MANAGEMENT INFLUENCES ON PLANT COMMUNITY COMPOSITION IN THE PRAIRIE POTHOLE REGION

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Management influences on plant community composition in the Prairie Pothole Region

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ABSTRACT

Remnant prairies in the Prairie Pothole Region (PPR) should serve as repositories of native plant species, yet disrupted ecological process, invasive species, potential nitrogen deposition, climate change, and numerous other factors threaten native species diversity in remnant prairies. This study sought to assess how historical and adaptive management practices influence plant community composition in remnant prairies. We grouped sites based on recent or long-term management histories, and explored differences in floristic diversity, quality, and the abundance of individual species and groups of species between site groupings. Our assessments determined that long-term management history determines present day species composition, and that reinstating native disturbance regimes following extended periods of rest is effective for shifting plant community composition to a more desirable state. A continued commitment to restoring ecological function is likely required to target invasive species and conserve native species diversity on remnant prairies in the PPR.

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C-value	Coefficient of Conservatism
dbRDA	Distance-Based Redundancy Analysis
FQI	Floristic Quality Index
NMS	Nonmetric Multidimensional Scaling
NPAM	Native Prairie Adaptive Management
PERMANOVA	Permutational Analysis of Variance
PERMDISP	Permutational Analysis of Multivariate Dispersion
PPR	Prairie Pothole Region
R-value	Pearson’s Correlation Coefficient
USFWS	United States Fish and Wildlife Service

1. LITERATURE REVIEW

1.1. Plant Biodiversity in the Prairie Pothole Region

The Prairie Pothole Region (PPR) of North America is characterized by millions of depressional pothole wetlands surrounded by a mosaic of cropland, restored grassland, and remnant unplowed tall- and mixed grass prairie. Remnant unplowed prairie, or “native” prairie, has been reduced to 3% and 25% of its former extent for the tallgrass and mixed-grass prairies, respectively, and is further threatened by agricultural development, urbanization, climate change, mismatched management practices, and invasive species (Samson and Knopf 1994). Remnant prairies are repositories of native plant biodiversity and provide crucial ecosystem services, including habitat for wildlife and pollinators, livestock forage production, and carbon sequestration (Gascoigne et al. 2011). These services are enhanced by biodiverse plant assemblages. For example, Tilman et al. (1996, 2001) found that diverse grasslands had greater above- and belowground biomass production than monocultures, and that resource utilization was greatest in diverse grasslands. With that, diverse grasslands exhibited greater stability in above- and belowground biomass production over two-, five- or ten-year periods (Tilman et al. 2006). Homogenous structure characteristic of monocultures such as croplands or invasive species dominance results in decreased habitat quality for many grassland wildlife species (Ellis-Felege et al. 2013; Hovick et al. 2015; Vickruck et al. 2019). Conserving native species diversity is vital for preserving ecological integrity and maintaining the services provided by remnant native prairie in the PPR (Fuhlendorf and Engle 2001).

Native upland vegetation in the PPR includes species of variable physiognomies including grasses, sedges, ferns, forbs, cacti, low shrubs and trees (Northern Great Plains Floristic Quality Assessment Panel, 2001). The families Asteraceae, Fabaceae, and Poaceae represent the majority of species diversity in the region (Coupland 1992). At the regional level, species composition is largely determined by landscape fragmentation, temperature and precipitation gradients (Coupland 1992; Paradeis et al. 2010; Grant et al. 2020a). Lower diversity assemblages occur in the fragmented landscapes in southeastern North Dakota and higher diversity assemblages in the grassland-dominated landscapes of northwestern North Dakota (Paradeis et al. 2010; Grant et. al 2020b). Overall, C4 grasses are predominant at warmer lower latitudes and C3 grasses at cooler higher latitudes. Low shrub and native-dominated communities are more prevalent in the drier, cooler climes of northcentral and northwestern North Dakota than the warmer and wetter conditions of southeastern South Dakota (Grant et al. 2020a). Conversely, introduced species occupy greater amounts of prairie in south central North Dakota and eastern South Dakota (Grant et al. 2020a).

Long-term and interannual climate variability influence grassland species richness (Knapp et al. 2002), diversity (Collins et al. 2012; Derner 2015), and primary production (Knapp et al. 2002; Jonas et al. 2015; Kirwan et al. 2021). Climate forecasts predict warmer temperatures and increased precipitation in central North America (Fischer et al. 2014), and an assessment of climate trends in the past century found that climate in the PPR is trending warmer and wetter (Millet et al. 2008). The east-west precipitation gradient is becoming more polarized as the eastern extent becomes wetter and the western extent drier. Increasing average temperatures increase the length of the growing season; in North Dakota, the number of frost-free days has increased by nearly two weeks since 1879 (Badh et al. 2009). These changes may benefit introduced cool-season grasses: additional growing days occur in the spring and fall when cool-season species are photosynthetically active (DeKeyser et al. 2013), and increased precipitation is correlated to increased cover of cool-season grasses and decreased cover of native forbs

(Dennhardt et al. 2021). However, these effects may not be evident in plant communities dominated by warm-season native species (Collins et al. 2012).

At local scales, species composition is driven by soil texture, slope, aspect, human disturbance and land use practices. Coarse, well-drained sandy soils, loamy soils, and clayey soils support distinct community assemblages (Coupland 1992; Sedivec and Printz 2012). Areas with steeper slopes and south or west-facing aspects generally contain greater frequencies of native species than flatter areas (Grant et al. 2020b), and loamy soil ecological sites (Sedivec and Printz 2012) are associated with greater vulnerability to invasion by introduced species (DeKeyser et al. 2009; DeKeyser et al. 2013). Landscapes with less grassland continuity and more “edges” (defined by Grant et al. 2020b to be abrupt boundaries between prairie and croplands or roads) will exhibit greater frequencies of introduced species as roads and adjacent verges serve as invasion corridors for introduced plants (Hansen and Clevenger 2005; Meunier and Lavoie 2017). Patterns of invasion are species-specific with some species colonizing more densely along road edges and other species found more ubiquitously (Van Ripper and Larson 2009; Gifford et al. 2013; Grant et al. 2020b). Prairies with a long-term history of defoliation contain different species assemblages than prairies managed with deferment or rest (Murphy and Grant 2005; Gifford et al. 2013; Connell et al. 2020), and distinct changes in plant community composition may occur following a few decades without defoliation (DeKeyser et al. 2009).

1.1.1. Fire

Fire suppression has been noted as a factor influencing native species loss and introduced species dominance throughout the prairie region (Leach and Givnish 1996; DeKeyser et al. 2009). Prescribed burning emerged as a tool for emulating natural fire in an attempt to restore ecological processes (Engle and Bidwell 2001), increase spatial and structural heterogeneity

(Fuhlendorf and Engle 2001), and bolster native species abundance (Grant et al. 2009; Dixon et al. 2019). Burning may influence plant community composition by altering nutrient availability (Ojima et al. 1994; Blair 1997; Veen et al. 2008), litter and thatch accumulation (Ehrenreich and Aikman 1963; Kral et al. 2018), microbial activity (Dooley and Treseder 2012), and soil water availability (Anderson et al. 1970). Plant community response to prescribed burning varies with the ecology of individual species or functional groups (Curtis and Partch 1948; Engle and Bultsma 1984; Knapp 1985; Howe 1994b; Shay et al. 2001; Brudvig et al. 2007), the seasonality of burning (Biondini et al. 1989; Howe 1994b; Bennett et al. 2019), the frequency of burning (Kobiela et al. 2017; Dickson et al. 2019), prior year precipitation (USFWS, unpublished data) and species composition prior to burning (Blankespoor and Larson 1994; Ereth et al. 2017; Alhering et al. 2020).

The seasonal timing of burning may influence species composition due to phenological differences between cool- and warm-season species (Dickson et al. 2019). Late summer burning benefits cool-season grasses by targeting warm-season grasses during their emergence and growth periods (Howe 1994b). Cool-season grasses are not as strongly impacted because they are not as photosynthetically active during late summer (Dickson et al. 2019). Spring burning favors warm-season grasses by reducing the competitive advantage of cool-season grasses (Engle and Bultsma 1984; Steuter 1987; Bennett et al. 2019). These effects may be amplified in years with above average moisture conditions in the growing season following a spring burn (Blankespoor and Larson 1994). Spring burning has variable effects on forb populations: it has been noted to reduce forb abundance (Kline 1986) and species diversity (Biondini el al. 1989) but increase forb density (Biondini et al. 1989). Precipitation may moderate the effects of spring burning on forb growth persistence (Biondini et al. 1989). The seasonal effects of burning may not be evident if burning occurs in variable seasons or is conducted at infrequent intervals (Dickson et al. 2019). Implementing a variable cycle of spring and fall burning is recommended in communities where native cool-season species may be harmed by repeated spring burning (Sather 1996).

Frequent burning has been associated with decreases in introduced species cover (Li et al. 2013; Kobiela et al. 2017) and increases in native species richness (Brudvig et al. 2007; Kobiela et al. 2017) and cover (Ahlering et al. 2020). These compositional shifts may be most evident in sites with a high proportion of introduced invaders (Ereth et al. 2017; Ahlering et al. 2020). Annual burning may lead to decreased forb abundance by damaging belowground bud banks (Kline 1986; Dalgleish and Hartnett 2009; Russell et al. 2015). However, surviving forbs exhibit greater vigor than plants in unburned areas (Briggs and Knapp 2001). The effects of a single prescribed burn on species composition may be short-lived (Blankespoor and May 1996; Spasojevic et al. 2010; Bahm et al. 2011; Kral et al. 2018; Dickson et al. 2019), especially in communities dominated by introduced invasive species (Wilson and Stubbendieck 2000).

1.1.2. Grazing

Prairie plant communities evolved with grazing pressure by native herbivores. Though native herbivores have been largely extirpated from the PPR, livestock grazing is commonly implemented on remnant native prairie (Murphy and Grant 2005; Dixon et al. 2019). Grazing affects species composition and diversity (Biondini and Manske 1996; Collins et al. 1998; Towne et al. 2005; Manning et al. 2017), soil properties (Greenwood and McKenzie 2001; Fuhlendorf et al. 2002), nutrient cycling (Johnson and Matchett 2001; Knapp et al. 2002), and litter accumulation rate (Potvin and Harrison 1984, Naeth et al. 1991). Plant community response to grazing varies with the seasonality of grazing (Hendrickson et al. 2020) and stocking density (Hickman et al. 2004; Dornbusch et al. 2020).

Grazing in different seasons influences plant community composition due to the variation in response of individual species or functional groups to grazing (Gaujour et al. 2012). In communities dominated by cool-season introduced species, grazing in the early spring (typically early to mid-May) may impact the vigor of cool-season introduced species while avoiding damage to or favoring the growth of warm-season native species (Smith and Owensby 1978; Stacy et al. 2005; Hendrickson et al. 2020). Early spring grazing may favor warm-season species by reducing the competitive advantages that cool-season species obtain by emerging and initiating growth earlier in the growing season (Bennett et al. 2019). Native warm-season grasses may increase in cover (Hendrickson et al. 2020) and biomass production (Stacy et al. 2005) following early spring grazing than late spring grazing (after June 1).

Stocking density influences selective herbivory and biomass utilization (Smart et al. 2010; Gaujour et al. 2012), thus differences in plant community assemblages may arise following grazing at differing stocking densities (Vermeire et al. 2008). Short-duration grazing at high stocking densities may be effective for targeting introduced species and increasing native species richness, diversity and abundance (Hickman et al. 2004; Dornbusch et al. 2020). Conversely, low to moderate stocking rates over the majority of the growing season (i.e. season-long grazing) have been associated with declines in native species abundance and increases in introduced species abundance (Smith and Owensby 1978; Murphy and Grant 2005; Dornbusch et al. 2020).

1.1.3. Fire and Grazing Interactions

Prescribed fire and livestock grazing interact to influence plant community composition (Fuhlendorf et al. 2009). The majority of research on this topic has been conducted in the Southern Great Plains, thus additional research is warranted to establish burn-graze interactions in the Northern Great Plains. Herbivores preferentially graze plants in recently burned areas due to their greater palatability and nutritional content (Allred et al. 2011), which lessens grazing pressure in previously disturbed areas and allows them to recover. As the time since burning increases, grazing pressure will decrease and litter will accumulate (Fuhlendorf and Engle 2004; Fuhlendorf et al. 2006). As litter accumulates and increases fuel load and fuel continuity, the probability of fire occurring increases and the burn-graze interaction repeats (Fuhlendorf and Engle 2001). Managing grasslands with burning and grazing supports a mosaic of plant communities in various stages of regrowth (Fuhlendorf et al. 2006); thus, management that utilizes a combination of short-interval burning followed with intense herbivory is recommended for increasing heterogeneity in plant community composition and structure (Fuhlendorf et al. 2009).

1.1.4. Invasive Species

Introduced species invasion is the second most influential factor affecting native biodiversity globally; nearly half of the species on the U.S endangered species list are in decline due to negative impacts from invasive species (Wilcove et al. 1988). In the PPR, introduced invasive species comprise over 60% percent of plant cover on USFWS lands (Grant et al. 2020a) and are present on greater than 75% of non-federal rangelands (NRCS 2014). As introduced plant species displace native species, community structure and composition become more homogenous with ensuing impacts on ecosystem processes and services (DeKeyser et al. 2009; Toledo et al. 2014; Printz and Hendrickson 2015).

Standard management practices for combatting introduced species dominance in the PPR include prescribed fire, livestock grazing, or a combination of these approaches (Gasch et al. 2019). Alternative management approaches that include diversifying management to include multiple species grazing may more effectively control introduced species invasion in novel environments (DeKeyser et al. 2010; Printz and Hendrickson 2015). Management that emphasizes restoring ecological processes may be the most effective approach for controlling introduced species in the PPR (Dixon et al. 2019).

1.1.4.1. Kentucky bluegrass

Kentucky bluegrass (*Poa pratensis* L.) is a rhizomatous, perennial cool-season grass introduced to the Great Plains in the late 1800s (Carrier and Bort 1916). It is widely planted for use as an ornamental turfgrass, pasture forage, and roadside stabilization (Palit et al. 2021). It is among the most widespread invasive introduced species in the PPR and is the predominant grass species in all but the southeastern and northwestern extents of the region (Grant et al. 2020a). Its widespread invasion is implicated in the decline of native species richness and abundance (Cully et al. 2003; Miles and Knops 2009; Larson and Larson 2010; DeKeyser et al. 2013; White et al. 2013), and may cause additional impacts to ecological processes and ecosystem services (Toledo et al. 2014; Printz and Hendrickson 2015).

Kentucky bluegrass is a highly competitive invader. It initiates growth before many native species (Nieland and Curtis 1956) and may thus experience less competition for resources such as light, moisture, and nutrients. Its rhizomatous habit can allow it to spread by up to two square meters of horizontal growth within a two-year period (Kannenberg and Wrede 1934).

Kentucky bluegrass competes against native species by producing dense stands of tillers and thick root mats, or “thatch” (Bonos and Murphy 1999). Thatch is a dense mat of senesced and live plant material, roots, and decomposing litter (Hilfer and Limb 2020). Kentucky bluegrass thatch suppresses native species persistence by creating a physical and chemical barrier to germination and growth (Bosy and Reader 1995), as well as altering germination cues such as light and temperature fluctuation (Rice 1985; Gasch et al. 2019). It changes soil surface hydrology by increasing hydrophobicity in dry soils and decreasing it in wet soils (Nouwakpo et al. 2019). Though it is a prolific seed producer (Evans and Canode 1971), it is predominantly apomictic and reproduces sexually less than 20% of the time (Akerberg 1939).

Kentucky bluegrass responds variably to prescribed burning. Repeat early spring burning timed to coincide with the boot stage is effective for reducing Kentucky bluegrass (Launchbaugh and Owensby 1978; Towne and Owensby 1984; Engle and Bultsma 1984; Schacht and Stubbendieck 1985; Svedarsky et al. 1986; Knops 2006; Li et al. 2013). Burning while Kentucky bluegrass is in the boot stage may cause plants to allocate resources to tillers instead of rhizomes, reducing the opportunity for sod formation (Dahl and Hyder 1977). However, others have noted little or no effect of repeat spring burning on Kentucky bluegrass abundance (Kobiela et al. 2017; Kral et al. 2018). Kral et al. (2018) found that late season and dormant season burns were more effective than spring burns for reducing Kentucky bluegrass cover three years after initial burning. The authors suggest that fall and dormant season burning may increase native warm- and cool-season species vigor by avoiding burn damage and removing accumulated litter. The effects of burning on Kentucky bluegrass patches may be short-lived if warm-season species are not present in the plant community (Schacht and Stubbendieck 1985). Variable effects of burning on Kentucky bluegrass may also be attributed to differences in soil moisture conditions (Schact and Stubbendieck 1985; Grace et al. 2001; DiTomaso et al. 2006).

Kentucky bluegrass is tolerant of grazing and persists even when exposed to long-term annual grazing pressure (Murphy and Grant 2005; Gifford and Otfinowski 2013). Kentucky bluegrass internodes do not elongate during growth and meristems remain low to the ground (Dahl and Hyder 1977), thus allowing it to regrow following defoliation. Low- and moderate-intensity continuous grazing practices are noted to increase Kentucky bluegrass abundance (Weaver 1954; Donkor et al. 2002; Murphy and Grant 2005; Dornbusch et al. 2020). This may occur because cattle preferentially graze native warm-season species, especially big bluestem, over Kentucky bluegrass (Weaver 1948; Sather 1996). Intensive early-spring grazing appears to decrease (Smith and Owensby 1978) or moderate (Dornbusch et al. 2020; Hendrickson et al. 2020) Kentucky bluegrass abundance. The mixed effects of early-spring targeted grazing on Kentucky bluegrass may be attributed to differences in precipitation: Kentucky bluegrass may be more tolerant to grazing during periods of increased precipitation (Donkor et al. 2002; Hendrickson et al. 2020). Conversely, Kentucky bluegrass may be killed when grazed or mowed during drought (Sather 1996).

Climate change has lengthened the growing season and increased precipitation in the PPR, and these changes may favor Kentucky bluegrass expansion (Badh et al. 2009; DeKeyser et al. 2015). Additional growing days occur in the spring and fall when Kentucky bluegrass is photosynthetically active. Increased precipitation favors Kentucky bluegrass spread (Dennhardt et al. 2021) and yield (Owensby et al. 1970). Though Kentucky bluegrass proliferates in moist soils (Stevens 1950) and is most productive in moist pasture (Etter 1951), it may persist through drought by utilizing water deeper in the soil profile (DaCosta et al. 2004). Additionally, Kentucky bluegrass' shallow, mat-forming roots allow it to rapidly uptake water during intermittent rain events (Dong et al. 2014).

Kentucky bluegrass abundance is higher in grassland-dominated landscapes that have been managed for livestock production since the early 1900s (Murphy and Grant 2005; Gifford and Otfinowski 2013; Grant et al. 2020b). Grazing may have historically facilitated Kentucky bluegrass invasion in native grasslands (Gifford and Otfinowski 2013), though it is now present in comparable frequencies on native grasslands with differing grazing histories (Murphy and Grant 2005). Kentucky bluegrass frequencies are highest in landscapes with continuous grassland and lower road density (Grant et al. 2020b). These areas are primarily used for livestock production, or are managed with livestock for conservation purposes (Grant et al. 2020b).

1.1.4.2. Smooth brome

Smooth brome (*Bromus inermis* Leyss.) is rhizomatous, perennial cool-season grass that was introduced in North America in the late 1800s (Sedivec and Barker 1997). It is widely planted for livestock forage, roadside stabilization, and wildlife habitat improvement (Salesman and Thomsen 2011) and was bred to establish and grow rapidly and densely under variable conditions (Wilkins and Humpherys 2003). Smooth brome invasion is associated with altered resource availability and declines in native species richness and abundance (Fink and Wilson 2011; Stotz et al. 2019).

Smooth brome was bred to establish and grow rapidly and densely under variable conditions (Wilkins and Humpherys 2003). It initiates growth in colder temperatures and lower light conditions (Grilz et al. 1994) and can initiate growth early in the growing season before many native species emerge. Smooth brome may also undergo a second growth period in the fall

(Willson and Stubbendieck 2000). Fall tillers do not elongate and meristematic tissue remains belowground; thus, plants may not be as vulnerable to defoliation during this period (Willson and Stubbendieck 2000; Otfinowski et al. 2007). Smooth brome's rhizomatous growth habit allows it to invade unoccupied interspaces and nutrient-limited areas. Resource transfer occurs between established "mother" plants and new rhizomatous clones, and established patches can outcompete cespitose species for light, nutrients, and soil moisture (Otfinowski and Kenkel, 2010). In addition to asexual reproduction, smooth brome is a prolific seed producer (Otfinowski et al. 2008). The majority of seeds are dispersed within a meter of the parent plant (Otfinowski et al. 2008), but long-range dispersal may be accomplished by animals, wind, and hay production (Otfinowski et al. 2007). However, smooth brome may negatively impact its own seedling germination, growth and survival rates within dense patches (Carrigy et al. 2016).

Smooth brome is prevalent in areas with high proportions of cropland edges (Grant et al. 2020b). Smooth brome abundance increases near roadways (Gifford and Otfinowski 2013; Grant et al. 2020b), and road verges and cropland edges may serve as invasion fronts and propagule sources affecting nearby native prairie (Hansen and Clevenger 2005; DeKeyser et al. 2013). Nitrogen drift from croplands to nearby prairie (Murphy and Grant 2005) may increase smooth brome tiller density and biomass within patches (Vinton and Goergen 2006). Smooth brome litter is nitrogen rich and decomposes faster than native species litter (Vinton and Goergen 2006) and may further alter nitrogen cycling rates in patches (Jordan et al. 2008, Piper et al. 2014). Though its litter decomposes rapidly (Vinton and Goergen 2006), increased litter can provide a barrier to native species germination by altering light availability (Stotz et al. 2017), soil moisture (Fink and Wilson, 2011), and soil temperature (Facelli and Pickett 1991). Changes in light and resource availability caused by smooth brome invasion may suppress the germination and growth of native species and lower likelihood of persistence (Myster 2006; Williams et al. 2006, Dillemuth et al. 2009).

