



## Vegetation and climate characteristics of arid and semi-arid grasslands in North America and their biome transition zone

T. Hochstrasser<sup>\*</sup>, Gy. Kröel-Dulay<sup>†</sup>, D.P.C. Peters<sup>‡,\*</sup>, J.R. Gosz<sup>§</sup>

<sup>\*</sup> Graduate Degree Program in Ecology, Natural Resource Ecology Laboratory, and Department of Rangeland Ecosystem Sciences, Colorado State University, Fort Collins, CO 80523-1499, U.S.A.

<sup>†</sup>Institute of Ecology and Botany, Hungarian Academy of Sciences, Vácrátot H-2163, Hungary

<sup>‡</sup>United States Department of Agriculture-Agricultural Research Service, Jornada Experimental Range, Box 30003, MSC 3JER, NMSU, Las Cruces, NM, U.S.A.

<sup>§</sup>Department of Biology, University of New Mexico, Albuquerque, NM 87131, U.S.A.

(Received 7 March 2001, accepted 28 September 2001)

The objective of this study was to investigate the relationship among species richness, functional group composition, and climate for three sites representing the shortgrass steppe, the Chihuahuan desert grasslands and their biome transition zone. We found that perennial species richness increased as the climate became more favorable for plant growth. The biome transition zone was more similar to the Chihuahuan desert grassland site in most climate and vegetation characteristics, partly because of the shorter biogeographic distance between the two sites. This study clarified the ecological position of the biome transition zone site with respect to the adjacent biomes.

© 2002 Elsevier Science Ltd.

**Keywords:** annuals; Chihuahuan desert grasslands; ecotone; perennials; regional analysis; shortgrass steppe; species area curve

Nomenclature: USDA NRCS (1999)

### Introduction

Regional or geographic patterns in species richness are often related to climate (Wright, 1983; Currie & Paquin, 1987; Wright *et al.*, 1993; Gross *et al.*, 2000). In semi-arid and arid environments, plant species richness increases with higher water

\*Corresponding author. Fax: +1-505-646-5889. e-mail: [debpeter@nmsu.edu](mailto:debpeter@nmsu.edu)

availability (Shmida, 1985; Ward & Olsvig-Whittaker, 1993; Kutiel *et al.*, 2000). This relationship is often interpreted as the increasing branch of a hump-shaped relationship between the energy captured by vegetation in photosynthesis (a process dependent on water availability) and species richness (Wright *et al.*, 1993). Climatic variables that affect water availability include total precipitation and temperature as well as their temporal distributions. The correlation between species richness and climate within a region is typically based on observations at the local scale at different sites within biomes (alpha diversity, *sensu* Whittaker, 1972) (Shmida, 1985; Gross *et al.*, 2000). There have been few studies of species diversity patterns across biome transitions (Risser, 1995). Thus, it is unknown how this regional relationship between climate and species richness is affected by these transition zones. Because biome transition zones are expected to be among the most sensitive areas to directional changes in climate and they can have important effects on plant and animal composition (Solomon, 1986; di Castri *et al.*, 1988; Bestelmeyer & Wiens, 2001), it is critical to understand the relationship between climate and species diversity at broad scales.

For biome transition zones, it has been proposed that landscape-scale species richness (gamma diversity, *sensu* Whittaker, 1972) is higher than in adjacent biomes (Neilson, 1993). Many species reach the edge of their physiological tolerance at the edge of biomes (Shmida & Wilson, 1985; Gosz, 1992). Therefore, minor changes in soils, topography or disturbance at biome transition zones can result in thresholds in response of the vegetation. The predicted result is high spatial heterogeneity in species composition (beta diversity, *sensu* Whittaker, 1972) and therefore high landscape-scale species richness (gamma diversity) for the biome transition zone compared with adjacent biomes (Neilson, 1993). Our goal was to investigate the relationship between species richness and climate for two dry grassland biomes and their transition zone located along a north-south gradient in North America. Following the above hypotheses, we expected that local-scale species richness (alpha diversity) would follow patterns in climate. Spatial heterogeneity (beta diversity) was expected to peak at the biome transition zone and, as a consequence, landscape-scale species richness (gamma diversity) would be highest at the biome transition zone.

Two grassland biomes of particular importance in North America are the shortgrass steppe located along the eastern slope of the Rocky Mountains and the Chihuahuan desert grasslands located in the central Rio Grande valley and extending into Northern Mexico (Lauenroth & Milchunas, 1992; Schmutz *et al.*, 1992). These biomes meet to form a transition zone in central New Mexico (McLaughlin, 1986). Plant communities at this transition zone are dominated or codominated by the perennial  $C_4$  grasses, *Bouteloua gracilis* (Willd. ex Kunth) Lag. ex Griffiths, the dominant species of the shortgrass steppe, and *Bouteloua eriopoda* (Torr.) Torr., the dominant species of Chihuahuan desert grasslands (Gosz, 1993). Several species have been found to reach the edge of their distribution at this biome transition zone (Gosz, 1992). However, it has not been investigated how species richness and climate of this biome transition zone compare with core areas of the adjacent biomes.

In arid ecosystems dominated by perennial grasses, highly variable presence and abundance of annual species makes cross-site comparisons of richness difficult (Ward & Olsvig-Whittaker, 1993). Therefore, it may be important to distinguish responses of annual and perennial species. Long-term data are more useful than short-term data for examining relationships between annual species richness and climate (Bowers, 1987). However, few, if any, long-term datasets exist for biomes and their transition zones, and in many cases these data have been collected using different methods. Thus, a combination of short-term studies using standard methods across sites and long-term data often collected with different methods may provide the most information about regional patterns in species richness. We had three specific objectives: (1) to characterize climate across multiple temporal scales for three sites selected to represent two grassland biomes and their transition zone, (2) to evaluate

the above hypotheses by contrasting species richness of annuals and perennials at multiple scales between these sites, and (3) to compare the year of sampling with multi-year patterns in species richness and long-term climate.

## Method

### *Study site descriptions*

We selected three sites to represent the core areas of the shortgrass steppe and Chihuahuan desert biomes as well as their transition zone. These sites were selected because long-term vegetation and climate data were available for them.

#### *Shortgrass steppe site (SGS)*

The site selected to represent the shortgrass steppe biome was the Central Plains Experimental Range located in northcentral Colorado (40·8°N, 104·8°W, 1650 m, a.s.l.). The topography is gently rolling with level uplands separated by swales. Soils range from a clay loam to loamy sand. Moderate grazing by cattle occurs throughout the site at intensities maintained since 1939 (Klippel & Costello, 1960). The pasture selected for sampling is exposed to moderate grazing. Total basal cover ranges from 25% to 40%. Plant communities are dominated by *B. gracilis*; other grasses, succulents, shrubs, and forbs account for the remainder of cover (Lauenroth & Milchunas, 1992). The average ( $\pm$  S.D.) above-ground net primary production is 172 ( $\pm$  41)  $\text{g m}^{-2}$  (ungrazed) and 103 ( $\pm$  23)  $\text{g m}^{-2}$  (grazed) (Sims & Singh, 1978). A complete site description is available at <http://sgs.cnr.colostate.edu>.

#### *Chihuahuan desert grassland site (CD)*

The Jornada Experimental Range (32·5°N, 106·8°W, 1350 m a.s.l.) in southern New Mexico was selected to represent Chihuahuan desert grasslands. These grasslands occur on soils varying in texture from sandy loams to loamy sands with an indurated calcium carbonate layer at 15 to > 50 cm depths. Grazing by cattle occurs throughout the site at varying intensities. Our sampling was conducted in a pasture that has been lightly grazed since 1967 (R. Beck, pers. comm.). Grassland communities are dominated by *B. eriopoda*; other grasses, succulents, shrubs, and forbs account for the remainder of cover (Paulsen & Ares, 1962). Total basal cover ranges from 5% to 20% (Gibbens & Beck, 1988). Average ( $\pm$  S.D.) above-ground net primary production is 148 ( $\pm$  33)  $\text{g m}^{-2}$  (ungrazed) and 109 ( $\pm$  65)  $\text{g m}^{-2}$  (grazed) (Sims & Singh, 1978). A complete site description is available at <http://jornada.nmsu.edu>.

