

PLANT COMMUNITY COMPOSITION OF CAMP GRAFTON TRAINING CENTER
(SOUTH UNIT) FROM 1998-2013

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MASTER OF SCIENCE

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ABSTRACT

A vegetation monitoring study was conducted from 1998 to 2013 at Camp Grafton South (CGS) in Eddy County, North Dakota to assess how climatic, grazing, and military training disturbance affects plant community composition. The objectives of this study were to 1) describe the prairie vegetation at CGS across three topographic positions and 2) explore any shifts in plant community composition in correlation with time. Frequency data was collected at 45 randomly selected transects on lowland, midland, and upland grassland plant communities on native prairie. Plant communities were compared using non-metric multidimensional scaling (NMS) ordination. NMS ordination showed that the three plant communities were distinct from one another, and that the frequency of the invasive graminoids Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.) increased. Increases in precipitation, temperature, and growing season days appear to be the primary influence on the changes in plant communities from 1998-2013.

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INTRODUCTION

The extent of native grasslands in North America has been dramatically reduced over the past five decades. Approximately 70% of tall-grass prairies, 30% mixed-grass prairies, and 50% short-grass prairies have been lost due to an increased disturbance regime, agricultural conversion, and an altered climate (Samson and Knopf 1994; Samson et al. 2004). In some areas, the loss has been up to 99% (Cully et al. 2003). These losses have left the remaining prairie isolated and disjointed. The fragmentation of prairie has altered the successional pathways in these communities and left them susceptible to invasion by exotic species (Hobbs and Huenneke 1992; Leach and Givnish 1996; Higgins et al. 2002). The loss of these prairies has negative effects on diversity of localized plant and animal communities, as well as broad regional impacts on biodiversity.

In the Northern Great Plains, Kentucky bluegrass (*Poa pratensis* L.) and smooth brome (*Bromus inermis* Leyss.) are the most prevalent prairie invaders (Cully et al. 2003; Murphy and Grant 2005). Some areas of the North Dakota National Wildlife Refuge system have over 70% frequency of Kentucky bluegrass and smooth brome; conversely, frequencies of native grasses are below 5% (Grant et al. 2009). These grasses have been shown to replace native prairie vegetation with monocultures and degrade ecosystem services. These species compete well against native grasses and are difficult to supplant once established. The suitability of Kentucky bluegrass and smooth brome to the current disturbance and climate regimes in the Northern Great Plains is accelerating the rate at which native grasslands are being reduced (White et al. 2013; Wilson and Pinno 2013).

Specific ecological impacts of the loss of native prairie may be highly variable across space and time, but one way to document the effects is through long-term vegetation surveys. Beginning in 1995, vegetation data was collected on Camp Grafton Training Facility, Camp

Grafton South (CGS) grasslands found within the transition zone between tall-grass and mixed-grass prairies in Eddy County, North Dakota (Prosser 1998). The objectives of this study were to 1) describe the prairie vegetation at CGS across three topographic positions for 15 years and 2) explore any shifts in plant community composition in correlation with time.

Using the frequency data from 1998 to 2013, we described the vegetation across three landscape positions: upland, midland, and lowland. We used non-metric multidimensional scaling (NMS) ordination to identify shifts in the plant communities and tested for correlations with specific species.

LITERATURE REVIEW

Determinants of Northern Great Plains Grassland Plant Communities

The species composition of plant communities in grasslands are the result of an interaction between disturbance and climate variability (Tilman 1999; Collins and Smith 2006). In the transition zone between the mixed-grass and tall-grass prairies in the upper Great Plains, the disturbance regime is a combination of fire and grazing. Because the grassland ecosystem evolved under grazing and fire pressure, a mixture of these disturbances is required to maximize plant species diversity (Stohlgren et al. 1999; Collins and Calabrese 2012). Alterations to the disturbance regime over the past several decades have resulted in a shift in plant community composition (Samson et al. 2004; Murphy and Grant 2005). Similarly, the changing climate plays a role in the shift of dominance within these plant communities. Precipitation, temperature, and growing season length have all departed from historical averages (NOAA, 1948-2013), and these factors dictate plant community dynamics. Additionally, burning of fossil fuels and agricultural practices have led to an increase in nutrient deposition, especially nitrogen (N), that alters soil nutrient cycling from historical norms (Dessierud and Naeth 2013).

In the transitional grasslands of North Dakota, disturbance in the form of fire has been widely variable. The practice of fire suppression dominated rangelands for many years because of the belief that the fire would destroy valuable forage for livestock production. Some research has proven this belief unfounded, and numerous studies document the benefits of prescribed fire on grassland communities (Shay et al. 2001; Fuhlendorf and Engle 2001; Harrison et al. 2003; Towne and Kemp 2008). Prescribed burning is now a common tool utilized to manage rangelands, although optimal timing and frequency of burning is still disputed.

Grazing techniques in the Northern Great Plains grasslands have also been highly variable. Historically, rangelands have been managed to maximize livestock production;

consequently, many of the rangelands have been overgrazed. Conversely, some managers have completely removed grazing to avoid consequences of overgrazing. Both extremes in grazing intensity lead to shifts in resource availability and creation of novel ecosystems (Cid et al. 1991; Patton et al. 2007; Collins and Caberese 2012).

Climate variability in relation to plant community composition may be measured by precipitation, temperature, and length of growing seasons. In the Northern Great Plains, each of these measures has departed from 30 year averages. The area has been experiencing a wet cycle for the past 20 years, and the trend is expected to continue. While the amount of precipitation has increased, it has occurred with less frequent but more intense precipitation events, leading to long periods of time without an influx of water. The mean average temperature has also increased from historical norms. This temperature increase is largely a result of more mild spring and autumn weather (NOAA, 1948-2013). Thus, the length of the growing season, defined as the number of days between the last thaw and the first freeze, has increased (Badh et al. 2009).

Tied to climate variability is the increased effect of anthropogenic activities on these ecosystems. Burning of fossil fuels and intensive agricultural practices have altered the balance of nutrients within the prairie soils (Vinton and Goergen 2006; Munson et al. 2012). In the Northern Great Plains, soil N is historically a limiting resource for plant growth. With increased N deposition, species with a strong competitive ability for soil N no longer have an advantage (Wedin and Tilman 1990).

Effects of Invaders in Northern Great Plains

Variations in climate and disturbance regimes create changing conditions that may no longer favor historically dominant native plant species and have led to reduced species diversity

(Hobbs and Huenneke 1992). This reduction leaves an ecosystem that may be more susceptible to further establishment of invasive species (Larson 2003; Fridley et al. 2007), which creates a continuing positive feedback for invasions across the Northern Great Plains grasslands. Additionally, the disturbance events that normally allow for high species richness and turnover will be altered, which will result in the creation of novel successional pathways. Prairies with high resource availability and a frequent disturbance regime may be especially vulnerable to exotic species invading these pathways (Smith and Knapp 1999).

These plant invaders may alter hydrology, nutrient cycling, and productivity (Vitousek 1982), and these alterations can result in dense monocultures of exotic species (D'Antonio and Vitousek 1992; Otfinowski et al. 2007). The loss of species diversity and richness that accompany the creation of these monocultures alters ecosystem processes and community structure and function (Leach and Givnish 1996; Miles and Knops 2009). As native species diversity declines, net biomass productivity will also decline (Biondini 2007). This negative correlation is the result of an inability to adapt to changing conditions. If conditions are not suitable to the monoculture species, then the entire season of growth will be compromised. In diverse grasslands, a variety of species are productive under a range of conditions, which allows for more consistent biomass production (Isbell and Wilsey 2011).

Monocultures result in an alteration of community structure. Monocultures have homogeneous structure, while a desirable rangeland should be heterogeneous in vegetative height, thickness and species diversity. Not only will this diversity ensure a more stable ecosystem capable of competition with exotic species, spatial heterogeneity on rangelands is essential for the support of wildlife populations. Many grassland wildlife species; especially

birds, and invertebrates require a variety of habitat types in close proximity as they progress through life history stages (Fuhlendorf and Engle 2001; Grant et al. 2010).

Prevalent Invaders in Northern Great Plains

Kentucky Bluegrass

Kentucky bluegrass is an exotic, cool-season perennial sod-forming grass that reproduces primarily through rhizomes. It is prevalent in both disturbed and undisturbed areas across the Northern Great Plains (MacDougall and Turkington 2005). Once established, it is not clear what allows Kentucky bluegrass to become so dominant in the tall- and mixed-grass prairie communities. However, several characteristics have been identified that make this invader a strong competitor for resources both above and below ground.

Kentucky bluegrass begins growth and reproduction earlier in the season than many of the native species on the transitional grasslands. This early growth habit offers an advantage in competing for light, soil nutrients, and water resources (D'Antonio and Vitousek 1992). When native grasses begin to grow in the spring, Kentucky bluegrass forms a foliage layer that intercepts light from reaching the immature native graminoids (Bookman and Mack 1983; Cully et al. 2003). Increased access to sunlight offers a significant advantage in this region because light availability is a limiting factor in undisturbed grasslands ecosystem (Turner and Knapp 1996; MacDougall and Turkington 2005). Furthermore, Kentucky bluegrass forms a dense root mat layer once established. This layer blocks light to native cool-season grasses in the spring, and it also inhibits growth of warm-season C4 grasses later in the year even after the foliage canopy begins to recede (Cully et al. 2003). The thatch layer reduces germination of forbs (Bosy and Reader 1995) and inhibits infiltration until saturated (Taylor and Blake 1982).

