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Sherry Leis

Lloyd W. Morrison

Michael D. Debacker

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Spatiotemporal Variation in Vegetation Structure Resulting from Pyric-Herbivory

SHERRY A. LEIS[1], LLOYD W. MORRISON, AND MICHAEL D. DEBACKER

Department of Biology, Missouri State University, 901 S. National Avenue, Springfield, MO 65897, USA (SAL, LWM)
National Park Service, Heartland Inventory and Monitoring Network, Wilson's Creek National Battlefield, 6424 W. Farm Road 182, Republic, MO 65738, USA (LWM, MDD)

ABSTRACT Pyric-herbivory is a process that is widely assumed to create greater habitat heterogeneity in grasslands at the landscape scale than could be achieved by either fire or grazing alone. Yet, few studies have actually quantified the effects of pyric-herbivory on vegetation structure within layers of the grass canopy. Here we quantify the effects of pyric-herbivory on a pasture at Tallgrass Prairie National Preserve in Kansas. We subdivided the pasture into three patches and burned one patch each year in a three-year rotation. We estimated visual obstruction for 25-cm strata and recorded maximum vegetation height. We found that recently burned patches exhibited less visual obstruction in comparison to patches burned 13 and 25 months prior, creating heterogeneity at the landscape scale, and we noted that structure recovered at half the length of the fire return interval. We did not observe an intermediate vegetation structure (consisting of an open understory with a canopy cover), which pyric-herbivory has been hypothesized to create. We found almost no differences among years, indicating that pyric-herbivory operated similarly within the observed range of precipitation, topography, fire intensity, and stocking rate. Despite these consistencies, the effects of pyric-herbivory on vegetation structure may vary with different stocking levels.

KEY WORDS habitat heterogeneity, patch burn grazing, patch contrast, pyric-herbivory, tallgrass prairie, visual obstruction

Ecological disturbances are fundamental to maintaining grasslands (Axelrod 1985, Anderson 2006). The organisms and processes involved, however, respond to disturbance at different rates and on varied spatial scales. Managing and maintaining North American grasslands is increasingly challenging as these habitats continue to decline due to fragmentation from urban and exurban development, energy extraction, cultivation, and myriad other sources (Samson and Knopf 1994). Land managers generally strive to maintain or increase biodiversity (Howe 1994, Woodwell 2010), which requires knowledge of the varied habitat requirements among species.

One suggested way to increase biodiversity is through habitat heterogeneity (Wiens 1973, Howe 1994, Fuhlendorf and Engle 2001, Fuhlendorf et al. 2006, 2009). A juxtaposition of varied habitats within a landscape provides for greater community diversity. Pyric-herbivory describes the synergistic relationship between the processes of fire and grazing (Fuhlendorf et al. 2009). Fire occurs in grasslands both naturally and anthropogenically (Pyne et al. 1996), and the attraction of grazing animals to recently burned areas has been well documented (Fuhlendorf et al. 2009). Forage tends to become less palatable and less accessible over time, so that as time since burn increases, grazing pressure is reduced. Shifts in burned areas and grazing intensity create a mosaic of disturbance histories on the landscape, and this mosaic represents the varied response of the biotic community across the landscape. This principle is increasingly being applied by land managers using a practice often called patch burn grazing to create habitat heterogeneity, increase biodiversity, and recouple processes that historically acted synergistically (Fuhlendorf and Engle 2001, NRCS 2004).

Vegetation structure (e.g., the density and arrangement of foliage) determines habitat suitability for many animals, thereby affecting wildlife composition at a variety of scales (Weins 1973, Turner 1989, Chapman et al. 2004, Bell et al. 2010). One measure of vegetation structure is visual obstruction within layers of the grass canopy (Nudds 1977). Grassland bird habitat requirements in relation to vegetation structure have been studied extensively and vary by species (e.g., Wiens 1973). For example, grasshopper sparrows (*Ammodramus savannarum*) prefer short, clumped grasses and their abundance is negatively correlated with increased visual obstruction (Patterson and Best 1996). Henslow's sparrows (*A. henslowii*), however, prefer taller, less disturbed grasslands for calling and nesting (Coppedge et al. 2008), while killdeer (*Charadrius vociferous*) nest on bare ground (Stokes and Stokes 1996). Greater prairie chickens (*Tympanuchus cupido*) and northern bobwhite (*Colinus virginianus*) are known to utilize different habitats for disparate life history needs. Courtship occurs in areas with reduced visual obstruction (e.g., short grass and open space), while brood rearing occurs in areas with protective overhead cover, but a sparse understory or surface layer. Areas of dense vegetation offer protection from predators and are utilized for nesting (Bidwell et al. 1991, Svedarsky et al. 2003). Small mammal species also demonstrate preferences for varied habitats (Tews et al. 2004) as do insects (Tscharntke and Greiler 1995, Bakker et al. 2003, Engle et al. 2008, Debinski et al. 2011, Doxon et al. 2011).

