RESEARCH ARTICLE

SHORT-TERM EFFECTS OF REPEATED WILDFIRES IN OAK-JUNIPER WOODLANDS

Charlotte M. Reemts[1]* and Laura L. Hansen[2]

[1]The Nature Conservancy, 318 Congress Avenue, Austin, Texas 78701, USA

[2]1406 Main Street, Suite 275, Fredericksburg, Texas, USA

*Corresponding author: Tel.: 001-254-493-6041; e-mail: creemts@tnc.org

ABSTRACT

Fire can shape both the structure and composition of vegetation communities, especially those dominated by species with different regeneration strategies. The dominant species of oak-juniper communities in central Texas include resprouters (oaks [*Quercus* spp.]) and a reseeder (Ashe juniper [*Juniperus ashei* Buchholz]). We studied the effects of two overlapping wildfires (1996 and 2009) on oak-juniper woodlands on Fort Hood Military Reservation, Texas, USA. We estimated burn severity and measured vegetation regeneration along permanent transects in once-burned, twice-burned, and nonburned areas. Burn severity was highly variable, but was higher in 1996 than in 2009. In the first growing season after the second fire (2009), understory stem density was 3 to 4 times higher than in 1996, but that difference had disappeared by the third growing season. Overstory density did not differ after the two fires, but density on slopes was 3 to 10 times higher than on mesas. Overall species composition was similar after the two fires, but differed from nonburned areas due to the absence of Ashe juniper. Ashe juniper was still absent from twice-burned areas in

RESUMEN

El fuego puede modelar tanto la estructura como la composición de las comunidades de plantas, especialmente aquellas dominadas por especies con diferentes estrategias de regeneración. Las comunidades de encino-junípero en la región central de Texas, incluyen especies dominantes que rebrotan, como los encinos (*Quercus* spp.) y otras que regeneran por semillas, como el junípero (*Juniperus ashei* Buchholz). En este trabajo estudiamos los efectos de dos incendios ocurridos en una misma área (1996 y 2009) en bosques de encino-junípero en la Reservación Militar de Fort Hood, Texas, EUA. Estimamos la severidad de los incendios y medimos la regeneración de la vegetación a lo largo de transectos permanentes en áreas quemadas una vez, dos veces y no quemadas. La severidad de los incendios fue altamente variable, aunque mayor en 1996 que en 2009. En la primera estación de crecimiento después del segundo incendio (2009), la densidad de tallos del subdosel fue entre 3 y 4 veces mayor que la de 1996, aunque esa diferencia desapareció en la tercera temporada de crecimiento. No hubo diferencia en la densidad del dosel después de los dos incendios, aunque la densidad en áreas con pendientes fue entre 3 y 10 veces mayor que en áreas planas (mesas). La composición general de especies fue similar después de los dos incendios, y difirió de la de las áreas no quemadas por la ausencia de junípero. Hasta el año 2011, el junípero no se

2011, whereas small numbers of junipers (21 ± 34 stems ha⁻¹) had colonized the once-burned areas within three years. Our data suggest that wildfires controlled the historical distribution of Ashe juniper, but not of resprouting species, in the Edwards Plateau, and that long intervals between wildfires are required for Ashe juniper to become a canopy dominant in these woodlands.

había recuperado en las áreas quemadas en 1996 y 2009, mientras que en aquellas áreas quemadas solo una vez, un bajo número de juníperos (21 ± 34 tallos ha⁻¹) las había colonizado a tres años del incendio. Nuestros datos sugieren que el fuego controlaba la distribución histórica del junípero, pero no de las especies rebrotantes en la Planicie Edwards, y que son necesarios intervalos largos entre los incendios para que el junípero se convierta en una especie dominante del dosel en sus bosques.

INTRODUCTION

Fire is a natural disturbance throughout the southwestern United States, although fire regimes vary greatly from frequent low-severity fires to infrequent high-severity (crown) fires (Floyd *et al.* 2000, Baker and Shinneman 2004). Variations in fire regimes can shape vegetation structure and species composition on local scales (as in the case of mixed-severity fires) through landscape scales (Turner and Romme 1994). Vegetation response to a particular fire depends on fire severity, climatic conditions (e.g., drought), and post-fire regeneration strategies.

Oak-juniper (*Quercus* spp.-*Juniperus* spp.) woodlands in the Southwest are co-dominated by resprouters and seeders. Most oak species resprout vigorously after fire (Boyd and Bidwell 2002, Rodríguez-Trejo and Myers 2010) and can suppress regeneration of co-dominant seeding species (Haire and McGarigal 2008, Reemts and Hansen 2008). The dominant juniper species include both seeders and resprouters (Adams 2008). Many junipers can be top-killed by fire when small (Noel and Fowler 2007), but large individuals often survive prescribed fires (Ansley and Rasmussen 2005). Survival of resprouting junipers after

wildfire can be more than 50 % (Johnson *et al.* 1962). Recolonization by seeding junipers can be slow in woodlands (Reemts and Hansen 2008), but more rapid in grassland and shrublands (Ansley and Rasmussen 2005).

The effects of wildfires on species composition in oak-juniper woodlands depend on the fire return interval, fire season, and regeneration strategies of the dominant species. In communities co-dominated by seeding juniper species, extensive, high-severity fires can shift dominance to resprouting oak species (Floyd *et al.* 2000, Reemts and Hansen 2008), and repeated fires can restrict junipers to fire refugia (Floyd *et al.* 2000). Repeated summer prescribed fires can also reduce or eliminate junipers from a community (Ewing *et al.* 2005). Some oak species can survive high-frequency fires, at least in the short term (Harrell *et al.* 2001), but they may be more vulnerable to growing-season fires (Harrington 1989).

