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# The Future of the Big Sagebrush Ecosystem: Plant Community Response to Grazing, Wildfire, and Invasive Annual Grass in a Changing Climate

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# THE FUTURE OF THE BIG SAGEBRUSH ECOSYSTEM: PLANT COMMUNITY RESPONSE TO GRAZING, WILDFIRE, AND INVASIVE ANNUAL GRASS IN A CHANGING CLIMATE

A thesis submitted to
the Graduate College of
Marshall University
In partial fulfillment of
the requirements for the degree of
Master of Science
In
Biology
by
Margaret Eleanor England
Approved by
Dr. Kyle Palmquist, Committee Chairperson
Dr. Anne Axel
Dr. John Bradford

Marshall University
May 2022

## APPROVAL OF THESIS

We, the faculty supervising the work of Margaret Eleanor England, affirm that the thesis, *The Future of the Big Sagebrush Ecosystem: Plant Community Response to Grazing, Wildfire, and Invasive Annual Grass in a Changing Climate*, meets the high academic standards for original scholarship and creative work established by the Biology Department and the College of Arts and Sciences. This work also conforms to the editorial standards of our discipline and the Graduate College of Marshall University. With our signatures, we approve the manuscript for publication.

Kyle Palmquist 9 March 2022

Dr. Kyle Palmquist, Department of Biology Committee Chairperson Date

Anne C Axel 9 March 2022

Dr. Anne Axel, Department of Biology Committee Member Date

JOHN BRADFORD Digitally signed by JOHN BRADFORD
Date: 2022.03.09 08:03:56 -07'00'

Dr. John Bradford, USGS Committee Member Date

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Finally, I would like to thank the friends, family, and community I’ve found along this journey for the support they have offered me and the sanity they provided while finishing the majority of my thesis during a difficult time. Thank you for being the people who make this all worth it.

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# ABSTRACT

Climate change is increasingly affecting the plant communities across the world. In the Western United States, these changes are affecting plant communities and their risk of invasive species, as well as the frequency and severity of wildfire. Big sagebrush (*Artemisia tridentata* Nutt.) ecosystems of the Western United States are facing threats of increasingly frequent wildfire and invasion of the annual grass cheatgrass (*Bromus tectorum* L.), which may be exacerbated by global climate change. Past studies have found cheatgrass to exhibit a positive feedback loop with wildfire, and climate change is expected to facilitate expansion of the cheatgrass range. Livestock grazing, particularly overgrazing, can also promote cheatgrass invasion and subsequent decline of native species. The goal of this work is twofold: (1) to simulate where cheatgrass invasion is most likely to occur, and what the resulting impacts on fire frequency and the native plant community will be under future climate scenarios, and (2) to determine the response of cheatgrass and native plant functional types to different grazing treatments. We modeled changes in plant community composition and fire frequency under future climate conditions and livestock grazing intensity treatments using an individual-based plant simulation model, STEPWAT2, for 200 sites across the big sagebrush ecosystem. We used global circulation models for established representative concentration pathway (RCP) emissions scenarios 4.5, and 8.5 for mid-century, and end-century conditions, and implemented livestock grazing treatments as a predetermined portion of biomass removed for each functional type for each simulation year. We found that sites within the northeastern ecoregions of our study area, including the Snake River Plain, the Wyoming Basins, and the Great Plains, were the most likely to become invaded by cheatgrass in the future as climate becomes more suitable for cheatgrass. On average across all sites, we simulated declines in biomass for native perennial forbs, big sagebrush, and $C_3$ perennial grasses under future climate scenarios, and simulated increases in cheatgrass and $C_4$ perennial grass biomass. Sites which had a simulated increase in cheatgrass invasion burned more frequently, which resulted in lower simulated big sagebrush biomass than uninvaded sites. We found that functional types which are most sensitive to climate change had similar responses to climate regardless of livestock grazing treatment, and the implementation of livestock grazing in any intensity did not fully counteract the effects of climate on native or invasive plant functional types. Livestock grazing had a larger effect on plant communities than climate for all plant functional types except big sagebrush, and in the case of native $C_3$ perennial grasses livestock grazing exacerbated the effects of climate on biomass loss. These results suggest that climate change may lead to the increased spread of cheatgrass and increased wildfire in big sagebrush ecosystems and a reduction in biomass for most native plant functional types, irrespective of livestock grazing intensity. These findings may help to inform land management decisions and conservation planning within the big sagebrush region in light of a changing climate.

# CHAPTER 1

# THE FUTURE OF THE BIG SAGEBRUSH ECOSYSTEM: PLANT COMMUNITY RESPONSE TO WILDFIRE AND INVASIVE ANNUAL GRASS IN A CHANGING CLIMATE

## INTRODUCTION

Climate change, increases in disturbance, and their interactions are accelerating non-native species invasions throughout the world resulting in the loss of native biodiversity (Abatzoglou and Kolden 2011, D'Antonio and Vitousek 1992, Mack 1981). Warming has increased the probability of wildfire in many locations due to dry, more flammable fuels and fire weather that is more conducive for ignition and fire spread (Westerling et al. 2006). Increases in wildfire frequency or increases in livestock grazing intensity often decrease native biomass and increase bare ground, providing opportunities for non-native species to establish and proliferate (D'Antonio and Vitousek 1992, Mack 1981). Warming-fire interactions are projected to intensify in the coming decades with important implications for native biodiversity.

Currently, big sagebrush (*Artemisia tridentata* Nutt.) ecosystems of the Western United States (U.S.) are threatened by the invasion of cheatgrass (*Bromus tectorum* L.), an invasive annual cool-season ($C_3$) grass, and subsequent increases in wildfire frequency (Balch et al. 2013, Brooks et al. 2004, Coates et al. 2016, Knick et al. 2003) through a positive feedback loop between cheatgrass abundance and wildfire occurrence (Bradley et al. 2018, D'Antonio and Vitousek 1992). Increases in disturbance, particularly wildfire and livestock grazing, along with increases in cool-season precipitation and warming have facilitated the spread of cheatgrass and resulted in ecosystems state transitions from native shrublands to non-native grasslands throughout large areas of the Western U.S (Bradley et al. 2018, Knapp 1996, Mack 1981, Pilliod et al. 2017).

Cheatgrass is native to the semi-arid plains of central Asia as well as parts of Europe and northern Africa, where the majority of precipitation occurs during the cool-season. In the Intermountain West, cheatgrass germinates and initiates growth during the cool-season before native $C_3$ grasses and forbs and individuals typically reach reproductive maturity by the onset of the dry summer season (Kostivkovsky and Young 2000, Morrow and Stahlman 1984). Monocultures of cheatgrass can contain greater than 10,000 individuals per $m^2$ (Young and Evans 1985). Once established, cheatgrass creates a continuous, fine, flammable fuel bed, increasing the frequency and spread of wildfire (Balch et al. 2013, Brooks et al. 2004), with areas in the Snake River Plain now burning as often as every 3 to 5 years compared to historical mean fire return intervals (FRI) of 100 years (Brooks et al. 2004, Whisenant 1990). Even small amounts of cheatgrass (1-5% cover) can substantially increase fire probability (Bradley et al. 2018). After wildfire, cheatgrass is capable of recolonizing more rapidly than native species and can quickly dominate a recently disturbed landscape due to its high seed production and ability to draw down soil moisture before native species emerge (Young and Evans 1978, Young and Evans 1985).

Big sagebrush, the dominant species in these ecosystems, is sensitive to increases in wildfire driven by cheatgrass invasion as it has evolved with relatively infrequent fire (mean FRI often > 50 years, although there is considerable variability across the biome) (Baker 2013, Bukowski and Baker 2013, Heyerdahl et al. 2006). As a result, big sagebrush is not well adapted to frequent fire: it has no capacity to resprout post-fire after being top-killed, and thus recolonization occurs exclusively from seed (Lesica et al. 2007, Schlaepfer et al. 2014, Wijayratne and Pyke 2012). In addition, the poor dispersal of seeds (Young et al. 1989), low seed viability (Wijayratne and Pyke 2009, Wijayratne and Pyke 2012), and the narrow soil moisture and temperature conditions required for regeneration (reviewed in Schlaepfer et al. 2014) place additional constraints on big sagebrush recovery after fire. As a result, big sagebrush is slow to recolonize after fire and it may take several decades for big sagebrush biomass to recover to pre-disturbance levels (Lesica et al. 2007, Shinneman and McIlroy 2016). Collectively, climate-driven cheatgrass invasion and increased wildfire frequency have resulted in declines of native plant species richness and abundance and reduced habitat quality for sagebrush-dependent wildlife species (Ashton et al. 2016, Bansal and Sheley 2016, Wisdom et al. 2005).

Despite significant impacts of the cheatgrass-fire cycle over large areas, some portions of the big sagebrush region are relatively unaffected by these dynamics due to the striking geographic pattern of cheatgrass abundance in the Intermountain West. Cheatgrass has successfully invaded large portions of the big sagebrush region, where climate conditions have favored invasion, specifically: areas with winter-dominated soil moisture patterns and warm, dry growing seasons primarily in the Great Basin and the Snake River Plain (Balch et al. 2013, Bradley 2010, Brummer et al. 2016, Mack 1981, Pilliod et al. 2017, Taylor et al. 2014). In these locations, big sagebrush ecosystems are often less resilient and resistant to wildfire, resulting in greater susceptibility to invasion by cheatgrass post-fire (Chambers et al. 2007, Chambers et al. 2014). In contrast, the northeastern part of the big sagebrush region (i.e., Wyoming Basins and Great Plains) and areas elsewhere at high elevation have generally resisted invasion due to either cold conditions or a larger fraction of growing-season precipitation, which are not climatically suitable conditions for cheatgrass (Bradley 2009, Bradley et al. 2018, Brummer et al. 2016, Taylor et al. 2014). In addition to climate, a significant barrier restricting the establishment and subsequent dominance of cheatgrass is a well-developed layer of native perennial grasses and forbs, which tend to be more abundant in cold, moist sites and in regions with higher growing-season precipitation (such as the Great Plains) (Bradley et al. 2018, Brummer et al. 2016, Chambers et al. 2007, Reisner et al. 2013, Taylor et al. 2014, Williamson et al. 2019).

Our understanding of whether existing geographic differences in cheatgrass abundance and the associated impacts will persist into the latter half of the 21st century in response to warming, drying, and increased wildfire activity is limited (but see Brummer et al. 2016). Projected warming and slight increases in cool-season precipitation are likely to increase suitability for cheatgrass as a result of wetter winter soil conditions and a drier extended growing season (Abatzoglou and Kolden 2011, Palmquist et al. 2016a, b, Pilliod et al. 2017), creating opportunities for cheatgrass establishment and proliferation (Brummer et al. 2016, Concilio et al. 2013, Palmquist et al. 2021). To better understand invasion risk and fully characterize the cheatgrass-fire cycle under future conditions, approaches are needed that simulate the effects of climate-wildfire interactions on plant communities comprised of multiple functional types, including cheatgrass and native functional types. We used an individual-based plant simulation model (STEPWAT2, Palmquist et al. 2018a, b) to determine the response of big sagebrush plant communities to climate change, cheatgrass invasion, and wildfire driven by cheatgrass abundance. Our simulation modeling approach represents a process-based representation of soil moisture and competitive interactions between cheatgrass and native species for fluctuating limiting resources to characterize the response of widespread big sagebrush plant communities to cheatgrass-wildfire dynamics under current and future conditions.

Our goal was to determine where and how the cheatgrass-fire cycle will result in substantial changes to big sagebrush plant communities, and how these interactions will be affected by a changing climate. Specifically, we evaluated three questions: First, what is the potential for spread of the cheatgrass-fire cycle into currently unimpacted areas? Second, which areas will remain vulnerable, which areas will become more vulnerable, and which areas will remain resistant to cheatgrass invasion in the future? Third, how will cheatgrass-wildfire dynamics affect the biomass and composition of native plant functional types under a future climate? Accurately projecting which geographic regions will potentially be most and least vulnerable to cheatgrass invasion under future conditions will help to guide effective management decision-making in these ecosystems to protect species of conservation concern.

## METHODS

### Study Area and Site Selection

We examined plant community dynamics in big sagebrush ecosystems, which are widespread across Western North America, and historically encompassed more than 100 million hectares (West 2000) and currently occupy approximately 76 million hectares (Rigge et al. 2020). These habitats are important for over 350 species of conservation concern, including threatened greater sage-grouse (*Centrocercus urophasianus*) and endangered pygmy rabbits (*Brachylagus idahoensis*) (Connelly et al. 2004, Raphael et al. 2001, Remington et al. 2021, Rowland et al. 2006). Big sagebrush ecosystems encompass several distinct ecoregions spanning the Intermountain West which are highly variable in elevation, topography and climate, including the Great Basin, the Wyoming Basins, the Columbia Basin, the Colorado Plateau, the Snake River Plain, and Northwestern parts of the Great Plains (Stiver et al. 2006, West 1983). Each of these ecoregions contains a unique mixture of grasses, shrubs, and forbs, which vary in composition and importance according to climate, fire history, grazing pressure, and land-use (West 1983, West 2000). Effective conservation of big sagebrush ecosystems therefore requires an understanding of plant species composition and spatial heterogeneity across their geographic extent.

We selected 200 sites dominated by big sagebrush which represent the range of climatic variability and encompass the spatial extent of big sagebrush plant communities in the Western U.S. (Appendix B). Mean annual temperature and mean annual precipitation of the 200 sites ranged from 0.1 to 13°C and 176 to 850 mm, respectively. When possible, we selected sites within areas with a high density of breeding greater sage-grouse populations based on Doherty et al. (2016) within each of seven Sage-grouse Management Zones (MZs) designated by the Western Association of Fish and Wildlife Agencies (Stiver et al. 2006) (Appendix B). The selection of these sites is described in additional detail in Palmquist et al. (2021).

## STEPWAT2 Modeling

We simulated big sagebrush plant communities in response to climate and cheatgrass-wildfire dynamics using STEPWAT2, an individual-based, gap dynamics plant simulation model described and validated by Palmquist et al. (2018a, 2018b) and using rSFSTEP2 (https://github.com/DrylandEcology/rSFSTEP2/releases/tag/v.1.0.0) via R version 3.6.0, an R program that executes STEPWAT2. STEPWAT2 integrates a process-based soil water balance model that runs on a daily basis and represents multiple soil layers (SOILWAT2, Schlaepfer et al. 2012) and an individual-based plant simulation model that runs on an annual time step (STEPPE, Coffin and Lauenroth 1990). STEPWAT2 simulates establishment, competition, growth, and mortality of multiple plant species and functional types based on soil water availability generated by SOILWAT2, along with species- and functional type-specific life-history traits. Soil water available for transpiration (mm) is simulated daily for each soil layer and plant functional type within SOILWAT2, aggregated on a monthly basis, and then determines resource availability for corresponding functional types within STEPPE. Transpired water in each soil layer is partitioned to each STEPPE functional type based on the matching of each functional type's monthly active roots in each soil layer and the monthly soil water available for transpiration within each soil layer (see Palmquist et al. 2018a). Inputs include daily weather, monthly climate, soil properties for multiple soil layers, and multiple life-history parameters for each functional type and species (Palmquist et al. 2018a). Output includes total aboveground biomass (g/m$^2$) for each species and functional type, and wildfire occurrence (Palmquist et al. 2018a), in addition to ecohydrological and climatic variables simulated within SOILWAT2 (Schlaepfer et al. 2012b).

STEPWAT2 simulations were designed similarly to those described in Palmquist et al. (2021). We represented each site as a 1 m$^2$ patch, which was simulated for 300 years and 200 iterations to characterize average conditions for that location based on multiple sources of variation (e.g., interannual climate variability, stochastic demographic processes). Simulations were conducted for 300 years because the simulations start with bare ground and it often takes 100 to 150 years for the plant community to reach steady-state conditions. We ran simulations for each site for 200 iterations to account for variation in model output between each simulation run resulting from stochastic processes, including establishment and mortality. A patch size of 1 m$^2$ was simulated based on the average resource space of an individual of the dominant species and to reflect the average area that a full-sized big sagebrush individual occupies based on its root system (~ 1 m$^2$; Sturges 1977) and based on average big sagebrush density (~1.5 individuals/m$^2$; Palmquist et al. 2018a).

