Examination of Fire-Related Succession Within the Dry Mixed-Grass Subregion of Alberta With the Use of MODIS and Landsat

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Abstract

Fire is an important disturbance process historically present across the northern Great Plains. Previous research from northern dry mixed-grass prairie suggests that C4 (warm season) grasses replace C3 (cool season) climax species with increasing fire, particularly in the spring. This hypothesis was tested at a landscape scale at Canadian Forces Base Suffield Alberta, by exploring the relationship between ecosystem states (C3 dominant, C3/C4 codominant, C4 dominant) inferred from a MODIS multitemporal plant functional type classification (pseudo R^2: 0.598, overall accuracy: 0.74) and interyear fire history digitized from the Landsat archive (1972–2007). Probit regression showed that succession processes were different between range sites, where C4-dominant pixels were positively related to fire ($P < 0.001$, pseudo $R^2 = 1$) and completely replaced C3-dominant pixels on loamy range sites after 14 fires in 36 yr. In contrast, C3- and C3/C4-codominant pixels were related with fire on Blowouts range sites ($P < 0.001$, pseudo $R^2 = 1$), where C3/C4-codominant pixels replaced C3-dominant pixels with increasing fire. Finally, there were no statistically significant relationships between ecosystem states and fire for Sands range sites. Analysis of recovery showed that after loamy pixels experienced three to six fires in 18 yr followed by 18 yr of rest, C3-dominant pixels were reduced by over 30% compared to unburned pixels. Finally, intrayear fire timing (2001–2009) was explored with the use of Wilcoxon signed-rank tests between the spatial extent of spring and summer fires, with the use of MODIS burned-area data. Results indicate that fires are not limited to the spring season ($P < 0.05$), but occur across the entire growing season. Although fire timing does not appear to play a role in driving succession, this ecosystem is generally sensitive to repeated fire, with recovery of C3 climax species taking decades.

Key Words: dry mixed grass, fire ecology, plant functional type, rangeland, succession

INTRODUCTION

Fire is a landscape-level disturbance historically present across the Great Plains, serving an important role in nutrient cycling, modifying vegetative structure, and plant succession (Daubenmire 1968; Wells 1970; Wright and Bailey 1982; Bragg 1995; Anderson 2006). However, human activities have altered fire regimes in the Great Plains (Hart and Hart 1997) such that the extent, frequency, and timing of fires are departed from their historical norms (Leach and Givnish 1996; Umbanhowar 1996). Because of a lack of historical information, experimental research is important in guiding the management of fire in rangelands (Scheintaub et al. 2009).

The effects of fire are different among rangeland ecosystems in North America. In tall-grass prairie (dominated by warm-season grasses with the use of the C4 photosynthetic pathway), fire has been shown to increase productivity (Wright and Bailey 1982; Briggs and Knapp 1995) and alter species composition (Abrams and Hulbert 1987; Stueter 1987; Collins and Gibson 1990). However, in northern mixed-grass prairie (dominated by cool-season grasses using the C3 photosynthetic pathway), fire can reduce productivity (Clarke et al. 1943; Redmann 1978), modify the ratio between C3 and C4 species (Steuter

1987), and the recovery of water-conserving litter can take many years (Dix 1960).

In northern mixed-grass prairie, regressive changes in species composition (retrogression; Glenn-Lewin and van der Maarel 1992) have been observed as a result of fire. In northern mesic mixed-grass prairie, fire reduced the cover of C3 climax species, including fescue (*Festuca hallii* [Vasey] Piper; Gerling et al. 1995), and wheatgrass (*Agropyron* [Hook.] Scribn.; Coupland 1973). Furthermore, spring fires have been shown to stimulate the production of western wheatgrass (*Pascopyrum smithii* [Rybd.] A. Love) and the warm-season grass blue grama (*Bouteloua gracilis* [Willd. Ex Kunth] Lag. Ex Griffiths; White and Currie 1983), particularly as a result of repeated fire (Shay et al. 2001). Within northern dry mixed-grass prairie, Vermeire et al. (2011) showed that western wheatgrass replaced needle and thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth) as the dominant species, following a single fire. In contrast, Erichsen-Arychuk et al. (2002) found that a single summer fire and drought did not affect the cover of needle and thread, but did differentially affect the cover of wheatgrass; wheatgrass cover was higher in burned than unburned treatments on upland sites, but the reverse was found on lowland sites.

Fire-related retrogression in northern mixed-grass prairie may be directly related to the selective suppression of a species or functional group (e.g., C3 species) based on fire timing, particularly spring fires (Anderson et al. 1970; White and Currie 1983; Schacht and Stubbendieck 1985; Redmann et al. 1993; Shay et al. 2001), or indirectly through the modification of structure (litter) important for conserving scarce moisture (Dix 1960; Redmann 1978; Willms et al. 1986; Dormaar and

Willms 1990; Willms et al. 1993; Dormaar et al. 1994; Vermeire et al. 2005). The removal of litter increases soil temperatures (Vermeire et al. 2005) and decreases productivity (Willms et al. 1986), because litter serves to reduce evapotranspiration, making more water available for plant growth (Willms et al. 1993).

Although the restoration of fire to rangelands has been recommended as a tool to support conservation (Bailey and Anderson 1978; White and Currie 1983; Gross and Romo 2010), information is typically unavailable to guide management because fire-history proxies (e.g., charcoal) are a limiting factor in identifying historical regimes. Experimental research is therefore important to fill the void (Scheintaub et al. 2009). However, very few field-based rangeland studies have been conducted at sufficient temporal scales to detect succession, or separate human impacts from natural variability (Washington-Allen et al. 2003). In contrast, ecological indicators derived by remote sensing can provide information at spatial and temporal scales relevant for rangelands management (Tueller 1989; Washington-Allen et al. 2006).

Remote sensing of plant functional types (PFTs) exploits the phenological differences between C3 (cool season) grasses, and C4 (warm season) grasses, with a classification scheme that falls between species-specific and broad vegetation types (Ustin and Gamon 2010). A remote-sensing approach designed to exploit phenological differences between PFTs is relevant in answering ecological questions (Adjorlolo et al. 2012), including land-use effects on ecosystem function (Tieszen et al. 1997) and ecosystem changes as a result of environmental change (Davidson and Csillag 2003). PFT-based remote sensing has the potential to complement field-based studies of fire ecology, by providing spatially explicit landscape-level information about plant composition.

The primary objective of this study was to examine the effect of repeated fires across a 36-yr (1972–2007) time span on plant communities across different range sites within the northern dry mixed-grass prairie. We achieved this by analyzing the spatial relationships between contemporary (2009) ecosystem states (C3 dominant, C3/C4 codominant, C4 dominant) inferred from a moderate resolution imaging spectroradiometer (MODIS) normalized difference vegetation index (NDVI) 250-m PFT classification (pseudo $R^2 = 0.598$, overall accuracy $= 74\%$, weighted kappa $= 0.53$), and interyear fire history digitized from the Landsat archive: the longest-available free satellite–remote-sensing archive (Woodcock et al. 2008). Based on previously established state-and-transition models, we hypothesized that 1) the proportion of C3-dominant communities would be negatively correlated with the total number of fires, whereas the proportion of C4-dominant communities would be positively correlated with the total number of fires, in the process of retrogression; 2) the proportion of C4-dominant communities would be lower, and the proportion of C3-dominant communities would be higher in pixels subjected to rest from fire compared to those undergoing burning, in the process of progressive succession; and 3) that fire timing—collected by MODIS monthly burned area data (Roy et al. 2008)—was not restricted exclusively to the spring months, and as a result, was not related to long-term succession.

