Long-Term Effects of a Summer Fire on Desert Grassland Plant Demographics in New Mexico

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Abstract

Plant demographic responses to an experimental summer fire were monitored for 12 yr on the Sevilleta National Wildlife Refuge, New Mexico, to determine recovery rates of burned plants and evaluate fire effectiveness in preventing shrub invasion of desert grasslands. Fourteen common species of grasses, shrubs, yucca, and cacti were measured for mortality, resprouting, regrowth, herbivory, and reproduction. After the first postfire growing season, black grama (*Bouteloua eriopoda* [Torr.] Torr.) declined 80% in size, whereas blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths) exhibited no decline. Linear regression indicated that *B. eriopoda* needed 11 yr to recover. Spike dropseed (*Sporobolus contractus* A.S. Hitchc.) and purple three-awn (*Aristida purpurea* Nutt.) showed postfire declines in plant sizes, requiring 4- and > 5-yr recovery times, respectively. Sand muhly (*Muhlenbergia arenicola* Buckl.) exhibited no fire impact. Snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby) sustained 61% fire mortality and reduction in regrowth canopy size. Creosotebush (*Larrea tridentata* [Sesse & Moc. ex DC.] Coville) had 12% mortality, but survivors recovered over 12 yr. Fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.) sustained 62% mortality, but recovered plant size in 5–6 yr. Winterfat (*Krascheninnikovia lanata* [Pursh] A. D. J. Meeuse & Smit) suffered 7% mortality, but required 9+ yr to recover. Pale desert-thorn (*Lycium pallidum* Miers) survived fire, recovering prefire canopy size in 3 yr. Torrey joint-fir (*Ephedra torreyana* Watson) exhibited < 1% mortality, and recovered in 2–3 yr. Soapweed yucca (*Yucca glauca* Nutt.) had < 2% mortality, recovered plant sizes in 2 yr, and increased numbers of rosettes 17%. Chollas (*Opuntia imbricata* [Haw.] DC. and *Opuntia clavata* Engelm.) suffered high mortality rates and required > 12 yr recovery times. Results demonstrated that summer fire may counter some shrub and cacti invasion in central New Mexico, but once shrubs mature, fire is less effective in removing woody plants to restore southwestern grasslands.

Resumen

Las respuestas demográficas de vegetación a un fuego experimental de verano fue monitoreado por 12 años en el Refugio Nacional de Fauna Silvestre Sevilleta, Nuevo México, para determinar las tasas de recuperación de plantas quemadas y evaluar la eficacia del fuego para la prevención de invasiones de arbustos en los pastizales de desierto. Catorce especies comunes de pastos, arbustos, yuca y cactus fueron medidas para determinar la mortalidad, el rebrote, el crecimiento, la herbívoria y la reproducción. Después de la primera temporada de crecimiento posterior a la quema, el tamaño de la navajita negra (*Bouteloua eriopoda* [Torr.] Torr.) disminuyó en un 80%, mientras que la navajita azul (*B. gracilis* [Willd. ex Kunth] Lag. ex Griffiths) no mostró ninguna disminución. El modelo de regresión linear indica que *B. eriopoda* necesitó 11 años para recuperarse. El zacate espigado (*Sporobolus contractus* A.S. Hitchc.) y el zacate tres barbas (*Aristida purpurea* Nutt.) también mostraron una reducción en el tamaño de las plantas después del fuego, y necesitaron 4 y >5 años de recuperacion respectivamente. El mal forrage (*Muhlenbergia arenicola* Buckl.) no mostró ningún efecto al fuego. El romerito (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby) sufrió una mortalidad de 61% y una reducción el rebrote del tamaño del dosel por el incendio. La gobernadora (*Larrea tridentata* [Sesse & Moc. ex DC.] Coville) tuvo una mortalidad de 12%, pero las plantas sobrevivientes se recobraron en 12 años. El chamiso (*Atriplex canescens* [Pursh] Nutt.) sufrió 62% de mortalidad, pero el tamaño de planta se recuperó en 5–6 años. EL senecio (*Krascheninnikovia lanata* [Pursh] A. D. J. Meeuse & Smit) sufrió una mortalidad de 7%, pero tomo 9+ años para recuperarse. La mora de lobo (*Lycium pallidum* Miers) sobrevivió el fuego, recuperando tamaño del dosel en 3 años. La caniatilla (*Ephedra torreyana* Watson) mostró <1% mortalidad y se recuperó en 2–3 años. La yuca (*Yucca glauca* Nutt.) tuvo una mortalidad menor al 2%, recobró su tamaño en 2 años y aumentó el número de panículas en 17%. Las chollas (*Opuntia imbricata* [Haw.] DC. y *O. clavata* Engelm.) mostraron altas tasas de mortalidad y requirieron >12 años para su recuperación. Los resultados demuestran que un incendio en verano podria contrarrestar la invasión de arbustos y cactus en el centro de Nuevo Mexico, pero una vez que los arbustos están establecidos, el fuego es menos efectivo para remover plantas leñosas y restaurar los pastos del suroeste.

Key Words: desertification, grazing, herbivory, prescribed fire, range restoration, shrub invasion

INTRODUCTION

The importance of rangeland fires in the southwestern United States has long been recognized in deterring the invasion of woody plant species into grasslands (e.g., Humphrey 1958; Kozlowski and Ahlgren 1974). Most temperate and subtropical grasslands are fire-maintained ecosystems, and their resident

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species have evolved to coexist with fire (Wright and Bailey 1982; DeBano et al. 1998). Fire has the ability to kill aboveground portions of grasses, forbs, and woody plants, but belowground meristematic tissues of some perennial species survive and resprout. Although numerous plant species, particularly woody plants with well-established root systems, can produce stump-sprouts and recover from fire, young plants with insufficient root mass often die in grassland fires (Humphrey 1958; Bahre 1991). As such, recurrent fires in grasslands can prevent establishment of young shrubs and cacti, thus maintaining an open grassland ecosystem. The reduction of rangeland fire frequency in the American Southwest during the 20th century, due to both active suppression and fine fuel removal via high stocking rates of livestock, has likely contributed to the ongoing expansion of desert scrub vegetation into former arid and semiarid grasslands (Bahre 1991; McPherson 1995).

In the Rio Grande valley of New Mexico, desert shrub species have steadily increased their distributions and densities at the expense of grasslands (Branscomb 1958; Buffington and Herbel 1965; York and Dick-Peddie 1969; Hennessy et al. 1983; Grover and Musick 1990). The current "front" of northward-moving desert shrubland is presently located in Socorro County on the Sevilleta National Wildlife Refuge (NWR). Formerly a Spanish land grant and cattle ranch, the Sevilleta NWR sustained historically high stocking rates of sheep (1800s through mid-1940s) and cattle (1940s–1970s). Natural or prescribed fires were essentially nonexistent during this time (based on lack of fire scars in nearby piñon–juniper savannas; Betancourt et al. 1993). The Sevilleta NWR was established in early 1974, and all livestock were removed from the refuge during 1974–1976. Vegetation changes since 1976 have been substantial in short-grass steppe habitats on the Sevilleta NWR, with grasses becoming dominant in place of forbs; shrub-dominated habitats have changed little during this time, indicating that shrub expansion has slowed (Ryerson and Parmenter 2001). Natural fires from lightning strikes on the Sevilleta NWR have been common as the grassland fuel load increased following livestock removal, and prescribed fires have become a management tool of the US Fish and Wildlife Service staff.

The purpose of the present study was to assess the impact of prescribed, experimental summer fires on the native plant populations in a short-grass steppe ecotone area located on the edge of a shrub-dominated Chihuahuan Desert scrubland (Peters et al. 2006). Scattered shrubs, yucca, and cacti have already become established in the Sevilleta NWR grasslands, and with future climate change (warming temperatures) and increasing CO_2 (Archer 1995; Polley et al. 1997, 2002; Morgan et al. 2007), additional desert woody plant expansion is anticipated. However, fire is hypothesized to prevent further establishment of woody plants in this area, and may play an important role in reducing or eliminating established woody species already on site. Thus, the specific objective of the experiment was to determine the impact of fire (mortality/survivorship, regrowth rates, reproduction, and postfire impacts of native herbivores) on each of 14 species of common grasses, shrubs, yucca, and cacti that occur in the short-grass steppe of the Sevilleta NWR.