For each site, we simulated common and widespread plant species of big sagebrush plant communities, represented by 10 functional types: big sagebrush, $C_3$ perennial grasses, $C_4$ perennial grasses, $C_3$ annual grasses, $C_3$ perennial cool-season forbs, $C_3$ perennial warm-season forbs, $C_3$ annual cool-season forbs, and $C_3$ annual warm-season forbs, non-sagebrush shrubs, and succulents (see Palmquist et al. 2021). STEPWAT2 simulates both intraspecific and interspecific competition between plant individuals. Larger individuals within the same species receive soil water resources first and a larger share of the resources (intraspecific competition). Interspecific competition occurs through several processes driven by species-specific differences in resource acquisition, which are largely based on species phenology, rooting depth distributions, and intrinsic growth rates (see Palmquist et al. 2018a for additional detail). Although we simulated $C_3$ perennial cool-season forbs and $C_3$ perennial warm-season forbs separately, we summarize biomass for $C_3$ perennial forbs for simplicity and because cool-season and warm-season functional types responded in similar ways. Here, we focus on summarizing the effects of climate change and cheatgrass-driven wildfire for the dominant plant functional types in these ecosystems represented by coarser groups: big sagebrush, $C_3$ perennial grasses, $C_4$ perennial grasses, perennial forbs, and cheatgrass.

We simulated each site under current and future climate conditions derived from 13 Global Climate Models (GCMs) for representative concentration pathways (RCPs) 4.5 (a less severe emissions scenarios) and 8.5 (a more severe emissions scenario). To evaluate a range of future climate projections, we used 13 GCMS which perform well in the Western US (Rupp et al. 2013) and are representative of existing GCM families (Knutti et al. 2013): CanESM2, CESM1-CAM5, CSIRO-Mk3-6-0, FGOALS-g2, FGOALS-s2, GISS-E2-R, HadGEM2-CC, HadGEM2-ES, inmcm4, IPSL-CM5A-MR, MIROC5, MIROC-ESM, and MRI-

CGCM3. Climate data from these GCMs under RCP4.5 and RCP8.5 were extracted for 30-year clusters representing current (1981-2010), mid-century (2031-2060), and end-century (2071-2100) conditions. Current climate data were extracted from Daymet (Thornton et al. 2018). Future climate data for each GCM-RCP combination were downloaded from the Downscaled CMIP3 and CMIP5 Climate and Hydrology Projects archive on June 23, 2020 (Maurer et al. 2002, Maurer et al. 2007) and then downscaled using the hybrid-delta approach to generate future daily weather from current daily weather data and monthly future projections (Hamlet et al. 2010, Tohver et al. 2014). We used a first-order markov weather generator within SOILWAT2 to generate 300 years of weather data with the same statistical properties as the 30-year clusters of weather data.

Plant communities were simulated under light grazing by livestock to isolate the effects of climate change and cheatgrass-wildfire dynamics on plant community biomass and composition. Livestock grazing occurred annually and was implemented for each functional type by removing a fraction of the current year's growth. Biomass removed by livestock grazing was based on data presented in Milchunas and Lauenroth (1993) on the effects of grazing in global shrublands (see Appendix C). We simulated each site with soil properties that correspond to a silt loam (30% sand, 18% clay), the most common soil type that big sagebrush plant communities occur on (see Palmquist et al. 2021, Appendix S3). We simulated the effects of climate-driven shifts in soil moisture seasonality and depth on the functional type composition in the 200 sites, and according to established climate-functional type relative abundance equations (Brummer et al. 2016, Paruelo and Lauenroth 1996, Teeri and Stowe 1976). These soil and climate driven community responses were implemented using R package rSOILWAT2 (Schlaepfer et al. 2020) and this approach is described in detail in Palmquist et al.

(2021). This implementation results in differences in vegetation parameters for multiple functional types across sites based on current conditions and shifts in functional type composition for each site from current to future conditions in response to changing climate.

We simulated the potential expansion of cheatgrass in the future using a positive cheatgrass-wildfire feedback loop within STEPWAT2. Fire probability based on cheatgrass biomass was calculated each year using an equation derived from data presented in Balch et al. (2013) and Bradley et al. (2018). This equation characterizes the relationship between percentage cover of cheatgrass and annual fire probability based on MODIS fire data presented in Bradley et al. (2018) (see Appendix D for a detailed description). Since cheatgrass abundance is tracked as biomass ($g/m^2$) in STEPWAT2, we also implemented an equation that converts cheatgrass biomass to percentage cover each year. This equation was based on an allometric equation between cheatgrass percent cover and cheatgrass biomass ($g/m^2$) derived for big sagebrush ecosystems in the Great Basin (Mahood et al. 2021). This implementation allowed us to determine a fire probability for each simulation year based on cheatgrass biomass in that year (see Appendix D).

We also implemented additional simulations without the cheatgrass-wildfire loop enabled to quantify the effects of the cheatgrass-wildfire loop under a future climate, relative to the effect of climate change alone. Fire probability was based solely on cheatgrass abundance, which is an important factor that determines the likelihood of wildfire in big sagebrush ecosystems, and did not incorporate fuel load or weather data.

## Analysis

We calculated median mean biomass for each functional type under future and current conditions, and summarized changes in biomass from current to future conditions under different climate scenarios. First, we calculated mean biomass over the final 30 years of simulated data after plant communities had reached steady-state conditions. We did this for current conditions and for each GCM-RCP-time period combination for each of the 200 sites. Second, we calculated the change in biomass (g/m$^2$) from current to future conditions under each GCM-RCP-time period combination, along with percentage change from current to future conditions relative to the current maximum biomass (hereafter % change of historical maximum biomass). Thereafter, we sorted mean biomass, change in biomass, and % change of historical maximum biomass to identify the median among the 13 GCMs for each RCP-time period combination. Finally, we calculated differences in current and future biomass (g/m$^2$) with the cheatgrass-wildfire loop enabled and with fire excluded to determine the effect of the cheatgrass-wildfire cycle relative to the effects of climate change.

We also calculated mean fire return-interval (FRI) (the mean number of years between fire events) for current conditions and for each future climate scenario, along with changes in FRI from current to future conditions as described above for biomass. We explored spatial patterns of changes in plant functional type biomass and FRI using geographic maps for the 200 sites. In addition, we interpolated simulation output from the 200 sites to create gridded plant functional type biomass surfaces for the big sagebrush region using a multivariate matching algorithm developed by Renne et al. (2021) and described in Palmquist et al. (2021). This approach allowed us to extrapolate results from the 200 sites to produce range-wide maps of plant functional type biomass. We used R version 3.6.0 (R Core Development Team 2020) and RStudio version 1.2.1335 (RStudio 2021) for all analyses.

# RESULTS

## Potential for Cheatgrass Spread into Currently Unimpacted Areas

Under current conditions, cheatgrass was simulated in 193 of the 200 sites based on current climate and climate-cheatgrass abundance relationships derived and described in Palmquist et al. (2021), however its abundance varied substantially across sites (Appendix E). The seven sites where cheatgrass was not simulated under current conditions were moist, cold, high-elevation or high latitude locations (mean MAP = 551 mm, mean MAT = 2.05 °C, mean elevation = 2560 m, Appendix E), and hence were not climatically suitable for cheatgrass. However, by mid-century under both RCP4.5 and RCP8.5, climate became more suitable for cheatgrass in those 7 sites, and as a result, cheatgrass was simulated in all 200 sites under all future climate scenarios. Simulated increases in climate suitability due to warming, resulted in small interpolated areas (1.5% of the study area) previously unoccupied by cheatgrass becoming more suitable for cheatgrass under all future climate scenarios (gray areas in Figure 1A).

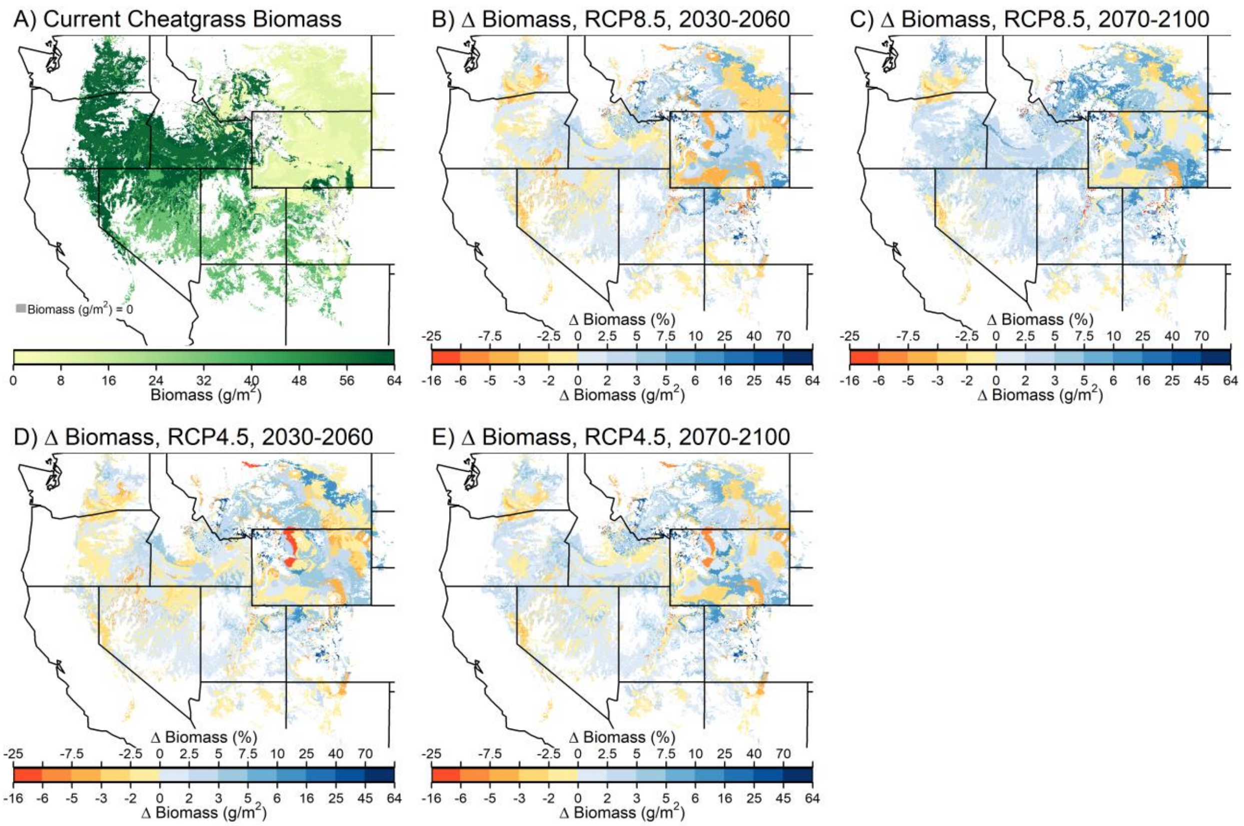

**Figure 1. Interpolated Cheatgrass Maps**

Interpolated cheatgrass biomass ($g/m^2$) for current conditions (1981-2010) (A), change in biomass from current to mid-century (2031-2060) and end-century (2071-2100) under RCP8.5 (B, C), and RCP4.5 (D, E). Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage change of the maximum historical biomass.

## Geographic Patterns of Resistance and Vulnerability

We simulated increases in cheatgrass biomass in the majority of sites under all future scenarios and time periods (Table 1, Figure 2). For most sites, those increases were small, representing median changes across all sites of 0.8 to 2.8% depending on the RCP-time period (Figure 2, Appendix E). Large increases in cheatgrass biomass (>50%) were simulated for 1.5% of sites, while increases between 5 to 15% were simulated in 11 to 22% of sites depending on the future climate scenario (Figure 2, Appendix E). We also simulated small declines in cheatgrass biomass (up to -10%) in 18% to 39% of sites depending on the RCP and time period (Table 1).

| | RCP4.5 | | | | RCP8.5 | | | |
|---|---|---|---|---|---|---|---|---|
| | Mid-century | | End-century | | Mid-century | | End-century | |
| | Gain | Loss | Gain | Loss | Gain | Loss | Gain | Loss |
| Sagebrush | 45% | 55% | 38% | 63% | 41% | 59% | 24% | 76% |
| Cheatgrass | 62% | 39% | 72% | 29% | 67% | 34% | 82% | 18% |
| C3Pgrass | 31% | 69% | 19% | 81% | 24% | 77% | 8% | 92% |
| C4Pgrass | 87% | 13% | 93% | 8% | 91% | 10% | 98% | 3% |
| Pforb | 33% | 68% | 26% | 75% | 28% | 73% | 16% | 84% |

**Table 1. Biomass Gain/Loss Percentage Per Site**
Percentage of the 200 sites that gained or lost biomass of each plant functional type under each RCP and time period.

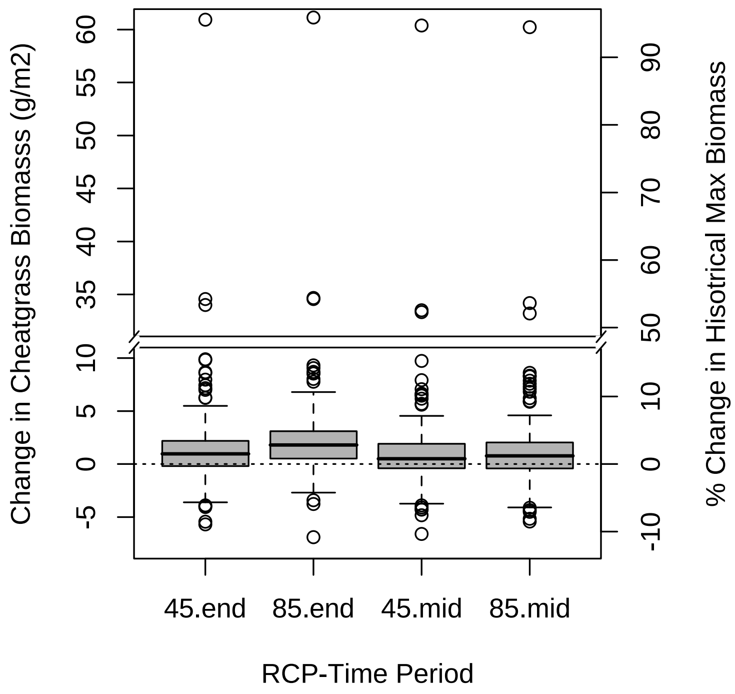

**Figure 2. Boxplot of Changes in Cheatgrass Biomass**
Changes in cheatgrass biomass (g/m$^2$) and percentage change in historical maximum biomass from current (1981-2010) to future conditions for the 200 sites under each RCP-time period combination. Results are for RCP4.5 (45), RCP8.5 (85), mid-century (mid), and end-century (end).

Areas with the greatest simulated increases in cheatgrass biomass were located in the eastern portion of the study area, including parts of the Great Plains, Wyoming Basins, Colorado Plateau, and Snake River Plain, where simulated cheatgrass biomass under current conditions was low (Figure 1). In contrast, we simulated small increases to small decreases in cheatgrass biomass in currently invaded areas in the Great Basin, Columbia Basin, and throughout large areas of the Colorado Plateau, and Snake River Plain (Figure 1). Increases in cheatgrass biomass were generally larger and more widespread under RCP8.5 than RCP4.5, and by end-century under both scenarios.

Under current conditions, invaded sites in the Western half of the study area had more frequent fire (lower FRI, fire every 56 to 69 years) than sites with lower cheatgrass biomass in the East (fire every 73 to 500 years) (Figure 3A, Appendix E). Under a future climate, fire became more frequent in sites with simulated increases in cheatgrass biomass, even when increases in cheatgrass biomass were small (Figures 3B-E, 4). Decreases in mean FRI (indicative of more frequent fire) were larger under RCP8.5 end-century conditions, but we simulated decreases in FRI under all future scenarios, especially in the Great Plains and Wyoming Basins (Figure 3B-E). Cheatgrass biomass was strongly correlated with changes in mean FRI under both mid-century and end-century conditions (Figure 4). Sites with small decreases in cheatgrass biomass had either no change or increases in mean FRI, while simulated increases in cheatgrass biomass consistently led to more frequent fire (decreases in mean FRI) (Figure 4).

