

Effects of Fire Frequency and Intensity on Velvet Mesquite in an Arizona Grassland

Carl E. Bock,¹ Linda Kennedy,² Jane H. Bock,¹ and Zach F. Jones³

Authors are ¹Professors Emeriti, Department of Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0334; ²Director, Appleton-Whittell Research Ranch, HC1 Box 44, Elgin, AZ 85611; and ³Visiting Professor, Biology Department, The Colorado College, Colorado Springs, CO 80903.

Abstract

Increases of velvet mesquite (*Prosopis velutina* Woot.) in southwestern grasslands might have been caused by livestock consumption of fuels that once burned with sufficient frequency and intensity to kill the trees. However, attempts to control mesquite with fire usually have failed. We measured fire damage and 5 years of postfire recovery for 225 mesquite trees > 1 m tall, following a 2002 wildfire that included grasslands differing in fire history, presence vs. 34-year livestock exclusion, and predominance of native vs. exotic grasses. The fire burned 100% of ground cover in ungrazed areas and 65% on grazed lands. Top-kill was 100% for trees in exotic ungrazed grasslands (the areas with highest fuel loads), 79% for trees in ungrazed native grasslands, and 28% for trees in grazed grasslands. Most top-killed trees produced ground sprouts, so that by 2006 the combined foliage volume from ground sprouts and surviving branches was 78% (± 3.2 SE) of preburn foliage volume in grazed areas, 66% (± 3.3) in ungrazed exotic grasslands, and 57% (± 4.0) in ungrazed native grasslands. Fire damage was greater among surviving trees in ungrazed areas that had burned twice (1987 and 2002) than among those that had burned only once since 1968 (in 2002), especially in native grasslands where postfire foliage recovery for twice-burned trees was only 47% (± 6.3) by 2006. Only 1 of 84 trees died in the area burned once, whereas 12 of 66 (18.2%) died in the area burned twice, including several individuals > 3 m tall. These results suggest that repeated fires likely could have prevented the historic spread of velvet mesquite into southwestern grasslands, but probably could be used to control mesquite today only in areas where abundant herbaceous growth provides sufficient fine fuels.

Resumen

El aumento del “Velvet mesquite” (*Prosopis velutina* Woot.) en los pastizales del suroeste puede haber sido causado por el consumo de los combustibles por el ganado que una vez quemaron el pastizal con suficiente frecuencia e intensidad para matar los árboles. Sin embargo, los intentos para controlar el “Mesquite” con fuego usualmente han fallado. Medimos el daño por el fuego y la recuperación 5 años después de la quema en 225 árboles de “Mesquite” mayores de un metro de altura, después de un fuego natural ocurrido en 2002 el cual abarcó pastizales con diferente historial de quema, la presencia vs. 34 años de exclusión al ganado y la predominancia de zacates nativos vs. exóticos. El fuego quemó el 100% de la cobertura del suelo en las áreas sin apacentar y el 65% en las apacentadas. La muerte de la parte aérea de los árboles fue: 100% en los pastizales de zacates exóticos sin apacentar (las áreas con la mayor carga de combustible), 79% en los pastizales nativos sin apacentar, y 28% en los pastizales apacentados. La mayoría de los árboles con muerte aérea produjeron rebrotes del suelo y para el 2006 el volumen de follaje combinando los rebrotes y las ramas sobrevivientes fue 78% (± 3.2 SE) del volumen presente antes de la quema en las áreas apacentadas, 66% (± 3.3) en los pastizales con zacates exóticos, y 57% (± 4.0) en los pastizales nativos sin apacentar. El daño por fuego fue mayor entre los árboles sobrevivientes en las áreas sin apacentar que se habían quemadas dos veces (1987 y 2002) que entre aquellas quemadas una sola vez desde 1968 (en el año 2002), especialmente en los pastizales nativos donde, en el 2006, la recuperación del follaje después del fuego en árboles quemados dos veces fue solo el 47% (± 6.3). Solo uno de 84 árboles murió en el área quemada solo una vez, mientras que 12 de 66 (18.2%) murieron en el área quemada dos veces, incluyendo varios individuos de mas de 3 m de altura. Estos resultados sugieren que los fuegos repetidos probablemente pudieron haber prevenido la invasión histórica del “Velvet mesquite” a los pastizales del suroeste y probablemente pudiera ser usado para controlar el “Mesquite” solo en áreas donde el crecimiento abundante de herbáceas provee suficiente combustible fino.

Key Words: burn, exotic grasses, foliage volume, fuels, grazing, livestock

INTRODUCTION

Cover and density of various trees and shrubs, including mesquite (*Prosopis* sp.), have increased over the past 150 years

in arid and semiarid ecosystems of North America, as part of a worldwide trend (Buffington and Herbel 1965; Archer 1989, 1995; Van Auken 2000). Historic advances of mesquite into southwestern rangelands have been attributed to the independent and interactive effects of climate change, activities of rodents and livestock, and partial or complete loss of fire from these ecosystems (Archer et al. 1995; McPherson 1995; Owens et al. 2002). One possibility is that consumption of fine fuels by livestock has caused fires to burn with insufficient frequency or intensity to kill invading mesquite (Bahre and Shelton 1993; Drewa 2003).

Research was supported by the Arizona Game and Fish Dept, and by the Ecology Program of the National Science Foundation.

