

Importance of species diversity in the revegetation of Alberta's northern fescue prairies

Jay Woosaree¹ · Rafael Otfinowski²

Received: 16 March 2017 / Revised: 30 August 2017 / Accepted: 25 October 2017 /

Published online: 31 October 2017

© Springer Science+Business Media B.V. 2017

Abstract Restoration of grassland ecosystems is critical to the provision of ecosystem services, however, legacies of historic disturbances pose a challenge to grassland restoration. In the northern Great Plains of North America, continued fragmentation and disturbance of northern fescue prairies has prompted more stringent criteria to regulate the revegetation of native prairies disturbed by industrial activities. Here, we evaluate methods of revegetating northern fescue prairies, disturbed by energy development, and test the hypothesis that higher richness of species seeded within disturbed areas improves the structure, diversity, and composition of revegetated communities. Our results demonstrate that disturbed northern fescue prairies are able to recover their structural elements, including vegetative and ground cover and plant litter, irrespective of the number of species in the seed mixes, even though revegetated areas remained similar in all measures of community diversity. Despite this, revegetated areas remained compositionally different from adjacent native prairies, 7 years following seeding treatments. Based on our observations, the persistent differences in the species composition of disturbed and undisturbed prairies highlight that all efforts should be practiced to minimize the scale of disturbance of northern fescue prairies through energy development.

Keywords Ecological function · Native prairie · Restoration · Species richness · Grassland diversity

Communicated by Anurag chaurasia.

✉ Rafael Otfinowski
r.otfinowski@uwinnipeg.ca

¹ Woosaree Environmental Inc., Edmonton, AB T6K 0T1, Canada

² Department of Biology, University of Winnipeg, 515 Portage Avenue, Winnipeg, MB R3B 2E9, Canada

Introduction

Restoration of grassland ecosystems is critical to the provision of ecosystem services, including carbon storage, water regulation, and biodiversity (Gos et al. 2016; Lal 2011; Liebman et al. 2013). However, in many regions only small fragments of grasslands remain (Roch and Jaeger 2014), often isolated by areas of intense agriculture (Öster et al. 2009). Efforts to restore native and semi-natural grasslands are occurring throughout North America and other parts of the world to increase biodiversity and reconnect natural landscapes (Gerla et al. 2012). However, legacies of historic disturbances pose a challenge to grassland restoration (Foster et al. 2003). As a result, restoration thresholds need to be tested and long term monitoring continued to evaluate restoration success (Kreuter et al. 2016) and help guide restoration science and practice (Higgs et al. 2014).

In the northern Great Plains in North America, rough fescue prairies, once a dominant vegetation community in the Aspen Parkland ecoregion, have become increasingly rare as a result of the extirpation of plains bison (*Bison bison*), suppression of natural fires, and increased agricultural production and energy development (Anderson and Bailey 1980; Trotter 1986; Campbell et al. 1994). These impacts have increased the fragmentation and loss of rough fescue prairies and increased the abundance of invasive species (Ofinowski et al. 2007; Qiu et al. 2007). Less than 5% of historic fescue prairie remains in Manitoba and Saskatchewan (Qiu et al. 2007) and public land and conservation managers are concerned with continued development that threatens prairie remnants (Alberta Environment and Parks 2016). As a result, provinces in western Canada continue to apply more stringent criteria to regulate the revegetation of disturbed native prairies. For example, in Alberta, recent regulations stipulate that disturbed prairies must be revegetated to pre-disturbance conditions and recommend minimizing disturbance (Alberta Environment 2010).

Historically, restoration of native grasslands disturbed by energy development relied on re-contouring of land and the seeding of agronomic, exotic forages to stabilize soil (Kreuter et al. 2016). However, many of these species are highly competitive and their use excludes native prairie species from re-establishing in revegetated areas (Downey et al. 2013). In some cases, exotic forages such as smooth brome grass (*Bromus inermis*), crested wheatgrass (*Agropyron cristatum*), Kentucky bluegrass (*Poa pratensis*), and Canada bluegrass (*Poa compressa*), invade native prairies adjacent to disturbed areas, reducing their diversity and simplifying their structural composition (Bakker et al. 2003; Carrigy et al. 2016).

In Alberta, land management agencies have stopped recommending invasive, exotic forages to revegetate oil and gas leases situated on native grassland and have recently adopted a set of best practices to guide restoration in areas of northern fescue prairie (Alberta Environment and Parks 2016). Cultivars of wheatgrasses are commonly used in revegetation, as they are most available in large quantities, relatively cheap, and establish rapidly. Although wheatgrass cultivars provide a valuable alternative to invasive, exotic forages, some public land and conservation managers are concerned about the loss of species diversity, their persistence, and their effects on native species (Alberta Environment and Parks 2016) in revegetated areas, compared with adjacent, native prairie communities. The problem is further confounded by older regulations that stipulated rapid establishment of 80% plant cover on disturbed areas (Alberta Environment 2010). In response, industries often used high seeding rates to increase vegetative cover of disturbed areas (Downey et al. 2013).

Another important question relates to the diversity of restored areas. Current regulations stipulate the re-establishment of the diversity and structure of communities comparable to



Fig. 1 Distribution of study sites in east-central Alberta, Canada used to evaluate the importance of species richness in the revegetation of northern fescue prairies disturbed by energy development in east-central Alberta, Canada. Inset map (<http://data.canadensys.net/>)

undisturbed, reference communities (Alberta Environment 2010). However, long-term evaluations of the efficacy of various revegetation techniques is lacking, as is the effect of these treatments on the re-establishment of species diversity (Kreuter et al. 2016). For example, several studies from areas of tallgrass prairie in North America have found that regardless of the diversity of seed mixes used for restoration, sites never reach comparable levels of diversity to reference sites and actually decrease in diversity over time (Camill et al. 2004; Hansen and Gibson 2014; Klopff et al. 2017). In this research, we evaluate the long-term revegetation of abandoned wellsites located in areas of northern fescue prairie in east-central Alberta. The goal of this project is to evaluate methods of revegetating wellsites and to test the hypothesis that more species-rich seeding mixes improve the structure, diversity, and composition of revegetated communities.

