



ARTICLE

Feast or famine: How is global change affecting forage supply for Yellowstone's ungulate herds?

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Abstract

The ecological integrity of US national parks and other protected areas are under threat in the Anthropocene. For Yellowstone National Park (YNP), the impacts that global change has already had on the park's capacity to sustain its large migratory herds of wild ungulates is incompletely understood. Here we examine how two understudied components of global change, the historical increase in atmospheric CO₂ and the spread of nonnative, invasive plant species, may have altered the capacity of YNP to provide forage for ungulates over the last 200-plus years. We performed two experiments: (1) a growth chamber study that determined the growth rates of important invasive and native YNP grasses that are forages for ungulates under preindustrial (280 ppm) versus modern (410 ppm) CO₂ levels and (2) a field study that compared the effect of defoliation (clipping) on the shoot growth of invasive and native mesic grassland plants under ambient CO₂ conditions in 2019. The growth chamber experiment revealed that modern CO₂ increased the growth rates of both invasive and native grasses, and invasive grasses grew faster regardless of CO₂ conditions. The field results showed a continuum of positive to negative responses of shoot growth to defoliation, with a subgroup of invasive species responding most positively. Altogether the results indicated that the historical increase in CO₂ and the spread of invasive species, some of which were planted to provide forage for ungulates in the early and mid-1900s, have likely increased the capacity of forage production in YNP. However, rising CO₂ has also resulted in regional warming and increased aridity in YNP, which will likely reduce grassland productivity. The challenge for global change biologists and park managers is to determine how competing components of global change have already affected and will increasingly affect forage dynamics and the sustainability of Yellowstone's iconic ungulate herds in the Anthropocene.

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KEYWORDS

Anthropocene, atmospheric CO₂, climate change, grasslands, grazing, herbivory, invasive plants, ungulates, Yellowstone National Park

INTRODUCTION

Global change threatens the ecological integrity of US national parks and other protected areas in several ways (Beissinger et al., 2017; Hanson et al., 2014). Human development is increasingly encroaching on parks and disrupting the movements of ungulates across park boundaries (Berger, 2017). Global climate, driven by increasing concentrations of CO₂ and other greenhouse gases, is warming and altering precipitation patterns and ecological processes within park ecosystems (Gonzalez, 2017; Hanson et al., 2014; Rammer et al., 2021). Further, the spread of nonnative, invasive animal and plant species in parks jeopardizes the conservation and functioning of native communities (Foxcroft et al., 2013; Simberloff, 2017).

These Anthropocene pressures on park ecosystems have compelled a reevaluation of the management goals for US national parks. In the 1960s, the US National Park Service (NPS) adopted the recommendations of Leopold et al. (1963) calling for parks to preserve “vignettes” of nature that existed before the arrival of Europeans in North America. The recommendations of the “Leopold Report” provided a clear management target guiding the NPS for half a century. However, recognizing that global-level factors have changed and will increasingly change ecological dynamics in national parks and, thereby, make the preservation of a pre-European condition a wistful management goal, the NPS Science Advisory Committee (Colwell et al., 2012) and others more recently (Beissinger & Ackerly, 2017; Cole & Yung, 2010; White et al., 2013) recommended that US national parks shift management priorities from historical preservation to the conservation of critical ecological processes. Current NPS policies allow individual parks to adopt a variety of management priorities, ranging from historical preservation to sustaining ecological integrity (USDI 2006).

In this paper, we focus on the impacts of global change on the capacity of Yellowstone National Park (YNP) to provide forage to support herds of migratory ungulates. YNP is occupied by the largest ungulate herds in North America. These animals are a major attraction for millions visiting the park each year and have become an important model system to study plant–wild ungulate dynamics and the positive feedbacks that grazing has on grassland production (Frank et al., 2018; Geremia et al., 2019; Middleton et al., 2018). However, the

integrity of the ecological processes that sustain Yellowstone’s ungulate populations is under threat by several global change components, only two of which have received some attention. The first, the encroachment of human development at the boundaries of YNP, has hampered animals following their natural migratory routes entering and exiting YNP (Middleton et al., 2020). To curb the spread of *Brucella* (the bacteria causing brucellosis) to cattle, bison (*Bison bison*) movements outside of YNP are particularly tightly regulated (White et al., 2011). Second, the climate of YNP has warmed in the last several decades, resulting in an increasing frequency and intensity of forest fires (Turner et al., 2017) and declining soil moisture levels at elevations below ca. 2000 m (Thoma et al., 2015), which impacts the production of forage resources throughout much of the annual range of YNP ungulates. In this study, we consider how two other components of global change that have received less attention, the spread of invasive plants and the historical increase in atmospheric CO₂ concentrations, and their interaction have impacted the production of forage for ungulates in YNP.

