

Effects of Fire and Neighboring Trees on Ashe Juniper

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Abstract

The survival of Ashe juniper (*Juniperus ashei* Buchh.) plants of all sizes was compared between paired burned and unburned plots in four savanna sites on the eastern Edwards Plateau. Smaller plants were less likely to survive a fire than larger plants, over the entire range of plant sizes. Overall fire survival rates varied from ~45% (0- to 50-cm-tall plants) to ~92% (> 2-m-tall plants). The high rate of survival of small plants indicates that fires like those typically used in this region are not likely to control even the early stages of the encroachment of Ashe juniper. If fire is to be used to maintain savannas in this region, multiple burns, more intense fires, or supplementary mechanical removal will probably be needed. Junipers 0 to 200 cm tall were significantly more likely to be growing under the canopy of a tree (defined as a plant > 2 m tall of any species) than in the open. Small (0 to 50 cm tall) junipers under a tree canopy were significantly more likely to be alive than plants in the same size class growing in the open, suggesting facilitation of small Ashe juniper by neighboring trees. There was, however, no significant effect of neighboring trees on the rate at which small Ashe juniper survived fire, contrary to our initial expectation.

Resumen

Se comparó la probabilidad de sobrevivir de individuos de *Juniperus ashei* Buchh. de todos los tamaños en parcelas quemadas y en parcelas no quemadas en cuatro sitios de estudio en la porción este de la Meseta Edwards. En todo el rango de tamaños, las plantas pequeñas mostraron menor probabilidad de sobrevivir a las quemaduras comparadas con las plantas de mayor tamaño. En general, la probabilidad de sobrevivir a las quemaduras varió de aproximadamente 45% (plantas de 0 a 50 cm de altura) hasta 92% (plantas > 2 m) indicando que el tipo de quemaduras típicamente utilizados en esta región probablemente no es lo suficientemente efectivo para controlar la expansión de *J. ashei*, ni siquiera en los primeros estadios de colonización. Si se utilizan quemaduras para el mantenimiento de las sabanas en esta región, probablemente será necesario aplicarlas con mayor frecuencia, así como provocar fuegos de mayor intensidad o complementar con la remoción mecánica de *J. ashei*. Las plantas de 0 a 200 cm se encuentran con una frecuencia significativamente mayor debajo de la copa de otros árboles (árboles se definen en este estudio como plantas de más de 2 m de altura de cualquier especie) que en la matriz herbácea. Las plantas pequeñas (0–50 cm de altura) de *J. ashei* que se encontraban bajo la copa de árboles tenían una probabilidad significativamente mayor de encontrarse vivas comparadas con las plantas del mismo tamaño que se encontraban en la matriz herbácea, hecho que sugiere una interacción de facilitación hacia las plantas pequeñas por parte de los árboles vecinos. Sin embargo, contrario a nuestras expectativas, en este estudio no se encontró un efecto significativo de la presencia de árboles vecinos en la probabilidad de sobrevivir de las plantas pequeñas de *J. ashei* a la aplicación de fuego.

Key Words: Edwards Plateau, facilitation, fire survival, *Juniperus ashei*, survival rates, Texas

INTRODUCTION

Many factors are thought to be responsible for maintaining savannas, including fire, herbivory, and certain patterns of rainfall and plant water uptake (e.g., Knoop and Walker 1985; Dublin et al. 1990; Laycock 1991; Higgins et al. 2000). However, at present many savannas and grasslands are undergoing “woody plant encroachment,” that is, an increase in the proportion of area under the canopies of woody species (McPherson 1997; Scholes and Archer 1997; Van Auken 2000). Well-known examples include the spread of eastern red cedar (*Juniperus virginiana* L.) into former tallgrass

grasslands (e.g., Hoch and Briggs 1998; Briggs et al. 2002), the conversion of south Texas savannas into woodlands dominated by honey mesquite (*Prosopis glandulosa* Torr.; Archer et al. 1988; Archer 1989, 1995), and the expansion of pinyon pine–juniper woodlands in the western United States (e.g., Blackburn and Tueller 1970; Eddleman 1987; Knapp and Soule 1998; Brockway et al. 2002).

Increases in the cover of juniper species are converting formerly more open vegetation to woodland in at least three different ecosystems in central Texas. On the eastern Edwards Plateau, increases in the number and size of Ashe juniper (*Juniperus ashei* Buchh.) plants rapidly convert live oak (*Quercus fusiformis* Small) savannas to woodlands unless they are actively managed to prevent this (Buechner 1944; Smeins and Merrill 1988; Van Auken 1993; Smeins et al. 1997; Jessup et al. 2003). Increases in red-berry juniper (*Juniperus pinchotii* Sudworth) on the western Edwards Plateau and eastern red cedar to the east of the Edwards Plateau also create woodlands in sites that formerly had more open vegetation (McPherson

Funding was provided by the University of Texas and Sigma Xi to J.M.N.

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Manuscript received 11 June 2006; manuscript accepted 24 August 2007.

et al. 1988; McPherson and Wright 1990; Kramer and Rykiel 1996). It is thought that the increase in the abundances of these juniper species in central Texas is primarily due to domestic stock grazing, which reduces competition from grasses, and to the concurrent reduction in fire frequency and fire intensity (Smeins 1980; Fonteyn et al. 1988; Fuhlendorf et al. 1996; Fuhlendorf and Smeins 1997), although the increase in atmospheric CO₂ concentration might also play a role (Archer et al. 1995; Polley 1997).

