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Plant Interspaces Resulting From Contrasting Grazing Management in Northern Mixed-Grass Prairie: Implications for Ecosystem Function

Justin D. Derner[1] *and Ashley J. Whitman*[2]

Authors are [1]*Rangeland Scientist, US Department of Agriculture–Agricultural Research Service (USDA–ARS), High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, USA; and* [2]*Graduate Student, Department of Renewable Resources, University of Wyoming, Laramie, WY 82071, USA.*

Abstract

We assessed plant interspaces in July 2007 using continuous line intercepts in twice-replicated pastures of northern mixed-grass prairie with contrasting grazing treatments: 1) long-term (25 yr) heavily grazed, dominated by the bunchgrass blue grama (*Bouteloua gracilis*), and 2) ungrazed, dominated by the rhizomatous grass western wheatgrass (*Pascopyrum smithii*). The number of plant interspaces was 26% higher in pastures heavily grazed, but the amount of soil surface occupied by plant interspaces was 27% greater without grazing. Plant interspaces were larger without grazing (14.8 ± 1.2 cm, mean ± 1 SE) than heavily grazed (8.9 ± 0.4 cm). Plant interspaces represented 87% and 68% of the total soil surface in the ungrazed and heavily grazed communities, respectively. The percentage of soil surface covered by plant interspaces < 20 cm was higher for the heavily grazed (94%) compared to the ungrazed (79%). Litter cover in the plant interspaces was higher without grazing (80 ± 1%) compared to the heavily grazed (57 ± 3%). Grazing-induced structural changes from a rhizomatous- to a bunchgrass-dominated vegetation community were manifest in the size and distribution of plant interspaces. Ecological consequences for erosion from raindrop impacts in larger plant interspaces in the ungrazed community are likely offset by greater litter cover in these communities; conversely, lower litter cover in heavily grazed pastures may increase erosion potential despite occurrence of smaller plant interspaces and less proportion of the soil surface covered by interspaces. Management practices that increase the cover of litter in plant interspaces should reduce the potential of erosion from water and wind in this semiarid rangeland.

Resumen

Determinamos los espacios entre plantas en Julio del 2007 utilizando la línea de intercepto continuo en potreros con dos repeticiones en un pastizal mediano abierto del noroeste de los Estados Unidos contrastando tratamientos de pastoreo 1): largo-plazo (25 años) con un pastoreo intenso, y dominado principalmente por el pasto navajita (*Bouteloua gracilis*), y 2) sin pastorear dominado principalmente por western wheatgrass (*Pascopyrum smithii*). El número de espacios entre plantas fue 26% mayor en el pastoreo intenso, pero la cantidad de superficie del suelo ocupada por los espacios entre las plantas fue 27% mayor en áreas sin pastoreo. Los espacios entre las plantas fueron mayores en áreas sin pastoreo (14.8 ± 1.2 cm, media ± 1 es) que en áreas con pastoreo intenso (8.9 ± 0.4 cm). Los espacios entre las plantas representaron 87% y 68% del total de la superficie del suelo en áreas sin pastoreo y en áreas con el pastoreo intenso, respectivamente. El porcentaje de la superficie del suelo cubierto por los espacios entre las plantas < 20 cm fue mayor (94%) para el área pastoreada intensamente que para el área sin pastoreo (79%). La cubierta del mantillo en los espacios entre las plantas fue mayor en el área sin pastoreo (80 ± 1%) comparado con el pastoreo intenso (57 ± 3%). El pastoreo induce cambios estructurales de rizomatoso a una comunidad dominada por especies amacolladas donde se manifiesta el tamaño y la distribución del espacio entre las plantas. Las consecuencias ecológicas debido a la erosión por el impacto de las gotas de lluvia en los espacios más grandes entre las plantas en las comunidades no pastoreadas puede compensarse por una cubierta mayor de mantillo en esas comunidades; por lo contrario una cubierta menor de mantillo como resultado de un pastoreo fuerte, puede incrementar el potencial de la erosión aunque los espacios entre las plantas sean menores y una menor proporción de los espacios entre las plantas se cubra. Prácticas de manejo que incrementen la cubierta de mantillo en los espacios entre las plantas podrían reducir el potencial de la erosión debido a la lluvia o el viento en pastizales de zonas semiáridas.