Invasive plant species have become widely distributed (Stohlgren et al., 2010) and threaten native plant communities throughout YNP (Simberloff, 2017). Numerous studies examining the effect of invasive plant species on park ecosystems (Simberloff, 2017) have connected the spread of invasive plants to changes in nutrient cycling, fire regimes, hydrology, ecosystem structure, competitive relations with native plants, and, of particular relevance to this study, increasing plant production (Asner & Vitousek, 2005; Erhenfeld, 2010; Esque et al., 2006; Vitousek, 1986; Von Holle et al., 2006, 2013). Plant invasion ecology research in YNP has largely investigated the distributions throughout the park of a few invasive species such as *Linaria vulgaris* (Pauchard et al., 2003), *Linaria dalmatica* (Larson, 2021), and *Cirsium arvense* (Wright & Tinker, 2012). How the increasing abundance of invasive species impacts forage production for YNP ungulate herds has not been considered.

Atmospheric CO₂ concentrations have increased sharply from ~270 ppm before the Industrial Revolution to 410 ppm in 2019 (Friedlingstein et al., 2019). Elevated CO₂ often stimulates plant growth, largely as a function of reducing the rate of photorespiration, particularly in C3 plants, and reducing the effects of water stress on leaf carbon assimilation rates (Dewar et al., 2018; Eamus, 1991;

Leakey et al., 2009). Most previous studies compared photosynthetic and plant growth rates between modern (350–400 ppm) and predicted future (>550 ppm) conditions. These studies revealed that future elevated levels of CO₂ will likely increase the performance of invasive species more than native species (Liu et al., 2017). The effects of historical CO₂ enrichment on plant growth is relatively understudied, yet critical for assessing how modern atmospheric CO₂ and its interaction with an increasing abundance of invasive species may have already altered fundamental ecosystem processes, such as the rate of plant production and forage supply for herbivore populations in YNP and other protected areas.

In this study, we performed two experiments to assess the effects of the historical increase in atmospheric CO₂ and the spread of invasive species on grassland production in YNP to explore how these global change factors have affected forage production and the capacity of present-day YNP to support ungulate populations compared to pre-European conditions. First, we grew three invasive and four native YNP grass species, all important forages for wild ungulates, under preindustrial (270 ppm) and modern (410 ppm) CO₂ levels in a controlled growth chamber experiment to examine how nativity, the rise in atmospheric CO₂, and their interaction affect plant growth and may have altered forage production since the Industrial Revolution. Second, we examined the effect of simulated grazing (clipping) on shoot regrowth post clipping between native and invasive plants in the field under ambient, modern CO₂ conditions to explore how the two plant groups respond to herbivory and may differentially contribute to forage production under the grazing regime in YNP. We hypothesized that (1) plant growth rates would be greater for invasive species at both CO₂ levels, and modern CO₂ would stimulate invasive grasses more than native grasses in the controlled growth chamber experiment; and (2) defoliation in the field would promote shoot growth more for invasive species compared to native species. Thus, we predicted that the combination of the historical increase in CO₂ and the spread of invasive species has likely increased the capacity of YNP to produce forage for ungulates.

MATERIALS AND METHODS

Study area

YNP supports eight ungulate species. Elk (*Cervus canadensis*), bison, and pronghorn (*Antilocapra americana*) are the predominant grassland grazers in YNP. The park also supports populations of bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*),

mule deer (*Odocoileus hemionus*), moose (*Alces alces*), and white-tailed deer (*Odocoileus virginianus*) that rarely graze grassland. The climate of YNP is characterized by long cold winters and short dry summers. Thirty-year (1989–2019) average temperature and precipitation at Tower Ranger Station, located at 2012 m elevation and 15 km from the field site in the Lamar Valley, were 2.7°C and 42.1 cm, respectively. During that 30-year period, 56% of the annual precipitation fell during the April to August growing season. Soils throughout the park have developed primarily on mineral material deposited during the Pleistocene (Keefer, 1987). Plant production and soil water, nitrogen, and phosphorus availability increase along catenas from relatively dry hilltop and slope grasslands to mesic slope-bottom and valley-bottom grasslands (Frank, 2008; Frank et al., 2011). YNP grasslands are predominately made up of C3 species, which are predicted to respond strongly to rising atmospheric CO₂ levels (Dewar et al., 2018; Eamus, 1991; Leakey et al., 2009). Between 1904 and 1952, more than 405 ha of the Northern Range were cleared of native vegetation. Unspecified “oatgrasses” and alfalfa (*Medicago sativa*) were used as nurse crops and replaced with invasive *Bromus inermis*, *Trifolium repens*, *Poa pratensis*, and *Elymus trachycaulus* over time to provide forage for ungulates (Skinner & Alcorn, 1947).

CO₂ experiment

Seeds from four native (*Achnatherum richardsonii*, *Bromus carinatus*, *Deschampsia cespitosa*, *Koeleria macrantha*) and three invasive (*B. inermis*, *Phleum pratense*, *P. pratensis*) C3 grass species were collected from the Northern Range of YNP (Houston, 1982) in July 2019 (Table 1). All seven species are forage for wildlife (Eddleman & McLean, 1969; Hobbs et al., 1981; Johnson, 1962; Stubbendieck & Hatch, 1997; Vallentine, 1961). Five of the seven species occur in mesic grasslands, where two invasives, *P. pratense* and *P. pratensis*, often dominate. *K. macrantha* and *A. richardsonii*, both native species, are more common in drier grasslands. Seeds were stratified at 4°C in wet sand for 6–8 weeks before germination.