The early growth habit of Kentucky bluegrass also offers an advantage when competing for below ground resources. The early spring growth of immature Kentucky bluegrass has no competition. Thus, it may locally deplete nutrients and water resources before native species start spring growth (Bosy and Reader 1995). Spreading along the landscape horizontally, it depletes resources that are close to the soil surface. Root growth is shallower than native grass species, with the rooting depth of a two year old plant no more than 30 cm (Bookman and Mack 1982). Kentucky bluegrass roots also fill the soil space and make it difficult for immature root systems of native species to break through to the depth required for nutrient absorption. A study with another graminoid invader, cheatgrass (*Bromus tectorum* L.), showed that the ability for Kentucky bluegrass to fill volumes with root mass is not affected by the presence of a cool-season annual (Bookman and Mack 1982).

Kentucky bluegrass may create a system of positive feedback with soil N cycling by producing large quantities of N-rich litter (Wedin and Tilman 1990). Many native grasses are strong competitors in N-limited ecosystems, but the increase in N availability in Kentucky bluegrass invaded soils reduces the competitive advantage of those native species (Desserd and Naeth 2013).

Several studies have been conducted to ascertain any allelopathic properties that Kentucky bluegrass may possess (Lipinska and Harkot 1998; Sanchez-Moreira 2003). While it is likely that there is some manner of allelopathy occurring in the invaded rangelands, the process is not clearly documented.

Smooth Brome

Smooth brome is an exotic, cool-season, sod-forming, perennial grass that spreads primarily by rhizomes (Otfinowski et al. 2007). This Eurasian grass was originally introduced to

provide soil stability in disturbed areas and as a valuable, drought resistant forage grass (Larson et al. 2001). Possibly because of these beneficial uses, smooth brome has often been overlooked as an invasive grass (Dillemuth et al. 2009). However, smooth brome has become established in many native prairies (D'Antonio and Vitousek 1992), and has impacts on resource cycling (Vinton and Goergen 2006) and biodiversity (Williams and Crone 2006; Wilson and Pinno 2013).

Smooth brome is effective at competing in both resource-rich and resource-poor environments. The rhizome connections between invading smooth brome clones and the mother clone allow some resource sharing. This sharing allows smooth brome to successfully invade areas with low nutrient availability (Ostrowski and Kenkel 2008). Similarly, in areas that have abundant resources, especially high soil moisture, smooth brome forgoes dormancy in the summer months and continues growth throughout the year (Blankespoor and Larson 1994).

Once established, smooth brome increases density to form monocultures through a positive feedback with soil conditions. Smooth brome may have a higher decomposition rate than naturally occurring native species (Hendrickson et al. 2001), and it produces litter that results in higher available N in the soil. The increased soil N shifts the advantage from native grasses that are strong N competitors to smooth brome (Vinton and Goergen 2006). However, soils with high clay content may resist accumulating soil N associated with the faster litter turnover by immobilizing the organic matter (Nosshi et al. 2006).

Continuous smooth brome growth without disturbance also increases density through increasing competitive advantages for light (Groya and Sheaffer 1981). Other forbs are suppressed through a deep litter layer that accompanies an undisturbed site (Goldberg 1987; Williams and Crone 2006). Beneath the litter layer, smooth brome may also be a strong

competitor for resources, although the majority of its roots remain in the upper 10 cm of soil (Otfinowski and Kenkel. 2008). In addition to increasing under non-use, smooth brome may also increase under disturbance as long as soil N levels remain high (Otfinowski and Kenkel 2010).

Fire and Plant Community Composition

Fire frequency and intensity is a driver of plant community composition in mixed-grass and tall-grass prairie ecosystems. While many of the rangelands in the Northern Great Plains had been subjected to years of fire suppression, fire is now recognized as an important process for a healthy grassland community (White and Curie 1983; Higgins et al. 2002). Substantial research has been conducted on the effects of prescribed burning in the transitional grasslands, but only some of the major trends identified will be discussed.

Immediately following a fire on native grassland, an area exists that is open to repopulation subject to traditional successional pathways. Most biomass and litter have been removed, which leaves high light availability, high available soil nutrient content in the form of ash, and no established species with which to compete (Wilson and Shay 1990). Thus, most transitional grasslands communities begin with annual grasses and forbs quickly emerging, and these give way to perennial graminoid species, which become the dominant functional group (Collins and Cabrese 2012). The dominance of graminoids, coupled with the absence of a litter layer, draws grazing ungulates to recently burned areas (Fuhlendorf and Engle 2001). Grazing pressure then reduces the canopy layer of the graminoids; thereby, allowing light to the soil surface and encouraging higher forb density (Hartnett et al. 1996; Coppedge and Shaw 1998). Thus, species diversity increases as time from the most recent fire event increases (Collins and

Barber 1986; Hartnett et al. 1996; Grant et al. 2010) until a threshold is crossed into non-disturbance.

Fire also results in large-scale structural heterogeneity on the grassland. Areas that have recently been burned are characterized by low species diversity, high graminoid production, and low forb density. Short intervals between burns do not allow for the establishment of shrubs and forbs that give the landscape diversity in height, shape, and growth form. Areas that have not been burned for several years display higher species diversity, lower graminoid production, and higher forb density. As time since the most recent burn increases, tall stature plants and some woody vegetation become established (Hartnett et al. 1996; Coppedge and Shaw 1998; Veen et al. 2008). This diversity between contiguous areas on the landscape encourages long-term trends in vegetation stability and favors the support of wildlife (Fuhlendorf and Engle 2001; DiTomaso et al. 2006; Grant et al. 2010).

Timing and frequency of fire regimes also affect plant community composition. Extended periods of time without fire increase exotic species and shrubby vegetation (Higgins et al. 2002; Ludwick and Murphy 2006). In a tall-grass prairie, cool-season plants dominated areas that had more time since the most recent burn, while warm-season grasses were more prevalent in recently burned areas (Steuter 1987; Collins and Cabrese 2012). Similarly, burning may reduce soil moisture and nitrogen availability, both of which increase the competitive ability of warm-season grasses (Shay et al. 2001). Spring burns target the litter layer and cool-season plant species that have begun growth. Thus, burning in the spring in a mixed-grass prairie may reduce the frequency of cool-season grasses and increase competitive effects of warm-season grasses later in the growing season (Dix 1960; Redmann et al. 1993). Fall burns may increase cool-season grasses the following spring (Travnicek et al. 2005). Summer burns have also been

shown to increase warm-season plant species in tall-grass prairie, as well as native grass cover and frequency (Johnson and Matchett 2001; Reed et al. 2005; Towne and Kemp 2008), although cool-season grasses may be hurt by the summer burns (Engle and Bultsma 1984).

Because native plant communities evolved with fire, it may be used as a tool to combat the spread of exotic species. However, no clear strategy has been found for how best to target Kentucky bluegrass with prescribed fire. As an early growing plant species, it is beneficial to have an early spring burn to hinder its dominance early in the growing season and reduce its competitive advantage (Engle and Bultsma 1984; Hendrickson and Lund 2010). However, consecutive years of burning may be required for lasting effect (Knops 2006). The destruction of the dense, matted litter layer will also allow native species to compete for light and space against invaders (DiTomaso et al. 2006). If burned early enough in the spring, the native warm-season grasses will still be dormant. Thus, the damage to the cool-season grasses should shift the competitive balance to the warm-season grasses. However, while removing invasive species with fire may be effective initially, there must be native species in the seed bank to replace the exotic for the treatment to retain efficacy over time (Willson and Stubbendieck 1996; Travnicek et al. 2005). Additionally, there is no way to target Kentucky bluegrass without harming other native cool-season grasses (Curtis and Partch 1948; Engle and Bultsma 1984; Becker 1989).

Further studies conducted outside of the transitional grasslands of the upper Great Plains demonstrate some negative effects of burning on Kentucky bluegrass. Becker (1989) noted a decrease in bluegrass cover and an increase in native grasses and forbs over five years of annual burning in Nebraska. Svedarsky et al. (1986) used ten years of biennial burning to stimulate little and big bluestem while controlling Kentucky bluegrass in Minnesota. Burning five out of every six years in Kansas almost entirely removed Kentucky bluegrass from the system

(McMurphy and Anderson 1965; Abrams 1988). Li (2013) found that frequent burning reduced Kentucky bluegrass on infertile grassland. Thus, there is evidence that burning may have negative effects on Kentucky bluegrass, but it is not a strict correlation.

Using prescribed fire to manage smooth brome is also very complex. Late spring burns may decrease the frequency and production of smooth brome. For burning to be effective, burning must occur annually for several years (Willson and Stubbendieck 1997). Because smooth brome tillers at a similar time as native cool-season grasses, burning will negatively affect exotic and native species alike. However, burns at the tiller elongation stage, usually mid-May in the Northern Great Plains, can significantly decrease smooth brome cover and increase native warm-season grasses (Willson and Stubbendieck 1997; DiTomaso et al. 2006; Bahm et al. 2011). Native grasses are especially successful in suppressing smooth brome in areas with high soil moisture (Blankespoor and Larson 1994). Areas that do not have native grasses in the seed bank can experience an increase in brome cover (Schact and Stubbendieck 1985). Reduction of smooth brome using fire is most effective when combined with herbicide use (Willson and Stubbendieck 1996; Bahm et al. 2011).