#### *Chihuahuan desert grassland/shortgrass steppe transition site (SGS/CD)*

The Sevilleta National Wildlife Refuge (34·5°N, 106·9°W, 1650 m a.s.l.) in central New Mexico was selected to represent the biome transition zone between the shortgrass steppe and the Chihuahuan desert (Gosz, 1992). Grazing by cattle has been excluded from the site since 1973, although grazing by native herbivores, such as pronghorn antelope and rabbits, occurs at low-to-moderate intensities. Soils range from sandy loam to loamy sand with a calcium carbonate layer at varying depths and stages of development from 15 to > 50 cm. Additional information is available at <http://sevilleta.unm.edu>.

The area within the SGS/CD selected for study was the McKenzie Flats where patches of variable size ( $<10$  to  $>1000\text{ m}^2$ ) and shape are clearly distinguished based upon their dominance or co-dominance by *B. gracilis* or *B. eriopoda* (Gosz, 1993). The area selected for sampling consists of patches where both species co-dominate to represent the transition zone between community types. Other species of annual and perennial grasses and forbs, cactus, and shrubs can be found in all patch types (Kröel-Dulay *et al.*, submitted). Cover of all species ranges from 30% to 50% (Peters, 2000a). Net primary productivity is estimated at  $193\text{ g m}^{-2}$  ( $\pm 50$  S.D.) (D. Moore, pers. comm.).

### *Climatic analyses*

Monthly weather data from 1916 to 1995 and daily data from 1940 to 1995 were used to characterize the climatic regime of each site for a range of temporal scales selected to represent different aspects of climate found to be important in dry grasslands. We calculated long-term (80 years) mean annual, seasonal, and monthly precipitation and temperature (average, minimum, and maximum) for each site. A 'season' was defined as a three-month time period: winter (January–March), spring (April–June), summer (July–September), and fall (October–December). We also characterized climatic variability because of its importance to local and regional patterns in vegetation (Conley *et al.*, 1992). The coefficient of variation is often used to describe variability in precipitation since it standardizes for the amount received (Conley *et al.*, 1992; Cowling *et al.*, 1994). Daily precipitation data were used to characterize the distribution of rainfall and drought events within each year because small rainfall events and drought are important to vegetation responses in arid and semi-arid ecosystems (Albertson & Weaver, 1944; Herbel *et al.*, 1972; Sala *et al.*, 1992). Rain events were separated into one of seven size classes based on amount of precipitation ( $\leq 5$ , 6–10, 11–15, 16–20, 21–25, 26–30,  $> 30\text{ mm event}^{-1}$ ) (Sala *et al.*, 1992). The distribution of droughts was determined by counting the number of sequences of consecutive days without rain for each year. Drought events were separated into one of eight size classes (1–5, 6–10, 11–15, 16–20, 20–25, 26–30, 31–40,  $> 40$  days without rain). The impacts of these drought events can vary with the season they are occurring in, but this was not addressed in this study.

We also used the long-term monthly data to compare the amount of precipitation received in different types of years based on the ENSO phenomenon. Patterns in precipitation are known to differ significantly in the winter and spring during El Niño conditions and in the summer during La Niña conditions for central New Mexico (Molles & Dahm, 1990), with important effects on the vegetation, such as seedling establishment of the dominant species at the SGS/CD site (Peters, 2000b). Similar analyses and comparisons have not been conducted for the other two sites. Because the southern oscillation index (SOI) is a key indicator of the state of this phenomenon, years with a larger negative SOI ( $\leq -1.0$  5-month running mean) were classified as El Niño (Molles & Dahm, 1990). Years with a large positive SOI ( $\geq 1.0$ ) were defined as La Niña; remaining years were considered 'other'.

### *Vegetation sampling*

At each site, we selected a homogeneous 50 ha area representative of the undisturbed vegetation under the current grazing management regime. We randomly located 30–40 pairs of quadrats ( $4\text{ m} \times 4\text{ m}$ ) within each area at points not affected by local disturbance regime (e.g. burrowing activity of kangaroo rats) and topographic differences. The two quadrats in each pair were separated by 8 m; a nested design was used where four  $1\text{ m} \times 1\text{ m}$  quadrats were located within each of the  $4\text{ m} \times 4\text{ m}$

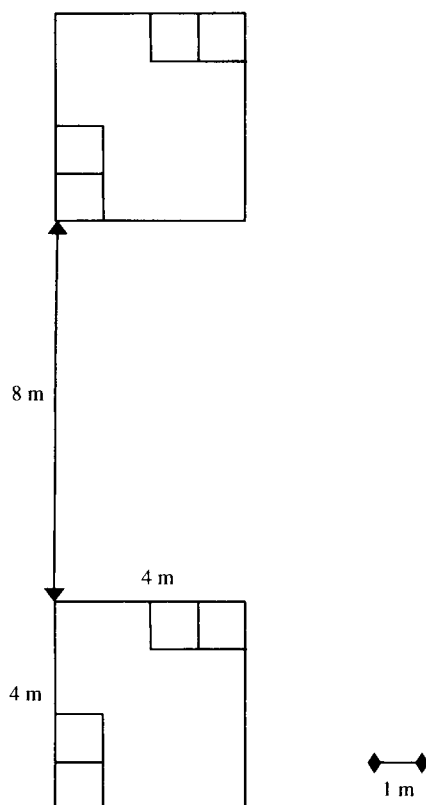
quadrats (Fig. 1). In each quadrat, we visually estimated the canopy cover (%) for each species. This sampling design was shown to be effective at describing multiple scales of pattern in vegetation for sand grasslands in Hungary (Kertész & Bartha, 1997; Kovács-Láng *et al.*, 2000; Gosz *et al.*, 2000). Sampling was conducted during the period of peak growth in vegetation for each site: August 1996 (SGS/CD, CD) and mid-June to mid-July 1997 (SGS).

*Year of sampling vs. long-term data*

In order to compare short-term and multi-year vegetation data with climate, we made two analyses. First, we compared the weather of the year of sampling to long-term climate. For this analysis, we used Bailey's moisture index developed for semi-arid climates to combine monthly precipitation and temperature into one expression of moisture availability (Bailey, 1979). This index is based on the premise that evaporation is exponentially related to temperature:

$$si(i) = \frac{0.18 \text{ PPT}(i)}{1.045^{\text{TEMP}(i)}}$$

where  $si(i)$  is the moisture index of month ( $i$ ),  $\text{PPT}(i)$  is the amount of precipitation (cm) received in month ( $i$ ), and  $\text{TEMP}(i)$  is the average temperature ( $^{\circ}\text{C}$ ) in month ( $i$ ).



**Figure 1.** Sampling design for vegetation sampling where canopy cover of each species in each 1 m x 1 m quadrat and 4 m x 4 m plot was estimated.

Values of this index decrease with increasing aridity. Yearly estimates of this index were calculated by summing monthly values.

Second, we compared our plant species richness data (*cf.* below) to multi-year vegetation data and growing season (April–September) precipitation from each site. The time period and method of sampling differed among sites. For the SGS, 4 years of richness data were available (1983–1986) that were collected in 0.25 m<sup>2</sup> circular plots located 7–10 m apart on randomly located transects (Milchunas & Lauenroth, 1995). For the SGS/CD, 6 years of data (1994–1999) were obtained from 400 m long transects using a line-intercept method (<http://sevilleta.unm.edu>). For the CD, 9 years of data (1989–1997) were available that were collected in 1 m<sup>2</sup> quadrats located 10 m apart (L. F. Huenneke, unpubl. data). Because these samples were collected on a small scale, our 1 m × 1 m quadrats were the most appropriate for comparison. The long-term data from the SGS and SGS/CD sites were compared with our data by adding species presence in adjacent sampling units until the total area was 1 m<sup>2</sup> (*sensu* Palmer, 1990; Gross *et al.*, 2000). At the SGS, the closest four plots along each transect were summed. At the SGS/CD, we assumed the line-intercept was 10-cm wide; thus, we summed all species that occurred within each 10 m line segment to obtain 1 m<sup>2</sup> ‘quadrats’. We averaged the species richness of each functional group in each year for each site.

### *Statistical analyses*

#### *Climate*

We tested for differences in monthly and seasonal precipitation, temperature, and moisture using a mixed model analysis of variance with year as a random effect since these variables may not be independent between sites in any given year (Mixed Model Procedure, SAS Institute Inc., 1988). Precipitation was square root transformed. *Post hoc* comparisons of means were conducted using Fisher’s least significant difference test with a significance level of 0.05. Differences in the coefficient of variation were determined using a 90% confidence interval (CI) defined by Chebyshev’s rule (CI = mean ± √10\* standard deviation) (Sokal & Rohlf, 1969). The amount of rainfall received during October–May and June–September in El Niño, La Niña, and other years, as well as the number of droughts and rainfall events per year in each category were compared using a one-way analysis of variance (ANOVA Procedure, SAS Institute Inc., 1988). Tukey’s studentized range test was used to test for differences among sites ( $\alpha=0.05$ ).

