Protection from livestock fails to deter shrub proliferation in a desert landscape with a history of heavy grazing

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Abstract. Desertification is often characterized by the replacement of mesophytic grasses with xerophytic shrubs. Livestock grazing is considered a key driver of shrub encroachment, although most evidence is anecdotal or confounded by other factors. Mapping of velvet mesquite (*Prosopis velutina*) shrubs in and out of exclosures in 1932, 1948, and 2006 in semiarid grasslands of southeastern Arizona, USA, afforded the opportunity to quantify livestock grazing effects on mesquite proliferation over 74 years in the absence of fire to test the widespread assumption that livestock grazing promotes shrub proliferation. In 1932, shrub cover, density, and aboveground biomass were compared on grazed (12%, 173 plants/ha, 4182 kg/ha) and newly protected areas (8%, 203 plants/ha, 3119 kg/ha). By 1948, cover on both areas increased to ~18%; yet, density on the protected area increased 300% (to 620 plants/ha), nearly twice that of the grazed area (325 plants/ha). From 1932 to 1948, differences in recruitment of new plants and growth of existing plants were reflected in biomass, which was higher on the protected area (415 plants/ha, 8788 kg/ha) relative to the grazed area (155 plants/ha, 7085 kg/ha), although mortality was equally low (~0.06%). In 2006, 42 years after an herbicide application reset mesquite cover to ~10% on both areas, aboveground mesquite mass was comparable on both areas (~4700 kg/ha), but cover and density on the protected area (22%, 960 plants/ha) exceeded that on the grazed area (15%, 433 plants/ha). Mesquite mass in 2006 was substantially below 1948 levels, so continued accrual is likely. That shrub recovery from herbicides on a biomass basis was much less than recovery on a cover basis suggests that remotely sensed biomass estimates should integrate land management history. Contrary to widely held assumptions, protection from livestock since 1932 not only failed to deter woody-plant proliferation, but actually promoted it relative to grazed areas. Results suggest (1) that thresholds for grassland resistance to shrub encroachment had been crossed by the 1930s, and (2) fire management rather than grazing management may be key to maintaining grassland physiognomy in this bioclimatic region.

Key words: arid rangelands; land cover change; land use legacy; livestock grazing; mesquite; Prosopis velutina; shrub encroachment; shrub proliferation; Sonoran Desert; woody biomass.

INTRODUCTION

Desertification is a global environmental problem (Millennium Ecosystem Assessment 2005). In many arid and semiarid rangelands, desertification is characterized by the replacement of mesophytic grasses with xerophytic shrubs and bare ground. This land cover change has ramifications for nutrient cycling (e.g., Wessman et al. 2004), primary production (e.g., Knapp et al. 2008), erosion (Neff et al. 2008, Okin et al. 2009*b*), and sustainable land use (Lambin et al. 2007). Livestock grazing is widely regarded as a driver in the process of woody-plant encroachment (Bahre 1991, Skarpe 1992, Archer 1994); however, evidence in support of this

assumption is mixed (Scholes and Archer 1997, Sankaran et al. 2008) and often casually inferred. Grazing–climate–fire interactions may be amplified or constrained by soils, topography, and land use history, thereby complicating the task of disentangling the contributions of individual drivers (House et al. 2003, Sankaran et al. 2005).

Direct assessments of livestock grazing as a driver of shrub proliferation are also hampered by six challenges that span spatial and temporal scales, as well as the availability of requisite data. First, information needed to assess livestock grazing pressure (e.g., stocking density, distribution, seasonality and duration of grazing) is seldom available. Second, livestock grazing influences on ecosystem processes are strongly mediated by seasonal and interannual variation in precipitation (e.g., Fensham 1998, Heitschmidt et al. 2005). Precipitation records often do not exist in drylands, and when they do, they are not generally distributed in a manner needed to capture the high degree of spatial variability. Third, long-term experimental manipula-

tions or observations are required to elucidate livestock grazing effects on vegetation (e.g., Mashiri et al. 2008). Fourth, grazing alters processes that influence patterns of vegetation at multiple spatial scales. Seed dispersal, trampling, dung deposition, and the selective utilization of plants influence fine-scale patterns, while alteration of fine-fuel biomass and continuity influence broad-scale disturbances such as fire (Archer 1994, Fuhlendorf et al. 2008). Fifth, effects of grazing may persist for decades following the removal of livestock, especially where soil erosion has occurred. Finally, the longevity of many woody species requires a multi-decadal perspective to capture the net outcome of climate–grazing interactions on recruitment, mortality, and stand development.

Shifts from herbaceous to woody-plant dominance constitute a potentially significant, but highly uncertain component of the North American terrestrial carbon budget (SOCCR 2007; Barger et al., *in press*). Recent efforts to understand the effects of land use on global change highlight the need to quantify the effects of livestock grazing on biomass and carbon pools, particularly in relation to woody-plant proliferation (Asner and Archer 2010). Projections of biomass change require knowledge of plant population structure (Hurtt et al. 2002), and long-term perspectives on plant demographics are required to predict the effects of livestock grazing on woody-plant stand development and biomass.

Long-term approaches to quantifying the effects of livestock grazing on shrub dynamics range from field observations to analysis of remotely sensed imagery. Logistical constraints associated with field data collection (Brown 1950) and persistence of treatment for livestock removal experiments render field-based studies problematic (Bock et al. 1993). Remote-sensing studies (e.g., Laliberte et al. 2004) offer the opportunity to characterize changes in woody-plant abundance over long timescales and large areas, but are typically unable to adequately quantify woody-plant population size-class structure due to detection limitations and the inability to clearly distinguish individual plants (Browning et al. 2008, 2009). Long-term field-based assessments indicate that relative to protected areas, livestock grazing can promote (60-year study by Yanoff and Muldavin 2008), have no effect (e.g., 17-year study by Glendening 1952), or dampen increases in shrub cover (35-year study by Smeins and Merrill 1988). Thus, robust generalizations have yet to emerge, perhaps owing to species-specific ecology and confounding interactions between soils, climate, and historic land use. Here, we used a unique data set spanning 74 years holding soils and climate constant with contrasting land use (i.e., livestock grazing) histories to quantify the effects of livestock removal on woody-plant cover, recruitment, and aboveground biomass.

Mesquite (*Prosopis* spp.) is a leguminous shrub that has extensively invaded semidesert grasslands in the southwestern United States. Its encroachment has been coincident with the intensification of livestock grazing in the late 1800s/early 1900s (Archer 1995, Fredrickson et al. 2006), but has livestock grazing promoted its invasion? We addressed this question using spatially explicit shrub census data from 1932, 1948, and 2006 to quantify changes in velvet mesquite (*P. velutina* var. Woot.) density, cover, biomass, and population structure on sites with a long-term history of livestock grazing and protection from livestock. Specifically, we sought to determine: (1) if livestock grazing promotes mesquite recruitment and increases in cover, density, and biomass as is widely assumed; (2) how removal of livestock in a historically grazed system influences mesquite stand structure over the long term; and (3) how changes in mesquite stand structure on grazed and protected areas translate into changes in aboveground carbon mass.