[1] Corresponding author email address: sleis@missouristate.edu

Vegetation structure in grasslands is influenced by a variety of factors. Variation in abiotic factors such as soil type and depth, precipitation, slope, and aspect create inherent levels of heterogeneity (Burke et al. 1998, 1999). Large and small scale disturbances also are key processes that can alter structure. For example, grazing, fire, and the interaction of the two have been shown to change vegetation structure (Vinton et al. 1993, Harrell and Fuhlendorf 2002, Coppedge et al. 2008, Allred et al. 2011). Furthermore, biotic factors influence vegetation structure. Prairie dogs, for example, actively reduce the stature of the plant community through grazing for improved predator detection (Hoogland 1995). Large ungulate grazing also can alter vegetation structure, but the effect varies depending on the stocking rate, evolutionary history of grazing, and synergy with other disturbances (Milchunas et al. 1988, Briske et al. 2008, Allred et al. 2011).

Wildlife studies have demonstrated the relationship between vegetation structure and habitat using indirect estimations of biomass (often as modifications of the Robel pole technique) as a surrogate for vegetation structure, or one-dimensionally using the angle of obstruction (Robel et al. 1970*a*, 1970*b*, Harrell and Fuhlendorf 2002, Coppedge et al. 2008). These studies, however, have not demonstrated how vegetation structure in grasslands might differ spatially and temporally within the layers of the plant canopy. Here we present a case study in which we directly measured vegetation structure in a pasture where pyric-herbivory was applied over a complete burn-graze cycle to determine if the goal of creating habitat heterogeneity was achieved. Specifically, our objectives were to evaluate 1) variation in vegetation structure (e.g., visual obstruction at different strata and vegetation height) within and among patches as a function of time since burn, and 2) consistency of burn patterns among different years.

STUDY AREA

Our study was conducted at Tallgrass Prairie National Preserve near Strong City, Kansas (712311.373 easting, 4257485.335 northing Zone 14N, UTM NAD83), USA. The 4,409 ha preserve is within the Flint Hills upland physiographic region and is primarily covered by tallgrass prairie vegetation, dominated by big bluestem (*Andropogon gerardii*) and little bluestem (*Schizachyrium scoparium*). The Preserve had considerable relief with elevation within Chase County that ranged from 335 to 457 m above sea level (United States Department of Agriculture 1974) and exposed rock, primarily cherty limestone and shale, averaging 9% cover in long-term monitoring plots in 2006 (James and DeBacker 2007). Formerly known as the Spring Hill Ranch, the Preserve has been continuously grazed for cattle production for over 120 years. Grazing practices have changed over time, but annual spring burning is a cultural tradition in the Flint Hills. For the two decades prior to 2006, intensive early stocking (Smith and Owensby 1978) was applied.

Our study focused on a single pasture, named “Big” pasture, where managers applied pyric-herbivory. We subdivided Big pasture (1,546 ha) into three patches of 563, 487, and 495 ha. Beginning in 2006, we burned one patch each year in a three-year rotation from the last week of March through mid-April. Fires were generally moderate in intensity and burned through the entirety of the patch. Precipitation for the 12 months (May–Apr) preceding each sampling event was 108.8 cm in 2009, 85.2 cm in 2010, and 82.9 cm in 2011 (remote automated weather station (RAWS) station KTAL data). Grazing by cattle began in April and continued through mid-July. The stocking rate (based on a 340.2-kg animal) was 0.70 ha/animal unit month (AUM) in 2009, 0.73 ha/AUM in 2010, and 0.76 ha/AUM in 2011. This amounted to heavy use on the burned patch, but light use of the pasture as a whole. On a traditionally grazed pasture (intensive early stocking systems are most common in the area), the stocking rates would be considered moderate based on utilization (Holechek et al. 2001).

