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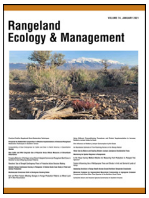

Original Research

Consequences of Rainfall Manipulations for Invasive Annual Grasses Vary Across Grazed Northern Mixed-Grass Prairie Sites☆

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ABSTRACT

Northern mixed-grass prairie rangelands are threatened by increasing drought severity and invasion by annual grasses. However, it is unclear whether climate change will amplify or dampen this invasion. We tested separate and combined effects of livestock grazing and experimental rainfall manipulation on invasion by annual brome grasses—cheatgrass (*Bromus tectorum* L.) and field brome (*Bromus arvensis* L.)—in two mixed-grass prairie sites (Montana and Wyoming, United States). To provide management-relevant results, we manipulated precipitation at five levels representing a gradient of precipitation reduction and implemented grazing strategies selected by stakeholders to represent realistic management choices: destock, stable, and heavy grazing scenarios. We measured soil moisture and three plant properties of invasive annual bromes (aboveground primary production, percent greenness, and percent cover) during two water manipulation yr (2019, 2020) and one recovery yr of natural rainfall (2021).

Imposed precipitation reduction generally decreased absolute annual brome biomass and induced earlier senescence. However, during the recovery year, we observed prolonged time to senescence in the formerly droughted plots. In Wyoming, summer grazing had little appreciable effect on annual bromes, perhaps because annual bromes mature early in the growing season (mid-June) and may therefore be less affected by summer grazing. However, in the first year after ending water treatments during a natural drought in Montana, under heavy grazing, annual brome production marginally increased from 32.4 ± 10.6 kg · ha^{-1} to 130.8 ± 111.8 kg · ha^{-1} (mean ± standard error) with prior severe precipitation reduction. The magnitude of responses tended to be site dependent, which may be due to inherent vegetation differences between our sites, as well as site-scale differences in natural precipitation patterns. Together, these results suggest that annual brome abundance may increase in the context of drought combined with heavy grazing, a more likely scenario with continuing climate change.

Introduction

Grazing lands are the most widespread terrestrial biome in the world (Ellis and Ramankutty 2008), covering ~40% of the global land surface (White et al. 2000; Suttie et al. 2005; Gibson 2009). Their structure and diversity are maintained by frequent disturbances including grazing, drought, and fire (Gibson 2009). The livelihoods and health of > 1 billion people worldwide rely specifically on herbaceous systems to graze livestock (Sayre et al. 2013), yet management of these lands is currently challenged by unprecedented climate regimes and intense pressure from invasive species (DiTomaso 2000; McCollum et al. 2017).

Invasive plant species alter landscapes and plant community dynamics, making management of working rangelands challenging (Belnap et al. 2012). Invasive weeds can harm livestock production due to decreased forage quality and quantity, slower animal weight gain, and decreased land value (DiTomaso 2000). Simultaneously, invasive plants compete with native plant communities, decreasing

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native productivity, diversity, and litter decomposition (Ogle et al. 2003; Henderson and Naeth 2005). Further, invasive grasses can directly alter soil nutrient content and availability and soil microbial composition (Parker and Schimel 2010; McLeod et al. 2021; Nasto et al. 2022), which can in turn affect ecosystem functioning and services (Parker and Schimel 2010; McLeod et al. 2021). Altogether, invasive species on rangelands are responsible for large-scale negative ecological and economic consequences (Pimentel et al. 2000, 2005; Poland et al. 2021).

While climate change and invasive species can independently affect ecosystems, there is also substantial evidence suggesting climate change will have an impact on invasive species (Dukes and Mooney 1999; Hellmann et al. 2008; Mainka and Howard 2010; Ziska et al., 2011; Bradley et al. 2016; Bezeng et al. 2017; Shabani et al. 2020). Further, while grasslands are adapted to and depend on disturbances including variable weather, global climate models predict increases in magnitude and frequency of climate extremes (Rosenzweig et al. 2001; Smith 2011; Ades et al. 2020), which could potentially alter grassland composition and function. Productivity of grasslands in mixed-grass prairies of the United States has a strong positive correlation with spring precipitation (Wiles et al. 2011), so altered precipitation patterns may greatly alter production from these systems. Precipitation patterns are expected to change, with summer droughts in the midwestern United States predicted to increase in frequency and intensity (Andresen et al. 2012) and surface soil moisture expected to decrease with increasing temperatures across the United States (Wehner et al. 2017). With these changes expected in the coming decades, it is critical to understand how increased drought intensity and frequency will impact invasive species on rangeland ecosystems.

The northern mixed-grass prairies of the North American Great Plains are an important ecoregion for biodiversity and livestock (including beef cattle) production (Samson and Knopf 1994; Martin et al. 1999; Samson et al. 2004). However, the mixed-grass prairie is threatened by both increased drought severity and invasive species (DiTomaso 2000; Henderson and Naeth 2005; Gaskin et al. 2021). Current grazing management practices may not be sustainable as the climate changes, and new approaches to management may be required to uphold land value and prevent overgrazing (Derner and Augustine 2016; Li et al. 2018). Additionally, across northern Great Plains rangelands, the invasive grasses field brome (*Bromus arvensis* L.) and cheatgrass (*Bromus tectorum* L.), hereafter referred together as annual bromes, or separately as field brome *(B. arvensis)* and cheatgrass *(B. tectorum),* are cause of concern for overall rangeland sustainability (Vermeire et al. 2009b; Germino et al. 2016). *B. arvensis* and *B. tectorum* are two widespread, well-established, C_3, winter-annual grass species (Wright and Wright 1948; Hulbert 1955; Oja et al. 2003). These species were intentionally introduced as forage for cattle, but while annual bromes provide forage in the spring, the optimal grazing period is short as the protein percentage decreases by ~97% on maturation in mid-June (Hulbert 1955; Morrow and Stahlman 1984; DiTomaso 2000; Oja et al. 2003; Chambers et al. 2007; Schachner et al. 2008; Vermeire et al. 2009b). Invasive annual brome grasses harm native rangeland communities by decreasing the quality and quantity of forage and competing with native plant species (Haferkamp et al. 1998, 1997; Ogle et al. 2003; Ashton et al. 2016). Intensive cattle grazing of cheatgrass during the boot stage before flowering has been shown to significantly reduce annual brome abundance in subsequent years (Diamond et al. 2012; Porensky et al. 2021), and some level of grazing may be required to maintain invasion resistance and native diversity in disturbance-adapted rangelands (Loeser et al. 2007; Porensky et al. 2020, 2013). However, in a Great Basin grassland, after a naturally occurring (single year) severe drought, both heavy grazing and no grazing produced increases in cheatgrass, with heavy grazing resulting in the most dramatic increase (Loeser et al. 2007). Therefore, the relationship between grazing and control of invasive annual bromes is complex, particularly under decreased precipitation conditions.