METHODS

Study site

The study was conducted on the Santa Rita Experimental Range (SRER) in southeastern Arizona, USA (31.8139° N, −110.8886° W; Fig. 1A), where increases in mesquite since 1900 have been well documented (McClaran 2003). Situated on an alluvial fan terrace on the western flank of the Santa Rita Mountains, physiognomy on the SRER ranges from desert scrub at lower elevations (875 m) to oak (*Quercus* spp.) savanna/woodland at the highest elevations (1,400 m). Annual precipitation is bimodal with a pronounced peak in summer (July–September monsoon) and a lesser peak in winter. Mean annual precipitation ranges from 296 mm at 866 m elevation to 498 mm at 1372 m elevation.

The SRER, representative of many of the grasslands of the Southwestern USA (Enquist and Gori 2008), was severely degraded by the turn of the century due to decades of heavy, year-round, unregulated cattle grazing (Fredrickson et al. 1998, Sayre 2002). Cattle were removed shortly after the establishment of the SRER in 1902 to promote vegetation recovery, and then reintroduced in 1916. Year-round grazing was practiced from 1916–1972, with stocking rates steadily decreasing from a maximum of 0.17 animal unit years/ha in 1918 (Fig. 1D; Ruyle 2003). A rotational grazing system (Mashiri et al. 2008) was implemented in 1972 and maintained through the date of our 2006 shrub census.

William McGinnies established two 1.8-ha plots (440 m × 40 m; 31.81346° N, −110.8875° W) in 1932 to evaluate herbivore effects on vegetation on a sandy loam upland ecological site (fine, mixed, superactive, thermic Ustic Paleargids [Breckenfeld and Robinett 2003]; National Resources Conservation Service [NRCS] Ecological Site Reference Number R041XC319AZ) at 1100 m elevation (Fig. 1C). McGinnies mapped the location of all mesquite shrubs and cacti within these plots and measured their canopy dimensions and height. Glendening (1952) replicated field measurements and mapping in 1948, and we extended the historic record
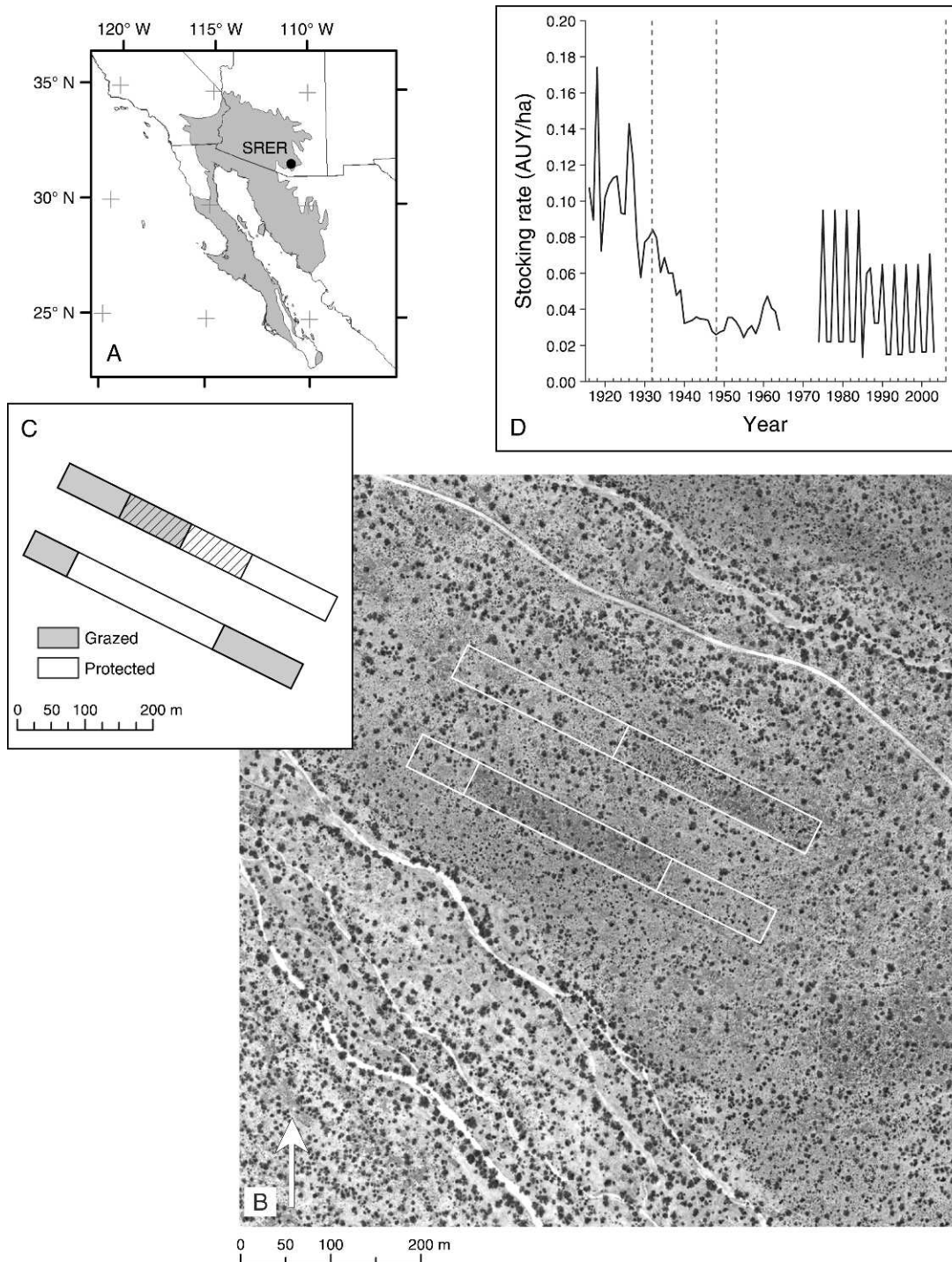
Fig. 1. (A) Location of the Santa Rita Experimental Range (SRER) within the Sonoran Desert biogeographic region in southeastern Arizona, USA, and (B) panchromatic 2005 image illustrating shrubs (dark spots; primarily *Prosopis velutina*) in an herbaceous matrix (gray areas) and the plots established by W. McGinnies in 1932 (outlined in white). (C) Grazed and protected areas within the long-term plots. Hatching in the 200 × 40 m subset of the north plot shows the area inventoried in 2006. The slightly darker shades of gray in protected areas in panel (B) indicate more herbaceous and litter cover. (D) Historic cattle stocking rates (AUY, animal unit years) for the area (from SRER Archive, School of Natural Resources and the Environment, University of Arizona, Tucson, Arizona, USA); dotted vertical lines denote the years when field surveys of plot vegetation were conducted.

with a 2006 field campaign. No fires have been recorded on this study site since the SRER was established.

McGinnies gridded the 1.8-ha plots with rebar at 10-m intervals and subdivided the area to create three treatments: (1) protected from jackrabbits (*Lepus californica eremicus* Allen and *L. alleni* Mearns), cottontails (*Sylvilagus auduboni arizonae* Allen), and cattle; (2) protected from cattle; and (3) accessible to cattle and lagomorphs. All plots were accessible to small mammals (e.g., Merriam [*Dipodomys merriami* Mearns] and banner-tailed [*D. spectabilis* Merriam] kangaroo rats, which are known to cache mesquite seeds [Reynolds and Glendening 1949]).

