



Long-Term Effects of Fire on the Grasslands and Juniper Savannas at Wupatki National Monument

Natural Resource Report NPS/SCPN/NRR—2020/2066



ON THE COVER

Photopoint for Southern Colorado Plateau Network monitoring plot in Wupatki National Monument.
NPS photo.

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Natural Resource Report NPS/SCPN/NRR—2020/2066

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Abstract

The effects of fire on the grassland and juniper savanna vegetation at Wupatki National Monument were examined by comparing burned and unburned plots 12 to 21 years following three wildland fires. Vegetation data were analyzed from 29 permanent vegetation plots monitored by the Southern Colorado Plateau Network. I used two-way ANOVAs to compare the mean cover of abundant species, functional groups, and soil surface features, between burned and unburned plots. I also compared species richness and mortality of *Juniperus monosperma* (one-seed juniper) between the burned and unburned plots. While tree mortality was greater in burned areas, there were no statistically significant differences in herbaceous or shrub cover, or in the cover of abundant species in burned and unburned areas. There was greater litter cover and dead shrub cover in the unburned areas. I found evidence of fire effects on the woody elements of this grassland and juniper savanna ecosystem, but fire effects on the herbaceous vegetation were negligible, suggesting that fire does not have long-term effects on the herbaceous vegetation in this ecosystem.

Acknowledgments

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Introduction

The influence that wildland fires have on the grasslands of Southwestern United States has not been well studied. Compared to other grasslands, such as tallgrass prairies, fire frequency in the grasslands of the southwestern United States is relatively low due to low biomass and a lack of fuel continuity (Burgess 1995). How fires affect species composition both in the short- and long-term is not well known. A number of studies have suggested that biomass recovers in 1 to 3 years following the fire, and impacts are rather benign (Jameson 1962, McPherson 1995). In contrast, other studies have suggested that fire can affect species composition and structure. Fires stimulate germination of seeds of certain species, particularly annual species, including nonnative annual grasses (McPherson 1995). Some native herbaceous species, such as *Bouteloua eriopoda* (black grama), have been reported to be sensitive to fire (Burgess 1995, McPherson 1995, Kilgore et al. 2009). Certain cactus and shrub species have also been reported to be sensitive to fire, and fire has been suggested to be responsible for maintaining the dominance of grasses (Archer 1994, Burgess 1995, McPherson 1995, Miller 2005, Van Auken 2009). Fires may also be responsible for maintaining the low tree densities in juniper savannas, although few studies have examined historical disturbance regimes in these ecosystems (Romme et al. 2009).

Wupatki National Monument (NM) provides an opportunity to study the long-term effects of fire in grasslands and juniper savannas on the Colorado Plateau. Between 1995 and 2002, four wildland fires burned 1221 ha (3017 acres) of grasslands and juniper savannas on the western side of Wupatki NM. Between 2007 and 2016, the Southern Colorado Plateau Inventory and Monitoring Network (SCPN) of the National Park Service established and monitored permanent vegetation monitoring plots across the grasslands and savannas within the monument. Nine of these plots were located in areas burned in three of the four fires. Long-term fire effects can be determined by the differences in vegetation composition and structure between burned and unburned plots 12 and 21 years following fire.

Methods

Study area

Wupatki NM is located in northern Arizona on the southern portion of the Colorado Plateau. Elevations in the monument range from 1310 to 1540 m (4300 to 5710 ft), with grasslands occurring in the higher elevations. Precipitation occurs in a bimodal pattern, with more than half occurring between July and October. Mean annual precipitation at the Wupatki Visitor Center (1496 m) was 20.7 cm with a range of 9.8 cm to 35.2 cm between 1942 and 2018 (using years where there were records for all 12 months; Climate Analyzer 2019). The higher elevation grasslands on the western side of the park receive more precipitation. The Volcanic Upland ecological site that comprises this ecosystem is associated with a precipitation zone of 25.4–35.6 cm (10–14 in) (U.S. Department of Agriculture, Natural Resources Conservation Service, and U.S. Department of the Interior, National Park Service [NRCS and NPS] 2015).

Much of the grasslands on the western portion of Wupatki NM are underlain with volcanic lava flows of primarily basalts, the majority of which range in age from 1 million to 600,000 years. These flows originated from obscured volcanic vents to the south and west of Wupatki NM (Billingsley et al. 2007, Graham et al. 2001). The soils are derived from a combination of underlying bedrock, aeolian deposits, and tephra from volcanic eruptions. The tephra is comprised of pyroclastic grains with capillary pore spaces that provide high moisture retention. The soils of the study area are Flaco, extremely gravelly coarse sand (NRCS and NPS 2015).

The vegetation is primarily grassland with areas of juniper savanna. *Hilaria jamesii* (James' galleta), is the dominant perennial grass, with *Bouteloua eriopoda* (black grama), *Hesperostipa neomexicana* (New Mexico needlegrass) and *Sporobolus* spp. (dropseed) occurring in lower abundance. Common forbs include the perennials *Sphaeralcea hastulata* (spear globemallow), *Astragalus* spp. (milkvetch) and *Zinnia grandiflora* (Rocky Mountain zinnia), and the annuals *Salsola tragus* (prickly Russian thistle), *Chenopodium leptophyllum* (narrowleaf goosefoot) and *Euphorbia* spp. (annual sandmats). The multi-stemmed, shrubby tree, *Juniperus monosperma* (one-seed juniper) is sparse, as are shrubs and cacti, which include *Ericameria nauseosa* (rubber rabbitbrush), *Ephedra torreyana* (Torrey's jointfir) and *Opuntia* spp. (prickly pear) (DeCoster and Swan 2011). Herbaceous species, particularly annual species, demonstrate interannual variability, presumably as a result of precipitation and other climatic factors (Muldalvin et al. 2008, DeCoster and Swan 2011).

