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# Targeting Introduced Species to Improve Plant Community Composition on USFWS-Managed Prairie Remnants

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**ABSTRACT:** The quality of plant community composition on US Fish and Wildlife Service (USFWS) lands in North Dakota and South Dakota has declined over the past several decades—the abundance of native species has decreased while the abundance of introduced species has rapidly increased. Extensive efforts have been made to improve plant community composition on USFWS prairies; however, there was not a unified approach to this end in North Dakota and South Dakota until the advent of the Native Prairie Adaptive Management (NPAM) program. The NPAM program provides decision support for the selection of management actions to improve plant community composition of tallgrass and mixed-grass prairies in the Northern Great Plains. We evaluated plant community composition on USFWS native tallgrass and mixed-grass prairie remnants enrolled in the NPAM program in North Dakota and South Dakota to examine effects of management on plant community composition. Our analysis suggests that incorporating certain management actions can improve plant community characteristics on the agency's tallgrass and mixed-grass prairies. We documented increased native species richness and decreased *Bromus inermis* (smooth brome) relative cover at sites that had been burned two or more times during a four-year period. In contrast, smooth brome relative cover was higher at sites managed by the exclusion of fire and intermittent light grazing or rest. Smooth brome is extremely invasive in native prairie remnants throughout the Northern Great Plains. Thus, our results have marked implications for managers working to reduce the prevalence of smooth brome on public and private lands.

*Index terms:* *Bromus inermis* Leyss., native prairie, North Dakota, South Dakota

## INTRODUCTION

North American grasslands are among the continent's most endangered ecosystems (Samson and Knopf 1994; Grant et al. 2009; DeKeyser et al. 2015). Grassland losses have been as high as 70% throughout the Great Plains, with wide variation by grassland type (Samson et al. 2004). For example, only an estimated 13%, 29%, and 52% of the historical extent of tallgrass, mixed-grass, and shortgrass prairies, respectively, remain on the landscape (Samson et al. 2004). In the Northern Great Plains (NGP) states of North Dakota and South Dakota, less than 3% of tallgrass prairies remain (Samson et al. 2004). Remaining native prairies are clearly essential to preserving biodiversity throughout the NGP (Samson and Knopf 1994). North American grasslands evolved under climatic variability and in concert with periodic disturbances (e.g., grazing and/or fire) (Fuhlendorf and Engle 2001; Murphy and Grant 2005). Management that excludes disturbances tends to result in fairly homogenous grasslands dominated by a few highly competitive species (Murphy and Grant 2005). Thus, in order to ensure that remnant prairie ecosystems remain intact, it is vital to maintain, or reinstate, certain disturbances (i.e., grazing and/or fire) (Biondini et al. 1989; Murphy and Grant 2005; Grant et al. 2009).

The US Fish and Wildlife Service (US-

FWS) manages about 90,000 ha of tallgrass and mixed-grass prairies east of the Missouri River in North Dakota and South Dakota, most as National Wildlife Refuges (NWRs) or Waterfowl Production Areas (WPAs) (Grant et al. 2009). In recent decades, researchers have documented declines in species composition on native prairies managed by the USFWS and have related these declines to management (Murphy and Grant 2005; Grant et al. 2009; Paradeis et al. 2010). Traditionally, management of native prairies on USFWS lands consisted of prolonged periods of rest and/or intermittent light grazing, at odds with the historical disturbance regimes of tallgrass and mixed-grass prairies (Murphy and Grant 2005; Grant et al. 2009). This low-intensity management, coupled with the exclusion of certain periodic disturbances, especially fire, led to a decline in the quality of plant community composition on USFWS prairies. The decline in composition was evidenced by a decrease in native plant species in conjunction with an increase in introduced species, especially *Bromus inermis* Leyss. (smooth brome) and *Poa pratensis* L. (Kentucky bluegrass) (Grant et al. 2009; DeKeyser et al. 2013; DeKeyser et al. 2015).

Smooth brome and Kentucky bluegrass negatively affect prairie ecosystems through displacing native species, altering community composition and competitive dynamics, reducing productivity and/or

diversity, and/or altering nutrient cycles (Christian and Wilson 1999; Reed et al. 2005; Vinton and Goergen 2006; Di-Alllesandro et al. 2013; DeKeyser et al. 2015). Smooth brome is a prevalent invader of NGP grasslands and can be an aggressive competitor both above- and below-ground (Johnson and Biondini 2001; Levang-Brilz and Biondini 2002; Rajaniemi and Reynolds 2004; Murphy and Grant 2005; Vinton and Goergen 2006; Biondini 2008; Grant et al. 2009; DiAlllesandro et al. 2013; Kobiela et al. 2016). Similarly, Kentucky bluegrass is a prolific invader throughout the NGP and its success in a given area often coincides with a decline in plant community quality (i.e., richness and productivity of native species) (Murphy and Grant 2005; Grant et al. 2009; DeKeyser et al. 2013; DeKeyser et al. 2015).

Upon recognition of declining conditions on prairie remnants throughout the NGP, USFWS land managers have increasingly reincorporated fire and grazing to repair, or maintain, the integrity of such prairies. In addition, USFWS managers are increasingly developing adaptive management approaches to address site-specific objectives (Grant et al. 2009; Moore et al. 2011). In the Prairie Pothole Region of the NGP, a partnership, known as the Native Prairie Adaptive Management (NPAM) program, was formed between the USFWS and US Geological Survey (USGS) to develop a framework for decision support in selecting management actions to achieve certain objectives (Gannon et al. 2013). The principal objective of the NPAM program is to increase the composition of native species found on native tallgrass and mixed-grass prairies while minimizing costs. The NPAM process relies on annual monitoring of vegetation by management unit to select the most appropriate management actions for the coming year.

