

2010

Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits

Marko J. Spasojevic

Department of Ecology and Evolutionary Biology, University of California-Irvine

Rebecca J. Aicher

Department of Ecology and Evolutionary Biology, University of California-Irvine

Gregory R. Koch

Department of Biological Sciences, Florida International University

Emily S. Marquardt

Department of Biology and Biochemistry, University of Houston

Nicholas Mirotchnick

Department of Ecology, Evolution and Environmental Biology, Columbia University

See next page for additional authors

Follow this and additional works at: https://digitalcommons.fiu.edu/fce_lter_journal_articles



Part of the [Ecology and Evolutionary Biology Commons](#)

Recommended Citation

Spasojevic, M.J., R.J. Aicher, G. Koch, E.S. Marquardt, N. Mirotchnick, T. Troxler, S.L. Collins. 2010. Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits. *Ecology* 91 (6): 1651-1659.

This material is based upon work supported by the National Science Foundation through the Florida Coastal Everglades Long-Term Ecological Research program under Cooperative Agreements #DBI-0620409 and #DEB-9910514. Any opinions, findings, conclusions, or recommendations expressed in the material are those of the author(s) and do not necessarily reflect the views of the National Science Foundation.

This work is brought to you for free and open access by the FCE LTER at FIU Digital Commons. It has been accepted for inclusion in FCE LTER Journal Articles by an authorized administrator of FIU Digital Commons. For more information, please contact dcc@fiu.edu, jkrefft@fiu.edu.

Authors

Marko J. Spasojevic, Rebecca J. Aicher, Gregory R. Koch, Emily S. Marquardt, Nicholas Mirotchnick, Tiffany G. Troxler, and Scott Collins

Fire and grazing in a mesic tallgrass prairie: impacts on plant species and functional traits

MARKO J. SPASOJEVIC,^{1,6} REBECCA J. AICHER,¹ GREGORY R. KOCH,² EMILY S. MARQUARDT,³ NICHOLAS MIROTCHEV,⁴
TIFFANY G. TROXLER,² AND SCOTT L. COLLINS⁵

¹*Department of Ecology and Evolutionary Biology, 321 Steinhaus Hall, University of California-Irvine,
Irvine, California 92697-2525 USA*

²*Department of Biological Sciences, Florida International University, Miami, Florida 33199 USA*

³*Department of Biology and Biochemistry, University of Houston, Houston, Texas 77204 USA*

⁴*Department of Ecology, Evolution and Environmental Biology, Columbia University, New York, New York 10027 USA*

⁵*Department of Biology, MSC03-2020, University of New Mexico, Albuquerque, New Mexico 87131 USA*

Abstract. Fire is a globally distributed disturbance that impacts terrestrial ecosystems and has been proposed to be a global “herbivore.” Fire, like herbivory, is a top-down driver that converts organic materials into inorganic products, alters community structure, and acts as an evolutionary agent. Though grazing and fire may have some comparable effects in grasslands, they do not have similar impacts on species composition and community structure. However, the concept of fire as a global herbivore implies that fire and herbivory may have similar effects on plant functional traits. Using 22 years of data from a mesic, native tallgrass prairie with a long evolutionary history of fire and grazing, we tested if trait composition between grazed and burned grassland communities would converge, and if the degree of convergence depended on fire frequency. Additionally, we tested if eliminating fire from frequently burned grasslands would result in a state similar to unburned grasslands, and if adding fire into a previously unburned grassland would cause composition to become more similar to that of frequently burned grasslands. We found that grazing and burning once every four years showed the most convergence in traits, suggesting that these communities operate under similar deterministic assembly rules and that fire and herbivory are similar disturbances to grasslands at the trait-group level of organization. Three years after reversal of the fire treatment we found that fire reversal had different effects depending on treatment. The formerly unburned community that was then burned annually became more similar to the annually burned community in trait composition suggesting that function may be rapidly restored if fire is reintroduced. Conversely, after fire was removed from the annually burned community trait composition developed along a unique trajectory indicating hysteresis, or a time lag for structure and function to return following a change in this disturbance regime. We conclude that functional traits and species-based metrics should be considered when determining and evaluating goals for fire management in mesic grassland ecosystems.

Key words: disturbance; fire; grassland; grazing; plant functional traits; prairie.

INTRODUCTION

Fire and herbivory are two of the most common globally distributed disturbances that have profound impacts on the structure and function of terrestrial ecosystems (Milchunas et al. 1988, Bond and Van Wilgen 1996). Recently, Bond and Keeley (2005) proposed that fire is, in essence, a global “herbivore.” Fire, like herbivory, is a top-down driver that converts organic materials into inorganic products, alters community structure, and acts as an evolutionary agent (Bond and Keeley 2005). Unlike herbivores, however, “combustive consumption” by fires is based on physical properties of available fuels, and can have rapid and

severe impacts over large areas (Whelan 1995). In addition, while fires often have relatively uniform impacts spatially, the effects of grazing are much more spatially and temporally variable (Fuhlendorf and Engle 2004, Collins and Smith 2006). Although grazing and fire have been proposed to be relatively similar (Bond and Keeley 2005), their impacts on species composition differ (Collins 1987, Keeley et al. 2003, Trager et al. 2004, Uys et al. 2004). For instance, in mesic tallgrass prairies, frequent fires are non-selective and decrease diversity, whereas selective grazing increases diversity (Collins and Smith 2006).

While patterns of species composition have been shown to differ in response to fire and grazing, the Bond and Keeley (2005) hypothesis suggests that these disturbances may have similar impacts on plant functional trait composition. Functional traits integrate the evolutionary and ecological history of a species

Manuscript received 16 March 2009; revised 28 July 2009; accepted 9 September 2009; final version received 16 October 2009. Corresponding Editor: J. J. Battles.