The vegetation of the Wupatki grasslands has experienced widespread human disturbance. Ancestral Puebloans moved into the area in the 7th century CE, and maintained large populations between 1064 and 1250 (Sullivan and Downum 1991). Navajos began grazing sheep in the area of what is now the monument beginning in the mid 19th century, but were displaced by cattle ranchers in 1886. After establishment of the monument in 1924, cattle grazing continued through leases, and finally ceased in 1988 (Cinnamon 1982, Cinnamon 1990).

The removal of vegetation through livestock grazing altered the fire regime and caused a large increase in the fire return interval. Between 1924 and 1995, only one fire that exceeded 1 ha occurred: in 1945 the Baxter Fire burned 160 ha in this area (Parker 2006). Prior to livestock grazing,

the fire return intervals ranged between 15 and 35 years (Cinnamon 1988, Ironside 2006). The recovery of the vegetation following the removal of livestock allowed fire to be reintroduced into the system. Seven fires burned through the western portion of the Wupatki NM between 1995 and 2017, burning a total of 2146 ha (Figure 1, Table 1). All but one of the fires were lightning-caused; the Antelope Fire was anthropogenic (caused by a cigarette from a motorist), but it did occur during the monsoon season when lightning fires occur. Only three of the seven fire perimeters included SCPN plots: West, State and Antelope, which occurred between 1995 and 2002. This period coincided with a severe drought—the driest period in the past 1200 years (Salzer and Kipfmüller 2005).

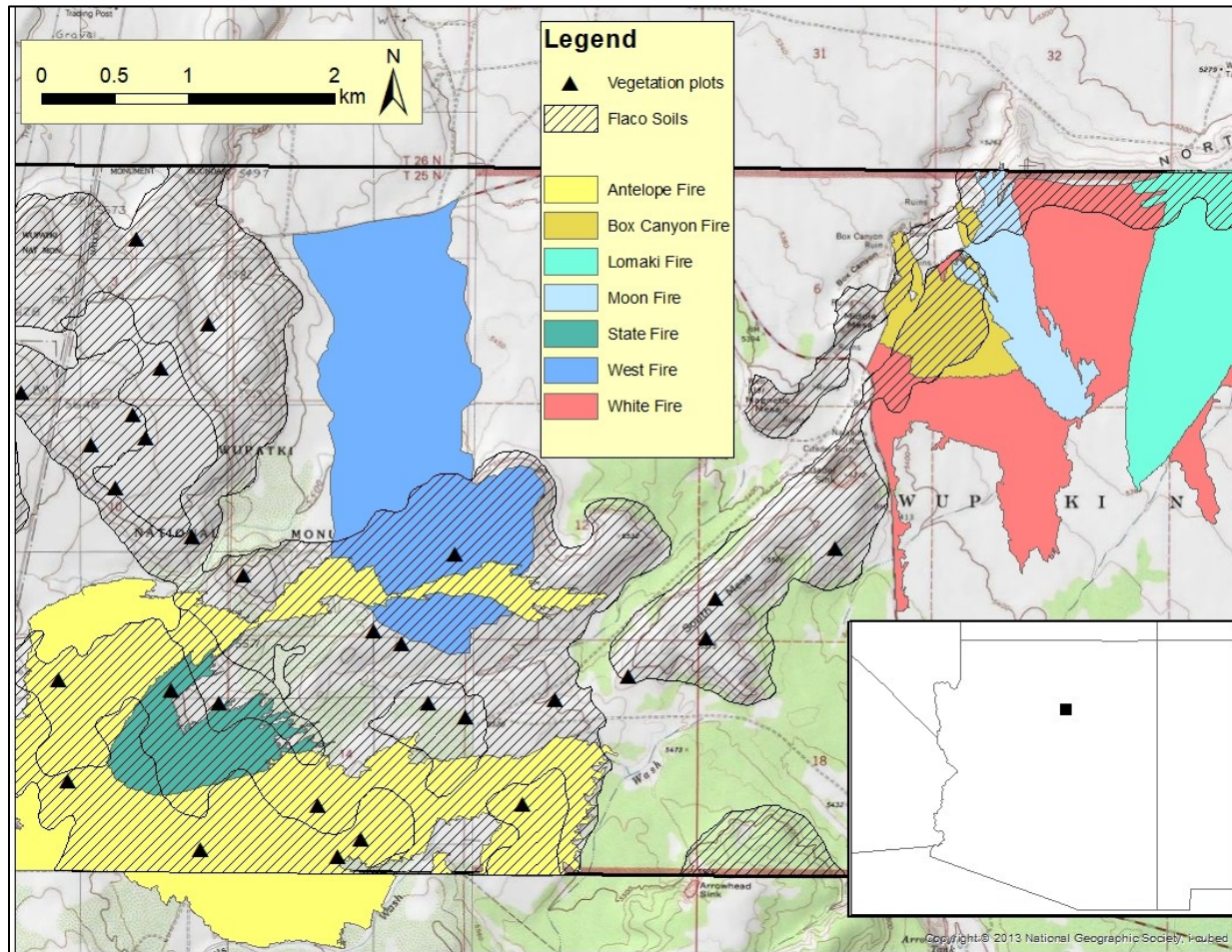


Figure 1. Perimeters of 7 wildland fires that burned on the western portion of Wupatki National Monument between 1995 and 2017, with locations of SCPN vegetation monitoring plots. Inset map shows location of study area within the state of Arizona.