Correspondence: Carl E. Bock, Ecology and Evolutionary Biology, University of Colorado, Boulder, CO 80309-0334. Email: carl.bock@colorado.edu

Manuscript received 13 December 2006; manuscript accepted 25 May 2007.

In contrast to prehistoric wildfires, contemporary prescribed fires might not achieve thresholds of frequency or intensity that are necessary to return former grasslands and open savannas to a steady state that is relatively free of woody plants (Fuhlendorf et al. 1996; McPherson 1997). Attempts to control honey mesquite (*Prosopis glandulosa* Torr.) with prescribed fire in Texas and New Mexico usually have failed, probably due to the lack of sufficient fuels (Owens et al. 2002; Drewa 2003; Ansley and Castellano 2006). Initial optimism about fire control of velvet mesquite (*Prosopis velutina* Woot.) in Arizona was based on studies where fuels were artificially increased around the bases of trees (Glendening and Paulson 1955). Subsequent studies under naturally occurring fuel loads revealed that few except the smallest velvet mesquite were killed by fire (Reynolds and Bohning 1956; Cable 1967; Martin 1983; McClaran 2003). However, this could have been due to low fuel loads resulting from long-term effects of grazing, and/or to the lack of repeated fires at the same sites (Bahre and Shelton 1993).

The Appleton–Whittell Research Ranch is a 3160-ha sanctuary of the National Audubon Society in the grasslands of southeastern Arizona (Bock and Bock 2000). It has been ungrazed by livestock since 1968, and as a result it supports dense stands of both native and exotic grasses compared to adjacent grazed areas (Bock et al. 1986; Bock and Bock 1993). An unusually intense April 2002 wildfire (the Ryan Fire) burned 90% of the Research Ranch as well as large portions of adjacent operating cattle ranches. Kupfer and Miller (2005) compared damage and postfire recovery of velvet mesquite on and adjacent to the Research Ranch in May 2003, 1 year after this burn. They found that negative fire effects on mesquite were proportional to preburn fuel loads, being highest in ungrazed stands of exotic African lovegrasses (*Eragrostis* spp.), intermediate in ungrazed native grasslands, and lowest in grazed grasslands. However, even in ungrazed areas only 6% of trees showed no signs of postfire recovery, and therefore appeared to have been killed by the fire.

The present study, also conducted on the Research Ranch and adjoining cattle ranches, expands on that of Kupfer and Miller (2005) in two ways. First, we followed mesquite recovery for an additional three growing seasons after the Ryan Fire (through 2006). Second, we compared trees on the Research Ranch that had not burned over the 34 years preceding the 2002 Ryan Fire with trees in another area that had burned one additional time in a July 1987 wildfire. Our study had two objectives. First, we compared fire damage and postfire recovery of mesquite in three habitats: ungrazed native grasslands, ungrazed exotic grasslands, and grazed grasslands that included mixtures of both native and exotic species. Second, we compared mortality and recovery of mesquite in ungrazed areas that had burned once vs. twice since 1968, to test the hypothesis that repeated wildfires might once have played a role in keeping southwestern grasslands relatively free of mesquite.

METHODS

Study Area and Sampling Design

The Research Ranch and adjacent operating cattle ranches are in the Sonoita Valley, Santa Cruz County, Arizona (lat

31°39'N, long 110°32'W). Elevations range from 1400 to 1550 m. Temperatures range from a mean daily January minimum of -3.0°C to a mean daily June maximum of 32.6°C . Annual precipitation averages 430 mm, about 60% of which occurs during the July–August summer monsoon (Bock and Bock 2000). The present study occurred in areas transected by the northern and eastern boundaries of the Research Ranch. Predominant native vegetative ground cover consisted of perennial bunchgrasses in the genera *Aristida*, *Bouteloua*, and *Eragrostis*, scattered low shrubs, especially *Baccharis pteronioides* DC and *Isocoma tenuisecta* Greene, and a large variety of forbs. Two African exotics, Lehmann lovegrass (*Eragrostis lehmanniana* Nees) and Boer lovegrass (*Eragrostis curvula* Nees var. *conferta* Stapf.), dominated parts of the Research Ranch where they had been planted in the 1940s and 1950s (Bock et al. 1986). The entire study area supported low densities of velvet mesquite that were the subject of the present study. Botanical nomenclature is from McLaughlin et al. (2001).

We measured preburn ground vegetation and postfire mesquite recovery at 75 sampling points on and adjacent to the Research Ranch. These points had been established in the 1980s for studies of the responses of ground vegetation to livestock grazing, wildfire, and the planting and spread of the exotic African grasses (Bock et al. 1984; Bock et al. 1986; Bock and Bock 1992). All the points were on level mesa tops with gravelly loam soils (McLaughlin et al. 2001). Twenty-five points were on parts of the ungrazed Research Ranch dominated by native grasses, 25 were on parts of the sanctuary dominated by the exotic lovegrasses, and 25 points were on portions of two adjacent operating cattle ranches that included mixtures of native and exotic grasses.

The Diamond C Ranch (11 grazed sampling points) was grazed by a herd of about 250 cows and their calves, at a density of about 1 cow–calf unit $\cdot 13 \text{ ha}^{-1}$ across the ranch as a whole. The herd was moved rotationally for short durations (< 1 week) on 63 small (about 50 ha) paddocks, following the principles of holistic resource management (R. Jelks, personal communication, 2007). Grazing on the Babacomari Ranch (14 sampling points) involved steers and heifers only, rotated seasonally through relatively large (> 500 ha) pastures grazed for about $45 \text{ d} \cdot \text{y}^{-1}$, at a stocking density of about 1 animal $\cdot 12 \text{ ha}^{-1}$ across the ranch as a whole (D. Ruppel, personal communication, 2005).

