IMPACTS OF INVASIVE PLANT SPECIES ON THE PLANT COMMUNITY IN THE

NORTHERN GREAT PLAINS

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Title

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MASTER OF SCIENCE

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ABSTRACT

Invasive species are encroaching rangelands in the U.S. and altering community composition and plant diversity. In the Northern Great Plains, exotic cool-season perennial grasses (Kentucky bluegrass, *Poa pratensis*; crested wheatgrass, *Agropyron cristatum*; smooth brome, *Bromus inermis*) have invaded rangelands with their ecological impacts less understood. This study analyzed a long-term (13-year) and landscape-scale dataset to identify potential impacts on site richness, diversity, community composition shifts, and species tolerant of invasion by Kentucky bluegrass, crested wheatgrass, and smooth brome. We found these three invaders cumulatively are associated with decreased site richness, maximum richness, and site diversity, especially native forb diversity. Clayey and loamy sites had a shift in plant community composition when invaded with Kentucky bluegrass and smooth brome. Clayey, loamy and limy residual ecological sites were more likely to be invaded, while very shallow, shallow loamy, and thin loamy sites were least likely to be invaded by cool-season invasive perennials.

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DEDICATION

I dedicate this thesis to my grandparents- Gary and Norma Bradow and LeRoy and Marilyn

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LIST OF ABBREVIATIONS

U.SUnited States
NGPNorthern Great Plains
CWCrested Wheatgrass
YSYellow Sweetclover
LSLeafy Spurge
CTCanada Thistle
JBJapanese Brome
DBDowny Brome
ANNBROAnnual Bromes
KBKentucky Bluegrass
SBSmooth Brome
NDNorth Dakota
NRCSNatural Resources Conservation Service
USFSUnited States Forest Service
ESDEcological Site Description
MLRAMajor Land Resource Area
LMNGLittle Missouri National Grasslands
NMGPNorthern Mixed Grass Prairie
GRNGGrand River National Grasslands
CIPCool-Season Invasive Perennials
NMDSNon-Metric Multidimensional Scaling
STMState and Transition Model

CHAPTER 1. INVASIVE PLANTS DECREASE PLANT DIVERSITY AND HAVE VARYING EFFECTS ON HERBAGE PRODUCTION IN THE NORTHERN GREAT PLAINS: A REVIEW

Introduction

Invasive plants comprise over half of the most widely distributed plant species in North America (Stohlgren et al., 2011). This proportion is double that seen in Argentina and Africa, and 50 times that seen in Europe (Stohlgren et al., 2011). Invasive species are a main cause for landscape plant species' homogenization (Stohlgren et al., 2011) and a decrease in native species richness (Gaertner et al., 2009; Ndhlovu et al., 2016). This invasion has become even more prevalent in rangelands of the United States (U.S.), which comprise 34.2% of the total land area (Loomis, 2002). Rangelands have experienced a dramatic increase in the presence of invasive species over the past 50 years (USDA, 2014), and more recently we have seen this occur in the Northern Great Plains (NGP; DeKeyser et al., 2013). Rangelands of the NGP provide an important agricultural value for livestock production while providing many ecosystem services for humans including recreation and critical pollination services (Samson et al., 2004). Many of these services rely on herbage production and plant diversity. This review will highlight areas of concern for the NGP and gaps in research. We will focus on the impacts of invasive plant species in the NGP rangelands.

Spread of Invasive Species

Invasive species are typically non-native and spread readily, often at the expense of the native species and cause environmental or economic harm (Beck et al., 2006). Invasive species have a strong propensity to establish and spread, deteriorating rangeland. Invasive species Tolerance for harsh conditions, ability to out-compete native plants and easier establishment

combine to aid in their spread (Ditomaso, 2000; James and Drenovsky, 2007; DeKeyser et al., 2015). The removal of fire, grazing pressure, and other disturbances is advantageous to some invasive species, such as Kentucky bluegrass, as periods of non-use or light-use on rangelands have expedited its expansion (DeKeyser et al., 2009; Toledo et al., 2014). Other invasive species have had similar successes (Carter and Lym, 2017).

Invasive species are widespread on rangelands in the U.S. (Figure 1; USDA, 2014). In some cases, these invasive species actually exceed the native species on the landscape (Figure 2; USDA, 2014). Plant communities and their functions are altered due to the increasing distribution and concentration of invasive plants. The impacts of invasive species always start small, but can expand to the presence displayed in Figure 1.

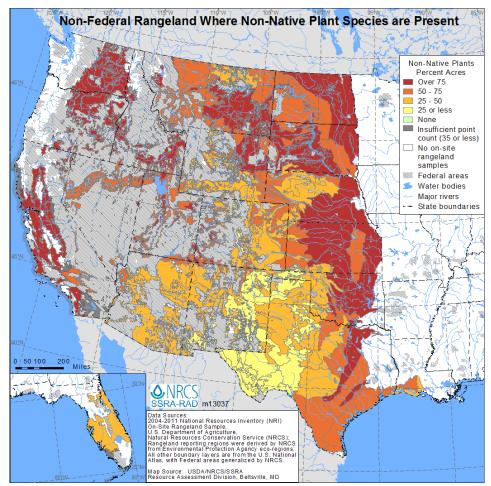


Figure 1. Presence of invasive plant species across the western U.S. (USDA, 2014).

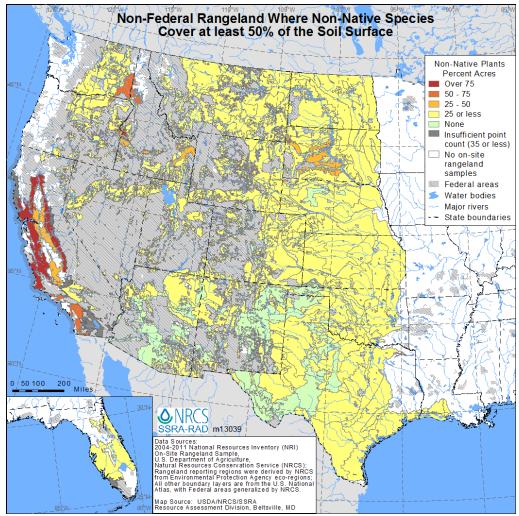


Figure 2. Presence of invasive plant species cover comprising 50 percent or greater of the soil surface across the western U.S. (USDA, 2014).

Invasive Species' Impact on the Landscape

The consequences of invasive plants to the landscape can be great, as reviewed by Vilà et al. (2011), and have a significant impact on many ecosystem functions. Worldwide, invasive plants decrease native species diversity, animal production, animal diversity, and litter decomposition. Some invasive plants were found to increase herbage production and soil microbial activity (Vilà et al., 2011). The review from Vilà et al. (2011) did not differentiate between species and broadly covered all invasive plants worldwide. In contrast, this review gains a better understanding of the impacts of invasive plants in the smaller NGP region by breaking down differences between species. Depending on the invasive species, different impacts can result from their invasion. This includes how they alter the environment around them, how they impact plant diversity or herbage production (West, 1993; DiTomaso, 2000).

Understanding species-specific patterns is important to allow for better management of invaded areas. Biodiversity and herbage production are crucial to many benefits on rangeland, and should be protected (Middleton and Grace 2004; Mangold et al., 2018). Biodiversity on rangelands supports resilience and resistance to invasion (Smith and Knapp, 1999). Once invaded, many of these invasive species are able to alter their environment and create new stable states where reversal to the previous native community is extremely difficult to attain (McIver et al., 2010; Bagchi et al., 2013; Toledo et al., 2014). Certain invasive species reduce rangeland's total herbage production, thus reducing the amount of livestock or wildlife it can support (Kobayashi et al., 2014). Many studies have analyzed the economic impacts of invasive species, and all have found a great expenditure devoted to the management of these troublesome species (Duncan et al., 2004; Mangold et al., 2018; Hendrickson et al., 2019). The dynamics of the various invasive species in the NGP need to be understood to determine management strategies to combat their spread and impacts (Bestelmeyer, 2006).

Invasive Species in the Northern Great Plains

The spread of invasive plant species has greatly impacted rangelands of the NGP. The NGP encompasses land in five different U.S. states and three Canadian provinces, with a grassland community now compromised by many invaders. The common invaders to the area were introduced in a variety of ways and impact the surrounding ecosystem differently (Table 1; DeKeyser et al., 2009).

Table 1. Common invasive plant species found in the Northern Great Plains, their potential sources, and how they alter their environment.

Invasive Plant Species	Purpose for introduction	Consequences	Citation
Kentucky Bluegrass (Poa pratensis)	Widely used in turfgrasses for lawns and grazing fields	Is active early in the growing season and can out-compete native species. Can create a thatch layer altering plants' microclimate	(DeKeyser et al., 2009, 2015; Toledo et al., 2014)
Cheatgrass (Bromus tectorum)	Cheatgrass Potentially through		(Zouhar, 2003; Mealor et al., 2012)
Japanese Brome (Bromus japonicus)	Unknown	Early maturation and seed dispersal	(Haferkamp and Heitschmidt, 1999)
Crested Wheatgrass (Agropyron cristatum)	Planted for soil protection of abandoned fields beginning in the 1930s; later seeded for early season, improved pasture, and hay land	Produces a homogenous stand	(Looman and Heinrichs, 1973)
Smooth Brome (Bromus inermis)	Interseeded for improved pastures, seeded for hay land	Aggressively colonizes and out-competes native species, thrives under non-use management of grasslands	(Duebbert et al., 1981)
Leafy Spurge (Euphorbia esula)	Spread through oat seeds	Creates large seed banks and out-competes native species	(Bakke, 1936; Haines et al., 2013)
Canada Thistle (Cirsium arvense)	Likely accidentally introduced in crops or hay	Out-competes native species and proliferates when disturbed	(Zouhar, 2001)
Sweetclovers (<i>Melilotus officionale</i> or <i>M. albus</i>)	Interseeded for improved pastures; seeded as a green manure crop and hay land	Increase nitrogen levels and alter species competition	(Duebbert et al., 1981; Van Riper and Larson, 2009; Van Riper et al., 2010)

Due to their quick establishment, herbage value, or drought tolerance, many invasive plant species were introduced purposefully with the intent of improving pastures, developing new pastures and hay lands, and conservation plantings (Looman and Heinrichs, 1973; Duebbert et al., 1981). Others were accidentally introduced with harsh consequences (Haferkamp and Heitschmidt, 1999; Zouhar, 2001). All invasive plants possess competitive characteristics allowing them to alter the surrounding plant community (Howard, 1996; Zouhar, 2003; Van Riper and Larson, 2009; Haines et al., 2013; DeKeyser et al., 2015). Many anthropogenic means caused the invasion and we must understand their consequences to develop best management practices to help deal with them.

Current Research on Invasive Species in the Northern Great Plains

The NGP is a large ecoregion of the U.S. and Canada. It is primarily comprised of mixedgrass and short-grass prairie, and is a productive system (Hendrickson et al., 2019). This review only covers studies located in the NGP ecoregion Figure 3. Studies conducted in the Nebraska Sandhills (not shown in Figure 3) were also included in the review.



Figure 3. The Northern Great Plains Ecoregion (light green), which also includes the Nebraska Sandhills Region in northern Nebraska (Hendrickson et al., 2019).

To better understand why invasive plants affect native plant diversity, herbage production, and ecosystem services, more research is needed despite the quantity and quality of existing studies. Biological invasions of all kinds, as reviewed by Lowry et al. (2013), have been extensively studied, with a significant rise in research after 2003. They found that many of the studies focused on the cause of invasions rather than the impacts of the invaders, many were field observational studies, and most were on primary producers (plants; Lowry et al., 2013). Although there were 1,200 studies focused on plants, these studies are spread across all continents and vegetation types (Lowry et al., 2013). Many different interactions in a rangeland community combine to create the ecosystem, and factors like weather, elevation, soil type, species composition, grazing, and microbes play a role (Naiman, 1988). Therefore, it is sometimes difficult to generalize studies from one ecosystem to another.