METHODS

Study Area and Ecology

Canadian Forces Base Suffield is situated within the Northern Great Plains of North America, approximately 20 km north of Medicine Hat, Alberta, within the dry mixed-grass subregion of Alberta (Strong and Leggat 1992; Fig. 1). Vegetation is dominated by native grassland, interspersed with areas of abandoned cultivation where the land was broken prior to the establishment of the base in 1971. CFB Suffield is the largest Army training facility in Canada, with a total area of 2 690 km^2. Land-use disturbances at CFB Suffield include vegetation and soil compaction resulting from wheeled and tracked military vehicles, frequent fires resulting from various munitions, bare ground resulting from excavation and trenching of military and petroleum infrastructure, and vegetation trampling and removal by cattle grazing. Since the inception of military training (1972), exercises and associated fires generally commence in May and end in October, and result in areas that burn frequently (Fig. 1). Although frequent fires occur in the central areas of the base corresponding with military training, infrequent fires occur across its entirety. This diversity of fire frequency permits the statistical analysis of the spatial arrangement of ecosystem states inferred from MODIS, relative to fire history.

Plant communities within the study area fall within the *Stipa-Bouteloua* faciation described by Coupland (1950). The predominant C3 grasses by canopy cover are needle and thread (ubiquitous), and western wheatgrass and northern wheatgrass (*Agropyron dasystachyum* [Hook.] Scribn.), both of which are consistently present on solonetzic and very coarse-textured soils (Adams et al. 2005; Smith 2013). Of the five C4 grass species present—blue grama, sandreed grass (*Calamovilfa longifolia* [Hook.] Scribn.), sand dropseed (*Sporobolus cryptandrus* [Torr.] A. Gray), plains muhlenbergia (*Muhlenbergia cuspidata* [Trin.] Rydb.), and little bluestem (*Schizachyrium scoparius* [A. Michx.] Nees), only blue grama exists with canopy cover consistently greater than five percent at the landscape scale (Smith 2013). These C4 species are in the northern extent of their range and exist under conditions that are marginal for growth, and are highly responsive to subtle changes in environmental conditions (Davidson and Csillag 2003). For example, spring growth of blue grama begins only when the 10-d moving average soil temperature of the upper 15 cm exceeds 10.5°C (Detling et al. 1978).

Predominant range sites subject to ongoing land use include Blowouts (5% of study area; hardpan and solonetzic pits co-occurring with Loamy sites), Loamy (30%; typically associated with morainal landforms, and includes loam, silt loam, silt, clay loam, sandy clay loam, and silty clay loam soils), and Sands (20%; typically associated with glaciofluvial or low-relief eolian landforms, and includes loamy sand and sand soils; Alberta Sustainable Resource Development 2010). Each range site gives rise to distinct vegetation communities (climax/reference), and land-use disturbance results in succession that can generally be described by state-and-transition models (Bestelmeyer et al. 2003).

By long-term monitoring of vegetation and land use, species compositional changes were revealed by detrended correspondence analysis/DCA (McCune and Grace 2002), where species'
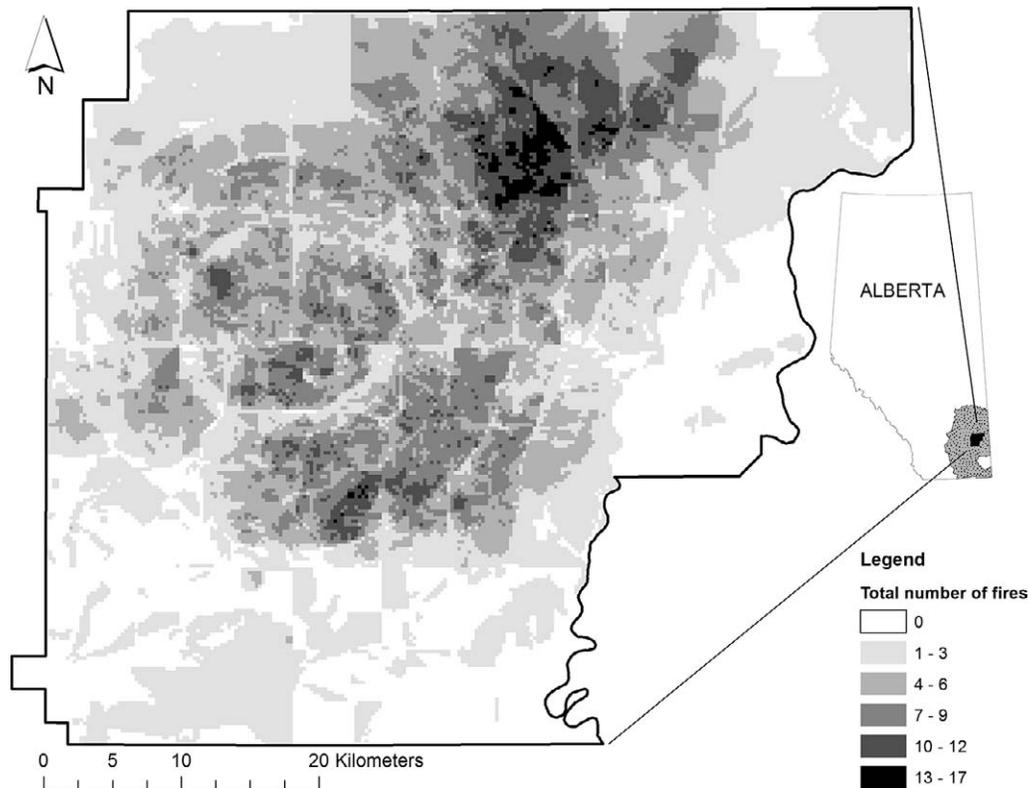
Figure 1. Total number of fires (1972–2007) within CFB Suffield, as digitized from the Landsat archive (inset: grey stipple=dry mixedgrass subregion of Alberta).

responses to fire can be visualized as an ordination plot, by arranging species' cover in multi-dimensional ecological space (Fig. 2). From this analysis, state-and-transition models were developed by correlation of land-use variables with DCA axes; the resulting interpretation was used to identify distinct successional states, where reference states (C3 dominant communities) undergo retrogression to C4 dominant communities, with increasing levels of disturbance particularly relating to fire (Smith 2013; Table 1). To investigate the relationship between fire and species composition, spatially explicit fire maps were required to develop a history of fire since training began.

Fire Mapping by Landsat Data

Landsat has been used in a variety of research designed to study fire (Chuvieco et al. 2002; Hudak and Brockett 2004; Smith et al. 2007). Such studies employ image transformations designed for Landsat, including the Tasseled Cap (Rogan and Yool 2001) and normalized burn ratio (NBR; Picotte and Robertson 2011), which is derived as

$$NBR = (B4 - B7)/(B4 + B7), \qquad [1]$$

where B4=digital number (DN) of TM/ETM+ band 4 and B7=DN of TM/ETM+ band 7.

NBR is useful for both delineating burn scars, and also identifying burn severity (Picotte and Robertson 2011). The results of these studies suggest that Landsat is an appropriate data source for mapping fire extent; however, automated detection is particularly problematic because of the spectral diversity of burned areas, and the time elapsed since fire

occurrence (Pereira and Setzer 1993; Chuvieco et al. 2006). As a result, some fire mapping projects rely solely on visual interpretation of Landsat data (Bastarrika et al. 2011).

In total, 61 Landsat images (including Multispectral Scanner/ MSS, Thematic Mapper/TM, and Enhanced Thematic Mapper Plus/ETM+) were used to digitize fire history, with the goal of using an early- and late-season image for each year. Data were downloaded from the EOS gateway (EOS 2006), georectified, and transformed to the Tasseled Cap (Kauth and Thomas 1976; Crist and Cicone 1984; Huang et al. 2001) and NBR (Roy et al. 2006) indices, which were used to assist in the manual delineation and digitization of burn scars. Where imagery for an entire year was unavailable, relative-difference images were made between images from the year before and the year after, to identify fires.

Burn scars were delineated by detecting high soil brightness values and/or low NBR values relative to the surrounding area, defined by a clear boundary. Although automated classification of burn scars was attempted, resulting outputs contained problematic errors of commission—where other land-use impacts (resulting in increased bare ground, also appearing as high soil brightness) were classified as burn scars. As a result, only manual interpretation was used. During digitization, burn polygons were verified against available military firefighting logs, which contain information on the spatial extent and location of fires, but have only been maintained since 2001.