The Ryan Wildfire ignited on 29 April 2002 at the northern edge of the San Rafael Valley south of the Research Ranch, passed through the sanctuary and adjacent parts of the Diamond C and Babacomari ranches on 30 April 2002, burning across all 75 of our sampling points, and eventually consumed over 15 000 ha in Santa Cruz and Cochise counties. Mesquite was in leaf at the time of the fire. There are four reasons why the Ryan Fire was unusually large and intense, such that it burned both grazed and ungrazed lands. First, the preceding summer had been wet and productive, so ground fuels were abundant. Second, the winter of 2001–2002 had experienced a severe drought, so that fuels were very dry going into spring. Third, the fire occurred in April, which is before the start of the growing season, so that nearly all grass and forb cover consisted of dead growth from the previous year. Finally,

winds during the fire were sustained at speeds up to $65 \text{ km} \cdot \text{h}^{-1}$.

An earlier wildfire on the Research Ranch ignited in the afternoon of 16 July 1987, and burned about 1 000 ha of the sanctuary before it was contained in the evening of 17 July. Mesquite was in leaf, but the summer monsoon was late that year and there was little green vegetative ground cover (Bock and Bock 1992). The 1987 fire combusted nearly all ground vegetation and burned all foliage on mesquites at 22 of the 50 sampling points on the Research Ranch (11 in native and 11 in exotic grasslands). Unlike the 2002 fire, the 1987 fire did not burn onto the adjacent cattle ranches.

Preburn Ground Cover and Fire Coverage

We had measured percentage vegetative ground cover at the 75 sampling points in August 2001 as part of a long-term vegetation monitoring program. We used these data in the present study as an indicator of fine fuel loads at the time of the April 2002 wildfire. Four 10-m transects were set out in cardinal compass directions from each point. We placed a 20×50 cm sampling frame at 2-m intervals along each transect, and visually estimated percentage canopy cover for each plant species inside each frame ($n = 20$ frames per plot). These data were pooled to generate cover values for grasses, forbs, and shrubs, which in turn were summed to give one overall measure of percentage ground vegetative canopy at each point.

In May 2002, less than 1 month after the Ryan Fire and before the start of vegetative growth, we recorded whether ground vegetation was blackened or not at 200 points spaced at 1-m intervals along 6 transects in the same general areas where we measured vegetative ground cover and postfire mesquite recovery. The 6 transects were distributed as follows: one each on the grazed Babacomari and Diamond C ranches, and one each in ungrazed native or ungrazed exotic grasslands that had burned either once (2002) or twice (1987 and 2002). We used these data (percent of ground points burned) as a measure of the completeness with which the fire had burned litter as well as standing grasses, forbs, and shrubs.

Mesquite Measurements

In June 2003, at the start of the second postfire growing season, we counted the number of mesquites inside a circle enclosing 500 m^2 centered on each of the 75 sampling points, and selected 3 trees > 1.0 m tall that were closest to each point for measurement of postfire recovery ($n = 225$ trees total sample: 75 each in grazed, ungrazed native, and ungrazed exotic grassland habitats). We restricted our study to trees > 1.0 m tall, because most shorter trees were burned so severely that remaining branches could not serve as a reliable estimate of preburn height or crown volume. For taller trees, the fire appeared to have spared all but the finest twigs from complete combustion, such that remaining branches were a reasonable estimate of preburn crown sizes, even in severely burned trees.

Burned velvet mesquite recovers from fire by growing back from surviving axillary buds on branches, and/or as sprouts coming from basal stem buds just below the ground surface (Cable 1967; Martin 1983). In June 2003, when we began mesquite measurements, the live foliage on many severely burned trees consisted only of ground sprouts. Foliage on

moderately damaged trees usually included mixtures of some branch recovery and new ground sprouts. The least-damaged trees had few or no ground sprouts, and their live crowns appeared to be essentially the same sizes as they had been before the burn. We used the same procedures to estimate postfire recovery of all trees. First we measured height of the tallest ground sprout, height of the tallest living foliage coming from prefire branches, and height of the tallest dead branch as an estimate of prefire height. Next, teams of two to five individuals observed each tree from a distance of about 10 m, from each of the four cardinal compass directions, and estimated live crown foliage volume and live ground sprout foliage volume as percentages of preburn volume (to the nearest 10%), using the extent of burned branch tips as a representation of the spread of the preburn crown. These independent estimates then were averaged for each tree. In some lightly-burned trees the longest branches all were green, and there was little or no sign of any fire-related loss of interior foliage. In these cases postburn branch foliage was considered to represent 100% of preburn foliage.

We repeated the tree measurements in June 2004 and 2006, using the burned crown still in place to estimate the volume of postburn foliage as a percent of preburn foliage. However, the results then were adjusted to account for possibility that some branches killed by the fire had since fallen from the trees. We made these adjustments by measuring the height of the tallest fire-killed branch still in place in 2004 and 2006, comparing it to the height of the tallest fire-killed branch in place in 2003, and adjusting our estimate of live foliage as a percent of preburn foliage proportionately. Differences in dead branch height between 2003 and 2004 were negligible, but many trees had lost substantial portions of their fire-killed branches by 2006.