⁶ E-mail: mspasoje@uci.edu

(Ackerly and Reich 1999, Cavender-Bares et al. 2004) and both fire and grazing act as evolutionary agents (Bond and Keeley 2005). While these two disturbances can both select for specialized traits, such as serotiny in the case of fire (Bond and Van Wilgen 1996) or thorns in the case of grazing (Belovsky et al. 1991, Young et al. 2003), fire and grazing may also both select for the same suite of more general traits. For example, both fire and grazing decrease the height of plants (Diaz et al. 2001, Noy-Meir and Kaplan 2002), and increase the abundance of C₄ species (Collins et al. 1998), legumes (Towne and Knapp 1996, Coppedge and Shaw 1998, Noy-Meir and Kaplan 2002), and nonnative plants (D'Antonio and Vitousek 1992, Seabloom et al. 2003). While species composition differs in burned and grazed grasslands, these disturbances may be selecting for similar traits that are distributed among different species. However, the effects of grazing and fire on the abundance of plant functional traits may differ depending on both the frequency and the intensity of burns and grazing (Engle and Bidwell 2001, Briggs et al. 2002, Heisler et al. 2003).

Changes in the fire regime can have strong effects on the species and trait composition of plant communities (Pausas 1999, Franklin et al. 2001, 2005, Kahmen and Poschlod 2008). While frequent fire has been shown to increase the abundance of species with the traits listed above, unburned communities tend to be composed of perennials, shrubs, C₃ species, broad-leaved evergreens, and deciduous species (Collins et al. 1998, Heisler et al. 2003, Grund et al. 2005, Kahmen and Poschlod 2008). Thus, removal of fire from a regularly burned system or the addition of fire to a previously unburned community should shift the community from dominance of one group to the other. However, these systems may exhibit hysteresis (Beisner et al. 2003, Suding et al. 2004, Suding and Hobbs 2009), and the change in fire regime may not shift the community from dominance of one group to the other, but instead to a state different than unburned or regularly burned grasslands.

Using 22 years of data from a mesic grassland, we examined the impacts of fire and grazing on species and trait composition. We hypothesized that (1) trait composition in grasslands that are grazed or burned will converge because these disturbances exert similar top-down pressures on vegetation and community physiognomy, and (2) the degree of trait convergence of grazed and burned grasslands will depend on the frequency of burning. Additionally, we examined the effects of changing the frequency of fire on species and trait composition. Given the high species richness in unburned plots and research showing that burned areas are compositional subsets of unburned sites (Collins et al. 1995), we hypothesized that (3) unburned sites will quickly change toward annually burned communities. However, given the reduced species pool and lower diversity of annually burned sites (Collins et al. 1998), we hypothesized that (4) annually burned grasslands

that had fire removed would exhibit hysteresis and slower convergence of species and trait composition with unburned grasslands.

METHODS

Study site

This study was based on data collected at the Konza Prairie Biological Station (KPBS), a 3487-ha native tallgrass prairie located in the Flint Hills of Kansas, USA ranging from 320 to 444 m above sea level. All data used in this study were from upland sites which are characterized by shallow, rocky, cherty, silty, clay loams. Replicate watersheds at KPBS have been burned experimentally at 1-, 4-, and 20-year intervals since 1972 (Knapp et al. 1998). In 1987, bison (see Plate 1) were introduced to a 1012-ha area of KPBS where they have free access to watersheds subjected to the above fire treatments. Herd size was maintained during our study period at approximately 225 individuals. This herd size was selected so that ≈25% of net primary production is consumed annually (Towne 1999). In 2001, fire treatments were reversed on four ungrazed watersheds (fire reversal treatments); burning was stopped on two watersheds that had been burned annually since 1972 and 1978 respectively, and annual burning treatments were started on two watersheds that had been burned infrequently since 1973 and 1980, respectively.

The vegetation at KPBS is predominantly native unplowed tallgrass prairie, with some woody vegetation in gallery forests along drainages (Knight et al. 1994) as well as in infrequently burned watersheds (Briggs et al. 2002). The grassland is dominated by a matrix of C₄ perennial grasses, including *Andropogon gerardii*, *A. scoparius*, *Sorghastrum nutans*, and *Panicum virgatum*. Although grass biomass dominates, interstitial forb species comprise greater than 75% of the species richness (Towne 2002). Common perennial forbs include *Aster* spp., *Kuhnia eupatorioides*, *Salvia azurea*, and *Solidago* spp. Woody species include *Symphoricarpos orbiculatus*, *Cornus drummondii*, *Prunus americana*, *Rhus glabra*, and *Juniperus virginiana* (Briggs et al. 2005).

Vegetation sampling

We used 22 years (1984–2006) of species composition data from grazed and ungrazed watersheds subjected to 1-year, 4-year, and 20-year fire frequencies, and fire reversal treatments. For reversal treatments we only have composition data up to 2004, three years after the reversal of fire treatment. Vegetation in each watershed was sampled in five permanently located 10-m² circular plots equally spaced along each of four 50-m transects for a total of 20 permanent plots per site in May and late August of each year. May and August data were combined so as to include both early and late season species. Percent cover of species in each plot was estimated using a modified Daubenmire scale (1 = <1%, 2 = 2–5%, 3 = 6–25%, 4 = 26–50%, 5 = 51–75%, 6

= 76–95%, 7 = 95–100%). Abundance of each species was determined by converting the Daubenmire scale to the midpoint of the cover range and then averaging species across the 20 plots at a site.

Trait groups

We constructed trait groups using a published trait database that included species from KPBS (Cleland et al. 2008). The traits included life history strategy (annual, biennial, or perennial), detailed life form (C_3 grass, C_4 grass, leguminous forb, non-leguminous forb, evergreen shrub, or deciduous shrub), height within the canopy, clonality, and nativity. Although certain plant traits exhibit plasticity, all of the traits we used do not vary substantially with environmental conditions. To create trait groups we performed hierarchical clustering on the trait data using Perl (Wall et al. 2000), which used a single linkage algorithm to merge clusters based on the minimum euclidean distance. Complete trait data were present for all species in the database for the trait group clustering. Our hierarchical clustering procedure included all species in our data set, and resulted in 15 trait group clusters (Table 1). The cut-off for the number of clusters was determined by the limited species pool (no trait groups could have only one species) and partly by looking at the results of successive iterations (up to 20 clusters). After 15 clusters, the successive subdivisions were no longer biologically relevant. However, we acknowledge that identifying the most biologically relevant trait groups is challenging (Lavorel and Garnier 2002, Petchey and Gaston 2002). Nonetheless, we feel that our trait groups represent a reasonable first approximation of response patterns to fire and grazing in this mesic grassland ecosystem.