Fire History and Spatial Attribute Database

A GIS database with the use of ArcMap 10.0 (Esri 2012) was constructed for each 250-m MODIS pixel, where its geographic
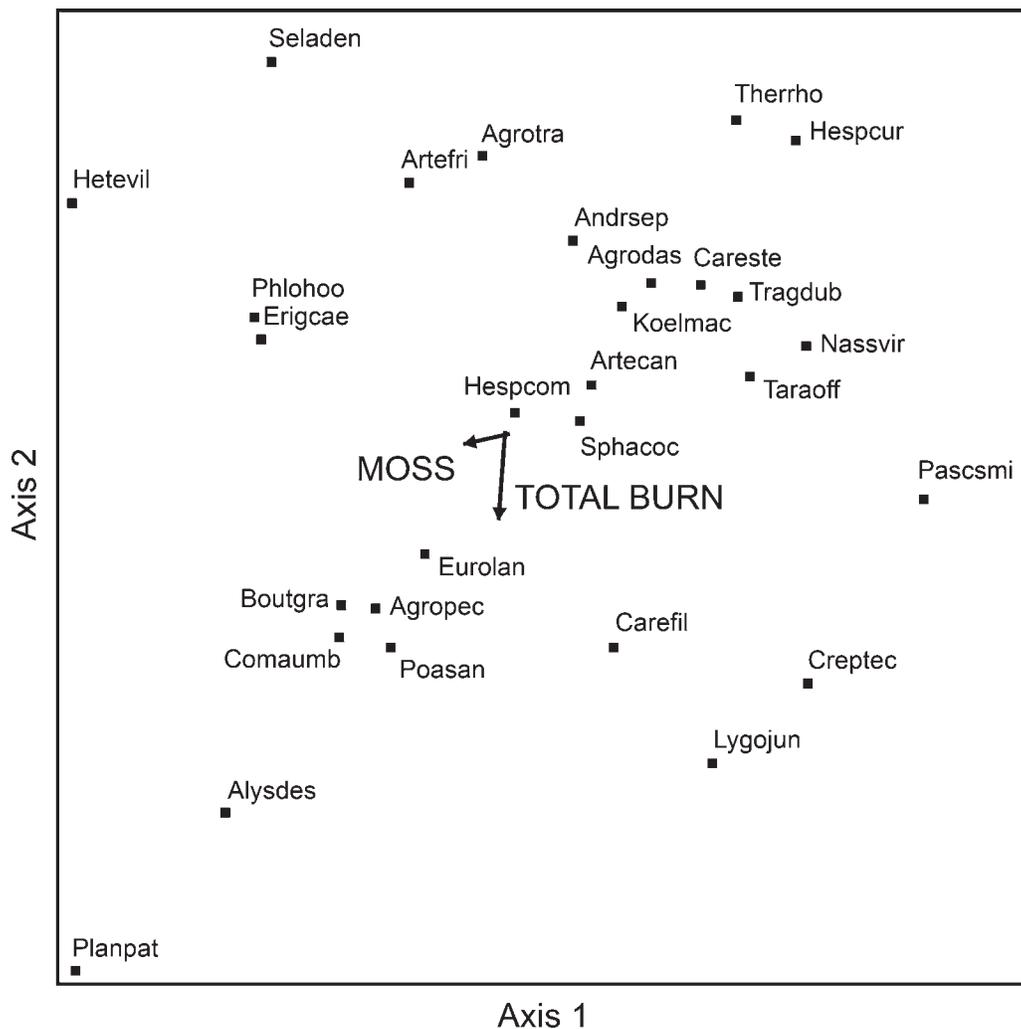
Figure 2. Ordination of species in ecological space for Loamy range sites with joint-plot overlays of environmental variables (moss=moss cover, total burn=number of fires) with $R^2 > 0.10$. Agrodas (*Agropyron dasystachyum*), Agrotra (*Agropyron trachycaulum*), Alydes (*Alyssum desertorum*), Andrsep (*Androsace septetrionalis*), Artecan (*Artemisia cana*), Artefri (*Artemisia frigida*), Boutgra (*Bouteloua gracilis*), Carefil (*Carex filifolia*), Careste (*Carex stenophylla*), Comaumb (*Comandra umbellata*), Creptec (*Crepis tectorum*), Erigcae (*Erigeron caespitosa*), Eurolan (*Eurotia lanata*), Hespcom (*Hesperostipa comata*), Hespcur (*Hespersostipa curtiseta*), Hetevil (*Heterotheca villosa*), Koelmac (*Koeleria macrantha*), Lygojun (*Lygodesmia juncea*), Nassvir (*Nassella viridula*), Pascsmi (*Pascopyrum smithii*), Planpat (*Plantago patagonica*), Poasan (*Poa sandbergii*), Phlohoo (*Phlox hoodii*), Seladen (*Selaginella densa*), Sphacoc (*Spharalcea coccinea*), Taraoff (*Taraxacum officionale*), Therrho (*Thermopsis rhombifolia*), and Tragdub (*Tragopogon dubius*). Ordination derived from 95 long-term monitoring plots.

centroid was recorded as an attribute and matched to geolocated environmental and land-use information. Associated attributes that were appended to each MODIS pixel included its current ecosystem state (inferred from PFT classification), fire history (1972–2007), range site, land use, and topographic position, all extracted by spatial join to the pixel centroid. For each year, presence/absence was used to describe fire history: where a fire intersected the centroid of the pixel, it was recorded as a fire event (1); otherwise absence was recorded (0).

Range-site data were extracted from a polygon database produced by Alberta Sustainable Resource Development (2010). Range-site data describe the relevant soil and topographic attributes that support different vegetation communities. Land-use presence/absence information for each pixel was also extracted into the following categories: garrison/built-up,

military training, and cattle grazing. A 1:250 000 digital elevation model (75 m) was downloaded from the Canadian Digital Elevation Database (CDED 2011), rescaled to a 250-m resolution product (bilinear interpolation), and used to derive topographic position with the topographic position index (TPI) tool for ArcMap (Jenness Enterprises 2006). Topographic position is a key variable to control in rangeland studies, because different topographic positions have different hydrogeological rates (erosion, hydrology) resistance, resilience, and potential for biotic communities (West 2003). TPI tool outputs were aggregated into four distinct topographic positions: valley, ridge, level, and slopes.

MODIS MCD45 Burned Area Product

As Landsat data were used only to identify interyear fire history, the MODIS MCD45 burned area product was used to

Table 1. Range sites and successional states represented by mean, (SD) canopy cover.

| Range site | Successional state | Sample size | Ecosystem state | Mean canopy cover (SD) by species | | | |
				Blue grama	Needle and thread	Northern wheatgrass	Western wheatgrass
Blowouts	Reference	10	C3	17.4 (8.6)	21.4 (12.3)	6.9 (10.5)	5.5 (7.9)
	Successional	5	C3/C4	19.8 (7.4)	14.5 (9.4)	5.3 (3.9)	1.3 (2.2)
Loamy	Reference	19	C3	10.6 (13.2)	36.4 (20.2)	8.8 (11.6)	7.8 (14.3)
	Successional 1	30	C3/C4	38.4 (14.1)	30.1 (8.2)	1.6 (2.4)	0.0
	Successional 2	3	C4	64.8 (5.7)	12.5 (1.9)	0.1 (0.2)	0.0
Sands	Reference	17	C3	16.0 (10.7)	52.8 (9.5)	2.5 (4.3)	0.8 (1.8)
	Successional	18	C4	40.1 (22.2)	22.9 (8.9)	2.5 (5.6)	0.0

identify precise intrayear fire timing for the years available (2001–2009). MCD45 data are available from the year 2000 onwards, provided as a monthly 500-m raster containing per-pixel burning and quality information, including the approximate Julian day of burning within a 16-d window (Roy et al. 2008). The MODIS burned area algorithm (Roy et al. 2005) detects rapid changes in vegetation growth, by assessing daily surface reflectance time series in a bidirectional reflectance model to deal with angular variations found in satellite data, and using a statistical measure to detect change probability from a previously observed state. After detecting statistically significant changes in vegetation, the algorithm assigns an approximate day of burning for each pixel.