Key Words: fetches, gap intercept, grassland structure, hydrologic function, indicator, monitoring, rangeland health, site integrity, vegetation heterogeneity

INTRODUCTION

Semiarid rangelands have discontinuous aboveground plant cover because of water limitation (Noy-Meir 1973; Milchunas et al. 1989). Direct measurements regarding the status of key ecological processes on these rangelands, including the water cycle, energy flow, and nutrient cycles, are difficult and/or expensive, but assessments of biological and physical components can be used as indicators of these ecological processes and related site integrity (Pyke et al. 2002; Pellant et al. 2005). The

At the time of research, Whitman was an undergraduate student, Department of Renewable Resources, University of Wyoming.

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Correspondence: Justin Derner, USDA–ARS, High Plains Grasslands Research Station, 8408 Hildreth Road, Cheyenne, WY 82009, USA. Email: Justin.Derner@ars.usda.gov

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proportion of the soil surface covered by plant interspaces, defined as the distance between two perennial plant stems or bases (i.e., fetches; Ludwig et al. 1999), is one indicator that addresses soil and hydrologic processes, as erosion from raindrop impact, wind, and overland flow occurs in these areas (Wilcox et al. 2003). Also, plant interspaces have lower soil aggregate stability (Bestelmeyer et al. 2006) as well as smaller pools of soil carbon and nitrogen and root biomass (Hook et al. 1991; Vinton and Burke 1995; Derner et al. 1997).

The number and size, as well as the configuration, of plant interspaces may influence redistribution of soil and soil nutrients at local, small scales or at larger scales with the potential for off-site transport of soil by water and/or wind (Ludwig et al. 1999; Okin et al. 2006). In addition, changes in the size and distribution of plant interspaces may be associated with differences in vegetation communities that relate to water flow patterns, infiltration, runoff, and redistribution or loss of litter (Pellant et al. 2005). Large plant interspaces generally have a more pronounced effect on ecosystem function than small interspaces (Goldberg and Werner 1983; McConnaughay and Bazzaz 1987, 1990; but see Aguilera and Lauenroth 1993b). Although spatial dynamics of canopy gaps in rangelands have been studied (e.g., Derner and Wu 2001, 2004), limited efforts on plant interspaces in rangelands of the western United States have been conducted (Aguilera and Lauenroth 1993b, 1995; Hook et al. 1994), with these studies largely addressing effects of disturbance and seedling recruitment, or in restored minelands (e.g., Herrick et al. 2006).

Livestock grazing affects structure and function of rangelands (Manier and Hobbs 2007) through effects on species composition and productivity (Milchunas and Lauenroth 1993), species replacement (Anderson and Briske 1995), vertical and horizontal distribution of vegetation (Marriott and Carrere 1998), and plant morphology (Briske and Richards 1995; Briske and Derner 1998). The effect of livestock grazing on plant interspaces, however, has received little attention (Tongway et al. 2003). Here we utilize contrasting vegetation communities resulting from a long-term (25 yr) stocking rate study in the northern mixed grass prairie to determine the influence of grazing on plant interspaces. Prior research has documented grazing effects on vegetation, animal, and soil responses in this rangeland ecosystem (Hart et al. 1988; Manley et al. 1997; Derner and Hart 2007; Derner et al. 2008; Ingram et al. 2008). Heavy stocking rates decreased the composition of the dominant perennial C_3 (cool-season), midheight, rhizomatous grass western wheatgrass (*Pascopyrum smithii* [Rydb] A. Love) while concurrently increasing the composition of the perennial C_4 (warm-season), shortgrass, bunchgrass blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Griffiths; Manley et al. 1997; Ingram et al. 2008). Blue grama is resistant to grazing and horizontal basal cover increases with grazing (Milchunas et al. 1989). As a result, the vertical and horizontal distribution of vegetation has been modified because of differences in plant morphology with the replacement of the rhizomatous grass by the bunchgrass. Changing the dominant growth form in these vegetation communities may impact plant interspaces, but this has not been quantified.

Our purpose in this study was to assess plant interspaces and litter cover within these interspaces in contrasting vegetation communities (ungrazed—western wheatgrass dominated and heavily grazed—blue grama dominated) in northern mixed-grass prairie. Our specific objectives were to determine if differences exist in 1) number and cumulative size of plant interspaces, 2) size of plant interspaces, 3) distribution of plant interspaces, and 4) litter cover in plant interspaces between these vegetation communities. Because of the differences in plant morphology between western wheatgrass and blue grama, we hypothesized that in the heavily grazed communities 1) the total number and cumulative size of plant interspaces would be less, 2) mean size of plant interspaces would be smaller, 3) a greater proportion of the plant interspaces would be observed in smaller (< 20 cm) sizes, and 4) litter cover in plant interspaces would be lower compared to the ungrazed communities.