The goal of our study was to evaluate plant species composition of native tallgrass and mixed-grass prairie remnants in North Dakota and South Dakota. Study sites were USFWS-managed native prairies enrolled in the NPAM program. Thus, management actions at each site were guided by the NPAM decision framework, rather than selected as part of this study.

We especially focused on prevalence of introduced species (specifically, smooth brome and Kentucky bluegrass) and management regimes employed at each site to relate plant community composition to management actions.

## METHODS

We selected 32 native tallgrass or mixed-grass prairie sites located on NWRs or WPAs east of the Missouri River in North Dakota and South Dakota (Figure 1). Sites were enrolled in the NPAM program and selected based on management history, accessibility, and soil characteristics. We exclusively selected loamy ecological sites

(Sedivec and Printz 2012) because these are known to be impacted by Kentucky bluegrass invasion (DeKeyser et al. 2009). We chose to include a single ecological site type to counteract the potential variability inherent with the large geographical extent of our study, especially the inclusion of both tallgrass and mixed-grass prairies. Loamy ecological sites are expected to possess characteristic plant communities due to similar conditions, including precipitation, slope, exposure, and soil conditions (Sedivec and Printz 2012). However, because our sites were scattered across a large geographical area, there was a prominent gradient in precipitation and we would expect a similar gradient to be reflected in annual production. Thus, our

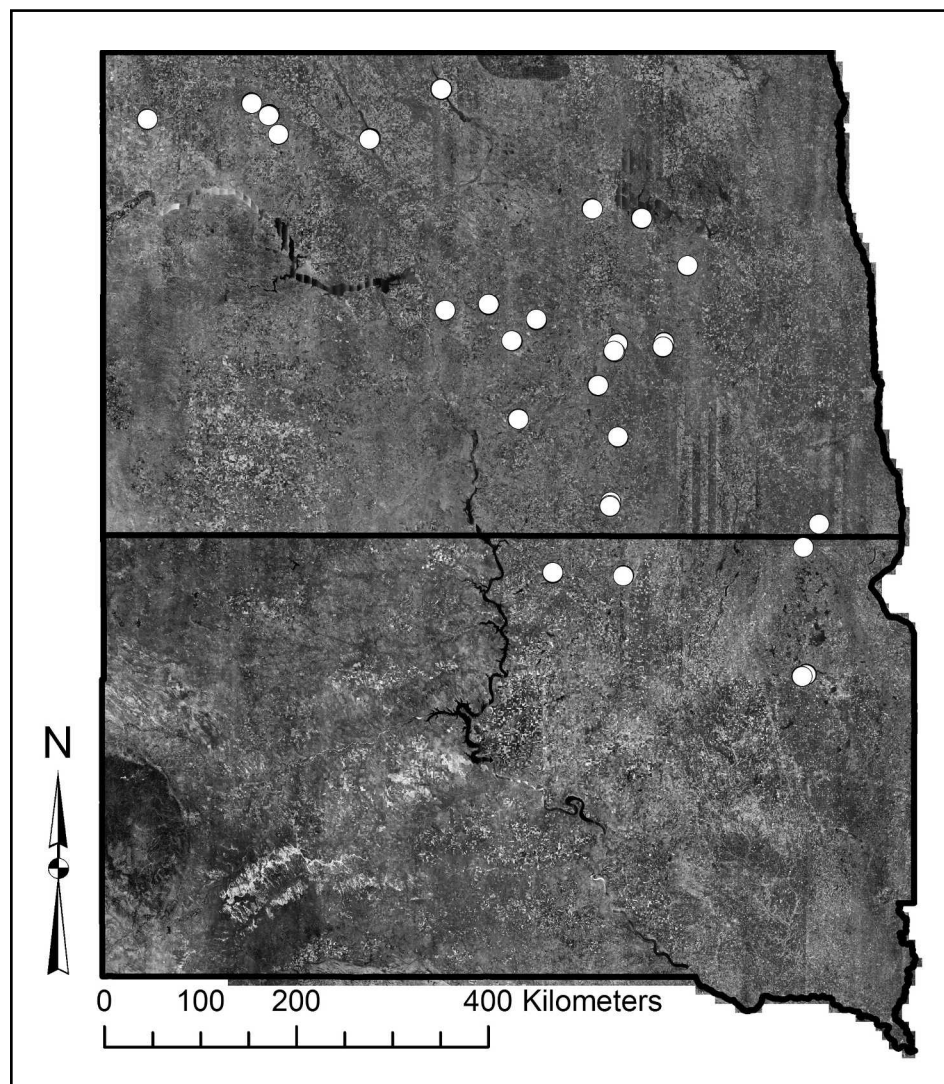


Figure 1. Study site locations (circles) in North Dakota and South Dakota (2014 National Agricultural Imagery Program).

analysis examined the impacts of management actions on species composition rather than production.

We obtained management records for each site from 2009 through 2013 to evaluate how plant communities were affected by NPAM-guided management. Sites were assigned to one of three categories intended to represent a gradient of management approaches from traditional USFWS management to intensive USFWS management, and related to the number of years where fire was used as a management strategy. The first group consisted of four sites that were managed following the traditional USFWS approach and were not burned between 2009 and 2013 (henceforth, unburned). The second group consisted of nine sites that were burned two or more times between 2009 and 2013 and represented the strongest departure from historical USFWS management. The third group consisted of 19 sites that were burned a single time (2009–2013) and represented a transition in management approaches from traditional (unburned) toward intensive (burned two or more times).

