

1 The influence of management relative to inherent landscape heterogeneity on the vegetation of a
2 tallgrass prairie

3
4 McGlinn, Daniel^{1*}, Earls, Peter¹ and Palmer, Michael¹

5
6 Daniel McGlinn

7 ¹ *Department of Botany, Life Sciences East 117, Oklahoma State University, Stillwater,*
8 *Oklahoma, 74078 USA; Email: danmcglinn@gmail.com*

9 * correspondence author

10
11 Peter Earls

12 *Email: earlsp@okstate.edu*

13
14 Michael Palmer

15 *Email: mike.palmer@okstate.edu*

Abstract

It is widely recognized that management using prescribed fire and grazing influences plant species richness and composition in many ecological communities. However, the contextual relevance of management is often unclear because the majority of our knowledge is based upon small-scale manipulative studies that are not ideally suited to quantify the importance of management relative to inherent landscape heterogeneity. The purpose of our study was to quantify the importance of fire and grazing by bison and/or cattle relative to inherent site and year effects on the vascular plant community in a tallgrass prairie. We accomplished this objective with an 11 year observational study on a preserve where management decisions were geared towards increasing community heterogeneity through the application of randomized burning and freely ranging grazers. We utilized variation partitioning and explanatory modeling within multiple regression and canonical ordination frameworks on species richness and composition respectively. Our results indicated that site effects, due to below ground differences, explained the majority of variation in richness and composition. Year effects, related to seasonal precipitation, appeared to influence richness but not composition. Management practices were relatively unimportant relative to inherent site and year drivers with respect to both richness and management; however, management effects were not negligible, and years of bison management was positively correlated with plant richness. We suggest that the emphasis of inherent sources of heterogeneity should be increased when setting and assessing conservation priorities that consider the tallgrass prairie plant community. Furthermore, our study demonstrates how observational studies can be used to place management effects into a broader ecological context.

Key words: *restoration, bison, vegetation monitoring, natural variability concept, vascular plants, Flint Hills*

Introduction

Natural variability concepts of land management, which promote spatial and temporal variability, are increasingly utilized in restoration ecology (Palmer et al. 1997). Underlying these concepts are two premises: 1) that historical conditions and processes can provide guidance for management, and 2) that spatial and temporal variability generated by disturbance are vital components of nearly all ecosystems (Landres et al. 1999). Managing for historical conditions is thought to benefit species that have evolved in that system and to minimize human alterations (Swanson et al. 1994). Spatial and temporal variability in management is thought to maintain biological diversity (MacArthur 1965, Petraitis et al. 1989). Although these concepts are grounded in ecological theory, as Palmer et al. (1997) note, the importance of managing for natural variability is rarely examined experimentally.

The application of natural variability concepts is relevant to the conservation and restoration of the North American tallgrass prairie ecosystem. In this ecosystem fire and grazing were important components of pre-Columbian North America disturbance regime (Anderson 1990) and still are today (Daubenmire 1968, Abrams et al. 1986, Collins 1992). Although historically the region was grazed by bison (*Bos bison* L.) and was burned in a variety of seasons, presently much of the remaining tallgrass prairie ecosystem is managed for cattle with annual spring burns (Fuhlendorf and Engle 2001). The purpose of annual spring burning is to maximize yields of palatable C4-grasses (Towne and Owensby 1984). Howe (1994) also noted that many restoration efforts on prairie remnants promote production of C4-grasses with spring season burning and a lack of grazing. These management practices may be a threat to the ecosystem's

biodiversity by only benefiting one competitively superior plant-functional group and by homogenizing an entire region's disturbance regime (Howe 1994, Fuhlendorf and Engle 2001, Nekola and White 2002).

In an effort to restore natural variability to grazing systems, Fuhlendorf and Engle (2001, 2004) suggested the interaction between fire and grazing could be used in a more variable manner in space and time to create a *shifting mosaic* in contrast to the traditional homogenous application of these management tools. They argued that a mosaic of burned and unburned patches more closely approximates the historical variability that would have existed on the landscape and will result in higher biodiversity than traditional homogenous management practices (annual spring burning). This hypothesis is guiding the management of the Tallgrass Prairie Preserve (TGPP), one of the largest preserves in the region of remaining tallgrass prairie (Hamilton 1996, 2007).

The scale of the TGPP (15,700 ha) coupled with the spatially and temporally varying application of fire provides both important opportunities and challenges for experimentally evaluating aspects of the natural variability hypothesis. One of the opportunities that the TGPP offers is a chance to carry out an observational study that investigates the relative importance of management in a tallgrass prairie ecosystem that is presumably in somewhat of a more pre-Columbian ('natural') state given its intact native vegetation, the presence of free ranging bison, and the variable burning regime. This opportunity is valuable because the majority of our knowledge on tallgrass prairie ecology either originates from relatively small scale experiments (e.g., Hulbert 1988) or from strictly controlled watershed treatments (e.g., Konza prairie LTER studies). Controlled studies are extremely valuable in elucidating ecological mechanisms that

1 underlie a system, but they are less useful in providing the ability to examine multiple driving
2 factors of community change within a broader ecological context. This can be better achieved by
3 an observational study if properly designed (Halle 2007, Hobbs et al. 2007, Weiher 2007).

4
5 With these opportunities in mind, the purpose of this study was to investigate the variation in
6 plant species richness and composition in space and time at the TGPP, and to quantify the
7 relative importance of management practices which included prescribed burning and grazing by
8 bison and/or cattle. Our goal was not to directly test whether or not variable management
9 regimes are effective tools for meeting conservation targets, but rather to examine the relative
10 influence that management has on the plant community when management is guided by the
11 natural variability hypothesis. Differences due to management within sites are likely to be
12 strongly confounded by year-to-year variation in climate (Anderson 1982, Gibson and Hulbert
13 1987, Adler and Levine 2007) and between sites by variation in soil (Critchley et al. 2002) and
14 topography (Abrams and Hulbert 1987, Briggs and Knapp 1995). However, these confounding
15 variables can be used as covariables in multiple regression and partial canonical correspondence
16 analysis (pCCA; Borcard et al. 1992) so that the amount of variation only explained by
17 management can be quantified relative to other explanatory variables.

18
19 Using a mixture of explanatory modeling and ordination techniques, we addressed three related
20 questions. Is there directional change in species richness and species composition through time?
21 What are the most important environmental variables for explaining plant richness and
22 composition? If space and time are factored out does disturbance significantly correlate with
23 richness or composition and, if so, in what way?

Methods

Study Site:

The TGPP is a 15,700 ha nature preserve located between 36.73° and 36.90° N latitude, and 96.32° and 96.49° W longitude, in Osage County, Oklahoma and owned by The Nature Conservancy (TNC). Over the course of the 11 year study period (1998-2008), total annual rainfall varied from 490 to 1250 mm. The preserve is situated at the southern extent of the Flint Hills region. The elevation of the preserve ranges from 253 to 366 m, and the underlying bedrock of the region is characterized by soils deriving from Permian sediment (Oviatt 1998). Due to long-term erosion, the surface layers of soil are thin and young; limestone and sandstone are frequently exposed at the surface, sometimes within close proximity of each other. Because of this rockiness the Flint Hills region, including the Tallgrass Prairie Preserve, has remained unplowed and has been instead utilized primarily as rangeland for cattle. Prior to the acquisition of the preserve by TNC in 1989, the majority of the site was managed for cow-calf and yearling cattle production with a 4- to 5-year rotation of prescribed burning and aerial application of broadleaf herbicides (1950-1989) (Hamilton 2007).

Approximately 90 % of the TGPP consists of grasslands. The majority of the grasslands are composed of tallgrass prairie habitats dominated by *Andropogon gerardii*, *Sorghastrum nutans*, *Sporobolus compositus*, *Panicum virgatum*, and *Schizachyrium scoparium*. Shortgrass prairie habitat occurs to a lesser extent on more xeric sites and is dominated by *Bouteloua* spp. Despite the application of herbicide earlier in the 20th century, the flora of the preserve appears relatively intact with a total of 763 species of vascular plants (to date) of which 12.1% are exotic (Palmer 2007).

1
2 *Management:*

3 The management at the TGPP was variable in space and time. In 1993, 300 bison were
4 introduced year-round onto a 1,960 ha portion of the preserve (Hamilton 1996, 2007). As the
5 bison herd increased in size, the area allotted to the herd was increased eight times to an area of
6 8,517 ha by 2007 (Fig. 1, 54% of preserve area). Initial bison stocking rates were increased in
7 1999 to 2.1 animal-unit months ha⁻¹ (see Hamilton 2007 for additional details). Within the bison
8 unit, animals were allowed to range freely and their movement was not obstructed by internal
9 fences. Watersheds within the bison unit were considered randomly for burning only if they met
10 the minimum fuel criteria of 900 kg ha⁻¹ of fine fuels. Within a given year, the season of burn of
11 the bison unit was split as follows: 40 % dormant spring (March - April), 20 % late growing
12 season (August - September), and 40 % dormant winter (October - December). The remainder
13 of the preserve was seasonally grazed by cattle and typically burned more frequently in the
14 dormant spring season, but some of the cattle pastures were utilized for smaller scale (2,350 ha)
15 patch-burn experiments in which only one-third of a given management unit was burned
16 annually (Hamilton 2007). Stocking within the cattle pastures included both intensive-early
17 stocking and season-long stocking, which contrasted with the year-round stocking in the bison
18 unit.

