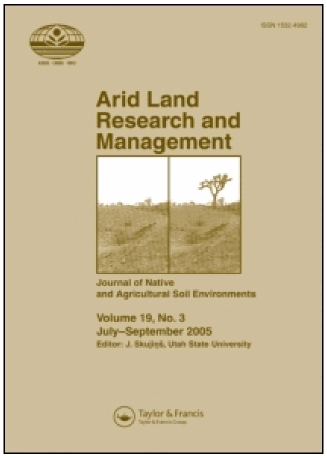

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Functional Group and Species Responses to Precipitation in Three Semi-Arid Rangeland Ecosystems

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The objective of this study was to compare forage production and foliar and basal cover responses of plant communities, plant functional groups, and individual species between years with below average (2004) and well above-average (2005) spring precipitation in three semi-arid rangeland ecosystems (shortgrass steppe, northern mixed-grass prairie, and sagebrush grassland). Foliar and basal cover at the time of a peak standing crop were visually estimated using modified Daubenmire cover categories, and forage production by species was harvested from areas that had been excluded from large herbivores. Responses of forage production to precipitation, but not foliar and basal cover, were similar for the three semi-arid ecosystems. Total forage production was more responsive (75–159%) than basal (8–35%) or foliar (2–29%) cover to increasing precipitation. Absolute (1016 kg · ha^{-1}) and relative (159%) increases in total forage production from 2004 to 2005 were greatest for the shortgrass steppe. Forage production increases were largely attributable to greater production by C3 perennial graminoids in each ecosystem; increases in basal and foliar cover for this plant functional group were observed in shortgrass steppe and sagebrush grassland, but not in northern mixed-grass prairie. Fine-scale inputs of species and plant functional group responses to precipitation will further the accuracy of forage prediction models in predicting both total biomass production and relative proportions of plant biomass.

Keywords bare ground, basal cover, foliar cover, forage production, northern mixed-grass prairie, sagebrush grassland, shortgrass steppe

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Introduction

Variation in forage production of semi-arid rangelands at global (Lauenroth, 1979), regional (Sala et al., 1988), and individual field scales (e.g., Lauenroth and Sala, 1992) is largely controlled by precipitation. For example, 43–66% of the variance in estimates of forage production in the central grassland region of North America is accounted for by regional trends in mean annual precipitation (Lauenroth et al., 1999). In addition, a high correlation ($r = 0.88$) was found between annual precipitation and forage production for 19 sites encompassing a shortgrass steppe to tallgrass prairie gradient from northeastern Colorado to eastern Kansas and Nebraska (Barrett et al., 2002). Regression relationships have been developed for predicting forage production from precipitation in many rangeland ecosystems (e.g., O'Connor et al., 2001; Khumalo and Holechek, 2005).

Precipitation also influences plant species distribution and ecosystem functioning in rangeland ecosystems (Sala et al., 1988; Zak et al., 1994; Epstein et al., 1997; Barrett et al., 2002). In contrast to the well-established relationships between precipitation and forage production, relationships between precipitation and vegetative cover are poorly understood. Basal cover of vegetation was not related to mean annual precipitation across a gradient from shortgrass prairie to tallgrass prairie (Lane et al., 1998), but basal cover and precipitation were good predictors of forage production for semi-arid African grassland (O'Connor et al., 2001).

Forage production can be more sensitive to fluctuations in precipitation than to long-term grazing treatments (Milchunas et al., 1994). Productive capacity of semi-arid rangelands in the northwestern area of the Great Plains is largely influenced by spring precipitation because they are dominated by perennial cool-season, mid-height grasses such as *Pascopyrum smithii* (Rydb) A. Love (western wheatgrass) and *Hesperostipa comata* (Trin. & Rupr.) Barkworth (needleandthread) (e.g., Biondini and Manske, 1996). Productivity of these semi-arid rangeland ecosystems in the Great Plains is affected proportionally more by interannual variability in precipitation compared to other ecosystems (Knapp and Smith, 2001).

Several relationships have been developed for predicting forage production from spring precipitation in these rangeland ecosystems (e.g., Hart and Samuel, 1985; Biondini and Manske, 1996; Biondini et al., 1998; Heitschmidt et al., 1999; Bork et al., 2001; Andales et al., 2006). Yet plant communities with varying dominant species within a northern mixed-grass prairie in western North Dakota displayed differential responses to precipitation (Redmann, 1975), suggesting that relationships between precipitation and finer-scale plant biomass information (functional groups, individual species) may be different than those relationships for the broader system. Plant functional groups, defined as sets of plants exhibiting similar responses to environmental conditions and having similar effects on dominant ecosystem processes (Walker, 1992; Noble and Gitay, 1996), can be used to summarize the complexity of individual species responses. The application and relevance of plant functional groups to management of rangelands has been reviewed by Díaz et al. (2002).