### Vegetation Sampling

We sampled vegetation at each site during summer 2012 using a Modified-Whittaker design in order to assess the plant community in its entirety (Stohlgren et al. 1995). Modified-Whittaker designs are useful for identifying rare or patchy plant species and for early detection of introduced species (Barnett and Stohlgren 2003). Three to five 20 m × 50 m (1000 m<sup>2</sup>) Modified-Whittaker plots were established on loamy ecological sites at each location during summer 2012. The number of plots at each site corresponded with the site's total area. Each Modified-Whittaker plot was randomly

assigned, located using GPS, and permanently marked to ensure we sampled the same plot in the subsequent year. We also sampled ten 1-m<sup>2</sup> nonoverlapping subplots, two 10-m<sup>2</sup> nonoverlapping subplots, and one 100-m<sup>2</sup> subplot, nested within the whole 1000-m<sup>2</sup> plot. We estimated percent cover for each plant species within the 1-m<sup>2</sup> subplots and recorded species presence for the 10-m<sup>2</sup> and 100-m<sup>2</sup> subplots and for the entire (1000-m<sup>2</sup>) Modified-Whittaker plot.

### Data Analysis

Our extensive vegetation sampling design yielded an abundance of data. Our intention was to conduct a thorough examination of the plant community, thus, we utilized a few separate analysis methods, incorporating both multivariate and univariate techniques (namely, multi-response permutation procedure (MRPP), nonmetric multidimensional scaling (NMS), one-way analysis of variance (ANOVA), and Tukey's honestly significant difference (HSD) test). Relative cover values were transformed prior to multivariate analyses using the arcsine square root transformation (McCune and Grace 2002; McCune and Mefford 2011). Multivariate analysis was conducted in PC-ORD (ver. 6.0, McCune and Mefford 2011) and univariate analysis was conducted in SAS (ver. 9.4, SAS Institute, Cary, NC, USA).

We used MRPP, with the relative Sørensen distance measure (McCune and Grace 2002), to evaluate plant species composition of our sites. More specifically, we used MRPP to compare the relative cover of every species encountered at our sites, based on management categories (as detailed above). We also used MRPP to make pair-wise comparisons between management categories (*P* values were adjusted for

multiple comparisons using the Bonferroni correction (Gotelli and Ellison 2013)). We used NMS to display relationships among our sites in species space and to explore individual species' correlations with the ordination axes, paying special attention to smooth brome and Kentucky bluegrass. In addition, we used one-way ANOVA to further explore how total species richness, native species richness, relative smooth brome cover, and relative Kentucky bluegrass cover responded to management actions employed at our sites using Tukey's HSD test to make comparisons between management categories.

### RESULTS

Our MRPP analysis of the community-level relative cover dataset determined that there were indeed differences in species composition between the unburned sites and those that were burned two or more times in 2012 (MRPP, *P* = 0.01) (Table 1). In addition, ANOVA indicated that total species richness (*P* < 0.01), native species richness (*P* < 0.01), and smooth brome relative cover (*P* = 0.03) responded to management in 2012, while Kentucky bluegrass relative cover did not (*P* = 0.76) (Table 2) (Figure 2). Mean species richness and native species richness were higher at sites that were burned two or more times (72.0 and 59.4 species, respectively) than sites that were burned once (59.6 and 49.5, respectively) or left unburned (50.3 and 40.8, respectively) (Figure 2). Additionally, smooth brome was less prevalent at sites that were burned two or more times (7.33% mean relative cover) than those that were unburned (30.1% mean relative cover) (Figure 2).

In 2013, MRPP analysis of relative cover (all species) again determined that spe-

**Table 1.** *P* values from multi-response permutation procedure (MRPP) pair-wise comparisons of plant species relative cover for native prairie remnants that were unburned, burned once, and burned two or more times (*P* values adjusted for multiple comparisons using the Bonferroni correction).

	Unburned vs. burned once	Unburned vs. burned two or more times	Burned once vs. burned two or more times
2012 Relative cover (all species)	<i>P</i> = 0.909	<i>P</i> = 0.013	<i>P</i> = 0.119
2013 Relative cover (all species)	<i>P</i> = 1.00	<i>P</i> = 0.029	<i>P</i> = 0.019

**Table 2.** ANOVA of species richness, native species richness, smooth brome relative cover, and Kentucky bluegrass relative cover of prairie remnants that were not burned, burned once, and burned two or more times.

