

Perennial Cool-season Grass Invasion in the Northern Great Plains: The Role of Plant-soil Feedback

Rakhi Palit^{1,2}, Shawn DeKeyser^{1,3*}, Caley Gasch⁴,
Esben Kjaer^{1,5}, and Eric G. Lamb⁶

Abstract – In March 2014, the first Cool-Season Invasive Grasses of the Northern Great Plains Workshop occurred in Fargo, ND. Presenters from North Dakota, South Dakota, Wyoming, and Saskatchewan mainly focused on topics related to Kentucky Bluegrass and Smooth Brome, such as distribution, ecology, physiology, genetics, herbicide control, and fire and grazing management effects. There were approximately 180 people at the Workshop where many collaborations were solidified and/or established, and a number of relevant research projects and publications resulted from the participants on the subjects presented (e.g., DeKeyser et al. 2015, Dennhardt et al. 2016, Ereth et al. 2017, Halvorson et al. 2022, Hendrickson et al. 2019 and 2021, Kobiela et al. 2017, Palit and DeKeyser 2022, Palit et al. 2021, Preister et al. 2019 and 2021, Printz and Hendrickson 2015, Sanderson et al. 2017, Toledo et al. 2014). These now long-standing collaborations have maintained relevant research for understanding these species' ecology and management. However, as is typical with research, new questions arose which need to be addressed. By the fall of 2022, collaborators from the first Workshop desired an update on current findings for the Northern Great Plains community and an outline for the direction of future research on these species.

The Second Perennial Cool-Season Invasive Grasses of the Northern Great Plains Workshop took place in Fargo, North Dakota in March 2023. Approximately 200 people from throughout the Northern Great Plains participated in the Workshop, which consisted of 16 oral and 7 poster presentations. Participants included federal, state, and provincial government land managers, academics, federal researchers, non-profit land managers, private land managers, and industry representatives interested in management of the grasslands of the Northern Great Plains. The Workshop ended with a roundtable discussion with all participants on the last day deliberating major needs and gaps of understanding in the management of native prairie areas with consideration for these invasive species. Several topics were listed as important for future research including: invasion thresholds, restoration prioritization, alternative stable states/novel ecosystem existence, maintenance of native diversity, future invasive species, climate change factors, impacts on cattle production, axillary bud production, remote sensing applications, economic impacts, fire/grazing/herbicide management, and social/policy change potential. The topic that had great interest during the roundtable discussion was the role of plant-soil feedbacks in the proliferation of these invasive species, and the importance of plant-soil feedbacks for maintaining healthy native prairie. We are in consensus with the Workshop participants, and believe plant-soil feedbacks are most likely playing important roles in maintaining native prairie and the invasion ecology of cool-season grass species. We also believe this is an area needing further research for our understanding. This opening article of this special issue will be an exploration of what we know about plant-soil feedbacks for three of the Northern Great Plains' most troublesome cool-season invasive grasses: Kentucky Bluegrass (*Poa pratensis*), Smooth Brome (*Bromus inermis*), and Crested Wheatgrass (*Agropyron cristatum*). Furthermore, this review article will briefly discuss the impacts of these invaders on native ecosystems and shed some light on the role of plant-soil feedback for

¹ School of Natural Resource Sciences, North Dakota State University, Fargo, ND, 58108. ² ORCID ID: 0009-0005-0802-9515. ³ ORCID ID: 0000-0002-7336-4169. ⁴ Matanuska Experiment Farm and Extension Center, Institute of Agriculture, Natural Resources, and Extension, University of Alaska Fairbanks, Palmer, AK, USA 99645. ORCID: 0000-0001-5755-8468. ⁵ ORCID ID: 0000-0003-1434-646X. ⁶ Department of Plant Sciences, University of Saskatchewan, Saskatoon, SK, Canada S7N5A8 ORCID ID: 0000-0001-5201-4541. * Corresponding author.

understanding their invasion mechanisms. This information will be helpful in formulating research direction and management strategies for these invasive rangeland species.

Introduction

Native prairie rangelands are considered some of the most endangered yet least protected ecosystems globally (DeKeyser et al. 2015; Grant et al. 2020a,b; Hendrickson et al. 2019; Hoekstra et al. 2005). The Great Plains, one of North America's largest ecosystems, has been significantly altered through European and American settlement primarily for agricultural purposes. Factors, including crop production, urbanization, energy production, fire suppression, overgrazing, and climate change have also negatively impacted the biodiversity of the remaining prairies (Askins et al. 2007, Duell et al. 2016, Samson and Knopf 1994). The invasion of non-native species is considered the second most crucial factor in endangering native species, right after land clearing and habitat fragmentation (Levine et al. 2003). In certain regions of the Northern Great Plains grasslands, the invasive species *Poa pratensis* L. (Kentucky Bluegrass) and *Bromus inermis* Leyss (Smooth Brome) can comprise approximately 62% of the total exotic species cover (Cully et al. 2003), and *Agropyron cristatum* (L.) Gaertn. (Crested Wheatgrass) has been shown to decrease native species by 35% where it invades (Heidinga and Wilson 2002, Vaness and Wilson 2007). Despite recognizing the rapid spread of invasive species as a critical factor leading to the significant loss of biodiversity in the native grasslands, our understanding of the underlying mechanisms of plant invasions and how invaders interact with the surrounding ecosystems, including both biotic and abiotic factors is limited (Grant et al. 2009, 2020a,b, 2006; Palit and DeKeyser 2022).

The displacement of native species by invasive species often leads to transformation of highly diverse ecosystems into more uniform novel ecosystems, resulting in reduced biodiversity at various trophic levels (Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006 and 2009). This transformation can negatively impact ecosystem services (Estes et al. 2011, Nouwakpo et al. 2019) and incur costs for landowners (Pyšek and Richardson 2010). Additionally, invasive species that share morphological and phenological traits with native species (e.g., Kentucky Bluegrass, Smooth Brome, and Crested Wheatgrass) can be challenging to manage using conventional methods, including prescribed fire, grazing, and herbicides, as these approaches may also hinder the growth of native species (Simmons et al. 2007, Toledo et al. 2014). The current management practices designed to combat the spread of invasive species unintentionally hinder the abundance and growth of surrounding native species and, thus, may not be optimal (Gasch et al. 2020, Palit et al. 2021). As stated, our understanding of the mechanisms underlying plant invasion and their impact on ecosystems remains limited, hindering the development of effective and cost-efficient management strategies that enhance native biodiversity. Preservation and restoration of remaining prairies play a vital role in safeguarding biodiversity, ecosystem functions, services, and economic purposes. Therefore, it is essential to investigate the factors that facilitate plant invasion in order to strengthen conservation efforts.

One of the primary objectives of invasion biology is to assess the impacts of invasive species on the ecosystem as a whole (Crooks 2002, Parker et al. 1999, Ruiz et al. 1999, Williamson 1996). The most common consequence of invasion is negative interactions between invasive species and their native neighbors. Invasive species potentially compete with native species for available resources, such as light, moisture, nutrients, water, and habitat. The concept of ecosystem engineering, when applied to biological invasions,

provides valuable insights into the effects of invasive species, and enables a deeper exploration of the broader role of invasive species in modifying habitats. The term ecosystem engineering was first coined by Jones et al. (1994) to describe the indirect or direct control of an organism on resource availability by causing physical changes to abiotic or biotic factors in the ecosystem (Crooks 2002; Jones et al. 1997a,b). Numerous invasive species can effectively regulate the availability and distribution of nutrients by directly getting involved in the biogeochemical cycles and modifying them. Moreover, apart from the differences in the process of nutrient uptake and consumption between invasive species and the natives, invaders can simply alter the nutrient availability by their large propagule pressure in the ecosystem (Crooks 2002, Williamson 1996).

