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Grazing effects on shrub-induced resource islands and herbaceous vegetation heterogeneity in sagebrush-steppe communities[☆]

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ABSTRACT

Spatial heterogeneity in plant communities promotes coexistence and diversity by providing a variety of niches for different species. In shrub-steppe communities, shrubs create distinct microsites under their canopies (canopy microsites) compared to areas between their canopies (interspace microsites). This creates spatial heterogeneity in soil nutrient availability and herbaceous vegetation. Grazing can influence spatial heterogeneity, but the effect of grazing on shrub-induced spatial heterogeneity is largely unknown. We investigated the long-term (+80 yrs.) effects of moderate grazing by cattle on sagebrush (*Artemisia*)-induced spatial heterogeneity in soil nutrients, herbaceous vegetation, and ground cover in sagebrush-bunchgrass steppe communities at eight sites in southeastern Oregon. Each site consisted of a long-term grazing enclosure and an adjacent grazed area. Almost all measured herbaceous vegetation (cover, density, diversity, and evenness) and ground cover variables differed between canopy and interspace microsites. Grazing did not influence the effects of microsites on most measured herbaceous vegetation characteristics and ground cover variables. Available soil nutrients were not influenced by grazing, but the majority differed between microsites. The limited effect of moderate grazing on shrub-induced spatial heterogeneity provides evidence that sagebrush exerts a strong influence on patterns of soil nutrients and herbaceous vegetation in sagebrush-bunchgrass communities. These results also demonstrate that moderate grazing by cattle can be compatible with maintaining spatial heterogeneity within shrub-steppe communities. In these ecosystems, maintaining and restoring shrubs is critical to promoting spatial heterogeneity, thereby encouraging coexistence and diversity.

1. Introduction

Grazing by livestock is the primary land use of rangelands throughout the world, providing food and fiber for humans. Thus, understanding the effects of grazing is important, especially as greater demand is placed on rangelands with increasing human populations. Grazing effects on environmental characteristics and plant community composition are of concern and have been

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investigated in many ecosystems (e.g., Johnson, 1956; Landsberg et al., 1999; Jing et al., 2014; Porensky et al., 2017). This has resulted in recommended management practices that are environmentally sustainable in contrast with historic grazing practices that often were not (Borman, 2005; Davies and Boyd, 2020). However, there remains important areas that are understudied, in particular, the effects of grazing on spatial heterogeneity. Spatial heterogeneity in plant communities is point to point dissimilarity in vegetation and/or environmental characteristics in space (Collins and Smith, 2006). Grazing can affect spatial heterogeneity, thereby, altering ecosystem processes and biodiversity (Alder et al., 2001). The effect of grazing on spatial heterogeneity likely varies by vegetation and environmental heterogeneity, scale, and grazing animal characteristics (Alder et al., 2001; Collins and Smith, 2006), thus warranting further investigation.

Spatial heterogeneity is important because it promotes coexistence by providing niches for a variety of species (Silvertown, 2004; Do Carmo et al., 2016; Feeser et al., 2018). Heterogeneity in arid and semi-arid plant communities can at least be partially attributed to shrubs and trees. Woody vegetation can create distinct canopy (under canopy) and interspace (between canopies) microsites, often resulting in resource islands (a.k.a., islands of fertility) in canopy compared to interspace microsites (Jackson and Caldwell, 1993a, 1993b; Herman et al., 1995). In particular, soil nutrient concentrations are generally greater in canopy compared to interspace microsites (Doescher et al., 1984; Burke et al., 1987; Davies et al., 2007). Woody vegetation also influences the microenvironment (e.g., temperature, light, and moisture) under their canopies (Pierson and Wight, 1991; Chambers, 2001; Davies et al., 2007), thereby, creating spatial heterogeneity in microsites in plant communities.

This shrub-induced heterogeneity in soil resources and microenvironments (i.e., interspace and canopy microsites) contributes to herbaceous vegetation heterogeneity in plant communities. The canopy microsite is often more favorable for herbaceous vegetation, especially in hot and dry ecosystems, leading to patches of greater vegetation abundance and cover (Holzapfel et al., 2006; van Zonneveld et al., 2012). This has been observed in many shrublands including the sagebrush (*Artemisia* L.) steppe of North America (Doescher et al., 1984; Burke et al., 1987; Wight et al., 1992; Davies et al., 2007). Though many plant species are favored by canopy microsites, others are favored by interspace microsites (Davies et al., 2007). Plant functional groups may also differ in their response to microsites, for example annual forbs may be more common in interspace microsites and perennial forbs more common in canopy microsites (Eckert et al., 1986; Davies et al., 2007). This creates a diversity of habitat for higher trophic levels within a plant community.