Uniquely, our study examines the consequences of an experimentally generated gradient of precipitation reduction crossed with varying levels of livestock grazing intensity on the productivity and percent cover of field brome and cheatgrass in northern mixed-grass prairies. Additionally, we assess how annual brome phenology changes under these treatment conditions. We tracked these responses across 2 yr of water reduction treatments (hereafter "precipitation reduction") and the first-yr post water reduction treatment (hereafter "recovery year"). Our hypotheses are as follows:

1) We hypothesized that summer grazing and precipitation reduction would have interactive effects on annual brome biomass, percent cover, and senescence. Specifically, we predicted that the combination of severe drought and heavy grazing would result in the largest increases in biomass and percent cover of field brome and cheatgrass, especially during the recovery year. This could be due to high cover of bare space via reductions in perennial plant cover (Porensky et al. 2013). Under heavy grazing following drought, cheatgrass has been shown to significantly increase in abundance and greatly contribute to alterations in plant community composition in similar regions (Souther et al. 2020). Cattle often preferentially graze the nonbrome plant community, decreasing perennial plant abundance (Rickard et al. 1975; Derner and Hart 2007). As grazing intensifies, especially under reduced precipitation conditions, decreases in the nonbrome, perennial vegetation can free up space for invasive annual bromes to increase (Haferkamp 2001).

2) We hypothesized that during precipitation reduction years, the biomass and percent cover of invasive annual bromes would decrease across precipitation reduction treatments due to the added stress of water loss (Richardson et al. 1989). Likewise, we predicted that precipitation reduction would cause annual bromes to senesce earlier in the season, with average percent green the lowest under the severest water reduction levels (Rice et al. 1992).

3) We hypothesized that in the recovery year following precipitation reduction, biomass and percent cover of invasive annual bromes would increase. We also hypothesized that in the recovery year, previous precipitation reduction would indirectly cause annual bromes to delay senescence, reflecting a possible drought-avoidance strategy of invasive annual bromes (Rice et al. 1992). After 2 yr of summer precipitation reduction, lowered resistance to invasion via suppression of perennial species under high precipitation reduction could lead to competitive release for bromes in the historically severe precipitation reduction plots (Jiménez et al. 2011; Diez et al. 2012). This could be due to legacy effects in the soil. For example, following drought, soil nitrogen can increase, which annual bromes are better able to use than the native plant community, allowing annual bromes to increase in abundance while indirectly suppressing native plant species (Meisner et al. 2013; Souther et al. 2020). In addition, while cheatgrass and field brome are considered winter annuals, they can be relatively plastic in germination timing, especially under altered precipitation, allowing them to better avoid drought-legacy effects in native-suppressed areas (Roundy et al. 2007; Espeland et al. 2016).

Methods

Study sites

The Northern Great Plains steppe ecoregion is dominated by temperate and semiarid mixed-grass prairie and spans 22 million ha across five states in the United States and two Canadian provinces (Martin et al. 1999), covering 38% of grassland area in

North America (Lauenroth 1979; Chimner and Welker 2011). Most precipitation occurs from May to June, with total average annual precipitation for the region ranging from < 250–500 mm (Reinhart and Vermeire 2017). This ecoregion is ecologically and economically important, with as much as 50% of the land area being used to support livestock (Holechek et al. 2011; Vold 2018) and an estimated ~11 million animal unit mo of livestock grazing (Reinhart and Vermeire 2017).

We experimentally manipulated rainfall and cattle management at one site in Custer County in eastern Montana (46.3366°N, −105.985°W) and another in Converse County in northeastern Wyoming (43.3025°N, −105.0575°W). The Montana site is centrally located in the Northern Great Plains steppe ecoregion at the Fort Keogh Livestock and Range Research Laboratory. The Wyoming site is located at the south end of the Northern Great Plains steppe ecoregion on private land within a shrubland-grassland ecotone (known locally as the Thunder Basin ecoregion) (Porensky et al. 2018).

Both the Montana and Wyoming sites have a semiarid climate (Fig. S1, available online at doi:10.1016/j.rama.2023.05.007; Curtis and Grimes 2004; Peterson and Reinhart 2012; Wilcox et al. 2015). Mean temperature for the Montana site ranges from −10°C in January to 24°C in July (Waterman et al. 2021), and elevation is 715–860 m above sea level (Peterson and Reinhart 2012). Ninety percent of annual net primary productivity at the Montana site is completed by July 1 (Vermeire et al. 2009a). Soils at this site are typically Mollisolls and Entisols (Peterson and Reinhart 2012). Mean temperature for the Wyoming site ranges from −5°C in December to 22°C in July and elevation is 1 097–1 585 m above sea level (Curtis and Grimes 2004; Porensky et al. 2018; Connell et al. 2019). Soils in this region are most commonly Aridisols and Entisols (Ebertowski 2005).

Common plant species at both sites include the shrub *Artemisia tridentata* Nutt. ssp. *Wyomingensis* Beetle and Young (Wyoming big sagebrush); perennial graminoids *Bouteloua gracilis* (Willd. Ex Kunth) Lag. ex Griffiths (blue grama), *Carex filifolia* Nutt. (threadleaf sedge), *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needle-and-thread grass), and *Pascopyrum smithii* (Rydb.) Á. Löve (western wheatgrass); annual grasses *Bromus tectorum* (cheatgrass), *Bromus arvensis* (field brome), and *Vulpia octoflora* (Walter) Rydb. (6-wk fescue); and the forb *Plantago patagonica* Jacq. (wooly plantain) (Russell et al. 2017; Porensky et al. 2018). Other reported plant species include the subshrub *Artemisia frigida* Wild. (prairie sagewort), the perennial grass *Bouteloua dactyloides* (Nutt.) J. T. Columbus (buffalograss), and the forbs *Tragopogon dubius* Scop. (yellow salsify), *Logfia arvensis* (L.) Holub (field cottonrose), and *Hedeoma hispida* Pursh. (rough false pennyroyal) in Montana (Russell et al., 2017) and the forbs *Alyssum desertorum* Stapf (desert madwort), *Lepidium densiflorum* Schrad. (common pepperweed), and *Sphaeralcea coccinea* (Nutt.) Rydb. (scarlet globemallow); and the cactus *Opuntia polyacantha* Haw. (Plains pricklypear) in Wyoming (Porensky et al. 2018).

Experimental design

Experimental design was identical at both sites and consisted of three fully replicated blocks (80.8 × 61.0 m), with three paddocks nested within each block. Paddocks (40.4 × 30.5 m) were randomly assigned to one of three livestock management strategy treatments. Grazing intensity was similar across paddocks in 2018 (pretreatment), when plots received the conventional practice for the system of moderate summer grazing. However, during precipitation reduction (2019–2020) and recovery (2021) yr, grazing intensity varied across the paddocks to correspond with how regional livestock managers might alter their management in response to drought. The “control” grazing strategy was a fixed grazing intensity (moderate) throughout the experiment. The other two grazing treatments varied grazing intensity to reflect destocking or heavy management scenarios (Fig. 1).