Beyond altering biogeochemical cycles, invasive species have been shown to alter soil microbiota, and these can create plant-soil feedbacks further favoring invasion (Callaway et al. 2004, Klironomos 2002, Levin et al. 2006, Suding et al. 2013, van der Putten et al. 2013, van der Putten et al. 2016; Fig. 1). For clarification, feedback refers to the processes in an ecosystem that either enhance or impair its resilience and functioning (Printz and Hendrickson 2015). Negative feedback contributes to the ecosystem stability, while positive feedback transforms the ecosystem into a different state. Plant-soil feedback refers to the process in which different plant species alter soil communities by cultivating specific microbiota for each species (Piper et al. 2015a, van der Putten et al. 2013). Soil microbial communities, including mycorrhizae and soil pathogens play a significant role in influencing plant performance, abundance, and community structure. This is particularly important in the context of invasive plants, as native pathogens in the rhizosphere can provide a competitive advantage to exotic species over native competitors (Batten et al. 2006, Suding et al. 2013, Trognitz et al. 2016, van der Putten et al. 2013). Exotic species may perform better in new locations because they have escaped pathogens from their original range. Generally, exotic invasive species benefit more from the release of soil-borne pathogens than from their exposure to symbionts like mycorrhizae (Blumenthal 2005, Kardol et al. 2006, van der Putten et al. 2013). For example, in North America, introduced species have shown a greater dependency on mycorrhizal fungi compared to native species (Pringle et al. 2009).

Researchers and land managers recognize the importance of reconstructing habitats that can withstand the abiotic stresses associated with changing climate conditions (Bork et al. 2019, Larson et al. 2022, Sanderson et al. 2017). One potential approach is relocating plant materials from a native habitat to a restoration site, where they may be better adapted to climate change. Previous studies have found that plant-soil interactions of nitrogen-fixing bacteria, arbuscular mycorrhiza, and root herbivores, have a significant impact on floral traits. This, in turn, enhances pollinator visits and pollinator potential (Casper and Castelli 2007, Heinen et al. 2018, Larson et al. 2022, Wolfe et al. 2005). Therefore, including soil microbiota in prairie restoration efforts can help establish and promote the growth of native plant communities. However, our understanding of the soil microorganisms that drive these processes in the prairie ecosystem is limited. Expanding our knowledge of how invaded microbial communities affect ecosystem function and native plant fitness would be extremely important in combating plant invasions and restoring native prairies.

The following sections are an exploration of current knowledge of plant-soil feedbacks for the most troublesome perennial cool-season invasive grasses of the Northern Great Plains: Kentucky Bluegrass, Smooth Brome, and Crested Wheatgrass. We will also highlight potential management scenarios which may impact plant-soil feedbacks in a way that favors native plants and the overall plant diversity of the remaining prairies of the region.

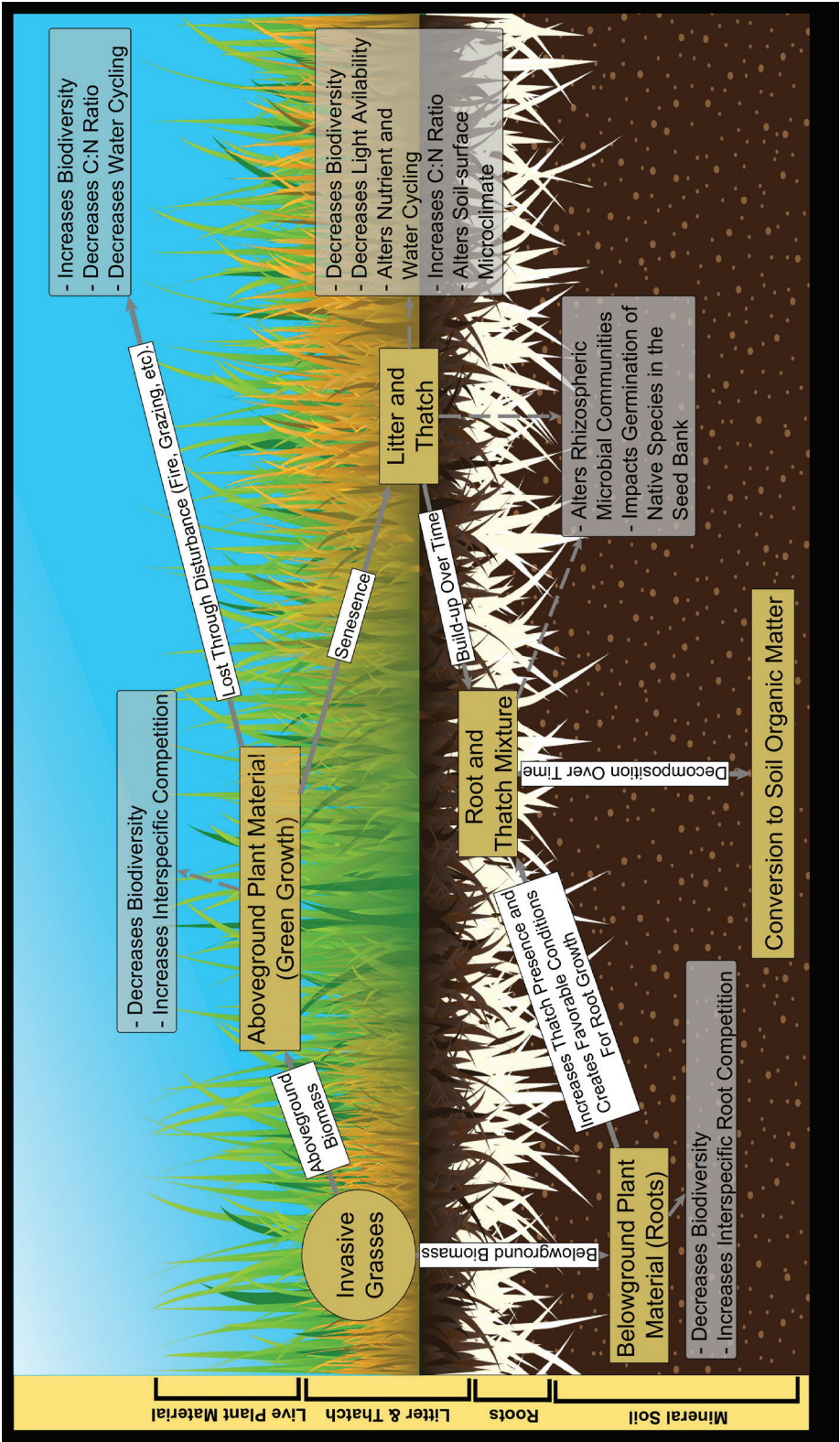


Figure 1. Conceptual diagram of plant-soil feedback of three perennial cool-season invasive grasses of the Northern Great Plains. Grey boxes refer to different invasion effects; white boxes refer to the factors/conditions that influence these invasion effects at the direction of the arrows.

Kentucky Bluegrass

Kentucky Bluegrass is a highly rhizomatous grass known for its “mat-forming” abilities (Uchytel 1993), and the grass is believed to have been introduced to North America as early as the 1600s (DeKeyser et al. 2015). As part of its mat-forming properties, Kentucky Bluegrass serves as an ecosystem engineer by also developing a thatch layer to enhance its ability to invade (Ellis-Felege et al. 2013, Hilfer and Limb 2020). Thatch refers to a combination of partially dead, decomposed, and living plant parts such as roots, rhizomes, leaves, stems, and aboveground green plant parts near the soil surface (Dornbusch et al. 2020, Printz and Hendrickson 2015). Over time, Kentucky Bluegrass forms a dense layer of thatch on the ground, which diminishes light availability and temperature fluctuations (Hilfer and Limb 2020, Nouwakpo et al. 2019, Palit et al. 2021). Kentucky Bluegrass leaves are uniquely well adapted to pushing through this thatch layer (Letts et al. 2015). Additionally, the water-holding capacity of thatch is lower than that of soil, resulting in faster drying and reduced contact between seeds and soil. These mechanisms greatly impede the successful germination, growth, and survival of native grasses and forbs in the surrounding area (Facelli and Pickett 1991, Gasch et al. 2019, Hilfer and Limb 2020, Palit et al. 2021). The thatch layer significantly impacts the hydrology and nutrient cycling of the soil surface (Chuan et al. 2020, Liang et al. 2017, Sanderson et al. 2017). Moreover, the abundance of roots in the soil gives Kentucky Bluegrass a competitive advantage in accessing soil moisture compared to the neighboring native plants (Palit et al. 2021, Printz and Hendrickson 2015). These interactive processes collectively create positive feedback that supports the growth and abundance of Kentucky Bluegrass while suppressing its native counterparts (Hilfer and Limb 2020, Palit et al. 2021). These plant-soil interactions in Kentucky Bluegrass play crucial roles in regulating plant invasions and maintaining ecosystem diversity (Elgersma et al. 2012, van der Putten et al. 2007). Plants modify the soil through both physical and chemical mechanisms, such as above and below-ground litter accumulations (e.g. Kentucky Bluegrass thatch and root mat) and utilization of soil pathogens and symbionts (Bell et al. 2020, van der Putten et al. 2013).