Data analysis

To describe differences in diversity between watersheds we calculated richness and Simpson's diversity index for each year of each watershed using PRIMER 5.2 (Clarke and Gorley 2001). We compared richness and diversity across years among watersheds using a repeated-measures ANOVA in JMP 5.1 (SAS Institute, Cary, North Carolina, USA). We used a nonmetric multidimensional scaling (NMDS) routine in PRIMER to describe differences among the unburned (U), annually burned (A), quadrennially burned (Q), and grazed (G) watersheds for species composition and trait composition using Bray-Curtis dissimilarity for each year for each watershed. Bray-Curtis dissimilarity is a semi-metric measure of dissimilarity used for continuous numerical data and does not group samples by shared zeros in the data set (Beals 1984).

"Stress" is a measure of departure from monotonicity in the relationship between the dissimilarity in the original n -dimensional space and distance in our two-dimensional ordination space (Kruskal and Wish 1978). In general, stress values less than 0.1 correspond to a good indication of the similarities between samples,

TABLE 1. Summary of trait groups constructed.

Trait group	Description
1	perennial C_4 grasses
2	perennial C_3 grasses that are clonal
3	perennial non-leguminous forbs that are short and clonal
4	perennial non-leguminous forbs that are short and not clonal
5	perennial non-leguminous forbs that are medium to tall and clonal
6	perennial non-leguminous forbs that are medium to tall and not clonal
7	perennial legumes that are short to medium and not clonal
8	deciduous shrubs that are not clonal
9	deciduous shrubs that are clonal
10	annual C_4 grasses
11	annual and perennial C_3 grasses that are not clonal
12	annual non-leguminous forbs that are short and not clonal
13	annual/biennial non-leguminous forbs that are medium/tall and not clonal
14	perennial legumes that are clonal
15	evergreen shrubs

whereas stress values greater than 0.2 indicate a poor relationship between original and final configurations (Clarke 1993). However, these are only general guidelines because stress tends to increase with increasing sample size (Clarke 1993). Differences in trait group composition between watersheds were compared in the final year of the data set using an ANOVA in JMP 5.1.

RESULTS

The effects of fire and grazing

Species composition.—We found that grazing and fire do not have similar impacts on species composition in grasslands (Fig. 1A). Overall, richness and diversity were both higher in grazed compared to burned communities (richness, $F_{1,3} = 25.8380$, $P < 0.001$, Simpson's diversity, $F_{1,3} = 15.4026$, $P < 0.001$). While the communities in each watershed were initially relatively similar (initial year mean dissimilarity = 30.3), they diverged in composition over 22 years (Fig. 1A, final year mean dissimilarity = 56.56, $df = 7$, $t = -8.69$, $P < 0.01$). The annually burned community was the most dissimilar and developed along a unique trajectory relative to the other communities (Fig. 1A).

Trait composition.—Patterns of trait composition were not as simple as species composition patterns. We found more convergence in trait composition between grazed and burned communities than for species composition (species composition final year mean dissimilarity = 56.6, trait composition final year mean dissimilarity = 43.6; $df = 7$, $t = -10.25$, $P < 0.01$), but that convergence depended upon fire frequency (Fig. 1B). The quadrennially burned community and the grazed community were most similar in their trajectories during the 22 years (they follow the same general path,