At each site, we used beef cattle *(Bos taurus)* to implement the grazing treatments. Utilization targets varied by grazing treatment and year according to the experimental design (see Fig. 1). For each block, different grazing intensities were achieved by varying the number of days a given herd had access to different paddocks within the block. During grazing bouts, we assessed livestock utilization using visual obstruction readings before, during (daily or subdaily as needed), and after grazing. We used a visual obstruction pole (modified from Robel et al. 1970) with alternating black and white bands modified to a 1-cm increment, a method with application in grasslands broadly (Ganguli et al. 2000). Temporary fencing was used to exclude cattle from a given paddock once the target forage utilization (30% for light, 50% for moderate, or 70% for heavy; see Fig. 1) was achieved. Due to spatial and temporal variation in forage production, this resulted in variable numbers of animals and days of grazing across sites, years, and blocks (summarized in Table S1, available online at doi:10.1016/j.rama.2023.05.007). Blocks were grazed sequentially, and all grazing was completed within 3 wk each year (WY: June 26–July 18, 2019; July 2–15, 2020; July 7–14, 2021; MT: August 13–23, 2019; July 30–August 8, 2020; August 9–12, 2021). Fort Keogh Livestock and Range Research Laboratory’s Institutional Animal Care and Use Committee evaluated our experiment and determined that our use of animals was consistent with standard livestock management and did not require special approval for either site.

Within each paddock, six 2 × 2 m plots were randomly assigned to different precipitation treatments. Each paddock had two control plots (no precipitation reduction) and one plot for each precipitation reduction level (25%, 50%, 75%, 99% reduction from ambient precipitation), giving a total of 54 plots per site. Plots were on average 3.5 m apart from one another and included a 0.5-m buffer from the edge of the shelter to prevent hydrological overlap and overland flow (Beier et al. 2012). We also used gutters to ensure intercepted rainfall was diverted away from each plot. To achieve our rainfall gradient, we constructed rainout shelters (modified from Yahdjian and Sala 2002). Rainout shelters were 3 × 4 m and covered the entire plot. In April 2019 and 2020, rainout shelters were erected. The shelters remained up until October, except for a brief grazing period in July (for Wyoming) or August (for Montana) to allow cattle to graze each paddock. This resulted in varying grazing and water treatments per year. To assess the effectiveness of our precipitation reduction treatments, we tested for water treatment differences in average soil moisture per plot (April–October) for each year and site separately. We measured soil moisture using time-domain reflectometry (TDR) with a Field Scout probe to determine percent volumetric water content (VWC) at a depth of 10 cm.

Data collection

Each plot was divided into four 1 × 1 m subplots used for different sampling approaches, including a permanent 1 m^2 species composition subplot and a 1 m^2 area used for aboveground biomass clipping. We collected all data types annually for 3 yr including the two precipitation reduction yr (2019–2020) and the recovery yr (2021) from each site. We measured plant species composition in late June each year by visually estimating foliar cover (i.e., calibrated to estimates generated by a 100 pin-point intercept frame) for each species to the nearest percent. Additionally, each year during peak biomass production (mid-late July), we clipped all aboveground biomass from two 0.5 × 0.2 m quadrats; the quadrats for each year were never adjacent to the prior yr’s clippings. In Wyoming, where grazing occurred in early July before clipping,

Forage Utilization % (July – August)

Grazing Treatment	Year	2018	2019	2020	2021
Destock		50%	50%	30%	30%
Stable		50%	50%	50%	50%
Heavy		50%	70%	70%	50%

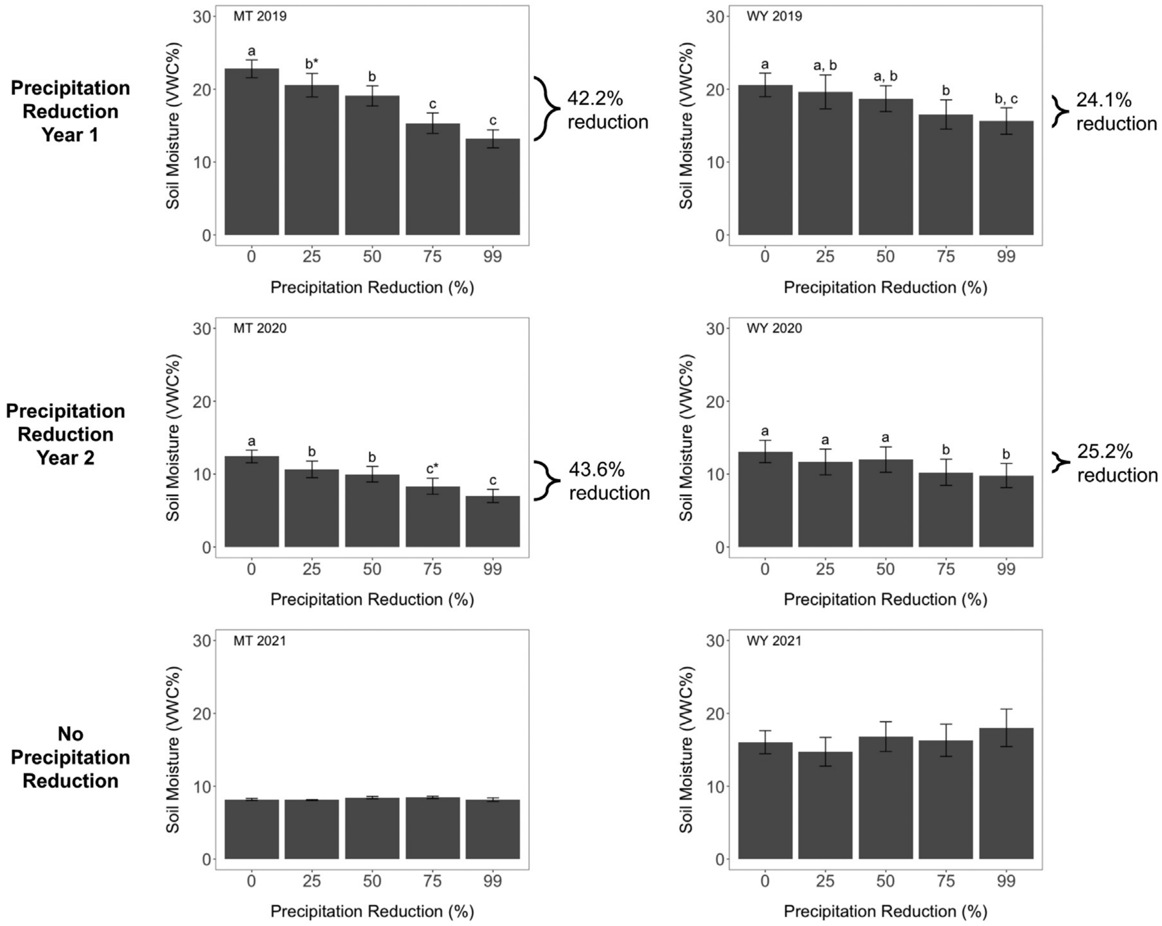

Figure 1. Experimental design from 2018 to 2021. In 2018 (pretreatment), precipitation was ambient, and grazing followed conventional practice; pretreatment data for aboveground biomass and percent cover were collected. **Top,** Our experiment consisted of three grazing treatments (light—30%, moderate—50%, heavy—70% forage utilization) to represent different livestock utilization methods each year (destock, stable, and heavy, respectively). We imposed grazing in either July or August in each of the 3 treatment yr (2019–2021). **Bottom,** In 2019 (precipitation reduction yr 1) and 2020 (precipitation reduction yr 2), we erected rainout shelters during the growing season (April–October) to impose rainfall reduction across a gradient of five levels (0%, 25%, 50%, 75%, 99% precipitation reduction). We did not impose precipitation reduction treatments in 2021; plots were exposed to ambient precipitation (recovery yr). Bar graphs show mean ± standard error of average growing season soil moisture in Montana (MT) and Wyoming (WY) across the precipitation reduction treatments through the 3 treatment yr. Model fit was assessed using linear mixed-model ANOVAs. Letters indicate significant differences at $P < 0.05$, and asterisks indicate marginal significance at $0.05 < P < 0.1$ based on Tukey honestly significant difference test.