The fire regime and historic extent of oak-Ashe juniper (*Juniperus ashei* Buchholz) woodlands in central Texas is debated (e.g., Wills 2005, Diamond and True 2008, Murray *et al.* 2012). Oak-juniper woodlands in this area include a number of different communities, ranging from oak savannas in various stages of juniper encroachment to mature

woodlands, which generally occur on shallower soils (Diamond 1997). Historically, woodland cover within the region varied, but likely occupied around half of the overall landscape and most of the slopes (Wills 2006, Diamond and True 2008, Murray *et al.* 2012; but see Wills 2005). Fire regime ranged from low-severity, frequent fires in the savanna communities, to high-severity, infrequent crown fires in the woodlands (Bray 1901, Gehlbach 1988, Diamond 1997). We focused on woodland communities on shallow soils, rather than on savannas.

Most hardwood species in the woodlands, including all oaks, resprout vigorously after being top-killed by fire (Reemts and Hansen 2008). A few species, such as prairie sumac (*Rhus lanceolata* [A. Gray] Britton), colonize burned areas primarily from seed, but can also resprout after fire (Rasmussen and Wright 1989). Ashe juniper does not resprout and, while small individuals can be killed by relatively low-intensity fires, larger individuals are killed only by high-intensity fires (Bryant *et al.* 1983, Fonteyn *et al.* 1988, Noel and Fowler 2007). Ashe juniper seeds are dispersed by birds and, to a lesser extent, some mammals, and dispersal is relatively inefficient (Chavez-Ramirez and Slack 1993, 1994). The woodland communities can successfully regenerate after a single fire, although regaining the original structure may take decades (Huss 1954, Gehlbach 1988). However, little is known about the effects of multiple wildfires on vegetation structure or species composition.

We examined the response of oak-juniper woodlands to two overlapping wildfires (1996 and 2009) on Fort Hood Military Reservation, Texas, USA, to determine how repeated fires influence regeneration. Because most of the woody species resprout and because of the relatively long interval (14 years) between fires, we predicted that vegetation structure and species composition after the second wildfire would be similar to the response after the first wildfire.

METHODS

Study Area

Fort Hood Military Reservation is an 87 890 ha army installation in Bell and Coryell counties, Texas, USA (Figure 1). Common vegetation communities include oak-Ashe juniper woodlands and oak shrublands on slopes and mesa tops. Grasslands and riparian woodlands are found in the valleys and on rolling lowlands; savannas dominated by Texas live oak (*Quercus fusiformis* Small.) and post oak (*Q. stellata* Wagnenh.) occur in the lowlands and on deeper soils on the mesas. Fort Hood includes breeding habitat for two federally endangered songbirds: the golden-cheeked warbler (*Setophaga chrysoparia* Sclater & Salvin) and the black-capped vireo (*Vireo atricapilla* Woodhouse). The installation is grazed year round at a stocking rate of ~2000 animal units. Military training requirements preclude cross-fencing, allowing cattle to roam freely.

Fire Descriptions

On 21 February 1996, military training activities started three grassland fires. Due to hot, dry, and windy conditions, the fires moved into adjacent woodlands where they burned mostly as crown fires. By the time the fires were controlled (on 7 March), they had burned more than 4000 ha of woodlands. The second fire, which burned from 3 to 12 April 2009, was smaller (608 ha; 360 ha overlapping with first fire). Both fires were preceded by above-average rainfall (11 to 13 months before the 1996 fire; 14 to 16 and 8 to 10 months before the 2009 fire; Figure 2). The 1996 fire occurred during a four-month period of below-average rainfall; rainfall during March to April 2009 was above average. Palmer Modified Drought Index was moderate in February 1996 and mid-range in April 2009; the Palmer Z-Index was extreme in February 1996 and mid-range in April 2009.
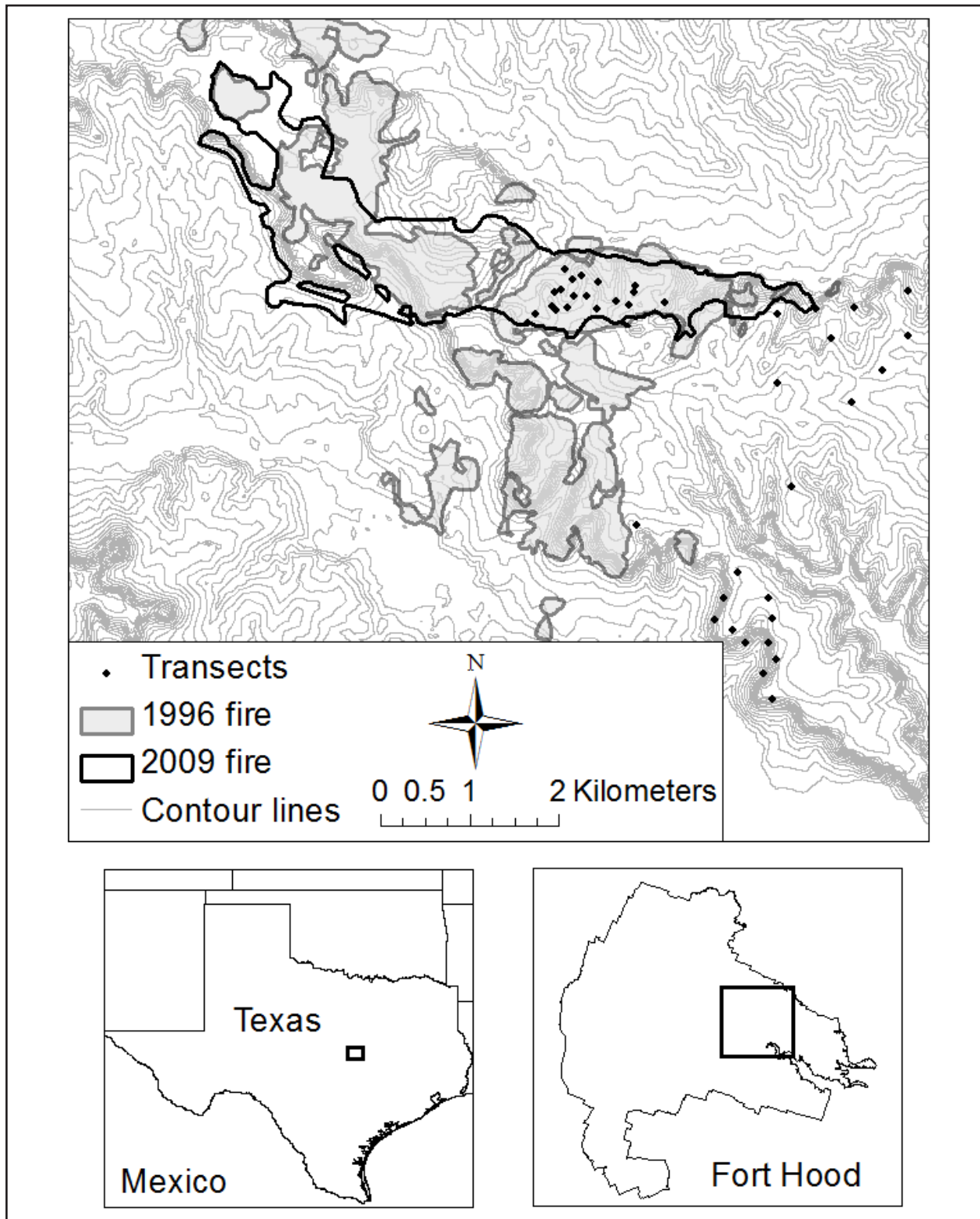
Figure 1. Location of two wildfires and sampled transects on Fort Hood, Bell and Coryell counties, Texas, USA. Only part of the 1996 wildfire and only those transects analyzed for this study are shown.
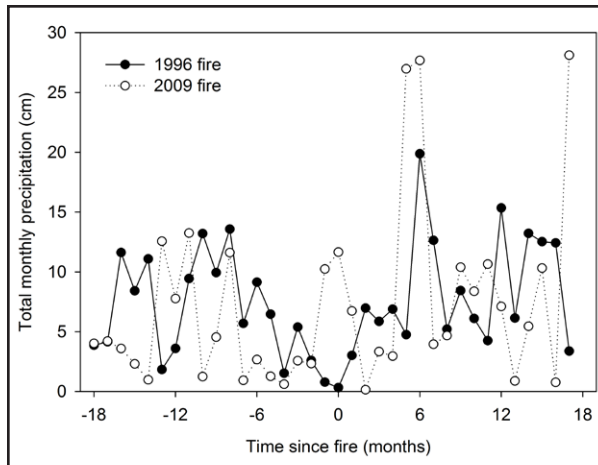
Figure 2. Total monthly rainfall (cm) for the three-year period around the time of the two wildfires based on the closest weather stations in Bell and Coryell counties, Texas, USA. Average monthly rainfall from 1990 to 2011 was 7.5 cm.

