

Differences in population size structures characterize grass response to long-term livestock removal

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Abstract

Questions: How does desert grassland vegetation respond to long-term grazing removal? Is grass response the result of differences in the number or the size of plants? Does the response differ over time and in relation to precipitation patterns?

Location: Santa Rita Experimental Range, southwestern United States.

Methods: Four times between 2011 and 2020, we measured the cover of woody plants and native and non-native perennial grasses, and the density, size, and biomass of individual perennial grasses on 40 permanent transects inside and outside 10 long-term (88–104-years old) livestock enclosures (0.1–4.0 ha) occurring on the same ecological site. We used linear mixed models to compare vegetation variables in grazed vs ungrazed transects through time and calculated the cumulative frequency distributions of grass plant diameters.

Results: The cover of woody plants did not differ by grazing treatment. Instead, the enclosures had a greater cover, density, and biomass of native grasses and cover and biomass of the most abundant native grass Arizona cottontop (*Digitaria californica*). Moreover, ungrazed populations of natives and Arizona cottontop showed a plant size structure skewed to larger sizes. Non-native grasses showed no differences between grazing treatments. Patterns of inter-annual precipitation influenced woody and grass plant abundance, but not their response to livestock removal.

Conclusions: Long-term grazing removal in desert grasslands affected native grass abundance, but not that of non-native grasses and woody plants. Response of native grasses to livestock removal was characterized more by plant size rather than the number of plants, and, importantly, the population size structure skewed to smaller plants in grazed areas suggests that grazing limits plant vigor and longevity. Absence of a non-native grass response likely reflects lower palatability and greater grazing resistance of non-natives. Absence of woody plant response is due to their low palatability and the permeability of enclosures to seed dispersal.

KEYWORDS

desert grassland, livestock enclosures, native grasses, perennial grasses, plant biomass, repeated measures, shrubs, vegetation dynamics

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1 | INTRODUCTION

Is grass response to long-term livestock removal the result of differences in the number of plants or the size of plants? In essence, this question asks if differences in recruitment (number of plants) or longevity (size of plants) are the dominant mechanism of response to removal of livestock grazing. Comparing population size structures between grazed and ungrazed settings provides evidence to address this question (Oñatibia & Aguiar, 2019; Oñatibia et al., 2020). Studies conducted in rangelands worldwide have shown contrasting effects of livestock grazing on the number and size of grasses, suggesting that mechanisms can change depending on the environment, plant species, livestock species, and management conditions. Concerning plant density (number of plants), many authors observed an increase in the number of plants, especially at high grazing intensity (Butler & Briske, 1988; Fuhlendorf et al., 2001; Oliva et al., 2005; Travers & Berdugo, 2020), while others a decrease (Pfeiffer & Hartnett, 1995; Oñatibia et al., 2020). Importantly, Oñatibia and Aguiar (2019) found that density response to grazing was inversely related to palatability, with lower density of more palatable species in grazed vs ungrazed settings, and the opposite for unpalatable species. Concerning plant size, the majority of studies showed a plant size distribution skewed to smaller sizes in grazed than ungrazed conditions (Sala et al., 1986; Butler & Briske, 1988; Pfeiffer & Hartnett, 1995; Fuhlendorf et al., 2001; Oliva et al., 2005; Oñatibia & Aguiar, 2019; Oñatibia et al., 2020).

We explored this question of number vs size for grass response to livestock removal in the semi-arid, low primary productivity desert grassland of southwestern North America (McClaran, 1995), where livestock use is well documented since its rapid expansion in the late 19th century, and livestock exclosures were established in the early 20th century to evaluate grazing impacts. Here, livestock exclosures and comparisons of different grazing histories revealed patterns of increased woody plant cover and decline in grass cover and production since livestock expansion in the late 19th century (e.g., Gardner, 1950; Smith & Schmutz, 1975; McClaran, 2003; McClaran et al., 2010; Browning & Archer, 2011), and, more recently, they helped to understand that the spread of non-native Lehmann lovegrass (*Eragrostis lehmanniana*) is not reliant on livestock grazing (McClaran & Anable, 1992; Bock et al., 2007). However, no previous work has used long-term livestock exclosures to explore the relative importance of plant number vs plant size in the response to long-term livestock removal.

It is understood that vegetation response to livestock removal can be influenced by factors such as (i) age and size of the exclosure, (ii) plant species, and (iii) fluctuations in climatic conditions. The timing of vegetation response to livestock removal may range from years (Chen & Tang, 2016; Sun et al., 2020) to several decades (Valone et al., 2002), with longer timings typical of low-productivity arid environments (Valone et al., 2002; Augustine et al., 2017; Wolf & Mitchell, 2021). For this reason, old and young exclosures differ in their ability to show vegetation changes after

livestock removal. Small exclosures can be more vulnerable than large ones to non-grazing processes such as seed dispersal from outside the exclosure (Bock et al., 2007). Response to livestock removal can also depend upon the grazing resistance of each plant species (Briske, 1996). Lastly, the fluctuations in climatic conditions can interact with grazing to generate different effects on vegetation. For instance, grazing may adversely affect the ability of grasses to recover after drought, thus causing higher mortality and reduced forage production compared to ungrazed areas (Holechek et al., 2003; Loeser et al., 2007; Chen et al., 2013; Oñatibia et al., 2020).

We minimized these sources of variation by measuring four times in 10 years (2011–2020) cover of woody plants and cover, density, biomass, and size of grass plants inside and outside 10 long-term (88–104 years old) exclosures on the Santa Rita Experimental Range (Arizona, USA). This experimental design allowed us to obtain a novel dataset for several reasons (Table 1; Table S1): (i) length of livestock removal (up to 104 years, corresponding to the longest time frame in exclosure studies published up to date, to our knowledge); (ii) large number of exclosures; (iii) consistency of soils (same Ecological Site); (iv) consistency of stocking rate during the study; (v) four repeated measurements, which provided the opportunity to assess the patterns related to climate variation; and most importantly (vi), three measures of grass abundance (cover, density, biomass) and individual plant size.

Based on results in the literature and our experimental approach, we formulated four hypotheses: (i) grass response (in terms of cover and biomass) to livestock removal is mainly the result of differences in population size structure rather than by differences in the absolute number of plants as demonstrated by previous works showing smaller sizes in grazed than ungrazed conditions (e.g., Butler & Briske, 1988; Oliva et al., 2005; Oñatibia et al., 2020); (ii) grazed grass populations have less cover and biomass and are skewed toward smaller sizes, particularly for native grasses because they are more palatable and less grazing-resistant than non-native grasses (Oñatibia & Aguiar, 2019); (iii) woody species' response does not differ inside and outside exclosures because they are not directly impacted by livestock and exclosures are too small to interfere with seed dispersal (Bock et al., 2007; Browning & Archer, 2011); and (iv) the patterns are consistent across the four repeated measurements because grazing pressure was moderate during the study, there were no extreme droughts or other disturbances such as fires, and vegetation has probably stabilized during more than 80 years of livestock removal (Valone et al., 2002).

2 | METHODS

2.1 | Study area

The study occurred on the 21,000 ha Santa Rita Experimental Range (SRER), 40 km south of Tucson, Arizona, United States (31°50'31" N, 110°51'36" W). The average annual precipitation and temperature

TABLE 1 Characteristics of the studies that used long-term exclosures (≥ 10 years old) in desert grasslands, in other vegetation types of the world (including grasslands, shrub grasslands, shrublands, savannas, and dune fields), and in the present study.