METHODS

We established 87 monitoring plots across the pasture (n = 34 in patch 1, n = 26 in patch 2, and n = 27 in patch 3). We sampled vegetation in May of each year from 2009 to 2011, corresponding to time since burn (TSB) periods of 1, 13, and 25 months. Sampling was conducted in May to correspond with the peak of breeding bird nesting and brood rearing activity. In some years, one or two plots in a patch were not sampled because we deemed that site conditions would not produce a representative sample, primarily due to conditions in ephemeral stream corridors (e.g., standing water).

We placed a 2.0 × 0.15 m profile board (Peitz et al. 2008) at the center of each plot. We characterized vegetation structure by estimating visual obstruction (e.g., the area of the profile board obscured by vegetation, both live and standing dead, between the board and observer) in 25-cm strata. The observer, located 15 m from the board at an azimuth direction of 0, estimated visual obstruction using a cover class index modified from Daubenmire (1959). For each 25-cm stratum, we classified visual obstruction within one of seven cover percentage classes: <1%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, and 96–100%. We used the class midpoints in statistical analyses. We employed eight 25-cm strata from ground-level to 2 m high. The eye position of the observer varied according to the stratum. Strata 0–0.25 m and 0.25–0.50 m on the profile board were read from 0.5 m high, strata 0.50–0.75, 0.75–1.0, and 1.0–1.25 m on the profile board were read from 1.0 m high, and the remaining strata were read from a height of 1.5 m.

We measured maximum vegetation height to the nearest cm in 2009 and 2010. In 2011, we recorded maximum vegetation height as within one of the eight strata and used the midpoint of that stratum in analyses. Observations of obstruction in the fourth and fifth strata were rare with only 25% and 7% of all plots across all years producing observations in those respective strata. Thus, our analyses focused on the first three strata and on vegetation height.

Examination of the data revealed substantial departures from normality. Thus we used a Kruskal-Wallis test, followed by a multiple comparison procedure with an experimentwise error rate of $\alpha = 0.15$ (Daniel 1990). We evaluated each year independently.

RESULTS

Our results were consistent among the three years evaluated. In the lowest stratum (0–0.25 m), mean visual obstruction in recently burned patches (TSB = 1) ranged from 25–40% and was less than for patches burned 13 and 25 months prior (TSB = 13 and TSB = 25) in all years. We found no difference between TSB = 13 and TSB = 25 in any of the three years (Fig. 1A). In the second stratum (0.25–0.50 m), mean visual obstruction was less for TSB = 1 (always <6%) than either TSB = 13 or TSB = 25 (both always >30%), and we found no difference between TSB = 13 and TSB = 25 in 2009 or 2010. In 2011, however, all three TSB treatments were different from each other (Fig. 1B).

Relatively little vegetation occurred in the third stratum (0.5–0.75 m). Nevertheless, mean visual obstruction was lower for TSB = 1 (near 0%) than either TSB = 13 or TSB = 25 (between 1 and 6%) in all years. We detected no difference between TSB = 13 and TSB = 25 in any of the three years for the third stratum (Fig. 1C).

Vegetation height revealed a pattern similar to visual obstruction. Mean vegetation height was lower for TSB = 1 (always <0.3 m) than either TSB = 13 or TSB = 25 (both always >0.6 m) in all years. We found no difference in any of the years between TSB = 13 and TSB = 25 (Fig. 1D).

We also evaluated within-patch variability in visual obstruction measurements. In the lowest stratum (0–25 cm), the sample standard deviation was always higher in recently burned patches (TSB = 1) than in either TSB = 13 or TSB = 25, due to the consistently high proportion of the board (always >89%) obstructed by vegetation in patches burned