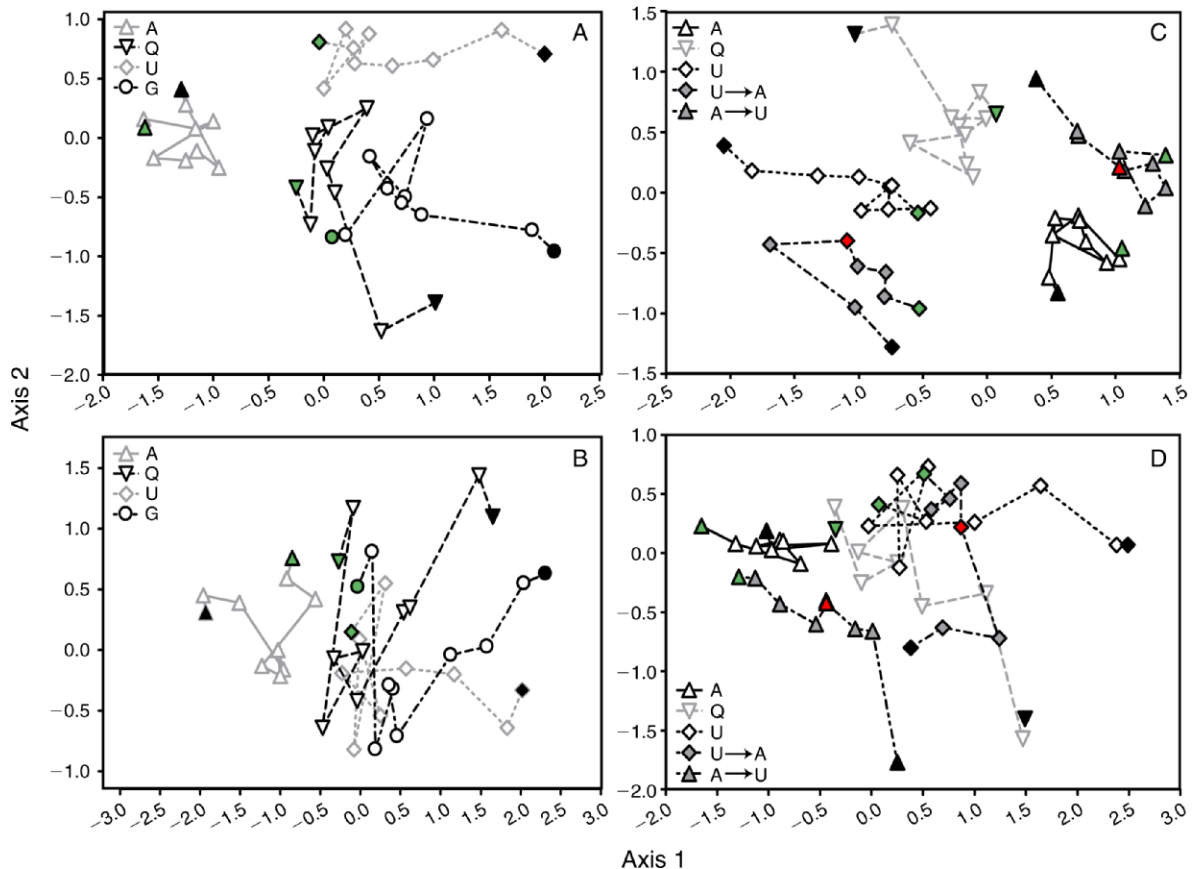


FIG. 1. Nonmetric multidimensional scaling plots of Bray-Curtis dissimilarity for (panel A) species composition (stress = 0.17) and (panel B) trait composition (stress = 0.15) between burned and grazed communities, and (panel C) species composition (stress = 0.18) and (panel D) trait composition (stress = 0.11) for fire reversal treatments over time. White triangles represent annually burned communities (A), white upside-down triangles represent quadrennially burned communities (Q), white diamonds represent unburned communities (U), and white circles represent grazed communities (G). Gray diamonds (U→A) represent a community that was initially unburned, but then had fire reintroduced annually. Gray triangles (A→U) represent a community that was initially annually burned, but then had fire removed from the system. In all cases, the green symbols represent the first year of the study, the black symbols represent the final year of the study, and the red symbols in panels C and D represent the year in which the fire treatment was reversed. For viewing purposes, not all years are shown. For treatments A, Q, U, and G, the first two years are shown, then every third year, and then the final three years. For treatments U→A and A→U, the first two years are shown, then every other year (including the year in which the fire treatment was reversed), and then the final two years.

though slightly offset) and in trait composition at year 22 of the time series (mean dissimilarity = 28.9, the most similar among all treatments). As with species composition, the annually burned watershed developed along a unique trajectory of trait composition.

The grazing and burning treatments had different effects on trait composition (Fig. 2). Burning annually favored C_4 grasses (trait group 1; $F_{3,76} = 143.21$, $P < 0.0001$). The unburned and grazed community was co-dominated by perennial C_4 and C_3 grasses (trait groups 1 and 2). The quadrennially burned community tended to be co-dominated by C_4 grasses and short non-clonal non-leguminous forbs (trait groups 1 and 4). The quadrennially burned community and the grazed community shared the highest relative abundance of annual C_4 grasses (trait group 10; $F_{3,76} = 7.33$, $P = 0.0002$), relatively high abundances of perennial C_4

grasses (trait group 1), and low abundances of perennial non-leguminous clonal forbs (trait groups 3 and 5), but the grazed community had higher abundance of C_3 grasses (trait group 2, $F_{3,76} = 96.44$, $P < 0.0001$; trait group 11, $F_{3,76} = 4.38$, $P = 0.0067$).

The effect of fire treatment reversal

Species composition.—We found that the fire reversal effects on species composition were dependent on treatment (Fig. 1C). The formerly unburned community that is now burned annually (U→A) was initially similar to the unburned and quadrennially burned treatments (Fig. 1C). As the U→A community developed, it became less similar to the unburned treatment and more similar to other annually burned communities at KPBS only three years after reversal of the fire treatment. Initially, the U→A community was co-dominated by

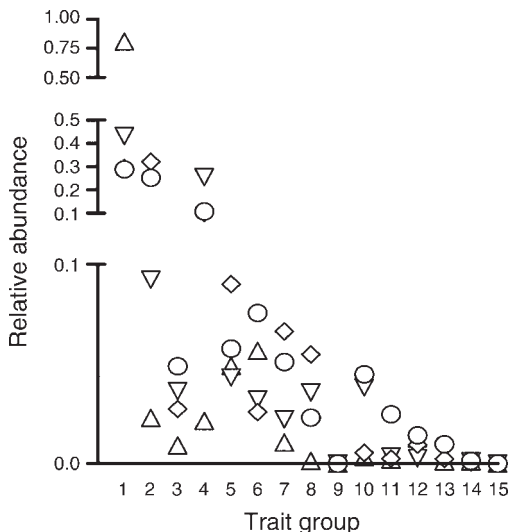


FIG. 2. Trait group composition of burned and grazed communities in 2006 based on mean abundance of trait groups (Table 1). White triangles represent annually burned communities, white upside down triangles represent quadrennially burned communities, white diamonds represent unburned communities, and white circles represent grazed communities. To improve presentation for viewing, standard error bars are not shown. Note the three different y-axis scales.

several species (*Andropogon gerardii*, *Salvia azurea*, and *Sorghastrum nutans*), but after fire was introduced, *Andropogon gerardii* became dominant in the community and both *A. scoparium* and *Lespedeza violacea* (an N-fixing legume) increased in abundance. Furthermore, we found that richness decreased once fire was reintroduced to the system ($F_{1,4} = 8.099$, $P < 0.001$, Fig. 3A). Diversity initially increased once the fire was reintroduced to the U→B community, but then decreased, resulting in no overall change through time ($F_{1,4} = 1.340$, $P = 0.261$, Fig. 3B).

The annually burned community that had fire removed (A→U) had an initial species composition similar to other annually burned communities at KPBS. As the A→U community developed over time, however, it exhibited hysteresis in that it did not return to a community type similar to the unburned community in the three years after reversal of the fire treatment (Fig. 1C). Instead, the A→U community initially followed a similar trajectory as the annually burned community but then switched to a unique trajectory. Additionally, we found that richness increased once fire was removed ($F_{1,4} = 8.099$, $P < 0.001$, Fig. 3A). The A→U community was initially dominated by *Andropogon gerardii* with *Poa pratensis* and *Ambrosia psilostachya*, but following fire removal both *P. pratensis* and *A. psilostachya* decreased in abundance and *Ceanothus herbaceus* (a shrub) and *Solidago canadensis* (a clonal forb) increased in abundance, yet there was no change in diversity in the three years after reversal of fire treatment ($F_{1,4} = 1.340$, $P = 0.261$, Fig. 3B).