Table 1. Large fires that burned in Wupatki National Monument between 1995 and 2002 with year, cause, and size, the number of SCPN vegetation plots located in these fire perimeters, and the year that they were sampled.

Fire	Year	Cause	Size (ha)	Plots sampled in 2014	Plots sampled in 2016
West	1995	Lightning	369	0	1
Moon	2000	Lightning	220	0	0
State	2002	Lightning	72	0	1
Antelope	2002	Human	550	4	3
White	2013	Lightning	572	0	0
Box Canyon	2016	Lightning	76	0	0
Lomaki	2017	Lightning	287	0	0

Vegetation sampling

Between 2007 and 2016, SCPN installed and monitored 30 permanent plots in the grasslands and juniper savannas of Wupatki NM. A sampling frame was created from the Flaco soils of the NRCS soils map (NRCS and NPS 2015). Plot locations within the sampling frame were determined using the Generalized Random Tessellation Stratified (GRTS) design, creating a random, spatially-balanced design (Figure 1) (Stevens and Olsen 2004).

Vegetation plots were 0.5 ha in size, measuring 71 x 71 m, and consisted of 3 parallel 50 m transects spaced 25 m apart. Five 2 x 5 m (10 m²) quadrats were arranged along each transect. Cover was estimated for each species, functional group and soil surface feature and placed in one of 12 cover classes (e.g., 2-5%, 5-10%). Living and dead junipers $\geq$ 15 cm diameter at root crown (DRC) were measured in a 20 x 50 (0.1 ha) subplot located between 2 of the transects (DeCoster et al. 2012). The revisit design for the monitoring entails a panel design, where 2 panels of 10 plots each are sampled every other year (i.e. panels A and B in 2012, panels B and C in 2014 and panels A and C in 2016).

Data analysis

Only one year of data was used from each plot. Data from the most recent sampling was used with 9 plots sampled in 2014 (one plot was inadvertently not sampled) and 20 plots sampled in 2016. GIS technology was used to identify which plots were inside and outside of the fire perimeters. Of the 29 plots monitored, 9 had burned and 20 had not burned. Of the 9 burned plots, one plot had burned in the West Fire of 1995, 7 plots had burned in the Antelope Fire of 2000, and one plot had burned in the State Fire of 2002 (Table 1). For the 20 plots sampled in 2016, 5 plots had burned; for the 9 plots sampled in 2014, 4 plots had burned. Of the 9 burned plots, 4 plots were sampled 12 years post-fire; 4 plots were sampled 14 years post-fire; and one plot was sampled 21 years post fire (Figure 1, Appendix).

For all analyses, the plot was the sample unit. Plot values for each metric (species, functional group, and soil surface feature) were derived by calculating the mean value of the cover class midpoints for

the 15 quadrats. It was not feasible to include time since fire as a predictor variable, due to its small range of values: all but one plot were sampled 12 or 14 years post-fire (see Appendix). Instead, the treatment of burned/unburned was used as the predictor variable. Two-way ANOVA was used to test for differences in the mean cover of each metric as a function of treatment (burned and unburned) and year (2014 and 2016), as well as a treatment $\times$ year interaction. A nonparametric Aligned Rank Transformation was used, as many of the data violated statistical assumptions of normality and homogenous variances (Wobbrock et al. 2019). Type III tests for the ANOVAs were used because of the unbalanced design (unequal number of burned and unburned plots for each sampled year). Due to interannual variation in vegetation cover resulting from precipitation (DeCoster and Swan 2011), it was necessary to include year as a factor. In 2014 there was 15.8 cm of precipitation, while in 2016 there was 35.2 cm (Climate Analyzer 2019). The following functional groups were tested: perennial grasses, forbs, shrubs, cacti, standing dead herbaceous and standing dead shrub. (Annual grasses only occurred in trace amounts and were therefore excluded from the analysis). For soil surface features, only abundant elements that may be susceptible to variation over time were tested. These variables included bare ground, undifferentiated crust, live plant base, dead herbaceous base, dead woody base, litter, and woody debris. (Features such as rock components were not tested). For species, 8 species with mean foliar cover of greater than $>0.05\%$ were tested. Plot species richness, or the number of species in a plot, was also tested. Species that were unique to burned and to unburned plots were identified using all plot visits between 2007 and 2016, including visits to 12 additional plots that were used in pilot sampling. A chi-squared test was used to test for differences in dead *Juniperus monosperma* trees in burned and unburned areas. Community composition was also analyzed by running a Detrended Correspondence Analysis (DCA) ordination of species cover values.

ANOVA tests were conducted using the R statistical package, v 3.5.1 with a significance level of 0.05. The DCA ordination was conducted using PC-Ord v. 7.07.