MODIS MCD45 data were downloaded from the Land Processes Distributed Active Archive Center (LP-DAAC 2005), reprojected to NAD83 UTM Zone 12, and converted to vector with the use of ArcMap 10.0. Vector data were then summarized as total area burned by month and total area burned by year. In order to assess the accuracy of the burned area product relative to manual digitization, the detection rate (DR) of MCD45 data was derived as:

$$DR_{(MCD45)} = \left[\text{total annual burned area}_{(MCD45)}\right] / \left[\text{total annual burned area}_{(Landsat)}\right] * 100. \quad [2]$$

Pixel Selection for Limiting Variance Prior to Statistical Analysis

It is critical that rangeland studies control for unwanted variability (West 2003) and also account for human causes of change (Washington-Allen et al. 2003) in order to preserve the signal of the relevant ecological processes of interest. In order to limit variation in the fire history and spatial-attribute database prior to statistical tests, pixels were removed when their PFT class could be affected by land use other than fire, or their presence was affected by topographic variance. For example, blue grama is naturally dominant on dry hillcrests (Smith 2013); the inclusion of such C4-dominant pixels could interfere with the establishment of statistical models that seek to explain their presence solely in relation to fire history.

The following were removed prior to further analysis: pixels that had burned between 2008 and 2009 (to remove any effect of fire-induced misclassification of PFTs); pixels located in cattle grazing pastures (where grazing-induced succession could be falsely associated with fire); pixels of garrison/built-up land use, where cultivation has occurred and introduced C3 species are deliberately grown; pixels with ridge (naturally dry and

sparse, favoring arid C4 species) and valley positions (naturally moist, favoring mesic C3 species; Smith 2013); and pixels of C3/C4-codominant and C4-dominant states, where no fires had occurred (i.e., succession associated with a different disturbance process). Although the removal of pixels effectively reduced sample sizes for analysis, it was important to remove as many factors that contribute to undesired noise attributed to environmental variability and land use as possible. After pixel selection, Blowouts (1 393 pixels), Loamy (4 713 pixels), and Sands (3 432 pixels) range sites, which did not contain previous cultivation, were then analyzed separately.

Statistical Analysis

Fire-Related Retrogression. All statistical analyses were conducted with the use of SPSS 19 (IBM Corp. 2010). Where most ecological studies favor the use of logistic regression to model the dependence of categorical data on proportional data ranging from 0 to 1 (Trexler and Travis 1993), probit regression is appropriate for response-based sampling, where sampling is not random but is instead stratified by the discrete variable of an outcome (Manski 1981). Probit regression was used to test for significant relationships between the proportions of each ecosystem state and the total number of fires experienced (response based).

Postfire Resilience and Progressive Succession. Because it is logistically difficult to investigate ecological change over long time spans, spatial sequences are often used as direct substitutes for temporal sequences in a concept known as *ergodicity* (Gregory et al. 2009). If the ergodic hypothesis in ecology (Molchanov 1992) is valid, then the climax state of a succession system represents a spatially developed time history of succession, and the areas making up a plant community should be proportional in a climax state of association to the times of their development in the succession series (Karev 1997). We suggest that the ergodic hypothesis is a useful framework in examining the process of recovery (resilience), by enabling comparisons of the proportions of ecosystem states under different disturbance regimes, where the disturbance history is well established and the time period is fixed. In order to examine the process of post-fire resilience and progressive succession, the fire history and spatial attribute database was further parsed into two treatments:

1) Burning treatment, where pixels were subjected to 18 yr of rest (1972–1989), followed by 18 yr of burning (1990–2007).

Table 2. Probit regression results with total number of fires (m) as predictor of ecosystem state.

Range site	Ecosystem state	m * x + b (SD)	McFadden's pseudo R^2	Significance	95% (CI) (lower, upper)	
Blowouts	C3	$-0.436 + 1.488$ (0.120)	1.0	0.000	-0.671	-0.201
	C3/C4	$0.234 - 1.886$ (0.033)	1.0	0.000	0.170	0.299
	C4	$0.096 - 2.542$ (0.114)	0.009	0.403	-0.129	0.320
Loamy	C3	$-0.301 + 1.312$ (0.028)	1.0	0.000	-0.356	-0.247
	C3/C4	$0.081 - 1.377$ (0.008)	0.023	0.000	0.064	0.097
	C4	$0.224 - 2.045$ (0.014)	1.0	0.000	0.196	0.252
Sands	C3	$-6.700 + 5.238$ (44.812)	0.011	0.881	-94.53	81.13
	C3/C4	$0.366 - 2.922$ (0.124)	0.011	0.003	0.124	0.609
	C4	$0.614 - 1.938$ (0.057)	0.008	0.000	0.502	0.726

2) Recovery treatment, where pixels were subjected to 18 yr of burning (1972–1989), followed by 18 yr of rest (1990–2007).

χ^2 tests were run to compare the frequency of each ecosystem state between burning and recovery treatments, and by the number of times burned for each range site, in order to determine the significance, direction, and magnitude of change. The Blowouts range site did not have sufficient sample sizes to run statistical tests.

Fire Timing. Fire timing was analyzed by comparing MODIS burn extent between spring (May–June) and summer (July–September) fires from 2001 to 2009, with the use of the Wilcoxon signed-rank test.

RESULTS

Fire-Related Retrogression
C3-dominant pixels were negatively related to fire ($P < 0.001$) on Blowouts (pseudo $R^2 = 1$) and Loamy (pseudo $R^2 = 1$, Table 2) range sites. C4-dominant pixels on Loamy range sites were positively related to fire ($P < 0.001$, pseudo $R^2 = 1$). However, C4-dominant pixels on Blowouts range sites were unrelated to fire ($P = 0.403$, pseudo $R^2 = 0.009$). Instead, C3/C4-codominant pixels in Blowouts were positively related to fire ($P < 0.001$, pseudo $R^2 = 1$).

In contrast to Loamy and Blowouts range sites, there was no relationship ($P = 0.881$, pseudo $R^2 = 0.011$) between C3-dominant pixels and fire on Sands range sites (Table 2). As visualized in Figure 3, succession processes are different between range sites, with the proportion of C3-dominant pixels decreasing in relation to the total number of fires for Blowouts and Loamy range sites, but not for Sands. In contrast, the proportion of C3/C4-codominant pixels on Loamy and Sands range sites appear to rise to a peak (approximately four–eight fires in 36 yr; Fig. 3) and then decrease in relation to the total number of fires.

Postfire Resilience and Progressive Succession
In all burning treatments with at least one fire in Loamy range sites, the proportions of C4-dominant and C3/C4-codominant pixels were significantly higher, and the proportion of C3-dominant pixels was significantly lower ($P < 0.05$) than the recovery treatment (Table 3). After three–six fires on Loamy

sites, C4-dominant pixels comprise the majority of ecosystem states of the burning treatment (88%). However, after the same number of fires in the recovery treatment—but with at least 18 yr of rest—the proportion of C3-dominant pixels are significantly higher than C4-dominant pixels ($P < 0.05$) and comprise the majority of ecosystem states (69%; Table 3).

In contrast to Loamy range sites, where the proportion of C4-dominant pixels ranged from 8% to 88% in the burning treatments, only 1–5% of pixels exist as C4 dominant in the Sands burning treatments. However, with 18 yr of rest following three–six fires in the Sands recovery treatment, there was a similar proportion of C3-dominant pixels (65%) to the Loamy recovery treatment (69%; Table 3).

