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Slow recolonization of burned oak–juniper woodlands by Ashe juniper (*Juniperus ashei*): Ten years of succession after crown fire

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Abstract

Fire is an important control on the distribution of plant communities on the Edwards Plateau in central Texas. Although the effects of fire in grasslands have been well studied, little is known about the recovery of mature oak–Ashe juniper (*Quercus* spp.–*Juniperus ashei*) woodlands after crown fire. These woodlands are the only nesting habitat of the endangered golden-cheeked warbler (*Dendroica chrysoparia*). In February 1996, crown fires burned more than 4000 ha of woodland on Fort Hood Military Reservation. Permanent transects were installed in moderately to severely burned areas on three soils types in 1996 and data were collected annually from 1996 to 2002 and again in 2005. We also sampled 36 transects in unburned areas on the same soil types in 2001 and 2005. Overall stem density (all species combined) in the burned areas recovered rapidly, at least in the smaller size classes (<1.8 m tall), and, by 2005, sapling stem density (>1.8 m tall, <5 cm dbh) was higher in burned areas than in unburned areas for all soil types (ANOVA, $p < 0.02$). Tree density (>5 cm dbh) in burned areas remained low until 2005 (2001: 20 ± 36 stems/ha; 2005: 326 ± 260 stems/ha). The dominant oak species recovered rapidly due to vigorous resprouting. Ashe juniper, a fire-sensitive species, recovered much more slowly. Only six Ashe juniper saplings (and no trees) were found in burned transects in 2005, compared to 646–871 trees/ha in unburned areas. Although Ashe juniper was largely absent from the burned areas, post-fire species composition was otherwise similar to unburned communities and became more similar with time (Sorenson similarity index in 1996: 0.70–0.83; 2005: 0.86–0.88). NMS ordination separated burned communities on different soils more than unburned communities, because all unburned areas were dominated by Ashe juniper. Due to the slow recovery of Ashe juniper, it will likely be decades before the burned areas are again suitable as breeding habitat for golden-cheeked warblers.
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Keywords: Oak–juniper woodlands; Crown fire; Ashe juniper; Succession; Edwards Plateau

1. Introduction

Fire plays an important role in controlling the local distribution of many plant communities (Romme, 1982; Trabaud and Galtie, 1996; Floyd et al., 2000; Miller and Tausch, 2000). In particular, fire is often thought to control transitions between grasslands and wooded communities (Smeins, 1980; Anderson and Brown, 1986; van Langevelde et al., 2003; Baker and Shinneman, 2005; Behling et al., 2007). Frequent fire usually favors grasslands and savannas, while less frequent fire allows the succession of open communities into woodlands and forests (Callaway and Davis, 1993; Miller et al., 2000; Behling et al., 2007). Fire may also maintain shrublands of fire-resistant species; lack of fire in such areas may allow fire-sensitive forests to invade (Floyd et al., 2000).

The vegetation in central Texas consists of both fire-dependent and fire-sensitive communities. Historical records indicate that grasslands and savannas were common, while woodlands and forests were generally confined to mesic canyons, riparian corridors and steep, rocky slopes (Smeins, 1980; Fonteyn et al., 1988). Diamond et al. (1995) recognized four oak–juniper woodland communities – the dominant woodland type – in central Texas. Live oak (*Quercus fusiformis*)–Ashe juniper savannas are found on deep, upland soils. Post oak (*Quercus stellata*)–blackjack oak (*Quercus marilandica*)–Ashe juniper communities occur on upland soils derived from silica-containing limestone and range from savannas to woodlands. Relatively frequent, low-intensity fires

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maintain these two communities as savannas; without fire, the abundance of Ashe juniper increases and the communities become woodlands or forests (Diamond et al., 1995; Diamond, 1997, personal observation). Shin oak (*Quercus sinuata* var. *breviloba*) and Ashe juniper co-occur on upland soils over massive limestone. Depending on soil depth and fire frequency, these communities can be shrublands or woodlands. The fourth community is found on slopes, in canyons, and along streams, and is comprised of Texas red oak (*Quercus buckleyi*) and other deciduous tree species that co-occur with Ashe juniper. Fire was largely absent from these mesic forests; crown fires would have occurred only after severe drought.

Mature examples of all four communities are used as nesting habitat for the golden-cheeked warbler (*Dendroica chrysoparia*), a federally endangered songbird (Kroll, 1980). Nesting habitat must include large junipers (the shredding bark is used for nest construction) as well as oaks and other deciduous species (Ladd and Gass, 1999). The historical abundance of nesting habitat was likely determined by fire: while all the oak species listed above resprout after being top-killed, Ashe juniper does not. Crown fires likely were a natural process in these communities, although data on their frequency and size are sparse, and little is known about the long-term effects of crown fires on these communities. Bray (1904) described a fire that burned for two days in July 1901, and destroyed ''many thousands of dollars' worth'' of juniper timber, but he does not specify the source of the fire. He also mentions that ''during the past 25 years far more cedar [juniper] timber has been burned than has been marketed''. Foster (1917) mentions that it is ''not unusual'' for burned juniper forests to be recolonized by juniper, but no timeframe for recovery is given. Huss (1954) found small junipers within 4 years after fire, but Ashe juniper did not become dominant until 26 years after fire. However, Huss studied grazed pastures, which may not be representative of post-fire succession in less disturbed communities. Gehlbach (1988) found no juniper 3 years after a crown fire in an undisturbed woodland, although Texas red oak and shin oak had resprouted vigorously within 5 months.