Materials and methods

Study area

To evaluate the role of species diversity in wellsite reclamation, we selected three northern fescue prairies situated within the Dark Brown Chernozemic soil zone in east-central Alberta (Alberta Agriculture and Forestry 2016). Sites were selected to be surrounded by representative, healthy northern fescue prairies (range condition: 75–100%). Topography in this area is hummocky to rolling with medium to fine textured glacial till deposits (Downing and Pettapiece 2006). Two of the sites, Brownfield (Lat. 52.3168°, Lon. – 111.4350°) and Neutral Hills (Lat. 52.2334°, Lon. – 110.9517°) were located within the Northern Fescue Natural Subregion (Downing and Pettapiece 2006), the third site, Hand Hills (Lat. 51.5001°, Lon. – 112.2851°), was located in the Central Parkland Natural Subregion (Fig. 1). Northern fescue prairies in this region are dominated by plains rough fescue (*Festuca hallii*), which forms dense stands on undisturbed sites. In lightly grazed areas, it commonly occurs with northern porcupine grass (*Hesperostipa curtisetata*), needle-and-thread grass (*Hesperostipa comata*), slender wildrye (*Elymus trachycaulus* subsp. *trachycaulus*), Hooker's oatgrass (*Helictochloa hookeri*), prairie junegrass (*Koeleria macrantha*), and a variety of perennial herbs, including prairie crocus (*Pulsatilla nuttalliana*), fringed sage (*Artemisia frigida*), wild blue flax (*Linum lewisii* var. *lewisii*), northern bedstraw (*Galium boreale*), and three-flowered avens (*Geum triflorum*) (Downing and Pettapiece 2006; Thorpe et al. 2015). Common upland sedges include blunt sedge (*Carex obtusata*), needle-leaved sedge (*Carex duriuscula*) and long-stolon sedge (*Carex inops*) (Thorpe et al. 2015). Moist, moderately well drained sites often support shrub communities, including shrubby cinquefoil (*Dasiphora fruticosa*), silverberry (*Elaeagnus commutata*), prickly rose (*Rosa acicularis*), and saskatoon (*Amelanchier alnifolia*) (Downing and Pettapiece 2006). Prairies surrounding the three study sites were grazed annually by cattle or harvested for hay and can be classified as healthy, modified by the presence of non-native forages, including smooth brome (*Bromus inermis*) and Kentucky bluegrass (*Poa pratensis*) (Adams et al. 2009). These sites receive a mean annual precipitation of 372 mm in the Northern Fescue Natural Subregion and 397 mm in the Central Parkland Subregion (Downing and Pettapiece 2006).

Table 1 Seeding treatments used to evaluate the importance of species richness in the revegetation of northern fescue prairies disturbed by energy development in east-central Alberta, Canada

Species	PLS/m ² (species)	PLS/m ² (total)	Proportion of mix (seed %)
Reclamation mix			
<i>Festuca hallii</i>	400	600	67
<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	200	600	33
Simple mix			
<i>Festuca hallii</i>	400	600	67
<i>Nassella viridula</i>	100	600	16.5
<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	45	600	7.5
<i>Koeleria macrantha</i>	30	600	5
<i>Hesperostipa curisetata</i>	25	600	4
Diverse mix			
<i>Festuca hallii</i>	400	600	67
<i>Nassella viridula</i>	50	600	8.3
<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	40	600	6.7
<i>Hesperostipa curisetata</i>	25	600	4.2
<i>Elymus lanceolatus</i> subsp. <i>lanceolatus</i>	20	600	3.3
<i>Koeleria macrantha</i>	15	600	2.5
<i>Pascopyrum smithii</i>	10	600	1.7
<i>Festuca saximontana</i>	6	600	1
<i>Heterotheca villosa</i>	10	600	1.7
<i>Vicia americana</i>	8	600	1.3
<i>Achillea millefolium</i>	2	600	0.3
<i>Anemone multifida</i>	2	600	0.3
<i>Erigeron glabellus</i>	2	600	0.3
<i>Gaillardia aristata</i>	2	600	0.3
<i>Hedysarum</i> spp.	2	600	0.3
<i>Penstemon procerus</i>	2	600	0.3
<i>Potentilla gracilis</i>	2	600	0.3
<i>Solidago rigida</i>	2	600	0.3

Nomenclature according to Canadensys (Brouillet et al. 2010). Two additional treatments: natural (disturbed, unseeded) and control (undisturbed prairie), were not seeded

Experimental design

At each site, we used the following five treatments to test the importance of species richness of seed mixes on the structure, diversity, and composition of revegetated fescue prairie communities: (1) natural (disturbed, unseeded); (2) reclamation mix (disturbed, seeded with two species); (3) simple mix (disturbed, seeded with five dominant species found in control prairie); (4) diverse mix (disturbed, seeded with 15 species); and (5)

control (undisturbed prairie) (Table 1). Direct seeding was used as it is the most widely accepted practice in the oil and gas industry and is a common technique used for prairie restoration (Rowe 2010). A Fabro plot-seeder (Fabro Enterprises Ltd, Swift Current, Saskatchewan) with double disk openers and rubber packer wheels was used for seeding. Sites were seeded using 20 cm row-spacing at a depth of 1.2–1.9 cm (1/2 to 3/4 inches). Seed mix composition was adjusted for seed weight and percent seed viability/purity. Seed viability was based on tetrazolium testing (TZ) from seed analysis certificates and expressed as a proportion. Legume seeds were scarified prior to seeding. Treatments were seeded at a rate of 600 PLS/m² (12–18 kg/ha) based on recommendations for native grass seed mixes (Hardy BBT Limited 1989; Kerr et al. 1993; Morgan et al. 1995). Pure live seed (PLS) was calculated as the product of the purity and viability of seed of each species and used to express the quality of each seed lot (Diboll 1997). In all seeded treatments, rough fescue was cross-seeded (diamond seeded) to the other species to reduce competitive effects of other species on fescue establishment. Species taxonomy follows *Canadensys* (Brouillet et al. 2010).