#### *Vegetation*

Using our different quadrat sizes and information about the distance between quadrats, we constructed a species–area curve for perennial and annual species in the following way. We determined the average cumulative species richness of four 1 m × 1 m quadrat nested within a 4 m × 4 m quadrat (4 m<sup>2</sup>) and of two 4 m × 4 m quadrats in a quadrat pair (32 m<sup>2</sup>) (*sensu* Palmer, 1990; Gross *et al.*, 2000). We also calculated the average cumulative species richness for three quadrat pairs within 100 m from each other (96 m<sup>2</sup>), for seven pairs within 400 m (224 m<sup>2</sup>), for 14 pairs within 600 m (448 m<sup>2</sup>), and for the whole 50 ha area (1000 m<sup>2</sup>). Thus, we estimated species richness for eight spatial scales (1, 14, 16, 32, 96, 224, 448, 1000 m<sup>2</sup>), where the largest scale (1000 m<sup>2</sup>) was considered to be an estimate of the species richness in the 50 ha area corresponding to the landscape-scale species richness (gamma diversity). The species richness within quadrat pairs (1, 14, 16, 32 m<sup>2</sup>) was considered to be the local-scale species richness (alpha diversity).

Spatial heterogeneity of the vegetation composition was described based on species composition at the local scale (1, 4, 16, and 32 m<sup>2</sup>). We used the distance measure corresponding to Jaccard's coefficient (1—Jaccard's coefficient). The mean of this distance measure between all possible quadrat pairs was termed habitat heterogeneity index ( $h$ ) by Qian *et al.* (1997):

$$h = \frac{2}{n(n-1)} \sum_{j < k}^{n(n-1)/2} \left( 1 - \frac{C_{jk}}{A_j + B_k - C_{jk}} \right)$$

where  $A_j$  and  $B_k$  are the numbers of species in the  $j$ th and  $k$ th plot under the  $i$ th pairwise comparison ( $i = 1$  to  $n(n-1)/2$ ,  $n$  = number of plots in the dataset, and  $j < k$ ), respectively,  $C_{jk}$  is the number of species common to both the  $j$ th and the  $k$ th plot. Only species that occurred in  $\geq 10\%$  of the quadrats were used. Means were compared between sites using a one-way analysis of variance (General Linear Models Procedure, SAS Institute Inc., 1988). *Post hoc* comparisons of means were conducted using Fisher's least-significant difference test with a significance level of 0.01.

### Multi-year data

Relationships between local-scale species richness for annuals and perennials and growing season precipitation were obtained using regression analysis (Regression Procedure, SAS Institute Inc., 1988). Differences between the multi-year data between sites and our 1 m  $\times$  1 m quadrats from each site were not assessed statistically since sampling methods differed among datasets and sample sizes were small (4–9 points). Thus, only qualitative comparisons were made.

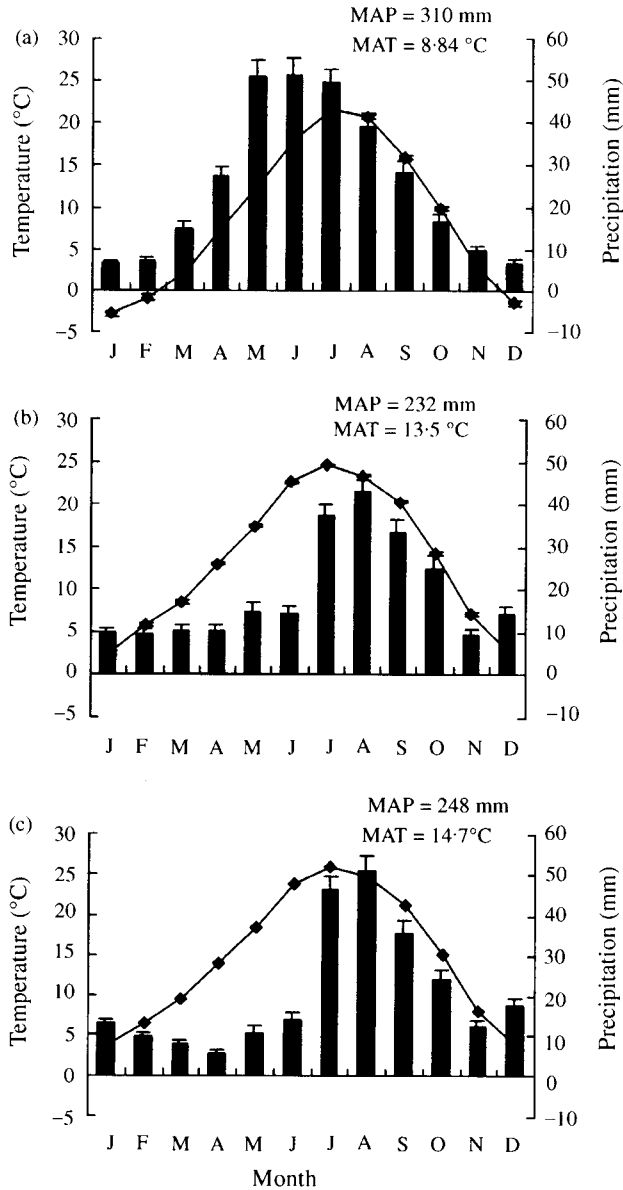
## Results

### Climate

Mean annual precipitation (MAP) over the past 80 years was highest at the shortgrass steppe site (310 mm; S.D. = 86) and similar for the Chihuahuan desert (248 mm; S.D. = 87) and transition zone sites (232 mm; S.D. = 79). The two southern sites also had similarly high inter-annual variability of precipitation (CV = 35) compared to the SGS site (CV = 28). The SGS site is characterized by a continental climate with peak amounts of precipitation in May, June, and July, whereas the CD and SGS/CD are characterized by a monsoonal pattern in precipitation with large amounts in July, August, and September (Fig. 2).

Mean annual temperature (MAT) increased from north to south. At the SGS site, monthly temperatures ranged from  $-2.8^\circ\text{C}$  (in January) to  $21.7^\circ\text{C}$  (in July), at the SGS/CD site from  $2.6^\circ\text{C}$  to  $24.6^\circ\text{C}$ , and at the CD site from  $3.8^\circ\text{C}$  to  $26.1^\circ\text{C}$ . Average monthly minimum and maximum temperature showed the same trend as the average temperature (results not shown). Maximum temperature was on average  $6^\circ\text{C}$  higher at the SGS/CD than at the SGS and  $1.5^\circ\text{C}$  lower at the SGS/CD than at the CD. Minimum temperature was on average  $3.5^\circ\text{C}$  higher at the SGS/CD than at the SGS and  $0.5^\circ\text{C}$  lower at the SGS/CD than at the CD.

When monthly precipitation was summarized according to season, summer (July–September) precipitation was largest at the CD, intermediate at the SGS and lowest at the SGS/CD (Fig. 3(a)). The transition site (SGS/CD) had spring moisture (April–June) statistically intermediate between the CD and the SGS. The difference in spring moisture between these sites is of strong biological importance, too (Gosz, 1992). The coefficient of variation in seasonal precipitation was largest in the spring for the CD