The interaction between plants and soil microbial communities plays a crucial role in determining the outcomes of competition between invaders and the native plant community (Hilbig and Allen 2015, Levine et al. 2006, Palit et al. 2021). In reference to Kentucky Bluegrass, studies have found that grass species with coarse root morphology and fewer root hairs, as well as those that thrive in nutrient-limited habitats, benefit more from arbuscular mycorrhizae than species with fine roots (Dhillon and Friesse 1992, Printz and Hendrickson 2015, Toledo et al. 2014). In a survey of approximately 96% mycorrhizal species, Kentucky Bluegrass had an infection rate of less than 15%, suggesting that it is a facultative species (Dhillon and Friesse 1992). Although, another study showed that Kentucky Bluegrass had no significant response to mycorrhizal association and was non-mycorrhizal (Eom et al. 2000, Printz and Hendrickson 2015).

There are many potential explanations for the invasiveness of certain exotic species when it comes to plant-soil feedback. Although some exotic species exhibit negative plant-soil feedbacks in the area they have invaded, they still manage to be invasive. This phenomenon could be attributed to the accumulation of local pathogens that are more harmful to native species than to exotic species (Eppinga et al. 2006, Mangla and Callaway 2008, van der Putten 2013). When the invaded microbial community has pathogens harmful to native plants or deficient in beneficial organisms required for their establishment and survival, this process can facilitate increased invasion (Batten et al. 2006). The newly invaded soil community may not be conducive to the re-establishment and growth of native plants, resulting in a negative

interaction that promotes further invasion.

Nitrogen is an essential and often limited nutrient for plants. It is projected that by 2030 there will be an increase in atmospheric nitrogen deposition globally, which could lead to a significant loss of plant biodiversity worldwide (Palit et al. 2021, Phoenix et al. 2006). Nitrogen deposition directly contributes to increased nitrogen availability in many plant communities (Shivega and Aldrich-Wolfe 2017). Studies suggest that this increase in nitrogen availability can result in decreased diversity and significant changes in the species composition (Palit et al. 2021, Printz and Hendrickson 2015). Furthermore, it can lead to lower carbon-to-nitrogen ratios in both above- and below-ground tissues (Yang et al. 2019).

Another possible feedback mechanism involves exotic plants altering physico-chemical properties of the soil in the invaded area. This alteration can have a direct positive plant-soil feedback for the exotic species, while simultaneously providing negative feedback for the surrounding native species (Simberloff and Gibbons 2004, van der Putten et al. 2013). For instance, changes in litter-soil-nutrient dynamics can give a species like Kentucky Bluegrass a competitive advantage, displacing other native species in the community (DeAngelis 2012). Typically, invasive C3 grasses (such as Kentucky Bluegrass and Smooth Brome) have higher nitrogen concentrations and lower recalcitrant carbon than certain native C4 grasses (Mahaney et al. 2008), which can lead to increased decomposition rates and faster nutrient cycling (Sanderson et al. 2017). Additionally, the higher plant and litter production of invasive C3 grasses may stimulate soil microbial activity and soil nitrogen mineralization processes.

In native mixed-grass prairies, nitrogen remains stored in soil organic matter, and prairie fires reduce the total nitrogen through volatilization and slow the conversion of organic nitrogen from a labile to a recalcitrant form. Additionally, fire negatively impacts soil microbial activities, thereby slowing down nitrogen cycling (Georgen and Chambers 2009). Changes in nitrogen availability resulting from altered community structure and atmospheric nitrogen deposition may promote the rapid spread and dominance of cool-season invasive grasses, such as Kentucky Bluegrass, in prairie ecosystems. A previous study found no clear evidence that Kentucky Bluegrass dominance or the associated land management techniques significantly impacted soil carbon and nitrogen levels, nor the structure and abundance of microbial communities (Gerhard et al. 2019). Moreover, they indicated soil abiotic characteristics, such as moisture and temperature, may have a greater influence on soil nutrient levels and microbial populations than litter chemistry. Conversely, a different study found increases in Kentucky Bluegrass abundance were associated with increases in both total soil N and soil organic C (Hendrickson et al. 2021). The shift in the prairie plant communities from native grass and forb dominated systems to Kentucky Bluegrass dominated grasslands reduces soil surface fire intensity by altering the fuel properties, including the distribution and moisture of the fuel, which in turn results in decreased nitrogen volatilization (Printz and Hendrickson 2015). Warmer soil temperatures can further accelerate the soil mineralization rates, enhancing the plant-available nitrogen. The enhanced soil nitrogen levels can also alter the soil microbiota, which in turn can facilitate the growth and establishment of exotic species. Elevated nitrogen levels in the ecosystem promote invasions also by inhibiting soil mycorrhizal colonies (Bradley et al. 2006, Printz and Hendrickson 2015). For example, where the fungicide Benomyl was applied to suppress soil mycorrhizal populations to less than 25%, the result was an increase in cool-season grasses, including Kentucky Bluegrass (Harnett and Wilson 1999). Although the added nitrogen may increase the overall production, many native species may lose their natural ability to compete, which they have under lower nitrogen conditions (Wedin and Tilman 1990).

Smooth Brome

Smooth Brome is a rhizomatous perennial grass of Eurasian origin and a widespread invader of native grasslands across the Great Plains of North America (Grant et al. 2020a, Otfinowski et al. 2007, Palit and DeKeyser 2022). Smooth Brome was introduced to North America in the 1880s as a forage grass for livestock (Newell and Keim 1943). Numerous cultivars are available that have been widely seeded for pasture, land reclamation, and on roadsides. Smooth Brome is a prolific seed producer that readily establishes on small disturbances such as gopher mounds in intact grasslands and, once established, spreads via rhizomes to create near-monoculture patches (Otfinowski and Kenkel 2008, Stotz et al. 2019). Smooth Brome is highly productive, often producing a continuous canopy and a thick litter layer (Otfinowski et al. 2007, Piper et al. 2015a). The combination of high shoot biomass, heavy litter accumulation, and fierce belowground and aboveground competition reduces native plant community diversity and impacts ecosystem services ranging from nutrient cycling to water purification (Bell et al. 2020 and 2023, Bennett et al. 2014, Fink and Wilson 2011, Lamb et al. 2016, Li et al. 2018, Piper et al. 2015b, Stotz et al. 2019, Stotz et al. 2017, Vinton and Goergen 2006).

Smooth Brome invasions originating from both historical and current plantings are very problematic for native grassland managers, given the challenge of controlling this prolific and productive species (Palit and DeKeyser 2022, Salesman and Thomsen 2011). Small patches can be eliminated using broad spectrum herbicides, but the recovering patches can be vulnerable to follow-on invasions by other species including Kentucky Bluegrass (Slopek and Lamb 2017). The aggressive growth and robust rhizome systems of Smooth Brome mean more extensive invasions can, at best, be partially controlled but not eliminated through management actions such as prescribed fire and grazing (Otfinowski et al. 2007, Palit and DeKeyser 2022, Salesman and Thomsen 2011). Please see the concurrent article by Gannon et al. (2024) in this issue for additional information of fire effects on Smooth Brome. Developing effective mitigation measures requires an enhanced understanding of the ecological mechanisms underlying Smooth Brome invasion.

There has been a series of detailed investigations into the ecological mechanisms underlying Smooth Brome invasion in two fescue grasslands in Saskatchewan, Canada (Bell et al. 2023; Piper et al. 2015a,b). These studies demonstrate that Smooth Brome invasion has had a profound impact on soil communities that ultimately are plant-soil feedbacks which enhance the invasion (Bell et al. 2023). Smooth Brome invasion first alters soil community assembly processes by selectively suppressing dominant soil bacteria, driving an increased abundance and diversity of rarer taxa (Piper et al. 2015b). These impacts on soil bacterial diversity are correlated with increases in litter or soil organic matter, but the causal mechanism appears to be the loss of plant root diversity in brome-invaded soils (Li et al. 2018, Mamet et al. 2017, Piper et al. 2015b). The loss of native plant roots initiates complex interactions among rhizosphere bacteria, fungi, and archaea (Bell et al. 2023b, Mamet et al. 2017, Mamet et al. 2019) which ultimately explain why the increased accumulation of litter under Smooth Brome is associated with increased nitrogen cycling rates (Piper et al. 2015a,b; Vinton and Goergen 2006). The available ammonium produced by higher mineralization rates is then likely taken up by Smooth Brome, because nitrification rates remain stable (Piper et al. 2015a). This increased nitrogen mineralization and uptake enhances aboveground Smooth Brome growth and biomass production, creating a positive feedback (Bell et al. 2023).