Because the semi-arid rangeland ecosystems in the northwestern portion of the Great Plains are dominated by perennial cool-season grasses, it is expected that this functional group, and the species associated with this group, will exhibit the greatest relative and absolute responses to spring precipitation. There is a need to determine whether precipitation-induced changes to forage production in semi-arid rangelands described above are species-specific, functional group-specific, or ubiquitous across species and functional groups. Our objective was to compare forage production and foliar and basal cover responses between years with below average (2004) and well above-average (2005) spring precipitation in three semi-arid rangeland ecosystems (shortgrass steppe, northern mixed-grass prairie, and sagebrush grassland). Specific hypotheses addressed in each of the three ecosystems include; 1) forage production, basal cover, and foliar cover are not equally responsive to precipitation; 2) perennial cool-season grasses are the most responsive plant functional group to precipitation; and 3) dominant perennial cool-season grass species display the greatest absolute and relative forage production and cover responses to precipitation.

Materials and Methods

Study Area

The shortgrass steppe site was located at the USDA-Agricultural Research Service, Central Plains Experimental Range in north central Colorado (40°49′ N, 107°46′ W). Mean annual precipitation at Nunn, Colorado is 361 mm. Soil is a sandy loam (fine-loamy, mixed, mesic Ustollic Haplargid). Cool-season graminoids include western wheatgrass, needleandthread, and *Carex duriuscula* C.A. Mey (needleleaf sedge). *Bouteloua gracilis* (H.B.K.) Lag. ex Griffith (blue grama) and *Buchloe dactyloides* (Nutt.) Engelm. (buffalograss) are the most common warm-season grasses. *Sphaeralcea coccinea* (Nutt.) Rydb. (scarlet globemallow) is the most frequent forb. The northern mixed-grass site was located at the USDA-Agricultural Research Service, High Plains Grasslands Research Station, approximately 7 km northwest of Cheyenne, Wyoming (41°11′ N, 104°53′ W). Mean annual precipitation in Cheyenne is 393 mm. Soil is a loam (mixed mesic Aridic Argiustoll). Cool-season graminoids include western wheatgrass, needleandthread, *Koeleria macrantha* (Ledeb.) J.A. Schultes (prairie junegrass) and needleleaf sedge. Blue grama is the dominant warm-season grass, scarlet globemallow is the most common forb, and *Artemisia frigida* Willd. (fringed sage) is the most frequent subshrub. The sagebrush grassland site was located at the University of Wyoming, McGuire Ranch (41°4′ N, 105°3′ W), approximately 56 km northeast of Laramie, Wyoming. Mean annual precipitation is 284 mm at Laramie. Soil is a loam (fine loamy, mixed, superactive, frigid Ustic Haplargid). Perennial cool-season graminoids include western wheatgrass, prairie junegrass, and *Poa secunda* J. Presi (Sandberg bluegrass). The most common forb is *Phlox hoodii* Richards (spiny phlox). *Artemisia tridentata* Nutt ssp. *wyomingensis* Beetle & Young (Wyoming big sagebrush) is the dominant shrub with *Chrysothamnus nauseosus* (Pallas ex Pursh) Britt (rubber rabbitbrush) also abundant.

Experimental Design

All three sites sampled in 2004 and 2005 had been excluded from large herbivores. For the shortgrass steppe and sagebrush grassland sites, where only one exclosure was used, we recognize that the sampling could be perceived as pseudoreplication. Potential statistical consequences and limitations of pseudoreplication have been discussed (see Hurlbert, 1984; Heffner et al., 1996); inferences from our findings are specific to our experimental locations and treatments. Further experimentation is required to determine the applicability of our results to a wider geographic area.