Glendening (1952) inventoried the plots in 1948 and noted no differences in mesquite cover on areas protected from or accessible to lagomorphs over the 1932–1948 period. Lagomorph exclosures were not maintained after 1948, thus preventing longer term assessments their effects. However, the spatially explicit long-term record permitted us to test for differences in mesquite density between nonoverlapping 20 × 20 m subplots protected for 16 years from lagomorphs and cattle and those protected from cattle only. Densities in 1948 were comparable on 20 × 20 m subplots protected from lagomorphs and livestock ($n = 5$, 27.4 ± 7.5 plants/400 m^2 [mean ± SE]) and on subplots protected only from livestock ($n = 5$, 20.8 ± 4.5 plants/400 m^2) (ANOVA $F_{1,8} = 0.38$, $P = 0.555$). We therefore pooled these treatments.

A 161-ha area encompassing the McGinnies plots was treated with an aerial herbicide (2,4,5-trichlorophenoxy-acetic acid) in May 1964 and 1965 as part of a mesquite management study. Herbicide effects (i.e., mortality, reduction of canopy cover) were not quantified on the long-term plots, but Cable (1976) reported mesquite mortality and canopy cover reductions of 50% and 90%, respectively, where the same herbicide was applied at a nearby site. To determine how the 1964/1965 herbicide might have influenced woody-plant cover, we compared our 2006 cover estimates to cover values from 30 m × 30 m plots not treated with herbicides (under the assumption that the herbicide affected mesquite plants on grazed and protected plots similarly). These plots ($n = 3$) were 1.2 km from the long-term exclosures, occurred on the same soil type, and had the same livestock grazing history. This also afforded an opportunity to determine if mesquite recovery from herbicide application, a land management practice widely applied on western rangelands (Scifres 1980), was influenced by the presence or absence of livestock.

The 1932 and 1948 field measurements were repeated May 2006 (described in the next section). High shrub densities limited this endeavor to a 200 × 40 m portion of the north plot centered on the livestock exclosure treatment boundary (Fig. 1C). This 0.8-ha area encompassed a 100 × 40 m area accessible to lagomorphs and livestock since 1916 (hereafter "grazed area") and an area of equal size protected from livestock since 1932

and protected from lagomorphs from 1932 to 1948, but accessible thereafter (hereafter "protected area").

Field data collection

Canopy diameter and height of woody plants (primarily *P. velutina*; some *Celtis pallida*, *Acacia greggii*, and cacti [*Opuntia* spp.]) were measured to the nearest 0.1 m in 1932. Plants were remeasured in 1948 and their locations mapped with a survey instrument consisting of a telescopic alidade and plane table (Glendening 1952). Rebar marking 10 × 10 m cell corners were geo-coded with a wide area augmentation system (WAAS; minimum 0.5 m positional accuracy) global positioning system (Leica GS20; Leica Geosystems, Heerbrugg, Switzerland) in 2006. We replicated historic canopy and height field measurements (to 0.1 m) for all woody plants within the 200 × 40 m subset of the north plot in May 2006, recorded Universal Transverse Mercator (UTM) coordinates at the bole of each mesquite plant, and translated them to cartesian coordinate space using an affine transformation and 10 ground control points (RMS error = 0.24 m). Canopy diameter was measured along the north–south axis and the longest orthogonal axis.

GIS data processing

Scaled, hand-drawn maps from 1932 and 1948 from the SRER archive were scanned (at 1200 dpi with an Epson 836XL scanner; Epson America, Long Beach, California, USA). Digital maps were spatially registered with ArcMap (version 9.0; ESRI 2004) to a 10 × 10 m grid generated in AutoCad. Point files for 1932 and 1948 plant locations were created within a geographic information system (GIS) database by digitizing plant locations demarcated on the spatially referenced field maps. Unique identifiers were assigned to each plant and field measurements were linked to point file attribute tables. Canopy diameter measurements were used to compute canopy area as that of a circle (see Browning et al. 2009 for validation). Overlapping canopy boundaries were dissolved in ArcMap to generate projected canopy cover to facilitate comparisons with cover estimates from aerial photography.

Mesquite cover and density

Field-estimated cover and plant density were calculated within 20 × 20 m subplots ($n = 10$ grazed, $n = 10$ protected) as per Glendening (1952). Cover and density estimates at this scale were not spatially autocorrelated over time (D. M. Browning, *unpublished data*), thus permitting comparison of 2006 values with those previously reported by Glendening (1952). Normality assessments (studentized residuals) and statistical comparisons were conducted with SAS (version 9.1; SAS Institute 2004). Changes in mesquite cover and density were analyzed using repeated measures analysis of variance (ANOVA). Paired *t* tests were used to evaluate

changes in cover and density; alpha = 0.05 was reduced to account for the appropriate number of comparisons.

Based on observed changes in mesquite cover between 1932 and 1948, Glendening (1952) predicted that landscapes would stabilize at 30% shrub cover. We tested this prediction by computing the probability of mesquite cover increase as the proportion of 20×20 m subplots exhibiting an increase in cover for a given initial condition for the 1932–1948 and 1948–2006 periods. Given the low sample size ($n = 10$ subplots per treatment per time period) and similarities in transition outcomes for grazed and protected subplots (based on preliminary analyses; data not shown), data were pooled across treatments and time periods, yielding 40 transitions.

Population structure and mesquite biomass

Differences in field-measured canopy area and tree height distributions on grazed and protected areas and within treatments across years were assessed using paired Kolmogorov-Smirnoff (K-S) tests; differences in mesquite canopy area and tree height were compared using ANOVA. A site-specific relationship between natural log-transformed velvet mesquite canopy area (CA) and aboveground biomass ($R^2 = 0.97$, $n = 32$ trees; Browning et al. 2008) was used to estimate mesquite biomass. The extent to which the CA–biomass relationship might differ on grazed vs. protected plots is unknown, so we proceeded under the assumption of no differences. Plot-level biomass was calculated by summing individual plant mass in each 0.4-ha grazing treatment. Biomass estimates based on height and basal area yielded results similar to those based on CA (S. R. Archer, *unpublished data*), suggesting these three morphometric variables scale similarly. Combining these variables did not significantly improvement biomass predictions.

RESULTS

Mesquite cover and density

Mesquite density and cover were comparable within 20×20 m subplots on grazed and protected areas in 1932; and density and cover estimates derived from the 0.8-ha area we inventoried were comparable to those reported for the entire 3.6-ha area in 1932 and 1948 by Glendening (1952) (black triangles in Fig. 2). Cover increased significantly and comparably on protected ($t = -5.09$, df = 9, $P = 0.001$) and grazed ($t = -3.38$, df = 9, $P = 0.008$) areas between 1932 and 1948 (Fig. 2A). Herbicide applications in 1964/1965 ostensibly reduced shrub cover on both areas by 90% (Cable 1976), but by 2006, cover had returned to levels statistically comparable to those in 1948 on both grazed ($t = 0.85$, df = 9, $P = 0.417$) and protected ($t = -1.05$, df = 9, $P = 0.323$) areas. Mean ($\pm$SE) mesquite cover on the protected area in 2006 (21.9% $\pm$ 1.8%) was significantly higher than that on the grazed area (15.4% $\pm$ 2.3%). In comparison,

cover on nearby grazed plots with no history of herbicide treatment was 35.6% $\pm$ 2.0%.