The changed soil processes observed following Smooth Brome invasion likely perpetuate the dominance of the invasive plants (Bell et al. 2023). There is some evidence from sites

in Alberta, Canada that negative plant-soil feedbacks, likely from pathogen accumulation, can diminish Smooth Brome performance over time (Salimbayeva 2021, Stotz et al. 2018). The long-term persistence of Smooth Brome invasions (Otfinowski et al. 2007, Salesman and Thomsen 2011), including in cases where negative soil feedbacks were observed (Salimbayeva 2021), demonstrates that the net impact of altered soil processes generally remains positive for Smooth Brome. More broadly, recent work on multiple invasions suggests that similar soil feedbacks may be important in the dominance of other invasive cool-season grasses (e.g. Kentucky Bluegrass; Bell et al. 2023).

The cascade of soil changes observed following invasion in fescue grasslands are critical to understanding how invasive Smooth Brome can achieve and maintain dominance (Bell et al. 2023, Mamet et al. 2019). The results from these studies can be tied to other research which can give insight to potential mechanisms of changes in soil ecology of sites invaded by Smooth Brome. For example, Smooth Brome generates heavy litter layers relative to the native species that it displaces (Fink and Wilson 2011, Otfinowski et al. 2007, Piper et al. 2015a, Williams and Crone 2006). While that litter is not a direct cause of the soil community reorganization observed under Smooth Brome (Mamet et al. 2017, Mamet et al. 2019, Piper et al. 2015b), the enhanced release of nitrogen from decomposition of that litter is ultimately important in maintaining Smooth Brome dominance (Piper et al. 2015a, Vinton and Goergen 2006). There is every reason to believe that the impacts of this litter on nitrogen cycling can be generalized across the invasive range of Smooth Brome. Thick litter layers are likely important in physically excluding many native species from Smooth Brome invaded sites (Lamb 2008, Letts et al. 2015, Williams and Crone 2006, Xiong and Nilsson 1999), and this is likely the cause of the loss of native plant roots following Smooth Brome invasion that is a critical driver of Smooth Brome impacts on soil communities (Li et al. 2018, Mamet et al. 2017).

Crested Wheatgrass

Crested Wheatgrass is a perennial, cool-season grass native to Eurasia. Its present range in North America spans the Northern Great Plains, the Intermountain West, and the Southwest (USDA NRCS 2021). The species was widely introduced to stabilize abandoned cropland in the 1930s as a cold-tolerant, drought-tolerant, easy-to-establish and high-yielding perennial forage, as summarized by Lesica and Deluca (1996). Since that time, it continues to be used in forage, conservation, reclamation, and urban seed mixes. As a result of these intentional plantings, it has replaced or encroached into native plant communities, including grasslands, shrublands, and forests (Zlatnik 1999).

Despite its anticipated soil stabilizing abilities, the benefits of Crested Wheatgrass have been limited, and the species has become a concern to land managers throughout its range (also summarized by Lesica and Deluca; 1996). Crested Wheatgrass is particularly competitive and persistent in arid and semi-arid regions, and it can dominate vegetation stands, effectively reducing plant species richness and diversity (Henderson and Naeth 2005, Lesica and Cooper 2019, Williams et al. 2017), and therefore reducing wildlife habitat and forage quality (summarized by Davies et al. 2011, Vaness and Wilson 2007).

Scalable control of Crested Wheatgrass has been difficult in locations where land managers desire to reduce its dominance and increase native species abundance and diversity. Tillage has repeatedly failed to accomplish this, even when combined with herbicide and native seedings, and such physical soil disturbance may actually facilitate secondary invasions (Fansler and Mangold 2011, Hulet et al. 2010, McAdoo et al. 2017). Repeated applications of herbicide (glyphosate), aimed to deplete the seedbank and prevent additional

invasions have also failed to reduce Crested Wheatgrass to acceptable levels (Morris et al. 2019). In a review of control methods, Wengreen et al. (2016) state that successful reseeding of other species requires less than 14% cover of Crested Wheatgrass, and in addition to the failures of tillage to accomplish this, neither grazing nor fire have been successful. The most promising efforts in reduction and native species expansion have used a combination of tillage + herbicide + seeding (Cox and Anderson 2004), or herbicide + clipping + native competition (Wilson and Pärtel 2003). In these “assisted succession” approaches, the goal is to direct the plant community with a combination of simultaneous Crested Wheatgrass suppression and native species promotion.

Perhaps the intensive agronomic-based approaches to Crested Wheatgrass control and native seeding are more successful because they disrupt the factors associated with the species’ resilience, including those belowground. There is mounting evidence (highlighted below) to support the notion that Crested Wheatgrass occupancy initiates belowground changes that create an alternative soil state, which reinforces its dominance and persistence. However, mechanistic studies that explicitly explore these feedbacks are limited. Here, we summarize current knowledge about soil characteristics associated with Crested Wheatgrass that play a role in its occurrence and management, and that may contribute to reinforcing Crested Wheatgrass persistence.

Soil structural and abiotic properties associated with Crested Wheatgrass are apparent on the soil surface and extend deeper in the profile. Stands of Crested Wheatgrass exhibit increased bare ground relative to native assemblages (McWilliams and Van Cleave 1960, Williams et al. 2017), which is presumably due to lower plant species diversity (Henderson and Naeth 2005) and hummock formation (McWilliams and Van Cleave 1960). Soil surface exposure increases susceptibility to erosion (McWilliams and Van Cleave 1960) and surface crusting, which hinders seedling emergence, permits larger and faster temperature fluctuations, and reduces air and water exchange rates (Hillel 2004). Collectively, these structural and abiotic conditions result in a less hospitable environment for seedlings and surface-dwelling organisms, effectively excluding species from establishing and occupying the stand.

In the rooting zone, soils dominated by Crested Wheatgrass develop and maintain less granular (aggregated) structure (Gasch et al. 2016), which is also critical for regulating thermal, atmospheric, and hydrologic dynamics (Hillel 2004). This may be due to a combination of Crested Wheatgrass’ affinity for coarse-textured soils (Nafus et al. 2020, Williams et al. 2017) as well as its production of a coarse root system with relatively low root biomass production (Dormaar et al. 1995). In addition to enabling infiltration and air exchange, soil aggregates provide structural complexity that houses diverse soil communities, stores carbon and other soil nutrients, and provides strength within the soil matrix to resist erosion and compaction (Voroney 2007).

It stands to reason that the surface sealing, under-developed aggregate structure, and associated micro-climate that occurs in Crested Wheatgrass stands directly governs belowground biogeochemistry and soil communities. Differences in soil carbon and nutrient pools have been observed between Crested Wheatgrass occupied soils and their native analogs (Dormaar et al. 1995, Smoliak and Dormar 1985). Crested Wheatgrass appears to contribute less carbon to soil carbon and organic matter stocks (Smoliak and Dormaar 1985), presumably through reduced carbon inputs derived from roots (Dormaar et al. 1995), reduced root exudation (Morris et al. 2019), and accelerated carbon mineralization (Chen and Stark 2000, Curtin et al. 2000). Soil nitrogen and carbon cycles are naturally coupled; nitrogen dynamics respond to shifts in plant communities as well. Chen and Stark (2000) measured elevated total nitrogen and nitrate concentrations and accelerated nitrogen mineralization

rates beneath Crested Wheatgrass in Utah, compared to soils beneath a patchy sagebrush community. While the specific mechanisms behind these shifts in nutrient pools and cycling rates are not known, research suggests that invasive plant species may influence soil biogeochemistry by changing the quantity, timing, distribution, and chemical nature of soil organic matter inputs, and by influencing the organisms that mediate decomposition and nutrient fluxes (Bradford et al. 2012, Kramer et al. 2012, Piper et al. 2015b).