Fire Timing
Based on MODIS MCD45 data, the majority (spatial extent) of detected fires occur in August (mean = 36%; range = 0–97%) and September (mean = 21%; range = 0–88%; Table 4). Results of the Wilcoxon signed-rank test showed that the spatial extent of spring fires (May–June) were less ($P < 0.05$) than summer fires (July–September). However, the mean detection rate of MCD45 burned area product is 37% (range = 19–80%), when compared to manually delineated burn scars from Landsat.

DISCUSSION

Fire-Related Retrogression
Although Blowouts pixels experienced fewer total fires than other ecological units, this range site appears more resistant to fire-related retrogression than Loamy, where C4-dominant pixels do not generally increase with total fires. Instead, C3/C4-codominant pixels increase at the expense of C3-dominant pixels. Because Blowouts range sites are less productive and are inherently moisture limiting in the dry mixed-grass prairie (Willms et al. 2002; Adams et al. 2005), we suggest that fires are likely to be less frequent because of the slower regrowth of litter. Furthermore, we suggest that shallow-rooted species like blue grama have no competitive advantage on this range site type because solonetzic soils place greater physical and chemical limitations on plants than other range sites, significantly impeding root growth (Willms et al. 2002).

In contrast to Blowouts, repeated fire in Loamy range sites resulted in the complete transition from C3-dominant pixels to C4-dominant pixels after 14 fires in 36 yr. These results are similar to the succession observed by Shay et al. (2001), where
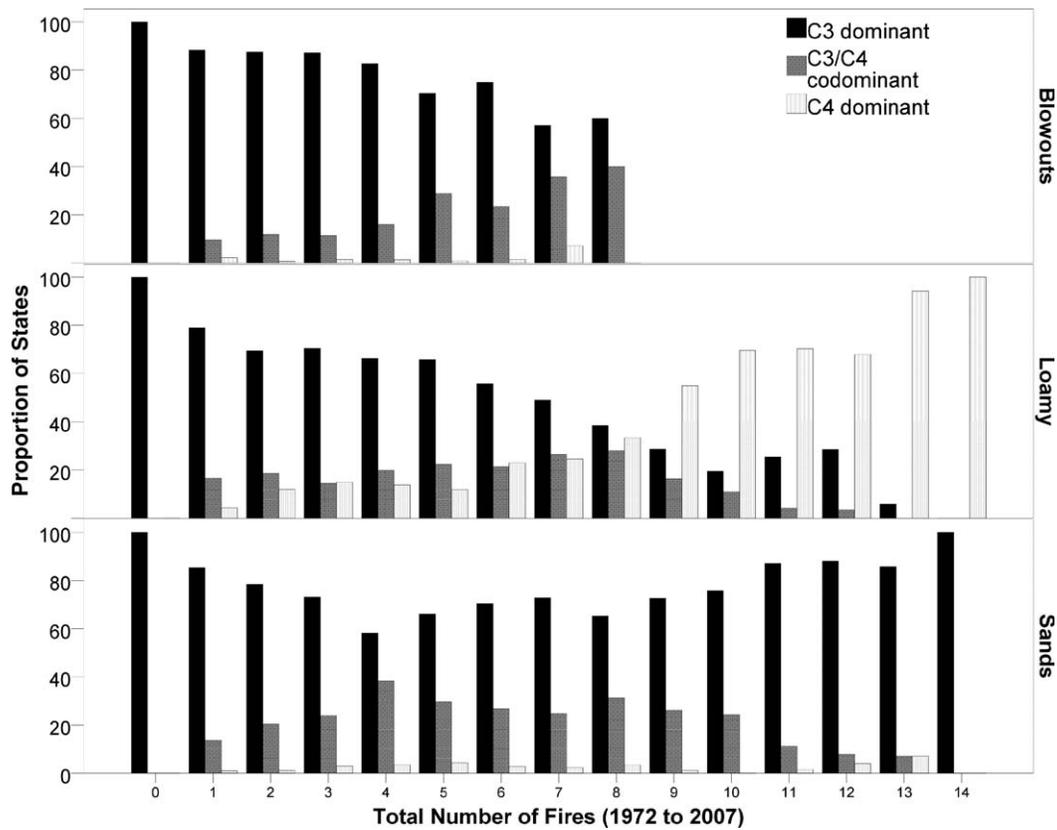
Figure 3. Proportion of ecosystem states by number of fires for Blowouts, Loamy, and Sands range sites.

frequent burning at CFB Shilo was associated with an increase in blue grama cover. This C4 species is very drought tolerant and is able to make efficient use of small precipitation events (Sala 1985), and can increase recruitment following drought (Fair et al. 1999). We suggest that on Loamy range sites, the long-term effects of fire are similar to grazing-related succession—by the persistent removal of litter. The elimination of litter results in elevated soil temperatures and increased evapotranspiration favoring C4 species, which are more tolerant of warmer and drier conditions. For example, Smoliak et al. (1972) showed that after 19 yr of continuous heavy grazing on *Stipa-Bouteloua* prairie, shallow-rooted species like blue grama replaced deeper-rooted species on the drier environment induced by heavy grazing. Hart (2001) observed similar trends on the short-grass steppe, where heavy grazing resulted in the increased cover of blue grama and a corresponding decrease of needle and thread.

In contrast to Loamy range sites (where C3-dominant pixels are removed after 14 fires in 36 yr), C4-dominant pixels were completely removed after 14 fires in 36 yr on Sands range sites. Because blue grama is a shallow-rooted species, we suggest that fire-related effects (litter reduction, increased evapotranspira-

Table 3. Frequency and proportions of ecosystem states by treatment (burning/recovery), and number of fires.

		Frequency of pixels of ecosystem states by number of fires										
		Not burned 1972–1989, burned 1990–2007 (E); burning treatment				Burned 1972–1989, not burned 1990–2007 (O); recovery treatment				Magnitude of change (O–E)		
Range site	Number of fires	C4 proportion of pixels	C4	C3/C4	C3	C4	C3/C4	C3	C3 proportion of pixels	C4	C3/C4	C3
Loamy	0	0%	0	0	1 281	0	0	1 281	100%	NA	NA	NA
	1	8%	15	25	152	18	101	446	79%	−5%[1]	5%[1]	0%
	2	18%	10	14	31	20	46	190	74%	−10%[1]	−8%[1]	18%[1]
	3–6	88%	15	1	1	14	12	59	69%	−72%[1]	8%[1]	64%[1]
Sands	0	0%	0	0	765	0	0	765	100%	NA	NA	NA
	1	1%	3	51	149	6	70	607	89%	0%	−15%[1]	15%[1]
	2	1%	1	28	79	2	33	134	79%	0%	−6%[1]	6%[1]
	3–6	5%	2	11	30	2	5	13	65%	5%	0%	−5%

[1]Significant difference ($P < 0.05$).

Table 4. Percent of total annual burned area (2001–2009) for summer months at CFB Suffield, derived from MODIS MCD45 burned area product compared to Landsat digitized burns.

Year	Percent of total annual burned area						Total annual burned area (ha)		MODIS detection rate (DR)
	May	June	July	August	September	May–September	MODIS MCD45	Landsat	
2001	0	0	0	97	0	97	4 950	25 888	19.1%
2002	0	0	0	0	0	0	0	0	NA
2003	0	0	1	10	88	99	19 025	42 906	44.3%
2004	2	0	44	0	34	80	1 250	2 588	48.3%
2005	17	0	0	0	0	17	1 650	5 056	32.6%
2006	0	2	15	54	29	100	28 575	35 681	80.1%
2007	5	0	1	79	10	95	4 550	15 469	29.4%
2008	9	0	2	82	3	95	4 350	21 613	20.1%
2009	47	0	0	0	23	70	22 300	40 100	55.6%
Mean	9	0	7	36	21	72	9 628	21 033	36.6%

tion) favor deep-rooted species that are able reach moisture deeper into coarse-textured soils, where soil moisture is severely limiting at the surface. Hugenholtz et al. (2010) suggest that wheatgrasses are able to develop deep root systems to cope with surface-moisture limitations in eolian landscapes. Furthermore, Coupland and Johnson (1965) showed that the average rooting depth of blue grama was 19 cm less than needle and thread, and 29 cm less than western wheatgrass. Such physiological differences in grass species may explain the stark differences in successional processes between range sites. As a result, the hypothesis regarding the fire-related retrogression of grass species from C3 to C4 species holds true only for Loamy range sites. The biophysical differences between range sites and physiological traits of dominant grasses likely result in different fire-succession processes.