Seedlings were grown in 1.6-L pots ($N = 4–5$ per species/CO₂ treatment combination) in Conviron BDR16 environmental chambers at 270 ppm and 410 ppm atmospheric CO₂ concentrations (± 20 ppm). Pots were filled with a 2:1 mixture of steam-sterilized topsoil and sand. To each pot, 8 g Osmocote Smart Release Plant Food (SDS#320000005091, The Scotts Company LLC, Marysville, OH) was added to ensure adequate nutrients throughout the experiment. Multiple stratified seeds were added to each pot and after germination thinned to one plant per pot. Plants were grown under 14 h day/night cycles, with

TABLE 1 Grass species included in growth chamber study.

Binomial name	Common name	Abbreviation	Nativity	Habitat	Harvest ^a (days)
<i>Achnatherum richardsonii</i>	Richardson's needlegrass	ACRI	Native	Dry	78
<i>Bromus carinatus</i>	California brome	BRCA	Native	Mesic	54
<i>Bromus inermis</i>	Smooth brome	BRIN	Invasive	Mesic	47
<i>Deschampsia cespitosa</i>	Tussock grass	DECE	Native	Mesic	50
<i>Koeleria macrantha</i>	Prairie junegrass	KOMA	Native	Dry	71
<i>Phleum pratense</i>	Timothy grass	PHPR	Invasive	Mesic	61
<i>Poa pratensis</i>	Kentucky bluegrass	POPR	Invasive	Mesic	62

^aNumber of days species grew before being harvested.

light levels gradually increasing to 1000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the first daytime hour and then back down to 0 $\mu\text{mol m}^{-2} \text{s}^{-1}$ during the last daytime hour. Temperature also increased gradually at the start of each day from 13°C (night) to 23°C (day, $\pm 0.2^\circ\text{C}$), common modern midsummer conditions in YNP. Relative humidity was set to maintain 60/80% ($\pm 1\%$) day/night conditions.

Each species was harvested before plants became root-bound (based on harvested root profiles) or shaded by neighbors. Because of the different seed germination periods and growth rates, species were harvested at different time points, ranging from 50 to 78 days after emergence. Harvested plant material was separated into above- and belowground tissues, dried at 50°C for 3 days, and weighed to determine plant dry weight. Aboveground biomass allocation was calculated as the dry weight of leaves relative to total dry weight (leaf mass fraction [LMF]).

Clipping experiment

A clipping study was performed in mesic grasslands in the Lamar Valley on the Northern Range in 2018 (Penner & Frank, 2021) to compare how invasive and native grassland species regrew after being defoliated in the field. Ten 2.5 × 2.5-m ungulate exclosures were established after snowmelt in the mesic grassland. Two 0.5-m² paired quadrats with similar plant species composition and total shoot biomass were established inside each exclosure and randomly assigned to be clipped or left as an unclipped control. Approximately half of the plant biomass was removed in each clipped quadrat in early June and again in early July, a rate well within the range that plant biomass is consumed in YNP grasslands (Frank et al., 2016). The effect of clipping on species growth rate was determined by comparing one-month changes in species biomasses in paired clipped

and unclipped quadrats after June and July clipping events. Biomass per species was estimated with the canopy intercept method (Frank & McNaughton, 1990).

Statistical analyses

Growth chamber experiment

A single varying-intercept model was separately fit to data on growth rates of shoot, root, and total biomass and LMF. Biomass data were natural log-transformed, which assumes constant relative growth rates (Hunt, 1982). Each model considered the main effects of CO₂ concentration and nativity and the interaction between them. CO₂ concentration (preindustrial, modern) and nativity (native, nonnative) were treated as categorical variables. Data were grouped by ($J = 7$) species. The mathematical notation for the model is

$$y_i = \alpha_{j[i]} + X_i\boldsymbol{\beta} + \varepsilon_i, \quad \text{for } i = 1, \dots, I \text{ and } j = 1, \dots, J,$$

where ε_i is given by $N(0, \sigma_y^2)$ and $\alpha_{j[i]}$ is given by $N(\mu_\alpha, \sigma_\alpha^2)$. The resulting likelihood is

$$P(y|\boldsymbol{\beta}, \mu_\alpha, \sigma_y^2, \sigma_\alpha^2) = \prod_{i=1}^I N(y_i|\alpha_{j[i]} + X_i\boldsymbol{\beta}, \sigma_y^2) \prod_{j=1}^J N(\alpha_{j[i]}|\mu_\alpha, \sigma_\alpha^2),$$

where y_i is the i th value of the dependent variable (biomass or LMF), $\boldsymbol{\beta}$ is a vector of linear model coefficients, X is a matrix of independent variable values, and j is the species group.

