52%) and INDVI (48%). Seasonal variation in SRAD explained the most variation while a predictor variable related to either water-availability (SOILW) or demand (VPD) was significant in every model except SOS. Temperature variables also appeared in each model and regression

tree splits based on different measures of temperature (TMAX, TMIN and AGDD) made little difference to modeling results (results not shown). SNOW was identified as a correlate in only the model that explained the timing of the entire growing season (INDVI model).

Biophysical models of SOS (Figure 2.7) indicated that the growing season started in the spring when average daily levels of solar radiation (SRAD) are above approximately 336 watts per meter-squared and average daily minimum temperatures (TMIN) are above -5.00 degrees Celsius. Although SNOW was not a significant predictor

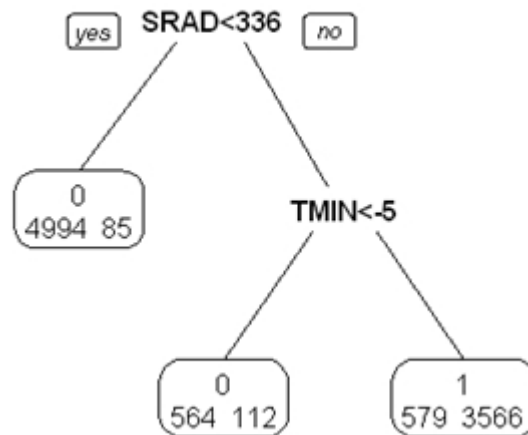


Figure 2.7. Decision-tree for biophysical model of SOS constructed with 100 grassland points over 9 years of study.

of SOS in binary response models, we note that continuous plots of snowmelt date versus SOS show an increasingly strong relationship in years and for locations where snow melted later in the spring (Figure 2.8). This relationship appeared to begin when and where snow melted after approximately March 31st.

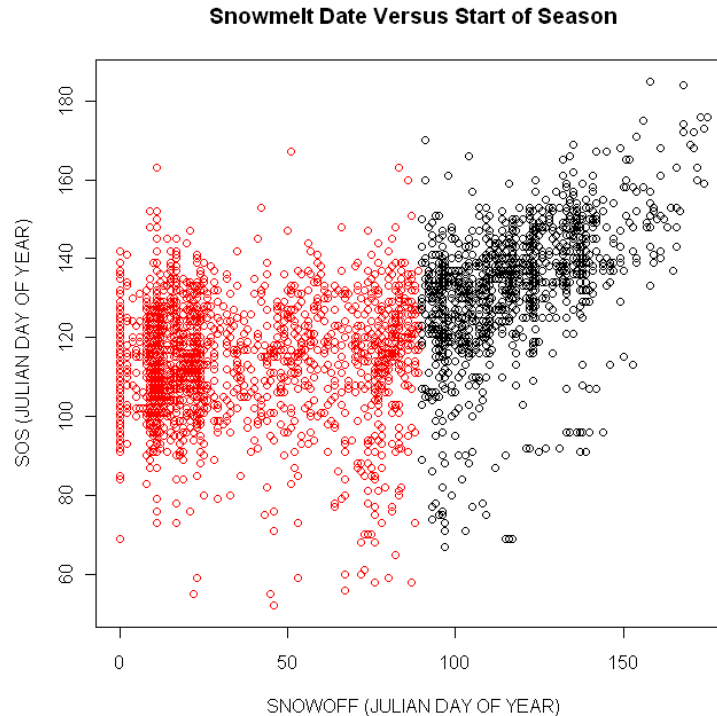


Figure 2.8. Relationship between date of spring snowmelt and grassland start of the growing season (SOS) in Upper Yellowstone River Basin, 2001 – 2009. Red points show years and locations for which snow-melt occurred prior to March 31st. The strength of the relationship increases the later in the year that snow-melt occurs.

EOS models (Figure 2.9) indicated that the growing season ended when average daily solar radiation in the fall dipped below approximately 393 watts per meter-squared, or earlier in the year when average daily soil-moisture was below 268 kilograms of water per meter-squared and average daily vapor-pressure deficit (VPD) was above 1,026 pascals. EOS dates were earliest for years and locations where there was high VPD at the time of EOS with a few exceptions. Some locations along the Yellowstone River just north of YNP exhibited the earliest EOS dates despite moderate VPD (Figure 2.10 tail extending towards the bottom-left corner of the figure). Field visits indicated that these

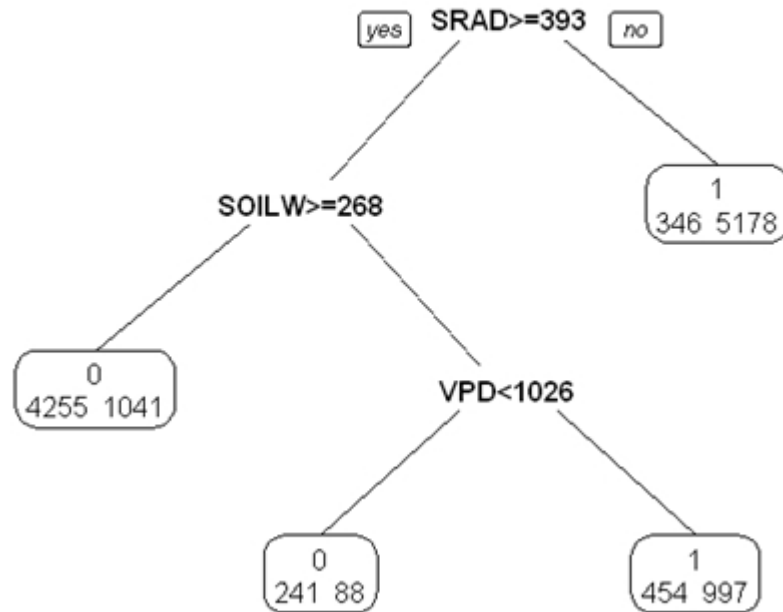


Figure 2.9. Decision-tree for biophysical EOS model constructed with 100 grassland points over 9 years of study.

areas appear to be quite dry although this was not captured well by climate data that was interpolated based in part on elevation (this area is of middle-elevation, but still quite dry). A difference in soil type and consequently moisture holding capacity may explain this localized difference in EOS dates and their relationship to climate, but was not captured by models.

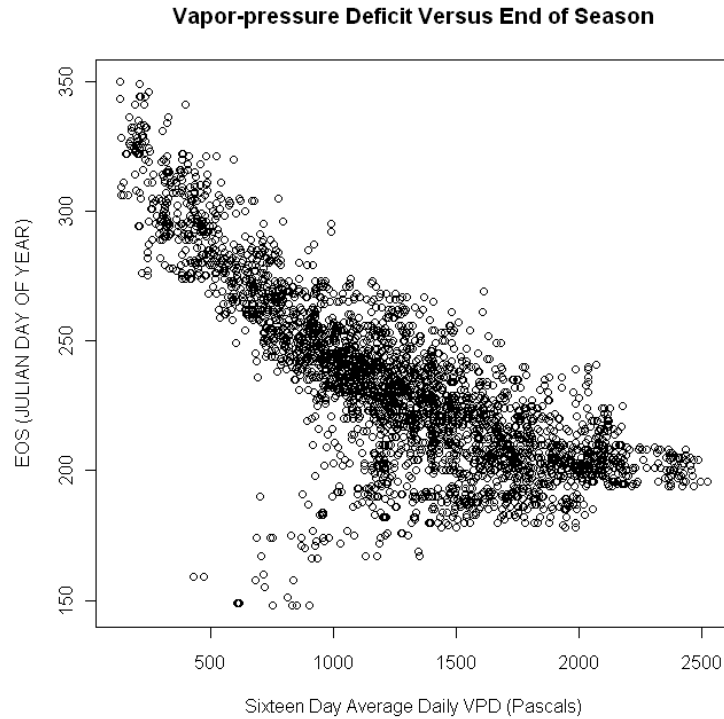


Figure 2.10. Relationship between vapor-pressure deficit (VPD) and grassland end of the growing season (EOS) in Upper Yellowstone River Basin, 2001 – 2009. The growing season ends earliest for locations and years that have high VPD at the time of EOS.

MAX models (Figure 2.11) indicated that annual peak greenness occurred in the summer when average daily minimum temperatures (TMIN) was above -0.38 degrees Celsius, average daily vapor-pressure deficit (VPD) was below 1,230 pascals and average daily solar radiation was above 426 watts per meter squared.

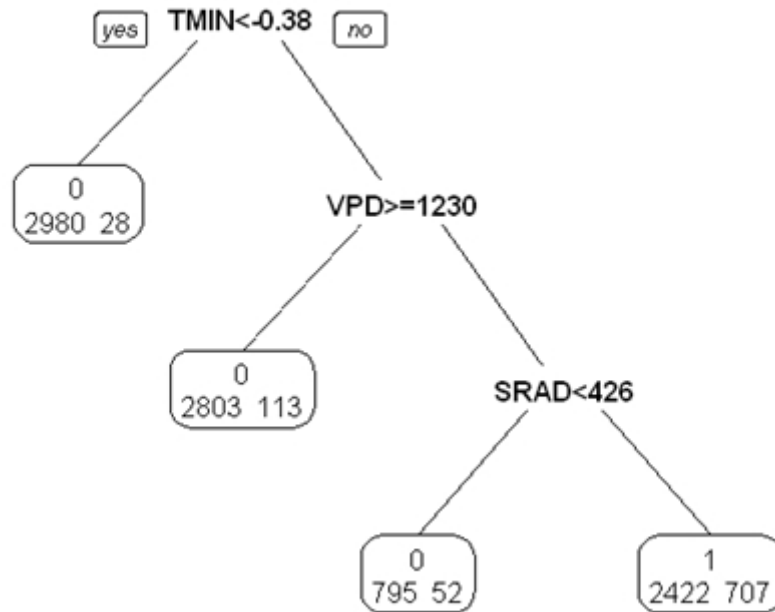


Figure 2.11. Decision-tree for biophysical MAX model constructed with 100 grassland points over 9 years of study.

Finally, models of INDVI (Figure 2.12) indicated that growing season conditions were defined in general by either SRAD above 318 watts per meter squared; or if SRAD was below 318 watts per meter-squared, then by snow-free conditions in the spring, SRAD that remained above 193 watts per meter squared in the fall, TMIN above -4.70 degrees Celsius and VPD that was below 555 pascals. INDVI generally increased for years and locations that received more growing season precipitation although there was considerable spread in this relationship (Figure 2.13).

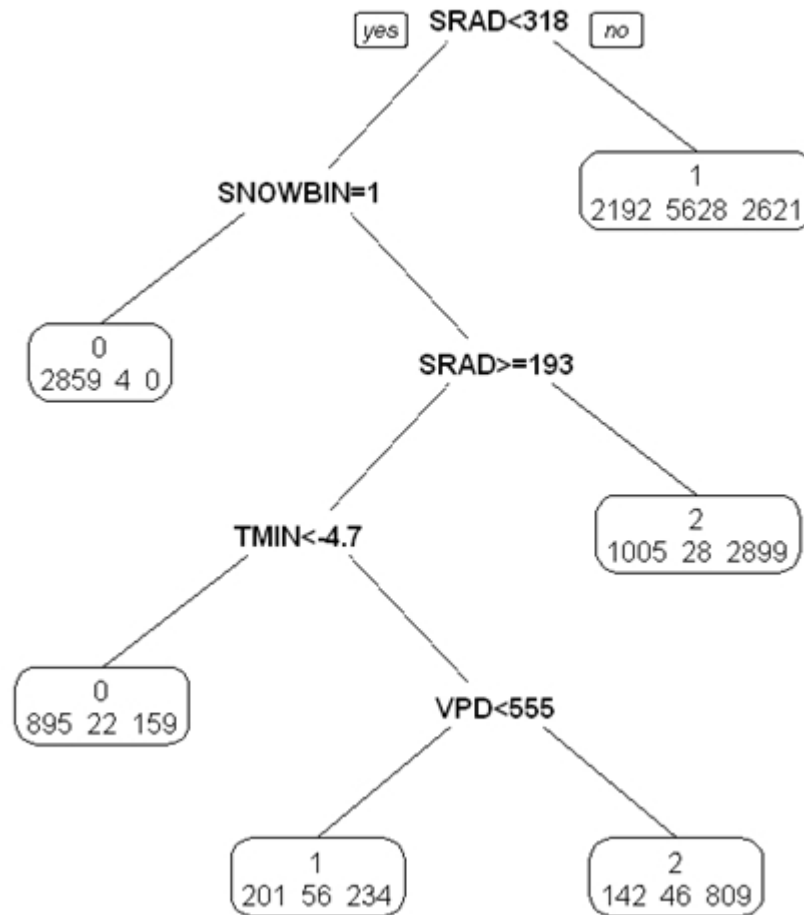


Figure 2.12. Decision-tree for biophysical INDVI model constructed with 100 grassland points over 9 years of study.

Predictive Models for an Average Year

The ability to predict LSP for an average year was good for SOS and MAX and modest for EOS and INDVI (Table 2.2 and Figure 2.13). RMSE for SOS was just over one week (8.71 days) with 95% of prediction errors falling within roughly two-weeks (-2.13 +/- 12.80) of actual SOS. Spatial-variation in TMAX and SRAD best predicted SOS across the study-area. This is in contrast to EOS which was explained by spatial-variation

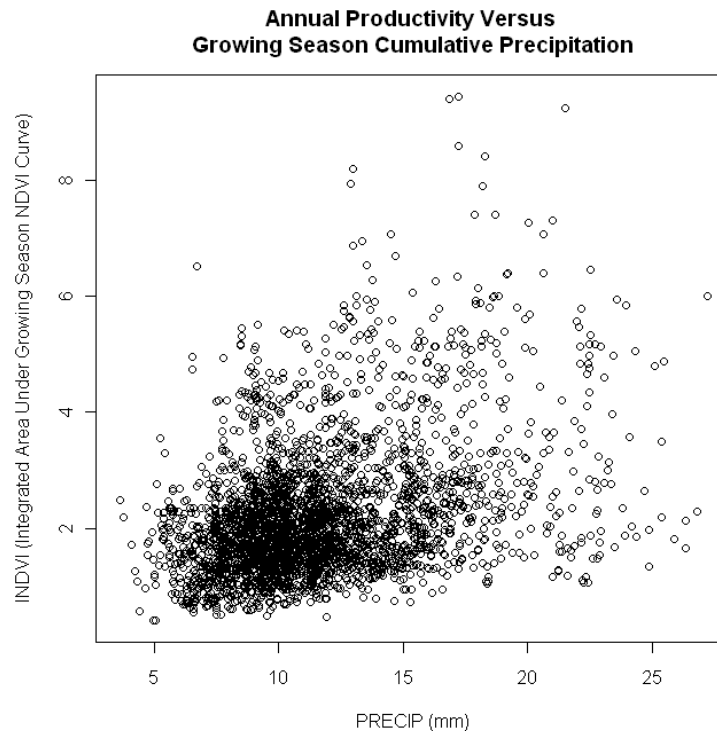


Figure 2.13. Relationship between cumulative growing season precipitation and total annual grassland productivity (INDVI) in the Upper Yellowstone River Basin, 2001 – 2009. Locations and years that receive more precipitation are generally more productive.

in SRAD and PRECIP. EOS RF models exhibited a RMSE of over three weeks (23.24 days). There was also substantial bias in models to predict EOS to be later than was observed in an independent dataset. This was common of middle-elevation pixels that made up the majority of grasslands in the study-area (Figure 2.14). Some prediction errors were up to 30 days later (-12.98 +/- 28.11). EOS in low- and high-elevation settings were commonly predicted by biophysical models to be earlier than was observed (Figure 2.14). RF models using spatial-variation in SNOW and PRECIP explained less than 40% of variation in magnitude of MAX. This result may have belied the model's predictive ability in that 95% of prediction errors were less than 27% of mean MAX (0.01 +/- 0.14; mean = 0.57).

For INDVI, spatial-variation in AGDD and PRECIP best predicted INDVI with 95% of errors being less than 50% of the mean (0.06 ± 2.14 ; mean = 4.47). Inspection of the distribution of errors for each model showed that they were all approximately normally-distributed.

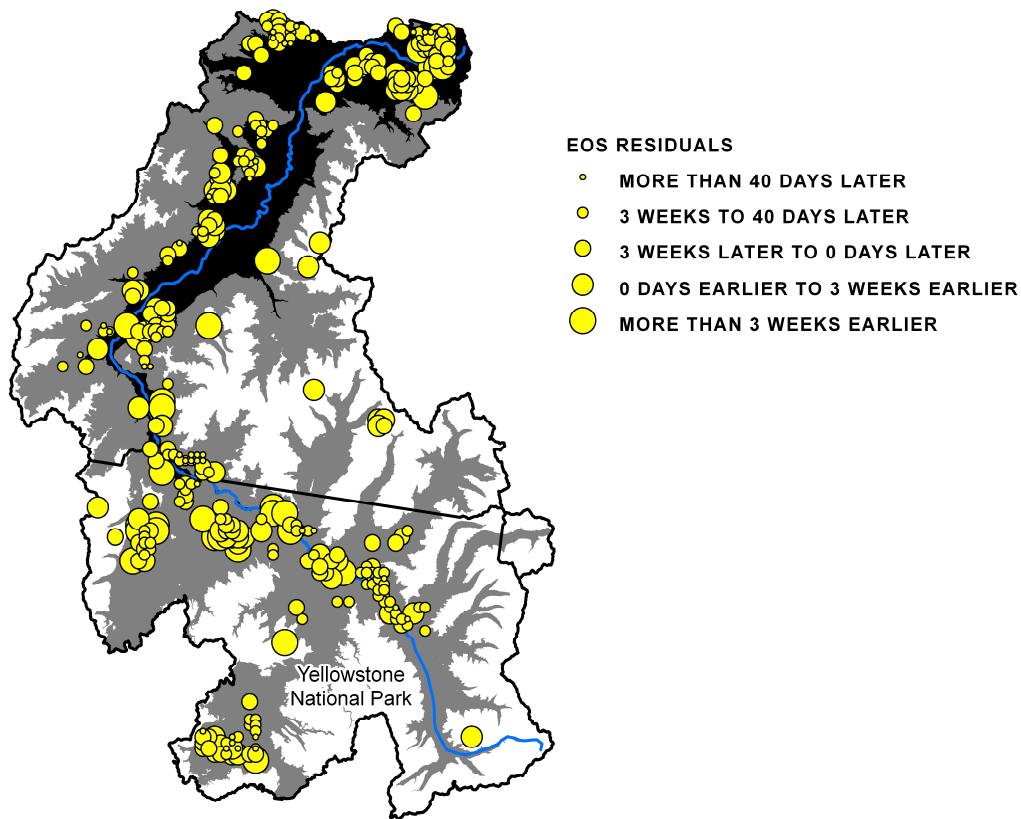


Figure 2.14. Spatial pattern of EOS model residuals for an average year across 360 natural grassland pixels. The size of points represents the size of residuals when comparing observed EOS to biophysically predicted EOS.