Grazing and Plant Community Composition

The transitional grassland ecosystem evolved under grazing pressure from large ungulates, so the stability of the plant community relies on some measure of grazing. Many native species respond to defoliation by increasing reproduction or photosynthetic rates (Georgiadis et al. 1989), and the defoliation of graminoids also creates opening in the canopy layer for forb density to increase (Milchunas et al. 1988; Harrison et al. 2003; Veen et al. 2008). Hoof action and trampling of standing dead or dormant grasses increases decomposition rates by increasing the interaction of plant tissue and soil microbes. Additionally, forcing dead plant

material onto the soil changes microclimates by reducing bare ground; this reduction keeps soil surface temperatures lower and allows the soil to retain moisture for longer periods of time (Naeth et al 1991). These factors allow for an enhanced nutrient cycle, especially N, in grazed grasslands (Jaramillo and Delting 1988; Holland et al. 1992).

While species richness and net primary productivity may increase under proper grazing conditions (Collins and Barber 1986), lack of grazing or grazing too heavily may have adverse effects on rangeland health (Murphy and Grant 2005; Collins and Smith 2006; DeKeyser et al. 2013). Removing grazing pressure from rangelands results in homogenized plant communities comprised of strong competitive species (Veen et al. 2003; DeKeyser et al. 2009). Species adapted to increase under grazing pressure, such as blue grama, are reduced in areas with no grazing (Brand and Goetz 1986). The primary large ungulate grazers in the Northern Great Plains, bison and cattle, preferentially feed on graminoids, so the removal of these animals results in increased graminoid production and cover but reduced forb diversity (Cid et al. 1991; Patton et al. 2007; Collins and Caberese 2012). Similarly, the removal of grazing pressure eliminates patches of disturbance that contribute to varied vegetation structure across the landscape (Fuhlendorf and Engle 2001).

Alternatively, excessive grazing results in a decrease in production (Dyer et al. 1993; Derner and Whitman 2009) and a shift in plant community composition. Short-stature warm-season grasses and forbs increase under intense grazing pressure; whereas, cool-season grasses decrease (Biondini and Manske 1996). This shift in community composition also alters community structure. Heavily grazed grasslands are characterized by exclusively short-stature herbaceous vegetation and very little litter (Higgins et al. 2002; Derner and Whitman 2009), which may impact wildlife habitat. Additionally, the lack of litter in heavily grazed systems

increases bare ground and leads to significantly reduced infiltration (Abdel-Magid et al. 1987). Negative consequences associated with overgrazing lead to unsustainable and changing ecosystems due to negative feedbacks within the plant community. Vegetation under heavy grazing pressure allocates fewer resources to reproductive structures and alters nutrient cycling (Jaramillo and Delting 1988; Holland et al. 1992), which may lead to conditions that do not favor native vegetation (Wedin and Tillman 1990).

In the Northern Great Plains, these shifts in resource cycling as a result of grazing intensity often result in the increase of Kentucky bluegrass and smooth brome (Sinkins and Otfinowski 2012; Wilson and Pinno 2013). Both grasses have been shown to increase under non-grazing conditions. This increase may result in native grasses and forbs being displaced (Stohlgren et al. 1999; Murphy and Grant 2005; DeKeyser et al. 2009). However, Kentucky bluegrass also increases in heavily over-grazed pastures (Beebe and Hoffman 1968; Patton et al. 2007). Kentucky bluegrass generally responds positively to defoliation (White et al. 2013), and it may continue to invade grasslands at a fixed rate regardless of grazing intensity (Silvertown et al. 1994). Smooth brome, alternatively, may invade aggressively in non-grazed areas but decrease in abundance as disturbance increases (Wilson and Pinno 2013).

Climate Variability and Plant Community Composition

Over the past two decades, average precipitation in northern and eastern North Dakota has increased from previous levels. Additionally, temperature averages have been increasing over that same time period, resulting in extended growing seasons (NOAA, 1948-2013). Forage production and species composition are driven by precipitation and temperature conditions, so the new climate regime in the Northern Great Plains may have significant long-term effects on plant community composition and community stability (Badh et al. 2009; DeKeyser et al. 2013).

For example, Kentucky bluegrass thrives in high moisture areas and it has been noted to dominate some wet areas in North Dakota Rangelands since 1950 (Stevens 1950). Kentucky bluegrass occurred first in areas of the United States with higher moisture content, and it has been shifting west into traditionally drier climates over the past several decades (Stevens 1950; DeKeyser et al. 2013).

Increases in water availability in North American prairies have been linked with increases in primary production (Sala et al. 1988; Milchunas et al. 1994) and changes in plant community composition and structure (Hautier et al. 2009; Collins et al. 2012). Although annual precipitation trends are increasing, the increasingly more variable climatic conditions often result in fewer, more intense precipitation events. Thus, extended periods without precipitation may also be affecting plant communities. Reduction in precipitation during the growing season reduced total herbaceous production up to 40%, with perennial cool-season grasses being the most affected. While herbaceous production may return to pre-drought levels only two years after the removal of drought conditions, the species composition of the community remains altered (Heitschmidt et al. 2005).

Species richness also shows a direct relationship to precipitation. Many tall-grass and mixed-grass prairies in North America are in a continental climate and subject to extreme fluctuations in precipitation, and species richness follows these fluctuations. Across many types of grasslands, increases in precipitation have been tied to greater species richness, especially in warm season grasses and forbs (Collins et al. 2012). Conversely, reduced precipitation may result in a drastic decline in species richness and a slow recovery from that decline. Additional research has shown a lag time before species diversity or richness is affected, as in the case of a wet year following a dry year (Biondini et al. 1998; Symstad and Jonas 1999; Collins et al.

2012). The variety of conditions and ecosystems make it difficult to generalize the results of these studies across time and space.

In addition to the altered precipitation regime, climate in the Northern Great Plains displays an increase in overall temperature and the number of days in a growing season (Badh et al. 2009). Temperature may play a crucial factor in several stages of plant development. Large temperature fluctuations at the beginning of a growing season may have adverse impacts on plants emerging from dormancy (Malyshev and Henry 2012). High temperatures during the growing season result in rapid evaporation that may reduce available water sources. A lengthened growing season could favor cool-season plants that benefit from the additional growing days in early spring and late fall.

A correlation was found between the morphological development of several native graminoid species and the number of growing degree days on a native mixed-grass prairie. Four different cool-season perennial grasses were shown to reach certain morphological development stages after a particular number of growing degree days (Frank and Hoffman 1989). The variability of developmental stages that the native grasses reached across a temporal scale reinforces that a heterogeneous landscape offers a variety of maturity, height, and cover levels which cannot be found in a monoculture (Frank and Hoffman 1989; Heitschmidt et al. 2005).

Similarly, growing degree days may have a linear relationship with N content on rangelands. An equation that may estimate the N content based on growing degree days and green:dead ratios of vegetation has shown some accuracy in the mixed-grass prairies in eastern Montana (Haferkamp et al. 2005). As growing degree days increase and soil N increases, exotic species like Kentucky bluegrass may become more dominant (Wedin and Tilman 1990; Laungani et al. 2012). While there may be a linear relationship between growing degree days

and soil N, the causation for this increase in N is likely a result of increased fossil fuel burning and nutrient deposition in agricultural practices (Vinton and Goergen 2006; Norton et al. 2008).

STUDY AREA

The study was conducted on Camp Grafton South (CGS), a military training base associated with the Camp Grafton Training Facility and an installation administered by the North Dakota Army National Guard, located in southeastern Eddy County, North Dakota. The study area is in east-central North Dakota at -98.67° longitude and 47.7° latitude, approximately 34 km (19 miles) east of New Rockford and approximately 56 km (35 miles) southeast of Devils Lake. The study area falls within MLRA 55B, classified as Central Black Glaciated Plains. The physiographic region is known as the Drift Plain, which formed from glacial lacustrine deposits during the Pleistocene era (USDA Natural Resource Conservation Service 2006).

The Drift Plain region extends across the center of the state, and its natural vegetation is characterized by a combination of mixed-grass and tall-grass prairie plants. The area has been called the Transition Grassland (Whitman and Wali 1975; Barker and Whitman 1989), and the potential natural vegetation was classified as moderately dense, short-to-medium tall Wheatgrass-Bluestem-Needlegrass association (Kuchler 1964).

The study site elevation ranges from 448.7 m to 538.1 m above sea level. The area is in a continental climate zone that experiences extreme temperature fluctuations. The 30-year mean annual temperature at McHenry, ND, approximately 24 km (15 miles) southeast of CGS, was 40.45 F (4.7 C). The 30-year mean annual precipitation was 20.64 inches (52.42 cm), up to 75% occurring in the form of rain during the growing season. The growing season, as defined by length of time from the last 0° C day in the spring to the first 0° C day in the fall, averaged 139 days over the past 30 years (NOAA, 1948-2013). The variation in elevation and topography in the study area leads to a zonation dominant plant species due to different tolerance ranges. Thus, the prairie was divided into upland, midland, and lowland areas.