The interactions of invasive species in the NGP will be slightly different from in other plant communities. This review will provide a more detailed review for invasive plants in the NGP compared to the more comprehensive review from Vilà et al. (2011). For example, there has been a plethora of studies identifying the consequences of invasive bromegrasses and woody encroachment in the Great Basin (Young et al., 1972; Young and Evans, 1973; Young and Longland, 1996; Bradley and Mustard, 2005; Creutzburg et al., 2011; Mealor et al., 2012; Gasch et al., 2013). Smooth brome and Kentucky bluegrass are two cool-season perennial non-native grasses invading rangelands in the NGP, and the consequences in this ecosystem are less understood (DeKeyser et al., 2013). Through this review, interactions not studied, or studied extensively in the NGP will be identified. The NGP ecosystem is vital to understand invasive species' impacts on wildlife habitat and livestock production. The NGP has long been recognized for having a unique ecosystem valuable to many wildlife species (Johnson, 2000; Higgins et al., 2002; Kirby et al., 2002). It is also extremely valuable to the livestock industry of the U.S., as ruminant animals can take advantage of the vast landscapes of grassland herbage (Hodur et al., 2007). Therefore, the protection of these assets is crucial for the future of the NGP.

Pollinators, wildlife habitat, and livestock production are dependent on the plant diversity and herbage production on rangelands (Middleton and Grace, 2004; Mangold et al., 2018). Therefore, the first objective of this paper is to analyze how invasive species in the NGP have influenced plant diversity and herbage production. Because some invasive species are more prevalent in other regions or are relatively new to the NGP, identification of gaps in the research is needed. The second objective for this paper is to identify what research has been done in this realm and areas for development.

Methods

A Web of Science search was done to identify studies on invasive species in the NGP. Specific criteria were used to choose which studies to use (Table 2). During this search, three reviews of different invasive species, or papers on current conditions of the NGP were identified (Christian and Wilson, 1999; DeKeyser et al., 2013; Toledo et al., 2014). These reviews also identified studies that mentioned any invasive species that impacted herbage production, community composition, or diversity. In total, this review will analyze the results of 22 studies that fit our search for the NGP.

Criteria:	Specification:	Purpose
Location	Within the Northern Great Plains region	To identify interactions and impacts of invasive species on the plant community and identify future research needs
Study Design	Rangeland field study Excluded a crop or planting study	There are many weed management strategies for crops; however, this review focuses on rangelands.
Species of Interest	Any invasive plant species	This review only pinpointed plant community interactions.
Results	Provide a difference between invaded and non-invaded sites on measures of diversity or herbage production	This identifies how invasive plants impact the land.
Other Study Variables	 Studies involving herbicide application- only results of different control pastures (those without herbicide application) were used to compare invaded and non- invaded sites Studies involving different grazing applications- grazing strategies were not analyzed in this study; only control pastures were used within this review 	A few of the results used in this review were from studies with a larger context/question and the invasion level impacts on the plant community was the focus for this review, so the other variables within these studies were excluded.

Table 2. Search criteria for the Northern Great Plains Invasive Species Study.

The 22 studies were unique; therefore, compiling their results required discretion and an understanding of their differences. The location, species of focus, variables tested, methods of sampling, etc. varied. Therefore, a vote-counting method of analysis (Cooper, 1998) was utilized for this group of studies. For each of the two measures, herbage production and biodiversity, if invasion had a significant negative impact, a significant positive impact, or an insignificant impact, it was designated as a -1, +1, and 0, respectively. If one study analyzed the effects of two different invasive species (eg. Kentucky bluegrass and smooth brome) separately, then both species were individually assessed within the review. Some studies analyzed many invasive

species at once and did not differentiate the invasion. Therefore, the invasive species in that study were grouped (Stohlgren et al., 1999; Ogle et al., 2003; Haines et al., 2013). Additionally, if a study had multiple locations with significant differences to the native plant community (i.e. a western wheatgrass dominated vs. a needle-and-thread dominated community), both were considered independently in the review if their results were explained independent of one another. With these expansions, the 22 studies in this review provided 25 unique interactions. In studies with different levels of invasion, the highest difference was considered in this review. For example, if there was a native, low invasion, and high invasion classification; the native and high invasion would be contrasted. To find areas studied and those that are understudied for Objective 2, the methods of each study were analyzed to know if they fit the criteria of the study. The location, species, number of sites, and measure of either diversity or herbage production were categorized.

Trends were identified from the analysis of the studies on invasive species' impacts on herbage production and biodiversity in the NGP. Some of the studies observed impacts on either herbage production or plant diversity and some observed impacts on both. Total herbage production and native plant production were separated in this review as a few studies analyzed both (Table 3).

Table 3. Results of all studies included in the northern great plains invasive species review. Row colors depict the various invasive species. ¹ Species included: CW= Crested Wheatgrass, YS= Yellow Sweetclover, LS= Leafy Spurge, CT= Canada Thistle, JB= Japanese Brome, DB= Downy Brome, ANNBRO= Annual Bromes, BG= Bluegrasses, KB= Kentucky Bluegrass, SB= Smooth Brome, ALL= Any invasive. (-), (+), 0 represents a negative, positive, or no significant impact on either plant diversity or herbage production; respectively.

Study	Species	Diversity	Total Herbage Production	Native Herbage Production	Location
Heidinga and Wilson, 2002	CW	(-)			Saskatchewan, Canada
Henderson and Naeth, 2005	CW	(-)	(+)		Saskatchewan, Canada
Looman and Heinrichs, 1973	CW		(+)		Saskatchewan, Canada
Smoliak and Dormaar, 1985	CW		(+)		Alberta, Canada
Sutter and Brigham, 1998	CW	(-)			Saskatchewan, Canada
Christian and Wilson 1999	CW	(-)			Saskatchewan, Canada
Van Riper and Larson, 2009	YS	0			SD
Van Riper and Larson, 2009	YS	(+)			SD
Larson and Larson, 2010	LS	(-)	0	(-)	ND
Hein and Miller, 1992	LS		(-)		MT
Belcher and Wilson, 1989	LS	(-)			Manitoba, Canada
Trammell and Butler, 1995	LS	0	(+)	(-)	ND
Butler and Cogan,2004	LS	(-)			ND
Lym and Kirby, 1987	LS		(-)		ND
Carter and Lym, 2017	CT			0	ND
Haferkamp and Heitschmidt, 1999	JB		(+)	(-)	MT
Haferkamp et al., 1997	JB			(-)	MT
Ogle et al., 2003	DB, JB		(-)		SD
Ashton et al., 2016	ANNBRO	(-)			7 National Parks
Trammell and Butler, 1995	ANNBRO	0	(+)	(-)	ND
Kral-O'Brien et al., 2019	BLUEGRASSES	(-)			ND and NE SD
DeKeyser et al., 2013	KB, SB	(-)			ND
Haines et al., 2013	LS, SB, KB	(-)			ND
Stohlgren et al., 1999	ALL	(-)			SD
Stohlgren et al., 1999	ALL	(-)			WY

Impacts of Invasive Species on Plant Species Diversity

Seventeen studies identified impacts of invasive plants on plant diversity in the NGP. Out of these 17 studies, 13 reported invasion decreased plant diversity in the community; additionally, three studies reported no difference and one study reported an increase in diversity with invasion of yellow sweetclover. Only Van Riper and Larson (2009), and Trammel and Butler (1995) reported either no difference or an increase in plant diversity with an increase in yellow sweetclover, leafy spurge, or annual bromes. Overall, invasive plant species have a detrimental effect on plant diversity of rangelands of the NGP. Data on bluegrass species, crested wheatgrass, bromegrasses, and leafy spurge all support that plant diversity decreases as invasive plant species increase (Belcher and Wilson, 1989; Sutter and Brigham, 1998; Christian and Wilson, 1999; Stohlgren et al., 1999; Heidinga and Wilson, 2002; Butler and Cogan, 2004; Henderson and Naeth, 2005; Larson and Larson, 2010; DeKeyser et al., 2013; Haines et al., 2013; Ashton et al., 2016; Kral-O'Brien et al., 2019). This finding is similar to the broad invasive plant species review by Vilá et al. (2011).

Only Van Riper and Larson (2009) reported either no impact or a positive impact on native species cover invaded with yellow sweetclover. This study occurred on a western wheatgrass (*Pascopyron smithii*) - green needlegrass (*Nassella viridula*)-dominated plant community that was sparsely vegetative and comprised of broom snakeweed (*Gutierrezia sarothrae*) and stiff sunflower (*Helianthus pauciflorus*) in the Badlands National Park in South Dakota. Trammel and Butler (1995) was the only study that reported no difference in plant diversity from leafy spurge and annual brome invasion on the Theodore Roosevelt National Park in western North Dakota (ND). Similar to Van Riper and Larson (2009), their study was located on semi-arid rangeland.

Plant diversity feeds into many of the ecosystem goods and services rangelands provide (Middleton and Grace, 2004). Therefore, maintaining diversity is crucial to rangeland management (Panetta and Gooden, 2017). With only 63% of the historic NGP rangelands remaining, these lands are pivotal to ensure wildlife and pollinators are sustained in the future (Kirby et al., 2002; Samson et al., 2004; Hendrickson et al., 2019; Kral-O'Brien et al., 2019). Sutter and Brigham (1998) found that reduced plant diversity in pastures invaded by crested wheatgrass contributed to the decline in grassland songbirds' population and diversity. Other

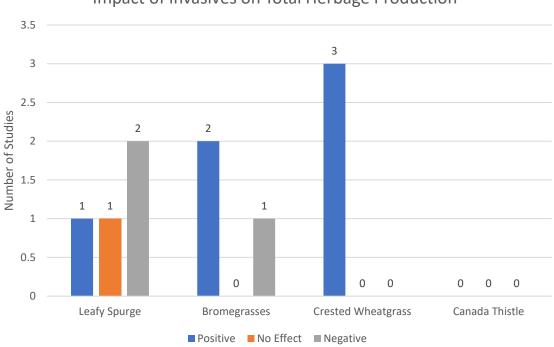
studies found cattle use (Lym and Kirby, 1987) and ungulate use, such as deer, bison, etc. (Trammell and Butler, 1995) declined as leafy spurge increased. Kral-O'Brien et al. (2019) reported increasing Kentucky bluegrass cover reduced the abundance and diversity of obligate grassland butterflies in the community. Our review reflects the results of a larger review finding that 113 of the papers on invasive plant species showed a negative impact on plant diversity, while 21 papers reported a positive impact, and two papers found no impact (Vilà et al., 2011). Similar to the global response to invasive species, rangelands in the NGP also have a decrease in plant diversity when invasive plant species increase.

Impacts of Invasive Species on Herbage Production

Twelve studies observed impacts of invasive species on herbage production. Ten studies focused on total herbage production (Table 3, Figure 4). Six found an increase in herbage production with increased invasive plants, three found a decrease, and one study reported no difference (Table 3, Figure 4). When studies only assessed native species production, five out of six studies found a negative impact associated with invasive plants. A study looking at Canada thistle (*Cirsium arvensis*) reported no difference in native species production between invaded and non-invaded sites (Figure 5). There were no studies analyzing the impact of bluegrasses (*Poa spp.*) on herbage production in the NGP.

Different invasive species have varying impacts on herbage production. These differences can be accounted for by differing characteristics, growth patterns, and environment (Bakke, 1936; Haferkamp et al., 1997; DeKeyser et al., 2013). Crested wheatgrass and smooth brome tend to increase total herbage production, while leafy spurge studies show mixed results. Overall, increases in invasive plants decrease native species herbage production (Table 1). This

finding can be explained because as invasive plants consume more resources, there are fewer resources available for the native species.