biomass plots were protected from same-yr grazing using movable grazing cages, and in Montana, grazing occurred after clipping. Thus, both biomass and cover measurements were not affected by current-year grazing treatments but could respond to prior-yr treatments. We separated annual grasses (in Montana, consisting largely of annual bromes) and annual bromes (in Wyoming) from the rest of the plant biomass. While ideally annual bromes would have been sorted out from other annual grasses in Montana, this was not done; however, the data are still beneficial for invasive annual bromes as there is only one other annual grass species at the site *(Vulpia octoflora)*. This species accounted for < 0.5% cover on average and has consistently low biomass compared with annual brome production, which can range from low to high biomass at this site (Vermeire et al. 2021). Thus, we feel confident in using these data as a proxy for invasive brome biomass. We collected soil moisture (VWC) and plant phenology (visual estimates of percent of green tissue on randomly selected, individually marked, and ungrazed plants) throughout the growing seasons (April–October) from 2019 to 2021. Percent of the plant tissue that was green was visually estimated to the nearest 1% (modified from USA-NPN National Coordinating Office 2012). To differentiate between senescence and temporary shifts in color (e.g., due to cold stress), percent green included reddish or purple tinted tissue but not brown, dried tissue. The same researcher collected the data for each time point across all plots at a site and often throughout the entirety of each growing season to reduce bias. While researchers were calibrated through training, each researcher could have varied in their measurement of percent green, thus highlighting the importance of having one researcher collect all percent green data at each time point. We present here relativized percent green results rather than raw values, as the change in percent green between control and treatment plots is more important than the raw values. Plant phenology measurements were done exclusively on field brome in Montana but were done on a combination of field brome

Table 1
Linear mixed-model analysis of variance (F statistics with P values) for aboveground biomass responses of invasive annual bromes to each yr's treatment conditions at the time of sampling. We assessed biomass response to each yr's applicable precipitation reduction and grazing treatments. W indicates water treatment; G, grazing treatment; WR, water treatment recovery. Numerical subscripts indicate yr abbreviations for 2019–2021. Significant values are shown in boldface type, with * indicating $P < 0.1$, ** $P < 0.05$, *** $P < 0.001$.

Site	Montana				Wyoming			
Yr	Data transformation	df	F value	P value	Data transformation	df	F value	P value
2019	ln(data + 0.1)				ln(data + 0.1)			
W_{19}		1, 44.00	19.29	**< 0.001*****		1, 44.00	0.10	0.76
2020	ln(data + 0.1)				ln(data + 0.1)			
W_{20}		1, 43.00	3.13	**0.08***		1, 43.00	3.93	**0.05***
G_{19}		1, 17.99	0.19	0.67		1, 7.47	0.00	0.98
$W_{20} \times G_{19}$		1, 43.00	0.01	0.92		1, 43.00	0.78	0.38
2021	Square root				N/A			
WR_{21}		1, 42.00	0.25	0.62		1, 42.00	3.42	**0.07***
G_{20}		2, 10.10	1.65	0.24		2, 9.72	1.22	0.34
$WR_{21} \times G_{20}$		2, 42.00	3.87	**0.03****		2, 42.00	1.41	0.25

and cheatgrass in Wyoming because field brome was not present in all plots.

Statistical analyses

We conducted all calculations and analyses in R version 3.6.2 (R Core Team 2019). We used Shapiro-Wilk, Anderson-Darling, Cramer-von Mises, and Kolmogorov-Smirnov tests to assess normality of the residuals of all response variables using the Olsrr package (Hebbali 2020). We transformed data when necessary to achieve normality (Tables 1–3 and S1–S2, available online at doi:10.1016/j.rama.2023.05.007). We ran linear mixed-model regressions using the lmerTest package (Kuznetsova et al. 2017), followed by Type III analysis of variance (ANOVA) with Satterthwaite's method (Satterthwaite 1941). Because water and grazing treatments varied by yr (see Fig. 1), we performed unique tests each year. Further, models include grazing treatments for the prior calendar yr because we applied grazing treatments in July–August, after most annual brome data were collected. For 2019 data, we tested only the effect of water treatments, as grazing treatments could not have affected annual brome response variables during that year. For 2020 data, we tested the effect of a second yr of water treatments, the two grazing treatments applied in 2019 (two paddocks were moderately grazed and one paddock was heavily grazed; see Fig. 1), and their interaction. For 2021 data, we tested for water treatment legacy effects, the three grazing treatments applied in 2020 (one paddock was grazed at each of the three grazing intensities—light, moderate, and heavy; see Fig. 1), and the interaction between water and grazing treatments. We assessed the precipitation reduction treatment as a continuous variable and the grazing treatment as a categorical variable in all analyses. As part of data exploration, we fit nonlinear models to all our variables; however, in each instance, linear models fit better based on Akaike's information criterion with correction for small sample size (AICc). Therefore, only results for linear models are presented here.

To assess how soil moisture changed with our water treatments, we used Type III mixed-model ANOVAs with random effects of block and paddock nested within block for each site and year separately. We first averaged soil moisture across all time points at each site (collected approximately bimonthly each yr April–October throughout the experiment) to avoid pseudo replication. We then used Tukey's test (Tukey 1977) adjusted for multiple comparisons using the Benjamini-Hochberg method (Benjamini and Hochberg 1995) to assess significant differences in soil moisture between precipitation reduction levels.

To assess how aboveground biomass changed with our water and grazing treatments, we used Type III mixed-model ANOVAs with random effects of block and paddock nested within block for each site and year separately.

We also assessed how annual brome phenology responded to our water and grazing treatments in two ways. To standardize our results, we assessed differences in percent green by comparing each precipitation reduction level (25%, 50%, 75%, 99% reduction) to the corresponding control (0% precipitation reduction) for each paddock (i.e., precipitation reduction treatment–control) at each time point. In Montana, we averaged percent green across both control plots (two control plots per paddock) first as we only collected percent green data on field brome. In Wyoming, because we collected percent green data on a combination of field brome and cheatgrass, we paired the precipitation reduction plots with control plots for each paddock and time point of the same species (i.e., field brome treatment plots paired with field brome control plots; cheatgrass treatment plots paired with cheatgrass control plots). Then, we analyzed how differences in percent green between precipitation reduction treatments and control plots change with our water and grazing treatments through each summer separately for each site and year. While data collection for percent green occurred from April to October, we conducted data analyses on percent green data collected from May to July only, before grazing treatments each year. To do this, we used repeated measures mixed-model ANOVAs with random effects of block, paddock nested within block, and plot nested within paddock. Second, from these phenology results through time, we looked for a single time point in each year that maximized differences in percent green across our water treatments. We then selected the data for this time point only to assess how standardized percent green changes across our treatments at that chosen date. We analyzed this using Type III mixed-model ANOVAs with random effects of block and paddock nested within block separately for each year and site.