Upland plant communities consist of Kentucky bluegrass, western wheatgrass (*Pascopyrum smithii* (Rydb.) Á. Löve), blue grama (*Bouteloua gracilis* (Willd. Ex Kunth) Lag. ex Griffiths), prairie sandreed (*Calamovilfa longifolia* (Hook.) Scribn.), threadleaf sedge (*Carex filifolia* Nutt.), prairie junegrass (*Koeleria macrantha* (Ledeb.) Schult.), needle-and-thread (*Hesperostipa comata* (Trin. & Rupr.) Barkworth), and plains muhly (*Muhlenbergia cuspidata* (Torr. ex Hook.) Rydb.) as principal graminoid components. Common forbs on upland sites are textile onion (*Allium textile* A. Nelson & J.F. Macb.), western rockjasmine (*Androsace occidentalis* Pursh), bastard toadflax (*Comandra umbellata* (L.) Nutt.), Nuttall's violet (*Viola nuttallii* Pursh), blacksamson echinacea (*Echinacea angustifolia* DC.), silver-leaf Indian breadroot (*Pediomelum argophyllum* (Pursh) J. Grimes), tarragon (*Artemisia dracuncululus* L.), prairie sagewort (*Artemisia frigida* Willd.), hairy false goldenaster (*Heterotheca villosa* (Pursh) Shinnery), Flodman's thistle (*Cirsium flodmanii* (Rydb.) Arthur), and stiff sunflower (*Helianthus pauciflorus* Nutt.) (Prosser 1998; Prosser et al, 2003a).

The dominant graminoids on midland plant communities are Kentucky bluegrass, western wheatgrass, blue grama, prairie sandreed, little bluestem (*Schizachyrium scoparium* (Michx.) Nash), sun sedge (*Carex inops* L.H. Bailey), porcupine grass (*Hesperstipa spartea* (Trin.) Barkworth), and green needlegrass (*Nassella viridula* (Trin.) Barkworth). Common forbs on midland sites at CGS include common yarrow (*Achillea millefolium* L.), groundplum milkvetch (*Astragalus crassicaarpus* Nutt.), bastard toadflax, white prairie aster (*Symphyotrichum ericoides* (L.) G.L. Nesom), American vetch (*Vicia americana* Muhl. ex Will.), purple milkvetch (*Astragalus agrestis* Douglas ex G. Don), northern bedstraw (*Galium boreale* L.), candle anemone (*Anemone cylindrical* A.Gray), curlycup gumweed (*Grindelia squarrosa* (Pursh) Dunal), blue lettuce (*Lactuca tatarica* (L.) C.A. Mey.), prairie fleabane (*Erigeron strigosus*

Muhl. ex Willd.), large Indian breadroot (*Pedimelum esculentum* (Pursh) Rydb.), purple prairie clover (*Dalea purpurea* Vent.), Missouri goldenrod (*Solidago missouriensis* Nutt.), and dotted blazing star (*Liatris punctata* Hook.). Western snowberry (*Symphoricarpos occidentalis* Hook.) is the most commonly found shrub on these midland areas (Prosser 1998; Prosser et al. 2003a).

The lowland plant communities consist of Kentucky bluegrass, smooth brome, big bluestem (*Andropogon gerardii* Vitman), and switchgrass (*Panicum virgatum* L.) as principal graminoid components. Forbs on lowland sites include oval-leaf milkweed (*Asclepias ovalifolia* Decne.), Canadian anemone (*Anemone canadensis* L.), Canada goldenrod (*Solidago canadensis* L.), white prairie aster, smooth blue aster (*Symphyotrichum laeve* (L.) Á. Löve & D. Löve), and Canada thistle (*Cirsium arvensis* (L.) Scop.) (Prosser 1998; Prosser et al. 2003a). All plant names are referenced from the USDA PLANTS database.

Despite being almost entirely composed of native rangeland that has never been converted to cropland, several invasive plant species are found on CGS. The most common invasive graminoid species found across all sites of CGS are Kentucky bluegrass and smooth brome grass. Leafy spurge (*Euphorbia esula* L.) and Canada thistle are the most pervasive invasive forbs.

The management goal for the grasslands at CGS is “to integrate the relationships of all organisms including human activity and nonliving elements of their environment” (Barker et al. 2001). Guided by this goal, CGS has been managed for minimal human use and implemented grazing and burning programs. Nearly all military training on CGS in the past 15 years has been classified as minimum impact training; such as patrolling, terrain/map analysis, and reconnaissance. Camp Grafton South has been predominantly utilized as rangeland subject to cattle grazing for over a century. Carrying capacities were calculated based on ecological site

composition to fulfill a moderate to full utilization (up to 50% disappearance of aboveground biomass) grazing regime since 1982. To complement the grazing regimen, prescribed burning has been employed when necessary at CGS to maintain the health of the prairie vegetation (Barker et al. 2001).

METHODS

Field Sampling

The study area at CGS was classified into upland, midland, and lowland areas based on soil and slope characteristics. Upland sites are characterized by steep shoulder slopes and found on summits of knolls. Generally the highest point on the landscape, these sites lose most of their soil moisture through runoff. Midland sites are characterized by having moderate back slopes and increased infiltration compared to the upland sites. Lowland sites occupy foot slope and toe slope positions on the landscape and have the highest infiltration rate and most soil moisture in the area (Prosser 1998; Prosser et al. 2003a).

Fifteen transect sites were selected at CGS each year from 1995-1997. The Idrisi software program was utilized to randomly select transect locations from within the designated prairie types which resulted in 45 transects that were selected to mimic this site type distribution. Eight transects were selected from within the designated lowland areas, 20 transects were selected within the designated midland areas, and 17 transects were selected within the designated upland areas (Prosser 1998).

Vegetation surveys were conducted at CGS from 1998-2013. The vegetation surveys focused on graminoid and forb species composition. Plant communities were described using a 0.25m² quadrat with a 0.1m² quadrat nested within. Forbs were recorded using the 0.25m² quadrat to determine species composition and density. Graminoids were recorded using the 0.1m² quadrat to determine presence/absence frequency data (Prosser et al. 2003b)

Each year, surveys were conducted on 15 transects on a rotating basis; thus, each transect was surveyed at least 4 times for this analysis period, with the exception of transects that were inaccessible due to flooding. The surveys were conducted in early to mid-July each year, which represents the peak production on these sites.

Data Analysis

Climate data was analyzed using T-tests to compare 30 year averages before the study and the most recent 30 year averages. Four sample periods were utilized from each transect in order to standardize the data for analysis. Each sample period corresponds to a frequency value collected within a group of years. The first sample period for each transect was taken from 1998-2001, second sample period taken from 2002-2005, third sample period from 2007-2010, and fourth sample period from 2011-2013. Frequency values were subjected to an arcsine-square-root transformation to improve normality by spreading values on the tails of the distribution and compressing the middle (Peck 2010).

Non-metric multidimensional scaling (NMS) ordination using a relative Sorenson distance measure was applied to relate plant community patterns to the period that samples were taken. The sample periods were subjected to a Monte Carlo randomization test. A permutation-based nonparametric multivariate analysis of variance (PerMANOVA) using a relative Sorenson distance measure was calculated to assess the difference of species between sample periods (Anderson 2001; McCune et al. 2002). The PerMANOVA returned p-values for pairwise comparisons between sample periods.

Four of forty-five transects were not sampled at least four times, so they were not included in the data analysis. The remaining sixteen upland transects, seventeen midland transects, and eight lowland transects were analyzed in separate groups to detect temporal trends within each topographical position. Additionally, all transects were combined for a final NMS ordination to determine if plant community composition is trending toward a single point regardless of landscape position. A multi-response permutation procedure (MRPP) was

performed on the first and fourth sample periods of each transect across all site types. The distance matrix was rank transformed using a relative Sorenson distance measure.

RESULTS

Climate

The thirty year average for mean annual temperature (MAT) at the McHenry weather station increased ($p=0.018$) during the study, with temperatures rising over 1.5° F compared to the pre-study averages (Table 1). The increase in MAT was driven by an increase in minimum temperatures. The average minimum temperature increased by over 2.0° F, from 27.6 F to 29.7° F, while the average maximum temperatures increased less than 1° F, from 50.3° F to 51.2° F (NOAA, 1948-2013). Similarly, growing season days (GSD) at CGS increased ($p=0.007$) during the study, with over eight more days per year compared to the pre-study averages (NOAA, 1948-2013).

Although the thirty year averages for mean annual precipitation (MAP) did not significantly increase ($p=0.106$) during the study period, the MAP averages during the study were 1.5 inches greater than pre-study averages.

Figure 1 represents the MAP, MAT, and GSD at CGS from 1948 to 2013. The trend lines indicate that all three measures of climate are increasing during this time period, with the MAP fluctuating more than either the MAT or GSD. The MAT shows the most gradual increase, with the GSD averages closely match the MAT averages.