Vegetation and Burn Severity Sampling

Following the first fire, we randomly located permanent transects in moderately to severely burned oak-juniper woodlands (Figure 1). We sampled most of these "once-burned" transects annually from 1996 to 2002, and again in 2005 and 2010; a few transects were first sampled in 1997. After the second fire, we sampled all "twice-burned" transects annually from 2009 to 2011. We sampled "non-burned" transects (in 2001, 2005, and 2010) in mature woodlands located adjacent to the burned areas on similar slopes and soils (Figure 1). While the fire history of these non-burned woodlands is not known, all are present in aerial imagery taken in 1938 and appear similar in maturity to the woodlands subsequently burned in 1996. Tree skeletons in the burned areas were also of similar size to trees in the nonburned areas.

We sampled 101 transects (for a full description, see Reemts and Hansen 2008); for this analysis, we focused on the 19 transects that burned in both fires (8 on mesas and 11 on slopes) and on the nonburned transects (20 on mesas and 11 on slopes). Mesa transects were

on Eckrant cobbly silty clay soils with shallow slopes (<8º); this soil series falls in the Low Stony Hill ecological site. On Fort Hood, the vegetation on this soil type includes bastard oak (*Quercus sinuata* Walter var. *breviloba* [Torr.] C.H. Mull) shrublands or bastard oak-Ashe juniper woodlands, equivalent to the scaly-bark oak/Vasey oak-Ashe juniper community described by Diamond (1997). Slope transects were on Real gravelly clay loam soils (5º to 30º) and were slightly more mesic. This soil series is in the Steep Adobe ecological site and supports a more diverse woodland, co-dominated by Buckley oak (*Q. buckleyi* Nixon & Dorr) and Ashe juniper, that also includes bastard oak, Texas ash (*Fraxinus albicans* Buckley), and Texas live oak in the canopy. In mesic canyons, Ashe juniper dominance decreases and additional species, such as bigtooth maple (*Acer grandidentatum* Nutt.) and chinkapin oak (*Q. muehlenbergii* Engelm.), are added. This community is equivalent to the Ashe juniper-Texas oak/deciduous species woodland of Diamond (1997).

Transects were 110 m long and followed either a random bearing (for level sites) or were perpendicular to the slope (i.e., followed contour lines). Nested 10 m × 10 m plots were located at 10 m intervals along the transects, and 7 of the 11 possible plots were randomly selected for sampling. From 1996 to 2002, we re-randomized the selected plots every year. Starting in 2005, we used the plot locations from the first sampling year on each transect.

We visually estimated burn severity for substrate and vegetation in July to August 1996 for the first fire and April 2009 for the second fire, using definitions from National Park Service fire monitoring methods (National Park Service 1992). For substrate, plots were classified as severely burned if litter was completely consumed and mineral soil was visible; moderately burned if litter was mostly consumed leaving coarse ash; lightly burned if litter was partially consumed or charred; and scorched if litter was partially blackened. For

vegetation, all plant parts except major stems were consumed in severely burned plots; foliage, twigs, and small stems were consumed in moderately burned plots; foliage and smaller twigs were partially to completely consumed in lightly burned plots; and foliage was scorched but still attached to supporting twigs in scorched plots.