Mesquite density increased over both time periods, more so on protected than on grazed areas (Fig. 2B). A significant grazing $\times$ year interaction ($F_{2,17} = 4.3$, $P = 0.031$) reflected increases in plant density between 1932 and 1948 ($t = -4.41$, df = 9, $P = 0.002$) and 1948 and 2006 ($t = -3.99$, df = 9, $P = 0.003$) on the protected area, whereas significant increases in plant density occurred only from 1932 to 1948 ($t = -3.82$ df = 9, $P = 0.004$) on the grazed area. Mesquite density on the protected area was significantly higher than that on the grazed area in 1948 (603 $\pm$ 108 vs. 318 $\pm$ 40 plants/ha) and 2006 (960 $\pm$ 173 vs. 433 $\pm$ 53 plants/ha; Tukey's Studentized Range test, $\alpha = 0.05$; Fig. 2B).

Changes in mesquite cover were spatially heterogeneous over the 74-year period (Fig. 3). The probability of a mesquite cover increase in 20×20 m plots was highest (0.8–1.0) when total cover was <25%, and declined to 0.5 when cover was 26% to 30% (Table 1). Where cover was >30%, the probability of increase was 0.0.

Precipitation

Mean annual precipitation (MAP; from 1922 to 2007 "Rodent Station" rain gauge situated 0.33 km from the study site) was 354 mm, with an average summer (June–September) precipitation of 207 mm (CV [coefficient of variation] = 0.35) and an average winter precipitation (October–May) of 147 mm (CV = 0.47). The time-series rainfall records indicate substantial interannual variability and numerous potential years or periods for episodes of shrub recruitment (e.g., rain years 1932, 1982–1985) and mortality (e.g., 1942–1950, 1974, 1996, and 2002; Fig. 4A).

The long interval between repeated measures of shrub density and cover preclude rigorous statistical assessments of the role of precipitation on mesquite recruitment and mortality. Broadly speaking, 53% of years between 1932 and 1948 surveys experienced rainfall 0.5 standard deviations (SD) or more below the long-term average; and 18% of the years were >0.5 SD above the long-term average. Rainfall between 1948 and 2006 encompassed both dry periods (e.g., from 1948 to 1960, 58% of years were <0.5 SD) and wet periods (e.g., in the 1970s and 1980s, 35% of years had rainfall >1.0 SD of long-term average).

Mesquite population structure

Mesquite canopy area was statistically comparable on grazed and protected areas when the exclosures were established in 1932, although tree height was slightly greater on the grazed area (Fig. 4B, E). Between 1932 and 1948, more mesquite plants appeared on the protected area (166 new plants, 415 new plants/ha) than on the grazed area (62 new plants, 155 new plants/ha). This was also reflected in an increase in number of small plants (canopy area < 1.0 m^2, height < 0.5 m). Owing to
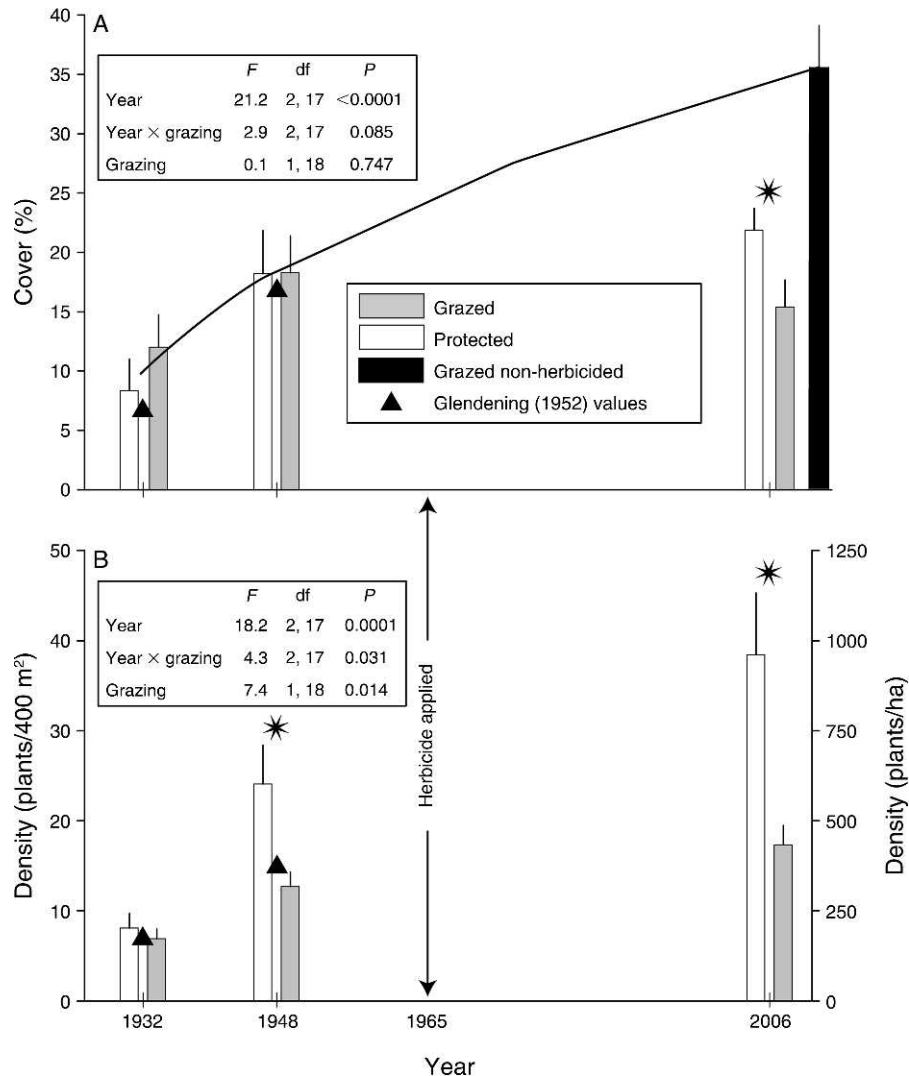
FIG. 2. (A) Bars depict mean (+SE; $n = 10$ plots, 20×20 m) percent velvet mesquite (*P. velutina*) canopy cover and (B) plant density on long-term grazed and protected areas on the Santa Rita Experimental Range. The entire area was treated with aerial herbicides in May 1964 and 1965. Density and cover values reported by Glendening (1952) are indicated (eighty-eight 20×20 m plots were statistically comparable, and so were pooled and are represented by black triangles). Results from repeated-measures ANOVA are summarized in inset boxes. Stars denote significant differences between grazing treatments ($\alpha = 0.05$). Mean shrub cover measured in 2004 within three 30×30 m plots in a nearby, non-herbicide-treated area on comparable soils is provided for comparison. The hypothesized trend in mesquite cover change in the absence of the herbicide treatment is depicted with the solid line in panel (A).

the appearance of these small plants, mean plant canopy area declined between 1932 and 1948, more so on protected plots than on grazed plots (Fig. 4C, F). Mortality over these 16 years was comparably low on both protected (0.07%) and grazed areas (0.06%), and plants that died on the grazed area were similar in size (canopy radius = 0.6 ± 0.5 m, maximum = 2.3 m] to those that died on the protected area [1.4 ± 0.5 m, maximum = 3.0 m; $t = 0.87$, df = 8, $P = 0.409$). Canopy area and height distributions were slightly, but significantly different on grazed and protected areas when the study was initiated (asymptotic Kolmogorov-Smirnov [K-S_a] = 1.81, $P = 0.003$; K-S_a = 1.39, $P = 0.042$; Fig.

