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Climate Change Impacts on Introduced Grass Invasion in the Prairie Pothole Region of the United States Great Plains

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Abstract – The Prairie Potholes Region of the northern Great Plains is under threat from the combined effects of introduced perennial grasses and climate change, which are driving plant community shifts and biodiversity loss. We synthesized current knowledge on how climate change drivers (i.e., precipitation variability, elevated atmospheric CO_2, and warming) and other local and regional biotic and abiotic factors, like soil nutrients and community diversity, impact grassland vegetation through their effects on Smooth Brome and Kentucky Bluegrass. Based on this synthesis, we provide a qualitative assessment of potential responses of Smooth Brome and Kentucky Bluegrass to different scenarios of seasonal water availability, warming climate, and elevated atmospheric CO_2 to inform future grassland management.

Introduction

The Prairie Pothole Region (PPR) occurs in the northern portion of the North American Great Plains and spans portions of Minnesota, North Dakota, South Dakota, Montana, Manitoba, Saskatchewan, and Alberta—encompassing approximately 700,000 km^2. Abundant ephemeral wetlands interspersed with grasslands define this landscape. The region spans a gradient of tallgrass prairie in the east to mixed grass prairie in the west. These grasslands are dominated by a combination of native C4 (e.g., *Andropogon gerardii* Vitman (Big Bluestem), *Schizachyrium scoparium* (Michx.) Nash. (Little Bluestem), *Bouteloua* spp. (grama grasses), etc.) and C3 (e.g., *Hesperostipa* spp. (needle grasses), *Nassella viridula* (Trin.) Barkworth (Green Needle Grass), *Pascopyrum smithii* P.A. Love (Western Wheatgrass), etc.) grasses with forbs (many in the Asteraceae and Fabaceae families) contributing to high species richness (Barker and Whitman 1988). These landscapes provide diverse ecosystem services of critical importance for local communities: carbon sequestration, nutrient cycling, wildlife habitat, and, in particular, forage production to graze cattle. This portion of the Great Plains has been drastically altered, with a majority of the landscape converted to croplands (Zhang et al. 2021) and remaining prairies highly invaded by introduced perennial grasses and noxious forbs (Grant et al. 2009). While native C4 grasses are the dominant functional group in tallgrass and mixed-grass prairies, Smooth Brome and Kentucky Bluegrass constitute the greatest proportion of C3 grasses within US Fish and Wildlife Service lands in the PPR (Grant et al. 2020a., Toledo et al. 2014).

The proliferation of introduced perennial grasses, namely *Bromus inermis* Leyss (Smooth Brome) and *Poa pratensis* L. (Kentucky Bluegrass) has severely reduced the plant diversity of the PPR (Jones et al. 2023). Both species were intentionally seeded in the United States from the Eurasian Steppe to provide forage for cattle and ensure soil stability, and their pro-

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liferation is facilitated by anthropogenic nitrogen enrichment (Dornbusch et al. 2018). While the negative effects of these species on the PPR have been widely acknowledged (Grant et al. 2009), they continue to be seeded in many parts of the country. The prolific vegetative and seed-based reproduction of these species enables them to spread rapidly. Smooth Brome homogenizes grassland communities by altering resources (e.g., soil nitrogen, soil moisture, light) and reducing local plant diversity (Hautier et al. 2018, Stotz et al. 2019). Additionally, Smooth Brome's ability to spread extensively via rhizomes enables it to invade under stressful conditions due to clonal integration (tillers/ramets in high-nutrient areas can transfer resources to tillers/ramets experiencing nutrient stress). Kentucky Bluegrass, a sod forming grass with similar homogenizing capacity, alters ecosystem processes like soil hydrology by forming dense litter layers, and has cascading effects across taxa (i.e., pollinators; Gasch et al. 2020). Introduced grasses—including Smooth Brome and Kentucky Bluegrass—tend to grow denser, taller, and earlier in the season (Molinari and D'Antonio 2014), facilitating their dominance over native vegetation under a variety of conditions. The persistence and future spread of these introduced grasses will depend strongly on climate change, with changes in precipitation, temperature, and carbon dioxide (CO_2) shaping competitive interactions between native and invasive grassland species in the PPR.

Highly variable temperature and precipitation are defining characteristics of the Great Plains climate (Barker and Whitman 1988, Ojima et al. 2021). Interannual climate variability is a critical driver of variation in the ecosystem functions—like productivity—of grasslands (Fay et al. 2011). This climate variability manifests within a single year as seasonal variation in temperature and precipitation (e.g., wet spring followed by dry summer) and interannually as variation in year-to-year changes in temperature and precipitation (e.g., dry spring in 2022 followed by a wet spring in 2023). This variability in climate makes predicting ecosystem responses (in terms of structure, composition, and function) particularly challenging. The PPR has a characteristic west to east, xeric to mesic gradient. Under current climate change, this gradient is becoming steeper (Millett et al. 2009). Current trends in the PPR indicate an overall trend of warming and wetting (Fig. 1; significant increases in precipitation, particularly in the mesic eastern portion; Easterling et al. 2017, Garbrecht et al. 2004) accompanied by increased variability.

Smooth Brome and Kentucky Bluegrass respond positively to soil moisture availability during the spring growing season (Printz and Hendrickson 2015). While the region is experiencing warming throughout the year, the winter has experienced the greatest increase in temperature compared to the growing season in recent decades (Vose et al. 2017). Continued winter warming would likely result in reductions in persistent snow cover, with consequences for hydrology and soil moisture availability during the following growing season. This effect on soil moisture is compounded by increased variation in precipitation in spring and fall compared to historical patterns. Variation in fall/winter and spring precipitation influence soil moisture during the subsequent growing season, with important implications for the spread of Smooth Brome and Kentucky Bluegrass.