Results

Species richness and cover of functional groups, soil surface features and species

Using Two Way ANOVA's, differences in the cover of the various functional groups (perennial grass, shrub, forb, cactus, standing dead herbaceous and standing dead shrub) were tested as a function of treatment, year, and the treatment $\times$ year interaction (Figure 2). The dominant functional groups were perennial grass and standing dead herbaceous. Mean cover of perennial grass was 37.0% in unburned plots and 37.3% in burned plots, which suggests that biomass between the burned and unburned plots were similar ($p = 0.866$). There were significant differences between years for perennial grass, standing dead herbaceous and standing dead shrub ($p < 0.001$, $p < 0.001$, and $p = 0.047$, respectively) (Table 2). This demonstrates high variability for these functional groups between the 2 sample years, likely the result of differences in precipitation in those 2 years. Including this factor in the analyses was critical to control for this among-year variation. Standing dead shrub was the only functional group that showed significant differences between burned and unburned areas ($p = 0.002$) (Table 2). For both 2014 and 2016, standing dead shrub cover was greater in unburned plots (Figure 2c). Mean standing dead shrub cover was almost 10 times greater in unburned plots than burned plots: 0.47% vs. 0.05%. Treatment $\times$ year interactions were not significant for any of the functional groups. There were no significant differences in the mean cover of forbs, shrubs and cacti between burned and unburned plots.

Differences in the cover of the various soil surface features groups (bare ground, dead herbaceous base, dead woody base, litter, live plant base, undifferentiated crust and woody debris) were tested as a function of treatment, year and the treatment $\times$ year interaction (Figure 3, Table 2). Litter was the only metric that showed significant differences between treatments ($p = 0.006$): mean cover of litter was 7.1% in burned plots and 12.1% in unburned plots. Four soil surface features showed significant differences among years, indicating interannual variability. None of the treatment $\times$ year interactions was significant.

Differences in cover of the most abundant species were tested as a function of treatment, year and the treatment $\times$ year interaction (Figure 4, Table 2). There were significant differences between years for many of the species, indicating interannual variability; however, there were no significant differences between treatments or with the treatment $\times$ year interactions, which indicates no long-term impacts to cover of the most abundant species.

Table 2. Results of two-way ANOVA's for each of the functional groups, soil surface features and species, as well as species richness in grassland and juniper savanna plots in Wupatki NM. Dependent variables included Treatment (burned and unburned), Year (2014 and 2016) and Treatment × Year interaction.

Metric	Category	Treatment		Year		Treatment × year	
		F value	p	F value	p	F value	p
Functional Groups	Cacti	0.407	0.529	0.337	0.567	1.113	0.302
	Forb	0.599	0.446	0.151	0.701	0.064	0.802
	Perennial grass	0.029	0.866	41.473^d	<0.001^{c,d}	2.270	0.144
	Shrub	0.025	0.875	0.287	0.597	0.054	0.818
	Standing dead herbaceous	0.100	0.754	41.967^d	<0.001^{c,d}	0.280	0.601
	Standing dead shrub	12.333^d	0.002^{b,d}	4.383^d	0.047^{a,d}	1.553	0.224
Soil surface features	Bare ground	0.134	0.718	32.428^d	<0.001^{c,d}	0.018	0.896
	Dead herbaceous base	2.132	0.157	18.100^d	0.003^{b,d}	1.341	0.258
	Dead woody base	3.145	0.088	1.395	0.249	0.007	0.935
	Litter	9.11^d	0.006^{b,d}	23.464^d	<0.001^{c,d}	1.760	0.197
	Live plant base	0.934	0.343	2.411	0.133	0.891	0.354
	Undifferentiated crust	1.071	0.311	32.508^d	<0.001^{c,d}	1.0437	0.317
	Woody debris	0.140	0.712	3.935	0.058	0.020	0.888
Species	<i>Astragalus</i> spp.	2.190	0.151	7.484^d	0.011^{a,d}	0.169	0.685
	<i>Bouteloua eriopoda</i>	0.307	0.584	1.752	0.198	0.003	0.958
	<i>Chenopodium</i> spp.	1.366	0.254	5.984^d	0.022^{a,d}	0.011	0.918

^a p < 0.5

^b p < 0.001

^c p < 0.001

^d indicates significant difference, also shown in bold font

Table 2 (continued). Results of two-way ANOVA's for each of the functional groups, soil surface features and species, as well as species richness in grassland and juniper savanna plots in Wupatki NM. Dependent variables included Treatment (burned and unburned), Year (2014 and 2016) and Treatment × Year interaction.

Metric	Category	Treatment		Year		Treatment × year	
		F value	p	F value	P	F value	p
Species (continued)	<i>Ericameria nauseosa</i>	0.365	0.551	0.115	0.736	<0.001	0.985
	<i>Euphorbia</i> spp.	2.306	0.141	5.686^d	0.025^{a,d}	4.168	0.052
	<i>Hesperostipa neomexicana</i>	1.903	0.180	4.828^d	0.037^{a,d}	0.028	0.868
	<i>Hilaria jamesii</i>	1.779	0.194	9.829^d	0.004^{b,d}	1.598	0.218
	<i>Salsola tragus</i>	0.372	0.547	1.288	0.267	1.198	0.284
	<i>Sporobolus</i> spp.	0.651	0.427	0.242	0.627	0.183	0.678
Plot species richness	—	0.591	0.449	0.751	0.394	3.714	0.065