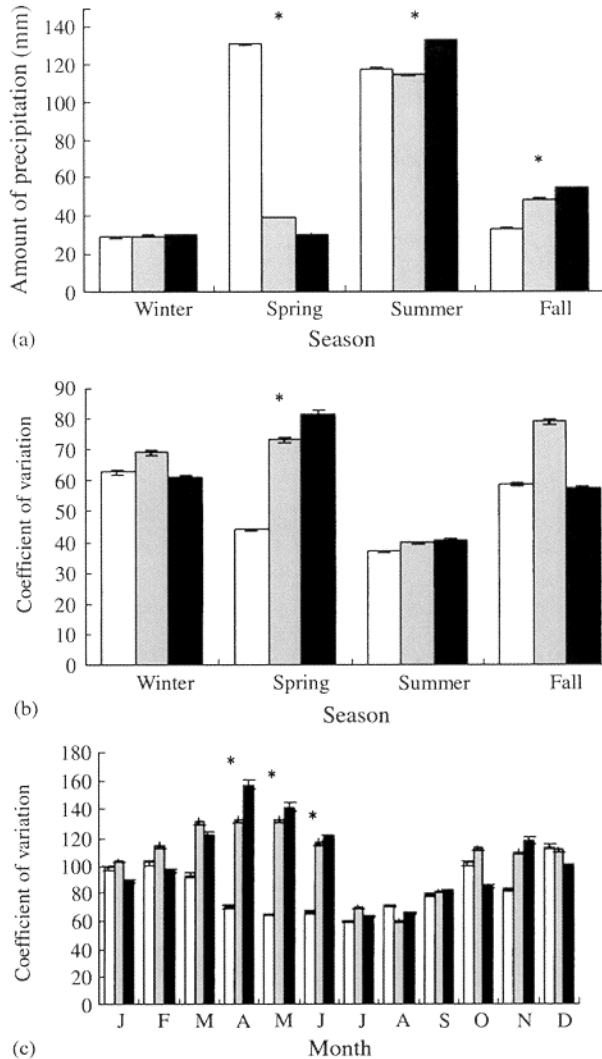


**Figure 2.** Long-term (1916–1995) monthly temperature (°C) (—) and precipitation (mm) (■) for three sites representing two biomes and their transition: (a) shortgrass steppe [SGS], (b) shortgrass steppe/Chihuahuan desert grassland [SGS/CD], (c) Chihuahuan desert grassland [CD]. Average and standard errors shown. Mean annual precipitation (MAP) and mean annual temperature (MAT) also shown.

site, whereas at the SGS/CD it was largest in the fall (Fig. 3(b)). On a monthly basis, July and August were least variable for all three sites (Fig. 3(c)). The SGS was less variable in the spring (March–June) compared to the two southern sites that had their highest variability during this time period.

On a daily basis, variability in precipitation at these sites implies that plants have to sometimes withstand long periods without rainfall. Drought during the spring may be

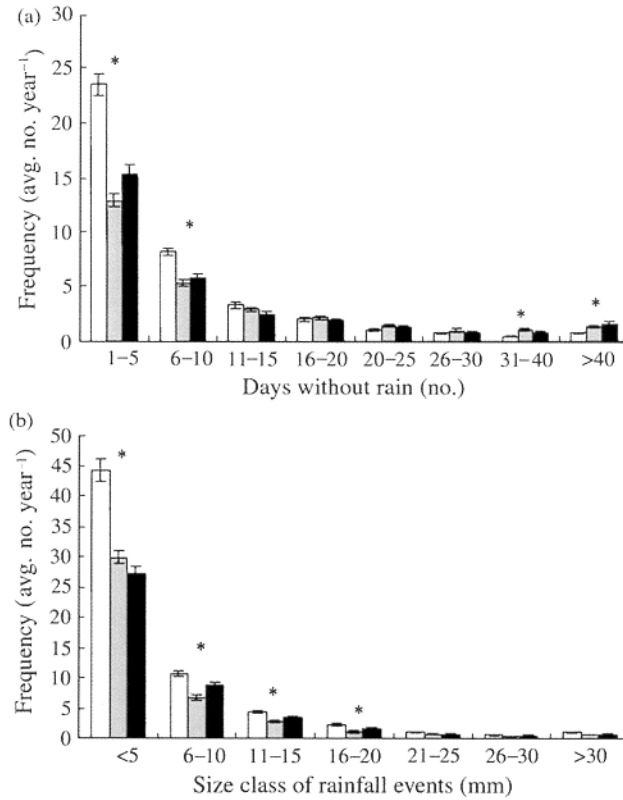




**Figure 3.** Seasonal precipitation for each site (abbreviations same as Fig. 2): (a) average seasonal precipitation summed over three-month periods, (b) coefficient of variation of seasonal precipitation, and (c) coefficient of variation of monthly precipitation. Average and standard errors shown. Stars indicate statistically significant differences ((a)  $\alpha = 0.05$ , (b) and (c)  $\alpha = 0.1$ ). (□) SGS; (■) SGS/CD; (■) CD.

particularly important in explaining differences in the vegetation of these sites. Although the distribution of the number of consecutive days without rain was similar among sites, important differences were found between the SGS and the two southern sites (Fig. 4(a)). A significantly larger number of extended droughts (e.g. >40 days without rain) occurred at the SGS/CD and CD sites compared with the SGS site. Plants at these sites also have to be capable of utilizing small rainfall events since the majority of events are  $\leq 5$  mm at all three sites (Fig. 4(b)). Even though we expected the number of large rainfall events to be highest at the most mesic site (SGS), high rainfall at this site resulted from a larger number of small- and medium-sized rainfall events.

Variability in total precipitation between October and May was related to the ENSO phenomenon at the two southern sites (Fig. 5). At these sites, precipitation was



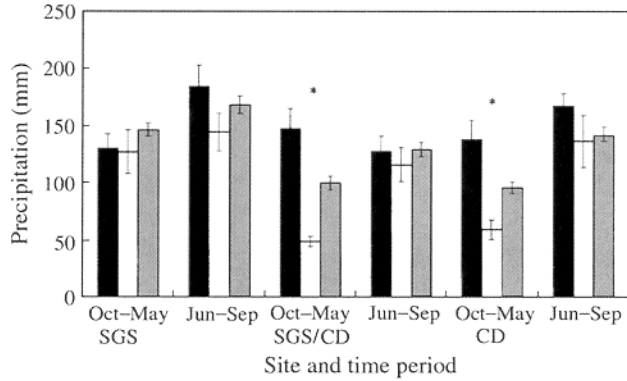
**Figure 4.** Frequency distributions of droughts and rainfall events based on daily weather data (1940–1995) for three sites: (a) average number/year of periods without rain in size class and (b) average number/year of rainfall events in one of seven size classes. Stars indicate statistically significant difference ( $\alpha=0.05$ ). (□) SGS; (■) SGS/CD; (■) CD.

highest in El Niño years and lowest in La Niña years during this period. June–September precipitation was not affected by El Niño or La Niña. By contrast, precipitation at the SGS site was similar for all types of years in both seasons.

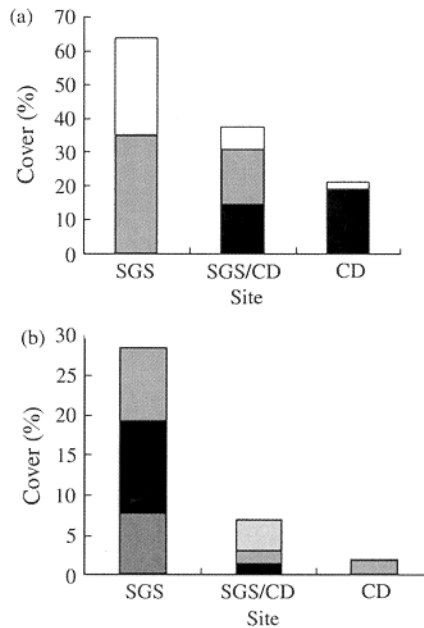
### Vegetation

Total cover of the vegetation decreased from north to south. *Bouteloua gracilis* had a higher total cover at the SGS site compared to the other sites, and *B. eriopoda* had similar cover at the SGS/CD and CD site (Fig. 6(a)). The contribution of other species to total cover decreased from the north (SGS) to south (CD). Functional group composition of subdominant species differed among sites (Fig. 6(b)). At the SGS, subdominant cover was evenly divided among  $C_4$  perennials, mainly the grass *Buchloe dactyloides*, succulent species, mainly *Opuntia polyacantha*, and a group of  $C_3$  perennials, mainly forbs and shrubs. At the SGS/CD, the cover of subdominants was mainly attributed to  $C_4$  annuals.  $C_3$  perennial forbs and shrubs were the most important subdominant species group at the CD site.

The total number of identified species (gamma diversity) at the biome transition zone (52) was more similar to the CD (50) than to the SGS site (67). Three species were unidentified at these sites. The two southern, more arid sites also had the most species in common (22) that included three species of perennial grasses, seven



**Figure 5.** Precipitation received at each site during one of three types of years (El Niño ( $n = 15$ ), La Niña ( $n = 9$ ) and 'other' ( $n = 56$ )) for two time periods. Average and standard error shown. Stars indicate statistically significant differences ( $\alpha = 0.05$ ). (■) El Niño; (□) La Niña; (▒) Other.