Smooth brome abundance varies with precipitation and temperature gradients. The tallgrass prairie communities of the eastern PPR have relatively warmer and wetter climates and are more adversely impacted by smooth brome invasion than cooler, drier areas in the north and west (Stotz et al. 2017, Grant et al. 2020a). The more extreme precipitation patterns and warmer temperatures predicted by climate models may enhance smooth brome vigor (Fischer et al. 2014). Where present, smooth brome may outcompete native species even under very dry conditions (Nernberg and Dale, 1997). North Dakota’s growing season has increased by 12 days in the past century (Badh et al. 2009), and a longer growing season may favor introduced cool-season grasses (DeKeyser et al. 2015).

Smooth brome may be controlled using repeat, late spring prescribed burns. Repeated burning has shown promise for suppressing smooth brome (Rosburg 2001; Brudvig et al. 2007, Kobiela et al. 2017), whereas single burns are ineffective at reducing smooth brome abundance over time (Willson and Stubbendieck 1997). Repeat burning during shoot elongation in late spring significantly reduces smooth brome tiller density and patch size (Blankespoor 1987; Blankespoor and Larson 1994; Willson and Stubbendieck 1997). During shoot elongation, carbohydrate stores in the roots are translocated to aboveground biomass; thus, targeted burns during this time may successfully limit smooth brome growth and reproduction (Willson and Stubbendieck 2000). However, the results of a ten year assessment on USFWS lands suggests that burning during elongation may be ineffective for controlling smooth brome in tallgrass prairies in eastern ND and SD (USFWS, unpublished data). Additional research on the effects of burning outside of the tiller elongation window may provide managers with a more diverse toolkit for targeting smooth brome with fire. Smooth brome tiller density was significantly reduced following one year of late fall burning (Preister 2018), though it's unclear what long-term effects single or repeat late fall burning may have on smooth brome abundance.

Targeted spring grazing has mixed effects on smooth brome abundance and vigor. Annual early spring grazing was effective for reducing smooth brome relative cover (Stacy et al. 2005; Smart et al. 2013), tiller density (Brown 1997) and seed production (Hopkins et al. 2003). Smooth brome occurs infrequently on annually-grazed rangelands, indicating that it may be intolerant to frequent, prolonged grazing (Murphy and Grant 2005). However, other studies have found limited or no differences in smooth brome abundance following annual early spring grazing treatments (Dornbusch et al. 2020; Hendrickson et al. 2020). Early spring targeted grazing at variable stocking densities resulted in no change in smooth brome abundance (Dornbusch et al. 2020; Hendrickson et al. 2020).

1.1.4.3. Forbs

Introduced forbs account for roughly 4.5% of plant community composition on USFWS lands in the PPR (Grant et al. 2020a). Four species, Canada thistle (*Cirsium arvense* L.), yellow sweet clover (*Melilotus officinalis* (L.) Lam.), wormwood (*Artemisia absinthium* L.) and leafy spurge (*Euphorbia esula* L.), have demonstrated invasive tendencies throughout the PPR (Evans 1982; Lesica and DeLuca 2000; Larson et al. 2001; Grant et al. 2020a). They are less prevalent on the landscape than Kentucky bluegrass or smooth brome (Grant et al. 2020a), but their ability to modify ecosystem processes and affect management outcomes may warrant monitoring and targeted management.

Canada thistle is a short-lived rhizomatous perennial found throughout a vast range of habitat types (Walkup 1991). It has demonstrated allelopathic interactions with various cultivated species (Stachon and Zimdahl 1980) and is listed as noxious within North Dakota and South Dakota. It increases in abundance following disturbance, though its rhizomatous habit and prolific seed production may allow it to spread in undisturbed areas (Heimann and Cussans 1996). Canada thistle's spines and thorns make it undesirable forage for both livestock and wildlife, and animals preferentially select for more palatable forage when available (Tierney 2013). It has shown sensitivity to repeat early-intensive grazing, but may increase under season-long or deferred management (De Bruijn and Bork 2006). Researchers have noted variable response to burning: repeat late spring burning reduced abundance (Hutchison 1992), early season burning had no effect (Hogenbirk and Wein 1991) or caused increased sprouting (Hutchison 1992), and late summer and fall burning were associated with declines in abundance (Kirsch and Kruse 1973) or increases in biomass and shoot density (Hogenbirk and Wein 1991). Additional research is needed to understand which factors influence Canada thistle response to prescribed fire.

Yellow sweet clover is a biennial legume widely used in wildlife habitat enhancement, roadside revegetation, forage and cover crops in PPR (Turkington et al. 1978). It is estimated to comprise 1.5% of species composition on USFWS units in the PPR (Grant et al. 2020a) and is the sixth most frequently encountered species on National Park Service (NPS) lands in western ND (Larson et al. 2001). Its widespread presence in the PPR is concerning due to its ability to alter nitrogen cycling (Lesica and DeLuca 2000), though its direct impacts on species composition are not well understood. Increased nitrogen availability is linked to increases in dominance and decreases in species richness independent of initial species abundances (Tilman 1987; Wilson and Shay 1990). Given the context of increased nitrogen availability in the highly agricultural PPR, native prairie invaded by yellow sweet clover may experience increases in nitrophilic introduced species and additional impacts to species diversity (Lesica and DeLuca 2000; Jarchow and Liebman 2012; Grant et al. 2020b). There are anecdotal accounts of Kentucky bluegrass increasing following sweet clover senesce (Printz and Hendrickson 2015), and greenhouse studies have demonstrated that Kentucky bluegrass produces more biomass when grown in soil conditioned with sweet clover (Dornbusch et al. 2018). The effects of sweet clover on nitrogen availability and facilitating invasion of other introduced species may be moderated in intact grasslands (Van Riper and Larson 2009; Van Riper et al. 2010).

Yellow sweet clover may be controlled using targeted grazing or consecutive burning. Targeted grazing during late summer and fall can reduce sweet clover density, but is unlikely to fully eliminate it due to the ability of seeds to remain viable in the seedbank for extended periods (Meyer 2005). Seed germination is triggered by burning (Heitlinger 1975), and repeated annual late spring burning is recommended for targeting sweet clover, while burning at infrequent intervals (>2 years) may promote its expansion (Kline 1986). Controlling sweet clover will require multi-year management approaches designed to address site-specific conditions.

Wormwood is a perennial forb listed as noxious within North Dakota and South Dakota. It was introduced to North America in the early 1800s for cultivation for medicinal and culinary purposes (Kaul et al. 1976). It escaped cultivation and is observed to invade along road verges, overgrazed rangelands, pastures and shelterbelts in the northern Great Plains (Evans 1982; Maw et al. 1985). It increases following soil disturbance (Evans 1982), though it is noted to be a weak competitor in intact grasslands (Selleck and Coupland 1961). Wormwood influences plant community dynamics by releasing alkaloid compounds that inhibit germination and growth and promote senescence in neighboring plants (Ueda and Kato 1980). These pungent alkaloid compounds in the leaf tissue also deter livestock and wildlife herbivory (Maw et al. 1985), and when present at high densities, wormwood may impact forage availability and increase grazing pressure on neighboring species (Selleck and Coupland 1961; Evans 1982). There is limited information on wormwood response to prescribed burning, though it appears sensitive to repeat spring burning (Steuter 1988; Rosburg 2001).

Leafy spurge is a rhizomatous perennial native to Eurasia. It was introduced to the northern Great Plains in the late 1800s (Watson 1985) and was listed as noxious in North Dakota in 1935 (Lym and Travnicek 2010). It comprises roughly 1% of floristic cover on USFWS lands in the PPR (Grant et al. 2020a). It is distributed primarily in untilled agricultural land and adjacent road verges (Bangsund and Leistritz 1991), and was estimated to 725,000 hectares in North Dakota at the peak of its invasion in the 1980s (Lym and Travnicek 2010). Leafy spurge negatively impacts native species diversity by forming dense canopies and root systems that limit germination and seedling growth in neighboring plants (Selleck et al. 1962; Butler and Cogan 2004). There are variable accounts of allelopathy in leafy spurge: decaying leafy spurge roots impacted the growth of cultivated species (Steenhagen and Zimdahl 2017), but perennial grasses grown in soil condition by leafy spurge exhibited no differences in biomass production compared to controls (Barreto and Fay 1981).

Leafy spurge may be controlled with targeted grazing and prescribed burning. Leafy spurge invasion is associated with decreased forage availability for cattle (Bangsund and Leistritz 1991) and may cause toxicity in cattle in horses (Callihan et al. 1990). Sheep and goat grazing during the growing season may reduce but not eradicate leafy spurge populations (Lym and Travnicek 2010). Prescribed fire may control leafy spurge populations by directly causing mortality to seeds; repeat burning is recommended to deplete leafy spurge seeds in the soil seedbank (Wolters et al. 1994; Vermeire and Rinella 2009). The timing of prescribed burning influences leafy spurge response: early spring burning increased leafy spurge stem densities compared with late-May burning or no burning (Masters 1994), but repeat fall burning may be effective for reducing the frequency of leafy spurge (Dix 1960; Prosser et al. 1999).

1.1.4.4. Shrubs

Shrubs account for roughly 10% of plant cover in the PPR (Grant et al. 2020a). Western snowberry (*Symphoricarpos occidentalis* Hook.) and silverberry (*Elaeagnus commutata* Bernh. Ex Rydb.) are native, rhizomatous low shrub species that have increased in abundance on native prairies in response altered disturbance regimes and climate (Bailey 1970; Van Auken 2000; Murphy and Grant 2005). Though found throughout the region, their occurrence is greatest in central, north central, and northwestern North Dakota (Grant et al. 2020a). Woody species encroachment in grasslands can facilitate changes in plant community composition (Dahl et al. 2020) by altering light and nitrogen availability (Lett and Knapp 2003), and significant declines in species richness may occur following shrub invasion in grassland communities (Ratajczak et al. 2012). In the PPR, low shrub encroachment creates environments conducive for secondary invasion by Kentucky bluegrass, smooth brome and Canada thistle (Smith 1985a, Grant et al 2020b). A region-wide assessment of USFWS lands found low shrub understories to be dominated by Kentucky bluegrass and smooth brome (Grant et al. 2020). Low shrub and introduced grass co-invasion may be exacerbated in loamy ecological sites (DeKeyser et al. 2009; DeKeyser et al. 2013; Grant et al. 2020b).

Low shrub response to defoliation is varied. Western snowberry stands decreased in density and canopy cover following repeated spring burning (Bailey and Anderson 1979; Smith 1985b), but increased two- to three-fold over pre-burn conditions following a singular fall or spring burn (Romo et al. 1993). Silverberry is vulnerable to spring burning and is slow to recover to pre-burn levels (Bailey and Anderson 1979; Arnold and Higgins 1986). Both western snowberry and silverberry are noted to increase in response to heavy grazing (Bailey 1970; Bailey et al. 1990), but western snowberry canopy cover may be reduced with targeted grazing treatments (Kirby et al. 1988; Reed et al. 2019). Silverberry cover may be reduced by repeated sheep browsing or mowing (Bailey 1970).

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2. TRENDS IN PLANT COMMUNITY COMPOSITION FOLLOWING A DECADE OF ENROLLMENT IN THE NATIVE PRAIRIE ADAPTIVE MANAGEMENT PROGRAM

2.1. Introduction

The prairies of central North America are among the most converted and least protected ecosystems (Hoekstra et al. 2005). Tallgrass and mixed-grass prairies of the Prairie Pothole Region (PPR) have declined by upwards of 99% and 70%, respectively, primarily due to agricultural conversion following Euro-American settlement in the 1800s (Samson and Knopf 1994). The native biodiversity of remnant prairie is further threatened by urbanization, agricultural conversion, climate change, fire suppression, certain grazing practices, and invasive plants (Samson and Knopf 1994; Grant et al. 2020a; Dennhardt et al. 2021). Introduced species invasion and disrupted disturbance regimes are implicated in the loss of native biodiversity in remnant prairies (DeKeyser et al. 2009; Grant et al. 2020a). Introduced species invasion and native species biodiversity loss has negative implications for preserving the ecological integrity, functioning and services provided by remnant native prairie (Toledo et al. 2014; Printz and Hendrickson 2015).

Disruptions to the ecological processes that shaped grassland communities occurred following Euro-American settlement (Samson and Knopf 1994). Resilient, disturbance-adapted plant communities were shaped by interactions between climate, herbivory and fire (Higgins 1986). The region supported year-round herds of bison (*Bos bison)* and elk (*Cervus elaphus*) (Hanson 1984) and natural and anthropogenic fires commonly occurred every 5-6 years (Bragg 1995). Following Euro-American settlement in the late 1800s, native herbivores were replaced with domestic livestock and naturally-occurring fires were suppressed.

The United States Fish and Wildlife Service (USFWS) manages over 100,000 hectares of prairie east of the Missouri River in North Dakota and South Dakota. These lands were traditionally managed to increase waterfowl production (Dixon et al. 2019). Waterfowl nesting density was determined to be highest in prairies with tall, dense herbaceous vegetation (Naugle et al. 2000). To achieve desired nesting structure, fire was suppressed and livestock occurred infrequently at light intensities (Murphy and Grant 2005). These management practices persisted through the 1990s and are implicated in the widespread proliferation of introduced species on prairies managed by USFWS (Grant et al. 2020a). Two introduced cool-season grasses, Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.), comprise greater than 50% of vegetative cover on USFWS-owned prairies (Murphy and Grant 2005; Grant et al. 2020a). Both species are associated with declines in native species diversity and abundance (Cully et al. 2003; Williams and Crone 2006; Fink and Wilson 2011; DeKeyser et al. 2013) and altered ecosystem function (Toledo et al. 2014; Printz and Hendrickson 2015). Their prevalence on USFWS-owned prairies indicates that native plant diversity may be imperiled.

Following the outcomes of regional floristic assessments (Murphy and Grant 2005; Grant et al. 2009), the USFWS partnered with the United States Geological Survey (USGS) to develop an adaptive process to guide management of USFWS prairies (Grant et al. 2009; Gannon et al. 2013). The Native Prairie Adaptive Management (NPAM) program emerged as a means to evaluate strategies intended to target introduced grasses and increase native species abundance while minimizing costs. The program provides annual decision support in the face of biological or environmental uncertainty by utilizing site-specific information and annual vegetation monitoring data to develop management recommendations each year. Annual management actions for mixed grass sites include graze, prescribed burn, prescribed burn and graze within the same management year, and rest. Management recommendations for tallgrass sites are being revised based on recent research, but formerly were burn within smooth brome elongation period, grazing within smooth brome elongation period, defoliate (burn, graze, or hay anytime outside of the smooth brome elongation window), and rest. The establishment of the NPAM program marked a formal shift in management paradigms on USFWS lands as burning and grazing became more commonplace. Restoring periodic disturbance to historically idle native prairie has demonstrated promise for improving floristic composition; notably, prairies burned at greater frequencies have greater native species richness and lower abundance of smooth brome than unburned prairie (Kobiela et al. 2017; Dixon et al. 2019). Annual belt-transect monitoring by USFWS staff have determined that native species abundance increased at sites enrolled in the NPAM program between 2010 and 2016 (Dixon et al. 2019). However, the species-level compositional changes in native abundance remain unclear.

In 2012, we established permanent monitoring plots across a subset of units enrolled in the NPAM program to assess plant community composition. We revisited these plots in 2020 with the intent to evaluate changes in native species composition over time. We related environmental and management variables at each site to shifts in species composition to determine which changes were associated with the NPAM program's management recommendations. Though the principal goal of the NPAM program is to increase native species cover, implied within that is control of introduced invasive species; thus, we included three predominate introduced species, Kentucky bluegrass, smooth brome, and yellow sweet clover (*Melilotus officinalis* (L.) Lam.) in our assessment.

2.2. Methods

2.2.1. Study Area

The PPR is a glaciated landscape that spans approximately 48 million hectares across five U.S. states (Millett et al. 2009). It is characterized by flat to gently rolling landscapes pockmarcked by millions of small wetlands, or "potholes", formed by glacial activity in the late Wisconsinian glaciation (Johnson et al. 2008). Land use in this region is dominated by intensive agricutlure in the flatter areas and livestock grazing on steeper slopes.

The PPR has a semi-arid to sub-humid climate with cyclic deluge and drought periods (Winter and Rosenberry 1998). Precipitation and temperature vary along orthogonal latitudinal and longitudinal gradient. Precipitation ranges between 30cm in the western extent to 90cm in the eastern extent, with the majority of precipitation (70%) falling during the growing season between April and September (Millett et al. 2008). Mean annual temperatures range between 10°C in the south and 1°C in the north, but daily temperatures may fluctuate to above 40°C or below -40°C (Millett et al. 2008). The average number of frost-free days is approximately 120 days (Badh et al. 2009).

2.2.2. Site Selection

We selected 30 native prairie sites on USFWS lands enrolled in the NPAM program in North and South Dakota (Figure 2.1) (Appendix A). The sites were selected based on site history, accessibility, and soil characteristics. The sites have been managed with various combinations of rest, grazing, burning, or a combination of burning and grazing since at least 2008. Prescribed burning is primarily conducted in early- to mid-May at moderate intensity. The seasonality of grazing and stocking density vary considerably between years and sites.

These sites have never been cultivated and contain predominantly loamy soil types. We selected sites with predominantly loamy soils because they are known to be vulnerable to invasion by introduced cool-season grasses and are the predominant soil types in the region (DeKeyser et al. 2009; DeKeyser et al. 2013). Additionally, we selected the loamy soil ecological site type (Sedivec and Printz 2012) to control for variability inherent in the large geographical extent of this study, especially with the inclusion of sites in both the tall- and mixed-grass prairies. Plant communities associated with the loamy ecological site are expected to have a comparable composition across the study area (Sedivec and Printz 2012).

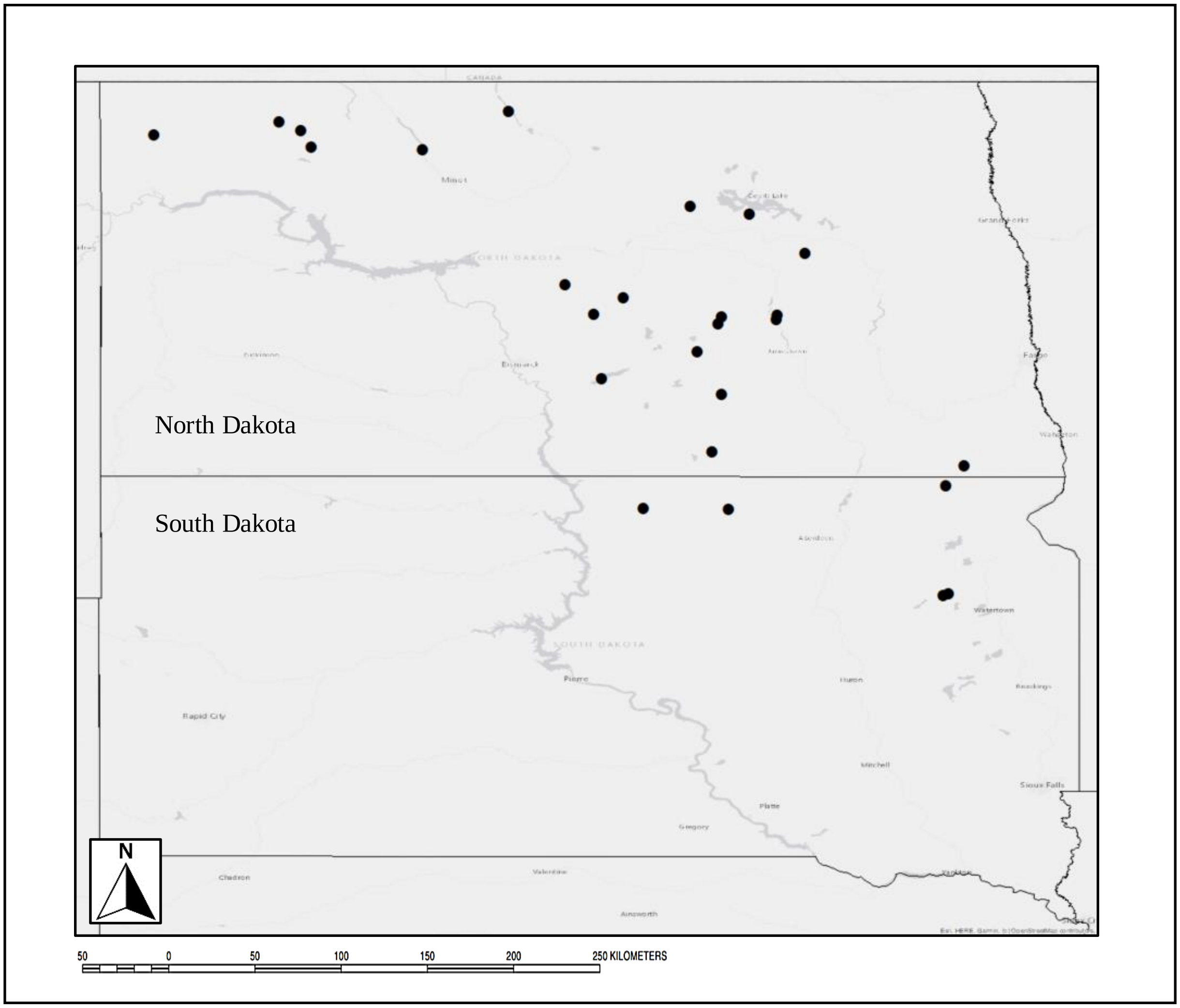

Figure 2.1. Location of 30 units (black circles) enrolled in the NPAM program throughout the Prairie Pothole Region of North Dakota and South Dakota.