^a p < 0.5

^b p < 0.001

^c p < 0.001

^d indicates significant difference, also shown in bold font

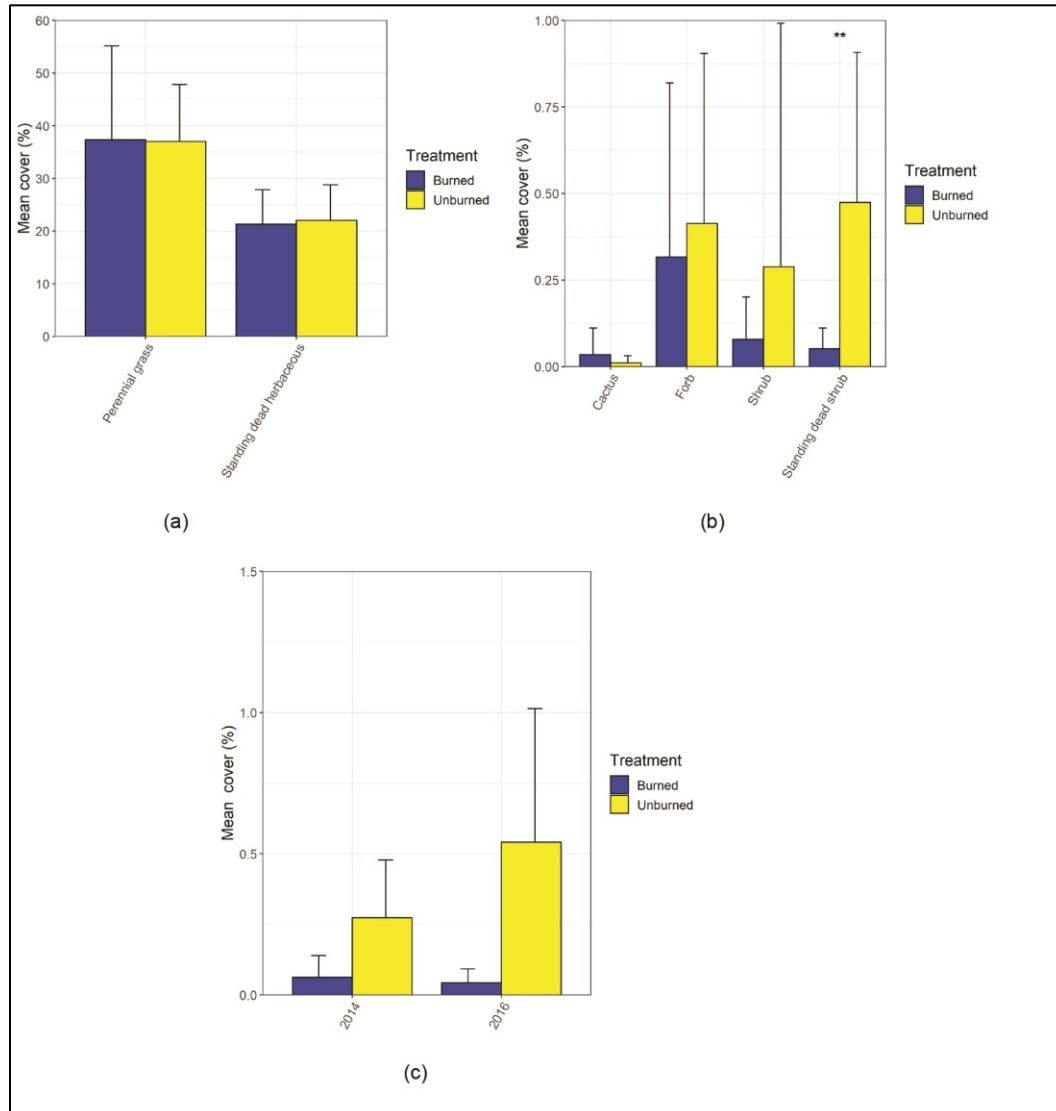


Figure 2. Mean cover of functional groups in burned and unburned grassland and juniper savanna plots in Wupatki NM. (a) Mean cover of perennial grass and standing dead herbaceous cover. (b) Mean cover of all other functional groups. (c) Mean cover of standing dead shrubs in burned and unburned plots by year. Note the three graphs have different scales on the y-axis. Asterisks indicate significant differences. Error bars represent one standard deviation.