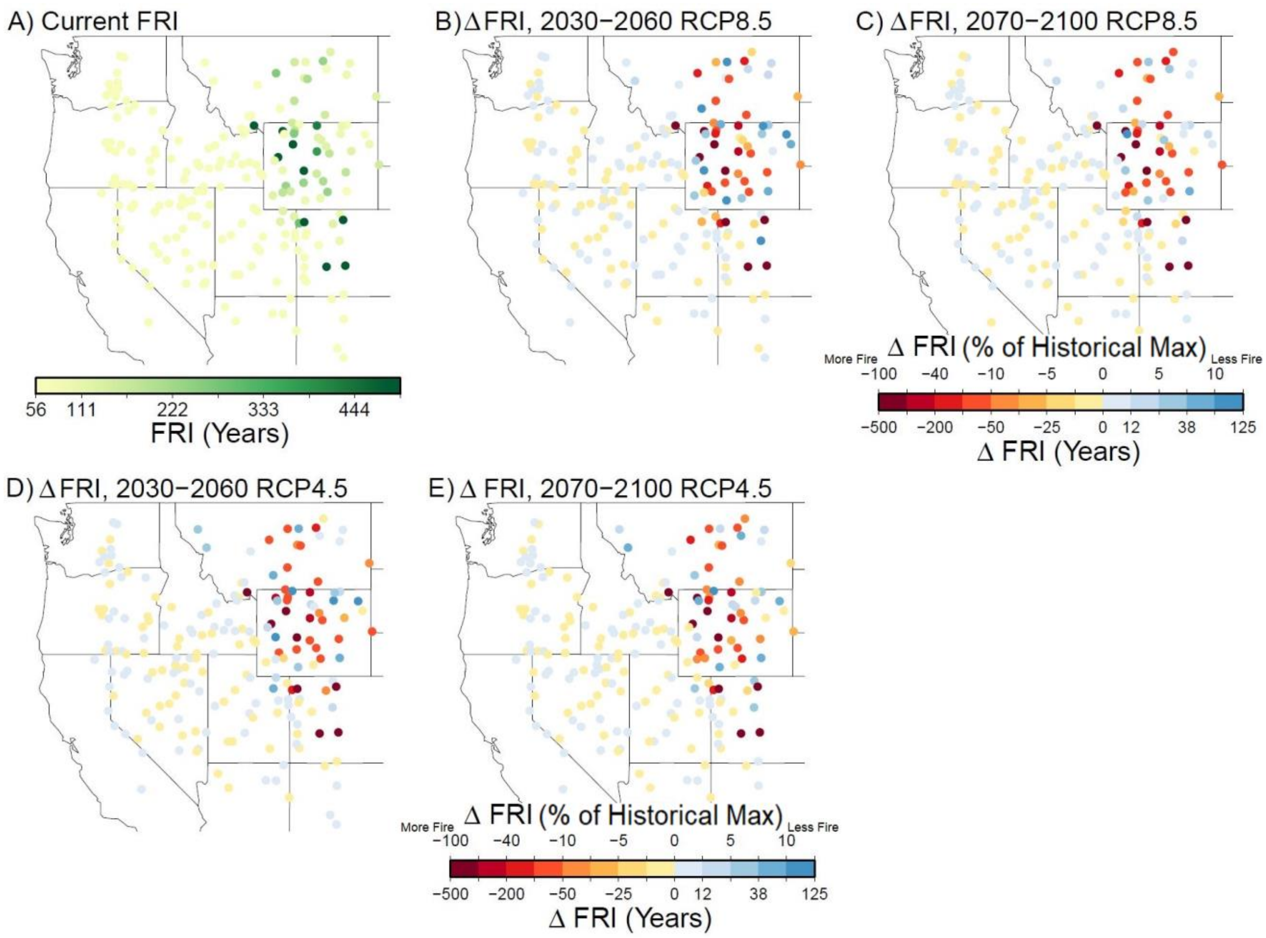

**Figure 3. Maps of FRI Simulations**

Current fire return interval (FRI) in years for the 200 sites (A) and change in FRI from current to future conditions under RCP8.5 (B, C) and RCP4.5 (D, E) for mid-century (2031-2060) and end-century (2071-2100), respectively. Each point represents the median FRI across simulations forced by 13 GCMs, and are colored by absolute change in FRI, which is also depicted as a percentage of the maximum historical FRI. FRI was capped at 500 years for 36 sites which had a FRI greater than 500 years or had no wildfire simulated.

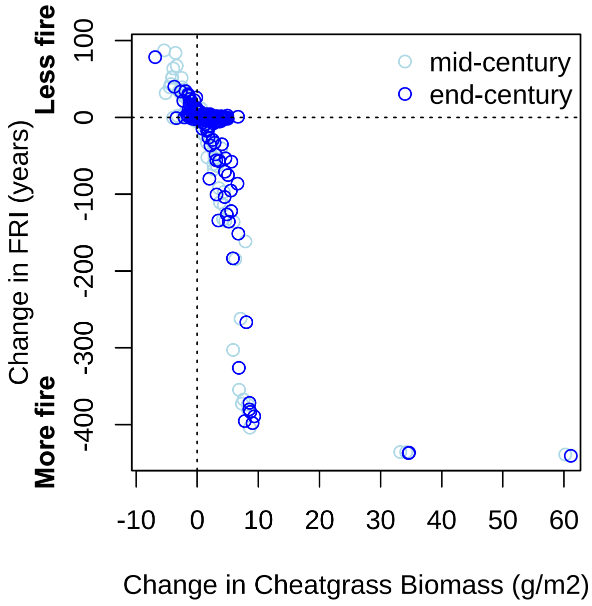

**Figure 4. Scatterplot of Changes in Cheatgrass and FRI**
Changes in cheatgrass biomass (g/m$^2$) from current to future conditions for the 200 sites under RCP8.5 versus changes in mean fire return-intervals (FRI, years) from current to future conditions. Decreases in mean FRI indicate more frequent fire under future conditions.

## Effects of the Cheatgrass-Wildfire Cycle on Native Plant Functional Types

The collective impact of climate change and increases in cheatgrass biomass and wildfire frequency resulted in moderate to large decreases in big sagebrush biomass over large areas under all climate scenarios (Figure 5B, C, Appendix F, G). The most significant losses occurred under RCP8.5 conditions by end-century (Figure 5B, C) and were concentrated in the Great Basin, the Great Plains and parts of the Snake River Plain. Under the least severe climate scenario (mid-century under RCP4.5), decreases in big sagebrush biomass were simulated in 55% of sites, and 63% of sites by end-century (Table 1). Despite this, we simulated regions of no change or small to moderate increases in big sagebrush biomass under all future climate scenarios and throughout the study area (Figure 5B, C, Appendix F, G). The largest contiguous zone of stability for big sagebrush under all future climate scenarios was located in the Columbia Basin (Figure 5B, C, Appendix F, G).

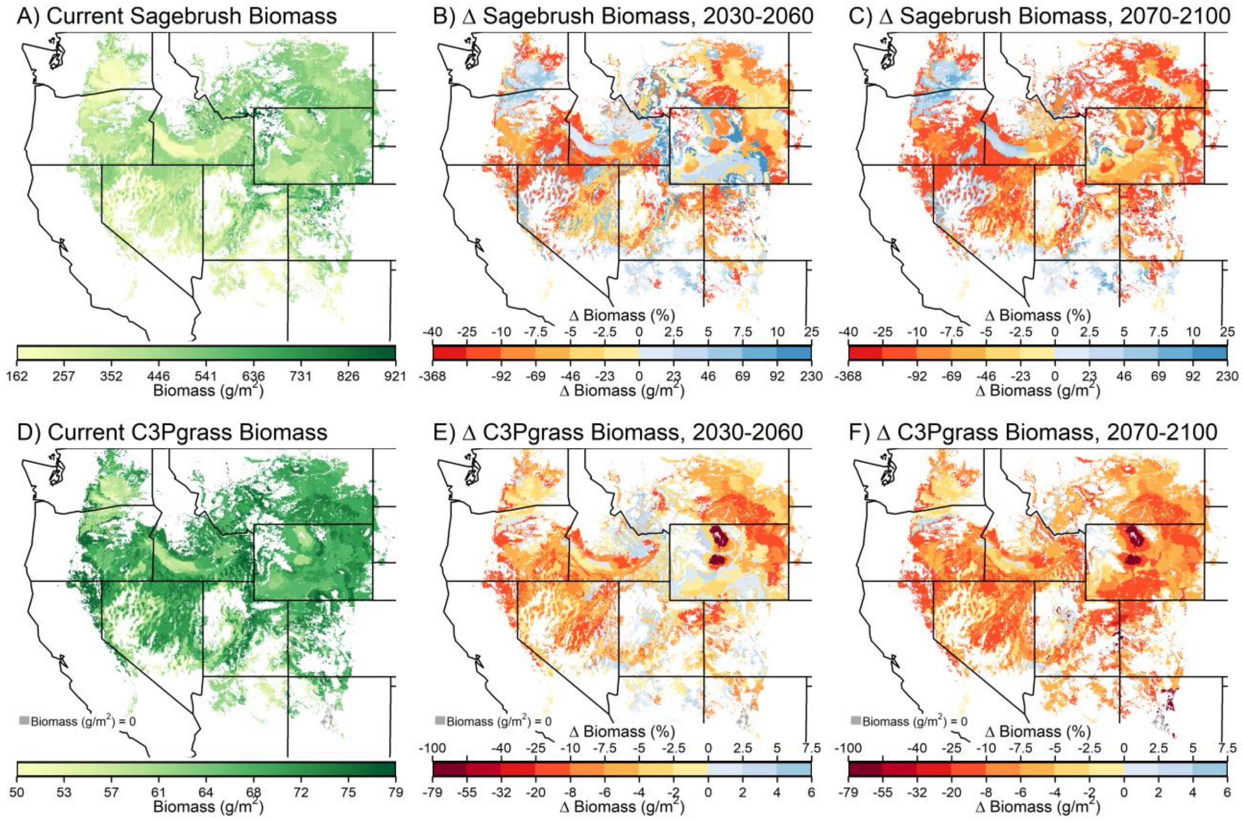

**Figure 5. Big Sagebrush and $C_3$ Perennial Grass Interpolated Maps**
Interpolated $C_3$ perennial grass and big sagebrush biomass (g/m$^2$) for current conditions (1981-2010) (A, D), change in biomass from current to mid-century (2031-2060) (B, E) and end-century (2071-2100) (C, F) under RCP8.5. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage change scaled to the maximum historical biomass.

$C_3$ and $C_4$ perennial grasses displayed equally strong but contrary trends. For both RCPs and time periods, $C_3$ perennial grasses declined across most of the study area (Figures 5E, F, Appendix F, H). By end-century under RCP8.5, 92% of sites had simulated decreases in biomass (Table 1), some of which were large and resulted in complete loss in some sites (Figure 5F,

Appendix H). There were only a few sites and interpolated areas where we simulated stability or increases in $C_3$ perennial grass biomass, most of which were located in the eastern half of the study area or at high-elevation elsewhere (Figures 5E, F, Appendix H). In contrast, we simulated consistent increases in $C_4$ perennial grasses (Figure 6B, C, Appendix I, J). By mid-century under RCP4.5, we simulated increases in $C_4$ perennial grass biomass in over 80% of sites, and in 98% of sites by end-century (Table 1). Under current conditions, many sites had little or no $C_4$ perennial grasses present, and by mid-century under both RCPs, almost all sites had $C_4$ perennial grasses present (Appendix I). Perennial forb biomass responded similarly to $C_3$ perennial grasses with widespread small to moderate declines under all future climate scenarios (Figure 6E, F, Appendix I, K). We simulated decreases in perennial forb biomass in 84% of sites by end-century under RCP8.5, compared to 75% under RCP4.5 (Table 1). Sites which currently have a high abundance of forbs had the greatest simulated decrease in biomass (Figure 6, Appendix I, K).

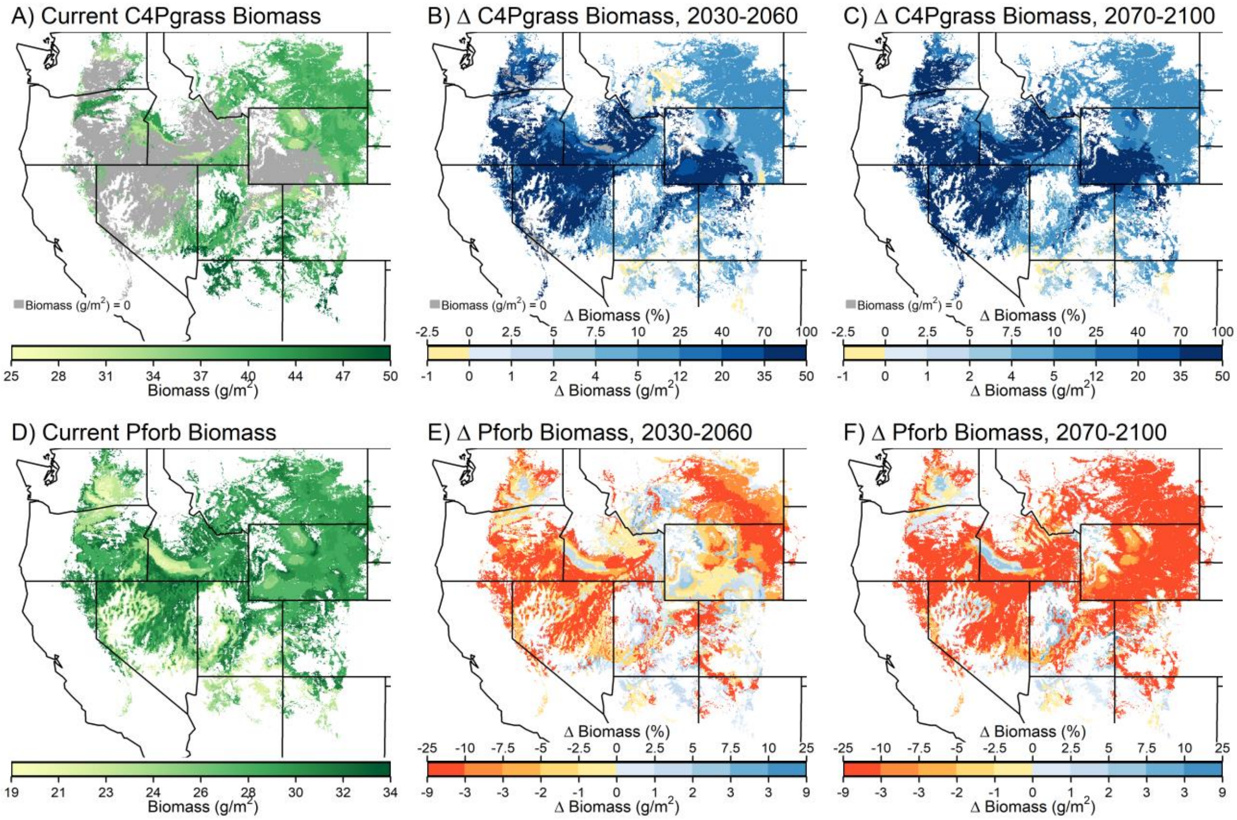

**Figure 6. $C_4$ Perennial Grass and Perennial Forbs Interpolated Maps**
Interpolated $C_4$ perennial grass and perennial forb biomass (g/m$^2$) for current conditions (1981-2010) (A, D), change in biomass from current to mid-century (2031-2060) (B, E) and end-century (2071-2100) (C, F) under RCP8.5. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage change scaled to the maximum historical biomass.

Wildfire driven by cheatgrass biomass substantially reduced big sagebrush biomass when compared to biomass from simulations without wildfire but with climate change represented (Figure 7). Declines in big sagebrush biomass due exclusively to cheatgrass-wildfire dynamics represented reductions of 56% to 61% across sites and RCPs. In contrast to big sagebrush, we simulated slight increases in median biomass across all sites for perennial grasses and forbs with wildfire simulated (Figure 7). Biomass differences for native herbaceous plant functional types (relative to biomass without wildfire simulated) were slightly higher under end-century conditions relative to mid-century and for RCP8.5 conditions relative to RCP4.5 (Figure 7).

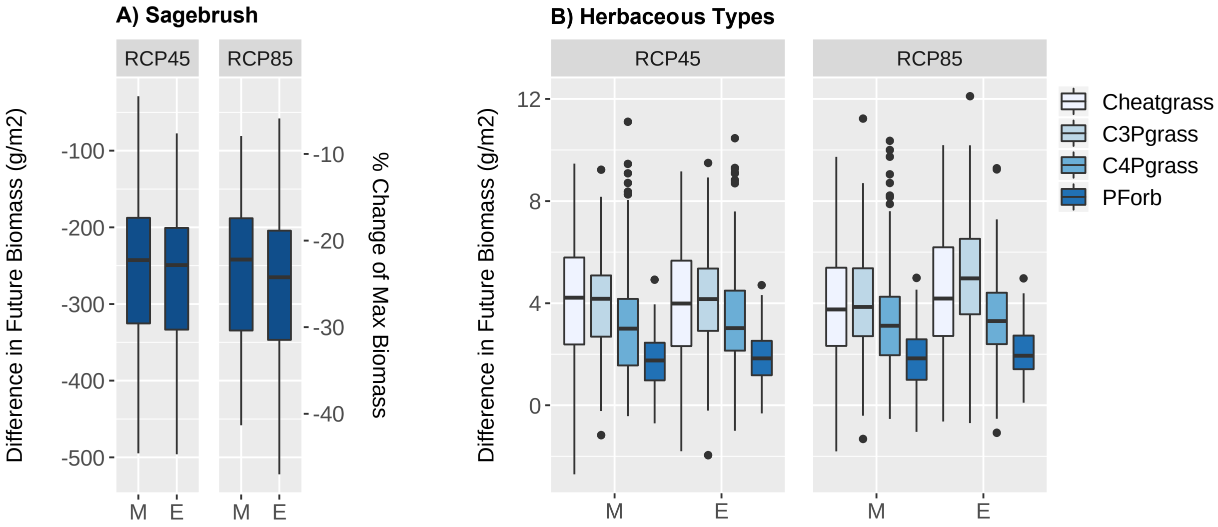

**Figure 7. Boxplot of Differences in Biomass with and without Wildfire**
Difference in future biomass between simulations run with the cheatgrass-wildfire loop enabled and without wildfire for mid-century (M) and end-century (E) under RCP4.5 and RCP8.5. Functional types represented are big sagebrush (panel A), cheatgrass, $C_3$ perennial grasses, $C_4$ perennial grasses, and perennial forbs (panel B). For big sagebrush (A), changes in biomass are also shown as a percentage change scaled to maximum future biomass without wildfire. Negative values indicate less biomass when wildfire was simulated.