4B, E). By 1948 these differences were substantially more pronounced (grazed K-S_a = 1.48, $P = 0.024$; protected K-S_a = 1.41, $P = 0.036$; Fig. 4C, F). Differences between 1932 and 1948 size distributions were amplified on the protected area (canopy area K-S_a = 2.28, $P < 0.0001$; height K-S_a = 1.28, $P = 0.076$) compared to the grazed area (canopy area K-S_a = 1.29, $P = 0.071$; height K-S_a = 0.82, $P = 0.506$).

The period from 1948 to 2006 was marked by high recruitment in both the grazed and protected areas, but more so on the protected area (grazed = 123 new plants, 308 new plants/ha; protected = 192 new plants, 480 new plants/ha; Figs. 3 and 4D). Mean and maximum canopy
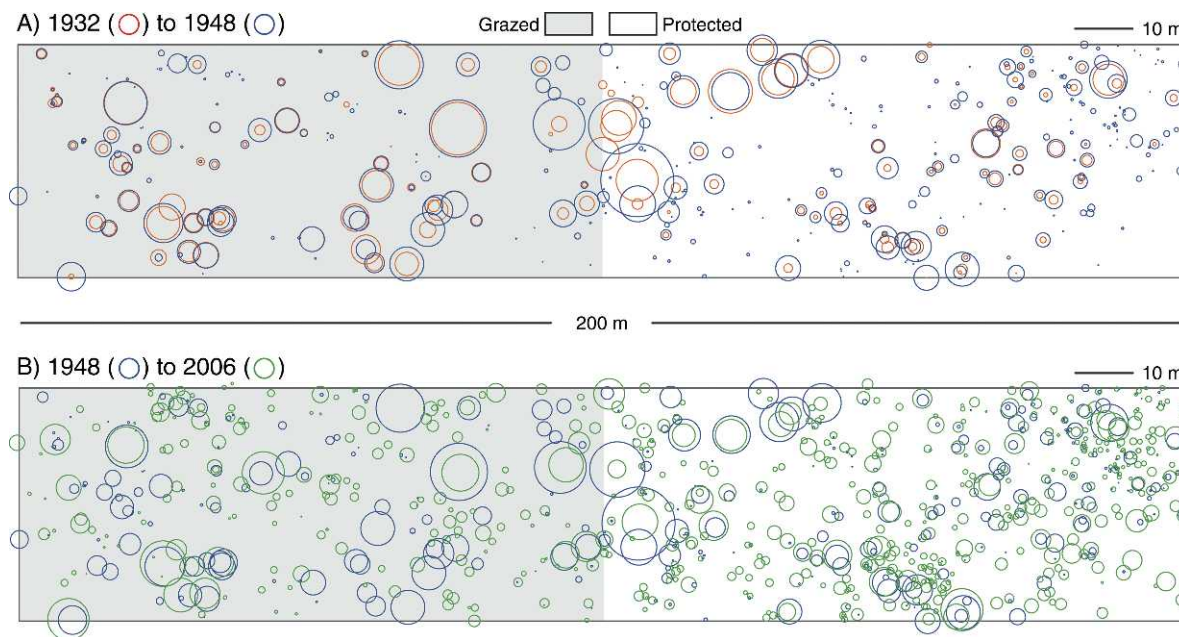
FIG. 3. Spatially explicit changes in mesquite canopy cover between (A) 1932 and 1948 and (B) 1948 and 2006 on (left) a long-term grazed and (right) a protected area on a sandy loam upland ecological site on the Santa Rita Experimental Range. Circles depict idealized canopies of individual mesquite plants in 1932 (red), 1948 (blue), and 2006 (green). The entire area was treated with aerial herbicides in May 1964 and 1965.

area were reduced, and canopy size distributions between 1948 and 2006 shifted toward significantly toward smaller plants on both areas by 2006 (K-S_a = 2.14, $P < 0.0002$ for grazed; K-S_a = 3.42, $P < 0.0001$ for protected), presumably reflecting the 1964/1965 herbicide application (Fig. 4C, D). Recruitment into taller height classes was evident on both grazed and protected sites by 2006. Although the number of plants was substantially higher on the protected area than on the grazed area in 2006, canopy size-class distributions were statistically comparable (K-S_a = 0.989, P = 0.281). Differences in tree height in 2006 were evidenced by the increasing dissimilarity of height distributions for grazed and protected areas (K-S_a = 2.21, $P < 0.001$; Fig. 4G), with the smallest plants on the protected area advancing to larger height classes. Mortality rates could not be quantified from 1948 to 2006 because historic maps had not been spatially referenced at the time of the 2006 sampling, and retrospective identification of individuals was problematic.

Mesquite aboveground biomass

Mean (±SE) aboveground mesquite plant biomass was comparable on grazed and protected areas in 1932 (23.6 ± 7.5 and 15.2 ± 4.6 kg/plant, respectively; $F_{1, 149}$ = 0.97, P = 0.326) and 1948 (22.8 ± 6.3 and 14.7 ± 5.6 kg/plant; $F_{1, 366}$ = 0.83, P = 0.364). In 2006, aboveground biomass of plants on grazed areas (10.8 ± 2.7 kg/plant) was significantly greater than that of plants on protected areas (4.8 ± 0.8 kg/plant; $F_{1, 559}$ = 7.99, P = 0.005). On a land area basis, mesquite aboveground biomass was comparable in 1932 on grazed (4182 kg/ha) and protected areas (3119 kg/ha; Fig. 5). Total mesquite biomass increased 2903 kg/ha and 5667 kg/ha from 1932 to 1948 on grazed and protected areas, respectively, owing mainly to growth of the largest plants. Biomass declined from 1948 to 2006 on both areas, presumably a consequence of the 1964/1965 herbicide application. Herbicide-induced loss of biomass from large trees (canopy areas > 51 m^2) more than offset increases in biomass associated with the appearance of new plants (Figs. 3 and 5). In 2006, 40 years after the herbicide was applied and 74 years after the grazing contrast was established, mesquite aboveground biomass (~4700 kg/ha) was comparable on grazed and protected areas. However, biomass contributions on the grazed area were from trees larger than those on the protected area (Fig. 5).

TABLE 1. Probability of increasing mesquite cover on the Santa Rita Experimental Range computed as the proportion of 20 × 20 m subplots that increased in cover for a given initial condition for the 1932–1948 and 1948–2006 periods.