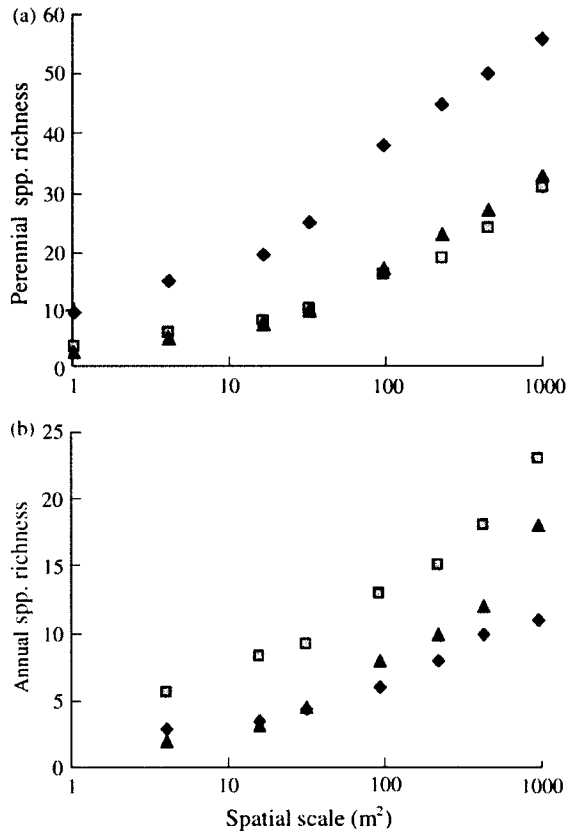
**Figure 6.** Average cover (%) at each site in  $4\text{ m} \times 4\text{ m}$  quadrats: (a) two dominant grasses (*Bouteloua gracilis*, *Bouteloua eriopoda*) and other/subdominant species combined: (□) Others; (▒) *B. gracilis*; (■) *B. eriopoda*; and (b) cover of subdominant species divided into five functional groups (C<sub>3</sub> and C<sub>4</sub> annuals include grasses and forbs, C<sub>3</sub> and C<sub>4</sub> perennials include grasses, forbs and subshrubs/shrubs): (□) C<sub>3</sub> Annuals; (▒) C<sub>4</sub> Annuals; (▒) C<sub>3</sub> Perennials; (■) C<sub>4</sub> Perennials; (■) Succulents.

perennial forbs, 10 annuals, and two succulents (Appendix). Few species were found at both the transition site and the shortgrass steppe site (6) that included three perennial grasses, one perennial forb, one annual, and one subshrub. Only three species were common to both the SGS and CD sites; these species were also found at the SGS/CD site, and included a perennial C<sub>4</sub> grass (*Aristida purpurea*), perennial C<sub>4</sub> forb (*Evolvulus nuttalianus*), and a C<sub>3</sub> subshrub (*Gutierrezia sarothrae*). Most species at

**Table 1.** Number of species by group found within a 50 ha area within each of three sites

Species group	Site		
	SGS	SGS/CD	CD
C <sub>3</sub> annual grasses and forbs	8	4	1
C <sub>4</sub> annual grasses and forbs	4	16	17
C <sub>3</sub> perennial grasses and forbs	32	12	13
C <sub>4</sub> perennial grasses and forbs	15	12	12
Shrubs and subshrubs	5	5	4
Succulents	3	3	3
Total	67	52	50

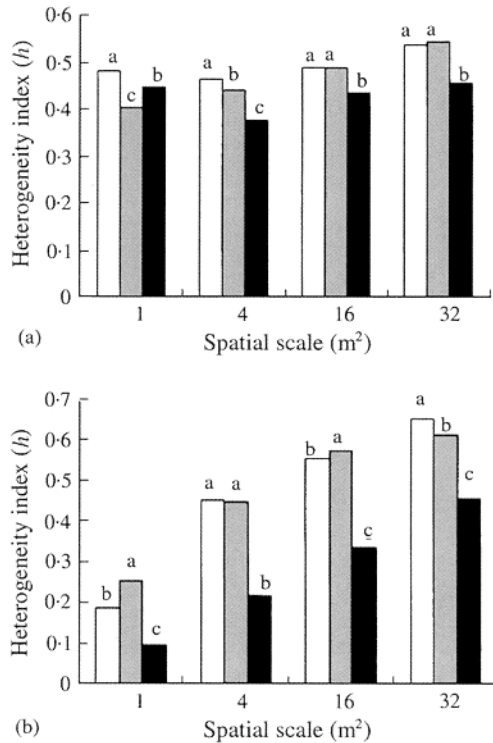
the SGS were C<sub>3</sub> perennial grasses and forbs (48%), whereas the other sites had a similar number of C<sub>4</sub> annuals, C<sub>3</sub> and C<sub>4</sub> perennial grasses, and forbs (23–34%) (Table 1). Numbers of shrub (4–5) and succulent species (3) were similar for all three sites. Number of C<sub>3</sub> annual species was low in all cases and decreased from the SGS (8) to the CD site (1).

**Figure 7.** Number of species within a 50 ha area (1000 m<sup>2</sup>) at eight spatial scales for three sites: (a) perennials (b) annuals. (◆) SGS; (■) SGS/CD; (▲) CD.

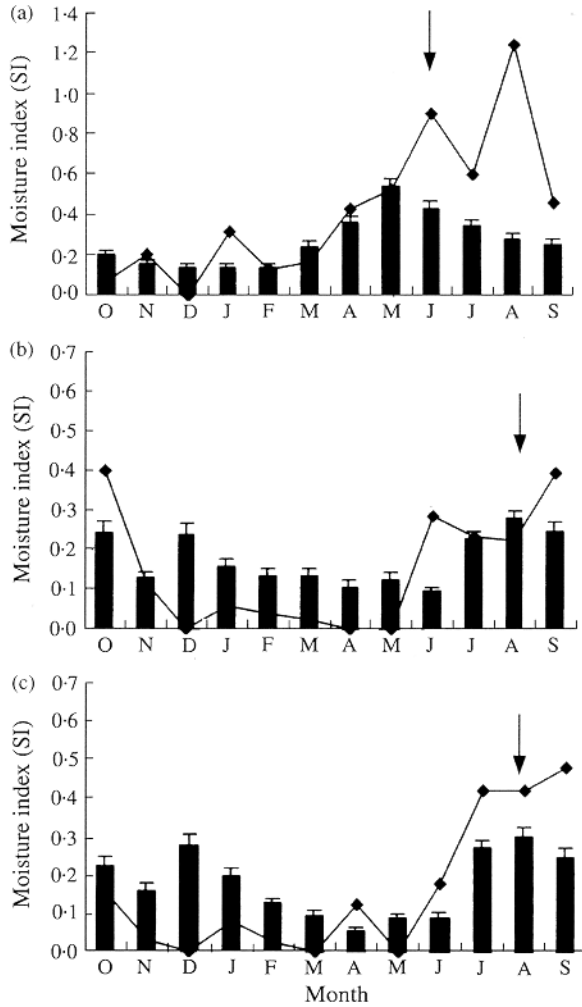
Perennial species richness was similar between the SGS/CD and the CD whereas annual species richness was highest at the transition zone from the local to the landscape scale (Fig. 7). The species–area curve of the perennial species was similar at the CD and the SGS/CD, and less steep at the SGS. Spatial heterogeneity varied both for the functional group sampled and the size of the sampling quadrat (Fig. 8). The spatial heterogeneity of perennial and annual species composition was generally higher at the SGS and the SGS/CD compared with the CD. At small spatial scales perennial species composition was most heterogeneous at the SGS, whereas at bigger spatial scales it was similar at the SGS and the SGS/CD. Quadrat size had a larger influence on spatial heterogeneity of annuals than perennials. These patterns may be partially explained by differences in numbers of species used to perform these calculations since spatial heterogeneity of species composition may increase as species number increases.

*Year of sampling vs. long-term data*

The value of Bailey's annual moisture index decreased from the SGS (3.3) to the two southern sites (SGS/CD = 2.1, CD = 2.2) indicating similar aridity for the two southern sites and a more mesic climate for the northern site (Fig. 9). For the year of sampling, moisture in the spring preceding sampling was below average for most months at the two southern sites and near the long-term average the SGS (Fig. 9). During the summer of the sampling (June–August), moisture levels were average or above average for all three sites.