Impact of Invasives on Total Herbage Production

Figure 4. The number of studies that listed invasive plant species having either a positive, negative, or no impact on total herbage production compared to less- invaded sites in the Northern Great Plains.

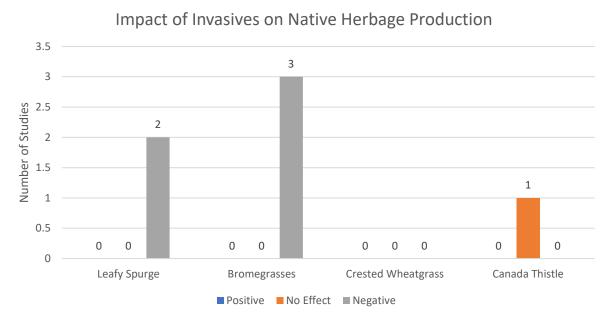


Figure 5. The number of studies listing invasive plant species having either a positive, negative, or no impact on native species' herbage production compared to less-invaded sites in the Northern Great Plains.

Leafy spurge studies had different findings on total herbage production. The mixed results could have been due to the studies' varying methods. Two studies (Lym and Kirby, 1987; Hein and Miller, 1992) found that leafy spurge decreased total herbage production. Hein and Miller (1992) studied leafy spurge presence and cattle utilization in Montana in response to herbicide application. Therefore, the results could have been influenced by cattle utilization, Picloram application, or year of study (Hein and Miller, 1992). Cattle grazing was also part of the study by Lym and Kirby (1987) where they showed leafy spurge decreased both native and total herbage production on grazed and ungrazed treatments. No impact on total herbage production was found in Larson and Larson's (2010) study which also looked at leafy spurge. However, they did report a negative impact on native herbage production. This study focused on how flea beetle control of leafy spurge can affect species composition and how leafy spurge and exotic grasses influence diversity and herbage production of native species. Total herbage

production increased in two of the three years (Trammell and Butler, 1995). Both studies testing native herbage production in response to leafy spurge invasion found a negative impact (Trammell and Butler, 1995; Larson and Larson, 2010).

Of the three studies reporting on crested wheatgrass, all mentioned a positive impact on total herbage production; however, none analyzed the impact on native production (Looman and Heinrichs, 1973; Smoliak and Dormaar, 1985; Henderson and Naeth, 2005). Other studies showed crested wheatgrass reduced native plant diversity (Sutter and Brigham, 1998; Christian and Wilson, 1999; Heidinga and Wilson, 2002; Henderson and Naeth, 2005). Therefore, one would expect a loss of native herbage production. This total increase in herbage production is probably due to the characteristics crested wheatgrass was selected for- its hardiness, value for herbage production, and productivity. Herbage production was higher on crested wheatgrass invaded sites than native rangeland sites, as it was seeded following the Dust Bowl era as a soil stabilizer and to improve pastures for livestock production (Looman and Heinrichs, 1973; Smoliak and Dormaar, 1985). Since increasing herbage production is one purpose for crested wheatgrass presence, these studies may have not thought to include its impact on native production or it simply wasn't their objective.

Studies focused on brome grasses showed variability in production findings, but less than leafy spurge. All the studies testing native herbage production found annual brome presence decreased the native plant production (Trammell and Butler, 1995; Haferkamp et al., 1997; Haferkamp and Heitschmidt, 1999). Many of the studies on annual bromes studied different species (Table 4). This makes it difficult to pinpoint which species drive different impacts. Across the span of three years, Trammell and Butler (1995) determined the influence of downy brome, Japanese brome, and smooth brome individually on the total herbage production in a

western wheatgrass-threadleaf sedge (*Carex filifolia*) dominated plant community. They found in eight of nine bromegrass-species-by-year combinations, the presence of each invasive bromegrass related to an increased total herbage production (Trammell and Butler, 1995). Haferkamp and Heitschmidt (1999) did not include a control site without invasion of Japanese brome, and only looked at the effect of Japanese brome removal. Upon removal, total biomass of the stand was less than when Japanese brome was not removed; therefore, this study is not the best indication of how total production is influenced by presence or absence of the species (Haferkamp and Heitschmidt, 1999). Ogle et al. (2003) contrasts these studies showing a significant decline in total herbage production with downy brome and Japanese brome presence . This is only the case in September, as opposed to the other three months data was collected where it had the opposite effect or no effect. September was chosen for this review because it was the latest date collected and accounted for the full growth of the growing season (Ogle et al. 2003).

Study	Smooth Brome	Downy Brome	Japanese Brome
Ashton et al. 2016	No	Yes	Yes
Trammell and Butler, 1995	Yes	Yes	Yes
DeKeyser et al. 2013	Yes	No	No
Ogle et al. 2003	No	Yes	Yes
Haferkamp et al. 1997	No	No	Yes
Haferkamp and Heitschmidt 1999	No	No	Yes

Table 4. Bromegrass studies and their respective species studied.

Many different interactions influence herbage production. These bromegrass studies focused on a wide array of species, native communities, grazing protocols, and combinations of variables that may affect production. The two factors most influential in terms of altering herbage production would be the plant community and weather conditions for the year. Every plant community will inherently have different production potential, so invasion may increase or decrease based on whether or not the invasive species has on average, greater or less production potential compared to the native plants. In addition, this review did not quantify the level of invasion from each study as it varied so much and some did not specify each level. Therefore, wide variability can be expected from sites with minimal invasion to heavy invasion. However, invasion consistently had a negative effect (n=5; Trammell and Butler, 1995; Haferkamp et al., 1997; Haferkamp and Heitschmidt, 1999; Larson and Larson, 2010) or no effect (n=1; Carter and Lym, 2017) on native herbage production.

Herbage production is crucial to livestock producers as it changes the carrying capacity of pastures (Meehan et al., 2018). Because of the small profit margins in the cattle industry (Henry, 2003), a decline in the number of cattle raised on a piece of land would be costly. Therefore, producers need to maintain the condition of their pastures and prevent increases in invasion on their land (Dunn et al., 2010; Wagg et al., 2017).

Limitations of Past Studies and Furthering Research

My review consisted of 22 studies to review and draw information from to address the invasive species' impact on herbage production and plant diversity in the NGP. The review limited the search criteria, which excluded many studies. However, this was to specifically target these two questions in the NGP ecosystem and provide a detailed analysis of the current knowledge of invasive species' impact within this unique region. All of the studies identified were unique; therefore, many assumptions were made for their comparison. First, although each study's methods are different, they can provide results to compare for invasion's impact. The second assumption is that each study location accurately represents the NGP. Third, each invasive species, although different, could be somewhat compared as influencing the community it invades. This review attempted to address each of these limitations either through selecting

criteria to limit differences, or through discussing each of these differences in the discussion section and what impact they may have had on the results.

Very few of the studies with results on plant diversity provided information on what species were lost. This piece of information may help identify key species for managers to look for to identify the progression or level of invasion. It could also aid in understanding the consequences of invasion if those species provide critical benefits to the ecosystem. Pollinator preference and wildlife habitat could be some of the potential losses from these sensitive species.

The species of interest also vary in their research presence for the NGP. For example, only one study was found for Canada thistle and it only focused on its impact on herbage production (Carter and Lym, 2017). The research on yellow sweetclover and bluegrasses only focused on their impact on diversity (Van Riper and Larson, 2009; DeKeyser et al., 2013; Haines et al., 2013; Kral-O'Brien et al., 2019). The results for herbage production in studies on leafy spurge and bromegrasses contradicted each other (Lym and Kirby, 1987; Hein and Miller, 1992; Trammell and Butler, 1995; Haferkamp and Heitschmidt, 1999; Ogle et al., 2003; Larson and Larson, 2010). Additionally, a few studies looked at the impacts of invasive species in general, not just an individual or group of species (Stohlgren et al., 1999; Haines et al., 2013). Future studies could help in furthering research on species rarely studied, filling in research gaps of those already studied, and compiling more data on those species where contradictions were seen. Overall, there is a plethora of research to be done on the impacts of invasive plant species on plant diversity and herbage production of the rangelands within the NGP. It is with this advancement of knowledge that livestock managers can make sound and effective decisions for sustainability on this unique landscape.

Management Implications

Invasive plants are a high priority for rangeland managers and various strategies are attempting to minimize their spread and decrease their presence. While eradication is desired, most often maintenance is the most feasible strategy due to labor, biological, and economic restrictions (Panetta and Gooden, 2017). Maintenance strategies aim to keep the invasive populations low, while not spending excessively to eradicate. On rangelands, depending on the invasive species, this can be accomplished through various disturbances including fire, grazing, and herbicide applications (Panetta and Gooden, 2017). Timing, intensity, and frequency of these events can be essential in controlling the invasive plant (Wallace et al., 2008; Kral et al., 2018; Menalled et al., 2018). Further research is needed to develop management strategies for various invasive species (Toledo et al., 2014).

In certain cases where total herbage production is increased, people may view the invasion as a positive impact. However, this may not be the best conclusion due to reduced plant diversity. Additionally, more herbage production may not be ideal depending on the type of herbage added. For example, more herbage production due to leafy spurge may initially seem positive to cattle producers; however, leafy spurge is generally avoided by cattle (Kronberg and Walker, 2007). Herbage value in an area is determined by both quantity and quality of the herbage. Downy brome is such an early-maturing grass that its herbage quality later in the season is much lower than the other actively growing plants in the community (Cook and Harris, 1968). Thus, more herbage does not necessarily mean better for livestock and wildlife.

CHAPTER 2. IMPACTS OF INVASIVE PLANT SPECIES ON PLANT RICHNESS, DIVERSITY, AND COMMUNITY COMPOSITION IN THE NORTHERN GREAT PLAINS

Introduction

Invasive plant species pose a threat to native rangelands across the United States (Pimentel et al., 2005, Vilà et al., 2011). This threat comes in many forms. Invasive plant species tend to outcompete native plants in the area, reducing plant diversity, and shifting community dynamics (Vilà et al., 2011). These impacts are not limited to plants, but also decrease animal diversity and abundance, and increase soil microbial diversity (Vilà et al., 2011). Consequently, rangeland managers attempt to control the spread and reduce the presence of invasive plant species (Larson and Larson, 2010; Link et al., 2017; Panetta and Gooden, 2017). In total, invasive plant species cost the U.S. almost 35 billion dollars annually in lost revenue, damage to the environment, and input costs for control measures (Pimentel et al., 2005).

Specifically, invasive plants cost six billion dollars annually to control on rangelands in the U.S. (Pimentel et al., 2005). Over 5.6 million hectares of California rangeland were invaded by yellow starthistle (*Centaurea solstitialis*) in 2002, an increase of 81% from 1985 (Pitcairn et al., 2006). Yellow starthistle transformed California's rangeland ecosystem and continues to spread (Sheley et al., 1996). Many invasive species, like saltcedar (*Tamarix* spp.), are successful for multiple reasons. Saltcedar has invaded the southwest region of the U.S., with its easily distributed seeds and high tolerance for little water or highly saline water, heat, cold, and flooding (DiTomaso, 1998). Saltcedar can alter its environment to inhibit native plant competition by lowering the water table and drawing salt to the surface, resulting in a harsh saline environment (DiTomaso, 1998). Not only do invasive plant species present an economic

cost to control, but also decrease biodiversity, strain management and policy, and threaten our rangelands (West, 1993; Stohlgren et al., 2011).