## DISCUSSION

Our simulations suggest continued suitability for cheatgrass in currently invaded areas and increased suitability for cheatgrass in currently uninvaded or mildly invaded sites, due to a warming climate. These changes are likely to result in increases in fire frequency, even in sites with small increases in cheatgrass biomass. Under the combined influence of climate change and wildfire driven by cheatgrass abundance, we simulated widespread moderate declines in biomass for all of the dominant plant functional types, with the exception of $C_4$ perennial grasses. More frequent wildfire substantially reduced big sagebrush biomass, relative to herbaceous functional types. Collectively, our simulations suggest substantial changes in big sagebrush plant community composition under a future climate, especially under the more severe emissions scenario (RCP8.5) and by end-century.

In our simulations, warmer future conditions increased habitat suitability for cheatgrass in currently cold, high elevation or high latitude sites. These findings are consistent with experimental studies that have documented positive effects of warming on cheatgrass, as long as sufficient moisture remains (Blumenthal et al. 2016, Compagnoni and Adler 2014, Zelikova et al. 2013) or studies that have projected expansion of cheatgrass in areas where it is currently limited by minimum winter temperatures (Abatzoglou et al. 2011, Bradley et al. 2018, Pilliod et al. 2017). In contrast, Larson et al. (2017) found that warming did not increase cheatgrass invasion in Southwestern Montana, a region that we projected to be more suitable for cheatgrass under future conditions. Larson et al. (2017) attributed this to less cool-season precipitation than in sites where warming benefited cheatgrass growth, along with increased stress for cheatgrass during the warm-season imposed by the warming treatments. In contrast to cold sites, we simulated smaller increases or no change in cheatgrass biomass in warm, dry invaded sites, which we interpret as continued suitability for cheatgrass in those areas. We also simulated small decreases in cheatgrass biomass for some sites throughout the study area. This is likely due to reductions in soil moisture driven by warming in the late spring when cheatgrass is phenologically active, which is consistent with Larson et al. (2017).

Slight increases in cold-season precipitation projected for the big sagebrush region (Bradford et al. 2020, Palmquist et al. 2016b) may also have benefitted cheatgrass in our sites.

As a winter annual, cheatgrass's phenological activity is centered on the cool-season and experimental studies have documented positive responses of cheatgrass to increases and negative responses to decreases in cool-season precipitation (Larson et al. 2017, Prevéy and Seastedt 2014, Prevéy and Seastedt 2015). Additional evidence that cheatgrass benefits from more precipitation falling during the cool-season come from studies that have leveraged natural precipitation variability among sites (Bradford and Lauenroth 2006, Concilio et al. 2013).

We simulated increases in wildfire frequency in sites where cheatgrass biomass increased, even when those increases were small. Consistent with our results, Bradley et al. (2018) documented that within the Great Basin, small increases in cheatgrass percent cover (changes from <1% to 1-5%) lead to considerably more area burned and increases in fire probability. Small increases in cheatgrass biomass may increase fine fuel continuity and allow for more rapid-fire spread (Bradley et al. 2018). Our results are consistent with many studies in the Great Basin which indicate wildfire promotes cheatgrass invasion and increases cheatgrass abundance (Balch et al. 2013, Brooks et al. 2004, Whisenant 1990), and suggest that warming will expand the cheatgrass-wildfire cycle into currently unimpacted areas.

Simulated biomass of big sagebrush, $C_3$ perennial grasses, and perennial forbs decreased over large portions of our study area due to climate change and more frequent wildfire caused by increases in cheatgrass biomass. Palmquist et al. (2021) evaluated climate change effects on the same 200 sites without representing wildfire and found variable responses among locations within the biome for currently moisture-limited vs. temperature-limited sites. Consistent with previous empirical and modeling studies (Harte et al. 2015, Palmquist et al. 2021, Perfors et al. 2003, Renwick et al. 2018), we simulated stability or slight increases in big sagebrush biomass in cold, moist sites (primarily in the eastern half of the study area) and in the Columbia Basin due to smaller reductions in soil water availability in those locations. In contrast, we simulated the largest decreases in big sagebrush biomass in warm, dry locations due to simulated declines in soil moisture under future conditions, primarily in the Great Basin and the Snake River Plain. Our results for big sagebrush are consistent with the geographic patterns and trends described in Palmquist et al. (2021), however, we simulated considerably larger magnitudes of big sagebrush decline due to wildfire. Collectively, these outcomes are consistent with building evidence that suggests habitat suitability will decrease for big sagebrush in the Great Basin in response to warming and drying (Neilson et al. 2005, Renwick et al. 2018, Schlaepfer et al. 2012a, Still and Richardson 2015).

Decreases in $C_3$ perennial grasses and perennial forbs under future climate can be explained by the overall trend toward a warmer and drier climate resulting in decreases in soil moisture, as outlined by Palmquist et al. (2021). In contrast to big sagebrush, $C_3$ perennial grasses, and perennial forbs, we simulated increases in $C_4$ perennial grass suitability and hence biomass under a warmer climate due to the higher photosynthetic efficiency of $C_4$ species in warm conditions (Ehleringer 1978, Epstein et al. 1997, Sage 2004), along with lower stomatal conductance relative to $C_3$ species (Knapp 1993). This is consistent with other studies that have projected increases in $C_4$ grass abundance under warmer conditions (Klemm et al. 2020).

Simulated increases in wildfire frequency substantially reduced big sagebrush biomass, but slightly increased native perennial grass and forb biomass, relative to simulations with wildfire excluded. Big sagebrush is a long-lived and slow-growing perennial shrub that has evolved under relatively infrequent fire and is slow to recolonize following a fire event (Heyerdahl et al. 2006, Lesica et al. 2007, Shinneman and McIlroy 2016). Thus, big sagebrush is poorly adapted to frequent wildfire, and big sagebrush abundance decreases as fire becomes more frequent (Whisenant 1990). Perennial grasses and forbs likely responded positively to increases in wildfire frequency due to increased resource availability caused by big sagebrush mortality, along with the ability of grasses and forbs to re-sprout post-fire and recolonize more rapidly after fire than big sagebrush (Young and Raymond 1978).

Our modeling approach represents soil moisture dynamics under a future climate, intraspecific and interspecific competition between multiple plant functional types for soil moisture, and wildfire based on cheatgrass abundance, but approaches some processes in a more simplified way. While cheatgrass abundance is highly predictive of wildfire occurrence in big sagebrush ecosystems, the wildfire module of STEPWAT2 does not currently represent the effects of warming, antecedent precipitation, or fuel loads on fire probability, therefore potentially underestimating wildfire frequency. In this context, our results are likely a conservative representation of fire effects on big sagebrush plant communities. In addition, we chose to represent each site by a single soil type which is the most common in the big sagebrush region to understand the individual and combined effects of climate change and cheatgrass-driven wildfire on big sagebrush plant communities. Other big sagebrush studies have found that soil texture and soil depth can influence soil moisture (in addition to climate) with consequences for plant functional type composition (Renne et al. 2019, Schlaepfer et al. 2012b). Thus, evaluating climate-wildfire effects while representing spatial variability in soil properties is an important and logical next step. Finally, dispersal of species into new areas was not explicitly represented and hence we interpret our results for $C_4$ perennial grasses with some caution. While our results suggest increasing climate suitability for $C_4$ perennial grasses over large areas, the increases in biomass we simulated will only be achieved if $C_4$ perennial grasses can disperse to and establish in sites with an existing plant community.

Understanding the effects of cheatgrass invasion and resulting changes in wildfire frequency on big sagebrush plant communities under a changing climate has important implications for conservation planning and decision-making. Warmer, drier conditions are likely to increase opportunities for cheatgrass establishment in portions of the big sagebrush region that are currently not climatically suitable, thereby increasing wildfire frequency. These potential increases in wildfire will disrupt native plant communities, with especially large impacts for big sagebrush, and result in negative effects for sagebrush-obligate wildlife species. Reversing cheatgrass invasion requires substantial effort and cost (Whisenant 1990), thus identifying where big sagebrush ecosystems will be more vulnerable or resistant to cheatgrass invasion is vital to inform management decisions and conservation investments. Our simulations suggest that increased fire frequency will negatively impact big sagebrush ecosystems and facilitate the invasion of cheatgrass into currently uninvaded or minimally invaded sites.

# CHAPTER TWO

# EFFECTS OF LIVESTOCK GRAZING ON THE BIG SAGEBRUSH PLANT COMMUNITIES IN A CHANGING CLIMATE

## INTRODUCTION

Livestock grazing is one of the most widespread land uses in drylands, which comprise ~ 40% of global land surface (Feng and Fu 2013) and can be an important force governing plant community composition (Milchunas and Lauenroth 1993, Augustine and McNaughton 1998). Livestock grazing can shift the competitive advantage among plant functional types as a result of herbivore selectivity and the ability of plants to recover following grazing (Noy-Meir 1993, Augustine and McNaughton 1998). The potential for plant regrowth following grazing depends on plant morphology, the evolutionary history of grazing, and environmental and climatic conditions (Milchunas et al. 1988, Noy-Meir 1993, Stohlgren et al. 1999, Rahmanian et al. 2020), while herbivore selectivity depends on the kind and number of herbivores as well as the duration of grazing (Augustine and McNaughton 1998).

In the future, livestock grazing may interact with shifting climate patterns to influence plant communities in unexpected ways (Lohmann et al. 2012), especially in drylands. Rising temperatures and changing precipitation regimes influence dryland ecohydrology and plant community composition, because water is already scarce and increases in temperature are projected to decrease water availability (Huang et al. 2017), with more profound effects projected for currently moisture-limited sites (Kleinhesselink and Adler 2018, Palmquist et al. 2021). Understanding the direction and regional patterns of livestock grazing and climate change impacts is critical to human livelihoods and sustainable ecosystem management.

In big sagebrush (*Artemisia tridentata* Nutt.) ecosystems, which are widespread drylands now covering approximately 76 million hectares in the Western United States (U.S.) (Rigge et al. 2020), grazing by livestock has been widely implemented since the 1800s (Connelly et al. 2004), in addition to grazing by native ungulates. This ecosystem was significantly altered during the western expansion of 1880-1905 from large increases in the number of livestock and from subsequent drought and overgrazing in the 1920s and 1930s (Mitchell and Hart 1987, Box 1990). Since then, livestock grazing has been a persistent land-use which supports western economies and has important implications for plant community structure (Connelly et al. 2004).

Big sagebrush ecosystems are the largest interconnected habitat type in the United States (US), historically encompassing arid and semiarid regions across more than 100 million hectares (West 2000). Multiple factors are threatening these ecosystems, including heavy grazing by livestock (Condon and Pyke 2018, Cutting et al. 2019), climate change (Renwick et al. 2018, Bradford et al. 2020, Palmquist et al. 2021), and increases in wildfire frequency (Whisenant 1990, Bradley et al. 2018), with negative effects for sagebrush-dependent species, including threatened greater sage-grouse (*Centrocercus urophasianus*) and endangered populations of pygmy rabbits (*Brachylagus idahoensis*) (Connelly et al. 2004, Cutting et al. 2019, Raphael et al. 2001, Remington et al. 2021, Rowland et al. 2006). A significant threat to big sagebrush ecosystems is the invasive annual grass cheatgrass (*Bromus tectorum* L.), and associated increases in wildfire frequency (Coates et al. 2016, Balch et al. 2013, Brooks et al. 2004, Knick et al., 2003). Cheatgrass invasion can initiate a positive feedback loop with wildfire (Whisenant 1990, D’Antonio and Vitousek 1992), both of which are expected to increase under a future climate due to warming (Brummer et al. 2016, Concilio et al. 2013, Howell et al. 2020). Heavy grazing has promoted the expansion of cheatgrass by decreasing the abundance of native perennial grasses, forbs, and biocrusts resulting in increases in bare ground and opportunities for cheatgrass establishment and proliferation (Mack 1981, Root et al. 2020, Williamson et al. 2020).

However, our understanding of how livestock grazing will interact with changes in climate and increases in wildfire to alter future big sagebrush plant communities remains limited. The big sagebrush region encompasses a large heterogenous landscape of several climatically distinct ecoregions which are projected to respond differently to future climate (Palmquist et al. 2016a, Renwick et al. 2018, Bradford et al. 2020, Palmquist et al. 2021) and the outcomes of different livestock grazing intensities are likely to vary depending on future climate heterogeneity. To better understand how livestock grazing may alter the response of plant communities under a future climate, we used an individual-based plant simulation model, STEPWAT2 (Palmquist et al. 2018a, b), to project the concurrent response of big sagebrush plant communities to future climate conditions, livestock grazing under different intensities, cheatgrass invasion, and wildfire based on cheatgrass abundance. Our simulation modeling approach represents a process-based representation of soil moisture and competitive interactions between cheatgrass and native plant functional types for fluctuating limiting resources to characterize the response of widespread big sagebrush plant communities to varying grazing intensity under current and future conditions. Our goal is to quantify how livestock grazing intensity will alter big sagebrush plant community responses under a changing climate. Specifically, (1) How will different intensities of livestock grazing alter native grass and forb biomass relative to invasive grass biomass under future conditions, and (2) How will these livestock grazing effects differ between future projected climate scenarios? Our results may help to identify effective and sustainable livestock grazing management strategies under future conditions across a diverse ecosystem.

## METHODS

### Study Area

Our study area encompasses the spatial extent of big sagebrush plant communities of the Western US (Appendix B). We selected 200 sites, which represent the range of climatic variability of big sagebrush ecosystems, encompassing mean annual temperature and mean annual precipitation from 0.1 to 13°C and 176 to 850 mm, respectively. When possible, sites were also chosen to represent high density of breeding populations of greater sage-grouse (Doherty et al. 2016). The selection of these sites is described in detail in Palmquist et al. (2021). Big sagebrush plant communities are characterized by an overstory of big sagebrush and an understory comprised primarily of perennial grasses and perennial forbs (West 1983, Pennington et al. 2017), which provide forage for cattle and native herbivores.

### STEPWAT2 Modeling

We used STEPWAT2, an individual-based plant simulation model described in and validated by Palmquist et al. (2018a, 2018b) and rSFTEP2 (https://github.com/DrylandEcology/rSFSTEP2/releases/tag/v.1.0.0), a R program that executes STEPWAT2, to model the effects of multiple climate and grazing scenarios on big sagebrush plant communities. STEPWAT2 integrates an individual-based plant simulation model that runs on an annual time step (based on STEPPE, Coffin and Lauenroth 1990) with a process-based soil water balance model that runs on a daily basis and represents multiple soil layers (SOILWAT2, Schlaepfer et al. 2012b). STEPWAT2 simulates establishment, growth, and mortality of multiple plant species and plant functional types based on soil water availability generated each year by

SOILWAT2, along with species- and functional type-specific life-history traits. This approach represents individual plant responses to fluctuating limiting resources that result from inter- and intraspecific competition. Larger individuals within the same species receive resources first and a larger share of the resources (intraspecific competition). Interspecific competition occurs through several processes driven by species-specific differences in resource acquisition, which are largely based on species phenology, rooting depth distributions, and intrinsic growth rates (see Palmquist et al. 2018a for additional detail). STEPWAT2 also simulates several disturbances including grazing and cheatgrass-driven wildfire implemented as a positive feedback loop between cheatgrass abundance and wildfire. Output includes total aboveground biomass (g/m2) for each species and functional type, species and functional type density, and wildfire occurrence, in addition to ecohydrological and climatic variables from SOILWAT2 (Schlaepfer et al. 2012b, Palmquist et al. 2018a).

Each site is represented as a 1 $m^2$ patch, simulated to reflect the average area that a full-sized big sagebrush individual occupies based on its root system (~ 1 $m^2$; Sturges 1977) and based on average big sagebrush density (~1.5 individuals/$m^2$; Palmquist et al. 2018a). Although each site is represented by 1 $m^2$, each patch is representative of conditions more general than at any particular 1 $m^2$ location because each STEPWAT2 simulation incorporates multiple sources of variation (e.g., 200 iterations of generated weather; stochastic demographic processes).