In 2012, we established and conducted vegetation monitoring at 30 USFWS management units enrolled in the NPAM program (Kobiela et al. 2017). We randomly placed three to five 1000 m^2 long-term Modified-Whittaker (Stohlgren et al. 1995) plots at in loamy soil types at each unit. The number of plots established was proportional to the area of the unit being surveyed. After monitoring in 2012 and 2013, we assessed the minimum number of plots necessary to survey at each site and determined that monitoring three plots per site was sufficient. In 2020, we re-monitored the plots at each site established in 2012. We randomly selected three plots for remeasurement at sites with more than three established plots.

2.2.3. Vegetation Monitoring and Data Analysis

We conducted vegetation monitoring between June and September of 2020. We used the Modified-Whittaker sampling method (Figure 2.2) to measure plant community composition and cover (Stohlgren et al. 1995). The Modified-Whittaker method utilizes a nested frequency design that is useful for comparing land use practices, investigating species-environment relationships, and detecting rare or exotic species (Stohlgren et al. 1995; Stohlgren et al. 1998). When compared with similar vegetation sampling methods, the Modified-Whittaker design reduces spatial autocorrelation and captures the highest species diversity by area (Stohlgren et al. 1995). The plot configuration is non-overlapping subplots of variable sizes positioned with a 1000 m^2 plot. We estimated percent cover for each species and ground cover class (litter, bare ground, or rock) in ten 1 m^2 plots. We recorded which species occurred within two 10 m^2 plots, one 100 m^2 plot, and one 1000 m^2 plot. Newly-encountered species were successively recorded at each scale.

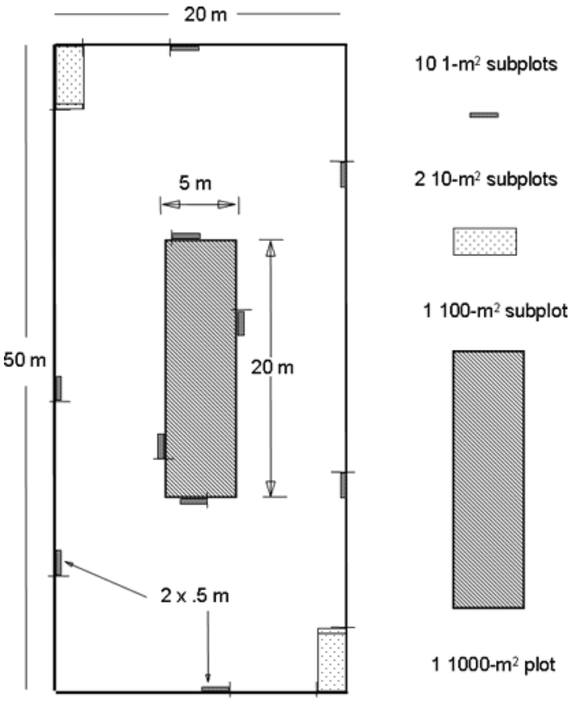

Figure 2.2. Modified-Whittaker sampling design. Modified from Stohlgren et al 1995.

We averaged and relativized species cover estimates across all plots at each site. Prior to the multivariate analyses, rare species (species with fewer than two occurrences) were eliminated to reduce noise in the dataset (Peck 2016) and relative cover values were transformed using the arcsine square root transformation to improve normality (McCune and Grace 2002). Multivariate analysis was conducted using PC-ORD (version 7, MjM Software Design, Gleneden Beach, OR, USA) and R (R Core Development Team; Oksanen et al. 2015). Univariate analysis was conducted using SAS Enterprise Guide (version 7.1, SAS Institute, Cary, NC, USA).

We determined the management history for each site between the years 2010 and 2019. We selected the year range 2010-2019 to reflect the maximum period of management influence based on the timing of all sites entering into the NPAM program (2010) and the most recent management year prior to monitoring (2019). We recorded the burn + graze treatment as two independent management actions; i.e. sites that received a burn + graze treatment will have two management actions (one burn and one graze) recorded for that calendar year.

We tested for correlations between species abundance and five environmental variables using distance-based redundancy analysis (dbDRA; Legendre and Anderson 1999). We used relative cover as the response matrix and used the Bray-Curtis distance measure to create our distance matrix. We retained environmental variables in the final model if they increased the explanatory power of the model; the environmental variables we tested are listed in Table 2.1. We conducted variance partitioning for each variable to determine which variables were correlated with variation in relative cover. We used correlation coefficients (r-values) to examine individual species relationships to dbDRA ordination axes. Species with r-values $\geq |0.4|$ were included for interpretation.

Table 2.1. Explanatory variables included in the dbDRA assessment.

Explanatory variable	Description
Number of burns	The number of times a site was burned between 2010 and 2019
Number of grazes	The number of times a site was grazed between 2010 and 2019
Years since burn	The number of years since a site was burned*
Years since graze	The number of years since a site was grazed*
Northing	The Universal Transverse Mercator northing value for a site

*Based on the actual year, not the USFWS management year. For example, a burn could be conducted in October 2015 but be recorded as occurring in the USFWS 2016 management year. If that were the most recent burn at that site, that burn would be recorded as occurring in 2015, or five years since the 2020 monitoring action.

We performed a one-way Permutation Multivariate Analysis of Variance (PERMANOVA) to test for significant differences in species compositions between groups based on burn frequency (Table 2.2). Conducting prescribed burning is resource-intensive and may be limited by environmental conditions, therefore examining how the plant community responds to differing levels of prescribed burn frequency will inform how often this management practice should be implemented. PERMANOVA requires a balanced design with equal numbers of samples in each group; thus, our study included two groups with 15 sites each. We used the

Relative-Sorenson distance measure and performed 1000 permutations ($p < 0.05$) (Anderson 2014).

Table 2.2. PERMANOVA grouping factor, levels, number of occurrences, and descriptions.

Factor	Levels	Number of sites	Description
Burn Frequency	0-2 burns	15	Burning occurred 0, 1 or 2 times between 2010 and 2019
	3+ burns	15	Burning occurred 3, 4, or 5 times between 2010 and 2019

We used the Coefficients of Conservatism for the Vascular Flora of the Dakotas and adjacent Prairies manual to assign each species a coefficient of conservatism value (C-value) and calculate a floristic quality index (FQI) value for each site (Northern Great Plains Floristic Quality Assessment Panel 2001). This index is a species richness estimate that assigns value rankings to native species based on their tolerance to disturbance. Low values indicate that a species is able to persist in severely disturbed areas while high values indicate that a species is restricted to relatively intact natural areas. Introduced species are not assigned C-values and are not included in the calculation of the FQI value.

We used paired T-tests to compare species richness, native species richness, FQI, and relative cover for a set of individual species, genera, and functional groups between 2012 and 2020 (Tables 2.3-2.5). For each diversity metric, individual species, or group of species, we calculated the change in value or relative cover between 2012 and 2020 and used two sample T-tests to assess if the changes were significantly different between sites burned 0-2 times and 3 or more times. The individual species were selected a priori for analysis by USFWS staff (Table 2.4). The native species are of special interest to managers due to their sensitivity to management actions (pers. com. C. Dixon, 2021). The introduced species were included due to their prevalence on USFWS-owned landscapes and ability to alter grassland composition and functioning (Table 2.5) (Toledo et al. 2014; DeKeyser et al. 2015; Grant et al. 2020a). Genera and specific epithets follow the United States Department of Agriculture Plant Database (USDA 2022).

Table 2.3. Description of diversity metrics, physiognomic groups, and functional groups compared between 2012 and 2020.

Metric	Description
Species richness	Number of species
Native species richness	Number of native species
FQI	Floristic quality index
Native species	Relative cover of all native species
Graminoids	Relative cover of all graminoid species
Warm-season graminoids	Relative cover of native warm-season graminoids
Cool-season graminoids	Relative cover of native cool-season graminoids
Forbs	Relative cover of all forb species
Shrubs	Relative cover of all shrub species

Table 2.4. List of native graminoid species and genera groups. The common name, physiognomy, and season are listed for each species or genera group.

Species or genera	Common name	Physiognomy	Season
Andropogon gerardii Vitman	Big bluestem	Grass	Warm
Bouteloua curtipendula Michx.	Sideoats grama	Grass	Warm
Bouteloua gracilis (Wiild. ex Kunth) Lag. ex Griffiths	Blue grama	Grass	Warm
Calamovilfa longifolia (Hook.) Scribn.	Prairie sandreed	Grass	Warm
Carex spp.	Sedge	Sedge	Cool
Hesperostipa commata (Trin. & Rupr.) Barkworth	Needle and thread	Grass	Cool
Hesperostipa spartea (Trin.) Barkworth	Porcupinegrass	Grass	Cool
Nasella viridula (Trin.) Barkworth	Green needlegrass	Grass	Cool
Pascopyrum smithii (Rydb.) A. Love	Western wheatgrass	Grass	Cool
Scizachyrium scoparium (Michx.) Nash	Little bluestem	Grass	Warm

Table 2.5. List of special interest introduced species. The common name, physiognomy, and season are listed for each species.

Species	Common name	Physiognomy	Season
Bromus inermis Leyss.	Smooth brome	Grass	Cool
Melilotus officinalis (L.) Lam.	Yellow sweet clover	Forb	Cool
Poa pratensis L.	Kentucky bluegrass	Grass	Cool

2.3. Results

2.3.1. Burn Frequency Effects on Species Composition

We monitored 30 sites and observed a total of 157 species (Appendix B). We eliminated 36 rare species (species with one or two occurrences) and performed the dbDRA and PERMANOVA analyses on the remaining 121 species. Values for each dbDRA explanatory variable for all sites are reported in Appendix C.

The dbDRA ordination produced a 2-dimensional solution that represented 44.3% of variation in the dataset (Table 2.6). The final model included number of burns, years since graze, and northing as significantly correlated to species composition (Table 2.7, Figure 2.3).

Table 2.6. Proportion of variance represent by each dbDRA axis based on the correlation between ordination distances and distances in the original space.

Axis	Incremental	Cumulative
1	27.6%	27.6%
2	16.7%	44.3%

Table 2.7. ANOVAs for the final dbDRA model. Each ANOVA was permuted 999 times with the vegan pack in R (Oksanen et al. 2015). Degrees of Freedom (Df), Sums of Squares (SS), F, and P-values are listed. Asterisks indicate which explanatory variables were significant.

Overall model	Df	SS	F	P
Model	5	1.312	2.340	**0.001***
Residuals	24			
Environmental Variables				
Number of burns	1	0.258	2.300	**0.009***
Number of grazes	1	0.178	1.588	0.087
Years since burn (YSB)	1	0.098	0.873	0.579
Years since graze (YSG)	1	0.282	2.519	**0.003***
Northing	1	0.495	4.422	**0.001***

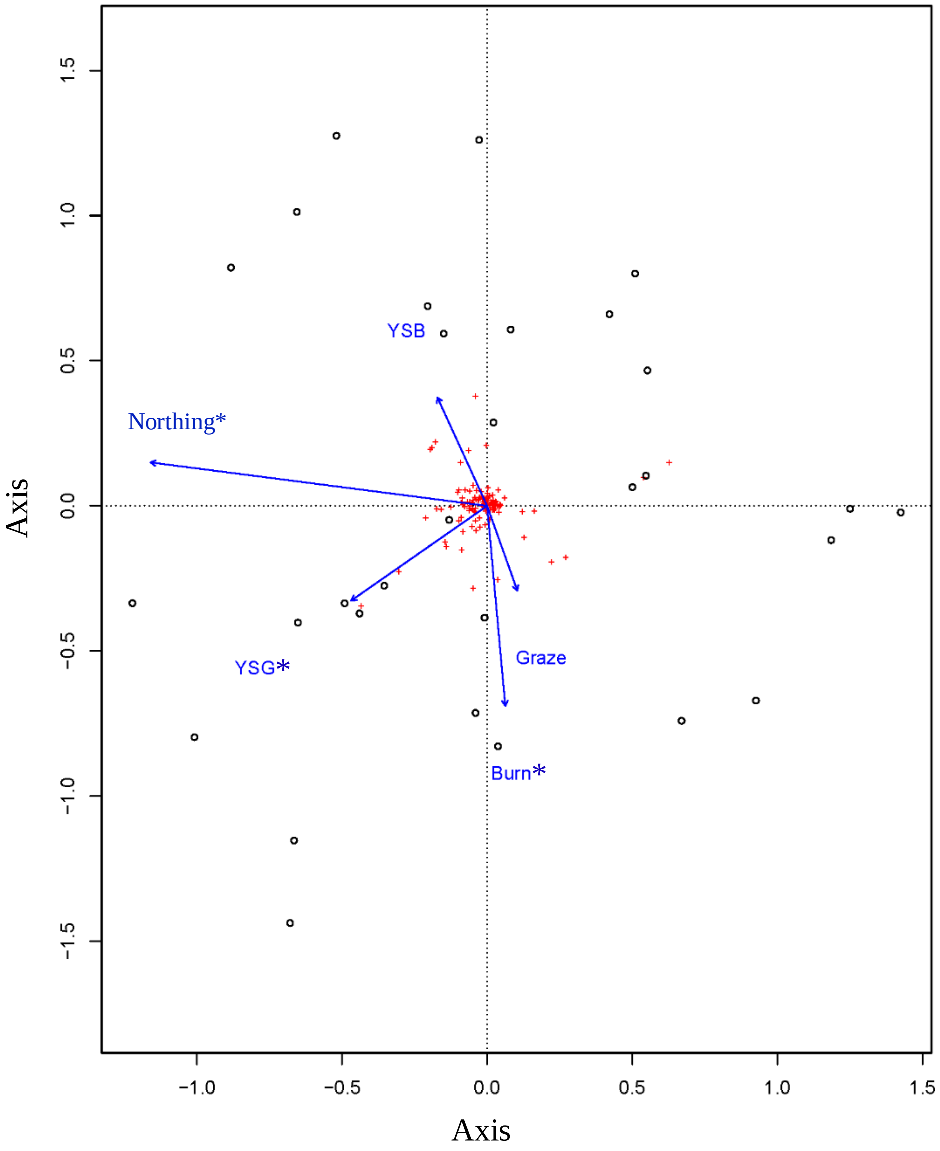

Figure 2.3. Ordination from the distance-based redundancy analysis (dbDRA), axes 1 and 2. Each site is indicated by an open circle, and all species included in the analysis are shown as red crosses. Environmental variables are displayed as vectors; significant variables are denoted with an asterisk.

We examined the r-values correlated with each axis to explore patterns underlying species relationships (Table 2.8). Axis 1 represented 27.6% of variation in the dataset (Figure 2.3). This axis represents a gradient in site location and years since a site was grazed. Species that are positively correlated with Axis 1 are more abundant in the mixed-grass prairies of northwestern and northcentral North Dakota, whereas negatively correlated species are more prevalent in the tallgrass prairies of southeastern South Dakota. Sites positioned along the negative end of Axis 1 have generally been grazed more recently than sites positioned along the positive end. Axis 2 represented 16.7% of variation in the dataset and is correlated with number of burns (Figure 2.3). Positively correlated species were more abundant at sites burned fewer times between 2010 and 2019, and negatively correlated species were more abundant at sites burned more frequently between 2010 and 2019.

Table 2.8. Species correlations to the ordination axes. Only species with r-values >|0.4| are listed (bold). C-value and Growth form are included for each species.

Species	C-value	Physiognomy	Axis 1	Axis 2
Achillea millefolium	3	Forb	**0.461**	0.180
Ambrosia psilostachya	2	Forb	-0.297	**-0.416**
Amorpha canescens	9	Shrub	-0.052	**-0.598**
Andropogon gerardii	5	Grass	**-0.542**	-0.320
Apocynum cannabinum	4	Forb	**-0.440**	-0.118
Artemisia campestris	5	Forb	0.225	**-0.510**
Artemisia frigida	4	Shrub	**0.527**	-0.309
Artemisia ludoviciana	3	Forb	**0.636**	**-0.580**
Astragalus flexuosus	4	Forb	0.311	**0.508**
Avenula hookeri	9	Grass	**0.425**	0.111
Bouteloua curtipendula	5	Grass	**-0.405**	-0.298
Bouteloua gracilis	7	Grass	**0.484**	-0.262
Brickellia eupatorioides	5	Forb	**-0.400**	-0.199
Bromus inermis	*	Grass	**-0.626**	0.091
Calamovilfa longifolia	5	Grass	**0.449**	-0.255
Carex brevior	4	Sedge	**-0.586**	-0.175
Carex duriuscula	4	Sedge	**0.401**	-0.203
Carex inops	7	Sedge	**0.533**	-0.113
Chenopodium album	*	Forb	**-0.537**	0.012
Cirsium arvense	*	Forb	-0.119	**0.473**
Comandra umbellata	8	Forb	**0.566**	-0.092
Elaeagnus commutata	5	Shrub	0.252	**0.479**
Elymus canadensis	3	Grass	**0.510**	0.280
Equisetum laevigatum	3	Fern	**-0.449**	-0.019
Euphorbia esula	*	Forb	0.280	**-0.463**

Table 2.8. Species correlations to the ordination axes (continued). Only species with r-values >|0.4| are listed (bold). C-value and Growth form are included for each species.

Species	C-value	Physiognomy	Axis 1	Axis 2
Galium boreale	4	Forb	0.336	**0.448**
Glycyrrhiza lepidota	2	Forb	0.100	**0.494**
Helianthus pauciflorus	8	Forb	0.274	**-0.637**
Hesperostipa comata	6	Grass	**0.578**	-0.609
Hesperostipa spartea	8	Grass	**-0.529**	-0.054
Juncus arcticus	5	Forb	0.234	**0.418**
Liatris punctata	7	Forb	**0.460**	-0.067
Lygodesmia juncea	2	Forb	**0.432**	-0.194
Medicago lupulina	*	Forb	**-0.476**	0.134
Medicago sativa	*	Forb	**-0.445**	-0.098
Melilotus officinalis	*	Forb	**-0.634**	0.195
Oenothera suffrutescens	4	Forb	**0.455**	0.095
Oxalis violacea	7	Forb	**-0.422**	-0.11
Pascopyrum smithii	4	Grass	**0.538**	-0.166
Phleum pratense	*	Grass	**-0.427**	0.019
Poa pratensis	*	Grass	0.224	**0.570**
Pulsatilla patens	9	Forb	**0.472**	0.292
Selaginella densa	6	Fern	**0.446**	-0.135
Solidago missouriensis	5	Forb	**0.510**	**-0.490**
Solidago mollis	6	Forb	**0.479**	-0.224
Sonchus arvensis	*	Forb	0.101	**0.509**
Symphyotrichum ericoides	2	Forb	**0.477**	-0.202
Symphyotrichum sericeum	10	Forb	**-0.619**	-0.024
Thermopsis rhombifolia	6	Forb	0.236	**0.431**
Vicia americana	6	Forb	**0.490**	0.392

The results of PERMANOVA determined that sites with differing burn frequencies (0-2 times or 3+ times) between 2010 and 2019 have distinct species compositions (Table 2.9).

Table 2.9. Results from the PERMANOVA analysis of burn frequency and species composition. Degrees of Freedom (Df), sums of squares (SS), means of squares (MS), pseudo F and p-value are listed.

Factor	Df	SS	MS	Pseudo F	P-value
Burn Frequency	1	0.249	0.249	1.874	**0.025***

2.3.2. Changes in species composition between 2012 and 2020

Our between-year comparisons of community diversity and the abundance of individual species, genera, physiognomic and functional groups determined that shifts in species composition have occurred between 2012 and 2020 (Tables 2.10-2.14). There were no significant differences in mean total species richness and mean native species richness between 2012 and 2020, but FQI was significantly (P < 0.0322) higher in 2020 (x̄= 35.57225, SD= 6.783384) than in 2012 (x̄=33.74921, SD= 5.317231).

Table 2.10. Mean and standard deviation for three community diversity metrics in 2012 and 2020 with degrees of freedom (Df), t-value (t), and p-value. Asterisks indicate significant differences in mean values between years.

Diversity metric	Mean	SD	Df	t	P-value	
Total species richness						
2012		57.1667	11.5999	29	0.33	0.7412
2020		56.2667	13.1567			
Native species richness						
2012		47.4667	10.4510	29	0.29	0.7705
2020		48.1667	12.7849			
FQI						
2012		33.7492	5.31723	29	2.25	**0.0322***
2020		35.5723	6.78338			

The relative cover of all graminoids decreased significantly (P < 0.025) between 2012 (x̄=60.8258, SD=13.1505) and 2020 (x̄=54.3396, SD=11.8615). There were no significant differences in native warm-season graminoid cover between 2012 (x̄=1.6399, SD=2.5784) and 2020 (x̄=3.0421, SD=4.4887), but native cool-season graminoids decreased significantly (P < 0.0041) between 2012 (x̄=9.5174, SD=9.043) and 2020 (x̄=5.7036, SD=6.8025). Shrub relative cover increased significantly (P < 0.0007) between 2012 (x̄=10.3608, SD==6.8674) and 2020 (x̄=14.9274, SD= 8.6972). There were no significant differences between native species cover in 2012 (x̄=43.2179, SD=13.3142) and 2020 (x̄=45.7672, SD=17.9503) or forb relative cover in 2012 (x̄=26.9220, SD=11.0956) and 2020 (x̄=30.1541, SD=10.0371).