Statistical Analyses

Because we studied the effects of only one fire in one ungrazed area, the conservative approach would be to consider the trees we measured as pseudoreplicates. Therefore, statistical inferences should be limited to the particular areas represented by this study (Wester 1992). Data for ground vegetation canopy in 2001, preburn mesquite height and density, postburn height of ground sprouts and live branch foliage, and postburn foliage volume as a percent of preburn foliage volume, all met assumptions for parametric statistical analyses (Sokal and Rohlf 1995). Therefore, we compared these variables between habitats, and between areas burned once vs. twice, using analyses of variance (ANOVA). We first performed repeated measures ANOVA of mesquite recovery data, with year as the repeated measure on each tree. However, highly significant interactions between treatment and year made it difficult to interpret treatment effects. Furthermore, we were less interested in the testing for differences in the trajectories of postfire recovery than we were in differences between habitats and treatments (one vs. two fires) at the end of the study. Therefore, we restricted our statistical comparisons of mesquite recovery to 2006, using 1-way ANOVA to examine differences among habitats, and 2-way ANOVA to examine the independent and interactive effects of habitat and fire frequency in ungrazed areas only. In some cases we also have shown data

Table 1. Mean (SE) preburn vegetative conditions and percent of 400 points at which ground vegetation was burned during an April 2002 wildfire, in ungrazed native, ungrazed exotic, and grazed grasslands in southeastern Arizona.

	Habitat			Statistics
	Native	Exotic	Grazed	
Mesquite height (cm)	249.9 (11.2)	223.1 (7.9)	252.0 (10.4)	$F_{2,222} = 2.63$ ($P = 0.08$)
Mesquite density ¹ (trees · 500 m ⁻²)	0.6 (0.1)	1.2 (0.2)	2.2 (0.2)	$F_{2,72} = 15.39$ ($P < 0.001$)
Ground vegetation ¹ (percent canopy)	79.0 (2.7)	92.1 (1.2)	61.8 (2.8)	$F_{2,72} = 42.85$ ($P < 0.001$)
Percent ground vegetation burned	99.5	100.0	64.5	$\chi^2 = 313.8$ ($P < 0.001$)

¹Each habitat different from the other two ($P < 0.05$) in Scheffé posthoc comparisons of mean values.

from 2003 and 2004 for comparative purposes. We compared the preburn heights of trees killed vs. spared by the fire using the nonparametric Mann-Whitney *U*-test, because highly unequal sample sizes and heterogeneity of variances precluded parametric testing.

We used the Chi-square contingency statistic (χ^2) to compare 1) the amount of ground vegetation that was burned vs. unburned among habitats, 2) the number of fire-killed vs. surviving trees in areas burned once vs. twice, 3) the number of trees with tops killed vs. alive among habitats, and 4) the number of trees with or without ground sprouts among individuals with tops killed vs. alive.

All statistical tests were performed in Statview 5.0.1 (SAS Publishing 1999), with $P < 0.05$ considered significant and $0.05 < P < 0.10$ as marginally significant. Unless otherwise noted, values shown are means \pm standard error.

RESULTS

Preburn Vegetation and Fire Coverage

The combined canopy of grasses, forbs, and low shrubs was highest in ungrazed exotic grasslands, intermediate in ungrazed native grasslands, and lowest in grazed grasslands, at the height of the growing season the year before the April 2002 wildfire (Table 1). Combustion of this ground vegetation was virtually complete in both native and exotic ungrazed grasslands as a result of the fire, but only 258 of 400 points sampled were burned in grazed grasslands (64.5%; Table 1). Preburn mesquite density averaged 1.3 trees · 500 m⁻² at the 75 points, and was highest in grazed grasslands, lowest in ungrazed native grasslands, with ungrazed exotic grasslands intermediate (Table 1). There was a marginally significant difference in mesquite height among habitats, with trees in exotic ungrazed grasslands being somewhat shorter than those in the other two habitats (Table 1). However, Scheffé pairwise posthoc comparisons of mean heights between habitats were not significant ($P > 0.12$ in each case).

Mesquite Recovery Among Habitats

All 75 trees in exotic ungrazed grasslands were completely top-killed by the Ryan Fire, whereas there was some live branch foliage in 2003 in 21% of trees in ungrazed native grasslands and in 72% of trees in grazed areas ($\chi^2_2 = 95.7$, $P < 0.001$). Top-killed trees were more likely to have ground sprouts than trees with live branch foliage (88.4% vs. 62.9%; $\chi^2_1 = 19.98$, $P < 0.001$). By 2006, maximum ground sprout height was greater among 155 top-killed trees (109.3 \pm 3.8 cm) than it was

among 70 trees that were not top-killed (72.0 \pm 6.3 cm; $F_{1,223} = 37.57$, $P < 0.001$).

The foliage volume of burned mesquite in grazed grasslands, excluding ground sprouts, had recovered to an average 58% of preburned levels by the fifth postfire growing season (2006), compared to 22% among trees in ungrazed native grasslands, and only 1.3% in ungrazed exotic grasslands (Fig. 1; $F_{2,222} = 76.76$, $P < 0.001$). If ground sprouts were included, the foliage volume of mesquite in grazed grasslands had recovered to nearly 80% of preburn volume by 2006 (Fig. 2), which was significantly higher than that of trees in ungrazed native grasslands, with trees in ungrazed exotic grasslands being intermediate (Fig. 2; $F_{2,222} = 9.10$, $P < 0.001$).