Field clipping experiment

Species relative abundance in the mesic Yellowstone grassland was calculated using mean species abundance data for

each enclosure ($n = 10$) in June before clipping occurred. The daily rate of shoot growth was determined for clipped and control treatments for each species. Daily shoot growth was calculated according to Penner and Frank (2021) as

$$\text{Daily growth} = \frac{S_2 - S_1}{t_2 - t_1},$$

where S equals shoot biomass at the first (t_1) and second (t_2) time points. The effect of clipping on plant growth in each enclosure ($n = 10$) was derived by subtracting the daily growth in the control quadrat from that of the clipped quadrat. Thus, positive and negative values reflect positive and negative effects of clipping on daily growth, respectively. Daily growth for each species was only calculated for enclosures (replicates) where the species occurred in both clipped and control quadrats. Results are presented for species with sample sizes ≥ 3 . A paired t -test was used to determine significant differences in daily growth between clipped and control treatments for a species. The effect of nativity on plant growth responses to clipping in June and July was examined with one-way ANOVAs.

RESULTS

Growth chamber experiment

Shoot, root, and total plant growth rates were greater for invasive compared to native species (Table 2, Figure 1). CO₂ enrichment enhanced shoot and total plant growth

TABLE 2 Model results examining effects of CO₂ concentration, nativity, and their interaction on ln shoot, ln root, and ln total plant growth rate and leaf mass fraction.

Independent variable	Dependent variables	F value	Probability
Ln daily shoot production	CO ₂	43.29	<0.0001
	Nativity	33.85	0.0043
	CO ₂ × Nativity	0.07	0.7907
Ln daily root growth ^a	Nativity	29.43	0.0056
	CO ₂ × Nativity	6.00	0.0174
Ln daily whole plant growth	CO ₂	24.34	<0.0001
	Nativity	43.76	0.0027
	CO ₂ × Nativity	2.97	0.0905
Leaf Mass Fraction ^a	Nativity	8.39	0.0443
	CO ₂ × Nativity	7.53	0.0082

Note: Significant ($\alpha = 0.05$) results are in bold.

^aCO₂ was removed from analysis after inspection of its interactions with nativity.

rates for both native and invasive plants in the experiment (Table 2, Figure 1). Root growth rate increased with CO₂ more for native species than invasive species. Allocation to leaves (LMF) was greater for native compared to invasive grasses (Table 2, Figure 2). However, elevated CO₂ increased LMF for invasive grasses but not for natives. Removing *A. richardsonii* and *K. macrantha*, two grasses found in dry grasslands and adapted to more stressful conditions than the remaining grasses that grow in mesic grasslands, had no qualitative effect on the findings, with the exception that there was only an interaction between CO₂ and nativity on LMF and not a main nativity effect (Appendix S1: Table S1).

Field clipping experiment

Invasive species represented 91% of the shoot biomass of the mesic grassland in June at the beginning of the clipping experiment. Seven of the 25 species were invasive, and five of those seven were the most abundant (Figure 3; Appendix S1: Table S2).

Responses of daily growth to clipping in both June and July ranged from positive to negative among species (Figure 4). Nativity had a marginal effect on the response of plants to clipping in June ($p = 0.078$) and no effect in July ($p = 0.73$). However, species that responded most positively to clipping in June and July were subgroups of invasive species, which in at least one of the 2 months included each of the three invasive species grown in the CO₂ experiment (BRIN, PHPR, POPR). In June, six of the seven species whose mean responses were enhanced by clipping the most were invasive, although three displayed statistically nonsignificant trends (Figure 4). Collectively those six invasive species represented 86% of the species biomass measured in June, with *P. pratensis* (POPR) contributing over 45% of the biomass (Figure 3). In July, the four species stimulated the most by clipping were all invasive, one of which exhibited a nonsignificant trend (Figure 4). Those top four ranked invasive species in July represented 78% of the June mesic grassland composition (Figure 3). The mean response of the invasive *Phleum pratense* to clipping was negative in June and positive in July (Figure 4). Low sample sizes likely impacted discriminating statistically significant responses to clipping for some species.

DISCUSSION

This study explored how two components of global change, CO₂ enrichment and invasive species, have altered grassland production in YNP. As expected, shoot