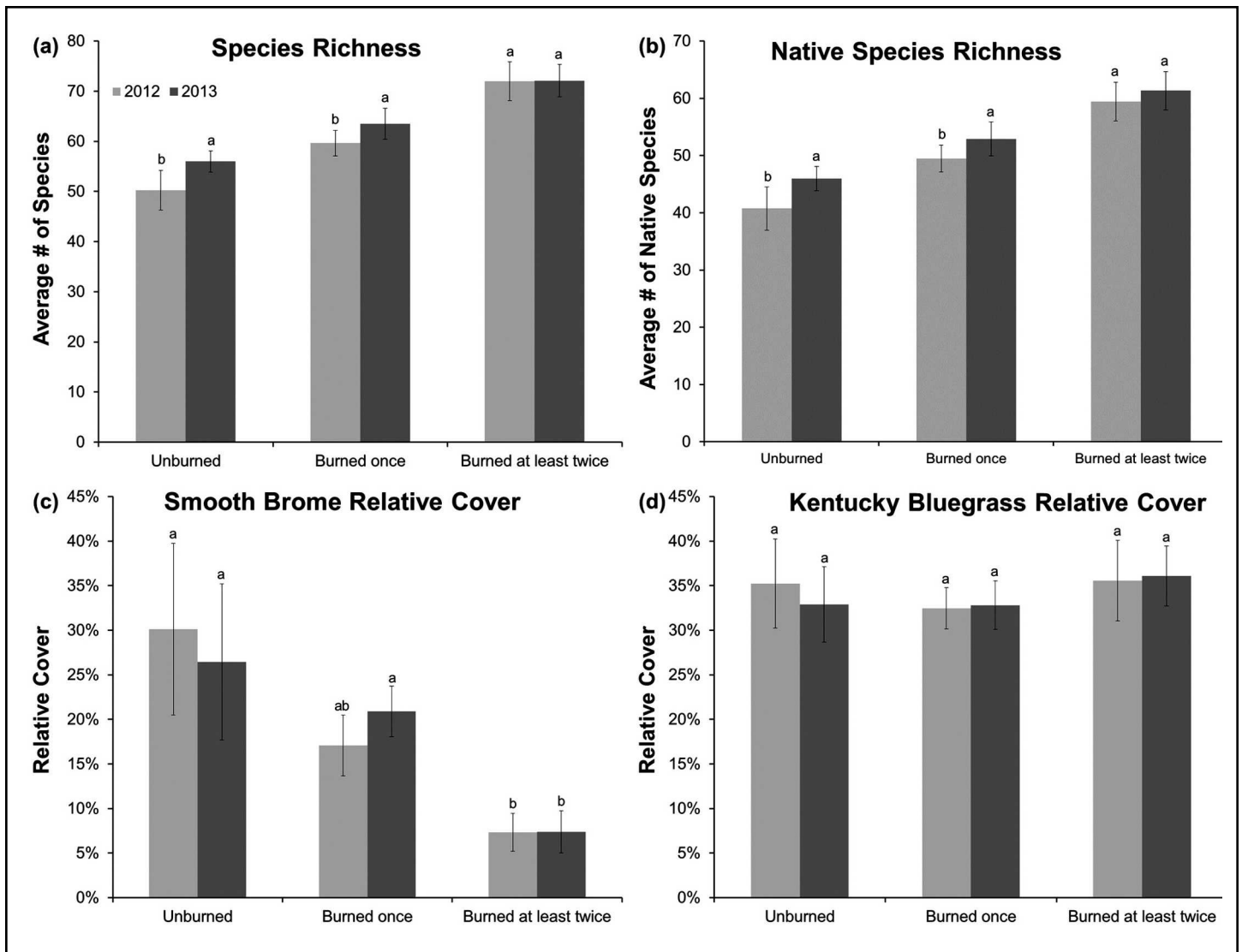
	Degrees of freedom	Sum of squares	Mean square	<i>F</i>	<i>P</i>
<b>Species richness (2012)</b>					
Model	2	1559	779.4	6.47	0.005
Error	29	3495	120.5		
Corrected total	31	5054			
<b>Native species richness (2012)</b>					
Model	2	1105	552.6	5.69	0.008
Error	29	2818	97.2		
Corrected total	31	3923			
<b>Smooth brome relative cover (2012)</b>					
Model	2	0.1499	0.074	4.03	0.029
Error	29	0.5397	0.019		
Corrected total	31	0.6896			
<b>Kentucky bluegrass relative cover (2012)</b>					
Model	2	0.007	0.0035	0.28	0.756
Error	29	0.3585	0.0124		
Corrected total	31	0.3655			
<b>Species richness (2013)</b>					
Model	2	823.3	411.7	2.91	0.07
Error	29	4100	141.4		
Corrected total	31	4923			
<b>Native species richness (2013)</b>					
Model	2	757.9	379	2.84	0.075
Error	29	3874	133.6		
Corrected total	31	4632			
<b>Smooth brome relative cover (2013)</b>					
Model	2	0.1458	0.0729	5.16	0.012
Error	29	0.4095	0.0141		
Corrected total	31	0.5553			
<b>Kentucky bluegrass relative cover (2013)</b>					
Model	2	0.0069	0.0035	0.28	0.756
Error	29	0.3543	0.0122		
Corrected total	31	0.3612			

cies composition of unburned sites was different from those that were burned two or more times ( $P = 0.03$ ) (Table 1). In addition, species composition of sites that were burned once was distinct from sites that were burned two or more times ( $P = 0.02$ ) (Table 1). Again, ANOVA indicated that smooth brome relative cover ( $P =$

0.01) responded to management, while total species richness ( $P = 0.07$ ), native species richness ( $P = 0.07$ ), and Kentucky bluegrass relative cover did not ( $P = 0.76$ ) (Table 2, Figure 2). Smooth brome was less prevalent at sites that were burned two or more times (7.38% mean relative cover) than those that were burned once (20.9%

mean relative cover) or not at all (26.4% mean relative cover) (Figure 2).

NMS analysis of the 2012 relative cover (all species) produced a final solution with three dimensions (final stress = 13.51, instability < 0.001; Figure 3) with each of the three axes representing a gradient of



**Figure 2.** Mean ( $\pm$  standard error) species richness (a), native species richness (b), smooth brome relative cover (c), and Kentucky bluegrass relative cover (d) by management approach for 2012 and 2013. Different letters indicate significant differences ( $P < 0.05$ , Tukey's honestly significant difference (HSD)) within a single year.