Although a long-term trend toward increased precipitation in recent decades is part of the natural variability of this region (Ojima et al. 2021), there is uncertainty in how the combined effects of future increases in precipitation, temperature, and CO_2 will influence moisture availability throughout the growing season. In addition, interannual and interdecadal climatic variability makes predicting drought risk and severity more difficult depending on parameters included—which have their own complicated relationships with climate and vegetation (Cook et al. 2015, Feng et al. 2017). The Great Plains, particularly the PPR, has experienced extreme droughts and flooding on a decadal basis over the 20th

century (Conant et al. 2018). Increasing climatic variation in an already variable climate poses a significant challenge for researchers and land managers interested in predicating future climate and ecological dynamics of the PPR. Specifically, anticipating how 2 dominant introduced grasses will respond to this changing variation in their specific ecological contexts is a major barrier to grassland conservation in the PPR.

This synthesis was conducted to integrate current understanding of introduced perennial grass responses to climate change with research on potential mechanisms driving their proliferation, in order to better inform management of the PPR. In the following sections, we discuss the potential influence of warming temperatures, elevated atmospheric CO_2, precipitation seasonality and variability, and interactions of the above on these 2 species. While explicit research on mechanisms of proliferation and responses to climate change in Smooth Brome and Kentucky Bluegrass has increased in recent decades, this synthesis draws on the wealth of research on varying responses between C3 and C4 grasses to climate change to further inform our discussion. For a breakdown of C3 and C4 grass similarities and differences, see Table 1. We integrate this information to qualitatively assess potential

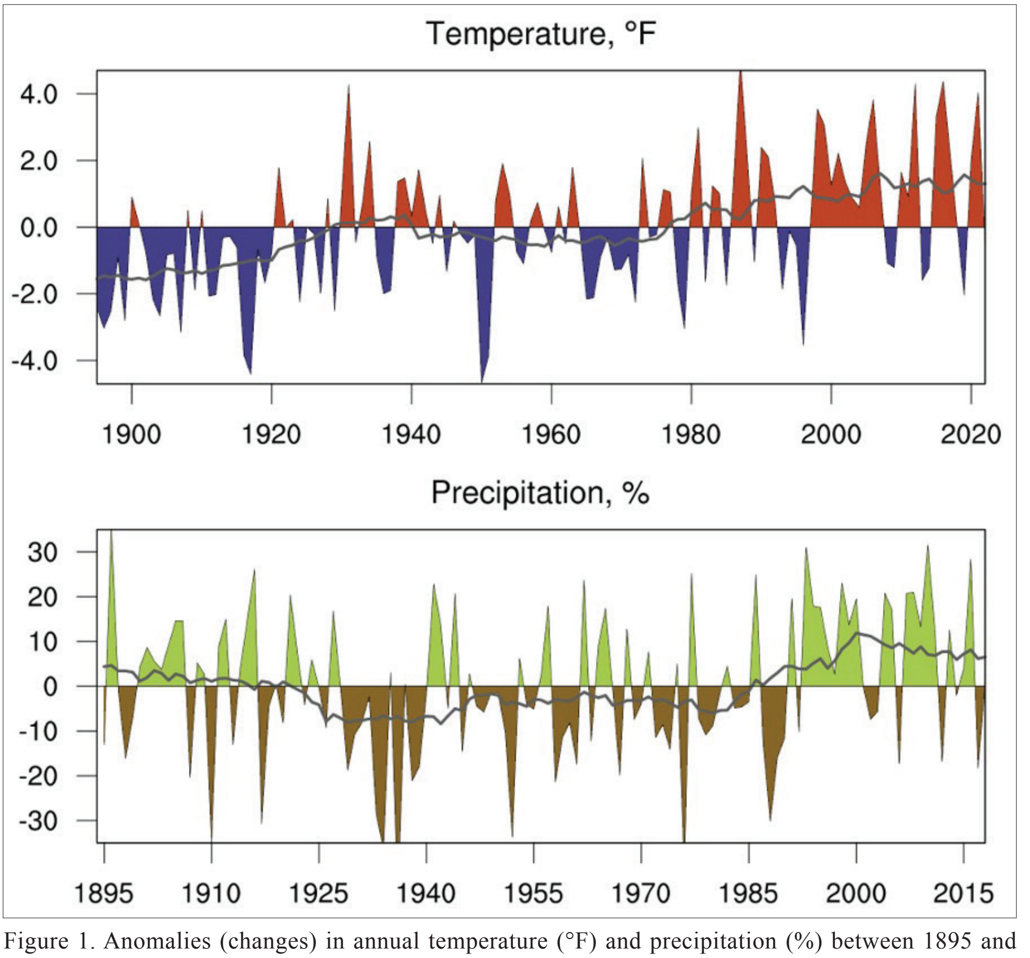

Figure 1. Anomalies (changes) in annual temperature (°F) and precipitation (%) between 1895 and 2022 for the PPR (45–49°N, 97–99.5°W) relative to the 20th century mean. The gray trendline is a 20-year running mean. The temperature and precipitation have increased by 2°F and 10%, respectively, in recent decades. Data Source: NOAA NCEI nclimgrid

responses of Smooth Brome and Kentucky Bluegrass to different scenarios of seasonal water availability, a warming climate, and elevated atmospheric CO_2.