Table 1. The 30 year averages in mean annual temperature (MAT), mean annual precipitation (MAP), and growing season days (GSD) at McHenry weather station before study (1968-1997) and during study (1984-2013) (NOAA, 1948-2013).

| 30 year average | MAT (°F) | MAP (in.) | GSD |
|------------------------------|----------|-----------|----------|
| Prior to study (1968 – 1997) | 38.97 | 19.00733 | 132.6250 |
| During study (1984 – 2013) | 40.50 | 20.56833 | 140.7167 |

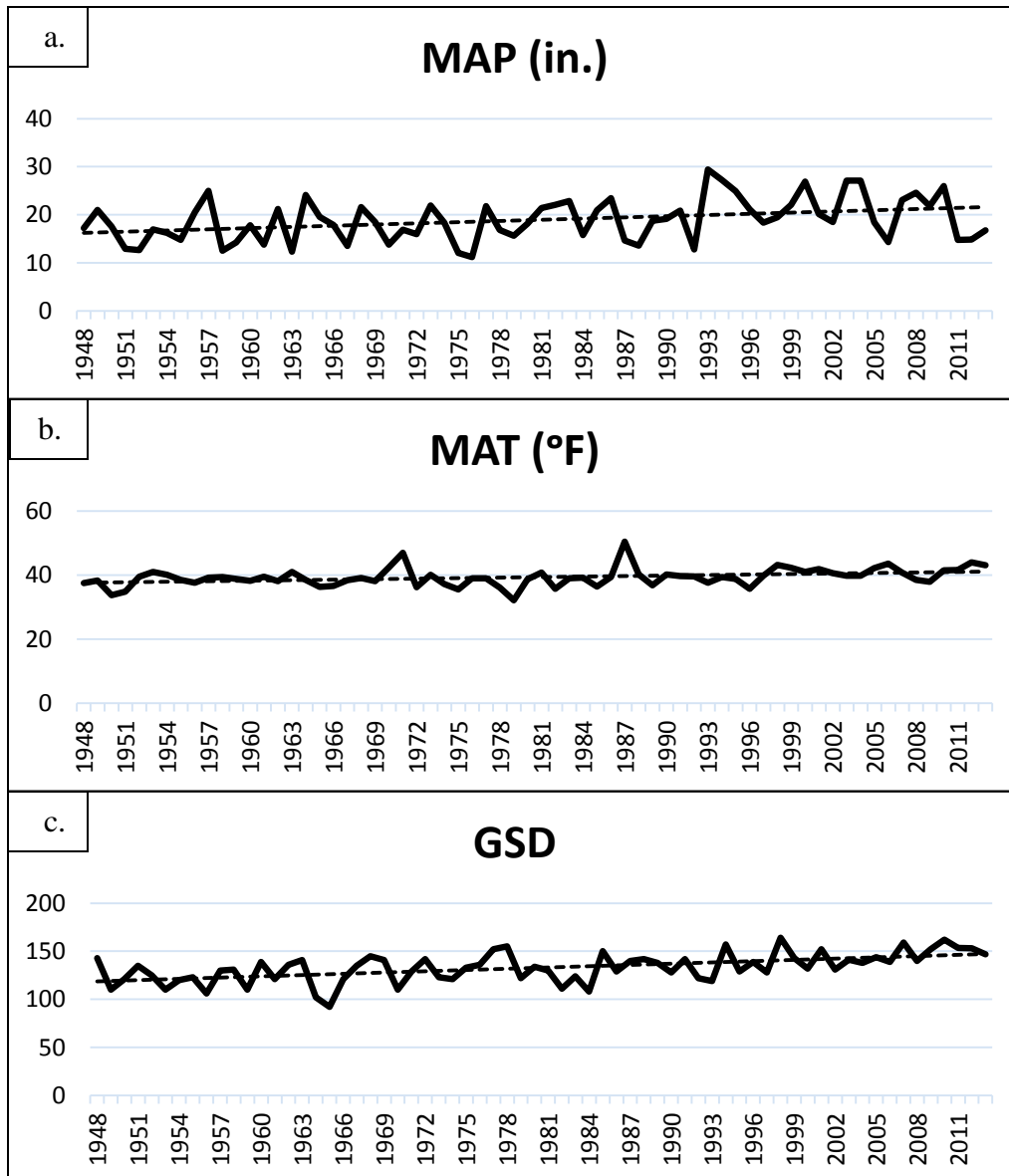


Figure 1. The a) mean annual precipitation (MAP); b) mean annual temperature (MAT); and c) growing season days (GSD) at McHenry, ND weather station from 1948-2013 (NOAA, 1948-2013).

Upland Plant Community

Non-metric multidimensional scaling (NMS) scores using the relative Sorenson distance measure returned a three-dimensional solution. The first and second axes are displayed in Figure 2. The sites for each time period are surrounded by a minimum convex polygon. Coefficients

of determination for the correlations between ordination distances on the axis determined by the NMS scores were calculated for each axis. The R-squared value for the first axis was 0.412. The second axis increment was 0.209, resulting in a cumulative value of 0.621 for both the first and second axes. The third axis increment was 0.159. Thus, the three axes cumulative R-squared value was 0.779 or 78% of the variability in the data was explained.

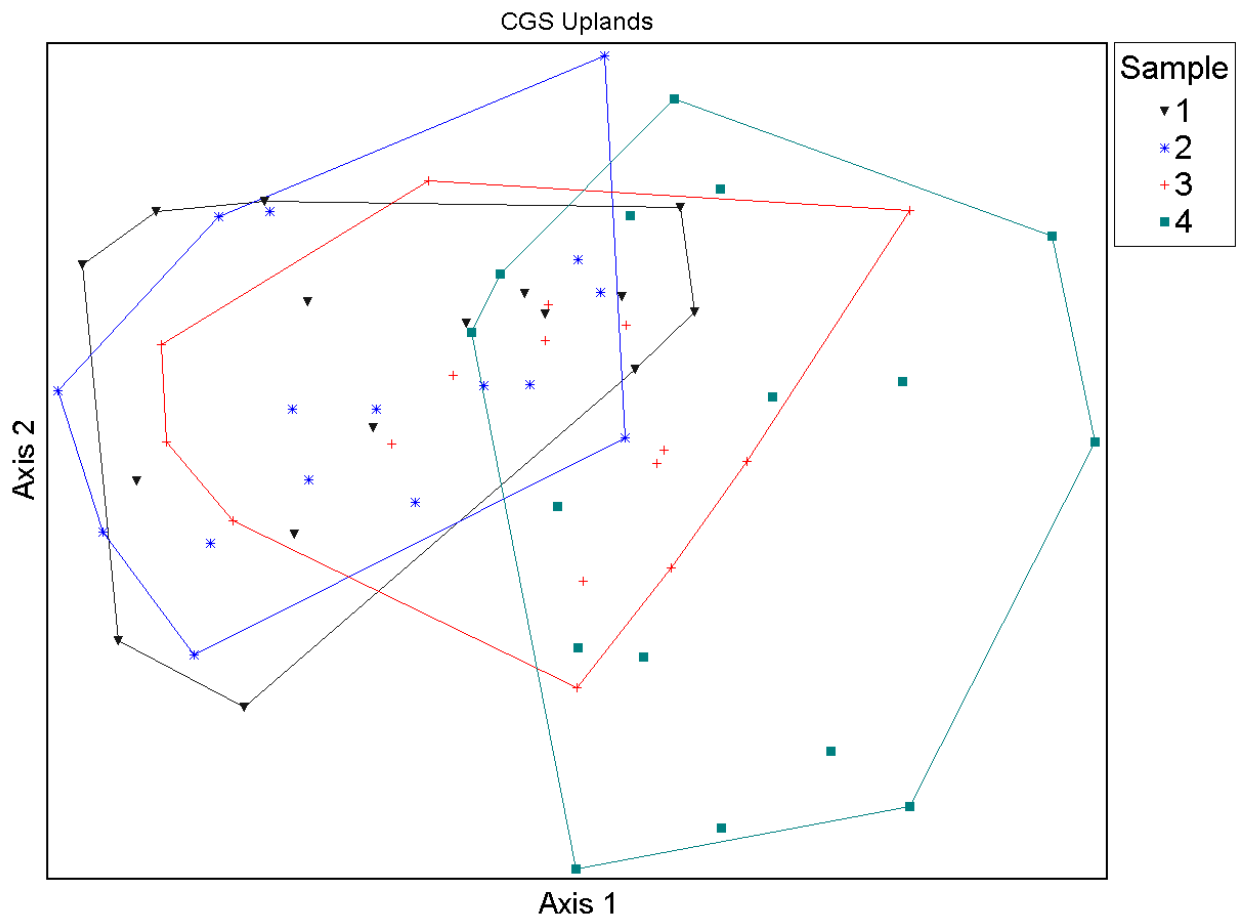


Figure 2. Non-metric multidimensional scaling ordination of the 16 upland sites at Camp Grafton South for Sample 1 (taken between 1998-2001), Sample 2 (taken between 2002-2005), Sample 3 (taken between 2007-2010), and Sample 4 (taken between 2011-2013) near McHenry, North Dakota. Minimum convex polygons surround different sample periods.

Correlation scores between species and axis were deemed interpretable at an absolute value greater than 0.4. Twenty species had negative correlations (< -0.4) with the first NMS

axis. Of these prairie sagewort, white prairie aster, silver-leaf Indian breadroot, and fall rosette grass (*Dichanthelium wilcoxianum* (Vasey) Freckmann) had the highest correlation scores, each of which was less than -0.6. Kentucky bluegrass and needle-and-thread were positively correlated with the first axis. The second axis had four species that were negatively correlated: switchgrass, (*Panicum virgatum* L.), reed canary grass, violet wood sorrel (*Oxalis violacea* L.), and field pussytoes (*Antennaria neglecta* Greene) (values ranged between -0.572 and -0.406). Porcupine grass was the only species that showed a positive correlation with the second NMS axis. The third axis had only one correlated species, thread-leaf sedge, which was positively correlated.

The PerMANOVA pairwise comparisons between each sample determined that plant community shifts occurred between the first and fourth sample period ($p=0.0002$), as well as between the second and fourth sample period ($p=0.0002$) (Figure 2). All other pairwise comparisons had no difference ($p \leq 0.05$) between sample periods using the Bonferroni's correction. Graminoid and forb frequency change over time is presented in Table 2.