Heterogeneity in microsites and herbaceous vegetation is important for maintaining structure and function in the sagebrush ecosystem of western North America. Under sagebrush canopies are favorable for the establishment and growth of many plant species (Eckert et al., 1986; Pierson and Wight, 1991; Callaway et al., 1996; Chambers, 2001; Davies et al., 2007). This is particularly important as recruitment of many native perennial species is infrequent (Svejcar et al., 2017). Heterogeneity in sagebrush communities is also important to higher trophic levels, like sage-grouse, a species of conservation concern (Aldridge and Brigham, 2002; Doherty et al., 2010). The differences between canopy and interspace locations are also likely important for various insects and small animals that require distinct habitats.

The effects of disturbances on spatial heterogeneity in sagebrush communities are a concern as this may affect plant community assemblage and higher trophic levels. Disturbances (e.g., exotic annual grass invasion, fire, grazing) likely influence the heterogeneity of microsites and herbaceous vegetation in sagebrush communities. Annual grass invasion increases homogeneity in sagebrush communities (Davies and Nafus, 2013). Fire can increase or decrease heterogeneity in sagebrush communities, depending on scale and completeness of the burn (Davies et al., 2009a; Davies and Bates, 2020). Livestock grazing, which is nearly ubiquitous across the sagebrush ecosystem, effects on shrub-induced spatial heterogeneity are largely unknown. Cattle graze interspaces more readily than under sagebrush canopies (France et al., 2008), which may dampen or exaggerate the effects of shrubs on microsite plant communities. Grazing by removing photosynthetic tissue may have a greater influence on herbaceous vegetation than the effects of sagebrush-induced microsites. Grazers can also alter microsite environments by reallocating nutrients through deposition of urine and feces (Steinauer and Collins, 2001), which may mediate the resource island effect of sagebrush. If grazing alters the spatial heterogeneity of a plant community, it may significantly impact ecosystem functions and processes (Alder et al., 2001). To better understand functional relationships in shrublands and guide management, information detailing the effects of grazing on shrub-induced heterogeneity is needed.

The purpose of this study was to investigate the influence of moderate grazing by cattle on spatial heterogeneity at the local scale (canopy and interspace microsites) in sagebrush communities. We accomplished this by comparing microsite vegetation, ground cover, and soil nutrient availability inside and outside long-term (+80 yrs.) grazing exclosures in the northern Great Basin. We hypothesized that grazing would 1) modulate the effects of canopy and interspace microsites, thereby, decreasing the resource island effect and 2) subsequently, leading to less spatial heterogeneity in herbaceous vegetation associated with shrub-induced microsites in sagebrush communities.

2. Methods

2.1. Study Area

The experiment was conducted on the Northern Great Basin Experimental Range (NGBER) approximately 56 km west of Burns, Oregon, USA (lat 43°29'N, long 119°43'W). Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* (Beetle and A. Young) S.L. Welsh) was the dominant shrub at all study sites. The dominant perennial bunchgrass was Thurber's needlegrass (*Achnatherum thurberianum* (Piper) Barkworth), Idaho fescue (*Festuca idahoensis* Elmer), or bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Löve) depending on the study site. Other perennial bunchgrass species at the study sites included Sandberg bluegrass (*Poa secunda* J.

Presl), prairie Junegrass (*Koeleria macrantha* (Ledeb.) J.A. Schultes), squirreltail (*Elymus elymoides* (Raf.) Swezey), needle and thread (*Hesperostipa comata* (Trin. and Rupr.) Barkworth), and Indian ricegrass (*Achnatherum hymenoides* (Roem. and Schult.) Barkworth). Climate at the NGBER is representative of the northern Great Basin with cold, wet winters and hot, dry summers. Average long-term annual precipitation (1991–2020) at the study area was 252 mm (PRISM, 2021). Crop year precipitation (Oct. 1, 2020–Sept. 30, 2021) was 175 mm (PRISM, 2021). Elevation at the study sites ranges from 1390 to 1489 m above sea level. Topography at the study sites is variable with slopes ranging from 0 to 15° and aspects from north to south. Soils at the study sites are Aridisols and Andisols with shallow to moderately deep soil profiles before reaching a restrictive layer. Historic fire return intervals are estimated to be 50–100 + years for these sagebrush plant communities (Wright and Bailey 1982; Mensing et al., 2006). There was no record or evidence that these plant communities burned in the last + 80 years.