Differences among habitats in postfire foliage recovery (including ground sprouts) varied according to tree size (Fig. 3). Trees between 100–200 cm preburn height recovered to an average 74% of preburn foliage volume by 2006, with only a marginally significant difference among habitats ($F_{2,74} = 2.85$, $P = 0.064$). Trees 200–300 cm tall recovered to an average of 66% preburn foliage volume by 2006, and recovery was greater in grazed than in ungrazed native grasslands, with ungrazed exotic grasslands intermediate ($F_{2,91} = 5.67$, $P = 0.005$). Recovery of trees > 300 cm tall averaged 60% in 2006 and differed among habitats, being lowest in ungrazed exotic, intermediate in ungrazed native, and highest in grazed grasslands ($F_{2,51} = 5.94$, $P = 0.005$).

Mesquite Mortality and Recovery in Relation to Fire Frequency

By 2006, 13 of the 225 mesquite trees we sampled (5.8%) showed no signs of any green foliage, and we assumed they had died as a result of the 2002 fire. All 13 dead trees were on ungrazed plots (5 in exotic grasslands, 8 in native grasslands), representing 8.7% of the 150 trees measured in ungrazed habitat. Twelve of the 13 dead trees were among the 66 on plots that had burned in the July 1987 wildfire as well as in 2002 (18.2%), whereas only one dead tree was among the 84 on ungrazed areas that had burned only in 2002 (1.2%)—a highly significant difference ($\chi^2_1 = 13.48$, $P < 0.001$). Fire-caused mortality apparently was not related to tree size, because the mean height of the 13 dead trees (213.5 \pm 25.4 cm, range 100–330) did not differ from that of the trees in ungrazed areas that survived the fire (243.4 \pm 5.9 cm, range 100–600; $Z = 1.04$, $P = 0.30$).

Postfire regrowth among trees that survived the 2002 fire was higher for individuals that had been burned only once compared to those that had been burned twice (Fig. 4). However, this result was much more striking for trees in ungrazed native than in ungrazed exotic grasslands, resulting

Post-fire Re-growth Excluding Ground Sprouts

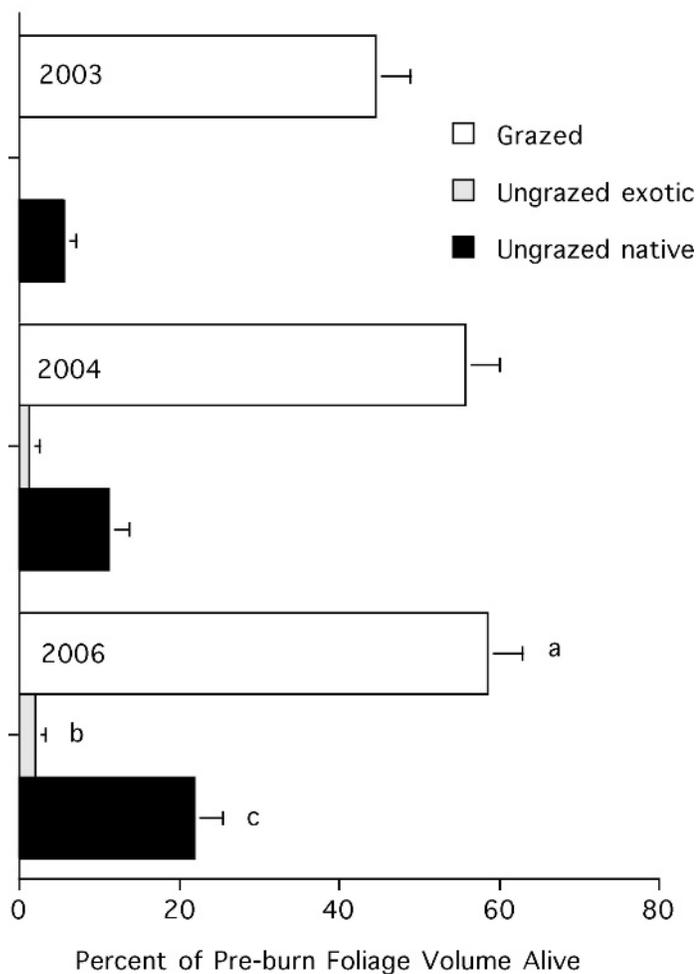


Figure 1. Mean (SE) percentage of preburn foliage volume alive for mesquite trees in three grassland habitats ($n = 75$ trees · habitat⁻¹), in 3 years following a 2002 wildfire in southeastern Arizona. Data include foliage volume estimates for branches in place before the fire, but not foliage on postfire ground sprouts. Letters adjacent to 2006 results indicate homogeneous subsets in pairwise posthoc comparisons of means.

in a significant interaction between habitat and fire frequency (habitat effect: $F_{1,133} = 2.65$, $P = 0.11$; fire frequency effect: $F_{1,133} = 14.34$, $P < 0.001$; interaction: $F_{1,133} = 4.75$, $P = 0.031$).