METHODS

Study Area

This study was conducted on the Sevilleta NWR, Socorro County, New Mexico. The Sevilleta NWR encompasses nearly 100 000 ha, including two mountain ranges (Los Pinos Mountains and Sierra Ladrones) with the Rio Grande valley in between. The refuge straddles transition zones between the Chihuahuan Desert, the Great Plains short-grass steppe, the Colorado Plateau shrub-steppe, and the Mogollon mixed-conifer woodlands. Since its formation, the Sevilleta NWR has been managed by the US Fish and Wildlife Service for conservation, research, and environmental education. The Sevilleta NWR became part of the National Science Foundation's Long Term Ecological Research (LTER) network in 1988 (Parmenter 1999).

The prescribed fire experiment was undertaken in an ecotonal zone of Chihuahuan Desert scrubland and short-grass steppe in the southeastern portion of a broad plain known locally as McKenzie Flats (lat 34°18′18″N, long 106°41′10″W; elevation 1 610 m). The site was dominated by a variety of grasses, including blue grama (*Bouteloua gracilis* [Willd. ex Kunth] Lag. ex Griffiths), black grama (*Bouteloua eriopoda* [Torr.] Torr.), purple three-awn (*Aristida purpurea* Nutt.), sand muhly (*Muhlenbergia arenicola* Buckl.) and several dropseeds (of which the most abundant was spike dropseed [*Sporobolus contractus* A.S. Hitchc.]). Scattered shrubs included creosotebush (*Larrea tridentata* [Sesse & Moc. ex DC.] Coville), fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), snakeweed (*Gutierrezia sarothrae* [Pursh] Britt. & Rusby), winterfat (*Krascheninnikovia lanata* [Pursh] A. D. J. Meeuse & Smit), pale desert-thorn (*Lycium pallidum* Miers), and Torrey joint-fir (*Ephedra torreyana* Watson). In some areas, soapweed yucca (*Yucca glauca* Nutt.) was locally abundant. The most common cacti were walking stick cholla (*Opuntia imbricata* [Haw.] DC.) and club cholla (*Opuntia clavata* Engelm.). Soils were classified as Berino-Dona Ana association, consisting of fine-loamy, mixed, thermic Typic Haplargids (Johnson 1988); slope was nearly flat (approximately 1%–2%) with a northwest aspect. Mean annual precipitation (1989–2006) on McKenzie Flats was 244 mm, with a mean daily minimum temperature of -7.3°C in January and a mean daily maximum of 33.2°C in July. Precipitation patterns during the study (1991–2004) are shown in Figure 1 (Sevilleta LTER, Deep Well meteorological data: http://sev.lternet.edu/).

Experimental Prescribed Fire Design

As part of a collaborative effort between the Sevilleta LTER program and the US Fish and Wildlife Service, a series of controlled burns on experimental plots were conducted in July 1993. Sixteen 9-ha plots (300×300 m, separated by 300-m interspaces) were established in a 4×4 grid pattern on McKenzie Flats in 1991; eight plots were randomly assigned to a prescribed fire treatment, and the other eight were not burned. Preburn measurements of grasses and snakeweed (see methods below) were taken in 1991, 1992, and early summer 1993. Postfire plant recovery measurements were begun in autumn 1993. US Fish and Wildlife Service fire records for the Sevilleta NWR indicated that the area of the experiment had

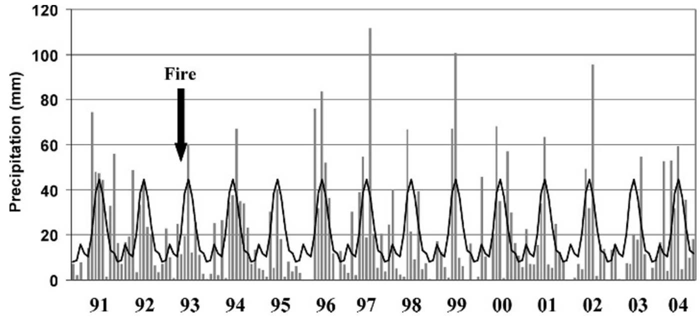

Figure 1. Precipitation patterns during the study period, 1991–2004, on McKenzie Flats, Sevilleta National Wildlife Refuge, New Mexico. Histograms represent total monthly precipitation amounts; line indicates long-term monthly means. Experimental fires were conducted in July 1993. Note drought conditions during spring–summer–fall 1995 through winter–spring 1996; summer drought ended with above-average monsoons in July 1996.

not burned since the refuge was formed (1974), giving a period of at least 20 yr since the last possible range fire; however, with high livestock stocking rates and low fuel loads (based on early 20th century photographs) on McKenzie Flats during prerefuge times, it was possible that fire had not occurred on the site for many decades.

Experimental Prescribed Fire Weather Conditions

Most natural fires on the Sevilleta NWR occur in early to midsummer when vegetation is dry (premonsoon) and ignition events from lightning are common. The objective of this experiment was to simulate, to the greatest extent possible, the effects of a natural fire on vegetation by burning during this time of year. Personnel from the US Fish and Wildlife Service conducted the burns during 6–9 July 1993. The burns were implemented under the prescription of wind speeds of 8–24 $m \cdot s^{-1}$, and relative humidity $< 20\%$. During the burns, daytime maximum temperatures averaged 36.8°C, and relative humidity averaged 15.3% (range = 13.5%–18.7%; weather data from the Sevilleta LTER Deep Well meteorological station on McKenzie Flats, located approximately 5 km northwest of the burn plots). Wind speeds during the burn days averaged $3.2 \pm 0.6\ m \cdot s^{-1}$ (hourly mean $\pm 95\%$ CI), with mean maximum wind speeds of $11.4 \pm 3.3\ m \cdot s^{-1}$; the maximum wind gust speed was $14.3\ m \cdot s^{-1}$. In contrast, wind speeds during thunderstorms in 1993 ($n = 22$ storms) on McKenzie Flats were characterized by mean hourly wind speeds of $5.0 \pm 0.7\ m \cdot s^{-1}$ and mean maximum wind speeds of $10.9 \pm 1.5\ m \cdot s^{-1}$, with a maximum gust speed of $21.8\ m \cdot s^{-1}$. As such, the mean hourly wind speeds on burn days were significantly slower than during actual thunderstorms (3.2 vs. $5.0\ m \cdot s^{-1}$, t test with unequal variances, $P < 0.001$), but mean maximum wind speeds were not significantly different between burn days and thunderstorms (11.4 vs. $10.9\ m \cdot s^{-1}$, t test with unequal variances, $P = 0.796$).

Experimental Prescribed Fire – Fuel Loads and Fire Behavior

Prior to the fires in May 2003, canopy cover of total plant species on McKenzie Flats averaged 40.8% (data from Sevilleta LTER Program: http://sevilleta.unm.edu/research/local/plant/transect/documents/cover_sum.lst), dominated by black grama (24.7% cover) and blue grama (7.9%); herbaceous plant litter cover averaged 29%. Aboveground herbaceous plant biomass (oven-dried) was spatially extremely variable, with typical values on unburned areas of McKenzie Flats (measured in 1989–1992) averaging $192 \pm 52\ g \cdot m^{-2}$ (mean $\pm 95\%$ CI; D. Moore, unpublished Sevilleta LTER data, 1992).

Fires were ignited using drip torches, and personnel took extra effort to reignite areas that did not burn completely because of patchy fuel loads or light wind conditions to achieve maximum fire coverage. Flame heights were dependent on fuel loads and wind speeds at various times of day, and varied from 20 cm during light wind in grass fuels to 2 m in higher winds when burning creosotebush with accumulated subcanopy piles of Russian thistle (*Salsola kali* L.). Flame-front rate of spread varied from $1.5\ m \cdot min^{-1}$ through grasses under light winds, up to $12\ m \cdot min^{-1}$ when burning through creosotebush/Russian thistle stands. The Sevilleta Refuge Manager ensured that all vegetation study subplots (see below) within the eight large fire plots were completely burned.

Plant Measurements

Plants were measured using two taxon-specific methods: grasses and snakeweed were sampled using a repeat-photographic analysis technique; larger shrubs, yucca, and cacti were mapped and sampled with direct measurements/observations for plant size and condition. Grasses and snakeweed were sampled on 12 subplots on each of the 16 large 9-ha experimental plots (total of 192 subplots). Subplots were 3×4 m rectangles permanently marked in the corners with steel rebar stakes, and were randomly distributed across each 9-ha plot. Subplots were sampled with a boom-camera instrument consisting of a camera suspended approximately 5 m off the ground with a Gimble mount from a portable bipod support structure. A field technician with an infrared remote control triggered the camera when it was centered over the plot, and a color slide of the plot was produced (Kodak® Ektachrome® ASA 200 film, shutter speed 1 000, F22). Each plot had four bright orange caps placed on the corner stakes to clearly mark the subplot corners in the photographs; a color chart and plot-identifying label also appeared in each photograph. Following the first preburn photographic sampling in 1991, color prints of the slides were taken to the field sites, and all plants in each photograph were ground-truthed for positive species identifications. Subplots were photographed prior to the experimental fires during the summer for 2 yr (1991 and 1992), and again in June 1993. Following the fires in July 1993, repeated photographs were taken for 5 yr each October during 1993–1997.