Within the plots, we recorded stem density of all woody species in four categories: "seedlings" (<0.3 m tall), "shrubs" (between 0.3 m and 1.8 m tall), "saplings" (≥1.8 m tall, <5 cm diameter at breast height [dbh]), and "trees" (≥5 cm dbh). We did not distinguish between resprouts from top-killed individuals and regeneration from seed. We counted the stem density of seedlings, shrubs, and saplings in 5 m × 5 m plots. Stems that split above the root crown were counted as one. Saplings were divided into five dbh classes: 0 cm to 0.9 cm, 1.0 cm to 1.9 cm, 2.0 cm to 2.9 cm, 3.0 cm to 3.9 cm, and 4.0 cm to 4.9 cm.

We sampled trees in 10 m × 10 m plots. From 1996 to 2002, we recorded the stem density of trees in 5 cm or 10 cm dbh classes. Starting in 2005, we recorded dbh (to the nearest 0.1 cm) for each tree. If saplings or trees branched above the root crown, only the largest stem was measured and counted. In the study area, Ashe juniper is the species that most commonly has multiple branches rather than multiple stems; Ashe juniper is therefore somewhat under-represented in the basal area data.

Statistical Analyses

While we sampled multiple transects in the burned areas, these transects represent subsamples of the two wildfire events and we lack true replication. However, our data are still useful for comparing vegetation responses to these two fires (Wester 1992) and provide an opportunity to document a poorly studied phenomenon (i.e., repeated wildfires on the Edwards Plateau) for comparison with future studies elsewhere in the region.

We compared burn severity between the 1996 and 2009 fires using a chi-square analysis (SAS 9.2, SAS Institute, Cary, North Carolina, USA). We used plots as sampling units because fire intensity was patchy and fire severity within a single transect often spanned three or even four burn severity categories. We compared burn severity (substrate and vegetation separately) between years within topographic position; we also compared substrate and vegetation burn severity within a year and topographic position.

We analyzed changes in stem density and basal area using mixed models with the Kenward-Roger approximation for denominator degrees of freedom (MIXED in SAS 9.3). Because the plot locations within a transect varied among years, we averaged plot-level values for each transect. For each analysis, we selected an appropriate covariance structure using the adjusted Akaike Information Criterion (AICc). We compared understory density (seedlings + shrubs), overstory density (saplings + trees), and basal area (saplings + trees) from burned sites in years 0, 1, and 2 with data from nonburned sites, conducting separate analyses for each year. Throughout this study, year 0 is defined as the year of the fire (1996 and 2009). We also conducted a repeated measures analysis comparing density and basal area in the once-burned and twice-burned sites through time (years 0 to 2). Significance tests were adjusted to account for multiple comparisons using the simulated distribution of the maximum of a multivariate t random vector (SAS Institute 2009).

To examine changes in species composition, we used nonmetric multidimensional scaling with a Sorenson distance measure (PC-ORD 6.0, MjM Software, Gleneden Beach, Oregon, USA). For each transect, we summed average basal area for the shrub, sapling, and tree layers. Shrubs were included because many transects did not have saplings or trees in the first few years after fire. Shrub dbh was not recorded, but most shrubs (woody stems

between 0.3 cm and 1.8 m tall) had a dbh of <1 cm. For the purposes of this analysis, we converted shrub density into basal area by assuming that the average shrub dbh was 0.1 cm. We used data from the following years: once-burned transects from 1997 (not all transects were sampled in 1996) and 2005; twice-burned transects from 2009 to 2011; and nonburned transects from 2005 and 2010. We eliminated species with fewer than three occurrences from the analysis and applied a square-root transformation. A two-dimensional ordination was chosen based on a Monte Carlo permutation test and scree plot.

RESULTS

Visual estimates of burn severity differed among years for substrate and vegetation on both mesas and slopes, with burn severity estimates being higher in 1996 than in 2009 ($\chi_3^2 >$ 25, $P \leq 0.001$ for all; Figure 3). On mesas, estimated vegetation burn severity was higher than that of substrate burn severity in 1996 ($\chi_2^2 = 13$, $P = 0.001$), but not in 2009 ($\chi_3^2 = 4$, $P = 0.2$). On slopes, vegetation burn severity estimates were higher than estimated substrate burn severity in both years (1996: $\chi_2^2 = 21$, $P \leq 0.001$; 2009: $\chi_2^2 = 11$, $P = 0.004$).

In the first growing season after fire (year 0), understory stem density in twice-burned transects was higher than density in both once-burned and nonburned transects for slopes and mesas ($t < 7.07$, $P \leq 0.001$ for all; Figure 4; Table 1). In year 1, stem density in twice-burned transects remained higher than in non-burned transects for slopes and mesas ($t < 3.8$, $P \leq 0.001$ for both); density on slopes was also higher than in once-burned transects ($t = 4.12$, $P \leq 0.001$). In year 2, density in twice-burned transects was higher than in nonburned transects only on mesas ($t = 3.16$, $P = 0.02$). Understory stem density did not differ between mesas and slopes in any year. Stem density in twice-burned transects on mesas was higher in year 0 than in subsequent years ($t \leq 7.45$, $P \leq$

0.001 for both; Table 2); density in years 1 and 2 did not differ. On slopes, density decreased significantly each year ($t \leq 10.61$, $P \leq 0.001$ for all).