Fort Hood Military Reservation (Bell and Coryell counties, Texas) hosts one of the largest breeding populations of golden-cheeked warblers (Anders and Dearborn, 2004). In February 1996, three grass fires were ignited by military training activities. Following more than a year of below-average rainfall and fueled by high temperatures and strong winds, these fires spread into the adjacent oak–juniper woodlands, becoming crown fires. The fires, which burned for over 2 weeks, consumed more than 4000 ha of woodland, including 2108 ha of golden-cheeked warbler habitat (Goering, 1998; Anders and Dearborn, 2004). Since 1996, we have monitored succession in the burned areas to answer the following questions: (1) Did the physiognomy and species composition of these communities change after the fires? (2) Did plant communities on different soils respond similarly to the crown fires? (3) How long will it be before these areas are again suitable habitat for the golden-cheeked warbler?

2. Methods

2.1. Study area

Fort Hood Military Reservation is located in Bell and Coryell counties, in central Texas. It occupies 87,890 ha within the Lampasas Cut Plains, at the intersection of the Edwards Plateau and the Crosstimbers-Southern Tallgrass Prairies ecoregions (Olsen et al., 2001). A topographically complex area, Fort Hood features flat, steep-sided mesas, capped by Edwards limestone and separated by wide valleys. Historically, Fort Hood likely had a variety of vegetation communities, including tall- or mixed-grass prairies, oak savannas, oak shrublands, oak–juniper woodlands, riparian woodlands and forests and floodplain forests (Van Auken et al., 1979, 1980, 1981).

2.2. Sampling design

In the summer of 1996, we established 58 permanent transects in moderately to severely burned golden-cheeked warbler habitat. Burn severity was evaluated based on guidelines in the National Park Service Fire Monitoring Handbook (National Park Service, 1992). In moderately burned areas, foliage, twigs and small stems were consumed by the fire, and litter was burned to a coarse, light-colored ash. In severely burned areas, most of the vegetation was consumed, leaving only a few tree trunks, while litter was burned to a fine, white ash. Transects were located randomly on three soil types (Table 1): Evant silty clay (clayey, montmorillonitic, thermic, shallow petrocalcic paleustoll), Eckrant cobbly silty clay (clayey–skeletal, montmorillonitic, thermic lithic haplustolls) and Real gravelly clay loam (loamy–skeletal, carbonatic, thermic, shallow typic calciustolls). Seven more transects were added in 1997. In 2001, we added 36 transects in unburned oak–juniper woodlands, for a total of 101 transects. These 'control' transects were selected to represent mature communities on the same soils as the burned transects (Table 1). Data were collected from the burned areas every summer from 1996 to 2002, and in 2005. We sampled unburned transects in 2001 and 2005.

Table 1
Descriptions of transect stratification classes

Soil	Dominant oak species	Slope (°)	Number of transects	
			Burned	Unburned
Evant silty clay (Ev)	Post oak (*Quercus stellata*)	1–12	12	5
Eckrant-rock outcrop complex (Er)	Shin oak (*Q. sinuata* var. *breviloba*)	1–13	30	20
Real-rock outcrop complex (Re)	Texas red oak (*Q. buckleyi*)	5–42	23	11

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). Woody plant stem density (number of stems) was sampled using nested plots (25, 100 m^2). Plots were located at 10 m intervals along the right side of the transects and 7 of the 11 possible plots were randomly selected for sampling. From 1996 to 2002, the selected plots were re-randomized every year. In 2005, the locations from the first sampling year for each transect were used.

Stem density of all woody species were recorded in four categories: ''seedlings'' (<0.3 m tall), ''shrubs'' (between 0.3 and 1.8 m tall), ''saplings'' (≥1.8 m tall, <5 cm diameter at breast height (dbh)) and ''trees'' (>5 cm dbh). In the seedling size class, we could not distinguish resprouts from top-killed individuals and regeneration from seed. The stem density of seedlings, shrubs and saplings were counted in 5 m × 5 m plots. For multi-stemmed shrubs, stems that split above the root crown were counted as one. Saplings were divided into five dbh classes: 0–0.9, 1.0–1.9, 2.0–2.9, 3.0–3.9 and 4.0–4.9 cm. For multi-stemmed individuals, only the largest stem was measured and counted. Trees were sampled in 10 m × 10 m plots. From 1996 to 2002, we recorded the stem density of trees in 5- or 10-cm dbh classes. In 2005, dbh (to the nearest 0.1 cm) was recorded for each tree. If the trunk branched above the root crown, only the largest stem was measured and counted. Photos were taken at the beginning and end of each transect for visual reference.

2.3. Statistical analysis

Average stem density for each vegetation layer was analyzed using a repeated measures, linear mixed model ANOVA. All analyses used unstructured, autoregressive or autoregressive-moving average covariance structures; the structure with the lowest Akaike's information criterion (AIC) was selected for each vegetation layer. Basal area for sapling and pre-2005 tree data was calculated from the midpoints of dbh classes as basal area = $\pi(\text{dbh}/2)^2$. Average plot basal area was analyzed using the same procedure described above. Least squares means (lsmeans) of stem density and basal area were calculated for each year-soil combination. Burned and unburned transects were analyzed separately. For the 2005 density and basal area data, we conducted a separate general linear model ANOVA testing the effects of burn status and soil type. Lsmeans were calculated for each burn–soil combination. The 2005 density analysis was repeated for four important species: Ashe juniper, shin oak, post oak and Texas red oak. Data for post oak were analyzed only on Evant soils, because this species rarely occurs on other soil types. All analyses were conducted in SAS 9.1 (SAS Institute, 2003).