For each site, we simulated common and widespread plant species representative of 10 functional types: big sagebrush, $C_3$ perennial grasses, $C_4$ perennial grasses, annual $C_3$ grasses, perennial $C_3$ cool-season forbs, perennial $C_3$ warm-season forbs, annual $C_3$ cool-season forbs, and annual $C_3$ warm-season forbs, non-sagebrush shrubs, and succulents (see Appendix C). We focused on sagebrush, cheatgrass, $C_4$ and $C_3$ perennial grasses, and forbs for our analysis as the most dominant functional types of this ecosystem. Each functional type was represented by a single species which is widely distributed and abundant in big sagebrush ecosystems (see Palmquist et al. 2018a).

We simulated each site for 200 iterations and 300 years under current and future climate conditions using 13 Global Climate Models (GCMs) for representative concentration pathways (RCPs) 4.5 and 8.5 to evaluate different future climate scenarios. We ran simulations for 200 iterations to account for variation in model output between each simulation run resulting from stochastic processes, such as seedling establishment. We used 13 GCMS which perform well in the Western US (Rupp et al. 2013) and are representative of the existing GCM families (Knutti et al. 2013): CanESM2, CESM1-CAM5, CSIRO-Mk3-6-0, FGOALS-g2, FGOALS-s2, GISS-E2-R, HadGEM2-CC, HadGEM2-ES, inmcm4, IPSL-CM5A-MR, MIROC5, MIROC-ESM, and MRI-CGCM3. For each site, we extracted current (1981-2010) daily climate data from Daymet (Thornton et al. 2018). Future climate data for each site-GCM-RCP combination for mid-century (2031-2060) and end-century (2071-2100) were extracted from the Downscaled CMIP3 and CMIP5 Climate and Hydrology Projects archive (Maurer et al. 2002, Maurer et al. 2007) and then downscaled using the hybrid-delta approach to generate future daily weather from current daily weather and monthly future projections (Hamlet et al. 2010, Tohver et al. 2014). We used a first-order markov weather generator within SOILWAT2 to generate 300 years of weather data with the same statistical properties as the 30-year clusters of weather data.

We simulated each site with soil properties that correspond to a silt loam (30% sand, 18% clay), which represents the most frequent soil type for big sagebrush plant communities (see Bradford et al. 2019, Palmquist et al. 2021, Appendix S3). We simulated differences in plant functional composition in the 200 sites based on each site’s climate (current or future) and according to established climate-relative abundance equations in the literature (Brummer et al. 2016, Paruelo and Lauenroth, 1996, Teeri and Stowe, 1976). This was implemented using R package rSOILWAT2 (Schlaepfer et al. 2020) and is described in detail in Palmquist et al. (2021). This implementation results in differences in vegetation parameters for multiple functional types across sites based on current conditions and shifts in functional type composition for each site from current to future conditions in response to changing climate.

We simulated livestock grazing annually at light, moderate, and heavy intensities. This was implemented for each functional type by removing a fraction of the current year's growth allowing for variation in livestock grazing impacts on different functional types. Biomass removed by grazing was based on data in Milchunas and Lauenroth (1993) which characterized the effects of grazing on multiple plant functional types in shrublands globally (see Appendix C). For each livestock grazing intensity, grasses and forbs had more biomass removed than big sagebrush and succulents to represent livestock forage preferences.

Similar to Chapter 1, all simulations were run with a positive feedback loop between cheatgrass biomass and wildfire enabled. Wildfire based on cheatgrass biomass was modeled based on data from Bradley et al. (2018) and Balch et al. (2013), that characterize fire probability based on cheatgrass percent cover. We derived a relationship between percent cover of cheatgrass and FRI based on MODIS fire data presented in Bradley et al. (2018) (see Appendix D). However, within STEPWAT2, we track cheatgrass abundance using biomass (g/m$^2$). As such, we also implemented an equation that converts cheatgrass biomass (g/m$^2$) to percent cover each year, so we could then calculate fire probability. This equation was based on an allometric equation between cheatgrass percent cover and cheatgrass biomass (g/m$^2$) presented in Mahood et al. (2021) and derived for big sagebrush ecosystems in the Great Basin. This relationship was then incorporated into the STEPWAT2 fire module to simulate fire each year based on cheatgrass abundance.

### Analysis

We calculated median mean biomass for each functional type under future and current conditions, and summarized changes in biomass from current to future conditions under different climate scenarios and livestock grazing intensities. First, we calculated mean biomass over the final 30 years of simulated data after plant communities had reached steady-state conditions. We did this for current conditions and for each GCM-RCP-time period-grazing combination for each of the 200 sites. Second, we calculated the change in biomass ($g/m^2$) from current to future conditions under each GCM-RCP-time period-grazing combination, along with percentage change from current to future conditions relative to the current maximum biomass (hereafter % change of historical maximum biomass). Thereafter, we sorted mean biomass, change in biomass, and % change of historical maximum biomass to identify the median among the 13 GCMs for each RCP-time period-grazing combination. Finally, we used the resulting biomass values to calculate the absolute and percentage change in biomass that results from a shift in livestock grazing intensity (light to moderate, moderate to heavy, light to heavy) under different RCP-time period combinations. We used R version 3.6.0 and R Studio version 1.2.1335 for analyses of simulation output (R Core team 2020, R Studio Team 2020).

## RESULTS

For most sites, $C_3$ perennial grass simulated biomass declined from current to future conditions under all livestock grazing intensity treatments, with more significant losses under moderate and heavy grazing (-16.8% and -16.1% respectively) for RCP8.5 (Figures 8A, 9, Appendix L). The lowest overall $C_3$ perennial grass biomass was simulated under heavy grazing and RCP8.5 end-century conditions (Figure 8A). In contrast, $C_4$ perennial grasses increased relative to current conditions under all livestock grazing and climate scenarios but increased the most under light grazing, and RCP8.5, end-century conditions (Figure 8B). $C_4$ perennial grass biomass increased from current to future conditions under all climate-grazing scenarios, but those simulated increases were smaller under heavy livestock grazing (Figure 9). Under each RCP and time period, $C_4$ perennial grasses both declined under a shift from light to moderate grazing, from moderate to heavy grazing, and declined substantially from light to heavy grazing (Figure 10). $C_3$ perennial grasses exhibited a slightly different response with the smallest declines in biomass occurring under a shifte from moderate to heavy grazing, and comparable declines under a shift from light to moderate and light to heavy grazing (Figure 10).

Perennial forbs decreased in most sites under all future climate scenarios but exhibited smaller percentage decreases in biomass under more intense livestock grazing treatments when compared to light grazing (Figure 9). However, some sites had simulated increases in perennial forb biomass under all climate-grazing scenarios. Future perennial forb biomass decreased significantly compared to current conditions under light grazing, particularly under RCP8.5, end-century conditions (Figure 8E). Comparatively, perennial forb biomass decreased only slightly under all livestock grazing treatments by mid-century under RCP4.5 conditions (Figure 9). Light and moderate livestock grazing had relatively little effect on perennial forb biomass under RCP4.5 conditions. Under each climate scenario and time period, perennial forb biomass increased under a shift from light to heavy grazing, and increased slightly under a shift from light to moderate or moderate to heavy grazing (Figure 10).

Simulated current cheatgrass and big sagebrush biomass exhibited little variation across livestock grazing intensity treatments (Figure 8C, 9D). Most sites had small increases in cheatgrass biomass, however, some sites exhibited large simulated increases in biomass under all climate and grazing scenarios, while others exhibited small decreases (Figure 9). Cheatgrass biomass declined slightly under moderate and heavy livestock grazing by end-century under RCP8.5 and RCP4.5, relative to light grazing, current conditions (Figure 8C). In general, percent changes in cheatgrass biomass were less variable under heavy grazing (Figure 9). Under each climate scenario and time period, cheatgrass declined more significantly when the livestock grazing regime shifted from light to heavy grazing relative to shifts from light to moderate or moderate to heavy grazing (Figure 10). Big sagebrush biomass declined slightly under end-century and RCP8.5 conditions for all livestock grazing treatments compared to current biomass (Figure 8D). Under RCP4.5, mid-century conditions big sagebrush decreased slightly across livestock grazing treatments (<-1%) and exhibited smaller decreases under heavy grazing conditions (Appendix L). Big sagebrush biomass declined the most under RCP8.5 and end-century conditions (Figure 9). Big sagebrush declined slightly when the livestock grazing management regime shifted from moderate to heavy grazing or light to moderate grazing, but declined more substantially between light and heavy grazing under each climate scenario and time period (Figure 10).

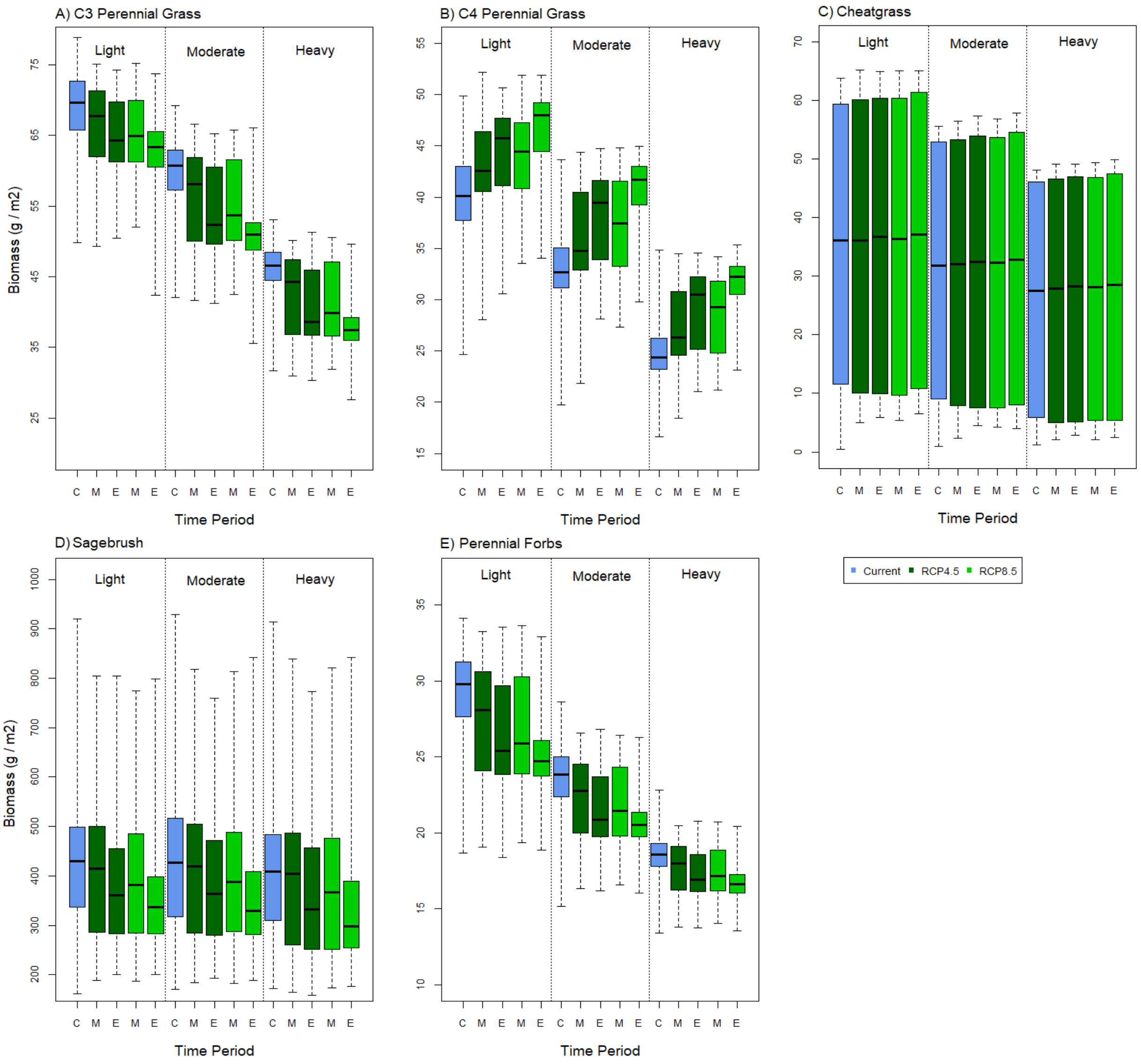

**Figure 8. Current and Future Biomass for each Climate-Livestock Grazing Intensity Scenario**

Current and future biomass (g/m$^2$) for each functional type under each livestock grazing intensity. Future biomass is shown for mid-century (“M”) and end-century (“E”) under RCP4.5 and RCP8.5. and represents the median biomass that resulted from forcing by 13 GCMs.

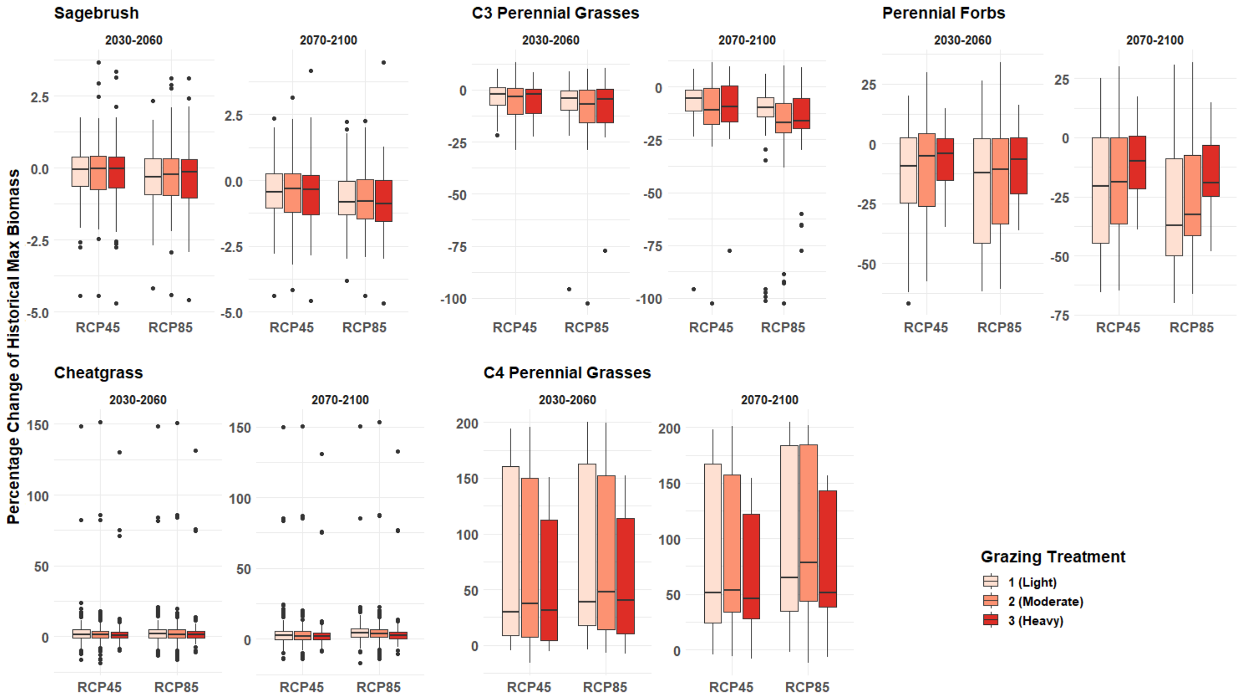

**Figure 9. Percentage Change of Biomass from Current to Future Conditions for each Livestock Grazing Intensity**

Percentage change in biomass from current conditions to mid-century (2031-2060) and end-century (2071-2100) under each livestock grazing intensity for each functional type. Values represent future median biomass under each climate-livestock grazing scenario subtracted by median biomass under current conditions for the same grazing treatment, scaled relative to the maximum possible biomass across all sites under current conditions.