Precipitation Seasonality and Variation

Fluctuations in precipitation are the dominant driver of grassland processes such as productivity, with other climate change drivers—namely increased temperatures and elevated CO_2 (see below)—having a secondary impact (Mueller et al. 2016). Warming temperature and elevated CO_2 become key ecological drivers under drought conditions, where elevated CO_2 differentially affects C3 and C4 species. In the tallgrass and mixed-grass prairies of the PPR, C3 versus C4 responses to these climatic changes could shift community dynamics to favor introduced perennial C3 grasses over native perennial C4 grasses (see *Elevated CO_2 and Warming Temperatures* below for greater detail). In addition to interacting with increased temperatures and CO_2 levels, precipitation indirectly impacts plant communities through its influence on soil moisture and nitrogen availability (Carrillo et al. 2012, Mueller et al. 2016).

The effects of precipitation seasonality and interannual variation also differ across the region, tracking the east to west, mesic to xeric gradient. The more xeric, mixed-grass prairie side of the PPR will likely be more sensitive to change. Drier grasslands tend to be more responsive to variable precipitation, resulting in greater species turnover and compositional changes compared to mesic grasslands (Cleland et al. 2013). This susceptibility to turnover may enable Smooth Brome and Kentucky Bluegrass to invade regions where dry climates have historically limited their abundances (Grant et al. 2020a).

The earlier emergence of Smooth Brome and Kentucky Bluegrass compared to many native (warm season) species results in unique species and season-specific changes in cover following changes in precipitation. Compared to historical patterns, increased precipitation during the spring and fall will likely impact the prevalence of Smooth Brome and Kentucky Bluegrass and benefit C3 over C4 species due to C3 grass' earlier phenology and green-up. Both Smooth Brome and Kentucky Bluegrass respond positively to increased precipitation (Grant et al. 2020a, Stotz et al. 2019), driven by their earlier phenologies (Printz and Hendrickson 2015). In addition to their expected positive response to increases in precipitation, introduced grasses tend to be especially resilient to stressful environmental conditions in

Table 1. Description of generalized characteristics of C3 and C4 grasses, the 2 dominant functional groups in the PPR and the Great Plains broadly. Coarse characterizations of phenology and climate tolerance are included to inform our prediction for introduced perennial grasses responses to climate change (Millett et al. 2009). However, we note that this table does not capture the full range of variability among functional groups, nor the effects of climate change on phenology (e.g., through extended growing seasons). Tolerance implies sustained photosynthetic activity and carbon assimilation under various climate conditions.

Photosynthetic Pathway	Seasonality	Phenology	Climate Tolerance	Common Species in the PPR
C3	Cool season	Emerge: Mar-Apr Flower: May-Jun Senesce: Jul	- Sensitive to high temperatures - Cold tolerant - Most responsive to elevated CO_2	Kentucky Bluegrass Smooth Brome Green Needlegrass Needle-and-thread Western Wheatgrass
C4	Warm season	Emerge: Apr-May Flower: Jul-Aug Senesce: Sep-Oct	- Drought tolerant - Heat tolerant	Big Bluestem Little Bluestem Side-oat Grama

terms of biomass production (Duell et al. 2016). This resilience is driven by senescence or reduced growth in C3 grasses during warm, dry summer months, enabling them to persist through summer drought.

There have been mixed responses of introduced grasses to increasingly hot and dry summers. For example, Kentucky Bluegrass is particularly drought tolerant in the PPR, despite turf grasses typically being more susceptible to drought than other grass growth forms (Printz and Hendrickson 2015). However, to limit water stress driven by elevated evapotranspiration during hot and dry conditions, C3 grasses generally tend to reduce their stomatal conductance and consequently carbon assimilation (Taylor et al. 2014); this results in reduced growth, which may limit Smooth Brome and Kentucky Bluegrass spread. In addition to limits on growth, summer droughts may limit the recruitment of new individuals of Smooth Brome and Kentucky Bluegrass. Without adequate soil moisture, Smooth Brome seedlings have reduced survival and growth (Carrigy et al. 2016). While recruitment of new individuals may be lower during summer droughts, clonal integration may enable Smooth Brome to persist or even spread during droughts (Otfinowski and Kenkel 2008). Clonal integration is a process whereby Smooth Brome transfers resources from individual ramets (single tillers or clusters of tillers linked belowground to genetically identical ramets) in more resource rich environments (e.g., microsites with greater soil moisture) to new ramets in more stressful environments (e.g., microsites with lower soil moisture).

Climate change, along with the prevalence of Smooth Brome and Kentucky Bluegrass, could have synergistic negative effects on the regions' hydrology and native vegetation. For example, Kentucky Bluegrass reduces water infiltration (Printz and Hendrickson 2015) which could compound reduced water availability because of changing precipitation patterns. Depending on fall precipitation, winter snowpack, and snowmelt timing, Kentucky Bluegrass could have a significant effect on soil moisture availability. In many areas of the PPR, Kentucky Bluegrass is the dominant species, potentially altering local hydrology with consequences for soil-water dynamics and native vegetation (Nuowakpo et al. 2019). Smooth Brome impacts the community in unique ways compared to Kentucky Bluegrass—the former directly alters ecosystems it invades while also indirectly affecting them through its impact on native vegetation. In the PPR, Smooth Brome was not found to reduce soil moisture, but it did limit light penetration to understory vegetation and the soil likely due to its greater leaf area compared to Kentucky Bluegrass (Stotz et al. 2019; J. Laron, University of Washington, Seattle, WA, 2016 unpubl. data). In addition, Smooth Brome homogenized PPR grassland plant communities by reducing native cover and altering soil resource availability (Stotz et al. 2017). We need to account for the synergistic effects of climate change with introduced grasses on the native communities of the PPR to increase conservation and restoration success.