A dataset recording the presence and absence of cheatgrass at nearly 5,000 locations during 2009 within the Paradise Valley, MT was provided by B. Maxwell. These field plots overlapped with 54 MODIS pixels, 10 of which were identified in the

present study as natural grasslands. Detection rates (number of times observed divided by number of plots visited) of cheatgrass in these 10 pixels averaged 12% (range of 0 - 40%). Four of these pixels were used to construct biophysical models of natural grassland phenology and for three of those no cheatgrass presence was recorded. There was a 30% detection rate of cheatgrass in the final pixel used for model construction. Agricultural fields as well as sagebrush and conifer cover were common in pixels of higher rates of cheatgrass occurrence. Examination of these pixels showed that the LSP signal was more consistent with the effects of agricultural management practices and overstory species than it was with cheatgrass contamination. Cheatgrass did not appear to affect natural grassland phenology results.

Discussion

Results of the present study highlight the utility of both LSP methods and interpolated climate grids for the discovery of the main climate correlates and potential drivers of vegetation phenology at landscape scales. Results also supported hypotheses that emphasized water-limitations to plant growth in the study-area, while there was limited evidence of the importance of temperature and snow-dynamics. Finally, variation left unexplained by LSP models are likely the result of the methods used to generate them and by patterns of vegetation disturbance that have not been accounted for by models.

Table 2.2. Modeling results. Biophysical drivers explain the timing of LSP events across space (study-area) and through time (2001-2009). RF predictors explain spatial-variation in the timing (SOS and EOS) or magnitude (MAX and INDVI) of LSP for an average year.

Phenology Metric	Biophysical drivers ³	R-Squared and Number of Tree Splits for Timing ⁴	Top 2 RF Predictors by Importance Rank for Average Year ⁵ (n=100)	RF Prediction Error for Average Year ⁵ RMSE (95% C.I.)
SOS ¹		0.78 2		8.71 (-2.13 +/- 12.80) ‡
	SRAD	0.76	TMAX	
	TMIN	0.02	SRAD	
EOS ¹		0.70 3		23.24 (-12.98 +/- 28.11) ‡
	SRAD	0.64	SRAD	
	VPD	0.04	PRECIP	
	SOILW	0.02		
MAX ²		0.52 3		0.07 (0.01 +/- 0.14) †
	TMIN	0.30	SNOW	R ² = 0.39
	VPD	0.19	PRECIP	
	SRAD	0.03		
INDVI ²		0.47 5		1.10 (0.06 +/- 2.14) †
	SRAD	0.24	AGDD	R ² = 0.37
	SNOW	0.15	PRECIP	
	TMIN	0.06		
	VPD	0.02		

¹ Binary response variable

² Binary response variable for identification of drivers and continuous response variable for prediction

³ All predictor variables listed in Tale 2.1 were considered in each LSP model

⁴ Models were built on 100 unique locations, 9 years and twenty-two 16-day time-periods per year. Tree splits maximized the proportion of variation in the response variable explained by variation in an explanatory variable. Splits were undertaken if they explained at least 2% of the variation in the response.

⁵ Random Forest (RF) models predict LSP response across the study area for an average year; Importance rank is determined by % increase in mean squared error with the variable included versus not included

‡Units for SOS and EOS are in DAYS

†MAX and INDVI are unitless

Biophysical Correlates of Land Surface Phenology

Seasonal variation in SRAD (which is related to seasonal variation in photoperiod) was found to be the main biophysical correlate and potential driver of SOS, EOS and INDVI. For each of these three LSP regression-tree models, SRAD provided the first data split ending in a terminal node if SRAD thresholds were not met (see decision-trees in Results section). This result suggests that if SRAD (or photoperiod) is not above/below certain threshold levels then vegetation will not respond to changes in other climatic conditions (e.g. spring-warming prior to a certain date does not elicit a vegetation response; Partanen et al. 1998). This is consistent with existing understanding of photoperiod and variation in daily inputs of solar radiation as representing the outer envelope of climatic controls on phenology (Jolly et al. 2005). However, some experimental studies suggest that photoperiod is a stronger driver of spring ephemeral plant growth than daily solar radiation inputs (Gandin et al. 2011); while still others suggest that temperature and precipitation are stronger predictors of grassland phenology specifically than photoperiod (Huber et al. 2011; Lesica and Kittleson 2010; White et al. 1997). Photoperiod, solar radiation and temperature are all highly-correlated, making it difficult to distinguish with observational studies to which aspect of climate plants respond. In cases, it seems possible that the best predictors of phenology are not necessarily the aspects of climate that trigger biochemical processes in plants; but rather, SRAD for example, is merely the most reliable predictor of LSP across the present study-area. This tendency may be most pronounced when developing a single model of phenology for multiple plant populations that are locally adapted to different climatic

conditions (Chuine et al.1999). The present study included steep environmental gradients where there appeared to be a switch from one primary climate-driver to another as setting changed (e.g. influence of snow cover on SOS). As such, identifying a more mechanistic understanding of the actual biophysical controls on plant growth and how these change across environmental gradients remains an active and complex area of research with obvious relevance to anticipating climate-change impacts (i.e. correlates will not predict well into novel climate space; Cleland et al. 2006).

Consistent with hypotheses, the present study found some evidence of a minimum temperature threshold for SOS (-5 degrees C; Table 2.2 and Appendix A); while differences in TMAX and SRAD explained variation in SOS across the study-area (Table 2.2). Seasonal variation in SRAD and temperature are collinear and disentangling their unique contributions remains a challenge. Acknowledging uncertainty, the results of both RF and single-tree models suggest that temperature and SRAD share a role in determining SOS; perhaps SRAD as the outer-envelope and temperature as the primary predictor of variation within that envelope. In general, these findings are consistent with the work of Jolly et al. (2005) who posited that broad-scale plant development could be predicted to begin when minimum temperatures reached approximately -2 degrees C. This also appears to be consistent with observations that many plant species of the mountain west can grow at or near freezing temperatures even under snow-cover (Kimball et al. 1973). Contrary to hypotheses, snow-dynamics were not identified as a correlate of SOS in binary modeling exercises despite its known influence on mountain phenology (Fagre 2003; Jonas et al. 2008; Körner 2005). Instead, results (Figure 2.8)

suggest that the timing of snowmelt influences SOS for only higher-elevations and/or years with later spring snowmelt. It follows that middle-elevations may represent a zone where there is a switch from temperature and photoperiod controls to snow-dynamics as primary drivers of SOS. Similar to the work of Pepin and Lundquist (2008) who asserted that high-elevation areas near the 0 degree C mean-annual-temperature isotherm are at the greatest risk of future warming; we posit that vegetation-dynamics in areas where there is currently a transition from one biophysical driver of phenology and productivity (temperature or photoperiod driven SOS and water-limited productivity) to another (snow-dynamics driven SOS and annual productivity limited by growing season length) may also be at greatest risk of future climate change.

An interaction between water-availability and demand appeared to control EOS for lower-elevations while photoperiod best predicted EOS for higher-elevations where evaporative demand never reached high-levels. Spatial-variation in SRAD and PRECIP best predicted EOS across the study-area (Table 2.2). This is consistent with hypotheses that focused on late-season water-deficit as the primary determinant of EOS. Others note that vapor-pressure deficits below roughly 900 pascals exert little influence on plant growth while those above 4,100 pascals can force plant stomata closed even in the presence of sufficient soil-moisture (Jolly et al. 2005; Osonubi and Davies 1980; Tenhunen et al. 1982). Vapor-pressure-deficit within the study-area rarely reaches such extreme levels and models suggest that when there is sufficient soil-moisture grassland growth continues. It is only when VPD is high (16-day averages above 1,026 pascals) and soil-moisture is low, that grasslands senesce earlier than late-season photoperiod triggers.

Precipitation (commonly used as a surrogate for soil-moisture) has been noted to be a good predictor of grassland phenology in arid and semi-arid regions of the world (Lesica and Kittelson 2010; Wang et al. 2003; White et al. 1997); and soil-moisture can be a difficult parameter to estimate (Botta et al. 2006). Soil-moisture estimates used in the present study appeared to capture changes in the physical environment that triggered grassland senescence; however these estimates did not accurately predict EOS when applied to an independent dataset.

There are two main issues that confuse the generation of discrete EOS dates: 1) the gradual nature of grassland senescence (Reeves et al. 2006); and 2) bimodal growth that is characteristic of some arid and semi-arid grasslands (White et al. 1997; Penuelas et al. 2004). The timing of EOS in broad-leaf deciduous forests for example, is associated with 15-25% leaf-drop (White et al. 1997), and therefore detects a change in the target land cover's structure (i.e. biomass) in addition to reduced photosynthetic activity. EOS in grasslands however, is of a more gradual nature due to relative constancy of the target's physical structure (Reeves et al. 2006). Reeves et al. (2006) noted this dynamic when relating a grassland clipping experiment to satellite-derived estimates of gross primary-productivity. They concluded that the lack of growth in browning senescent vegetation was not captured as well as was early growth that was associated with both vegetation greening, and biomass accumulation. A similar dynamic is likely at work in the present study where the browning of grasses may not be sufficient to drop NDVI to low-enough levels to record EOS. This likely resulted in estimates of EOS for low-elevation settings that were later than actual (EOS dates in August and September for the

Paradise Valley when one would expect July). Bimodal growth patterns can also make detection of EOS a challenge. Grasslands in summer-dry arid and semi-arid regions often retain the ability to respond to single precipitation events even after senescence (Buyantuyev and Wu 2012; Wang et al. 2003); this is characterized as a “bimodal” pattern of growth and is often associated with winter annuals of many desert environments. Although there are no native winter annuals in the present study-area, there was some evidence of bimodal growth (e.g. small October-November increase shown in Figure 2.2 example although this is on the small end of bi-modality that was observed), whereby grasslands appeared to respond to fall precipitation with slightly increased NDVI values. This may have delayed EOS dates in some settings because LSP models used in the present study recorded the timing of EOS as the latest date that NDVI dropped from above to below half of its annual amplitude. In either of the above two cases, climate-driven models of EOS were likely parameterized in part on EOS dates that were later than actual. This meant that when they were used to predict the EOS of an independent dataset, errors were biased towards later EOS dates in general. To clarify, later than actual EOS dates appeared to be a problem limited to lower-elevations where species tend to be taller and growth slow so that the NDVI signal is determined more by biomass and less by absorption of radiation for photosynthesis (Jonas et al. 2008). Lower-elevation sites (and high-elevation sites) were underrepresented in the total dataset of 360 grasslands because most valley settings have been converted to human land uses. As a result, the spatially-balanced subsample of pixels chose most or all lower-elevation pixels for model construction and these models were then applied to an independent dataset that

represented mostly middle-elevation pixels where satellite-derived EOS may be closer to actual conditions. The result was that biophysical models commonly predicted later EOS dates than were observed in an independent dataset. The gradual nature of EOS and bimodal pattern of grassland growth in some ecosystems highlights the difficulties inherent in representing EOS as the timing of a discrete event (Jolly et al. 2005). Prediction of SOS did not suffer from the same issues because the structure of senescent grassland biomass is broken-down over winter by a number of physical processes including snow-compaction, driving winds, and the grazing and trampling of domestic and free-ranging herbivores.

Models suggested that the timing of MAX is controlled by TMIN and VPD, while SNOW and PRECIP explained variation in MAX across the study-area. Lower than ideal temperatures for vegetation growth can: inhibit plant-root uptake of water from the soil (Waring 1969); slow plant cell-division (Granier and Tardieu 1999); and in combination with high-solar radiation characteristic of much of the present study-area, can reduce maximum photosynthetic efficiency (Germino and Smith 2000). Other studies find a consistent time-lag between peak precipitation and peak greenness (i.e. MAX) in grasslands of the Great Plains (Wang et al. 2003); and that the timing of peak greenness is relatively insensitive to summer precipitation in Southern Arizona (Jenerette et al. 2010). NDVI as recorded by satellite (and therefore the timing of its annual maximum value) is sensitive to both vegetation biomass and the fraction of absorbed-photosynthetically-active-radiation. In this light, it should not be surprising that the timing of MAX is not more highly correlated with the timing of any single climatic

event; but rather it represents a gradual accumulation of biomass followed by short-lived vigorous growth under ideal growing conditions (i.e. when evaporative demand is low and temperatures are not). The specific timing and combination of climate factors that lead to MAX likely vary across the study-area coincident with fast growing species of short stature at high-elevations in contrast to taller and more slowly growing species at lower-elevations (Jonas et al. 2008).

RF predictive models are consistent with hypotheses that an interaction between temperature and water-availability would predict spatial-variation in MAX. Early- and mid-growing season soil-moisture for portions of the study-area is likely controlled by spring rains, while for other portions it is controlled by snowmelt. In both cases, summer precipitation is limited and therefore, the timing of soil-moisture depletion is dependent on the timing of the start of the growing season. For some middle- and most higher-elevations where SOS is delayed by snowmelt, soil-moisture levels remain high-enough for peak-growth later in the season when temperatures are ideal for rapid growth. This is in contrast to lower-elevations that depend on soil-water recharge from winter and early spring rains and likely deplete moisture reserves prior to temperatures reaching levels that are ideal for rapid growth.

Regression-tree models of the timing of INDVI did not identify the timing of the growing season as well as did SOS and EOS models separately. SRAD was the primary biophysical correlate in SOS and EOS models and spring versus fall SRAD conditions are similar; meaning that the predictive power of SRAD in INDVI models was diluted. AGDD and PRECIP explained variation in INDVI across space consistent with

hypotheses that water-availability and accumulations of temperature would explain spatial-variation in the magnitude of INDVI. Contrary to hypotheses, PMAT was not useful in explaining variation in INDVI. Soil properties are known to explain the distribution of plant form (tree versus shrub versus grassland, Despain 1990), within the study-area and explain spatial-variation in forest biomass accumulation (Hansen et al. 2000); however, this may have more to do with soil-moisture-holding capacity and water-availability that is better captured by spatial-variation in PRECIP. In either case, climate-driven RF models do not capture well spatial-variation in the magnitude of INDVI.

Comparison to Other Studies

Spatial patterns of LSP mapped by the present study match well those of prior efforts (Thein et al. 2009), with some important differences. Based on published maps, it appears that Thein et al. (2009) produce average (for the time-period 2001 – 2005) February SOS dates for low-productivity areas such as those in the vicinity of YNP's north entrance near Gardiner, MT. They state that these results are either mistakes in the data or limitations of the methods as applied to low-productivity areas where the annual amplitude of NDVI values is small. These anomalously early SOS dates are in contrast to the present study that produced average mid-March and April SOS dates for the same areas (although we do produce a few February SOS dates for individual years like 2005 and 2006), which the current authors think are representative of the real average timing of spring plant growth. This difference is likely due to the methods that each study used to handle snow-covered portions of the year in NDVI time-series. NDVI often increases concurrent with snowmelt (snow-cover depresses NDVI values) and independent of

changes in vegetation activity (Delbart 2005; Huete et al. 1999). Other researchers have noted a propensity for LSP methods that do not correct for snow-effects to estimate anomalously early SOS dates (Hudson Dunn and DeBeurs 2011). Although they do not state their methods for handling snow-cover explicitly, if Thein et al. (2009) included snow-covered NDVI observations as missing data (smoothers would project downward trends of the previous fall into the no-data gap and likely beyond actual background values), or '0' NDVI values (also likely below actual background values), this would explain the early SOS dates that they produced. This is because LSP metrics are based on the annual NDVI amplitude (the present study and Thein et al. both use 50% of annual amplitude for SOS) and methods that do not correct for snow-cover can introduce a increase in spring NDVI that is associated with snow-melt rather than vegetation activity. By substituting empirical estimates of snow-free background values for snow-covered portions of the year, the present study minimized long gaps in data and the tendency of NDVI to increase in early spring due to snowmelt. That said, estimating snow-free background values can be problematic for locations with long periods of snow-cover and for which plant growth commences soon after snow-melt (or even before snow-melt, see Kimball 1973) and growth continues until fall snow-cover. Ideally, estimates of background values would be snow-free and have no photosynthetic activity for a full 16-day NDVI period. This set of conditions may never occur for high-elevations in the study-area. Therefore, the present methods may delay SOS at higher-elevations by estimating a higher than actual background value (although SOS dates for high-elevations appear to be reasonable). Even when using corrections for snow-covered portions of the

year, low-productivity pixels with low annual NDVI amplitude pose challenges for the accurate estimation of LSP. Small errors in background value estimates, or sensor-errors can cause large changes in LSP results (i.e. signal to noise ratio increases with decreasing annual NDVI amplitude; Verbesselt et al. 2010). That said, the present methods appear to offer an improvement over previous methods that have been applied to the study-area.