2.2. Experimental design and measurements

To investigate the effects of grazing on microsites, we used a complete block design with eight blocks. Each block was in a different pasture and consisted of the factorial combinations of grazed or ungrazed, and sagebrush canopy or interspace microsites. The ungrazed treatments were 2-ha livestock grazing exclosures established in 1936. The grazed treatment plots were located adjacent (20 m) to the exclosures and within the same soil, topography, and vegetation association as the exclosures. Density data collected in 1937 revealed no differences in Sandberg bluegrass, large perennial bunchgrass, annual grasses, perennial forbs, and annual forbs between inside and outside the exclosures (Rose et al., 1994; Davies et al., 2010; Copeland et al., 2021). The grazed treatments were grazed by cattle at generally moderate levels, 30–50% use of available forage. From 1938–1949, livestock use was rotation grazing with stocking rates determined from rangeland production surveys conducted in 1938 and 1944 (Davies et al., 2009b). From 1949 to present, the grazing program was a deferred-rotation system with an occasional year of complete rest from grazing. Grazing pressure was 0.15–0.36 animal unit months (AUMs) per ha with an average pressure of 0.22 AUMs per ha. Grazed treatments were not grazed in 2021 prior to data collection.

Herbaceous vegetation cover and density were measured in 50 randomly selected sagebrush canopy and interspace microsites in each grazed and ungrazed treatment in June of 2021 for a total of 1600 microsites sampled (8 blocks X 50 replicates X 2 microsites X 2 grazing treatments = 1600 sampled microsites). Sagebrush and other shrub cover and density were not measured in this study because moderate grazing has little to no effect on them (Davies et al., 2009, 2010). Canopy microsites were under mature sagebrush plants. Interspace microsites were between sagebrush canopies. Vegetation cover and density were measured by species in two 0.2 m² (40 × 50 cm) quadrats in each microsite resulting in a total of 3200 quadrats (2 quadrats X 1600 sampled microsites = 3200 quadrats). In canopy microsites, a quadrat was placed on each side of the sagebrush stem. In interspaces, two quadrats were placed in its center adjacent to each other. Cover was visually estimated to the nearest 1% using markings along the quadrat that divided it into 5%, 10%, 25%, and 50% segments. Bare ground, ground litter, and soil biological crust cover were also estimated in the 0.2 m² quadrats. Density was determined by species by counting all individuals rooted inside the quadrat. Diversity (Shannon-Wiener Index) and evenness (Shannon Evenness Index) were calculated from density estimates.

Available soil nutrients (total inorganic nitrogen, potassium, phosphorus, calcium, and magnesium) were measured using plant root simulator probes (PRSTM-probes Western Ag Innovations, Saskatoon, Saskatchewan, Canada) placed in two canopy and two interspace microsites in each grazed and ungrazed treatment in each block. Each treatment replicate consisted of three anion and three cation PRSTM-probes. PRSTM-probes use an ion exchange membrane buried in the soil to attract and absorb ions to estimate the availability of soil nutrients to plants (Jowkin and Schoenau, 1998). The PRSTM-probes were buried vertically in the upper 20 cm of the soil profile from April 15th through July 15th. PRSTM-probes were extracted with 0.5 N HCl and analyzed colourimetrically with an autoanalyzer by Western Ag Innovations to determine nutrient concentrations.

2.3. Statistical analyses

We used analysis of variance (ANOVA) using a mixed model approach in SAS v. 9.4 (PROC MIXED SAS Institute Inc., Cary, NC) to determine the influence of grazing and microsites on herbaceous vegetation characteristics, ground cover, and soil nutrient availability. Fixed variables were microsite and grazed treatments and their interactions. Random variables were block and interactions between blocks and treatments. The interaction between grazing and microsite was included in all models, but only reported in the text when significant. Appropriate covariance structures were selected using the Akaike's Information Criterion (Littell et al., 1996). Data that violated assumptions of ANOVAs were log transformed. Data in the text and figures are presented in their original (non-transformed) dimensions. For analyses, herbaceous vegetation was grouped into five categories: perennial bunchgrass (excluding Sandberg bluegrass), Sandberg bluegrass, perennial forb, annual grass, and annual forb. Sandberg bluegrass was analyzed individually from other native bunchgrasses because it is smaller in stature, develops earlier in the growing season, and responds differently to disturbances (McLean and Tisdale, 1972; Yensen et al., 1992; Davies et al., 2021). The annual grass group was comprised solely of non-natives. Significance was set at $P \leq 0.05$ and response variable means were reported with standard errors (mean + S.E.).