Next, we used ordination to examine whether communities on different soils could be separated based on species composition. We chose non-metric multidimensional scaling (NMS, executed in PC-ORD 4.34, MjM Software Design, Gleneden Beach, OR, USA) as our ordination technique because it is well suited to non-normal data (McCune and Grace, 2002). We used basal area for the ordination. Because many transects did not initially have saplings or trees, we converted shrub density into basal area by assuming that shrubs had a dbh of 0.1 cm. This value was added to any sapling or tree basal area present. The first ordination, which used Sorenson distance, examined only 2005 data. A three-dimensional ordination was chosen based on a Monte Carlo permutation test. After the ordination was complete, we rotated the axes to maximize correlation with slope. The second ordination, again using Sorenson distance, examined data from 1997 and 2005 to evaluate whether burned transects had become more similar to unburned areas. We used 1997 data instead of 1996, because not all burned transects were sampled in 1996. Again, a three-dimensional ordination was chosen.

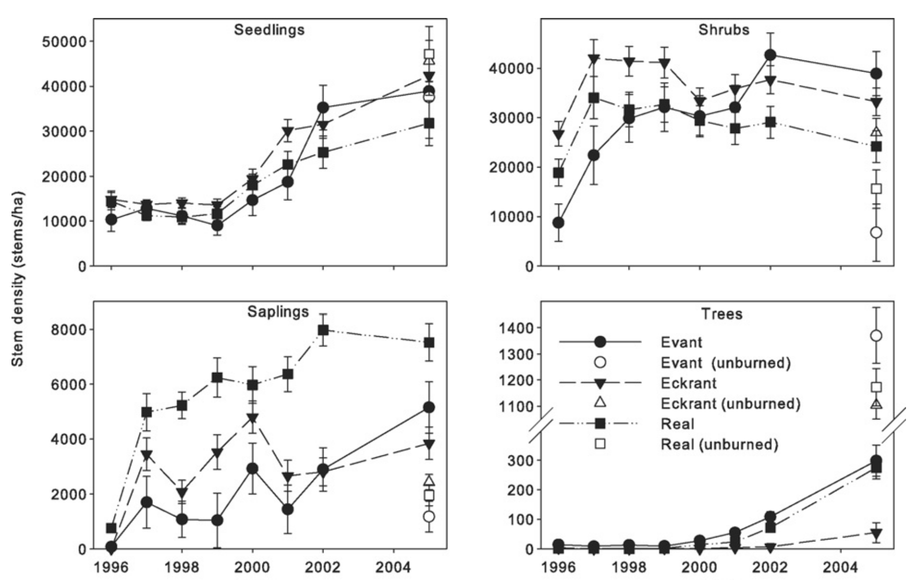

Fig. 1. Stem density in four vegetation strata on three soils. Seedlings were <0.3 m in height, shrubs were between 0.3 and 1.8 m in height, saplings were >1.8 m tall but <5.0 cm dbh and trees were >5.0 cm dbh. Evant soils are dominated by post oak (*Quercus stellata*), Eckrant soils are dominated by the shrubby shin oak (*Q. sinuata* var. *breviloba*) and Real soils are dominated by Texas red oak (*Q. buckleyi*). For unburned areas (open symbols), only data from 2005 are shown.

3. Results

3.1. Changes in physiognomy

Seedling density (of all species) followed a similar trajectory on all three soil types (Fig. 1). Density at the initial sampling varied between 10314 ± 2642 stems/ha (Evant soils) and 14863 ± 1782 stems/ha (Real soils). Seedling density increased most rapidly between 1999 and 2005. By 2005, seedling density in burned areas did not differ from density in unburned areas on any soil type ($F = 2.08$, d.f. = 1, $p = 0.15$).

Shrub density in 1996 was similar to that of unburned areas (Fig. 1). Density increased between 1996 and 1997, but then remained fairly constant until 2005, when density declined. In 2005, shrub density of burned areas on Evant soils was greater ($F = 4.26$, d.f. = 2, lsmeans $p < 0.001$) than shrub density of unburned areas. Although shrub density on Eckrant and Real soils appeared to be higher in the burned areas, this difference was not significant ($p = 0.11$ and $p = 0.10$, respectively).

Sapling density was initially low (<800 stems/ha on all soils), but increased rapidly between 1996 and 1997 (Fig. 1). Sapling density on Real soils was consistently higher than sapling density on Evant or Eckrant soils. In 2005, sapling density of burned areas was higher than density of unburned areas for all three soil types ($F = 4.11$, d.f. = 2, $p = 0.02$).

Tree density remained below 110 trees/ha until 2005 (Fig. 1). In 2005, tree density was highest on Evant soils (299 ± 53 trees/ha) and lowest on Eckrant soils (55 ± 34 trees/ha). Tree density was lower in burned areas for all soil types ($F = 206.71$, d.f. = 1, $p < 0.0001$).

Basal area was initially highest on Evant soils, due to a few trees that survived the fire (Fig. 2). By 2000, basal area on Real soils had surpassed that on Evant soils. Basal area was consistently lowest on Eckrant soils. In 2005, basal area of burned areas was lower than basal area of unburned areas for all soil types ($F = 525.38$, d.f. = 1, $p < 0.001$ for all).