In mixed-grass prairie, moisture is the most limiting factor for plant growth (Coupland 1958; Sala et al. 1988), and frequent litter removal impairs production on dry mixed prairie (Willms et al. 1986). Surface litter reduces evapotranspiration (Willms et al. 1993), but also reduces surface temperatures (Redmann 1978). Conversely, removal of litter increases surface soil temperatures (Vermeire et al. 2005), and drier soils on burned prairie have been attributed to increased evapotranspiration (Bremer and Ham 1999), and to reduced water capture (Debano 2000). Finally, the rate of litter accumulation is almost the same as the rate of decomposition (Coupland 1973), and litter build-up after fire takes many years (Dix 1960). Given these considerations, it is highly likely that the physical removal of litter by fire is the primary driver for succession, by increasing evapotranspiration and increasing soil temperatures. These physical changes to the soil surface result in different effects to PFTs, based on soil texture and chemistry—litter removal favors drought-tolerant C4 species on Loamy range sites, favors deeper-rooted C3 species on Sands range sites, but confers only limited advantage to C4 species on Blowouts range sites.

Postfire Resilience and Progressive Succession

With respect to postfire resilience, our results support the hypothesis that the proportion of C3-dominant communities increases, and the proportion of C4-dominant communities decreases with rest from fire on Loamy range sites. However,

even after 18 yr of rest following three–six fires, the proportion of Loamy C3-dominant pixels (69%) is still significantly lower than unburned pixels (C3-dominant pixels=100%). This outcome suggests that the complete re-establishment of climax C3 species after repeated fire in dry mixed-grass prairie may take decades. Dormaar and Willms (1990) found an important similarity, where removal of grazing pressure in overgrazed *Stipa-Bouteloua* communities did not necessarily result in succession back to the climax species. Further, Dormaar et al. (1994) argued blue grama is resistant to displacement by associated climax species, either by allelopathy (Dormaar and Willms 1990), or by competing more effectively in the drier environment (Weaver and Albertson 1956; Kemp and Williams 1980). Dormaar et al. (1994) also showed that the overgrazing-related dominance of blue grama was only released by cultivation, where needle and thread was able to rapidly re-establish its dominance. Finally, it appears that postfire resilience is also dependent on the number of times burned, where the proportion of C3-dominant pixels in recovery treatments declines with increasing fire, from 79% (one fire) to 69% (three–six fires).

Similar to Loamy range sites, the recovery of C3 species after repeated (three–six) fires on Sands range sites appears to take decades: C3-dominant pixels comprised only 65% of ecosystem states after 18 yr of rest. However, this low value may simply be caused by the small number of pixels ($n=20$) in the recovery treatment. Regardless, Sands range sites appear highly resistant to fire-induced increases of C4-dominant pixels. Although infrequent fire reduces the cover of C3 species, it appears that C4 species decrease with repeated fire, having no competitive advantage over C3 species on coarse-textured soil.

Fire Timing

Where previous studies have shown that spring fires favor C4 species at the expense of C3 species (Anderson et al. 1970; White and Currie 1983; Schact and Stubbendieck 1985; Redmann et al. 1993; Shay et al. 2001), MCD45 burn-area data indicate the majority of fires at CFB Suffield tend to occur in late summer, when C3 species are dormant. This suggests that fire timing is not directly related to successional processes in dry mixed-grass prairie. Even with the low mean rate of detection by MODIS (37%), MCD45 data reveal that fire is

not limited to any particular part of the growing season, and as such does not selectively favor C4 species by spring burning. Rather, the persistent removal of litter (and resulting increase in soil evapotranspiration) is a more probable cause for inducing succession.

MANAGEMENT IMPLICATIONS

Ecosystem states derived from PFT classification can be evaluated in the context of range health, which serves as a tool to evaluate ecosystem functions including net primary production (Adams et al. 2005). It is important to note that C3 species produce three–four times more above-ground biomass than C4 species in northern mixed-grass prairie (Clarke et al. 1943). This study has established that C3 PFTs are replaced with C4 PFTs with increasing fire on Loamy range sites, whereas Blowouts and Sands range sites are more resistant to succession because of their biophysical properties. Particularly for Loamy range sites, repeated fire in dry mixed-grass prairie therefore significantly reduces range health and productivity by the replacement of C3 species with C4 species.

In the absence of specific management objectives, we suggest that the maintenance of at least 50% of the landscape as C3-dominant communities is a useful starting point for fire-management goals at CFB Suffield, as a diversity of successional communities is favored to support endemic wildlife including species at risk (Rumboldt et al. 2011). Based on the regression equations produced, fire frequency must not exceed once every 5 yr ($\sim$ 7 fires in 36 yr) for Loamy range sites in order to maintain at least 50% of the area as C3 dominant. Although Blowouts and Sands range sites appear more resistant to succession of C4 species, it is impossible to manage them separately within the same landscape. We therefore recommend that fire be managed with frequency not exceeding once every 5 yr. However, because of the potential for C4-dominant communities to reach an alternative (and irreversible) steady state (Dormaar and Willms 1990; Dormaar et al. 1994), management and monitoring must focus on whether such sites can revert back to C3-dominant species in the long term.

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LITERATURE CITED

Abrams, M. D., and L. C. Hulbert. 1987. Effect of topographic position and fire on species composition in tallgrass prairie in northeast Kansas. *American Midland Naturalist* 117:442–445.

Adams, B. W., L. Poulin-Klein, D. Moisey, and R. L. McNeil. 2005. Rangeland plant communities and range health assessment guidelines for the dry mixedgrass natural subregion of Alberta. Lethbridge, AB, Canada: Rangeland Management Branch, Public Lands Division, Alberta Sustainable Resource Development. Pub. No. T/040. 106 p.

Adjorlolo, C., O. Mutanga, M. A. Cho, and R. Ismail. 2012. Challenges and opportunities in the use of remote sensing for C3 and C4 grass species discrimination and mapping. *African Journal of Range & Forage Science* 29(2):47–61.

Alberta Sustainable Resource Development. 2010. Grassland vegetation inventory (GVI) specifications, 5th ed. Edmonton, AB, Canada: Alberta Sustainable Resource Development.

Anderson, K. L., E. F. Smith, and C. E. Owensby. 1970. Burning bluestem range. *Journal of Range Management* 23:81–92.

Anderson, R. C. 2006. Evolution and origin of the central grassland of North America: climate, fire, and mammalian grazers. *Journal of the Torrey Botanical Society* 133:626–647.

Bailey, A. W., and M. L. Anderson. 1978. Prescribed burning of a Festuca-Stipa grassland. *Journal of Range Management* 31:446–449.

Bastarrika, A., E. Chuvieco, and M. P. Martin. 2011. Mapping burned areas from Landsat TM/ETM+ data with a two-phase algorithm: balancing omission and commission errors. *Remote Sensing of Environment* 115:1003–1012.

Bestelmeyer, B., J. Brown, K. Havstad, R. Alexander, G. Chavez, and J. Herrick. 2003. Development and use of state-and-transition models for rangelands. *Journal of Range Management* 56:114–126.

Bragg, T. B. 1995. The physical environment of the Great Plains grasslands. *In:* A. Joern and K. H. Keeler [eds.]. The changing prairie. New York, NY, USA: Oxford University Press. p. 49–81.

Bremer, D. J., and J. M. Ham. 1999. Effect of spring burning on the surface energy balance in a tallgrass prairie. *Agricultural and Forest Meteorology* 97:43–54.

Briggs, J. M., and A. K. Knapp. 1995. Interannual variability in primary production in tallgrass prairie—climate, soil moisture, topographic position, and fire as determinants of aboveground biomass. *American Journal of Botany* 82:1024–1030.