Table 2. Frequency (%) of dominant graminoid and forb species on the 16 upland sites at Camp Grafton South near McHenry, North Dakota from 1998-2013.

| | Period 1 1998-2001 | Period 2 2002-2005 | Period 3 2007-2010 | Period 4 2011-2013 |
|------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Graminoids | | | | |
| Kentucky bluegrass | 65.0 | 64.1 | 78.3 | 93.8 |
| Needle-and-thread | 41.6 | 41.5 | 66.0 | 40.3 |
| Prairie sandreed | 26.3 | 14.4 | 20.8 | 10.0 |
| Sun sedge | 63.8 | 56.8 | 58.3 | 15.8 |
| Forbs | | | | |
| Prairie heath aster | 17.5 | 20.6 | 16.8 | 1.0 |
| Missouri goldenrod | 7.8 | 9.0 | 4.5 | 0.0 |
| Prairie sagewort | 13.4 | 21.7 | 14.0 | 2.5 |
| Silver-leaf Indian breadroot | 19.0 | 20.1 | 12.8 | 4.0 |

The shifts in dominant vegetation were accompanied with differences in diversity indices (Table 3). Species richness declined ($p = 0.001$) between the second and fourth sample periods, and the Shannon's H diversity indices declined ($p = 0.008$) between the two sample periods. While no other pairwise comparisons returned significant values ($p \leq 0.05$), all indices peaked during the second sample period and declined dramatically to reach the lowest values in the fourth sample period.

Table 3. Plant species richness and diversity indices on the 16 upland sites at Camp Grafton South near McHenry, North Dakota from 1998-2013.

| | Period 1 1998-2001 | Period 2 2002-2005 | Period 3 2007-2010 | Period 4 2011-2013 |
|------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Species richness | 26.35 | 30.63 | 29.00 | 22.25 |
| Shannon's H | 2.80 | 2.96 | 2.92 | 2.58 |
| Simpson's D | 0.92 | 0.93 | 0.93 | 0.89 |

Midland Plant Community

Non-metric multidimensional scaling (NMS) scores using the relative Sorenson distance measure returned a three-dimensional solution (Figure 3). The sites for each time period are surrounded by a minimum convex polygon. Coefficients of determination for the correlations between ordination distances on the axis determined by the NMS scores were calculated for each axis. The R-squared value for the first axis was 0.314. The second axis increment was 0.289, resulting in a cumulative value of 0.603 for the first and second axis combined. The third axis increment was 0.199. Thus, the three axes cumulative R-squared value was 0.802 or 80% of the variability in the data was explained.

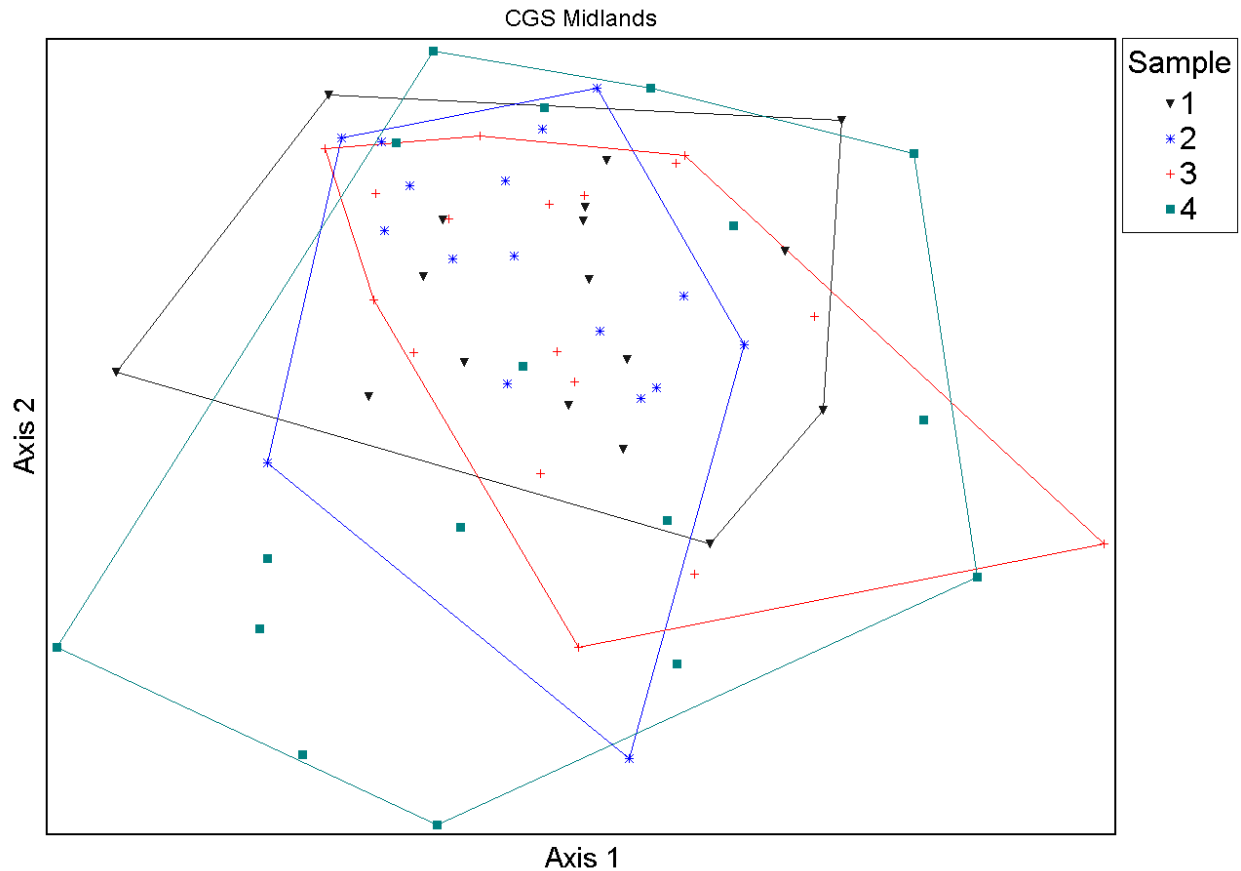


Figure 3. Non-metric multidimensional scaling ordination of the 17 midland sites at Camp Grafton South for Sample 1 (taken between 1998-2001), Sample 2 (taken between 2002-2005), Sample 3 (taken between 2007-2010), and Sample 4 (taken between 2011-2013) near McHenry, North Dakota. Minimum convex polygons surround different sample periods.

Correlations between species and axis were deemed interpretable at an absolute value greater than 0.4. Six species; blue grama, blue lettuce, plains muhly, white prairie aster, Flodman's thistle, and spikeoat (*Avenula hookeri* (Scrib.) Holub) had a negative correlation with the first NMS axis. Kentucky bluegrass, with a correlation score of 0.482, was the only species with a positive correlation on the first axis. The second axis had three species; woolly plantain (*Plantago patagonica* Jacq.), arctic rush (*Juncus arcticus* Willd.), and short-awn foxtail (*Alopecurus aequalis* Sobol.) with negative correlation scores. Nine species, mostly native shrubs and forbs, showed positive correlation scores on the second NMS axis, with western

snowberry and stiff sunflower having scores over 0.6. The third axis had six species with negative correlations; most of these species were native warm-season grasses, and prairie sandreed had the greatest negative correlation score of -0.682. Five species, including smooth brome and western snowberry, had positive correlation scores between 0.432 and 0.559 on the third NMS axis.

The PerMANOVA pairwise comparisons between each sample determined that plant community shifts occurred between the first and fourth sample period ($p=0.0006$), as well as between the second and fourth sample period ($p=0.0012$). All other pairwise comparisons had no difference in sample periods using the Bonferroni's correction. Graminoid and forb frequency change over time is shown in Table 4.

Table 4. Frequency (%) of dominant graminoid and forb species on the 17 midland sites at Camp Grafton South near McHenry, North Dakota from 1998-2013.

| | Period 1 1998-2001 | Period 2 2002-2005 | Period 3 2007-2010 | Period 4 2011-2013 |
|------------------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Graminoids | | | | |
| Kentucky Bluegrass | 94.7 | 97.2 | 98.1 | 93.7 |
| Blue grama | 26.8 | 29.2 | 37.9 | 37.7 |
| Prairie sandreed | 35.1 | 22.9 | 11.3 | 19.8 |
| Sun sedge | 69.6 | 51.1 | 57.7 | 6.4 |
| Forbs | | | | |
| Blue lettuce | 12.7 | 8.9 | 9.4 | 16.2 |
| Prairie heath aster | 20.1 | 23.7 | 37.4 | 35.1 |
| Silver-leaf Indian breadroot | 19.8 | 31.5 | 36.7 | 10.1 |
| Prairie sagewort | 13.2 | 11.1 | 24.7 | 13.7 |

The shifts in dominant vegetation were accompanied with differences in diversity indices (Table 5). Species richness declined ($p=0.001$) between the second and fourth sample periods, and the Shannon's H also declined ($p=0.004$) between the two sample periods. While no other

pairwise comparisons were no different ($p \leq 0.05$), all indices peaked during the second sample and declined to reach the lowest values in the fourth sample period.