Table 2.11. Mean relative cover and standard deviation of five species groups based on physiognomy or functional groups with degrees of freedom (Df), t-value (t), and p-value. Asterisks indicate significant differences in mean relative cover between years.

Species group	Mean relative cover (%)	Standard deviation	Df	t	P
Native species					
2012	43.2179	13.3142	29	0.86	0.3956
2020	45.7672	17.9503			
Graminoids					
2012	60.8258	13.1505	29	2.36	**0.0250***
2020	54.3396	11.8615			
Warm-season graminoids					
2012	1.6399	2.5784	29	1.86	0.0735
2020	3.0421	4.4887			
Cool-season graminoids					
2012	9.5174	9.0430	29	3.13	**0.0041***
2020	5.7036	6.8025			
Forbs					
2012	26.9220	11.0956	29	1.41	0.1695
2020	30.1541	10.0371			
Shrubs					
2012	10.3608	6.8674	29	3.78	**0.0007***
2020	14.9274	8.6972			

Introduced invasive species exhibited differing responses across time (Table 2.12). Kentucky bluegrass decreased significantly ($P < 0.0012$) between 2012 ($\bar{x}$=32.35559, SD=11.6606) and 2020 ($\bar{x}$=23.8618, SD=11.6606), while smooth brome increased significantly ($P < 0.0385$) between 2012 ($\bar{x}$=17.6742, SD=15.0747) and 2020 ($\bar{x}$=21.9956, SD=16.0026). Yellow sweet clover relative cover increased significantly ($P < 0.0220$) between 2012 ($\bar{x}$=2.6601, SD=5.3869) and 2020 ($\bar{x}$=5.1904, SD=9.1086).

Table 2.12. Mean relative cover and standard deviation of smooth brome, Kentucky bluegrass, and yellow sweet clover in 2012 and 2020 with degrees of freedom (Df), t-value (t), and p-value. Asterisks indicate significant differences in mean relative cover between years.

Species	Mean relative cover (%)	Standard deviation	Df	t	P
Smooth brome					
2012	17.6742	15.0747	29	2.17	**0.0385***
2020	21.9956	16.0026			
Kentucky bluegrass					
2012	32.3556	10.0384	29	3.59	**0.0012***
2020	23.8618	11.6606			
Yellow sweet clover					
2012	2.6601	5.3869	29	2.42	**0.0220***
2020	5.1904	9.1086			

The paired T-tests determined there were no significant differences in average relative cover for warm-season grass species between 2012 and 2020 (Table 2.13). Although not significant, the average relative cover of warm-season grass species in Table 2.13 increased between 2012 and 2020.

Table 2.13. Mean relative cover and standard deviation of five native warm-season grass species in 2012 and 2020 with degrees of freedom (Df), t-value (t), and p-value.

Species	Mean relative cover (%)	Standard deviation	Df	t	P
Big bluestem					
2012	0.8612	2.4453	29	0.80	0.4315
2020	1.2677	2.7888			
Sideoats grama					
2012	0.1258	0.5301	29	1.47	0.1536
2020	0.4281	1.6073			
Blue grama					
2012	0.3271	0.6424	29	0.83	0.4153
2020	0.5555	1.6760			
Prairie sandreed					
2012	0.0809	0.2680	29	1.09	0.2844
2020	0.2597	0.8311			
Little bluestem					
2012	0.1599	0.3910	29	1.27	0.2154
2020	0.3235	0.7432			

The paired T-tests determined that there were significant differences in average relative cover between years for three of the five native cool-season graminoid species (Table 2.14). The aggregate relative cover of sedges decreased significantly ($P < 0.0185$) between 2012 ($\bar{x}$=1.1007, SD=1.7533) and 2020 ($\bar{x}$=0.4302, SD=0.9783). Green needlegrass average relative cover was significantly ($P < 0.0001$) lower in 2020 ($\bar{x}$=0.4022, SD=0.7773) than in 2012 ($\bar{x}$=2.8171, SD=3.1439), and western wheatgrass average relative cover declined significantly ($P < 0.0108$) between 2012 ($\bar{x}$=1.9851, SD=2.8935) and 2020 ($\bar{x}$=0.8579, SD=1.4314).

Table 2.14. Mean relative cover and standard deviation of six native cool-season graminoid species in 2012 and 2020 with degrees of freedom (Df), t-value (t), and p-value. Asterisks indicate significant differences in mean relative cover between years.

Species	Mean relative cover (%)	Standard deviation	Df	t	P
Sedge sp.					
2012	1.1007	1.7533	29	2.49	**0.0185***
2020	0.4302	0.9783			
Needle and thread					
2012	2.5503	4.3854	29	0.06	0.9498
2020	2.5927	5.5104			
Porcupinegrass					
2012	0.1164	0.3841	29	1.30	0.2023
2020	0.3013	0.9072			
Green needlegrass					
2012	2.8171	3.1439	29	4.45	**0.0001***
2020	0.4022	0.7773			
Western wheatgrass					
2012	1.9851	2.8935	29	2.72	**0.0108***
2020	0.8579	1.4314			

2.3.3. Changes Between Years and Burn Grouping

We calculated the change in community diversity metrics and relative cover for the above set of individual species, genera, physiognomic and functional groups for sites burned 0-2 times or 3 or more times between 2010 and 2019. We used two sample T-tests to determine whether changes were significant between burn groupings.

Changes between years for each burn grouping were not significant for all but two species (Tables 2.15 and 2.16). Yellow sweet clover average relative cover increased significantly ($P < 0.0500$) at sites burned three or more times ($\bar{x}$=6.03, SD=7.530) compared to sites burned 0-2 times ($\bar{x}$=0.735, SD=3.750) (Figure 2.4), while green needlegrass average relative cover decreased significantly ($P < 0.0148$) at sites burned three or more times ($\bar{x}$=-3.580, SD=3.510) compared to sites burned 0-2 times ($\bar{x}$=-1.220, SD=1.300) (Figure 2.5).

Table 2.15. Mean change in diversity metrics for sites burned 0-2 times or 3+ times between 2010 and 2019 with standard deviation (SD), degrees of freedom (Df), t-value (t), and p-values (P).

Metric	Mean change (%)	SD	Df	t	P
Total species richness					
0-2 burns	-0.667	12.687	25.841	0.08	0.9330
3+ burns	-1.133	17.083			
Native species richness					
0-2 burns	0.867	10.921	25.394	0.07	0.9456
3+ burns	0.533	15.222			
FQI					
0-2 burns	1.710	4.114	25.128	0.12	0.903
3+ burns	1.936	5.850			

Table 2.16. Mean change in percent relative cover for individual species, genera, physiognomic or functional groups for sites burned 0-2 times or 3+ times between 2010 and 2019 with standard deviation (SD), degrees of freedom (Df), t-value (t), and p-values (P). Asterisks indicate significant differences in relative cover between burn groupings.

Species/group	Mean Change (%)	SD	Df	t	P
Native species					
0-2 burns	4.280	16.630	27.973	0.58	0.5667
3+ burns	0.816	16.120			
Graminoids					
0-2 burns	-6.800	16.310	27.483	0.11	0.9126
3+ burns	-6.180	14.200			
Warm-season graminoids					
0-2 burns	0.716	2.548	20.876	0.89	0.3815
3+ burns	2.042	5.103			
Cool-season graminoids					
0-2 burns	-2.089	5.435	25.805	1.4	0.1723
3+ burns	-5.423	7.279			
Forbs					
0-2 burns	2.536	11.644	27.228	1.40	0.7674
3+ burns	3.929	13.802			
Shrubs					
0-2 burns	6.110	7.960	22.826	1.29	0.2073
3+ burns	3.020	4.740			
Kentucky bluegrass					
0-2 burns	-9.051	11.479	26.452	0.23	0.8189
3+ burns	-7.938	14.692			
Smooth brome					
0-2 burns	4.481	14.500	28	0.19	0.8506
3+ burns	5.340	9.755			
Yellow sweet clover					
0-2 burns	0.735	3.750	14.122	2.12	**0.0500***
3+ burns	6.030	7.530			
Big bluestem					
0-2 burns	0.651	2.392	16.991	0.01	0.9929
3+ burns	0.637	4.142			
Sideoats grama					
0-2 burns	0.206	0.236	7.452	1.13	0.2928
3+ burns	1.057	2.092			
Blue grama					
0-2 burns	0.704	2.342	10.33	0.51	0.6200
3+ burns	0.175	1.769			
Prairie sandreed					
0-2 burns	-0.091	0.268	6.45	1.31	0.2341
3+ burns	0.818	1.798			
Little bluestem					
0-2 burns	0.119	0.877	6.00	0.74	0.4866
3+ burns	0.650	1.340			

Table 2.16. Mean change in percent relative cover for individual species, genera, physiognomic or functional groups for sites burned 0-2 times or 3+ times between 2010 and 2019 with standard deviation (SD), degrees of freedom (Df), t-value (t), and p-values (P) (continued). Asterisks indicate significant differences in relative cover between burn groupings.

Species/group	Mean Change (%)	SD	Df	t	P
Sedge spp.					
0-2 burns	-0.799	2.129	14.75	0.02	0.9868
3+ burns	-0.810	0.925			
Needle and thread					
0-2 burns	0.929	4.240	19.537	0.86	0.3994
3+ burns	-0.668	4.400			
Porcupinegrass					
0-2 burns	-0.104	0.189	6.556	1.58	0.1615
3+ burns	0.822	1.510			
Green needlegrass					
0-2 burns	-1.220	1.300	18.559	2.69	**0.0148***
3+ burns	-3.850	3.510			
Western wheatgrass					
0-2 burns	-1.191	1.755	21.761	0.31	0.7623
3+ burns	-1.479	2.910			

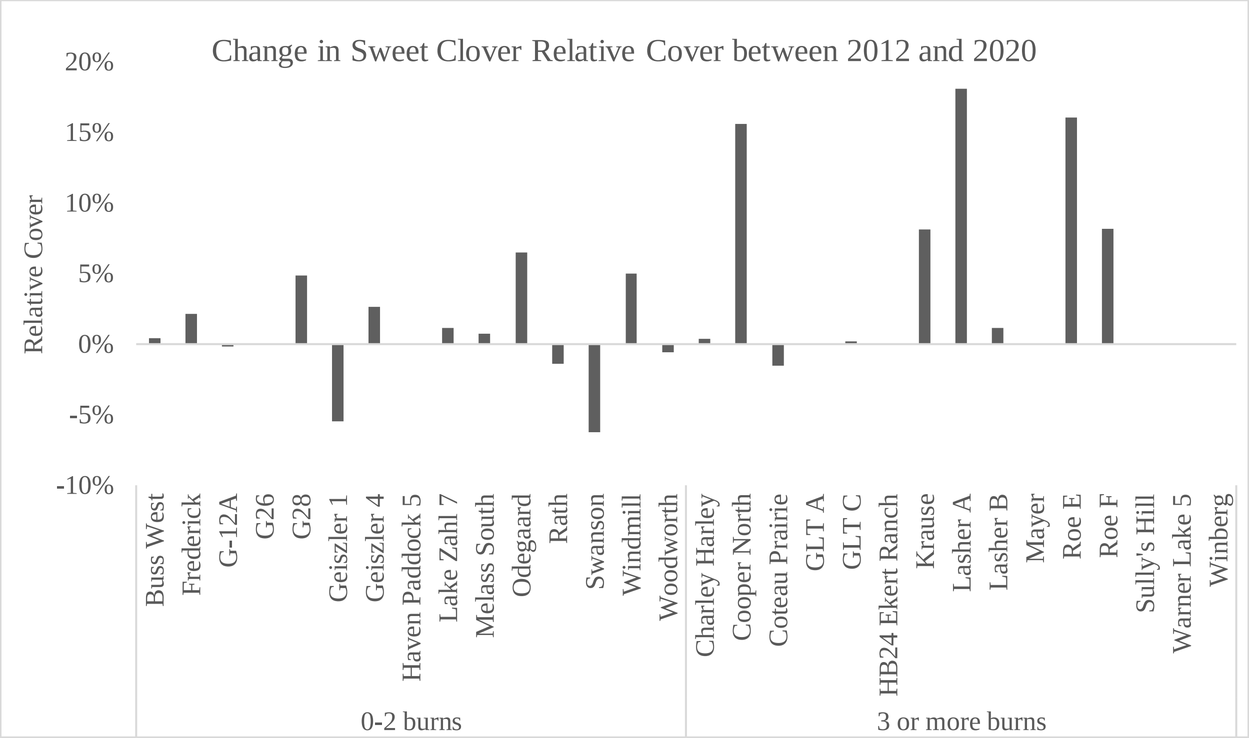

Figure 2.4. Change in yellow sweet clover relative cover between 2012 and 2020. Sites burned 0-2 times are on the left half and sites burned 3 or more times are on the right half.

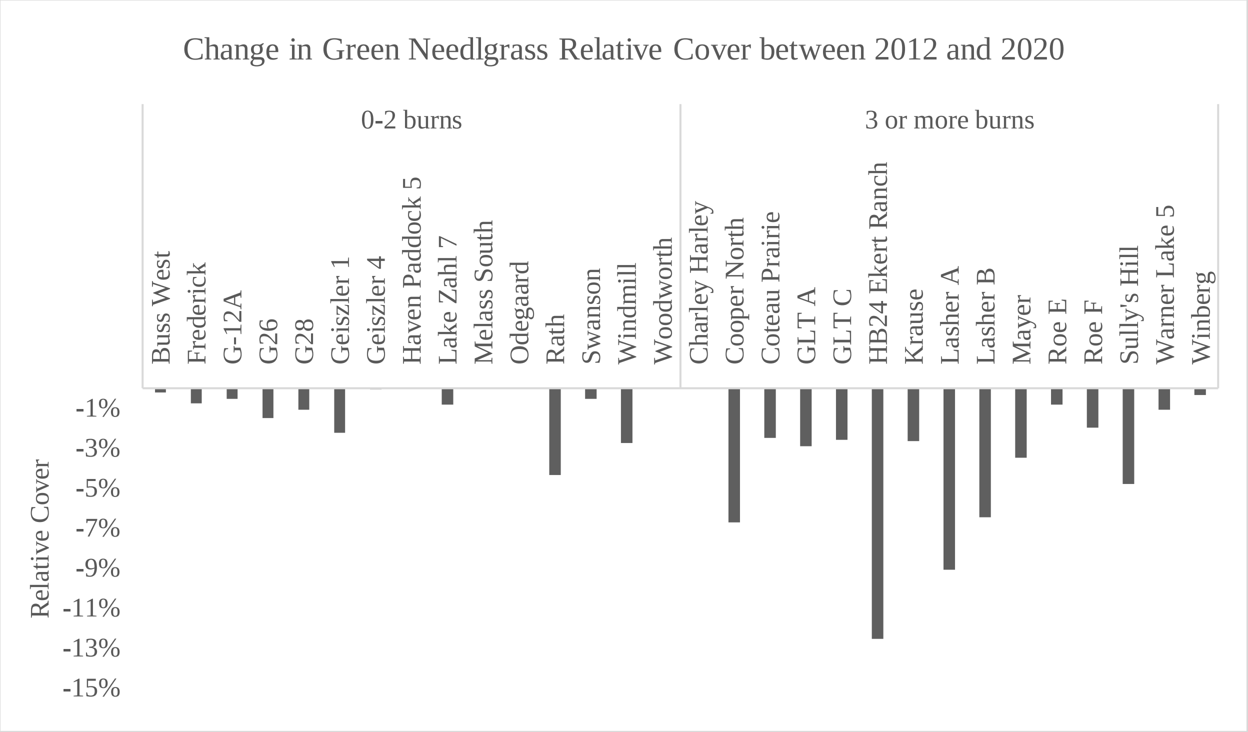

Figure 2.5. Change in green needlegrass relative cover between 2012 and 2020. Sites burned 0-2 times are on the left half and sites burned 3 or more times are on the right half.

2.4. Discussion

Our results demonstrate that shifts in plant community composition have occurred on sites enrolled in the NPAM program between 2012 and 2020. Native species assemblages are increasing significantly in floristic quality over time, and while we observed increases in native species richness and abundance between years, these changes were not significant. The abundance of certain species and groups increased or decreased significantly over time while others were more constant. Previous research found that NPAM sites with increased burn frequency had more desirable floristic composition (Kobiela et al. 2017), and while our analysis determined that shifts in species composition may be attributed to the number of times a site was burned, it did not reveal changes in most site diversity metrics or species abundance to be solely explained by burn frequency. In addition to the number of times a site was burned, our model identified site location and years since graze as significant factors influencing species composition among sites.

Site location (as represented by site northing) was a significant predictor of species composition in our study. Given the large geographic range of this study, we expected differences in site location to contribute variation in species composition. Factors that are likely correlated with site location include land use practices, grassland type (tallgrass vs. mixed grass), climate, phenology, and timing of monitoring. Tallgrass communities occur in the southeastern extent of the study area where landscapes tend to be dominated by restored grassland and cropland (Seabloom and van der Valk 2003). These sites have a warmer and wetter climate and plants emerge earlier in these systems (Grant et al. 2020a); thus, sampling generally occurred around June 1. In contrast, remnant mixed-grass communities occur in the central, northern, and western extent of the study area where surrounding land use is more evenly mixed between cropland and rangeland (Seabloom and van der Valk 2003). Mixed-grass prairies tend to be cooler and drier, especially in the northwestern extent of the study area (Grant et al. 2020a). Given the greater number of mixed-grass sites spread over a larger geographic extent, sampling for mixed-grass sites varied between mid-June to mid-August.

Increases in floristic quality suggest that the NPAM program's recommendations are promoting more conservative species and grasslands with greater ecological integrity; species with high conservatism values are restricted to natural, undegraded areas (Taft et al. 1997). Burning and grazing have been shown to promote species with higher conservation values in native prairie (Manning et al. 2017), thus we expected that increases in FQI might be attributed to more intensive management over time. Our analysis did not discern significant differences between burn frequency groupings, possibly due to combined influence of burning and livestock grazing on increasing floristic quality (Manning et al. 2017). Increases in floristic quality between 2012 and 2020 indicate that the NPAM program is improving the ecological integrity of historically idle remnant prairie by restoring periodic defoliation. Floristic quality is positively correlated with metrics indicative of soil fertility (Manning et al. 2017), thus plant communities with high floristic quality may be indicative of broader ecological integrity (Klopf et al. 2017).

We expected increased burning to have differing effects on the abundance of cool-season and warm-season graminoids due to phenology and the timing of burning. Cool-season species emerge and initiate growth prior to warm-season species, thus burning in the spring and early summer may target cool-season species like Kentucky bluegrass and smooth brome while avoiding damage to dormant warm season species (Bennett et al. 2019). The potential benefits of this control strategy come with trade-off as native cool-season graminoids may also be negatively impacted (Engle and Bultsma 1984; Toledo et al. 2014). Though we observed shifts in the abundance of native warm- and cool-season graminoids between 2012 and 2020, these changes were not attributed to increased burn frequency. Aside from green needlegrass, a species noted for its sensitivity to spring burning (Engle and Bultsma 1984; Gartner et al. 1986), more frequent spring burning does not seem to be the cause of changes in native graminoid communities.

Kentucky bluegrass relative abundance decreased by nearly 30% between 2012 and 2020. This decline in Kentucky bluegrass abundance is remarkable as this species has proved difficult to control, especially when intermixed with native species with similar phenological traits (Toledo et al. 2014). Kentucky bluegrass was positively correlated with Axis 2 and negatively correlated with Axis 3, which suggests this species is responding to increased burning on NPAM units. Decreases in Kentucky bluegrass were not significant between sites burned at different frequencies, however, which suggests that additional factors may be driving Kentucky bluegrass decline. Interactions between management practices, recent and long-term climate conditions, or an interaction of management practices and climate are likely influencing declines in Kentucky bluegrass abundance (USFWS unpublished report).

Our between-year comparison revealed a nearly 20% increase in smooth brome abundance, and we discerned no difference in smooth brome abundance between sites burned at differing frequencies. Our results differ from a previous floristic assessment of NPAM units that determined smooth brome abundance to be lowest at sites burned at greater frequencies over a four-year period (Kobiela et al. 2017). The disparity between our results suggests that the effects of burning on smooth brome abundance is variable, possibly due to the challenges of targeting smooth brome during its vulnerable elongation period (Priester et al. 2019). Recent research indicates that the timing of burning on NPAM units may not have been optimal for targeting smooth brome due to a mismatch between purported smooth brome development stages and its vulnerability to prescribed burning (USFWS unpublished report). USFWS tallgrass prairie burning guidelines rely on Willson and Stubbendieck’s (2000) provisional model, which suggests that burning should be implemented when the majority of the smooth brome population has reached the five-leaf vegetative stage (i.e. elongation stage) (Willson 1990). However, not all smooth brome populations achieve this stage (Priester et al. 2019), thus prescribed burning may have been inadvertently conducted outside of the smooth brome elongation period. Data from annual monitoring of tallgrass NPAM units by USFWS staff indicates that burning in the spring within the smooth brome elongation period recommended by Preister et al. (2019) may be less effective for targeting smooth brome abundance than burning before or after the elongation period (C. Dixon, pers.com.). Whether or not defoliation was conducted at the appropriate time, smooth brome appears to be more resilient to spring defoliation than was previously understood, and additional research is needed to identify management scenarios for controlling smooth brome invasion.