At present, the primary methods of stopping and reversing Ashe juniper encroachment are mechanical, despite issues of cost and, in some sites, soil erosion (Hamilton et al. 2004). There is considerable interest in using surface fires in place of mechanical methods to maintain savannas in this region, both by ranchers and by conservation land managers (Ueckert 1997; Lyons et al. 1998; Hamilton et al. 2004; C. Sexton, personal communication, July 2000).

Under what conditions can fires maintain savanna vegetation in central Texas? This study addressed this question by examining the effects of surface fires on Ashe juniper in four savannas of the eastern Edwards Plateau. These four fires were representative of current fire usage in this region in being winter burns of relatively low intensity. Prior to this study, it was known that surface fires kill some proportion of small Ashe juniper plants (Wink and Wright 1973; Ueckert 1980; Fonteyn et al. 1988), but the effectiveness of surface fires on Ashe juniper plants of different sizes had not been quantified. We expected to find that fire survival rates were positively correlated with plant size, so that only among small plants would a substantial proportion be killed. Although the first prediction was upheld, the second was not, as we discuss below.

The present study also tested the hypothesis that the effects of a surface fire upon an Ashe juniper individual depend on the presence of a larger neighboring tree. Because both the characteristics and the amount of fuel for a surface fire can differ between open grassy areas and areas under trees in these savannas (Fonteyn et al. 1988; Fuhlendorf et al. 1997), it seemed likely that mortality rates of small juniper plants would differ between these two phases of the spatial mosaic, with higher survival rates under trees due to the lack of grass and other herbaceous vegetation there.

METHODS

We located four study sites on the eastern Edwards Plateau that had comparable burned and unburned areas (Table 1). In each site, the burned area had recently had a prescribed winter fire. These were low intensity fires (Table 2) that left even very small Ashe juniper plants intact and easily measured. Two were headfires (Balcones and Hill Country) and two were backfires (Pace Bend and Pedernales); backfires are common in this region, despite, or because of, their low intensity, which makes them easy to control. The dominant woody species in these sites included Ashe juniper, Plateau live oak, and (in the Pace Bend and Pedernales Falls sites only) honey mesquite (*Prosopis glandulosa* Torr.). Both the woody and the herbaceous vegetation of these sites were typical of savannas of this region (Fowler and Dunlap 1986; Van Auken 1988). Common

herbaceous species in the study sites included the native grasses little bluestem (*Schizachyrium scoparium* [Michx.] Nash.), Texas wintergrass (*Nassella leucotricha* Trin. & Rupr.), various *Bouteloua* (grama) and *Aristida* (three awn) species, and the invasive nonnative grass King Ranch bluestem (*Bothriochloa ischaemum* [L.] Keng).

In each of the four sites, two circular 1-ha plots, one burned and one unburned but otherwise as similar as possible, were selected, for a total of eight 1-ha plots. Within each 1-ha plot, the height and species of every plant taller than 2 m (referred to henceforth as “trees”) were recorded. The position of each tree in the plot and whether it was dead or alive was also recorded.

Within each 1-ha plot Ashe juniper ≤ 2 m tall were sampled at two scales. Thirty medium-sized circular subplots (radius = 5.25 m, area = 86.6 m², hereafter referred to as 86-m² subplots) were randomly located in each of the eight 1-ha plots. Four hundred small-sized subplots (radius = 0.28 m, area = 0.25 m², hereafter referred to as 0.25-m² subplots) were also randomly located in each of the eight 1-ha plots, independent of the locations of the 86-m² subplots. If a subplot of either size fell on a road or brush pile, it was discarded and replaced by another randomly located subplot of the same size. Within each of the 86-m² subplots, the height of each Ashe juniper plant between 50 cm and 200 cm tall and whether it was alive or dead were recorded. Within each of the 0.25-m² subplots, the height of each Ashe juniper plant less than 50 cm and whether it was alive or dead were recorded. There was some overlap of subplots within a plot, especially between different 86-m² subplots, but plant densities were sufficiently low (see below) that no plants were counted twice.

To estimate the effect of tree canopies on the spatial arrangement and survival of smaller Ashe juniper plants, the canopy radius of each tree between 2 m and 3 m tall was assumed to be 1.5 m (i.e., it was assumed to have a circular canopy 3 m in diameter). The canopy radius of trees 3 to 4 m tall was assumed to be 2 m, and the canopy radius of trees 4 to 6 m tall was assumed to be 2.5 m. ArcView GIS (version 3.2a; ESRI, Redlands, CA) was used to produce a map of each 1-ha plot. These maps were used to estimate the proportion of each 1-ha plot covered by one or more tree canopies of any species, and the proportion of each 86-m² subplot that was under one or more tree canopies of any species. The area of each 86-m² subplot under one or more tree canopies was divided by the total area of the subplot, yielding the proportion of that plot under tree canopy. Each 0.25-m² subplot was simply classified as “under a tree canopy” if its center point fell under one or more canopies, or “in the open” if its center point did not fall under a tree canopy.

The proportion of plants alive in a burned plot is not equal to the fire survival rate in that plot, because plants also die for other reasons, as shown by the presence of dead plants in the unburned plots. Even in the unburned plots, the proportion of plants alive is not necessarily equal to the survival rate. (For example, the survival rate would be overestimated if dead plants had disappeared before counting.) Therefore, the rate at which plants survived fire (fire survival rate) was calculated by dividing the observed number of plants that survived in the burned plot(s) by an estimate of the number of plants that would have survived in the burned plot(s) had there been no fire. The number of expected survivors in the absence of fire

Table 1. Characteristics of the study sites. Each site had a burned plot and an unburned plot. Soil types according to Werchan et al. (1974; Travis County), Dittmar et al. (1977; Medina County), and Dittmore and Allison (1979; Blanco County).