19
20 *Data collection:*

21 Because of the temporally variable and spatially aggregated nature of the management, we opted
22 to annually re-sample a semi-random, spatially stratified set of twenty square 100 m² plots
23 located at the intersections of the 1-km UTM grid (Fig. 1.). The only criteria that we imposed on

1 the selection of our plots was that they contain less than 20 % of woody cover, standing water, or
2 exposed rock. A semi-unbiased spatial stratification of samples is an ideal sampling method for
3 ensuring that samples are representative of the broader variation in grassland communities across
4 the preserve (Palmer 1995). We opted to annually resample our sites in order to observe the
5 vegetation at a given site in multiple management states (e.g., one year post burn, bison vs. cattle
6 grazed), and to provide information on inherent year-to-year variation. We resampled our plots
7 every June from 1998 to 2008 and recorded the percent cover of all vascular plant species at the
8 100 m² scale.

9
10 Each year we combined four 15 cm soil cores collected at each corner of the quadrat and sent
11 these to Brookside Labs (New Knoxville, Ohio) to be analyzed for soil cations, pH, and other
12 variables. We recorded topographic data on slope and aspect in the field. For analyses, aspect
13 was converted to an index of northness [northness = cos(aspect)] (Roberts 1986). We did not
14 consider a corresponding index of eastness because of difficulties in ecological interpretation and
15 exploratory results indicated it was unimportant (not shown).

16
17 Climatic variation was quantified with total monthly precipitation data that was downloaded
18 from the Oklahoma Mesonet Foraker site (36.841° N, -96.428° W; elevation: 330 m; Fig. 1)
19 which is located on the preserve (McPherson et al. 2007). We calculated total precipitation for
20 three arbitrarily defined season variables (four months each): June through September (summer),
21 October through January (winter), and February through May (spring).

1 We derived management variables including years of bison grazing, years since last burn, and
2 number of burns in the past five years from a GIS database that we developed based on TNC's
3 recorded burn and grazing history. We recognize that the number of burns in the past five years
4 is negatively correlated with years since last burn (see Appendix A) and reflects somewhat of an
5 arbitrary cutoff point (five years), but we chose to include this variable in our models despite
6 these shortcomings because we wished to quantify the short term burn history of a site. If a site
7 is burned frequently then years since burn does not convey any information on the history of the
8 site. We chose not to include season of burn as an explanatory variable because 83% (67 out of
9 80) of the prescribed fire events recorded on our study sites took place during the dormant
10 season. It is important to note that all of these management variables were dynamic in time (i.e.,
11 they were not fixed treatments).

13 *Data analysis:*

14 Our goal when modeling richness and species composition was to develop explanatory models
15 and not predictive models, *sensu* Mac Nally (2000). Therefore, we were primarily concerned
16 with comparing the explanatory strength of variables that were chosen a priori rather than
17 developing a single most accurate or necessarily most parsimonious model. We made this
18 conscious decision for two related reasons. Firstly, there are two published analyses that utilized
19 portions of our dataset which indicate in part which variables may yield the greatest explanatory
20 power (Palmer et al. 2003, Brokaw 2004). Secondly, we believe that, given the observational
21 nature of this study, many of our explanatory variables are likely to act as proxy variables, and
22 therefore we wish to clarify our interpretations by only examining a relatively small set of all
23 potential explanatory variables and models.

1
2 We utilized ordinary least squares (OLS) and generalized least squares (GLS) to dissect
3 relationships between species richness and our various explanatory variables. GLS models were
4 considered because they allow us the ability to incorporate correlational models for the residuals
5 of the model. When examining specific explanatory models, we compared 10 isotropic
6 correlational models (5 one parameter and 5 two parameter) for the residuals of each explanatory
7 model (see Appendix B for description of models). The model with the lowest AIC value was
8 then chosen to estimate effect sizes and carry out conditional *F*-tests for each explanatory
9 variable of interest. If a model with one less parameter had an AIC within 3 of the minimum,
10 then visual examination of model fit was used to judge which was more the more appropriate
11 model. The GLS models were fit with a restricted maximum likelihood algorithm which is the
12 preferred method for generating unbiased estimates of variance in models that have a relatively
13 large number of parameters (Diggle et al. 1994). The R package *nlme* version 3.1-90 was used to
14 carry out all GLS model fitting and diagnostics (Pinheiro et al. 2008).

15
16 We utilized variation partitioning (or commonality analysis) to estimate the unique and shared
17 fractions of explained variation in three factors (or classes of variables): sites, years, and
18 management on richness (Legendre and Legendre 1998, Peres-Neto et al. 2006). Sites and years
19 were coded as dummy variables and the management factor was composed of the three
20 management variables described above. We carried out partitioning with OLS as well as with
21 GLS multiple regression. For each fraction of the OLS analysis we report both the coefficient of
22 determination and its adjustment for number of variables, R^2 and R^2_{adj} respectively. For the
23 GLS fractions we calculated a generalized formulation of the coefficient of determination, R^2_{GLS} ,

1 that is appropriate for GLS models (Nagelkerke 1991). For the variation partitioning the
2 correlation structure of all models was assumed to be first-order autoregressive so that
3 comparisons between fractions could be more easily interpreted.

4
5 In all analyses we treated species richness as a continuous variable with normally distributed
6 error. We recognized that in some modeling contexts it is more appropriate to consider richness
7 as a Poisson distributed variable (Candy 1997, Palmer and Hussain 1997). However, because the
8 normal distribution provides a good approximation of a Poisson random variable when the mean
9 is larger than approximately 20; we feel that our usage of normal errors (instead of Poisson) is
10 justified given that richness was never below 48 in our samples. We also recognize that some
11 authors consider richness to only be one facet of grassland biodiversity and that other diversity
12 indices can yield more insight into the ecology of the system (Wilsey et al. 2005, Chalcraft et al.
13 2009). This may be potentially true, but in this study richness was so strongly correlated with all
14 of the indices examined in Wilsey et al. (2005) that additional analyses on various diversity
15 indices would have yielded little additional insight (see Appendix C).

16
17 We utilized both indirect and direct gradient analyses to examine species composition. Prior to
18 all ordinations, we square-root transformed all species cover data, down-weighted rare species,
19 and log-transformed variables (Palmer 1990). Detrended Correspondence Analysis (DCA; Hill
20 and Gauch 1980) was used to visually inspect directional change in the plant composition
21 through time and to estimate the amount of variation composition displayed across a hypothetical
22 environmental gradient. Non-metric multidimensional scaling (NMS), another indirect
23 ordination technique, was used to confirm the general conclusions of the DCA.

1
2 For the analysis of species composition we also carried out variation partitioning but with partial
3 canonical correspondence analysis (pCCA) (Borcard et al. 1992, Okland 1999). The factors used
4 in the variation partitioning were as defined above for richness. We calculated Peres-Neto et al.'s
5 (2006) formulation of the adjusted fraction of variation explained in CCA using a permutation
6 approach (R^2_{CCAadj}). To our knowledge, correlational models for the residuals have not been
7 theoretically developed within the direct ordination context and therefore these methods were not
8 applied in our analysis of species composition. However, when testing the importance of
9 dependent variables that accounted for the within-site variability in species composition, we
10 conducted a toroidal shift Monte Carlo test (Legendre 1993, ter Braak and Šmilauer 2002b). This
11 method of permutation maintains the observed order of the samples within a site while nullifying
12 the temporal relationship of samples between sites. When the constraining variable was site
13 specific, we carried out permutations that randomly shuffled samples only within their year of
14 occurrence which agrees with our assumption of spatial independence between sites but not
15 years. All randomization tests were conducted with 999 iterations to determine significance of
16 all canonical axes for all partial CCA analyses under the reduced model (Legendre and Legendre
17 1998, p308). As in the analysis on richness, we constructed models to examine the importance
18 of specific explanatory variables with estimates of variation explained and conditional F -tests.
19 We performed multivariate analyses with CANOCO version 4.5 (ter Braak and Šmilauer 2002a)
20 and the R package *vegan* version 1.15-1 (Oksanen et al. 2008, R Development Core Team 2008).

Results

Variance in species richness

The average species richness over the 11 year study was 76.24 (± 0.86). The between-year variance ($\sigma = 9.13$) in richness was approximately equal to the between-site variance ($\sigma = 8.93$). There were not strong directional changes in total richness (not shown) or in the four functional groups through time (Fig. 2). Forbs were significantly more species rich than all other functional groups. Variation partitioning of the unbiased OLS estimate of variance explained (R_{adj}^2 ; Table 1), indicated that between-site differences accounted for the majority of variability in richness ($R_{\text{adj}}^2 = 0.48$), followed by year-to-year differences ($R_{\text{adj}}^2 = 0.13$). However, after the within-site temporal autocorrelation was considered (using a first-order auto-regressive term), the strength of site identity relative to year identity was diminished quite a bit according to Nagelkerke's (1991) generalized definition of the coefficient of determination. In both OLS and GLS based variation partitioning, the management class of variables accounted for a much smaller percentage of explained variance in richness (2-4 %), but still contributed a significant amount of explained variation as judged by conditional (type III) *F*-tests at an alpha level of 0.05 (Table 2). The shared component of variation between management and site was larger than the influence of management alone, but the same was not true when comparing year and management after correcting for temporal autocorrelation in which case the shared component was effectively zero.