Trait composition.—The trait composition of the reversal treatments followed a trend similar to that of species composition. We found that fire reversal treatments had different effects on trait composition depending on the reversal treatment (Fig. 1D). The U→A community was initially similar to the unburned and quadrennially burned treatments (Fig. 1D), but as this community developed, it became less similar to the unburned treatment and more similar to the annually burned community. Once fire was returned to the unburned community (U→A), perennial C₄ grasses dominated (trait group 1, Fig. 4), similar to other annually burned communities at KPBS. However, the

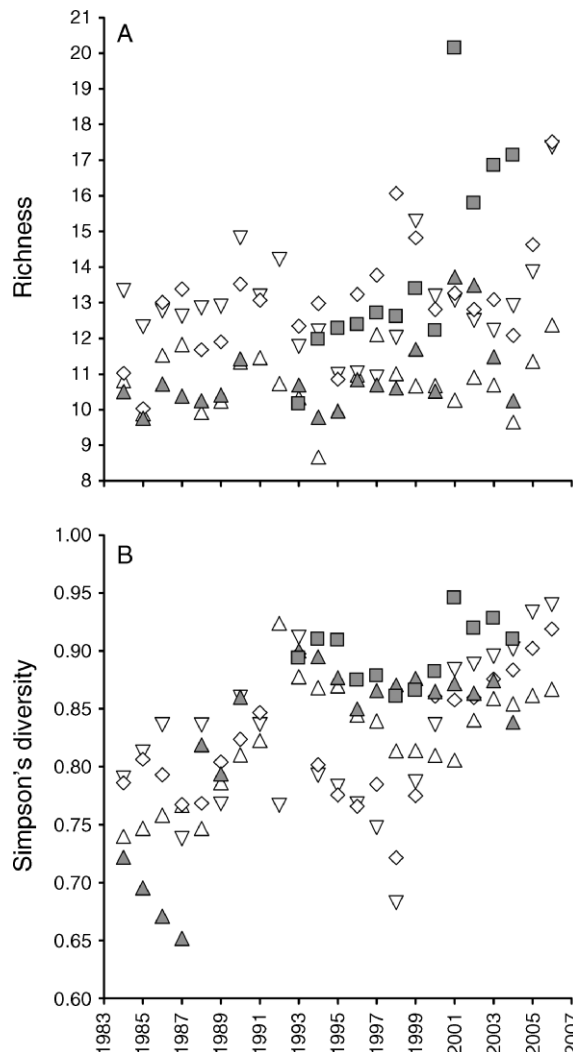


FIG. 3. (A) Richness and (B) diversity over time in reversal treatments. White triangles represent annually burned communities, white upside down triangles represent quadrennially burned communities, and white diamonds represent unburned communities. Gray squares represent a community that was initially unburned, but then had fire reintroduced annually. Gray triangles represent a community that was initially annually burned, but then had fire removed from the system. Fire treatments were reversed in 2001.

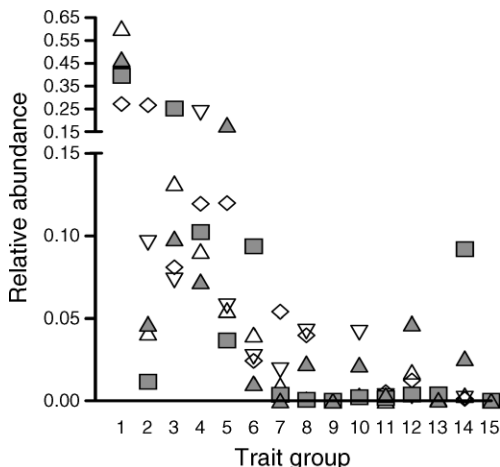


FIG. 4. Trait group composition of reversal communities in 2004 (the final year of data for the reversal treatments) based on mean abundance of trait groups (Table 1). White triangles represent annually burned communities, white upside down triangles represent quadrennially burned communities, and white diamonds represent unburned communities. Gray triangles represent a community that was initially unburned, but then had fire reintroduced annually. Gray diamonds represent a community that was initially annually burned, but then had fire removed from the system. To improve presentation for viewing purposes, standard error bars are not shown.

U→A community was unique because it had higher abundances of trait groups 5 ($F_{4,96} = 8.31$, $P < 0.0001$) and 12 ($F_{4,96} = 26.83$, $P < 0.0001$) compared to all other communities (Fig. 4).

The annually burned community from which fire had been removed (A→U) was initially similar to other annually burned communities in trait group composition. Over time, however, the A→U community did not develop towards a composition similar to unburned communities. Instead, once fire was removed, the A→U treatment proceeded along a unique path and was dominated by trait groups 1 and 3, and had high abundances of species from trait groups 6 ($F_{4,96} = 68.25$, $P < 0.0001$) and 14 ($F_{4,96} = 98.24$, $P < 0.0001$; Fig. 4).

DISCUSSION

The effects of fire and grazing

Our results support Bond and Keeley's (2005) assertion that fire behaves as a non-selective, globally-distributed herbivore, but only when grassland community composition is viewed from a functional trait perspective. We did not find support for our first hypothesis that grazing and fire have similar impacts on community composition; instead, communities that were either grazed or burned diverged in composition over time (Fig. 1A). Similar results have been found in many studies, as these disturbances have different effects on community composition and diversity (e.g., Collins 1987, Morrison 2002, Keeley et al. 2003, Trager et al. 2004, Uys et al. 2004).