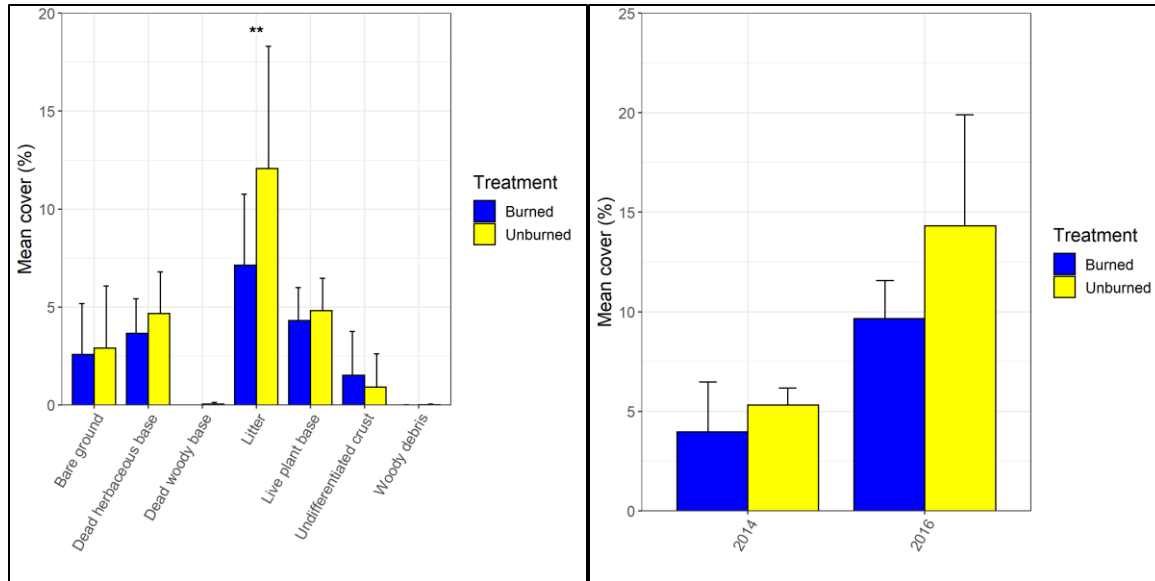


Figure 3. Mean cover of soil surface features in burned and unburned grassland and juniper savanna plots in Wupatki NM. (Left) Mean cover of soil surface features. (Right) Mean cover of litter in burned and unburned plots by year. Note the two graphs have different scales on the y-axis. Asterisks indicate significant differences. Error bars represent one standard deviation.

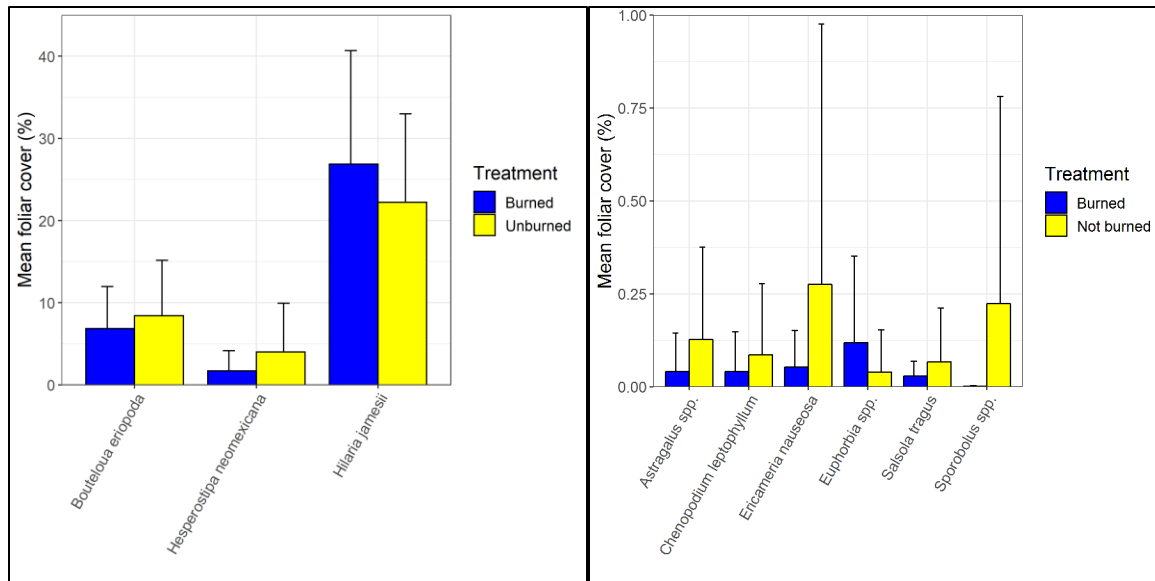


Figure 4. Mean species cover in burned and unburned grassland and juniper savanna plots in Wupatki NM. (Left) Mean foliar cover of the abundant species. (Right). Mean foliar cover of the less abundant species. Note the two graphs have different scales on the y-axis. No significant differences were detected. Error bars represent one standard deviation.

Species richness and community composition

The differences in species richness (number of species) among the plots were tested as a function of treatment and year and the treatment x year interaction (Table 2). Mean plot species richness was 12.7 species in unburned plots and 13.0 species in burned plots. Plot species richness ranged from 6

to 23 species. There were no significant differences between treatments nor years. Ordinations illustrate differences in species composition in multi-dimensional space, based on dissimilarities in species abundances. The Detrended Correspondence Analysis (DCA) plot ordination shows a concentration of burned plots in the center left portion of the plot, but there is large overlap between burned and unburned plots, suggesting small differences in species composition (Figure 5).