In the Northern Great Plains (NGP), many cool-season perennial grasses are invading rangelands (DeKeyser et al., 2013). The primary invasive grasses are Kentucky bluegrass (Poa pratensis), smooth brome (Bromus inermis), and crested wheatgrass (Agropyron cristatum; Bradley and Mustard, 2005; Henderson and Naeth, 2005; DeKeyser et al., 2013; Ellis-Felege et al., 2013; Printz and Hendrickson, 2015; Grant et al., 2020). There are many drivers to the increase and success of invasive species like Kentucky bluegrass including overgrazing, climate change, fire exclusion, and its own self-reinforcing ecosystem feedbacks such as alteration of nutrient cycling, hydrology, and light penetration (Toledo et al., 2014). Crested wheatgrass was planted after the Dust Bowl to stabilize soil; however, it has invaded native pastures and creates homogenous patches (Heidinga and Wilson, 2002). Not only are these invasive species expensive monetarily to control or in lost revenue, they also pose a large threat to biodiversity and production in the ecosystem and on management decisions and policy (West, 1993). For many of the invasive species, their dominance is attributed to a decline in disturbance events (DeKeyser et al., 2009; Kral et al., 2018). With only about 26% of the historic Dakotas mixedgrass prairie remaining, management and understanding of the remnants is crucial (Samson et al., 2004). The objectives of this study are to determine how crested wheatgrass, Kentucky bluegrass, and smooth brome invaded areas are different than non-invaded areas in regards to richness, diversity, and plant community composition. In addition, two other objectives are to see which species are more characteristic of invaded sites and what ecological sites are more likely to be invaded.

Methods

Study Area

The study area lies within the Little Missouri National Grasslands (LMNG), which spans 4,162 sq. km and 416,047 hectares of western North Dakota, and found within the Northern Mixed Grass Prairie (NMGP) (Figure 6). In addition, the Grand River National Grasslands (GRNG; also found within the NMGP), spans 626.4 sq. km and 62,639 hectares of northwestern South Dakota, was also included in this study. The National grassland study sites are managed by the United States Forest Service (USFS) for multiple uses. Livestock herbivory is the primary disturbance, with privately owned cattle generally stocked at a moderate stocking rate. The allotments studied are sub-divided into pastures and managed with either rotational or continuous grazing. Long-term monitoring data from the study sites was available for this evaluation, providing a large sample size across twelve years (2008-2019). This time span provided multiple wet and dry cycles, and the large land area surveyed provides a landscape-level analysis of the NGP.

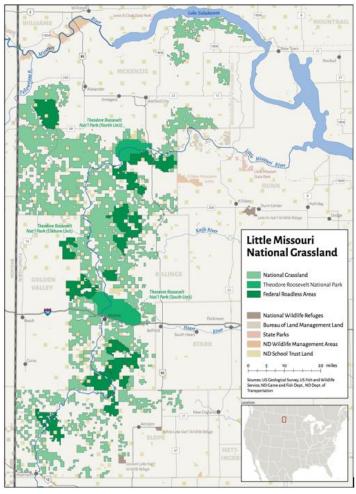


Figure 6. The Little Missouri National Grassland, the majority of the study area in western ND (Bohannon and Blinnikov, 2019).

The area has a mean annual temperature of 5.5 degrees Celsius on the northern range of the area and 8 degrees Celsius in the southern range of the area and an annual precipitation of 45 and 37 cm respectively (NDAWN, 2020). The LMNG is comprised of soil orders including mollisols, entisols, vertisols, and inceptisols (USDA-NRCS, 2019). Primary grasses of the ecosystem include *Pascopyron smithii*, *Bouteloua gracilis*, and *Hesperostipa comata* (Singh et al., 1983). Invasion of the native rangeland by *Poa pratensis*, *Agropyron cristatum*, and *Bromus* species have in general, altered the plant community in the NGP (Henderson and Naeth, 2005; DeKeyser et al., 2013).

Plot Selection

The study plots were selected using ArcGIS (v. 10.2; Redlands, 2013). The USFS assigned which allotments were to be monitored each summer. Each allotment's major ecological sites were assessed in the monitoring, and so two to three plots dependent on the size of the allotment were randomly assigned within each allotment's major ecological site. The purpose was to gather an accurate representation of each allotment and each ecological site. These random plots were given a 200-meter buffer from water sources (streams, tanks, ponds, etc.) and oil pads. The plots also have a 50-meter buffer from fences, trails, roads, and oil pipelines. Different grazing allotments or pastures found within the LMNG and GRNG were studied during different years based off USFS assignment. Data were collected at 80-180 plots per year from early-June to late-August during the growing season. Data were collected at each plot once during the study. The study compiled data from four different USFS Ranger Districts in western ND and SD (Table 5). Grant et al. (2020) had a similar long-term data set from US Fish and Wildlife Service-managed prairies from ND, SD, and northeastern MT where no point was visited twice. They determined trends and characterized differences between sites with invasion and those without (Grant et al., 2020).

Grand River	Medora	McKenzie	Little Missouri
2008	2008 2017	2008 2014	2011
2013	2009 2018	2009 2016	2012
2014	2010 2019	2010 2017	2013
	2011	2011 2018	
	2012	2012 2019	
	2013	2013	

Table 5. Years of study for each USFS Ranger District.

Field Methods

Each study plot contained two 75-meter transects, one placed from north to south and the second placed east to west (Figure 7). They crossed at 37.5 meters and was the center on each plot.

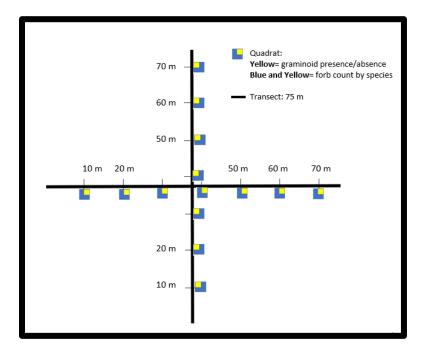
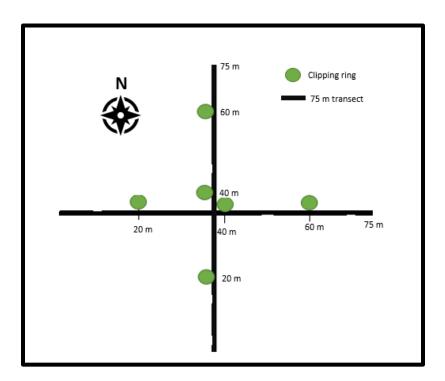


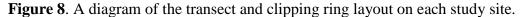
Figure 7. Layout of the aerial view of each study plot with transects and quadrat placements.

Seven quadrats (0.25 m² frame with a nested 0.0625 m² frame inside) were placed along each transect every 10 meters on the right side of the transect for a total of 14 sampling points (Figure 7). Within the smaller frame (0.0625 m²) at every sample point, each grass, sedge, or rush species found was identified and recorded by species, plot, and sampling point location. Within the larger frame (0.25 m²) at every sampling point, all forb species were recorded and number of stems/plant species counted (density).

To obtain herbage production for each plot and proportion of invasive grasses, production clippings were collected every 20 m along each (north to south and east to west) transect for a total of six collection sites (Figure 8). The clipping frame was a ring with an area of 0.178 sq. m.

They were placed directly to the left of the transect line and plants were clipped to the soil surface. Live material was separated by species and all standing litter was collected in separate bags. Each plant originating within the ring was clipped at the base, identified to species by its six letter Latin code (USDA NRCS, 2020), and placed into a bag.





To confirm and classify the plot ESD, a soil pit was excavated to 50 centimeters. We assessed for soil texture, horizon depths, carbonate presence via an acid test (1 mol HCl), and compared the soil and plant community to its NRCS expected ESD. The ESD was typically very close to what it was expected to be; however, some landscape-level differences caused a change to the recorded ESD.

Analysis of Raw Data

Forb density was calculated for each forb species within the plot using the forb counts per plot.

forb density
$$(plants/0.25m^2) = \frac{sum of the count of species in all 14 quadrats(4)}{14}$$

The proportion of each of the cool- season perennial invasive grasses for each site was calculated using the herbage production by species clippings.

proportion invasive
$$x = \frac{\text{sum of the weight of all the invasive x in all 6 clipping rings}}{\text{sum of the weight of all live material in all 6 clipping rings}}$$

Species Richness

Richness was determined for each site by determining how many species (forb or graminoid) were present. The richness measure was based off the graminoid presence/absence data and forb density data. The richness for all sites were then plotted against the proportion of invasive cool-season grasses (crested wheatgrass, Kentucky bluegrass, smooth brome, and all three) in a site with a simple linear regression model fit to the trend. The proportions were determined based on the herbage production data for the site (i.e. what percentage of the total production of the site was from Kentucky bluegrass). All of the sites were analyzed using R functions (R Development Core Team, 2020). An additional richness analysis on a subset of the data was performed because of a trend seen when plotting suggesting that as invasion increased, the maximum richness was limited. Therefore, a trend line was fitted on the maximum richness for each 5% increase in proportion invasion for all the sites for all of the cool-season invasive perennials (CIP; individually and cumulative) to better illustrate this observation.

Species Diversity

Forb diversity was determined for each site using Simpson's forb diversity (Simpson, 1949). The forb density data was analyzed using R and the Simpson's diversity for the forbs were plotted against the proportion of invasive cool-season grasses (individually and cumulative) in a site with a linear model fit to the trend (R Development Core Team, 2020).

Plant Community Composition

The data set's most prominent ecological sites were thin loamy (273 sites), loamy (450 sites), and clayey (132 sites). Therefore, these were the three ecological sites used to test if invasion by the CIPs had an effect on the plant community. The plant community composition was based on the graminoid and forb abundance data. Species with only one occurrence or less were excluded from the analysis as they were considered very rare. In addition, the data was relativized and scaled so that the species all were proportionate to one another.

The data for each ecological site was analyzed through Fuzzy Set Ordinations in PC-ORD version 7.08 (Roberts, 1986). The level of crested wheatgrass, Kentucky bluegrass, smooth brome, and cumulative CIP invasion were tested against the Fuzzy Set Ordination of the community to determine if any of them were significantly associated with the community changes. This analysis was then compared to a Nonmetric Multi-dimensional Scaling (NMS) ordination (unconstrained) using PC-ORD version 7 (MjM Software Design, Gleneden Beach, OR) for the same three community (ecological site) datasets (Peck, 2010). These ordinations both used the Sorenson (Bray-Curtis) distance measure to find patterns and dissimilarity within the community data (Bray and Curtis, 1957). The fuzzy set ordination analyses that were significant (P<0.05) were further analyzed using NMS ordinations to display their unconstrained ordination relationship. For the NMS ordination, the selected model and axes were based on having a p-value of less than or equal to 0.05, having a stress test of less than 25, and having an instability of less than 0.0001. Only the first two axes were utilized for all of our analyses as they accounted for the majority of the variation in the ordination with the third axis contributing to less than 0.175% of the variation.

Species Characteristic of Invaded and Non-Invaded Sites

This analysis built off the plant community analysis's NMS ordinations. The NMS ordinations provided correlation coefficients for all species in the dataset that showed how strongly correlated a species is for each axis in the ordination. The value (positive or negative) of the correlation coefficient for an axis indicates which end of the axis (positive or negative, respectively) with which the species is associated. After reviewing the NMS ordinations with a significant community composition shift from Kentucky bluegrass and smooth brome, the axes which were significantly correlated with the CIP were reviewed for significant correlations for all the other species. This provided a species rankings for being more and less correlated with low and high invasion of the three different invaders. The cutoff for species correlation coefficients that were reported as strong correlations was set at greater than [0.3].

The total invasion level (combined CIP level) was calculated for each site based on the proportion of the total herbage production for the site that is comprised of one of the three CIPs. The sites in the dataset were sorted into their respective ecological site. The top nine ecological sites (loamy, thin loamy, clayey, claypan, limy residual, shallow loamy, sandy, thin claypan, and very shallow) were analyzed using the density plot function in R (R Development Core Team, 2020). This provided the distribution curve of how many of the total sites (in the specific ecological site) fit across the gradient of 0 to 100% invasion. These graphs are then compared to see the distribution of how many sites are invaded vs. not invaded. The dependent variables of this study include the site richness, diversity, community composition, species associated with invasion, and number of sites at different levels of invasion (Table 6).