Variation Unexplained by Models

There was spatial (for an average year) and temporal (timing across space and through time) variation in LSP that was unexplained by climate-driven models. This was likely the result of the methods and data used to construct models and variation in grassland disturbance that was not accounted for by models.

The present study required spatially-continuous input datasets in order to characterize vegetation response across the study-area. This meant introducing some error into models via imperfections in gridded climate data with unknown effects on modeling results. Plots of EOS versus VPD for example, appear to highlight an area in the Gardiner Basin for which VPD estimates are poor and present unexplained variation in an otherwise strong relationship between LSP and its climate correlate (tail of points extended towards lower-left hand corner of Figure 2.10). Perhaps more important than errors in climate datasets, variation in vegetation response across steep environmental gradients may have resulted in model parameter estimates that are likely averages of several distinct vegetation-climate relationships. This challenge is similar to what White et al. (1997) found across latitude in a continental-scale study of North America and what Chuine et al. (1999) pointed out is a difficulty in developing climate-driven models of

phenology across large areas. With these short-comings in mind, models developed for the present study are likely of only limited utility for predicting the future impacts of climate change since they may not capture the “true” climate-drivers of LSP, nor the magnitude of vegetation response (i.e. their parameter estimates and temporal transferability are untested; Dobrowski et al. 2011). Despite these limitations, models can be interpreted as a mean response to climate of a single, important, natural land cover type (grasslands) in the northern GYE. Models were also sufficient to meet the third study-objective, to predict natural LSP under average climate conditions for areas presently under human land use.

Domestic and free-ranging herbivores (i.e. grazers) are common throughout the study-area in spatially- and temporally-varying densities and this was not accounted for in LSP models. Grasslands on private-lands for example, were identified specifically because they had significant grazing resources (i.e. are grasslands) as identified by Montana Cadastral datasets. However, information on the intensity of domestic livestock grazing on private-lands was unavailable. Grazers can substantially impact net primary-productivity (Frank and McNaughton 1993; Frank et al. 2002; McNaughton et al. 1996) by removing biomass and stimulating vigorous re-growth. Studies conducted on grasslands within YNP observed that grazers stimulated above-ground primary-productivity by 21% (Frank et al. 2002) while removing 36% of total summer grass biomass in the Hayden Valley (Olenicki and Irby 2005). The net effect of reduced biomass and increased growth rates on summer NDVI and annual INDVI is relatively unknown. However, we note that when applied to pixels in the Hayden Valley that were

not used in model construction; predictive models overestimated INDVI in every case, by an average of 11% (results not shown). The Hayden Valley likely represents higher native (*Bison bison*) grazing intensity relative to the rest of the study-area and this appears to suggest that models that are constructed using locations of lower grazing intensity will routinely overestimate INDVI in areas of higher grazing intensity. It seems likely that spatially- and temporally-varying grazing intensity accounts for a significant portion of the variation in LSP that is left unexplained by climate-driven models. Developing reliable satellite-based estimates of primary-productivity in domestic and free-ranging grazing ecosystems is a non-trivial task (McNaughton et al. 1985).

Implications for Science and Management

The present study contributes to broad-scale understanding of the biophysical drivers of grasslands phenology in the GYE and highlights some of the conservation challenges faced by public land and wildlife managers. Landscape patterns of grassland phenology provide a basis for understanding the movements, population dynamics and space use of migratory ungulates in this ecosystem. Results demonstrate that early-season grassland growth, which represents a critical resource for ungulates, is primarily limited to private lands north of YNP. This may explain why some ungulates cross (or try to cross) the park's northern boundary during late winter and early spring months in many years. To the extent that spatial and temporal variation in climate drives grassland phenology, future climate change has the potential to alter patterns of productivity in ways that could alleviate, or exacerbate issues related to ungulate use of private lands. As

models of future climate scenarios improve, the approach presented in this study could be used to project future patterns of grassland phenology and help to anticipate climate change impacts to migratory ungulate habitat.

Because important portions of the grassland grazing system within the study-area lie on private lands, there is also the possibility that they undergo land use change in the future. The study-area at present remains rural and agricultural in character, but exurban development is projected to increase rapidly in coming years with largely unknown ecological effects. Like climate change, land use change has the potential to substantially alter landscape patterns of grassland phenology via human-activity and land management practices. Land use change also often brings new residents who sometimes embrace different values and aesthetic preferences for their biophysical surroundings than are espoused by current residents. Like climate change, the cumulative impacts of land use change have tremendous ability to alleviate or exacerbate the challenges of managing migratory ungulates. Because many changes (land use and climate driven) are expected to occur on private lands; managers require the best scientific understanding of likely future scenarios of grassland phenology in order to anticipate and plan for management and conservation challenges.

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CHAPTER 3

LAND USE MODIFIES LAND SURFACE PHENOLOGY FROM ITS NATURAL
BIOPHYSICAL STATE IN THE UPPER YELLOWSTONE RIVER BASINAbstract

Human land use around U.S. National Parks is intensifying; some studies find at rates that exceed regional and national averages. This is of concern to the conservation and management communities because human activity around parks can compromise species conservation goals. Most prior research has focused on the ecological effects of habitat fragmentation and/or impacts to hydrology. An understudied effect of land use change around parks investigates its impact on spatial and temporal patterns of vegetation productivity. With Yellowstone National Park at its core, The Greater Yellowstone Ecosystem supports the largest migratory herds of elk and bison left in North America. This area is experiencing land use change that has some in the wildlife and land management communities concerned that change will affect wild ungulate migration patterns, increase human-wildlife conflict and risk of disease transmission to domestic livestock, and possibly even attract large predators into human-populated areas. The present study examines these concerns within the context of land use impacts on patterns of grassland phenology and productivity (the primary forage of migratory ungulates) by comparing predicted patterns of phenology in the absence of human-activity to that observed under human land use. Results suggest that the primary impact is on the timing of productivity and occurs late in the growing season when irrigation of private-lands

artificially extends grassland growth into late-summer and fall months. Results also suggest that land use in low-elevation settings introduces a more heterogeneous pattern of phenology and productivity than is expected in the absence of human-activity. Low-elevation heterogeneous patterns on private lands under current land use mimic the total pattern of phenology across the rest of the study-area; which may suggest that private lands could offer a substitute for an ungulate migration strategy that crosses longer-distances and elevations. Although the future impacts of land use change on patterns of grassland productivity and ungulate migration patterns is largely unknown; results of the present study offer quantification of concerns related to land use effects on patterns of grassland phenology and productivity.

Introduction

Human land use around U.S. National Parks is intensifying; some studies find at rates that far exceed regional and national averages (Davis and Hansen 2011; Radeloff et al. 2010; Wade and Theobald; Wittemeyer et al. 2008). This is of concern because parks represent only portions of larger ecosystems (Gimmi et al. 2011; Hansen and Defries 2007; Hansen et al. 2011; Moon and Farmer 2010). Therefore, human activity (i.e. land use) can compromise the successful conservation of biodiversity in and around parks. Most prior work has focused on the effects of habitat fragmentation and/or land cover change impacts on hydrology (Ambrose and Bratton 1990; Svancara et al. 2009; Hansen et al. 2011). However, another broad-scale effect of land use on natural systems is that it often modifies landscape-scale patterns of vegetation phenology and primary-

productivity (Buyantuyev and Wu 2009; de Beurs and Henebry 2004, 2008; White et al. 2002; Zhang 2004). In many ecosystems, species-diversity and primary-productivity are positively related (Phillips et al. 2008; Williams et al. 2005) and large parks tend to protect low-productivity areas while urban and agricultural land uses are concentrated in high-productivity areas (Luck 2008; Scott et al. 2001). This pattern combined with observations that land use is altering broad-scale patterns of species richness via presumed impacts on primary-productivity (Williams et al. 2005), raises concerns about land use effects on protected-areas. Although these concerns are not new, investigations to date have remained cursory and largely limited to qualitative descriptions of change (Alcaraz-Segura et al. 2009; Tang et al. 2012). Better understanding land use effects on vegetation-phenology and -productivity is an important research topic that is highly relevant to biodiversity conservation and land use change around parks.

Remote Sensing Phenology and Land Use

A variety of remote-sensing methods have been proposed to both estimate vegetation phenology and primary-productivity, as well as to monitor land use change around protected-areas (Alcaraz-Segura et al. 2009; Garbulsky and Paruelo 2004; Tang et al. 2012). These methods are often based on indices of land surface reflectance (the Normalized Difference Vegetation Index, NDVI, for example) and the physical properties of leaf chlorophyll and other pigments involved in photosynthesis to absorb red portions of the electromagnetic spectrum while reflecting near-infrared portions (Huete 2002). Monitoring of land use is then based on the impacts that human activity has on land cover and vegetation. Land surface phenology (LSP, a term used to

distinguish it from field-based measures of phenology; Moody and Johnson 2001) has evolved from earlier remote-sensing studies to track seasonal changes in surface reflectance (NDVI) as recorded by dense time-series of satellite images. From annual time-series, LSP methods generate a suite of metrics that correspond to the timing and magnitude (i.e. productivity) of vegetation development (Jonsson and Eklundh 2002, 2004). Interannual changes in these metrics are then interpreted as either variability associated with short-term climate fluctuations (Anyamba and Eastman 1996; Myneni et al. 1997; Reed et al. 1994; White et al. 1997), or more persistent change as a response to a number of factors including: natural disturbance and recovery (Beck and Goetz 2012; Peckham et al. 2008; Verbesselt et al. 2010); longer-term climate change (Jeong et al. 2011; Linderholm 2006; Myneni et al. 1997; Parmesan and Yohe 2003); or land use change (Lunetta et al. 2006; Narumalani et al. 2004; Neigh et al. 2008).

Land Use Impacts on Phenology and Productivity

Land use can modify LSP in at least two distinct ways: by removing or replacing native land cover; and/or by changing the physical environment to which vegetation responds. The former case is straight-forward and involves activities such as: planting agricultural crops which has a tendency to increase primary-productivity (Buyantuyev and Wu 2009; Imhoff et al. 2004; Wardlow and Egbert 2008); harvesting timber, which initially reduces NDVI (Guerric et al. 2011; Roberts et al. 2004); the intentional introduction and maintenance of non-native species such as residential landscaping which can have a variety of effects including earlier start of the growing season and increased productivity as compared to wildland conditions (White et al. 2002; Shustack et al.

2008); and the unintentional introduction of weedy species with phenologies that are distinct from native vegetation (Clinton et al. 2010; Shustack et al. 2008). Changes to the physical environment can include: fertilization that changes soil properties and tends to increase primary-productivity (Imhoff et al. 2004; Schubert et al. 2010); irrigation of agricultural and residential landscapes that extends the growing season later into the fall in water-limited ecosystems (Buyantuyev and Wu 2012; Johnson and Belitz 2012); and temperature warming as a result of urban-heat-island effects that results in earlier vegetation growth in the spring in urban environments than surrounding rural and wildland settings (Kato et al. 2005; Zhang 2004).

The availability of studies that specifically develop the magnitude, direction and nature of change associated with individual land uses varies by land use type. Studies of agricultural and urban land uses are common and in general find that urbanization leads to an earlier start and later end of the growing season (although see Gazal et al. 2008) and reduced productivity compared to rural and wildland surroundings (although see Buyantuyev and Wu 2009) (Imhoff et al. 2004; White et al. 1997; Zang 2004). Agricultural land uses tend to increase productivity and result in a later end of the growing season in semi-arid ecosystems (Imhoff et al. 2004; Neigh et al. 2008). Studies of suburban and exurban land uses are fewer and in general find that productivity decreases with increasing population densities (Zhao 2011; Zhao et al. 2007), although these studies have largely been restricted to the eastern half of the U.S. One study found that the productivity of exurban land uses was higher than the agricultural land use that it replaced due to increases in the proportion of tree-cover (Zhao et al. 2007).

Generalizations of land use impacts on vegetation phenology and productivity are difficult and often found to be distinct to the environmental setting of the study-area (Buyantuyev and Wu 2009; Gazal et al. 2008; Williams et al. 2008). This variability highlights the importance of locally-focused studies that develop the ecological consequences of specific land use transitions that are of greatest concern. To the author's knowledge, there have been no prior studies that examine the effects of specific land uses on phenology and productivity in areas surrounding national parks in general or the Greater Yellowstone Ecosystem (GYE) specifically.

Most investigations of the impacts of land use on phenology compare LSP from urban areas to those observed in surrounding rural or wildland areas and infer change in a space for time substitution (although see Imhoff et al. 2000 for an interesting alternative to this method). A short-coming of this approach is that it does not account for systematic bias in the location of urban areas relative to rural areas (Jochner et al. 2012). Urban areas are commonly located in lower-elevation river valleys and on more productive soils than neighboring rural or wildland areas (Jochner et al. 2012; O'Neill and Abson 2009; Scott et al. 2001). Therefore, the biophysical setting of LSP in areas now occupied by urban land uses likely includes warmer spring temperatures and an earlier start of the growing season for example, than surrounding rural areas (Jochner et al. 2012). Most studies that find different LSP in urban versus rural areas attribute this difference to warming as a result of urban-heat-island effects (see White et al. 2002 and Zhang et al. 2004 for two of many examples); while other studies find differences along socio-economic gradients that are presumably related to variation in aesthetic preferences for different residential

landscapes and the management practices necessary to maintain them (Buyantuyev and Wu 2012). Common attempts to correct for differences in the location of phenology study-sites include the use of elevation and/or latitude as a surrogate for changes in biophysical setting (principally climate and soils) that are thought to affect LSP (Hudson-Dunn and deBeaurs 2011; Hwang et al. 2011; Jochner et al. 2012). However, using surrogates for biophysical setting often obscures the likely modes of change by which land use (i.e. human activity) changes phenology (e.g. urban-heat-island effects as compared to introduction of non-native species or aesthetic preferences that co-vary with socio-economic status). Ideally, investigations of land use impacts on LSP should both correct for differences in biophysical setting of land uses and develop the likely ways that human-activity is affecting LSP. The benefit of exploring modes of change is that it can guide future research and may highlight opportunities for management of unwanted change.

Grasslands of the Greater Yellowstone Ecosystem

Grass and shrublands (hereafter “grasslands”) are an important natural land cover type that is often underrepresented on public-lands and has disproportionately been the subject of human development on private-lands throughout the Northern Rocky Mountains, U.S. including in the GYE (Piekielek and Hansen accepted). Grasslands in the GYE provide habitat for the largest migratory herds of elk, (*Cervus elaphus*), and bison, (*Bison bison*) remaining in North America. Migratory ungulates in this ecosystem are thought to track grassland productivity across the landscape while simultaneously attempting to avoid deep winter snowpack and high predator densities (White et al. 2010;

Proffitt et al. 2011; Thein et al. 2009). Prior to European settlement, seasonal movements likely included utilization of low-elevation valley-settings that are now largely in private-ownership during winter and early spring months because snowpack was light and these were locations of earliest spring forage development (Skinner 1925). Little summer precipitation (in the absence of irrigation) leads to early-summer grassland senescence and ungulates historically moved to progressively higher-elevations throughout the year where grassland growth continued. Today, bison are largely not allowed to leave Yellowstone National Park (YNP) boundaries and only the Northern Yellowstone elk herd continues to make long-distance movements onto private lands each year.

Several contemporary management issues now bring the seasonal space-use of ungulates in the GYE to the forefront of the public, manager's and researcher's attention. First, the discovery of the disease brucellosis (*Brucella abortus*, a disease that causes abortion in wildlife and domestic cattle) in free-ranging herds (Cross et al. 2010) makes the co-mingling of both elk and bison with domestic livestock a major economic and wildlife management concern (Bidwell 2010; Cross et al. 2007; Proffitt et al. 2011). Second, there has been a recent socio-cultural shift in local residents' attitudes towards "New-western" ideals including valuing natural amenities such as wildlife viewing, over traditional values focused on agricultural productivity. New-western values and turnover in large ranch property ownership raises concerns about the privatization of elk herds and management of wildlife resources for the public (Gosnell et al. 2006; Gosnell and Travis 2005; Haggerty and Travis 2006; Robbins 2006). These concerns come in part from changes in private ranch management practices that are meant to encourage wildlife

presence on private-lands while excluding hunting access; thereby limiting wildlife management options and potentially jeopardizing the preservation of natural ungulate migration. In the most extreme cases, it has been reported that practices include irrigating high-quality forage crops without harvesting them in an effort to attract year-round herds of elk on private-lands (Haggerty and Travis 2006). Studies from across the Northern Rockies suggest an elk preference for private-lands over public (Proffit et al. 2011), and an attraction to the fertilized and irrigated grasses of alfalfa hay-crops, golf courses and residential landscaping on private-lands (Krausman et al. 2009; Henderson and O' Herren 1992; Lubow 2002; Thompson and Henderson 1998; Wait and McNally 2004). Within the socio-ecological context of YNP (including the unique natural resources that it protects) and recently observed change on surrounding lands, investigations of the landscape-scale impacts of land use on grassland phenology is of high research and management interest.

Study Objectives and Hypotheses

The objective of the current study is to quantify the impacts of specific land uses on grassland phenology and productivity in a study-area that is relevant to the effects of human activity on wildlife management around YNP (Figure 3.1). This is accomplished by applying biophysical models of LSP in the absence of human-activity (hereafter referred to as "wildland LSP") (Piekielek and Hansen unpublished, Chapter 2 this dissertation) to the study area and comparing them to present-day observations of LSP under human land use.