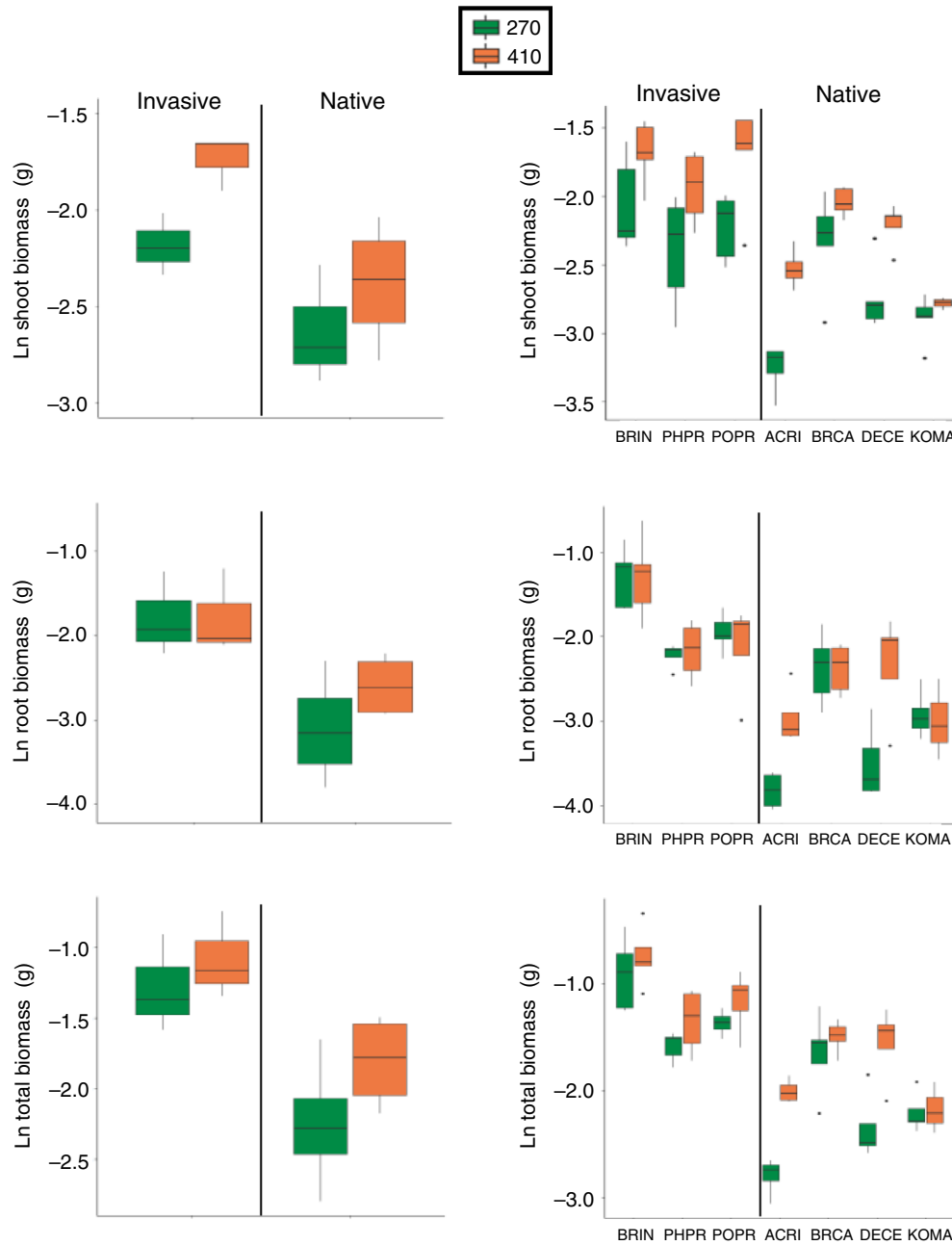


FIGURE 1 Boxplots for ln (natural logarithm) shoot, ln root, and ln total biomass of invasive and native Yellowstone National Park grasses (left) and by species (right). ACRI, *Achnatherum richardsonii*; BRCA, *Bromus carinatus*; BRIN, *Bromus inermis*; DECE, *Deschampsia cespitosa*; KOMA, *Koeleria macrantha*; PHPR, *Phleum pratense*; POPR, *Poa pratensis*.

and root production were greater for invasive compared to native grasses, and modern (410 ppm) CO₂ increased whole plant growth compared to preindustrial CO₂ (270 ppm) in the growth chamber experiment. Interestingly, invasive species had a significant growth advantage over native species, even under low CO₂. Although changes in CO₂ benefited both plant groups, elevated CO₂ caused invasive grasses to increase allocation to shoots and therefore increase the biomass available to herbivores. Thus, the combination of CO₂ enrichment

and abundant invasive grasses may have increased grassland production in YNP and the availability of forage to grazing ungulates compared to preindustrial conditions.

These findings are consistent with two separate large bodies of work documenting that invasive plants grow faster than native herbaceous species (Baker & Stebbins, 1965; Rejmánek & Richardson, 1996) and that rising CO₂ concentrations facilitate C3 plant growth (Dewar et al., 2018; Eamus, 1991; Leakey et al., 2009). Faster growth rates of invasive species are frequently