3. Results

3.1. Cover

Perennial bunchgrass cover was influenced by grazing and microsite (Fig. 1A; $P = 0.047$ and 0.029, respectively). Grazing

decreased perennial bunchgrass cover in both microsites. Canopy microsites generally had greater perennial bunchgrass cover compared to interspaces. Sandberg bluegrass cover was greater in grazed compared to ungrazed areas (Fig. 1B; $P = 0.018$) and in canopy compared to interspace microsites ($P < 0.001$). Sandberg bluegrass cover was on average 2.1-fold greater in the canopy compared to the interspace, regardless of grazing treatment. The response of perennial forb cover to grazing varied by microsite (Fig. 1C; $P = 0.007$). Perennial forb cover in grazed and ungrazed interspaces were similar. In contrast, perennial forb cover was less in

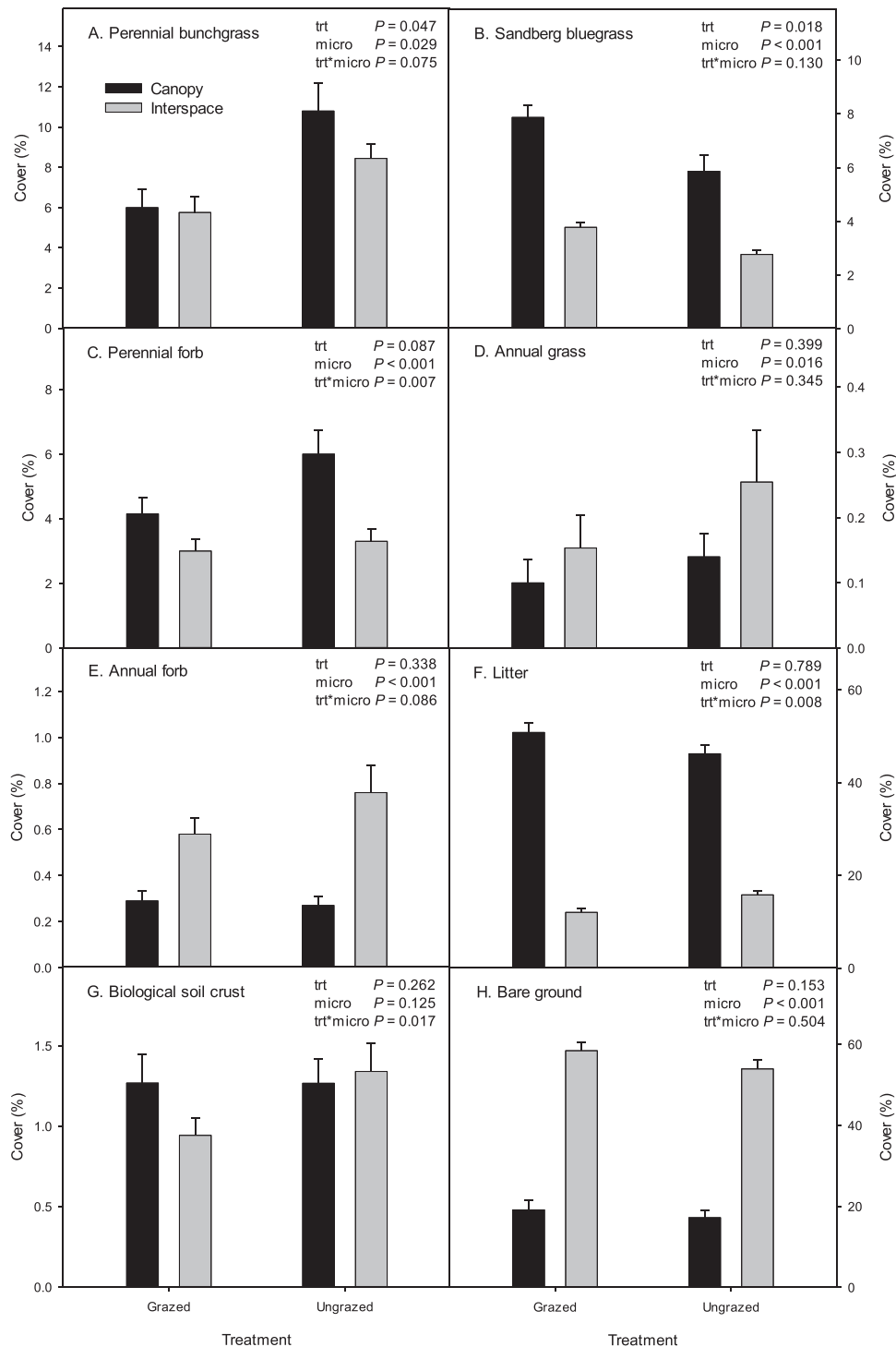


Fig. 1. Herbaceous vegetation, ground litter, biological soil crust, and bare ground cover (mean + S.E.) in moderately grazed and ungrazed canopy and interspace microsites. Trt = treatment (grazed and ungrazed), micro = microsites, and trt*micro = treatment by microsite interaction.