Prior work (Piekielek and Hansen unpublished, Chapter 2 this dissertation) identifies interactions between water-availability and demand as the principal limitation to plant-growth for low-elevations within the study-area with one exception: during early spring months water is not a limiting factor and the timing of spring growth is dictated principally by seasonal variation in solar radiation (i.e. photoperiod). Based on these observations we present the following hypotheses. Each hypothesis compares predicted wildland LSP to that which is observed under different land uses:

1. The timing of the start of the growing season (SOS) in residential areas trends towards later because many homes artificially support ornamental trees and shrubs. SOS may be later in agricultural settings due to planting dates and/or the unique phenologies of crops.
2. The timing of the end of the growing season (EOS) is later across all land uses because irrigation decouples vegetation from local precipitation regimes that include late-summer drying. This land use effect becomes successively more pronounced as residential land use intensifies (rural to urban) coincident with greater proportions of irrigated land area. Irrigated agricultural land use exhibits later than predicted EOS, however crop harvest may add variability to this relationship in some cases.
3. Magnitudes of peak annual greenness (MAX) are lower than predicted wildland MAX in high-density residential settings because significant portions of these areas have been converted to non-vegetated land covers (e.g. pavement, buildings etc). MAX gets progressively higher from high-

to moderate-intensity residential settings along with increasing proportions of vegetated and managed land cover; and then decreases in rural settings that are expected to be similar to wildland conditions. MAX is highest in agricultural settings due to irrigation and because agricultural crops are planted densely and exhibit rapid growth.

4. Patterns of total annual productivity (INDVI) under land use mirror those of MAX via the same assumed modes of change.

Methods

Study-area and Wildland Growing Conditions

The 7,400 square kilometer study-area (Figure 3.1) encompasses the upper Yellowstone River Basin and the public-private interface along YNP's northern boundary. The Paradise Valley is the main southwest to northeast low-elevation, privately-owned valley in the northern half of the study-area (Figure 3.1). Low-elevation private-lands were natively occupied by grasses and shrubs of mixed species (*Pseudoroegneria spicata*, *Festuca idahoensis* and *Artemisia* spp. for example). The study was inclusive in its definition of grasslands and focused on grass and/or shrublands as defined by: Despain et al. (1990) within YNP; the National Land cover Classification (Comer et al. 2003) on public-lands outside of YNP; and as defined below (Land use section) on private-lands. Low-elevations and northern portions of the study-area receive infrequent winter snow-cover and mild temperatures as compared to higher-elevations and more southern portions of the study-area. The growing season begins earliest at low-elevations and on south- and west-facing aspects and moves progressively upslope to

starting latest at higher-elevations and on north- and east-facing slopes. Low-elevations receive little summer precipitation and the growing season ends early in the year due to water-deficit (Piekielek and Hansen, unpublished, Chapter 2 this dissertation). The growing season ends progressively later as you move up to middle-elevations where water-limitations are relaxed due to a later start of the growing season and more summer precipitation. At the highest-elevations in the study-area temperature can be harsh year-round, snow-cover lasts up to 250-days per year and the growing season is short and ends early. The most optimal grassland growing conditions are generally found in middle-elevations where soils are deep (compared to higher-elevations), there is sufficient soil-moisture for growth and temperature and snow-conditions are not as harsh as those found at higher-elevations (Piekielek and Hansen unpublished, Chapter 2 this dissertation).

Land Use

The study-area was frequented by Native Americans prior to European exploration that began in the early 1800s and eventually led to the establishment of YNP in 1872 (Jacoby 2001). Areas outside of YNP that are now in federal ownership (primarily U.S. Forest Service) have experienced a variety of human uses from logging to grazing of domestic livestock; however, present-day human-activity in these areas is primarily recreational. There are a number of communities within the study-area

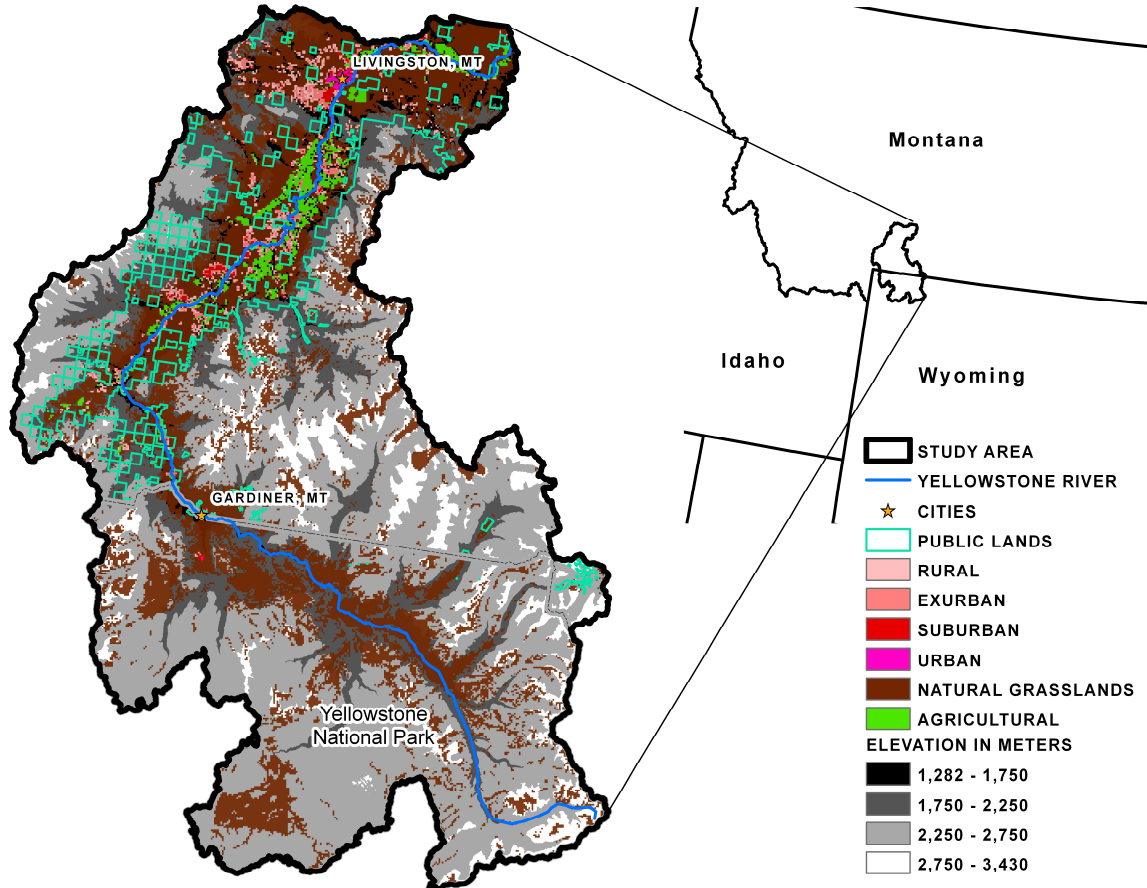


Figure 3.1. Map of study-area including location of land use, ownership and distribution of public and undeveloped grasslands. The “checkerboard” pattern of land ownership is an artifact of the Public-land Survey System and railroad land grants.

including Mammoth, WY (population 263; U.S. Census Bureau data) that is within YNP boundaries and the gateway community of Gardiner, MT (population 875; U.S. Census Bureau data) at the park’s north entrance. Livingston, MT (population 7,044; U.S. Census Bureau data) is the largest community and lies at the northern-most extent of the study-area.

On private-property, land uses range from agricultural to a variety of residential and commercial uses (Table 3.1, Figure 3.1). Maintained residential landscapes vary dramatically from very little disturbance of native vegetation to the maintenance of large

well-watered lawns and ornamental trees and shrubs of non-native species. Horses are commonly grazed in small to moderate numbers on residential properties. Commercial uses include a large private hunting ranch (reportedly almost 35,000 acres of mixed owned and leased lands), guest ranches and an 11,000 acre high-end luxury development and nature preserve. The area is a popular tourist destination and location to build second and vacation homes.

Agricultural practices include raising domestic livestock and cultivation of alfalfa-grass hay crops and small grains (wheat and barley). Hay fields typically yield one-cutting annually in dryland areas and in irrigated areas yield two-cuttings (first in late-June, second in late July). It is also common haying practice to “stockpile” which leaves late-summer and fall growth (from August to end of season) as winter-forage for livestock and also in order to maximize crop survival overwinter. Livestock are often allowed to graze in irrigated hay fields throughout early and middle portions of the summer. Many hay fields are kept on a short fallow rotation schedule of approximately three years and/or can be mixed with production of small grains. Approximately 90% of agricultural lands are irrigated within the study-area. Water for irrigation comes from the Yellowstone River directly, irrigation projects, and private wells. Of the remaining 10% of cultivated lands that are not irrigated, most are used to grow hay to feed domestic livestock as well as to grow winter annuals (U.S.D.A. National Agricultural Statistics Service).

Data from several sources were used to create a 250-meter spatial resolution land use map of the study-area. Montana Cadastral Mapping Program data was downloaded

during the summer of 2009. Montana Cadastral data are geo-referenced, vector-based datasets that describe land use by property-parcel as recorded for valuation and taxation purposes. Land uses are identified as occupied-residential, vacant-residential, actively-managed agricultural or fallow-agricultural and designate whether agricultural land is irrigated or not. In this dataset, irrigated agricultural lands were on-screen digitized using 2005 National Agricultural Imagery Program (NAIP) aerial photography. Cadastral data further classify non-irrigated agricultural lands by whether they have either significant potential for timber-extraction (i.e. are forested) or for domestic livestock grazing (i.e. are grasslands). To identify agricultural lands, we separated actively-managed and irrigated-lands from fallow and non-irrigated lands. Polygons of irrigated agricultural lands were used to produce a continuous data field of “percent irrigated agriculture” at the 250-meter scale for quantitative analysis of land use effects. This data layer was spatially-averaged to a 1-kilometer scale so that both LSP metrics and percent irrigated agriculture became an average of the subset of sixteen 250-meter pixels within each 1-kilometer pixel that was used to characterize agricultural lands.

In most studies, residential land uses are mapped using a density of occupied homes per unit area. Home locations were assumed to be at the centroid of small (less than 20 acres, or approximately one 250-meter pixel) property-parcels. Because some parcels within the study-area are quite large (e.g. over 1000 acres, or approximately 64, 250-meter pixels), actual homes sites were digitized for properties over 20 acres in size. Home sites were identified using NAIP aerial photography from the year 2009. The density of occupied homes within each 250-meter pixel was used to estimate a

continuous “housing density” layer at the 1-kilometer scale for quantitative analysis of residential land use effects on LSP. These data are summarized into common residential land use classes for presentation in Table 3.1.

Because the land use map was static and derived from a variety of data sources spanning multiple time-periods, we also took steps to validate this data layer and explore how much land use likely changed throughout the study-period. Validation was achieved by comparing the present land use map to land use classifications derived from aerial photography interpretation from years 2003 and 2009. A field visit to a combination of randomly selected sites as well as sites where there was disagreement between data sources was also performed during the summer of 2012.

Generating LSP

Because LSP metrics observed under human land use were compared to LSP as predicted by biophysical models for an average year (average of 2001 – 2009) it was important to use identical data (MODIS NDVI) and methods (TIMESAT algorithm, Jönsson and Eklundh 2002, 2004) as was used in biophysical modeling exercises (Chapter 2 this dissertation). However, quantitative comparisons made using 1-kilometer data were unproductive due to substantial mixing of the land use signal with other land covers. We therefore transitioned to using 250-meter NDVI (MODIS MOD13Q1 data product) to generate LSP metrics for the time-period 2001 to 2009 at a spatial resolution that better captured patterns of land use. LSP was generated for an average year in the same way as was done in biophysical modeling (i.e. an average of years 2001 – 2009).

Final LSP maps depicted SOS, EOS, MAX and INDVI for 250-meter resolution pixels across the study-area.

Land Use Effects on Wildland Land Surface Phenology

The land use map described above was used to select 1-kilometer (collections of up to sixteen 250-meter pixels) “study-sites” where LSP under human land use was compared to LSP under predicted wildland conditions. Study-sites were chosen that had little forest presence within 250-meter pixels (conifer forest at higher elevations and riparian deciduous forest along the Yellowstone River) and where land use was spatially-aggregated. Spatial aggregation was selected for so-as to eliminate pixels of the lowest percentages of land use cover where effects were assumed to be undetectable by the present methods. Land uses of long and linear shape (e.g. some flood irrigated agricultural fields and residential properties along rivers) were largely omitted from the study. The attributes of 250-meter pixels (up to sixteen per 1-kilometer study-site) under land use (LSP, housing density and percent agriculture) were spatially-averaged in order to compare them with 1-kilometer biophysically predicted wildland LSP. In total, 353 agricultural and 477 residential study-sites (1-kilometer pixels) were identified. For comparison and exploration of broad-scale pattern, we also present the maps of 1-kilometer LSP under human land use that were generated using 1-kilometer NDVI data (MODIS MOD13A2) as input. All LSP metrics represented average conditions based on data from years 2001 – 2009 (n = 9).

LSP observed under land use was compared to wildland LSP in several graphical and quantitative ways. In each case, the operational spatial scale of analysis was 1-kilometer based on the coarsest resolution of input datasets. Only weak relationships were found between continuous measures of land use (housing density and percent agricultural cover) and their effects on LSP; we therefore focused on comparisons across all intensities of residential and agricultural use. Because biophysical models used to predict wildland LSP had known distributions of errors, we interpreted differences between observed LSP under human land use and predicted wildland LSP within the context of these known errors. Empirical distribution functions were used to quantify the percentage of calculated differences (between observed land use LSP and predicted wildland at study-sites) that were above (i.e. greater than) and below (i.e. less than) the 95% confidence windows of biophysical model errors. Finally, maps of biophysically predicted wildland LSP were compared to maps of land use LSP in order to examine changes in landscape-scale patterns. Mapping results are presented for only pixels that are covered by some active human land use (undeveloped private and wildland grasslands are excluded) in order to focus on change as a result of land use.

Results

In general, grasslands make up 33% of the study-area with this being split somewhat evenly between public and private-lands (Table 3.1 and Figure 3.1). Undeveloped uses occupy the most private grassland area (11% of study-area) followed

by agricultural (2% of study-area), rural (1% of study-area), exurban (1% of study-area), and urban and suburban occupy the least area (less than 1% of study-area each).

Agreement between land uses mapped by the present study as compared to land use mapped from two other data sources and time-periods was modest (Table 3.2). More than half of the disagreement between irrigated agricultural areas identified in 2003 and those identified by the present study were consistent with either irrigation projects that were abandoned (between 2003 and 2005), or a propensity for the 2003 map to identify all private land parcels as under agricultural management. Disagreement between the present land use map and 2009 aerial photography centered around misidentification of irrigated agricultural lands (in 2009) as undeveloped lands by the present study. Nearly all of the areas of disagreement between residential areas identified in the 2003 land use map and those identified by the present study were consistent with intensifying land use (low-density residential to high-density, or agricultural to residential). What disagreement remained appeared to be related to housing densities that were identified in the 2003 map based on the number of structures that could be seen using aerial photography as opposed to the number of occupied homes as was identified by the present study. Field validation of land use maps suggested that some inconsistencies were related to scale and arbitrary placement of the 250-meter land use grid so that land uses were split in sometimes unnatural ways (e.g. a subdivision being split into two low-density residential pixels).

Table 3.1. Land use characteristics of study-area

Land use class	Makeup of Study-area (%)	Definition
Other	67	Not Grassland
Public Wildland Grasslands	18	Grasslands on public-land
Private Undeveloped Grasslands	11	Occupied* housing density: < 1 home per 80ac; vacant residential or undeveloped private- land
Agricultural	2	Actively managed* irrigated agricultural land
Rural	1	40.01 < Occupied* housing density acres per home < 80
Exurban	1	10.01 < Occupied* housing density acres per home < 40
Suburban	< 1	1.71 < Occupied* housing density acres per home < 10
Urban	< 1	0 < Occupied* housing density acres per home < 1.7

**Note: 'actively managed' and 'occupied' were determined based on 2009 Montana Cadastral data*

These results highlight the dynamic nature of human land use through time and the difficulties in characterizing land use at moderate spatial scales that are often-times more coarse than the pattern of land use itself. This last issue is especially common in the case of higher-density residential uses that take place on small property parcels.

Table 3.2. Land use map validation comparison with other data sources and time-periods. Percentages indicate the degree to which the land use map produced by the present study agreed with other land use maps at 250 randomly identified points within the study-area.

Land Use Source	2003 Air Photo Classification	2009 NAIP Photography
Irrigated Agriculture	59%	77%
Residential	53%	80%

Predictive power of wildland biophysical LSP models within the current study-area was found to be good for SOS and MAX and moderate for EOS and INDVI (Table 3.3). Mean prediction error for SOS was roughly one week (8.71 days) and up to two-weeks (15 days, 95% confidence interval). Mean prediction error for MAX was 0.07 and up to 0.15 (unitless, NDVI). EOS model errors were negatively biased, predicting later dates than observed more often than earlier dates. EOS models were accurate to within roughly three weeks (23.24 days) on average and sometimes predicted EOS up to 40 days later than observed. INDVI models were accurate to within 1.10 (unitless, integrated area under NDVI growing season curve) on average with errors up to 2.20 (95% confidence interval).

Table 3.3. LSP Biophysical model prediction performance for an average year (2001 – 2009). Errors were calculated by applying biophysical models to an independent dataset (n=260) and subtracting predicted LSP from actual. Root-mean-squared-errors and 95% confidence intervals are reported based on distribution of 260 errors (see Chapter 2 this dissertation for complete description of methods).