In the laboratory, large-format color prints of the slides were examined to identify individual plants of the dominant grass species for size change measurements. Individual grass patches had to be clearly distinguishable in all photographs through time, and had to have survived over the course of the study (1991–1997). Technicians then took measurements of plant diameter, and in the case of ring-forming grasses (e.g., blue grama and sand muhly), ring width. For black grama, a stoloniferous grass, the number of "patches" composing an individual also was recorded; i.e., a single "individual" black grama patch in a prefire photograph would actually be composed of several stolon-generated basal stem clusters. In the postfire photograph, these separate basal clusters could be identified, counted, and measured. Through time, as these small "patches" regrew, they would expand and coalesce, eventually re-forming the original large patch. The measurements from the photographs allowed the calculation of the time required to restore the original grass architecture in the subplots. Plants from both burned and unburned plots were selected for statistical comparisons.

Snakeweed was included in this portion of the fire study, in spite of it being a small, woody shrub. Its small canopy size was conducive to including it in the photographic analyses, rather than the woody vegetation measurements (described below). From the photographs, samples of 134 snakeweed plants (67 on burned plots, 67 on unburned) were measured annually to assess not only regrowth rates, but mortality rates as well.

Woody plants species (shrubs, yucca, cacti) were measured to determine the mortality and regrowth recovery rates following fire; as such, only woody plants that actually burned in the fires were measured. To acquire an adequate population sample size of the common species, individuals of woody plants were mapped and measured on three of the eight burned plots following the fires in 1993. A rodent live-trapping "web" (see Parmenter et al. 2003 for trap web description) had been installed on each 9-ha plot, with permanent, numbered steel rebar stakes. Using these stakes as permanent reference points, field technicians surveyed each 9-ha plot and located all burned shrubs, yucca, and cacti. The experimental fires had killed the aboveground parts of these plants, but had not consumed the branches and upper leaves; hence, woody plant species could be easily identified to species, verified that they had been alive before the fire, and accurately measured postfire for height and diameter. Each burned plant was mapped using a compass direction and distance from the nearest rodent trap stake. Plants were then measured for height and canopy diameter. Observational data on evidence for presence of stump sprouts, herbivory, flowering, and seed awns or fruits were recorded. Postfire recovery of woody plants was measured annually for 5 yr (1993–1997), and at 9 and 12 yr postfire (2001 and 2004, respectively).

Statistical Analyses

In all analyses of plant demographic variables, individual plants were treated as the experimental units (replicates); hence, species-specific sample sizes were determined by the actual number of individual plants found within the burned areas that met the criteria for long-term sampling (see Methods: Plant Measurements above). This approach acknowledged that the collective population of plants would be exposed to a range of localized fuel loads, and hence, variable fire temperatures and fire duration. As such, the analyses were designed to test for postfire demographic responses of the overall plant populations subjected to the experimental fires.

Pre- and postfire differences among burned and unburned grass populations of each species were analyzed using repeated measures analysis of variance (RMANOVA). Data on plant or patch size/numbers from prefire measurements (1991 through June 1993) were analyzed first to assess any preexisting differences between treatments or years. A second analysis tested fire effects after the burns. For snakeweed, a RMANOVA was used for prefire evaluation of burned/unburned populations; however, because of the high postfire mortality suffered by this species, repeated measures could not be employed for postfire analyses (because of the large number of missing cells). Instead, separate analyses of variance (ANOVAs; with unequal sample sizes) were used for each postfire year. The significance level for all analyses was set at $P \leq 0.05$.

For all shrub, cholla, and yucca species, the analyses for postfire effects were predicated on the condition that the individuals had been severely burned (verified by field inspections). Therefore, statistical analyses were designed to evaluate and quantify the postfire trends of the incremental recovery patterns relative to the mean initial prefire plant size (heights and canopy diameters) of the same individuals. For both grasses and woody plants, linear regression models were fit to postfire plant data to estimate time (years) for each species to fully recover from the fire in terms of plant height and canopy size. Mortality of burned woody plants was recorded over the period of study, and if mortalities occurred during the first two postfire growing seasons, these events were interpreted to be directly related to fire-induced factors. In view of the observed extremely low "background" (i.e., non–fire related) mortality rates of these long-lived shrub species (e.g., Bowers et al. 1995; Webb 1996; Ryerson and Parmenter 2001), annual shrub mortality under natural nonfire conditions was assumed to be negligible. For example, in northern Arizona, Webb (1996) documented 23 desert shrub species and 10 cacti and yucca that live >100 yr, including many genera and species examined in this study (e.g., creosotebush, four-wing saltbush, joint-fir, thornbush, and yucca).

RESULTS

Grasses

Black Grama. Fire had a large negative impact on black grama in terms of both patch size and patch number (Figs. 2A and 2B). Prefire results indicated no differences in mean patch size ($n = 22 \cdot \text{treatment}^{-1}$) between treatments ($P > 0.73$) or years ($P > 0.46$); however, postfire differences were highly significant for the fire treatment ($F = 8.48$, df = 1,42, $P < 0.006$), years ($F = 7.86$, df = 4,168, $P < 0.0001$), and treatment × years interaction ($F = 3.13$, df = 4,168, $P < 0.016$). The fire burned virtually all aboveground biomass, reducing the mean plant patch size from 0.71 m^2 to zero; regrowth during the summer of 1993 regained some of the patch size, finishing the season at 0.12 m^2 (Fig. 2A). Steady incremental increases in patch size continued during 1994–1997, but after five growing seasons, black grama had only recovered 51% of its prefire patch size. Linear regression analysis of patch recovery through time predicted full recovery would be achieved in 11 yr ($patch[m^2]) = 0.062(years) + 0.05$, $r = 0.99$, df = 3, $P < 0.01$). The fire also increased the number of patches (Fig. 2B), with significant differences for treatment ($F = 18.84$, df = 1,42, $P < 0.001$), years ($F = 10.25$, df = 4,168,

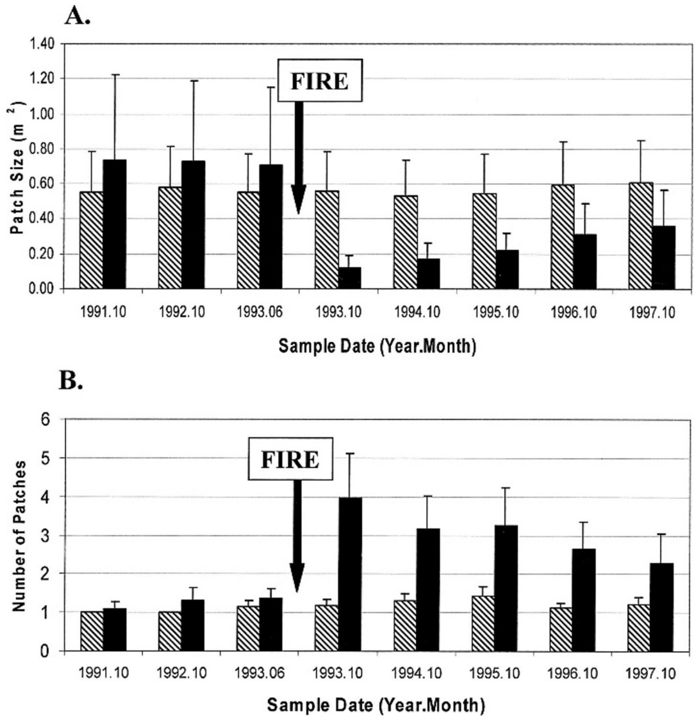

Figure 2. Fire-induced changes in **A**, black grama (*Bouteloua eriopoda*) plant patch size and **B**, patch numbers on the Sevilleta National Wildlife Refuge, New Mexico. Fire treatment occurred in July 1993. Diagonal lined bars indicate unburned; solid black bars, burned. Error bars represent 95% confidence interval of the mean.