MATERIALS AND METHODS

Site Description

The experiment was conducted on northern mixed-grass prairie at the US Department of Agriculture–Agricultural Research Service High Plains Grasslands Research Station, approximately 7 km northwest of Cheyenne, Wyoming (41°11′N, 104°53′W). Mean annual precipitation (132 yr) is 381 mm with a peak in May. Soils are coarse textured and well drained, comprised of Ascalon loams (mixed mesic Aridic Argiustolls; Stevenson et al. 1984). The ecological site is Loamy 12–17″ Precipitation Zone for Major Land Resource Area 67 (Site ID R067XY122WY), which is the primary ecological site in the region. Vegetation is predominantly grasses. Perennial cool-season graminoids include western wheatgrass, needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.] Barkworth), prairie junegrass (*Koeleria macrantha* [Ledeb.] J.A. Schultes), and needleleaf sedge (*Carex duriuscula* C.A. Mey). Blue grama is the primary perennial warm-season grass, scarlet globemallow (*Sphaeralcea coccinea* [Nutt.] Rydb.) is the primary forb, and fringed sage (*Artemisia frigida* Willd.) is the primary subshrub.

Vegetation Communities

In 1982, on the study area that had previously been grazed very lightly by livestock and wildlife, light, moderate, and heavy stocking rates were applied to twice-replicated, season-long grazed pastures (approximately 130 d, mid-June–mid-October). In addition, two 0.5-ha exclosures were established in 1982 to prevent large herbivore grazing. For this study, we sampled the heavy stocking rate (53.4 steer-days $\cdot$ ha^{-1}, or 40 animal unit days $\cdot$ ha^{-1} using 0.75 as an animal unit equivalent for yearling steers; Holechek et al. 1998) pastures and the exclosures that represent contrasting grazing management and have different vegetation communities (Ingram et al. 2008). Vegetation communities, which were similar in 1982, have diverged with the grazing treatments, as blue grama has displaced western wheatgrass as the dominant species in the heavily grazed pastures, whereas western wheatgrass remains the dominant species in the exclosures (Manley et al. 1997). From vegetation sampling in 2004, warm-season perennial grasses comprised 42% of the aboveground biomass in the heavily grazed pastures but only 4% in the exclosures (Ingram et al. 2008). Conversely, cool-season perennial grasses constituted 62% of the biomass in the exclosure and 33% in the heavily grazed pastures.

Aboveground productivity was 16% lower with heavy grazing (960 vs. 1 138 $kg \cdot ha^{-1}$), standing dead was 6-fold greater in the exclosures (260 vs. 43 $kg \cdot ha^{-1}$), and litter was 3.5 times greater in the exclosures (1 447 vs. 413 $kg \cdot ha^{-1}$; Ingram et al. 2008).

Plant Interspaces

Plant interspaces were measured 9–13 July 2007 using modified methods from Herrick et al. (2005) on four randomly located 20-m line transects in each replicated heavily grazed pasture and exclosure. Plant interspaces were measured to the nearest 1 cm as the distance between two perennial plant stems/bases with a minimum intercept of 2 cm, which was the mean size of plant stem/bases in preliminary sampling. Plant stems/bases could be live or dead but had to be anchored in the soil, and annual plants were not included, as they are highly variable in this ecosystem (Manley et al. 1997). In addition, litter cover in each plant interspace was visually determined using cover categories where $0 = < 1\%$ $1 = 1–25\%$ cover, $2 = 26–50\%$, $3 = 51–75\%$, and $4 = 76–100\%$. Midpoints of litter cover classes were used in statistical analyses.

For each transect, we calculated 1) the total number and cumulative size of plant interspaces (cm), 2) the percentage of the transect length occupied by plant interspaces (%), 3) the mean size of plant interspaces (cm), and 4) the litter cover in plant interspaces (%).