Biophysical Model	Root-mean-squared Prediction Error	Confidence Interval (95%) of Predictions Errors
Start of Season (SOS) (days)	8.71	-2.13 +/- 12.80
End of Season (EOS) (days)	23.24	-12.98 +/- 28.11
Annual peak growth (MAX) (NDVI)	0.07	0.01 +/- 0.14
Annual productivity (INDVI) (INDVI)	1.10	0.06 +/- 2.14

Comparisons of predicted wildland to observed LSP under residential land use showed some differences that were within the range of common model prediction errors (95% confidence intervals) and some that were outside of this range (Table 3.4). SOS for land use sites was similar to somewhat later (a mean of 5 days later) than predicted wildland. Twenty-six percent of residential sites exhibited later SOS than predicted wildland and 5% earlier and these were outside of the range of common biophysical model prediction errors (i.e. 69% were within common model prediction errors and therefore deemed an insignificant difference). EOS was substantially later (a mean of 40 days) than predicted wildland with 86% of sites exhibiting later EOS dates that were outside of common biophysical prediction errors and no sites exhibiting earlier EOS. MAX and INDVI for residential sites were similar to somewhat higher (means of 0.09

and 1.55) than predicted wildland. Thirty-five percent exhibited MAX and INDVI that were higher than predicted wildland and outside of the range of biophysical model prediction errors although 6% of residential sites exhibited MAX that was lower than predicted wildland and outside of the range of prediction errors.

Table 3.4. Comparison of LSP observed under residential land use versus predicted wildland condition using 477 study-sites.

LSP Metric	Land Use Range	Predicted Wildland Range	Mean Difference	Larger Positive Difference	Larger Negative Difference
SOS	71 - 163	105 – 137	5	26%	5%
EOS	181 - 330	201 – 265	40	86%	0%
MAX	0.28 – 0.92	0.45 – 0.69	0.09	35%	6%
INDVI	2.41 – 12.20	3.64 – 5.31	1.55	35%	0%

Comparisons of predicted wildland to observed LSP under irrigated agricultural land use showed some differences that were outside of the range of common model prediction errors (95% confidence intervals) (Table 3.5). SOS was similar to somewhat

Table 3.5. Comparison of LSP observed under agricultural land use versus predicted wildland condition using 353 study-sites.

LSP Metric	Land Use Range	Predicted Wildland Range	Mean Difference	Larger Positive Difference	Larger Negative Difference
SOS	78 - 139	105 – 137	7	25%	2%
EOS	180 - 315	201 – 265	47	85%	0%
MAX	0.36 – 0.91	0.47 – 0.67	0.14	47%	1%
INDVI	2.4 – 10.40	3.65 – 5.31	2.20	50%	0%

later (a mean of 7 days later) than predicted wildland conditions. Twenty-five percent of SOS dates in irrigated agricultural settings were later and 2% earlier than wildland and outside of common biophysical model prediction errors. EOS was substantially latter than predicted wildland (a mean of 47 days later). Eighty-five percent of irrigated agricultural EOS were later (0% earlier) and outside of biophysical model errors. MAX and INDVI were both generally higher than predicted wildland (means of 0.14 and 2.20; Figure 3.2) with approximately 50% of sites exhibiting MAX and INDVI that was higher and outside of the range of biophysical model errors.

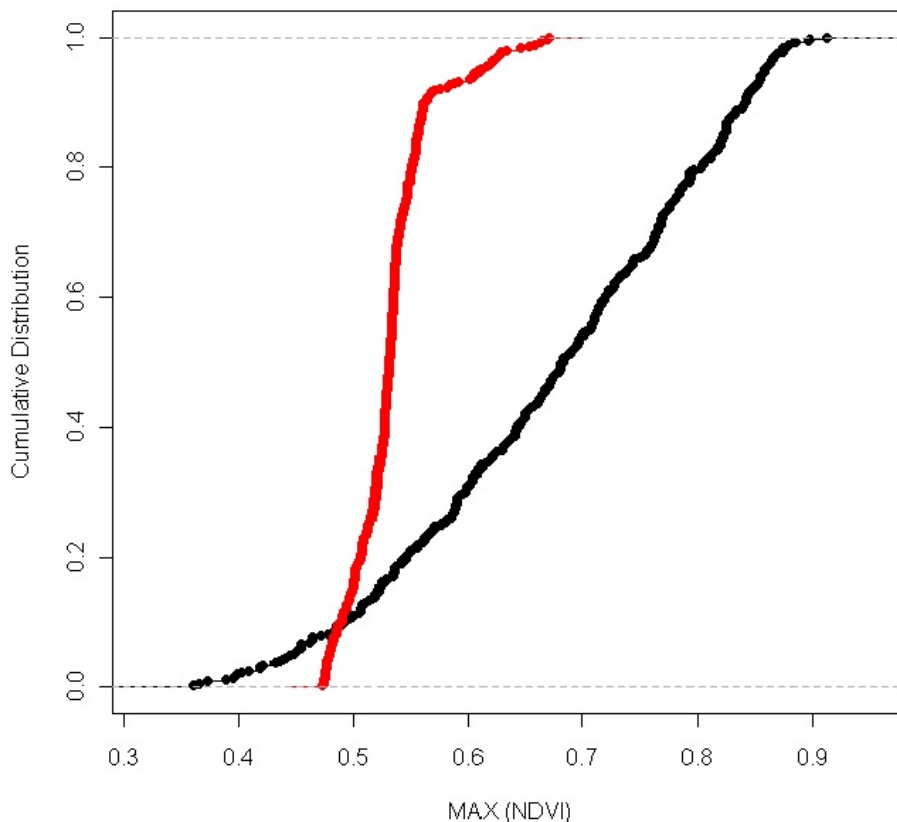


Figure 3.2. Empirical cumulative distribution functions of MAX under agricultural land use (black line) versus predicted wildland condition (red line) ($n=353$). Half of ag. sites are higher and outside of common model wildland biophysical prediction errors (Table 3.5).

Maps of the spatial pattern of predicted wildland as compared to observed land use LSP exhibited some similarities and some differences (Figures 3.3-3.6). Consistent with quantitative results, SOS appears to be largely unchanged from wildland conditions under land use. The growing season begins in April and May for most private-lands in the study-area (Figure 3.3). This is in contrast to EOS, which appears to undergo dramatic change from wildland conditions (Figure 3.4). EOS throughout much of the Paradise Valley and northern portions of the study-area (around Livingston, MT, see Figure 3.1 for location) is predicted to occur in July or August under wildland conditions. Under land use, EOS is observed to occur in September and October for the same areas. Other northern portions of the study-area (farther from Livingston) exhibit mixed EOS dates from July through November (Figure 3.4). Annual peak growth rates (MAX) for wildland conditions were predicted to be between 0.41 and 0.6 with large contiguous areas of similar MAX and little variation across private-lands of the study-area (Figure 3.5). Under land use, MAX ranged from 0.3 to 0.84 with dramatically different MAX values immediately adjacent to each other (Figure 3.5). Maps of INDVI largely mirrored those of MAX exhibiting a more heterogeneous pattern of INDVI under land use as compared to predicted wildland conditions (Figure 3.6).

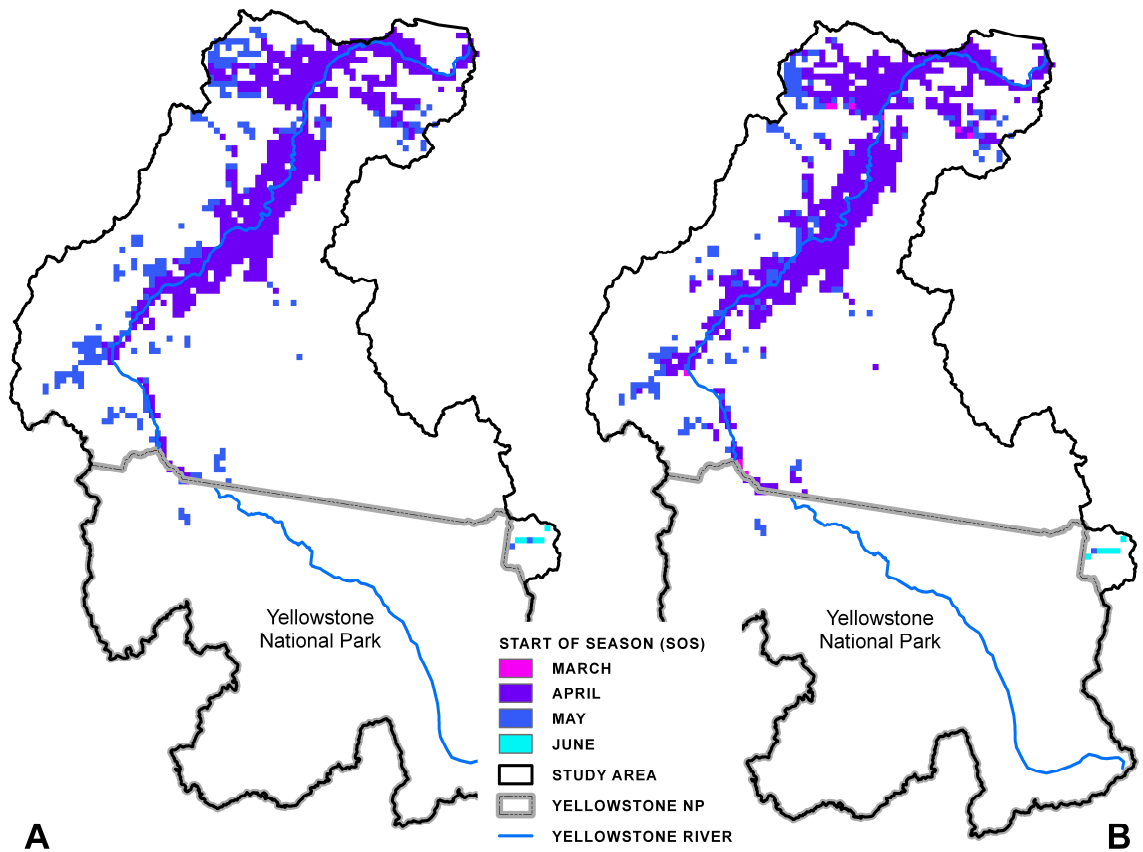


Figure 3.3. (A) Comparison of biophysically predicted average (2001 – 2009) timing of the start of the growing season (SOS), versus (B) observed SOS under human land use using 1-kilometer data. Study results find few differences between predicted wildland and land use SOS.

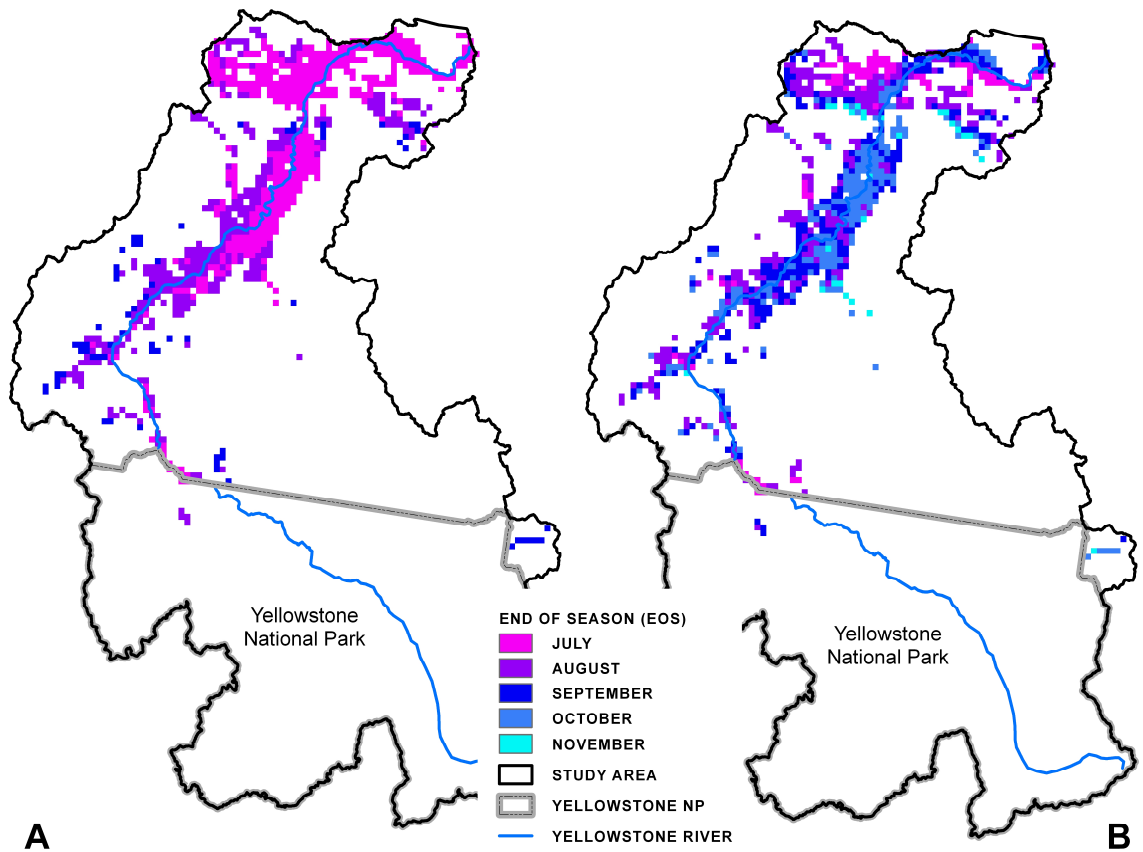


Figure 3.4. (A) Comparison of biophysically predicted average (2001 – 2009) timing of the end of the growing season (EOS), versus, (B) observed EOS under human land use using 1-kilometer data. Under human land use the growing season is lengthened in the fall by over 40 days on average across land use types.

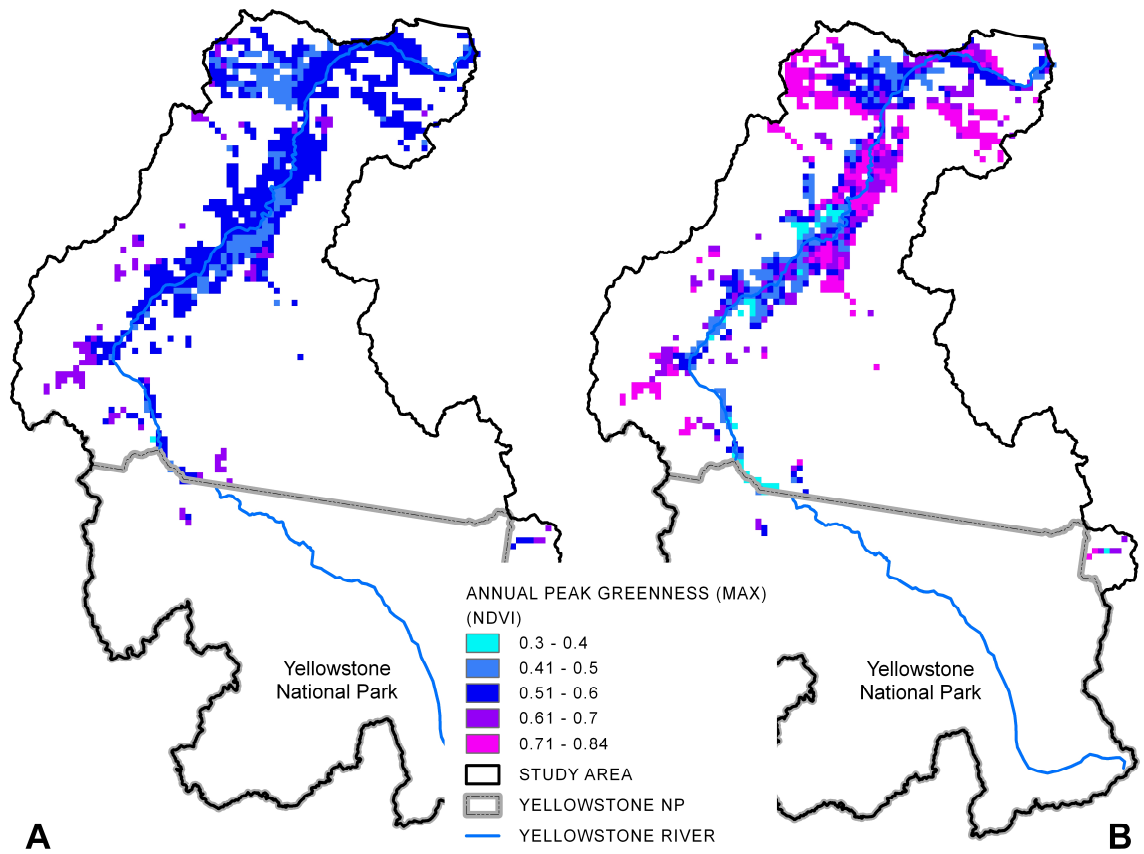


Figure 3.5. (A) Comparison of biophysically predicted average annual peak greenness (MAX) (A), versus, (B) observed MAX under human land use using 1-kilometer data. Grasslands under human land use generally exhibit higher average MAX than their predicted wildland condition.