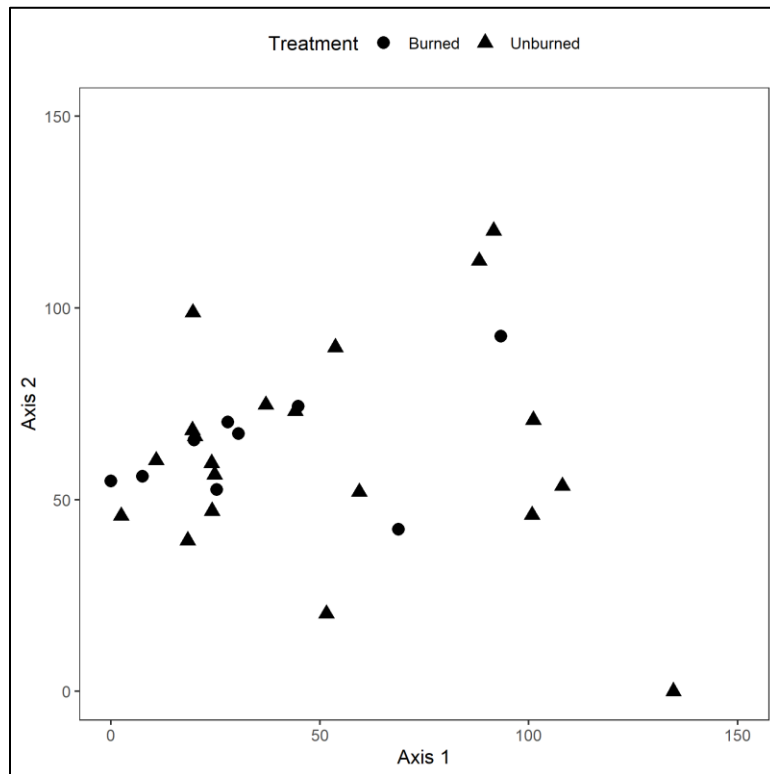


Figure 5. Detrended Correspondence Analysis (DCA) ordination plot of herbaceous/shrub species cover showing burned and unburned plots.

A species biplot (not shown) suggests that plots on the right side of the plot are associated with higher abundance of *Hesperostipa neomexicana*, *Bouteloua eriopoda*, and *Ericameria nauseosa*; they are also associated with a number of species of low abundance, such as *Krascheninnikovia lanata* (winterfat), *Chloracantha spinosa* (spiny chloracantha), *Evolvulus nuttallianus* (shaggy dwarf morning-glory) and *Escobaria vivipara* (spiny star). The plots on the left side are associated with the annual species *Chenopodium leptophyllum* and *Euphorbia* spp.

Species unique to burned and unburned plots were identified. This analysis included species that had occurred in these plots in previous years, and in 12 additional plots used for pilot sampling. Thirteen species were unique to unburned plots, and 4 species were unique to burned plots. However, these species were present in only one or two plots. There were 3 nonnative, annual species in the plots: *Salsola tragus* (prickly Russian thistle), which occurred in moderate abundance in both burned and unburned plots; and *Mollugo cerviana* (threadstem carpetweed), which occurred in one burned plot, and *Bromus tectorum* (cheatgrass), which occurred in one unburned plot, both in trace amounts (<

001% mean foliar cover). Other native annual species, such as *Euphorbia* spp. and *Chenopodium leptophyllum* occurred in moderate abundance in both burned and unburned plots.

Trees

Foliar cover of *Juniperus monosperma* was not measured in the quadrats; instead, their stems were measured in 0.10 ha subplots. There were 41 stems of *Juniperus monosperma* greater than 15 cm DRC that occurred in the plots in 2014 and 2016, 33 of which were living and 8 of which were standing dead. Only one of the standing dead trees occurred in the unburned plots; the remaining 7 standing dead trees occurred in the burned plots. In other words, 41% of the dead trees were in the burned plots, compared to 4% in the unburned plots. A chi-squared test demonstrated that there were significant differences in the number of dead trees in burned and unburned plots (chi-squared = 12.487, $p < 0.001$), indicating that tree mortality was greater in burned areas.

Discussion and Conclusion

Two general models have been proposed for the effects of fires on the grasslands of the Southwest. The first suggests that the impacts of fire are short-term: biomass recovers to pre-fire levels within 3 years, and species composition remains relatively unchanged over the long term (Jameson 1962, McPherson 1995). A second model suggests that long-term effects of fire may occur through the mortality of fire-sensitive species (e.g. *Bouteloua eriopoda*) or life forms (i.e. shrubs and cacti), and/or by promoting the regeneration of annual species (Archer 1994, Burgess 1995, McPherson 1995, Miller 2005, Kilgore et al. 2009, Van Auken 2009). With the exception of standing woody material, the grasslands of Wupatki NM, which burned between 1995 and 2002, appear to have recovered their pre-fire structure by 2014–2016, in 12 to 21 years post-burn. It is unclear, however, to what extent the overall composition of the grasslands have changed because of drought and other factors. In other words, was the composition of the unburned plots in 2014 and 2016 similar to their composition in 1994?

The greatest effect of the fires appears to be the mortality of *Juniperus monosperma*. In Southwestern grasslands, fires have been cited as responsible for maintaining the dominance of perennial grasses though the mortality of shrubs and other woody plants (Archer 1994, Burgess 1995, Miller 2005, Van Auken 2009). Park staff confirmed that trees died following the fires (pers. comm. Paul Whitefield). There is not strong evidence that ground fires historically acted to maintain juniper savannas across the Southwest (Romme et al. 2009). However, a number of researchers have documented the increased density of *Juniperus monosperma* in and around Wupatki over the past century (Cinnamon 1988, Hassler 2009, Parker 2009, Clifford et al. 2011). They logically inferred this was caused by the removal of fire from the system, although favorable climatic conditions may have also facilitated its establishment (Arnold et al. 1964, Cinnamon 1988, Ironside 2006, Parker 2009). Generally, surface fires kill smaller stems of this species, while larger stems are susceptible to individual tree torching and crown fires (Jameson 1962, Johnsen 1962, Arnold et al. 1964). The lack of herbaceous cover beneath the trees (Chong 1993, Baril et al. 2018) may also decrease their susceptibility to fires. The fire-induced mortality of trees in this study supports the argument that fires historically maintained this system as grasslands and open savannas. After a large disruption of the fire regime associated with European-American settlement and livestock grazing, its reintroduction into the ecosystem is allowing fire to resume its historic role in maintaining open grasslands and savannas.