Table 5. Plant species richness and diversity indices on the 17 midland sites at Camp Grafton South near McHenry, North Dakota from 1998-2013.

| | Period 1 1998-2001 | Period 2 2002-2005 | Period 3 2007-2010 | Period 4 2011-2013 |
|------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Species richness | 27.77 | 30.18 | 27.06 | 21.88 |
| Shannon's H | 2.96 | 3.22 | 3.06 | 2.88 |
| Simpson's D | 0.94 | 0.95 | 0.94 | 0.93 |

Lowland Plant Community

Non-metric multidimensional scaling (NMS) scores using the relative Sorenson distance measure returned a three-dimensional solution. The first and second axes are displayed in Figure 4. The sites for each time period are surrounded by a minimum convex polygon. Coefficients of determination for the correlations between ordination distances on the axis determined by the NMS scores were calculated for each axis. The R-squared value for the first axis was 0.39. The second axis increment was 0.266, resulting in a cumulative value of 0.656 for both the first and second axes. The third axis increment was 0.221. Thus, the three axis cumulative R-squared value was 0.877 or 87% of the variability in the data was explained.

Correlations between species and axis were deemed interpretable that had an absolute value greater than 0.4. Eight species, a mix of native cool-season grasses and forbs, were found to have negative correlation scores on the first NMS axis, and 13 species, predominantly native forbs, were found to have positive correlation scores. Prairie sagewort, upright prairie coneflower (*Ratibida columnifera* (Nutt.) Woot. & Standl.), white sagebrush (*Artemisia ludoviciana* Willd.), and common yarrow all had scores of greater than 0.673. Twelve species had negative correlation scores on the second NMS axis, with yellow sweetclover (*Melilotus*

officianlis (L.) Lam.), black medic (*Medicago lupulina* L.), and common yellow oxalis (*Oxalis stricta* L.) each having values less than -0.615. Kentucky bluegrass had the greatest positive correlation score on the second NMS axis of 0.683; needle-and-thread, thread-leaf sedge, and leadplant (*Amorpha canescens* Pursh) also having positive correlations. No species had a negative correlation score on the third NMS axis and 11 species belonging to a variety of functional-structural groups had positive correlation scores. Wild bergamont (*Monarda fistulosa* L.) had the greatest correlation score of 0.606.

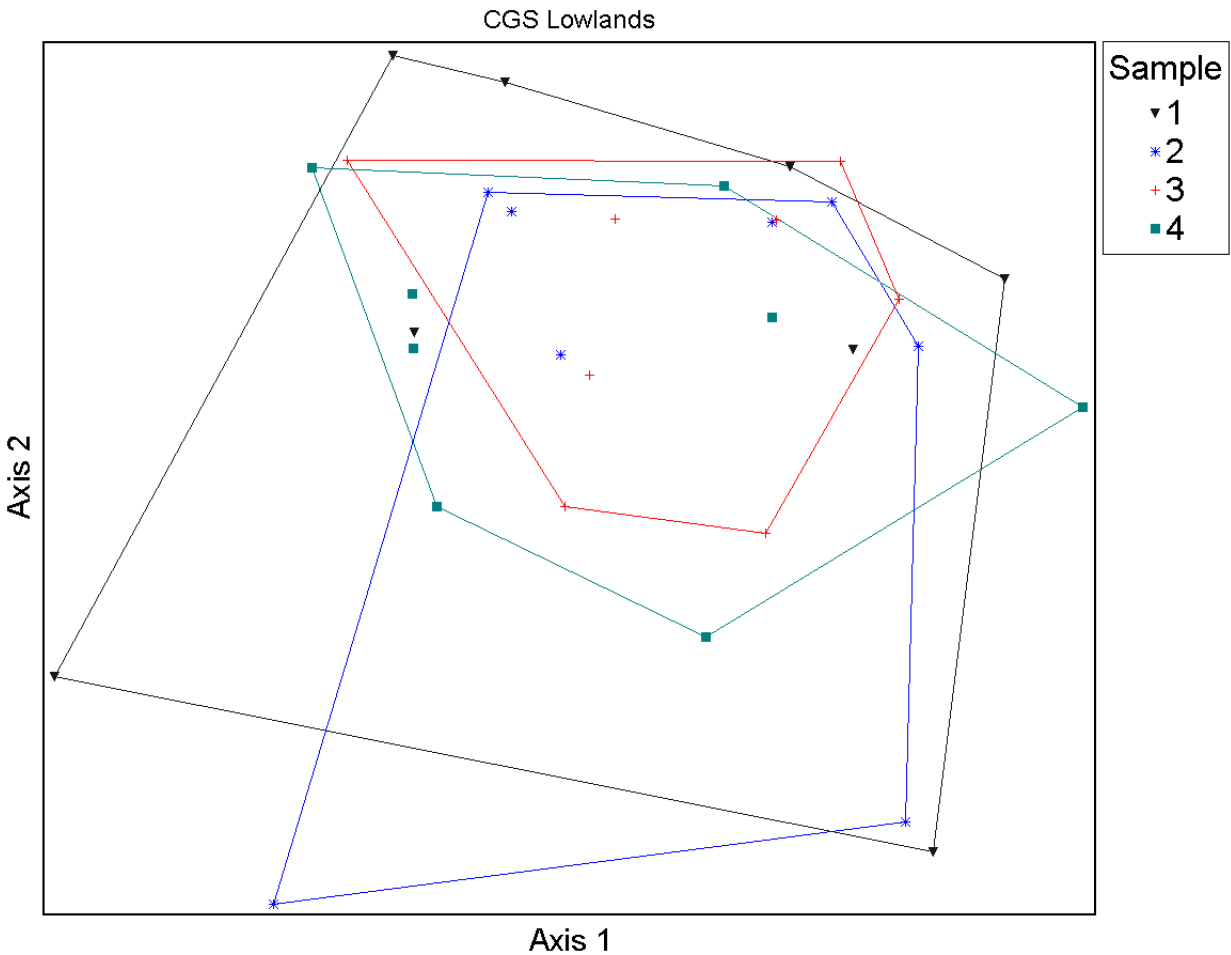


Figure 4. Non-metric multidimensional scaling ordination of the eight lowland sites at Camp Grafton South for Sample 1 (taken between 1998-2001), Sample 2 (taken between 2002-2005), Sample 3 (taken between 2007-2010), and Sample 4 (taken between 2011-2013) near McHenry, North Dakota. Minimum convex polygons surround different sample periods.

The PerMANOVA pairwise comparisons between each sample determined that plant community shifts between any of the samples were not significant ($p>0.05$) using the Bonferroni's correction. The Monte Carlo randomization test indicated ($p=0.5288$) that species differences between samples were possibly explained by randomness. Graminoid and forb frequency change over time is presented in Table 6.

Table 6. Frequency (%) of dominant graminoid and forb species on the eight lowland sites at Camp Grafton South near McHenry, North Dakota from 1998-2013.

| | Period 1 1998-2001 | Period 2 2002-2005 | Period 3 2007-2010 | Period 4 2011-2013 |
|-----------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Graminoids | | | | |
| Kentucky Bluegrass | 58.1 | 69.5 | 99.5 | 86.5 |
| Little bluestem | 13.1 | 10.5 | 9.5 | 2.5 |
| Sun sedge | 40.6 | 42.5 | 44.5 | 1.5 |
| Smooth brome | 20.6 | 22.5 | 44.5 | 49.5 |
| Forbs | | | | |
| White sagebrush | 19.9 | 33.0 | 32.5 | 9.5 |
| Prairie heath aster | 18.8 | 26.5 | 29.5 | 15.0 |
| Silver-leaf breadroot | 11.8 | 20.5 | 22.5 | 6.9 |
| Prairie sagewort | 11.0 | 9.5 | 11.0 | 5.5 |

Table 7. Plant species richness and diversity indices on the eight lowland sites at Camp Grafton South near McHenry, North Dakota from 1998-2013.

| | Period 1 1998-2001 | Period 2 2002-2005 | Period 3 2007-2010 | Period 4 2011-2013 |
|------------------|-----------------------|-----------------------|-----------------------|-----------------------|
| Species richness | 20.00 | 26.63 | 24.88 | 21.25 |
| Shannon's H | 2.49 | 2.80 | 2.76 | 2.49 |
| Simpson's D | 0.88 | 0.91 | 0.91 | 0.89 |

While individual species did change in abundance, the plant community did not shift ($p>0.05$). This fact is further exhibited by the diversity indices (Table 7). The values follow the trend of the upland and midland sites in that the highest values were found in the second sample period and lowest in the fourth sample period. However, none of the differences in pairwise comparisons were different ($p>0.05$).

All Sites

Non-metric multidimensional scaling (NMS) scores using the relative Sorenson distance measure returned a three-dimensional solution. The first and second axes are displayed in Figure 5. Coefficients of determination for the correlations between ordination distances on the axis determined by the NMS scores were calculated for each axis. The R-squared value for the first axis was 0.331. The second axis increment was 0.217, resulting in a cumulative value of 0.548 for both the first and second axes. The third axis increment was 0.189. Thus, the three axis cumulative R-squared value was 0.737 or 74% of the variability in the data was explained.

Correlations between species and axis were deemed interpretable that had an absolute value greater than 0.4. Western snowberry had the greatest negative correlation score on the first NMS axis at -0.706. Smooth brome, white sagebrush, and Cuman ragweed (*Ambrosia psilostachya* DC.) also had negative correlations. Blue grama and needle-and-thread both had positive correlations on the first NMS axis. The second NMS axis had eight species, a mix of native forbs, warm-season grasses, and sedges, with negative correlations with plant community compositions; the greatest negative score was fall rosette grass at -0.614. Kentucky bluegrass was the only species with a positive correlation on the second NMS axis. The third axis had only one species with a negative correlation, sun sedge. The NMS returned correlation scores for six species that were significant and positively correlated with the third NMS axis.