Understandably, these physio-chemical soil characteristics that are associated with Crested Wheatgrass carry over into the soil microbial community. Indeed, multiple studies have observed reduced soil microbial abundance in soils occupied by Crested Wheatgrass. (Gasch et al. 2016, Jordan et al. 2012, Reinhart and Rinella 2021). These reductions are consistent with reduced microbial substrate contributions by Crested Wheatgrass roots. Gasch et al. (2016) found that Wyoming soils reclaimed with Crested Wheatgrass hosted only one-fourth of the total microbial abundance compared to undisturbed soils or soils reclaimed with native cool season grasses, and those differences persisted across a 29-year chronosequence. These differences were also reflected in all microbial groups measured (bacteria, actinomycetes, saprophytic fungi, and arbuscular mycorrhizal [AM] fungi). Studies in Montana have confirmed a negative relationship between the Crested Wheatgrass-AM fungi relationship in more depth, through field surveys and greenhouse experiments. Reinhart and Rinella (2021) found that field-collected Crested Wheatgrass roots from multiple locations were lacking AM fungal molecular signatures, which were present in all other grass and shrub species surveyed. Under controlled greenhouse conditions, Jordan et al. (2012) found that Crested Wheatgrass plants grown in field-collected soils had less AM fungal root colonization, and soils conditioned by Crested Wheatgrass held fewer AM fungal taxa compared to native species. In a related study (Jordan et al. 2008), Crested Wheatgrass and other invasive species performed well in soil conditioned by Crested Wheatgrass, whereas two native forb species suffered—and these changes were associated with the soil biotic makeup. Luckily, graminoid species were indifferent to the soil modifications and effectively prevented prolonged effects of the unfavorable soil condition. Plant-soil feedbacks are potentially at play in both Crested Wheatgrass self-perpetuation and in soil-plant community recovery after removal of Crested Wheatgrass (Perkins and Nowak 2012). Again, the mechanisms behind these observations are limited to speculation, but the associated physical, chemical, and biological nature of soils beneath Crested Wheatgrass stands likely plays a role in its success.

Despite the challenges in controlling Crested Wheatgrass density and cover, some studies have shown promise in remediating the negative belowground effects of the species as a way of potentially disrupting the factors supporting its perpetuation. Wallace et al. (2009) observed that four to five years after biosolids application, Crested Wheatgrass-dominated soils had higher carbon and nitrogen concentration and more aggregation, compared to soils treated with nitrogen and phosphorus fertilizer. Mummey and Ramsey (2017) successfully used *Onobrychis viciifolia* Scop. (Sainfoin) as a “bridge species” to boost AM fungal populations in soil and native plant roots. The Sainfoin conditioning phase also increased soil phosphorus and potassium availability, which would benefit native species establishment. Collectively, these control and remediation efforts suggest that success will require intensive management, employing multiple tools to modify the plant community and soil condition.

Management implications

A combination of plant traits and associated belowground characteristics seem to be important factors in the persistence of Kentucky Bluegrass, Smooth Brome, and Crested Wheatgrass and the prevention of native species establishment. There is strong evidence

that these species can influence the biogeochemical cycles in ways that promote their own growth, while inhibiting the growth of many native species. These same species are most likely altering soil biota by promoting microbiota that benefit their growth, while eliminating microbiota essential for native plant growth. While we know some things about how Kentucky Bluegrass, Smooth Brome, and Crested Wheatgrass stands respond (or do not respond) to various control methods, it would benefit us to understand how soil properties and microbial communities might play a role in facilitating their persistence and preventing native species establishment.

These plant-soil feedbacks present a management challenge because plant root interactions and soil microbial assembly processes cannot be directly managed. However, understanding the ecological mechanisms underlying the feedbacks can provide clues to break the invasion cycle. The key role of litter in many of the soil mechanisms described for Kentucky Bluegrass, Smooth Brome, and Crested Wheatgrass point to litter as a practical management target that may reduce the vigor, dominance, and persistence of these species. Excess litter is a tractable and achievable management objective that, while unlikely to eliminate invasions, may limit spread and impact on biodiversity and ecosystem services. For example, reductions in Smooth Brome abundance are often observed following treatments that, among other effects, remove shoot biomass or litter such as fire, haying, and grazing (Salesman and Thomsen 2011). Additionally, disturbances like the combination of fire and grazing and variably stocked rotational grazing that remove litter and promote grazing in discrete areas can mitigate the spread of both Kentucky Bluegrass and Smooth Brome (Duquette et al. 2022). These treatments may be effective because they are disrupting the Smooth Brome and Kentucky Bluegrass-soil feedbacks. While not studied to the same degree as Smooth Brome, similar cascades of invasion and soil community disruption driven by litter likely occur under Kentucky Bluegrass and Crested Wheatgrass invasion (Bell et al. 2023). Reductions in litter buildup may be a practical management intervention for many invasive cool season grasses.

Overall, to strengthen our understanding of plant-soil feedback on the invasion dynamics of rangeland species, future research should prioritize understanding the contribution of soil properties and microbial communities in promoting invasion success and inhibiting the establishment of native species. Additionally, it is crucial to expand our understanding of the influence of invaded microbial communities on ecosystem function and the fitness of native plants. This knowledge is essential in effectively combating plant invasions and restoring native prairies.

Acknowledgements

We would like to thank the Northern Great Plains Section of the Society for Range Management for helping monetarily with the publication of this special issue, and their support of the Workshop. We would also like to thank all of the sponsors of the Workshop in March, 2023 including the following: NDSU Agricultural Experiment Station, NDSU Central Grassland Research Extension Center, NDSU Hettinger Research Extension Center, The North Dakota Chapter of The Wildlife Society, USDA Natural Resources Conservation Service, Audubon Dakota, North Dakota Grazing Lands Coalition, The Nature Conservancy, Millborn Seeds, Agassiz Seed and Supply, North Dakota Natural Resources Trust, North Dakota Game and Fish Department, and Envu. We would like to thank all of the participants and presenters at the Workshop, and all authors who contributed to this special issue. Finally, we would like to thank the *Prairie Naturalist* for agreeing to host this special issue.

Literature Cited

- Askins, R.A., F. Chavez-Ramírez, B.C. Dale, C.A. Haas, J.R. Herkert, F. L. Knopf, and P.D. Vickery. 2007. Conservation of grassland birds in North America: Understanding ecological processes in different regions. *Ornithological Monographs* 64:iii–46.
- Batten, K.M., K.M. Scow, K.F. Davies, and S.P. Harrison. 2006. Two invasive plants alter soil microbial community composition in serpentine grasslands. *Biological Invasions* 8:217–230.
- Bell, J.K., S.D. Siciliano, and E.G. Lamb. 2020. A survey of invasive plants on grassland soil microbial communities and ecosystem services. *Scientific Data*. 7:86.
- Bell, J.K., S.D. Siciliano, and E.G. Lamb. 2023. Seasonality and bacterial community assembly processes dominate prairie ecosystem service disruption during invasion. *Soil Biology and Biochemistry*. 184:109120.
- Bennett, J.A., G.C. Stotz, and J.F. Cahill Jr. 2014. Patterns of phylogenetic diversity are linked to invasion impacts, not invasion resistance, in a native grassland. *Journal of Vegetation Science*. 25:1315–1326.
- Blumenthal, D. 2005. Interrelated causes of plant invasion. *Science* 310:243–244.
- Bork, E.W., M.P. Lyseng, D.B. Hewins, C.N. Carlyle, S.X. Chang, W.D. Willms, and M.J. Alexander. 2019. Herbage biomass and its relationship to soil carbon under long-term grazing in northern temperate grasslands. *Canadian Journal of Plant Science* 99:905–916.
- Bradford, M.A., M.S. Strickland, J.L. DeVore, and J.C. Maerz. 2012. Root carbon flow from an invasive plant to belowground foodwebs. *Plant and Soil* 359:233–244.
- Bradley, K., R.A. Drijber, and J. Knops. 2006. Increased N availability in grassland soils modifies their microbial communities and decreases the abundance of arbuscular mycorrhizal fungi. *Soil Biology and Biochemistry* 38:1583–1595.
- Calloway, R.M., G.C. Thelen, S., Barth, P.W. Ramsey, and J.E. Gannon. 2004. Soil fungi alter interactions between the invader *Centaurea maculosa* and North American natives. *Ecology* 85(4):1062–1071.
- Casper, B.B., and J.P. Castelli. 2007. Evaluating plant–soil feedback together with competition in a serpentine grassland. *Ecology letters* 10:394–400.
- Chen, J., and J.M. Stark. 2000. Plant species effects and carbon and nitrogen cycling in a sagebrush–Crested Wheatgrass soil. *Soil Biology and Biochemistry* 32:47–57.
- Chuan, X.Z., C.N. Carlyle, E.W. Bork, S.X. Chang, and D.B. Hewins. 2020. Extracellular enzyme activity in grass litter varies with grazing history, environment, and plant species in temperate grasslands. *Science of the Total Environment* 702:14.
- Cox, R.D., and V.J. Anderson. 2004. Increasing native diversity of cheatgrass-dominated rangeland through assisted succession. *Journal of Range Management* 57:203–210.
- Crooks, J.A. 2002. Characterizing ecosystem-level consequences of biological invasions: The role of ecosystem engineers. *Oikos* 97(2):153–166.
- Cully, A.C., J.F. Cully Jr., and R.D. Hiebert. 2003. Invasion of exotic plant species in tallgrass prairie fragments. *Conservation Biology* 17(4):990–998.
- Curtin, D., F. Selles, H. Wang, R.P. Zentner, and C.A. Campbell. 2000. Restoring organic matter in a cultivated, semiarid soil using Crested Wheatgrass. *Canadian Journal of Soil Science* 80:429–435.
- Davies, K.W., C.S. Boyd, J.L. Beck, J.D. Bates, T.J. Svejcar, and M.A. Gregg. 2011. Saving the sagebrush sea: An ecosystem conservation plan for big sagebrush plant communities. *Biological Conservation* 144:2573–2584.
- DeAngelis, D.L. 2012. Dynamics of nutrient cycling and food web. Springer Science and Business Media. Vol. 9.
- DeKeyser, E.S., L.A. Dennhardt, and J. Hendrickson. 2015. Kentucky Bluegrass (*Poa pratensis*) invasion in the northern Great Plains: A story of rapid dominance in an endangered ecosystem. *Invasive Plant Science and Management*. 8:255–261.
- Dennhardt, L.A., E.S. DeKeyser, S.A. Tennefos, and S.E. Travers. 2016. There is no evidence of geographical patterning among invasive *Poa pratensis* L. populations in the northern Great Plains. *Weed Science*. 64:409–420.