	Desert grasslands median (min–max)	Other vegetation types median (min–max)	Present study
Maximum age of the exclosure (years) ^a	28 (14–74) N = 16	30 (10–83) N = 61	104
Number of exclosures	1 (1–9) N = 16	3.5 (1–36) N = 62	10
Average exclosure size (ha)	72.4 (0.15– 1×10^5) N = 16	1.0 (0.01–6800) N = 49	1.1
Number of measurements	1 (1–6) N = 16	1 (1–30) N = 62	4
Length of the experiment (years) ^b	1 (1–74) N = 16	1 (1–72) N = 60	10
Number of growth forms (herbaceous/non-herbaceous)	2 (1–2) N = 16	2 (1–2) N = 63	2
Number of variables (cover, density, biomass)	1 (1–3) N = 15	2 (1–3) N = 64	3
Number of studies accounting for repeated measurements ^c	2/5	10/21	Yes

Note: For vegetation types other than desert grasslands, papers were selected only if published between 2000 and 2021. The criteria used to select the papers, the database including selected exclosure studies, and the description of the methodology used to calculate the median values for “Average exclosure size,” “Number of measurements,” and “Length of the experiment” are provided in the Appendices S1 and S2. N = number of papers used to calculate the median value for each category of data.

^aIt refers to the oldest exclosure in case there is more than one exclosure and/or to the most recent sampling in case there is more than one measurement.

^bYears from the first to the last measurement.

^cNumber of studies that used a repeated-measurement approach in the statistical analysis (e.g., repeated-measurement ANOVA, mixed models with sampling unit in the random part) out of the number of studies with more than one measurement.

on the SRER are 379 mm (McClaran & Wei, 2014) and 18.5°C (PRISM Climate Data, 2021), respectively. About 50%–60% of the annual total precipitation falls during the summer months and both annual and summer precipitation are characterized by high interannual variability (McClaran & Wei, 2014). Soils are in the thermic temperature regime and aridic and ustic moisture regimes (Breckenfeld & Robinett, 2003).

The vegetation is desert grassland, a mixture of different growth forms including grasses, forbs, shrubs, short trees, and cacti (Burgess, 1995). Common native perennial grasses are Arizona cottontop (*Digitaria californica*), Rothrock grama (*Bouteloua rothrockii*), threeawns (*Aristida* spp.), and Bush muhly (*Muhlenbergia porteri*), while Lehmann lovegrass is the most common non-native perennial grass. The dominant tree and shrub are mesquite (*Prosopis velutina*) and burroweed (*Isocoma tenuisecta*), respectively. Cane cholla (*Cylindropuntia spinosior*), Chainfruit cholla (*C. fulgida*), and Engelmann prickly pear (*Opuntia engelmannii*) are among the dominant cacti. In general, native grasses are more palatable to livestock than non-native grasses, mesquite is occasionally eaten as fresh leaves and seed pods, but cacti and small shrubs are not eaten by livestock.

2.2 | Experimental design and grazing system

In this study, we selected 10 long-term livestock exclosures on the SRER ranging in elevation from 1050 to 1250 m a.s.l. and located in the Sandy Loam Upland Ecological Site (including “baboquivari,” “diaspar,” and “sasabe” soil series; Figure 1; Appendix S3). Sandy Loam Upland Ecological Site has deep and well-drained soils with about 30% clay content in the subsurface horizons and occupies fan terraces with at most 8% slope (Breckenfeld & Robinett, 2003). The selected exclosures were built between 1916 and 1932, thus they were 88–104 years old in 2020. They ranged in size from 0.1 to 4.0 ha (Appendix S3).

In 2010, at each exclosure, two linear permanent transects of 100 ft (30.5 m) were placed within the excluded area (ungrazed treatment) and two outside of it (grazed treatment), at an average distance of 76 ± 7.3 m (mean \pm standard error). The transects were positioned in a stratified random manner to represent the vegetation structure and composition within and outside the exclosure. Because of this paired design, we assumed that at each exclosure: (i) the vegetation before exclusion did not differ between grazed and ungrazed transects; and (ii) the presence of livestock was the

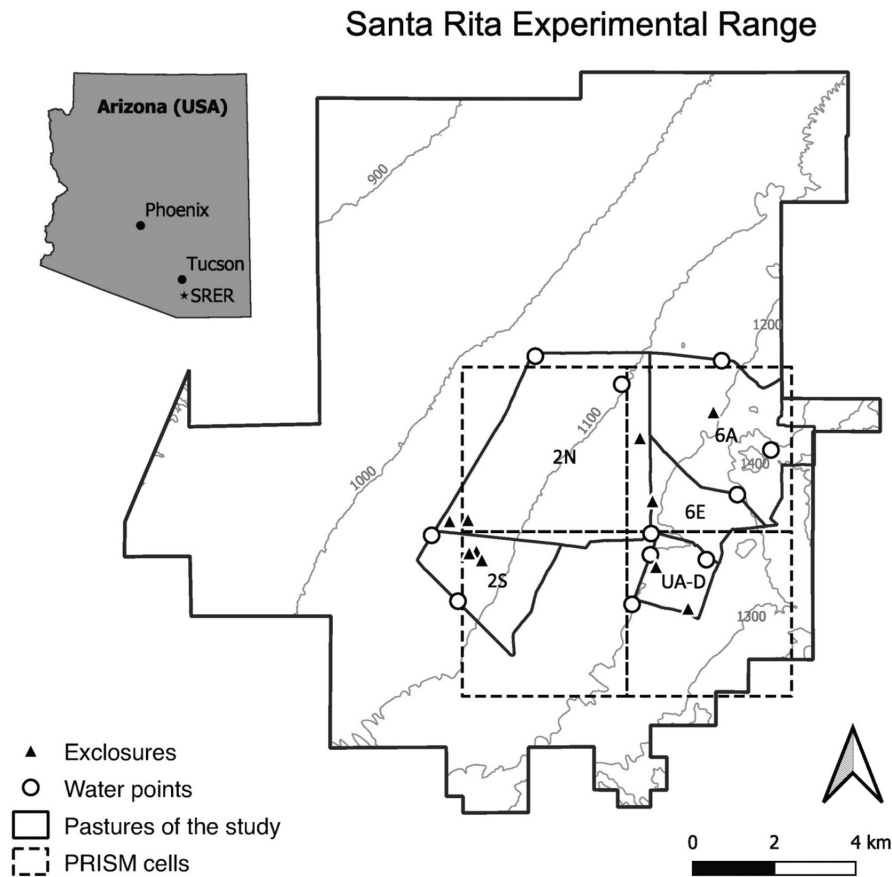


FIGURE 1 Exclosures, livestock waters, and pastures used in this study, and PRISM cells used for the precipitation trend analysis on the Santa Rita Experimental Range, Arizona, United States.

only differentiating factor between inside- and outside-exclosure conditions.