DISCUSSION

Results of our study are consistent with those of Kupfer and Miller (2005), insofar as mesquite top-kill following the 2002 Ryan Fire was greatest among trees in exotic ungrazed grasslands (100%) and least among trees in grazed areas (28%), with trees in ungrazed native grasslands intermediate (79%; Fig. 1). However, by following the same burned trees for 5 years (through 2006) instead of only into the second postfire year (2003), it became clear that this pattern was short-lived because of regrowth from ground sprouts. By 2006 the

Post-fire Re-growth Including Ground Sprouts

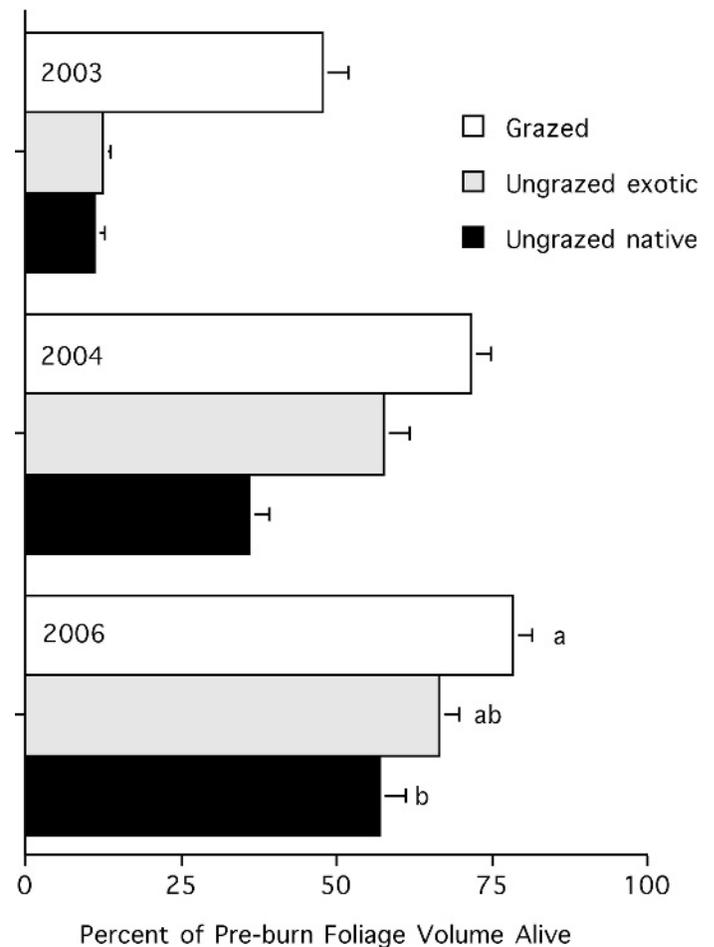


Figure 2. Same as Fig. 1, but postfire foliage volume estimates include ground sprouts. Shared letters for 2006 results indicate homogeneous subsets in pairwise posthoc comparisons of means.

recovery of preburn foliage volume among trees in ungrazed exotic grasslands was marginally higher than that among trees in ungrazed native grasslands, except for the largest trees (Figs. 2 and 3). This was a surprising result, because exotic ungrazed grasslands had substantially higher fuel loads than ungrazed native grasslands (Kupfer and Miller 2005). Our data therefore suggest the possibility of overcompensation for loss of branch growth through the production of ground sprouts, such that severely burned trees actually might produce a greater foliage volume than less severely burned trees, at least through five postfire growing seasons.

Results of our study also suggest that susceptibility of mesquite to fire damage and mortality was higher among previously-burned trees than among those that had been unburned for more than 30 years, even though the prior burn had occurred 15 years earlier (Fig. 4). Mortality resulting from the 1987 fire was only 6% (Bock and Bock 1992) among the same group of trees on the same set of 22 plots where mortality was 18% following the second fire in 2002. This suggests that there was nothing about the location or attributes of the twice-burned trees that made them inherently more vulnerable to fire

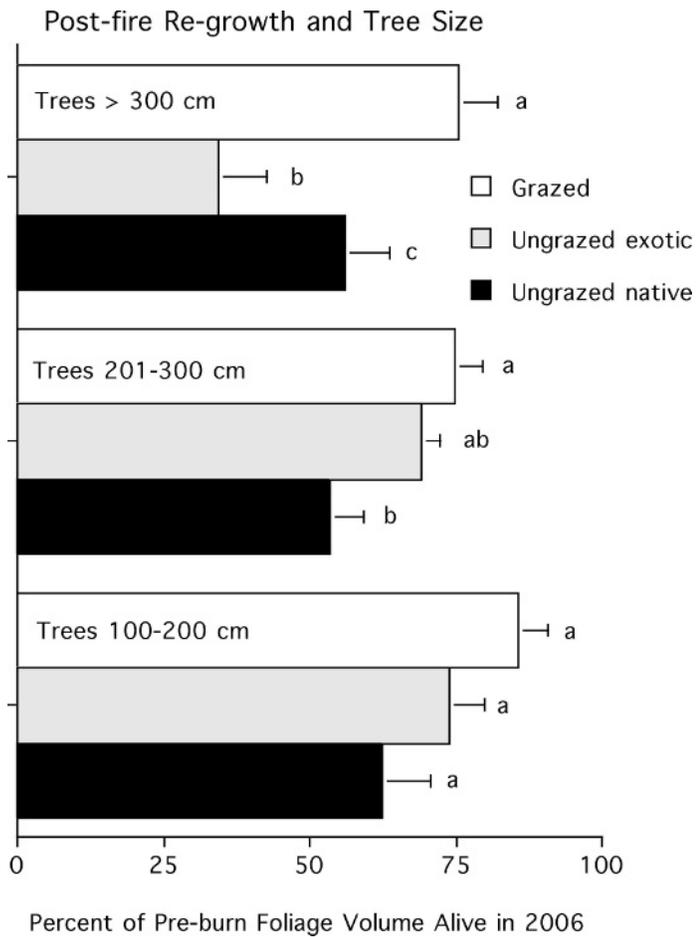


Figure 3. Mean (SE) percentage of preburn foliage volume alive, including ground sprouts, for mesquite trees of three height classes in three grassland habitats, during the fifth postfire growing season after a 2002 wildfire. Shared letters indicate homogeneous subsets in pairwise posthoc comparisons of means within size classes.

than the others we measured in 2003–2006, except that they had been burned twice in 15 years instead of only once.