$P < 0.0001$), and treatment × years interactions ($F = 6.58$, df = 4,168, $P < 0.0001$). Given a prefire arbitrary value of each plant representing one patch, the fire exposed an average of four smaller basal stem clusters after the first growing season (Fig. 2B, postfire). As black grama recovered through time, these patches expanded and coalesced, thereby reducing patch numbers as patch size increased. Linear regression analysis indicated that 8.3 yr would be required for black grama patches to combine sufficiently to form the original prefire patch configuration ($patch\ number = -0.39[years] + 4.23$, $r = 0.96$, df = 3, $P < 0.01$). Although not directly measured in this study, mortality of black grama during another fire experiment on McKenzie Flats in 1993 was reported to be 31% (see Gosz and Gosz 1996). Black grama did not produce seed until 1994 during the second growing season after the fire.

Blue Grama. In contrast to black grama, blue grama (a ring-forming grass in central New Mexico) showed no significant changes to the fire treatment. Prefire results indicated no difference in patch size ($n = 20 \cdot \text{treatment}^{-1}$) between treatments, although patch size did decline slightly between 1991 and June 1993 ($F = 5.44$, df = 2,76, $P < 0.006$). Although postfire patch size continued to fluctuate significantly through time ($F = 2.48$, df = 4,152, $P < 0.047$), there were no significant treatment effects observed. Similarly, the ring width of each patch exhibited no significant differences before or after the fire treatment. In a previous report on mortality and biomass production for blue grama on McKenzie Flats, Gosz and Gosz (1996) found only 8% mortality from the fire, and biomass production by October 1993 was statistically indistinguishable between burned and unburned plants. Blue grama successfully produced seed by October 1993, the same growing season in which it was burned.

Spike Dropseed. The response of spike dropseed ($n = 12 \cdot \text{treatment}^{-1}$) to fire was similar to that of black grama, but recovery was much faster (Fig. 3). The prefire results indicated no differences between treatments or years, but significant differences for postfire patch size values for years ($F = 11.76$, df = 3,88, $P < 0.0001$) and treatment × years interactions ($F = 6.55$, df = 3,88, $P < 0.0001$); the fire treatment was nearly significant ($F = 3.45$, df=1,22, $P < 0.077$). Postfire patch size recovery was achieved in 4 yr ($patch[m^2]) = 0.016(years) + 0.012$, $r = 0.98$, df = 3, $P < 0.01$. Field observers found no individuals with seed in October 1993; most spike dropseed plants did not produce seeds until 1994, two growing seasons postfire.

Purple Three-Awn. Fire had a substantial impact on purple three-awn, and postfire recovery patterns appeared to be inhibited by the drought of 1995–1996 (Fig. 4). Prefire results showed no differences in plant size ($n = 12 \cdot \text{treatment}^{-1}$) between treatments, although significant fluctuations through time were observed ($F = 4.63$, df = 2,40, $P < 0.016$). Following the experimental burns, purple three-awn exhibited highly significant fire treatment differences ($F = 21.93$, df = 1,20, $P < 0.0001$) and yearly differences ($F = 5.48$, df = 4,80, $P < 0.0006$). Plant patch size regrowth appeared to be rapid in 1993–1994, and may have attained prefire size by 1995, except that the severe drought in 1995–1996 apparently curtailed growth. By 1997, the burned plants had still not fully recovered their former patch size (Fig. 4). Still, some plants burned in 1993 successfully produced seeds in the spring of 1994.

Sand Muhly. The response of sand muhly, the other ring-forming grass in the study, was very similar to that of blue grama, in that there were no impacts from the experimental fires ($n = 11 \cdot \text{treatment}^{-1}$); however, changes through time were observed for both patch size ($F = 4.82$, df = 6,120, $P < 0.0002$) and ring width ($F = 3.59$, df = 6,120, $P < 0.003$). Field observations of the study area did not record any mortality of sand muhly, and as was the case with blue grama, some individuals produced seed stalks by October 1993.

Shrubs

Snakeweed. Fire impacts on snakeweed proved substantial in terms of both canopy size (Fig. 5A) and population size (Fig. 5B). The original sample population declined from 67 shrubs per treatment in 1993 to a total of five per treatment in 1997. The experimental fire resulted in the immediate deaths of 41 shrubs (61%), and of the 26 shrubs remaining in the burned sample population, half of those died the following year. The unburned population also sustained some mortality during 1993–1995, but suffered major losses during the drought of 1995–1996 (Fig. 5B). Two postfire individuals that appeared to be dead in the dry autumn of 1995 resprouted in 1996, but then died by 1997. Mean canopy size of snakeweed declined by 81% following the fire ($F = 107.82$, df = 1,412, $P < 0.0001$), and surviving individuals never regained their prefire size (Fig. 5A).

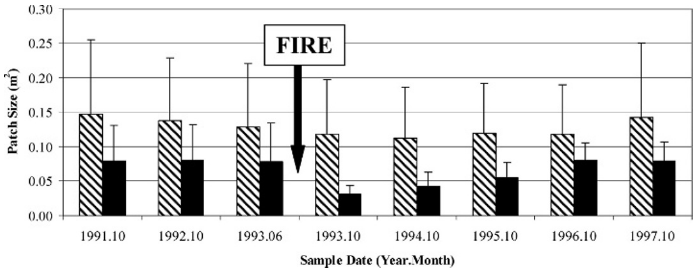

Figure 3. Fire responses of spike dropseed (*Sporobolus contractus*) patch size on the Sevilleta National Wildlife Refuge, New Mexico. Fire treatment occurred in July 1993. Diagonal lined bars indicate unburned; solid black bars, burned. Error bars represent 95% confidence interval of the mean.

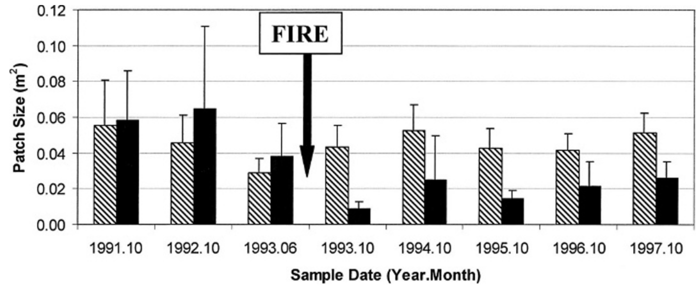

Figure 4. Fire responses of purple three-awn (*Aristida purpurea*) patch size on the Sevilleta National Wildlife Refuge, New Mexico. Fire treatment occurred in July 1993. Diagonal lined bars indicate unburned; solid black bars, burned. Error bars represent 95% confidence interval of the mean.

Separate ANOVAs for each postfire year (1993–1997) corroborated this result. Snakeweed plants subjected to fire were not observed to flower and produce seed until 1994, two growing seasons after the fire.

Creosotebush. Within the study area examined for woody vegetation, 82 burned creosotebush were mapped and measured through time. Most shrubs had all their aboveground biomass killed by the fire; a few had an occasional branch still alive. Many of the shrubs were severely charred due to the accumulation of dried, wind-blown Russian thistle beneath the canopy that substantially increased the fuel load; flames in such circumstances typically exceeded 2 m high (R. R. Parmenter, personal observation, July 1993). Only two shrubs (2.4%) died from the fire; the remaining 80 produced sprouts at ground level shortly after the fire. Of these, eight additional shrubs had died by autumn 1994, for a total of 12.2% mortality from the fires. The surviving stump-sprouts continued to grow annually, reaching prefire shrub height in 12 yr, and nearly achieving their prefire diameter in that time (Figs. 6A and 6B). The severe drought summer of 1995 (year 3 in Figs. 6A and 6B) did not appear to inhibit the regrowth of creosotebush. Flowers and fruits were first observed on the regrowing stump sprouts in 1995 during the third postfire growing season. Herbivores, principally black-tailed jackrabbits (*Lepus californicus* Gray), commonly fed upon the stump sprouts, clipping off the tips of branches to consume cambium layers of the stems. Discarded branch tips and clusters of jackrabbit feces under the shrub were often observed, particularly in first postfire period of 1993 when 22 of 72 surviving shrubs (31%) sustained jackrabbit herbivory. Herbivory levels varied over the years, from a low of 1.5% in 1994 to 64% in 2004. However, no additional postfire mortality was observed during this time, and at the end of 2004, all 72 surviving creosotebush appeared large and healthy.