Exclosures were in five different pastures (i.e., 2N, 2S, 6A, 6E, and UA-D) used by cattle herds (Figure 1). Pastures ranged in size from 268 (UA-D) to 1857 ha (2N) and the density of livestock water ranged from 0.22 to 1.11 km⁻². The average minimum distance between water and exclosures was 994.2 ± 330.6 m. All pastures shared a common stocking rate history. From 1916 up to the late 1920s, the stocking rate was around 10 Livestock Units (LU) km⁻² year⁻¹. By the 1940s, it was reduced to around 4 LU km⁻² year⁻¹, to achieve sustainable forage utilization (<50%). From 2008 to 2020, the stocking rate was uniform, with an average value of 2.7 LU km⁻² year⁻¹ (Appendix S4). All pastures were grazed year-long from 1916 to the 1970s. Then, in pastures 2S and 6A, a rotational grazing system was implemented for 30 years, consisting of a three-year cycle with two grazing periods (March–October and November–February) and 12 months of rest between each use (Mashiri et al., 2008). In pasture 6E, from 1971 to 2005, there were periods of 4–9 months of grazing followed by one year of rest from grazing. In pasture UA-D, the rotational grazing system occurred from 1972 to 1989, then the year-long was re-implemented until 2006. In pasture 2N, year-long grazing lasted from 1916 to 2006. Starting in 2006, a new grazing scheme was implemented in all pastures of the SRER, with short grazing periods (1–3 months) followed by longer rest periods (8–12 months). Despite some pastures experienced a different grazing system (year-long or rotational), Mashiri et al. (2008) found

no difference in vegetation dynamics between pastures that experienced year-round vs seasonal rotation of livestock grazing from 1972 to 2006.

2.3 | Vegetation measurements

At each transect, the following vegetation characteristics were measured: (i) the canopy cover of woody plants (i.e., mesquite, burroweed, and cacti); (ii) the basal cover and (iii) the density of each perennial grass species; and (iv) the basal diameter of each perennial grass plant. The woody plant canopy cover and the grass basal cover were measured in units of 0.1 ft (~3 cm) along the transect line according to the line intercept method of Canfield (1941). The density of perennial grasses was assessed by counting all individuals in a 12-inches-wide (0.305-m) belt along the right side of each transect, and for each grass plant, the basal diameter was measured with a graduated tape (diameter > 3.5 cm) or a caliper (diameter ≤ 3.5 cm). Individual grass plants (i.e., populations of one or more tillers; Briske, 1991) were counted and measured as spatially independent units when they were at least 5 cm apart from the other plants (Lauenroth & Adler, 2008). The 5-cm rule was set to distinguish separate individuals in the case of large plants fragmenting into smaller plants and this occurred <5% of the time. Vegetation measurements were performed during the dormant season (January–May) every 3 years from 2011 to 2020, for a total of four measurements

in 10 years. We distinguished dormant and dead plants by the presence of yellow or green-greenish leaves/stems. These data and photographs are accessible at <https://cals.arizona.edu/srer/content/exclosure-transects>. The complete list of plant species measured on the transects is given in Appendix S5. Nomenclature of plant species follows the USDA PLANTS Database (2022; <https://plants.usda.gov/home>).

2.4 | Precipitation measurements

To assess the precipitation trend, the winter (October of preceding year–May), the summer (June–September), and the 12-month water year (October–September) Standardized Precipitation Indices (SPI; McKee et al., 1993) were calculated for the 2008–2020 period. Even though the study started in 2011, we calculated the index since 2008 to consider the influence of the previous years on vegetation. Summer rainfall is particularly meaningful in the desert grasslands of the southwestern United States because it is the biggest contributor to grass biomass production of the current year (Cable, 1975). The winter precipitation, instead, does not directly impact grass production, but it influences plant vigor and potential for growth in the following summer (Cable, 1975; Martin, 1975). We retrieved SPI data from the SPI Explorer Tool V2.0 (<https://uaclimateextension.shinyapps.io/SPItool/>), which uses the PRISM Climate data set (PRISM Climate Data, 2021). We averaged the data from four PRISM cells that were representative of the exclosure locations (Figure 1). The reference period for SPI calculation was 1895–2020. SPI data were used to interpret the year and grazing \times year interactions results for vegetation response.

2.5 | Data analysis

To compare the vegetation between grazed and ungrazed conditions and assess changes over time, a set of vegetation variables was calculated for each transect and year. Canopy cover of mesquite, burroweed, and cacti and basal cover of perennial grasses was expressed in percentage value by dividing the measured tenths of feet by the total length of the transect. For grasses, basal cover, density, and biomass were computed for four categories of perennial grass species: total grasses, native grasses, non-native grasses, and Arizona cottontop (Appendix S5). We chose to analyze separately Arizona cottontop because it is an important forage species and the most abundant native grass in the data set (45% and 54% of natives' density and biomass, respectively). Non-native grasses included *Eragrostis curvula*, *E. lehmanniana*, and *Pennisetum ciliare* (Appendix S5). *Eragrostis lehmanniana* represented 89% and 80% of non-natives' density and biomass, respectively, and for this reason, it was not analyzed separately. For biomass, we applied the following formula developed by Nafus et al. (2009) at the SRER to each measured grass plant: biomass (g) = $e^{1.441} \times \text{diameter (cm)}^{1.253}$. Then, values were summed for each grass category. To investigate grass

population size structure, we calculated the density and biomass of two plant size classes for each grass category, i.e., diameter ≤ 3 cm and diameter > 3 cm, as representative of small and large plants, respectively. We used the 3-cm threshold because the frequency histogram of the whole grass population showed an inflection point around this value (Appendix S6). All vegetation variables were averaged between the two grazed transects and the two ungrazed transects at each exclosure to avoid pseudoreplication. Thus, we had 10 replicates for each combination of grazing treatment and year.

Finally, we constructed grazed and ungrazed cumulative frequency distribution curves of basal diameter for native and non-native grasses and Arizona cottontop, following the approach of Oñatibia et al. (2020) and Oñatibia and Aguiar (2019). To construct the grazed and ungrazed plant size curves, we combined all plants measured in grazed and ungrazed transects, respectively. The curves were calculated separately for each measurement year.

2.6 | Statistical analysis

Vegetation variables were analyzed through linear mixed models (LMMs). Grazing, year, and their interaction were set as fixed factors, and the transect (resulting from the average between pseudoreplicates) was specified as a random factor to account for the repeated-measure structure over time. Tukey's post-hoc tests were performed on significant effects ($p < 0.05$). In the case of no significant interaction, this term was removed from the model and only grazing and year effects were tested. Assumptions of residuals' normality and homoscedasticity were graphically checked (Zuur et al., 2009). Mesquite canopy cover and the density of large Arizona cottontop plants satisfied the assumptions, whereas the other variables were log- or square-root-transformed to achieve residuals' normality and homoscedasticity (Appendix S7). Non-transformed values are reported in the figures and table for ease of interpretation.

Grazed and ungrazed cumulative frequency distributions of plant size were compared according to the D statistic and p -value of the Kolmogorov–Smirnov test. The D statistic represents the maximum distance in the cumulative frequency distribution (0–1.0) between two curves.

The R software (R Core Team, 2018) was used for all statistical analyses. LMMs were run with the *lme4* package (Bates et al., 2015), post-hoc tests were computed with the *emmeans* package (Lenth, 2018), and Kolmogorov–Smirnov tests were performed with the *ks.test* function from the *stats* package.

3 | RESULTS

3.1 | Precipitation

The winter, summer, and 12-month water year precipitation trends showed both below and above-average SPI values (Figure 2). The periods 2008–2010 and 2017–2020 experienced a mixture of wet

and dry years. The period 2011–2013 was generally dry for summer, winter, and 12-month measures. The period 2014–2016 was generally wet, especially in summer. Specifically, moderate drought (SPI -1.00 to -1.49) occurred in winter 2011 (-1.43), 2013 (-1.06), and 2018 (-1.02), summer 2009 (-1.14), and in 12-month in 2011 (-1.42), 2013 (-1.01), and 2017 (-1.23). Severe drought (SPI -1.50 to -1.99) occurred in 12-month in 2009 (-1.55), and no extreme drought (SPI ≤ -2.00) occurred during the study period (drought classification based on McKee et al., 1993).