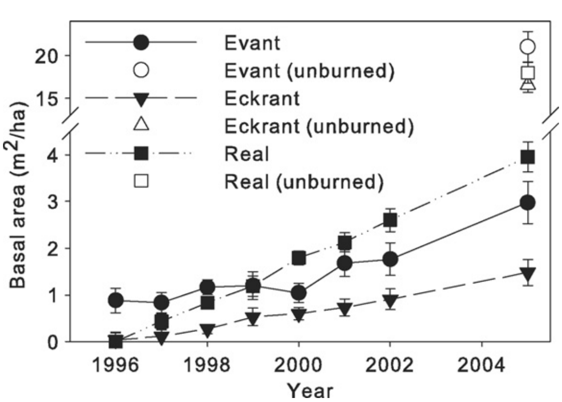

Fig. 2. Basal area of saplings and trees for all species. Evant soils are dominated by post oak (*Quercus stellata*), Eckrant soils are dominated by the shrubby shin oak (*Q. sinuata* var. *breviloba*) and Real soils are dominated by Texas red oak (*Q. buckleyi*). For unburned areas (open symbols), only data from 2005 are shown.

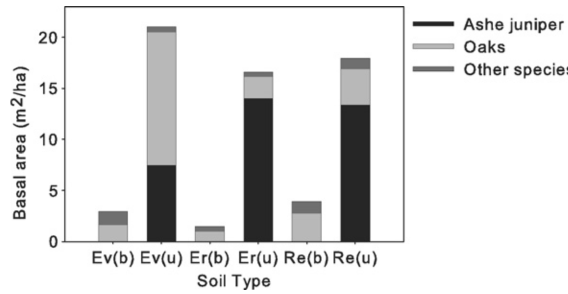

Fig. 3. Comparison of 2005 basal area (sapling and tree strata) in burned (b) and unburned (u) areas. Evant soils (Ev) are dominated by post oak (*Quercus stellata*), Eckrant soils (Er) are dominated by the shrubby shin oak (*Q. sinuata* var. *breviloba*) and Real soils (Re) are dominated by Texas red oak (*Q. buckleyi*). Ashe juniper (*Juniperus ashei*) is abundant in all unburned sites.

3.2. Changes in species composition

In 2005, Ashe juniper was still almost completely absent from the burned areas (Fig. 3). In contrast, juniper basal area in the unburned areas ranged from 7.5 m^2/ha (Evant soils) to 14 m^2/ha (Real soils). In the burned areas, non-oak species made up a greater percentage of the basal area than they did in unburned areas. On Evant soils, oak dominance (percentage of basal area, excluding Ashe juniper) declined from 96 to 56%. Smaller differences were found on Eckrant and Real soils, where oak dominance (again excluding Ashe juniper) dropped from 83 to 67% and from 77 to 70%, respectively.

NMS ordination distinguished between burned and unburned transects, but communities on different soils were less well separated (Fig. 4). For this ordination, final stress (a measure of departure from monotonicity) and instability of the three-dimensional solution were 13.4 and 0.000008. Slope was positively correlated with axis 1 (Table 2). Texas red oak, which is generally found on slopes, was also correlated with axis 1. Axis 3 appeared to be a successional gradient: Ashe juniper, which is characteristic of mature communities, was strongly positively correlated with axis 3, while flameleaf sumac (*Rhus lanceolata*)

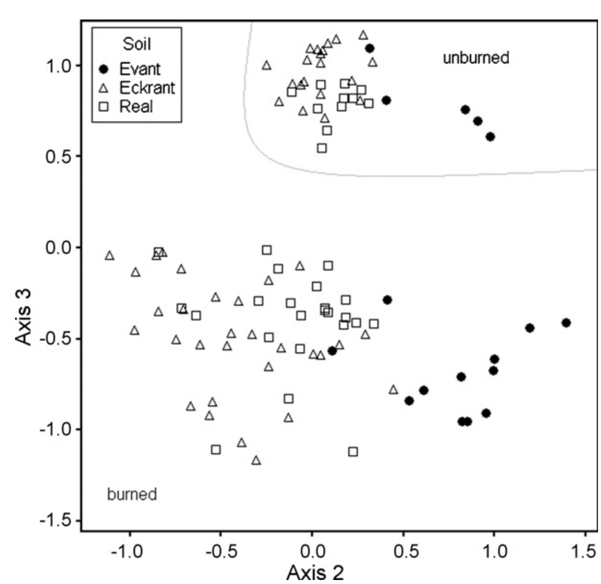

Fig. 4. NMS ordination of 2005 basal area (saplings and trees).

Table 2
Linear (Pearson's r) and rank (Kendall's tau) correlations between slope, select plant species and NMS ordination axes for 2005 data

Variable	Axis 1		Axis 2		Axis 3	
	r	tau	r	tau	r	tau
Slope	**0.58**[a]	**0.42**	0.02	0	0.4	−0.1
Ashe juniper (*Juniperus ashei*)	–[b]	–	–	–	**0.89**	**0.53**
Texas red oak (*Quercus buckleyi*)	**0.76**	**0.65**	–	–	0.10	0.04
Shin oak (*Q. sinuata* var. *breviloba*)	−0.06	−0.03	**−0.34**	**−0.48**	–	–
Post oak (*Q. stellata*)	–	–	**0.37**	**0.45**	0.16	−0.18
Blackjack oak (*Q. marilandica*)	–	–	**0.48**	**0.44**	–	–
Flameleaf sumac (*Rhus lanceolata*)	0.19	0.12	0.32	0.01	**−0.52**	**−0.58**
Catbrier (*Smilax bona-nox*)	–	–	0.56	0.28	–	–
Poison ivy (*Toxicodendron radicans*)	0.01	0.15	−0.12	−0.18	**−0.44**	**−0.34**

[a] The strongest correlation for each variable is in bold.
[b] Correlations are not shown when the relationship between a variable and an axis was humped.