Fourwing Saltbush. Unlike creosotebush, fourwing saltbush sustained high mortality rates from the fires. Of the 26 shrubs monitored, 15 (58%) failed to resprout in 1993 following the fire, and another individual died in 1994 for a total mortality of 62%. The surviving shrubs produced stump-sprouts shortly after the fire, and these grew quickly in both canopy diameter and height (Figs. 7A and 7B). The severe drought year of 1995 (year 3 in Figs. 7A and 7B) appeared to arrest regrowth, but growth continued in 1996 and subsequent years. Prefire shrub height was achieved in five growing seasons, and prefire diameter was estimated to have recovered in 6 yr (extrapolated from data in Fig. 7A; [*patch diameter* (*cm*)] = 8.65[*years*] + 12.40, $r = 0.98$, df = 4, $P < 0.001$). Fruits were first observed in 1997, during the fifth growing season after the fire. Herbivores (apparently rabbits, and possibly mule deer [*Odocoileus hemionus* (Rafinesque)]) browsed stump-sprout branch tips of fourwing saltbush, with an incidence of 55% in 1993. Herbivory varied from 10%–30% during 1994–1997, but no browse damage was detected in 2001 and 2004.

Winterfat. Of a sample of 30 winterfat shrubs, only two (7%) were killed by the fire. Stump-sprouts produced shortly after the fire grew quickly for the first 2 yr (1993–1994), but the drought of 1995–1996 caused a decline in both canopy area and height (Figs. 8A and 8B). Growth following the drought slowly increased height and diameter, with prefire shrub height being attained in postfire year 9. Shrub diameter had achieved 88% of prefire size by year 12, and was extrapolated to recover prefire canopy diameter in 14 yr ([*patch diameter* (*cm*)] = 1.63[*years*] + 26.75, $r = 0.78$, df = 5, $P < 0.05$). In spite of the relatively slow regrowth rates, most winterfat shrubs set seed each year starting in 1995, only three growing seasons after the fire. Herbivory on winterfat stump-sprouts was common, with 46% of shrubs sustaining browsing impacts in 1993 after the fire. Herbivory levels during the following years varied from 0% to 20%.

Pale Desert-Thorn. This species was relatively rare on the experimental area, with only five shrubs having been burned. However, pale desert-thorn proved to be a fire-tolerant species, suffering no fire mortality and recovering quickly. Stump-sprouts recovered the prefire canopy size in only three growing seasons (Fig. 9A), although total prefire height was not achieved until 9 yr postfire (Fig. 9B). Fruit and seed production was observed in 1996, during the fourth postfire growing season. No herbivore impacts were observed during 1993–1995, but herbivores browsed three of the shrubs (60%) in 1996 and two shrubs (40%) in 1997. Two of the shrubs had died by the 2001 sample. In 2004, the three remaining shrubs all sustained considerable herbivory levels, as evidenced by the decline in mean canopy diameter and height in Figures 9A and 9B.

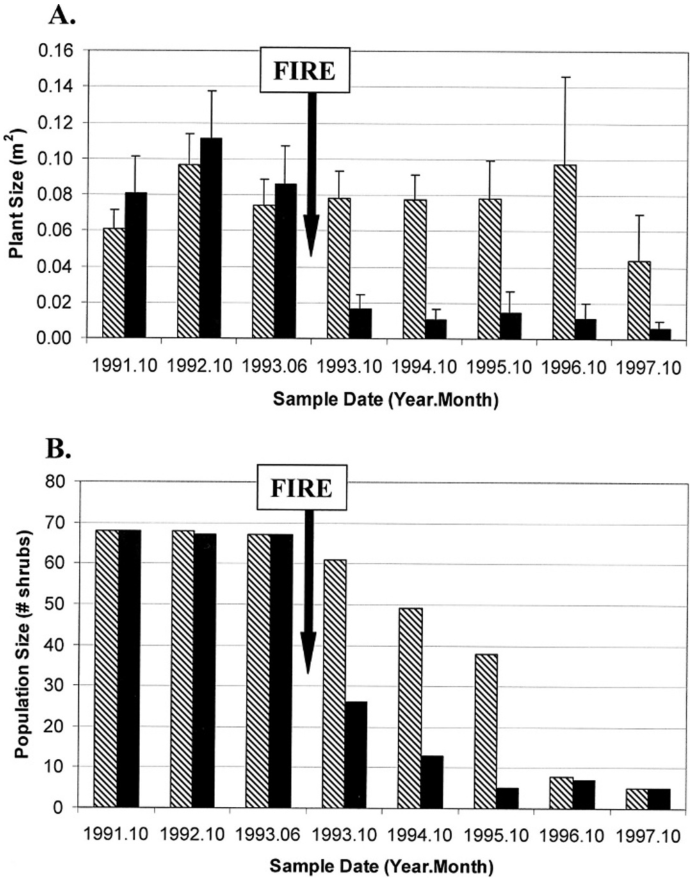

Figure 5. Fire responses of **A,** snakeweed (*Gutierrezia sarothrae*) plant canopy size and **B,** plant population size on the Sevilleta National Wildlife Refuge, New Mexico. Fire treatment occurred in July 1993. Diagonal lined bars indicate unburned; solid black bars, burned. Error bars represent 95% confidence interval of the mean.

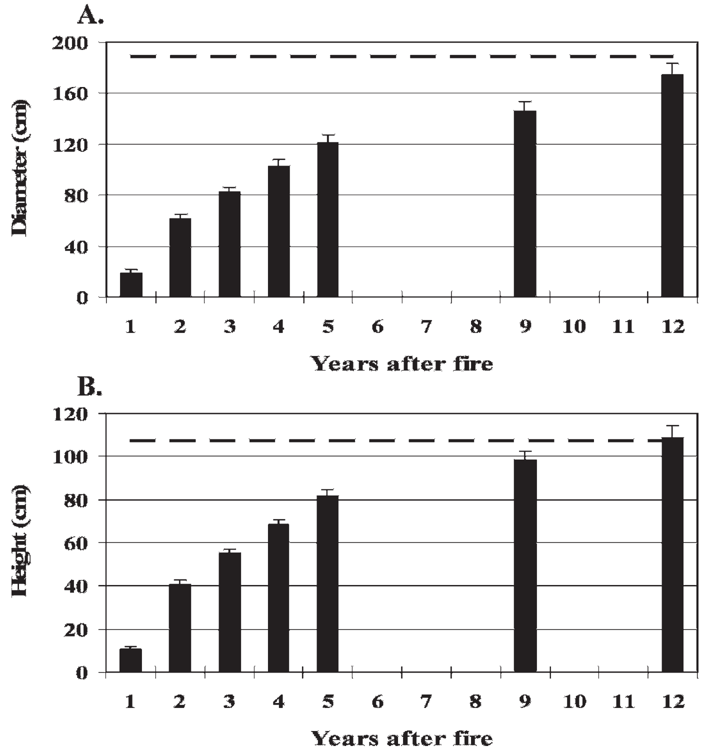

Figure 6. Postfire regrowth patterns of creosotebush (*Larrea tridentata*) on the Sevilleta National Wildlife Refuge, New Mexico. **A,** Shrub canopy diameter. **B,** Shrub height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

Torrey Joint-Fir. This diminutive shrub species appeared to be the most fire-adapted shrub species on the study site. Of a sample population of 137 individuals, only a single plant (0.7%) failed to regenerate after the fire. Shortly after the fire, large numbers of stump-sprouts (dozens to hundreds per shrub) were produced, and these grew quickly (Figs. 10A and 10B). Prefire height was achieved in the second growing season (Fig. 10B), with prefire canopy size being equaled by year 3 (Fig. 10A). Shrub height following the fire actually exceeded the mean shrub height before being burned, and this difference was sustained for at least through 2001. The drought of 1995–1996 did not appear to impact Torrey joint-fir, as it had already regrown to prefire conditions. Reproduction was first recorded in 1995, with cones and cone scars visible during the third postfire growing season. Herbivores utilized Torrey joint-fir heavily during the first postfire growing season, with 76% of shrubs showing evidence of browsing in 1993. In subsequent years, however, herbivory levels declined, ranging from 1% to 18% between 1994 and 2001. Only one additional Torrey joint-fir plant died during the study.

Yucca

Soapweed yucca also appeared to be very well adapted to fire, suffering only a single mortality (1.6%) from a sample population of 62 individuals. Postfire regrowth of the vegetative rosettes occurred very quickly from stump-sprouts, with prefire plant size being accomplished in two growing seasons (Figs. 11A and 11B). As with Torrey joint-fir shrubs, the postfire plant size exceeded the prefire size, and this size increase was perpetuated through 2001. Reproductive flowering stalks with fruits and seeds were first observed in 1997, during the fifth postfire growing season.