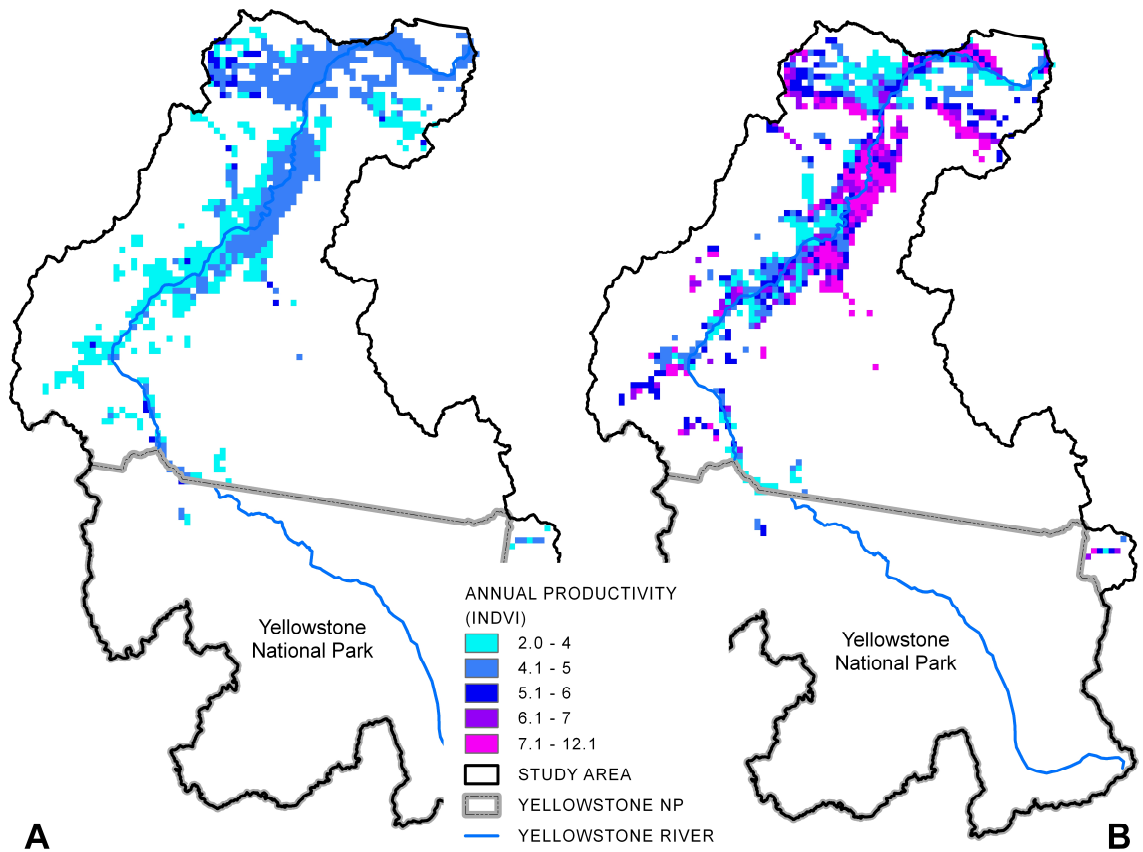


Figure 3.6. (A) Comparison of biophysically predicted average (2001 – 2009) total annual productivity as measured by NDVI (INDVI), versus (B) observed INDVI under human land use using 1-kilometer data. Grasslands under human land use exhibit higher average annual productivity than their predicted wildland condition and this is more pronounced for irrigated agricultural land uses than it is for residential land uses.

Discussion

Summary of Results

In general, land use did not appear to modify SOS from its wildland biophysical state whereas it substantially modified EOS to later dates. Irrigated agricultural land use also generally increased MAX and INDVI. Patterns of LSP for areas under human land use appeared to trend towards more spatial heterogeneity on private-lands for all LSP metrics except SOS. Results suggest the likely modes of change due to human-activity and have ecological implications for landscape-scale environmental conservation and management in the northern GYE.

Modes of Land Surface Phenology Change and Constancy Under Land Use

Start of the Growing Season (SOS): Previous studies have observed SOS dates that are: over a week earlier (8.70 days) than surrounding rural areas in New York City (Zhang et al. 2004), and up to three weeks (20 days) earlier throughout the Northeastern and Midwestern U.S. (White et al. 2002) as a result of urban-heat-island effects. Gazal et al. (2008) aimed to test the prevailing “earlier SOS-urban-warming” paradigm with a global study of deciduous trees in temperate ecosystems and observed earlier, but variable (1-23 days earlier) budburst dates in cities relative to surrounding rural areas. In addition to urban-warming as the likely mechanism of change, other studies suggest that invasive and/or managed species in urban environments account for differences in the timing of springtime vegetation development (Buyantuyev and Wu 2012; Shustack et al.

2009). Studies that observe earlier SOS in urban versus surrounding rural areas are in contrast to the present study that found no land use effect on SOS. There are several possible explanations for this difference including some methodological, some physiographical and some socio-ecological.

Urban and suburban settings are rare in the present study-area (together accounting for only ~1% of the total land-area); as such, we focus our interpretation of these results on a discussion rather than conclusions. It has been pointed out by others (Jochner et al. 2012) that there is substantial bias in the location of urban areas towards biophysical settings that likely exhibit earlier than rural and wildland SOS dates under wildland conditions. This is also true of urban and suburban areas within the present study that are located at low-elevations near the Yellowstone River. The present study's correction for this bias by using predicted wildland conditions based on biophysical setting could account for the lack of evidence of a land use effect on SOS. Other possibilities are that the urban/suburban areas of the present study are simply not large enough (Livingston, MT population ~7,000), or are within the wrong landscape context to support urban-warming. Although urban-heat-island effects have been well-documented in high biomass ecosystems where human infrastructure replaces forest that has a high capacity for evapotranspiration (i.e. Eastern and Midwestern U.S.); recent findings suggest that urban-warming is either dampened or altogether absent in semi-arid low-biomass systems like the grasslands of the present study-area (Imhoff et al. 2010).

The most likely explanation for the absence of a land use effect on SOS is socio-ecological and related to the phenology of preferred urban and suburban vegetation.

Intensively maintained lawns and landscaping are rare in the study-area and occur primarily across dispersed low-density residential settings as opposed to within urban and suburban settings. Often shading lawns in urban and suburban settings (and obscuring them from the view of satellites) are a variety of ornamental native and non-native deciduous trees. Ash (*Fraxinus* spp.) and Maple (*Acer* spp.) make up the majority of the urban forest canopy in Livingston, MT, according to urban forest statistics published online by the city of Livingston (http://www.livingstonmontana.org/living/urban_forest.html).

Across the study-area, residential tree-cover is generally associated with housing density with high-densities of each gradating to lower-densities. The consequence of this pattern is that the urban and suburban SOS signal (as measured by satellite) is dominated by common ornamental tree species that tend towards later leaf-out dates compared to surrounding native grasses (McGregor and Barkley 1986). If there is a trend towards earlier SOS for non-native grass lawns within the study-area it is obscured by overstory ornamental species. Further research using ground-based observations is needed to better understand urban/suburban modifications (or lack thereof) to wildland SOS in the study-area. Similarly, future modification of SOS remains unknown as urban/suburban vegetation dynamics will be shaped by the aesthetic and recreational preferences of future residents (Buyantuyev and Wu 2012). It is interesting to note that there was only a very weak relationship between housing density and all of the LSP metrics including SOS; suggesting that how many homes per unit area may not be as important as how those lands are managed.

End of the Growing Season: Late-summer drying characterized by interactions between low soil-moisture and high evaporative-demand, limits plant growth (EOS) of wildland grasslands within the present study-area (Chapter 2 this dissertation). At the most extreme levels of evaporative demand plant growth ceases even in the presence of sufficient soil moisture (Jolly et al. 2005; Osonubi and Davies 1980; Tenhunen et al. 1982); however those conditions are rare to absent in the present study-area. Instead, biophysical models suggested that plant growth continues when there is sufficient soil-moisture even in the presence of high evaporative-demand (Chapter 2 this dissertation). Therefore, widespread irrigation of crops and residential landscapes provides the most likely explanation for the observed delay in EOS under human land use. Irrigation augments late-season soil-moisture and decouples plant growth from local climate regimes (Buyantuyev and Wu 2012). This land use effect was most pronounced in agricultural areas where the proportion of irrigated land area is greatest.

Water resources for irrigation of agricultural lands are limited and declining across the U.S. (Clemmens et al. 2008) as they are reallocated to other uses including residential. Up to 75% of residential water use is allocated to irrigating residential landscapes in arid and semi-arid environments (Milesi et al. 2005). This national trend is also true of Southwestern Montana where some agricultural water-resources are being reallocated from crops to residential and in-stream uses as exurban development replaces agricultural lands (Gosnell et al. 2007). While irrigation of agricultural crops may decline in the future, residential expansion may offset this change, resulting in similar effects on landscape-scale EOS. This suggests that monitoring future land use change and

associated patterns of irrigation is an important priority for the present study-area. While satellite methods to monitor agricultural water-use are well-developed (Thenkabail et al. 2009), only recently have they been developed for residential landscapes (Johnson and Belitz 2012).

Peak Annual Greenness (MAX) and Total Annual Productivity (INDVI): Peak annual growth rates (MAX) and total annual productivity (INDVI) (together referred to here as “productivity”) of wildland grasslands in low-elevation settings of the present study-area are primarily constrained by lack of available water during times of year that are optimal for plant growth in other ways (high solar radiation and temperature; Chapter 2 this dissertation). Agricultural land use commonly exhibited higher productivity than predicted wildland conditions. However, there was only limited evidence found for increases associated with residential land uses (higher values in general, but many within common biophysical model errors). Increased productivity on agricultural lands is likely due to densely planted crops that are intensively management (fertilized and irrigated) (Buyantuyev and Wu 2009; Imhoff et al. 2004). Within a broader geographic context, intensively-managed vegetation is not limited to agricultural lands, but rather is motivated by socio-economics and aesthetic or other preferences (recreational for example) for shaping vegetation to meet human needs (Buyantuyev and Wu 2012; Gobster et al. 2007). Urban and suburban parks and golf courses are not agricultural by land use type, but are associated with substantial increases in primary-productivity due to intensive management (Johnson and Belitz 2012; Milesi et al. 2003). There is one golf course within the study-area covering three MODIS pixels

that also showed significant increases in grassland productivity but was excluded from the analysis because it provided only a single study-site. In arid and semi-arid regions of the U.S. (Arizona and California) other studies have observed increases in primary-productivity as a result of land uses other than irrigated agriculture (Buyantuyev and Wu 2012; Williams et al. 2005). Land use within the present study-area appears to be shifting away from agricultural uses (Haggerty and Travis 2006); however this may not mean a return to more natural levels of grassland productivity on private-lands. Similar to affects on EOS, should residential areas expand and/or the socio-economic characteristics and recreational preferences of new-residents change; land use modification of grassland productivity (other than agricultural) will also likely change. Cultural norms, aesthetic and recreational preferences and landscape change remains a sorely understudied topic that is highly relevant to land use modifications of grassland productivity (Buyantuyev and Wu 2012; Nassauer et al. 2009).

Spatial Heterogeneity of Land Surface Phenology Under Land Use

The location and nature of land use within the study-area has modified spatial and temporal patterns of LSP; with the principle outcome being greater heterogeneity of grassland phenology and productivity on private-lands and less contrast between public and private-lands. Biophysical controls on LSP operate at a coarse-spatial scale (panel A of Figures 3.3-3.6), while human activity can relax those controls and operates at finer-spatial scales (panel B of Figures 3.3-3.6) (Williams et al. 2008). Under wildland conditions within the study-area, grassland productivity generally increases as you move

from low- to middle-elevation and then declines at the highest elevations (Chapter 2 this dissertation). Under land use, this pattern changes so that some of the most productive grasslands are found at lower-elevations and immediately adjacent to lower-productivity wildland and undeveloped grasslands. Stated another way, the full spectrum of wildland grassland productivity within the study-area is now represented on private-lands under mixed land uses. To the extent that migratory ungulates respond to study-area wide heterogenous patterns of grassland productivity, they may also respond to finer-scale heterogeneity associated with human-activity.

Implications for Management and Conservation

Land use change is of local concern within the GYE (Gude et al. 2007; Parmenter et al. 2003); however rates of change are slow relative to other national parks around the country (Davis and Hansen 2011; Piekielek and Hansen *accepted*). Land area dedicated to agricultural uses in the GYE is in decline while area dedicated to rural and exurban uses are on the rise (Parmenter et al. 2003). Site-selection for newly constructed homes has implications for wildlife habitat conservation and human demographic trends and socio-economic factors that appear to explain home-location choice in the GYE are not encouraging for future conservation efforts (Petersen et al. 2008). Future exurban land use change is expected to occur disproportionately within riparian areas, bird diversity hot spots and grasslands (among other habitat types) (Gude et al. 2007). Based on the results of the present study, when grasslands are replaced by exurban development we should expect the growing season to be lengthened and possibly for productivity to increase. We should also expect spatial heterogeneity in late growing season conditions

to increase at low-elevations and decrease across larger spatial scales. The impacts of exurban uses on landscape-scale vegetation phenology and productivity will likely increase in the future along with land use intensification. The specific impacts will depend on whether exurban development replaces undeveloped or other (agricultural for example) land uses, and the preferences of future residents.

Seasonal use of private-lands north of YNP (within the study-area) by migratory elk and concerns about the privatization of wildlife could be exacerbated (or improved) by future land use change. In general, elk are recognized to readily adapt migration strategies to take advantage of forage resources and refuge from predators provided by human development (Geist 1982; Kloppers et al. 2005; Mckenzie 2001; Thompson and Henderson 1992). Within the small community of Mammoth, WY, elk are noted to have already habituated to regular human activity (Cassirer et al. 1992); and during winter months at lower-elevations, they appear to prefer private-lands of lower-predator densities and higher-productivity over adjacent wildland areas (Proffitt et al. 2011). Residential land use change and associated changes in habitat selection by elk have been documented throughout western North America including: The Hualapai Mountains of Arizona (Tucker et al. 2004), Estes Park, Colorado (Berris 1987; Lubow et al. 2002); southwestern Colorado (Wait and McNally 2004), Alberta, Canada (Hebblewhite et al. 2006; Mckenzie et al. 2005), and western Montana (Burcham et al. 1999; Thompson and Henderson 1998). Should some (or most) YNP elk abandon their seasonal migration back to public lands there are several possible ecological consequences ranging from relatively mild to more severe. More elk on private-lands for longer periods of time would almost

certainly mean more conflict with land owners, pets, and drivers on roadways regardless of whether wildlife-viewing is valued by residents or not. Conflicts could rise to a level that places a strain on resources that are dedicated to management of wildlife-human conflicts as has happened in many locales in southwestern MT with high populations of urban and suburban deer (Krausman et al. 2009). More elk on private-lands for longer periods of time would also increase the risk of disease transmissions to domestic livestock, which is already of high concern. Finally, if elk numbers increase on private-lands in concert with decreasing numbers within YNP, it is possible that specialist predators like wolves (*Canis lupus*) may adapt their patterns of space use along with their primary prey. Wolves are thought to be adaptive to “modest levels” of human disturbance which could be interpreted as exurban environments (Weaver et al. 1996). A variety of large carnivores have followed their prey into human-settlements in the Rocky Mountains U.S. and around the world with less-than-desirable consequences for both human residents and carnivores (Ogutu et al. 2005, 2009; Baron 2004). This last possibility may represent a worst-case future-scenario that would seriously compromise the ability of wildlife and park managers to ensure the protection of two iconic Yellowstone species, elk and wolves.

Many of the management concerns surrounding other ungulate species in expanding exurban environments are similar to those surrounding elk. White-tailed deer are recognized to thrive in urban to exurban environments where they are afforded day time cover (Swihart et al. 1995) and access to the high-quality forage of managed lawns and other residential landscaping (DeNicola et al. 2000). A number of studies document

higher survival rates for urban and exurban white-tailed deer than for rural and wildland populations (Etter et al. 2002; Storm et al. 2007). Mortality in urbanizing environments is primarily associated with vehicle collisions rather than hunting or starvation (Etter et al. 2002). In addition to the nutritional content of exurban forage, the present study adds the timing of forage availability (extended growing season as a result of irrigation) as an important aspect of human modification of ungulate habitats. In the absence of irrigated residential and agricultural landscapes, ungulates may be forced to look elsewhere for green forage during late-summer and fall months.

For species other than ungulates the impact of urbanizing landscapes is less well-developed. As a result, the expected future impacts of land use change and associated modification of grassland productivity is less clear. Other studies suggest that areas of higher-productivity (riparian deciduous forest for example) on private-lands surrounding YNP are hotspots for birds (Hansen and Rotella 2002); and increased vegetation productivity as a result of land use has been associated with increased bird richness in other locales (Buyantuyev and Wu 2009). In this light, the artificial maintenance of expanding urban and suburban forests on private lands within the study-area may provide more habitat for native birds. However, human activity can also provide an avenue for invasive species introductions that may jeopardize native species persistence (Williams et al. 2008) and Gude et al. (2007) suggest that human development of bird hotspots in the GYE would likely lead to increased risks of extinction for many native birds.

Many small mammals are herbivorous and rely on day-time cover much the same way that ungulates do. Therefore, they may also benefit from lower-density residential

development and increases in the duration and magnitude of forage productivity associated with human activity. However, many are also susceptible to predation by domestic pets, principally cats (Bock et al. 2002); making the aggregated effects of increased forage availability and predation unclear. Moving up to the higher trophic levels of mesopredators, the impact of increased productivity associated with land use change will likely be mediated by primary-consumers, tolerance of mesopredators by humans, and the adaptability of individual species to human activity.

It is expected that changes in coarse-scale patterns of vegetation phenology and productivity have broad ecological consequences that cross trophic-levels; however, the nature and timing of those consequences remain not well-understand (Buyantuyev and Wu 2012; Williams et al. 2005).