Table 3
Linear (Pearson's r) and rank (Kendall's tau) correlations between slope, select plant species and NMS ordination axes for 1997 and 2005 data

Variable	Axis 1		Axis 2		Axis 3	
	r	tau	r	tau	r	tau
Slope	0.16	0.17	0.20	0.08	**0.39**	**0.28**[a]
Ashe juniper (*Juniperus ashei*)	−0.44	−0.48	**0.83**	**0.68**	–	–[b]
Texas red oak (*Quercus buckleyi*)	–	–	**0.42**	0.32	**0.42**	**0.43**
Shin oak (*Q. sinuata* var. *breviloba*)	–	–	**0.43**	**0.29**	−0.25	−0.25
Post oak (*Q. stellata*)	**−0.40**	**−0.38**	–	–	–	–
Flameleaf sumac (*Rhus lanceolata*)	−0.20	0.12	–	–	**0.53**	**0.46**

[a] The strongest correlation for each variable is in bold.
[b] Correlations are not shown when the relationship between a variable and an axis was humped.

and poison ivy (*Toxicodendron radicans*), which are more common in early successional areas, were negatively correlated with axis 3. Post oak and blackjack oak, the dominant species on Evant soils, were positively correlated with axis 2, while shin oak was negatively correlated with axis 2.

Burned areas appeared to become more similar to unburned areas over time (Fig. 5, NMS ordination final stress: 12.7; instability: 0.00001). Ashe juniper was somewhat negatively correlated with axis 1 and strongly positively correlated with axis 2 (Table 3); unburned transects were clustered in the upper left corner of the graph. Flameleaf sumac was correlated with axis 3. Sorenson similarity indices also increased from 1996 to 2005 (Table 4).

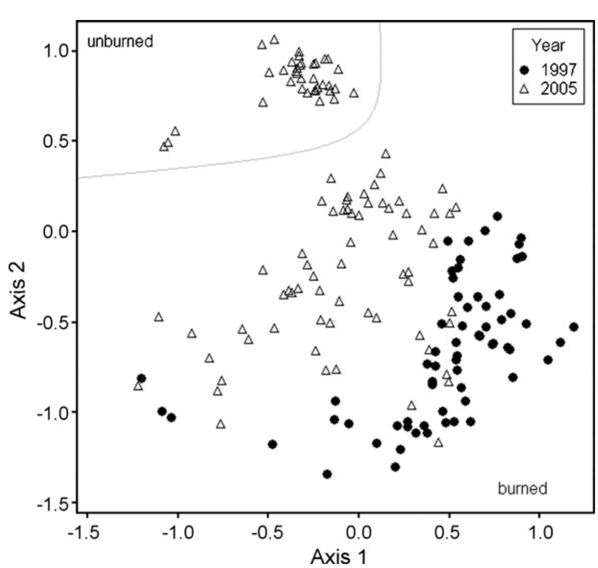

Fig. 5. NMS ordination of basal area data (shrubs, saplings and trees) from 1997 (closed circles) and 2005 (open triangles). Data were not collected in unburned areas in 1997.

3.3. Regrowth of important species

Ashe juniper seedling density remained low throughout the study period (Fig. 6). In 2005, seedling density in the burned areas (across all soil types) was 76 ± 267 seedlings/ha, compared with 6192 ± 389 seedlings/ha in the unburned areas ($F = 168.19$, d.f. = 1, $p < 0.0001$). Shrub density in 2005 on Eckrant and Real soils was lower than on unburned soils ($F = 3.68$, d.f. = 1, lsmeans $p < 0.0001$ for both), but not on Evant soils (lsmeans $p = 0.07$).

Table 4
Number of species in burned and unburned areas by soil type (in 2005)

Soil	Burned		Unburned	Sorenson similarity index[a]	
	1996	2005	2005	1996	2005
Evant	23	31	25	0.83	0.86
Eckrant	26	44	40	0.70	0.88
Real	26	49	42	0.71	0.86

[a] Sorenson similarity compares species composition in burned areas in 1996 and 2005 to unburned areas in 2005.

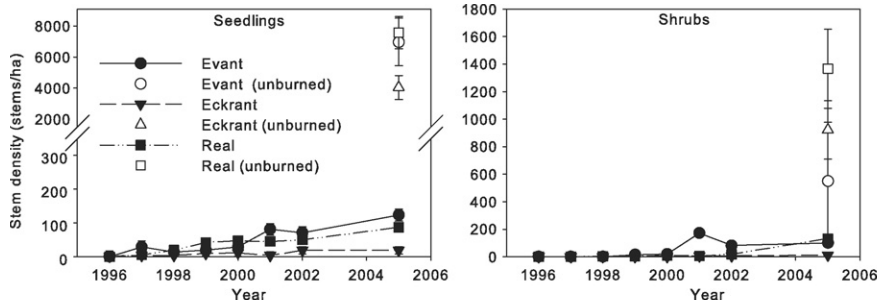

Fig. 6. Ashe juniper (*Juniperus ashei*) stem density in two vegetation strata on three soils. Seedlings were <0.3 m in height, shrubs were between 0.3 and 1.8 m in height, saplings were >1.8 m tall but <5.0 cm dbh and trees were >5.0 cm dbh. Sapling and tree data are not shown, because only six saplings and no trees were found in 2005. For unburned areas (open symbols), only data from 2005 are shown.