Correlations between forbs and environmental variables were variable by species, which suggests that increases in forb abundance may be attributed to species that are responding favorably to NPAM management recommendations. One introduced forb species, yellow sweet clover, appears to be responding positively to increased burn frequency; indeed, it was significantly more abundant at sites burned three or more times between 2012 and 2020 (Figure 2.4). Like many leguminous species, yellow sweet clover germination is stimulated by fire, and seedling density may increase for several years post-fire (Heitlinger 1975). While consecutive multi-year spring burning is recommended for targeting yellow sweet cover, burning at greater than two-year intervals may promote its expansion (Kline 1986). Increases in yellow sweet clover abundance at sites burned three or more times over a nine-year period suggests that the NPAM program's burn frequency recommendations may have inadvertently benefitted this species.

Increases in smooth brome and yellow sweet clover populations on NPAM units have negative implications for ecological functioning and biodiversity, especially within remnant tallgrass prairies. Remnant tallgrass prairies in the PPR typically exist in more isolated and fragmented landscapes where surrounding land types are restored grasslands or cropland (Seabloom and van der Valk 2003; Paradeis et al. 2010). Cropland edges serve as invasion fronts and propagule sources for smooth brome and yellow sweet clover (Van Riper and Larson 2009; DeKeyser et al. 2013), thus prairies with high proportions of cropland edges contain greater abundances of introduced species (Grant et al. 2020b). Additionally, remnant prairies located in cropland-dominated landscapes may have increased nitrogen concentrations as result of topsoil and fertilizer drift from adjoining croplands (Murphy and Grant 2005). Increased nitrogen availability is associated with shifts from diverse native assemblages to communities dominated by introduced species independent of initial community composition (Tilman 1987; Wilson and Shay 1990). Smooth brome has demonstrated increased vigor and growth following nitrogen addition (Vinton and Goergen 2006), and smooth brome and yellow sweet clover have each shown the ability to alter nitrogen cycling by increasing available nitrogen content in the soils they occupy (Vinton and Goergen 2006; Jordan et al. 2008; Van Riper et al. 2010; Dornbusch et al. 2018). This may in turn create favorable conditions for their own growth and establishment and facilitate invasion by other introduced species (Vinton and Goergen 2006; Dornbusch et al. 2018). Our results (Figure 2.4) and recent research (Grant et al. 2020a) show greater abundances of smooth brome and yellow sweet clover in the tallgrass prairies of the PPR. These species may be interacting with environmental conditions suited for their proliferation at these sites (e.g. increased propagule pressure and nitrogen availability), as well as management practices that may be inadvertently favoring their expansion (e.g. prescribed burning). Additional research is needed to understand the mechanism by which these species are becoming more abundant in tallgrass prairies.

The NPAM program’s management recommendations were expected to reduce the abundance of native shrub species, specifically western snowberry (*Symphoricarpos occidentalis* Hook. and (*Elaeagnus commutata* Bernh. x Rydb.). Many native shrub species are noted to proliferate following periods of fire suppression (Grant and Murphy 2005; Murphy and Grant 2005), and prescribed burning is recommended to control their encroachment in herbaceous communities (Bailey et al. 1990; Romo et al. 1993). Our observations were not consistent with these studies: shrub relative cover increased significantly over time, and shrub abundance did not differ between sites burned 0-2 times or three or more times. Once shrubs establish, managing fire regimes alone may not be effective for controlling shrub expansion (Briggs et al. 2005). A study of shrub expansion in the central tallgrass prairie observed comparable increases in shrub cover at sites burned every four years and sites burned once in a 20-year period (Heisler et al. 2003). This study and ours indicate that trends in shrub invasion may not be reversed with increased burn frequency, and that factors aside from prescribed burn frequency are driving shrub encroachment in prairie remnants. In addition to fire suppression, increased atmospheric CO_2 concentrations, climate change, and nitrogen deposition are implicated as causes of woody encroachment (Ratajczak et al. 2012), and it's probable that these factors are driving shrub expansion in the PPR. Increases in shrub cover are associated with changes in plant community composition and reduced species richness (Van Auken 2000; Ratajczak et al. 2012). Woody species may facilitate secondary invasion by Kentucky bluegrass and smooth brome by altering nutrient and moisture conditions in shrub understories (Lett and Knapp 2003); indeed, an assessment of floristic composition on USFWS lands in North Dakota and South Dakota showed that shrub understories were more frequently dominated by Kentucky bluegrass and smooth brome than native species assemblages (Grant et al. 2020a). Our analysis demonstrates that the NPAM program's management recommendations are not reversing trends in shrub expansion on remnant prairies.

2.5. Conclusion

This study assessed correlations between environmental and management variables and species composition at sites enrolled in the NPAM program, and related changes in species quality, diversity, and abundance to differing management regimes. Site location was the strongest predictor of species composition in our study, which underscores the necessity of the NPAM program’s site-specific management recommendations. While our analyses determined that variation in present day species composition are likely attributed to increased burning and sites burned at differing frequencies had unique species compositions, most of the individual species and functional groups assessed did not show significant differences in average relative cover between management regimes. However, between 2012 and 2020, prairies enrolled in the NPAM program experienced decreases in Kentucky bluegrass abundance and increases in native species diversity, abundance, and quality. These outcomes indicate that management practices that restore natural ecological processes may be effective for combatting Kentucky bluegrass dominance and native species decline.

2.6. Management Implications

The principal goal of the NPAM program is to increase the abundance of native species while targeting Kentucky bluegrass and smooth brome at least cost. In this study, native species, Kentucky bluegrass, smooth brome, and yellow sweet clover exhibited variable responses to the NPAM program’s management recommendations. Our results depict the inherent difficulty of restoring a highly-invaded ecosystem where individual species have differing responses to management actions and the timing of growth of introduced species overlaps with native species (Toledo et al. 2014; Grant et al. 2020b). Predicting management outcomes may be improved by understanding the mechanisms and ecological processes driving changes in species composition on remnant prairies (Dixon et al. 2019).

Research is needed to identify widely-applicable and cost-effective methods to control smooth brome invasion. The outcomes of long-term empirical research do not support burning during the elongation stage to control smooth brome invasion (this study; USFWS unpublished reports). Other studies of smooth brome patterns of occurrence in the PPR indicate that extended periods of annual moderate- to high-intensity grazing (>1.8 AUM) may be effective for combatting smooth brome invasion (Murphy and Grant 2005; Coleman et al. unpublished data). Plant communities where smooth brome is the dominant invader may benefit from repeat grazing, though changes may not be apparent over short periods (Dornbusch et al. 2020; Hendrickson et al. 2020). With that, it's likely that the impacts of the NPAM program's management recommendations on plant community composition are not fully apparent. A long-term commitment to restoring ecological processes may be required to increase and maintain native species abundance on remnant prairies in the PPR.

2.7. Future Research

The analyses reported in this study are based on two annual measurements of a set of permanent plots established on NPAM units throughout the PPR: the first monitoring event was conducted in 2012 and the second in 2020. If the NPAM program continues to be implemented, additional monitoring events could provide an ongoing assessment of how the program's recommendations affect native species composition over time.

We initially proposed to analyze the tallgrass sites and mixed-grass sites separately due to apparent differences in their plant community composition (Bragg 1995). Tallgrass communities are largely comprised of native warm-season species, while mixed-grass prairies are intermediate between tallgrass and shortgrass systems and contain a mix of native cool- and warm-season species. These differences are reflected in the NPAM program's modelling framework: management recommendations for tallgrass and mixed-grass sites are derived from differing parameters based on the phenology of the native species (Gannon et al. 2013). Despite these differences, the number of tallgrass sites included in this study was too few (N=5) to evaluate patterns in species composition across sites (Peck 2016), thus we elected to group the tallgrass sites with the mixed-grass sites. Future analyses should conduct a separate assessment for the mixed-grass sites, and more permanent Modified-Whittaker plots should be established on tallgrass sites. Though long-term plant community data will be lacking for new tallgrass sites, within-year comparisons will produce meaningful feedback for USFWS managers.

The effects of the NPAM program's management recommendations on forb community composition remain unclear. We observed near significant increases in forb abundance over time, which suggests that some forb species are benefitting from more intensive management practices. Future studies should evaluate forb species based on their expected response to management practices; this could be achieved by assigning all species to "low-seral" and "high-seral" groups based on their C-value (Travnicek et al. 2005). Additional groupings may be derived from the relationships between functional traits and C-values established by Ficken and Rooney (2020).

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3. LAND USE HISTORY AND PLANT COMMUNITY COMPOSITION IN THE PRAIRIE POTHOLE REGION

3.1. Introduction

Grassland ecosystems are globally imperiled and rank among the highest converted and least protected biomes (Hoekstra et al. 2005). North American grasslands are threatened by agricultural development, urbanization, energy development, climate change, and introduced species invasion (Samson and Knopf 1994). In the tall- and mixed-grass prairies of the Prairie Pothole Region (PPR) of North Dakota and South Dakota, native prairie landscapes have been reduced to less than 3% and 25% of their former extent, respectively (Samson and Knopf 1994). Remnant unbroken prairie should be a repository of native plant diversity in a highly modified landscape, but native prairie inventories have confirmed widespread invasion by introduced species (DeKeyser et al. 2013; Grant et al. 2020). Introduced species invasion is associated with declines in native species biodiversity and prairie condition (Cully et al. 2003; DeKeyser et al. 2013). Diverse native plant communities provide and support numerous ecosystem services (Gascoigne et al. 2011), and degradation of native prairie floristic quality has negative implications for ecosystem services and functions (Ellis-Felege et al. 2013; Toledo et al. 2014; Hovick et al. 2015).

Plant communities in the PPR evolved with interacting fire, grazing, and climate processes that shaped and maintained resilient plant communities adapted to frequent disturbance (Higgins 1986; Fuhlendorf and Engle 2004). Following Euro-American settlement, fire suppression, mismatched grazing practices, and climate change have influenced shifts in plant communities from diverse native communities to prairies dominated by a few introduced species (DeKeyser et al. 2009; Stotz et al. 2017; Grant et al. 2020), chiefly Kentucky bluegrass (*Poa* *pratensis* L.) and smooth brome (*Bromus inermis* Leyss.). These cool-season grasses are estimated to comprise upwards of 50% of floristic cover across the PPR, and are known to have detrimental effects on native plant diversity through direct competition and modifying ecological processes (Dillemuth et al. 2009; Toledo et al. 2014).

The United States Fish and Wildlife Service (USFWS) manages roughly 90,000 hectares of native prairie east of the Missouri River in North Dakota and South Dakota. Service-owned prairies were historically managed (1930s-1990s) to increase waterfowl production (Dixon et al. 2019). Fires were suppressed, and livestock grazing was infrequent and occurred at low stocking rates (<1.8 AUMs/ha) (Grant et al .2009; Dixon et al. 2019). In contrast, private- and state-owned native prairies were managed with no fire and annual moderate- to high-intensity grazing (>1.8 AUMs/ha) since at least the 1950s (Murphy and Grant 2005). Murphy and Grant (2005) conducted a comparative study of two USFWS-owned management areas and nearby privately-owned prairie. Their study established that differing management histories may influence species-specific patterns of invasion, notably that smooth brome was significantly less prevalent on privately-owned prairie. The limited geographic setting of this study limits generalizations about the condition of privately-owned prairies throughout the PPR, thus additional assessment is necessary to explore the effect of historical management practices on plant community composition.

Our goal was to compare species composition on USFWS-owned native prairie to nearby native prairie with a history of livestock grazing to examine the influence of long-term management history on plant community composition. Our comparisons focus on measures of native species abundance, richness, and quality, as well as prevalence of predominant introduced species. The outcomes of this study will offer insight into degree of introduced species invasion and patterns of invasion between lands with differing management paradigms.

3.2. Methods

3.2.1. Study Area

The PPR is a glaciated landscape that spans approximately 48 million hectares across five U.S. states (Millett et al. 2009). It is characterized by flat to gently rolling landscapes pockmarcked by millions of small wetlands, or “potholes”, formed by glacial activity in the late Wisconsinian glaciation (Johnson et al. 2008). Land use in this region is dominated by intensive agricutlure in the flatter areas and livestock grazing on steeper slopes.

The PPR has a semi-arid to sub-humid climate with cyclic deluge and drought periods (Winter and Rosenberry 1998). Precipitation and temperature vary along latitudinal and longitudinal gradients: precipitation varies between 30cm in the western extent and 90cm in the eastern extent, with the majority of precipitation (70%) falling during the growing season between the months of April and September (Millett et al. 2008). Mean annual temperatures range between 10°C in the south and 1°C in the north, but temperatures may range to above 40°C and below -40°C (Millett et al. 2008). The average number of frost-free days has increased over time to approximately 120 days (Badh et al. 2009).

3.2.2. Site Selection

We established 26 paired sites throughout the North Dakota and South Dakota extent of the PPR (Figure 3.1). We selected sites based on land use history, accessibility, and soil characteristics. We selected sites with predominantly loamy soils because they are known to be vulnerable to invasion by introduced cool-season grasses and are the most dominant soils in the region (DeKeyser et al. 2009; DeKeyser et al. 2013). Additionally, we selected the loamy soil ecological site type (Sedivec and Printz 2012) to control for variability inherent in the large geographical extent of this study. Plant communities associated with the loamy ecological site will have a comparable composition across the study area (Sedivec and Printz 2012).

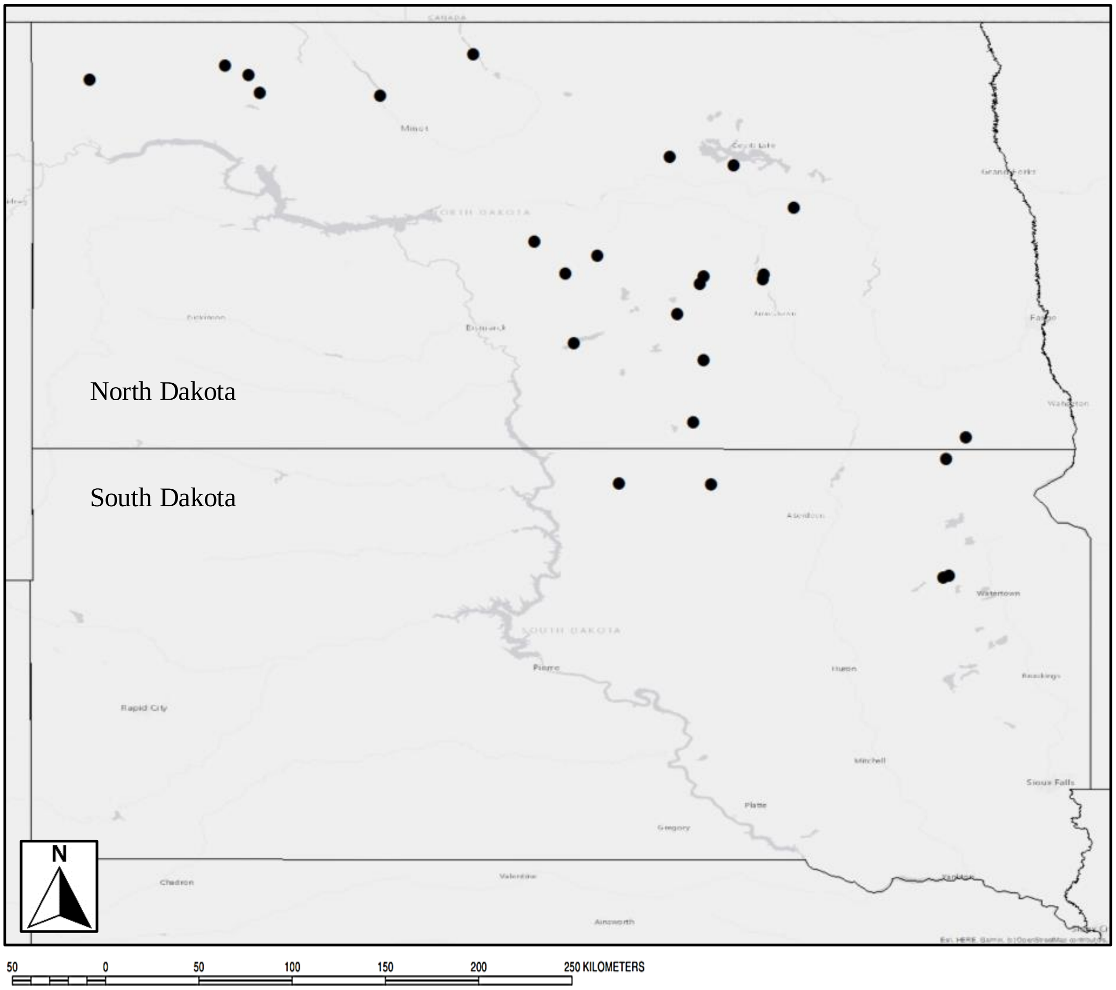

Figure 3.1. Location of 26 paired sites (black circles) throughout the Prairie Pothole Region of North Dakota and South Dakota.

We selected 26 sites managed by USFWS to represent sites without a long-term history of grazing (Appendix D). The USFWS sites have been managed annually with various combinations of livestock grazing, prescribed burning, and rest for the past 12-15 years, but prior to this period, these areas were primarily managed with deferment or infrequent low to moderate intensity season-long grazing (Dixon et al. 2019). We identified private- and state-owned tracts of native prairie within a 10km radius of a paired USFWS site (Appendix E). These lands are known to have a long-term history of livestock grazing (Murphy and Grant 2005). Grazing regimes varied between sites.

We identified areas with predominantly loamy soils using soil maps produced by SoilWeb (Soil Survey Staff 2021) and used the Create Random Points tool in ArcMap (ESRI version 10.7) to create random waypoints in those soil types. Once in the field, we conducted ground-truthing for each point's position on the landscape and associated vegetation. Our study focused on never-cultivated native prairie, thus we searched for evidence of prior cultivation such as distinct field edges, furrows, and rock piles (Grant et al. 2009).

3.2.3. Vegetation Monitoring and Data Analysis

We conducted vegetation monitoring between June and August of 2021. We established five 10m x 10m plots in loamy soil types at each paired site. We estimated the percent of absolute canopy cover of each species rooted in the plot. Species comprising less than 1% cover were recorded as 0.5%.

We averaged and relativized species cover estimates across all plots at each site. Rare species (species with two or fewer occurrences) were eliminated to reduce noise in the dataset (Peck 2016). Relative cover values were transformed using the arcsine square root transformation to improve normality (McCune and Grace 2002). Multivariate analysis was conducted using PC-ORD (version 7, MjM Software Design, Gleneden Beach, OR, USA) and R vegan (R Core Development Team 2010). Univariate analysis was conducted using SAS Enterprise Guide (version 7.1, SAS Institute, Cary, NC, USA).

We used Permutation Multivariate Analysis of Variance (PERMANOVA) to test for significant differences in species compositions between groups based on grassland type and grazing history (Table 3.1). To test for differences in grassland type in our dataset, we randomly selected a set of four paired mixed-grass sites to compare to the four paired tallgrass sites so that we could meet the balanced design requirement for PERMANOVA (Anderson 2014). We used permutational analysis of multivariate dispersions (PERMDISP) to test for differences in dispersion between grazing history groups in the R *vegan* package (Clarke 1993; Anderson 2006). We used the Bray-Curtis distance measure and performed 1000 permutations ($p < 0.05$) (Anderson 2014).

Table 3.1. PERMANOVA grouping factor, levels, number of occurrences, and descriptions.

Factor	Levels	Occurrences	Description
Grassland type	Tallgrass	4	Sites located in the tallgrass prairie
	Mixed-grass	4	Random subset of sites in the mixed-grass prairie
Grazing history	Historically grazed	26	Private or state-owned lands with a long-term history of grazing
	USFWS	26	USFWS management units enrolled in the NPAM program

We performed Nonmetric Multidimensional Scaling (NMS) ordination in PC-ORD to explore structure in the dataset. We used the Relative-Sorenson distance measure and performed 500 iterations to reduce from six axes to three axes. The final number of axes was based on guidelines provided by Grace and McCune 2002: final stress < 20, an instability criterion < 0.00001, and a step-down in dimensionality when the axis reduced stress by at least 5%. Correlation coefficients (Pearson r-values) were used to correlate individual species to ordination axes. All species with r-values ≥ |0.4| were included for interpretation.

We used the Coefficients of Conservatism for the Vascular Flora of the Dakotas and adjacent Prairies manual to assign each species a coefficient of conservatism value (C-value) and calculate a floristic quality index (FQI) value for each site (Northern Great Plains Floristic Quality Assessment Panel 2001). The FQI provides a species richness estimate that assigns value rankings to native species based on their tolerance to disturbance. Low values indicate that a species is able to persist in severely disturbed areas while high values indicate that a species is restricted to relatively intact natural areas. Introduced species are not assigned C-values and are not included in the calculation of the FQI value.

We performed paired T-tests to determine if there were significant differences in diversity measures, site characteristics, and plant community composition between paired sites. We tested for differences in total species richness, native species richness, FQI values, and relative cover for a set of individual species, functional groups, species assemblages, bare ground, and litter. Genera and specific epithets follow the United States Department of Agriculture Plant Database (USDA 2022).

3.3. Results

We monitored 26 paired sites and observed a total of 189 species (Appendix F). We eliminated 34 rare species prior to performing the PERMANOVA and NMS analyses, and performed the analysis on the remaining 155 species.

The PERMANOVA analysis did not discern significant differences in species composition between tallgrass and mixed-grass sites (Table 3.2), thus we did not separate sites by grassland type when exploring the influence of grazing history on species composition. The PERMANOVA determined that sites with differing grazing histories have distinct species compositions (Table 3.2). The PERMDISP analysis found no differences in variation between groups, which suggests that the PERMANOVA result is due to significant differences in the location of the group centroid rather than differences in dispersion between groups (Table 3.2, Figure 3.2) (Anderson 2001).

Table 3.2. Results from the PERMANOVA and PERMDISP analyses of grassland type, grazing history, and species composition. Degrees of freedom (Df), sums of squares (SS), means of squares (MS), pseudo F and p-values are listed. Significant P-values are indicated by an asterisk.