Each study site (100 m × 100 m) was divided into four 50 × 50 m plots and each was randomly assigned one of four seeding treatments (Table 1). Control treatments were situated in areas of undisturbed fescue prairie, adjacent to each site. A 5 m border was left around each plot, creating a 10 m buffer zone between neighbouring treatments. Four 30 m long transects were set up within each treatment (north–south orientation), ten meters apart. Transects were also established in each control, undisturbed prairie. These were placed 10–15 m from the sides of restored areas and parallel to them. Transects in control areas were 60 m long and surrounded the wellsite on four sides (north–south and east–west). Longer transects in the control areas permitted sampling along the entire length of each study site (100 m). Along each transect, 16 sampling points were selected at regular intervals (2 m—seeded areas, 4 m—control areas) and used to assess vegetation in each treatment plot. Daubenmire quadrats (20 × 50 cm, inside dimensions; Daubenmire 1959), placed northeast of each sampling point, were used to describe plant community structure and composition. Percent cover at ground level of live vegetation, plant litter, and bare ground were monitored for 10 years following seeding (1997–2000, 2004, 2007–2008). Vegetative cover was estimated using six cover classes (0–5%, 5–25%, 25–50%, 50–75%, 75–95%, 95–100%; Daubenmire 1959) and divided into the following categories: plains rough fescue; volunteer, non-seeded species (weedy grasses and forbs); and woody species. Few woody species were recorded and these were excluded from the analyses. Weedy species were defined as vascular, flowering plants, non-native to Canada (Brouillet et al. 2010).

Data analyses

We used linear mixed-effects models to compare community structure among the five seeding treatments. Structural measurements, including vegetative and litter cover, bare soil, abundance of weeds and plains rough fescue, were $\log(x + 1)$ transformed, but remained not normally distributed (Shapiro–Wilk test: $W = 0.88812$ – 0.9381 , $p < 0.0003$). As a result, we examined the effect of seeding treatments on the structure of plant communities using linear mixed-effects models (Bolker et al. 2009) (package “lme4” in R version: 1.1-10) and used the restricted maximum likelihood (REML) algorithm to estimate fixed-effect parameters. Fixed-effect variables accounted for the year since seeding (1997, 1998, 1999, 2000, 2007, 2008) and seeding treatment. In addition, study sites ($n = 3$) were assigned as random effects for each model.

Table 2 Linear mixed-effects models comparing differences in the structure of plant communities among five seeding treatments used to revegetate areas of northern fescue prairie disturbed by energy development in east-central Alberta, Canada

Variables describing the structure of plant communities were log ($x + 1$) transformed. Fixed-effect variables accounted for the year since seeding (ann: 1997–2000, 2007–2008) and seeding treatment (see Table 1 for details of seeding treatments). Sites ($n = 3$) were assigned as the random effect for each model

Variable	Fixed effects	F value	DF	p	AIC
Model					
Cover	Ann	39.75	5	< 0.0001	89.72
	Treat	7.65	4	< 0.0001	
	Ann:treat	1.29	20	0.2225	
	Error		58		
Litter	Ann	64.55	5	< 0.0001	183.95
	Treat	2.95	4	0.027	
	Ann:treat	3.14	20	< 0.001	
	Error		58		
Bare soil	Ann	54.33	5	< 0.0001	210.11
	Treat	11.22	4	< 0.0001	
	Ann:treat	3.33	20	< 0.001	
	Error		58		
Weed cover	Ann	0.18	5	0.9674	256.33
	Treat	29.20	4	< 0.0001	
	Ann:treat	0.25	20	0.9994	
	Error		58		
Fescue	Ann	4.03	5	< 0.001	238.65
	Treat	21.50	4	< 0.0001	
	Ann:treat	2.93	20	< 0.0001	
	Error		58		

We compared the diversity of plant communities among revegetation treatments using measures of within-community and between-community diversity. Between-community diversities were defined as slopes of species area curves, calculated using species shared and unique to a pair of quadrats (Oksanen et al. 2016). We separated within-community diversity into species richness (s), diversity (H') effective richness, and evenness (Pielou’s J), and compared their means within each seeding treatment using one-way ANOVA, blocked by study site. Diversity ($H' = - \sum p_i \log p_i$), effective richness ($N_1 = e^{H'}$), and evenness [$J = H'/\log(s)$], describe plant communities based on the proportional abundance of their species and the shape of their frequency distributions and can be used to examine the effect of management treatments (Legendre and Legendre 2012). In contrast with species richness (s), effective richness (N_1) expresses the entropy of species diversity (H') in terms of the number of species (Hill 1973). Differences in the composition of plant communities among seeding treatments were further contrasted using redundancy analysis (Legendre and Legendre 2012). Ordination axes were based on log-transformed species abundances and were selected to maximize linear combinations between species abundances and the seeding treatments. Gaps in survey years were created as a consequence of the availability of resources and field staff and were not part of the initial experimental design. As a result, data collected during five survey years (1998, 1999, 2000, 2007, 2008) were used to analyze the structure of the restored communities and data collected during the 2004 surveys were used to compare the species composition of restored communities. All statistical analyses were conducted using R (version 3.3.2) (R Core Team 2016).