Table 6. Study van	riables and their ex	planation.
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Variable	ble Type Classification				
Level of Invasion	Independent A continuous scale of composition in the plot, based on the percent frequency		Based on proportion of site forage production (0-1) comprised of Kentucky bluegrass, crested wheatgrass, smooth brome, or all three cumulative.		
Species Richness	Dependent	The number of species (forb and graminoid) in a given plot	Analysis performed on all plots over the 12 years, results will focus on comparison across invasion level.		
Species Diversity	Dependent	Simpson's Diversity- considers the number of species present, as well as the relative abundance of each species	Analysis performed on all plots over the 12 years, results will focus on comparison across invasion level.		
Species Composition	Dependent	Two-dimensional ordinations based off of Bray-Curtis distances from forb density and graminoid frequency of each plot	Fuzzy set ordination and NMS ordination performed on the sites within the top three ecological sites over the 12 years, results will focus on comparison across invasion level of each CIP.		
Species Associated with Invaded Sites	Dependent	List of multiple species based on strong (> 0.3) r- correlation values for the NMS ordination axes	Stems from the community composition analysis		
Ecological Sites more likely to be Invaded	Dependent	Classification based off density plots of each ecological sites' number of plots across the gradient of invasion	Density plot of top nine ecological site's plots against level of total CIP invasion		

Results

Impacts of Cool-season Invasive Grasses on Site Richness

Species richness decreased ($P \le 0.05$) with increased proportion of crested wheatgrass (Figure 9). Kentucky bluegrass and smooth brome level of invasion did not affect (P > 0.05) site richness (Figures 10 and 11). The maximum richness was limited for all three CIPs (Figures 12-14, 16). Crested wheatgrass had sites that reached almost 100% invasion levels; whereas, Kentucky bluegrass only reached levels of around 75% invasion and smooth brome 50% invasion (Figures 12-14).

Since there were a plethora of sites impacted by two or three of these CIPs, the combined total of crested wheatgrass, Kentucky bluegrass, and smooth brome on a site was analyzed. As total CIP invasion increased, the total species richness declined ($P \le 0.05$; Figure 15). In addition, maximum richness for each five percent increment of invasion decreased more rapidly as total invasion increased (Figure 16). We found roughly a 35% decrease in the potential maximum richness of a site when going from 0% invaded to 75% invaded (Figure 16).

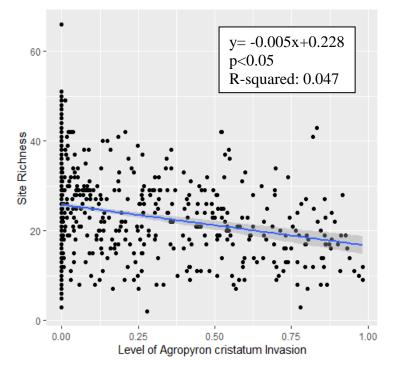


Figure 9. Plant species richness on all ecological sites combined across crested wheatgrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

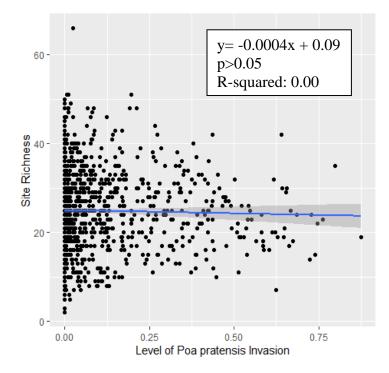


Figure 10. Plant species richness on all ecological sites combined across Kentucky bluegrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

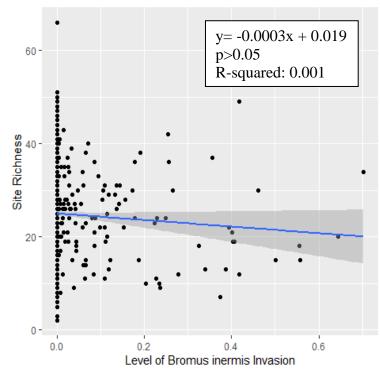


Figure 11. Plant species richness on all ecological sites combined across smooth brome proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

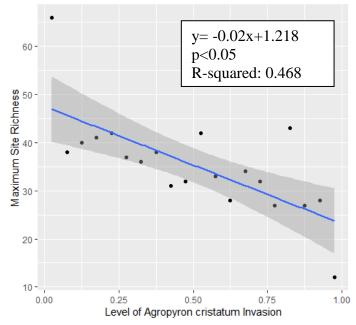


Figure 12. Maximum plant species richness on all ecological sites combined across crested wheatgrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

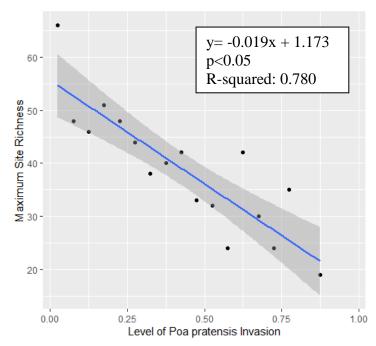


Figure 13. Maximum plant species richness on all ecological sites combined across Kentucky bluegrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

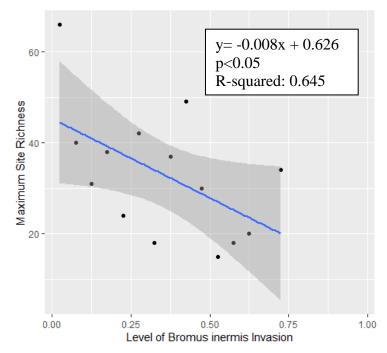


Figure 14. Maximum plant species richness on all ecological sites combined across smooth brome proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

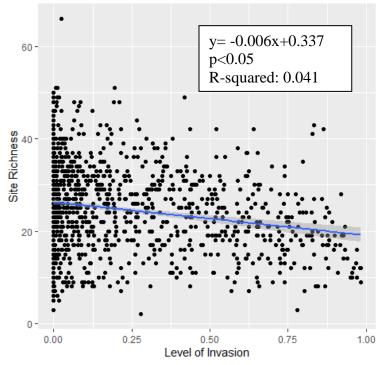


Figure 15. Plant species richness on all ecological sites combined across total proportion level of crested wheatgrass, Kentucky bluegrass, and smooth brome combined on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

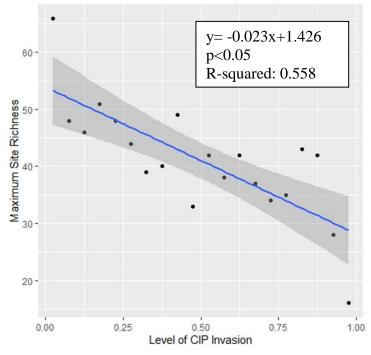


Figure 16. Maximum plant species richness on all ecological sites combined across total proportion level of crested wheatgrass, Kentucky bluegrass, and smooth brome combined on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

Impacts of Cool-season Invasive Grasses on Species Diversity

Crested wheatgrass and smooth brome invasion had a significant negative relationship (P<0.05) with species diversity (Figure 17, 19). Increased levels of Kentucky bluegrass invasion did not negatively (P>0.05) affect species diversity (Figure 18). As for native forb diversity, the same pattern was seen for both increased invasion of crested wheatgrass and smooth brome, with decreased diversity (P \leq 0.05) of native forbs on the sites (Figures 20 and 22) while Kentucky bluegrass did not decrease native forb diversity (Figure 21).

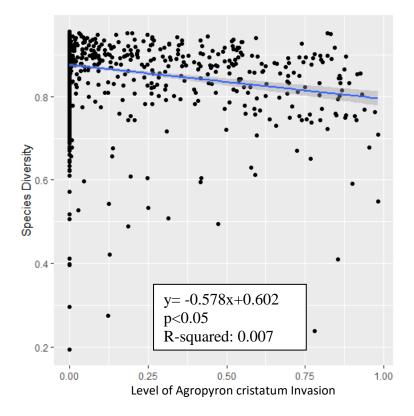


Figure 17. Plant species diversity on all ecological sites combined for crested wheatgrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

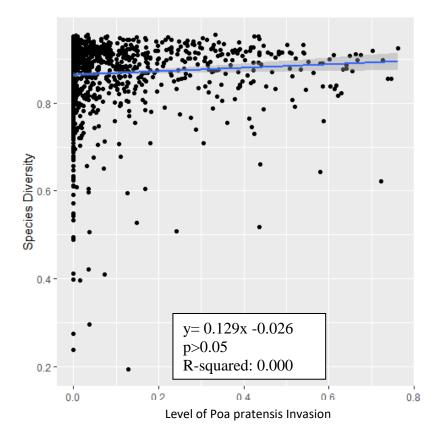


Figure 18. Plant species diversity on all ecological sites combined for Kentucky bluegrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

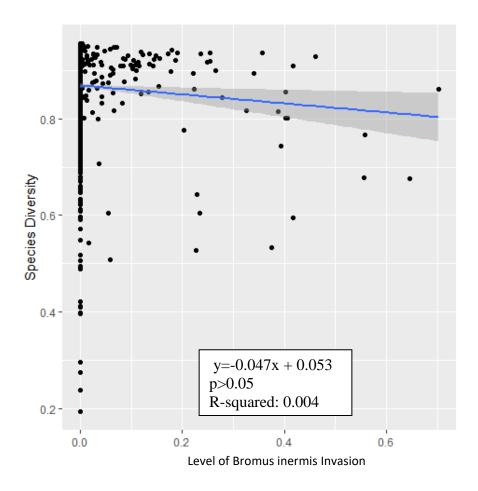
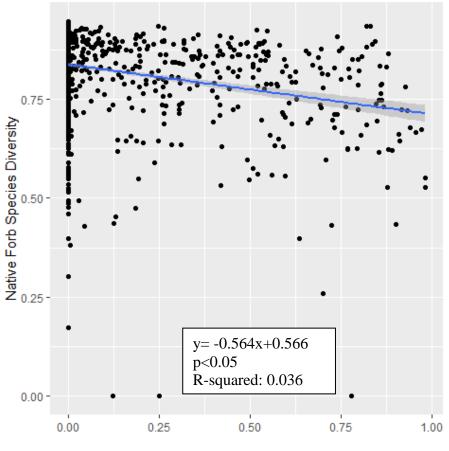


Figure 19. Plant species diversity on all ecological sites combined for smooth brome proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.