Lastly, we addressed how percent cover of invasive annual bromes respond to water and grazing treatments. In these analyses, we excluded all plots that never included invasive annual bromes, as we cannot attribute this to our treatment conditions. We excluded two plots entirely at our Wyoming site that never contained either field brome or cheatgrass. For analyses with cheatgrass cover, we also excluded eight additional plots at our Wyoming site that never contained cheatgrass. This aligns with previous work (Ashton et al. 2016), and analyses including these plots where invasive annual bromes were never present yielded similar results but did not fit our distributional assumptions as well (Table S2, available online at doi:10.1016/j.rama.2023.05.007). To determine how percent cover (foliar cover) of field brome and cheatgrass respond to our water and grazing treatments, we used Type III mixed-model ANOVAs with random effects of block and paddock nested within block for each site, year, and species separately. During data exploration, we also assessed how the pretreatment (2018) percent cover data at the Montana site covaried with each year's response using Type III mixed-model ANCOVAs with

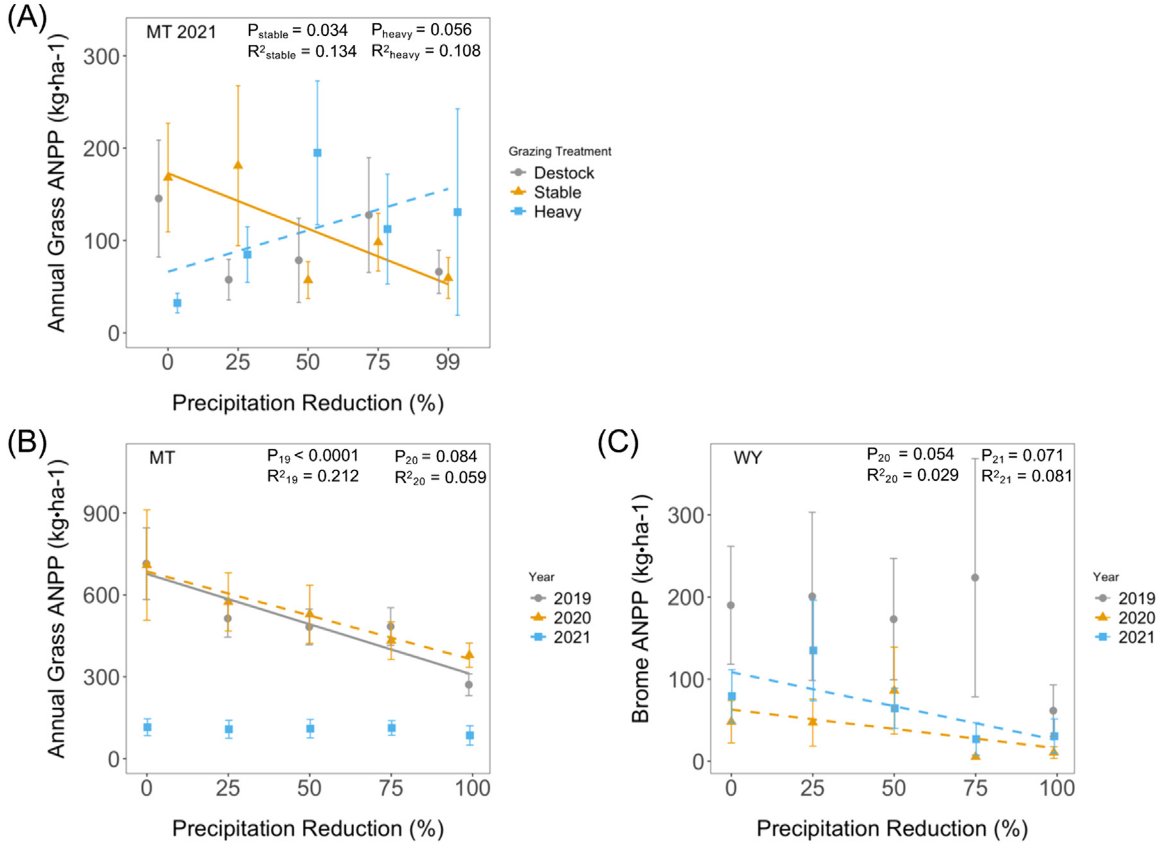

Figure 2. Mean ± standard error of aboveground net primary production (ANPP) of annual grass species for precipitation reduction treatments at Montana (MT) by **A,** grazing treatment or **B,** year, and **C,** of annual brome species at Wyoming (WY) by year. P values and marginal R^2 values for **A,** grazing treatments with significant or marginally significant precipitation reduction effects and **B–C,** significant or marginally significant effects of precipitation reduction for each yr are shown. Solid lines indicate significant main effects of water treatment ($P < 0.05$), and dashed lines indicate marginally significant results ($0.05 < P < 0.1$) as calculated from the linear mixed-model analyses of variance (see Table 1).

random effects of block and paddock nested within block (data not shown). However, AICc scores were similar with and without the covariate, so we proceeded with analyses without the covariate to simplify the models. We also collected pretreatment (2018) percent cover data for the Wyoming site, but we had to move the plots in 2019, so data could not be compared with subsequent years' data at the plot scale. Results are reported as means ± standard error (SE), and statistical results are reported as significant when $P < 0.05$ and marginally significant when $0.05 < P < 0.10$.

Results

Soil moisture

At both sites, water manipulations created a gradient of soil moisture during the growing seasons of 2019 and 2020 (water treatment $F_{4,\,41} = 35.7$, $P < 0.001$ for 2019 in Montana, water treatment $F_{4,\,41} = 30.1$, $P < 0.001$ for 2020 in Montana, water treatment $F_{4,\,41} = 6.7$, $P < 0.001$ for 2019 in Wyoming, water treatment $F_{4,\,41} = 4.6$, $P = 0.004$ for 2020 in Wyoming; see Fig. 1), though this pattern was somewhat weaker at Wyoming in 2020, when that site was experiencing a natural drought. Further, we saw a slightly stronger reduction in soil moisture in 2020 than in 2019 in Wyoming, though this reduction was not as consistent in 2020 as in 2019 (see Fig. 1). In 2021, soil moisture was similar across treatments in Montana (water treatment $F_{4,\,41} = 1.4$, $P = 0.244$), which was experiencing a natural drought. In Wyoming, which experienced wetter conditions in 2021, soil moisture was not significantly different across treatments (water treatment $F_{4,\,41} = 1.9$, $P = 0.129$; see Fig. 1).