One 1.9 ha (12 m × 1600 m) exclosure was established in 1939 at the shortgrass steppe site on an area that had previously been subjected to moderate, continuous season-long (May to October) grazing by cattle. Sixty 0.1 m^2 (0.2 × 0.5 m) quadrats were systematically spaced within this exclosure. Foliar and basal cover at the time of peak standing crop (early August) were visually estimated using modified Daubenmire (1959) cover categories where 1 = 0–5% cover; 2 = 6–15%; 3 = 16–25%; 4 = 26–40%; 5 = 41–60%; and 6 = 61–100%. Cover of individual species was determined by converting each Daubenmire scale value to the midpoint of the cover range (Towne et al., 2005; Hickman and Derner, 2007). Species were assigned to a functional group class: C4 perennial grasses, C3 annual grasses, C3 perennial graminoids, perennial forb, annual forb, subshrub or shrub. Above-ground biomass was clipped at ground level by species in every 5th quadrat, resulting in 12 clipped quadrats. The quadrat was our experimental unit for this site.

Two 0.5-ha exclosures were established in 1981 at the northern mixed-grass site where prior grazing was light to none. Two 50-m permanent transects were randomly located in each exclosure and 25, 0.1 m^2 (0.2 × 0.5 m) quadrats were randomly located on each transect. Foliar and basal cover at the time of peak standing crop (mid-July) were visually estimated as previously described. Above-ground biomass was clipped at ground level by species in three 0.18-m^2 quadrats randomly located along each transect. The transect was our experimental unit for this site.

A 6-ha exclosure was established in early 2004 at the sagebrush grassland site where prior management was season-long (June–October) grazing by cattle at a moderate stocking rate. Six 25-m long permanent transects were randomly located in the exclosure and eight 0.1 m^2 (0.2 × 0.5 m) quadrats were randomly located on each transect. Foliar and basal cover at the time of peak standing crop (early-July) were visually estimated as previously described. Above-ground biomass in these quadrats was clipped at ground level by species; biomass was not clipped from the primary shrub Wyoming big sagebrush. The transect was our experimental unit for this site.

Statistical Analyses

Forage production and cover data were analyzed using a one-way analysis of variance (ANOVA, SAS, 1999) with year as the single factor within each site. Cover data were arcsine square-root transformed before analysis to conform to assumptions of normality and homogeneity. Because sites were not fully replicated, we performed separate analyses on each site. The alpha level of 0.10 was used in all comparisons to determine significance.

Results

Precipitation

Spring (April–June) precipitation was higher in 2005 than 2004 for all three ecosystems, with the 2005 amounts greater than the long-term means due to the exceptionally wet June (Figure 1). In addition, all three study sites experienced a wetter-than-average early fall period (September) in 2004. Absolute increases in spring precipitation between years were greatest for shortgrass steppe (89 mm), intermediate for the northern mixed-grass prairie (68 mm), and lowest for the sagebrush grassland (38 mm) site.

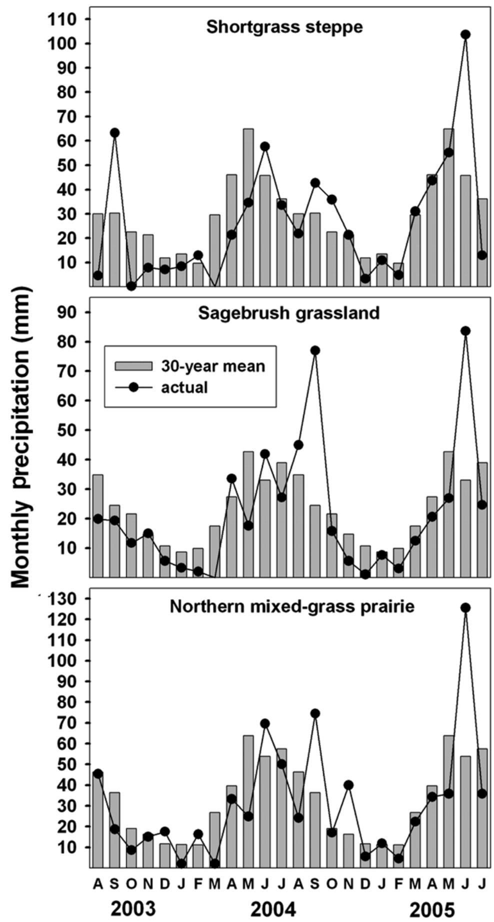

Figure 1. Actual and long-term mean (30-year) monthly precipitation amounts for the shortgrass steppe (Nunn, CO), sagebrush grassland (Laramie, WY), and northern mixed-grass prairie (Cheyenne, WY) study sites.