PERMANOVA						
Factor	N	Df	SS	MS	Pseudo F	P-value
Grassland type	8	1	0.290	0.290	1.6649	0.074
Grazing history	52	1	26656.00	26656.00	1.9349	**0.021***
PERMDISP						
Grazing history	52	1	0.001	0.001	0.089	0.757

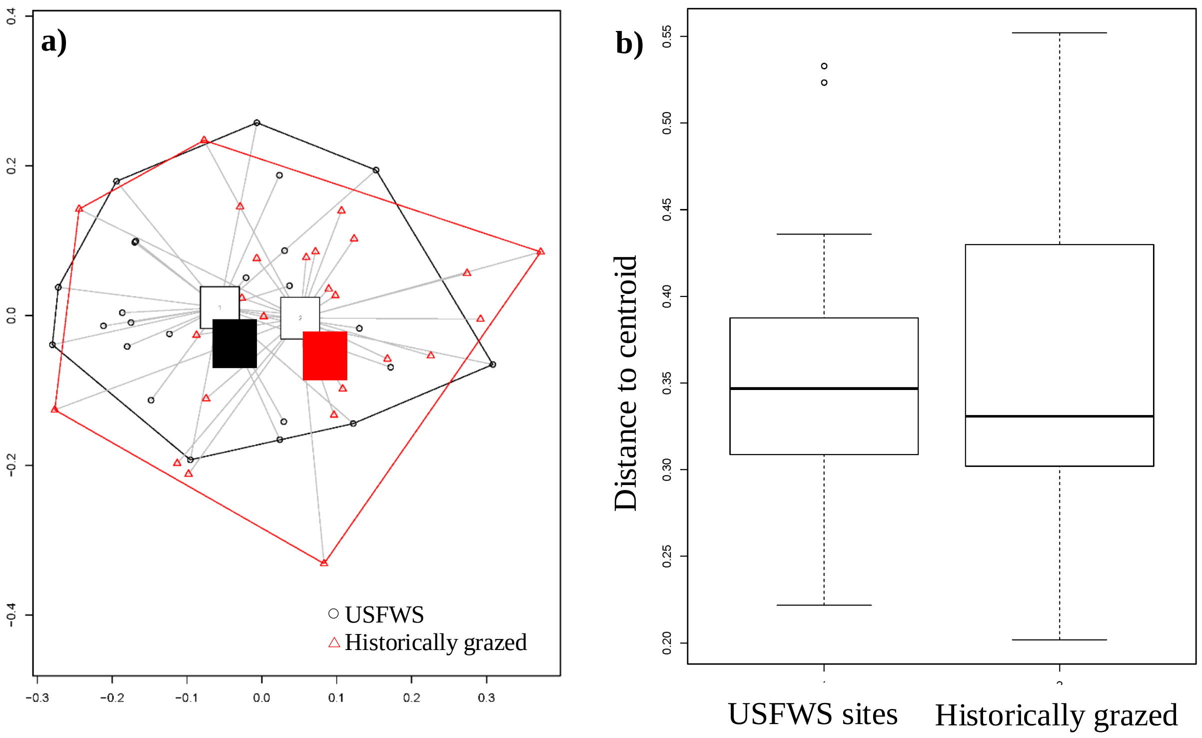

Figure 3.2. Ordination of sites showing distance to centroid for each site based on grazing history grouping (left). Black circles represent USFWS sites, and red triangles represent historically grazed sites. Boxplot of the average and range of distances to centroid between groups (right). The PERMDISP test did not discern significant differences in variation between groups based on grazing history.

The NMS ordination produced a three-dimensional solution with a final stress of 14.17. The three axes combined represented 85.9% of variation (Table 3.3). We examined the r-values correlated with each axis to explore patterns underlying species relationships (Table 3.4).

Table 3.3. Proportion of variance represented by each axis based on the correlation between ordination distances and distances in the original space.

Axis	Incremental	Cumulative
1	38.1%	38.1%
2	29.8%	67.9%
3	18.0%	85.9%

Table 3.4. Species correlations to the ordination axes. Only species with r-values ≥| 0.4| are listed (bold). The C-value and Physiognomy are included for each species.

Species	C-value	Physiognomy	Axis 1	Axis 2	Axis 3
Agropyron cristatum	*	Grass	**-0.409**	0.039	-0.007
Allium stellatum	7	Forb	-0.104	**-0.433**	-0.223
Ambrosia psilostachya	2	Forb	-0.050	**-0.595**	-0.090
Andropogon gerardii	5	Grass	-0.007	**-0.631**	0.074
Anemone canadensis	4	Forb	0.210	0.123	**0.578**
Antennaria microphylla	7	Forb	**-0.513**	-0.083	-0.363
Artemisia frigida	4	Shrub	**-0.693**	0.322	-0.273
Artemisia ludoviciana	3	Forb	**-0.415**	0.182	0.151
Bouteloua curtipendula	5	Grass	-0.118	**-0.500**	-0.264
Bouteloua gracilis	7	Grass	**-0.709**	-0.205	-0.397
Bromus inermis	*	Grass	**0.612**	-0.279	-0.051
Calamovilfa longifolia	5	Grass	-0.330	**-0.431**	0.187
Cirsium arvense	*	Forb	0.287	-0.168	**0.435**
Convolvulus arvensis	*	Forb	-0.102	**-0.501**	0.184
Carex filifolia	7	Sedge	**-0.429**	0.169	-0.160
Carex inops	7	Sedge	**-0.560**	0.024	-0.088
Echinacea angustifolia	7	Forb	**-0.553**	0.04	0.288
Elaeagnus commutata	5	Shrub	0.180	**0.434**	**0.409**
Erigeron strigosus	3	Forb	-0.058	**-0.473**	-0.187
Galium boreale	4	Forb	0.193	**0.408**	**0.540**
Glycyrrhiza lepidota	2	Forb	0.224	-0.002	**0.470**
Gutierrezia sarothrae	6	Shrub	**-0.424**	0.158	-0.009
Helianthus pauciflorus	8	Forb	-0.125	-0.116	**0.590**
Hesperostipa comata	6	Grass	**-0.555**	0.158	0.014

Table 3.4. Species correlations to the ordination axes (continued). Only species with r-values ≥|0.4| are listed (bold). The C-value and Physiognomy are included for each species.

Species	C-value	Physiognomy	Axis 1	Axis 2	Axis 3
Hesperostipa spartea	8	Grass	-0.190	**-0.416**	-0.066
Liatris ligulistylis	10	Forb	-0.125	**0.404**	0.165
Liatris punctata	7	Forb	**-0.527**	-0.108	0.087
Lygodesmia juncea	2	Forb	**-0.508**	-0.036	-0.064
Oenothera suffrutescens	4	Forb	**-0.447**	0.156	0.205
Oligoneuron rigidum	4	Forb	0.009	-0.070	**0.414**
Oxalis violacea	7	Forb	0.196	**-0.504**	-0.026
Panicum virgatum	5	Grass	-0.114	**-0.470**	-0.187
Pascopyrum smithii	4	Grass	**-0.478**	0.381	**-0.422**
Pediomelum argophylla	4	Forb	**-0.477**	-0.130	-0.084
Penstemon gracilis	6	Forb	**-0.556**	0.096	-0.133
Phleum pratense	*	Grass	0.079	**-0.449**	-0.164
Physalis virginiana	4	Forb	-0.033	**-0.431**	0.263
Poa pratensis	*	Grass	**0.449**	**0.409**	-0.364
Polygala alba	5	Forb	**-0.485**	-0.149	-0.161
Potentilla arguta	8	Forb	-0.136	0.269	**0.406**
Pulsatilla patens	9	Forb	**-0.478**	-0.183	0.297
Ratibida columnifera	3	Forb	-0.370	-0.340	**-0.470**
Selaginella densa	6	Fern	**-0.418**	0.235	-0.134
Solidago canadensis	1	Forb	0.381	**-0.428**	0.314
Solidago missouriensis	5	Forb	**-0.493**	0.258	-0.008
Solidago mollis	6	Forb	**-0.424**	0.194	-0.066
Sphaeralcea coccinea	4	Forb	**-0.592**	0.161	-0.265
Symphyotrichum ericoides	2	Forb	**-0.411**	0.021	0.009
Symphoricarpos occidentalis	3	Shrub	0.352	**0.527**	0.122
Verbena stricta	2	Forb	-0.067	**-0.501**	-0.183
Viola pedatifida	8	Forb	0.066	**-0.462**	-0.050

Axis 1 represented 38.1% of variation and appears to represent a gradient in floristic quality: negatively correlated species were primarily conservative native species, whereas smooth brome and Kentucky bluegrass were positively correlated (Figures 3.3 and 3.4). Additionally, species that are negatively correlated with Axis 1 are associated with the Historic Climax Plant Community (HCPC) of the loamy ecological site (USDA-NRCS 2016). These species are noted to be more abundant with periodic disturbance, and may proliferate following periods of heavy continuous grazing (e.g. fringed sage (*Artemisia frigida* Willd.*)* and blue grama (*Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths) (Stubbendieck et al. 2017).

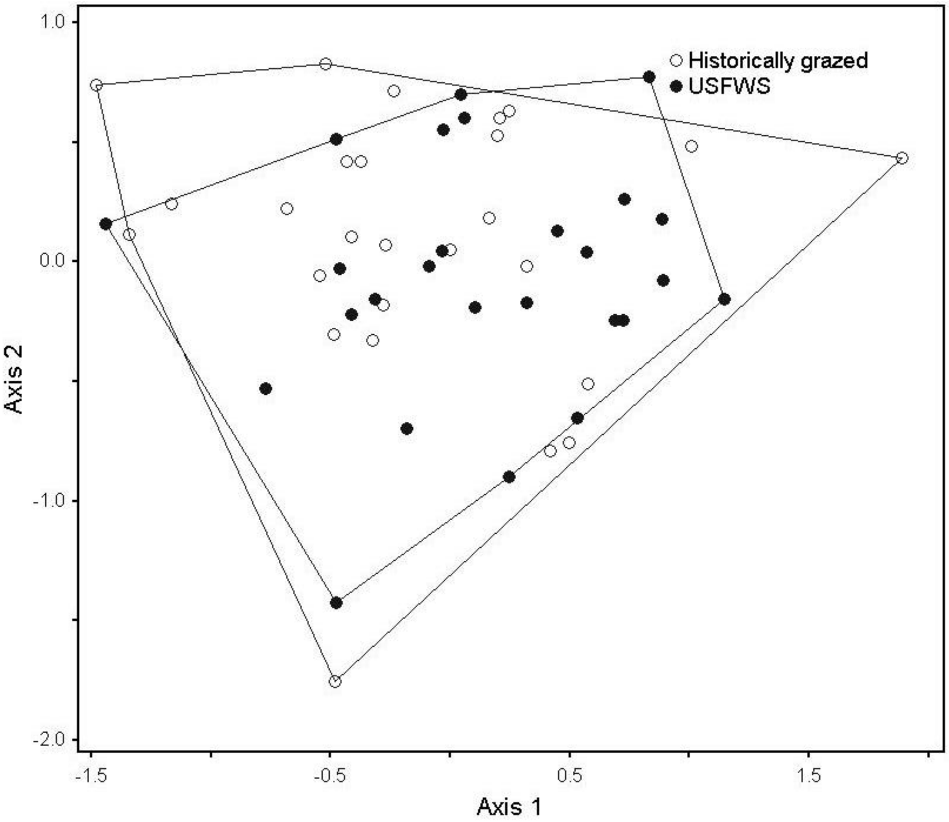

Figure 3.3. NMS ordination graph of species composition of each site grouped by grazing history, Axis 1 and Axis 2. Each symbol represents a site.

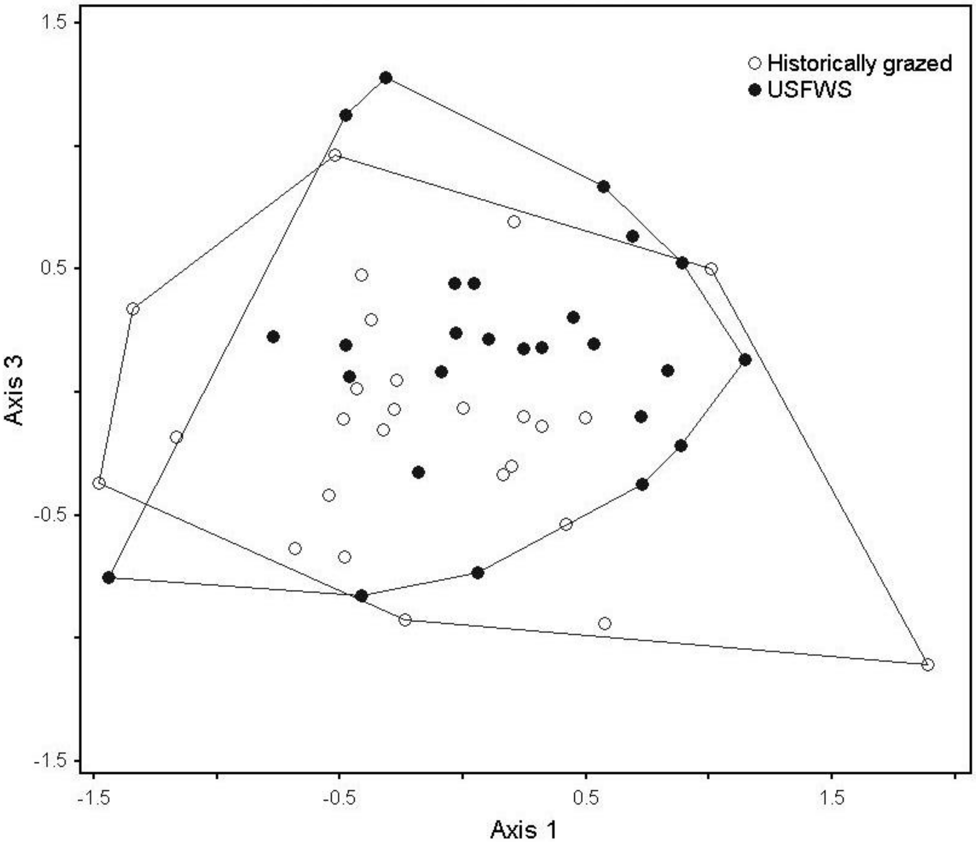

Figure 3.4. NMS ordination graph of species composition of each site grouped by grazing history, Axis 1 and Axis 3. Each symbol represents a site.

Axis 2 represented 29.8% of variation; low shrub species (Murphy and Grant 2005) and Kentucky bluegrass were positively correlated and a mix of warm-season grasses and native forbs were negatively correlated (Figure 3.3 and 3.5). Axis 3 represented 18.0% of variation (Figure 3.4 and 3.5). This axis appears to show a weak relationship with grazing; negatively correlated species are known to increase with heavy grazing (Stubbendieck 2017), while positively correlated species tended to be less abundant at sites with a history of grazing.

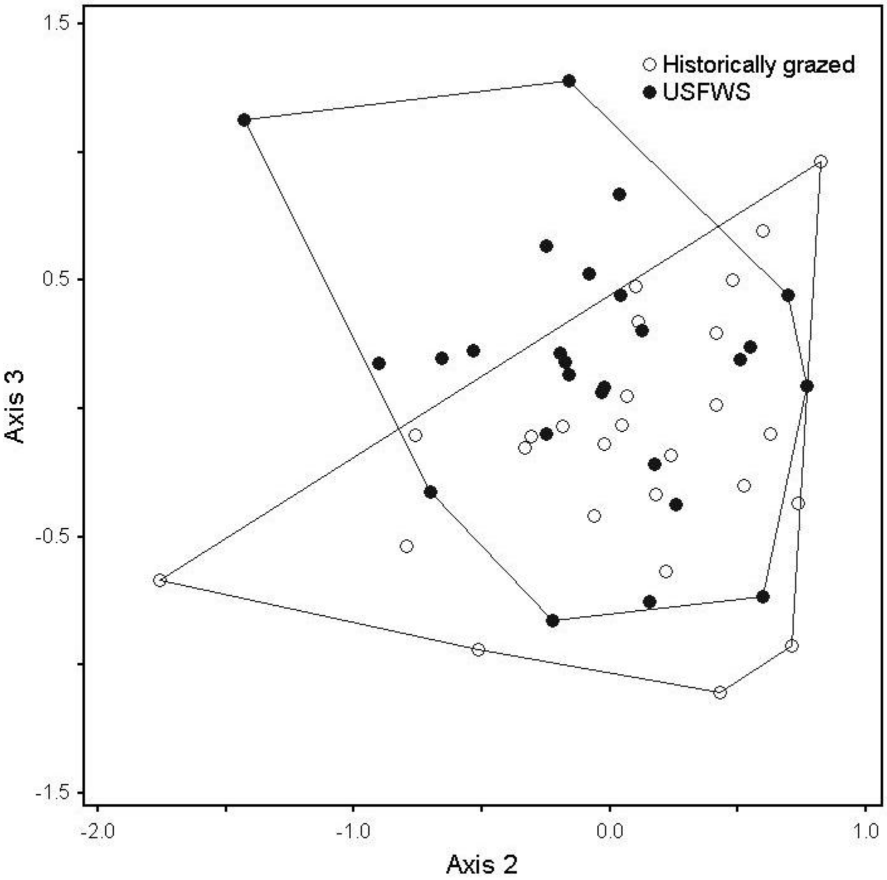

Figure 3.5. NMS ordination graph of species composition of each site grouped by grazing history, Axis 2 and Axis 3. Each symbol represents a site.

The paired T-test determined that total species richness was significantly ($P < 0.0057$) greater for historically grazed sites ($\bar{x}$ =52, SD=11.53) than USFWS sites ($\bar{x}$ =44.77, SD=8.02) (Table 3.6, Figure 3.6a). FQI values were significantly ($P < 0.0415$) higher for historically grazed sites ($\bar{x}$ =37.37, SD=6.61) than USFWS sites ($\bar{x}$ =34.42,5.44) (Table 3.6, Figure 3.6b). Additionally, smooth brome was significantly ($P < 0.0186$) less prevalent at historically grazed sites ($\bar{x}$ =13.3% relative cover, SD=13.3%) than USFWS sites ($\bar{x}$ =23.3% relative cover, SD=16.9%) (Table 3.6, Figure 3.6c). The HCPC assemblage had significantly ($P < 0.0393$) higher relative cover at historically grazed sites ($\bar{x}$=15.89, SD=11.49) than USFWS sites ($\bar{x}$=15.89, SD=10.38) (Table 3.6, Figure 3.6d). There were no significant differences in native species richness, vegetative cover, bare ground cover, litter cover, and the relative cover of native species, Kentucky bluegrass, and low shrubs between historically grazed and USFWS paired sites (Table 3.6). Low shrubs include western snowberry and (*Symphoricarpos occidentalis* Hook.) and silverberry (*Elaeagnus commutata* Bernh. ex Rydb.) (Grant et. al 2020a).

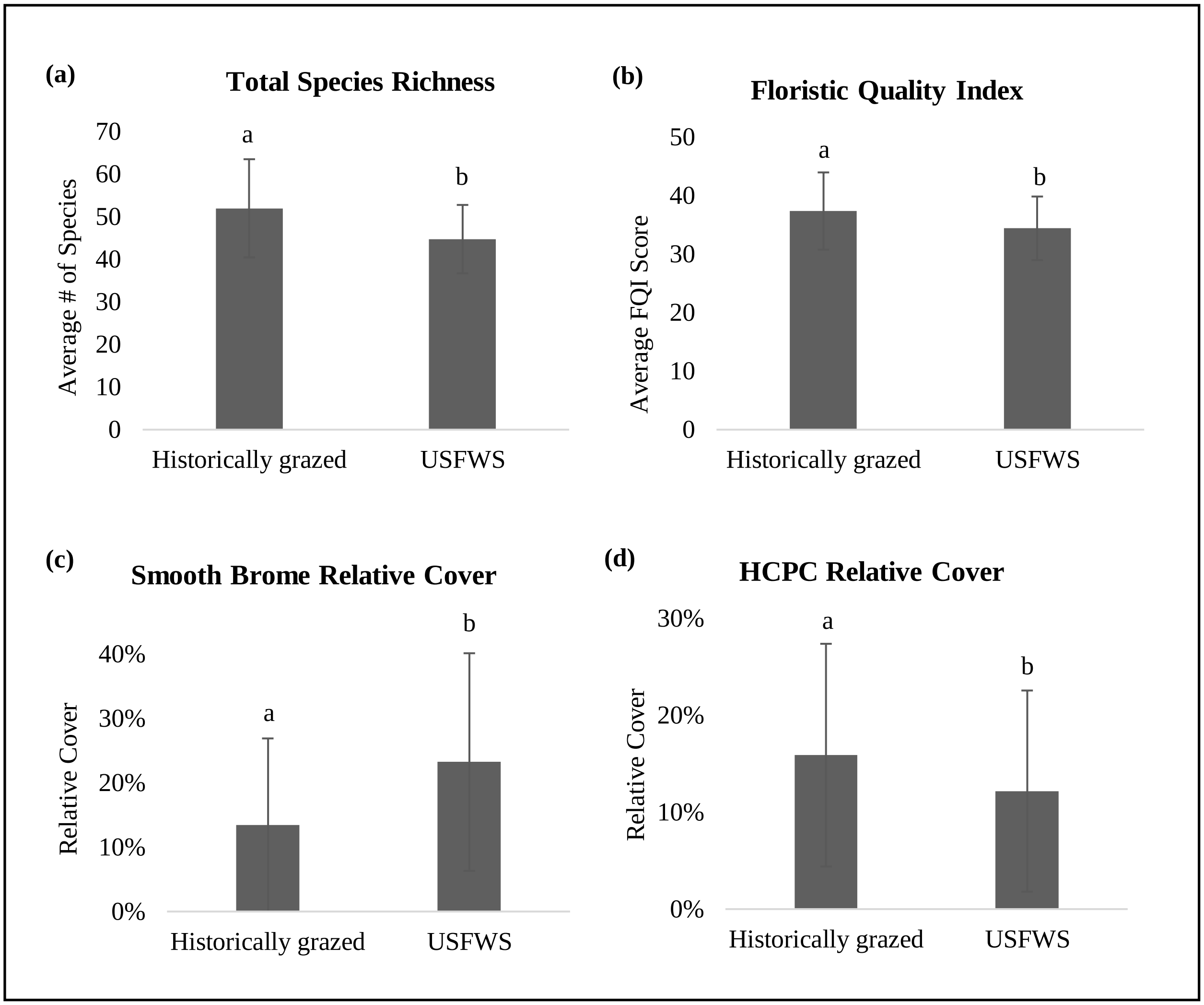

Figure 3.6. Mean (± standard deviation) total species richness (a), Floristic Quality Index (FQI) (b), smooth brome relative cover (c), and HCPC species relative cover (d) between historically grazed and USFWS paired sites. Different letters indicate significant differences ($P < 0.05$) between sites.