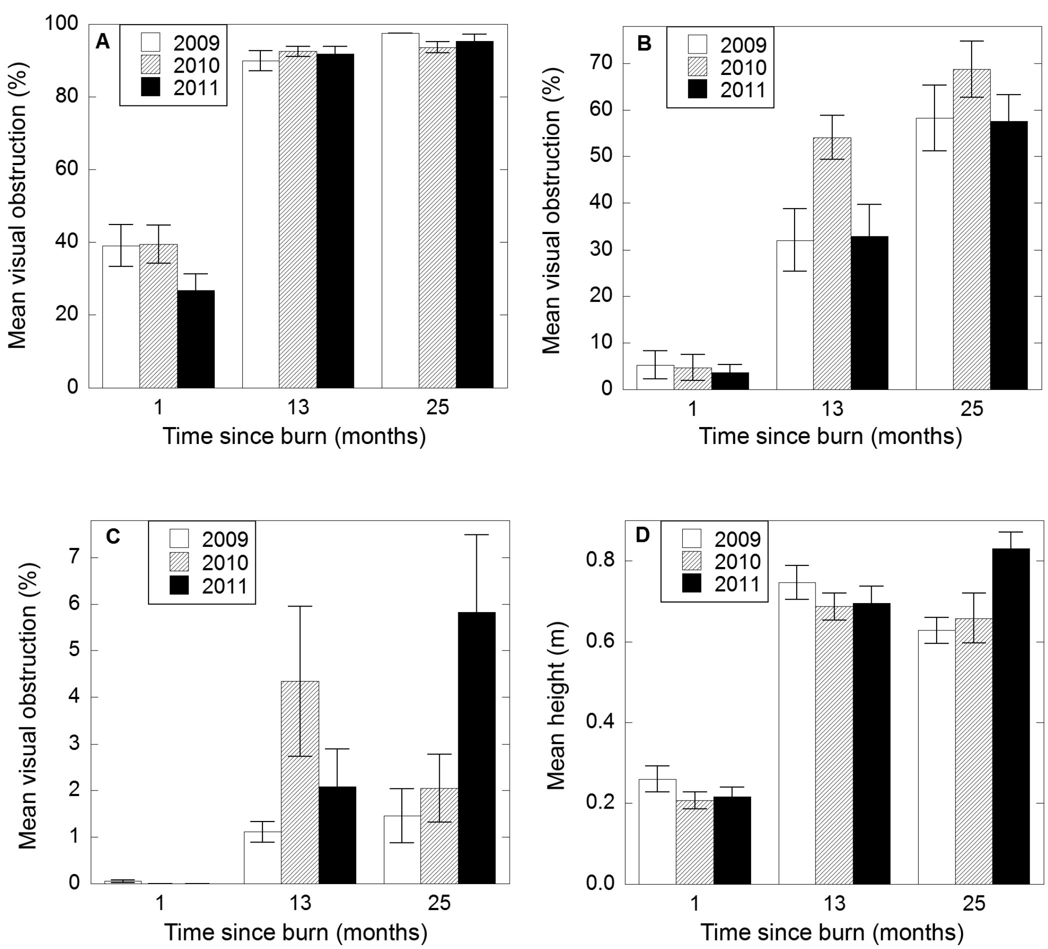

Figure 1. Mean visual obstruction for strata (A) 0–0.25 m, (B) 0.25–0.5 m, (C) 0.5–0.75 m, and (D) mean vegetation height, as a function of time since burn in months. Error bars represent 1 SE. Note differences in scale of y-axes.

13 and 25 months prior (Fig. 2A). Observations of any obstruction were rare in the second stratum of recently burned patches (TSB = 1) resulting in a low sample standard deviation. The degree of visual obstruction in the second stratum for TSB = 13 and TSB = 25, however, varied greatly among plots, resulting in a higher sample standard deviation (Fig. 2B). We recorded obstruction in the third stratum (50–75 cm) for only four plots in recently burned patches. The sample standard deviation was relatively low for TSB = 13 and TSB = 25 in the third stratum, although it did vary among years (Fig. 2C). We found no robust patterns in the sample standard deviation for height among years or TSB categories. There was generally greater variation among plots with increasing time since burn for 2010 and 2011, but not for 2009 (Fig. 2D, Table 1).

DISCUSSION

This study was designed as a case study to evaluate the application of pyric-herbivory, a current management practice, at Tallgrass Prairie National Preserve. Across the pasture, at the landscape scale, we found that heterogeneity was created through application of pyric-herbivory. The relative differences among the TSB categories for the three strata and vegetation height are summarized qualitatively for comparison in Table 1. Recently burned patches exhibited sparser and shorter vegetation in comparison to patches burned 13 and 25 months prior. This heterogeneity among patches has been termed patch contrast, and describes the degree of differences among patches that are otherwise similar (Kotliar and Wiens 1990, McGranahan et al. 2012).