In addition, fire stimulated an increase in the number of rosettes produced per plant. The number of yucca rosettes before the fire was $2.44 \cdot \text{plant}^{-1}$, and this number initially dropped significantly 22% after the fire to $1.91 \cdot \text{plant}^{-1}$ in the autumn of 1993 (RMANOVA, $F = 7.03$, $\text{df} = 6{,}325$, $P < 0.00001$). But in 1994, the mean number of rosettes significantly increased 64% to $3.14 \cdot \text{plant}^{-1}$. Rosettte numbers then slowly declined in subsequent years (1995: $2.98 \cdot \text{plant}^{-1}$; 1996: $2.85 \cdot \text{plant}^{-1}$; 1997: $2.77 \cdot \text{plant}^{-1}$) and stabilized at a significantly higher mean of $2.86 \cdot \text{plant}^{-1}$ through 2001, resulting in an average 17% increase in rosette numbers from prefire levels. A RMANOVA LSD test showed significant differences between rosette means in prefire 1993, postfire autumn 1993, and 1994–2001 (LSD $\text{df} = 325$, $P < 0.05$). Herbivores (blacktailed jackrabbits and woodrats [*Neotoma micropus* Baird and *Neotoma albigula* Hartley]) heavily utilized soapweed yucca, with 48% of plants browsed after the fire in 1993. Browsing continued in subsequent years, varying in intensity from 0% to 38%, with the drought summer of 1995 having the 38% browsing level.

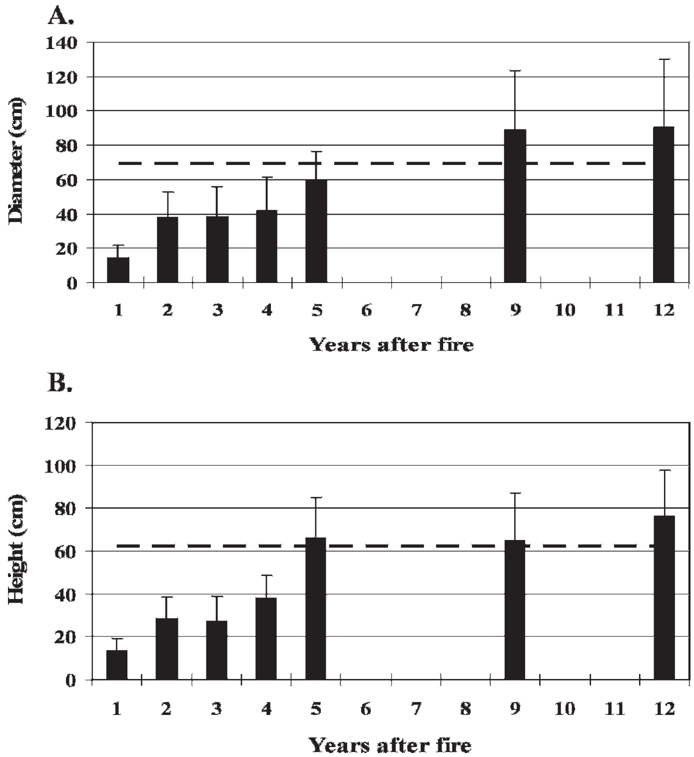

Figure 7. Postfire regrowth patterns of fourwing saltbush (*Atriplex canescens*) on the Sevilleta National Wildlife Refuge, New Mexico. **A,** Shrub canopy diameter. **B,** Shrub height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

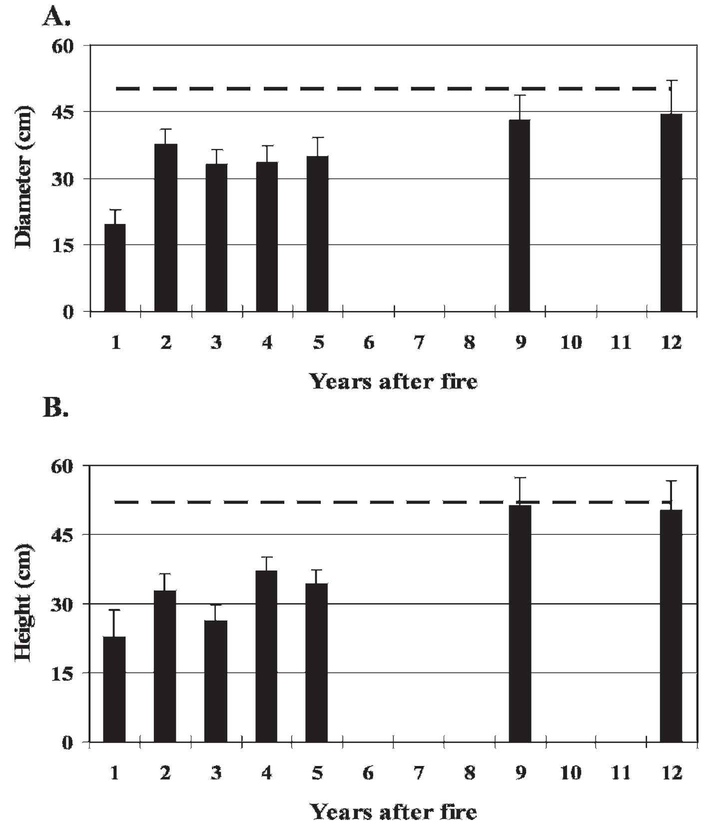

Figure 8. Postfire regrowth patterns of winterfat (*Krascheninnikovia lanata*) on the Sevilleta National Wildlife Refuge, New Mexico. **A,** Shrub canopy diameter. **B,** Shrub height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

Cacti

Walking-Stick Cholla. Of a prefire population of 61 chollas, 39 (64%) were killed outright by the fire. Others died in the following years, such that by 1997 (5 yr postfire), mortality had reached 89%. Smaller individuals (mean of 55 cm high) suffered higher mortality, with larger plants (mean of 71 cm high) surviving because of having a greater stem diameter that resisted the flames and branches that were higher off the ground and farther away from the heat. Some plants were killed aboveground, but produced branch sprouts near the ground shortly after the fire; others survived with live branches at higher levels in the plant. Branch sprouts grew slowly to increase diameter and height (Figs. 12A and 12B), and nearly achieved prefire diameter in 12 yr; however, surviving plants only recovered 71% of their prefire height during that same time. The drought summer of 1995 appeared to slow the regrowth of branch sprouts (year 3 in Figs. 12A and 12B). Fruit production was first observed during 1995, although fruits were generally limited to the larger individuals. Herbivory on walking stick cholla was relatively light (9%) immediately after the fire, and remained low throughout the study, with the exception of the drought summer of 1995, during which time 38% of the chollas were partially fed upon by woodrats.

Club Cholla. This species of cholla is a very low-growing, clump-forming cactus (unlike the tall, single-stalked walking stick cholla described above), whose vulnerability to fire is mostly limited to the clump's periphery where it comes into close contact with more flammable grasses and forbs. Typically, club cholla only grows one to two segments tall, rarely reaching 10 cm in height; hence, postfire regrowth would best be assessed using patch diameter. Of a prefire population of 44 club chollas, the fires inflicted 43% mortality in the first year, and by year 5, mortality had increased to 64%. Patch diameter was reduced by 37% in the fire through loss of peripheral elements, and recovery was very slow (Fig. 13A). Even after 12 yr, patch diameter had not recovered to prefire levels. Plant height remained the same throughout the study, due to the low-growing habit of this species (Fig. 13B). Fruits were first observed in 1997, during the fifth postfire growing season. Herbivory, probably from wood rats, was high shortly after the fires, with 100% of the population showing some sign of herbivore damage; this was generally limited to peripheral sections of the plants, where the fire had burned off the protective spines. Herbivory in later years varied from zero to 26%.