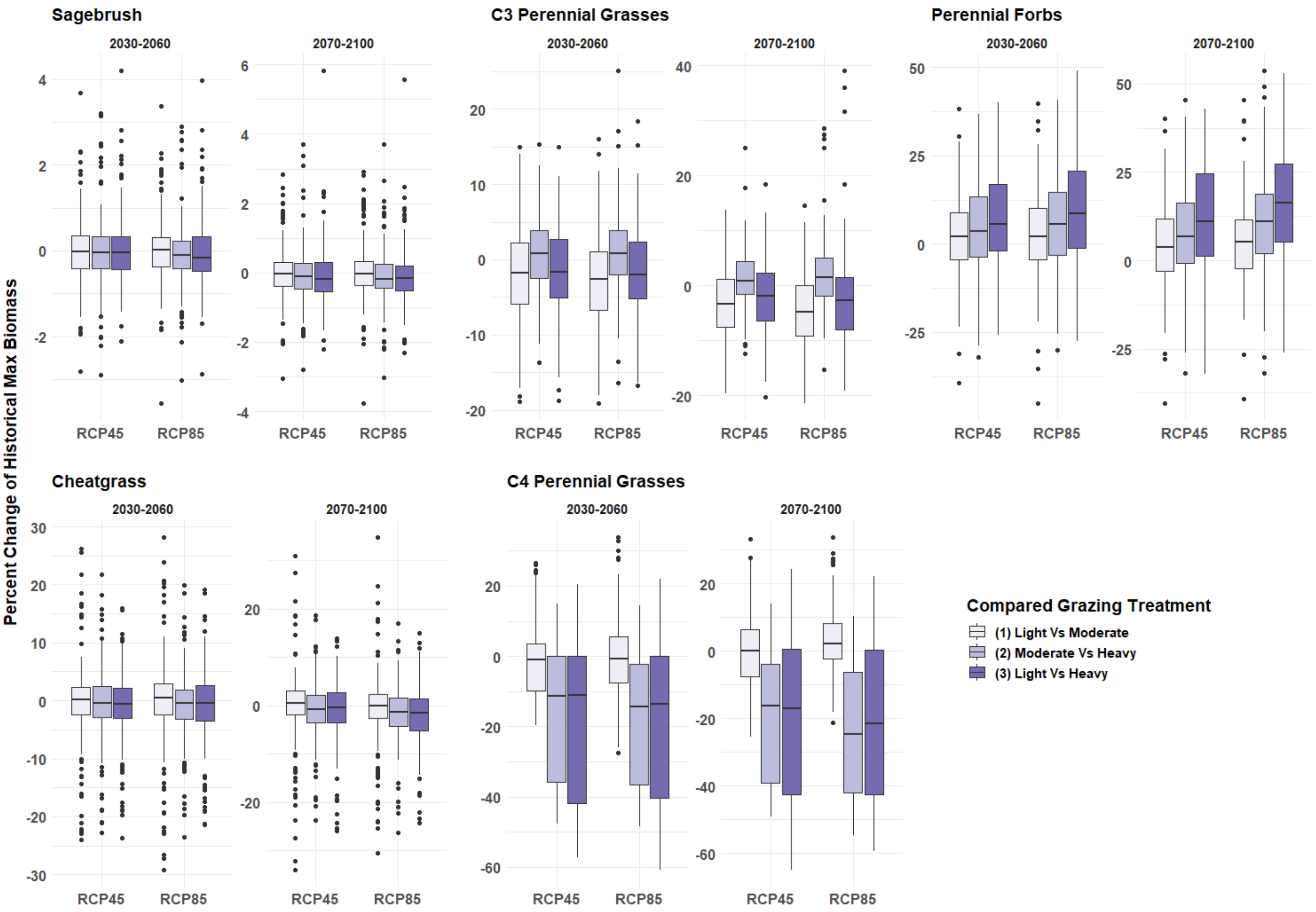

**Figure 10. Percentage Change in Biomass Between Livestock Grazing Treatments**
Percentage change scaled to the maximum historical biomass (g/m$^2$) for each plant functional type when livestock grazing management shifted from light to moderate (1), moderate to heavy (2), and light to heavy (3) under RCP4.5 and RCP8.5, and mid-century (2031-2060) and end-century (2071-2100) time periods. Values represent the difference in biomass in response to a shift from a less intense livestock grazing regime to a more intense regime. A negative value indicates more biomass is lost under the more intense livestock grazing treatment.

## DISCUSSION

We simulated greater declines in perennial grass and perennial forb biomass under increasingly heavy grazing, as a result of these plant functional types being favored as forage by livestock. For these functional types, heavy livestock grazing had a more significant impact than climate change alone. $C_4$ perennial grasses, big sagebrush, and cheatgrass responded less significantly to livestock grazing intensity treatments compared to other plant functional types. Collectively, our results suggest differential responses of plant functional types to climate change and livestock grazing intensity with implications for future plant functional type composition.

Climate change effects on plant functional type biomass interacted with the impacts of grazing in different ways. Despite losses in biomass due to livestock grazing, $C_4$ perennial grasses and cheatgrass still exhibited increases in biomass from current to future conditions within a given grazing intensity treatment. Comparatively, simulated big sagebrush biomass declined in most sites under all climate change scenarios, but showed little difference between livestock grazing intensity treatments. This resulted from the selective removal of grasses by livestock, resulting in greater available resources for shrubs and higher shrub biomass. Under all scenarios, cheatgrass biomass was not significantly reduced by increasing livestock grazing intensity. Climate change effects on some functional types such as $C_3$ perennial grasses were exacerbated by a shift from light to moderate or heavy grazing, and for some functional types, such as cheatgrass, heavy targeted grazing may help to reduce some effects caused by climate change. However, these findings suggest that even intense livestock grazing pressure may not counteract the projected increases in cheatgrass biomass that are likely to occur in response to climate change and increases in wildfire frequency (see Chapter 1).

Our findings are consistent with previous studies which suggest that heavy grazing by livestock may reduce native plant abundance in the future (Condon and Pike 2019, Root et al. 2020, Williamson et al. 2020). Contrary to expectations, heavy grazing did not substantially reduce $C_4$ perennial grass biomass and did not significantly affect cheatgrass invasion levels under future conditions. This likely results from the positive response of $C_4$ perennial grasses and cheatgrass to warmer future conditions (Epstein et al. 1997, Pilliod et al. 2017) and the relatively grazing-resistant nature of $C_4$ perennial grasses (due to clonal growth) and cheatgrass (due to prolific seed production and rapid colonization post-disturbance). Our findings also agree with other studies that have suggested climate change and livestock grazing will interact to increase cheatgrass invasion in most cases (Williamson et al. 2020).

Other studies have suggested that timing and/or spatial targeting of livestock grazing is necessary to act as a management strategy to reduce cheatgrass abundance (Perryman et al 2020, Porensky et al. 2021). However, we simulated little change in cheatgrass biomass under any livestock grazing intensity treatment. Future studies should explore the relative impact of seasonal targeted livestock grazing on cheatgrass under varying grazing intensity to understand the potential role of livestock grazing as a land management tool under a changing climate.

Limitations to this study result primarily from a somewhat simplistic representation of livestock grazing, along with limitations described previously in Chapter 1. Although our simulations did represent livestock forage preferences for herbaceous plant functional types, we simulated relatively homogenous grazing within each site and fixed grazing intensity across years. This may lead to an underestimation of the amount of biomass removed at least in some years, potentially resulting in an underestimation of the effect of livestock grazing on herbaceous plant functional types.

Collectively, our results suggest that livestock grazing treatments may have little to no effect on cheatgrass abundance in a future climate and mostly negative effects for native plant functional types (especially perennial forbs and $C_3$ perennial grasses). Overall, livestock grazing may not be an effective management strategy for the reduction or prevention of cheatgrass invasion and may exacerbate climate-driven loss of native plant communities.

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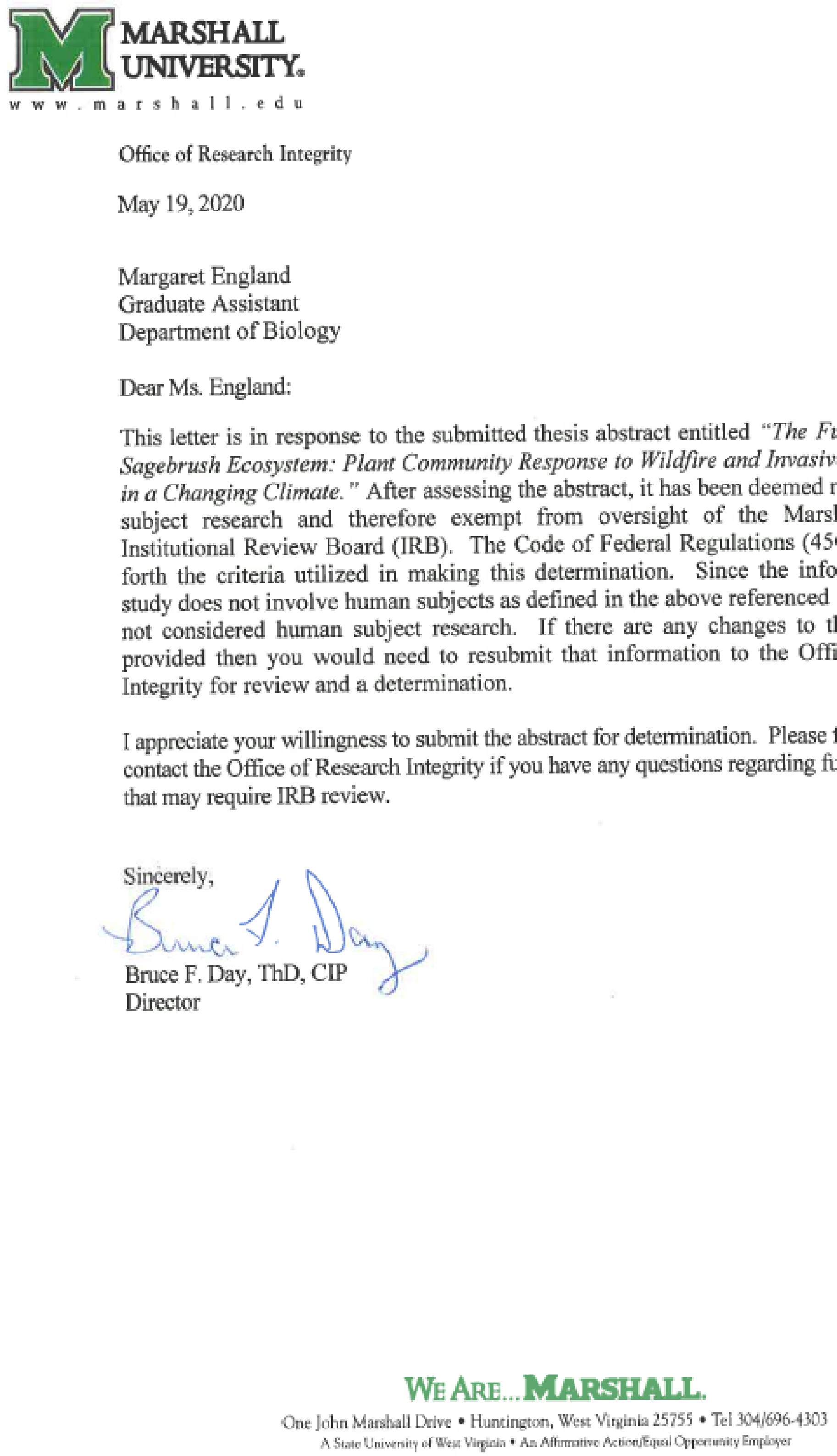
## Appendix A: Office of Research Integrity Approval Letter



MARSHALL
UNIVERSITY.
www.marshall.edu

Office of Research Integrity

May 19, 2020

Margaret England
Graduate Assistant
Department of Biology

Dear Ms. England:

This letter is in response to the submitted thesis abstract entitled *"The Future of the Big Sagebrush Ecosystem: Plant Community Response to Wildfire and Invasive Annual Grass in a Changing Climate."* After assessing the abstract, it has been deemed not to be human subject research and therefore exempt from oversight of the Marshall University Institutional Review Board (IRB). The Code of Federal Regulations (45CFR46) has set forth the criteria utilized in making this determination. Since the information in this study does not involve human subjects as defined in the above referenced instruction, it is not considered human subject research. If there are any changes to the abstract you provided then you would need to resubmit that information to the Office of Research Integrity for review and a determination.

I appreciate your willingness to submit the abstract for determination. Please feel free to contact the Office of Research Integrity if you have any questions regarding future protocols that may require IRB review.

Sincerely,

Bruce F. Day

Bruce F. Day, ThD, CIP
Director

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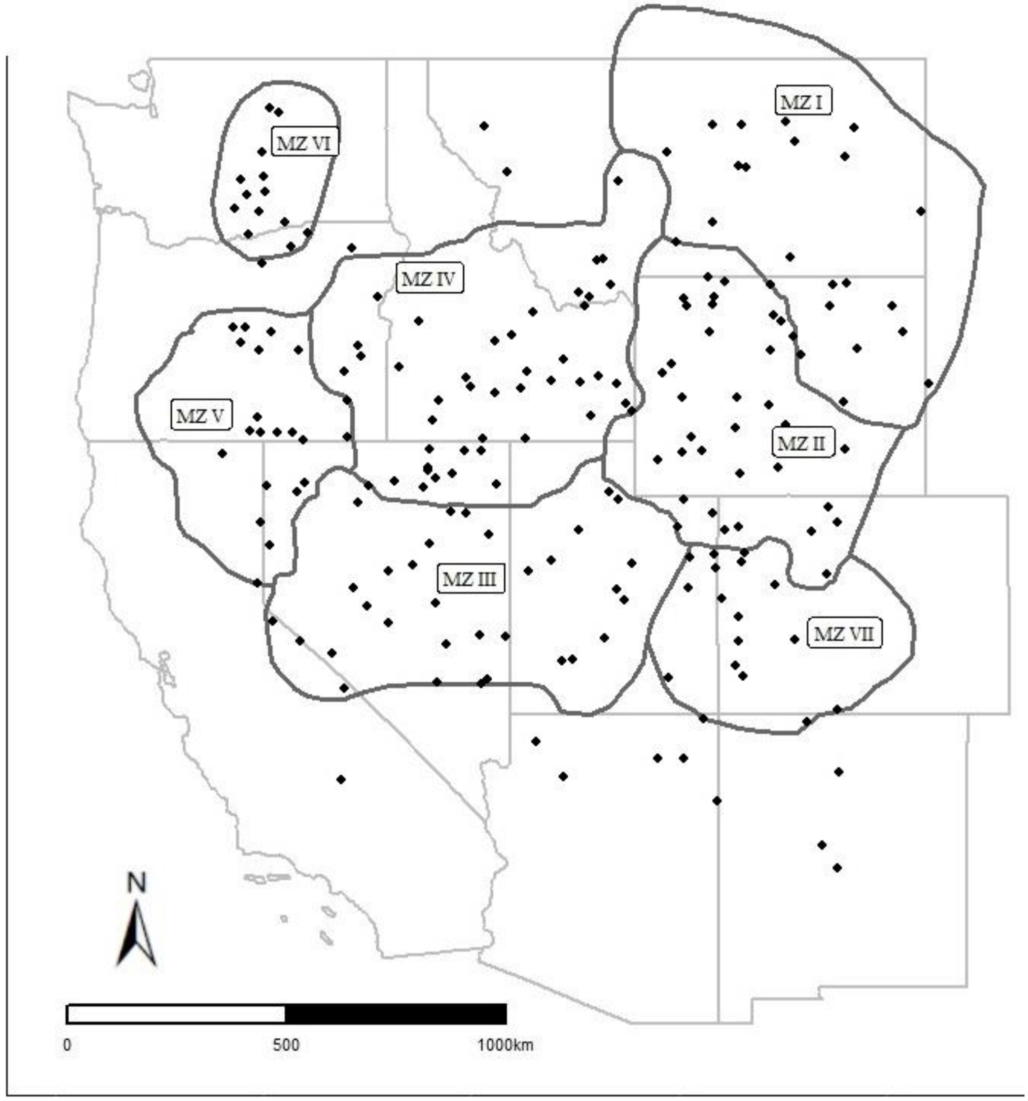
# APPENDIX B: STUDY SITE MAP



**Appendix B. Study Site Map**

Map of all 200 simulation sites within respective Sage-Grouse Management Zones (MZ). MZ I through MZ VII correspond to the Great Plains, Wyoming Basins, Southern Great Basin, Snake River Plain, Northern Great Basin, Columbia Basin, and the Colorado Plateau, respectively.