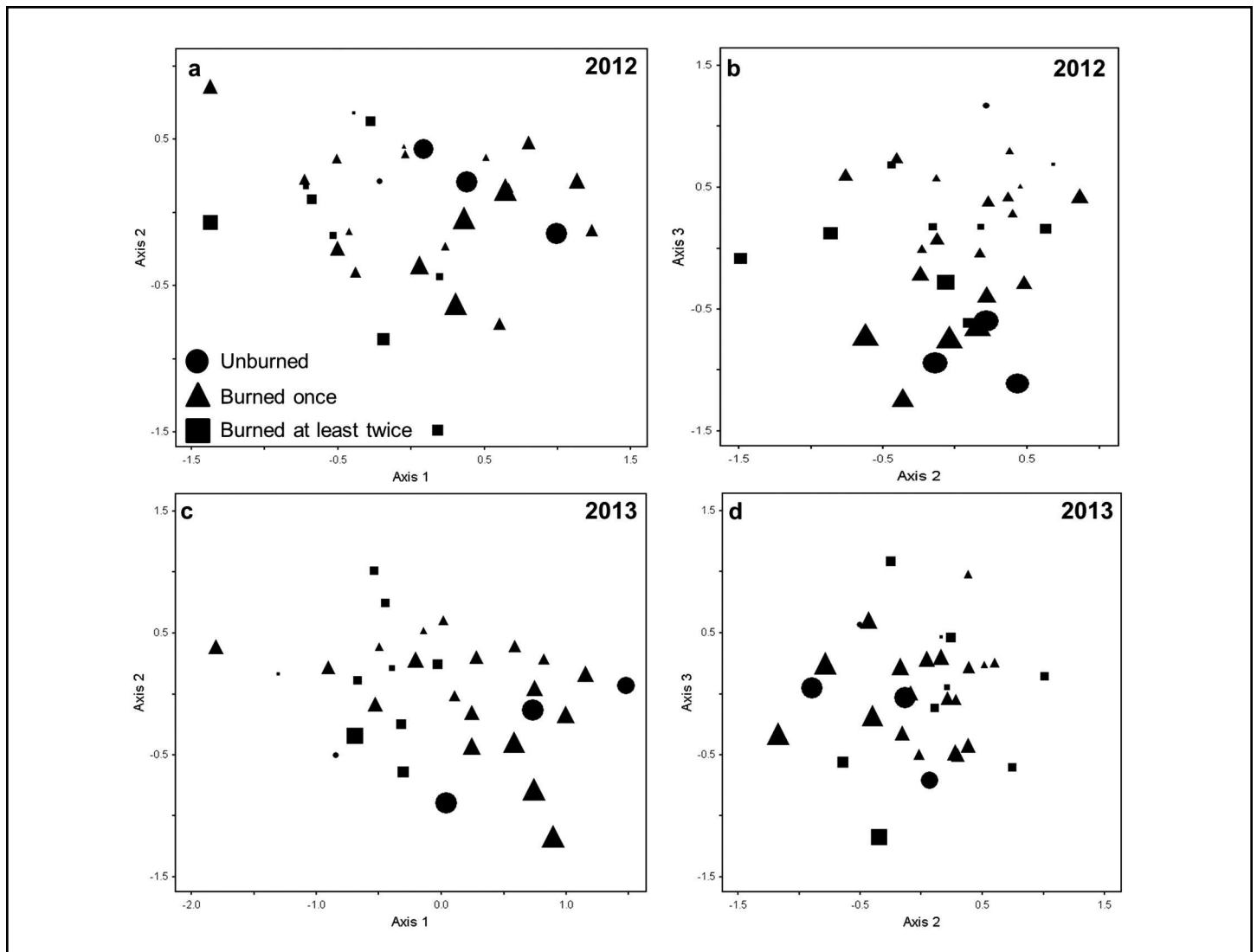
species quality (Appendix A). For example, the species positively correlated with Axis 3 tended to be native species typically encountered throughout the NGP. Conversely, the species negatively correlated with Axis 3 tended to be introduced species or native species indicative of disturbed conditions in the NGP. NMS analysis of relative cover (all species) sampled in 2013 also produced a final solution with three dimensions (final stress = 12.66, instability < 0.001; Figure 3). Similarly, each of the three axes was determined to represent a gradient of species quality in 2013 (Appendix B).

## DISCUSSION

Traditional USFWS management of tall-grass and mixed-grass prairie remnants was characterized by prolonged periods of rest with occasional light grazing (Murphy and Grant 2005; Grant et al. 2009). Research has shown that prolonged periods of rest led to a decline in the abundance of native species and an increase in the abundance of introduced species throughout the NGP (e.g., smooth brome and Kentucky bluegrass) (Grant et al. 2009; DeKeyser et al. 2013; DeKeyser et al. 2015). Our results

confirmed that the traditional USFWS approach to management fails to maintain or improve floristic quality on native tall-grass and mixed-grass prairie remnants in North Dakota and South Dakota. We found that sites with management histories most closely resembling the traditional USFWS management model had the lowest species richness (2012) and highest relative cover of smooth brome (2012 and 2013).

We observed higher total species richness and native species richness in 2012 on sites that were burned two or more times in the



**Figure 3.** Nonmetric multidimensional scaling ordinations for 2012 (a and b) and 2013 (c and d) of relative cover (all species) for sites that were unburned, burned once, or burned two or more times. Each symbol represents one site. The size of the symbol in ordination space indicates the relative cover of smooth brome at that site.

few years before our vegetation surveys. The higher species richness observed on such sites in 2012 likely reflects the evolution of tallgrass and mixed-grass prairies in concert with disturbance regimes that included relatively frequent grazing and fire (Fuhlendorf and Engle 2001; Murphy and Grant 2005). Native species were better able to withstand fire than smooth brome. Thus, the relative cover of smooth brome decreased as burn frequency increased. Our results support a growing body of research that has shown the maintenance of diverse native prairie plant communities to depend on the inclusion of a disturbance regime that mimics historical patterns (Biondini et

al. 1989; Murphy and Grant 2005; Grant et al. 2009).