The most important variable for site-to-site differences was log Ca which was negatively correlated with richness (standardized coefficient [β] = -0.28) (Table 2). Topography did not seem to have a strong influence on richness as neither slope nor northness explained much variation in richness. The most important seasonal rainfall variable was summer rain which was

negatively correlated with richness ($\beta = -0.19$); winter rain and spring rain appeared equally important and both were positively associated with richness ($\beta = 0.15$ and 0.14 respectively). The single most important management variable was years of bison which was positively associated with richness ($\beta = 0.43$). Both years since burn and number of burns in the past five years were negatively associated with richness but neither variable was found to explain significantly more variation in richness than due to chance.

Variance in species composition:

The DCA scatterplot indicated that change in species composition through time was not directional (Fig. 3). Furthermore, sites remained relatively separate from one another in ordination space which indicates that variation in species composition was greater between sites than within sites. There was not a strong difference in sample scores between sites that were bison versus cattle grazed along the first or second DCA axes. Furthermore, when samples switched from cattle to bison, their trajectory through time did not change substantially. The results of the NMDS (not shown) corroborated these qualitative results.

Variation partitioning based upon CCA indicated that site effects explained the majority of the variation in species composition ($R^2_{CCAadj} = 0.46$, Fig. 4). Year and management effects on species composition were negligibly small after adjustment, but both were still found to be significant in randomization tests at the 0.05 level (Table 3). There was a somewhat large shared site and management fraction ($R^2_{CCAadj} = 0.08$) of explained variation. The pCCAs that considered site specific explanatory variables after factoring out year and management effects indicated that log Ca was the most important site specific variable ($R^2_{CCAadj} = 0.07$; Table 3).

Although management explained only a very small proportion of the variation in species composition, we feel that for applied purposes it is still worth examining the management effects on particular species using a pCCA biplot (Fig. 5). The pCCA biplot displays only the 90 most abundant species (although all 307 species were included in the analysis) with respect to the three management variables after factoring out year and site effects as dummy variables. It appeared that both C3 and C4 grasses (open and filled black circles on biplot respectively) appeared to decrease in cover with increased years of bison grazing. *Lespedeza cuneata* (sericea lespedeza), an invasive species, was positively correlated with years of bison grazing. However, this species is a target for herbicide application by the TNC so care must be taken in interpretation of this result. Annual and ruderal species such as *Chamaesyce nutans* (eye bane), *Plantago virginica* (Virginia plantain), *Ambrosia artemisiifolia* (annual ragweed), and *Andropogon virginicus* (broomsedge bluestem) all were positively associated with the number of burns in the past five years.

Discussion

The purpose of our study was to examine the influence of a variable management regime on plant richness and composition relative to site-to-site and year-to-year variability. Our results suggested that the grasslands of the TGPP are not undergoing strong directional changes in richness or composition through time (i.e. they do not appear to be on a clear trajectory). Rather, samples appear to maintain their differences over time and respond somewhat idiosyncratically to management effects. This is not to say that management effects on richness and composition

independent of site and year effects were negligible, but simply that the management effects were relatively unimportant relative to inherent sources of landscape heterogeneity.

Role and drivers of site-to-site variation

The bulk of the variation in richness and composition was due to differences between sites which we believe primarily reflects belowground differences between our samples. We found that Ca explained the predominant amount of site-to-site variability in both richness and composition (Table 2). We interpret Ca's importance to be due to its role as a proxy variable for many other soil properties which are generally indicative of limestone derived soils (Palmer et al. 2003, Brokaw 2004). Using the same 20 sites analyzed in this study (only for the year 2002), Brokaw (2004) found that out of a set of 12 different soil nutrients and total carbon that the two most important variables for explaining plant composition (using pCCA) were total C (C_t) and residual P (P_r). These variables were strongly positively correlated with the majority of soil nutrients and Ca and interpreted as a general indicator of limestone parent materials. These findings suggest that the important role that Ca played in our study does not necessary contradict the body of work that suggests that below ground nutrients are the predominant drivers (not cations) of plant richness and composition in tallgrass prairie ecosystems (Turner et al. 1997, Burke et al. 1998, Baer et al. 2003, 2004).

Why was the relationship between Ca and richness negative? The positive relationship between Ca and soil nutrients (that Brokaw [2004] found in our samples) suggests one possible explanation. If soil high in Ca are the productive, nutrient rich sites, then plant species at these sites may experience stronger competitive exclusion and therefore have lower richness (Grime

1973, Tilman 1982). Pärtel's (2002) species pool hypothesis offers an alternative hypothesis for the negative correlation between richness and Ca (Palmer et al. 2003). The species pool hypothesis postulates that negative correlations between richness and pH (or Ca given their tight correlation) will occur in regions in which habitats high in pH were evolutionarily scarce. Palmer et al. (2003) found that the data from the Tallgrass Prairie Preserve (including this study's sites as well as many others) appeared to support Pärtel's hypothesis in the grasslands but not in the woodlands.

Role and drivers of year-to-year variation

Year-to-year variation was a better explanatory variable of richness than composition. This indicates that changes in year-to-year composition were primarily idiosyncratic. Relative to site and management factors, the year factor explained almost equal amounts of variation in richness as site effects (21% compared to 25%) with 9 fewer parameters. With respect to species composition, year effects were more comparable with the small influence of management (both were < 1%).

Climatic variability is the most obvious driver of year-to-year variation (that is independent of management effects). In the tallgrass prairie plant community water is typically viewed as an important limiting resource, and it is generally positively associated with richness in grasslands (Cornwell and Grubb 2003, Adler and Levine 2007, Wilson 2007). In our study, richness was positively correlated with the winter and spring seasonal precipitation variables, but negatively correlated with the summer precipitation variable. Although all the season variables explained a significant amount of variance in richness, it appeared that the independent negative effect of the

summer variable was largest with respect to richness (Table 2). Following Adler and Levine (2007), increased precipitation may act on richness directly by making the environment more benign and thus allowing more species to coexist. However, if this was generally true, then it is difficult to explain the strong negative correlation observed for summer rainfall. An alternative season specific hypothesis that may explain the negative relationship with summer rainfall is that increased precipitation in the summer previous to sampling yields higher above ground cover of C4 grasses. This increased level of above ground productivity could act to both inhibit germination of annuals and biennials later at the beginning of the next growing season as well as increase asymmetric light competition due to increased litter (Grace 2001). The positive influence of spring and winter rains may also be explained by the critical role that rainfall plays in stimulating germination in the annuals and biennials during the dormant seasons. In this sense precipitation is viewed as a non-resource variable that indirectly influences richness by increasing above ground primary productivity the summer prior to sampling and by influencing germination of species rich plant groups.

Independent management effects

Despite the occurrence of 80 recorded fire events across our twenty sites and the usage of different grazers, our results indicated that management effects were relatively minor in comparison to inherent site and year heterogeneity. This result is in conflict with the dominant paradigm of tallgrass prairie ecology which asserts that management tools such as fire and grazing are the dominant drivers of diversity and composition in the plant community (Collins 1987, Gibson and Hulbert 1987, Anderson 1990). Although the importance of site and year effects is not a novel insight in this system, they are rarely observed to dominate the influence of

1 management so strongly. There are several reasons that likely led to this result. Our samples
2 cover a larger spatial extent than the majority of other tallgrass prairie studies given the large size
3 of the TGPP. Additionally, due to the observational nature of our study, we did not compare our
4 samples to control sites that received no burning and/or grazing although some of our sites went
5 as long as 10 years without experiencing fire. And lastly, by utilizing site and year dummy
6 variables, we provided a conservative (but we believe more honest) estimate of the independent
7 influence of management.

8
9 Although management explained little variation overall, years of bison grazing had a strong
10 positive relationship with richness (Table 2). This suggests that “bison management” is having a
11 positive influence on richness at the TGPP. We stress bison management rather than the
12 influence of bison directly because the average fire return interval was generally longer and the
13 season of burn was more variable in the bison units when compared with the cattle units
14 (Hamilton 2007). Also the bison units were grazed year round, while the cattle units were only
15 seasonally grazed. Therefore, we are fairly confident bison management is having a positive
16 effect on richness, but we are less confident that this is due actually to the presence of bison in
17 comparison to cattle.

18
19 One explanation for the positive correlation between years of bison and richness may be related
20 to the dietary differences between cattle and bison. Bison are thought to selectively forage on
21 graminoids rather than forbs (in contrast to cattle which behave more as generalists) (Coppedge
22 et al. 1998b, Knapp et al. 1999). This dietary behavior may release forbs from competitive
23 exclusion due to the dominant C4 grasses. Although we did not record data on the total cover of

1 each functional group, years of bison grazing was negatively correlated with the cover of the
2 majority of C3 and C4 species (Fig. 5). Both of these findings lend modest support to the
3 hypothesis that bison may increase richness of tallgrass prairie by decreasing the cover of
4 graminoids relative to sites that were grazed seasonally by cattle.

5
6 Towne et al. (2005) undertook a more controlled approach to investigating the effects of bison
7 and cattle grazing on plant richness and composition at the Konza tallgrass prairie over a 10 year
8 period in annually burned pastures. They also found that overall the differences between bison
9 and cattle were slight but that bison grazed patches had a higher cover of some forb species and
10 gained forb species at a more rapid rate through time. They concluded the differential responses
11 of vegetation to bison or cattle grazing may be predominately due to differences in management
12 of these grazers rather than inherent differences in their biology. A similar effect may be taking
13 place at our study site as well.