Land unit	County	Latitude/Longitude	Distance between plots	Sampling date	Soil	Last grazed
Balcones Canyonlands National Wildlife Refuge, Martin (burned) and Old Salem (unburned) Tracts (US Fish and Wildlife Service)	Travis	burned plot: 30°31'1.6"N 98°01'25.9"W	1 360 m	July 2000	Brackett	1999
		unburned plot: 30°30'19.4"N 98°01'25.9"W		July 2000		1997
Hill Country State Natural Area (Texas Parks and Wildlife Department)	Medina/Bandera	burned plot: 29°37'17.8"N 99°09'52.6"W	540 m	December 2000	Pratley	not known
		unburned plot: 29°37'3.6"N 99°09'36.6"W		December 2000		Brackett
Pace Bend Park (burned plot: Travis County Parks and Natural Resources Division; unburned plot: Baptist Churches of Central Texas)	Travis	burned plot: 30°27'38.9"N 98°00'24.2"W	1 280 m	August 2000	Altoga	~ 1989
		unburned plot: 30°28'19.9"N 98°00'35.6"W		October 2000		Pedernales
Pedernales Falls State Park (Texas Parks and Wildlife Department)	Blanco	burned plot: 30°18'57.8"N 98°14'30.3"W	700 m	July–August 1999	Hensley	~ 1970
		unburned plot: 30°19'17.8"N 98°14'18.5"W		October 2000		Hensley

was estimated as the proportion of plants in the unburned plot(s) that were alive, times the total number of plants in the burned plot(s). This method of calculating fire survival rates assumes that any bias in the estimate of the non-fire-related death rate is the same in both treatments.

RESULTS

Ashe Juniper Plants 0 to 50 cm Tall

The proportion of Ashe juniper plants 0 to 50 cm tall alive at the time of sampling was 69% ($N = 145$) in unburned plots and

Table 2. Fire characteristics. Quantitative information about the fire at Hill Country State Natural Area is no longer available (K. Blair, personal communication, October 2006). That site was burned in February 2000 under conditions most similar to those of the Balcones Canyonlands fire (D. Riskind, K. Blair, personal communication, October 2006). Fuel moisture and flame height at Balcones Canyonlands were obtained from Forest Technology System (www.ftsinc.com), Fire Weather Stations, Fuel Stick Sensors, and BehavePlus 3.0.2 software, and an estimate of $3 \text{ tons} \cdot \text{acre}^{-1}$ of fine fuel. NR indicates not recorded.

Land unit	Balcones Canyonlands	Pace Bend	Pedernales Falls
Date	6 February 2000	24 February 1999	9 February 2000
Time	1300 h–1800 h	1139 h–1700 h	0920 h–1340 h
Air temperature			
Start	14°C	21°C	22°C
Finish	16°C	22°C	29°C
Maximum	17°C	22°C	29°C
Relative humidity			
Start	71%	54%	82%
Finish	66%	56%	33%
Wind speed			
Start	11.4 km · hr ⁻¹	3.2 km · hr ⁻¹	0 km · hr ⁻¹
Finish	5.6 km · hr ⁻¹	6.4 km · hr ⁻¹	4.8 km · hr ⁻¹
Maximum	22.4 km · hr ⁻¹	19.3 km · hr ⁻¹	4.8 km · hr ⁻¹
Herbaceous fuel moisture	13%	NR	NR
Woody fuel moisture	88%	NR	NR
Flame height	1.3–1.7 m	0.6–0.8 m	0.6–0.8 m

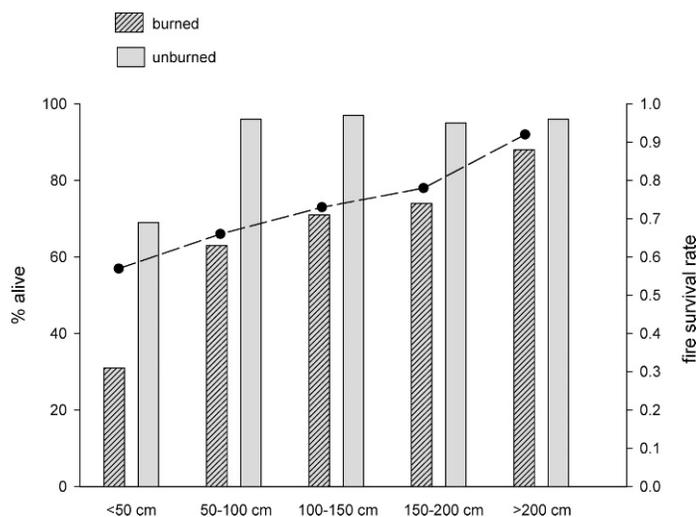


Figure 1. Proportion of Ashe junipers alive in each size class on the sampling date, and estimated rates of fire survival. Bars: percent of Ashe juniper plants that were alive in each height class. Circles and lines: fire survival rate for each height class. Size class and fire survival rate are correlated ($r_s = 1.0$, $P < 0.0001$). Plants from each of the four plots receiving the same treatment (burned or unburned) have been pooled for this figure only.