Table 3.5. Mean, standard deviation (SD), t-value (t), and P-value for paired USFWS and historically grazed sites for 11 variables. Degrees of freedom is equal to 25 for all tests. Asterisks indicate significant differences between paired sites.

Variable	Mean	SD	t	P-value
Total species richness				
USFWS	44.77	8.02	3.02	**0.0057***
Historically grazed	52.00	11.53		
FQI				
USFWS	34.42	5.44	2.15	**0.0415***
Historically grazed	37.37	6.61		
Native richness				
USFWS	40.15	8.67	1.82	0.0812
Historically grazed	44.73	12.05		
Native relative cover (%)				
USFWS	52.58	17.62	0.28	0.7814
Historically grazed	53.94	10.65		
HCPC relative cover (%)				
USFWS	12.18	11.49	2.17	**0.0393***
Historically grazed	15.89	10.38		
Kentucky bluegrass relative cover (%)				
USFWS	20.29	10.77	1.20	0.2400
Historically grazed	24.11	15.63		
Smooth brome relative cover (%)				
USFWS	23.23	16.90	2.52	**0.0186***
Historically grazed	13.45	14.03		
Low shrub relative cover (%)				
USFWS	7.10	6.52	0.39	0.7026
Historically grazed	7.80	6.88		
Vegetative cover (%)				
USFWS	54.96	12.42	0.86	0.3989
Historically grazed	57.53	10.41		
Bare ground cover (%)				
USFWS	2.38	4.76	0.37	0.7113
Historically grazed	2.00	1.48		
Litter cover (%)				
USFWS	39.46	11.99	0.16	0.8728
Historically grazed	38.90	12.50		

3.4. Discussion

Grazing is a major influence shaping prairie plant community composition (Fuhlendorf and Engle 2001), and its absence is associated with shifts from diverse native plant communities to grasslands dominated by introduced cool-season grasses (DeKeyser et al. 2009). This study assessed differences in plant community composition between sites with or without a long-term history of livestock grazing. Our analysis determined that paired sites with differing grazing histories have unique species compositions, with significant differences arising in species richness, floristic quality, and the prevalence of introduced cool-season grasses. These differences may be legacies of divergent management paradigms through the latter half of the 1900s (Murphy and Grant 2005); USFWS-owned prairies were historically managed with infrequent, low-intensity livestock grazing and occasional fire (Dixon et al. 2019), whereas historically grazed prairies typically experienced annual moderate to high intensity grazing and fire suppression (Murphy and Grant 2005).

We detected greater total species richness and floristic quality on sites with a long-term history of grazing. This difference in total species richness may be attributed to the moderating effect of grazing disturbance: grazing may support the persistence of uncommon species by reducing the competitive advantage of dominant species (Howe 1999). Moderate livestock grazing has been shown to maintain higher species richness in mesic grasslands (such as the prairies of the PPR) than either light grazing, heavy grazing, or grazing exclusion (Milchunas et al. 1988; Gao and Carmel 2020). Grazing reduces plant height, vegetative cover, and plant litter, which increases light availability and opens gaps for less competitive species to establish (Olff and Ritchie 1998). Our analysis did not detect any differences in amount of vegetative cover, accumulated litter or bare ground between paired sites, likely due to present-day management practices on the USFWS-owned prairies (Gannon et al. 2013). While we did not observe differences in native species richness between paired sites, native species communities at historically-grazed lands included greater abundances of uncommon or rare species. These species, especially short-statured perennials like littleleaf pussytoes (*Antennaria microphylla* Rydb.) and lesser spikemoss (*Selaginella densa* Rydb.) may persist when taller, dominant species are grazed (Towne et al. 2005).

Sites with historic livestock grazing contained greater abundances of species that are associated with Historic Climax Plant Communities (HCPC) in the PPR (USDA-NRCS 2016). The HCPC is derived from study of remnant prairie, research, and expert opinion, and is intended to represent the plant community and ecological condition prior to Euro-American settlement (Twidwell et al. 2013). HCPC serve as reference conditions because they represent the ecological state in which soil resources and native biodiversity are best conserved (Bestelmeyer et al. 2003). Though these communities likely no longer exist due to the ubiquity of introduced species and land use changes (Hobbs et al. 2009), the HCPC concept may serve as a reference state for guiding restoration and predicting plant community transitions (Twidwell et al. 2013). In our study, the greater occurrence of HCPC-associated species on historically grazed sites underscores the role of grazing in maintaining native species assemblages in the PPR (Fuhlendorf and Engle 2001). HCPC in the PPR are maintained by periodic disturbance, and extended rest or heavy grazing results in shifts in plant community composition (USDA-NRC 2016); thus, retaining aspects of the historic disturbance regime appears to have been partially effective in maintaining HCPC assemblages in the PPR. The lower abundance of these species on USFWS-owned prairies suggests these plant communities have transitioned to an alternative stable state where reestablishing burning and grazing may not be sufficient to shift species composition towards HCPC (USDA-NRCS 2016).

Introduced cool-season grasses exhibited differing patterns of occurrence between paired sites. Smooth brome was less prevalent at sites with a long-term history of grazing, while Kentucky bluegrass abundance was comparable between paired sites. Murphy and Grant (2005) likewise observed significantly lower smooth brome frequencies on privately-owned lands used for livestock production. They suggest that smooth brome may be intolerant of continuous moderate to heavy grazing due to the vulnerability of its meristems to being removed or damaged during grazing. Smooth brome tillers elongate from meristems located well above the soil surface, thus making the plant vulnerable to defoliation during the tiller elongation period (Willson and Stubbendieck 2000; Otfinowski et al. 2007). Repeat defoliation during tiller elongation may impact smooth brome vigor and competitiveness by reducing tiller density (Brown 1997) and foliar cover (Stacy et al. 2005). However, these effects have not been demonstrated in short-term studies evaluating targeted grazing impacts on smooth brome abundance (Dornbusch et al. 2020; Hendrickson et al. 2020). Smooth brome may be tolerant of repeat defoliation over multi-year periods in favorable environmental conditions (Hendrickson et al. 2020), thus making short-term assessments of grazing impacts on smooth brome vigor difficult to evaluate. The findings of our study and others (Murphy and Grant 2005) suggest that livestock grazing may be used to moderate smooth brome invasion if conducted over a period of decades, though the mechanism for why these plant communities are more resilient to invasion remains unclear.

We observed comparable abundance of Kentucky bluegrass between paired sites, which suggests that differences in historic management practices did not have an effect on Kentucky bluegrass abundance. Kentucky bluegrass is known to proliferate with prolonged rest or continuous, low to moderate grazing practices (Murphy and Grant 2005; DeKeyser et al. 2009; Dornbusch et al. 2020), and recent reviews of Kentucky bluegrass ecology in the Northern Great Plains suggest that environmental factors, such as increased propagule pressure, atmospheric CO_2 concentrations, nitrogen deposition, and climate change, may also be contributing to Kentucky bluegrass invasion (DeKeyser et al. 2015; Dennhardt et al. 2021; Palit et al. 2021). These findings, coupled with our results, suggest that alternative management approaches may be required to control Kentucky bluegrass expansion (DeKeyser et al. 2010; Dornbusch et al. 2020).

Western snowberry and silverberry, the two native species included in our low shrub grouping, have increased from 1-5% cover to greater than 20% cover on USFWS-owned lands (Grant et al. 2020). Low shrub expansion may be occurring on historically-grazed lands as well; our data did not show significant differences in low shrub abundance between paired sites. Western snowberry and silverberry proliferate with fire suppression (Bailey and Anderson 1979), thus a shared history of fire suppression between sites may account for similarities in low shrub abundance. Additionally, western snowberry and silverberry are noted to increase following periods of prolonged grazing (Bailey 1970; Bailey et al. 1990), perhaps due to selective herbivory pressures on surrounding herbaceous species (Bailey 1970).

Low shrub expansion is ecologically concerning due to its association with introduced species co-invasion. Grant et al. (2020) observed landscape-level patterns in low shrub occurrence in the PPR, with the greatest frequencies occurring in the relatively-intact prairies of northcentral and northwestern North Dakota. Though Kentucky bluegrass and smooth brome are subdominant to native species assemblages in these areas, Kentucky bluegrass and smooth brome more frequently dominated shrub understories (>80%) than native grasses and forbs (13%). Western snowberry and silverberry may create conditions conducive for secondary invasion by altering light, nutrient, and moisture in their understories (Lett and Knapp 2003; Grant et al. 2020), as well as providing a protective barrier to herbivory (Bailey 1970). Low shrub expansion may coincide with increases in Kentucky bluegrass and smooth brome in otherwise intact native prairie, though it's unclear to what extent co-invasion occurs on non-Service prairies in the PPR.

3.5. Conclusion

Grazing is a key process in maintaining species diversity on remnant native prairie in landscapes increasingly altered by anthropogenic pressures (Collins et al. 1998). This study established that paired sites with differing long-term grazing histories have distinct plant community compositions. The results are consistent with other assessments of species composition in the PPR, and confirm that historical management practices are a determinant in present day species composition. USFWS-owned prairies are generally less species-rich, lower in floristic quality, and contain more smooth brome than their historically-grazed counterparts. Prolonged periods without disturbance are associated with declines in native species and increases in introduced species (Grant et al. 2009; DeKeyser et al. 2013), and our results suggest that the consequences of rest may persist despite present-day management practices intended to improve species composition (Gannon et al. 2013). Grazing alone does not inhibit Kentucky bluegrass expansion, though it appears to moderate Kentucky bluegrass' detrimental effect on native species diversity.

3.6. Management Implications

Grassland stewards should prioritize acquiring lands or forming partnerships with landowners who have a demonstrated long-term history of moderate intensity livestock grazing. Though these lands may be substantially invaded by Kentucky bluegrass, opportunities may exist for conserving uncommon or rare native species on these lands. Re-establishing periodic early spring burning (5- to 6-year intervals) may be successful for targeting Kentucky bluegrass on private- and state-owned rangelands (Engle and Bultsma 1984; Towne and Owensby 1984), and repeated burning over extended periods may be required to significantly impact its abundance (Kobiela et al. 2017; Kral et al. 2018). The sparsity of smooth brome on grazed landscapes is important, as smooth brome's ability to negatively impact native species diversity and persistence makes it a particularly troubling invader (Myster 2006; Williams and Crone 2006, Dillemuth et al. 2009). Once established, smooth brome is difficult to control and creates conditions suitable for its own proliferation and secondary invasion by other introduced species (Vinton and Goergen 2006; Jordan et al. 2008, Piper et al. 2014). Managing to control Kentucky bluegrass, smooth brome, and low shrubs may prove challenging as they are reported to have differing responses to burning and grazing. In a region where native prairie exists primarily in isolated fragments under varying ownership, forming partnerships to implement cohesive management approaches on a landscape-scale may be imperative to combat introduced grass invasion and native species decline.

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APPENDIX A. LIST OF NPAM UNITS SURVEYED WITH USFWS DISTRICT, LATITUDE, AND LONGITUDE FOR EACH SITE

Site Name	USFWS District	Latitude	Longitude
Buss West	Waubay	46.90364	97.48659
Charley Harley	Sand Lake	45.86959	99.17021
Cooper North	Sand Lake	45.68415	99.83289
Coteau Prairie	Lostwood	48.49403	102.4027
Frederick	Chase Lake	47.33327	99.9886
G-12A East	Long Lake	46.69402	100.1554
G26	Arrowwood	47.18385	98.79375
G28	Arrowwood	47.15896	98.80285
Geiszler 1	Kulm	46.16097	99.2921
Geiszler 4	Kulm	46.13648	99.29759
GLT A	Souris	48.76742	100.8733
GLT C	Souris	48.76877	100.8706
Haven Paddock 5	Arrowwood	47.67145	98.57426
HB 24 Ekert Ranch	Souris	48.46972	101.5403
Krause	Tewaukon	46.02104	97.34006
Lake Zahl 7	Lostwood	48.58888	103.6304
Lasher A	Audubon	47.42487	100.4355
Lasher B	Audubon	47.42572	100.4295
Mayer	Kulm	46.58037	99.22248
Melass South	Devils Lake	48.03164	99.46857
Odegaard	Chase Lake	46.90868	99.41079
Rath	Long Lake	47.19401	100.2165
Roe E	Waubay	45.03549	97.46116
Roe F	Waubay	45.0305	97.4557
Sully’s Hill	Devils Lake	47.97027	99.00577
Swanson	Lostwood	48.68913	102.6539
Warner Lake 5	Waubay	45.02116	97.50307
Winberg	Chase Lake	47.17845	99.22378
Windmill	Lostwood	48.61712	102.4883
Woodworth	Chase Lake	47.12543	99.24986

APPENDIX B. LIST OF SPECIES ENCOUNTERED AT USFWS NPAM UNITS WITH C-VALUE, LIFE SPAN, GROWTH FORM AND FAMILY

Species	C-value	Life Span	Growth Form	Family
Achillea millefolium	3	Perennial	Forb	Asteraceae
Agoseris glauca	8	Perennial	Forb	Asteraceae
Agropyron cristatum	*	Perennial	Grass	Poaceae
Agrostis scabra	1	Perennial	Grass	Poaceae
Allium stellatum	7	Perennial	Forb	Liliaceae
Allium textile	7	Perennial	Forb	Liliaceae
Ambrosia psilostachya	2	Perennial	Forb	Asteraceae
Amorpha canescens	9	Perennial	Shrub	Fabaceae
Andropogon gerardii	5	Perennial	Grass	Poaceae
Androsace occidentalis	5	Annual	Forb	Primulaceae
Anemone canadensis	4	Perennial	Forb	Ranunculaceae
Anemone cylindrica	7	Perennial	Forb	Ranunculaceae
Antennaria neglecta	5	Perennial	Forb	Asteraceae
Apocynum cannabinum	4	Perennial	Forb	Apocynaceae
Arabis hirsuta	7	Biennial	Forb	Brassicaceae
Aristida purpurea	4	Perennial	Grass	Poaceae
Artemisia absinthium	*	Perennial	Forb	Asteraceae
Artemisia campestris	5	Biennial	Forb	Asteraceae
Artemisia filifolia	6	Perennial	Shrub	Asteraceae
Artemisia frigida	4	Perennial	Shrub	Asteraceae
Artemisia ludoviciana	3	Perennial	Forb	Asteraceae
Asclepias ovalifolia	9	Perennial	Forb	Asclepiadaceae
Asclepias speciosa	4	Perennial	Forb	Asclepiadaceae
Asclepias syriaca	0	Perennial	Forb	Asclepiadaceae
Asclepias verticillata	3	Perennial	Forb	Asclepiadaceae
Asclepias viridiflora	8	Perennial	Forb	Asclepiadaceae
Astragalus adsurgens	8	Perennial	Forb	Fabaceae
Astragalus agrestis	6	Perennial	Forb	Fabaceae
Astragalus canadensis	5	Perennial	Forb	Fabaceae
Astragalus flexuosus	4	Perennial	Forb	Fabaceae
Astragalus pectinatus	8	Perennial	Forb	Fabaceae
Avenula hookeri	9	Perennial	Grass	Poaceae
Bouteloua curtipendula	5	Perennial	Grass	Poaceae
Bouteloua dactyloides	4	Perennial	Grass	Poaceae
Bouteloua gracilis	7	Perennial	Grass	Poaceae
Brickellia eupatorioides	5	Perennial	Forb	Asteraceae
Bromus ciliatus	10	Perennial	Grass	Poaceae
Bromus inermis	*	Perennial	Grass	Poaceae

Species	C-value	Life Span	Growth Form	Family
Calamovilfa longifolia	5	Perennial	Grass	Poaceae
Calystegia sepium	0	Perennial	Forb	Convolvulaceae
Campanula rotundifolia	7	Perennial	Forb	Campanulaceae
Carex brevior	4	Perennial	Sedge	Cyperaceae
Carex duriuscula	4	Perennial	Sedge	Cyperaceae
Carex filifolia	7	Perennial	Sedge	Cyperaceae
Carex inops	7	Perennial	Sedge	Cyperaceae
Carex pellita	4	Perennial	Sedge	Cyperaceae
Carex praegracilis	5	Perennial	Sedge	Cyperaceae
Carex sartwellii	5	Perennial	Sedge	Cyperaceae
Carex tetanica	9	Perennial	Sedge	Cyperaceae
Carex vulpinoidea	2	Perennial	Sedge	Cyperaceae
Carex xerantica	10	Perennial	Sedge	Cyperaceae
Chenopodium album	*	Annual	Forb	Chenopodiaceae
Cirsium arvense	*	Perennial	Forb	Asteraceae
Cirsium flodmanii	5	Perennial	Forb	Asteraceae
Cirsium undulatum	7	Perennial	Forb	Asteraceae
Cirsium vulgare	*	Biennial	Forb	Asteraceae
Comandra umbellata	8	Perennial	Forb	Santalaceae
Convolvulus arvensis	*	Perennial	Forb	Convolvulaceae
Conyza canadensis	0	Annual	Forb	Asteraceae
Crataegus chrysocarpa	6	Perennial	Shrub	Rosaceae
Dalea purpurea	8	Perennial	Forb	Fabaceae
Dichanthelium leibergii	8	Perennial	Grass	Poaceae
Dichanthelium oligosanthes	6	Perennial	Grass	Poaceae
Dichanthelium wilcoxianum	8	Perennial	Grass	Poaceae
Distichlis spicata var. stricta	2	Perennial	Grass	Poaceae
Echinacea angustifolia	7	Perennial	Forb	Asteraceae
Elaeagnus commutata	5	Perennial	Shrub	Elaeagnaceae
Elymus canadensis	3	Perennial	Grass	Poaceae
Elymus canadensis	3	Perennial	Grass	Poaceae
Elymus repens	*	Perennial	Grass	Poaceae
Equisetum laevigatum	3	Perennial	Fern	Equisetaceae
Erysimum inconspicuum	7	Perennial	Forb	Brassicaceae
Euphorbia esula	*	Perennial	Forb	Euphorbiaceae
Fragaria virginiana	4	Perennial	Forb	Rosaceae
Galium boreale	4	Perennial	Forb	Rubiaceae
Geum triflorum	8	Perennial	Forb	Rosaceae
Glycyrrhiza lepidota	2	Perennial	Forb	Fabaceae
Helianthus maximilianii	5	Perennial	Forb	Asteraceae
Helianthus nuttallii	8	Perennial	Forb	Asteraceae
Helianthus pauciflorus	8	Perennial	Forb	Asteraceae

Species	C-value	Life Span	Growth Form	Family
Hesperostipa comata	6	Perennial	Grass	Poaceae
Hesperostipa spartea	8	Perennial	Grass	Poaceae
Heterotheca villosa	3	Perennial	Forb	Asteraceae
Heuchera richardsonii	8	Perennial	Forb	Saxifragaceae
Juncus arcticus	5	Perennial	Forb	Juncaceae
Koeleria macrantha	14	Perennial	Grass	Poaceae
Lactuca tatarica	1	Perennial	Forb	Asteraceae
Lathyrus venosus	8	Perennial	Forb	Fabaceae
Liatris ligulistylis	10	Perennial	Forb	Asteraceae
Liatris punctata	7	Perennial	Forb	Asteraceae
Linum perenne	6	Perennial	Forb	Linaceae
Linum rigidum	5	Annual	Forb	Linaceae
Lithospermum canescens	7	Perennial	Forb	Boraginaceae
Lotus purshianus	3	Annual	Forb	Fabaceae
Lygodesmia juncea	2	Perennial	Forb	Asteraceae
Medicago lupulina	*	Perennial	Forb	Fabaceae
Medicago sativa	*	Perennial	Forb	Fabaceae
Melilotus officinalis	*	Annual	Forb	Fabaceae
Monarda fistulosa	5	Perennial	Forb	Lamiaceae
Muhlenbergia cuspidata	8	Perennial	Grass	Poaceae
Muhlenbergia racemosa	4	Perennial	Grass	Poaceae
Nassella viridula	5	Perennial	Grass	Poaceae
Oenothera suffrutescens	4	Perennial	Forb	Onagraceae
Oligoneuron rigidum	4	Perennial	Forb	Asteraceae
Onosmodium bejariense	7	Perennial	Forb	Boraginaceae
Oxalis violacea	7	Perennial	Forb	Oxalidaceae
Oxytropis lambertii	5	Perennial	Forb	Fabaceae
Packera plattensis	6	Biennial	Forb	Asteraceae
Panicum virgatum	5	Perennial	Grass	Poaceae
Pascopyrum smithii	4	Perennial	Grass	Poaceae
Pediomelum argophylla	4	Perennial	Forb	Fabaceae
Pediomelum esculenta	9	Perennial	Forb	Fabaceae
Penstemon glaber	7	Perennial	Forb	Scrophulariaceae
Penstemon gracilis	6	Perennial	Forb	Scrophulariaceae
Phalaris arundinacea	0	Perennial	Grass	Poaceae
Phleum pratense	*	Perennial	Grass	Poaceae
Physalis virginiana	4	Perennial	Forb	Solanaceae
Poa palustris	4	Perennial	Grass	Poaceae
Poa pratensis	*	Perennial	Grass	Poaceae
Polygala alba	5	Perennial	Forb	Polygalaceae
Potamogeton gramineus	6	Perennial	Forb	Potamogetonaceae
Potentilla arguta	8	Perennial	Forb	Rosaceae