Fig. 2 Differences in the structural elements of revegetated northern fescue prairies in east-central Alberta, Canada, including total vegetative cover (a), litter and bare soil (b, c), cover of weedy grasses and forbs (volunteer, non-seeded species) (d), and abundance of plains rough fescue (*Festuca hallii*) (e). Structure within revegetated prairies was contrasted among five seeding treatments, following disturbance from energy development. Boxplots illustrate medians, upper and lower quartiles, and the minimum and maximum values of each variable

Results

Plant community structure

Vegetative cover increased significantly between 1997 and 2008 ($F_{5,58} = 39.75$, $p < 0.0001$; Table 2, Fig. 2a), however differences among treatments did not change consistently with time and the interaction between the year of seeding and seeding treatment was not significant ($F_{20,58} = 1.29$, $p = 0.2225$). Litter cover was initially highest among control treatments ($F_{4,58} = 2.95$, $p = 0.027$; Table 2, Fig. 2b), however plant litter accumulated with time for the remaining treatments ($F_{20,58} = 3.14$, $p < 0.001$; Table 2) with values of plant litter in the year 2000 higher compared to other years (Fig. 2b). Over time, increasing vegetative cover was reflected in a decline in the proportion of bare soil found in all treatments ($F_{5,58} = 54.33$, $p < 0.0001$; Table 2), however the low proportion of bare soil in the control treatment (Fig. 2c), contributed to the significant interaction between the sampling year and the remaining seeding treatments ($F_{20,58} = 3.33$, $p < 0.001$). The proportion of weeds remained highest in the natural revegetation treatment ($F_{4,58} = 29.20$, $p < 0.0001$; Table 2, Fig. 2d) and did not significantly change with time for any of the revegetation treatments ($F_{20,58} = 0.25$, $p = 0.9994$; Table 2). In contrast, although fescue cover remained highest in the control treatment ($F_{4,58} = 21.50$, $p < 0.0001$; Fig. 2e), it increased significantly between 1997 and 2008 for all treatments ($F_{20,58} = 2.93$, $p < 0.0001$; Table 2, Fig. 2e).

Plant community diversity and composition

Plant communities remained significantly different among the seeding treatments. Beta-diversities among plant communities changed significantly between treatments ($F_{4,14} = 1.8271$, $p = 0.002$). Despite this, means of species richness, diversity, effective richness, and evenness were not significantly different among seeding treatments ($p > 0.05$; Table 3). Differences in the composition of revegetated plant communities were influenced by the abundance of native and weedy species. The first axis of the constrained ordination ($F_{1,10} = 4.32$, $p = 0.003$) accounted for 22.6% of the correlation between species abundances and seeding treatments and separated quadrats found in the reference community, characterized by a higher abundance of native sedges (*Carex* spp.) and bryophytes (Fig. 3) from quadrats in all disturbed treatments. The second ordination axis ($F_{1,10} = 2.42$, $p = 0.008$) accounted for an additional 12.7% of correlation between species abundances and seeding treatments and separated quadrats in the simple and diverse revegetation treatments, dominated by rough fescue (*Festuca hallii*), green needlegrass (*Nassella viridula*), and common yarrow (*Achillea millefolium*), from those in the natural revegetation treatment, dominated by the exotic smooth brome (*Bromus inermis*) (Fig. 3).

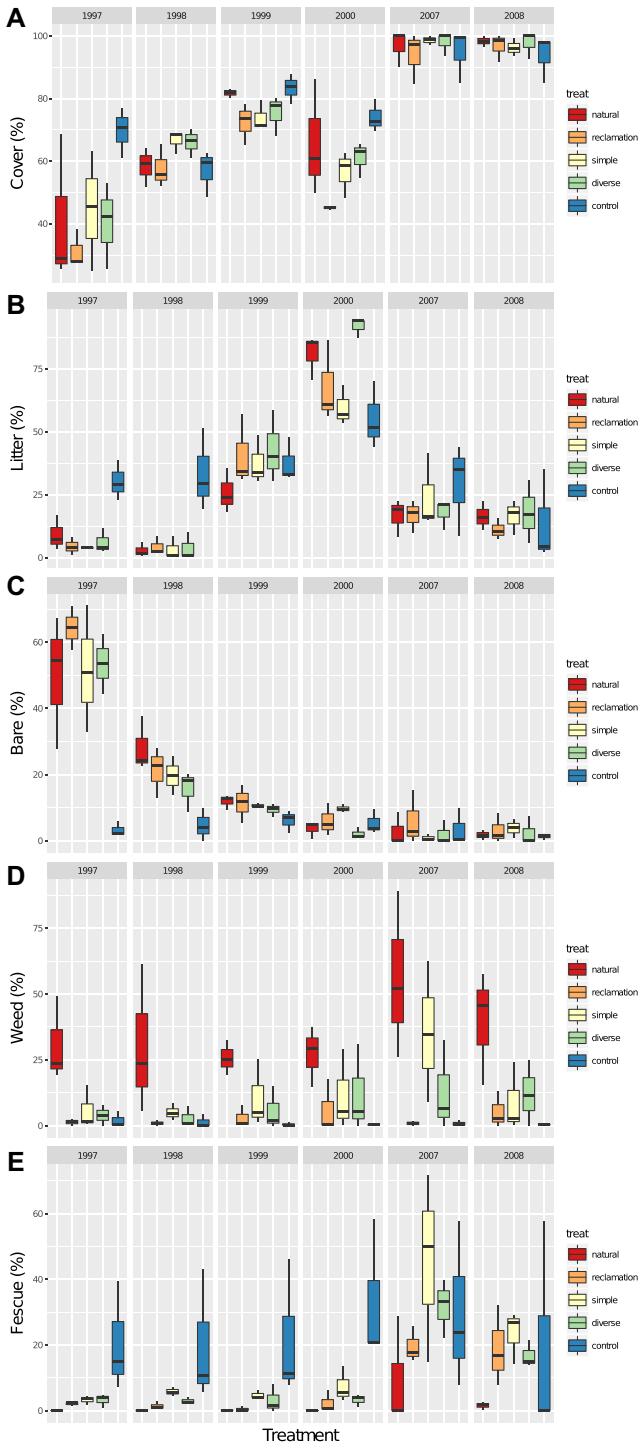


Table 3 Means (\pm SD) of top ten most abundant species within five treatments used to revegetate northern fescue prairies disturbed by energy development in east-central Alberta, Canada