The response of native vegetation to climate change will also determine the success of perennial grass invaders. For example, the encroachment of native shrubs in the PPR, facilitated by reduced fire management (Dixon et al. 2019, Murphy and Grant 2005), has resulted in grass invasion (Grant et al. 2020b). The effects of climate change on native vegetation, particularly C4 grasses, also has implications for the PPR's ability to withstand invasion. C4 grasses are adept at taking advantage of warm and wet conditions to compete against C3 grasses (Hoeppner and Dukes 2012). However, these C4 species are most active during the warm summer months, when water availability is generally projected to decrease, although plant responses to this expected drying remain uncertain. Ultimately, the seasonality of changes in water availability determines which guild of grasses (C3 or C4) benefits most.

Elevated CO_2 and Warming Temperatures

While changes in the amount and timing of precipitation have a dominant effect on PPR plant community dynamics (Mueller et al. 2016), elevated CO_2 and warming temperatures also affect the proliferation of introduced perennial grasses. We draw inference from research on the effects of warming and CO_2 in grasslands beyond the PPR, resulting in a broad research base for this synthesis. In grassland systems, elevated CO_2 and increasing temperatures (especially during the growing season) generally increase overall plant biomass for most species and accelerate soil respiration, with CO_2 having a greater effect on productivity than increases in temperature do (Dieleman et al. 2012). Warming can ameliorate the progressive nitrogen limitation that is associated with elevated CO_2 conditions. The 2 drivers result in varying plant response: elevated CO_2 stimulates root elongation to offset associated nutrient limitation, while warming reduces root growth by facilitating nutrient availability via increased nitrogen mineralization (Carrillo et al. 2012, Dieleman et al. 2012). Increased temperature, associated with reduced water availability, has mixed effects on grasses (particularly for C3 over C4) due to differing physiological drivers limiting carbon assimilation (Sage and Kubien 2007). Dry and hot conditions have also been observed to suppress total production, shoot production, and species richness of grassland communities (Hoeppner and Dukes 2012). Determining how introduced perennial grasses and native plants will respond to elevated CO_2 and warmer temperatures requires teasing apart the ecological and physiological drivers of their growth and spread.

With increasing temperatures, rates of which have been particularly high during the cold winter months and early spring in recent decades (Vose et al. 2017), the length of the growing season is expected to increase. Early start of the growing season has the potential to increase the prevalence of Smooth Brome and Kentucky Bluegrass, since both are C3 (cool-season) grasses that become active early in the season. Smooth Brome also has increased survival and growth under warmer conditions (Grant et al. 2020b, Stotz et al. 2017), a process which may become more common during spring tiller elongation under elevated warming. Under future increases in temperature, there is greater potential for false springs (seasonal warming followed by cold snaps; Ault et al. 2013), which could harm Smooth Brome and Kentucky Bluegrass, since they are most apt to take advantage of warmer springs and emerge early. However, Smooth Brome is a cold tolerant species (Palit and DeKeyser 2022), and therefore may be able to withstand cold snaps. Additionally, extended fall seasons have the potential to support a second growth period for cool-season perennial grasses.

The effects of elevated CO_2 on introduced perennial grasses are moderated by other climate change drivers in the PPR. Warming and elevated CO_2 have mixed effects on plant-available nitrogen (Carrillo et al. 2012). Elevated CO_2 is speculated to favor C3 species (Smooth Brome and Kentucky Bluegrass) over C4 grasses (Ehleringer and Björkman 1977, Ehleringer et al. 1997, Sage and Kubien 2007). However, elevated atmospheric CO_2 levels over time can decrease nitrogen mineralization rates and benefit C4-dominated grassland patches over those dominated by C3 species (Reich and Hobbie 2013, Reich et al. 2018). The mechanisms driving this inverse relationship between nitrogen availability and C3/C4 dominance remain poorly understood. The high nitrogen content of Smooth Brome litter may ameliorate nitrogen limitation (Palit and DeKeyser 2022) and enable Smooth Brome—and potentially other C3 grasses—to outcompete C4 grasses under elevated CO_2. Further, elevated CO_2-induced increases in soil moisture, resulting from greater plant water use efficiency, are important for sustaining elevated plant productivity, nitrogen uptake, and nitrogen cycling (Dijkstra et al. 2010). Based on both short term (1–3 years) and long term (>20 years) experiments, the effects of elevated CO_2 and increased temperatures interact in complicated ways with other abiotic drivers of plant growth (Reich et al. 2018).

The differing effects of CO_2 and temperature on grasslands affect dominance and tradeoffs between C3 and C4 gasses; particularly relevant in the PPR where there is a transition from tallgrass (dominated by C4) to mixed grass (co-dominance between C3 and C4), and, to the west of the PPR, shortgrass (a system not explored further here). Both C3 and C4 grasses have higher carbon assimilation under elevated CO_2 conditions, though physiologically they respond differently (i.e., C3 increases tiller densities while C4 increases leaf area; Wand et al. 1999). While the short-term positive effects of elevated CO_2 on C3 growth might imply a long-term advantage of C3 grasses over C4 grasses with increasing carbon emissions, this benefit will be mediated by nitrogen availability. The rapid increase in CO_2 since the Industrial Revolution might have been expected to result in a range expansion of mixed-grass C3/C4 grasslands and range contraction of tallgrass C4 grasslands, but no such pattern has been observed in the past 300 years, suggesting that the spatial distribution of these grassland types has been stable under historical environmental variation (Griffith et al. 2017). Important uncertainties remain that attest to the need for long-term studies on the effects of climate change drivers on grassland communities (see *Research Needs* below) and the oscillating effects of elevated CO_2 depending on other system-and site-specific limiting factors (e.g., soil nitrogen; Reich and Hobbie 2013, Reich et al. 2018).