DISCUSSION

The postfire responses of native grassland plant species observed in this study were generally consistent with previous studies from other parts of the Southwest, although some differences were noted. For example, blue grama recovered from burning in a single growing season, and its ability to

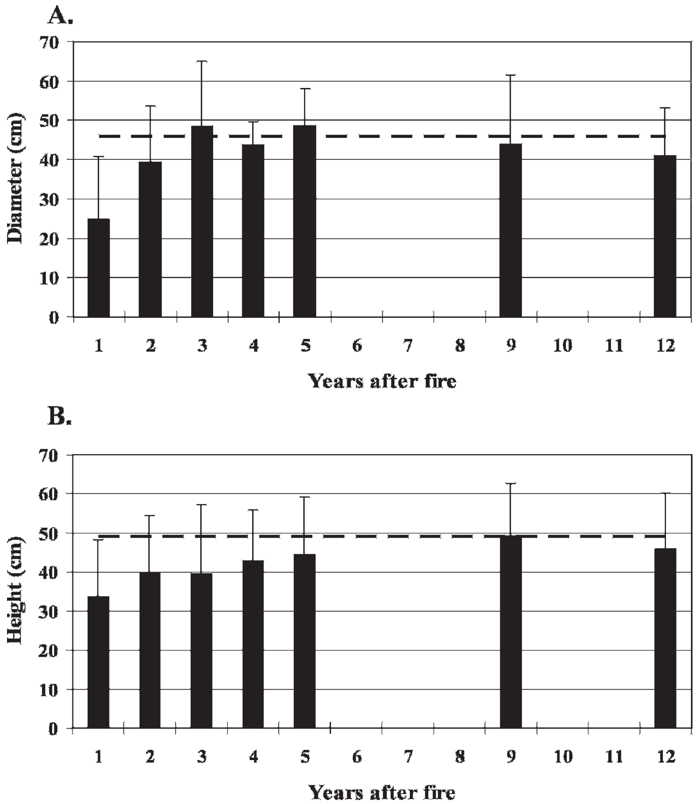

Figure 9. Postfire regrowth patterns of pale desert-thorn (*Lycium pallidum*) on the Sevilleta National Wildlife Refuge, New Mexico. **A**, Shrub canopy diameter. **B**, Shrub height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

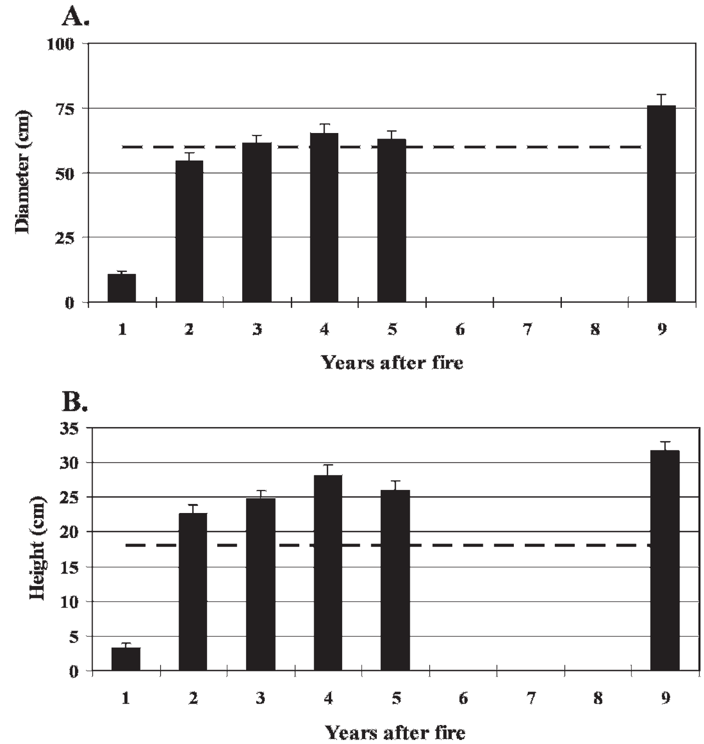

Figure 10. Postfire regrowth patterns of Torrey joint-fir (*Ephedra torreyana*) on the Sevilleta National Wildlife Refuge, New Mexico. **A**, Shrub canopy diameter. **B**, Shrub height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

tolerate burning has been observed in other settings (reviewed by Ford [1999]; see also White and Loftin 2000; Ford 2001). A second ring-forming grass, sand muhly, also showed high tolerance to fire in this study. Although this species apparently has not been studied before with respect to fire, other muhly species show a range of positive and negative responses to fire (Gaines et al. 1958; Dwyer and Pieper 1967; Schripsema 1978; Anderson and Bailey 1979; Wright and Bailey 1980; Andariese 1982; Harris and Covington 1983; Oswald and Covington 1984; Walsh 1995). Black grama exhibited extremely negative responses to fire, with high mortality (Gosz and Gosz 1996) and long recovery time (Fig. 2). Similar negative fire responses in black grama have been noted throughout its range (Reynolds and Bohning 1956; Jameson 1962; Cable 1965; Wright 1980; Drewa and Havstad 2001; Peters and Gibbens 2006). The other grass species examined in this study (purple three-awn and spike dropseed) also showed negative fire impacts and multiyear recovery times, a finding that is generally consistent with previous studies on *Aristida* (Christensen 1964; Trlica and Schuster 1969; Wright 1974; Steuter and Wright 1983) and *Sporobolus* species (Hopkins et al. 1948; Christensen 1964; Stinson and Wright 1969; Wright 1980; Rasmussen et al. 1986; Higgins et al. 1989; but see Schacht and Stubbendieck 1985 for positive fire effects on *Sporobolus*).

Shrub species also displayed a range of responses to fire in this study, some of which appeared unusual with regard to previous studies. The most conspicuous divergence from current understanding was creosotebush, which in this study suffered only 12% mortality, with all surviving plants produced stump sprouts. In contrast, previous studies on fire and creosotebush have reported mortality rates of 61%–97% (Dalton 1962; McLaughlin and Bowers 1982; Brown and Minnich 1986), and several authors have described creosotebush as poorly adapted to fire because of its limited sprouting ability (Humphrey 1974; Brown and Minnich 1986); however, if fire does not kill the root crown, resprouting and regrowth can be rapid (O'Leary and Minnich 1981; Loftin 1987). The Sevilleta NWR is at the northern edge of the range of creosotebush, and the cooler temperatures and higher precipitation on this site, compared to other desert regions of the Southwest, may have contributed to the high survival and regrowth rates.

Other shrub species in this study exhibited high mortality and slow recovery times, particularly snakeweed and fourwing saltbush. Snakeweed has been found to be particularly susceptible to fire (Christensen 1964; Britton and Ralphs 1979; Humphrey 1984; Gatewood 1992) although it occasionally shows little response (e.g., Drewa and Havstad 2001) or recovers within several years (Christensen 1964). Fourwing saltbush is known to be poorly adapted to frequent fires, but can stump-sprout following low-intensity fires (Wright and Bailey 1980; Conrad 1987).

In contrast, several shrub species in this study appeared to be fire tolerant, with low fire-induced mortality but variable recovery times. Torrey joint-fir and pale desert-thorn both showed high survivorship and recovered in 2–3 yr. Torrey

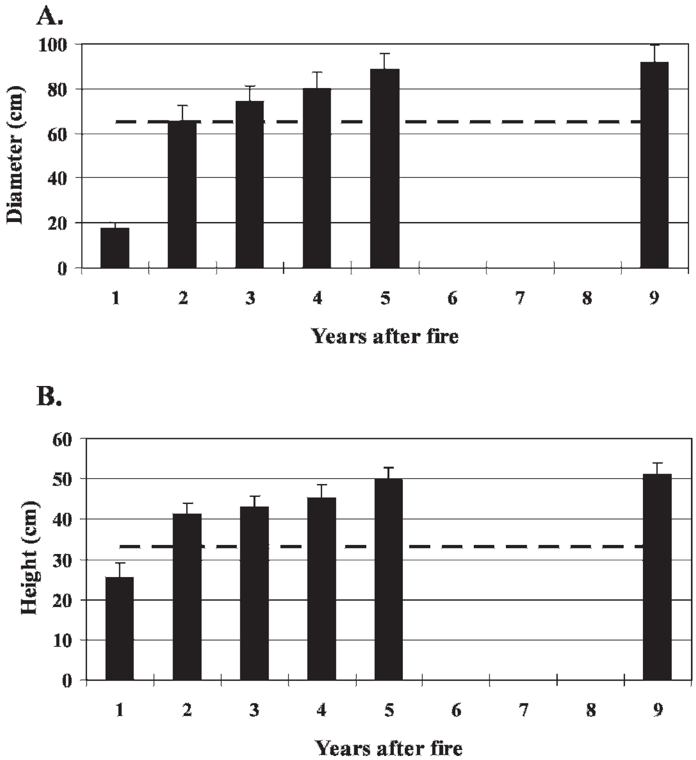

Figure 11. Postfire regrowth patterns of soapweed yucca (*Yucca glauca*) on the Sevilleta National Wildlife Refuge, New Mexico. **A**, Plant canopy diameter. **B**, Plant height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