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CHAPTER 4

PATCH DYNAMICS OF GRASSLAND PHENOLOGY IN THE UPPER
YELLOWSTONE RIVER BASINAbstract

Patch-dynamics studies have historically focused on vegetation cover and structure as a result of disturbance and succession over time-scales of years to decades. Examination of the size and spatial arrangement of distinct vegetation patches has led to improved understanding of a variety of spatially-complex ecological relationships including meta-population dynamics. More recently, the importance of the seasonal timing of vegetation development (green-up, budburst etc.) and senescence (or leaf-drop etc.) has garnered increased attention due to its ability to help to explain some species' distributions and life-history adaptations. This topic is especially well-developed for mobile, large-bodied herbivores where the timing and spatial location of nutritious forage is relevant to individual, population and species-level traits, behaviors and relationships. Numerous studies are now using synoptic estimates (satellite derived indices for example) of forage quantity and quality to demonstrate strong relationships between herbivore space use and different stages of forage phenological development. However, missing from recent studies has been the application of a patch-dynamics perspective that spatially-aggregates areas of similar forage conditions through time into patches and considers their timing and spatial arrangement. Development of the patch-dynamics of forage phenology compliments existing studies that consider the relationship between

forage phenology and herbivore presence, but not patterns of forage patches. We use satellite-derived estimates of vegetation phenology to describe the patch-dynamics of the grazing system (i.e. grasslands) of the Northern Greater Yellowstone Ecosystem. The patch-dynamics approach reveals that the heterogeneous environments of the Yellowstone Plateau provides young nutritious green forage for herbivores for almost half of the year; which may provide a unique resource within the Northern Rocky Mountains. In addition to improving our understanding of herbivore-forage relationships; the patch-dynamics of vegetation phenology is also likely applicable to a broader suite of species ecologies and ecological processes where the spatial arrangement and timing of vegetation development plays an important role.

Introduction

A central question in ecology seeks to understand the persistence, abundance and movements of organisms in relation to resource heterogeneity in both space and time (Jonzen et al. 2004; Mueller et al. 2011; Searle et al. 2010; Weins 1976). The concept of patch-dynamics has been especially useful to this task and has led to improved understanding of a variety of topics including: metapopulation dynamics (Amarasekare and Possingham 2001; Hanski 1999); minimum dynamic areas for reserve design and biodiversity conservation (Cromsigt et al. 2009; Pickett and Thompson 1978); and conditional dispersal strategies (Bowler and Benton 2005). Patch-dynamics highlights the importance of natural and anthropogenic disturbance and succession as drivers of heterogeneity in vegetation cover and structure in ecosystems (Forman 1995; Pickett and

White 1985). In combination with hierarchy theory, the patch-dynamics concept also provides a framework for linking landscape pattern to ecosystem process at multiple spatial scales (Gillson 2004; Wu and Loucks 1995).

Patch-dynamics studies have historically been focused on vegetation cover and structure as a result of disturbance and succession over time-scales of years to decades (Pickett and White 1985). For example, when a mature conifer forest burns in the Greater Yellowstone Ecosystem (GYE) the grasslands, shrublands and broad-leaf deciduous forest that often occupy that patch post-fire provide habitat for a variety of wildlife species until conifer forest reestablishes (Gallant et al. 2003). Throughout seasons (rather than years) vegetation development (green-up, budburst etc.) and senescence (or leaf-drop etc.) is also of known importance to organisms and can help to explain life-cycle adaptations (Pettorrelli et al. 2009). This topic is especially well-developed for herbivores where the seasonal development (i.e. phenology) of forage is relevant to the space-use, (Boone et al. 2006; Hebblewhite et al. 2008; Mueller et al. 2008), body-mass and foraging strategies (Cromsigt et al. 2009; Mysterud et al. 2001; Wilmshurst et al. 2000), timing of parturition (Ryan et al. 2007) reproductive success and juvenile survival (Pettorrelli et al. 2007) and population size (Andrea et al. 2008a, 2008b; Pettorrelli et al. 2009; Wang et al. 2009) of a diversity of herbivores. Forage-phenology describes seasonal changes in the quantity (i.e. biomass) and quality (i.e. nutrient content, especially nitrogen) of forage throughout the year. Forage quality generally decreases with plant development as the proportion of plant material that is indigestible by herbivores increases (Frank et al. 1998; Frank and McNaughton 1992; White 1983).

There is a trade-off between consuming forage of high-quality in small quantities and consuming lower-quality forage in larger quantities. Understanding this tradeoff in the context of different feeding and digestive strategies has helped to explain herbivore abundance, diversity and competition (Cromsigt et al. 2009; Pettorelli et al. 2009; Wilmshurst et al. 2000).

Prior forage-phenology studies have largely focused on the timing and characteristics of areas that were actually used by herbivores rather than the spatial and temporal patterns of forage patches. This choice highlights an assumption that herbivores make optimal decisions in terms of their foraging behavior (MacArthur and Pianka 1966) (although the unit of maximization remains debatable, Bergman et al. 2011) and that spatial relationships (e.g. proximity, patch size etc.) are generally unimportant. This assumption goes untested without investigation of the landscape context (i.e. pattern of patches available) within which space use takes place. A patch-dynamics approach to mapping forage-phenology would also likely offer insight to the ecological processes and relationships (many of which are related to climate) responsible for patterns of forage patches, (Cebrian et al. 2008; Mysterud et al. 2001; Post et al. 2008). In-so-doing, investigation of the patch-dynamics of forage-phenology may also contribute to our understanding of the impacts of climate change on herbivores (Pettorelli et al. 2005; Post et al. 2008; Sharma et al. 2009; Turnen et al. 2009).

Vegetation-phenology and productivity were historically estimated at the plot scale based on field measurements that were of limited temporal frequency and spatial coverage (Reeves et al. 2006). These datasets precluded a patch-dynamics approach that

requires estimating stages of phenological development at fine temporal scales and across often broad spatial coverage. More recently, satellite estimates of vegetation-phenology (the normalized-difference-vegetation-index, NDVI, in particular) have proven to be quite useful for estimating forage-development and answering a variety of questions in animal ecology (see Petorelli et al. 2011 for a review). For mobile large-bodied herbivores, there appears to be a strong relationship between NDVI, spatio-temporal patterns of forage chemistry (i.e. quality) and the content of herbivore fecal matter (Christiansen and Creel 2009; Hamel et al. 2009; Showers et al. 2006). These results suggest a strong link between seasonal forage development that can be observed synoptically via satellite and animal behavior such as migration, foraging strategies and space use. In particular, this relationship has been observed to begin when NDVI reaches approximately half of its annual amplitude in the spring for grasslands in the GYE (Christiansen and Creel 2009).

In addition to the NDVI of forage, its rate of change during spring months also appears to be an important factor mediating the relationship between herbivores and forage-phenology (Pettorelli et al. 2007). The rate of change is related to the rate of green-up (i.e. vegetation development and biomass accumulation). It therefore controls access by herbivores to high-quality forage by limiting the time that forage spends in early stages of growth. Rapid green-up may “smooth-over” spatial heterogeneity in the timing of forage growth that is thought to be an important determinate of access to high-quality forage in mountain ecosystems (Myserud et al. 2001; Pettoelli et al. 2009). During gradual green-up for example, an herbivore may be able to make small upslope

movements or movements to alternate aspects and remain in patches of forage in early stages of development. This is in contrast to rapid green-up conditions where movements are longer or the duration of access to forage in early stages of development is diminished. Collectively, the spatial location, timing of early stages of development and rate of NDVI change describe the patch-dynamics of forage-phenology.

To the author's knowledge no prior study has mapped the patch-dynamics of vegetation phenology. In addition to being relevant to herbivores, the timing and spatial location of vegetation development is also likely important to other species ecology such as to mediating the relationship between ground prey and their predators (Klassen et al. 2010; Newbury et al. 2007) and for the diet selection of omnivores (Bojarska et al. 2012). It may also be applicable to other ecological processes that are contagious such as the spread of fire or disease.

The objectives of the current study are to develop methods to map the patch-dynamics of vegetation phenology using the latest tools and methods. We demonstrate the approach for grasslands of the GYE due to their importance to a variety of large-bodied herbivores of high conservation and research interest. In lieu of formal hypotheses we present the following expectations for results based on current ecological understanding of grassland phenology in the GYE.

Expected Results Based on Current Ecological Understanding

The study-area is characterized by steep environmental gradients (in topography, soils and climate) which are known to influence vegetation cover and phenology

(Despain 1990). The Yellowstone River Valley is broadest in the northern most portion of the study-area (Figure 4.1) and this is in stark contrast to the variable terrain and incised headwater valleys of the Yellowstone Plateau (southern portions of the study-area). Based on current ecological understanding we offer the following expectations for the patch-dynamics of grasslands in the Upper Yellowstone River Basin study-area: Grasslands green-up earliest in low-elevation and northern portions of the study-area where patches are large and compact in shape as a result of relatively homogenous biophysical conditions. Green-up of middle- and higher-elevation patches follows with the largest patches occurring in the Lamar Valley (the broadest river valley of headwaters areas) of YNP. By late summer, the only grassland patches left in early stages of development are at higher elevations within YNP. Rates of grassland development are positively related to elevation due to climatic limitations to growth imposed by shorter growing season length.

Methods

Study Area

The study-area encompasses the northern-most portion of the GYE and is bounded by the Upper Yellowstone River Basin including portions of Yellowstone National Park (YNP) and adjacent private lands (Figure 4.1). Grasslands in the GYE support the last remaining long-distance migratory herds of ungulates in the lower 48 states (Berger 2004; White et al. 2009). Grasslands are patchily distributed across steep environmental gradients. There is a positive relationship between elevation and

precipitation in the study-area and negative relationship between elevation and temperature. The highest-elevations receive much of their precipitation as snow and continuous snow-cover is common for up to approximately 250-days per year. Summer precipitation is light throughout the study-area. This is especially true of low-elevations where late-summer drying limits vegetation-productivity (Chapter 2 this dissertation). See chapters 2 and 3 of this dissertation for a more detailed description of the study-area including grassland species, land use and climate.

Overview of Methods to Identify Natural Grasslands

Details of methods to identify natural grasslands in this ecosystem are given in Chapter 2 of this dissertation. In summary, grass and/or sagebrush land cover (together referred to here as “grasslands”) on both public and undeveloped private lands were identified using a variety of spatially-explicit data layers. Grasslands that provide substantial grazing resources for both wildlife and domestic livestock were included in the analysis.

Summary of Methods to Identify Forage-phenology

The present study used NDVI data from the MODIS AQUA (MYD13Q1) and TERRA (MOD13Q1) sensors in order to produce maps at the finest spatial and temporal scales possible using standard MODIS products. MODIS AQUA and TERRA data production is staggered in time (16-day intervals) to enable the generation of datasets with 8-day return. In contrast to MODIS TERRA data products used in Chapter 2 that began in year 2000; MODIS AQUA data became available beginning January 1st, 2003.

As such, data in the present study described NDVI at 250-meter spatial resolution for each 8-day period from January 1st, 2003 to December 31st, 2009.

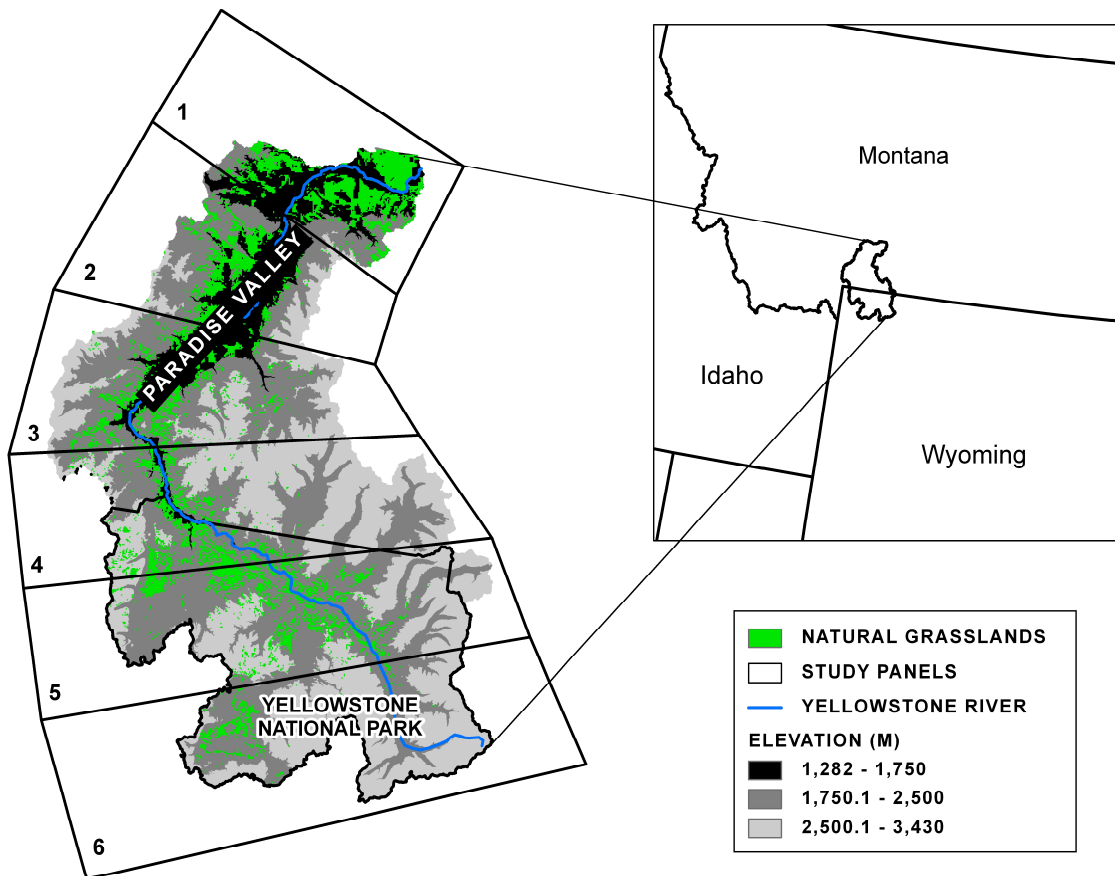


Figure 4.1. The location of natural grassland cover within the study-area and location of study panels.

Time-series of grassland NDVI were used as input to statistical smoothing techniques (TIMESAT, Jonsson and Eklund 2002, 2004) in order to identify the start of the growing season on a pixel-by-pixel basis (details of these methods are given in Chapter 2 of this dissertation). In summary, methods identified the ordinal day of the year when smoothed and gap-filled NDVI surpassed 50% of its annual amplitude as the start

of the grassland growing season. Over winter NDVI is of little relevance to wildlife (Pettorelli et al. 2009; Mueller et al. 2011) and field-study in the GYE confirms that the 50% of annual amplitude level marks the beginning of strong relationships between spring NDVI and migratory herbivore fecal chlorophyll content (Christianson and Creel 2009). Increasing NDVI values are associated with early and middle stages of vegetation development whereas decreasing values are associated with senescence (Reeves et al. 2006). We identified the time-periods for which NDVI was increasing from 50% of annual amplitude to peak greenness as most relevant to a broad selection of herbivores of different body sizes and requirements for forage quality and quantity.

Rate of Grassland Development

In addition to the timing of green grassland presence; we also characterize the rate of vegetation development. The rate of development considers both annual change in NDVI (i.e. magnitude of MAX values) and the amount of time required to transition from background to maximum values with a focus on the steepest portion of the annual NDVI curve (i.e. the portion of the NDVI curve that typically spans the 50% level and excludes transitional periods near 0 and 100% of annual amplitude which are of more shallow slope). Rate of grassland development was identified for each pixel as the change in NDVI from 20% to 80% levels divided by the amount of time required for this transition to take place on a year by year basis. This is equivalent to the first-derivative of what is typically the steepest part of the increasing portion of an annual NDVI curve.

Since each patch was made up of multiple pixels, a set of methods to determine the rate of NDVI change for each patch was also required. First, the complete distribution

of NDVI rates of change across the study-area was examined for each year and four classes were identified as the quartiles of each annual distribution so that the slowest developing 25% of pixels were members of class 1 while pixels in the fastest growing 25% were members of class 4. Classes representing different rates of development were incorporated into patches as the majority rate of development class represented by pixels in each patch.

Mapping Patches and Pattern

Forage patches were identified by aggregating pixels that simultaneously exhibited increasing NDVI values at each time-step (8-days). Spatial aggregation was performed according the following set of rules: 1) Pixels within 250-meter of one another (including on the diagonal) were considered to be part of the same patch; 2) Patches less than 5 pixels large were not considered; and 3) Holes in patches smaller than 5 pixels were incorporated into patches, while holes in patches that were larger than 5 pixels were preserved. Patch area was calculated in ArcGIS by creating a polygon layer from input raster datasets using the above rule-set for aggregating pixels and dealing with holes in patches.

Results included maps of forage patches of different rates of development for each 8-day interval from 2003 to 2009. For the sake of presentation and understanding spatial pattern, we present results for each of six study-panels in the study-area (Figure 4.1).

Evaluating Results

In order to evaluate the success of our methods, we qualitatively compare results to current ecological understanding of grassland phenology and migratory herbivore space use in this ecosystem. ‘Current ecological understanding’ is discussed in the introduction as the expected pattern of results. We also compare results to the known space-use of the Northern Yellowstone elk herd as described in White et al. (2010).

Results

Summary of Results

Results exhibit spatial and temporal patterns that are consistent with current ecological understanding of grassland phenology and space use of migratory ungulates in the study-area. Spring green-up progresses from north to south (panels 1 to 6) and upslope in the study-area. Low-elevation grasslands (up to roughly 1,750 meters) green-up in April, are organized into large contiguous patches of low and moderate rates of green-up and have reached peak greenness by July. Middle-elevation grasslands (roughly 1,750 to 2,500 meters) begin growth in May, are organized primarily into small and medium sized patches and green-up more quickly than lower elevations. At the highest elevations (above 2,500 meters) grasslands largely green-up very quickly in June, are organized into small patches and reach peak-greenness by July.

Spring Green-up

The grassland growing season begins earliest in study panel 1 and low-elevation valleys of panels 2, 3 and 4. Locations where growth starts early also have slower rates of

development (Figure 4.2 and Table 4.1). The start of the growing season gradually progresses upslope and southward (study-panels 2 – 6) throughout the spring (Figure 4.2), reaching middle-elevations by mid- to late-May and the highest-elevations by early- to mid-June (Figures 4.2). There is a positive relationship between the timing of early growth and the rate at which grasslands develop.