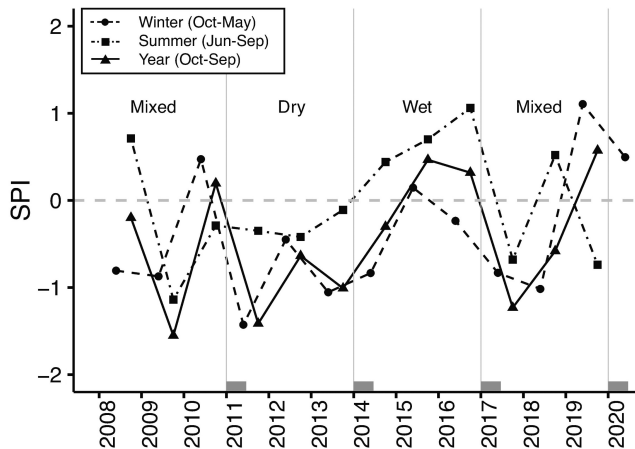


FIGURE 2 Standardized Precipitation Index (SPI) for winter (October–May), summer (June–September), and corresponding 12-month (October–September) precipitation from 2008 to 2020. SPI values are increments of the standard deviation of the population. The horizontal line at 0 SPI represents the long-term 1895–2020 average for each season, SPI negative values are drier than the average and SPI positive values are wetter than the average. Vertical lines and gray rectangles on the x-axis indicate years when vegetation measurements were made from January through May. Labels (dry, wet, and mixed) indicate the qualitative precipitation condition of the 3 years before each measurement.

3.2 | Mesquite, burroweed, and cacti cover

Grazing was not a significant factor in the dynamics of cover for mesquite, burroweed, and cacti, but year was significantly related to all dynamics of cover (Figure 3). Cover of mesquite increased in both 2017 and 2020, reaching about 30% cover in the last measurement year (Figure 3a). Burroweed cover significantly increased in 2017 (Figure 3b). The cover of burroweed in grazed transects was greater but not significantly different than ungrazed transects ($p = 0.057$). Only cacti showed a significant grazing \times year interaction ($p = 0.042$), with cover increasing over time in ungrazed but not in grazed transects (Figure 3c).

3.3 | Grass basal cover, density, and biomass

Grazed transects had significantly less basal cover of native grasses and Arizona cottontop than ungrazed transects (Figures 4b,d), whereas the basal cover of total and non-native grasses did not differ between grazing treatments (Figures 4a,c). Total, native, and non-native grasses showed a significant increase in cover in 2020 compared to the previous years, while Arizona cottontop cover was significantly higher in 2020 compared to 2017. The interaction term grazing \times year was not significant in all grass basal cover models.

Grazing did not affect the density of total and non-native grasses and Arizona cottontop (Figures 5a,c,d), but the density of native grasses was significantly greater in ungrazed than grazed transects (Figure 5b). All grass categories showed a significant increase in density in 2020, when the values doubled compared to the first measurement year. The interaction term grazing \times year was not significant in all grass density models.

On ungrazed transects, biomass of native grass and Arizona cottontop was about two-fold greater than grazed transects (Figures 6b,d). Total grass biomass was greater but not significantly different in the ungrazed than grazed treatment ($p = 0.078$), while

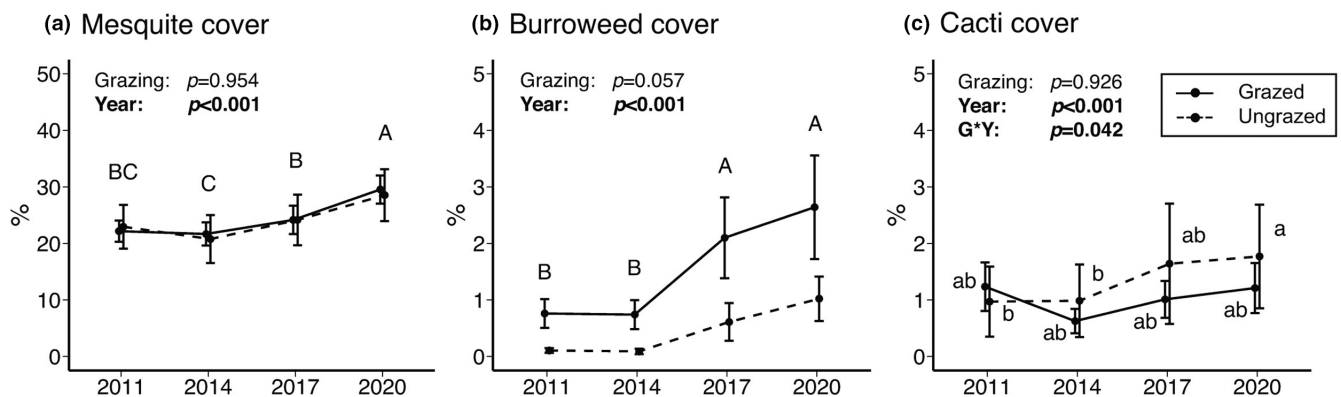


FIGURE 3 Canopy cover of (a) mesquite, (b) burroweed, and (c) cacti from 2011 to 2020 in grazed and ungrazed treatments. Values and bars represent means and standard errors, respectively. p -values of the main effects in the linear mixed models are reported, significant effects ($p < 0.05$) are in bold. Uppercase and lowercase letters indicate Tuckey post-hoc comparisons among years and among years and treatments, respectively.

FIGURE 4 Basal cover of (a) total, (b) native, (c) non-native, and (d) Arizona cottontop perennial grasses from 2011 to 2020 in grazed and ungrazed treatments. Values and bars represent means and standard errors, respectively. *p*-values of the main effects in the linear mixed models are reported, significant effects ($p < 0.05$) are in bold. Letters indicate Tuckey post-hoc comparisons among years.