The effects of increased temperature and elevated CO_2 on native vegetation depends on the invasion state. Warming and species diversity (which is higher in sites with lower invasion rates and cover; Stotz et al. 2017) both have positive effects on net primary productivity. Slow-growing plants, which likely constitute many long-lived native perennials in this region, have stronger responses to elevated CO_2 than faster, more acquisitive species (e.g., Smooth Brome and Kentucky Bluegrass; Ali et al. 2013). The stronger response may enable established, native species to offset the negative effects of projected aridification in summer. However, juvenile introduced grasses may also take advantage of increased CO_2 to overcome the drought-induced survival bottleneck between seedling and established, mature plants (Carrigy et al. 2016).

Interactive Effects of Climate Change Drivers

The response of introduced grasses and native vegetation to climate change is often driven by the interaction of 1 or 2 climate change drivers. Here, we briefly explore some examples of the ways climate change drivers interact to affect grassland vegetation in the PPR. The negative effects of drought (spring, summer, or fall) may be offset by plant physiological responses to elevated CO_2 (Mankin et al. 2017). Increased water availability because of elevated CO_2 enables plants to uptake carbon without losing as much water to evapotranspiration, although recent evidence suggests that elevated atmospheric aridity may offset these gains in water use efficiency at a global scale (Li et al. 2023). Further, plant diversity interacts with nitrogen availability, CO_2, temperature, and precipitation. Increased nitrogen availability from atmospheric deposition and introduced legumes like *Melilotus officinalis* (L.) Lam. (Yellow Sweet Clover) can reduce the ability of native plants to compete with introduced grasses like Kentucky Bluegrass leading to reduced plant diversity (Dornbusch et al. 2018, Lesica and DeLuca 2000, Palit et al. 2021). Once established, low diversity grasslands with reduced structural complexity are less resilient to climate change and elevated CO_2 compared to more diverse communities with greater potential for species turnover. Smooth Brome and Kentucky Bluegrass may thus be less impacted by climate change compared with native communities (Cantarel et al. 2013, Duell et al. 2016). One driver of resilience in native-dominated communities could be the increased cover of C4 grasses under warm and wet conditions during the late growing season when they are most active (Hoeppner and Dukes 2012). The interruption by periodic extreme drought will have very different effects on grassland vegetation in the PPR depending on seasonality and other local abiotic factors.

Here we explore how introduced grasses could respond to the seasonality of drought under a general regional wetting trend (Table 2). While much of the western United States is experiencing increased intensity and duration of drought (Williams et al. 2020), the PPR is experiencing increased precipitation in the majority of the region. However, because climate change is expected to amplify the Great Plains' climatic variability, this wetting is projected to be disrupted by periods of extreme drought, which may intensify in the future with increased temperatures (Cook et al. 2020). The seasonal timing of these droughts is likely to have significant impacts on local vegetation, particularly the prevalence of introduced perennial grasses and the ability of native vegetation to withstand invasion. We propose 3 drought scenarios: below-average early season "holdover" soil moisture (due to fall/winter drought or early snowmelt), spring drought, and summer drought. We also consider the scenario of above-average moisture in summer, which affects the senescence timing of cool-season grasses. Each scenario is detailed in Table 2 with respective impacts on soil moisture and introduced perennial grass.

Suggested Management Actions

The grasslands of this region are working landscapes (Dixon et al. 2019), and the sustainable use of these prairies depends on the ability to take appropriate management actions

Table 2. Scenarios of above- and below- average seasonal precipitation in the context of long-term climate change, and their effects on seasonal soil moisture variation and introduced perennial cool-season grasses. The Prairie Pothole Region is expected to experience warming, elevated atmospheric CO_2 levels, and an overall increase in precipitation, though these increases in precipitation are likely to be interrupted by periodic droughts that may occur within different seasons resulting in unique effects on the abiotic and biotic environment.

Regional Climate Trends	Seasonal Climate/ Weather Scenario	Effect on Soil Moisture	Predicted Effect on Introduced Grasses
Increased temperature; elevated CO_2; overall increase in precipitation (highly variable)	Drought: fall/winter	Initially deficient in early spring	Slows spring emergence
	Drought: spring	Diminishes quicker following soil thaw without additional input from spring precipitation	Slows late spring and early summer growth and flowering
	Drought: summer	Steady reduction over the course of the season; decline exaggerated by warming summer temperatures	Smaller effect due to early phenology of introduced C3 species
	Above-average precipitation: summer	Maintains higher-than usual soil moisture; could be counteracted by increased evapotranspiration under warmer temperatures	Delays warm-season senescence