Forage Production

Total forage production was greater in 2005 than 2004 for all three ecosystems (Figure 2). The relative increase in forage production was greatest in the shortgrass steppe (159%, 1657 vs. 641 kg ha^{-1}), intermediate in the sagebrush grassland (95%, 1176 vs. 604 kg ha^{-1}), and lowest in the northern mixed-grass prairie (75%, 1990 vs. 1139 kg ha^{-1}). For all ecosystems, forage production of the C3 perennial graminoid functional group was significantly greater in the year with higher spring precipitation. Relative increases for this functional group were in agreement with the trends in total forage production: shortgrass steppe (208%, 971 vs. 315 kg ha^{-1}) > sagebrush grassland (115%, 808 vs. 376 kg ha^{-1}) > northern mixed-grass prairie (95%, 1378 vs. 706 kg ha^{-1}). Western wheatgrass exhibited increases in forage production for all three ecosystems: shortgrass (582 vs. 113 kg ha^{-1}), northern mixed-grass prairie (764 vs. 149 kg ha^{-1}), and sagebrush grassland (246 vs. 136 kg ha^{-1}). In addition, we measured greater forage production for C4 perennial grasses (93%, 526 vs. 273 kg ha^{-1}) in shortgrass steppe and perennial forbs

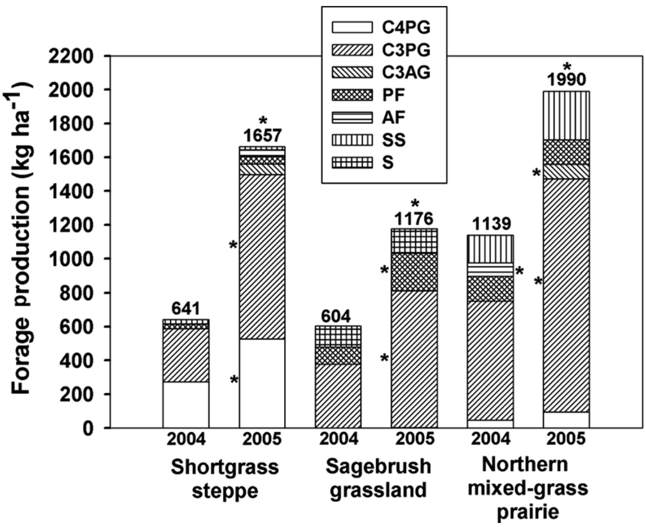

Figure 2. Forage production by plant functional groups (C4PG = C4 perennial grasses, C3PG = C3 perennial grasses, C3AG = C3 annual grasses, PF = perennial forbs, AF = annual forbs, SS = subshrubs and S = shrubs) for the shortgrass steppe (Nunn, CO), sagebrush grassland (Laramie, WY), and northern mixed-grass prairie (Cheyenne, WY) study sites in 2004 and 2005. Asterisk (*) indicates a significant ($P < 0.1$) difference between years within a study site for total forage production and for plant functional groups.

(120%, 220 vs. 100 kg ha^{-1}) in sagebrush grassland. C3 annual grass production increased in the northern mixed-grass prairie, whereas annual forbs decreased.

Basal Cover

Total basal cover of vegetation increased from 2004 to 2005 in the shortgrass steppe (36%) and sagebrush grassland (26%), but not in the northern mixed-grass prairie (Table 1). In the shortgrass steppe, basal cover was 53% greater for C3 perennial graminoids and 367% greater for C3 annual grasses. For C3 perennial graminoids, cover of needleleaf sedge and western wheatgrass increased by nearly 71%. Six weeks fescue [*Vulpia octoflora* (Walt.) Rydb.] was the single species that contributed to the increase in cover of C3 annual grasses. Cover of C3 perennial graminoids and perennial forbs in sagebrush grassland increased by 17% and 63%, respectively. Sandberg bluegrass cover increased by 56% in 2005. Basal cover of C3 annual grasses in the northern mixed-grass prairie was greater in 2005, but this increase was offset by a reduction in annual forb cover. Six weeks fescue was the only species that differed in basal cover between years. Bare ground decreased from 2004 to 2005 in the shortgrass steppe (33%) and northern mixed-grass prairie (24%), but not in the sagebrush grassland. Litter cover only increased in the shortgrass steppe (25%) from 2004 to 2005.