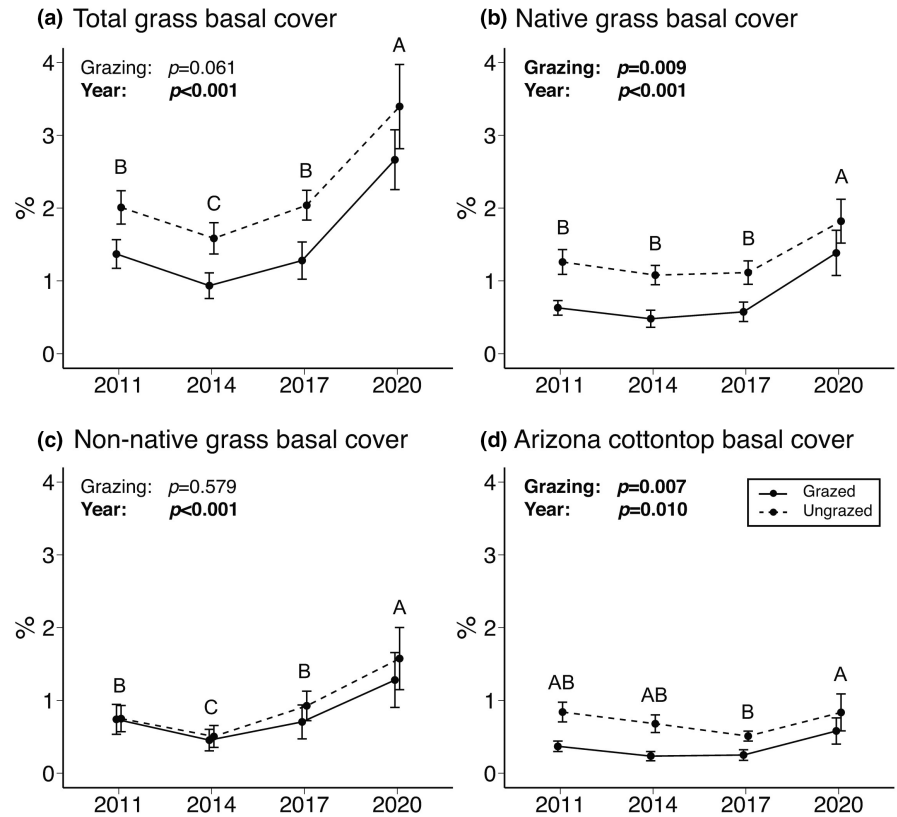
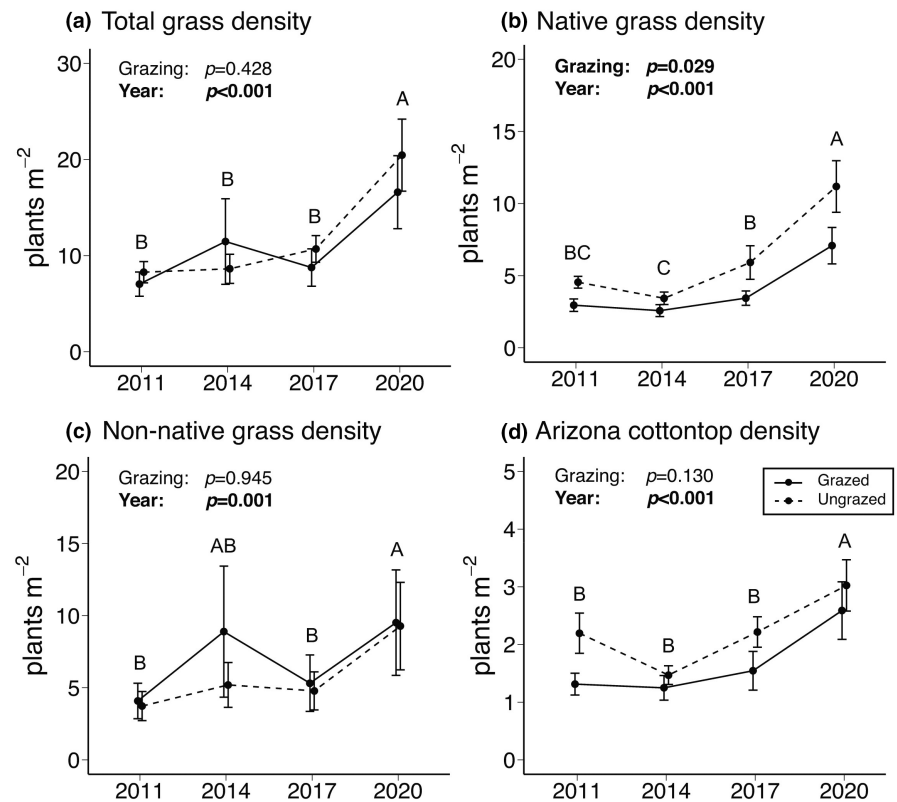


FIGURE 5 Density of (a) total, (b) native, (c) non-native, and (d) Arizona cottontop perennial grasses from 2011 to 2020 in grazed and ungrazed treatments. Values and bars represent means and standard errors, respectively. *p*-values of the main effects in the linear mixed models are reported, significant effects ($p < 0.05$) are in bold. Letters indicate Tuckey post-hoc comparisons among years.



the biomass of non-native grasses was comparable between treatments (Figures 6a,c). All categories showed a significant increase in biomass in 2017. As with grass density and cover, no grazing×year effect was observed for biomass in all grass categories.

3.4 | Grass population structure

Different responses of small and large plants to grazing and year were observed (Table 2). Density and biomass of small plants (≤ 3 cm

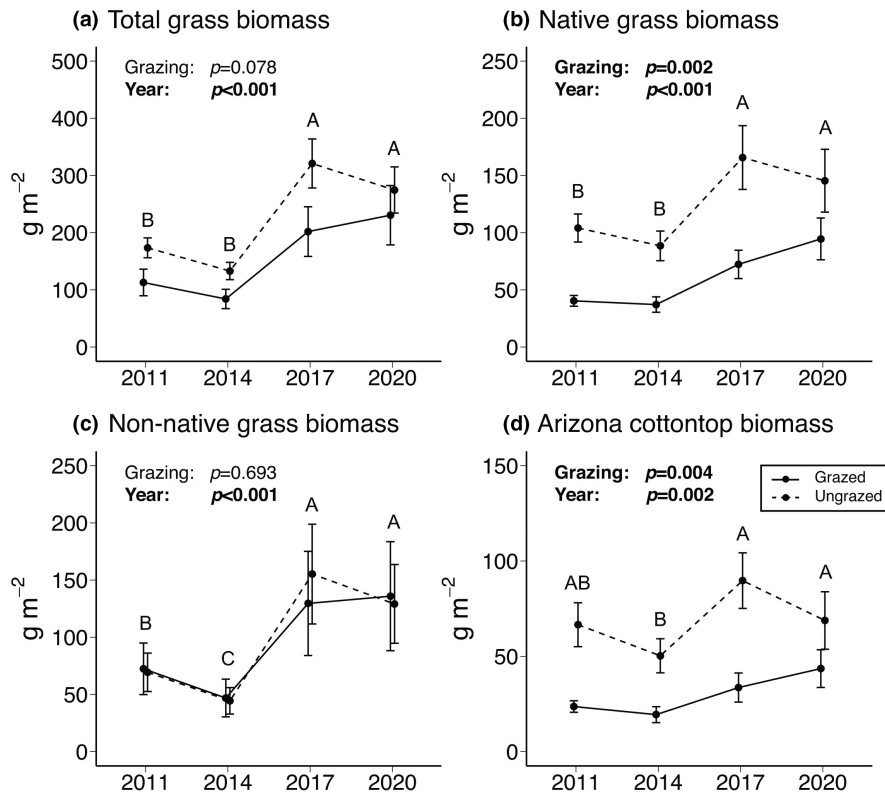


FIGURE 6 Biomass of (a) total, (b) native, (c) non-native, and (d) Arizona cottontop perennial grasses from 2011 to 2020 in grazed and ungrazed treatments. Values and bars represent means and standard errors, respectively. p -values of the main effects in the linear mixed models are reported, significant effects ($p < 0.05$) are in bold. Letters indicate Tuckey post-hoc comparisons among years.

diameter) did not differ between grazing treatments. However, for large plants (>3 cm diameter), density of native grasses and Arizona cottontop as well as biomass of total and native grasses and Arizona cottontop were less in grazed than ungrazed transects. Both size classes differed between years. Density and biomass of small plants increased significantly in 2020, whereas for large plants, they increased in 2017. Interaction between grazing and year occurred only for biomass of large native grasses. As a reference example, Arizona cottontop biomass trends over time and by grazing treatment and diameter class are shown in Figure 7.

All grazed vs ungrazed comparisons of cumulative frequency curves were significant (Kolmogorov-Smirnov test, $p < 0.05$), except for Arizona cottontop in 2020 ($p = 0.06$) (Figure 8). While D values for non-native grasses were ≤ 0.13 in all years, larger D values (≥ 0.19) were observed for natives and Arizona cottontop in 2011, 2014, and for Arizona cottontop only, in 2017. Here, grass populations were characterized by a greater fraction of large plants in ungrazed than grazed conditions (ungrazed curves shifted to the right). In 2017, regardless of the grazing treatment, populations were generally characterized by a greater fraction of large plants compared to all other years. In 2020, the grazed and ungrazed curves substantially overlapped for all grass categories (even though less pronounced in Arizona cottontop) and the D values were ≤ 0.10 .