14
15 Years since last burn was most strongly correlated with changes in species composition (Fig. 5),
16 but the other two management variables explained comparable amounts of variation (Table 3).
17 Other studies have noted the strong positive relationship between cover of legumes and C4
18 grasses with frequency of dormant season burning (Hulbert 1988, Towne and Knapp 1996,
19 Coppedge et al. 1998a, Peterson et al. 2007), although 84% of the burns in our samples occurred
20 during the dormant season, there was not a clear relationship between fire frequency and either
21 of these functional groups (Fig. 5). We found anecdotal evidence that ruderal species were
22 positively associated with the number of burns in the past five years (Fig. 5) which is to be

1 expected given that these samples were likely to have higher grazing pressure due to their more
2 nutritious regrowth (Coppedge and Shaw 1998, Fuhlendorf and Engle 2001).

3
4 *Management implications:*

5 Based on our results, we suggest that the importance of the template or inherent site-to-site
6 heterogeneity cannot be neglected when testing ecological theory, setting conservation goals, or
7 evaluating restoration progress. Despite the experimental evidence that studies have provided on
8 the strong role of management in our study system, these variables were not as important as
9 variation due to soil or climate. Therefore we suggest that ecologists and managers keep an open
10 mind to the potential drivers of their ecological systems and not simply the aspects that they can
11 manipulate.

12
13 Another implication of our results is that conservation priorities and restoration targets should be
14 viewed within the context of the important environmental gradients that shape community
15 composition (White and Walker 1997, Nekola and White 2002). Our study site, the TGPP,
16 occurs in the Flint Hills region of Oklahoma and Kansas where the largest amount of contiguous
17 unplowed tallgrass prairie remains. Future preserve design in this region should strongly
18 consider capturing as much of the limestone to sandstone gradient within the preserve as
19 possible, in order to capture a larger degree of complementarity in plant species composition.

20
21 *The importance of observational studies:*

22 It is important to recognize that even without control treatments that observation studies can
23 provide vital information about the ecology of a system (Underwood et al. 2000, Legg and Nagy

2006, MacNeil 2008). To examine long-term trends at our study site, it was more appropriate to conduct an observational study (rather than a manipulative one) given our interest in the role of inherent heterogeneity as well as the temporally dynamic nature of the management at the preserve. Our study demonstrates that long-term plots may be a potentially valuable source of information despite a lack of clearly defined treatments if they are placed objectively (Palmer 1993). This is not to say that experimental studies are not necessary for uncovering driving mechanisms, but rather that it is often valuable to complement them with observational studies such that the context of their results can be better interpreted.

Conclusions:

Management effects on plant richness and composition were relatively minor relative to inherent variation between sites and years. However, management effects were also not completely negligible, and a significant positive correlation between bison management and richness was detected. Inherent spatial environmental heterogeneity should be considered in setting and evaluating conservation targets. And lastly, long-term observational studies can be valuable for placing management effects into context.

Acknowledgments

DJM received funding from the U.S. Environmental Protection Agency (EPA) under the Greater Research Opportunities (GRO) Graduate Program. The U.S. EPA has not officially endorsed this publication, and the views expressed herein may not reflect the views of the Agency.

Additionally we wish to thank Bob Hamilton, members of LIBRA, and the Osage Nation for assistance with field work. The Oklahoma State University College of Arts and Science, The

Oklahoma Nature Conservancy, The Spatial and Environmental Information Clearinghouse, The Phileology Trust, The Swiss Federal Institute for Forest, Snow and Landscape Research, and the Oklahoma Water Resources Research Institute for assistance at various stages of research at the Tallgrass Prairie Preserve.

References:

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.

Abrams, M. D., A. K. Knapp, and L. C. Hulbert. 1986. A ten-year record of aboveground biomass in a Kansas tallgrass prairie: effects of fire and topographic position. *American Journal of Botany* **73**:1509-1515.

Adler, P. B. and J. M. Levine. 2007. Contrasting relationships between precipitation and species richness in space and time. *Oikos* **116**:221-232.

Anderson, E. 1990. The historic role of fire in North American grassland. *in* Fire in North American tallgrass prairies, Eds. S. L. Collins and L. L. Wallace. University of Oklahoma Press, Norman, Oklahoma.

Anderson, R. C. 1982. An evolutionary model summarizing the roles of fire, climate, and grazing animals in the origin and maintenance of grasslands: an end paper. Pages 297-308 *in* Grasses and grasslands: systematics and ecology, Eds. J. R. Estes, R. J. Tylr, and J. N. Brunken. University of Oklahoma Press, Norman, Oklahoma, USA.

Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2003. Soil resources regulate productivity and diversity in newly established tallgrass prairie. *Ecology* **84**:724-735.

1 Baer, S. G., J. M. Blair, S. L. Collins, and A. K. Knapp. 2004. Plant community responses to
2 resource availability and heterogeneity during restoration. *Oecologia* **139**:617-629.

3 Borcard, D., P. Legendre, and P. Drapeau. 1992. Partialling out the spatial component of
4 ecological variation. *Ecology* **73**:1045-1055.

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

8 Brokaw, J. M. 2004. Comparing explanatory variables in the analysis of species composition of a
9 tallgrass prairie. *Proceedings of the Oklahoma Academy of Science* **84**:33-40.

10 Burke, I. C., W. K. Lauenroth, M. A. Vinton, P. B. Hook, R. H. Kelly, H. E. Epstein, M. R.
11 Aguiar, M. D. Robles, M. O. Aguilera, K. L. Murphy, and R. A. Gill. 1998. Plant-soil
12 interactions in temperate grasslands. *Biogeochemistry* **42**:121-143.

13 Candy, S. G. 1997. Poisson vs normal-errors regression in Mac Nally (1996). *Austral Ecology*
14 **22**:233-235.

15 Chalcraft, D. R., B. J. Wilsey, C. Bowles, and M. R. Willig. 2009. The relationship between
16 productivity and multiple aspects of biodiversity in six grassland communities.
17 *Biodiversity and Conservation* **18**:91-104.

18 Collins, S. L. 1987. Interaction of disturbances in tallgrass prairie: a field experiment. *Ecology*
19 **68**:1243-1250.

20 Collins, S. L. 1992. Fire frequency and community heterogeneity in tallgrass prairie vegetation.
21 *Ecology* **73**:2001-2006.

- 1 Coppedge, B. R., D. M. Engle, C. S. Toepfer, and J. H. Shaw. 1998a. Effects of seasonal fire,
2 bison grazing and climatic variation on tallgrass prairie vegetation. *Plant Ecology*
3 **139**:235-246.
- 4 Coppedge, B. R., D. M. Leslie, and J. H. Shaw. 1998b. Botanical composition of bison diets on
5 tallgrass prairie in Oklahoma. *Journal of Range Management* **51**:379-382.
- 6 Coppedge, B. R. and J. H. Shaw. 1998. Bison grazing patterns on seasonally burned tallgrass
7 prairie. *Journal of Range Management* **51**:258-265.
- 8 Cornwell, W. K. and P. J. Grubb. 2003. Regional and local patterns in plant species richness with
9 respect to resource availability. *Oikos* **100**:417-428.
- 10 Critchley, C. N. R., B. J. Chambers, J. A. Fowbert, R. A. Sanderson, A. Bhogal, and S. Rose.
11 2002. Association between lowland grassland plant communities and soil properties.
12 *Biological Conservation* **105**:199-215.
- 13 Daubenmire, R. 1968. Ecology of fire in grasslands. *Advances in Ecological Research* **5**:209-
14 266.
- 15 Diggle, P. J., K.-Y. Liang, and S. L. Zeger. 1994. *Anaylsis of Longitudinal Data*. Clarendon
16 Press, Oxford.
- 17 Fuhlendorf, S. D. and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem
18 management based on evolutionary grazing patterns. *Bioscience* **51**:625-632.
- 19 Fuhlendorf, S. D. and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a
20 shifting mosaic on tallgrass prairie. *Journal of Applied Ecology* **41**:604-614.
- 21 Gibson, D. J. and L. C. Hulbert. 1987. Effects of fire, topography and year-to-year climatic
22 variation on species composition in tallgrass prairie. *Plant Ecology* **72**:175-185.

1 Grace, J. B. 2001. The roles of community biomass and species pools in the regulation of plant
2 diversity. *Oikos* **92**:193-207.

3 Grime, J. P. 1973. Competitive exclusion in herbaceous vegetation. *Nature* **242**:344-347.

4 Halle, S. 2007. Science, art, or application - the "Karma" of restoration ecology. *Restoration*
5 *Ecology* **15**:358-361.

6 Hamilton, R. G. 1996. Using fire and bison to restore a functional tallgrass prairie landscape.
7 Pages 208-214 *in* Transactions of the 61st North American Wildlife and Natural
8 Resources Conference, Eds. Wildlife Management Institute, Washington D.C.

9 Hamilton, R. G. 2007. Restoring heterogeneity on the Tallgrass Prairie Preserve: applying the
10 fire-grazing interaction model. Pages 163-169 *in* Proceedings of the 23rd Tall Timbers
11 Fire Ecology Conference: Fire in Grassland and Shrubland Ecosystems, Eds. R. E.
12 Masters and K. E. M. Galley. Allen Press, Tall Timbers Research Station, Tallahassee,
13 Florida, USA.

14 Hill, M. O. and H. G. Gauch. 1980. Detrended Correspondence analysis: an improved ordination
15 technique. *Vegetatio* **42**:47-58.

16 Hobbs, R. J., S. Yates, and H. A. Mooney. 2007. Long-term data reveal complex dynamics in
17 grassland in relation to climate and disturbance. *Ecological Monographs* **77**:545-568.