Although our sample size was small (12 trees killed out of 66 in twice-burned ungrazed grasslands), an 18% mortality rate should be sufficient to control mesquite with repeated burning. Importantly, the mortality and severe damage we measured among twice-burned trees was restricted neither to very small individuals nor to exotic grasslands. Fire-killed trees included individuals up to 3.3 m tall, the majority of which were in native ungrazed grasslands. Furthermore, postfire recovery of twice-burned trees that survived both fires was much lower in native than in exotic ungrazed grasslands (Fig. 4). A fire-return interval of less than 15 years, involving three or four rather than just two burns, could well result in even greater damage and mortality, but this possibility remains to be tested.

MANAGEMENT IMPLICATIONS

Our results, although limited in scope, support the hypothesis that repeated fire was an important factor limiting velvet mesquite in prehistoric southwestern grasslands (Bahre and

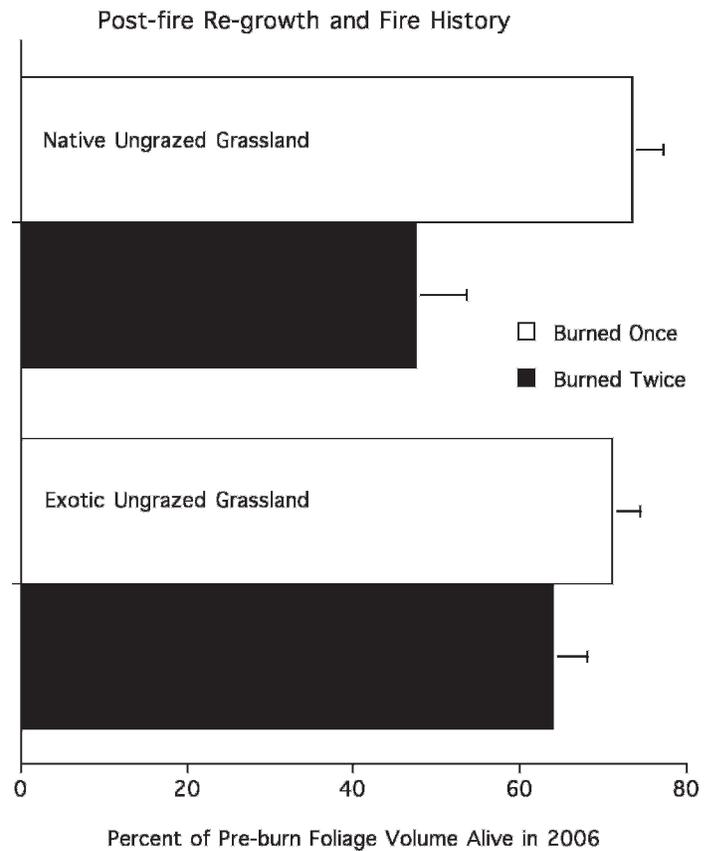


Figure 4. Mean (SE) percentage of preburn foliage volume alive in 2006, for mesquite trees in ungrazed native and ungrazed exotic grasslands that survived a 2002 wildfire, separated into trees from an area that also had burned in a 1987 fire ($n = 25$ in native and 29 in exotic grasslands) vs. trees in an area that had not burned in the earlier fire ($n = 42$ in native and 41 in exotic grasslands).

Shelton 1993; McPherson 1995). However, most attempts to control velvet mesquite with prescribed fire on contemporary rangelands have been marginally successful at best, whether sites were burned once (Reynolds and Bohning 1956; Martin 1983) or twice within 3 years (Cable 1967), because all but the smallest top-killed trees quickly recovered through ground sprouts (McClaran 2003). In exotic grasslands, livestock exclusion combined with repeated burning did not reduce velvet mesquite canopy (Geiger and McPherson 2005). However, results of the present study suggest that trees are more likely to be vulnerable to repeated fires in native than in exotic ungrazed grasslands, despite differences in fuels that would predict otherwise.

The most likely circumstances where prescribed fire might be effective against velvet mesquite would be repeated burning under dry conditions, in livestock-free areas where mesquite densities still are low enough to permit heavy growth of herbaceous ground cover (Ansley and Castellano 2006). We recommend further study of fire-induced mesquite damage and mortality under these conditions. Perhaps then Robert Humphrey's (1949:175) optimism about using "fire as a means of controlling velvet mesquite ... on southern Arizona ranges" will prove to have been justified.

ACKNOWLEDGMENTS

D. Ruppel and R. Jelks kindly granted permission to work on the Babacomari and Diamond C ranches, respectively. We thank the following individuals for field assistance: B. Audsley, K. Bishop, T. Crook, D. Goodheim, B. Loomis, A. Marshall, L. Schevets, C. Venot, and C. Wonkka.