Foliar Cover

Foliar cover results largely mirrored those for basal cover for all three ecosystems. Total foliar cover of vegetation increased from 2004 to 2005 in shortgrass steppe (21%) and sagebrush grassland (29%), but no differences were observed in northern mixed-grass prairie (Table 2). Foliar cover for the C3 perennial graminoids (29%),

Table 1. Basal cover (%) by plant functional group and dominant species (mean, SE), and bare ground and litter from the shortgrass steppe (Nunn, CO), sagebrush grassland (Laramie, WY), and northern mixed-grass prairie (Cheyenne, WY) study sites

	Shortgrass steppe		Sagebrush grassland		Northern mixed grass	
Functional group/species	2004	2005	2004	2005	2004	2005
Total	21.4 (2.0)	29.0 (1.2)*	23.1 (0.4)	29.1 (0.9)*	24.0 (1.2)	26.0 (1.7)
C3 perennial graminoids	7.0 (0.8)	10.7 (1.2)*	14.8 (0.7)	17.3 (0.9)*	12.5 (0.5)	13.9 (1.2)
Carex duriuscular	2.7 (0.4)	4.6 (0.8)*			2.5 (0.5)	3.0 (1.2)
Hesperostipa comata	1.8 (0.7)	1.7 (0.6)			4.8 (0.6)	5.5 (1.1)
Koleria macrantha			4.0 (0.5)	4.2 (0.4)		
Pascopyrum smithii	2.1 (0.3)	3.6 (0.6)*	4.5 (0.3)	4.1 (0.4)	4.6 (0.9)	5.0 (0.7)
Poa secunda			4.9 (0.6)	7.8 (0.8)*		
C3 annual grasses	0.3 (0.1)	1.4 (0.4)*	0 (0)	0 (0)	0.2 (0.1)	2.9 (1.1)*
C4 perennial grasses	11.3 (2.1)	13.9 (1.4)	0.1 (0.1)	0.3 (0.2)	3.0 (0.2)	1.9 (1.1)
Perennial forbs	1.8 (0.3)	2.4 (0.3)	4.0 (0.6)	6.5 (0.6)*	3.0 (0.6)	3.4 (0.1)
Annual forbs	0.4 (0.1)	0.3 (0.1)	0 (0)	0 (0)	2.5 (0.3)*	0.4 (0.1)
Subshrubs	0.6 (0.2)	0.2 (0.1)	0.4 (0.3)	0.1 (0.1)	2.8 (0.9)	3.6 (1.7)
Shrubs			3.7 (0.6)	4.9 (1.1)		
Bare ground	17.7 (2.4)*	11.8 (1.4)	36.9 (2.1)	31.8 (4.0)	8.9 (1.0)*	6.8 (0.6)
Litter	38.1 (2.5)	47.5 (2.9)*	17.2 (0.5)	14.6 (1.4)	48.1 (2.7)	54.9 (4.4)

*Indicates a significant ($P < 0.1$) difference between years within a study site.

Table 2. Foliar cover (%) by plant functional group and dominant species (mean, SE) from the shortgrass steppe (Nunn, CO), sagebrush grassland (Laramie, WY), and northern mixed-grass prairie (Cheyenne, WY) study sites

	Shortgrass steppe		Sagebrush grassland		Northern mixed grass	
Functional group/species	2004	2005	2004	2005	2004	2005
Total	40.5 (2.2)	48.9 (1.8)*	36.8 (1.5)	47.3 (2.9)*	44.5 (1.8)	45.5 (2.2)
C3 perennial graminoids	15.3 (1.8)	19.8 (2.1)*	22.0 (0.9)	26.6 (0.8)*	24.3 (0.8)	23.4 (1.9)
Carex duriuscular	5.8 (0.8)	7.9 (1.1)			5.1 (1.1)	4.6 (1.7)
Hesperostipa comata	4.1 (1.7)	3.2 (1.1)			5.6 (0.5)	8.8 (1.4)
Koleria macrantha			5.9 (0.7)	8.1 (0.8)*		
Pascopyrum smithii	4.7 (0.9)	7.4 (1.4)	6.3 (0.5)	6.3 (0.4)	9.5 (4.8)	9.3 (0.9)
Poa secunda			8.3 (0.8)	10.9 (1.0)*		
C3 annual grasses	0.4 (0.2)	2.2 (0.5)*	0 (0)	0 (0)	0.4 (0.2)	4.8 (2.1)*
C4 perennial grasses	20.0 (2.2)	21.3 (1.9)	0.3 (0.2)	0.5 (0.3)	4.9 (0.5)	3.0 (1.9)
Perennial forbs	2.4 (0.5)	4.1 (0.7)*	5.5 (0.6)	8.3 (0.6)*	4.7 (0.8)	7.0 (0.6)*
Annual forbs	0.5 (0.2)	0.4 (0.2)	0 (0)	0 (0)	3.7 (0.3)*	0.5 (0.2)
Subshrubs	1.4 (0.6)	0.9 (0.6)	0.4 (0.3)	0.3 (0.3)	6.4 (1.9)	6.8 (2.2)
Shrubs			8.6 (1.5)	11.5 (2.9)		

*Indicates a significant ($P < 0.1$) difference between years within a study site.