Annual brome responses

While we found no main effects of grazing on annual brome biomass (Fig. S2, available online at doi:10.1016/j.rama.2023.05.007; Table 1), we did find an interactive effect of water treatment and grazing on annual brome biomass in Montana in 2021, where biomass significantly decreased with severe precipitation reduction under stable grazing and marginally increased as precipitation reduction intensified under heavy grazing (Fig. 2A, see Table 1). Under stable grazing conditions, average biomass decreased 64.6% from 0% to 99% precipitation reduction. Conversely, under heavy grazing conditions, average annual brome biomass increased by 75.2% from 0% to 99% precipitation reduction (see Fig. 2A), though this increase was only marginally significant. Further, we found main effects of precipitation reduction on annual brome biomass. Annual brome biomass decreased linearly with precipitation reduction in 2019 (first yr of precipitation reduction) in Montana. In contrast, in Wyoming, all treatments maintained similar annual brome biomass except the 99% precipitation reduction treatment, which had on average less than half the biomass of other water treatments (see Fig. 2B, 2C, and Table 1). In 2020, the second yr of precipitation reduction, both sites displayed a marginally significant negative linear relationship between annual brome biomass and precipitation reduction. In Wyoming, this trend was also present in 2021 (recovery yr; see Fig. 2C, Table 1). In Montana, water treatments (ambient vs. 99% precipitation reduction) reduced average

Table 2

Repeated-measures linear mixed-model analysis of variance (F statistics with *P* values) for differences in annual bromes' percent green between precipitation reduction treatments and controls without precipitation reduction to each yr's treatment conditions at the time of sampling. We assessed this standardized percent green response to each yr's applicable precipitation reduction and grazing treatments. Data presented here were collected from summer months (May–July). W indicates water treatment; G, grazing treatment; WR, water treatment recovery. Numerical subscripts indicate yr abbreviations for 2019–2021. Data are approximately normal, so no data transformations were necessary. Significant values are shown in boldface type, with * indicating $P < 0.1$, ** $P < 0.05$, *** $P < 0.001$.

Site	Montana			Wyoming		
Yr	df	*F* value	*P* value	df	*F* value	*P* value
2019						
Date	1, 178	0.42	0.52	1, 232	2.50	0.12
W_{19}	1, 26	25.79	**<0.001*****	1, 21	0.09	0.77
Date × W_{19}	1, 178	0.24	0.63	1, 232	1.84	0.18
2020						
Date	1, 212	0.00	1.00	1, 189	0.54	0.46
W_{20}	1, 25	6.39	**0.02****	1, 13	0.44	0.52
G_{19}	1, 5	0.06	0.82	1, 3	2.27	0.23
W_{20} × G_{19}	1, 25	0.00	0.96	1, 13	0.06	0.81
Date × W_{20}	1, 212	0.14	0.71	1, 189	0.13	0.72
Date × G_{19}	1, 212	0.09	0.76	1, 189	0.06	0.81
Date × D_{20} × G_{19}	1, 212	0.03	0.86	1, 189	0.04	0.84
2021						
Date	1, 174	0.10	0.760	1, 253	0.24	0.62
WR_{21}	1, 24	10.25	**0.004****	1, 14	3.42	**0.09***
G_{20}	2, 4	2.80	0.17	2, 3	0.64	0.59
WR_{21} × G_{20}	2, 24	1.10	0.35	2, 14	1.29	0.31
Date × WR_{21}	1, 174	0.46	0.50	1, 253	0.08	0.78
Date × G_{20}	2, 174	0.04	0.96	2, 253	0.04	0.96
Date × WR_{21} × G_{20}	2, 174	0.01	0.99	2, 253	0.02	0.98

Table 3

Linear mixed-model analysis of variance (*F* statistics with *P* values) for differences in annual bromes' percent green between precipitation reduction treatments and controls without precipitation reduction to each yr's treatment conditions at the time of sampling. Data shown are from a single time point representing peak differences in percent green across the water treatments. Dates chosen for Montana are June 24, 2019; June 16, 2020; and June 16, 2021, and dates chosen for Wyoming are July 8, 2019; June 18, 2020; and June 16, 2021. We assessed this standardized percent green response to each year's applicable precipitation reduction and grazing treatments. W indicates water treatment; G, grazing treatment; WR, water treatment recovery. Numerical subscripts indicate yr abbreviations for 2019–2021. Data are approximately normal, so no data transformations were necessary. Significant values are shown in boldface type, with * indicating $P < 0.1$, ** $P < 0.05$, *** $P < 0.001$.

Site	Montana			Wyoming		
Yr	df	*F* value	*P* value	df	*F* value	*P* value
2019						
W_{19}	1, 26.00	24.56	**<0.001*****	1, 31.60	4.81	**0.04****
2020						
W_{20}	1, 25.00	3.78	**0.06***	1, 18.05	1.64	0.22
G_{19}	1, 25.55	0.08	0.77	1, 18.03	5.68	**0.03****
W_{20} × G_{19}	1, 25.00	0.13	0.73	1, 18.04	4.54	**0.05****
2021						
WR_{21}	1, 28.00	18.21	**<0.001*****	1, 30.10	0.44	0.51
G_{20}	2, 28.00	0.18	0.84	2, 5.50	0.48	0.65
WR_{21} × G_{20}	2, 28.00	1.15	0.33	2, 30.11	0.65	0.53

annual brome biomass by 62.1% in 2019 and 46.5% in 2020 (see Fig. 2b). In Wyoming, water treatments (ambient vs. 99% precipitation reduction) reduced average annual brome biomass 78.1% in 2020 and 61.5% in 2021 (see Fig. 2).

Throughout each growing season, grazing had no direct or interactive impacts on annual brome's percent green, but precipitation reduction treatments did result in within-season changes to brome phenology (Table 2). In Montana, the two most extreme precipitation reduction treatments resulted in earlier senescence of field brome in both 2019 and 2020, but in 2019 the two moderate precipitation reduction treatments delayed or had no effect on senescence (Fig. 3, see Table 2). Here, field brome experienced earlier senescence under more extreme precipitation reduction. This pattern was not present in Wyoming (see Table 2). In contrast, recovery yr results revealed significant, positive legacy effects of water treatments in Montana and marginally significant, positive legacy effects of water treatments in Wyoming, with foliar greenness declining earlier in ambient precipitation plots than the most extreme precipitation reduction plots (see Fig. 3, Table 2).

When we assessed a single time point that represented peak differences in percent green across water treatments, these trends tended to persist. In 2019 in Montana, we again found water manipulation significantly decreased percent green of field brome overall, except under 25% water reduction. Additionally, we found percent green marginally decreased in 2020, but in 2021, percent green significantly increased with precipitation reduction (Fig. 4, Table 3). Similar to Montana, in Wyoming in 2019, we found a significant decrease in percent green difference of annual bromes with precipitation reduction (see Fig. 4, Table 3). Additionally, in 2020 in Wyoming, we found an interaction between grazing and precipitation reduction on percent green difference, though post-hoc testing revealed no significant differences (see Table 3). We also found a main effect of grazing on percent green difference of annual bromes in 2020 in Wyoming, where percent green difference significantly decreased from stable to heavy grazing (see Table 3).

We found no significant effects of precipitation reduction or grazing on percent cover of field brome or cheatgrass at either site throughout the treatment yr (see Figs. S3-S4, Table S3, available online at doi:10.1016/j.rama.2023.05.007).

Discussion

The use of experimental manipulations is critical for understanding potential global change impacts; however, global change experiments are often limited in spatial and temporal scale (De Boeck et al. 2015) and rarely include recovery. Water manipulations using rain-out shelters are challenging due to the cost and difficulties of maintaining infrastructure (Svejcar et al., 1999; Yahdjian and Sala, 2002), while grazing experiments must deal with the logistical and financial challenges associated with large mammals (Bransby 1989), making manipulated precipitation and grazing experiments rare. Here, we uniquely combined the impacts of 2 yr of multi-intensity water removal treatments with summer grazing on invasive annual grasses.