- Dhillion, S.S., and C.F. Friese. 1992. The occurrence of mycorrhizas in prairies: Application to ecological restoration. Proceedings from the Thirteenth North American Prairie Conference. Windsor Ontario, Canada August 6–9, 1992. Department of Parks and Recreation, Windsor, Ontario, CA. 103–114 pp.
- Dormaar, J.F., M.A. Naeth, W.D. Willms, and D.S. Chanasyk. 1995. Effect of native prairie, Crested Wheatgrass (*Agropyron ristatum* [L.] Gaertn.), and Russian Wildrye (*Elymus junceus* Fisch.) on soil chemical properties. Rangeland Ecology and Management/Journal of Range Management Archives 48:258–263.
- Dornbusch, M.J., R.F. Limb, and K.K. Sedivec. 2020. Alternative grazing management strategies combat invasive grass dominance. Natural Areas Journal 40(1):86–95.
- 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.
- Duquette, C., D.A. McGranahan, M. Wanchuk, T. Hovick, R. Limb, and K. Sedivec. 2022. Heterogeneity-based management restores diversity and alters vegetation structure without decreasing invasive grasses in working mixed-grass prairie. Land 11(8):1135.
- Elgersma, K.J., S. Yu, T. Vor, and J.G. Ehrenfeld. 2012. Microbial-mediated feedbacks of leaf litter on invasive plant growth and interspecific competition. Plant and Soil 356:341–355.
- Ellis-Felege, S.N., C.S. Dixon, and S.D. Wilson. 2013. Impacts and management of invasive cool-season grasses in the northern Great Plains: Challenges and opportunities for wildlife. Wildlife Society Bulletin 37:510–516.
- Eom, A.D., Hartnett, and G.W.T. Wilson. 2000. Host plant species effects on arbuscular mycorrhizal fungal communities in tallgrass prairie. Oecologia 122:435–444.
- Eppinga, M.B., M. Rietkerk, S.C. Dekker, P.C. De Ruiter, and W.H. van der Putten. 2006. Accumulation of local pathogens: A new hypothesis to explain exotic plant invasions. Oikos 114:168–176.
- Ereth, C., J. Hendrickson, D. Kirby, E. DeKeyser, K.K. Sedivec, and M.S. West. 2017. Controlling Kentucky Bluegrass with herbicide and burning is influenced by invasion level. Invasive Plant Science and Management. Invasive Plant Science and Management 10:80–89.
- Estes, J.A., J. Terborgh, J.S. Brashares, M.E. Power, J. Berger, W.J.; Bond, S.R. Carpenter, T.E. Essington, R.D. Holt, J.B.C. Jackson et al. 2011. Trophic downgrading of planet earth. Science 333:301–306.
- Facelli, J. M., and S.T. Pickett. 1991. Plant litter: Its dynamics and effects on plant community structure. The botanical review 57:1–32.
- Fansler, V.A., and J.M. Mangold. 2011. Restoring native plants to Crested Wheatgrass stands. Restoration Ecology 19:16–23.
- Fink, K.A., and S.D. Wilson. 2011. *Bromus inermis* invasion of a native grassland: Diversity and resource reduction. Botany. 89:157–164.
- Fuhlendorf, S.D., D.M. Engle, J. Kerby, and R. Hamilton. 2009. Pyric herbivory: Rewilding landscapes through the coupling of fire and grazing. Conservation Biology 23:588–598.
- Fuhlendorf, S.D., and D.M. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. BioScience 51(8):625–632.
- Fuhlendorf, S.D., W.C. Harrell, D.M. Engle, R.G. Hamilton, C.A. Davis, and D.M. Leslie. 2006. Should heterogeneity be the basis for conservation? Grassland bird response to fire and grazing. Ecological Applications 16:1706–1716.
- Gannon, J.J., C.S. Dixon, S.C. Vacek, and B.A. Walker. 2025. Burning Questions: Synchronizing prescribed fire to *Bromus inermis* phenology. Prairie Naturalist Special Issue 2:19–39.
- Gasch, C., L. Gerhard and K. Sedivec. 2019. Shallow soil thermal and hydrological conditions beneath Kentucky Bluegrass thatch and in response to thatch removal. NDSU Central Grasslands Research Extension Center Annual Report: NDSU Extension. 37–41 pp.
- Gasch, C.K., S.V. Huzurbazar, A.F. Wick, and P.D. Stahl. 2016. Assessing impacts of Crested Wheatgrass and native species establishment on soil characteristics in reclaimed land using Bayesian posterior predictive distributions. Land Degradation and Development 27:521–531.
- 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.K. Nouwakpo, and K. 2020. Kentucky Bluegrass invaded rangeland: Ecosystem implications and adaptive management approaches. Rangelands 42:106–116.