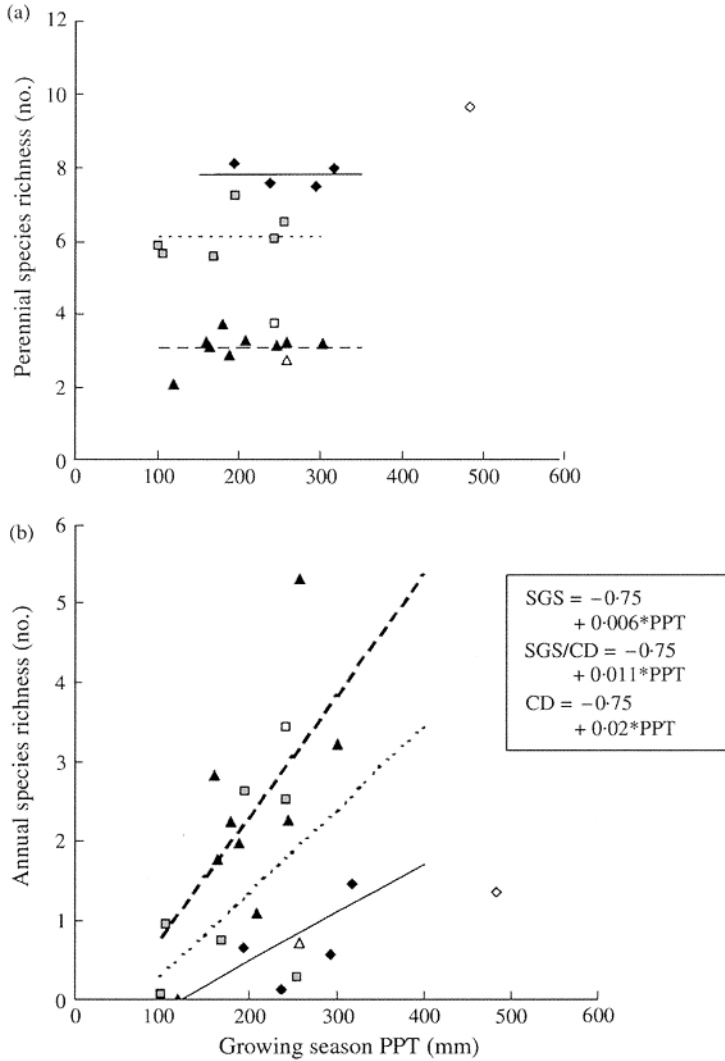
**Figure 8.** Spatial heterogeneity of species composition for four spatial scales within a 50 ha area at three sites: (a) perennial species (b) annual species. Different letters indicate significantly different results ( $\alpha = 0.01$ ) for a given quadrat size. (□) SGS; (■) SGS/CD; (■) CD.



**Figure 9.** Long-term average and standard error of monthly moisture index (■) and for the year of sampling (—) for three sites. (a) shortgrass steppe [SGS], (b) transition zone [SGS/CD], (c) Chihuahuan desert grassland [CD]. Months are arranged in the sequence of the water year starting with October and ending with September. The arrow indicates the time of sampling for each site.

Based on long-term data, perennial species richness was found insensitive of growing season precipitation for all the three sites (Fig. 10(a)). This suggests that our short-term data collected in a single year is a reliable measure for perennial species, and due to the standardized methodology can be used to compare the sites. However, the perennial species values collected in our short-term sampling are very different from long-term values for the SGS and the SGS/CD, where  $1\text{ m}^2$  long-term data were derived from different sampling designs. This implies that these long-term data cannot be used for cross-site comparisons due to differences in sampling designs between sites.

Contrary to perennials, annual species richness showed a statistically significant correspondence with growing season precipitation (April–September) at each site (Fig. 10(b)).



**Figure 10.** Species richness at the 1 m<sup>2</sup> scale from our sampling (open symbols) and multi-year data for each site (solid symbols) as a function of growing season (April–September) precipitation (PPT) (mm) in the year of sampling: (a) perennials, slopes of regression lines were not significantly different from zero (average is depicted as regression line) (b) annuals (equations for best-fitting regression line on graph). (◆) SGS; (□) SGS/CD; (▲) CD.

## Discussion

### *Patterns in climate*

The climate of these sites is typical for arid lands in that their mean annual precipitation (MAP) is low and highly variable (Huenneke & Nobel, 1996). MAP ranges from 160 to 1700 mm for grasslands all over the world (Ripley, 1992), which indicates that our sites are situated at the arid end of this range. The precipitation at these sites occurs primarily as small rainfall events, and prolonged periods without rain are common (Albertson & Weaver, 1944; Herbel *et al.*, 1972; Sala *et al.*, 1992).

The amount and seasonal of precipitation at these sites is influenced by continental scale climate phenomena, such as the strength of westerly winds and high-pressure systems (Neilson, 1987). These generating forces are strongly influenced by the Rocky Mountains, which form a biogeographic barrier between the SGS site and the two southern sites. The SGS site, which is located to the East of the Rocky Mountains, had a significantly higher amount and lower variability of MAP, as well as a different seasonality of precipitation in comparison with the two southern sites. The winter precipitation of the two southern sites was affected by the ENSO phenomenon, whereas it was unrelated to the Southern Oscillation at the SGS. The similarity in climate between the two southern sites corresponds to a previous study showing that they fall within the same general climatic region characterized by monsoon rains during the summer and fall (Comrie & Glenn, 1998).

However, there were also important differences between the climate of the two southern sites that may affect species composition. Higher minimum and maximum temperatures at the CD compared to the SGS/CD can have important effects on species distributions (Páruelo *et al.*, 1998; Alward *et al.*, 1999). Higher and less variable spring moisture at the SGS/CD compared to sites further south was also found in previous studies using a regional approach to climate analysis (Gosz, 1992; Comrie & Glenn, 1998). These seasonal differences may influence the dominance patterns and phenology of species at this transition site (Peters, in press). In a regional analysis of a biome transition zone in Europe, it was found that strong correlations exist between vegetation and certain climate characteristics but different vegetation types were related to different characteristics in climate (Moreno *et al.*, 1990).

#### *Patterns of species richness and functional group abundance*

Our results are similar to other studies (e.g. Cowling *et al.*, 1994; Kadmon & Danin, 1999; Kutiel *et al.*, 2000) showing that patterns in species diversity depend on functional group. Perennial species richness at the local scales (alpha diversity) were related to a long-term aridity gradient where richness was higher at the semi-arid SGS compared to the more arid CD and SGS/CD sites. Total species richness (gamma diversity) followed similar patterns as perennial species. An increase in perennial species richness with increasing precipitation has been found in other arid environments (Ward & Olsvig-Whittaker, 1993; Leiva *et al.*, 1997; Kutiel *et al.*, 2000; Kovács-Láng *et al.*, 2000; Gross *et al.*, 2000). These patterns are independent of the year of sampling since perennial species richness was not related to growing season precipitation.

Highest local-scale perennial species richness at the SGS site may correspond to the more mesic conditions, particularly in the spring when temperatures are cool, that allow more C<sub>3</sub> perennial grasses and forbs to coexist with the C<sub>4</sub> dominant, *B. gracilis*. These results are supported by the high cover attributed to perennials at the SGS site compared to the other two sites. The lack of a relationship between perennial species richness and growing season precipitation for all three sites is not surprising given the longevity and drought-tolerance of grasses and forbs in these grasslands (Dittberner, 1971; Fair *et al.*, 1999). Furthermore, many of these perennials have little ability to rapidly respond to short-term favorable conditions since seed storage in the soil is highly variable in time and space (Coffin & Lauenroth, 1989; Kemp, 1989).

By contrast, annual species richness was related to growing season precipitation in the year of sampling. Kutiel *et al.* (2000) also found that the proportion of annual species (out of total species found) was more closely related to rainfall in the year of sampling than the proportion of perennial species over 4 years. The increase in annual species richness with an increase in growing season precipitation within a site is common in dry grasslands and reflects the ability of these species to respond



opportunistically to favorable conditions (Bowers, 1987). High seed production, effective storage of seeds in the soil, and few requirements for germination allow annuals to respond rapidly when conditions are favorable, yet maintain seed sources through periods of drought (Danin & Orshan, 1990). Nutrients may accumulate in desert soils during drought that lead to an above average response upon drought relief (Charley & Cowling, 1968). This may explain the above-average annual species richness at the biome transition zone site in the year of sampling.