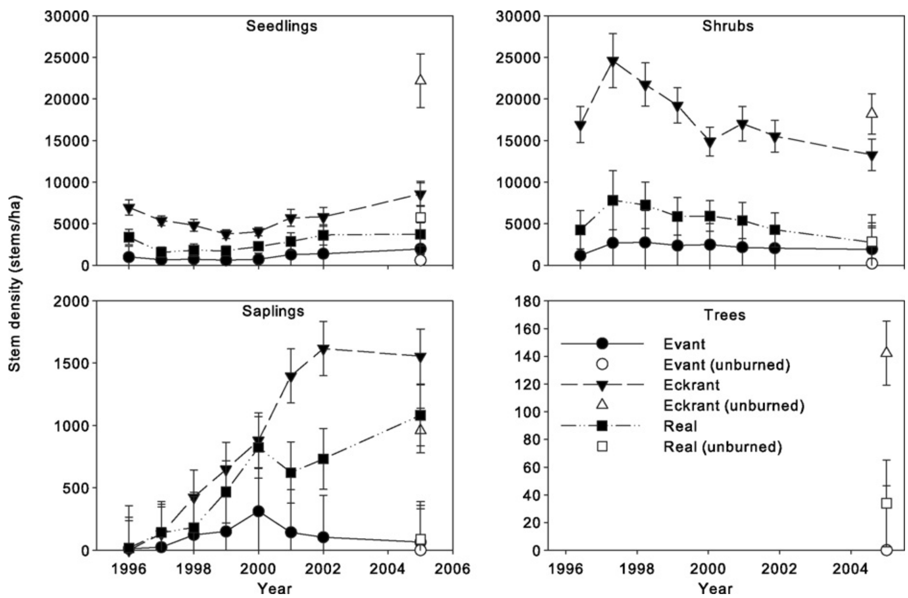

Fig. 7. Shin oak (*Quercus sinuata* var. *breviloba*) stem density in four vegetation strata on three soils. Seedlings were <0.3 m in height, shrubs were between 0.3 and 1.8 m in height, saplings were >1.8 m tall but <5.0 cm dbh and trees were >5.0 cm dbh. No trees were found in the burned areas in any year. For unburned areas (open symbols), only data from 2005 are shown.

Shin oak seedling density on Evant and Real soils returned to pre-burn levels within a growing season (Fig. 7), but remained low on Eckrant soils (8936 ± 2004 seedlings/ha versus 22180 ± 2414 seedlings/ha; $F = 3.60$, d.f. = 1, $p = 0.03$). Shrub and sapling density in 2005 were similar in burned and unburned areas (shrubs: $F = 0.25$, d.f. = 1, $p = 0.61$; saplings: $F = 2.26$, d.f. = 1, $p = 0.14$), but no resprouts had reached the tree size class.

Seedling density of post oak in 2005 was much lower in burned than in unburned areas (Fig. 8; $F = 11.83$, d.f. = 1, $p = 0.002$). Shrub density was initially higher in burned areas and then declined to 2005 levels as resprouts grew into the sapling size class. Tree density in burned areas remained low in 2005 (51 ± 67 trees/ha versus 435 ± 113 trees/ha; $F = 8.52$, d.f. = 1, $p = 0.007$).

Seedling density of Texas red oak on Eckrant and Evant soils returned to pre-burn levels soon after the fire (Fig. 9); in 2005, seedling density on Real soils was still much lower in the burned areas (1758 ± 539 seedlings/ha versus 9678 ± 780 seedlings/ha; $F = 17.86$, d.f. = 2, $p < 0.0001$). Shrub density was initially higher on Real soils, but quickly dropped as the resprouts grew into the sapling size class. Sapling density on Real soils in 2005 was higher in burned areas (3153 ± 196 saplings/ha) than in unburned areas (758 ± 284 saplings/ha; $F = 13.41$, d.f. = 2, $p < 0.0001$). Tree density remained low until 2005, when density returned to pre-burn levels for all soils ($F = 0.25$, d.f. = 1, $p = 0.6$). Basal area, however, remains much lower in the burned areas (Fig. 2).

4. Discussion

4.1. Recovery of Ashe juniper

In 2005, the 10th growing season after the fire, Ashe juniper abundance in the burned areas was still very low. While studies in Colorado have also observed delayed recovery of fire-sensitive juniper species (*Juniperus osteosperma* and *Juniperus scopulorum*) after crown fires (Floyd et al., 2000), we were somewhat surprised by the slow recolonization of Ashe juniper, because this species readily invades grassland and savanna