grazed compared to ungrazed canopy microsites. Annual grass and annual forb cover did not differ between grazed and ungrazed areas (Fig. 1D-E; $P = 0.399$ and 0.338 , respectively). Annual grass and annual forb cover were greater in interspace compared to canopy microsites ($P = 0.016$ and < 0.001 , respectively). The response of ground litter to grazing varied by microsite (Fig. 1F; $P = 0.008$). Litter was slightly greater in grazed compared to ungrazed canopy microsites and slightly less in grazed compared to ungrazed interspace microsites. Litter was 2.9–4.2-fold greater in canopy compared to interspace microsites. Soil biological crust cover response

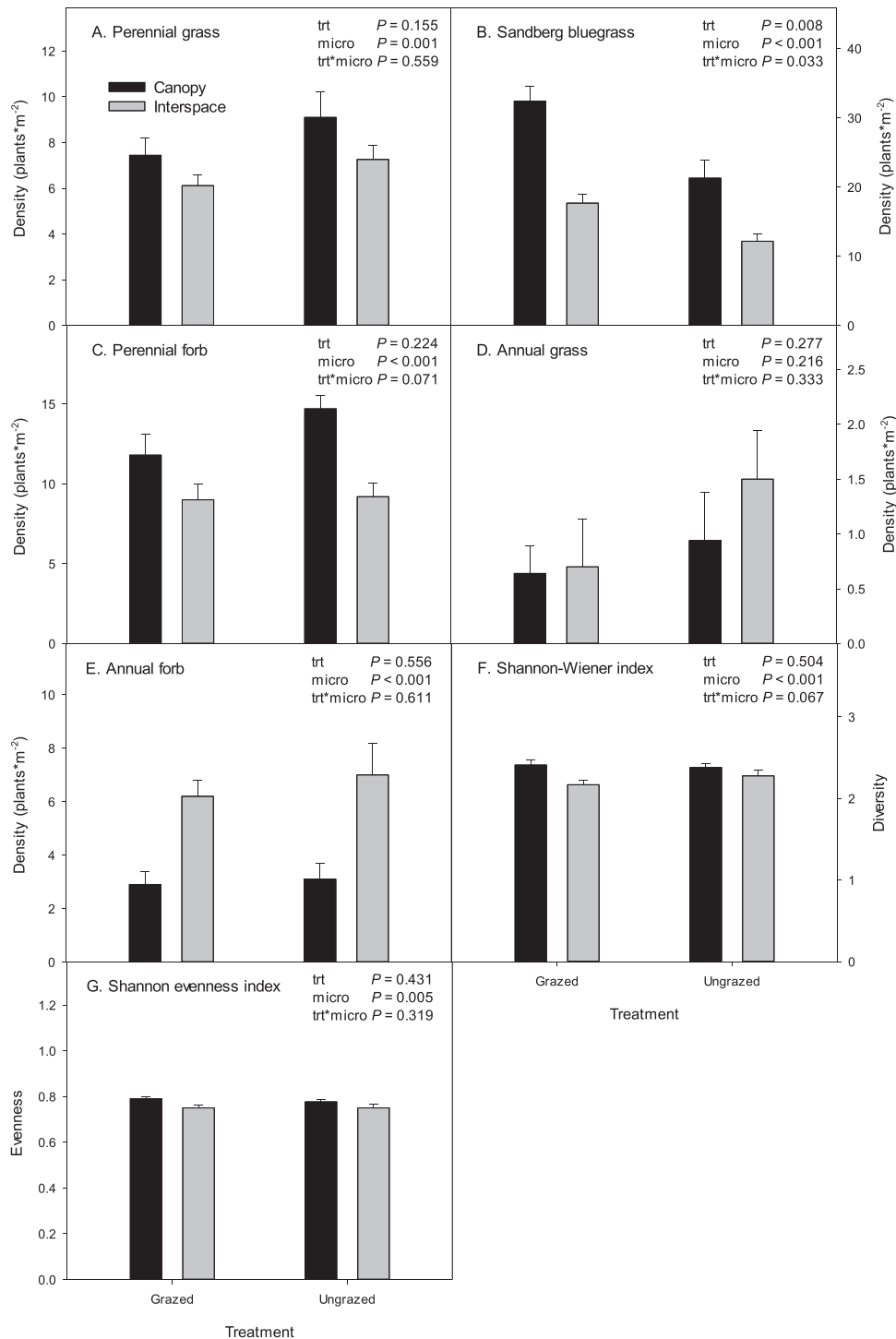


Fig. 2. Herbaceous vegetation density, diversity, and evenness (mean + S.E.) in moderately grazed and ungrazed canopy and interspace microsites. Trt = treatment (grazed and ungrazed), micro = microsites, and trt*micro = treatment by microsite interaction.