under highly variable climate conditions—no small task in a system where variation is the name of the game. The amount and timing of precipitation determine the effectiveness of grazing as a management tool (Hendrickson et al. 2020). Periods of long-term rest, when there is no burning or grazing, enable introduced perennial grasses to increase in abundance (Grant et al. 2020b). This potential invasion provides motivation to develop multi-action management plans that limit the opportunity for invasive grasses to increase in abundance or spread to new sites. Early spring grazing is commonly used to reduce the cover of Kentucky Bluegrass and Smooth Brome, which emerge especially early in the growing season (Hendrickson et al. 2020). However, the effectiveness of spring grazing is dependent on precipitation and additional management actions. Periodic burning can remove nitrogen through volatilization (Palit et al. 2021)—potentially limiting invasive grass spread—and grazers prefer recently burned grasslands (Allred et al. 2011). The greatest impact on invasive grasses may come from a fall burn followed by targeted grazing early the following spring. This management tactic could also be leveraged with drought timing. Following fall droughts with targeted spring grazing could reduce the cover of Smooth Brome and/or Kentucky Bluegrass (which might have reduced reserves to support regeneration because of the dry fall; Bam et al. 2022), but further study is needed to establish the efficacy of this tactic.

Research Needs

Teasing apart the interactive effects of climate change and elevated atmospheric CO_2 on the spread of introduced perennial grasses is a challenging task. While experimental, observational, and modeling work has led to useful insights into the dynamics of Smooth Brome and Kentucky Bluegrass, which pose the greatest threat to the PPR, many unknowns remain. Long-term studies on the effect of climate change on introduced grass invasions are needed because short-term studies are limited in their ability to predict long-term population, community, and ecosystem dynamics. The effects of climate change in the long term are likely also dependent on biogeochemical processes (e.g., nitrogen cycling) that operate on various spatial and temporal scales to determine community composition. When we fail to account for these factors, we may incorrectly predict or model long term community responses to climate change (Reich et al. 2018). In addition, lag effects of invasion decrease our ability to predict community and species level responses to climate change in the PPR (Crooks 2005). For example, particularly wet seasons may provide Smooth Brome and Kentucky Bluegrass with boosted resiliency that may last multiple years. Lags in population and community responses to variation in the amount and timing of precipitation are challenging to execute in experiments or capture in observational studies.

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Literature Cited

Ali, A.A., B.E. Medlyn, K.Y. Crous, and P.B. Reich. 2013. A trait-based ecosystem model suggests that long-term responsiveness to rising atmospheric CO_2 concentration is greater in slow-growing than fast-growing plants. Functional Ecology 27:1011–1022.

Allred, B.W., S.D. Fuhlendorf, D.M. Engle, and R.D. Elmore. 2011. Ungulate preference for burned patches reveals strength of fire–grazing interaction. Ecology and Evolution 1:132–144.

Ault, T.R., G.M. Henebry, K.M. de Beurs, M.D. Schwartz, J.L. Betancourt, and D. Moore. 2013. The false spring of 2012, earliest in North American record. Eos, Transactions American Geophysical Union 94:181–182.

Bam, S., J.P. Ott, J.L. Butler, and L. Xu. 2022. Belowground mechanism reveals climate change impacts on invasive clonal plant establishment. Scientific Reports 12:2860.

Barker, W., and W. Whitman. 1988. Vegetation of the Northern Great Plains. Rangelands 10:266–272.

Cantarel, A.A.M., J.M.G. Bloor, and J.-F. Soussana. 2013. Four years of simulated climate change reduces above-ground productivity and alters functional diversity in a grassland ecosystem. Journal of Vegetation Science 24:113–126.

Carrigy, A.A., G.C. Stotz, M.A. Dettlaff, G.J. Pec, Inderjit, N. Erbilgin, and J.F. Cahill. 2016. Community-level determinants of Smooth Brome (Bromus inermis) growth and survival in the aspen parkland. Plant Ecology 217:1395–1413.

Carrillo, Y., F.A. Dijkstra, E. Pendall, J.A. Morgan, and D.M. Blumenthal. 2012. Controls over soil nitrogen pools in a semiarid grassland under elevated CO_2 and warming. Ecosystems 15:761–774.

Cleland, E.E., S.L. Collins, T.L. Dickson, E.C. Farrer, K.L. Gross, L.A. Gherardi, L.M. Hallett, R.J. Hobbs, J.S. Hsu, L. Turnbull, and K.N. Suding. 2013. Sensitivity of grassland plant community composition to spatial vs. temporal variation in precipitation. Ecology 94:1687–1696.

Conant, R. T., D. Kluck, M. T. Anderson, A. Badger, B. M. Boustead, J. D. Derner, L. Farris, M. Hayes, B. Livneh, S. McNeeley, D. Peck, M. Shulski, and V. Small. 2018. Northern Great Plains. U.S. Global Change Research Program Impacts, Risks, and Adaptation in the United States: Fourth National Climate Assessment, Volume II. Pp 941–986.

Cook, B.I., T.R. Ault, and J.E. Smerdon. 2015. Unprecedented 21st century drought risk in the American Southwest and Central Plains. Science Advances 1:e1400082.

Cook, B.I., J.S. Mankin, K. Marvel, A.P. Williams, J.E. Smerdon, and K.J. Anchukaitis. 2020. Twenty-first century drought projections in the CMIP6 forcing scenarios. Earth's Future 8:e2019EF001461.

Crooks, J.A. 2005. Lag times and exotic species: The ecology and management of biological invasions in slow-motion. Écoscience 12:316–329.

Dieleman, W.I.J., S. Vicca, F.A. Dijkstra, F. Hagedorn, M.J. Hovenden, K.S. Larsen, J.A. Morgan, A. Volder, C. Beier, J.S. Dukes, J. King, S. Leuzinger, S. Linder, Y. Luo, R. Oren, P. De Angelis, D. Tingey, M.R. Hoosbeek, and I.A. Janssens. 2012. Simple additive effects are rare: A quantitative review of plant biomass and soil process responses to combined manipulations of CO_2 and temperature. Global Change Biology 18:2681–2693.