- Gerhard, L., C. Gasch, and K. Sedivec. 2019. Soil Nutrient and Microbial Response to Kentucky Bluegrass Invasion and Land Management Techniques. Central Grasslands Research Extension Center Annual Report.
- 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. Resiliency of Native Prairies to Invasion by Kentucky Bluegrass, Smooth Brome, and Woody Vegetation. *Rangeland Ecology and Management* 73:321–328.
- Grant, T.A., T.L. Shaffer, and B. Flanders. 2020b. 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.
- Goergen, E.M., and J.C. Chambers. 2009. Influence of a native legume on soil N and plant response following prescribed fire in sagebrush steppe. *International Journal of Wildland Fire* 18: 665–675.
- Hartnett, D.C., and G.W. Wilson. 1999. Mycorrhizae influence plant community structure and diversity in tallgrass prairie. *Ecology* 80(4):1187–1195.
- Heidinga, L., and S.D. Wilson. 2002. The impact of an invading alien grass (*Agropyron cristatum*) on species turnover in native prairie. *Diversity and Distributions* 8(5):249–258.
- Heinen, R., A. Biere, J.A. Harvey, and T.M. Bezemer. 2018. Effects of soil organisms on aboveground plant-insect interactions in the field: Patterns, mechanisms and the role of methodology. *Frontiers in Ecology and Evolution* 6:106. <https://doi.org/10.3389/fevo.2018.00106>.
- Henderson, D.C., and M.A. Naeth. 2005. Multi-scale impacts of Crested Wheatgrass invasion in mixed-grass prairie. *Biological Invasions* 7:639–650.
- Hendrickson, J.R., K.K. Sedivec, D. Toledo, and J. Printz. 2019. Challenges facing grasslands in the Northern Great Plains and North Central Region. *Rangelands* 41:23–29.
- Hendrickson, J. R., M.A. Liebig, J. Printz, D. Toledo, J.J. Halvorson, R.G. Christensen, and S.L. Kronberg. 2021. Kentucky Bluegrass impacts diversity and carbon and nitrogen dynamics in a Northern Great Plains rangeland. *Rangeland Ecology and Management* 79:36–42.
- Hilbig, B.E., and E. B. Allen. 2015. Plant-soil feedbacks and competitive interactions between invasive *Bromus diandrus* and native forb species. *Plant and Soil* 392:191–203.
- Hilfer, H., and R. Limb. 2020. Thatch Removal: A New Method for Managing Kentucky Bluegrass in the Northern Great Plains. NDSU Central Grasslands Research Extension Center Annual Report.
- Hillel, D. 2004. *Introduction to Environmental Soil Physics*. Elsevier-Academic Press, Amsterdam, The Netherlands. 494 pp.
- Hoekstra, J.M., T.M. Boucher, T.H. Ricketts, and C. Roberts. 2005. Confronting a biome crisis: Global disparities of habitat loss and protection. *Ecology Letters* 8(1):23–29.
- Hulet, A., B.A. Roundy, and B. Jessop. 2010. Crested Wheatgrass control and native plant establishment in Utah. *Rangeland Ecology and Management* 63:450–460.
- Jones, C.G., J.H. Lawton, and M. Shachak. 1994. Organisms as ecosystem engineers. *Oikos* 689:373–386.
- Jones, C.G., J.H. Lawton, and M. Shachak. 1997a. Ecosystem engineering by animals: Why semantics matters. *Trends Ecology and Evolution* 12:275.
- Jones, C.G., J.H. Lawton, and M. Shachak. 1997b. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology* 78:1946–1957.
- Jordan, N.R., L. Aldrich-Wolfe, S.C. Huerd, D.L. Larson, and G. Muehlbauer. 2012. Soil-occupancy effects of invasive and native grassland plant species on composition and diversity of mycorrhizal associations. *Invasive Plant Science and Management* 5:494–505.
- Jordan, N.R., D.L. Larson, and S.C. Huerd. 2008. Soil modification by invasive plants: Effects on native and invasive species of mixed-grass prairies. *Biological Invasions* 10:177–190.
- Kardol, P., T.M. Bezemer, and W.H. van der Putten. 2006. Temporal variation in plant-soil feedbacks controls succession. *Ecology Letters* 9:1080–1088.
- Klironomos, J.N. 2002. Feedback with soil biota contributes to plant rarity and invasiveness in communities. *Nature* 417(6884):67–70.

- Kramer, T.D., R.J. Warren, Y. Tang, and M.A. Bradford. 2012. Grass invasions across a regional gradient are associated with declines in belowground carbon pools. *Ecosystems* 15:1271–1282.
- Lamb, E.G. 2008. Direct and indirect control of species richness and evenness by litter, resources, and biomass. *Ecology* 89:216–225.
- Lamb, E.G., T. Winsley, C.L. Piper, S.A. Freidrich, and S.D. Siciliano. 2016. A high-throughput belowground plant diversity assay using next-generation sequencing of the trnL intron. *Plant and Soil* 404:361–372.
- Larson, J.L., R.C. Venette, and D.L. Larson. 2022. Restoration for resilience: The role of plant–microbial interactions and seed provenance in ecological restoration. *Natural Areas Journal* 42(2):152–159.
- Lesica, P., and S.V. Cooper. 2019. Choosing native species for restoring Crested Wheatgrass fields on the great plains of northeast Montana. *The American Midland Naturalist* 181:327–334.
- Lesica, P., and T.H. DeLuca. 1996. Long-term harmful effects of Crested Wheatgrass on Great- plains grassland ecosystems. *Journal of Soil and Water Conservation* 51:408–409.
- Letts, B., E.G. Lamb, J.M. Mischkolz, and J.T. Romo. 2015. Litter accumulation drives grassland plant community composition and functional diversity via leaf traits. *Plant Ecology* 216: 357–370.
- Levine, J.M., C.M.D. Antonio, J.S. Dukes, K. Grigulis, and S. Lavorel. 2003. Mechanisms underlying the impacts of exotic plant invasions. *Proceedings of the Royal Society of London* 270:775–781.
- Levine, J.M., E. Pachepsky, B.E. Kendall, S.G. Yelenik, and J.H.R. Lambers. 2006. Plant–soil feedbacks and invasive spread. *Ecology letters* 9(9):1005–1014.
- Li, Z., E.G. Lamb, C.L. Piper, and S.D. Siciliano. 2018. Plant belowground diversity and species segregation by depth in a semi-arid grassland. *Écoscience* 25:1–7.
- Liang, X., D. Su, Z. Wang, and X. Qiao. 2017. Effects of turfgrass thatch on water infiltration, surface runoff, and evaporation. *Journal of Water Resource and Protection* 9(7):799–810.
- Mahaney, W.M., K.A. Smemo, and K.L. Gross. 2008. Impacts of C4 grass introductions on soil carbon and nitrogen cycling in C3-dominated successional systems. *Oecologia* 157:295–305.
- Mamet, S.D., E.G. Lamb, C.L. Piper, T. Winsley, and S.D. Siciliano. 2017. Archaea and bacteria mediate the effects of native species root loss on fungi during plant invasion. *ISME J.* 11:1261–1275.
- Mamet, S.D., E. Redlick, M. Brabant, E.G. Lamb, B.L. Helgason, K. Stanley, and S.D. Siciliano. 2019. Structural equation modeling of a winnowed soil microbiome identifies how invasive plants re-structure microbial networks. *The ISME Journal*. 13:1988–1996.
- Mangla, S., and R.M. Callaway. 2008. Exotic invasive plant accumulates native soil pathogens which inhibit native plants. *Journal of Ecology* 96:58–67.
- McAdoo, J.K., J.C. Swanson, P.J. Murphy, and N.L. Shaw. 2017. Evaluating strategies for facilitating native plant establishment in northern Nevada Crested Wheatgrass seedings. *Restoration Ecology* 25:53–62.
- McWilliams, J.L., and P.E. Van Cleave. 1960. A comparison of Crested Wheatgrass and native grass mixtures seeded on rangeland in eastern Montana. *Rangeland Ecology and Management / Journal of Range Management Archives* 13:91–94.
- Morris, C., L.R. Morris, and T.A. Monaco. 2019. Evaluating the effectiveness of low soil-disturbance treatments for improving native plant establishment in stable Crested Wheatgrass stands. *Rangeland Ecology and Management* 72:237–248.
- Mummey, D.L., and P.W. Ramsey. 2017. Can sainfoin improve conditions for establishment of native forbs in Crested Wheatgrass stands? *Ecological Restoration* 35:127–137.
- Nafus, A.M., T.J. Svejcar, and K.W. Davies. 2020. Native vegetation composition in Crested Wheatgrass in northwestern great basin. *Rangeland Ecology and Management* 73:9–18.
- Newell, L.C., and F.D. Keim. 1943. Field performance of brome grass strains from different regional seed sources. *Agronomy Journal*. 35:420–434.
- Nouwakpo, S.K., D. Toledo, M. Sanderson, and M. Weltz. 2019. Under-standing 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(4):360–371.
- Otfinowski, R., and N. Kenkel. 2008. Clonal integration facilitates the proliferation of smooth brome clones invading northern fescue prairies. *Plant Ecology*. 199:235–242.