For overstory stem density, both once- and twice-burned stem density was lower than in nonburned transects in year 0 ($t < 8.08$, $P \leq 0.001$ for all; Figure 4; Table 3). In year 1, stem density in once-burned transects on slopes was higher than on mesas ($t = 4.06$, $P \leq 0.001$). On mesas, density in both once- and twice-burned transects was lower than in nonburned transects ($t < 5.82$, $P \leq 0.001$). In year 2, stem density in both once- and twice-burned transects was higher on slopes than on mesas ($t < 3.28$, $P \leq 0.01$). On mesas, density in once-burned transects was lower than in nonburned transects ($t = 3.97$, $P = 0.001$). On slopes, stem density in year 0 was lower than density in subsequent years for both once- and twice-burned transects ($t \leq 3.04$, $P \leq 0.04$); density in years 1 and 2 did not differ.

Basal area was higher in nonburned transects than in once- or twice-burned transects for all three years ($t \leq 12.23$, $P \leq 0.001$; Tables 4 and 5), but did not differ between mesas and slopes. On slopes, basal area was higher in year 2 than in years 0 to 1 for both once- and twice-burned transects ($t \leq 3.32$, $P \leq 0.02$).

For the ordination, final stress was 14.02, while instability was less than 0.001. Ordination indicated that species composition changed immediately after fire, but became more similar to nonburned areas over time (Figure 5). Species composition after the second fire was similar to that after the first fire, but twice-burned transects were grouped lower along Axis 2 than once-burned transects. Species composition in nonburned areas did not change between 2005 and 2010. Axis 1 was negatively correlated with basal area of juniper (nonburned areas had much higher basal area of juniper, Table 6). Basal area of bastard oak, Texas ash, Buckley oak, and Texas live oak were also negatively correlated with Axis 1, while poison ivy (*Toxicodendron radicans* [L.]
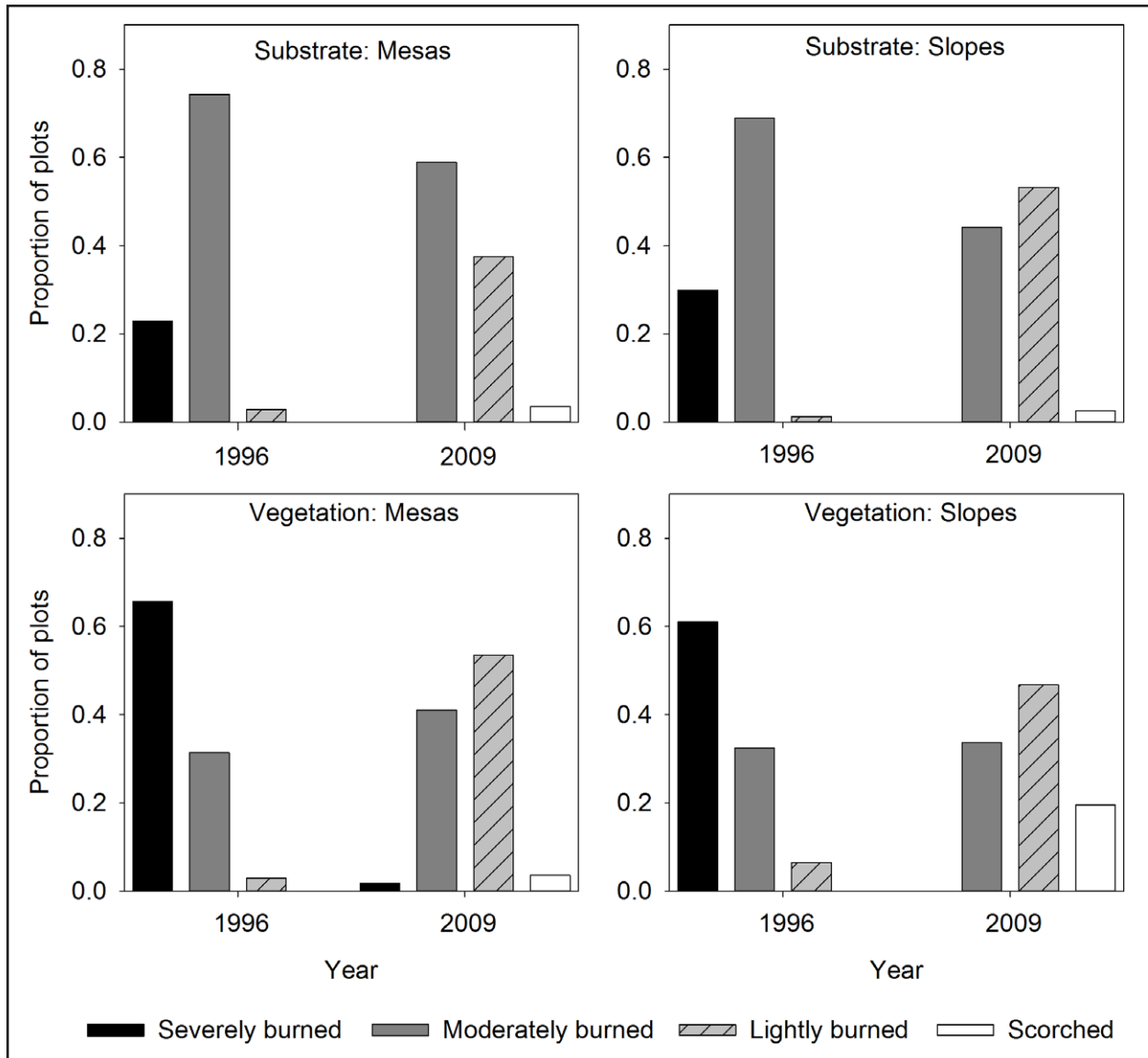
Figure 3. Burn severity in 1996 and 2009 by topographic position on Fort Hood Military Reservation (Texas, USA). Substrate: severely burned = litter consumed, mineral soil visible; moderately burned = litter mostly consumed with coarse ash; lightly burned = litter partially consumed or charred; scorched = litter partially blackened. Vegetation: severely burned = all plant parts except major stems consumed; moderately burned = twigs and small stems consumed; lightly burned = foliage and small twigs partially to completely consumed; scorched = foliage scorched but still attached.

Kunze) was positively correlated. Axis 2 was positively correlated with basal area of Buckley oak.