We hypothesized that precipitation reduction and summer grazing would have an interactive impact on invasive annual bromes. We found evidence of this interactive effect on annual brome biomass at the Montana site only during the recovery yr in 2021 (see Fig. 2A). Stable grazing conditions led to a decrease in annual brome biomass under precipitation reduction, while heavy grazing led to a marginal increase in annual brome production when combined with prior precipitation reduction. When water stress is severe, heavier grazing can promote annual brome abundance, possibly by reducing native plant biomass, thus reducing competition for resources (Davies et al. 2014, 2011). As these are disturbance-adapted systems, our results from summer grazing make sense given previous work on heavy or overgrazing of water-stressed systems. Grazing has been shown to maintain grassland states (Gibson 2009), but varying intensities of grazing (e.g., moderate vs. heavy) can alter the plant community (Veblen et al. 2016; Wells et al. 2022). Low to moderate grazing may have neutral or positive impacts on invasion resistance (Porensky et al. 2020) through direct negative impacts on annual bromes (Stechman and Laude 1962; Haferkamp and Karl 1999) and positive effects on the

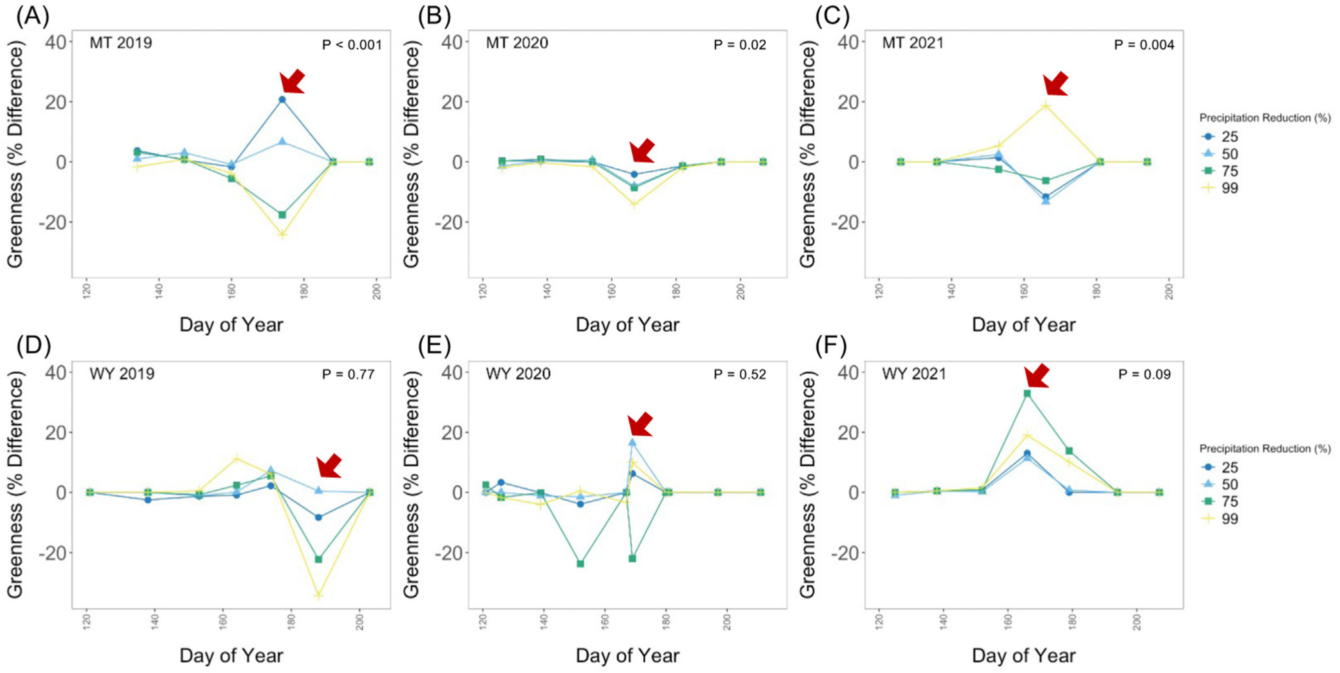

Figure 3. Changes in average percent green difference (treatment – control) of annual bromes within each growing season (**A–C**) in Montana (MT) and (**D–F**) Wyoming (WY) from 2019 to 2021. Colored lines represent the water treatments. Julian day of the year is along the x-axis. *P* values are for the water treatment main effect. *Arrow* indicates the time point with the greatest difference in standardized percent green among water treatments chosen for further analyses (see Table 3, Fig. 4).

grazing-adapted native plant community (Collins and Barber 1986; Patton et al. 2007). Spring grazing is commonly used to manage invasive annual bromes (Daubenmire 1940; Harmoney 2007; Diamond et al. 2012; Porensky et al. 2021), but some evidence suggests that late-season (Stechman and Laude 1962; Schmelzer et al. 2014) or season-long (Haferkamp and Karl 1999) grazing can decrease annual brome production. However, given that our grazing treatments occurred in the summer after annual bromes had matured (and likely dropped seeds), it makes sense that we did not find strong main effects of our grazing treatments on annual brome performance in the next growing seasons, as annual bromes are not preferable forage later in the season (Haferkamp 2001).

The response of invasive annual bromes to drought can be variable, in part depending on the timing and severity of the drought (Bradley et al. 2016) and the nature of legacy effects. We hypothesized that in addition to interactive effects of precipitation reduction and grazing, we would see main effects of water reduction on annual bromes, where brome biomass and percent cover would decrease during imposed precipitation reduction years but would increase in the recovery year. Following a year-long severe natural drought, the percent cover of cheatgrass increased for 3 yr before declining, while the dominant native species experienced declines following drought (Souther et al. 2020). Further, fall precipitation has been shown to affect annual brome biomass in the following summer (Rinella et al. 2020) and increased fall water can increase annual grass production, especially under spring drought (Vermeire and Rinella 2020). Other evidence suggests summer drought can impact invasive annual bromes, with summer drought favoring annual brome production over native species (Bradley et al. 2016). Generally, our hypothesis was supported for biomass (see Fig. 2, Table 1), but not cover (see Figs. S2, S3, Table S2) during precipitation reduction years, though the timing and magnitude of support differed between sites.

In years of average to above-average spring/summer precipitation, native perennial species can better resist invasive annual bromes as greater water availability occurs simultaneously with periods of native plant growth, helping to compensate for moisture losses depleted by annual grasses (Chambers et al. 2016). Alternatively, in similar systems, drought conditions during the growing season have been found to favor winter annual grasses and annual brome production since their growth periods are early in the spring when moisture inputs from snowmelt and rain are often large and evaporative losses are small (Meyer et al. 1997; Bradford and Lauenroth 2006; Bradley 2009; Bradley et al. 2016; Johnston and Garbowski 2020). In our study, limiting water during the growing season (April—October) tended to reduce annual brome biomass while having no significant effects on percent cover. Only when a third year of low water (natural 2021 drought in Montana) occurred, and was combined with heavy grazing, did we see an increase in annual brome production (see Fig. 2A). In all other less extreme treatment comparisons, annual brome production was unaffected or declined (see Fig. 2B and 2C). This suggests that as drought periods become longer and more extreme (Zhang et al. 2021), annual bromes may experience a competitive advantage, especially after multiyear droughts, but that the threshold by which this advantage is reached may be high. Furthermore, field experiments with rainout shelters have been shown to underestimate the response of plant biomass to drought compared with natural conditions, suggesting annual brome responses may be more extreme during natural drought (Kröel-Dulay et al. 2022).