Initial mesquite cover (%)	Probability of increase
≤10	1.0
11–20	0.8
21–25	0.8
26–30	0.5
>30	0.0

Note: Preliminary analysis indicated no differences between long-term grazed and protected plots (n = 10 each) over two time periods (1932–1948 and 1948–2006), so data were pooled to yield 40 transitions.
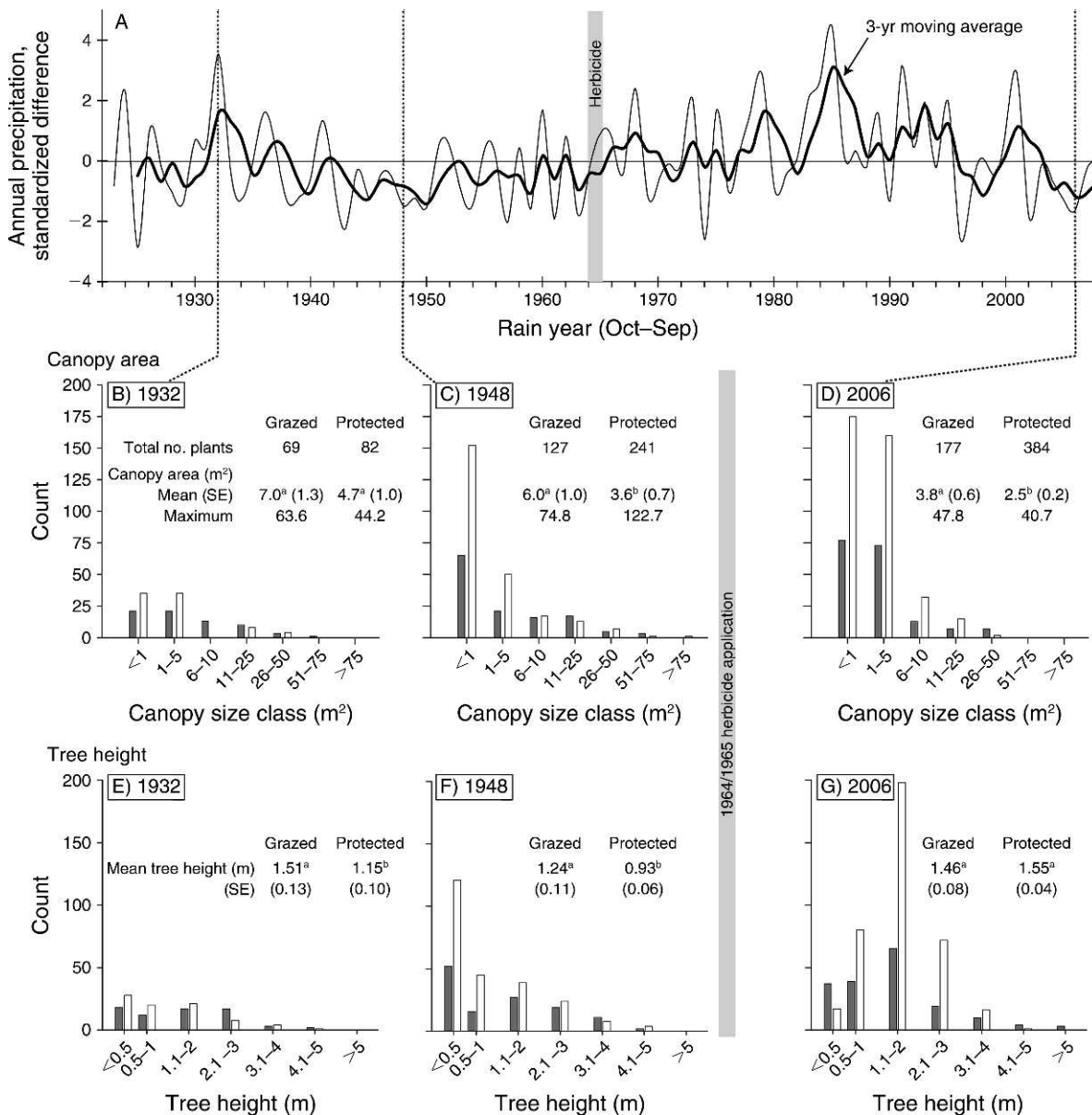
FIG. 4. (A) Annual precipitation from 1922 to 2008 at a rain gauge (Santa Rita Experimental Range "Rodent Station") 0.3 km from the study site. Precipitation is represented as the standardized difference (annual average minus the long-term average divided by standard deviation). (B–D) Size-class distributions of mesquite shrubs based on field-measured canopy area in (B) 1932, (C) 1948, and (D) 2006, and (E–G) tree height in (E) 1932, (F) 1948, and (G) 2006 on long-term grazed (shaded bars) and protected areas (open bars). Descriptive statistics are summarized in each panel: panels (B–D) show the total number of plants and canopy area (mean ± SE, maximum); panels (E–G) show tree height (mean ± SE). Different superscripts denote significant differences ($\alpha = 0.05$). Vertical dotted lines in panel (A) refer to the year; the vertical gray bar indicates the 1964/1965 herbicide application.

DISCUSSION

Knowledge of land use history is paramount to interpreting present patterns of vegetation structure in managed ecosystems and can influence future land cover change (Foster et al. 2003, Peters et al. 2006). However, the paucity of spatially explicit historical records makes it difficult to account for legacy effects (Rango et al. 2005). This study documents the outcome of historic effects of two common rangeland land use practices (livestock grazing and brush management) on vegetation over 74 years (Fig. 6). Results challenge the common assumption that livestock grazing promotes woody-plant encroachment. How representative are the changes in shrub cover observed on the McGinnies field plots? As an independent test, we quantified changes in shrub cover using time series aerial photography (1936, 1971, 1996, 2005) of three additional livestock exclosures on the SRER and the grazed areas surrounding them.
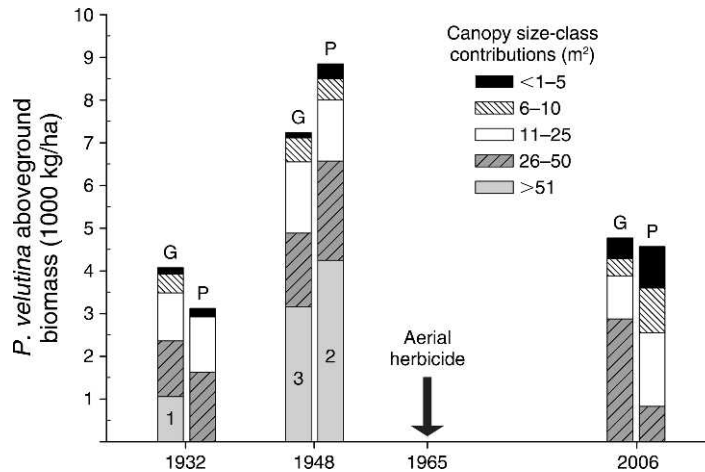
Fig. 5. Contributions of mesquite canopy size classes to total aboveground biomass in 1932, 1948, and 2006 on long-term grazed (G) and protected (P) areas on the Santa Rita Experimental Range. Values shown in the >51-m² segments represent the number of plants in that size class. Biomass was estimated using a site-specific allometric relationship for field-measured canopy area.