We categorized our sites to represent a gradient of management approaches employed by USFWS managers in North Dakota and South Dakota from a traditional (unburned) to an intensive approach (burned two or more times). Our results indicated that the intensive approach has the potential to improve plant community composition on USFWS-managed native prairies in North Dakota and South Dakota. Plant community composition improved and smooth brome cover decreased at sites burned two or more times. However,

these improvements were not observed on the unburned sites or on sites that were burned only once between 2009 and 2013. Our results suggest that using fire as a management tool has the potential to improve conditions on USFWS native prairies in North Dakota and South Dakota. Of course, there is no single approach to management that ought to be applied to all native prairies in North Dakota and South Dakota. However, implementing the NPAM program may help improve floristic condition of native prairies in North Dakota and South Dakota through its use of annual vegetation monitoring to customize future management actions

toward meeting a specific goal.

Smooth brome and Kentucky bluegrass readily outcompete many native species (Vinton and Goergen 2006; Bahm et al. 2011; DeKeyser et al. 2015). While smooth brome cover was lower on the sites that were burned two or more times than on the unburned sites, there was no difference in Kentucky bluegrass cover at our sites. Many researchers have found smooth brome and Kentucky bluegrass remarkably resilient to control measures such as fire, grazing, and herbicide treatments (Vinton and Goergen 2006; DeKeyser et al. 2010; Bahm et al. 2011; DeKeyser et al. 2013; DeKeyser et al. 2015). Thus, we were pleased to find that management impacted smooth brome relative cover at our sites (however, Kentucky bluegrass remains a problem). To effectively reduce the prevalence of Kentucky bluegrass at our sites, managers must continue to be diligent in identifying problem areas and persistent in their efforts to target the undesired species. More research on ways to reduce introduced species, especially Kentucky bluegrass, is critically needed. However, we believe that extended rest of native prairies in North Dakota and South Dakota—especially excluding fire and grazing—will only continue to foster conditions in which introduced species outcompete native species and continue to degrade native plant communities.

## MANAGEMENT IMPLICATIONS

For decades, USFWS-owned tallgrass and mixed-grass prairies were managed similarly and generally subjected to prolonged periods of rest and/or intermittent light grazing with no fire (Murphy and Grant 2005; Grant et al. 2009). Such management is at odds with the historical disturbance regimes to which tallgrass and mixed-grass prairies are adapted but continues to degrade plant community composition on USFWS prairies in North Dakota and South Dakota (Murphy and Grant 2005; Grant et al. 2009; DeKeyser et al. 2013; DeKeyser et al. 2015). However, declining conditions on these native prairies did not go unnoticed—many researchers have documented the decrease in native species

and corresponding increase in introduced species and related these changes to inappropriate management of native prairie systems (Murphy and Grant 2005; Grant et al. 2009; DeKeyser et al. 2013; DeKeyser et al. 2015). Today, USFWS managers are increasingly changing their management approach to improve conditions of native prairies in the NGP (Moore et al. 2011; Gannon et al. 2013). The NPAM program has the potential to greatly benefit USFWS managers during this transition by providing a valuable framework to help align management actions with specific goals. The NPAM program relies on annual monitoring to tailor future management actions to better target site-specific problems, thereby improving native species composition (Gannon et al. 2013).

While the NPAM program was undergoing development, management units were enrolled based on logistics (e.g., feasibility to burn, graze, and monitor on an annual basis) rather than plant community composition, thus, our sites may have had differing levels of floristic quality prior to their enrollment in the NPAM program. However, our analysis revealed that more frequent burning was the factor associated with the highest floristic quality on our sites. Thus, prescribed fire should be increased when and where possible to a frequency that more closely resembles the historical patterns for NGP prairies.

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## LITERATURE CITED

- Bahm, M.A., T.G. Barnes, and K.C. Jensen. 2011. Herbicide and fire effects on smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*) in invaded prairie remnants. *Invasive Plant Science and Management* 4:189-197.
- Barnett, D.T., and T.J. Stohlgren. 2003. A nested-intensity design for surveying plant diversity. *Biodiversity and Conservation* 12:255-278.
- Biondini, M. 2008. Allometric scaling laws for water uptake by plant roots. *Journal of Theoretical Biology* 251:35-59.
- Biondini, M.E., A.A. Steuter, and C.E. Grygiel. 1989. Seasonal fire effects on the diversity patterns, spatial-distribution and community structure of forbs in the Northern Mixed Prairie, USA. *Vegetatio* 85:21-31.
- Christian, J.M., and S.D. Wilson. 1999. Long-term ecosystem impacts of an introduced grass in the Northern Great Plains. *Ecology* 80:2397-2407.
- DeKeyser, E.S., G. Clambey, K. Krabbenhoft, and J. Ostendorf. 2009. Are changes in species composition on central North Dakota rangelands due to non-use management? *Rangelands* 31:16-19.