We also hypothesized that annual bromes would senesce earlier in the season during precipitation reduction years but would delay senescence in the recovery year. In general, this hypothesis was supported (see Fig. 3, Table 2). We found support that annual bromes senesced more quickly under severe water reduction in 2019 at both sites, except under 25% water reduction in Montana, and weak support for this in Montana in 2020 when assessing differences at a single time point (Fig. 4, Table 3). The increase in percent green under moderate water reduction in Montana may be due to the competitive advantage of bromes over natives to use moisture early in the season (Howell et al. 2020). Further, following imposed water treatments, we found annual bromes delayed

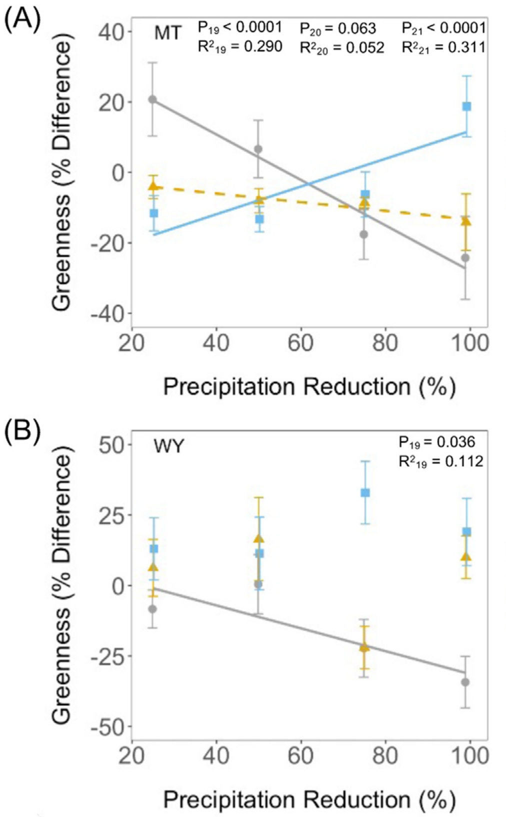

Figure 4. Mean ± standard error of percent green difference of annual bromes at **A,** Montana (MT) and **B,** Wyoming (WY) from 2019 to 2021. Data shown are from a single time point representing peak differences in standardized percent green across the water treatments. Dates chosen for MT are June 24, 2019, June 16, 2020, and June 16, 2021, and dates chosen for WY are July 8, 2019, June 18, 2020, and June 16, 2021. *Solid lines* indicate significant effects of water treatment ($P < 0.05$), and *dashed lines* indicate marginally significant results ($0.05 < P < 0.1$) as calculated from the linear mixed-model analyses of variance (see Table 3). P values and marginal R^2 values for significant or marginally significant effects of precipitation reduction for each yr are shown.

time to senescence in Montana, with weaker support for this in Wyoming. This differential response could be due to benefits of drought to annual bromes relative to native plant species or could reflect the different magnitudes of water treatment imposed and could indicate high capacity of phenological plasticity that allows varying response of annual bromes to drought. Additionally, previous year's drought may indirectly delay senescence of annual bromes due to a release from (resource) competition with perennial grasses still weakened by prior drought (Rice et al. 1992). Invasive annual bromes, growing early in the season, can take advantage of available moisture (and nutrients) that native plants are not able to use (Howell et al. 2020), especially if native plants recover slowly after drought (i.e., drought legacy effects).

Our results suggest that annual bromes vary in their resistance (i.e., current-yr effect) and resilience (i.e., legacy effects) to droughts by field site. We found that annual bromes were more resistant to drought in Wyoming than Montana but more resilient to drought in Montana than Wyoming. This variation by site may represent inherent vegetation differences. At the Wyoming site, annual brome phenology overlaps less with native plant phenology due to the greater abundance of C_4 grasses (Porensky et al. 2018). Thus, growing-season precipitation reduction combined with active native plant growth in the late summer/fall could draw down resources (e.g., nitrogen, water), negatively impacting annual brome growth in the fall/winter/early spring period (Ogle et al. 2003), whereas at the Montana site, cool-season C_3 grasses dominate. These grasses generally grow at the same time as invasive annual bromes, leading to stronger current-yr water effects (Haferkamp et al. 2005).

Alternatively, these mixed results of precipitation reduction on invasive annual bromes could be due to differences in water treatment effectiveness (Hoover et al. 2018). In our two implemented water treatment yr (2019–2020), we were able to impose a significant gradient of precipitation reduction conditions at both sites (see Fig. 1). However, the magnitude of soil moisture effect was greater in Montana. Specifically, our first yr of imposed precipitation reduction (2019) was a relatively average year at the Montana site. In contrast, the Wyoming site experienced a wet yr, which likely minimized the effectiveness of the rainout shelters. In 2019 and 2020, 99% rainfall reduction represented a greater reduction in soil moisture availability in Montana than in Wyoming (see Fig. 1). Overall, while still significant, our water reduction treatments (2019, 2020) were of smaller magnitude in Wyoming than Montana, which may have led to weaker and/or delayed treatment effects. Further, while 2021 was the recovery yr, Montana experienced low ambient precipitation conditions. Therefore, rather than serving as a recovery yr, we had a natural drought at the Montana site, which already received more severe precipitation reduction in 2019–2020. Considering the soil moisture availability differences between sites, the decrease in biomass of annual bromes during both water treatment yr in Montana makes sense, as does the more moderate responses seen in Wyoming. Further work will be needed to distinguish between these two hypotheses (which could also be acting together in our study).

Implications

Invasive annual bromes are known to decrease available high-quality forage for livestock (Haferkamp et al. 1998, 1997, 1994; DiTomaso 2000), decrease native species diversity, and lead to broad-scale soil erosion in similar regions of the Great Basin (Knapp 1996). Further, high annual brome abundance can decrease livestock performance by decreasing animal weight gains (Haferkamp et al. 2001). With an ever-growing human population, increased food demand, and severe consequences of climate change, it is crucial to understand how we can sustainably manage our rangeland ecosystems. Our results suggest that grazing management choices during drought can influence annual brome production, and drought can also have impacts on forage quality by affecting annual brome senescence patterns. However, responses may vary depending on particular site, climatic, and topographic conditions. Overall, the greater the magnitude of water reduction, the greater the reduction in annual brome biomass, but when a natural drought is combined with heavy grazing (which is common in drought years), there is potential for annual brome invasion to increase in subsequent years. In addition, in the year following reduced precipitation, legacy effects of water reduction can delay annual brome senescence. In a positive light, the threshold at which reduced precipitation and grazing stress interact to decrease rangeland sustainability may be quite high due to drought and grazing resistance of native vegetation. This highlights the need to maintain native populations of plants in these ecosystems as extreme scenarios become even more common in the future.

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Author Contributions

SEK, KJK, LMP, KOR, KRW designed the experimental platform while MDTF designed the invasion study. All authors collected data, and MDTF, SEK, and KRW performed analyses. MDTF wrote the manuscript, and all authors edited the manuscript.

Data Availability Statement

The datasets and code for this study can be found in the Grazing_drought_invasion repository (https://github.com/mdtrimas/Grazing_drought_invasion) on GitHub (DOI 10.5281/zenodo.8021689).

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.rama.2023.05.007.

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