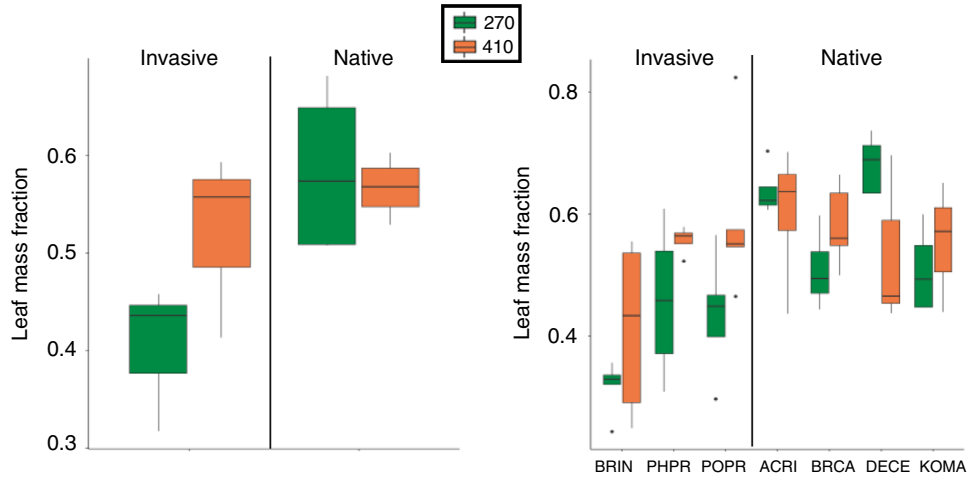


FIGURE 2 Boxplots for leaf mass fraction of invasive and native Yellowstone National Park (YNP) grasses (left) and by species (right). ACRI, *Achnatherum richardsonii*; BRCA, *Bromus carinatus*; BRIN, *Bromus inermis*; DECE, *Deschampsia cespitosa*; KOMA, *Koeleria macrantha*; PHPR, *Phleum pratense*; POPR, *Poa pratensis*.

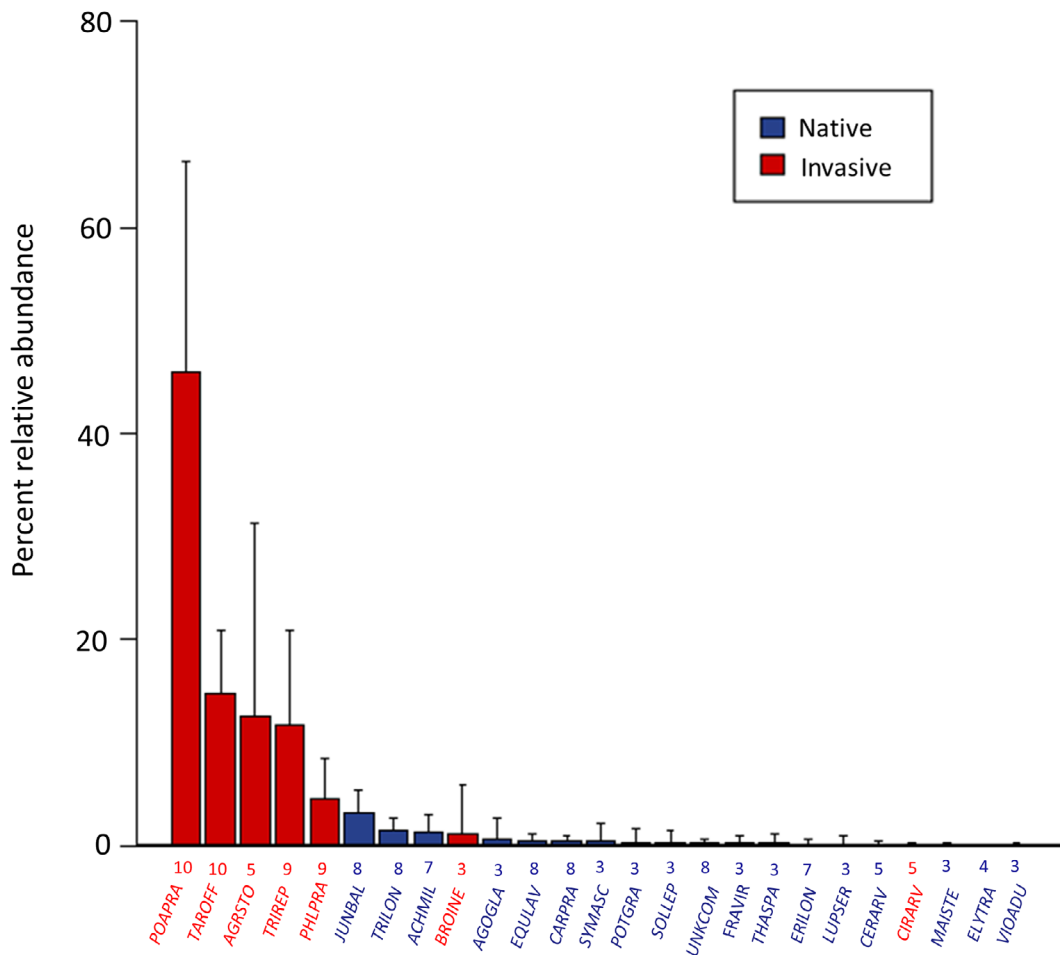


FIGURE 3 Mean (\pm standard error) relative abundance of species in 10 randomly located plots in Lamar Valley. Invasive and native species are indicated in red and blue, respectively. The number of plots in which each species occurred are provided. See Appendix S1: Table S2 for species identifications.