Natural Species	Reclamation		Simple		Diverse		Control	
	Mean \pm SD	Species	Mean \pm SD	Species	Mean \pm SD	Species	Mean \pm SD	Species
<i>Bromus inermis</i>	18.8 \pm 13.8	<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	8.2 \pm 3.3	<i>Festuca hallii</i>	11.4 \pm 9.2	<i>Festuca hallii</i>	14.4 \pm 18.3	<i>Bryophyte</i>
<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	8.2 \pm 9.2	<i>Artemisia ludoviciana</i>	7.8 \pm 11.7	<i>Nassella viridula</i>	12.7 \pm 10.8	<i>Achillea millefolium</i>	14.1 \pm 7.3	<i>Carex</i> spp.
<i>Poa pratensis</i>	6.2 \pm 10.8	<i>Vicia americana</i>	6.6 \pm 8.4	<i>Elymus trachycaulus</i> subsp. <i>subsecundus</i>	7.4 \pm 7.0	<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	10.3 \pm 9.5	<i>Festuca hallii</i>
<i>Artemisia ludoviciana</i>	4 \pm 4.4	<i>Achillea millefolium</i>	4.4 \pm 6.0	<i>Achillea millefolium</i>	6 \pm 10.0	<i>Nassella viridula</i>	2.9 \pm 2.1	<i>Pulsatilla nuttalliana</i>
<i>Ribes hirtellum</i>	3.8 \pm 6.5	<i>Symphoricarpos occidentalis</i>	4.2 \pm 4.1	<i>Poa</i> spp.	4.2 \pm 6.7	<i>Cerastium arvense</i>	2.8 \pm 4.9	<i>Bouteloua gracilis</i>
<i>Cerastium arvense</i>	3.3 \pm 5.8	<i>Festuca hallii</i>	3.7 \pm 3.6	<i>Elymus trachycaulus</i> subsp. <i>trachycaulus</i>	3.3 \pm 3.1	<i>Taraxacum officinale</i>	2.8 \pm 3.2	<i>Geum triflorum</i>
<i>Artemisia frigida</i>	2.9 \pm 4.6	<i>Fragaria virginiana</i>	2.1 \pm 3.6	<i>Bromus inermis</i>	3.3 \pm 2.9	<i>Artemisia frigida</i>	2.5 \pm 2.2	<i>Koeleria macrantha</i>
<i>Carex</i> spp.	2.1 \pm 3.6	<i>Rosa woodsii</i>	1.5 \pm 2.6	<i>Artemisia frigida</i>	2.8 \pm 3.7	<i>Vicia americana</i>	2.2 \pm 2.0	<i>Antennaria parvifolia</i>
<i>Taraxacum officinale</i>	1.8 \pm 2.8	<i>Solidago missouriensis</i>	0.9 \pm 1.4	<i>Vicia americana</i>	2.6 \pm 3.8	<i>Ribes hirtellum</i>	1.6 \pm 2.7	<i>Artemisia frigida</i>
<i>Cirsium arvense</i>	1.7 \pm 1.9	<i>Artemisia frigida</i>	0.8 \pm 1.4	<i>Symphoricarpos occidentalis</i>	2.3 \pm 4.0	<i>Mulgedium pulchellum</i>	1.5 \pm 1.1	<i>Hesperostipa comata</i>

Table 3 continued

Natural Species	Reclamation		Simple		Diverse		Control	
	Mean ± SD	Species	Mean ± SD	Species	Mean ± SD	Species	Mean ± SD	Species
Richness (s)	15 ± 5.3		16 ± 7.5		13 ± 6		15 ± 3.6	
Shannon's diversity (<i>H'</i>)	1.92 ± 0.49		2.19 ± 0.63		1.92 ± 0.43		1.99 ± 0.35	
Effective richness (<i>eH'</i>)	7.22 ± 3.72		10 ± 5.14		7.27 ± 3.32		7.59 ± 2.79	
Evenness [<i>J=H'/ln(s)</i>]	0.7 ± 0.09		0.8 ± 0.08		0.77 ± 0.08		0.73 ± 0.06	

Exotic species are highlighted in bold. Means of species diversity (richness, Shannon's diversity, effective richness, evenness) among treatments were not significant (one-way ANOVA, $p > 0.05$)