31% ($N = 182$) in burned plots (all sites pooled; Fig. 1). The overall fire survival rate was therefore 45%.

Plants 0 to 50 cm tall were disproportionately found under tree canopies. Overall, only 28% of the total area of the 1-ha plots was under the canopies of large trees, and 27% (860 of 3200) of the 0.25-m² subplots had their centers under tree canopies, but 41% of plants 0 to 50 cm tall were in those subplots. In two of the three plots with enough plants for statistical testing, there were significantly more plants in subplots under trees, and significantly fewer in subplots in the open, than one would expect from the distribution of subplots (Table 3).

Sample sizes were too small to test the effects of sites, treatments (burned/unburned), and cover (under a canopy or not) on plant state (live/dead) simultaneously. At Pedernales Falls, which had the greatest number ($N = 247$) of 0 to 50 cm tall plants, burning significantly decreased the proportion of living plants (treatment \times state [live or dead], $df = 1$, $\chi^2 = 26.96$, $P < 0.0001$) and being under a tree significantly increased it (cover \times state, $df = 1$, $\chi^2 = 5.17$, $P = 0.02$), whereas the interaction of burning and cover was nonsignificant (treatment \times cover \times state, $df = 1$, $\chi^2 = 0.04$, $P = 0.85$; three-

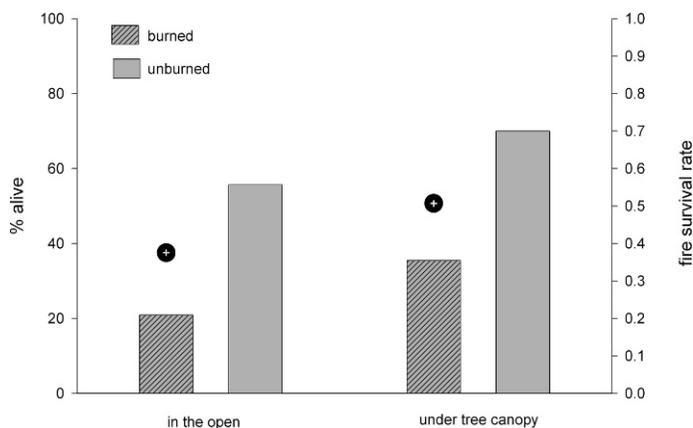


Figure 2. Proportion of small Ashe junipers alive under trees and in the open grassy areas between trees and estimated rates of fire survival. Bars: percent of Ashe juniper plants 0 to 50 cm tall that were alive, under tree canopy or in the open, at the Pedernales Falls site. Circles: fire survival rates of these plants.

way categorical model, [PROC CATMOD; SAS 1999]; Fig 2). In other words, the difference between the fire survival rate in the open (38%) and under trees (51%) was not significant. A parallel analysis of the plants of all four sites pooled (not shown) had very similar results.

Ashe Juniper Plants 50 to 200 cm Tall

The overall fire survival rate increased with plant size within this size class, from 65% (plants 50 to 100 cm tall) to 78% (plants 150 to 200 cm tall; all sites pooled; Fig. 1). There were a total of 1415 plants 50 to 200 cm tall in unburned plots and 1034 in burned plots.

To increase sample sizes for statistical analysis, the three size classes (50 to 100 cm, 100 to 150 cm, and 150 to 200 cm) of Figure 1 were pooled, and for each 86-m² subplot a new variable, subplot status, was calculated with the values “high” ($\geq 50\%$ of the plants in the subplot alive) and “low” ($< 50\%$ of the plants in the subplot alive). Burning significantly reduced the proportion of subplots with $\geq 50\%$ of their plants alive; in a three-way categorical model (SAS PROC CATMOD) both treatment (burned or unburned) and site also had significant effects on survival (treatment \times status [high or low], $df = 1$, $\chi^2 = 7.49$, $P = 0.006$; site \times status, $df = 3$, $\chi^2 = 10.46$, $P = 0.015$). It was not possible to test the effect of the interaction of site and treatment on subplot status because three sites had no 86-m² subplots in their unburned plots that were scored “low” ($< 50\%$ of plants alive).

Table 3. Distribution of small (0 to 50 cm tall) Ashe junipers. Only three of the eight 1-ha plots had sample sizes large enough for statistical testing. There were 400 0.25-m² subplots in each 1-ha plot. All plants 0 to 50 cm tall in a single 1-ha plot were pooled for these tests. The distribution of subplots (proportion under tree canopies and proportion in the open) provided the external expectation for each test. A significant result indicates that more of the small plants were in subplots under canopies, and fewer in subplots in the open, than expected from the distribution of subplots. ***, $P < 0.001$; NS indicates nonsignificant.

Site	No. of plants	No. (%) of plants in subplots under tree canopies	No. (%) of subplots under tree canopies	χ^2
Pace Bend unburned	34	20 (59%)	128 (32%)	11.2***
Pedernales burned	129	62 (48%)	83 (21%)	58.5***
Pedernales unburned	118	30 (25%)	117 (29%)	0.83(NS)

Like plants 0 to 50 cm tall, plants 50 to 200 cm tall were more common under tree canopies than they were in the open. On average, the 30 86-m² subplots in each plot had 25% of their area under the canopies of one or more trees, but on average a 50 to 200 cm tall plant was in a subplot with 36% canopy cover. There was a significant positive correlation between the number of plants 50 to 200 cm tall in a subplot and the proportion of the subplot under one or more tree canopies ($r_s = 0.38$, $P < 0.0001$, $N = 240$).