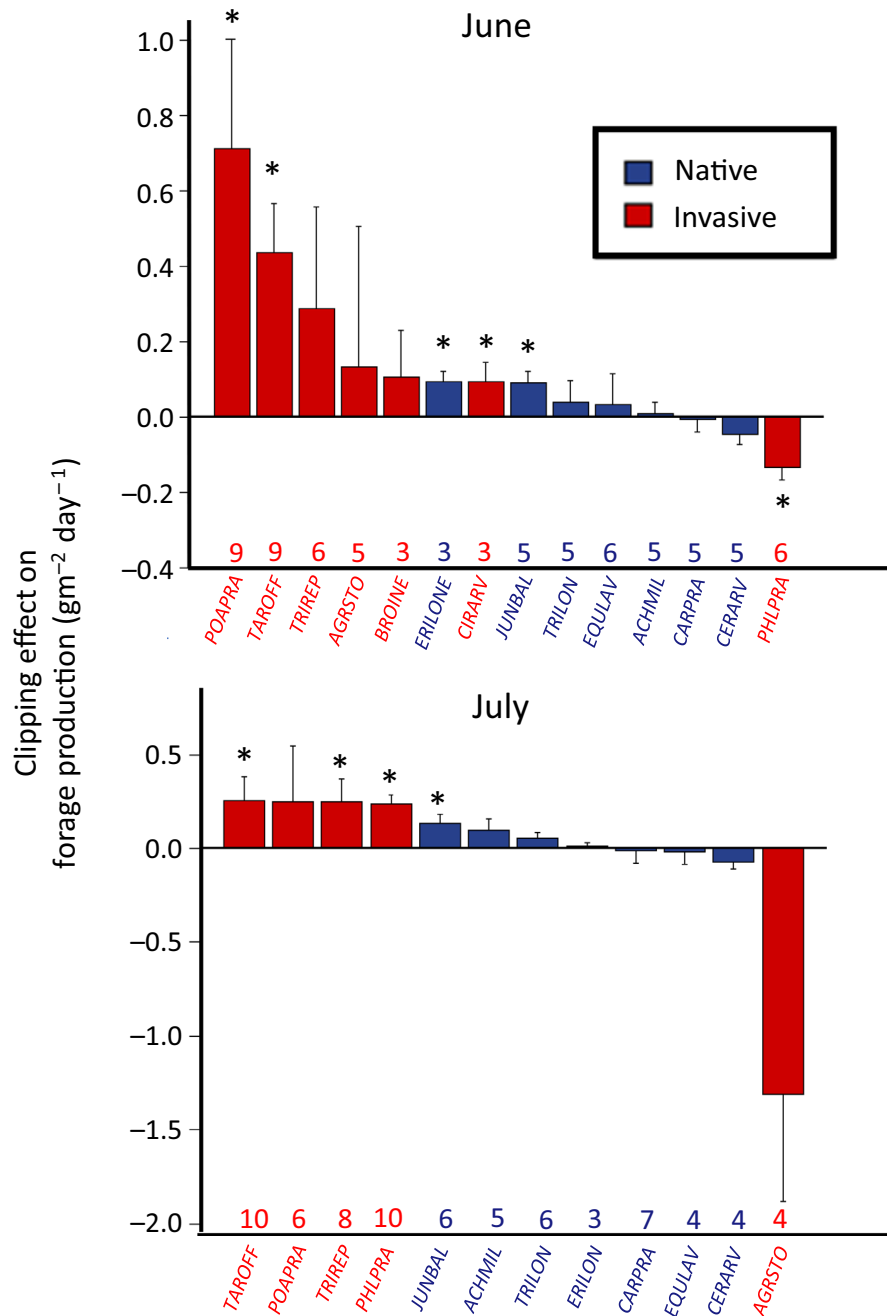


FIGURE 4 Mean (\pm standard error) effect of clipping on forage (shoot) production for native and invasive species in June and July in mesic grassland of the Lamar Valley. Species means were calculated from exclosures where the species was present in clipped and unclipped quadrats. Identification and the number of exclosures included in calculating the clipping effect for each species are provided. Asterisk (*) denotes probability ≤ 0.05 . See Appendix S1: Table S2 for species identifications.

attributed to more acquisitive growth strategies supported by higher leaf nitrogen and carbon assimilation in invasive plants compared to more conservative resource-use strategies in native species (Pyšek & Richardson, 2007). In this study, we further found that greater plasticity in allocation to leaves may support enhanced growth of invasive species under CO₂ enrichment. Higher CO₂ enhances growth rates of C3 plants by reducing rates of

photorespiration, increasing the activity of Rubisco (V_cmax, Leakey et al., 2009), and increasing leaf level water use efficiency (WUE) (Dewar et al., 2018; Gimeno et al., 2018). Since plants were watered to saturation daily in the growth chamber experiment, increased WUE likely had limited impact on the CO₂-induced increase in grass production. Thus, the growth-facilitating effects of CO₂ enrichment under water-

limiting conditions that often occur in YNP grasslands may be even greater than those measured in this study. However, other factors, such as nutrient availability and acclimation to higher CO₂, will likely constrain productivity benefits in the long term.