Statistical Analyses

To determine the influence of grazing (ungrazed vs. heavily grazed) on plant interspace parameters, we used a one-way analysis of variance (SAS Institute, Inc. 1999), using transect means of variables. The alpha level of 0.05 was used in all comparisons to determine significance. Comparisons of the distribution of plant interspace sizes were conducted using the Kolmogorov–Smirnov two-sample nonparametric test (Conover 1980). Because there were only two replications of each treatment, we used transects as our sampling unit rather than the entire pasture, which limits interpretations of our findings largely to this experimental location and treatments due to pseudoreplication (see Hurlbert 1984; Heffner et al. 1996). However, the length of imposed nongrazing and heavy stocking rate treatments (25 yr since 1982) and the vegetation composition and production differences associated with these treatments (Ingram et al. 2008) suggests that our findings can provide insights into the influence of plant interspaces and litter in these interspaces on ecosystem function.

RESULTS

The number of plant interspaces was 26% higher in the heavily grazed ($n = 154$ per 20-m transect) compared to the ungrazed ($n = 122$) communities ($P < 0.019$; Fig. 1a). The cumulative amount of transect length occupied by plant interspaces, however, was 27% greater for the ungrazed ($1\,734 \pm 10$ of 2 000 cm) than the heavily grazed pastures ($1\,365 \pm 71$ of 2 000 cm; $P < 0.0001$). Plant interspaces represented 87% and 68% of the total transect length in the ungrazed and heavily grazed communities, respectively (Fig. 1b). Mean plant interspace size was 66% larger in the ungrazed (14.8 ± 1.2 cm) than the heavily grazed (8.9 ± 0.4 cm) treatment ($P = 0.0005$; Fig. 1c). Litter cover in the plant interspaces was higher in the absence of grazing ($80 \pm 1\%$) compared to the heavily grazed pastures ($57 \pm 3\%$; $P < 0.0001$).