Shrub cover on these sites, with soils comparable to those in the McGinnies exclosure, generally tracked those observed on the McGinnies field plots, with cover values on the protected areas being consistently higher than those on the grazed areas (data not shown). Thus, there is reason to believe that the shrub cover changes reported herein are indicative of changes occurring over a broader area.
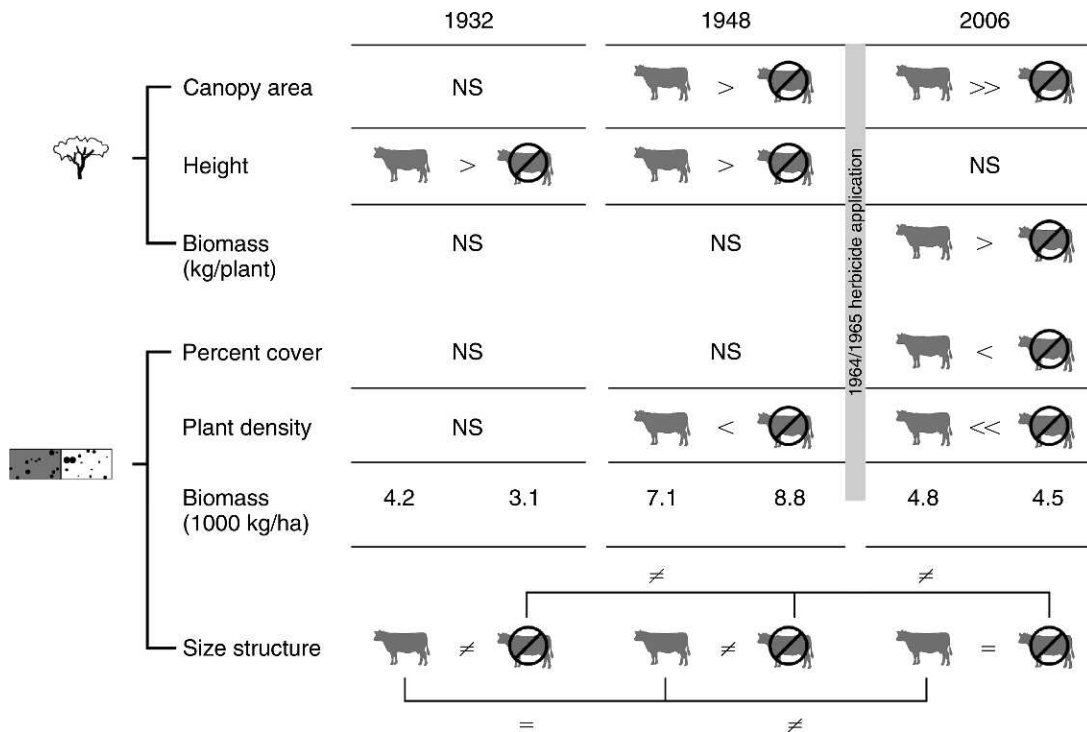

Fig. 6. Summary of effects of livestock removal on plant- and plot-level aspects of velvet mesquite (Prosopis velutina) dynamics over 74 years on the Santa Rita Experimental Range. Livestock were removed in 1932, and an aerial herbicide was applied in May 1964 and 1965 (vertical gray bar); herbicide effects over grazed ("cow") and protected ("no cow") areas were assumed equal. Metrics were based on field measurements of individual plants (Figs. 2, 4, and 5). See Methods section for details. NS and equal signs signify no statistically significant difference between groups. Single and double greater-/less-than symbols represent the magnitude of the difference between groups. Not-equal signs signify significant differences between groups using nonparametric K-S tests. For all tests, alpha was equal to 0.05.

Historic brush management and mesquite stand structure

Woody-plant proliferation has long been recognized as a land management issue in drylands, and shrub management practices involving herbicides, mechanical manipulation, and fire have been widely practiced in the Great Plains and western USA since the 1940s (Bovey 2001). As a result, present-day patterns of shrub cover and density often reflect the legacies of past shrub management (Asner et al. 2003, Heaton et al. 2003). We were fortunate to have knowledge of such activities; without it, our interpretation of mesquite stand development, dynamics, and biomass would have been misguided.

Stand structure and mass following brush management reflects the number surviving plants, the recruitment and growth of plants establishing from seed, and the vegetative regeneration of plants damaged by the treatment (e.g., Gibbens et al. 1992). Mesquite mortality and canopy cover reductions following the 1964/1965 herbicide applications were on the order of 50% and 90%, respectively (Martin and Ward 1966, Cable 1976). *Prosopis* spp. are capable of vegetatively regenerating following disturbances that damage aboveground portions of the plant (Hamilton et al. 2004), and they produce a long-lived seed bank (Tschirley and Martin 1960). The recovery of mesquite density and canopy cover in Fig. 2 therefore reflects a combination of recruitment and regeneration of plants damaged by the herbicide.

Stand recovery over the 40+ years post-disturbance, though substantial, was not complete. Cover had rebounded to pretreatment levels by 2006, but this was 43% lower than would have existed on grazed areas had the herbicide not been administered. However, from a shrub biomass perspective, the effects of the herbicide were substantially greater, as 2006 biomass was 50% (protected) and 65% (grazed) that of 1948 pretreatment levels (Fig. 5). These herbicide-induced reductions in aboveground carbon (C) mass would likely have been accompanied by substantial reductions in soil organic carbon and nitrogen (e.g., McClaran et al. 2008). Thus, our data illustrate how a lack of land use history knowledge could lead to substantive misinterpretations of structure–function relationships and errors in their projection through time.

Cover and density data indicate shrub recovery from the herbicide perturbation was either enhanced in the absence of livestock or that the presence of livestock had a suppressive effect on shrub recovery. Browsing or trampling of mesquite seedlings by livestock could potentially reduce mesquite establishment in the post-herbicide period, although evidence in the literature in support of this possibility is scant. Alternatively, alterations of grass–shrub interactions due to livestock might account for the observed patterns and are explored in the subsequent sections.

Precipitation and shrub dynamics

Drylands are often characterized as "event-driven" systems wherein plant populations grow or decline in response to rare events (Walker 1993) related to disturbance (Sousa 1984) or thresholds for recruitment during years of high precipitation or mortality during stressful years (Reynolds et al. 2004, Schwinning et al. 2004). Unfortunately, given the long time intervals between sampling dates and the 1964/1965 herbicide treatment, we cannot directly determine if or when such events might have occurred. Rainfall records at the site indicate numerous potential years or periods for episodes of shrub recruitment and mortality; and the occurrence of distinctive peaks or gaps in plant size-class distributions would be an indicator of recruitment or mortality events. However, shrub size distributions in 1932 showed no obvious spikes or gaps (Fig. 4B, E). Total shrub numbers increased dramatically from 1932 to 1948 (Fig. 4C, F); furthermore, mortality over this time period derived from tracking individual plants on the McGinnies plots was only ~0.06%, despite five years of consistently below-average rainfall preceding this sampling date (1942–1947; Fig. 4A). Our data, though limited in its temporal resolution, appears to support the notion that shrub recruitment and mortality in this dryland system may be more tied to "continuous" recruitment or mortality factors than to episodic factors (e.g., Watson et al. 1996, 1997*a*, *b*).

Livestock influences on mesquite stand dynamics

Concerns over unlimited, open livestock grazing and widespread soil erosion in the Southwest USA led to the formation of the SRER in 1902 (Ruyle 2003). Cattle were excluded from the SRER upon its creation, but E. O. Wooton, an early scientist on the site, observed "There is no doubt that the prediction made by Griffiths (1904), that the mesquites and other shrubs would increase in size and number, is slowly coming true..." (Wooton 1916:18). Livestock were reintroduced on the SRER in 1916, but the fact that mesquite abundance has increased since that time amidst substantial decreases in cattle stocking intensity (Fig. 1D), suggests changes in ecosystem processes and feedbacks favoring shrub invasion were already underway when the SRER was established in 1902 (e.g., Browning et al. 2008, Okin et al. 2009*a*). Indeed, in the absence of fire, increases in shrub abundance were actually greater on areas protected from livestock since 1932 than on areas grazed by livestock. Although counterintuitive, these results are in line with long-term data from Smeins and Merrill (1988) and Asner et al. (2009), who also observed greater levels of shrub cover and shrub cover increase on protected sites relative to grazed sites.