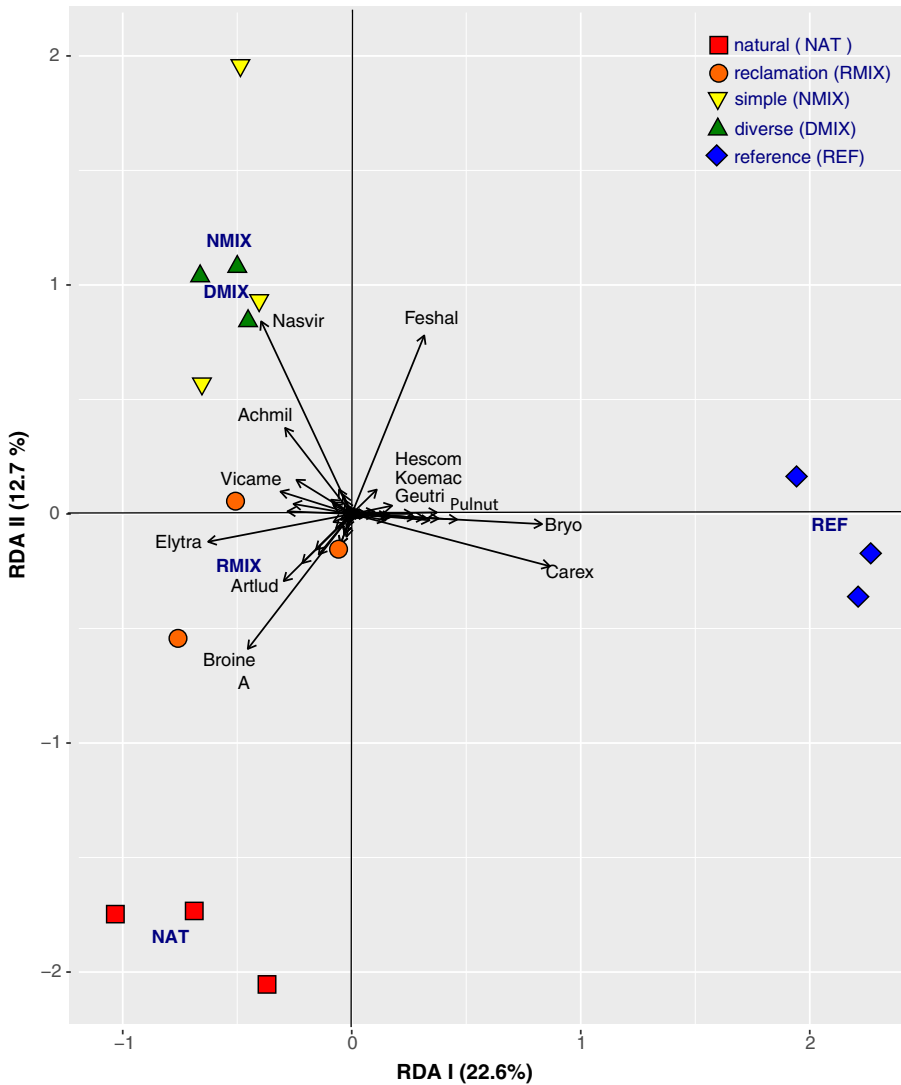


Fig. 3 Redundancy analysis of the abundances of plant species constrained by five seeding treatments across three sites disturbed by energy development in east-central Alberta, Canada. Species vectors were scaled proportional to eigenvalues and only species with eigenvectors elements ≥ 0.3 or ≤ -0.3 are presented for clarity. Achmil (*Achillea millefolium*), Broine (*Bromus inermis*), Bryo (bryophyte), Carex (*Carex* spp.), Elytra (*Elymus trachycaulus* subsp. *trachycaulus*), Feshal (*Festuca hallii*), Geutri (*Geum triflorum*), Hescom (*Hesperostipa comata*), Koemac (*Koeleria macrantha*), Nasvir (*Nassella viridula*), Pulnut (*Pulsatilla nuttalliana*), Vicame (*Vicia americana*). Nomenclature according to Canadensys (Brouillet et al. 2010)

Discussion

Our results demonstrate that disturbed northern fescue prairies are able to recover their structural elements, including vegetative and ground cover and plant litter, irrespective of the species richness of seeding treatments. Despite significant differences in the composition of plant communities among revegetation treatments, richness, diversity, and evenness of revegetated communities did not differ significantly in response to the seeding richness. The observed success to recover structural elements of revegetated communities challenges the traditional aim of restoration to maintain the fidelity of historic reference communities (Hansen and Gibson 2014). As a result, despite persistent differences in the composition of revegetated communities compared with reference northern fescue prairies, even the low diversity seed mix provided soil cover and established a more structurally comparable plant community on areas of disturbed northern fescue prairie. These simple communities were dominated by slender wheatgrass (*Elymus trachycaulus*) and included a high cover of plains rough fescue (*Festuca hallii*), native forbs, and a low proportion of weeds.

The choice of methods to restore biodiversity depends on their feasibility, costs and the restoration goals (Torok et al. 2011; Gerla et al. 2012). Our results illustrate that even simple mixes of two native species can help re-establish community structure, including vegetative and soil cover, and establish a plant community with a reduced abundance of weeds. However, the success of grassland restoration depends on site conditions, legacies of historic disturbances, the availability of propagules and/or donor sites, and on the budget and time available for restoration (Foster et al. 2003; Torok et al. 2011). Restoration of disturbed northern fescue grasslands is slow and complicated by the intensity of historic disturbance. In our study, the period of 7 years was insufficient to re-establish plant communities that resemble the composition of undisturbed controls. Desserud and Naeth (2014) reported the persistence of exotic species 11 years after the disturbance by oil and gas activity and recommended the used of minimum disturbance methods in native grasslands, such as plow-in pipelines and small areas well sites. For example, Desserud et al. (2010) reported higher cover of mountain rough fescue (*Festuca campestris*) on pipeline right of ways in Alberta, characterized by low disturbance, regardless of their age. Regional climates and site conditions also effect the rate of and the trajectory natural revegetation. For example, in semiarid grasslands in the short-grass steppe region of North America, Coffin et al. (2004) suggest that community recovery could take longer than 50 years, and abandoned cultivated steppe in the hemi-boreal forest eco-region of Western Siberia did not resemble reference prairie communities 24 years after abandonment (Kämpf et al. 2016).

The success of natural restoration of disturbed grasslands depends on the integrity of surrounding landscapes and on the successful dispersal and establishment of native species (Öster et al. 2009). In our study, natural recovery of unseeded treatments was more variable within and especially among sites compared to other seeded treatments. Although weeds remained most prevalent in the natural recovery treatment, recruitment of resident native species may also have been lower compared to seeded areas due to beneficial soil packing from the seeding operation that likely favored plant establishment. However, seed recruitment of resident native species has become greater on the natural recovery areas over time and a small proportion of the community included native species, including prairie sage (*Artemisia ludoviciana*), northern gooseberry (*Ribes hirtellum*), field chickweed (*Cerastium arvense*), and fringed sage (*Aremisia frigida*). In addition, total

vegetative cover and biomass became comparable to seeded areas. Although these results are encouraging, the small size of our trial areas likely contributed to the establishment of native species (Öster et al. 2009).