18 Howe, H. F. 1994. Managing species diversity in tallgrass prairie: Assumptions and implications.
19 *Conservation Biology* **8**:691-704.

20 Hulbert, L. C. 1988. Causes of fire effects in tallgrass prairie. *Ecology* **69**:46-58.

21 Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G.
22 Towne. 1999. The keystone role of bison in North American Tallgrass Prairie. *Bioscience*
23 **49**:39-50.

1 Landres, P. B., P. Morgan, and F. J. Swanson. 1999. Overview of the use of natural variability
2 concepts in managing ecological systems. *Ecological Applications* **9**:1179-1188.

3 Legendre, P. 1993. Spatial autocorrelation: trouble or new paradigm? *Ecology* **74**:1659-1673.

4 Legendre, P. and L. Legendre. 1998. *Numerical Ecology*. Elsevier, Boston.

5 Legg, C. J. and L. Nagy. 2006. Why most conservation monitoring is, but need not be, a waste of
6 time. *Journal of Environmental Management* **78**:194-199.

7 Mac Nally, R. 2000. Regression and model-building in conservation biology, biogeography and
8 ecology: The distinction between - and reconciliation of - 'predictive' and 'explanatory'
9 models. *Biodiversity and Conservation* **9**:655-671.

10 MacArthur, R. H. 1965. Patterns of species diversity. *Biological Review* **40**:510-533.

11 MacNeil, M. A. 2008. Making empirical progress in observational ecology. *Environmental*
12 *Conservation* **35**:193-196.

13 McPherson, R. A., C. A. Fiebrich, K. C. Crawford, J. R. Kilby, D. L. Grimsley, J. E. Martinez, J.
14 B. Basara, B. G. Illston, D. A. Morris, K. A. Kloesel, A. D. Melvin, H. Shrivastava, J. M.
15 Wolfenbarger, J. P. Bostic, D. B. Demko, R. L. Elliott, S. J. Stadler, J. D. Carlson, and A.
16 J. Sutherland. 2007. Statewide Monitoring of the Mesoscale Environment: A Technical
17 Update on the Oklahoma Mesonet. *Journal of Atmospheric and Oceanic Technology*
18 **24**:301-321.

19 Nagelkerke, N. J. D. 1991. A note on a general definition of the coefficient of determination.
20 *Biometrika* **78**:691-692.

21 Nekola, J. C. and P. S. White. 2002. Conservation, the two pillars of ecological explanation, and
22 the paradigm of distance. *Natural Areas Journal* **22**:305-310.

1 Okland, R. H. 1999. On the variation explained by ordination and constrained ordination axes.
2 Journal of Vegetation Science **10**:131-136.

3 Oksanen, J., R. Kindt, P. Legendre, B. O'Hara, G. L. Simpson, P. Solymos, M. H. H. Stevens,
4 and H. Wagner. 2008. Vegan: community ecology package.

5 Oviatt, C. G. 1998. Geomorphology of Konza Prairie. Pages 35-47 in A. Knapp, J. Briggs, D.
6 Hartnett and S. Collins (eds.), Grassland Dynamics: Long-term ecological research in
7 tallgrass prairie, Eds. Oxford University Press, NY.

8 Palmer, M. A., R. F. Ambrose, and N. L. Poff. 1997. Ecological theory and community
9 restoration. Restoration Ecology **5**:291-300.

10 Palmer, M. W. 1990. Spatial scale and patterns of species-environment relationships in
11 hardwood forest of the North Carolina piedmont. Coenoses **5**:79-87.

12 Palmer, M. W. 1993. Potential biases in site and species selection for ecological monitoring.
13 Environmental Monitoring and Assessment **26**:277-282.

14 Palmer, M. W. 1995. How should one count species? Natural Areas Journal **15**:124-136.

15 Palmer, M. W. 2007. The vascular flora of the Tallgrass Prairie Preserve, Osage county,
16 Oklahoma. Castanea **72**:235-246.

17 Palmer, M. W., J. R. Arévalo, M. C. Cobo, and P. G. Earls. 2003. Species richness and soil
18 reaction in a northeastern Oklahoma landscape. Folia Geobotanica **38**:381-389.

19 Palmer, M. W. and M. Hussain. 1997. The unimodal (species richness-biomass) relationship in
20 microcommunities emerging from soil seed banks. Proceedings of the Oklahoma
21 Academy of Sciences **77**:17-26.

22 Pärtel, M. 2002. Local plant diversity patterns and evolutionary history at the regional scale.
23 Ecology **83**:2361-2366.

1 Peres-Neto, P. R., P. Legendre, S. Dray, and D. Borcard. 2006. Variation partitioning of species
2 data matrices: Estimation and comparison of fractions. *Ecology* **87**:2614-2625.

3 Peterson, D. W., P. B. Reich, and K. J. Wragg. 2007. Plant functional group responses to fire
4 frequency and tree canopy cover gradients in oak savannas and woodlands. *Journal of*
5 *Vegetation Science* **18**:3-12.

6 Petraitis, P. S., R. E. Latham, and R. A. Niesenbaum. 1989. The maintenance of species diversity
7 by disturbance. *Quarterly Review of Biology* **65**:393-418.

8 Pinheiro, J., D. Bates, S. DebRoy, D. Sarkar, and R. C. Team. 2008. nlme: Linear and Nonlinear
9 Mixed Effects Models.

10 R Development Core Team. 2008. R: a language and environment for statistical computing. R
11 Foundation for Statistical Computing, Vienna, Austria.

12 Roberts, D. W. 1986. Ordination on the basis of fuzzy set theory. *Vegetatio* **66**:123-131.

13 Swanson, F. J., J. A. Jones, D. A. Wallin, and J. H. Cissel. 1994. Natural variability --
14 implications for ecosystem management Pages 85-99 *in* Eastside forest ecosystem health
15 assessment. Volume II. Ecosystem management: principles and applications., Eds. M.
16 E. Jense and P. S. Bourgeron. USDA Forest Service, Missoula, Montana, USA.

17 ter Braak, C. J. F. and P. Šmilauer. 2002a. Canoco for Windows Version 4.5. Biometris - Plant
18 Research International, Wageningen, The Netherlands.

19 ter Braak, C. J. F. and P. Šmilauer. 2002b. CANOCO Reference manual and CanoDraw for
20 Windows User's guide: Software for Canonical Community Ordination (version 4.5).
21 Microcomputer Power, Ithaca, NY, USA.

22 Tilman, D. 1982. Resource Competition and Community Structure. Princeton University Press,
23 Princeton, NJ.

- 1 Towne, E. G., D. C. Hartnett, and R. T. Cochran. 2005. Vegetation trends in tallgrass prairie
2 from bison and cattle grazing. *Ecological Applications* **15**:1550-1559.
- 3 Towne, E. G. and A. K. Knapp. 1996. Biomass and density responses in tallgrass prairie legumes
4 to annual fire and topographic position. *American Journal of Botany* **83**:175-179.
- 5 Towne, G. and C. Owensby. 1984. Long-term effects of annual burning at different dates in
6 ungrazed Kansas tallgrass prairie. *Journal of Range Management* **37**:392-397.
- 7 Turner, C. L., J. M. Blair, R. J. Scharz, and J. C. Neel. 1997. Soil N and plant responses to fire,
8 topography, and supplemental N in tallgrass prairie. *Ecology* **78**:1832-1843.
- 9 Underwood, A. J., M. G. Chapman, and S. D. Connell. 2000. Observations in ecology: you can't
10 make progress on processes without understanding the patterns. *Journal of Experimental*
11 *Marine Biology and Ecology* **250**:97-115.
- 12 USDA and NRCS. 2008. The PLANTS Database. National Plant Data Center, Baton Rouge, LA
13 70874-4490 USA.
- 14 Weiher, E. 2007. On the Status of Restoration Science: Obstacles and Opportunities. *Restoration*
15 *Ecology* **15**:340-343.
- 16 White, P. S. and J. L. Walker. 1997. Approximating nature's variation: selecting and using
17 reference information in restoration ecology. *Restoration Ecology* **5**:338-349.
- 18 Wilsey, B. J., D. R. Chalcraft, C. M. Bowles, and M. R. Willig. 2005. Relationships among
19 indices suggest that richness is an incomplete surrogate for grassland biodiversity.
20 *Ecology* **86**:1178-1184.
- 21 Wilson, S. D. 2007. Competition, resources, and vegetation during 10 years in native grassland.
22 *Ecology* **88**:2951-2958.
- 23
- 24

Tables

Table 1. Variation partitioning of richness into the its components for site (S), year (Y), and management (M) variables. Note that the factors: site, year, and management consist of q explanatory variables. The site and year factors these variables were coded as dummy variables (see *Methods* for explanation). The partitioning was conducted with respect to the unadjusted and adjusted OLS coefficients of determination (R^2 and R^2_{adj} respectively) as well as coefficients of determination for GLS models incorporating a single autoregressive term (R^2_{GLS}).