to grazing varied by microsite (Fig. 1G; $P = 0.017$), but was very low ($< 1.4\%$) regardless of grazing treatment and microsite. Soil biological crust cover was similar between grazed and ungrazed canopy microsites. In contrast, soil biological crust cover was less in grazed compared to ungrazed interspace microsites. Bare ground was not influenced by grazing (Fig. 1H; $P = 0.153$), but varied by microsite ($P < 0.001$). Bare ground was 3-fold greater in interspace compared to canopy microsites.

3.2. Density and diversity

Grazing did not influence the density of large perennial bunchgrasses (Fig. 2A; $P = 0.155$). Large perennial bunchgrass density was 1.2–1.3-fold greater in canopy compared to interspace microsites ($P = 0.001$). The response of Sandberg bluegrass density to grazing varied by microsite (Fig. 2B; $P = 0.033$). Sandberg bluegrass density increased more in the canopy compared to the interspace with grazing. Grazing did not influence perennial forb density ($P = 0.224$). Perennial forb density was 1.3–1.6-fold greater in canopy compared to interspace microsites (Fig. 2C; $P < 0.001$). Annual grass density was not influenced by grazing or microsite (Fig. 2D; $P = 0.277$ and 0.216 , respectively). Annual forb density did not differ between grazed and ungrazed areas (Fig. 2E; $P = 0.556$), but varied between microsites ($P < 0.001$). Annual forb density was 2.2–2.3-fold greater in interspace compared to canopy microsites. Diversity was not influenced by grazing (Fig. 2F; $P = 0.504$), but was greater in canopy compared to the interspace microsites ($P < 0.001$). Similarly, evenness did not differ between grazed and ungrazed treatments (Fig. 2G; $P = 0.431$), but was greater in the canopy compared to the interspace ($P = 0.005$).