Because we found no differences among years (with the exception of the second stratum in 2011), we can infer that the fire-grazing interaction operated similarly despite observed variability in precipitation, topography, fire intensity, and stocking rates. A similar fire-grazing interaction along a precipitation gradient from mixed prairie in the southwest to eastern tallgrass prairie was observed by McGranahan et al. (2012). Although our study was limited in that we were not able to incorporate true controls, nor evaluate the effects of burning and grazing independently, this work verifies that as the burned and subsequently grazed patches rotate through

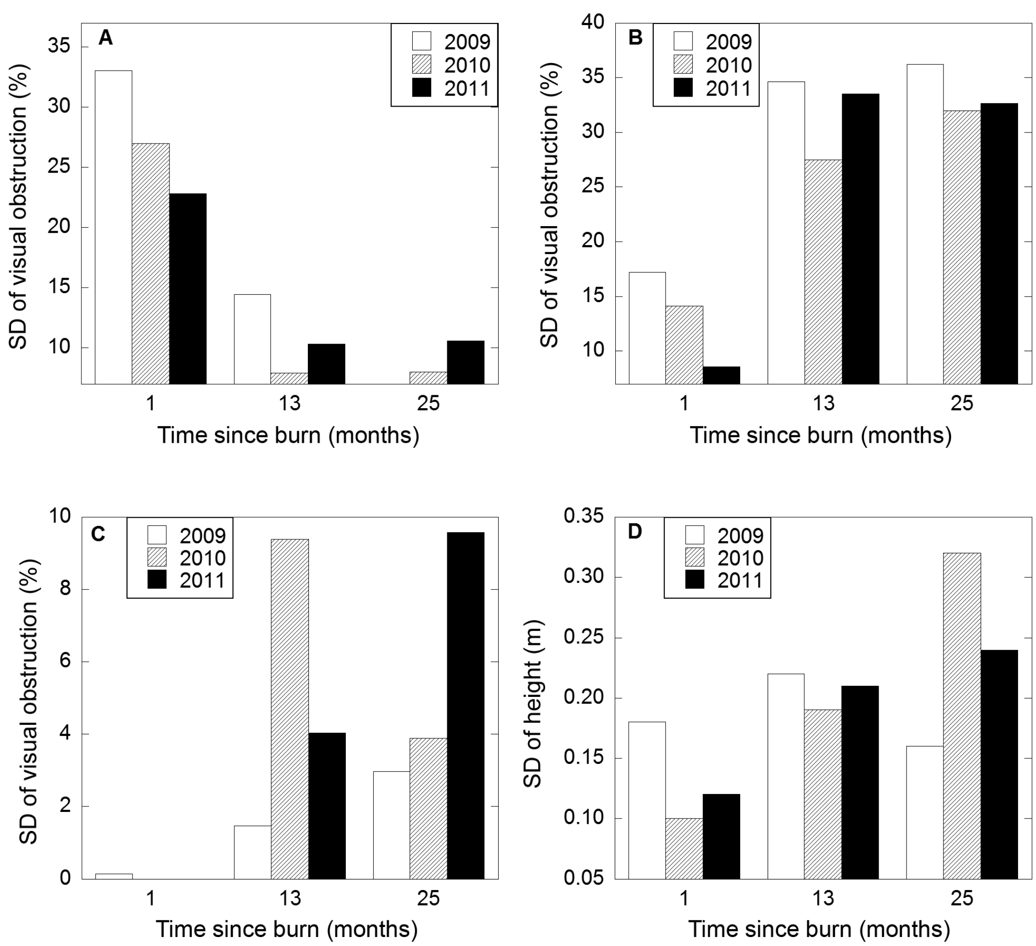

Figure 2. Standard deviations among plots for visual obstruction in strata (A) 0–0.25 m, (B) 0.25–0.5 m, (C) 0.5–0.75 m, and (D) vegetation height, as a function of time since burn in months. Note differences in scale of y-axes.

Table 1. Qualitative differences among time since burn categories versus vegetation strata and height. First entry refers to means; second entry (in parenthesis) refers to standard deviation. Means of visual obstruction are compared absolutely (on a 0–100% scale) among the three strata; standard deviations are compared relatively for each vegetation variable.