- DeKeyser, E.S., L.A. Dennhardt, and J. Hendrickson. 2015. Kentucky bluegrass (*Poa pratensis*) invasion in the Northern Great Plains: A story of rapid dominance in an endangered ecosystem. *Invasive Plant Science and Management* 8:255-261.
- DeKeyser, E.S., M. Meehan, G. Clambey, and K. Krabbenhoft. 2013. Cool season invasive grasses in Northern Great Plains natural areas. *Natural Areas Journal* 33:81-90.
- DiAllesandro, A., B.P. Kobiela, and M. Biondini. 2013. Invasion as a function of species diversity: A case study of two restored North Dakota grasslands. *Ecological Restoration* 31:186-194.
- Fuhlendorf, S.D., and D.E. Engle. 2001. Restoring heterogeneity on rangelands: Ecosystem management based on evolutionary grazing patterns. *BioScience* 8:625-632.
- Gannon, J.J., T.L. Shaffer, and C.T. Moore. 2013. Native prairie adaptive management: A multi region adaptive approach to invasive plant management on Fish and Wildlife Service owned lands. US Geological Survey Open File Report 2013-1279, Reston, VA. <<http://dx.doi.org/10.3133/ofr20131279>>.
- Gotelli, N.J., and A.M. Ellison. 2013. *A Primer of Ecological Statistics*, 2nd ed. Sinauer Associates, Sunderland, MA.
- Grant, T.A., B. Flanders-Wanner, T.L. Shaffer, R.K. Murphy, and G.A. Knutson. 2009. An emerging crisis across northern prairie refuges: Prevalence of invasive plants and a plan for adaptive management. *Ecological Restoration* 27:58-65.
- Johnson, H.A., and M.E. Biondini. 2001. Root morphological plasticity and nitrogen uptake of 59 plant species from the Great Plains grasslands, USA. *Basic and Applied Ecology* 2:127-143.
- Kobiela, B., M. Biondini, and K. Sedivec. 2016. Comparing root and shoot responses to nutrient additions and mowing in a restored semi-arid grassland. *Plant Ecology* 217:303-314.
- Levang-Brilz, N., and M.E. Biondini. 2002. Growth rate, root development and nutrient uptake of 55 plant species from the Great Plains grasslands, USA. *Plant Ecology* 165:117-144.
- McCune, B., and J.B. Grace, with a contribution from D.L. Urban. 2002. *Analysis of Ecological Communities*. MjM Software, Gleneden Beach, OR.
- McCune, B., and M.J. Mefford. 2011. *PC-ORD*. Multivariate analysis of ecological data. Version 6.0. MjM Software, Gleneden Beach, OR.
- Moore, C.T., E.V. Lonsdorf, M.G. Knutson, H.P. Laskowski, and S.K. Lor. 2011. Adaptive management in the US National Wildlife Refuge System: Science-management partnerships for conservation delivery. *Journal of Environmental Management* 92:1395-1402.
- Murphy, R.K., and T.A. Grant. 2005. Land management history and floristics in mixed-grass prairie, North Dakota, USA. *Natural Areas Journal* 25:351-358.
- Paradeis, B.L., E.S. DeKeyser, and D.R. Kirby. 2010. Evaluation of restored and native Prairie Pothole Region plant communities following an environmental gradient. *Natural Areas Journal* 30:294-304.
- Rajaniemi, T.K., and H.L. Reynolds. 2004. Root foraging for patchy resources in eight herbaceous plant species. *Oecologia* 141:519-525.
- Reed, H.E., T.R. Seastedt, J.M. Blair. 2005. Ecological consequences of C4 grass invasion of a C4 grassland: A dilemma for management. *Ecological Applications* 15:1560-1569.
- Samson, F., and F. Knopf. 1994. Prairie conservation in North America. *BioScience* 44:418-421.
- Samson, F.B., F.L. Knopf, and W.R. Ostlie. 2004. Great Plains ecosystems: Past, present, and future. *Wildlife Society Bulletin* 32:6-15.
- Sedivec, K.K., and J.L. Printz. 2012. Ecological sites of North Dakota. NDSU Extension Publication R-1556. <<https://www.ag.ndsu.edu/pubs/ansci/range/r1556.pdf>>.
- Stohlgren, T.J., M.B. Falkner, and L.D. Schnell. 1995. A Modified-Whittaker nested vegetation sampling method. *Vegetatio* 117:113-121.
- Vinton, M.A., and E.M. Goergen. 2006. Plant-soil feedbacks contribute to the persistence of *Bromus inermis* in tallgrass prairie. *Ecosystems* 9:967-976.

Appendix A: Species correlations (Pearson  $r > 0.4$ ) with nonmetric multidimensional scaling (NMS) of 2012 relative cover.

Species positively correlated with NMS Axes:

Axis 1	Axis 2	Axis 3
<i>Anemone canadensis</i> L.	<i>Comandra umbellata</i> (L.) Nutt.	<i>Artemisia frigida</i> Willd.
<i>Cirsium arvense</i> (L.) Scop.	<i>Festuca saximontana</i> Rydb.	<i>Artemisia ludoviciana</i> Nutt.
<i>Galium boreale</i> L.	<i>Hesperostipa comata</i> (Trin. & Rupr.) Barkworth	<i>Carex duriuscula</i> C.A. Mey.
<i>Glycyrrhiza lepidota</i> Pursh	<i>Poa pratensis</i> L.	<i>Carex inops</i> L.H. Bailey
<i>Helianthus maximiliani</i> Schrad.	<i>Pulsatilla patens</i> (L.) Mill.	<i>Dalea purpurea</i> Vent.
<i>Helianthus nuttallii</i> Torr. & A. Gray		<i>Euphorbia esula</i> L.
<i>Shepherdia argentea</i> (Pursh) Nutt.		<i>Helianthus pauciflorus</i> Nutt.
<i>Solidago canadensis</i> L.		<i>Hesperostipa comata</i>
<i>Spartina pectinata</i> Bosc ex Link		<i>Liatris punctata</i> Hook.
		<i>Nassella viridula</i> (Trin.) Barkworth
		<i>Oenothera suffrutescens</i> (Ser.) W.L. Wagner & Hoch
		<i>Pascopyrum smithii</i> (Rydb.) Á. Löve
		<i>Rosa arkansana</i> Porter
		<i>Solidago mollis</i> Bartlett
		<i>Symphoricarpos occidentalis</i> Hook.
		<i>Symphyotrichum ericoides</i> (L.) G.L. Nesom

Species negatively correlated with NMS Axes:

Axis 1	Axis 2	Axis 3
<i>Achillea millefolium</i> L.	<i>Ambrosia psilostachya</i> DC. Cuman	<i>Asclepias syriaca</i> L.
<i>Artemisia frigida</i>	<i>Astragalus flexuosus</i> Douglas ex G. Don	<i>Asclepias viridiflora</i> Raf.
<i>Bouteloua gracilis</i> (Willd. ex Kunth) Lag. ex Griffiths	<i>Astragalus laxmannii</i> Jacq.	<i>Bromus inermis</i> Leyss.
<i>Carex duriuscula</i>	<i>Brickellia eupatorioides</i> (L.) Shinnars	<i>Melilotus officinalis</i> (L.) Lam.
<i>Carex filifolia</i> Nutt.	<i>Carex brevior</i> Britton	
<i>Carex inops</i>	<i>Chenopodium album</i> L.	
<i>Conyza canadensis</i> (L.) Cronquist	<i>Cirsium arvense</i>	
<i>Distichlis spicata</i> (L.) Greene	<i>Cirsium flodmanii</i> (Rydb.) Arthur	
<i>Hesperostipa comata</i>	<i>Dichanthelium wilcoxianum</i> (Vasey) Freckmann	
<i>Koeleria macrantha</i> (Ledeb.) Schult.	<i>Gaillardia aristata</i> Pursh	
<i>Liatris punctata</i>	<i>Hesperostipa spartea</i> (Trin.) Barkworth	
<i>Lygodesmia juncea</i> (Pursh) D. Don ex Hook.	<i>Lotus unifoliolatus</i> (Hook) Benth.	
<i>Muhlenbergia cuspidata</i> (Torr. ex Hook.) Rydb.	<i>Melilotus albus</i> (L.) Lam.	
<i>Nassella viridula</i>	<i>Physalis virginiana</i> Mill.	
<i>Oenothera suffrutescens</i>	<i>Sorghastrum nutans</i> (L.) Nash	
<i>Pascopyrum smithii</i>	<i>Sporobolus heterolepis</i> (A. Gray) A. Gray	
<i>Pediomelum argophyllum</i> (Pursh) J. Grimes	<i>Taraxacum officinale</i> F.H. Wigg	

Continued

Appendix A (Cont'd)

Species negatively correlated with NMS Axes:

Axis 1	Axis 2	Axis 3
<i>Ratibida columnifera</i> (Nutt.) Wooton & Standl.	<i>Vernonia fasciculata</i> Michx.	
<i>Sphaeralcea coccinea</i> (Nutt.) Rydb.	<i>Vicia americana</i> Muhl. ex Willd.	
<i>Symphyotrichum ericoides</i>	<i>Viola pedatifida</i> G. Don	
<i>Thinopyrum intermedium</i> (Host) Barkworth & D.R. Dewey		
<i>Tragopogon dubius</i> Scop.		

Appendix B: Species correlations (Pearson  $|r| > 0.4$ ) with nonmetric multidimensional scaling (NMS) of 2013 relative cover.

Species positively correlated with NMS Axes:

Axis 1	Axis 2	Axis 3
<i>Anemone canadensis</i>	<i>Achillea millefolium</i>	<i>Agrostis scabra</i> Willd.
<i>Bromus inermis</i>	<i>Cirsium flodmanii</i>	<i>Amorpha canescens</i> Pursh
<i>Cirsium arvense</i>	<i>Comandra umbellata</i>	<i>Andropogon gerardii</i> Vitman
<i>Glycyrrhiza lepidota</i>	<i>Galium boreale</i>	<i>Comandra umbellata</i>
<i>Helianthus maximiliani</i>	<i>Geum triflorum</i> Pursh	<i>Helianthus pauciflorus</i>
<i>Sonchus arvensis</i> L.	<i>Hesperostipa comata</i>	<i>Hesperostipa spartea</i>
<i>Spartina pectinata</i>	<i>Nassella viridula</i>	<i>Melilotus albus</i>
	<i>Pediomelum esculentum</i> (Pursh) Rydb.	<i>Rosa arkansana</i>
	<i>Potentilla arguta</i> Pursh	<i>Symphoricarpos occidentalis</i>
		<i>Vernonia fasciculata</i>

Species negatively correlated with NMS Axes:

Axis 1	Axis 2	Axis 3
<i>Artemisia frigida</i>	<i>Agropyron cristatum</i> (L.) Gaertn.	<i>Asclepias viridiflora</i>
<i>Artemisia ludoviciana</i>	<i>Bromus inermis</i>	<i>Erysimum inconspicuum</i> (S. Watson) MacMill.
<i>Astragalus flexuosus</i>	<i>Calamovilfa longifolia</i> (Hook.) Scribn.	<i>Lactuca tatarica</i> (L.) C.A. Mey.
<i>Bouteloua gracilis</i>	<i>Helianthemum bicknellii</i> Fernald	<i>Melilotus officinalis</i>
<i>Carex filifolia</i>	<i>Lotus unifoliolatus</i>	
<i>Carex inops</i>	<i>Medicago lupulina</i> L.	
<i>Comandra umbellata</i>		
<i>Dichanthelium wilcoxianum</i>		
<i>Hesperostipa comata</i>		
<i>Heterotheca stenophylla</i> (A. Gray) Shinnars		
<i>Liatris punctata</i>		
<i>Nassella viridula</i>		
<i>Oenothera suffrutescens</i>		
<i>Pascopyrum smithii</i>		
<i>Pediomelum argophyllum</i>		

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Appendix B (Cont'd)

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Species negatively correlated with NMS Axes:

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Axis 1

Axis 2

Axis 3

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*Polygala alba* Nutt.

*Ratibida columnifera*

*Selaginella densa* Rydb.

*Sphaeralcea coccinea*

*Symphyotrichum ericoides*

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