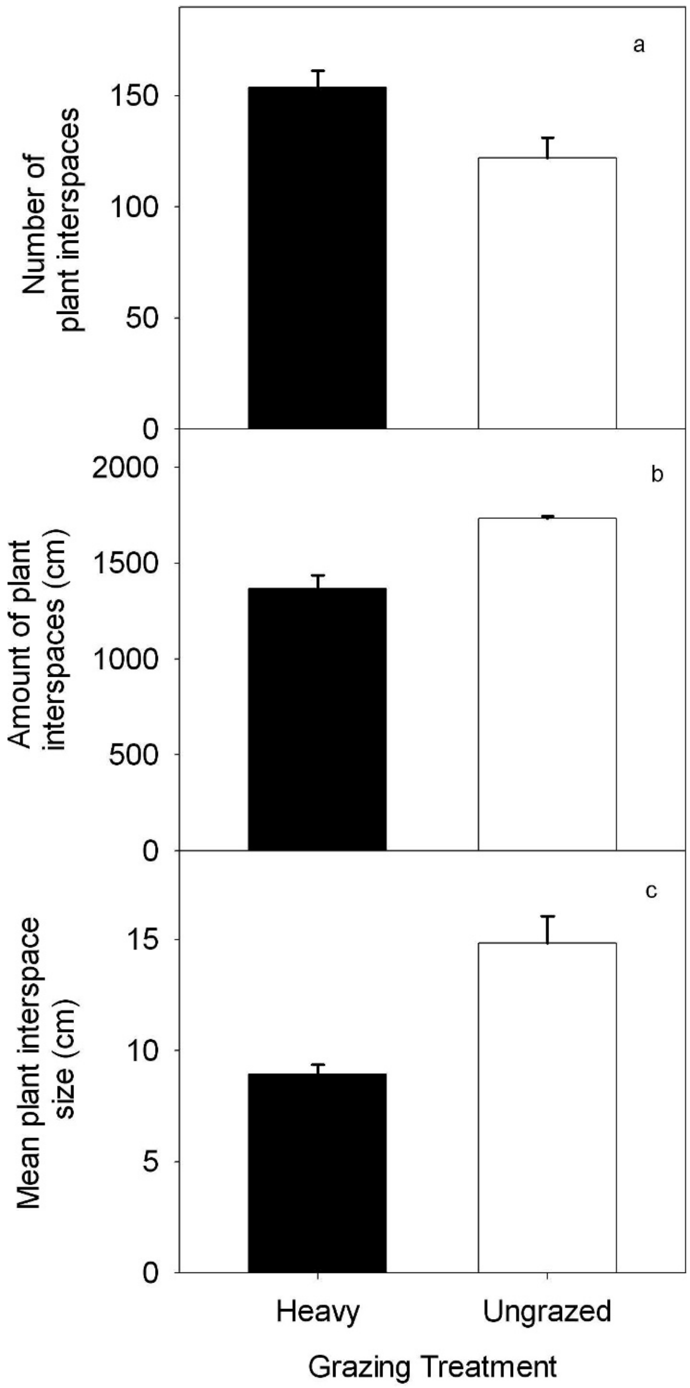

Figure 1. Mean (± 1 SE) number of plant interspaces per 20-m transect (**a**), percent of 20-m transect occupied by plant interspaces (**b**), and mean plant interspace size (**c**) for long-term (25 yr) heavy (40 animal unit days $\cdot$ ha^{-1}) and ungrazed plant communities in northern mixed-grass prairie at the High Plains Grasslands Research Station near Cheyenne, Wyoming.

Distributions of plant interspace sizes differed ($P < 0.0001$) between vegetation communities (Fig 2), as a higher proportion

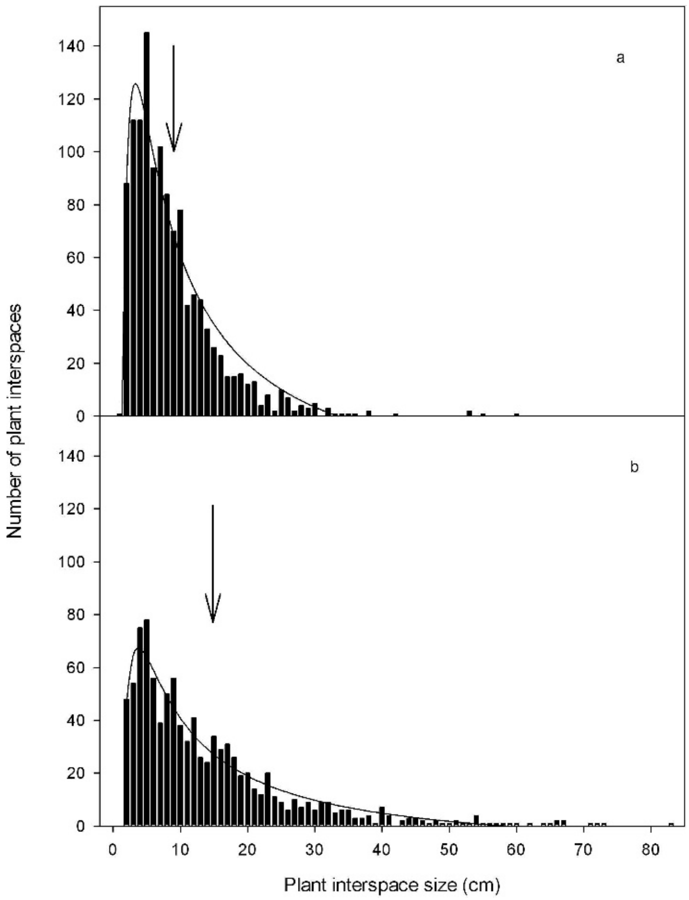

Figure 2. Distributions of size of plant interspaces for long-term (25 yr) heavy (40 animal unit days · ha^{-1}; **a**) and ungrazed (**b**) plant communities in northern mixed-grass prairie at the High Plains Grasslands Research Station near Cheyenne, Wyoming. Arrows indicate the mean value for plant interspace size in each community.

of interspaces occurred in the smaller sizes with heavy stocking rates. Conversely, a higher proportion of interspaces exceeding 20 cm in size were observed in the ungrazed communities.

DISCUSSION

Plant interspaces provide information pertaining to the patch openings of bare ground (i.e., fetch; Ludwig et al. 1999) and the proportion of the soil surface that is potentially exposed to erosion by water and/or wind (Pellant et al. 2005). Here, differences were observed in the number of plant interspaces, proportion of the soil surface identified as plant interspaces, mean plant interspace size, the distribution of plant interspaces, and litter cover in plant interspaces between contrasting vegetation communities with dissimilar dominant plant morphologies. This assessment of plant interspaces and litter cover within these interspaces provides further evidence of direct grazing-induced modifications to ecosystem structure and indirect alterations to ecosystem function in the northern mixed-grass prairie.