Furthermore, we found that the convergence in trait composition between burned and grazed grasslands is contingent upon fire frequency, which supports our second hypothesis. Grasslands burned with an intermediate frequency (once every four years), which is hypothesized to be the historical fire frequency in this region (Hulbert 1985), showed the greatest convergence in trait composition with grazed grasslands as compared to either unburned or annually burned grasslands. The greater convergence in trait composition of the quadrennially burned and grazed grasslands suggests that these communities may operate under similar deterministic assembly rules (i.e., Keddy 1992, Belyea and Lancaster 1999, Fukami et al. 2005), and fire and herbivory have some similar impacts at the trait-group level of organization. Because fires are nonselective consumers of plant biomass, high frequency burning likely exerts more selective pressure on trait composition of grassland communities than grazing by selective herbivores, which primarily consume graminoids (Senft et al. 1987). Thus, although fire and grazing provide similar pressures to grassland communities at intermediate frequencies, chronic fires have a greater impact on species and trait composition than light to moderate levels of chronic grazing because these disturbances differ in selectivity (Fuhlendorf and Engle 2004, Collins and Smith 2006).

Additionally, both intermediately burned and grazed communities had similarly high abundances of annual C₄ grasses (trait group 10) compared to the other communities. Fire and grazing have each been found to promote annual species as these plants are able to quickly recover following either disturbance (Diaz et al. 2001, Kahmen and Poschlod 2008, Savadogo et al. 2008). C₄ species often have a competitive advantage over C₃ plants in high light environments (Ehleringer and Monson 1993) such as those found when light is increased by the removal of the surrounding biomass by either burning or grazing. Burning may have a larger effect on increasing light availability than grazing because herbivores are selective and their impacts are more spatially variable than fires (Fuhlendorf and Engle 2004, Adler et al. 2005, Collins and Smith 2006). It is important to note that although our composition and trait ordination stress values (Fig. 1) were relatively high, we feel that given our large temporal data set (22 years), our stress values indicate good approximations of the similarity between samples because stress values tend to increase with sample size, yet all of our stress values are below 0.20.

The effects of fire treatment reversal

We found evidence to support our third and fourth hypotheses regarding grassland community convergence under the fire reversal treatments. Once the previously unburned community was burned, there was a peak in species richness followed by a decline. This is similar to several studies from a variety of systems (e.g., Adamson



PLATE 1. In 1987, bison were introduced to a 1012-ha area of the Konza Prairie Biological Station in Kansas (USA). Herd size is maintained at approximately 225 individuals, which consume ~25% of net primary production annually. Photo credit: S. L. Collins.

1935, Bell and Koch 1980, Trabaud and Lepart 1980, Posamentier et al. 1981, Hobbs and Atkins 1990). In these studies, the initial increase in richness was a result of species regenerating from the bud bank (Benson et al. 2004) or seeds in situ and may be related to the presence of species in the seed bank or with underground storage organs that were not present in the pre-fire community as adult plants (Whelan 1995). We observed an increase in clonal plants following the introduction of fire, suggesting similar regeneration of species from underground storage organs. Furthermore, species composition became more similar to that of intermediately burned grassland in multidimensional composition space, with an apparent trajectory toward annually burned composition, lending support for our third hypothesis. The unburned-to-annual burning treatment shifted toward dominance by both *A. gerardii* and *A. scoparium*, both perennial C_4 grasses common to annually burned grasslands on KPBS (Towne 2002). These results suggest that the reintroduction of fire to prairies that have had decades of fire suppression may quickly (in 3 years) restore both species and functional trait composition, and thus promote restoration of ecosystem function (Baer and Blair 2008).

Conversely, removal of fire from annually burned grassland did not cause species composition to become similar to that of unburned grassland. Instead, after fire disturbance was suppressed, species and functional trait composition began to develop along a trajectory (Fig. 1C, D) toward a unique community composition. While this reversal community was still dominated by peren-

nial C_4 grasses, similar to both high frequency and intermediately burned communities, it had much higher abundances of tall non-clonal perennial forbs and perennial clonal legumes than any other community (Fig. 4). The high abundance of C_4 species and N-fixing legumes is common after a disturbance that increases available light, such as a fire (Ehleringer and Monson 1993, Vitousek and Field 1999, Smithwick et al. 2005). Conversely, the unburned community exhibited the highest relative abundance of legumes but these are not clonal as in the annually burned-to-unburned reversal community. The high abundance of clonal legumes in formerly burned grassland indicates that these legumes may have regenerated from underground storage organs. The distinct trajectory under this type of fire reversal scenario may reflect a time lag necessary for the ecosystem to fully reorganize, in terms of community composition, before developing towards unburned grassland (Smith et al. 2009). This time lag may be a function of dispersal limitation (Dickson and Foster 2008) given that annually burned areas have lower in situ species diversity than infrequently burned areas. Thus, remeasuring species and functional trait composition after sufficient time will be needed to determine the degree to which convergence does or does not occur over time. However, this unique trajectory may result from hysteresis (Beisner et al. 2003, Suding et al. 2004, Suding and Hobbs 2009), and may indicate that the removal of fire from an annually burned grassland creates a novel state, different than either unburned or annually burned grasslands.

Conclusion

Our data provide some support for the Bond and Keeley (2005) hypothesis that fire acts as a non-selective, globally-distributed herbivore with regard to trait composition, rather than species composition, in North American tallgrass prairie. However, the degree of convergence between fire and herbivory is contingent upon fire frequency, and likely grazing intensity as well. In addition, we found that high fire frequency exerts stronger pressure on grassland composition and structure than moderate levels of grazing by bison, and that annual burning is not analogous to herbivory. Furthermore, reintroducing fire into grasslands following a long time interval without burning restores both species and trait composition within three years. However, fire suppression leads to unique grassland structure and composition that may not retain former ecological function. While we only have three years of data post-fire reversal, we suggest that fire management goals for grassland ecosystems may benefit from considering plant functional traits in addition to species-based metrics. Trait-based approaches comparing fire and herbivory are needed in other ecosystems in order to determine if fire is indeed a general global herbivore.

ACKNOWLEDGMENTS

This work resulted from a Distributed Graduate Seminar (Ushering in a New Era of Functional Ecology: Dynamics in a Changing Environment) conducted through the National Center for Ecological Analysis and Synthesis, a Center funded by NSF (Grant #EF-0553768), the University of California–Santa Barbara, and the State of California. We thank Dan Bunker for sharing his technical expertise, Elsa Cleland for organizing the Distributed Graduate Seminar from which this paper arose, the Konza Prairie Long-term Ecological Research program for data (data set PVC02), Leah De Rose-Wilson for assistance with trait clustering, and Matt Palmer, Dan Flynn, and two anonymous reviewers for providing comments on earlier drafts of the manuscript.