DISCUSSION

Contrary to our predictions, vegetation structure differed after the second fire: initial understory stem density was much higher in 2009 than after the first fire in 1996. Species with higher density after the second fire included resprouting trees (e.g., Buckley oak, Texas ash), shrubs (e.g., bastard oak, Mexican buckeye [*Ungnadia speciosa* Endl.], skunkbush sumac [*Rhus trilobata* Nutt.]), lianas (e. g., poison ivy, saw greenbrier [*Smilax bona-*
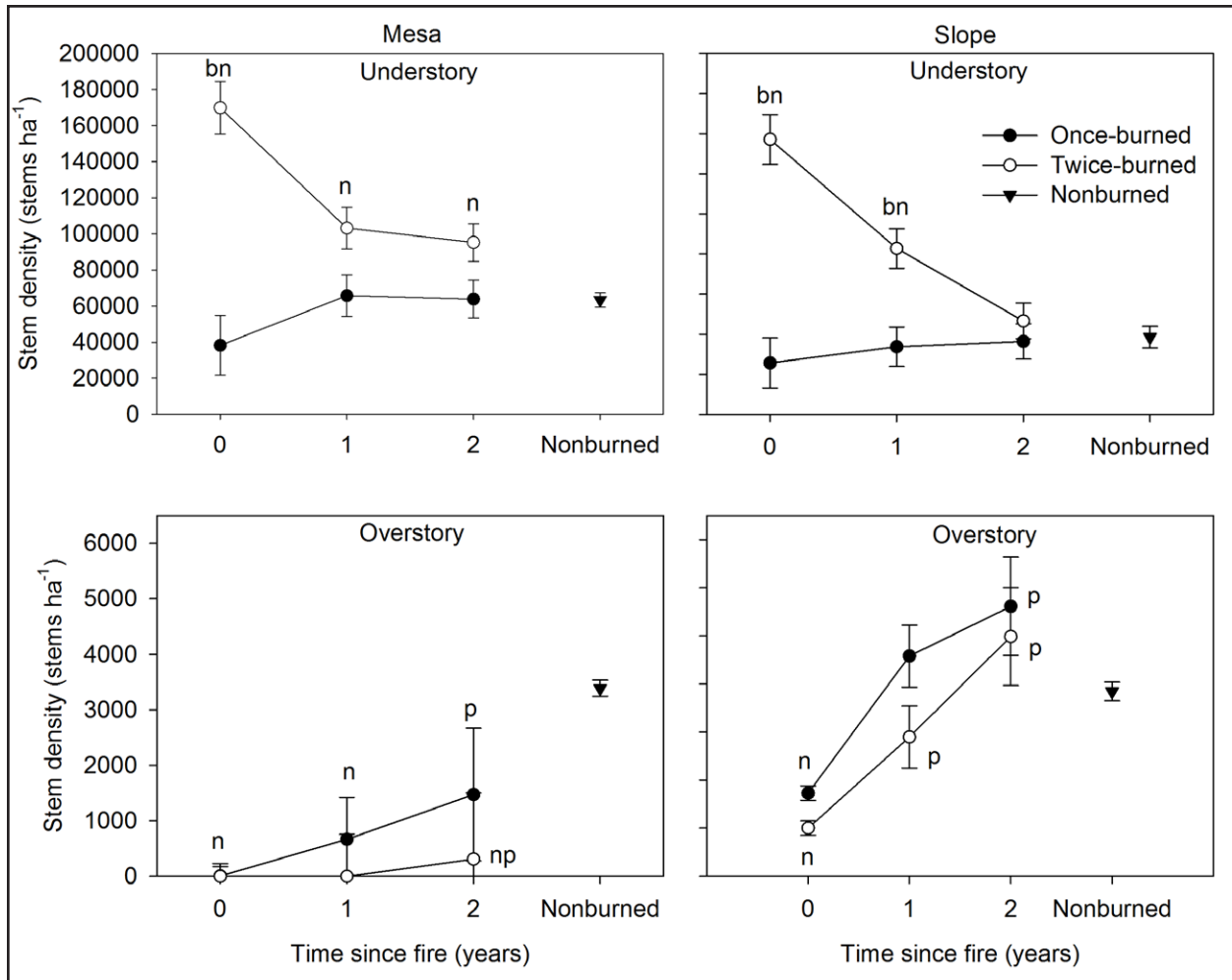
Figure 4. Understory (stems <1.8 m tall) and overstory (stems ≥1.8 m tall) density (least squares means ± standard error) after wildfires on Fort Hood Military Reservation (Texas, USA). Averaged data from non-burned transects collected in 2001, 2005, and 2010 are shown for comparison. b = significant difference between once-burned and twice-burned density in a given year; n = significant difference between burned and (average) nonburned density; p = significant difference between mesa and slope density in a given year ($\alpha = 0.05$).

Table 1. ANOVA tables for understory stem density: burn = burn status (once, twice, or nonburned); posi-

Effect	df	Year 0		Year 1		Year 2	
		F	*P*	*F*	*P*	*F*	*P*
burn	2	92.49	<0.001	18.07	<0.001	4.44	0.01
position	1	0.64	0.43	0.80	0.37	4.85	0.03
burn×position	2	0.18	0.84	0.21	0.81	1.51	0.22

Table 2. ANOVA tables for stem density and basal area comparisons through time: burn = burn status (once or twice); tsf = time since fire (0, 1, or 2); position = topographic position (mesa or slope).

Effect	df	Understory		Overstory		Basal area	
		F	*P*	*F*	*P*	*F*	*P*
burn	1	37.01	<0.001	2.04	0.16	0.74	0.40
tsf	2	20.62	<0.001	10.36	<0.001	11.84	<0.001
burned×tsf	2	48.36	<0.001	0.76	0.48	0.32	0.73
position	1	0.78	0.38	13.05	0.001	10.74	0.002
burn×position	1	0.24	0.62	0.12	0.73	0.03	0.85
tsf×position	2	1.85	0.17	4.95	0.01	6.95	0.002
burn×tsf×position	2	2.24	0.12	0.46	0.63	0.05	0.95

Table 3. ANOVA tables for overstory stem density: burn = burn status (once, twice, or nonburned); position = topographic position (mesa or slope).