Although plants 50 to 200 cm tall were clustered around large trees, there was no evidence for an effect of proximity to a large tree upon the proportion of plants in this size class that were alive. A logistic regression of subplot status as defined above against the proportion of subplot under canopy was nonsignificant (SAS PROC LOGISTIC; $df = 1$, $\chi^2 = 0.004$, $P = 0.95$). This test included only the 79 burned 86-m² subplots in which plants 50 to 200 cm tall occurred; there were too few subplots scored as having “low” status in the unburned plots to include unburned subplots in this analysis. Site was included as an independent term in this analysis and was significant, as expected ($df = 3$, $\chi^2 = 10.40$, $P = 0.016$).

Ashe Juniper Plants > 200 cm Tall

The overall fire survival rate of Ashe juniper plants > 200 cm tall (i.e., “trees”) was 92% (all sites pooled; Fig. 1). There were 1 112 trees of this size in unburned plots and 820 in burned plots.

At two sites there were enough dead trees in the > 200 cm size class to allow separate analyses. At Pace Bend, the proportion of trees in the burned plot that were alive (74%) was significantly less than the proportion of trees in the unburned plot that were alive (91%; $df = 1$, $\chi^2 = 33.27$, $P < 0.0001$). At Pedernales Falls, the comparable values (94% and 90%, respectively) were not significantly different ($df = 1$, $\chi^2 = 1.58$, $P = 0.21$).

Plants > 200 cm Tall of Other Species

There were a total of 1 211 plants > 200 cm tall (i.e., “trees”) of species other than Ashe juniper in the eight plots. Ninety-seven percent of them were alive in both the burned and unburned plots. Small sample sizes prevented analysis of species separately.

DISCUSSION

Effects of Fire on Ashe Juniper Survival

The results of this study indicate that the effectiveness for Ashe juniper control of fires of the sort typical in this region is less than land managers might desire. Although the fires studied here did kill Ashe juniper, even the Ashe juniper in smallest size class (0 to 50 cm tall) were not all killed by these fires (Fig. 1). Fire survival was size-dependent, and almost none of the Ashe juniper > 2 m tall were killed by these fires. These results are consistent with those of Wink and Wright (1973), who found that Ashe juniper > 1.8 m tall were more likely to survive a fire than Ashe juniper < 1.8 m tall. Fonteyn et al. (1988) also found fire survival rates of Ashe juniper increased with increasing plant size (up to stem diameters of 5 cm, i.e., about 1.5 m tall).

Fonteyn et al. (1988) reported much lower fire survival rates than we found, but half of their Ashe juniper were under post oak (*Quercus stellata* Wang.), a species not present in our sites, where they measured much higher fire temperatures than they did under live oak.

The fires of this study, like almost all prescribed fires in this region now, were winter burns of relatively low intensity (Table 2). The reasons for the low fire intensities in this region include county burn bans during hot, dry, and/or windy weather, liability issues, and public opinion, all of which are directed towards ensuring control of fires. Winter burns are less intense and therefore easier to control (Wright and Bailey 1982). Summer burns, or even winter burns conducted under hotter, drier, and windier conditions than these burns were, would probably have killed higher proportions of Ashe juniper and other woody plants than these winter burns did (Owens et al. 1998; Blair et al. 2004). If encroachment has progressed far enough, crown fires can occur in Ashe juniper-dominated sites. Crown fires kill adult Ashe juniper (Bryant et al. 1983), but are extremely dangerous. The plant communities that regenerate after a crown fire in such woodlands are largely unstudied.

Clustering and Facilitation of Ashe Juniper Plants

In this study, small- and medium-sized Ashe junipers were more common around large trees than in the open grassy areas between them. These large trees were primarily Ashe juniper or live oak. This pattern, a “skirt” of small Ashe junipers around every large tree, is very common throughout this region (Fonteyn et al. 1988; Fowler 1988; Jackson and Van Auken 1997). It is probably due in part to patterns of seed dispersal. Many seeds remain under the maternal tree (Owens and Schliesing 1995). The “berries” of Ashe juniper are dispersed by many mammals and birds, especially mockingbirds (*Mimus polyglottus*), cedar waxwings (*Bombycilla cedrorum*), and robins (*Turdus migratorius*), all of which defecate while perching in large trees (Chavez-Ramirez and Slack 1994), which could account for the association between small Ashe juniper individuals and live oak trees.

The clustering of small Ashe junipers around large trees also might be due to facilitation of the small Ashe junipers by neighboring trees. There was a significant positive relationship between the presence of a tree and the proportion of Ashe junipers 0 to 50 cm tall that were alive (Fig. 2). If small dead Ashe junipers disappear at the same rate in the open as under trees, the survival rate of small Ashe junipers must be higher under trees than in the open, implying direct or indirect facilitation. Facilitation of very small Ashe junipers by adult Ashe junipers, but not by adult live oaks, has been experimentally demonstrated (Batchelor 2004).

Fire and Neighboring Trees

Ashe juniper and similar *Juniperus* species suppress the growth of many herbaceous species, resulting in lower herbaceous biomass underneath them (Dye et al. 1995; Fuhlendorf et al. 1997). The litter under Ashe juniper and live oak trees is primarily composed of their own leaves and twigs. The characteristics, and perhaps the total amount, of fuel under tree clusters differs markedly from the fuel in open grassy areas between tree clusters (Fonteyn et al. 1988; Fuhlendorf et al.