Dijkstra, F.A., D. Blumenthal, J.A. Morgan, D.R. LeCain, and R.F. Follett. 2010. Elevated CO_2 effects on semi-arid grassland plants in relation to water availability and competition. Functional Ecology 24:1152–1161.

Dixon, C., S. Vacek, and T. Grant. 2019. Evolving management paradigms on U.S. Fish and Wildlife Service lands in the Prairie Pothole Region. Rangelands 41:36–43.

Dornbusch, M.J., R.F. Limb, and C.K. Gasch. 2018. Facilitation of an exotic grass through nitrogen enrichment by an exotic legume. Rangeland Ecology & Management 71:691–694.

Duell, E.B., G.W.T. Wilson, and K. R. Hickman. 2016. Above- and below-ground responses of native and invasive prairie grasses to future climate scenarios. Botany 94:471–479.

Easterling, D. R., J. R. Arnold, T. Knutson, K. E. Kunkel, A. N. LeGrande, L. R. Leung, R. S. Vose, D. E. Waliser, and M. F. Wehner. 2017. Precipitation change in the United States. U.S. Global Change Research Program Climate Science Special Report: Fourth National Climate Assessment, Volume I. Washington D.C. Pp. 207–230.

Ehleringer, J., and O. Björkman. 1977. Quantum yields for CO_2 uptake in C_3 and C_4 plants: Dependence on temperature, CO_2, and O_2 concentration. Plant Physiology 59:86–90.

Ehleringer, J.R., T.E. Cerling, and B.R. Helliker. 1997. C4 photosynthesis, atmospheric CO_2, and climate. Oecologia 112:285–299.

Fay, P.A., J.M. Blair, M.D. Smith, J.B. Nippert, J.D. Carlisle, and A.K. Knapp. 2011. Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. Biogeosciences 8:3053–3068.

Feng, S., M. Trnka, M. Hayes, and Y. Zhang. 2017. Why do different drought indices show distinct future drought risk outcomes in the U.S. Great Plains? Journal of Climate 30:265–278.

Garbrecht, J., M. Van Liew, and G.O. Brown. 2004. Trends in precipitation, streamflow, and evapotranspiration in the Great Plains of the United States. Journal of Hydrologic Engineering 9:360–367.

Gasch, C.K., D. Toledo, K. Kral-O'Brien, C. Baldwin, C. Bendel, W. Fick, L. Gerhard, J. Harmon, J. Hendrickson, T. Hovick, M. Lakey, D. McGranahan, S. Kossi Nouwakpo, and K. Sedivec. 2020. Kentucky bluegrass invaded rangeland: Ecosystem implications and adaptive management approaches. Rangelands 42(4):106–116.

Grant, T.A., B. Flanders-Wanner, T.L. Shaffer, R.K. Murphy, and G.A. Knutsen. 2009. An emerging crisis across northern prairie refuges: Prevalence of invasive plants and a plan for adaptive management. Ecological Restoration 27:58–65.

Grant, T.A., T.L. Shaffer, and B. Flanders. 2020a. Patterns of Smooth Brome, Kentucky Bluegrass, and shrub invasion in the northern Great Plains vary with temperature and precipitation. Natural Areas Journal 40:11–22.

Grant, T.A., T.L. Shaffer, and B. Flanders. 2020b. Resiliency of native prairies to invasion by Kentucky Bluegrass, Smooth Brome, and woody vegetation. Rangeland Ecology & Management 73:321–328.

Griffith, D.M., J.M. Cotton, R.L. Powell, N.D. Sheldon, and C.J. Still. 2017. Multi-century stasis in C3 and C4 grass distributions across the contiguous United States since the industrial revolution. Journal of Biogeography 44:2564–2574.

Hautier, Y., F. Isbell, E.T. Borer, E.W. Seabloom, W.S. Harpole, E.M. Lind, A.S. MacDougall, C.J. Stevens, P.B. Adler, J. Alberti, J.D. Bakker, L.A. Brudvig, Y.M. Buckley, M. Cadotte, M.C. Caldeira, E.J. Chaneton, C. Chu, P. Daleo, C.R. Dickman, J.M. Dwyer, A. Eskelinen, P.A. Fay, J. Firn, N. Hagenah, H. Hillebrand, O. Iribarne, K.P. Kirkman, J.M.H. Knops, K.J. La Pierre, R.L. McCulley, J.W. Morgan, M. Pärtel, J. Pascual, J.N. Price, S.M. Prober, A.C. Risch, M. Sankaran, M. Schuetz, R.J. Standish, R. Virtanen, G.M. Wardle, L. Yahdjian, and A. Hector. 2018. Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. Nature Ecology & Evolution 2:50–56.

Hendrickson, J.R., S.L. Kronberg, and E.J. Scholljegerdes. 2020. Can targeted grazing reduce abundance of invasive perennial grass (Kentucky Bluegrass) on native mixed-grass prairie? Rangeland Ecology and Management 73:547–551.

Hoeppner, S.S., and J.S. Dukes. 2012. Interactive responses of old-field plant growth and composition to warming and precipitation. Global Change Biology 18:1754–1768.

Jones, S. A., E. S. DeKeyser, C. Dixon, and B. Kobiela. 2023. Invasive species change plant community composition of preserved prairie pothole wetlands. Plants 12(6).