Effect	df	Year 0		Year 1		Year 2	
		F	*P*	*F*	*P*	*F*	*P*
burn	2	83.17	<0.001	16.2	<0.001	1.70	0.19
position	1	0.05	0.83	15.82	0.001	19.31	<0.001

Table 4. ANOVA tables for basal area: burn = burn status (once, twice, or nonburned); position = topographic position (mesa or slope).

Effect	df	Year 0		Year 1		Year 2	
		F	*P*	*F*	*P*	*F*	*P*
burn	2	203.3	<0.001	226.07	<0.001	219.81	<0.001
position	1	0.06	0.81	0.18	0.67	0.41	0.52
burn×position	2	0.09	0.91	0.05	0.95	0.01	0.99

Table 5. Average basal area (m^2 ha^{-1}, least squares means ± standard error) for slopes and mesas. For burned transects, values within a column with the same letter are not different. Values in burned transects are significantly lower than in nonburned transects ($\alpha = 0.05$). Nonburned values are averaged for 2001, 2005, and 2010.

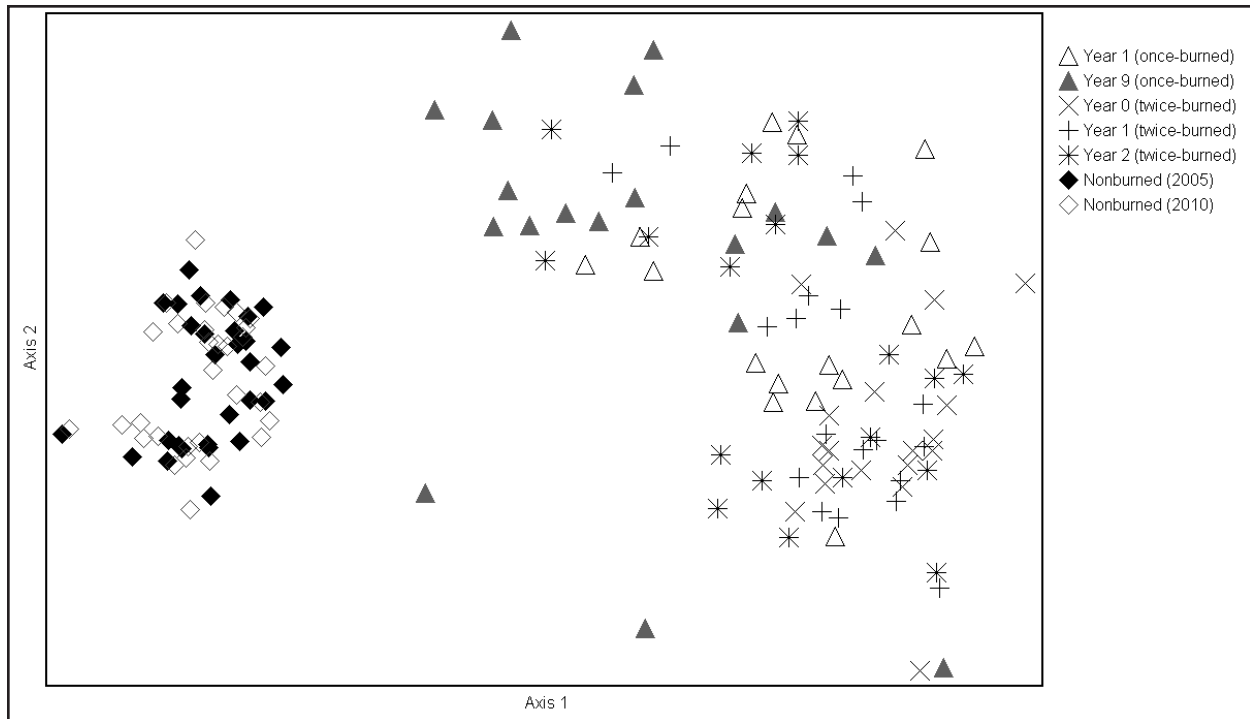| Time since fire (yr)	Mesas		Slopes	
	Once-burned	Twice-burned	Once-burned	Twice-burned
0	0 ± 2.13 a	0 ± 1.69 a	0.01 ± 1.43 a	0 ± 1.43 a
1	0.04 ± 1.66 a	0 ± 1.66 a	0.35 ± 1.42 a	0.23 ± 1.42 a
2	0.16 ± 1.66 a	0.02 ± 1.66 a	0.78 ± 1.42 b	0.64 ± 1.42 b
nonburned	19.40 ± 0.61		20.24 ± 0.83	

Figure 5. Nonmetric multi-dimensional scaling ordination of species basal area (shrubs, saplings, and trees) in burned and nonburned transects on Fort Hood Military Reservation (Texas, USA). Year 0 = summer immediately after the fire (i.e., 2009 for twice-burned transects).

Table 6. Correlations with nonmetric multi-dimensional scaling ordination axes for species with r > 0.4. Correlations are not shown for relationships that were bi-modal or humped.

Species	Axis 1			Axis 2		
	r	**R²**	**tau**	**r**	**R²**	**tau**
Ashe juniper	−0.922	0.868	−0.695			
Texas ash	−0.634	0.401	−0.576			
Bastard oak	−0.608	0.369	−0.370			
Buckley oak	−0.465	−0.216	−0.253	0.499	0.249	0.514
Texas live oak	−0.451	−0.204	−0.311			
Poison ivy	0.441	0.194	0.293			

nox L.]), and succulents (prickly pear [*Opuntia* spp.]), as well as a shrub that reseeds and resprouts (prairie sumac).