Level of Agropyron cristatum Invasion

Figure 20. Native forb species diversity on all ecological sites combined for crested wheatgrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

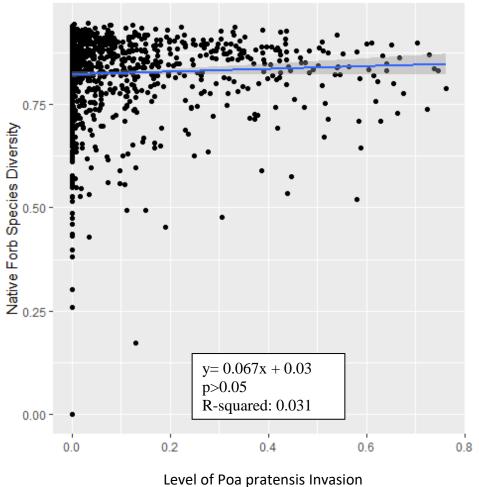


Figure 21. Native forb species diversity on all ecological sites combined for Kentucky bluegrass proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

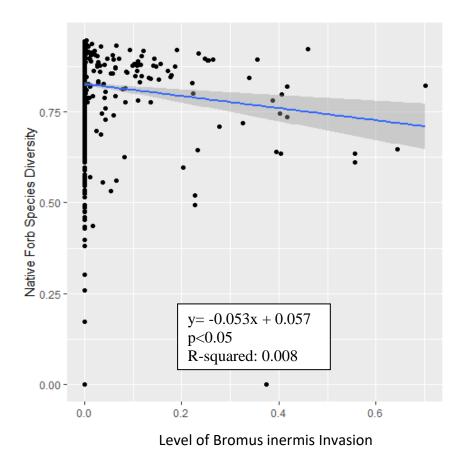


Figure 22. Native forb species diversity on all ecological sites combined for smooth brome proportions on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

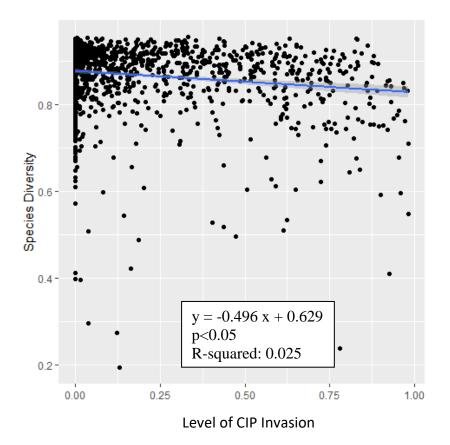


Figure 23. Forb species diversity on all ecological sites combined across total proportion level of crested wheatgrass, Kentucky bluegrass, and smooth brome combined CIP on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

As for the cumulative effect on species diversity, diversity decreased significantly $(P \le 0.05)$ as the proportion of invasive cool-season grass species increased (Figure 23). In addition, the native forb diversity was negatively affected more than the overall species diversity (Figure 24).

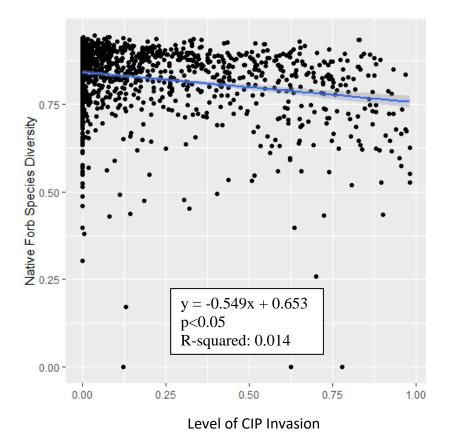


Figure 24. Native forb species diversity on all ecological sites combined across total proportion level of crested wheatgrass, Kentucky bluegrass, and smooth brome combined (CIP) on the Little Missouri National Grasslands. The shaded area is the 95% confidence interval.

Impacts of Cool-season Invasive Grasses on Plant Community Composition

When each ecological sites' community data was tested against each of the CIPs in the Fuzzy Set ordination, only five of the 12 analyses showed a significant effect of the CIPs on the community group composition. The Fuzzy Set Ordinations showed that crested wheatgrass did not have a significant effect (P>0.05) on any of the top three ecological sites' plant communities (Table 7). However, Kentucky bluegrass had a significant effect (P<0.05) on all three and smooth brome had a significant on loamy and clayey ecological sites' plant communities (Table 7). Because Kentucky bluegrass and smooth brome's plant community correlations were deemed significant, they were further evaluated with NMS ordination. Only Kentucky bluegrass had a significant correlation in the Fuzzy Set ordination for thin loamy sites, so only Kentucky bluegrass was analyzed with the NMS ordination for thin loamy sites.

Investing Species	Clayey		Loamy		Thin Loamy	
Invasive Species	R2	Random P	R2	Random P	R2	Random P
Proportion Crested Wheatgrass	0.0174	0.635	0.0326	0.293	0.0206	0.332
Proportion Kentucky Bluegrass	0.1144	0.006*	0.0967	0.015*	0.0719	0.02*
Proportion Smooth Brome	0.0795	0.03*	0.0778	0.033*	0.0519	0.066
Cumulative Proportion of CIPs	0.0758	0.058	0.0047	0.896	0.0369	0.133

Table 7. Statistical results of the plant community data Fuzzy Set Ordinations (*= statistically significant).

When analyzed using the NMS ordinations, the Fuzzy Set ordinations' significance was reaffirmed (Figures 25-29). Clayey sites had a significant correlation between the community composition of the sites and the level of Kentucky bluegrass and smooth brome (Figures 25 and 26). In this case, both smooth brome and Kentucky bluegrass invaded sites classify a similar group of the community data (the positive end of Axis 1; Figures 25 and 26).

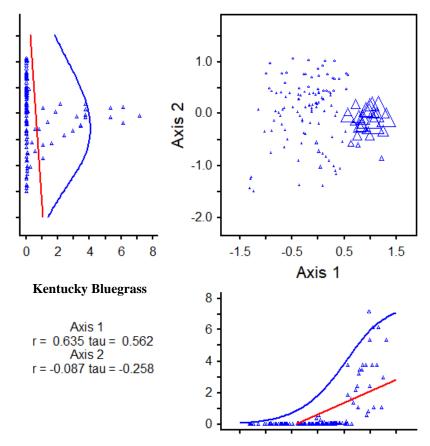


Figure 25. Clayey community Kentucky bluegrass NMS ordinations (the scale of the triangles, or plots, is dependent on the level of the invasive species). The two axes displayed are the first two axes of the NMS ordination which account for the majority of the variation amongst the sites. The graph provides the 2-D display of the NMS ordination as well as the breakdown for each axis. The red line is the linear regression for each axis and the blue line is the envelope that includes 95% of the values for each axis. The tau value describes the rank order correlation for the axis. Kentucky bluegrass invaded sites are more densely associated with the positive end of axis 1 and the middle or neutral portion of axis 2.

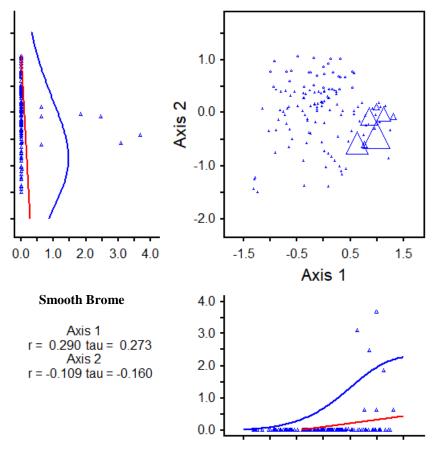


Figure 26. Clayey community smooth brome NMS ordinations (the scale of the triangles, or plots, is dependent on the level of the invasive species). The two axes displayed are the first two axes of the NMS ordination which account for the majority of the variation amongst the sites. The graph provides the 2-D display of the NMS ordination as well as the breakdown for each axis. The red line is the linear regression for each axis and the blue line is the envelope that includes 95% of the values for each axis. The tau value describes the rank order correlation for the axis. Smooth brome invaded sites are more densely associated with the positive end of axis 1 and the middle or neutral portion of axis 2.

Kentucky bluegrass and smooth brome showed similar significant results in their impact on the community composition on loamy ecological sites (Figures 27 and 28). Thin loamy sites do have a statistical correlation for Kentucky bluegrass invaded sites; however, there are far less sites invaded by Kentucky bluegrass in the thin loamy sites than either the clayey or loamy sites (Figure 29). The general statistical results from all three general NMS ordinations are listed in Table 8.

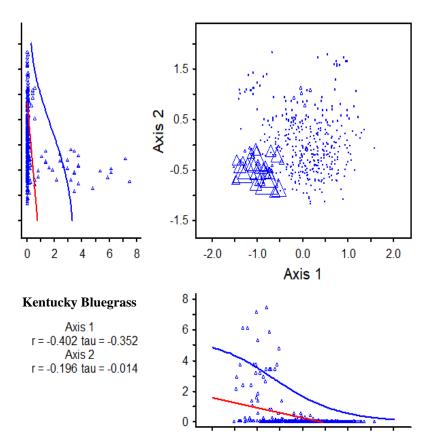


Figure 27. Loamy community Kentucky bluegrass NMS ordinations (the scale of the triangles, or plots, is dependent on the level of the invasive species). The two axes displayed are the first two axes of the NMS ordination which account for the majority of the variation amongst the sites. The graph provides the 2-D display of the NMS ordination as well as the breakdown for each axis. The red line is the linear regression for each axis and the blue line is the envelope that includes 95% of the values for each axis. The tau value describes the rank order correlation for the axis. Kentucky bluegrass invaded sites are more densely associated with the negative ends of both axis 1 and 2.

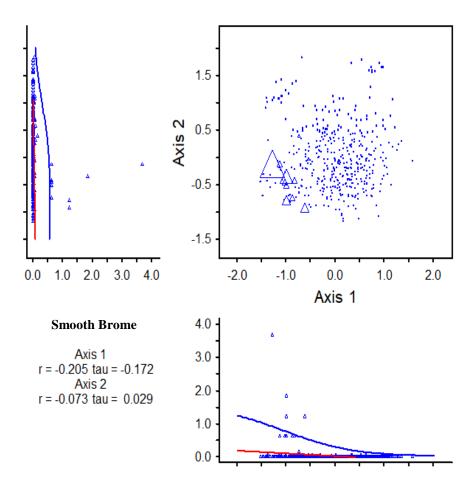


Figure 28. Loamy community smooth brome NMS ordinations (the scale of the triangles, or plots, is dependent on the level of the invasive species). The two axes displayed are the first two axes of the NMS ordination which account for the majority of the variation amongst the sites. The graph provides the 2-D display of the NMS ordination as well as the breakdown for each axis. The red line is the linear regression for each axis and the blue line is the envelope that includes 95% of the values for each axis. The tau value describes the rank order correlation for the axis. Smooth brome invaded sites are more densely associated with the negative ends of both axis 1 and 2.

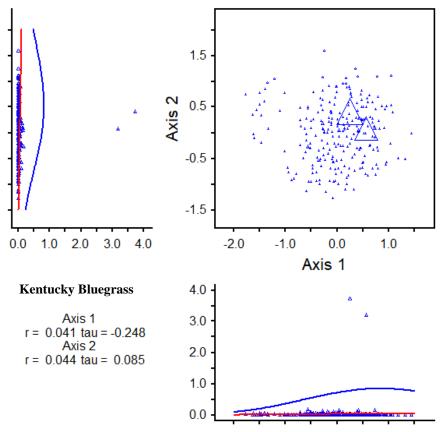


Figure 29. Thin loamy community Kentucky bluegrass NMS ordination (the scale of the triangles, or plots, is dependent on the level of Kentucky bluegrass). The two axes displayed are the first two axes of the NMS ordination which account for the majority of the variation amongst the sites in the ordination. The graph provides the 2-D display of the NMS ordination as well as the breakdown for each axis. The red line is the linear regression for each axis and the blue line is the envelope that includes 95% of the values for each axis. The tau value describes the rank order correlation for the axis. Kentucky bluegrass only significantly invaded two of the thin loamy sites, as seen here in the two larger triangles close to the middle of the NMS ordination.

Table 8 . Statistical results from the NMS Ordinations (Inc=	Increment, Cum= Cumulative).
---	------------------------------

		Cla	iyey	Loa	amy	Thin Loamy	
Final Stress for 3-Dimensional Solution		20.76		22.66		23.22	
Final Instability			0	0		0	
Number of Iterations		14	44	1	145 106		06
	Axis	Inc	Cum	Inc	Cum	Incr	Cum
R Squared Values	1	0.229	0.229	0.23	0.23	0.212	0.212
	2	0.215	0.444	0.194	0.425	0.155	0.367
	3	0.149	0.593	0.126	0.551	0.174	0.541

Species Characteristic of Invaded and Non-Invaded Sites

Certain species other than the CIPs had strong correlations with the plant community by ecological sites. The specific direction they are strongly correlated with on each ordination axis indicates which sites are most associated with a specific species. Figures 30-32 provide which species are associated with different communities in the three ecological sites. For those NMS ordinations with a strong invasive correlation, the species that are in the same area as the invasive species' sites are highly associated with that invasive species. However, if the species has a significant correlation to the opposite end of the axis than the invasive species, then they are highly characteristic of the non-invaded sites.