1996). Differences in fuel properties affect fire intensity (Wright and Bailey 1982; Whelan 1995), which could cause the rate of fire-induced mortality to differ between small Ashe juniper plants in the open and under trees, a fire \times neighbor interaction effect. If fire intensities were lower under trees, it would provide a mechanism by which larger trees could facilitate smaller ones. The results of this study, however, found only a weak, nonsignificant tendency for fire survival rate to be higher under trees (Fig. 2). We are aware of only two other studies testing comparable hypotheses, both of which found that juvenile pine fire-survival rates were lower close to adult pines than away from them (Grace and Platt 1995; Park 2003).

Why was there little or no effect of large trees on whether a small Ashe juniper survived a fire? Fire temperatures might not have been different near adult trees (Fonteyn et al. 1988). However, it was only possible to test the neighbor \times fire interaction effect statistically in one of the four sites, so it would be premature to conclude that it never exists. Moreover, the absence of a significant effect in that site might have been due to two of the approximations we had to make: 1) classifying all small plots as either under or not under a canopy, although the transition from the micro-environment found under a canopy to the micro-environment found in the open is not always sharp; and 2) estimating canopy radii from plant height, although the woody species involved differ in shape. With substantially more data, one could model survival as a function of distance to the center of the nearest tree and its species, bypassing these limitations and increasing the possibility of detecting an effect of proximity to a larger plant on fire survival.

What do These Results Suggest about Presettlement Savannas?

The results of this study indicate that it is unlikely that winter burns that resembled present prescribed burns could have maintained presettlement savannas. However, presettlement fires might have been much more effective than modern prescribed fires at maintaining savannas. Presettlement fires, especially summer fires, probably often occurred under conditions that were hotter, drier, and windier than the conditions under which prescribed burns are now conducted. Furthermore, although one of the study sites had not been grazed for a decade, and another for three decades, before they were burned, present vegetation there and elsewhere likely reflects many decades of intense grazing in the past (Smeins et al. 1997). Presettlement vegetation might have had quite different fuel characteristics, and therefore fire effects, than present vegetation does. Presettlement fires could have been set by lightning or by Native Americans. Before the eastern Edwards Plateau was settled by people of European descent, it was occupied for at least a century by Native Americans with a horse-based lifestyle, who might have set fires to attract herbivores to grass regrowth and to facilitate travel (Fehrenbach 1985).

MANAGEMENT IMPLICATIONS

Unfortunately, the results of this study indicate that single winter burns of the sort commonly used cannot accomplish the goal of controlling *J. ashei* encroachment into central

Texas savannas. It is possible that repeated winter burns of a site might control Ashe juniper by killing plants that survived previous burns. Fire damage to the lower branches of surviving Ashe juniper plants might reduce competition between Ashe juniper and surrounding grasses, which could result in more grass biomass, hence more fine fuel, hence a hotter second fire (Fuhlendorf et al. 1997; Fuhlendorf and Smeins 1997).

Ashe juniper does not resprout if it is burned to the ground. One would expect comparable fires to be even less effective in controlling resprouting species such as redberry juniper (*J. pinchotti*), the common species of the western Edwards Plateau, than they are in controlling Ashe juniper. Comparing Ashe juniper with other nonresprouting juniper species, such as eastern red cedar (*J. virginiana*), we would predict that in all cases survival of surface fires would be strongly size-dependent. All else being equal, surface fires might be more effective in controlling eastern red cedar than they are in controlling Ashe juniper because eastern red cedar typically invades sites that typically have greater herbaceous biomass than most sites invaded by Ashe juniper (Briggs et al. 2002). In the juniper-dominated woodlands of the western United States, in contrast, low productivity, grazing, or a closed canopy might cause the herbaceous biomass to be too low to sustain surface fires (West 1988) and low herbaceous biomass might reduce their effectiveness where they do occur.

ACKNOWLEDGMENTS

We thank the managers of the study sites and their staffs, especially the following: US Fish and Wildlife Service: D. Holle, W. Reiner, C. Schwoppe, and C. Sexton; Texas Parks and Wildlife Department: K. Blair, P. D. Fuentes, O. de la Garza, and D. Riskind; Travis Co. Parks and Natural Resources Department: C. Bergh and K. Terpening; Highland Lakes Camp: D. Dawdy. For assistance with field work we thank A. Sullivan, P. Batchelor, S. Brumbaugh, B. Gabbard, D. Maltby, L. Russell, and A. Strong. We thank Ana Gonzalez for the translation of the abstract, and three anonymous reviewers for comments on the manuscript.

LITERATURE CITED

- ARCHER, S. 1989. Have southern Texas USA savannas been converted to woodlands in recent history? *American Naturalist* 134:545–561.
- ARCHER, S. 1995. Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2:83–99.
- ARCHER, S., D. S. SCHIMEL, AND E. A. HOLLAND. 1995. Mechanisms of shrubland expansion: land use, climate or CO₂? *Climatic Change* 29:91–99.
- ARCHER, S., C. SCIFRES, C. R. BASSHAM, AND R. MAGGIO. 1988. Autogenic succession in a subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58:111–128.
- BATCHELOR, M. 2004. The balance between positive and negative effects in a savanna system [dissertation]. Austin, TX: University of Texas at Austin. 128 p.
- BLACKBURN, W. H., AND P. T. TUELLER. 1970. Pinyon and juniper invasion in black sagebrush communities in east-central Nevada. *Ecology* 51:841–848.
- BLAIR, B. K., J. C. SPARKS, AND J. FRANKLIN. 2004. Effective application of prescribed burning. In: W. T. Hamilton, A. McGinty, D. N. Ueckert, C. W. Hanselka, and M. R. Lee [EDS.]. *Brush management: Past, present, and future*. College Station, TX: Texas A&M University Press. p. 187–199.