Canadian Digital Elevation Database (CDED). 2011. Available at: http://www.geobase.ca/geobase/en/data/cded. Accessed 30 Sept 2012.

Chuvieco, E., M. P. Martín, and A. Palacios. 2002. Assessment of different spectral indices in the red-near-infrared spectral domain for burned land discriminations. *International Journal of Remote Sensing* 23:5103–5110.

Chuvieco, E., D. Riaño, F. M. Danson, and M. P. Martín. 2006. Use of a radiative transfer model to simulate the post-fire spectral response to burn severity. *Journal of Geophysical Research—Biosciences* 111. doi:10.1029/2005JG000143

Clarke, S. E., E. W. Tisdale, and N. A. Skoglund. 1943. The effects of climate and grazing on shortgrass prairie vegetation. Ottawa, ON, Canada: Ministry of Agriculture, Canadian Dominion Department of Agriculture Technical Bulletin 46. 53 p.

Collins, S. L., and D. J. Gibson. 1990. Effects of fire on community structure in tallgrass and mixed-grass prairie. *In:* S. L. Collins, and L. L. Wallace [eds.]. Fire in North American tallgrass prairies. Norman, OK, USA: University of Oklahoma Press. p. 81–98.

Coupland, R. T. 1950. Ecology of mixed prairie in Canada. *Ecological Monographs* 20:271–315.

Coupland, R. T. 1958. The effects of fluctuations in weather upon grasslands of the Great Plains. *Botanical Review* 24:273–317.

Coupland, R. T. 1973. Producers: I. Dynamics of above-ground standing crop. Matador Project. Saskatoon, Canada: Canadian IBP, IBP Program Technical Report 27. 159 p.

Coupland, R. T., and R. E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. *Journal of Ecology* 53:475–507.

Crist, E. P., and R. C. Cicone. 1984. A physically-based transformation of Thematic Mapper data—the TM Tasseled Cap. *IEEE Transactions on Geoscience and Remote Sensing* GE-22(3):256–263.

Daubenmire, R. 1968. Ecology of fire in grasslands. *Advances in Ecological Research* 5:209–266.

Davidson, A., and F. Csillag. 2003. A Comparison of three approaches for predicting C4 species cover of northern mixed grass prairie. *Remote Sensing of Environment* 86:70–82.

DeBano, L. F. 2000. The role of fire and soil heating on water repellency in wildland environments: a review. *Journal of Hydrology* 231:195–206.

Detling, J. K., W. J. Parton, and H. W. Hunt. 1978. An empirical model for estimating CO$_2$ exchange of *Bouteloua gracilis* (H.B.K.) Lag. in the short grass prairie. *Oecologia* 33:137–147.

Dix, R. L. 1960. The effects of burning on the mulch structure and species composition of grasslands in western North Dakota. *Ecology* 41:49–56.

Dormaar, J. F., B. W. Adams, and W. D. Willms. 1994. Effect of grazing and abandoned cultivation on a *Stipa-Bouteloua* community. *Journal of Range Management* 47(1):28–32.

Dormaar, J. F., and W. D. Willms. 1990. Effect of grazing and cultivation on some chemical properties of soils in the mixed prairie. *Journal of Range Management* 43:456–460.

Erichsen-Arychuk, C., E. W. Bork, and A.W. Bailey. 2002. Northern dry mixed prairie responses to summer wildfire and drought. *Journal of Range Management* 55:164–170.

Esri. 2012. ArcMap 10.0: ArcGIS Desktop 10.0 service pack 5 (Build 4400), Redlands, CA, USA: Esri.

EOS. 2006. Land Processes Data Active Archive Center Earth Observing System Data Gateway. Available at: http://lpdaac.usgs.gov. Accessed 30 September 2012.

Fair, J., W. K. Lauenroth, and D. P. Coffin. 1999. Demography of *Bouteloua gracilis* in a mixed prairie: analysis of genets and individuals. *Journal of Ecology* 87:233–243.

Gerling, H. S., A. W. Bailey, and W. D. Willms. 1995. The effects of burning of *Festuca hallii* in the parklands of central Alberta. *Canadian Journal of Botany* 73:937–942.

Glenn-Lewin, D. C., and E. van der Maarel. 1992. Patterns and processes of vegetation dynamics. *In:* D. C. Glen-Lewin, R. K. Peet, and T. T Veblen [EDS.]. Plant succession—theory and prediction. London, UK: Chapman & Hall. p. 11–44.

Gregory, K. J., I. G. Simmons, A. J. Brazel, J. W. Day, E. A. Keller, A. G. Sylvester, and A. Yáñez-Arancibia. 2009. Ergodicity. *In:* Environmental sciences: a student's companion. London, UK: Sage Publications Ltd. doi:10.4135/9781446216187.n83.

Gross, D. V., and J. T. Romo. 2010. Temporal changes in species composition in fescue prairie: relationships with burning history, time of burning, and environmental conditions. *Plant Ecology* 208:137–153.

Hart, R. H., and J. A. Hart. 1997. Rangelands of the Great Plains before European settlement. *Rangelands* 19:4–11.

Hart, R. H. 2001. Plant biodiversity on shortgrass steppe after 55 years of zero, light, moderate, or heavy cattle grazing. *Plant Ecology* 155:111–118.

Huang, C., B. Wylie, L. Yang, C. Homer, and G. Zylstra. 2001. Derivation of a Tasseled Cap transformation based on Landsat 7 at-satellite reflectance. Sioux Falls, SD, USA: Raytheon ITSS, USGS EROS Data Center. 10 p.

Hudak, A. T., and B. H. Brockett. 2004. Mapping fire scars in a southern African savannah using Landsat imagery. *International Journal of Remote Sensing* 25:3231–3243.

Hugenholtz, C. H., D. Bender, and S. A. Wolfe. 2010. Declining sand dune activity in the southern Canadian prairies: historical context, controls and ecosystem implications. *Aeolian Research* 2:71–82.

IBM Corp. Released 2010. IBM SPSS statistics for Windows, Version 19.0. Armonk, NY, USA: IBM Corp.

Jenness Enterprises. 2006. Topographic position index. Version 1.3a. Available from: http://www.jennessent.com. Accessed 11 September 2009.

Karev, G. P. 1997. On the ergodic hypothesis in biocenology. *Doklady Biological Sciences* 353:177–179.

Kauth, R. J., and G. S. Thomas. 1976. The Tasseled Cap—a graphic description of the spectral-temporal development of agricultural crops as seen by Landsat. Proceedings of the Symposium on Machine Processing of Remotely Sensed Data. Purdue University, West Lafayette, IN, USA. p. 4B41–4B51.

Kemp, P. R., and G. J. Williams III. 1980. A physiological basis for niche separation between *Agropyron smithii* (C3) and *Bouteloua gracilis* (C4). *Ecology* 61:846–858.

Land Processes Distributed Active Archive Centre (LP DAAC). 2005. MODIS Data Products. Available at: http://lpdaac.usgs.gov/modis/mod13q1v4.asp. Accessed 30 January 2011.

Leach, M. K., and T. J. Givnish. 1996. Ecological determinants of species loss in remnant prairies. *Science* 273:1555–1558.

Manski, C. F. 1981. Structural models for discrete data: The analysis of discrete choice. In S. Leinhardt [ED.]. Sociological methodology. San Francisco, CA, USA: Jossey-Bass. p. 58–109.

McCune, B., and J. B. Grace. 2002. Analysis of ecological communities. Gleneden Beach, OR, USA: MjM Software Design. 300 p.

Molchanov, A. M. 1992. Nonlinear biology. Pushchino, Russia: Pushchino Scientific Center of the Russian Academy of Sciences. p. 62–63 (in Russian).

Pereira, M. C., and A.W. Setzer. 1993. Spectral characteristics of fire scars in Landsat-5 TM images of Amazonia. *International Journal of Remote Sensing* 14:2061–2078.