4 | DISCUSSION

In the desert grasslands of southeastern Arizona (USA), long-term livestock removal (>85 years) increased grass abundance (cover and

biomass) of native grasses and, among them, Arizona cottontop, compared to pastures grazed at moderate stocking rates. Similar trends had been previously observed by other authors in the same biogeographical region (Smith & Schmutz, 1975; Bock et al., 1984; Valone et al., 2002; Allington & Valone, 2011). However, in our study, thanks to the measurements of plant size by single species, we could assess that native grass response to livestock removal was determined more by differences in plant size (i.e., greater number of larger plants resulting in greater biomass production and cover) rather than in the absolute number of plants (i.e., greater plant density). This pattern is clearly illustrated by Arizona cottontop, which showed no differences in plant density by grazing treatment. Further, it is consistent with research showing smaller grass plant sizes in grazed than ungrazed conditions (e.g., Butler & Briske, 1988; Oliva et al., 2005; Oñatibia et al., 2020).

These results lead us to accept our first hypothesis that response of grass cover and biomass to livestock removal is mainly the result of differences in size structure than absolute number of plants. Possible mechanisms leading to larger plants in ungrazed settings include greater longevity, increased survival rates to environmental stresses (e.g., drought), increased growth rates, and greater vigor, whereas increased grass mortality as well as shrinking of plant size following the death of some tillers can explain grass populations skewed to smaller sizes in grazed conditions (Butler & Briske, 1988; Briske & Richards, 1995; Hacker et al., 2006; Oñatibia & Aguiar, 2019; Oñatibia et al., 2020). Tussock fragmentation is also considered one important factor in reducing plant size and increasing plant density during grazing (Butler & Briske, 1988; Pfeiffer & Hartnett, 1995; Oliva et al., 2005). However, in our study, plant

TABLE 2 p-values and post-hoc comparisons of the linear mixed models performed on density and biomass of small (diameter ≤ 3 cm) and large grass plants (diameter > 3 cm).

Response variable	Small plants (diameter ≤ 3 cm)						Large plants (diameter > 3 cm)									
	p-values			Post-hoc comparisons			p-values			Post-hoc comparisons						
	Grazing	Year	Grazing × Year	Year/Treatment	2011	2014	2017	2020	Grazing	Year	Grazing × Year	Year/Treatment	2011	2014	2017	2020
Grass density					plants m ⁻² (mean ± standard error)						plants m ⁻² (mean ± standard error)					
Total	0.803	<0.001	0.550	Grazed	4.8 ± 0.89	10.2 ± 4.5	4.6 ± 1.02	12.4 ± 2.86	0.084	<0.001	0.255	Grazed	2.2 ± 0.46	1.2 ± 0.30	4.2 ± 1.01	4.2 ± 1.03
				Ungrazed	4.9 ± 0.83	6.3 ± 1.40	4.7 ± 0.79	16 ± 3.26				Ungrazed	3.4 ± 0.38	2.3 ± 0.23	6.0 ± 0.84	4.4 ± 0.7
					B	B	B	A					B	C	A	A
Native	0.242	<0.001	0.328	Grazed	2.1 ± 0.35	2.0 ± 0.33	2.0 ± 0.30	5.5 ± 0.98	0.001	<0.001	0.087	Grazed	0.9 ± 0.12	0.6 ± 0.10	1.4 ± 0.23	1.6 ± 0.32
				Ungrazed	2.6 ± 0.32	1.8 ± 0.27	3.0 ± 0.74	8.9 ± 1.56				Ungrazed	1.9 ± 0.24	1.6 ± 0.23	3 ± 0.47	2.3 ± 0.53
					B	B	B	A					B	B	A	A
Non-native	0.920	<0.001	0.733	Grazed	2.7 ± 0.86	8.3 ± 4.55	2.6 ± 1.01	6.9 ± 2.78	0.746	<0.001	0.794	Grazed	1.4 ± 0.43	0.6 ± 0.27	2.8 ± 1.00	2.6 ± 0.96
				Ungrazed	2.2 ± 0.67	4.5 ± 1.45	1.8 ± 0.49	7.1 ± 2.5				Ungrazed	1.5 ± 0.38	0.7 ± 0.19	3 ± 0.88	2.1 ± 0.60
					B	A	B	A					B	C	A	AB
Arizona cottontop	0.957	<0.001	0.117	Grazed	0.8 ± 0.16	0.9 ± 0.16	0.9 ± 0.23	1.7 ± 0.32	0.002	0.001	0.142	Grazed	0.5 ± 0.07	0.3 ± 0.08	0.6 ± 0.14	0.9 ± 0.20
				Ungrazed	1.0 ± 0.19	0.6 ± 0.09	0.8 ± 0.17	1.9 ± 0.26				Ungrazed	1.2 ± 0.21	0.9 ± 0.13	1.4 ± 0.21	1.1 ± 0.22
					B	B	B	A					AB	B	A	A
Grass biomass					gm ⁻² (mean ± standard error)						gm ⁻² (mean ± standard error)					
Total	0.987	<0.001	0.286	Grazed	37.6 ± 8.99	36 ± 9.65	33 ± 7.37	86 ± 21.08	0.009	<0.001	0.089	Grazed	75.4 ± 15.32	48.1 ± 10.61	168.7 ± 37.14	144.2 ± 32.03
				Ungrazed	39.4 ± 8.73	25.8 ± 4.84	26.3 ± 4.29	99.4 ± 22.44				Ungrazed	133.9 ± 11.37	106.9 ± 12.42	294.5 ± 40.57	175.1 ± 23.14
					B	B	B	A					C	C	A	B
Native	0.259	<0.001	0.358	Grazed	11.9 ± 1.52	13.4 ± 2.97	14.2 ± 2.4	36.7 ± 7.23	<0.001	<0.001	0.013	Grazed	28.5 ± 4.40 ^c	23.7 ± 5.40 ^c	58.0 ± 10.70 ^b	57.7 ± 11.72 ^b
				Ungrazed	18.8 ± 2.70	12.0 ± 1.90	15.4 ± 3.02	54.1 ± 10.19				Ungrazed	85.3 ± 11.48 ^b	76.3 ± 12.09 ^b	150.2 ± 25.6 ^a	91.4 ± 21.90 ^b
					B	B	B	A					A	B	A	A
Non-native	0.887	<0.001	0.353	Grazed	25.7 ± 8.43	22.6 ± 9.00	18.7 ± 7.47	49.4 ± 19.92	0.545	<0.001	0.635	Grazed	46.9 ± 14.89	24.4 ± 10.1	110.7 ± 38.49	86.5 ± 28.63
				Ungrazed	20.7 ± 6.41	13.8 ± 4.15	10.9 ± 3.40	45.4 ± 17.31				Ungrazed	48.6 ± 11.49	30.6 ± 8.22	144.3 ± 40.67	83.8 ± 19.53
					B	BC	C	A					B	C	A	A
Arizona cottontop	0.670	<0.001	0.186	Grazed	6.9 ± 1.42	6.7 ± 1.80	6.3 ± 1.66	12.8 ± 2.87	<0.001	0.002	0.237	Grazed	16.9 ± 2.61	12.7 ± 3.18	27.2 ± 6.42	30.7 ± 7.61
				Ungrazed	9.5 ± 1.72	4.5 ± 0.71	5.4 ± 1.45	15.0 ± 2.49				Ungrazed	57.1 ± 10.49	45.8 ± 8.73	84.3 ± 14.85	53.9 ± 13.36
					B	C	C	A					AB	B	A	AB

Note: Significant effects (p < 0.05) are highlighted in bold. Different uppercase letters in a column indicate significant differences between grazing treatments (grazing effect), different uppercase letters in a row indicate significant differences among years (year effect), and lowercase letters indicate significant differences among years and treatments (interaction effect), according to Tukey post-hoc tests.