- Otfinowski, R., N.C. Kenkel, and P.M. Catling. 2007. The biology of Canadian weeds. 134. *Bromus inermis* Leyss. Canadian Journal of Plant Science. 87:183–198.
- 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.
- Parker, I.M., D. Simberloff, and W.M. Lonsdale, K. Goodell, M. Wonham, P.M. Kareiva, M.H. Williamson, B. Von Holle, P.B. Moyle, J.E. Byers and L. Goldwasser. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1:3–19.
- Perkins, L.B., and R.S. Nowak. 2012. Soil conditioning and plant–soil feedbacks affect competitive relationships between native and invasive grasses. Plant Ecology 213:1337–1344.
- Phoenix, G.K., W.K. Hicks, S. Cinderby, J.C.I. Kuylenstierna, W.D. Stock, F.J. Dentener, K.E. Giller, A.T. Austin. et al. Atmospheric nitrogen deposition in world biodiversity hotspots: The need for a greater global perspective in assessing N deposition impacts. 2006. Global Change. Biology 12:470–476.
- Piper, C., E. Lamb, and S. Siciliano. 2015a. Smooth Brome changes gross soil nitrogen cycling processes during invasion of a rough fescue grassland. Plant Ecology. 216:235–246.
- Piper, C.L., S.D. Siciliano, T. Winsley, and E.G. Lamb. 2015b. Smooth Brome invasion increases rare soil bacterial species prevalence, bacterial species richness and evenness. Journal of Ecology. 103:386–396.
- Pringle, A., J.D. Bever, M. Gardes, J.L. Parrent, M.C. Rillig, and J.N. Klironomos. 2009. Mycorrhizal symbioses and plant invasions. Annual Review of Ecology Evolution and Systematics 40:699–715.
- 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.
- Pyšek, P., and D.M. Richardson. 2010. Invasive species, environmental change and management, and health. Annual Review of Environment and Resources 35:25–55.
- Reinhart, K.O., and M.J. Rinella. 2021. Molecular evidence for impoverished mycorrhizal communities of *Agropyron cristatum* compared with nine other plant species in the Northern Great Plains. Rangeland Ecology and Management 74:147–150.
- Ruiz, G.M., P. Fofonoff, A.H. Hines, and E.D. Grosholz. 1999. Non-indigenous species as stressors in estuarine and marine communities: Assessing impacts and interactions. Limnology and Oceanography 44:950–972.
- Salesman, J.B., and M. Thomsen. 2011. Smooth Brome (*Bromus inermis*) in tallgrass prairies: A review of control methods and future research directions. Ecological Restoration. 29:374–381.
- Salimbayeva, K. 2021. Temporal dynamics of plant-soil feedbacks and community consequences during *Bromus inermis* invasion. M.S. Thesis. Department of Biological Sciences, University of Alberta. 74 pp.
- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. BioScience 44(5):418–421.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. Wildlife. Society. Bulletin 32:6–15.
- Sanderson, M.A., H. Johnson, M.A. Liebig, J.R. Hendrickson, and S.E. Duke. 2017. Kentucky Bluegrass invasion alters soil carbon and vegetation structure on Northern Mixed-Grass prairie of the United States. Invasive Plant Science and Management 10:9–16.
- Shivega, W.G., and L. Aldrich-Wolfe. 2017. Native plants fare better against an introduced competitor with native microbes and lower nitrogen availability. AoB Plants 9(1): plx004.
- Simberloff, D., and L. Gibbons. 2004. Now you see them, now you don't!—population crashes of established introduced species. Biological Invasions 6:161–172.
- Slopek, J.I., and E.G. Lamb. 2017. Long-term efficacy of Glyphosate for Smooth Brome control in native prairie. Invasive Plant Science and Management. 10:350–355.
- Simmons, M.T., S. Windhager, P. Power, J. Lott, R.K. Lyons, and C. Schwoppe. 2007. Selective and non-selective control of invasive plants: The short-term effects of growing-season prescribed fire, herbicide, and mowing in two Texas prairies. Restoration Ecology 15:662–669.

- Smoliak, S., and J.F. Dormaar. 1985. Productivity of Russian wildrye and Crested Wheatgrass and their effect on prairie soils. *Journal of Range Management* 38:403–405.
- Stotz, G.C., E. Gianoli, and J.F. Cahill. 2018. Maternal experience and soil origin influence interactions between resident species and a dominant invasive species. *Oecologia*. 186:247–257.
- 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. 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.
- Suding, K.N., W. Stanley Harpole, T. Fukami, A. Kulmatiski, A.S. MacDougall, C. Steinand, and W.H. van der Putten. 2013. Consequences of plant–soil feedbacks in invasion. *Journal of Ecology* 101(2):298–308.
- Toledo, D., M. Sanderson, K. Spaeth, J. Hendrickson, and J. Printz. 2014. Extent of Kentucky Bluegrass and its effects on native plant species diversity and ecosystem services in the Northern Great Plains of the USA. *Invasive Plant Science and Management* 7:543–552.
- Trognitz, F., E. Hackl, S. Widhalm, and A. Sessitsch. 2016. The role of plant–microbiome interactions in weed establishment and control. *FEMS Microbiology Ecology* 92(10):138.
- Uchytel, R.R. 1993. *Poa pratensis*. USDA Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory.
- USDA NRCS. 2021. USDA PLANTS Database: *Agropyron cristatum* (L.) Gaertn. Available online at <https://plants.sc.egov.usda.gov/home/plantProfile?symbol=AGCR>. Accessed 12 April 2024.
- van der Putten, W.H., J.N. Klironomos, and D.A. Wardle. 2007. Microbial ecology of biological invasions. *ISME Journal* 1:28–37.
- van der Putten, W.H., R.D. Bardgett, J.D. Bever, T.M. Bezemer, B.B. Casper, T. Fukami, et al. 2013. Plant–soil feedbacks: The past, the present and future challenges. *Journal of Ecology* 101:265–276.
- van der Putten, W.H., M.A. Bradford, E. Pernilla Brinkman, T.F. van de Voorde, and G.F. Veen. 2016. Where, when, and how plant–soil feedback matters in a changing world. *Functional Ecology* 30(7):1109–1121.
- Vaness, B.M., and S.D. Wilson. 2007. Impact and management of Crested Wheatgrass (*Agropyron cristatum*) in the northern Great Plains. *Canadian Journal of Plant Science*. 87:1023–1028.
- Vinton, M., and E. Goergen. 2006. Plant and soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems*. 9: 967–976.
- Voroney, R.P. 2007. The soil habitat. Pp. 25–49, In E.A. Paul (Ed.). *Soil Microbiology, Ecology, and Biochemistry*. Academic Press, Amsterdam, The Netherlands. 532 pp.
- Wallace, B.M., M. Krzic, T.A. Forge, K. Broersma, and R.F. Newman. 2009. Biosolids increase soil aggregation and protection of soil carbon five years after application on a Crested Wheatgrass pasture. *Journal of Environmental Quality* 38:291–298.
- Wedin, D.A., and D. Tilman. 1990. Species effects on nitrogen cycling: A test with perennial grasses. *Oecologia* 84:433–441.
- Wengreen, K.A., M. Frisina, J.L. Hager, and B.F. Sowell. 2016. Restoring Crested Wheatgrass stands to big sagebrush for improved sage-grouse habitat: A literature review. *Environmental Management and Sustainable Development* 5:129–149.
- Williams, J.L., and E.E. Crone. 2006. The impact of invasive grasses on the population growth of *Anemone patens*, a long-lived native forb. *Ecology*. 87:3200–3208.
- Williams, J.R., L.R. Morris, K.L. Gunnell, J.K. Johanson, and T.A. Monaco. 2017. Variation in sagebrush communities historically seeded with Crested Wheatgrass in the eastern great basin. *Rangeland Ecology and Management* 70:683–690.
- Williamson, M. 1996. *Biological invasions*. Springer Science and Business Media.
- Wilson, S.D., and M. Pärtel. 2003. Extirpation or coexistence? Management of a persistent introduced grass in a prairie restoration. *Restoration Ecology* 11(4):410–416.
- Wolfe, B.E., B.C. Husband, and J.N. Klironomos. 2005. Effects of a belowground mutualism on an aboveground mutualism. *Ecology Letters* 8:218–223.

- Xiong, S., and C. Nilsson. 1999. The effects of plant litter on vegetation: A meta-analysis. *Journal of Ecology*. 87:984–994.
- Yang, S., W. Liu, C. Qiao, J. Wang, M. Deng, B. Zhang, and L. Liu. 2019. The decline in plant biodiversity slows down soil carbon turnover under increasing nitrogen deposition in a temperate steppe. *Functional Ecology* 33:1362-1372.
- Zlatnik, E. 1999. Fire effects information system, online database, species: *Agropyron cristatum*. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory. Available online at: <https://www.fs.fed.us/database/feis/plants/graminoid/agrcr/all.html>. Accessed 12 April 2024.