Heavy stocking rates induce changes in ecosystem structure of northern mixed-grass prairie by replacement of a midheight grass community with a shortgrass community, and the productive capacity of this rangeland ecosystem is reduced (Derner and Hart 2007). Structural changes from a rhizomatous- to a bunchgrass-dominated vegetation community are manifest in the size and distribution of plant interspaces. A greater number of plant interspaces was observed in the heavy grazing treatment dominated by the bunchgrass blue grama, but mean plant interspace size was less, resulting in lower total proportion of the soil surface covered by plant interspaces. Thus, heavy stocking rates have modified both the vertical (midheight to shortgrass) and horizontal (greater soil surface coverage by plants) vegetation structure in this rangeland ecosystem.

The effect of grazing-induced modifications to vegetation structure on ecological processes and functions associated with soil/site stability can be inferred from the plant interspace and litter cover findings. Soil aggregate stability is lower in plant interspaces compared to beneath plants (Bird et al. 2007). Plant interspaces provide sites for seedling establishment (McConnaughay and Bazzaz 1987; Aguilera and Lauenroth 1993a, 1993b) and are needed to achieve regeneration of dominant species, thereby influencing population dynamics of many species (Aguilera and Lauenroth 1995). Larger mean size of plant interspaces and the greater proportion of plant interspaces exceeding 20 cm in size in the ungrazed communities suggest that seedling emergence should be greater compared to the heavily grazed communities. Direct measurements of seedlings in the studied vegetation communities have not been conducted, but because litter decreases seedling establishment in grasslands (Jensen and Gutekunst 2003), we expect that higher levels of litter cover in the plant interspaces of the ungrazed communities may negate the advantage of larger plant interspaces.

The influence of grazing-induced modifications in vegetation structure associated with hydrologic processes can also be inferred from the plant interspace and litter cover findings. For example, infiltration rates are lower and runoff is higher with heavy grazing in semiarid rangelands (Thurow et al. 1988), including blue grama–dominated vegetation in shortgrass steppe (Feidler et al. 2002). Reduced infiltration has been observed on the heavily grazed communities in this northern mixed-grass prairie (Abdel-Magid et al. 1987). Reduced infiltration and corresponding higher runoff with heavy stocking rates is attributed to the higher number of plant interspaces and lower litter cover in these interspaces, thereby resulting in more potential soil detachment from raindrop impact and small-scale water erosion potential through greater sediment transport between interspaces (Weltz et al. 1998). There is a strong interaction between runoff-erosion processes and the distribution of plants and plant interspaces (Ludwig et al. 2005). In addition, plant interspaces store less water, produce less vegetation growth, and have lower infiltration compared to areas occupied by plants (Ludwig et al. 2005). Greater litter cover in the plant interspaces of the ungrazed communities may compensate for the larger sizes of interspaces and lower the water erosion potential. Small-scale redistribution of soil in the ungrazed community would likely be less because of the higher litter cover, but if a disturbance such as fire removes this litter, then the potential for larger-scale redistribution (perhaps even off-site) of soil increases because of the larger sizes of plant interspaces.

The vast majority of plant interspaces were less than 20 cm in this northern mixed-grass prairie, which is in agreement with findings in shortgrass steppe dominated by blue grama, where

86% of the interspaces fit this category (Hook et al. 1994). The percentage of plant interspaces < 20 cm was higher for the heavily grazed (94%) compared to the ungrazed (79%) communities in this rangeland ecosystem. For comparative purposes, Herrick et al. (2006) used a minimum plant interspace of 25 cm in native and reclaimed sagebrush grasslands. Therefore, the minimum interspace size for assessment and monitoring purposes should be ecosystem dependent and adjusted as appropriate for ecological site conditions (Herrick et al. 2005).

MANAGEMENT IMPLICATIONS

Grazing management practices in the northern mixed-grass prairie, through stocking rates, can shift the vertical and horizontal structure of vegetation communities via modifications in dominant grass species possessing contrasting plant morphologies. Differences in parameters of plant interspaces between ungrazed and heavily grazed communities reveal additional ecosystem structural modifications induced by grazing. Ecological consequences for erosion from raindrop impacts in larger plant interspaces in the ungrazed community are likely offset by greater litter cover in these communities; conversely, lower litter cover resulting from heavy stocking rates may increase erosion potential despite occurrence of smaller plant interspaces and less proportion of the soil surface covered by plant interspaces. Management practices that increase the quantity of litter, thereby increasing the cover of litter in plant interspaces, should reduce the potential of erosion from water and wind in this semiarid rangeland.

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