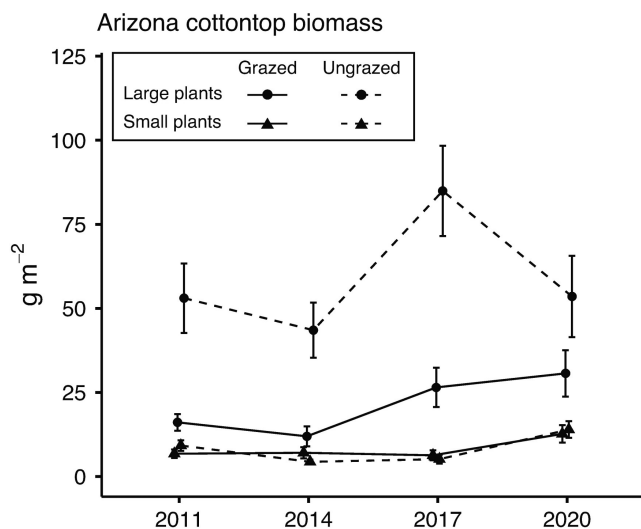


FIGURE 7 Arizona cottontop biomass by plant size class, small (diameter ≤ 3 cm) and large (diameter > 3 cm), from 2011 to 2020 in grazed and ungrazed treatments. The results of the linear mixed model are reported in [Table 2](#).

fragmentation occurred less than 5% of the time, and we did not observe greater plant density in the grazed compared to ungrazed treatment for any grass category, suggesting that plant fragmentation did not contribute to grass population dynamics. Similarly, we did not observe any difference between grazed and ungrazed areas in terms of plant recruitment, which can be expressed by the number of small plants (diameter ≤ 3 cm). In arid grasslands, grass recruitment is mostly limited by seed availability, as bare soil areas for seed germination are usually abundant (O'Connor, 1994). For this reason, O'Connor (1991, 1994), proposed that palatable native grasses may disappear when heavy grazing limits their seed production and therefore recruitment, but the results of our study suggest that the seed production by native grasses and Arizona cottontop was not hampered by the current moderate stocking rates.

We accept our second hypothesis that native grass, but not non-native grass species will be skewed toward smaller sizes in grazed than ungrazed settings based on results comparing large and small plants and cumulative frequency curves. We suggest that this difference between native and non-native grasses is driven by differences in palatability, grazing resistance, and seed production. First, Arizona cottontop is one of the most palatable species in desert grassland, and it is also very sensitive to intense utilization (Cable, 1971a, 1979), while Lehmann lovegrass is less palatable than native grasses but extremely tolerant to grazing (Cable & Bohning, 1959; Cable, 1971b). In general, this is consistent with a decrease in plant size for palatable grasses compared to non-palatable (Oñatibia & Aguiar, 2019). Second, while Arizona cottontop establishment patterns (e.g., seed production, germination, sprouting) can be strongly affected by rainfall variability, Lehmann lovegrass is very drought-resistant and an abundant seed producer (Cable & Bohning, 1959; Cable, 1971b; Sumrall, 1990; Cox et al., 1992). Indeed, after its first introduction on the SRER in the 1930s, Lehmann lovegrass spread in both

ungrazed and grazed areas thanks to the great ability to establish itself from seeds under different grazing intensities, water availabilities, and soil types (Cable, 1971b; McClaran & Anable, 1992). Moreover, the propagation of Lehmann lovegrass inside our enclosures may have been facilitated by the small enclosures' size (1.1 ha on average) and their permeability to seed dispersal. For example, in a southern Arizona desert grassland site with an enclosure larger (3160 ha) than the ones used in the present study, Bock et al. (2007) observed slower colonization of Lehmann lovegrass in ungrazed than grazed conditions.

We accept our third hypothesis that woody plant cover is not affected by long-term livestock removal because we observed no differences in cover between grazed and ungrazed settings for mesquite, burroweed, and cacti. We suggest this pattern occurred mainly because enclosures were too small to restrict seed dispersal and woody plants are not an important part of cattle diets. Burroweed and cacti are not palatable and therefore not directly impacted by livestock. Cattle do eat mesquite seed pods and young leaves, but their use of mesquite is not heavy enough to create a browseline or obvious damage to plants. In general, the increase in woody plant cover began in the late 19th century (Van Auken, 2000; Archer et al., 2017; Bestelmeyer et al., 2018), and for mesquite that increase appears to have slowed greatly suggesting that a carrying capacity has been approached (Huang et al., 2018). In contrast, although cover of burroweed and cacti is greater now than in the 19th century, their abundance displays decadal fluctuations due to climatic fluctuations and shorter life span than mesquite (McClaran, 2003; McClaran et al., 2010; Huang et al., 2018). Our finding of equivalent woody cover for long-term grazed and ungrazed settings is central to our interpretation of differences in grass abundance following long-term grazing removal. Mesquite cover is known to favor some native grass species and limit others but has little effect on Lehmann lovegrass abundance (Tiedemann et al., 1971; Tiedemann & Klemmedson, 1977; Gornish et al., 2021). Fortunately, the equivalence of mesquite cover in our grazed and ungrazed settings allows us to dismiss the mesquite effect on the grass response to long-term grazing removal.

We accept the fourth hypothesis that short-term (10 years in 3-yr increments) pattern of vegetation dynamics will occur in response to fluctuations in precipitation and growing conditions (i.e., general increase in cover of mesquite, burroweed, cacti, and grass between 2014 and 2020 as recovery from the dry period between 2011 and 2014 and recruitment of small grass plants in 2020 following wet summer condition in 2017), but the dynamics will not differ between long-term grazed and ungrazed settings. We emphasize that the absence of a grazing effect on the short-term vegetation dynamics most likely reflects a stabilization of vegetation differences after more than 80 years of livestock removal (Valone et al., 2002), the absence of other disturbances such as extreme drought and fires, and relatively moderate grazing intensity during the 2011–2020 period of study (O'Connor, 1991; Holechek et al., 2003; Loeser et al., 2007; Chen et al., 2013). Concerning the precipitation trends shown by SPI, our results did not show a significant interaction with