Lesica, P. L., and T. H. DeLuca. 2000. Sweetclover: A potential problem for the northern Great Plains. Journal of Soil and Water Conservation 55:259–261.

Li, F., J. Xiao, J. Chen, A. Ballantyne, K. Jin, B. Li, M. Abraha, and R. John. 2023. Global water use efficiency saturation due to increased vapor pressure deficit. Science 381:672–677.

Mankin, J. S., J. E. Smerdon, B. I. Cook, A. P. Williams, and R. Seager. 2017. The curious case of projected 21st-century drying but greening in the American West. *Journal of Climate* 30:8689–8710.

Millett, B., W.C. Johnson, and G. Guntenspergen. 2009. Climate trends of the North American prairie pothole region 1906–2000. Climatic Change 93:243–267.

Molinari, N.A., and C.M. D'Antonio. 2014. Structural, compositional and trait differences between native- and non-native-dominated grassland patches. Functional Ecology 28:745–754.

Mueller, K.E., D.M. Blumenthal, E. Pendall, Y. Carrillo, F.A. Dijkstra, D.G. Williams, R.F. Follett, and J.A. Morgan. 2016. Impacts of warming and elevated CO_2 on a semi-arid grassland are non-additive, shift with precipitation, and reverse over time. Ecology Letters 19:956–966.

Murphy, R., and T. Grant. 2005. Land management history and floristics in mixed-grass prairie, North Dakota, USA. Natural Areas Journal 25:351–358.

Nuowakpo, S.K., D. Toledo, M. Sanderson, and M. Weltz. 2019. Understanding the effects of grazing and prescribed fire on hydrology of Kentucky Bluegrass-dominated rangelands in the northern Great Plains. Journal of Soil and Water Conservation 74:360-371.

Ojima, D.S., R.T. Conant, W.J. Parton, J.M. Lackett, and T.L. Even. 2021. Recent climate changes across the Great Plains and implications for natural resource management practices. Rangeland Ecology & Management 78:180–190.
Otfinowski, R., and N.C. Kenkel. 2008. Clonal integration facilitates the proliferation of Smooth Brome clones invading northern fescue prairies. Plant Ecology 199:235–242.
Palit, R., and E.S. DeKeyser. 2022. Impacts and drivers of Smooth Brome (Bromus inermis Leyss.) invasion in native ecosystems. Plants 11:1340.
Palit, R., G. Gramig, and E.S. DeKeyser. 2021. Kentucky Bluegrass invasion in the northern Great Plains and prospective management approaches to mitigate its spread. Plants 10:817.
Printz, J.L., and J.R. Hendrickson. 2015. Impacts of Kentucky Bluegrass invasion (Poa pratensis L.) on ecological processes in the northern Great Plains. Rangelands 37:226–232.
Reich, P.B., and S.E. Hobbie. 2013. Decade-long soil nitrogen constraint on the CO_2 fertilization of plant biomass. Nature Climate Change 3:278–282.
Reich, P.B., S.E. Hobbie, T.D. Lee, and M.A. Pastore. 2018. Unexpected reversal of C3 versus C4 grass response to elevated CO_2 during a 20-year field experiment. Science 360:317–320.
Sage, R.F., and D.S. Kubien. 2007. The temperature response of C3 and C4 photosynthesis. Plant, Cell & Environment 30:1086–1106.
Stotz, G.C., E. Gianoli, and J.F. Cahill Jr. 2019. Biotic homogenization within and across eight widely distributed grasslands following invasion by Bromus inermis. Ecology 100:e02717.
Stotz, G.C., E. Gianoli, M.J. Patchell, and J.F. Cahill Jr. 2017. Differential responses of native and exotic plant species to an invasive grass are driven by variation in biotic and abiotic factors. Journal of Vegetation Science 28:325–336.
Taylor, S.H., B.S. Ripley, T. Martin, L.-A. De-Wet, F.I. Woodward, and C.P. Osborne. 2014. Physiological advantages of C4 grasses in the field: A comparative experiment demonstrating the importance of drought. Global Change Biology 20:1992–2003.
Toledo, D., M. Sanderson, K. Spaeth, J. Hendrickson, and J. Printz. 2014. Extent of Kentucky Bluegrass and its effect on native plant species diversity and ecosystem services in the northern Great Plains of the United States. Invasive Plant Science and Management 7:543–552.
Vose, R.S., D.R. Easterling, K.E. Kunkel, A.N. LeGrande, and M.F. Wehner. 2017. Temperature changes in the United States. U.S. Global Change Research Program Climate Science Special Report: Fourth National Climate Assessment, Volume I. Washington, D.C. Pp. 185–206.
Wand, S.J.E., G.Y. Midgley, M.H. Jones, and P.S. Curtis. 1999. Responses of wild C4 and C3 grass (Poaceae) species to elevated atmospheric CO_2 concentration: A meta-analytic test of current theories and perceptions. Global Change Biology 5:723–741.
Williams, A. P., E. R. Cook, J. E. Smerdon, B. I. Cook, J. T. Abatzoglou, K. Bolles, S. H. Baek, A. M. Badger, and B. Livneh. 2020. Large contribution from anthropogenic warming to an emerging North American megadrought. Science 368:314–318.
Zhang, X., T.J. Lark, C.M. Clark, Y. Yuan, and S.D. LeDuc. 2021. Grassland-to-cropland conversion increased soil, nutrient, and carbon losses in the US Midwest between 2008 and 2016. Environmental Research Letters 16:054018.