Given the historic importance of fire in maintaining the structure and diversity of northern fescue prairies (Anderson and Bailey 1980), burning could also be used to increase the emergence of native seeds stored in the seedbank (Ren and Bai 2017) and improve the ecological function of revegetated prairies (Klopf et al. 2017). Such recruitment from seed may not be feasible in larger areas and not viable to prevent the establishment of exotic species (Ravel 1993; Torok et al. 2011). In our experiment, naturally disturbed areas became dominated by smooth brome (*Bromus inermis*), an invasive exotic of the northern fescue prairies. The persistence of smooth brome and its ability to establish and restrict the establishment of native species following disturbance (Otfinowski and Kenkel 2009) could seriously impair the ability of the naturally revegetated areas to reestablish without intense management (Bakker et al. 2003).

Our results illustrate that the efficacy of using diverse seed mixes to restore disturbed areas depends on the measure of restoration success. For example, while, structurally the vegetative cover, bare soil, and the cover of weeds declined with time for all seeded treatments, the composition of seeded area remained distinct from adjacent native prairies. As a result, seed mixes have the potential to create ground cover and provide vegetative cover. Rapidly recovering ecological services should be measured and documented as soon as possible in order to help assure long-term support for restoration (Gerla et al. 2012). However, many important species characteristic of the northern rough fescue grasslands are not commercially available and may explain the differences in the composition of disturbed and native treatments. Despite the success to re-establish elements of the structural composition of disturbed northern fescue prairies, differences in the species composition of disturbed and undisturbed prairies illustrate that all efforts should be practiced to minimize the scale of disturbance of northern fescue prairies resulting from energy development.

Acknowledgements This research was funded by: Petroleum Technology Alliance of Canada through the Alberta Upstream Petroleum Research Fund and the University of Winnipeg. We gratefully acknowledged Patrick Porter, Land Management Branch, Alberta Environment & Parks, Wainwright; Heather Sinton, Alberta Environment & Parks, Calgary; Marshall McKenzie, Alberta Innovates Technology Futures, various industry operators that provided sites for the study and other collaborators from the former Alberta Research Council, namely Michelle Pahl, Byron James, and Natasha Page. We also acknowledge Nicholas Palaschuk, Department of Biology, University of Winnipeg.

References

- Adams BW, Ehler G, Stone C, Lawrence D, Alexander M, Willoughby M, Hincz C, Moisey D, Burkinshaw A, Carlson J, France K (2009) Rangeland Health Assessment for Grassland, Forest and Tame Pasture. Alberta Sustainable Resource Development Lands Division Rangeland Management Branch, Rangeland
- Alberta Agriculture and Forestry (2016) Agricultural Land Resource Atlas of Alberta—Soil Groups of Alberta. [http://www1.agric.gov.ab.ca/\\$department/deptdocs.nsf/all/agdex10307](http://www1.agric.gov.ab.ca/$department/deptdocs.nsf/all/agdex10307). Accessed 5 Feb 2017
- Alberta Environment and Parks (2016) Principles for Minimizing Surface Disturbance in Native Grassland: Principles, Guidelines and Tools for all Industrial Activity in Native Grasslands in the Prairie and Parkland Landscapes of Alberta. Edmonton, Alberta
- Anderson HG, Bailey AW (1980) Effects of annual burning on grassland in the aspen parkland of east-central Alberta. *Can J Bot* 58:985–996