- BRIGGS, J. M., G. A. HOCH, AND L. C. JOHNSON. 2002. Assessing the rate, mechanisms, and consequences of the conversion of tallgrass prairie to *Juniperus virginiana* forest. *Ecosystems* 5:578–586.
- BROCKWAY, D. G., R. G. GATEWOOD, AND R. B. PARIS. 2002. Restoring grassland savannas from degraded pinyon-juniper woodlands: effects of mechanical overstory reduction and slash treatment alternatives. *Journal of Environmental Management* 64:179–197.
- BRYANT, F. C., G. K. LAUCHBAUGH, AND B. H. KOERTH. 1983. Controlling mature Ashe juniper in Texas with crown fires. *Journal of Range Management* 36: 165–168.
- BUECHNER, H. K. 1944. The range vegetation of Kerr County, Texas, in relation to livestock and white-tailed deer. *American Midland Naturalist* 31:697–743.
- CHAVEZ-RAMIREZ, F., AND R. D. SLACK. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. *Oikos* 71:40–46.
- DITTMORE, W. H., JR., AND J. E. ALLISON. 1979. Soil survey of Blanco and Burnet Counties, Texas. Washington, DC: US Department of Agriculture, Soil Conservation Service. 116 p.
- DITTMAR, G. W., M. L. DEIKE, AND D. L. RICHMOND. 1977. Soil survey of Medina County, Texas. Washington, DC: US Department of Agriculture, Soil Conservation Service. 90 p.
- DUBLIN, H. T., A. R. E. SINCLAIR, AND J. MCGLADE. 1990. Elephants and fire as causes of multiple stable states in the Serengeti-Mara woodlands. *Journal of Animal Ecology* 59:1147–1164.
- DYE, K. L., D. N. UECKERT, AND S. G. WHISENANT. 1995. Redberry juniper–herbaceous understory interactions. *Journal of Range Management* 48:100–107.
- EDDLEMAN, L. E. 1987. Establishment and stand development of western juniper in central Oregon. In: R. L. Everett [ed.]. Proceedings: Pinyon–juniper Conference. Ogden, UT: US Department of Agriculture, Forest Service, Intermountain Research Station. p. 255–259.
- FEHRENBACH, T. R. 1985. Lone star: A history of Texas and the Texans. New York, NY: Collier Books. 761 p.
- FONTEYN, P. J., M. W. STONE, M. A. YANCY, J. T. BACCUS, AND N. M. NADKARNI. 1988. Determination of community structure by fire. In: B. B. Amos and F. R. Gehlbach [eds.]. Edwards Plateau vegetation: Plant ecological studies in central Texas. Waco, TX: Baylor University Press. p. 79–90.
- FOWLER, N. L. 1988. Grasslands, nurse trees, and coexistence. In: B. B. Amos and F. R. Gehlbach [eds.]. Edwards Plateau vegetation: Plant ecological studies in central Texas. Waco, TX: Baylor University Press. p. 91–100.
- FOWLER, N. L., AND D. W. DUNLAP. 1986. Grassland vegetation of the eastern Edwards Plateau. *American Midland Naturalist* 115:146–155.
- FUHLENDORF, S. D., AND F. SMEINS. 1997. Long-term importance of grazing, fire and weather patterns on Edwards Plateau vegetation change. In: C. A. Taylor, Jr. [ed.]. 1997 Juniper Symposium Proceedings. College Station, TX: Texas Agricultural Experiment Station. p. 7.19–7.29.
- FUHLENDORF, S. D., F. SMEINS, AND W. E. GRANT. 1996. Simulation of a fire-sensitive ecological threshold: a case study of Ashe juniper on the Edwards Plateau of Texas, USA. *Ecological Modelling* 90:245–255.
- FUHLENDORF, S. D., F. SMEINS, AND C. A. TAYLOR, JR. 1997. Browsing and tree size influences on Ashe juniper understory. *Journal of Range Management* 50:507–512.
- GRACE, S. L., AND W. J. PLATT. 1995. Effects of adult tree density and fire on the demography of pregrass stage juvenile longleaf pine (*Pinus palustris* Mill.). *Journal of Ecology* 83:75–86.
- HAMILTON, W. T., A. MCGINTY, D. N. UECKERT, C. W. HANSELKA, AND M. R. LEE. 2004. Brush management; past, present, and future. College Station, TX: Texas A&M University Press. 283 p.
- HIGGINS, S. I., W. J. BOND, AND W. S. W. TROLLOPE. 2000. Fire, resprouting and variability: a recipe for grass–tree coexistence in savanna. *Journal of Ecology* 88:213–229.
- HOCH, G. A., AND J. M. BRIGGS. 1998. Expansion of eastern red cedar in the northern Flint Hills, Kansas. In: J. T. Springer [ed.]. Proceedings of the sixteenth North American prairie conference. Kearney, NE: University of Nebraska. p. 9–15.
- JACKSON, J. T., AND O. W. VAN AUKEN. 1997. Seedling survival, growth, and mortality of *Juniperus ashei* in the Edwards Plateau region of central Texas. *Texas Journal of Science* 49:267–278.
- JESSUP, K. E., P. W. BARNES, AND T. W. BOUTTON. 2003. Vegetation dynamics in a *Quercus–Juniperus* savanna: an isotopic assessment. *Journal of Vegetation Science* 14:841–852.