Factors (q)	OLS		GLS (AR1)
	R^2	R^2_{adj}	R^2_{GLS}
$S \mid Y \cup M$ (19)	0.48	0.48	0.27
$Y \mid S \cup M$ (10)	0.13	0.13	0.18
$M \mid S \cup Y$ (3)	0.04	0.04	0.02
$S \cap Y \mid M$	0.01	-0.02	0.25
$S \cap M \mid Y$	0.05	0.05	0.04
$Y \cap M \mid S$	0.08	0.07	< 0.01
$S \cap Y \cap M$	-0.01	-0.02	< 0.01
Total (32)	0.77	0.74	0.77

Table 2. The conditional explanatory power of specific explanatory variables on species richness. The variables site, year, and management are as defined in Table 1. The model used to account for within site temporal autocorrelation in the residuals is displayed with the estimated range and nugget (see *Methods* for details on the selection of the correlation model). Cells marked as “--” indicate that their values are identical to cells above. The standardized regression coefficient (β) is also given to indicate the strength and direction of the response of richness as well as an estimate of variation explained and the results of conditional *F*-tests (approximate tests).

Explanatory Variables	Covariables	Temporal Autocorrelation Model (range, nugget)	β	R^2_{GLS}	<i>F</i> -ratio	<i>p</i> -value
Factors (<i>q</i>)						
site (19)	year + management	Gaussian (3.92, 0.55)	NA	0.25	5.80	< 0.001
year (10)	site + management	--	NA	0.21	12.87	< 0.001
management (3)	site + year	--	NA	0.01	4.07	0.008
Site Specific Variables						
log Ca	slope + northness + year + management	Exponential (10.91, 0.32)	-0.28	0.05	6.51	0.012
slope	log Ca + northness + year + management	--	-0.10	< 0.01	0.71	0.400
northness	log Ca + slope + year + management	--	0.24	0.01	3.71	0.056
Year Specific Variables						
summer rain	winter rain + spring rain + site + management	Exponential (0.85)*	-0.19	0.03	26.65	< 0.001
winter rain	summer rain + spring rain + site + management	--	0.15	0.02	15.47	< 0.001
spring rain	summer rain + winter rain + site + management	--	0.14	0.01	11.43	0.001
Management Variables						
years of bison	years since last burn + # of burns in 5 years + site + year	Gaussian (3.92, 0.55)	0.43	0.01	7.61	0.006
years since burn	years of bison + # of burns in 5 years + site + year	--	-0.11	< 0.01	3.52	0.062
# of burns in 5 years	years of bison + years since last burn + site + year	--	-0.11	< 0.01	1.34	0.249

*a one parameter model (i.e., the nugget was assumed to be zero)

Table 2. The results of Monte Carlo randomization tests using the results of pCCA under the reduced model. Each randomization test was conducted with 999 iterations. The variables site, year, and management are as defined in Table 1. Cells marked as “--” indicate that their values are identical to cells above.

Explanatory Variable	Covariables	Type of Randomization*	R^2_{CCA}	R^2_{CCAadj}	F-ratio	p-value
Factors (<i>q</i>)						
site (19)	year + management	random shuffle	0.50	0.46	13.471	0.001
year (10)	site + management	toroidal shift	0.04	< 0.01	2.248	0.001
management (3)	site + year	random shuffle	0.01	< 0.01	2.145	0.001
--	--	toroidal shift	--	--	--	0.001
Site Specific Variables						
log Ca	slope + northness + year + management	random shuffle	0.13	0.12	19.735	0.001
slope	log Ca+ northness + year + management	random shuffle	0.03	0.03	8.152	0.001
northness	log Ca + slope + year + management	random shuffle	0.02	0.01	5.219	0.001
Management Variables						
years of bison	years since last burn + # of burns in 5 years + site + year	random shuffle	< 0.01	< 0.01	2.314	0.001
--	--	toroidal shift	--	--	--	0.001
years since burn	years of bison + # of burns in 5 years + site + year	random shuffle	< 0.01	< 0.01	2.102	0.001
--	--	toroidal shift	--	--	--	0.001
# of burns in 5 years	years of bison + years since last burn + site + year	random shuffle	< 0.01	< 0.01	1.616	0.001
--	--	toroidal shift	--	--	--	0.021

* random shuffle permutations were constrained to occur within a year, toroidal shifts were constrained within a given a site and preserved the temporal order of samples (see *Methods* for more explanation)

Figures

The Nature Conservancy's
Tallgrass Prairie Preserve, Osage Co., OK, USA

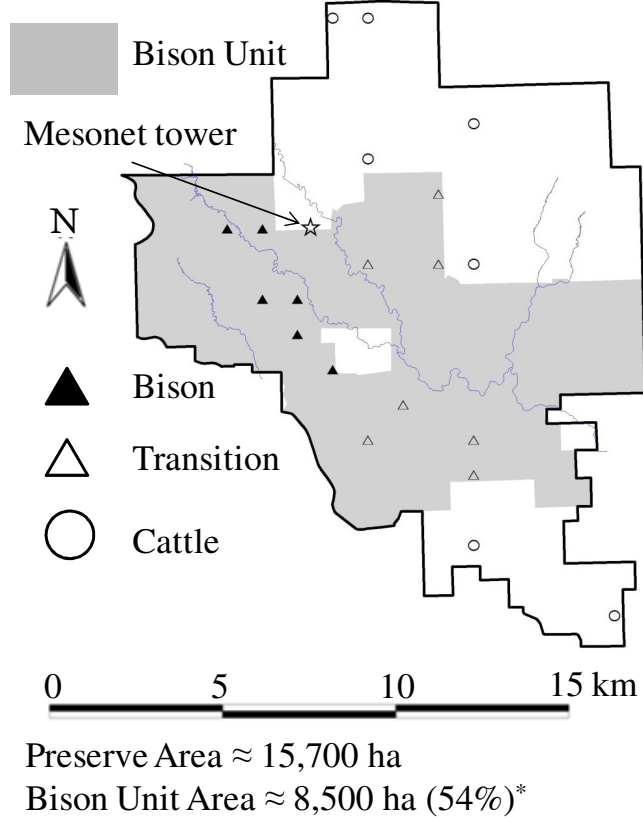


Fig. 1 A map of the Tallgrass Prairie Preserve. The shaded area denotes the bison unit which increased in area during the duration of the study. The Mesonet tower where the climate data was recorded is marked on the map as a star (☆). The twenty quadrats sampled each year of this study are displayed on the map. The sites that were bison at the beginning of the study (1998) are displayed with filled triangles (▲), those that transitioned during the study from cattle to bison are denoted by unfilled triangles (Δ), and the other cattle grazed samples are denoted by unfilled circles (○). *Area of bison unit is as of May 1, 2008.

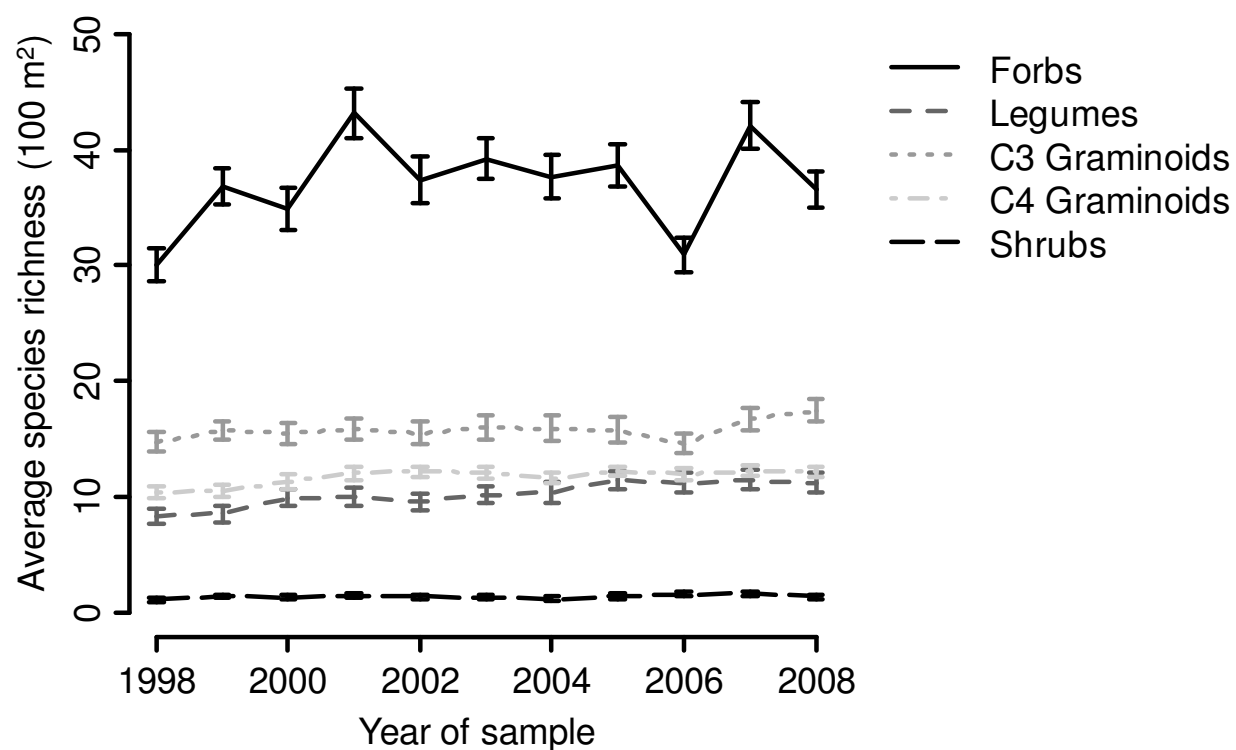


Fig. 2. The average species richness of five functional groups: forbs (that are not legumes), legumes, C3 graminoids (grasses, sedges, and rushes), C4 graminoids, and shrubs (woody plants) over the course of the study. The error bars display $\bar{x} \pm 1$ standard error.