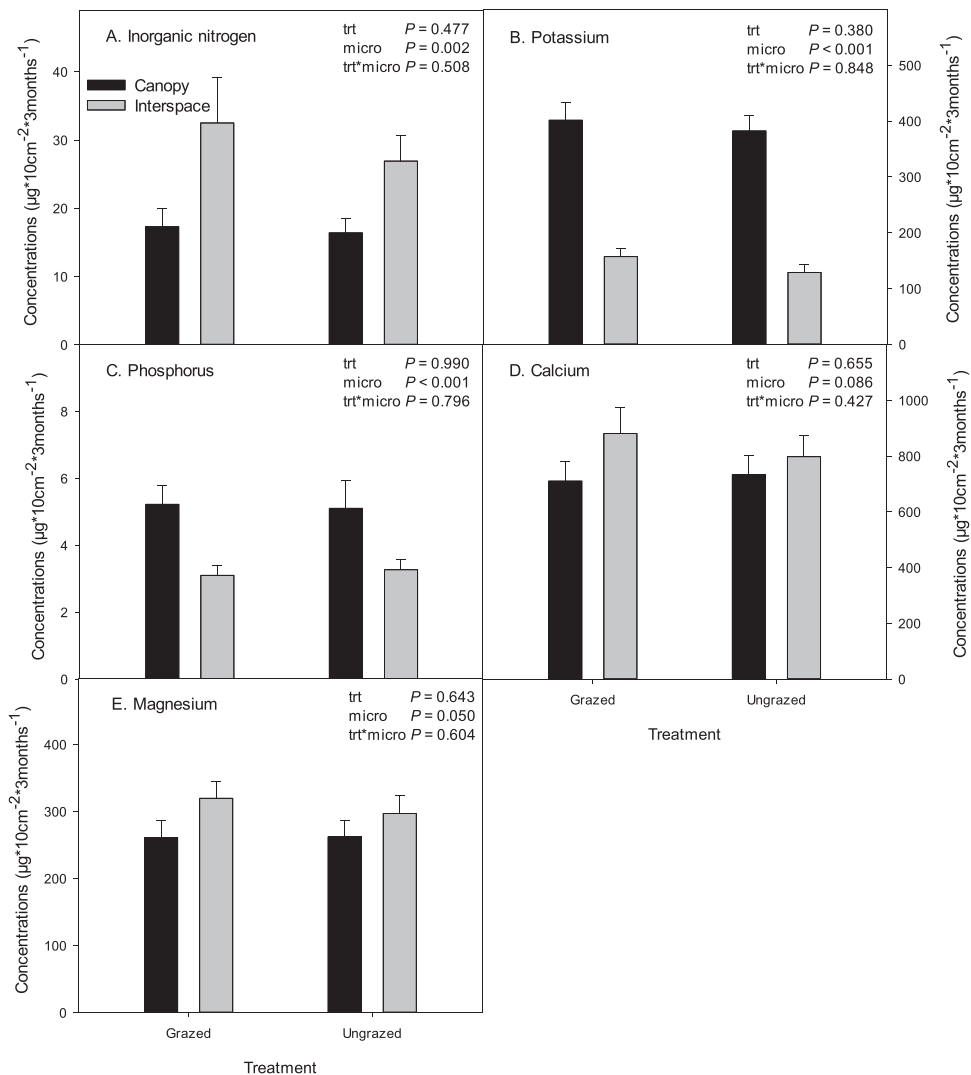


Fig. 3. Plant available soil nutrient concentrations (mean + S.E.) in moderately grazed and ungrazed canopy and interspace microsites. Trt = treatment (grazed and ungrazed), micro = microsites, and trt*micro = treatment by microsite interaction.

3.3. Available soil nutrients

Total inorganic nitrogen concentrations were not influenced by grazing (Fig. 3A; $P = 0.477$), but differed between microsites ($P = 0.002$). Total inorganic nitrogen was 1.6–1.9-fold greater in interspace compared to canopy microsites. Potassium concentrations were similar between grazed and ungrazed areas (Fig. 3B; $P = 0.380$), but differed between microsites ($P < 0.001$). Potassium was 2.6–3.0-fold greater in canopy compared to interspace microsites. Phosphorus concentrations were not influenced by grazing (Fig. 3C; $P = 0.990$), but were 1.6–1.7-fold greater in canopy compared to interspace microsites ($P < 0.001$). Calcium concentrations were not influenced by grazing or microsite (Fig. 3D; $P = 0.655$ and 0.086 , respectively). Magnesium concentrations were similar between grazed and ungrazed areas (Fig. 3E; $P = 0.643$), but differed between microsites ($P = 0.050$). Magnesium concentrations were 1.1–1.2-fold greater in interspace compared to canopy microsites.

4. Discussion

Understanding the effects of grazing on spatial heterogeneity is critical to maintain diversity and ecological processes and functions. In shrubland communities, the spatial heterogeneity created by shrubs influences plant community assemblage and higher trophic levels (Herman et al., 1995; Callaway et al., 1996; Davies et al., 2007). In our current study, long-term, moderate grazing by cattle had limited effects on spatial heterogeneity in herbaceous vegetation cover and density associated with shrub canopies and no effect on shrub-induced heterogeneity in nutrients, bare ground and diversity. This is counter to our hypotheses that grazing would mediate the effects of canopy and interspace microsites; thereby, decreasing the resource island effect and spatial heterogeneity of herbaceous vegetation within sagebrush communities. Our results imply that moderate grazing by cattle is unlikely to alter the spatial heterogeneity created by shrubs in shrub-steppe communities. In contrast, grazing by bison decreased spatial heterogeneity in tallgrass prairie (Collins and Smith, 2006) and livestock exclusion increased spatial heterogeneity in shortgrass steppe (Alder and Lauenroth, 2000). Our results likely differed because 1) shrubs create strong vegetation and micro-environment patterns, and 2) grazing intensity, frequency, and timing probably varied between our study and these other studies.

Though grazing influenced spatial heterogeneity of herbaceous vegetation and ground cover in a few instances, moderate grazing by cattle appears to have minimal effects on spatial heterogeneity in herbaceous vegetation and ground cover created by shrubs. Grazing effects only varied by microsite for perennial forb, ground litter, and biological soil crust cover, and Sandberg bluegrass density. These few effects of grazing on spatial heterogeneity were not unidirectional. Grazing increased and decreased differences between microsites (i.e., increased and decreased spatial heterogeneity) simultaneously, depending on response variable. Grazing in other systems increased spatial heterogeneity in some communities (Bakker et al., 1983; McNaughton, 1984) and decreased it in others (Sala et al., 1986; Fuhlendorf and Smeins, 1998; Collins and Smith, 2006); these contrasting results may be a product of different response variables being evaluated among studies. Considering our results and aforementioned prior works, we conclude that grazing effects on spatial heterogeneity of vegetation likely varies by scale, plant community, existing pattern of patchiness, response variable measured, and grazing pressure.