# APPENDIX C: TABLE OF GRAZING INTENSITY TREATMENTS

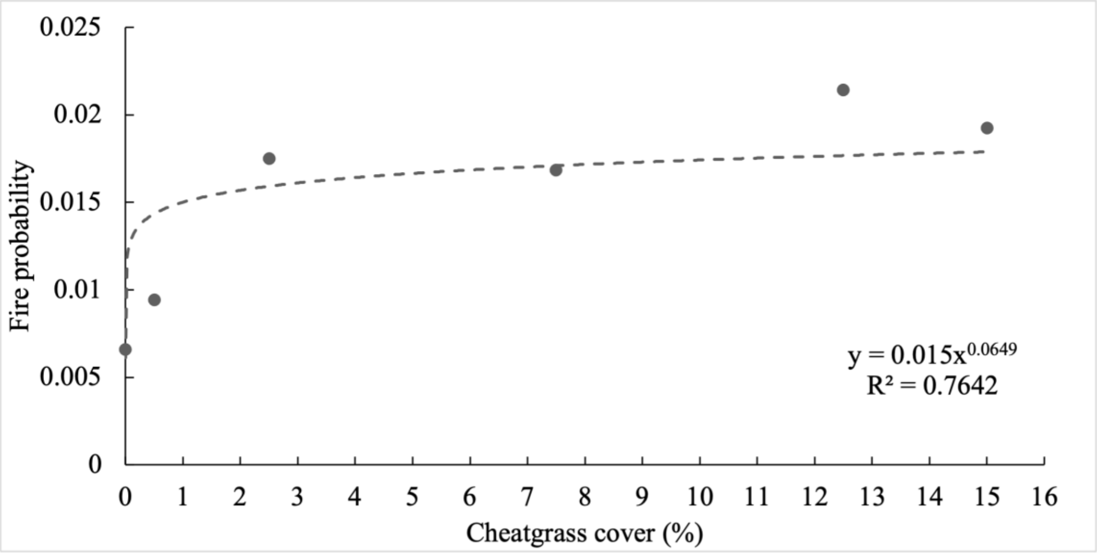
| Functional Type | Light Grazing | Moderate Grazing | Heavy Grazing |
|---|---|---|---|
| Big sagebrush | 0 | 0.01 | 0.10 |
| Annual $C_3$ cool-season forbs | 0.24 | 0.41 | 0.58 |
| Annual $C_3$ warm-season forbs | 0.24 | 0.41 | 0.58 |
| Perennial $C_3$ cool-season forbs | 0.24 | 0.41 | 0.58 |
| Perennial $C_3$ warm-season forbs | 0.24 | 0.41 | 0.58 |
| Annual $C_3$ grasses | 0.24 | 0.41 | 0.58 |
| $C_3$ perennial grasses | 0.24 | 0.41 | 0.58 |
| $C_4$ perennial grasses | 0.24 | 0.41 | 0.58 |
| Non-sagebrush shrubs | 0.24 | 0.41 | 0.58 |
| Succulents | 0 | 0.01 | 0.10 |

**Appendix C. Table of Grazing Intensity Treatments**

Proportion of this year’s growth removed for each functional type under each grazing intensity treatment.

## APPENDIX D: CHEATGRASS/WILDFIRE EQUATION

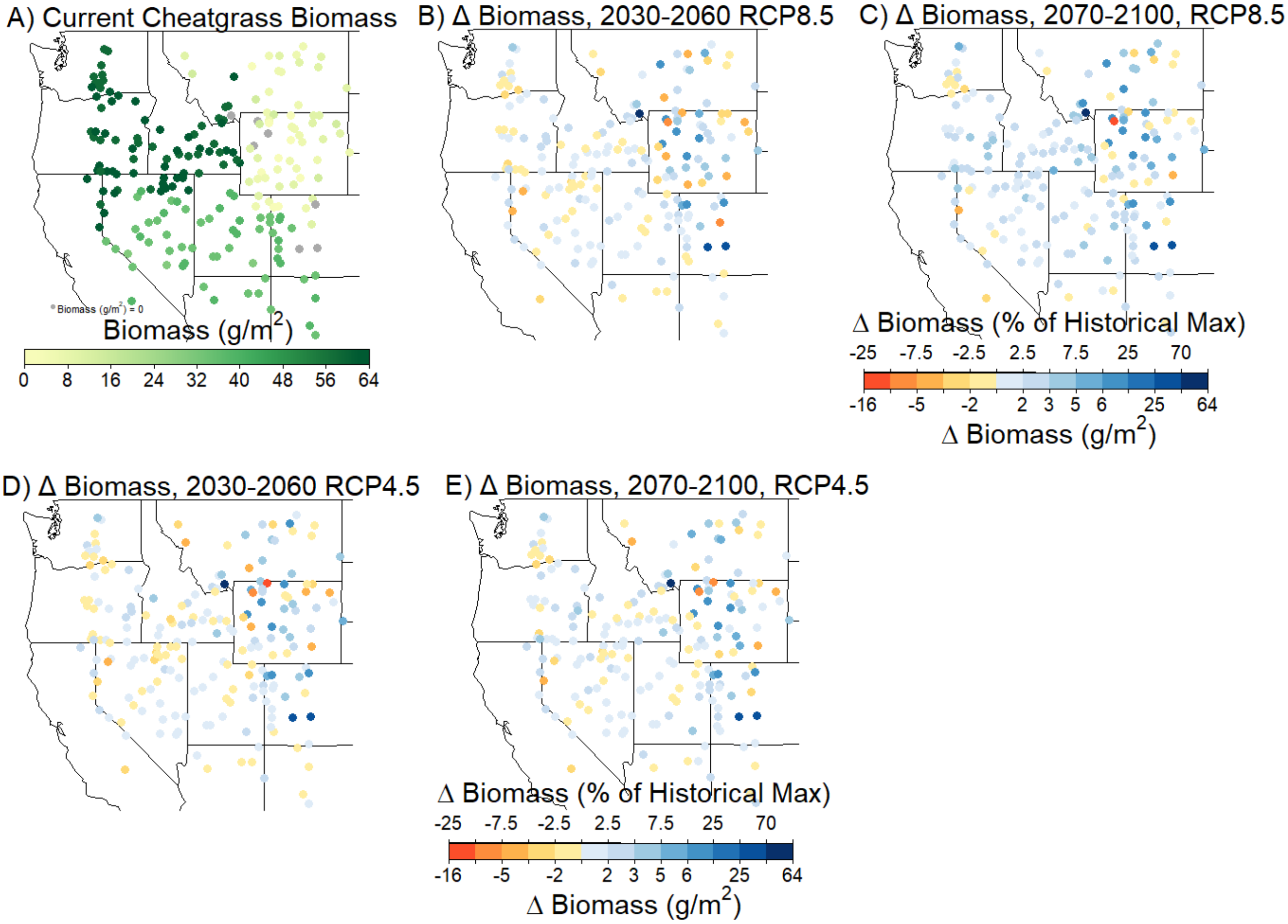
We developed a relationship between percent cover of cheatgrass and the probability of fire based on cheatgrass percentage cover and MODIS fire data presented in Bradley et al. (2018). We converted the percentage of grid cells burned over a 15-year period from Figure 5 in Bradley et al. (2018) to annual fire probability and a corresponding fire return-interval (FRI) for each level of cheatgrass percent cover presented in Bradley et al. (2018). We then rescaled the annual fire probability to overcome known discrepancies between MODIS annual fire probability and USGS annual fire probability described in Balch et al. (2013) that result from poor detection of small fires in the MODIS data. This allowed us to achieve a more accurate fire probability for the big sagebrush region. This rescaling was done by multiplying annual fire probability derived from the MODIS data by 0.49, which represents a ratio of the average fire return-interval from USGS fire data presented in Balch et al. (2013) to the average fire return-interval from MODIS fire data presented in Bradley et al. (2018)(97/196 years). The relationship between cheatgrass percent cover and annual fire probability was then determined mathematically via power regression analysis to be $y=0.015x^{0.0649}$.



## Appendix D. Cheatgrass/Wildfire Equation.

The relationship between cheatgrass and fire probability was developed using data in Bradley et al. (2018) and Balch et al. (2013).

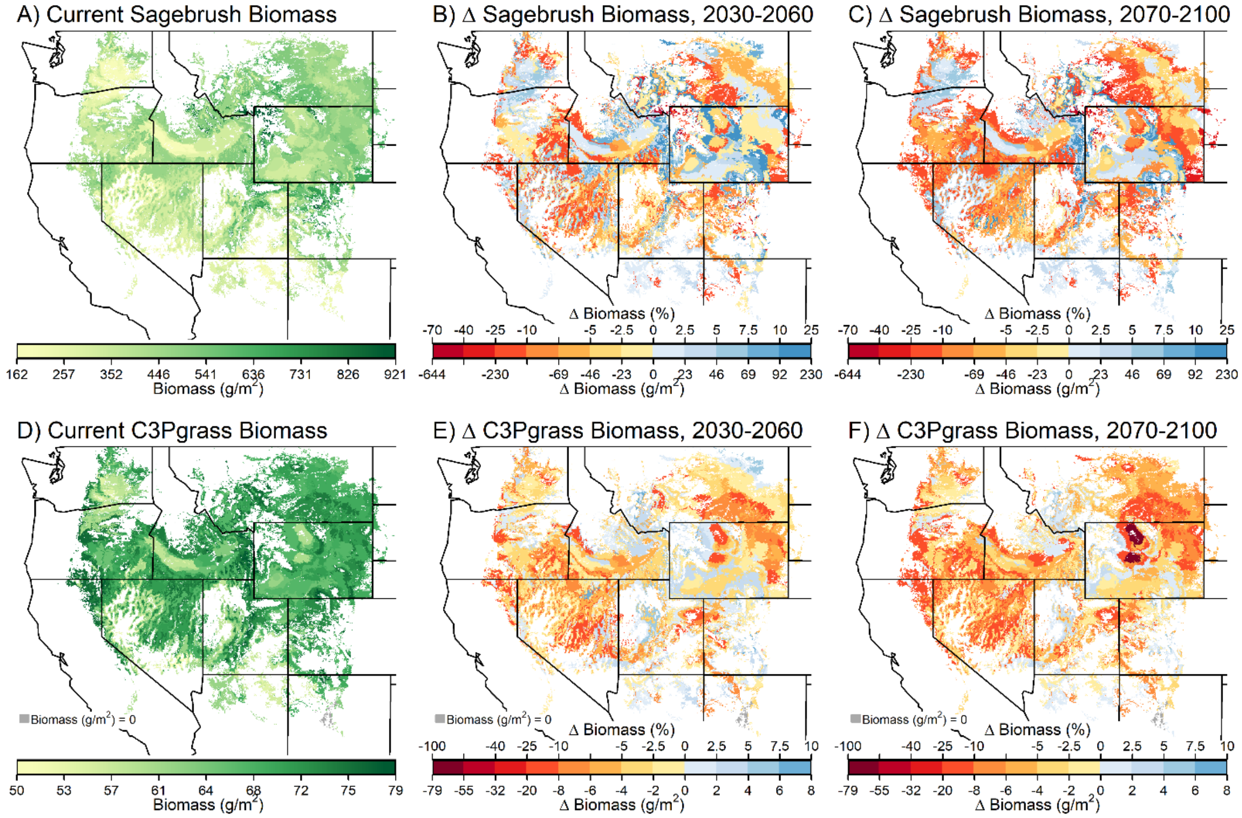
# APPENDIX E: CHEATGRASS BIOMASS SITE MAPS



**Appendix E. Cheatgrass Biomass Site Maps**

Current cheatgrass biomass (g/m$^2$) for the 200 sites (A) and change in cheatgrass biomass from current to future conditions under RCP 8.5 (B, C) and RCP4.5 (D, E) for mid-century (2031-2060) and end-century (2071-2100), respectively. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage of the maximum historical biomass.

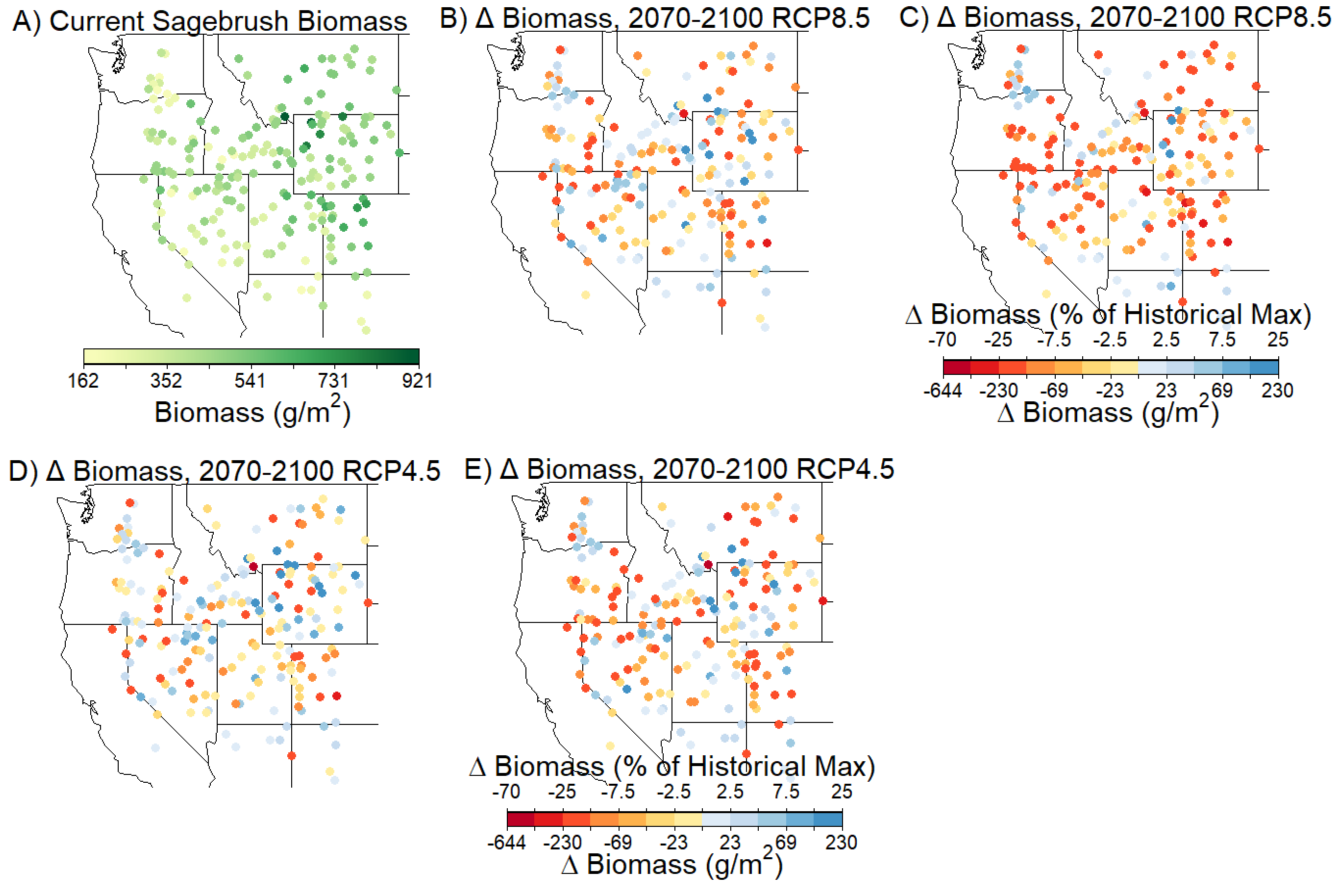
# APPENDIX F: BIG SAGEBRUSH AND $C_3$ PERENNIAL GRASS INTERPOLATED MAPS FOR RCP4.5



**Appendix F. Big Sagebrush and $C_3$ Perennial Grass Interpolated Maps for RCP4.5**

Interpolated $C_3$ perennial grass and sagebrush biomass (g/m$^2$) for current conditions (1981-2010) (A, D), change in biomass from current to mid-century (2031-2060) (B, E) and end-century (2071-2100) (C, F) under RCP4.5 (B, C), and RCP4.5. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage change scaled to the maximum historical biomass.

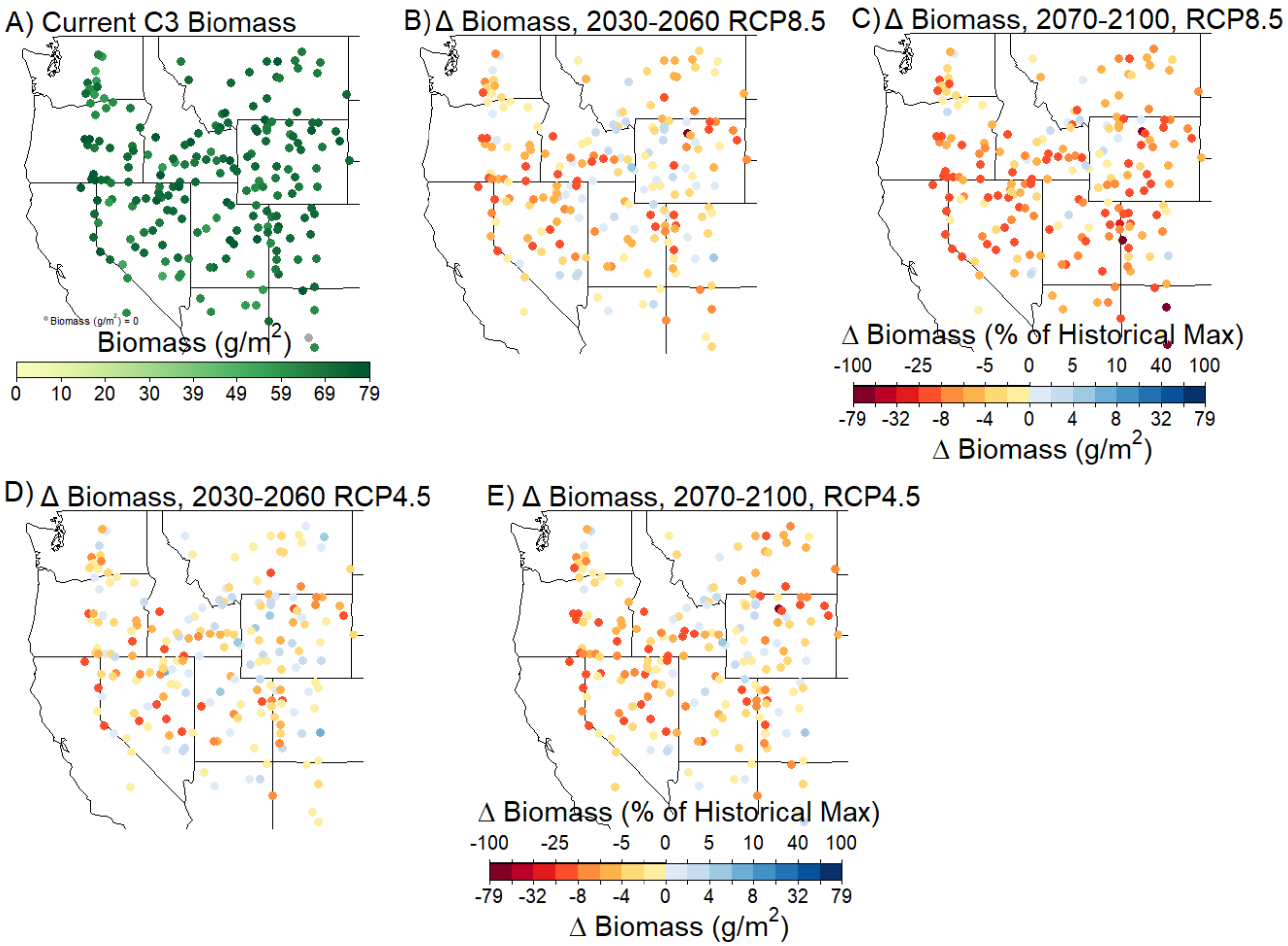
# APPENDIX G: BIG SAGEBRUSH BIOMASS SITE MAPS



**Appendix G. Big Sagebrush Biomass Site Maps**

Current sagebrush biomass (g/m$^2$) for the 200 sites (A) and change in sagebrush biomass from current to future conditions under RCP 8.5 (B, C) and RCP4.5 (D, E) for mid-century (2031-2060) and end-century (2071-2100), respectively. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage of the maximum historical biomass.