The MRPP performed to compare plant communities across all site types indicated that the upland sites were different from both midland ($p=0.0003$) and lowland ($p=0.00001$) sites. Plant communities on midland sites were also different ($p=0.0015$) from those on lowland sites.

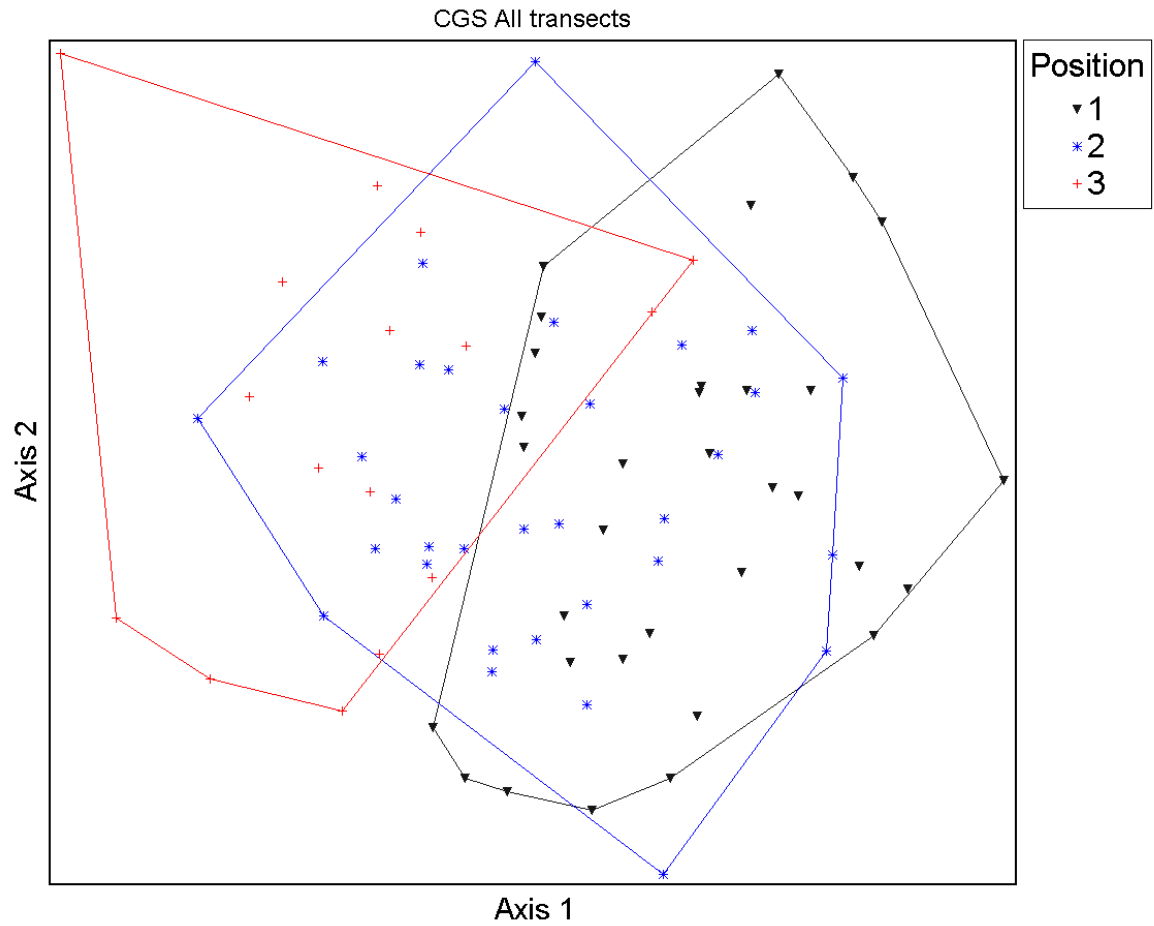


Figure 5. Non-metric multidimensional scaling ordination of the 1) 16 upland; 2) 17 midland; and 3) eight lowland sites at Camp Grafton South for Sample 1 (taken between 1998-2001) and Sample 4 (taken between 2011-2013) near McHenry, North Dakota. Minimum convex polygons surround different site positions.

DISCUSSION

The plant communities at CGS are trending towards lower species richness and dominance by cool-season grasses. Overall, Kentucky bluegrass is the strongest driver of the plant communities in the upland and midland sites. Native cool-season grasses like needle-and-thread are also increasing in the upland sites, while the invasive cool-season smooth brome is increasing in the midland sites. In both the uplands and lowland sites, native forbs and warm season grasses are decreasing. The lowland sites were dominated by Kentucky bluegrass and smooth brome at the beginning of the study, and the communities did not change significantly throughout the sampling period.

The plant communities of the upland and midland sites are undergoing a transition, but no change was found on the lowland sites between any of the sampling periods. The lowland community had already shifted away from the native state when the study started. Lowlands are more susceptible to Kentucky bluegrass invasion because of higher moisture conditions. Some wetter areas in North Dakota were already invaded by the late 1940s (Stevens 1950). While these sites may still have increasing amounts of exotic species, the plant community may be changing more slowly because they have already crossed some threshold of native to exotic state.

When comparing the upland, midland, and lowland sites, the vegetation compositions were different from one another throughout the study period. This difference is expected because of the variability in soil types, water infiltration and holding capacity, and light availability across the landscape (Abrams and Hulbert 1987; Knapp et al. 1993; Hook and Burke 2000). However, transects at each of these location types showed increases in Kentucky bluegrass and smooth brome, as well as decreases in frequency of sedges, warm season grasses, and native forbs. Despite these similarities, the NMS ordination did not clearly indicate that

plant community composition was moving toward a single invaded state. Eventually, Kentucky bluegrass and smooth brome may create monocultures that erase the species differences across the topographic gradient. However, the variety of soil characteristics and light availability at the microsite level dictate plant community composition more strongly than the presence of other species (Smeins and Olsen 1970; Hook and Burke 2000; Kolb et al. 2002). Thus, sites at different location types that are invaded by the same exotic species still retain unique species composition when compared across the landscape.

The effects of these invaders on measures of species richness and diversity are unclear. A general trend across all transects is that the greatest highest measures in Shannon's H and Simpson's D occurred during the second sampling period and lowest during the fourth sampling period. The corresponding increases in exotic species frequency may partially explain these changes in diversity (Kolb 2002); however, increasing precipitation, temperature, and growing season days over the course of the sampling periods may also be impacting the change in diversity (Frank and Hoffman 1989; Adler and Levin 2007). These climate shifts, in combination with the increased exotic species, have reduced species diversity over time.

Although the 15 year period encompasses a wet cycle when compared to historical averages, the years between the third and fourth sample period had a decline in precipitation from previous years (NOAA, 1948-2013). The prairie plant community is driven by an increase in Kentucky bluegrass and needle-and-thread. The rising frequencies of these two cool-season grasses may be a result of a shifting climate. While precipitation declined, the average temperature and growing season days were both much higher in the final years of the study than the beginning years. Because the additional growing season days extend the spring and fall,

these cool-season grass species may be benefiting from the increase growing season days (Bartholomew and Williams 2005).

The cool-season plant species also benefit from the disturbance regime at CGS. The increase in precipitation over the study period may have increased overall production (Milchunas et al. 1994; Biondini et al. 1998; Patton et al. 2007), but the stocking rates for the pastures remained static (Barker et al. 2001). The understocked pastures would show an increase in litter which reduces light availability for forbs or warm-season grasses (Collins and Caberese 2012). The litter layer produced by Kentucky bluegrass would have been especially detrimental to warm season grasses and forbs as it likely created a positive feedback with some soil nutrients (Wedin and Tilman 1990; Desserud and Naeth 2013). Additionally, the spread of Kentucky bluegrass and smooth brome probably resulted in many of the forb seedlings being suppressed (Bosy and Reader 1995; Williams and Crone 2006). Similarly, the timing for grazing may be benefitting the cool-season grasses. The growing seasons have been beginning earlier at CGS in recent years, but the timing of grazing has not changed. Therefore, the cool-season grasses experience a longer period of time without disturbance than in years before the study.

Smooth brome was not a significant part of the upland plant community, but it was increasing on the midland and lowland sites. The increase in the lowland and midland sites may be explained by smooth brome's ability to increase in density in the absence of disturbance (Wilson and Pinno 2013). If the stocking rate remains low and there is a lack of fire, smooth brome grass will continue to increase through its positive feedback with light and resource conditions (Groya and Sheaffer 1981; Otfinowski et al. 2007). It is likely that smooth brome has not been present on the uplands sites to displace the natives. Although Kentucky bluegrass and

smooth brome will both exist on the same prairie, it is unclear how the two species will compete with one another when the native species are depleted.

With only frequency data, it is difficult to make conclusions about species abundance and diversity. A major drawback to using only frequency data is that it cannot account for production of each plant counted, nor can it account for landscape structure, such as vegetation height, cover, or a measurement of bare ground. For example, Kentucky bluegrass occurred at 100% frequency throughout the study period at several transects, but it most likely increased in biomass through that time. The inability of frequency data to account for production changes in ubiquitous species makes measurements of diversity based on frequency data alone limited. These drawbacks notwithstanding, the frequency data is an excellent method to get a complete vegetation census on a site. Even if increases in biomass of invaders like Kentucky bluegrass and smooth brome occur, the frequency data will still highlight the existence, or subsequent loss, of rare species (Prosser et al. 2003b).

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