Why would woody-plant abundance increase more on areas protected from livestock than on areas with livestock? *Prosopis* spp. encroachment into livestock exclosures in the Chihuahuan Desert, USA, coincided with an influx of sands from nearby coppice dunes that buried grasses and promoted shrub establishment and dune formation (Peters et al. 2006, Okin et al. 2009*b*). However, coppice dune formation is not a feature of the

landscapes at SRER, and there was no evidence for off-site factors influencing on-site shrub dynamics on our site. Our data indicate differences in mesquite abundance and size structure are the result of differences in recruitment, rather than differences in mortality, for both the grazed and the protected areas (Fig. 6).

Two key aspects of recruitment are seed dispersal and seedling establishment. Removal of livestock might reduce the spread of mesquite, as cattle are well known to be highly effective agents of *Prosopis* spp. dispersal (Brown and Archer 1988). However, there was already an upland population of mesquite plants of seed-bearing size present in 1932 when the McGinnies exclosures were established and rodents known to disperse mesquite seeds were present (e.g., banner-tailed kangaroo rats; Glendening 1952). Furthermore, dispersal of seed by livestock prior to 1932 likely created a substantial seed bank on the areas subsequently protected from livestock. Thus, while removal of livestock might have diminished seed dissemination, mesquite was not likely dispersal-limited on the protected area.

If seed dispersal was not a constraint, then increases in mesquite abundance on protected sites relative to grazed sites would reflect enhanced seedling establishment. How might removal of livestock promote shrub seedling establishment? Browsing herbivores are known to limit woody-plant abundance (Weltzin et al. 1997, Staver et al. 2009), and their removal would thus promote increases in woody-plant abundance. The direct deleterious effects of livestock (trampling or browsing) could therefore explain enhanced recruitment on protected sites. However, we are not aware of published evidence for cattle having such impacts on mesquite.

The explanation for higher *Prosopis* spp. recruitment in the absence of livestock could also lie with the herbaceous vegetation response to livestock removal in degraded systems. In historically degraded systems such as the SRER, removal of livestock may allow a level of herbaceous recovery that stabilizes soil surfaces, reinstates surface hydrological processes, and ameliorates harsh near-surface soil conditions (e.g., temperature) to promote shrub seedling establishment (e.g., O'Connor 1995). Because *Prosopis* spp. are known to be little affected by herbaceous competition (Jurena and Archer 2003), increases in herbaceous production and cover following relaxation of grazing may have altered microclimatic conditions to favor rather than inhibit mesquite seedling recruitment. Our data cannot address the possible mechanisms, but point to the need for studies specifically investigating why shrub recruitment would be greater on protected rather than grazed areas.

Land management, shrub proliferation, and carbon accounting

Carbon accounting on extensively managed dryland ecosystems requires knowledge of co-occurring livestock grazing, shrub proliferation, and shrub management influences. Each of these varies in space and time and can interact to create mosaics of above- and below-ground carbon stocks (e.g., Asner et al. 2003, Asner and Archer 2010, Liu et al. 2010). Does grazing affect C pools in systems where woody-plant abundance has increased? Nosetto et al. (2006) found shrub carbon storage on grazed areas to be comparable to that on areas where livestock had been excluded for 15 years in northwest Patagonia. In our system with its history of long-term grazing, removal of livestock elevated shrub proliferation relative to that occurring in the grazed areas and increased biomass (and hence carbon mass) in the aboveground shrub pool by ~24% between 1932 and 1948. Unfortunately, we do not have herbaceous production for grazed and protected areas, so we do not know the net effect on the total aboveground pool. However, relaxation of grazing typically results in an increase in herbaceous production and should thus further increase total aboveground C pools. As shrubs establish and grow, the carbon content of soils beneath their canopies increases (Throop and Archer 2008). Long-term projections of ecosystem carbon pools will therefore depend largely on changes in shrub population structure as young (small) shrubs transition into older (larger) classes (e.g., Fig. 5). Furthermore, our data suggest that, while grazing may be mediating rates of carbon storage and the time to reach equilibrium conditions, it may not necessarily influence total carbon storage. Instead, other land use activities (e.g., management of brush by herbicides, fire, et cetera) are likely of much greater importance.

The effects of management-induced reductions in shrub cover on the carbon cycle are largely unknown, but will depend on the type (e.g., mechanical, fire, herbicide) and season of treatment, treatment efficacy, and the extent to which soils are disturbed. Decomposition processes are altered subsequent to shrub removal owing to changes in vegetation structure that influence microclimate and soil movement (Throop and Archer 2007), and soil organic C pools are known to be responsive to shrub removal and reestablishment at decadal timescales (Tiedemann and Klemmedson 1986). Our case study found that differences in shrub biomass evident on grazed and protected areas in 1948 disappeared following the 1964/1965 herbicide application. Interestingly, plot-level shrub biomass in the post-herbicide period was comparable on grazed and protected sites despite substantial differences in plant size-class distributions (more but smaller shrubs on the protected site, and fewer but larger shrubs on the grazed site). This observation suggests that scaling relationships describing variation in population density with plant size (Enquist et al. 1998) may be useful in robustly characterizing landscape-scale changes in biomass occurring with woody-plant proliferation or brush management. Other studies on the site indicate the herbicide-induced resetting of shrub cover would have also decreased soil carbon stocks substantially (McClaran et al. 2008), but the extent to which the presence/absence

of livestock might mediate this response is unknown. Present-day cover and aboveground woody biomass levels are substantially below their potential, so it is likely that above- and belowground biomass will continue to accrue on both the grazed and protected sites. The fact that shrub recovery from the herbicide application measured on a mass basis (Fig. 5) was much less than recovery measured on a cover basis (Fig. 2A) suggests caution must be exercised when using cover-based remote sensing estimates to estimate changes in aboveground C pools on landscapes with contrasting land management histories.

Heavy grazing by livestock in the late 1800s and early 1900s is a shared history for many of the world's rangeland ecosystems (Ash et al. 1997, Holecheck et al. 2003). The fact that shrub proliferation occurred on both protected and grazed sites suggests thresholds of grassland resistance to shrub establishment (e.g., Archer 1989) had been crossed by 1932 when the grazing exclosures were established. One consequence of livestock grazing is the removal of fine fuels and the virtual cessation of fire (e.g., Madany and West 1983, Savage and Swetnam 1990), and this was the case on our site. Although the historical importance of fire in the desert grasslands of the Southwestern USA is debatable (e.g., McPherson 1995, Drewa and Havstad 2001), our results clearly indicate that in the absence of fire, the post-1930s Santa Rita grasslands are susceptible to shrub encroachment.

Our observation that protection from livestock grazing facilitated recruitment-driven increases in mesquite abundance was unexpected and suggests that, in the absence of fire, grass–shrub interactions during the critical shrub seedling establishment phase may be fundamentally different on sites with contrasting grazing histories. Given that conservation initiatives in grasslands often focus on restoring areas with histories of heavy grazing, future studies should assess mechanisms and conditions whereby protection from grazing (in our case by cattle) promotes rather than curtail shrub encroachment. Furthermore, while brush management has been widely used on western rangelands in the USA since the 1940s to stem the tide of woody-plant proliferation in grazed grasslands (Bovey 2001, Hamilton et al. 2004), research on this land management practice has been short term and largely focused on herbaceous (forage) production (Archer et al., in press). Its historical and current effects on biodiversity, plant population biology and ecosystem processes are potentially substantial (Archer 2009) and should be more formally recognized, quantified, and documented in ecological studies.

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