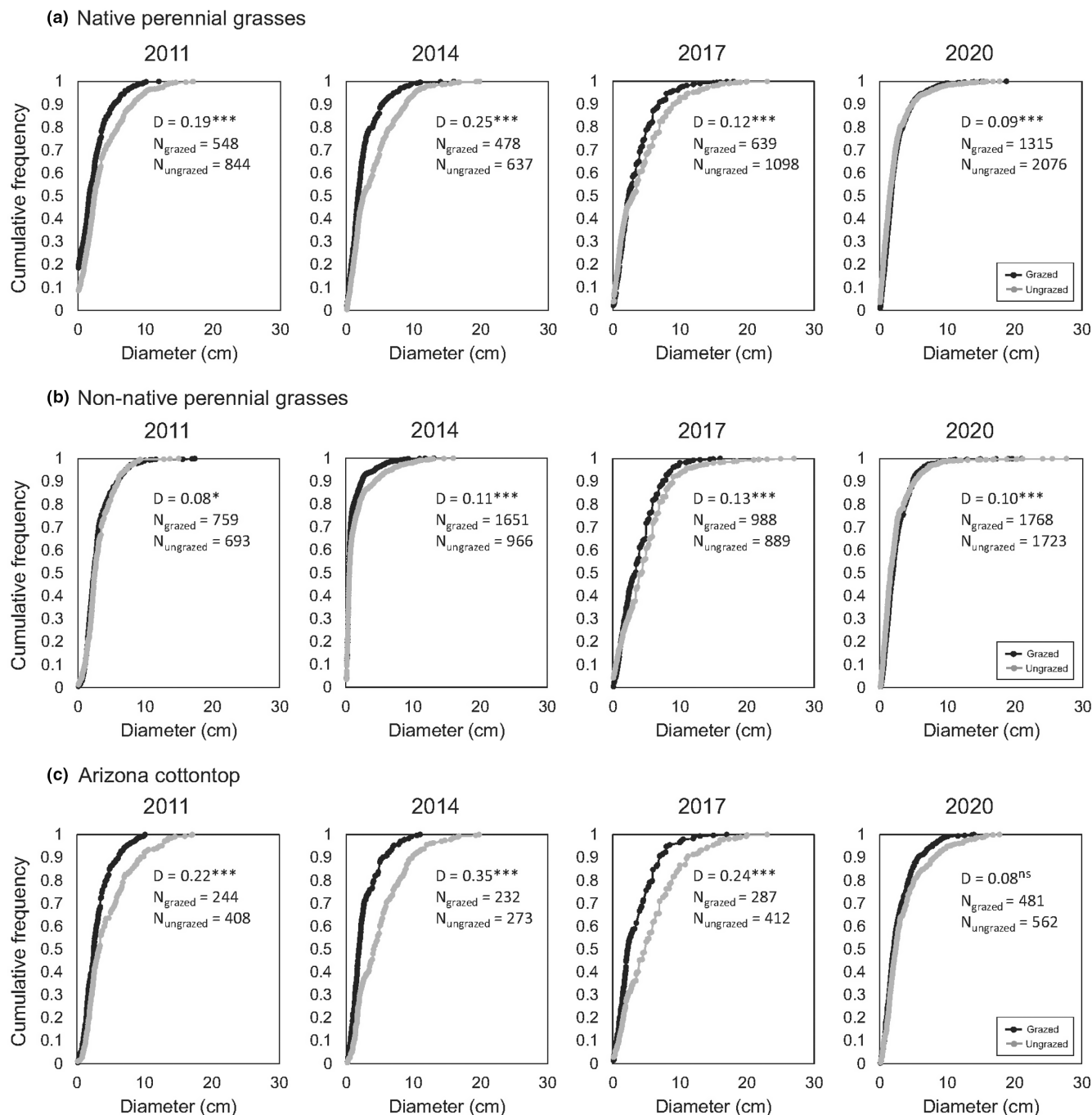


FIGURE 8 Cumulative frequency distributions of plant diameters for (a) native, (b) non-native, and (c) Arizona cottontop perennial grasses in grazed and ungrazed transects in all measurement years (2011, 2014, 2017, and 2020). The D statistic and significance of the Kolmogorov-Smirnov test and the number of plants in grazed and ungrazed curves are reported for each pair. Significance levels: ns, $p \geq 0.05$; *, $p < 0.05$; ***, $p < 0.001$.

grazing (grazed vs ungrazed) and year, even though there was a general trend of drier winter conditions in 2011–2014. It is possible that more extreme drought or greater grazing intensity may have resulted in a grazing \times year interaction. We also assumed the vegetation differences inside vs outside the exclosures have stabilized as most vegetation responses typically occur in the first years (e.g., Chen & Tang, 2016) or decades (e.g., Valone et al., 2002; Wolf & Mitchell, 2021) after grazing removal, especially for perennial grasses

which have shorter lifespans (<15 years at the SRER; Canfield, 1957) than shrubs (<40 years for burweed, <50 years for cacti, and up to 200 years for mesquite; Archer, 1989; McClaran, 2003; McClaran et al., 2010). Then, we can speculate that the differences in grass size structure we observed between grazed and ungrazed settings began to appear early in the more than eight decades of livestock removal, and most likely following the first multi-year period of wet growing conditions.

Our findings have implications for livestock management and the conservation of native grass species in the desert grassland. Under moderate livestock grazing intensity, native grass abundance is less than exists in long-term ungrazed areas. But even in grazed areas, there was a sustained (2011–2020) abundance of total native grasses and the dominant Arizona cottontop species. However, we are concerned that native grass abundance may decline in grazed areas given that the smaller plants found in grazed areas are likely to experience greater mortality than larger plants during drought (Butler & Briske, 1988; Pfeiffer & Hartnett, 1995; Fuhlendorf et al., 2001), and that drought frequency has increased since the mid-1990s (McClaran & Wei, 2014) and more frequent drought conditions are projected (Cook et al., 2015).

In summary, this study demonstrated that long-term livestock removal in desert grasslands affects native grass response, but not that of non-native grasses and woody species. Moreover, vegetation response is largely influenced by interannual precipitation variability, and especially by the amount of summer rainfall. Finally, results showed that differences in population size structure characterize the response of native grasses (i.e., biomass production and cover) to long-term livestock removal. We are confident in our findings thanks to the strength of both our database and experimental design, which are based on: (i) a large number (10) of long-term livestock exclosures (88–104 years) established on the same Ecological Site; (ii) consistent stocking rates in the grazed pastures during the study; (iii) four repeated measurements, which provided the opportunity to have a solid pattern of data also in relation to climate variations; and most importantly, (iv) three measures of grass abundance (cover, density, biomass) and plant size by single species and not by broad functional groups (i.e., grasses). In this regard, we emphasize the value and importance of measuring plant size and reporting population size structure for understanding the mechanisms behind grass response to livestock removal (Oñatibia et al., 2020; Travers & Berdugo, 2020).

AUTHOR CONTRIBUTIONS

Mitchel P. McClaran conceived the research idea and the experimental design of the study; Mitchel P. McClaran, Ginevra Nota, Nicolò Anselmetto, and Alessandra Gorlier contributed to the data collection; Ginevra Nota performed the statistical analyses; Ginevra Nota, with contributions from Nicolò Anselmetto, Alessandra Gorlier, and Mitchel P. McClaran, wrote the paper; all authors agree with the final manuscript.

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DATA AVAILABILITY STATEMENT

The original data sets including the vegetation measurements used in this study are stored and available for download on the Santa Rita Experimental Range (SRER) website at <https://cals.arizona.edu/srer/content/exclosure-transects>. Only exclosures 1A, 2B, 4, 5, 6, 23, 28, 35A, 35B, and 40 were used in this study. The livestock history data including the stocking rates of each pasture of the SRER are stored on the SRER website at <https://cals.arizona.edu/srer/content/monthly-livestock-use-pasture-1908>. Only pastures 2S, 2N, 6A, 6E, and UA-Cell D refer to this study.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. Criteria used for the selection of the papers included in the enclosure studies database (Table S1) and references.

Appendix S2. Methodology used to calculate the median values reported in the manuscript (Table 1).

Appendix S3. Characteristics of the 10 enclosures studied on the Santa Rita Experimental Range.

Appendix S4. Average stocking rate from 2008 to 2019 on the Santa Rita Experimental Range.

Appendix S5. List of plant species measured in the 10 enclosures studied on the Santa Rita Experimental Range.

Appendix S6. Frequency histogram of plant size (diameter classes) for all perennial grasses measured on the Santa Rita Experimental Range.

Appendix S7. Transformations of the response variables used for modeling with linear mixed models.

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