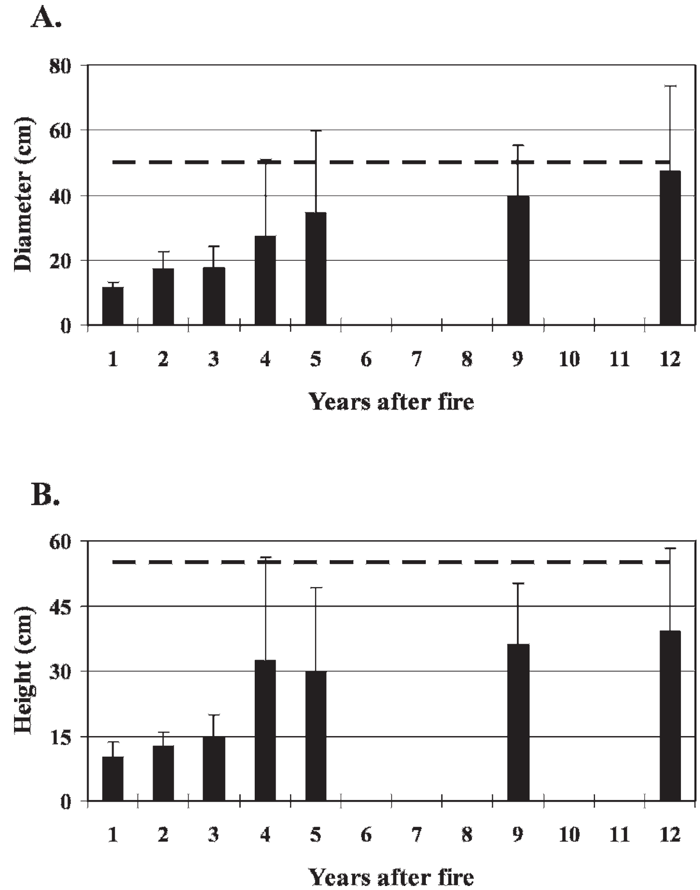

Figure 12. Postfire regrowth patterns of walking stick cholla (*Opuntia imbricata*) on the Sevilleta National Wildlife Refuge, New Mexico. **A**, Plant canopy diameter. **B**, Plant height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

joint-fir and pale desert-thorn have not been studied previously for fire responses, but pale desert-thorn was believed to stump sprout after low-severity fires (Loftin 1987). Winterfat also exhibited low mortality, though prefire size recovery was slow; however, survivors began producing seed very quickly. Previous studies of fire impacts on winterfat indicated that fire intensity was very important, with severe fires causing 100% mortality (Pellant and Reichert 1984) and light fires allowing resprouting (Dwyer and Pieper 1967).

Soapweed yucca also proved to be tolerant of fires, recovering quickly via sprouting following top kill of above-ground portions of the plants; fire actually stimulated a 17% increase in the number of postfire sprouts per plant. As with some shrub species, previous research has shown that fire intensity plays a role in survivorship and recovery of soapweed yucca, with low-intensity burns allowing greater survival (Webber 1953; Masters et al. 1988; Higgins et al. 1989).

Chollas (both walking stick cholla and club cholla) in this study were highly susceptible to fire, with high mortality rates and slow recovery times. This result was consistent with previous findings in which chollas were reduced in density and cover following fire in desert grasslands, and that smaller plants were more susceptible to fire-induced mortality than larger plants (Humphrey 1949; Reynolds and Bohning 1956; Cable 1967; Wright 1972; Martin 1983).

The collective results of this study demonstrated the wide range of responses to summer fire of the dominant grassland plant species in the middle Rio Grande valley of New Mexico. Many of these native plants appeared to be fire tolerant, and had the capacity not only to survive and regrow quickly, but also to reproduce within several growing seasons after being burned. A few species of grasses, shrubs, and cacti were more susceptible to fire impacts, suffering moderate to high mortality with survivors requiring longer time periods to recover. Considering all the recovery times of the 14 species observed in this study, it would appear that most of the grassland's dominant species would have recouped their prefire sizes (diameters and heights) within 10–12 yr.

Pre-historic fire return intervals in the arid and semiarid grasslands of the Southwest are not definitively known, and even surrogate estimates from historic postsettlement records are biased (fire return interval estimates are probably too long) because of fine fuel removal by cattle, sheep, and horses during the high livestock stocking levels in the 19th and 20th centuries. Nonetheless, minimum fire return interval estimates based on existing historic records, known species-specific postfire recovery times, and fire scar records on nearby trees have ranged from 5 to 15 yr (Johnsen 1962; Wright and Bailey 1982; also see review by McPherson [1995] and references therein). The results of this study in the middle Rio Grande valley appear consistent with this range of values as a minimum estimate of fire return interval, because it takes approximately a decade for

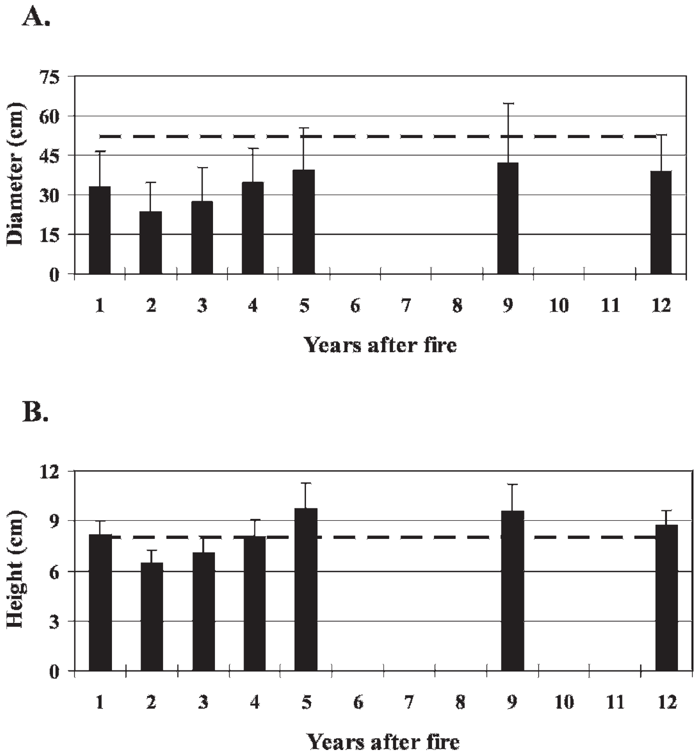

Figure 13. Postfire regrowth patterns of club cholla (*Opuntia clavata*) on the Sevilleta National Wildlife Refuge, New Mexico. **A,** Plant canopy diameter. **B,** Plant height. Histograms are means; error bars, 95% confidence intervals of the mean. Dashed horizontal line represents prefire mean value.

vegetation architecture (both vertical and horizontal) to recover to prefire values. Whether or not the actual fire return interval is on a decadal order here remains to be seen; intense grazing operations continue in the Rio Grande valley, and even on the Sevilleta NWR, the presence of graded roads prevents natural fires from realizing their full potential areal extent (e.g., in the history of the Sevilleta NWR, a natural or prescribed grassland fire has never crossed a graded road [US Fish and Wildlife Service Sevilleta NWR, unpublished fire history data]). It is likely that fire return intervals are greater than 10 yr, and may actually occur only two to three times per century, given existing constraints on fuel loads and uninterrupted fuel dispersion patterns.

MANAGEMENT IMPLICATIONS

The data from this experimental fire study have shown that summer fire can reduce shrub and cholla densities in central New Mexico, although the magnitudes of the responses are species-specific. Creosotebush, one of the major shrub species responsible for desertification of Southwestern rangelands, mostly survived the experimental fire in this study. The shrubs studied were large, well-established individuals, and future fire experiments will need to be conducted to determine if multiple, sequential fires can increase shrub mortality in this and other woody plant species (e.g., White et al. 2006). Although not greatly effective in removing mature creosotebush on this study site, fire may likely play an important long-term role in preventing recruitment of seedling creosotebush shrubs into the population. As such, continued use of natural and prescribed fires in this environment is recommended.

Summer fire had a deleterious effect on some grasses (particularly black grama), but surviving grass clumps showed steady recovery during the first five postfire growing seasons. Other grass species (blue grama and sand muhly) were only minimally affected by fire, and recovered within a single growing season. As such, the use of summer fire as a management tool had a range of positive, negative, and neutral impacts on the native range flora on this study site, and for land managers, the trade-offs of temporary reductions in desirable grass species must be balanced against the benefits of reducing woody plant densities and recruitment. The results of this study indicated that natural and prescribed summer fires can be successfully utilized by land managers for maintaining the physiognomic character of the shortgrass-steppe ecosystem in central New Mexico.

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