LITERATURE CITED

- ANSLEY, R. J., AND M. J. CASTELLANO. 2006. Strategies for savanna restoration in the southern Great Plains: effects of fire and herbicides. *Restoration Ecology* 14:420–428.
- ARCHER, S. 1989. Have southern Texas savannas been converted to woodlands in recent history? *American Naturalist* 134:545–561.
- ARCHER, S. 1995. Tree–grass interactions in a *Prosopis*–thornscrub savanna parkland: reconstructing the past and predicting the future. *Ecoscience* 2:83–99.
- ARCHER, S., D. S. SCHIMMEL, AND E. A. HOLLAND. 1995. Mechanisms of shrubland expansion—land-use, climate or CO₂? *Climatic Change* 29:91–99.
- BAHRE, C. J., AND M. L. SHELTON. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. *Journal of Biogeography* 20:489–504.
- BOCK, C. E., AND J. H. BOCK. 1993. Cover of perennial grasses in southeastern Arizona in relation to livestock grazing. *Conservation Biology* 7:371–377.
- BOCK, C. E., AND J. H. BOCK. 2000. The view from Bald Hill; thirty years in an Arizona grassland. Berkeley, CA: University of California Press. 197 p.
- BOCK, C. E., J. H. BOCK, K. L. JEPSON, AND J. C. ORTEGA. 1986. Ecological effects of planting African lovegrasses in Arizona. *National Geographic Research* 2:456–463.
- BOCK, C. E., J. H. BOCK, W. R. KENNEY, AND V. M. HAWTHORNE. 1984. Responses of birds, rodents, and vegetation to livestock enclosure in a semidesert grassland site. *Journal of Range Management* 37:239–242.
- BOCK, J. H., AND C. E. BOCK. 1992. Vegetation responses to wildfire in native versus exotic Arizona grassland. *Journal of Vegetation Science* 3:439–446.
- BUFFINGTON, L. D., AND C. H. HERBEL. 1965. Vegetation changes on a semi-desert grassland range from 1958 to 1963. *Ecological Monographs* 35:139–164.
- CABLE, D. R. 1967. Fire effects on semidesert grasses and shrubs. *Journal of Range Management* 20:170–176.
- DREWA, P. B. 2003. Effects of fire season and intensity on *Prosopis glandulosa* Torr. var. *glandulosa*. *International Journal of Wildland Fire* 12:147–157.
- FUHLENDORF, S. D., F. E. 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.
- GEIGER, E. L., AND G. R. MCPHERSON. 2005. Response of semi-desert grasslands invaded by non-native grasses to altered disturbance regimes. *Journal of Biogeography* 32:895–902.
- GLENDENING, G. E., AND H. A. PAULSON, JR. 1955. Reproduction and establishment of velvet mesquite as related to invasion of semidesert grasslands. Technical Bulletin Number 1127. Washington, DC: US Department of Agriculture. 50 p.
- HUMPHREY, R. R. 1949. Fire as a means of controlling velvet mesquite, burroweed, and cholla on southern Arizona ranges. *Journal of Range Management* 2:173–182.
- KUPFER, J. A., AND J. D. MILLER. 2005. Wildfire effects and post-fire responses of an invasive mesquite population: the interactive importance of grazing and non-native herbaceous species invasion. *Journal of Biogeography* 32:453–466.
- MARTIN, S. C. 1983. Responses of semidesert grasses and shrubs to fall burning. *Journal of Range Management* 36:604–610.
- MCCCLARAN, M. P. 2003. A century of vegetation change on the Santa Rita Experimental Range. In: M. P. McClaran, P. F. Ffolliott, and C. B. Edminster [TECHNICAL COORDINATORS]. Proceedings: Santa Rita Experimental Range: 100 years (1903–2003) of accomplishments and contributions. Ogden, UT: US Department of Agriculture, Forest Service, RMRS-P-30. p. 16–33.
- MCLAUGHLIN, S. P., E. L. GEIGER, AND J. E. BOWERS. 2001. Flora of the Appleton–Whittell Research Ranch, northeastern Santa Cruz County, Arizona. *Journal of the Arizona–Nevada Academy of Science* 33:113–131.
- MCPHERSON, G. R. 1995. The role of fire in desert grasslands. In: M. P. McClaran and T. R. Van Devender [EDS.]. The desert grassland. Tucson, AZ: University of Arizona Press. p. 130–151.
- MCPHERSON, G. R. 1997. Ecology and management of North American savannas. Tucson, AZ: University of Arizona Press. 208 p.
- OWENS, M. K., J. W. MACKLEY, AND C. J. CARROLL. 2002. Vegetation dynamics following seasonal fires in mixed mesquite/acacia savannas. *Journal of Range Management* 55:509–516.
- REYNOLDS, H. G., AND J. W. BOHNING. 1956. Effects of burning on a desert grass-shrub range in southern Arizona. *Ecology* 37:769–777.
- SAS PUBLISHING. 1999. Statview 5.0.1. Cary, NC: SAS Institute. 528 p.
- SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry. New York, NY: W. H. Freeman. 859 p.
- VAN AUKEN, O. W. 2000. Shrub invasions of North American semiarid grasslands. *Annual Review of Ecology and Systematics* 31:197–215.
- WESTER, D. B. 1992. Viewpoint: replication, randomization, and statistics in range research. *Journal of Range Management* 45:285–290.