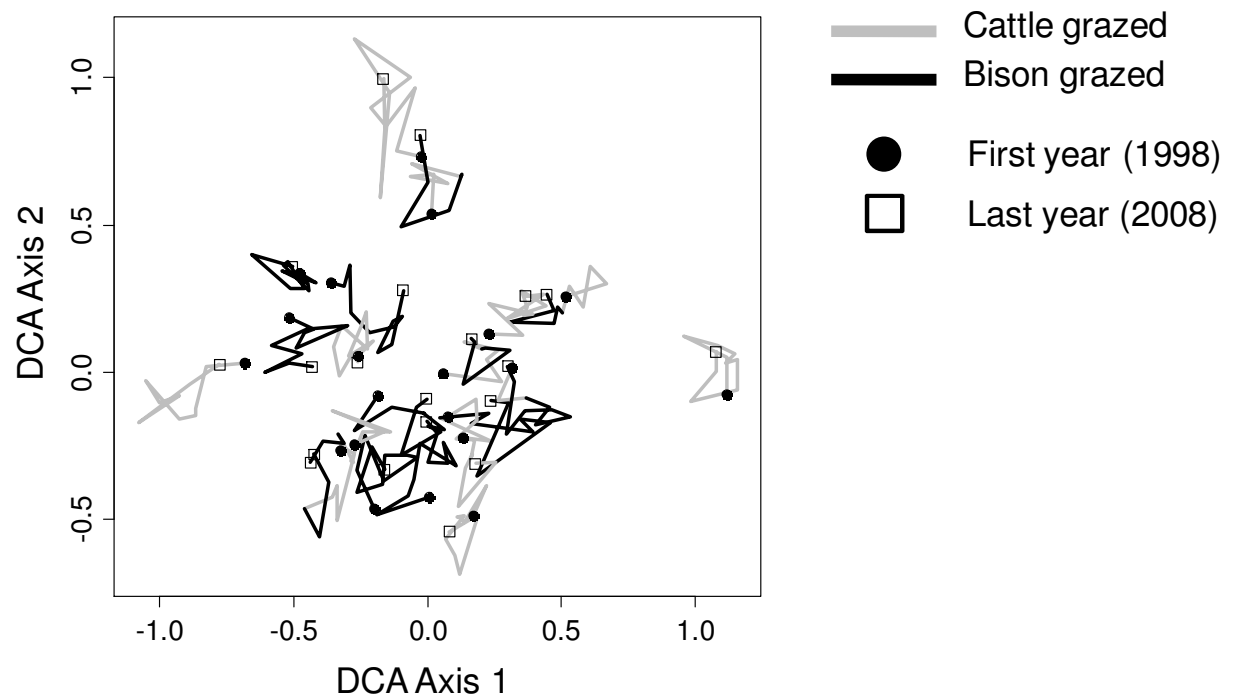
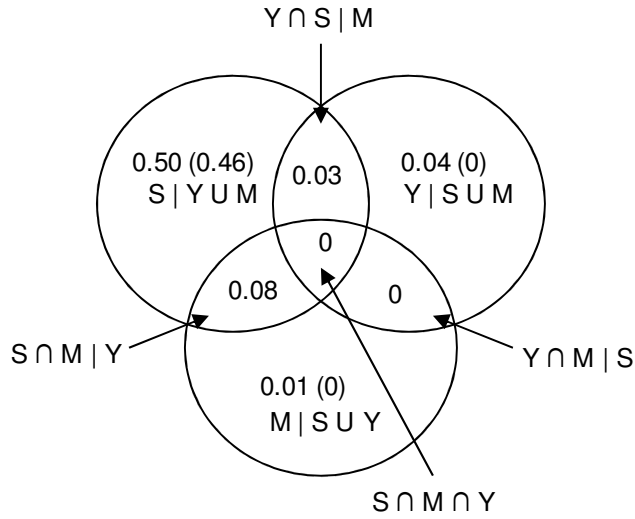


Fig. 3. DCA scatterplot displaying the 20 sites from 1998 to 2008. The eigenvalues were 0.152 and 0.108 for the first and second axis respectively. The time series is indicated by a line segment (—) with joints at each year, a dark black line joins years in which the plot experienced bison grazing and a grey line demarcates years in which the plot experienced cattle grazing. The 1998 samples are indicated by circles (●) and the 2008 samples are indicated by squares (□).



Total inertia = 1.48
 $R^2 = 0.63$ (0.57)

Fig. 4. A Venn diagram displaying the R^2 (R^2_{adj}) of each fraction resulting from the variation partitioning of species composition using pCCA. The three factors (classes of explanatory variables) were site (S), year (Y), and management (M). Note that R^2 in this context should not be interpreted as fraction of explained variance but rather fraction of explained inertia. For the shared fractions we only report the unbiased R^2_{adj} values.

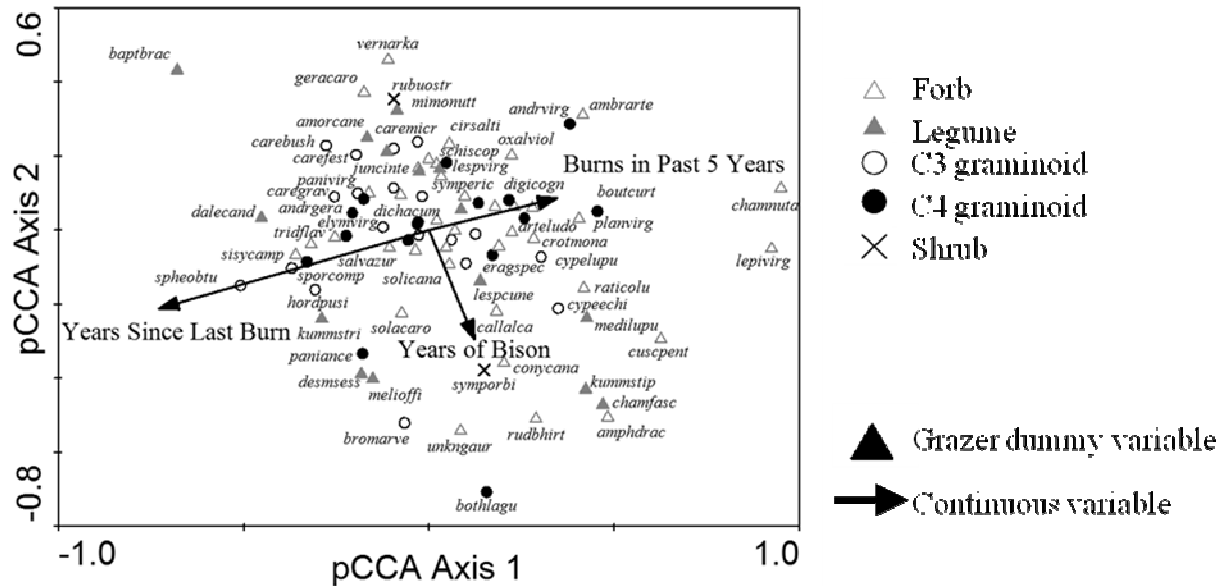


Fig. 5. A pCCA biplot displaying the influence of the management variables with the sites and years as covariables. The management variables in the model are indicated by black arrows. Only the 90 most abundant species of the 307 total are displayed for clarity. Abbreviations represent the first four letters of the genus and the first four of the letters of the species (see Appendix C). The symbol of each species depends on which functional type it belongs to (see legend).

Appendix A. The collinearity between each of the management variables.

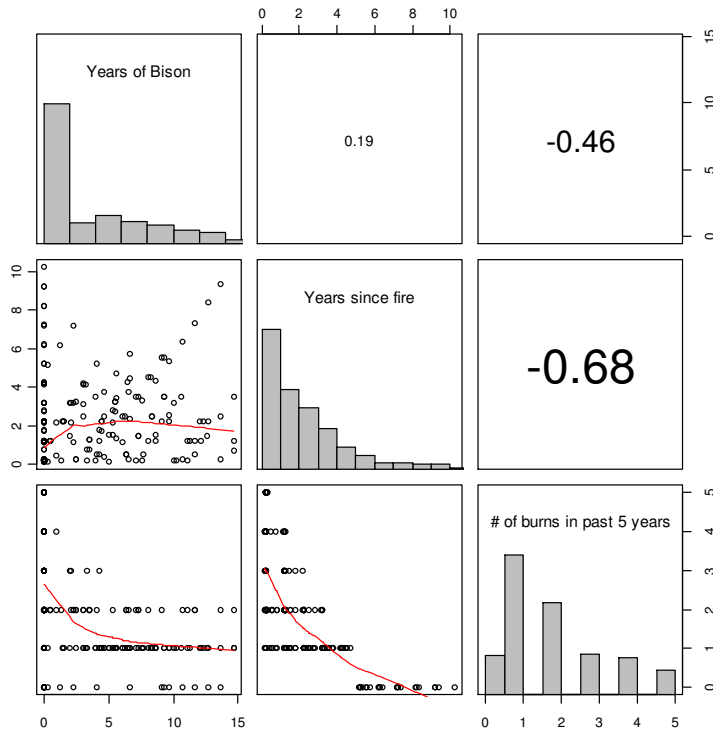


Fig. A.1. Each management variable displaying a histogram of the number of observations of a given value over the entire course of the study. The magnitude and direction of the correlation of two variables is indicated by the cells in the upper triangle. The lower triangle indicates the scatterplot of the two variables. A lowess smoothing function was applied to the scatterplots to aid visual interpretation.