Moderate grazing also influenced some herbaceous vegetation characteristics similarly between microsites. Most notably, grazing decreased large perennial bunchgrass cover and increased Sandberg bluegrass cover and density in both canopy and interspace microsites. However, microsite differences in these vegetation characteristics remained regardless of grazing. Grazing is expected to reduce large perennial bunchgrass cover as it decreases the contribution of prior years' growth to cover, a major contributor to total perennial grass cover (Davies et al., 2016). Reductions in large perennial bunchgrass cover were offset by increases in Sandberg bluegrass, a short-statured native bunchgrass. Similar to our current study, moderate grazing in the winter also increased Sandberg bluegrass cover and density when it decreased exotic annual grass cover and density (Davies et al., 2021). Sandberg bluegrass is probably susceptible to shading because of its short stature (Davies et al., 2021), thus it likely increased with grazing because of less cover (i.e., shading) from large bunchgrasses.

The influence of long-term, moderate grazing on resistance to annual grass invasion is of great interest because exotic annual grasses pose a major threat to spatial heterogeneity and diversity in sagebrush and other steppe communities (Knapp, 1996; Davies, 2011; Jones et al., 2020). Moderate grazing in these communities did not favor exotic annual grasses, providing strong evidence that it did not decrease resistance to annual grasses and is compatible with the sustainability of these plant communities. Additionally, most herbaceous vegetation characteristics including diversity and evenness were not influenced by grazing, further suggesting that moderate cattle grazing is in line with the conservation of this ecosystem. In contrast, repeated, heavy grazing during the growing season can decrease resistance to annual grass invasion (Daubenmire, 1940, 1970; Mack, 1981), likely leading to an annual grass-fire cycle (D'Antonio and Vitousek, 1992; Brooks et al., 2004; Balch et al., 2013) and ultimately the loss of microsite differences. Grazing effects will vary by timing, intensity, and frequency of use as well as other factors (Davies and Boyd, 2020), therefore, it is critical to identify and acknowledge the effects of different types of grazing. Moderate grazing did not promote annual grass invasion in our study, but this should not be interpreted as suggesting that all types of grazing produce a similar response in these plant communities.

Shrub-induced spatial heterogeneity of soil nutrients at the within plant community scale were not influenced by more than 80 years of moderate grazing by cattle. In contrast, cattle grazing in steppe meadows increased the spatial heterogeneity of soil available nitrogen (Liu et al., 2016). Similar to our study, short-term (3 yrs) grazing by sheep did not influence strong soil heterogeneity related to hummock-hollow microtopography in dune grasslands (Gibson, 1988). In our study, the strong effect of shrubs on soil nutrients probably overpowers any effect of grazing on spatial distribution of soil nutrients. Grazing redistribution of resources, from urine and fecal deposition (Steinauer and Collins, 2001), does not appear to be substantial enough in this ecosystem to influence the resource island effect of shrubs. In our current study, shrubs were driving spatial heterogeneity in soil nutrients regardless of grazing. These

findings do not agree with speculation that grazing, not shrubs, created resource islands in shrublands (Allington and Valone, 2014). This is important as spatial heterogeneity in soil resource availability influences vegetation heterogeneity, plant community assemblage, and diversity in these communities. Efforts to sustain and encourage spatial heterogeneity in soil resource availability in shrub communities should focus on maintaining and restoring shrubs in these communities.

5. Conservation and management implications

Shrubs were a pivotal contributor to spatial heterogeneity in plant communities in our study ecosystem. The majority of measured vegetation characteristics and soil nutrient concentrations differed between canopy and interspace microsites. These differences were largely unaffected by over 80 years of moderate grazing by cattle. These results provide robust evidence that sagebrush exerts a strong influence on the patterns of variability in herbaceous vegetation, ground cover, and soil nutrients. Livestock production, when grazing is managed properly (i.e., moderate grazing), appears compatible with maintaining shrub-induced spatial heterogeneity in herbaceous vegetation and microsites in shrub-steppe communities. Our results strongly imply that management should focus on maintaining shrubs in these communities to promote spatial heterogeneity. In sagebrush communities, especially those with low resilience and resistance to annual grass invasion, this should include preventing frequent and catastrophic wildfires that may lead to the permanent loss of sagebrush. When shrubs are lost in these communities, their restoration should be a priority to ensure the persistence of spatial heterogeneity.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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