Fifteen plant species were strongly correlated with clayey sites invaded by Kentucky bluegrass and smooth brome, while there was no species strongly correlated with non-invaded clayey sites (the opposite side of axis one; Figure 30). Two of these species strongly correlated with Kentucky bluegrass and smooth brome invasion are western snowberry (*Symphoricarpos occidentalis*) and yellow sweetclover (*Melilotus officionalis*; Figures 30 and 31). Eleven plant species were strongly correlated to the loamy sites with higher Kentucky bluegrass and smooth brome invasion, while there is only one species, scarlet globemallow (*Sphaeralcea coccinea*), that was strongly associated with non-invaded loamy sites (Figure 31, axis one). Because the thin loamy ordination lacked a strong correlation with a CIP, no species were compared to identify correlations with invasion. However, there were some strong correlations for the plant community (Figure 32). Scarlet globemallow and rush skeletonweed (*Lygodesmia juncea*) were associated with each other in the thin loamy sites and are different than the nine-species association on the opposite end of the NMS ordination's axis one (Figure 32).

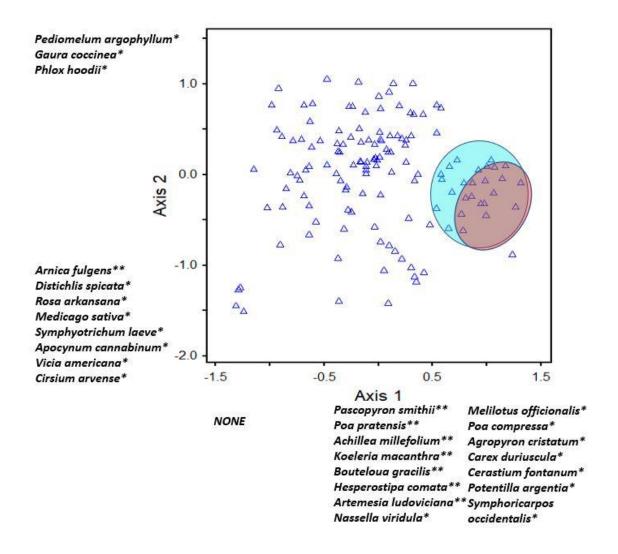


Figure 30. Clayey ecological sites' plant species correlations associated with Kentucky bluegrass and smooth brome invasion on the Little Missouri National Grasslands. The species listed on each side of the axis are associated with that respective side of the axis on the NMS ordination. The blue ellipse outlines the area highly associated with Kentucky bluegrass (*Poa pratensis*) invasion. The red ellipse outlines the area highly associated with smooth brome (*Bromus inermus*) invasion. One asterisk (*) represents a r-value of greater than |0.4| (stronger correlation). The species on the positive side of axis 1 are correlated with smooth brome and Kentucky bluegrass invasion.

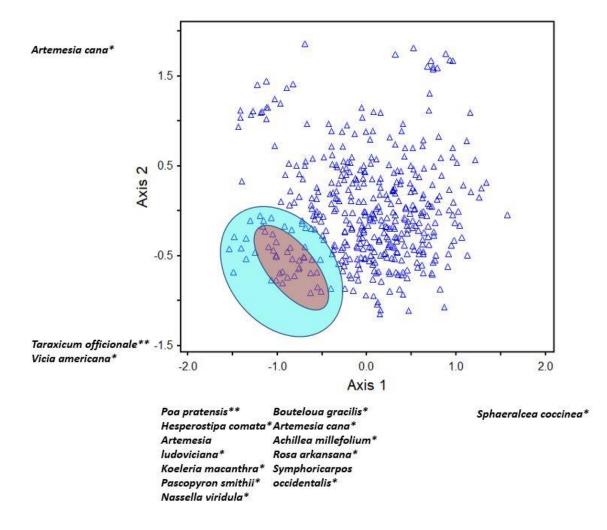


Figure 31. Loamy ecological sites' plant species correlations associated with Kentucky bluegrass and smooth brome invasion on the Little Missouri National Grasslands. The species listed on each side of the axis are associated with that respective side of the axis on the NMS ordination. The blue ellipse outlines the area highly associated with Kentucky bluegrass (*Poa pratensis*) invasion. The red ellipse outlines the area highly associated with smooth brome (*Bromus inermus*) invasion. One asterisk (*) represents a r-value of greater than |0.4| (stronger correlation). The species on the negative sides of axis 1 and axis 2 are correlated with smooth brome and Kentucky bluegrass invasion.

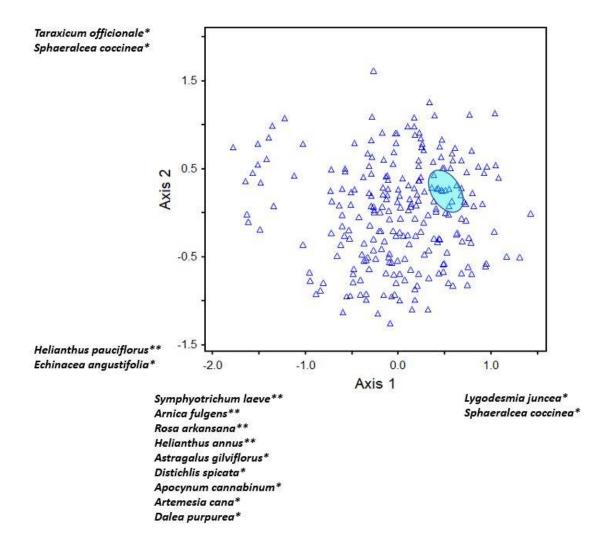


Figure 32. Thin loamy ecological sites' plant species correlations associated with Kentucky bluegrass and smooth brome invasion on the Little Missouri National Grasslands. The species listed on each side of the axis are associated with that respective side of the axis on the NMS ordination. The blue ellipse outlines the area highly associated with Kentucky bluegrass (*Poa pratensis*) invasion. One asterisk (*) represents a r-value of greater than |0.3| (strong correlation) and two asterisks (**) represents a r-value of greater than |0.4| (stronger correlation). The species on the same side of the axes are correlated with each other. If a species is on the opposite end of the axis, then they have a negative correlation.

Ecological Sites more likely to be Invaded

Reviewing the distribution curves displaying the invasion levels for each ecological site, the clayey, loamy, claypan, thin claypan, and limy residual ecological sites have a higher level of invasion relative to the very shallow, thin loamy, and shallow loamy ecological sites (Figure 33). The flatter the line going from 0-100 percent invasion indicates a higher proportion of being invaded.

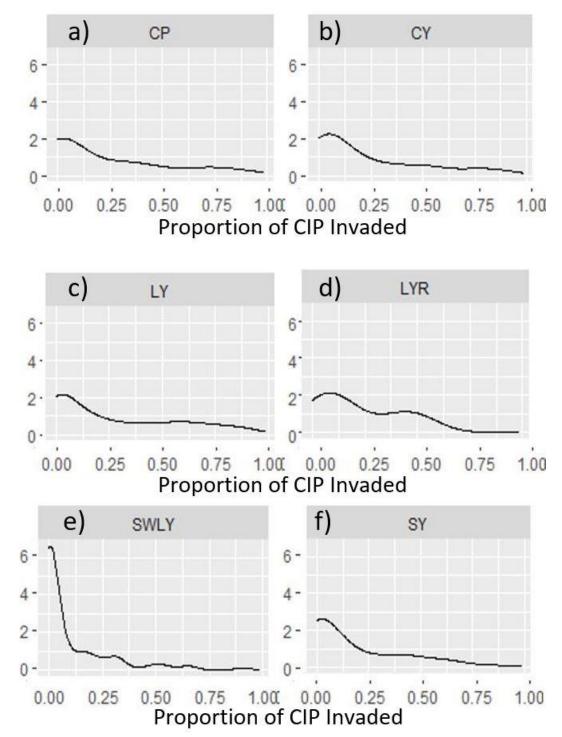


Figure 33. Density plots for the top nine ecological sites' distribution across total cool-season invasive plants (CIP) invasion level on the Little Missouri National Grasslands.

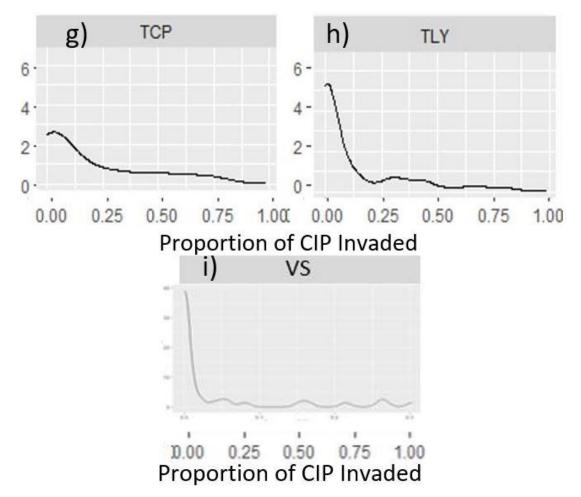


Figure 33. Density plots for the top nine ecological sites' distribution across total cool-season invasive plants (CIP) invasion level on the Little Missouri National Grasslands (continued). a) CP= claypan, b) CY= clayey, c) LY= loamy, d) LYR= limy residual, e) SWLY= shallow loamy, f) SY= sandy, g) TCP= thin claypan, h) TLY= thin loamy, i) VS= very shallow. All of the graphs have an x-axis of 0 to 1, the proportion of the invasion of crested wheatgrass, Kentucky bluegrass, or smooth brome. Graphs a-h have a y-axis scale of 0-6, but graph i has a y-axis scale of 0-40 as very shallow has such a high proportion of their sites without invasion.

Discussion

Impacts of Cool-season Invasive Grasses on Species Richness and Forb Diversity

Invaders, in general, decreased species richness and native forb diversity. These results are consistent with Vilà et al.'s (2011) review findings, as well as others (West, 1993; Stohlgren et al., 1999; DiTomaso, 2000). Our findings indicate that the invaded sites had no difference in total forb diversity than the non-invaded sites, which is different than most other studies.

Intuitively, richness should decrease as a particular species' proportion increases due to the inherently less ecological space and resources for another species to capitalize on. Based on maximum richness, these invasive species limit the potential for richness on these sites. As invasion increases, the potential richness for a site decreases by about 66%. In addition, we do not know which remaining plant species are in those sites as invasion increases. They could be species that are highly resilient to invasive species, or are invasive forbs themselves like yellow sweetclover and dandelions.

Increasing smooth brome cover has been shown to decrease species richness in a site. Smooth brome invasion initially decreases the abundance of different species, then the site begins to lose other species (Stotz et al., 2019). Kral-O'Brien et al. (2019) found that as Kentucky bluegrass cover increased, plant species diversity decreased. This finding contradicts our finding showing Kentucky bluegrass, overall, did not affect forb diversity. One potential explanation for this difference is based on observation of the Kentucky bluegrass invaded sites found in this semi-arid region. Similar to Van Riper and Larson (2009) who also worked on sites in western North Dakota, the invasive plant cover may be too low to impact the native plant species. Many of the sites invaded by Kentucky bluegrass in this region may be capable of maintaining plant diversity until the thatch/litter layer begins to cover the majority of the site. This only occurs when the proportion of Kentucky bluegrass is very high. One potential reason why the invasion level of Kentucky bluegrass and smooth brome doesn't completely take over the system is due to the lower level of precipitation this area sees as compared to further east in the NGP. The drought years may be enough of a disturbance/limitation for these grasses that even when they thrive during the normal or wet years, they are outcompeted when dry.