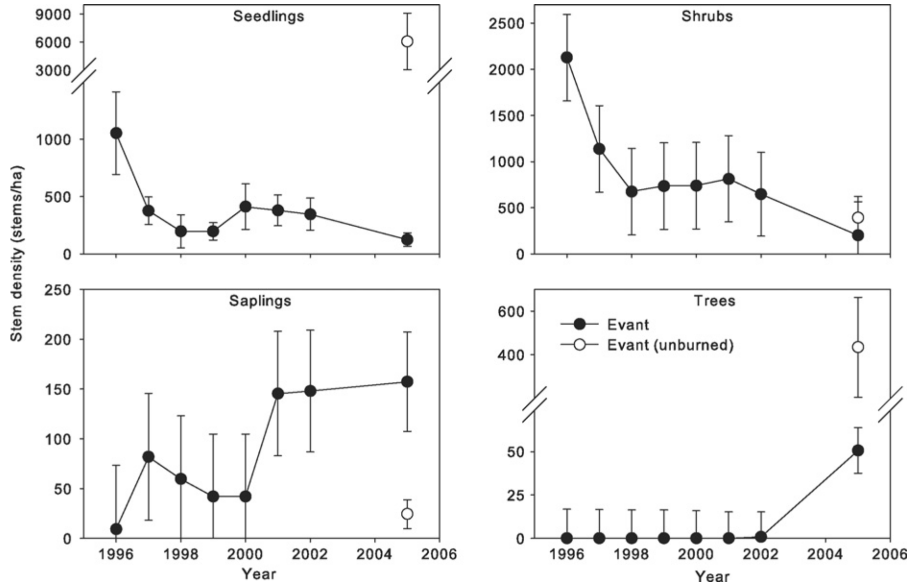

Fig. 8. Post oak (*Quercus stellata*) stem density in four vegetation strata on three soils. Seedlings were <0.3 m in height, shrubs were between 0.3 and 1.8 m in height, saplings were >1.8 m tall but <5.0 cm dbh and trees were >5.0 cm dbh. Only data from Evant soils are shown; post oak was only rarely found on Eckrant or Real soils. For unburned areas (open symbols), only data from 2005 are shown.

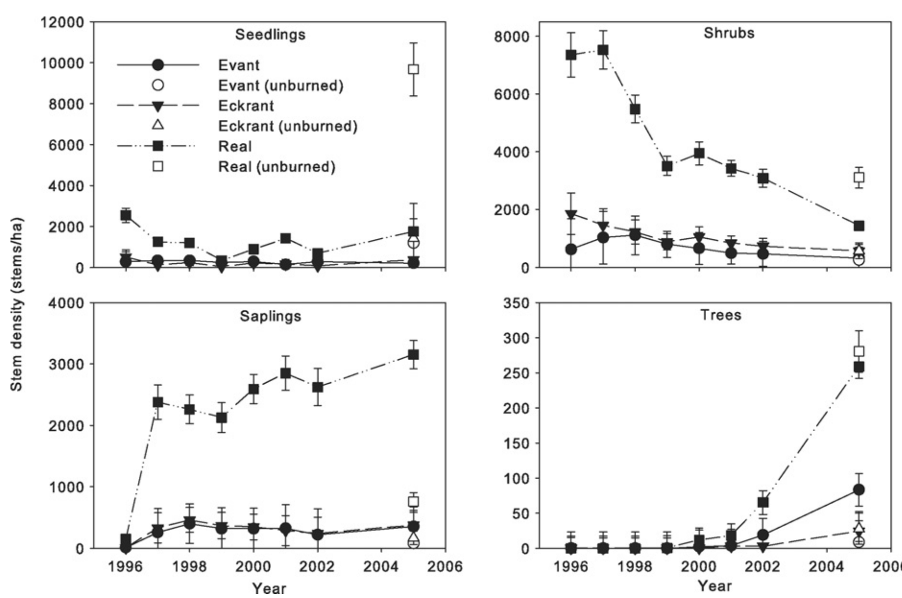

Fig. 9. Texas red oak (*Quercus buckleyi*) stem density in four vegetation strata on three soils. Seedlings were <0.3 m in height, shrubs were between 0.3 and 1.8 m in height, saplings were >1.8 m tall but <5.0 cm dbh and trees were >5.0 cm dbh. For unburned areas (open symbols), only data from 2005 are shown.

communities when fire is removed. For example, Rasmussen and Wright (1989) found Ashe juniper stem densities of 74–734 stems/ha in pastures 8–14 years after prescribed fire and about 25% of trees were taller than 1 m. Similarly, a model developed by Fuhlendorf et al. (1996) indicated that a grassland would become a closed-canopy juniper woodland in 75 years with no fire. McLemore et al. (2004) found that a former prairie had been converted into an Ashe juniper woodland in about 70 years. In contrast, after 10 years, we found stem densities of just over 200 stems/ha on Evant and Real soils, and only 30 stems/ha on Eckrant soils (Fig. 6). Only six individuals were taller than 1.8 m. A similar lack of juniper regeneration has been observed after other crown fires on Fort Hood (C. Reemts and L. Hansen, personal observation).

This slow recolonization can be attributed to several factors. Ashe juniper seeds usually germinate in late winter and early spring (Van Auken et al., 2004), so the intense crown fires in February killed that year's seedling crop. Furthermore, juniper seeds appear to be fire-sensitive. In our study, the first juniper seedlings were not found until 1997 (Fig. 6).

The extent of the crown fire may also have slowed the re-introduction of Ashe juniper seeds. While some trees remained in less severely burned parts of the crown fires, relict trees, which could serve as local seed sources, were absent from our sample areas. Juniper seeds are dispersed by several species of birds and mammals (Chavez-Ramirez and Slack, 1993, 1994). While mammals can carry seeds for great distances, they often deposit seeds in unfavorable locations (along trails) and in clumps that are vulnerable to seed predators (Chavez-Ramirez and Slack, 1993). Cedar waxwings (*Bombycilla cedrorum*), one of the dominant bird dispersers, also deposits seeds in clumps under flock roosting sites. The colonization rate at our site may increase now that a few sapling-sized juniper individuals are present within the burned area: trees begin producing seeds when 1–1.5 m in height (Smeins and Fuhlendorf, 1997).

Finally, competition from resprouting species probably limited seedling growth. Ashe juniper seedling establishment and survival are highest in shaded conditions, but growth is greatest at canopy edges and in grasslands (Smeins and Fuhlendorf, 1997; Van Auken et al., 2004). Thus, juniper growth was likely inhibited by the dense regrowth of oaks. This hypothesis is supported by the low density of juniper seedlings and shrubs on Eckrant soils (Fig. 6), which had the highest stem densities (Fig. 1).