The dramatic increase in stem density could be a response to the repeated fires: some woody plants gradually lose the ability to resprout as they increase in size (Babb 1992, Vesk and Westoby 2004, Franklin *et al.* 2006). Because the trees burned in the second fire

were much younger and smaller than those burned in the first fire (based on the size of the tree skeletons), the increase in stem density could be a more vigorous resprouting response. In Oklahoma, for example, sand shinnery oak (*Quercus havardii* Rydb.) cover was higher after two prescribed fires than after a single fire (Harrell *et al.* 2001). Similarly, Gambel oak (*Quercus gambelii* Nutt.) density increased af-

ter repeated prescribed fires in spring or fall (Harrington 1985). Very short fire return intervals can reduce resprouting capacity (e.g., Pond and Cable 1960), but the relatively long interval between the wildfires in this study apparently allowed plants to recover their resprouting capacity.

The increased understory stem density could also have been caused by differences between the two fires. Because wildfires are unplanned, uncontrolled events, there are inevitable differences between repeated fires in the same area. In our study, differences between the fires include season, climatic conditions, and severity. The first fire burned while most plants were still dormant (February), while the second fire burned in the early growing season, after most woody species were leafed out (April). Carbohydrate reserves are expected to be lowest soon after leaf-out (Harrington 1989). Fires during this time of carbohydrate depression could decrease resprouting ability and, in fact, repeated summer prescribed fires decreased Gambel oak density by 20 % (Harrington 1985). In our study, however, stem density increased after the early growing season fire compared to the late dormant season fire.

Climatic conditions during the fires also differed. Both fires were preceded by above-average precipitation, which may have increased fine fuel loads in the grasslands where the fires were initiated (Swetnam and Baisan 1996). However, the 1996 fire occurred during a drought, while the 2009 fire occurred during an average year. The drought in 1996 could have pre-disposed plants to post-fire mortality or reduced root reserves available for sprouting, while the higher rainfall in 2009 could have prevented some mortality. Indeed, mortality of the resprouting red-berry juniper (*Juniperus pinchotii* Sudw.) after prescribed fire was higher in drought years than in average years (Steuter and Britton 1983). In contrast, three winter prescribed fires (December to February) during droughts increased Texas

live oak understory frequency compared to pre-fire frequency (Taylor *et al.* 2012).

Finally, fire severity also differed, at least in the sampled transects (the original transects were deliberately established in areas burned with moderate to high severity and therefore do not measure the overall severity of the 1996 fire). Although no above-ground stems survived either fire (in the transects), the higher severity in the 1996 transects may have killed some shallow root systems or meristematic tissue. The presence of Ashe juniper could have contributed to differences in fire severity between the two fires. Ashe juniper is most flammable during the winter and spring (Owens *et al.* 1998); large Ashe juniper trees were still absent from once-burned areas at the time of the second fire.

Although understory density was much higher after the second fire, overstory density (stems > 1.8 m) was more similar. This similarity suggests that shrub and liana species (which tend not to grow into the overstory) may be more abundant after the second fire, particularly on mesas, where overstory density in twice-burned areas was still lower than in nonburned areas in 2011. Bastard oak, which tends to grow as a large shrub or small tree, and poison ivy were both linearly correlated with an ordination axis.

Despite the changes in stem density, overall species composition in once- and twice-burned areas remained similar. This lack of change is not surprising, given that most of the woody species resprout. Sand shinnery oak communities, which are also dominated by resprouting species, similarly show little change in species composition after fire (Harrell *et al.* 2001).

The most noticeable difference in species composition was the almost complete absence of Ashe juniper from the burned areas. By 2005 (nine years after the first fire), overstory Ashe juniper density had reached 10 ± 10 stems ha^{-1} on slopes, with no overstory stems on mesas (compared with more than 1000

stems ha⁻¹ in nonburned areas). Recovery after the second fire proceeded even more slowly, with no Ashe juniper found three growing seasons after fire (vs. 21 ± 34 stems ha⁻¹ in 1998). These results suggest that fire plays an important role in determining the distribution and extent of Ashe juniper in the Edwards Plateau. Indeed, fire suppression has long been cited as a major cause of juniper expansion into grasslands (Foster 1917, Wills 2005), although, in some cases, juniper may simply be reclaiming areas from which it had been harvested (Diamond and True 2008, Murray *et al.* 2012). Dynamics of encroachment into grasslands, however, appear to differ from recolonization of burned woodlands. Fires in grasslands usually reduce juniper cover or density, but do not eliminate the species entirely (Rasmussen and Wright 1989, Noel and Fowler 2007), leaving some trees to serve as seed sources for further encroachment (Fuhlendorf *et al.* 1996, Johnson and Miller 2008). In contrast, the wildfires in our study burned large areas with few relict trees, greatly reducing seed availability. Others have found that Ashe juniper was absent for at least three years after fire (Gehlbach 1988) and that oaks have higher basal area than junipers in burned areas decades after fire (Yao *et al.* 2012). Competition from resprouting plants likely also played a role in limiting recolonization: Ashe juniper seedlings grow fastest in unshaded conditions (Jackson and Van Auken 1997, Van Auken *et al.* 2004).

Woodlands co-dominated by Ashe juniper were part of the pre-settlement vegetation of the Edwards Plateau, although their location and extent is debated (Amos and Gehlbach 1988, Diamond 1995, Wills 2005, Murray *et al.* 2012). Our results suggest that decades must have passed between crown fires in woodlands where Ashe juniper was dominant, and that the oldest woodlands are likely in fire-protected sites (mesic canyons or rocky areas with low fuel loads). Furthermore, repeated crown fires, at least at the interval observed here, do not appear to limit the distribution of other woody species. Thus, repeated fire could shift the community from an oak-juniper woodland to an oak-dominated shrubland, but such fires are unlikely to convert woodlands on shallow soils into oak savannas.

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