This study did not detect any difference in shrub cover between burned and unburned plots; foliar cover of shrubs in the study area was low, less than 0.5% and had large among-plot variation. Standing dead shrub cover, however, was found to be significantly greater in the unburned area relative to the burned areas. A possible explanation of greater standing dead shrubs in unburned areas is that shrubs in the burned had been consumed in the fires. There is substantial anecdotal evidence of shrub mortality from fires at these sites (pers. comm. Paul Whitefield). The shrubs in the unburned areas may have died in subsequent droughts between 2002 and 2009, thus creating greater cover of dead woody shrubs. There was a decrease in the foliar cover of the shrub *Ericameria nauseosa* (rubber rabbitbrush) in these plots between 2007 and 2009 (DeCoster and Swan 2011). This suggests

that fires may have caused shrub mortality, but through the interaction of other disturbances, burned and unburned vegetation became more similar over time.

While short-term effects were not examined in this study, fires often cause changes to the soil surface by increasing bare ground and removing litter and woody debris (Fitzgerald et al. 2001, Drewa et al. 2006). In this study, litter was found to have lower cover in burned plots relative to the unburned plots 14 to 21 years following the fires. These differences likely have persisted because of low decomposition rates in the arid environment.

Fire has the potential to cause herbaceous species to increase or decrease, but this study did not find significant differences in the abundance of the 8 most abundant species. Perennial grasses are generally considered to be adapted to fire and grazing, due to their apical meristem being protected at the base of their tiller (McClaran 1995). *Bouteloua eriopoda*, however, has been shown to be sensitive to fire, due to its stoloniferous growth form (Burgess 1995, McPherson 1995), but there was not a significant difference for this species in this study. The large overlap of burned and unburned plots in ordination space suggests small differences in species composition. The fact that species that were unique to burned and unburned plots did not occur in more than 2 plots makes it difficult to suggest that any of these species can be considered either fire-tolerant or fire-sensitive. Fire does not appear to be causing the spread of nonnative species in this ecosystem. Only *Salsola tragus* occurred in moderate abundance, and had similar abundance in burned and unburned plots.

This study also did not detect differences in species richness between areas that were burned and unburned. Species diversity in these grasslands is low, relative to other grasslands on the southern portions of the Colorado Plateau (DeCoster and Swan 2013a, DeCoster and Swan 2013b). One explanation for reduced species diversity is the century of intensive livestock grazing, coupled with the removal of fire from the ecosystem. With 30 years since the cessation of grazing, the grasslands are likely still in the recovery process, and the potential effects of fire on species diversity may be masked by the legacy of livestock grazing. Alternatively, the low species richness of these grasslands may simply be the result of the unique geology and soils of this ecosystem.

This study demonstrated that the primary long-term effect of fires on the grassland and savannas of Wupatki NM is the direct killing of stems of *Juniperus monosperma*. The reintroduction of fire into this ecosystem appears to be reversing the trend of increased tree density through the 20th century, thus assuming its historical role in maintaining low tree densities. The effects of fire on the shrub/herbaceous layer and ground surface of these systems, however, are more subtle: decreased litter and dead shrubs, but no changes in species composition. The lack of significant differences, on one hand, may be the result of a small sample size and high variability. The lack of precipitation around the times of the fires may have also influenced how the fire influenced the vegetation. It is possible that immediate recovery from the fire could have proceeded differently if substantial rain events followed the fire, e.g. with the germination of new species. Alternatively, the lack of significant differences may indicate that long-term fire effects in these grasslands are minimal. Any short-term changes of vegetation structure and composition disappear in the first 2 decades post-fire. This study suggests that there are few long-term effects of fire in the grasslands, and that the composition of the burned and unburned areas likely converge within 14 years.

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Appendix: Southern Colorado Plateau Network upland monitoring plots at Wupatki National Monument

Table A-1. List of plots used in the analysis with sample year, the fire in which they burned, and years since fire.

Plot	Sample year	Fire	Years since fire
L01	2016	Not burned	—
L02	2016	Not burned	—
L03	2016	Antelope	14
L04	2016	Not burned	—
L05	2014	Not burned	—
L06	2016	Not burned	—
L08	2014	Not burned	—
L09	2016	West	21
L10	2014	Antelope	12
L13	2016	State	14
L20	2016	Not burned	—
L21	2016	Not burned	—
L22	2016	Not burned	—
L24	2016	Not burned	—
L26	2014	Not burned	—
L27	2014	Not burned	—
L30	2016	Not burned	—
L31	2014	Antelope	12
L32	2014	Not burned	—
L33	2014	Antelope	12
L34	2016	Not burned	—
L35	2016	Not burned	—
L36	2016	Antelope	14
L37	2014	Antelope	12
L38	2016	Not burned	—
L39	2016	Not burned	—
L01	2016	Not burned	—

Plot	Sample year	Fire	Years since fire
L02	2016	Not burned	—
L03	2016	Antelope	14
L04	2016	Not burned	—
L05	2014	Not burned	—
L06	2016	Not burned	—
L08	2014	Not burned	—
L09	2016	West	21
L10	2014	Antelope	12
L13	2016	State	14
L20	2016	Not burned	—
L21	2016	Not burned	—
L22	2016	Not burned	—
L40	2016	Antelope	14
L41	2016	Not burned	—

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