4.2. Changes in species composition and physiognomy

Differences in species composition among soils were greater in burned than in unburned areas (Fig. 4), reflecting the dominance of Ashe juniper in unburned communities (Fig. 3). However, even in burned areas, NMS ordination did not clearly distinguish among communities on different soils. The overlap was especially great between Eckrant and Real soils, likely because these two soil types are usually found adjacent to each other and share many species. Shin oak, for example, is most abundant on Eckrant soils, but is also commonly found on Real soils (Fig. 7). Transects on Evant soils were better separated because post oak and blackjack oak are found almost exclusively on this soil type (Amos and Gehlbach, 1988).

Recovery on each soil type generally followed the trajectory of the dominant oak species (Figs. 1, 7–9). For example, sapling density on Real soils was consistently higher than on other soils, in part because Texas red oak resprouts vigorously after fire. Gehlbach (1988) noted this vigorous sprouting of Texas red oaks after fire: within 5 months after a crown fire, he counted 39.5 ± 15.9 stump and root sprouts around burned individuals. Furthermore, Real soils are also more mesic than Evant or Eckrant soils, enabling many species to grow rapidly: possumhaw holly (*Ilex decidua*), shin oak, flameleaf sumac and Texas ash (*Fraxinus texensis*) were also abundant in 2005. On Eckrant soils, shin oak contributed 63% of the initial shrub density. Other abundant species included live oak, poison ivy, Texas red oak and Texas ash. By 2005, the most common species were shin oak, flameleaf sumac, Texas ash, live oak and Texas red oak. While Gehlbach (1988) found that shin oak initially had fewer resprouts than Texas red oak, more of the resprouts survived after 30–50 years, suggesting that communities on Eckrant soils will retain their high stem density for longer than communities on Real or Evant soils.

Fonteyn et al. (1988) suggested that a mixed-oak savanna that had been converted to a dense Ashe juniper–oak woodland by fire exclusion could be reverted to a savanna by a single, intense summer fire. Although Ashe juniper might be eliminated, or at least greatly decreased, by such a fire, our study suggests that multiple fires are necessary for the conversion of a woodland to a savanna because the density of resprouting species must be reduced. Tree density (Fig. 1) and basal area (Fig. 2) are still much lower than in unburned areas, but the high density of saplings suggests that the burned areas will again become woodlands. Even in transects on Evant soils, which are most similar to the communities Fonteyn et al. (1988) describe, sapling stem density in burned areas was more than four-fold that of unburned areas (5153 ± 934 stems/ha versus 1177 ± 565 stems/ha). Similarly, Trabaud and Galtie (1996) describe how recurring wildfires convert oak-dominated forests into shrublands. Frequent, repeated fires are necessary before resprouting oaks are negatively affected (Diaz-Delgado et al., 2002; Delitti et al., 2005), although high-intensity fires can reduce the proportion of individuals of a particular species that resprout (Penfound, 1968). Vulnerability to repeated fire depends on the species: sand shinnery oak (*Quercus havardii*) showed no effects from two fires only 2 years apart (Harrell et al., 2001). Decades of annual summer burning were required to reduce hardwood density in loblolly pine (*Pinus taeda*) stands (Waldrop et al., 1992).

NMS ordination suggests that the burned areas are becoming more similar to the unburned areas with time (Fig. 5). This increasing similarity is not surprising, since there was a large overlap in species composition between the burned and unburned areas even in 1996 (Table 4). As more late-successional species colonized the burned areas, the overlap in species composition increased. The greatest differences between burned and unburned areas are now the relative abundance of species and the much lower basal area in the burned areas.

4.3. Implications for golden-cheeked warblers

The 1996 crown fires burned approximately 15% of the golden-cheeked warbler habitat on Fort Hood (Goering, 1998; Anders and Dearborn, 2004). In the second breeding season following the fire (1997), the relative abundance of golden-cheeked warblers in one of the burned areas declined by more than 80%, with the remaining birds restricted to unburned remnants within the burned area (Baccus et al., 2007). In 2005, golden-cheeked warbler density in that area was still around 1997 levels. Because of the slow recovery of Ashe juniper, the burned areas will likely not host large numbers of golden-cheeked warblers for several more decades. However, overall golden-cheeked warbler populations on Fort Hood were not greatly affected by the fires (Anders and Dearborn, 2004), perhaps because the birds relocated to available habitat elsewhere on post (Baccus et al., 2007).

Crown fires were likely a natural, if infrequent, occurrence in these habitats, since they are often surrounded by frequently burned grasslands and savannas (Bray, 1904; Diamond, 1997).

However, increased urban development in much of the range of the golden-cheeked warbler has caused fragmentation and destruction of mature oak–juniper woodlands, threatening the recovery of the warbler (Kroll, 1980; Diamond et al., 1995). For this reason, crown fires in existing golden-cheeked warbler habitat should be suppressed.

5. Conclusion

Historical accounts indicate that crown fires were likely a natural occurrence in Ashe juniper–oak woodlands and that fire restricted these communities to relatively protected slopes and canyons, as well as rocky areas with low fine fuel loads (Bray, 1904; Diamond, 1997). Our data suggest that infrequent, high-severity fires could have controlled the distribution of Ashe juniper, but not of most other woody species. Because most deciduous species resprout vigorously after fire, multiple, high-intensity fires would have been necessary to convert dense woodlands into open savannas. Because Ashe juniper, a critical component of golden-cheeked warbler nesting habitat, recolonizes burned areas very slowly and because remaining mature woodlands are threatened by development, these communities should be protected from crown fire.

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