LITERATURE CITED

- Ackerly, D. D., and P. B. Reich. 1999. Convergence and correlations among leaf size and function in seed plants: a comparative test using independent contrasts. *American Journal of Botany* 86:1272–1281.
- Adamson, R. S. 1935. The plant communities of Table Mountain III: a six years' study of regeneration after burning. *Journal of Ecology* 23:44–55.
- Adler, P. B., D. G. Milchunas, O. E. Sala, I. C. Burke, and W. K. Lauenroth. 2005. Plant traits and ecosystem grazing effects: comparison of U.S. sagebrush steppe and Patagonian steppe. *Ecological Applications* 15:774–792.
- Baer, S. G., and J. M. Blair. 2008. Grassland establishment under varying resource availability: a test of positive and negative feedback. *Ecology* 89:1859–1871.
- Beals, E. W. 1984. Bray-Curtis ordination: an effective strategy for analysis of multivariate ecological data. *Advances in Ecological Research* 14:1–55.
- Beisner, B. E., D. T. Haydon, and K. Cuddington. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* 1:376–382.
- Bell, D. T., and J. M. Koch. 1980. Post-fire succession in the northern Jarrah forest of Western-Australia. *Australian Journal of Ecology* 5:9–14.
- Belovsky, G. E., O. J. Schmitz, J. B. Slade, and T. J. Dawson. 1991. Effects of spines and thorns on Australian arid zone herbivores of different body masses. *Oecologia* 88:521–528.
- Belyea, L. R., and J. Lancaster. 1999. Assembly rules within a contingent ecology. *Oikos* 86:402–416.
- Benson, E. J., D. C. Hartnett, and K. H. Mann. 2004. Belowground bud banks and meristem limitation in tallgrass prairie plant populations. *American Journal of Botany* 91:416–421.
- Bond, W. J., and J. E. Keeley. 2005. Fire as a global “herbivore”: the ecology and evolution of flammable ecosystems. *Trends in Ecology and Evolution* 20:387–394.
- Bond, W. J., and B. W. Van Wilgen. 1996. *Fire and plants*. Chapman and Hall, London, UK.
- Briggs, J. M., A. K. Knapp, J. M. Blair, J. L. Heisler, G. A. Hoch, M. S. Lett, and J. K. McCarron. 2005. An ecosystem in transition. Causes and consequences of the conversion of mesic grassland to shrubland. *BioScience* 55:243–254.
- Briggs, J. M., A. K. Knapp, and B. L. Brock. 2002. Expansion of woody plants in tallgrass prairie: a fifteen-year study of fire and fire-grazing interactions. *American Midland Naturalist* 147:287–294.
- Cavender-Bares, J., D. D. Ackerly, D. A. Baum, and F. A. Bazzaz. 2004. Phylogenetic overdispersion in Floridian oak communities. *American Naturalist* 163:823–843.
- Clarke, K. R. 1993. Nonparametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18:117–143.
- Clarke, K. R., and R. N. Gorley. 2001. *Primer v5*. PRIMER-E Ltd., Plymouth, UK.
- Cleland, E. E., et al. 2008. Species responses to nitrogen fertilization in herbaceous plant communities, and associated species traits. *Ecology* 89:1175.
- Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology* 68:1243–1250.
- Collins, S. L., S. M. Glenn, and D. J. Gibson. 1995. Experimental analysis of intermediate disturbance and initial floristic composition: decoupling cause and effect. *Ecology* 76:486–492.
- Collins, S. L., A. K. Knapp, J. M. Briggs, J. M. Blair, and E. M. Steinauer. 1998. Modulation of diversity by grazing and mowing in native tallgrass prairie. *Science* 280:745.
- Collins, S. L., and M. D. Smith. 2006. Scale-dependent interaction of fire and grazing on community heterogeneity in tallgrass prairie. *Ecology* 87:2058–2067.
- Coppedge, B. R., and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass prairie. *Journal of Range Management* 51:258–264.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Diaz, S., I. Noy-Meir, and M. Cabido. 2001. Can grazing response of herbaceous plants be predicted from simple vegetative traits? *Journal of Applied Ecology* 38:497–508.
- Dickson, T. L., and B. L. Foster. 2008. The relative importance of the species pool, productivity and disturbance in regulating grassland plant species richness: a field experiment. *Journal of Ecology* 96:937–946.
- Ehleringer, J. R., and R. K. Monson. 1993. Evolutionary and ecological aspects of photosynthetic pathway variation. *Annual Review of Ecology and Systematics* 24:411–439.
- Engle, D. M., and T. G. Bidwell. 2001. The response of central North American prairies to seasonal fire. *Journal of Range Management* 54:2–10.
- Franklin, J., A. D. Syphard, H. S. He, and D. J. Mladenoff. 2005. Altered fire regimes affect landscape patterns of plant succession in the foothills and mountains of southern California. *Ecosystems* 8:885–898.
- Franklin, J., A. D. Syphard, D. J. Mladenoff, H. S. He, D. K. Simons, R. P. Martin, D. Deutschman, and J. F. O'Leary.