Picotte, J. J., and K. Robertson. 2011. Timing constraints on remote sensing of wildland fire burned area in the southeastern US. *Remote Sensing* 3:1680–1690.

Redmann, R. E. 1978. Plant and soil water potentials following fire in a northern mixed grassland. *Journal of Range Management* 31:443–445.

Redmann, R. E., Romo, J. T., and B. Pylypec. 1993. Impacts of burning on primary productivity of Festuca and Stipa-Agropyron grasslands in central Saskatchewan. *American Midland Naturalist* 130:262–273.

Rogan, J., and S. R. Yool. 2001. Mapping fire-induced vegetation depletion in the Peloncillo Mountains, Arizona and New Mexico. *International Journal of Remote Sensing* 22:3101–3121.

Roy, D. P., L. Boschetti, and S. N. Trigg. 2006. Remote sensing of fire severity: assessing the performance of the Normalized Burn Ratio. *IEEE Geoscience and Remote Sensing Letters* 1:112–116.

Roy, D. P., L. Boschetti, C. O. Justice, and J. Ju. 2008. The Collection 5 MODIS burned area product – global evaluation by comparison with the MODIS active fire product. *Remote Sensing of Environment* 112:3690–3707.

Roy, D. P., Y. Jin, P. E. Lewis, and C. O. Justice. 2005. Prototyping a global algorithm for systematic fire-affected area mapping using MODIS time series data. *Remote Sensing of Environment* 97:137–162.

Rumboldt, K. S., F. Blouin, B. A. Downey, B. L. Downey, C. A. Koenig, D. J. Jarina, P. F. Jones, J. P. Landry-DeBoer, and E. R. Wesley. 2011. MULTISAR: a multi-species conservation strategy for species at risk 2010–2011 report. Edmonton, AB, Canada: Alberta Sustainable Resource Development, Fish and Wildlife Division. Alberta Species at Risk Report No. 141. 84 p.

Sala, O. E. 1985. Root profiles and the ecological effect of light rain showers in arid and semiarid regions. *American Midland Naturalist* 114:406–408.

Sala, O. E., W. J. Parton, L. A. Joyce, and W. K. Lauenroth. 1988. Primary production of the central grassland region of the United States. *Ecology* 69:40–45.

Schacht, W., and J. Stubbendieck. 1985. Prescribed burning in the Loess Hills mixed prairie of southern Nebraska. *Journal of Range Management* 38:47–51.

Scheintaub, M. R., J. D. Derner, E. F. Kelly, and A. K. Knapp. 2009. Response of the shortgrass steppe plant community to fire. *Journal of Arid Environments* 73:1136–1143.

Shay, J., D. Kunec, and B. Dyck. 2001. Short-term effects of fire frequency on vegetation composition and biomass in mixed prairie in south-western Manitoba. *Plant Ecology* 155:157–167.

Smith, A. M. S., N. A. Drake, M. J. Wooster, A. T. Hudak, Z. A. Holden, and C. J. Gibbons. 2007. Production of Landsat ETM+ reference imagery of burned areas within Southern African savannahs: comparison of methods and application to MODIS. *International Journal of Remote Sensing* 28:2753–2775.

Smith, B. 2013. Multi-temporal remote sensing of rangeland vegetation for investigation of fire-related ecology at Canadian Forces Base Suffield, Alberta [thesis]. Calgary, AB, Canada: University of Calgary. 124 p.

Smoliak, S., J. F. Dormaar, and A. Johnston. 1972. Long-term grazing effects on *Stipa-Bouteloua* prairie soils. *Journal of Range Management* 25:246–250.

Steuter, A. A. 1987. C3/C4 production shift on seasonal burns: northern mixed prairie. *Journal of Range Management* 40(1):27–31.

Strong, W. L., and K. R. Leggat. 1992. Ecoregions of Alberta. Edmonton, AB, Canada: Alberta Forestry, Lands, and Wildlife. Pub. No. T/245. 59 p.

Tieszen, L. L., B. C. Reed, N. B. Bliss, B. K. Wylie, and D. Donovan. 1997. NDVI, C3 and C4 production, and distribution in Great Plains land cover classes. *Ecological Applications* 7(1):59–78.

Trexler, J. C., and J. Travis. 1993. Nontraditional regression analyses. *Ecology* 74(6):1629–1637.

TUELLER, P. T. 1989. Remote sensing technology for rangeland management. *Journal of Range Management* 42:442–453.

UMBANHOWAR, C. E. JR. 1996. Recent fire history of the northern great plains. *American Midland Naturalist* 135:115–121.

USTIN, S. L., AND J. A. GAMON. 2010. Remote sensing of plant functional types. *The New Phytologist* 186(4):795–816.

VERMEIRE, L. T., J. L. CROWDER, AND D. B. WESTER. 2011. Plant community and soil environment response to summer fire in the northern Great Plains. *Rangeland Ecology & Management* 64:37–46.

VERMEIRE, L. T., D. B. WESTER, R. B. MITCHELL, AND S. D. FUHLENDORF. 2005. Fire and grazing effects on wind erosion, soil water content, and soil temperature. *Journal of Environmental Quality* 34:1559–1565.

WASHINGTON-ALLEN, R. A., N. E. WEST, AND D. R. RAMSEY. 2003. Remote sensing–based dynamical systems analysis of sagebrush steppe vegetation in rangelands. *In:* N. Allsopp, A. R. Palmer, S. J. Milton, K. P. Kirkman, G. I. H. Kerley, C. R. Hurt, and C. J. Brown [EDS.]. Proceedings of the 7th International Rangelands Congress, 26 July–1 August 2003; Durban, South Africa. p. 416–418.

WASHINGTON-ALLEN, R. A., N. E. WEST, D. R. RAMSEY, AND R. A. EFROYMSON. 2006. A protocol for retrospective remote sensing–based ecological monitoring of rangelands. *Rangeland Ecology & Management* 59(1):19–29.

WEAVER, J. E., AND F. W. ALBERTSON. 1956. The grasslands of the Great Plains: their nature and use. Lincoln, Nebraska, USA: Johnsen Publishing Co. 404 p.

WELLS, P. V. 1970. Historical factors controlling vegetation patterns and floristic distributions in the central plains region of North America. In: W. Dort and J. K. Jones [EDS.]. Pleistocene and recent environments of the Central Great Plains. Lawrence, KS, USA: University of Kansas Press. p. 211–221.

WEST, N. E. 2003. Theoretical underpinnings of rangeland monitoring, *Arid Land Research and Management* 17(4):333–346.

WHITE, R. S., AND P. O. CURRIE. 1983. Prescribed burning in the northern great plains: yield and cover responses of 3 forage species in the mixed grass prairie. *Journal of Range Management* 36:179–183.

WILLMS, W. D., J. F. DORMAAR, B. W. ADAMS, AND H. E. DOUWES. 2002. Response of the mixed prairie to protection from grazing. *Journal of Range Management* 55:210–216.

WILLMS, W. D., S. M. MCGINN, AND J. F. DORMAAR. 1993. Influence of litter on herbage production in the mixed prairie. *Journal of Range Management* 46:320–324.

WILLMS, W. D., S. SMOLIAK, AND A. W. BAILEY. 1986. Herbage production following litter removal on Alberta native grasslands. *Journal of Range Management* 39:536–539.

WOODCOCK, C. E., A. A. ALLEN, M. ANDERSON, A. S. BELWARD, R. BINDSCHADLER, W. B. COHEN, F. GAO, S. N. GOWARD, D. HELDER, E. HELMER, R. NEMANI, L. OREAPOULOS, J. SCHOTT, P. S. THENKABAIL, E. F. VERMOTE, J. VOGELMANN, M. A. WULDER, AND R. WYNNE. 2008. Free access to Landsat imagery. *Science* 320:1011.

WRIGHT, H. A. AND A. W. BAILEY. 1982. Fire ecology United States and Southern Canada. Toronto, Ontario, Canada: John Wiley and Sons, Inc. 501 p.