- Bakker JD, Wilson SD, Christian JM, Li X, Ambrose LG, Waddington J (2003) Contingency of grassland restoration on year, site, competition from introduced grasses. *Ecol Appl* 13:137–153
- Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-SS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. *Trends Ecol Evol* 24:127–135
- Brouillet L, Coursol F, Meades SJ, Favreau M, Anions M, Bélisle P, Desmet P (2010) VASCAN, the Database of Vascular Plants of Canada. <http://data.canadensys.net/vscan/>. Accessed 24 Aug 2017
- Camill P, McKone MJ, Sturges ST, Severud WJ, Ellis E, Limmer J, Martin CB, Navratil RT et al (2004) Community- and ecosystem-level changes in a species-rich tallgrass prairie restoration. *Ecol Appl* 14:1680–1694
- Campbell C, Campbell ID, Blyth CB, McAndrews JH (1994) Bison extirpation may have caused aspen expansion in western Canada. *Ecography* 17:360–362
- Carrigy AA, Stotz GC, Dettlaff MA, Pec GJ, Inderjit Erbilgin N, Cahill JF (2016) Community-level determinants of smooth brome (*Bromus inermis*) growth and survival in the aspen parkland. *Plant Ecol* 217:1395–1413
- Coffin D, Lauenroth WK, Burke I (2004) Recovery of vegetation in a semiarid grassland 53 years after disturbance. *Ecol Appl* 6:538–555
- Daubenmire R (1959) A canopy-coverage method of vegetational analysis. *Northwest Sci* 33:43–64
- Desserud PA, Naeth AM (2014) Predicting grassland recovery with a state and transition model in a natural area, central Alberta, Canada. *Nat Area J* 34:429–442
- Desserud P, Gates CC, Adams B, Revel RD (2010) Restoration of foothills rough fescue grassland following pipeline disturbance in southwestern Alberta. *J Environ Manag* 91:2763–2770
- Diboll N (1997) Designing seed mixes. In: Packard S, Mutel CF (eds) *The tallgrass restoration handbook*. Island Press, Washington, pp 135–150
- Downey BA, Blouin F, Richman JD, Downey BL, Jones PF (2013) Restoring mixed grass prairie in southeastern Alberta, Canada. *Rangelands* 35:16–20
- Downing DJ, Pettapiece WW (2006) Natural regions and subregions of Alberta. Government of Alberta Report No.: Pub. No. T/852. Edmonton, Alberta
- Environment Alberta (2010) Reclamation criteria for wellsites and associated facilities for native grasslands. Government of Alberta, Edmonton
- Foster D, Swanson F, Aber J, Burke I, Brokaw N, Tilman D, Knapp A (2003) The importance of land-use legacies to ecology and conservation. *Bioscience* 53:77–88
- Gerla PJ, Cornett MW, Ekstein JD, Ahlering MA (2012) Talking big: lessons learned from a 9000 hectare restoration in the northern tallgrass prairie. *Sustainability* 4:3066–3087
- Gos P, Loucougaray G, Colace M-P, Arnoldi C, Gaucherand S, Dumazel D, Girard L, Delorme S, Lavorel S (2016) Relative contribution of soil, management and traits to co-variations of multiple ecosystem properties in grasslands. *Oecologia* 180:1001–1013
- Hansen MJ, Gibson DJ (2014) Use of multiple criteria in an ecological assessment of a prairie restoration chronosequence. *Appl Veg Sci* 17:63–73
- Higgs E, Falk DA, Guerrini A, Hall M, Harris J, Hobbs RT, Jackson ST, Rhemtulla JM, Throop W (2014) The changing role of history in restoration ecology. *Front Ecol Environ* 12:499–506
- Hill MO (1973) Diversity and evenness: a unifying notation and its consequences. *Ecology* 54:427–432
- Kämpf I, Mathar W, Kuzmin I, Hölzel N, Kiehl K (2016) Post-Soviet recovery of grassland vegetation on abandoned fields in the forest steppe zone of Western Siberia. *Biodivers Conserv* 25:2563–2580
- Kerr DS, Morrison LJ, Wilkinson KE (1993) Reclamation of native grasslands in Alberta: A review of the literature. Alberta Land Conservation and Reclamation Council Report No. RRTAC 93-1. Edmonton, Alberta
- Klopf RP, Baer SG, Bach EM, Six J (2017) Restoration and management for plant diversity enhances the rate of belowground ecosystem recovery. *Ecol Appl* 27:355–362
- Kreuter UP, Iwaasa AD, Theodori GL, Ansley RJ, Jackson RB, Fraser LH, Naeth MA, McGillivray S, Moya EG (2016) State of knowledge about energy development impacts on North American rangelands: an integrative approach. *J Environ Manag* 180:1–9
- Lal R (2011) Sequestering carbon in soils of agro-ecosystems. *Food Policy* 36:S33–S39
- Legendre P, Legendre L (2012) *Numerical ecology*. Elsevier, Amsterdam
- Liebman M, Helmers MJ, Schulte LA, Chase CA (2013) Using biodiversity to link agricultural productivity with environmental quality: results from three field experiments in Iowa. *Renew Agr Food Syst* 28:115–128
- Hardy BBT Limited (1989) *Manual of plant species suitability for reclamation in Alberta—2nd Edition*. Alberta Land Conservation and Reclamation Council Report No. RRTAC 89-4. Edmonton, Alberta
- Morgan JP, Collicutt DR, Thompson JD (1995) *Restoring Canada's native prairies*. Prairie Habitats, Argyle

- Oksanen J, Blanchet GF, Friendly M, Kindt R, Legendre P, McGlenn D, Minchin PR, O'Hara RB, Simpson GL, Solymos P, M. Stevens MHH, Szocs E, Wagner H (2016) vegan: Community Ecology Package. R package version 2.4-1. <https://CRAN.R-project.org/package=vegan>
- Öster M, Ask K, Cousins SAO, Eriksson O (2009) Dispersal and establishment limitation reduces the potential for successful restoration of semi-natural grassland communities on former arable fields. *J Appl Ecol* 46:1266–1274
- Otfinowski R, Kenkel NC (2009) Covariance between disturbance and soil resources dictates the invasibility of northern fescue prairies. *Biol Invas* 12:1349–1361
- Otfinowski R, Kenkel NC, Dixon P, Wilmshurst JF (2007) Integrating climate and trait models to predict the invasiveness of exotic plants in Canada's Riding Mountain National Park. *Can J Plant Sci* 87:1001–1012
- Qiu J, Fu Y-B, Bai Y, Wilmshurst J (2007) Patterns of amplified restriction fragment polymorphism in natural populations and corresponding seed collections of plains rough fescue (*Festuca hallii*). *Can J Bot* 85:484–492
- Ravel RD (1993) Canada's rough fescue grasslands. A trial restoration project in Alberta is yielding encouraging results. *Restor Manag Notes* 11:117–124
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria <https://www.R-project.org/>
- Ren L, Bai Y (2017) Burning modifies composition of emergent seedlings in fescue prairie. *Rangeland Ecol Manag* 70:230–237
- Roch L, Jaeger JAG (2014) Monitoring an ecosystem at risk: what is the degree of grassland fragmentation in the Canadian Prairies? *Environ Monit Assess* 186:2505–2534
- Rowe HI (2010) Tricks of the trade: techniques and opinions from 38 experts in tallgrass prairie restoration. *Restor Ecol* 18:253–262
- Thorpe J, Baldwin K, Allen L (2015) Great plains rough fescue prairie. Canadian National Vegetation Classification Macrogroup, Sault Ste. Marie
- Torok P, Vida E, Deak B, Lengyel S, Tothmeresz B (2011) Grassland restoration on former croplands in Europe: an assessment of applicability of techniques and costs. *Biodivers Conserv* 20:2311–2332
- Trottier GC (1986) Disruption of rough fescue, *Festuca hallii*, grassland by livestock grazing in Riding Mountain National Park, Manitoba. *Can Field Nat* 100:488–495