	Time since burn (yrs)		
Visual obstruction	0	1	2
0–25 cm stratum	Moderate (High)	High (Low)	High (Low)
25–50 cm stratum	Low (Low)	Moderate (High)	Moderate (High)
50–75 cm stratum	Low (Low)	Low (Low–High)	Low (Low–High)
Vegetation height	Low (Low)	High (Low–Moderate)	High (Low–High)

the pasture, structural heterogeneity is increased in both space and time. Furthermore, it clarifies some long held assumptions about how vegetation structure changes through the recovery period.

Management application of pyric-herbivory is often touted as a way to create an intermediate type of vegetation structure that is not achievable with fire or grazing alone. An intermediate vegetation structure consists of an open understory (ground layer) with a canopy cover. We did not observe this type of habitat in our study. In patches burned 13 and 25 months earlier, we did see the development of an upper canopy and it was variable both within and between patches. The dominant grasses, however, recovered quickly in burned patches and occupied the ground layer within a year. We did not collect data on the litter layer, which could help to further inform this discussion. The importance of this type of structure often is regarded as a key necessity for brood rearing of gallinaceous birds (Jones 1963, Svedarsky et al. 2003).

It is unclear whether different stocking rates or patch sizes would produce support for the "intermediate structure" model. Given the choice among multiple burned patches of various sizes and shapes, bison (*Bison bison*) and domestic cattle show a preference for smaller patches and proximity to patch edges (Allred et al. 2011). Smaller patches also create a juxtaposition of burned and unburned areas in close proximity. Furthermore, grazers prefer locations with access to nutritious and accessible new growth (e.g., burned patches) in proximity to sources of bulk fiber (e.g., unburned patches; Allred et al. 2011), and variations in patch size or stocking rate may better favor these preferences.

In a patch burn grazing system, the optimal size and spatial arrangement of patches with respect to target species or communities may vary. For example, greater prairie chickens may have home ranges up to 2,500 ha but conduct their activities within smaller patches of that area (Patten et al. 2011). Given that vegetation structure recovered more quickly than expected, burning multiple patches throughout the year in conjunction with grazing may maintain greater landscape structural heterogeneity over time. Topography may create inherent heterogeneity in addition to that caused by pyric-herbivory in some areas, but other areas with little relief or soil type differentiation may benefit from additional burn patches in a given year.

Stocking rate is a key component of any grazing system. When pyric-herbivory is applied in a managed pasture setting, overstocking may lead to increased utilization outside the burn patch resulting in less patch contrast (McGranahan et al. 2012). Alternatively, understocking may result in poor patch contrast in that grazing will not keep up with forage production and the grazing lawn structure (reminiscent of a golf course putting green) will not be created. In our study, the stocking rate effectively created the grazing lawn structure without leading to high levels of utilization in the unburned patches.

The type of habitat we observed in recently burned patches is common in much of the Flint Hills as a result of widespread use of the intensive early stocking system. This regime calls for annual spring burning and double stocking over a shortened grazing season (Smith and Owensby 1978). Species such as killdeer, 13-lined ground squirrel (*Spermophilus tridecemlineatus*) and deer mouse (*Peromyscus maniculatus)* thrive in such an environment (Streubel and Fitzgerald 1978, Kaufman et al. 1990). On the other hand, the habitat provided in recently burned areas is not suitable for species such as

Henslow's sparrow or the cotton rat (*Sigmodon* sp.; Cameron and Spencer 1981, Coppedge et al. 2008). Outside the Flint Hills, fire is less accepted and less frequently employed by private landowners for pasture management (Fuhlendorf et al. 2011, Mohler and Goodin 2012, Pyne 2012). Consequently, habitat similar to what we observed in patches burned 25 months prior is common.

MANAGEMENT IMPLICATIONS

This case study of pyric-herbivory and vegetation structure, along with a growing body of research, suggest that pyric-herbivory is a management technique that is widely beneficial in tallgrass prairie. Application of this technique in grasslands is likely to create greater habitat heterogeneity, which in turn is expected to increase biodiversity. Critical intermediate structures may be the most difficult to create, however. Managers should also consider how managed areas contribute to habitat in the larger vicinity of their reserves. If an area is surrounded by short, sparse grassland, for example, managers might consider increasing vegetation height and density to increase heterogeneity at the landscape scale by applying pyric-herbivory and possibly adjusting stocking rates. Finally, future research involving control plots and evaluation of burning and grazing independently would further elucidate the effects of pyric herbivory in grasslands.

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