Species	C-value	Life Span	Growth Form	Family
Potentilla pensylvanica	9	Perennial	Forb	Rosaceae
Prunus americana	4	Perennial	Shrub	Rosaceae
Pulsatilla patens	9	Perennial	Forb	Ranunculaceae
Ratibida columnifera	3	Perennial	Forb	Asteraceae
Rosa arkansana	3	Perennial	Shrub	Rosaceae
Rosa woodsii	5	Perennial	Shrub	Rosaceae
Schizachyrium scoparium	6	Perennial	Grass	Poaceae
Selaginella densa	6	Perennial	Fern	Selaginellaceae
Solidago canadensis	1	Perennial	Forb	Asteraceae
Solidago missouriensis	5	Perennial	Forb	Asteraceae
Solidago mollis	6	Perennial	Forb	Asteraceae
Sonchus arvensis	*	Perennial	Forb	Asteraceae
Spartina pectinata	5	Perennial	Grass	Poaceae
Sphaeralcea coccinea	4	Perennial	Forb	Malvaceae
Spiraea alba	7	Perennial	Shrub	Rosaceae
Sporobolus heterolepis	10	Perennial	Grass	Poaceae
Stachys pilosa	3	Perennial	Forb	Lamiaceae
Symphoricarpos occidentalis	3	Perennial	Shrub	Caprifoliaceae
Symphyotrichum ericoides	2	Perennial	Forb	Asteraceae
Symphyotrichum falcatum	4	Perennial	Forb	Asteraceae
Symphyotrichum laeve	5	Perennial	Forb	Asteraceae
Symphyotrichum lanceolatum	3	Perennial	Forb	Asteraceae
Symphyotrichum sericeum	10	Perennial	Forb	Asteraceae
Taraxacum officinale	*	Perennial	Forb	Asteraceae
Thalictrum venulosum	6	Perennial	Forb	Ranunculaceae
Thermopsis rhombifolia	6	Perennial	Forb	Fabaceae
Toxicodendron rydbergii	3	Perennial	Shrub	Anacardiaceae
Tragopogon dubius	*	Biennial	Forb	Asteraceae
Trifolium pratense	*	Perennial	Forb	Fabaceae
Vicia americana	6	Perennial	Forb	Fabaceae
Viola nuttallii	8	Perennial	Forb	Violaceae
Viola pedatifida	8	Perennial	Forb	Violaceae
Zizia aptera	8	Perennial	Forb	Apiaceae

*Introduced species are not assigned a c-value

APPENDIX C. VALUES FOR EXPLANATORY VARIABLES ASSESSED IN DBRDA MODEL

Site	Burn	Graze	Years Since Burn	Years Since Graze	Northing
Buss	1	8	3	1	5314104
CH	3	3	2	1	5079572
Cooper	4	5	2	1	5059293
Coteau	2	5	2	1	5374470
Frederick	0	4	0	3	5242674
G12	1	9	5	1	5171811
G26	1	9	4	1	5225616
G28	2	4	5	1	5222848
Geiszler 1	1	5	9	1	5111974
Geiszler 4	1	6	8	1	5109255
GLT A	3	8	1	1	5403294
GLT C	3	8	1	1	5403439
Haven	1	10	8	1	5279872
HB24	5	2	2	1	5371627
Krause	5	5	2	1	5097725
Lake Zahl	1	5	10	2	5382661
Lasher A	4	3	2	2	5253379
Lasher B	4	3	2	2	5253465
Mayer	4	1	2	4	5158558
Melass	1	4	8	2	5319923
Odegaard	0	5	0	1	5195098
Rath	2	7	3	2	5227442
Roe E	3	5	2	1	4988045
Roe F	4	4	2	1	4987499
Sully's Hill	5	1	2	6	5312996
Swanson	1	3	9	1	5395555
Warner	3	5	4	1	4986391
Winberg	3	2	1	2	5225019
Windmill	1	2	10	4	5387939
Woodworth	0	7	0	1	5219133

APPENDIX D. LIST OF USFWS UNITS SURVEYED WITH USFWS DISTRICT, LATITUDE, AND LONGITUDE FOR EACH SITE

Unit Name	USFWS District	Latitude	Longitude
Buss West	Waubay	46.90364	97.48659
Charley Harley	Sand Lake	45.86959	99.17021
Cooper North	Sand Lake	45.68415	99.83289
Coteau Prairie	Lostwood	48.49403	102.4027
Frederick	Chase Lake	47.33327	99.9886
G-12A East	Long Lake	46.69402	100.1554
G26	Arrowwood	47.18385	98.79375
G28	Arrowwood	47.15896	98.80285
Geiszler 4	Kulm	46.13648	99.29759
GLT A/C	Souris	48.76742	100.8733
Haven Paddock 5	Arrowwood	47.67145	98.57426
HB 24 Ekert Ranch	Souris	48.46972	101.5403
Krause	Tewaukon	46.02104	97.34006
Lake Zahl 7	Lostwood	48.58888	103.6304
Lasher A/B	Audubon	47.42487	100.4355
Mayer	Kulm	46.58037	99.22248
Melass South	Devils Lake	48.03164	99.46857
Odegaard	Chase Lake	46.90868	99.41079
Rath	Long Lake	47.19401	100.2165
Roe E/ F	Waubay	45.03549	97.46116
Sully’s Hill	Devils Lake	47.97027	99.00577
Swanson	Lostwood	48.68913	102.6539
Warner Lake 5	Waubay	45.02116	97.50307
Winberg	Chase Lake	47.17845	99.22378
Windmill	Lostwood	48.61712	102.4883
Woodworth	Chase Lake	47.12543	99.24986

APPENDIX E. LIST OF USFWS PAIRED SITES WITH LAND OWNERSHIP, LATITUDE, AND LONGITUDE FOR EACH SITE

USFWS Site	Paired Site Ownership	Latitude	Longitude
Buss West	State of South Dakota	45.86776	97.41595
Charley Harley	Private landowner	45.68600717	99.16804396
Cooper North	State of South Dakota	45.68914284	99.84225161
Coteau Prairie	Private landowner	48.48794364	102.400814
Frederick	State of North Dakota	47.37396945	99.97045324
G-12A East	State of North Dakota	46.68964623	100.1502722
G26	Private landowner	47.19183	98.78407
G28	Private landowner	47.11831365	98.78359918
Geiszler 4	Private landowner	46.13199725	99.29367933
GLT A/C	Private landowner	48.78158249	100.8928582
Haven Paddock 5	State of North Dakota	47.67804565	98.54528081
HB 24 Ekert Ranch	Private landowner	48.53047096	101.5281762
Krause	Private landowner	46.02243658	97.36290201
Lake Zahl 7	State of North Dakota	48.63741478	103.6682506
Lasher A/B	State of North Dakota	47.42136329	100.4320807
Mayer	Private landowner	46.58316337	99.22526343
Melass South	Private landowner	48.04208	99.37209
Odegaard	Private landowner	46.89927143	99.43827797
Rath	Private landowner	47.17077592	100.2275149
Roe E/F	Private landowner	45.03354	97.43331
Sully’s Hill	Private landowner	48.69510111	102.6528672
Swanson	Private landowner	45.03558896	97.49229898
Warner Lake 5	Private landowner	47.18212286	99.21693465
Winberg	Private landowner	48.61545702	102.4933345
Windmill	Private landowner	47.11097587	99.25587348

APPENDIX F. SPECIES ENCOUNTERED AT PAIRED SITE WITH C-VALUE, LIFE SPAN, GROWTH FORM, AND FAMILY

Species	C-value	Life Span	Growth form	Family
Achillea millefolium	3	Perennial	Forb	Asteraceae
Agoseris glauca	8	Perennial	Forb	Asteraceae
Agrimonia striata	5	Perennial	Forb	Rosaceae
Agropyron cristatum	*	Perennial	Grass	Poaceae
Allium stellatum	7	Perennial	Forb	Liliaceae
Ambrosia psilostachya	2	Perennial	Forb	Asteraceae
Amelanchier alnifolia	6	Perennial	Shrub	Rosaceae
Amorpha canescens	9	Perennial	Shrub	Fabaceae
Amorpha nana	9	Perennial	Shrub	Fabaceae
Andropogon gerardii	5	Perennial	Grass	Poaceae
Anemone canadensis	4	Perennial	Forb	Ranunculaceae
Anemone cylindrica	7	Perennial	Forb	Ranunculaceae
Antennaria microphylla	7	Perennial	Forb	Asteraceae
Apocynum cannabinum	4	Perennial	Forb	Apocynaceae
Aristida purpurea	4	Perennial	Grass	Poaceae
Artemisia absinthium	*	Perennial	Forb	Asteraceae
Artemisia campestris	5	Biennial	Forb	Asteraceae
Artemisia dracunculus	4	Perennial	Forb	Asteraceae
Artemisia frigida	4	Perennial	Shrub	Asteraceae
Artemisia ludoviciana	3	Perennial	Forb	Asteraceae
Asclepias ovalifolia	9	Perennial	Forb	Asclepiadaceae
Asclepias speciosa	4	Perennial	Forb	Asclepiadaceae
Asclepias syriaca	0	Perennial	Forb	Asclepiadaceae
Asclepias verticillata	3	Perennial	Forb	Asclepiadaceae
Asclepias viridiflora	8	Perennial	Forb	Asclepiadaceae
Aspargus officinalis	*	Perennial	Forb	Liliaceae
Astragalus adsurgens	8	Perennial	Forb	Fabaceae
Astragalus agrestis	6	Perennial	Forb	Fabaceae
Astragalus canadensis	5	Perennial	Forb	Fabaceae
Astragalus crassicarpus	7	Perennial	Forb	Fabaceae
Astragalus flexuosus	4	Perennial	Forb	Fabaceae
Astragalus gilviflorus	7	Perennial	Forb	Fabaceae
Astragalus pectinatus	8	Perennial	Forb	Fabaceae
Avenula hookeri	9	Perennial	Grass	Poaceae
Bassia scoparia	*	Annual	Forb	Chenopodiaceae
Bouteloua curtipendula	5	Perennial	Grass	Poaceae
Bouteloua dactyloides	4	Perennial	Grass	Poaceae
Bouteloua gracilis	7	Perennial	Grass	Poaceae

Species	C-value	Life Span	Growth form	Family
Brickellia eupatorioides	5	Perennial	Forb	Asteraceae
Bromus ciliatus	10	Perennial	Grass	Poaceae
Bromus inermis	*	Perennial	Grass	Poaceae
Bromus tectorum	*	Annual	Grass	Poaceae
Calamovilfa longifolia	5	Perennial	Grass	Poaceae
Calylophus serrulatus	7	Perennial	Forb	Onagraceae
Campanula rotundifolia	7	Perennial	Forb	Campanulaceae
Carex brevior	4	Perennial	Sedge	Cyperaceae
Carex duriuscula	4	Perennial	Sedge	Cyperaceae
Carex filifolia	7	Perennial	Sedge	Cyperaceae
Carex inops	7	Perennial	Sedge	Cyperaceae
Carex tetanica	9	Perennial	Sedge	Cyperaceae
Cerastium arvense	2	Perennial	Forb	Caryophyllaceae
Chenopodium album	*	Annual	Forb	Chenopodiaceae
Cirsium arvense	*	Perennial	Forb	Asteraceae
Cirsium flodmanii	5	Perennial	Forb	Asteraceae
Cirsium undulatum	7	Perennial	Forb	Asteraceae
Cirsium vulgare	*	Biennial	Forb	Asteraceae
Comandra umbellata	8	Perennial	Forb	Santalaceae
Convolvulus arvensis	*	Perennial	Forb	Convolvulaceae
Conyza canadensis	0	Annual	Forb	Asteraceae
Crataegus chrysocarpa	6	Perennial	Shrub	Rosaceae
Cynoglossum officinale	*	Biennial	Forb	Boraginaceae
Dalea candida	8	Perennial	Forb	Fabaceae
Dalea purpurea	8	Perennial	Forb	Fabaceae
Descurainia sophia	*	Annual	Forb	Brassicaceae
Dichanthelium leibergii	8	Perennial	Grass	Poaceae
Dichanthelium oligosanthes	6	Perennial	Grass	Poaceae
Dichanthelium wilcoxianum	8	Perennial	Grass	Poaceae
Echinacea angustifolia	7	Perennial	Forb	Asteraceae
Elaeagnus commutata	5	Perennial	Shrub	Elaeagnaceae
Elymus canadensis	3	Perennial	Grass	Poaceae
Elymus repens	*	Perennial	Grass	Poaceae
Elymus trachycaulus	6	Perennial	Grass	Poaceae
Equisetum laevigatum	3	Perennial	Fern	Equisetaceae
Erigeron strigosus	3	Annual	Forb	Asteraceae
Erysimum asperum	3	Biennial	Forb	Brassicaceae
Erysimum inconspicuum	7	Perennial	Forb	Brassicaceae
Escobaria missouriensis	10	Perennial	P-forb	Cactaceae
Euphorbia esula	*	Perennial	Forb	Euphorbiaceae
Fragaria virginiana	4	Perennial	Forb	Rosaceae
Gaillardia aristata	5	Perennial	Forb	Asteraceae

Species	C-value	Life Span	Growth form	Family
Galium boreale	4	Perennial	Forb	Rubiaceae
Gentianella amarella	7	Annual	Forb	Gentianaceae
Geum aleppicum	4	Perennial	Forb	Rosaceae
Geum triflorum	8	Perennial	Forb	Rosaceae
Glycyrrhiza lepidota	2	Perennial	Forb	Fabaceae
Grindelia squarrosa	1	Biennial	Forb	Asteraceae
Gutierrezia sarothrae	6	Perennial	Shrub	Asteraceae
Haplopappus spinulosus	7	Perennial	Forb	Asteraceae
Helianthus maximilianii	5	Perennial	Forb	Asteraceae
Helianthus pauciflorus	8	Perennial	Forb	Asteraceae
Hesperostipa comata	6	Perennial	Grass	Poaceae
Hesperostipa spartea	8	Perennial	Grass	Poaceae
Heterotheca villosa	3	Perennial	Forb	Asteraceae
Heuchera richardsonii	8	Perennial	Forb	Saxifragaceae
Hordeum jubatum	0	Perennial	Grass	Poaceae
Hymenopappus tenuifolius	8	Biennial	Forb	Asteraceae
Hymenoxys richardsonii	8	Perennial	Forb	Asteraceae
Juncus arcticus	5	Perennial	Forb	Juncaceae
Juniperus communis	5	Perennial	Shrub	Cupressaceae
Koeleria macrantha	7	Perennial	Grass	Poaceae
Lactuca serriola	*	Annual	Forb	Asteraceae
Lactuca tatarica	1	Perennial	Forb	Asteraceae
Lathyrus venosus	8	Perennial	Forb	Fabaceae
Liatris ligulistylis	10	Perennial	Forb	Asteraceae
Liatris punctata	7	Perennial	Forb	Asteraceae
Lilium philadelphicum	8	Perennial	Forb	Liliaceae
Linaria vulgaris	*	Perennial	Forb	Scrophulariaceae
Linum perenne	6	Perennial	Forb	Linaceae
Lithospermum canescens	7	Perennial	Forb	Boraginaceae
Lonicera tatarica	*	Perennial	Shrub	Caprifoliaceae
Lotus purshianus	3	Annual	Forb	Fabaceae
Lygodesmia juncea	2	Perennial	Forb	Asteraceae
Maianthemum stellata	5	Perennial	Forb	Liliaceae
Medicago lupulina	*	Perennial	Forb	Fabaceae
Medicago sativa	*	Perennial	Forb	Fabaceae
Melilotus officinalis	*	Annual	Forb	Fabaceae
Monarda fistulosa	5	Perennial	Forb	Lamiaceae
Muhlenbergia cuspidata	8	Perennial	Grass	Poaceae
Nassella viridula	5	Perennial	Grass	Poaceae
Oenothera biennis	0	Biennial	Forb	Onagraceae
Oenothera nuttallii	8	Perennial	Forb	Onagraceae
Oenothera suffrutescens	4	Perennial	Forb	Onagraceae

Species	C-value	Life Span	Growth form	Family
Oligoneuron rigidum	4	Perennial	Forb	Asteraceae
Onosmodium bejariense	7	Perennial	Forb	Boraginaceae
Oxalis violacea	7	Perennial	Forb	Oxalidaceae
Oxytropis lambertii	5	Perennial	Forb	Fabaceae
Oxytropis splendens	9	Perennial	Forb	Fabaceae
Panicum virgatum	5	Perennial	Grass	Poaceae
Pascopyrum smithii	4	Perennial	Grass	Poaceae
Pediomelum argophylla	4	Perennial	Forb	Fabaceae
Pediomelum esculenta	9	Perennial	Forb	Fabaceae
Penstemon gracilis	6	Perennial	Forb	Scrophulariaceae
Phalaris arundinacea	0	Perennial	Grass	Poaceae
Phleum pratense	*	Perennial	Grass	Poaceae
Phlox hoodii	6	Perennial	Forb	Polemoniaceae
Physalis virginiana	4	Perennial	Forb	Solanaceae
Plantago major	*	Perennial	Forb	Plantaginaceae
Plantago patagonica	1	Annual	Forb	Plantaginaceae
Poa pratensis	*	Perennial	Grass	Poaceae
Polygala alba	5	Perennial	Forb	Polygalaceae
Populus tremuloides	4	Perennial	Tree	Salicaceae
Potentilla arguta	8	Perennial	Forb	Rosaceae
Potentilla gracilis	5	Perennial	Forb	Rosaceae
Potentilla hippiana	8	Perennial	Forb	Rosaceae
Potentilla pensylvanica	9	Perennial	Forb	Rosaceae
Prunus americana	4	Perennial	Shrub	Rosaceae
Prunus virginiana	4	Perennial	Shrub	Rosaceae
Pulsatilla patens	9	Perennial	Forb	Ranunculaceae
Ratibida columnifera	3	Perennial	Forb	Asteraceae
Rosa arkansana	3	Perennial	Shrub	Rosaceae
Rosa woodsii	5	Perennial	Shrub	Rosaceae
Rubus idaeus	5	Perennial	Shrub	Rosaceae
Rumex crispus	*	Perennial	Forb	Polygonaceae
Salix bebbiana	8	Perennial	Shrub	Salicaceae
Salsola iberica	*	Annual	Forb	Chenopodiaceae
Schizachyrium scoparium	6	Perennial	Grass	Poaceae
Selaginella densa	6	Perennial	Fern	Selaginellaceae
Shepherdia argentea	5	Perennial	Shrub	Elaeagnaceae
Sisyrinchium campestre	10	Perennial	Forb	Iridaceae
Solidago canadensis	1	Perennial	Forb	Asteraceae
Solidago missouriensis	5	Perennial	Forb	Asteraceae
Solidago mollis	6	Perennial	Forb	Asteraceae
Sonchus arvensis	*	Perennial	Forb	Asteraceae
Sorghastrum nutans	6	Perennial	Grass	Poaceae
Spartina pectinata	5	Perennial	Grass	Poaceae
Sphaeralcea coccinea	4	Perennial	Forb	Malvaceae

Species	C-value	Life Span	Growth form	Family
Spiraea alba	7	Perennial	Shrub	Rosaceae
Sporobolus heterolepis	10	Perennial	Grass	Poaceae
Stachys pilosa	3	Perennial	Forb	Lamiaceae
Symphoricarpos occidentalis	3	Perennial	Shrub	Caprifoliaceae
Symphyotrichum ericoides	2	Perennial	Forb	Asteraceae
Symphyotrichum falcatum	4	Perennial	Forb	Asteraceae
Symphyotrichum laeve	5	Perennial	Forb	Asteraceae
Symphyotrichum lanceolatum	3	Perennial	Forb	Asteraceae
Symphyotrichum sericeum	10	Perennial	Forb	Asteraceae
Tanacetum vulgare	*	Perennial	Forb	Asteraceae
Taraxacum officinale	*	Perennial	Forb	Asteraceae
Teucrium canadense	3	Perennial	Forb	Lamiaceae
Thalictrum venulosum	6	Perennial	Forb	Ranunculaceae
Thermopsis rhombifolia	6	Perennial	Forb	Fabaceae
Toxicodendron rydbergii	3	Perennial	Shrub	Anacardiaceae
Tragopogon dubius	*	Biennial	Forb	Asteraceae
Trifolium pratense	*	Perennial	Forb	Fabaceae
Ulmus americana	3	Perennial	Tree	Ulmaceae
Verbena stricta	2	Perennial	Forb	Verbenaceae
Vicia americana	6	Perennial	Forb	Fabaceae
Viola pedatifida	8	Perennial	Forb	Violaceae
Zigadenus venenosus	7	Perennial	Forb	Liliaceae
Zizia aptera	8	Perennial	Forb	Apiaceae

*Introduced species are not assigned a c-value