We found that the scale of the sampling quadrat can have an important influence on the level of spatial heterogeneity (beta diversity) detected. The spatial heterogeneity of perennial species composition was high at the SGS and the SGS/CD and lowest at the CD. Because the SGS/CD was similar to the CD in other vegetation characteristics, our results indicate that spatial heterogeneity of perennial species composition is particularly high at the transition zone site. In another study (Kröel-Dulay *et al.*, submitted), we found that species composition differs between patches of the two dominant species at the SGS/CD site. Our cover data show that dominance increases from the SGS to the CD. The CD site is characterized by many rare species, which corresponds to the common perception that dominance increases as aridity increases (Ward & Olsvig-Whittaker, 1993).

#### *Evaluation of hypotheses*

Perennial species richness (alpha diversity) of the three sites followed an aridity gradient. Therefore, the first hypothesis that species richness (alpha diversity) increases with more favorable climatic condition was supported by our data, after we distinguished between functional groups of plant species. In general, the two southern sites were more similar to each other in most vegetation characteristics than to the SGS site. The similarities of these two sites can be explained by their position in relation to the Rocky Mountains, which form a major biogeographic barrier. The biogeographic proximity of the two southern sites results from both the similarity in climate as well as their short geographic distance (257 km *vs.* SGS/CD to SGS 955 km). Similarity in climate can explain similarities in functional group composition (Cowling *et al.*, 1994), and geographic proximity can increase dispersal between sites and therefore increase the floristic similarity of the sites (Leiva *et al.*, 1997). It remains to be understood if climate or geographic proximity was more important in determining the strong similarity of vegetation characteristics in these two sites.

Although high spatial heterogeneity of perennial species composition (beta diversity) was found at the transition zone, this did not result in higher landscape-level species richness (gamma diversity) as predicted due to the mixing of different regional floras and high spatial heterogeneity in the environment at biome transition zones (Shmida & Wilson, 1985; Neilson, 1993). However, our results are limited since we only sampled a small part of the landscape at each site (50 ha) that was dominated by grasses. All three sites contain additional grassland and shrubland types that contribute to species richness. Furthermore, differences in landuse (grazing), topography, soils, and animal-generated soil disturbances can have important effects on species richness at each site (Cornelius *et al.*, 1991; Singh *et al.*, 1996; Fields *et al.*, 1999; Ryerson & Parmenter, 2001). Variation in these factors could not be accounted for in our sampling. So this hypothesis may be more appropriately tested at a larger spatial scale than the extent of our sampling. However, rigorous hypothesis testing at larger scales may prove difficult (Rice & Westoby, 1983).

Similar to our study, it was found that ant species composition was more similar at the SGS/CD and the CD, than at the southern sites and the SGS (Bestelmeyer & Wiens, 2001). However, ant species richness was similar among all three sites. Ant species richness is also expected to peak at biome transition zones. Based on patterns

in species composition, highest ant species richness was suggested to occur north of the SGS/CD site near the Colorado/New Mexico border where seasonal precipitation changes from monsoonal (summer–fall peak) to continental (spring–summer) (Comrie & Glenn, 1998). In another study, the probabilities of establishment of the two dominant grasses (*Bouteloua gracilis* and *B. eriopoda*) were shown by simulation modelling to be equal for both species south of the SGS/CD site in southcentral New Mexico (Minnick & Coffin, 1999). Additional plant diversity studies at more sites along the gradient are needed to determine if peaks in species diversity occur at transition zones based on different vegetation and climate characteristics than examined in this study.

#### *Long-vs. short-term vegetation sampling in arid environments*

Our single year–single season sample of the vegetation with standardized methods could reveal important differences and similarities between these sites in perennial species richness. The long-term data that were available from these sites were not gathered with standard methods, thus they could not be used for cross-site comparisons. Different sampling methods can have a strong effect on the number of species detected at any given site (Stohlgren *et al.*, 1998). Nevertheless, within each site, the long-term data were able to reveal the dynamics of species richness over time. In the absence of standardized long-term data from each site, a combination of long- and short-term standardized data can be used. However, in order to compare these grassland sites, long-term sampling with standardized methods would be best.

### **Summary**

Using long-term data, we found that annual, but not perennial, species richness (local or alpha diversity) was related to the weather in the year of sampling at all three of these arid and semi-arid grassland sites. Long-term data could not be used for cross-site comparison because they were gathered with different methodology at the different sites. Using short-term data collected with standardized methodology, we found that perennial species richness decreased as the climate became less favorable for plant growth along the north–south gradient. Spatial heterogeneity in perennial species composition (beta diversity) was high at the shortgrass steppe and the transition zone site. However, this did not translate into higher perennial species richness at the landscape-level (gamma diversity) at the transition zone site. Instead, landscape-level species richness was similar between the biome transition zone and the Chihuahuan desert grassland site. The biome transition zone site was more similar to the Chihuahuan desert grassland site in most climate and vegetation characteristics, which may have been partly due to the shorter biogeographic distance between the two sites. Using both long- and short-term climate and vegetation data helped to clarify the ecological position of the biome transition zone site with respect to the adjacent biomes, but also highlighted the need for long-term studies with standardized methodology.

This study was supported by grants from the National Science Foundation to Colorado State University and New Mexico State University (INT-9896168) and to the University of New Mexico (DEB-9411976). G. Kröel-Dulay was also supported by a grant from the Hungarian National Science Foundation (OTKA 21166). T. Hochstrasser received a scholarship for research and further education (bourse de recherche et de perfectionnement) from the University of Lausanne, Switzerland and the Francis C. Clark Award for Excellence in Soil Biology through Colorado State University. Miklos Kertész developed the sampling design, and Sandor Bartha, Miklos Kertész and Edit Kovács-Láng gave valuable advice during field

sampling. Esteban Muldavin, John Anderson, Cindy Villa and Kelly Rimar helped with species identification. We thank Jim Zumbrunnen, Robin Reich and Sarah Goslee for statistical advice. We thank Brandon Bestelmeyer, Laura Huenneke, Ron Neilson, and an anonymous reviewer for helpful comments on the manuscript. Special thanks to Daniel Milchunas, Laura Huenneke and the Sevilleta LTER for availability and use of multi-year species richness data. All three sites are National Science Foundation supported Long Term Ecological Research sites. The SGS LTER is administered by the USDA-ARS and the US Forest service, the Sevilleta LTER by the US Fishery and Wildlife Service and the Jornada LTER by the USDA-ARS and New Mexico State University. This is Sevilleta Long-Term Ecological Research Program publication number 255.

### References

- Albertson, F.W. & Weaver, J.E. (1944). Nature and degree of recovery of grassland from the great drought of 1933 to 1940. *Ecological Monographs*, **14**: 393–479.
- Alward, R.D., Detling, J.K. & Milchunas, D.G. (1999). Grassland vegetation changes and nocturnal global warming. *Science*, **283**: 229–231.
- Bailey, H.P. (1979). Semi-arid climates: their definition and distribution. In: Hall, A.E., Cornell, G.H. & Lawton, H.W. (Eds), *Agriculture in Semi-arid Environments*, pp. 73–97. New York: Springer-Verlag, 340 pp.
- Bestelmeyer, B.T. & Wiens, J.A. (2001). Local and regional-scale responses of ant diversity to a semiarid biome transition zone. *Ecography*, **24**: 381–392.
- Bowers, M.A. (1987). Precipitation and the relative abundances of desert winter annuals: a 6-year study in the northern Mohave desert. *Journal of Arid Environments*, **12**: 141–150.
- Charley, J.L. & Cowling, S.W. (1968). Changes in soil nutrient status resulting from overgrazing and their consequences in plant communities of semi-arid areas. *Proceedings of the Ecological Society of Australia*, **3**: 28–38.
- Coffin, D.P. & Lauenroth, W.K. (1989). Spatial and temporal variation in the seed bank of a semiarid grassland. *American Journal of Botany*, **76**: 53–58.
- Comrie, A.C. & Glenn, E.C. (1998). Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. *Climate Research*, **10**: 201–215.
- Conley, W., Conley, M.R. & Karl, T.R. (1992). A computational study of episodic events and historical context in long-term ecological processes: climate and grazing in the northern Chihuahuan desert. *Coenoses*, **7**: 1–19.
- Cornelius, J.M., Kemp, P.R., Ludwig, J.A. & Cunningham, G.L. (1991). The distribution of vascular plant species and guilds in space and time along a desert gradient. *Journal of Vegetation Science*, **2**: 59–72.
- Cowling, R.M., Esler, K.J., Midgley, G.F. & Honig, M.A. (1994). Plant functional diversity, species diversity and climate in arid and semi-arid southern Africa. *Journal of Arid Environments*, **27**: 141–158.
- Currie, D.J. & Paquin, V. (1987). Large-scale biogeographical patterns of species richness of trees. *Nature*, **329**: 326–327.
- Danin, A. & Orshan, G. (1990). The distribution of Raunkiaer life forms in Israel in relation to the environment. *Journal of Vegetation Science*, **1**: 41–48.
- di Castri, F., Hansen, A.J. & Holland, M.M. (Eds). (1988). A New Look at Ecotones. Biology International, Special Issue 17. Paris: International Union of Biological Sciences. 163 pp.
- Dittberner, P.L. (1971). A demographic study of some semidesert grassland plants. M.Sc. Thesis, New Mexico State University, Las Cruces, NM. 81 pp.
- Fair, J.L., Lauenroth, W.K. & Coffin, D.P. (1999). Demography of *Bouteloua gracilis* in a mixed grass prairie: analysis of genets and individuals. *Journal of Ecology*, **87**: 233–243.
- Fields, M.J., Coffin, D.P. & Gosz, J.R. (1999). Burrowing activities of kangaroo rats and patterns in plants species dominance at a shortgrass steppe–desert grassland ecotone. *Journal of Vegetation Science*, **10**: 123–130.
- Gibbens, R.P. & Beck, R.F. (1988). Changes in grass basal area and forb densities over a 64 year period on grassland types of the Jornada Experimental Range. *Journal of Range Management*, **41**: 186–192.