Appendix B. Isotropic variogram models for within site temporal autocorrelation of the residuals of the GLS models of species richness.

For each GLS model the single and double parameter formulations of five different models were compared using AIC which penalizes for the additional parameter.

Table B.1 The single parameter formulation of five isotropic variogram models. This table is recreated from Table 5.2 in Pinherio et al. (2008).

Model name	Single parameter formulation
Exponential	$\gamma(s, \rho) = 1 - \exp(-s / \rho)$
Gaussian	$\gamma(s, \rho) = 1 - \exp[-(s / \rho)^2]$
Linear	$\gamma(s, \rho) = 1 - (1 - s / \rho)I(s < \rho)$
Rational quadratic	$\gamma(s, \rho) = (s / \rho)^2 / [1 + (s / \rho)^2]$
Spherical	$\gamma(s, \rho) = 1 - [1 - 1.5(s / \rho) + 0.5(s / \rho)^3]I(s < \rho)$

In the table above, s is the distance between two observations (in our case number of years) and ρ is the range of the model or the distance at which observations are no longer correlated. The two parameter version of each model can be formulated simply by the addition of a third parameter, the nugget (c_o):

$$\gamma_{nugg}(s, c_o, \rho) = \begin{cases} c_o + (1 - c_o)\gamma(s, \rho), & s > 0, \\ 0, & s = 0. \end{cases}$$

Appendix C. The relationship between richness and several other diversity indices examined in Wilsey et al. (2005).

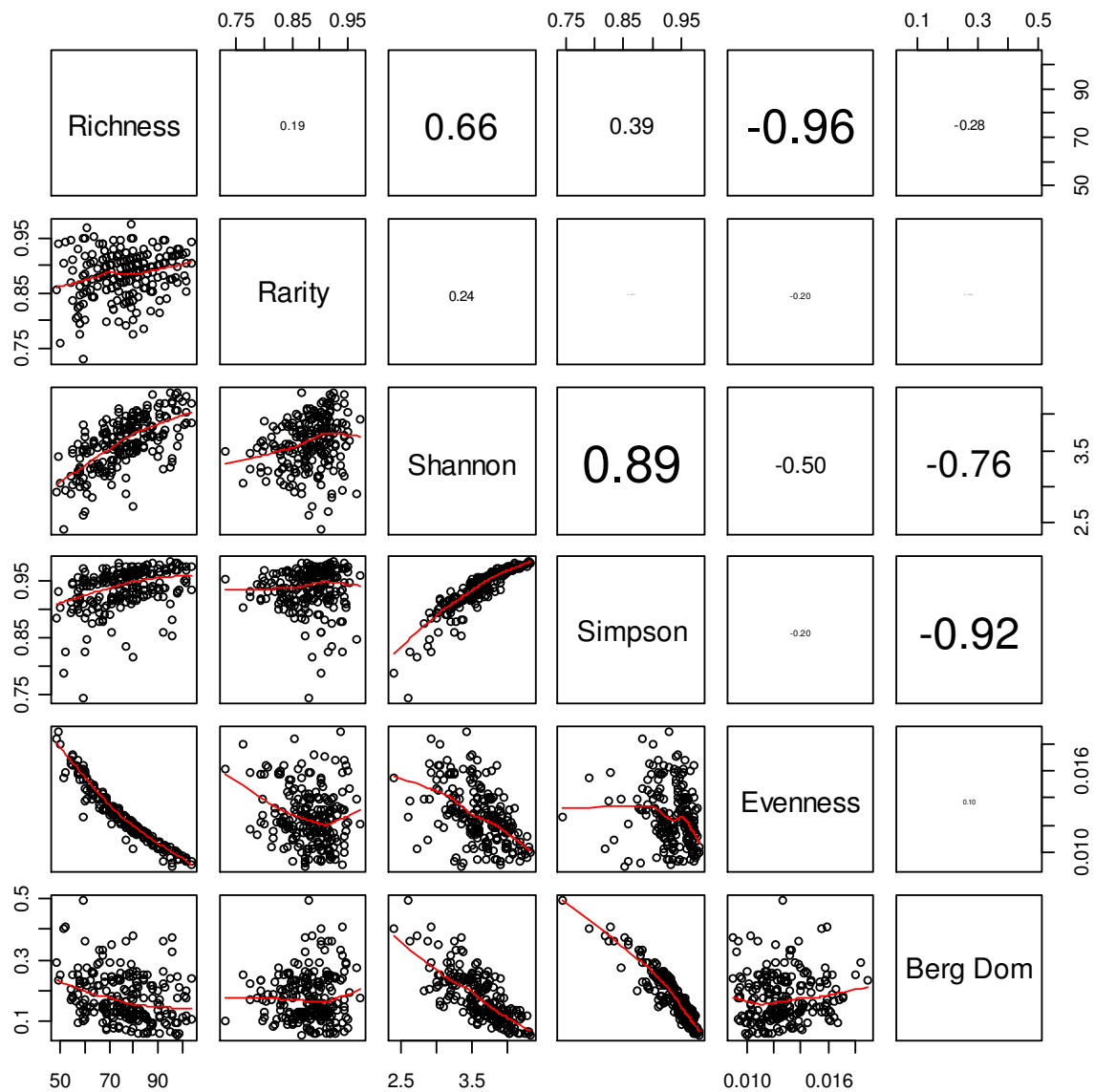


Fig. C1. The relationship between richness and each diversity indice. The linear correlation coefficients are indicated in the upper triangular matrix. A lowess smoothing function was applied to the scatterplots to aid visual interpretation.

Appendix D. The abbreviations for the species name in Fig. 5 the pCCA biplot of management effects. Only the 90 most abundant species were displayed symbolically and of those only 59 names were displayed to decrease visual clutter

Table D.1. nomenclature follows the PLANTS database (USDA and NRCS 2008)

Abbreviated name	Binomial	Functional Group
ambrarte	<i>Ambrosia artemisiifolia</i>	F
amphdrac	<i>Amphiachyris dracunculoides</i>	F
arteludo	<i>Artemisia ludoviciana</i>	F
callalca	<i>Callirhoe alcaeoides</i>	F
chamnuta	<i>Chamaesyce nutans</i>	F
cirsalti	<i>Cirsium altissimum</i>	F
conycana	<i>Conyza canadensis</i>	F
crotmona	<i>Croton monanthogynus</i>	F
cuscpent	<i>Cuscuta pentagona</i>	F
gaurunko	<i>Gaura sp.</i>	F
geracaro	<i>Geranium carolinianum</i>	F
lepivirg	<i>Lepidium virginicum</i>	F
oxalviol	<i>Oxalis violacea</i>	F
planvirg	<i>Plantago virginica</i>	F
raticolu	<i>Ratibida columnifera</i>	F
rudbhirt	<i>Rudbeckia hirta</i>	F
salvazur	<i>Salvia azurea</i> var. <i>grandiflora</i>	F
sisycamp	<i>Sisyrinchium campestre</i>	F
solacaro	<i>Solanum carolinense</i>	F
solicana	<i>Solidago canadensis</i>	F
symperic	<i>Symphyotrichum ericoides</i>	F
vernarka	<i>Vernonia arkansana</i>	F
amorcan	<i>Amorpha canescens</i>	L
baptbrac	<i>Baptisia bracteata</i>	L
chamfasc	<i>Chamaecrista fasciculata</i>	L
dalecand	<i>Dalea candida</i>	L
desmsess	<i>Desmodium sessilifolium</i>	L
kummstip	<i>Kummerowia stipulacea</i>	L
kummstri	<i>Kummerowia striata</i>	L
lespcune	<i>Lespedeza cuneata</i>	L
lespvirg	<i>Lespedeza virginica</i>	L
medilupu	<i>Medicago lupulina</i>	L
melioffi	<i>Melilotus officinalis</i>	L
mimonutt	<i>Mimosa nuttallii</i>	L

bromarve	<i>Bromus arvensis</i>	C3
carebush	<i>Carex bushii</i>	C3
carefest	<i>Carex festucacea</i>	C3
caregrav	<i>Carex gravida</i>	C3
caremicr	<i>Carex microdonta</i>	C3
cypeechi	<i>Cyperus echinatus</i>	C3
cypelupu	<i>Cyperus lupulinus</i>	C3
dichacum	<i>Dichanthelium acuminatum</i>	C3
elymvirg	<i>Elymus virginicus</i>	C3
hordpusi	<i>Hordeum pusillum</i>	C3
juncinte	<i>Juncus interior</i>	C3
spheobtu	<i>Sphenopholis obtusata</i>	C3
andrgera	<i>Andropogon gerardii</i>	C4
andrvirg	<i>Andropogon virginicus</i>	C4
bothlagu	<i>Bothriochloa laguroides ssp. torreyana</i>	C4
boutcurt	<i>Bouteloua curtipendula</i>	C4
digicogn	<i>Digitaria cognata</i>	C4
eragspec	<i>Eragrostis spectabilis</i>	C4
paniance	<i>Panicum anceps</i>	C4
panivirg	<i>Panicum virgatum</i>	C4
schiscop	<i>Schizachyrium scoparium</i>	C4
sporcomp	<i>Sporobolus compositus</i>	C4
tridflav	<i>Tridens flavus</i>	C4
rubuostr	<i>Rubus ostryifolius</i>	W
symporbi	<i>Symphoricarpos orbiculatus</i>	W