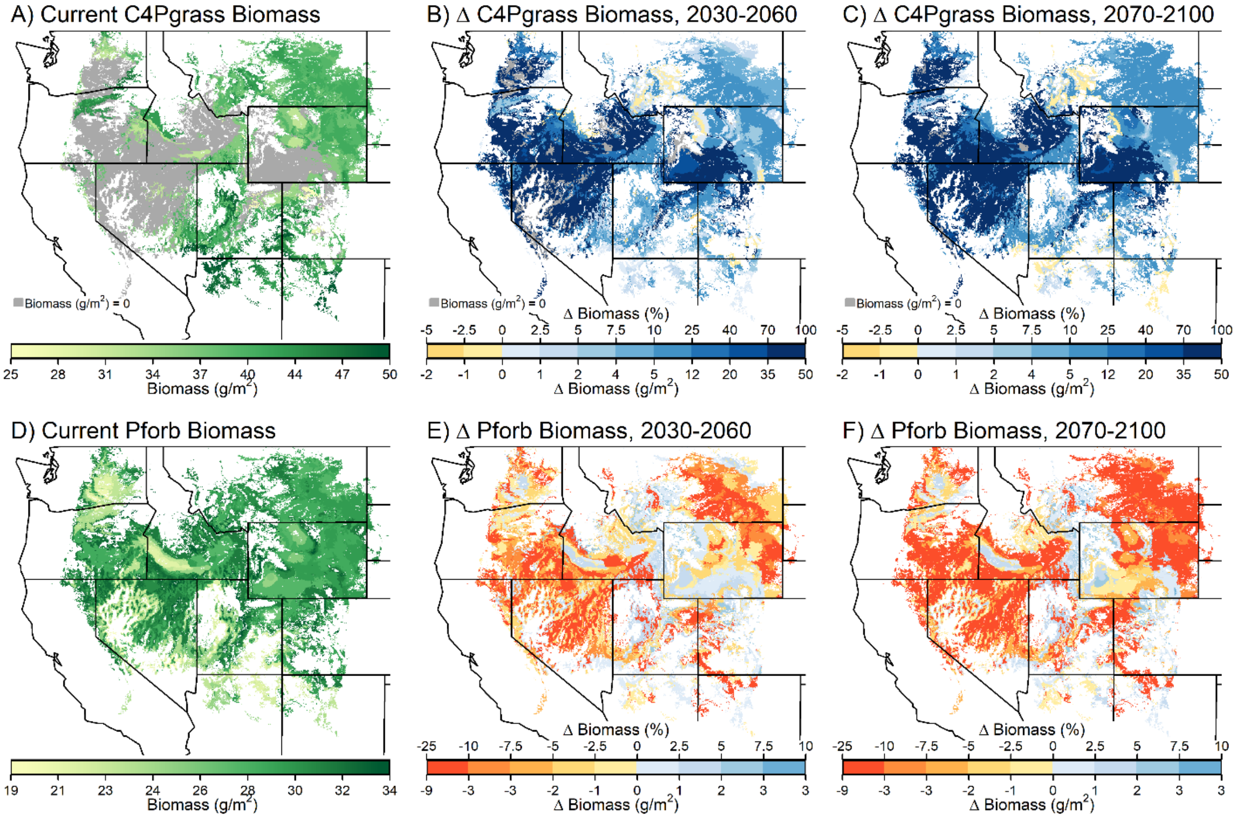
# APPENDIX H: $C_3$ PERENNIAL GRASS BIOMASS SITE MAPS



**Appendix H. $C_3$ Perennial Grass Biomass Site Maps**

Current $C_3$ perennial grass biomass (g/m$^2$) for the 200 sites (A) and change in $C_3$ perennial grass biomass from current to future conditions under RCP 8.5 (B, C) and RCP4.5 (D, E) for mid-century (2031-2060) and end-century (2071-2100), respectively. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage of the maximum historical biomass.

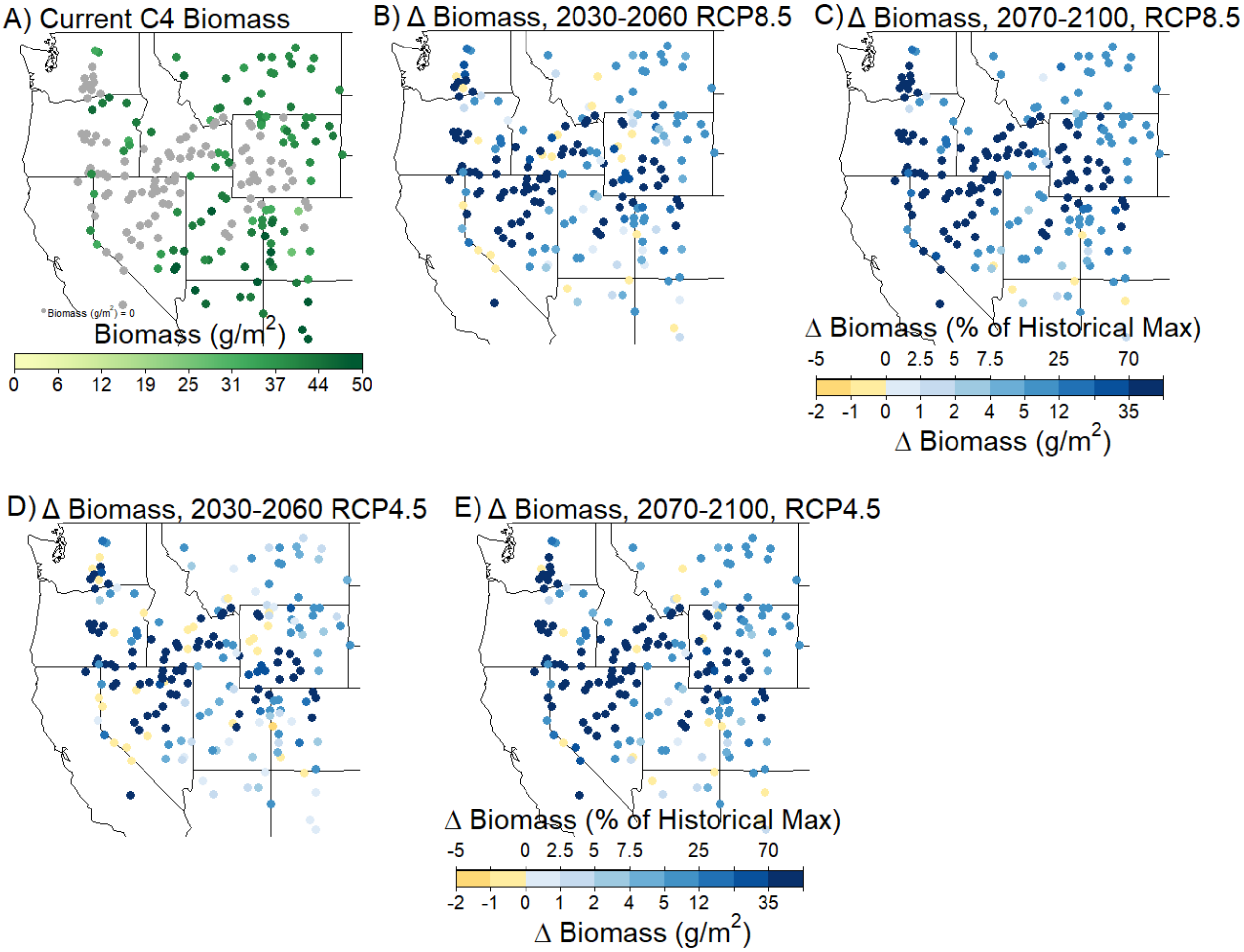
# APPENDIX I: $C_4$ PERENNIAL GRASS AND PERENNIAL FORBS INTERPOLATED MAPS FOR RCP4.5



**Appendix I. $C_4$ Perennial Grass and Perennial Forbs Interpolated Maps for RCP4.5**

Interpolated $C_4$ perennial grass and perennial forb biomass (g/m$^2$) for current conditions (1981-2010) (A, D), change in biomass from current to mid-century (2031-2060) (B, E) and end-century (2071-2100) (C, F) under RCP4.5 (B, C), and RCP4.5. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage of the maximum historical biomass.

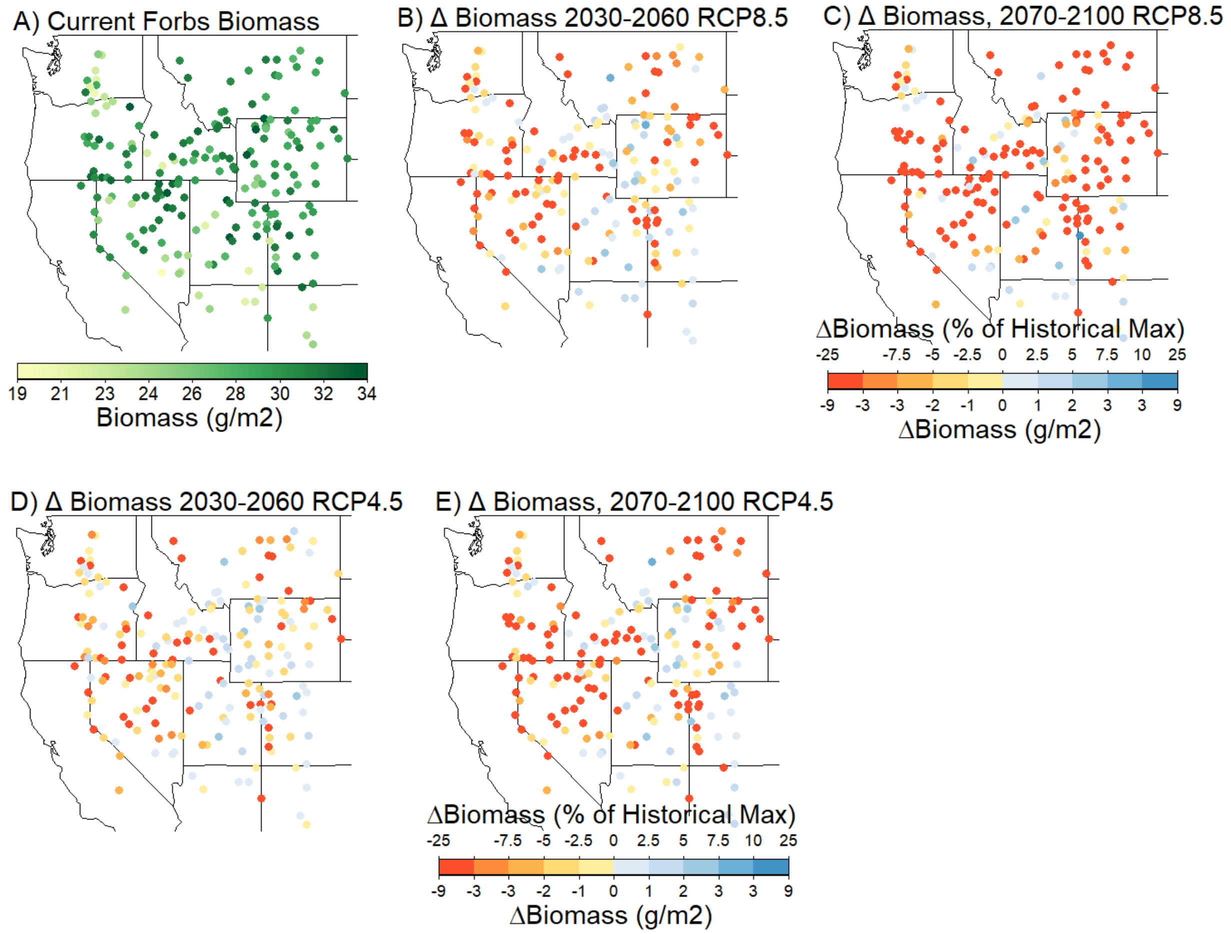
# APPENDIX J: $C_4$ PERENNIAL GRASS BIOMASS SITE MAPS



**Appendix J. $C_4$ Perennial Grass Biomass Site Maps**

Current $C_4$ perennial grass biomass (g/m$^2$) for the 200 sites (A) and change in $C_4$ perennial grass biomass from current to future conditions under RCP 8.5 (B, C) and RCP4.5 (D, E) for mid-century (2031-2060) and end-century (2071-2100), respectively. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage of the maximum historical biomass.

# APPENDIX K: PERENNIAL FORBS BIOMASS SITE MAPS



**Appendix K. Perennial Forbs Biomass Site Maps**

Current perennial forb biomass ($g/m^2$) for the 200 sites (A) and change in perennial forb biomass from current to future conditions under RCP 8.5 (B, C) and RCP4.5 (D, E) for mid-century (2031-2060) and end-century (2071-2100), respectively. Future maps represent median biomass across simulations forced by 13 GCMs and are colored by absolute change in biomass, which is also depicted as a percentage of the maximum historical biomass.

# APPENDIX L: TABLE OF PERCENT CHANGE SCALED TO THE MAXIMUM BY GRAZING TREATMENT

| | RCP 4.5 2031-2060 | | | RCP4.5 2071-2100 | | |
|---|---|---|---|---|---|---|
| | **Light** | **Moderate** | **Heavy** | **Light** | **Moderate** | **Heavy** |
| **Sagebrush** | -0.06 | -0.04 | -0.03 | -0.43 | -0.32 | -0.36 |
| **Cheatgrass** | 1.25 | 1.16 | 0.68 | 2.39 | 2.35 | 1.82 |
| **$C_4$ Perennial grass** | 29.48 | 37.39 | 31.61 | 51.51 | 53.49 | 46.32 |
| **$C_3$ Perennial grass** | -2.32 | -3.21 | -2.17 | -5.40 | -10.86 | -9.24 |
| **Perennial forbs** | -9.30 | -5.09 | -4.03 | -20.39 | -18.70 | -10.05 |

| | RCP8.5 2031-2060 | | | RCP8.5 2071-2100 | | |
|---|---|---|---|---|---|---|
| | **Light** | **Moderate** | **Heavy** | **Light** | **Moderate** | **Heavy** |
| **Sagebrush** | -0.31 | -0.22 | -0.14 | -0.81 | -0.79 | -0.88 |
| **Cheatgrass** | 1.90 | 1.65 | 1.63 | 4.42 | 3.99 | 2.83 |
| **C4 Perennial grass** | 38.82 | 47.75 | 39.98 | 64.60 | 78.57 | 50.97 |
| **C3 Perennial grass** | -4.17 | -6.82 | -4.64 | -9.63 | -16.81 | -16.09 |
| **Perennial forbs** | -12.13 | -10.88 | -6.57 | -37.26 | -32.67 | -19.06 |

**Appendix L.** Percent change scaled to the maximum from current conditions for each grazing treatment, for each RCP (RCP4.5 and RCP8.5), and for each time period (mid-century and end-century).