Impacts of Cool-season Invasive Grasses on Plant Community Composition

Crested wheatgrass did not reveal a significant correlation with shifting the community of the ecological sites. This may be due to the human influence associated with sites that are invaded by crested wheatgrass. The majority of sites with high crested wheatgrass levels were seeded at one point to crested wheatgrass with little consideration to the plant community (Looman and Heinrichs, 1973; Henderson and Naeth, 2005). Therefore, sites with crested wheatgrass invasion are scattered across the landscape with a high variation in the communities associated with its presence, because its presence was not dependent on the community but rather on whether the sites were seeded in the past.

Smooth brome was only associated with shifting clayey and loamy sites. This is most likely due to the few sites this study had with smooth brome invasion on thin loamy sites. This is primarily because thin loamy sites are less prone to invasion (Grant et al., 2020) and because, out of the three CIP invaders, smooth brome invaded the least amount of sites in the dataset. Thin loamy had the least amount of invasion of the top three ecological sites in this study. In total, there are only nine loamy sites in the dataset with greater than 10% smooth brome invasion.

The shift in plant community based on invasion supports the state and transition model (STM) hypothesis that invaders can cause a shift in stable states for a plant community (Briske et al., 2005; Bagchi et al., 2013; McGranahan et al., 2013). The STM explains how a particular ecological site can have multiple different stable states within which the plant community can reside given management history, physical characteristics of the site, and other factors (Bestelmeyer et al., 2003; Bagchi et al., 2013). Clayey and loamy sites did experience a shift in the plant community with increased invasion of Kentucky bluegrass and smooth brome. Crested wheatgrass lacked significance in the three ecological sites tested, and thin loamy sites did not

have sufficient invasion of CIP to identify a major difference. Perlinski et al. (2014) showed using a long-term dataset on the Santa Rita Experimental Range that refining a STM for an ecological site looking at the invasion of Lehmann's lovegrass (*Eragrostis lehmanniana*) was also possible. They found stable states driven by lovegrass invasion were similar to those seen within this study. Stotz et al. (2019) showed smooth brome was influential in driving plant community composition from uninvaded sites to invaded sites. They also described how, across the landscape, smooth brome-invaded sites were highly similar in composition to each other, therefore creating a more homogenous landscape.

After we performed our NMS ordinations we saw a trend that needs to be explored further. We found Kentucky bluegrass, in particular, did not influence the community in a linear or gradient manner, but more as a presence/absence once it crosses a potential threshold around 20-35% invasion. The proportion of the invasive species in a site varies from small to large in the area in which the invasion is highly correlated (as seen in Figures 18 and 19), meaning that there is invasion but unclear of the gradient from non-invaded to highly invaded. Therefore, this threshold may be a better analysis for Kentucky bluegrass's impact on communities than the gradient models. This is also why the Fuzzy Set R-squared values are less significant than expected for the data- it didn't follow the gradient for which this analysis tested.

Species Characteristic of Invaded and Non-Invaded Sites

Certain plant species have a strong correlation with invaded sites or non-invaded sites. It would be interesting to know at what point of invasion progression certain species are lost or gained. The major species more prevalent in invaded sites and less prominent in non-invaded sites reflect some of those identified in the STM models' characteristics of the invaded states for the three major ecological sites. The STMs for loamy, clayey, and thin loamy sites were

reviewed and the reference state (non-invaded) and the invaded state vegetation descriptions for each showed a few similarities to what was found in this study. For clayey sites, yellow sweetclover, cudweed sagewort (*Artemesia ludoviciana*), and western snowberry (*Symphoricarpos occidentalis*) were identified as plant species associated with the invaded state in the STM as well as during our study. For loamy sites, cudweed sagewort, American vetch (*Vicia americana*), and western snowberry were identified as plant species associated with the invaded state in our study and the STM; whereas, scarlet globemallow (*Sphaeralcea coccinea*) was identified in both our findings and the STM associated with native sites.

The differences in the thin loamy community are most likely based off of site characteristics rather than invasion due to most of our sites having less CIP invasion. Site characteristics could be whether a site was more clayey or sandy, or how steep the slope was. These characteristics can change the plant community as seen in our findings, with common dandelion (*Taraxicum officionale*) and scarlet globemallow-dominated community shifting to a stiff sunflower (*Helianthus pauciflorus*) and narrowleaf purple coneflower (*Echinacea angustifolia*) dominated community.

In the clayey and loamy sites from our study, one can conclude there are less correlations for species on the opposite end of the invasion (i.e. there are very few species highly associated with non-invaded sites). This can potentially be interpreted as the clayey or loamy sites without Kentucky bluegrass and smooth brome are more diverse and variable in their plant species composition than those that were invaded. So, there is less chance of a singular species being characteristic of many of the non-invaded sites.

Yellow sweetclover, an invasive forb, was highly characteristic of invaded sites and positively associated with invasion in the clayey ecological sites in our study. Yellow

sweetclover was also highly prevalent in much of the loamy sites in our study. Yellow sweetclover, a legume, fixes atmospheric nitrogen in the soil that can readily be utilized by Kentucky bluegrass and smooth brome, creating a competitive advantage over native plants (Van Riper et al., 2010; Dornbusch et al., 2018). Compared to western wheatgrass, Kentucky bluegrass's production increases more when yellow sweetclover is present and fixes more nitrogen (Dornbusch et al., 2018). Another study found that the coumarin in yellow sweetclover has inhibitory effects on the germination of other species' seedlings (CaiXia et al., 2016).

Another species of concern, western snowberry, is an encroaching woody shrub that was positively associated with CIP invaded clayey and loamy ecological sites. Western snowberry alters the plant community in an inhibitive manner for other vegetation due to reducing water and other resources in the soil (Pelton, 1953). The encroachment of this shrub has decreased the available palatable forage for livestock and wildlife, and restricted access as well (McCarty, 1967; Grant et al., 2004). The association between western snowberry, yellow sweetclover, and invasive CIP species like Kentucky bluegrass and smooth brome show that invasive species can benefit each other in their spread and form new stable states.

It may be difficult to recognize how invaded an area is just based off the presence of the invader. Key species' presence/absence could aid in knowing how degraded an area is. The species noted here that are quick to decrease when an invader encroaches are helpful in identifying the stages of invasion and knowing when a return to native or across the threshold is less likely. Of course, better study designs targeted towards identifying these species are necessary as this study only provided an indication of which were more present in invaded and non-invaded sites. In addition, species that are more susceptible and disappear first may be of concern because of the resources or unique ecosystem services that they provide (Van Riper and

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Larson 2009). For example, if black samson (*Echinacea angustifolia*) was lost, it could impact the native pollinators negatively.

The plant species associations identified from our study may have resulted from having plant communities more susceptible to Kentucky bluegrass/smooth brome, certain species be more resilient to their invasion, or species that invade the area with them.

Ecological Sites more likely to be Invaded

Loamy, clayey, claypan, limy residual, thin claypan, and sandy sites are more likely to be invaded by Kentucky bluegrass, smooth brome, and crested wheatgrass. The more fertile soils may have been, at one-point in history, cropland that was either allowed to revegetate naturally or else seeded back to a plant species or mixture. Often times they were seeded back to crested wheatgrass (Looman and Heinrichs, 1973) or else neighboring invaded areas more easily encroached (Grant et al., 2020).

In this study, we see that thin loamy, very shallow, and shallow loamy sites are all less likely to be invaded than the other six top ecological sites in our dataset. These ecological sites describe our more "marginal" soils, which Grant et al. (2020) also found to be the soils least likely to be invaded. The areas least likely to be invaded in Grant et al.'s study were those with a higher prevalence of native species, on a steep slope with western or southern exposures, on poorer soils, farther away from cropland or roads, and with higher biodiversity. We found native plant species like little bluestem, sedges, and hood's phlox are more likely to be found on steeper slopes and poorer soils farther away from cropland and roads. Sites with little bluestem and sedges were also typically associated with more native forbs than observed on invaded sites. Understanding which ecological sites are more likely to be invaded may help rangeland managers identify which areas to focus invasive species management. It also may help predict which areas are susceptible to invasion in the future.

There have been few studies analyzing the impacts of Kentucky bluegrass on the native plant community's richness, diversity, and composition (Toledo et al., 2014). Most studies focused on management, whether it be grazing, seeding, fire, or herbicide studies (Hendrickson and Lund, 2010; Link et al., 2017; Otfinowski et al., 2017; Kral et al., 2018). There needs to be more studies like this or Grant et al. (2020) that attempt to describe the impacts across a landscape. To get more specific results without the variability, more studies should focus on ecological sites, disturbance history, and climate data. More studies like DeKeyser et al. (2013) that revisit the sites years later to compare changes due to invasion can help better understand the impacts in different regions. Studies with climate data associated with the sites can be more reliable in assessing climate change on the impacts of invasive species on native plant communities.

Study Limitations

This large dataset inherently comes with a larger amount of variability than other more controlled and short-term datasets. All of these variables can impact the interpretation of change to the plant community. This data set did not give detailed account of location, climate, or disturbance history. The location was more limited to the four different regions of the LMNG, and the ecological site was determined to better classify the locations based on their topological space, soil classification and texture, and carbonate content. Climate varied from severe droughts in 2008, 2012, and 2017 to extreme moisture in 2011, 2013, and 2014 (NOAA, 2020). While the disturbance history is unknown, there are some generalizations for these sites. All sites were

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managed by the USFS and grazed by private ranchers who obtain a grazing permit for the allotments. The USFS has general guidelines that the land is to be moderately grazed. They are generally grazed season-long and by beef cattle in this region. Especially in the larger allotments, the density of grazing can vary greatly from one area of the pasture to another. In addition, the USFS may have used prescribed fire to manage some of the allotments in the past, although these would be few. Therefore, because the dataset is so robust in all of the variables it accounts for, the more difficult it is to draw out conclusions or trends on specifics like how invasion level affects the site.

Within all of these variables; however, is a strength. We can analyze and better understand a large region, given all of its variables, and assess trends and groupings that still encapsulate the different areas or conditions. For example, even though the variability is high in the dataset, the fact that in 1,500 sites the maximum richness was limited so distinctly is something worth noting. Also, across all of the sites and variation, invasion can limit the diversity of native forbs.

As with many ecological studies, there are more sites in the dataset that are not invaded than along the gradient of invasion which skews the data towards zero. This can be difficult in some analyses like our richness and diversity linear models. This data set also has fewer sites with smooth brome than Kentucky bluegrass or crested wheatgrass. Therefore, the smooth brome analyses are more skewed towards zero than the others.

Management Implications

With the loss of richness and diversity, a shifting in the plant community, and a general consensus of invasive species, rangeland managers should try to prevent invasion, minimize it, and mitigate it. There is a potential loss in beneficial, native species and a potential gain of even

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more invasive and/or ecosystem altering species when the NGP is invaded by Kentucky bluegrass, smooth brome, and crested wheatgrass. Knowing which sites are less prone to invasion (very shallow, thin loamy, and shallow loamy) can give rangeland managers an indication that those should be the easiest to protect from CIP invaders. The sites more prone to invasion, like loamy and clayey sites, may already be invaded, and if they are not, could be more difficult to keep from being invaded by CIP, so diligent management strategies to suppress or prevent invasion like managed grazing, prescribed burning, and general monitoring is necessary (DeKeyser et al., 2009; 2013; 2015; Ellis-Felege et al., 2013; Link et al., 2017; Grant et al., 2020). The species associated with invaded sites, like yellow sweetclover and western snowberry, confound the damaging potential from invasive species to landowners' property. The loss of forage resources, alteration of ecosystem services, and loss of native diversity are all causes for concern. More research should be conducted to learn how Kentucky bluegrass and smooth brome influence the plant community. In this study we found an indication that 20-30% Kentucky bluegrass invasion may be an important ecological threshold in altering the plant community rather than a gradient. This should be explored further. Due to the magnitude of this dataset, we were able to gain a broad picture of these three CIPs in the NGP, but more research is necessary.

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