Landscape Pattern of Green Grassland Patches

In northern study-panels and lower-elevations grassland patches are fairly large, homogeneous and compact in shape (Figure 4.2 panels A and B, Table 4.1). Middle-elevations and valley settings in the southern portion of the study-area can also contain large contiguous patches, however they tend to be more linear and of greater shape complexity (Figure 4.2 panels B and C, Table 4.1). High-elevation patches are mostly small in size and widely dispersed throughout study-panels 4, 5 and 6.

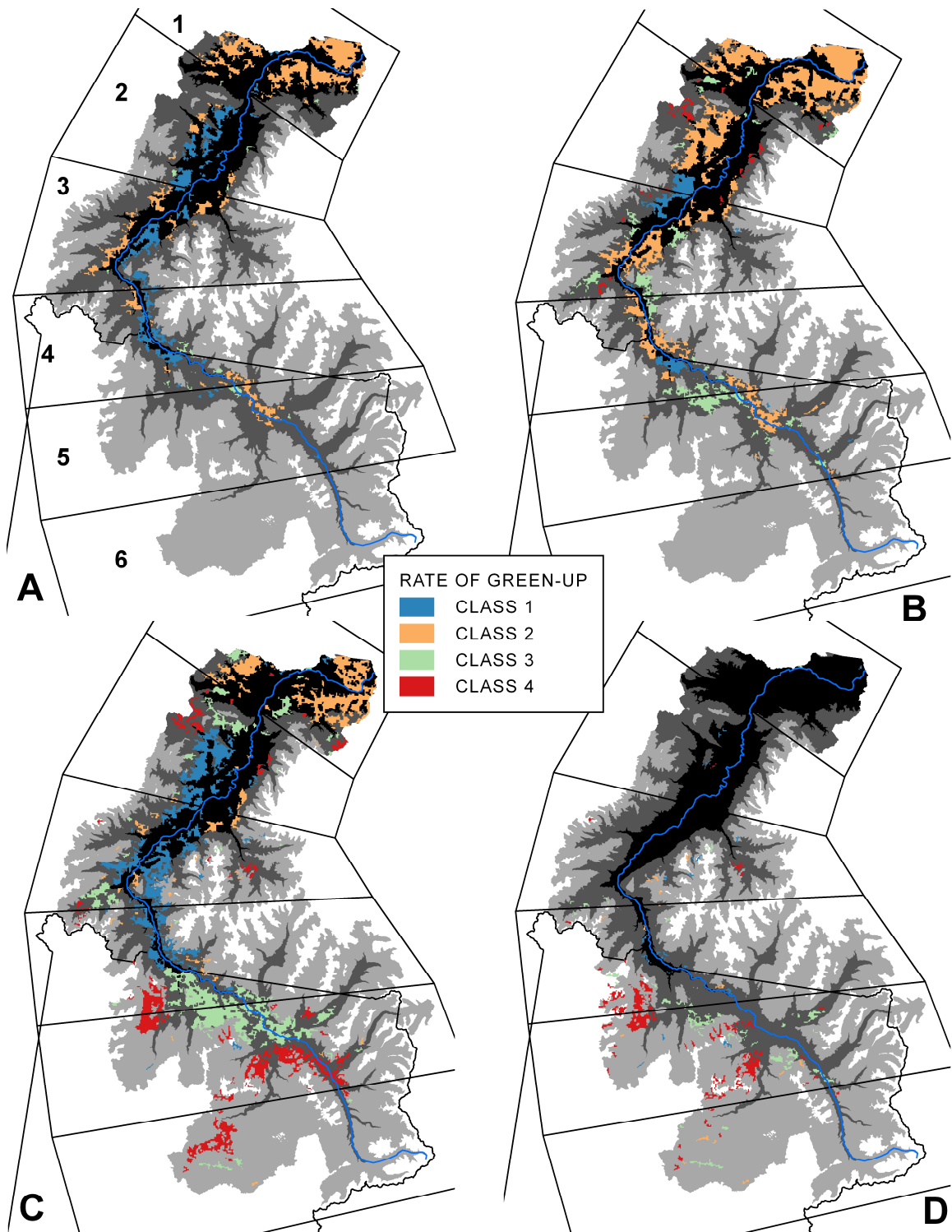
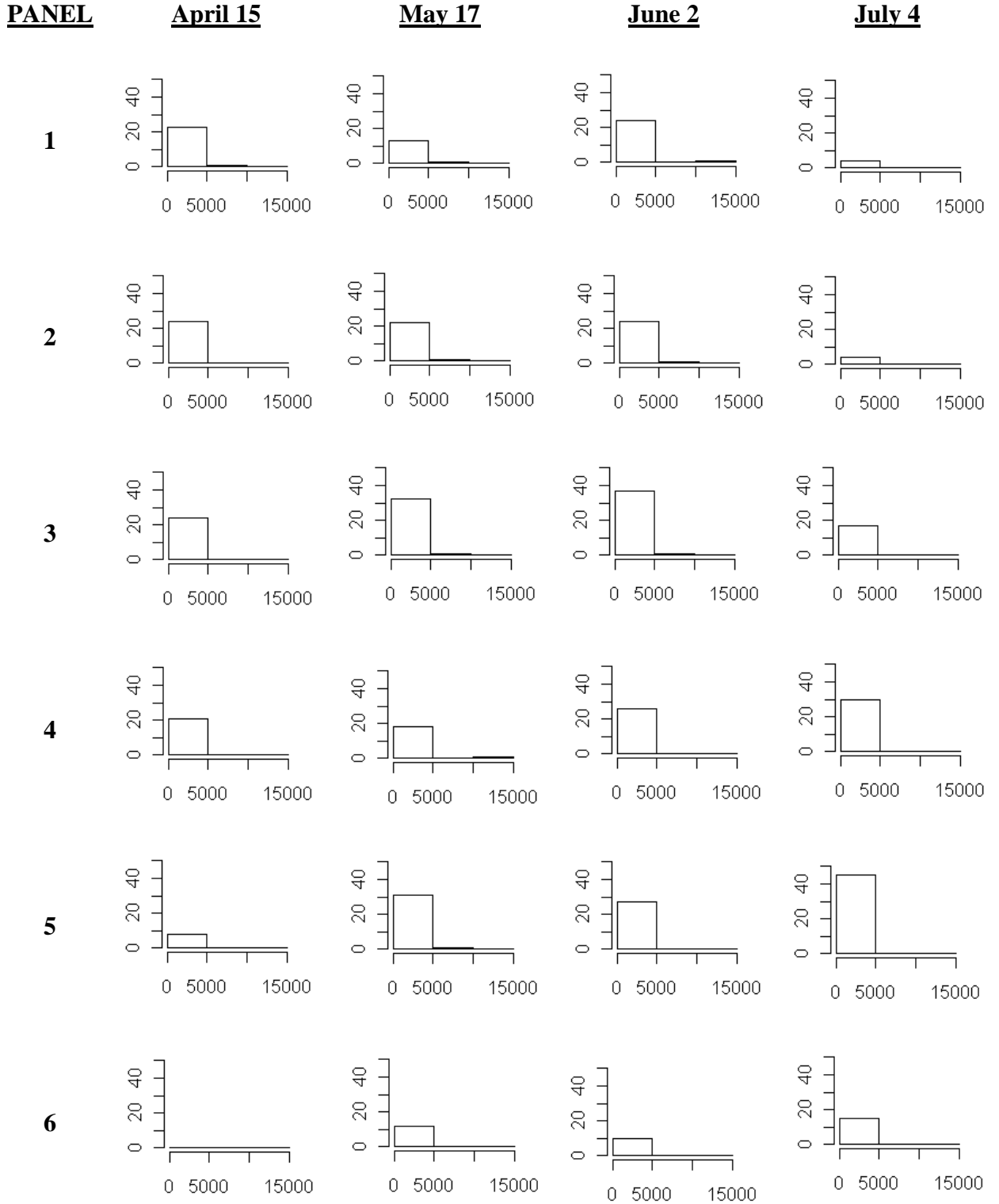


Figure 4.2. Typical pattern of spring green-up by rate of green-up class and study-panel. A) April 15th; B) May 17th; C) June 2nd; D) July 4th; (see Figure 4.1 for elevation classes shown with background shaded relief and location of study panels).

Table 4.1. Distribution of patch sizes by study panel throughout a typical year. X-axis shows size classes in hectares and Y-axis frequency.



Discussion

The present methods capture seasonal and interannual variation in patterns of grassland patches in the GYE and match well current ecological understanding of green-up and herbivore space use. The present methods could be easily modified to map the patch-dynamics of vegetation phenology with a focus on other species and their specific requirements for seasonal vegetation development or other ecological processes of interest.

Patterns of Grasslands Patches Relative to Herbivore Space Use

The following discussion summarizes growing season space use that would likely maximize exposure to large grassland patches of early to middle stages of development in a typical year without resorting to long-distance movements. The following also ignores areas currently under active human land use and any human influence on animal movements: March and April would be spent capitalizing on large patches of early growth that develops slowly in the low-elevations of study-panels 1, 2 and 3 (i.e. the Paradise Valley, see Figure 4.1 for location); late-April into May would see gradual movement southward and/or upslope tracking medium-sized patches as they begin to green-up; May into June would be spent on the large grassland patches of study-panels 4, 5 and 6; and July and August would be spent at the highest-elevations in the western-portions of study-panels 5 and 6 where the last remaining grassland patches remain in early to middle stages of development.

This pattern matches the actual present-day movements of Northern Yellowstone elk that spent winters outside of YNP as described in White et al. (2010); with the exception that some of these animals migrated to summer range west of the present study-area.

It is interesting to note that within YNP borders (see Figure 4.1 for location) there are grassland patches of at least moderate number and size that typically remain in early to middle stages of growth for approximately five months of the year (mid-April through August, results not shown for August). This pattern of forage-phenology may be unique in a broader geographic context and contribute to the diversity and abundance of large-bodied herbivores found in this ecosystem. It also may help to explain their seasonal migration strategy and how this might change in the absence of human intervention (see White et al. 2010 for a discussion of migration timing and human hunting pressure). In other parts of North America that support large-bodied herbivores, lower-elevations that provide early-season growth (and often winter range) have in many cases been developed for human use while parks and preserves protect high-elevations that have a shorter grassland growing season. YNP on the other hand preserves grasslands in a diversity of biophysical settings ranging in elevation, aspect, landscape position and soil types so that forage in early to middle stages of development is available for sometimes half of the calendar year. Comparing this duration of time to other protected-areas and surrounding ecosystems that support (and have lost) large-bodied herbivores could provide insight to the broad-scale patterns of forage availability that are required of large-bodied herbivores.

Applicability to Other Species

We also see potential for application of the present methods to a broader set of species that rely on seasonal vegetation development to meet other than food resource needs. For example, grasslands provide cover-habitat and seasonal protection from predators for some species. In a study of raccoon (*Procyon lotor*) foraging behavior in grasslands where ground-nesting birds and their eggs represent a food resource; Newbury and Nelson (2007) found that raccoons did not search grasslands for nests during the nesting season despite being known nest-predators. This result suggests that the nesting season is well-timed so that grasses have developed to the point of providing sufficient cover habitat from nest-predators so that predator foraging strategies do not include searches for nests. The evolution of loop migration of marsh hawks in Africa and southern Europe provides another example of how predator foraging strategies may be related to grassland development (Klassen et al. 2009). Many species rely on pulses of resources (often related to vegetation productivity in terrestrial ecosystems) for survival and their life-history strategies are well-coordinated with the timing and spatial location of seasonal (and episodic) resource pulses (Yang et al. 2010). We suggest that explorations of the spatial and temporal patterns of vegetation-productivity can shed-light on a wide-variety of ecological relationships in addition to further developing of our understanding of forage-phenology and herbivore space use.

Limitations and Recommendations for Future Applications

There remain a number of important limitations to the current methods and datasets on which they rely. Perhaps most importantly, a 250-meter spatial resolution and 8-day return interval clearly limits application to species that make habitat selections at fine spatial and temporal scales. Application may also be limited for species whose habitats do not undergo seasonal changes in vegetation as observed by satellite; or where vegetation fluctuates at shorter than weekly timescales. Vegetation in desert environments is known to respond over very short time-scales to precipitation events and this response may be missed by an 8-day satellite return interval. With the aforementioned limitations in mind, we present the following characteristics of studies for which the present methods are likely most applicable:

1. The habitat of interest is patchily distributed; seasonally-dynamic and its spatial and temporal distributions have implications for species or processes of interest.
2. Vegetation-productivity of habitat patches is organized at moderate-spatial and greater than weekly-temporal scales.
3. The relationship between vegetation-productivity and the species of interest is more important for the growing season than for non-growth portions of the year.

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CHAPTER 5

CONCLUSIONS AND FUTURE RESEARCH

Direction for Future Research

There remain a number of outstanding and underdeveloped research topics relevant to the present dissertation's results. First, although we identified moderate-scale climate correlates of grassland phenology we also document what appears to be switching of climate-drivers across the study-area and methodological limitations in distinguishing the relative contributions of climate drivers that vary together throughout seasons (e.g. photoperiod and temperature). Future research could include field experiments or controlled laboratory studies, the results of which should continue to improve understanding of climate-phenology relationships. Future research could also include the generation and local testing of interpolated of climate data. Although testing the accuracy of these datasets has been extensive elsewhere; accuracy within the present study-area is largely unknown and was a potential source of error in phenology models. These research activities would inform and greatly improve landscape-scale models of grassland phenology that are necessary in order to predict the likely ecological effects of climate change.

Second, the detection of statistically significant land use effects was limited by the accuracy of biophysical models (see above research needs), but also by the spatial resolution of remote-sensing data and the fine-scaled pattern of land use. At present, there

is not a single satellite platform that possesses both the spatial and temporal resolution required to more accurately depict land use effects on phenology (although data-fusion methods that may meet requirements have been proposed, see Gao et al. 2006). Future research that capitalizes either on new satellite platforms, or tests the applicability of data-fusion methods will likely be better able to detect the fine-scaled effects of residential development (in contrast to more coarse-scaled agricultural effects that appeared to be adequately captured in the present study). Related to this, the modes of change (i.e. human activity) discussed in the present dissertation (especially for residential land use classes such as exurban that are projected to increase within the study-area) are speculative and would benefit greatly from social-science investigations of actual landscape maintenance practices of local residents as well as variation in and motivation for maintenance practices. This could include recruitment of volunteers to keep diaries of residential landscaping activities (i.e. modifications to the physical and biological environment of grasslands under human land use). If this were done in conjunction with remote sensing investigations at finer-spatial and –temporal scales results would likely provide compelling evidence of the mechanisms by which land use and human-activity affect broad-scale patterns of phenology. Land use effects on phenology remains understudied and in need of development on several fronts (both social and natural science investigations).

Finally, there are a host of unanswered questions related to the role of grassland phenology in determining migratory ungulate movement and space use. Migratory ungulates in the GYE are intensively studied, the technology and datasets have been

collected and this kind of analysis has already been performed with other species and populations around the world; and yet it remains an outstanding research question within the GYE. Elk especially, due to management concerns surrounding this species, seem to be a prime candidate for analyses of movement-patterns relative to natural and human-modified grassland phenology and productivity. The major challenge here appears to be assembling a research team with knowledge of animal behavioral ecology, access to wildlife relocation data and expertise in the use of remote sensing datasets and spatial analyses techniques.

Conclusions

Results presented in this dissertation highlight the utility of new datasets and statistical methods for discovering climate-phenology relationships, land use effects on phenology and the patch-dynamics of green forage across landscapes. These results are relevant to a variety of conservation and management concerns related to land use change surrounding Yellowstone National Park and migratory ungulate space use.

Within the GYE, solar radiation (loosely interpreted as photoperiod) appears to impose an outer-envelope on the timing of grassland phenology. Within this envelope, phenology is controlled by seasonal variation in water-availability, evaporative demand and temperature (Chapter 2). This was largely consistent with hypotheses and current ecological understanding that has been developed by other studies. However, there also appeared to be a switch in climate-drivers across environment gradients that deserves further research attention and would help to anticipate the effects of future climate

change. Other studies have noted the difficulty in developing single models of phenology-climate relationships across diverse biophysical settings.

All land uses within the study-area extended the grassland growing season to later in the year as compared to predicted wildland conditions (Chapter 3). The likely mode of change is irrigation of agricultural crops and residential landscapes. Agriculture also boosted two measures of grassland productivity: peak annual greenness and estimates of total annual productivity. This is likely due to irrigation and densely planted crops that grow rapidly. Interestingly, we did not detect a land use effect on the timing of the start of the growing season which has been extensively documented in other studies. The spatial pattern of grassland productivity was modified under human land use so that the full gradient of spatial and temporal variation in grassland productivity across the study-area is now represented on private lands (as opposed to across the steep environmental gradients represented across the entire study-area). The potential ecological implications of altered grassland productivity include attraction of migratory ungulates (and their predators) to human-settlements and agricultural areas. During field visits in the middle of the summer of 2012, an elk herd of approximately 40 individuals was observed to be feeding on hay and alfalfa fields in the Paradise Valley that were in early stages of second growth (i.e. within weeks of first hay cutting). This is of note because most experts would expect elk to be frequenting higher-elevation meadows where forage remained in early stages of growth and not in low-elevation settings where most wildland grasslands had already senesced. Should Yellowstone elk modify their behavior to include more use of

private lands as has happened elsewhere in the Rocky Mountains; it will present a host of conservation and management challenges for wildlife and land managers.

New data and methods now allow for the mapping of spatial and temporal patterns of seasonally-productive grassland habitat patches in ways that match current ecological understanding. Spatial and temporal patterns of green forage patches become the basis for understanding contemporary ungulate population dynamics, movement and space use. To the extent to which climate drives forage phenology and patch-dynamics, it also provides an entry-point to understanding the likely effects of expected future climate change on migratory ungulates in the GYE.

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