Two meta-analyses synthesized large bodies of work examining the effects of elevated CO₂ on native versus invasive plant species. Sorte et al. (2013) found a nonsignificant trend for elevated CO₂ increasing growth of invasive plants more than native plants. In a more recent study (Liu et al., 2017) that included a larger set of plant performance variables (e.g., growth, survival, reproduction, photosynthetic rate), elevated CO₂ increased the performance of invasive species significantly more than that of native species. Both meta-analyses focused on studies comparing plant performance at existing ambient conditions at the time of each study versus a forecasted future (>550 ppm) CO₂ concentration. They did not include responses to CO₂ below modern levels (e.g., 410 ppm), which are often greater than responses to predicted future CO₂ concentrations. Here we did not find that invasive grasses increased their performance in response to modern compared to preindustrial CO₂ levels more than native grasses, which was not what we had predicted. However, shifts in biomass allocation to leaves could poise invasive grasses to take greater advantage of further increases in CO₂ concentration.

Our results reveal that the historical increase in CO₂ has facilitating effects on growth rates of both native and invasive grasses that are eaten by wildlife (Eddleman & McLean, 1969; Hobbs et al., 1981; Johnson, 1962; Stubbendieck & Hatch, 1997; Vallentine, 1961). This suggests that CO₂ enrichment has already increased grassland forage production and the capacity of YNP to support grazing ungulates compared to preindustrial times. However, anthropogenic CO₂ emissions have also caused regional warming and increased aridity on rangelands occupied by Yellowstone ungulates (Thoma et al., 2015), which may constrain the stimulatory effects of rising CO₂ on forage production. The interactive effects of CO₂ enrichment and warming on native and invasive grasses are largely unknown and may vary between mesic and dry grasslands where grasses face different abiotic conditions and grazing intensities (Frank et al., 2016).

Invasive species, particularly grasses, dominate the Lamar Valley and other mesic grassland plant communities (Geremia et al., 2019) throughout Yellowstone's Northern Range. Some of those invasive species, *B. inermis*, *T. repens*, and *P. pratense*, were planted for forage in the early and mid-1900s. The other invasive species have spread into the park, reflecting their range

expansions throughout the northern Rocky Mountain region. Mesic grasslands throughout much of YNP experience intense and chronic grazing (Frank et al., 2018; Geremia et al., 2019). Results from the field defoliation experiment revealed a spectrum of positive to negative responses to clipping, which, reported elsewhere (Penner & Frank, 2021), resulted in a net increase in shoot production during June. A subset of four or five invasive species shown to be important forages for wildlife (Hansen et al., 1990; Hobbs et al., 1981; Stubbendieck & Hatch, 1997) were stimulated the most among all species in both June and July, although several of those positive responses were nonsignificant trends. These results confirmed our prediction that regrowth after defoliation would be greater for nonnative compared to native species. Previously, grazers were shown to increase annual shoot production in YNP, particularly in mesic grasslands (Frank et al., 2016, 2018). The rates of regrowth of mesic community species after clipping in this study (Figure 4) suggests that the facilitating effects of grazing on mesic grassland production is primarily due to the overcompensating response of some of the invasive species to defoliation, which is a function of clipping stimulating their relative growth rates (Penner & Frank, 2021). Invasive plants generally have higher concentrations of important dietary minerals for ungulate grazers (e.g., nitrogen, phosphorus) compared to native plants (Zhang et al., 2022). Thus, the greater growth response of invasive plants to defoliation is an additional pathway by which invasive plants likely have enhanced forage supply and quality for herbivores.

The large migratory herds of Yellowstone ungulates are an attraction for the millions of annual visitors to YNP. The capacity of the YNP ecosystem to sustain its herds of ungulates is a function of the soil and plant processes that deliver sufficient forage to support its abundant ungulate community. Prior to the Industrial Revolution, the temporal variation in those processes and the production of forage largely ebbed and flowed according to the vagaries of fluctuating climatic conditions. However, temperatures in YNP have warmed and are expected to continue to warm (Thoma et al., 2015), which should result in increasing aridity. The interactive effects of elevated CO₂ and warming on plant production are complex and will likely change over time. Such multifaceted and changing environmental conditions highlight why the NPS aspiration of preserving vignettes of pre-European America (Leopold et al., 1963) is impossible under present and continually changing environmental conditions and why managing to conserve critical ecological processes has been recommended recently (Beissinger & Ackerly, 2017; Colwell et al., 2012). The difficult challenges facing global change biologists and park managers are to, first,

understand how the combination of global change factors, some operating in opposing ways, will influence forage dynamics and, second, utilize that knowledge to develop policies to sustain Yellowstone's iconic herds of ungulates in the Anthropocene.

AUTHOR CONTRIBUTIONS

Jason Fridley helped with statistical analyses. Douglas A. Frank helped design the experiments, analyze the data, and draft the manuscript. Katie M. Becklin helped design the growth chamber experiment, analyze data, and draft the manuscript. Jacob F. Penner conducted the field experiment and commented on the manuscript. K. Alice Lindsay conducted the growth chamber experiment and helped draft the manuscript. Chris J. Geremia assisted with seed collection in YNP for the growth chamber experiment, assisted in the field experiment, and commented on the manuscript.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (Frank et al., 2022) are available in Dryad at <https://doi.org/10.5061/dryad.br15dvcd>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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