- KNAPP, P. A., AND P. T. SOULE. 1998. Recent *Juniperus occidentalis* (western juniper) expansion on a protected site in central Oregon. *Global Change Biology* 4:347–357.
- KNOOP, W. T., AND B. H. WALKER. 1985. Interactions of woody and herbaceous vegetation in a southern African savanna. *Journal of Ecology* 73: 235–252.
- KRAMER, K. A., AND E. J. RYKIEL. 1996. Succession via vegetation clusters: is the post oak savanna becoming a closed-canopy woodland? *Bulletin of the Ecological Society of America Supplement* 77:244.
- LAYCOCK, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- LYONS, R. K., M. K. OWENS, AND R. V. MACHEN. 1998. Juniper biology and management in Texas. B-6074. College Station, Texas: Texas Agricultural Extension Service. 11 p.
- MCPHERSON, G. R. 1997. Ecology and management of North American savannas. Tucson, AZ: University of Arizona Press. 208 p.
- MCPHERSON, G. R., AND H. A. WRIGHT. 1990. Establishment of *Juniperus pinchotii* in western Texas: environmental effects. *Journal of Arid Environments* 19:283–287.
- MCPHERSON, G. R., H. A. WRIGHT, AND D. B. WESTER. 1988. Patterns of shrub invasion in semiarid Texas grasslands. *American Midland Naturalist* 120:391–397.
- OWENS, M. K., C.-D. LIN, C. A. TAYLOR, JR., AND S. G. WHISENANT. 1998. Seasonal patterns of plant flammability and monoterpenoid content in *Juniperus ashei*. *Journal of Chemical Ecology* 24:2115–2129.
- OWENS, M. K., AND T. G. SCHLIESING. 1995. Invasive potential of Ashe juniper after mechanical disturbance. *Journal of Range Management* 48:503–507.
- PARK, A. 2003. Spatial segregation of pines and oaks under different fire regimes in the Sierra Madre Occidental. *Plant Ecology* 169:1–20.
- POLLEY, H. W. 1997. Viewpoint: atmospheric CO₂, soil water, and shrub/grass ratios on rangelands. *Journal of Range Management* 50:278–284.
- SAS. 1999. Statistical Analysis Systems. Version 8. Cary, NC: SAS Institute.
- SCHOLLES, R. J., AND S. R. ARCHER. 1997. Tree–grass interactions in savannas. *Annual Review of Ecology and Systematics* 28:517–544.
- SMEINS, F. E. 1980. Natural role of fire on the Edwards Plateau. In: L. D. White [ed.]. Proceedings: Prescribed Burning of the Edwards Plateau. College Station, TX: Texas Agriculture Extension Service. p. 4–16.
- SMEINS, F. E., S. FUHLENDORF, AND C. A. TAYLOR, JR. 1997. Environmental and land use changes: a long-term perspective. In: C. A. Taylor, Jr. [ed.]. 1997 Juniper Symposium Proceedings. College Station, TX: Texas Agricultural Experiment Station. p. 1.3–1.21.
- SMEINS, F. E., AND L. B. MERRILL. 1988. Longterm change in a semi-arid grassland. In: B. B. Amos and F. R. Gehlbach [eds.]. Edwards Plateau vegetation: plant ecological studies in central Texas. Waco, TX: Baylor University Press. p. 101–114.
- UECKERT, D. N. 1980. Manipulating range vegetation with prescribed fire. In: L. D. White [ed.]. Prescribed range burning in the Edwards Plateau of Texas. College Station, TX: Texas Agriculture Experiment Station. p. 27–44.
- UECKERT, D. N. 1997. Juniper control and management. In: C. A. Taylor, Jr. [ed.]. 1997 Juniper Symposium Proceedings. College Station, TX: Texas Agricultural Experiment Station. p. 5.23–5.34.
- VAN AUKEN, O. W. 1988. Woody vegetation of the southeastern escarpment and plateau. In: B. B. Amos and F. R. Gehlbach [eds.]. Edwards Plateau vegetation: Plant ecological studies in central Texas. Waco, TX: Baylor University Press. p. 43–55.
- VAN AUKEN, O. W. 1993. Size distribution patterns and potential change of some dominant woody species of the Edwards Plateau region of Texas. *Texas Journal of Science* 45:199–210.
- VAN AUKEN, O. W. 2000. Shrub invasions of semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197–216.

- WERCHAN, L. E., A. C. LOWTHER, AND R. N. RAMSEY. 1974. Soil survey of Travis County, Texas. Washington, DC: US Department of Agriculture, Soil Conservation Service. 126 p.
- WEST, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. *In*: M. B. Barbour and W. D. Billings [EDS.]. North American terrestrial vegetation. Cambridge, UK: Cambridge University Press. p. 209–230.
- WHELAN, R. J. 1995. The ecology of fire. Cambridge, UK: Cambridge University Press. 346 p.
- WINK, R. L., AND H. A. WRIGHT. 1973. Effects of fire on an Ashe juniper community. *Journal of Range Management* 26:326–329.
- WRIGHT, H. A., AND A. W. BAILEY. 1982. Fire ecology: United States and southern Canada. New York: John Wiley and Sons. 501 p.