2001. Simulating the effects of different fire regimes on plant functional groups in Southern California. *Ecological Modelling* 142:261–283.
- Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* 41:604–614.
- Fukami, T., T. M. Bezemer, S. R. Mortimer, and W. H. van der Putten. 2005. Species divergence and trait convergence in experimental plant community assembly. *Ecology Letters* 8:1283–1290.
- Grund, K., M. Conedera, H. Schroder, and G. R. Walther. 2005. The role of fire in the invasion process of evergreen broad-leaved species. *Basic and Applied Ecology* 6:47–56.
- Heisler, J. L., J. M. Briggs, and A. K. Knapp. 2003. Long-term patterns of shrub expansion in a C-4-dominated grassland: fire frequency and the dynamics of shrub cover and abundance. *American Journal of Botany* 90:423–428.
- Hobbs, R. J., and L. Atkins. 1990. Fire-related dynamics of a *Banksia* woodland in south-western Western Australia. *Australian Journal of Botany* 38:97–110.
- Hulbert, L. C. 1985. History and use of Konza Prairie Research Natural Area. *Prairie Scout* 5:63–93.
- Kahmen, S., and P. Poschod. 2008. Effects of grassland management on plant functional trait composition. *Agriculture Ecosystems and Environment* 128:137–145.
- Keddy, P. A. 1992. Assembly and response rules—2 goals for predictive community ecology. *Journal of Vegetation Science* 3:157–164.
- Keeley, J. E., D. Lubin, and C. J. Fotheringham. 2003. Fire and grazing impacts on plant diversity and alien plant invasions in the southern Sierra Nevada. *Ecological Applications* 13:1355–1374.
- Knapp, A. K., J. M. Blair, and J. M. Briggs. 1998. Long-term ecological consequences of varying fire frequency in a humid grassland. Pages 173–178 in T. L. Pruden and L. A. Brennan, editors. *Fire in ecosystem management: shifting the paradigm from suppression to prescription*. Tall Timbers Research Station, Tallahassee, Florida, USA.
- Knight, C. L., J. M. Briggs, and M. D. Nellis. 1994. Expansion of gallery forest on Konza-Prairie-Research-Natural-Area, Kansas, USA. *Landscape Ecology* 9:117–125.
- Kruskal, J. B., and M. Wish. 1978. *Multidimensional scaling*. Sage Publications, Beverly Hills, California, USA.
- Lavorel, S., and E. Garnier. 2002. Predicting changes in community composition and ecosystem functioning from plant traits: revisiting the Holy Grail. *Functional Ecology* 16:545–556.
- Milchunas, D. G., O. E. Sala, and W. K. Lauenroth. 1988. A generalized-model of the effects of grazing by large herbivores on grassland community structure. *American Naturalist* 132:87–106.
- Morrison, D. A. 2002. Effects of fire intensity on plant species composition of sandstone communities in the Sydney region. *Austral Ecology* 27:433–441.
- Noy-Meir, I., and D. Kaplan. 2002. Species richness of annual legumes in relation to grazing in Mediterranean vegetation in northern Israel. *Israel Journal of Plant Sciences* 50:S95–S109.
- Pausas, J. G. 1999. Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. *Journal of Vegetation Science* 10:717–722.
- Petchey, O. L., and K. J. Gaston. 2002. Functional diversity (FD), species richness and community composition. *Ecology Letters* 5:402–411.
- Posamentier, H. G., S. S. Clark, D. L. Hain, and H. F. Recher. 1981. Succession following wildfire in coastal heathland (Nadgee Nature Reserve NSW). *Australian Journal of Ecology* 6:165–175.
- Savadogo, P., D. Tiveau, L. Sawadogo, and M. Tigabu. 2008. Herbaceous species responses to long-term effects of prescribed fire, grazing and selective tree cutting in the savanna-woodlands of West Africa. *Perspectives in Plant Ecology, Evolution and Systematics* 10:179–195.
- Seabloom, E. W., W. S. Harpole, O. J. Reichman, and D. Tilman. 2003. Invasion, competitive dominance, and resource use by exotic and native California grassland species. *Proceedings of the National Academy of Sciences USA* 100:13384–13389.
- Senft, R. L., M. B. Coughenour, D. W. Bailey, L. R. Rittenhouse, O. E. Sala, and D. M. Swift. 1987. Large herbivore foraging and ecological hierarchies. *BioScience* 37:789–799.
- Smith, M. D., A. K. Knapp, and S. L. Collins. 2009. A framework for assessing ecosystem dynamics in response to chronic resource alterations induced by global change. *Ecology* 90:3279–3289.
- Smithwick, E. A. H., M. G. Turner, M. C. Mack, and F. S. Chapin. 2005. Postfire soil N cycling in northern conifer forests affected by severe, stand-replacing wildfires. *Ecosystems* 8:163–181.
- Suding, K. N., K. L. Gross, and G. R. Houseman. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends in Ecology and Evolution* 19:46–53.
- Suding, K. N., and R. J. Hobbs. 2009. Threshold models in restoration and conservation: a developing framework. *Trends in Ecology and Evolution* 24:271–279.
- Towne, E. G. 1999. Bison performance and productivity on tallgrass prairie. *Southwestern Naturalist* 44:361–366.
- Towne, E. G. 2002. Vascular plants of Konza Prairie Biological Station: an annotated checklist of species in a Kansas tallgrass prairie. *SIDA, Contributions to Botany* 20:269–294.
- Towne, E. G., and A. K. Knapp. 1996. Biomass and density responses in tallgrass prairie legumes to annual fire and topographic position. *American Journal of Botany* 83:175–179.
- Trabaud, L., and J. Lepart. 1980. Diversity and stability in garrigue ecosystems after fire. *Vegetatio* 43:49–57.
- Trager, M. D., G. W. T. Wilson, and D. C. Hartnett. 2004. Concurrent effects of fire regime, grazing and bison wallowing on tallgrass prairie vegetation. *American Midland Naturalist* 152:237–247.
- Uys, R. G., W. J. Bond, and T. M. Everson. 2004. The effect of different fire regimes on plant diversity in southern African grasslands. *Biological Conservation* 118:489–499.
- Vitousek, P. M., and C. B. Field. 1999. Ecosystem constraints to symbiotic nitrogen fixers: a simple model and its implications. *Biogeochemistry* 46:179–202.
- Wall, L., T. Christianse, and J. Orwant. 2000. *Programming Perl*. Third edition. O'Reilly Media, Sebastopol, California, USA.
- Whelan, R. J. 1995. *The ecology of fire*. Cambridge University Press, Cambridge, UK.
- Young, T. P., M. L. Stanton, and C. E. Christian. 2003. Effects of natural and simulated herbivory on spine lengths of *Acacia drepanolobium* in Kenya. *Oikos* 101:171–179.