C3 annual grasses (450%), and perennial forbs (71%) increased in the shortgrass steppe. Consistent with basal cover responses in sagebrush grassland, foliar cover of C3 perennial grasses (21%) and perennial forbs (51%) increased. Prairie junegrass (37%) and Sandberg bluegrass (31%), both C3 perennial grasses, exhibited increases in foliar cover. Cover of C3 annual grasses increased in the northern mixed-grass prairie by 11-fold, and perennial forb cover increased by 49%. However, annual forb cover decreased.

Discussion

Spring precipitation (April–June) had a substantial impact on forage production at the study sites in these three semi-arid rangeland ecosystems. Semi-arid rangeland ecosystems have the capacity for considerable forage production responses when unusually high precipitation levels occur, such as those in June 2005 (Knapp and Smith, 2001). Forage production was more responsive to increased precipitation in 2005 than were either basal or foliar cover in all three ecosystems. Absolute and relative increases in total forage production were greatest for the shortgrass steppe ecosystem. Increases in forage production were largely attributable to greater production by C3 perennial grasses in each ecosystem; increases in basal and foliar cover for this plant functional group were observed in the shortgrass steppe and sagebrush grassland ecosystems, but not the northern mixed-grass prairie. Northern mixed-grass prairie was not responsive to spring precipitation in terms of total basal and foliar cover, with decreases in one plant functional group (annual forbs) offsetting increases in another functional group (C3 annual grasses). Dominant C3 perennial graminoid species displayed the greatest absolute and relative responses to spring precipitation for forage production, but not for basal and foliar cover. Findings from these sites in the three semi-arid rangeland ecosystems suggest that spring precipitation amount is a primary driver influencing productivity of these systems through impacts on C3 perennial graminoids.

Responses of plant growth to spring precipitation in these three semi-arid ecosystems provide opportunities for strategic (long-term) and tactical (short-term) predictions of forage production (e.g., Andales et al., 2006). This response is meaningful in semi-arid rangelands which experience high interannual variability in precipitation (Knapp and Smith, 2001; Watterson, 2005), and subsequently high interannual variability in forage production (Sala et al., 1988; Knapp and Smith, 2001). Although forage production generally increases with increasing precipitation across terrestrial ecosystems (Sala et al., 1988; Paruelo et al., 1999; Knapp and Smith, 2001; Huxman et al., 2004), the relationship between forage production and precipitation at individual locations is closer for more xeric than mesic sites (Huxman et al., 2004). Forage production in highly productive systems ($>8000\,kg\,ha^{-1}$) is more strongly correlated with growing season maximum temperatures and production levels in the prior year, whereas precipitation is the best correlate with forage production when production is lower (Huxman et al., 2004).

Forage production is better predicted by current than prior year precipitation when sites do not have the capacity to receive additional water due to topography and/or landscape position (Bork et al., 2001). Sites in this study all occurred on nearly level topographical positions. About 40% of the variation in forage production in shortgrass steppe is explained by annual precipitation (Lauenroth and

Sala, 1992), with another 17% explained by previous year forage production (Oesterheld et al., 2001).

For the northern mixed-grass prairie, about 60% of the variation in forage production is explained by April, May, and June precipitation (Derner and Hart, 2007), with very low explanatory power for temperature (Smoliak, 1986). Greater predictive ability in the northern mixed-grass prairie than shortgrass steppe is due to the higher proportion of C3 perennial graminoids. Spring precipitation can alter the production, composition, and structure of sagebrush steppe in the Great Basin (Bates et al., 2006), but we are unaware of similar findings for our study site. We note that our sagebrush grassland study site had just been fenced to exclude cattle grazing at the beginning of this experiment. Some of the measured C3 perennial grass biomass increase at this site could be due to the release of grazing pressure. In contrast, exclosures had been in place at the other two sites for several decades. Due to the selective grazing of C3 relative to C4 species (Hart, 2001), C3 species in these ecosystems are generally reduced in the plant community relative to C4 species with heavy grazing (e.g., Hart and Ashby, 1998). Our findings of large relative and absolute biomass production responses of these semi-arid rangeland ecosystems to spring precipitation suggest that modification of precipitation amounts and/or distribution due to global climate change may have implications to the productivity of these systems (e.g., Weltzin et al., 2003).

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