- Gosz, J.R. (1992). Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In: Hansen, A.J. & di Castri, F. (Eds), *Landscape Boundaries. Consequences for Biotic Diversity and Ecological Flows*, pp. 55–75. New York: Springer-Verlag, 452 pp.
- Gosz, J.R. (1993). Ecotone hierarchies. *Ecological Applications*, 3: 369–376.
- Gosz, J.R., Peters, D.P.C., Bartha, S., Kertész, M., Kovács-Láng, E. & Kröel-Dulay, G. (2000). Organization of grasslands along ecological gradients: US–Hungarian LTER grassland cooperation. In: Lajtha, K. & Vanderbilt, K. (Eds), *Proceedings of the ILTER Regional Workshop*, pp. 67–78. Corvallis, OR: Oregon State University Press. 128 pp.
- Gross, K.L., Willig, M.R., Gough, L., Inouye, R. & Cox, S.B. (2000). Patterns of species density and productivity at different spatial scales in herbaceous plant communities. *Oikos*, 89: 417–427.
- Herbel, C.H., Ares, F.N. & Wright, R.A. (1972). Drought effects on a semidesert grassland range. *Ecology*, 53: 1084–1093.
- Huenneke, L.F. & Nobel, I.R. (1996). Ecosystem function of biodiversity in arid ecosystems. In: Mooney, H.A., Cushman, J.H., Medina, E., Sala, O.E. & Shulze, E.-D. (Eds), *Functional Roles of Biodiversity. A Global Perspective*, pp. 99–128. Chichester: John Wiley & Sons, 493 pp.
- Kadmon, R. & Danin, A. (1999). Distribution of plant species in Israel in relation to spatial variation in rainfall. *Journal of Vegetation Science*, 10: 421–432.
- Kemp, P.R. (1989). Seed banks and vegetation processes in deserts. In: Leck, M.A., Parker, V.T. & Simpson, R.L. (Eds), *Ecology of Soil Seed Banks*, pp. 257–281. San Diego, CA: Academic Press, 462 pp.
- Kertész, M. & Bartha, S. (1997). Spatial organization of open sand grasslands in Hungary. *Bulletin of the Ecological Society of America*, 78: 268.
- Klippel, G.E. & Costello, D.F. (1960). Vegetation and cattle responses to different intensities of grazing on short-grass ranges on the central Great Plains. *US Department of Agriculture Technical Bulletin No. 1216*, 82 pp.
- Kovács-Láng, E., Kröel-Dulay, G., Kertész, M., Fékéte, G., Mika, J., Dobi-Wantuch, I., Rédei, T., Rajkai, K., Hahn, I. & Bartha, S. (2000). Changes in the composition of sand grasslands along a climatic gradient in Hungary, and implications for climate change. *Phytocoenologia*, 30: 385–407.
- Kröel-Dulay, G., Ódor, P., Peters, D.P.C. & Hochstrasser, T. (submitted). Plant species associations with different patch types at a semiarid-arid grassland ecotone. *Journal of Vegetation Science*.
- Kutiel, P., Kutiel, H. & Lavee, H. (2000). Vegetation response to possible scenarios of rainfall variations along a Mediterranean–extreme arid climatic transect. *Journal of Arid Environments*, 44: 277–290.
- Lauenroth, W.K. & Milchunas, D.G. (1992). Short-grass steppe. In: Coupland, R.T. (Ed.), *Natural Grasslands. Ecosystems of the World*, Vol. 8A, pp. 183–225. Amsterdam: Elsevier Science Publishers, 469 pp.
- Leiva, M.J., Chapin, F.S., III & Ales, F.R. (1997). Differences in species composition and diversity among Mediterranean grasslands with different history—the case of California and Spain. *Ecography*, 20: 97–106.
- McLaughlin, S.P. (1986). Floristic analysis of the Southwestern United States. *Great Basin Naturalist*, 46: 47–65.
- Milchunas, D.G. & Lauenroth, W.K. (1995). Inertia in plant community structure: state changes after cessation of nutrient-enrichment stress. *Ecological Applications*, 5: 452–458.
- Minnick, T.J. & Coffin, D.P. (1999). Geographic patterns of simulated establishment of two *Bouteloua* species: implications for distributions of dominants and ecotones. *Journal of Vegetation Science*, 10: 343–356.
- Molles, M.C. & Dahm, C.N. (1990). A perspective of El Niño and La Niña: global implications for stream ecology. *Journal of the North American Benthological Society*, 9: 68–76.
- Moreno, J.E.M., Pineda, F.D. & Rivas-Martínez, S. (1990). Climate and vegetation at the Eurosiberian–Mediterranean boundary in the Iberian Peninsula. *Journal of Vegetation Science*, 1: 233–244.
- Neilson, R.P. (1987). Biotic regionalization and climatic controls in western North America. *Vegetatio*, 70: 135–147.
- Neilson, R.P. (1993). Transient ecotone response to climatic change: some conceptual and modelling approaches. *Ecological Applications*, 3: 385–395.
- Palmer, M.W. (1990). The estimation of species richness by extrapolation. *Ecology*, 71: 1195–1198.

- Paruelo, J.M., Jobbágy, E.N.G., Sala, O.E., Lauenroth, W.K. & Burke, I.C. (1998). Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications*, **8**: 194–206.
- Paulsen Jr. H.A. & Ares, F.N. (1962). Grazing values and management of black grama and tobosa grasslands and associated shrub ranges of the Southwest. *U.S. Department of Agriculture Technical Bulletin No. 1270*, 56 pp.
- Peters, D.P.C. (2000a). Plant species dominance and disturbance at a grassland–shrubland ecotone. *Bulletin of the Ecological Society of America*, **81**: 175.
- Peters, D.P.C. (2000b). Climatic variation and simulated patterns in seedling establishment of two dominant grasses at a semiarid–arid grassland ecotone. *Journal of Vegetation Science*, **11**: 493–504.
- Peters, D.P.C. (in press). Plant species dominance at a grassland–shrubland ecotone: an individual-based gap dynamics model of herbaceous and woody species. *Ecological Modelling*.
- Qian, H., Klinka, K. & Sivak, B. (1997). Diversity of the understory vascular vegetation in 40 year-old and old-growth forest stands on Vancouver Island, British Columbia. *Journal of Vegetation Science*, **8**: 773–780.
- Rice, B. & Westoby, M. (1983). Plant species richness at the 0.1 hectare scale in Australian vegetation compared to other continents. *Vegetatio*, **52**: 129–140.
- Ripley, E.A. (1992). Grassland climate. In: Coupland, R.T. (Ed.), *Natural Grasslands. Ecosystems of the World*, Vol. 8A, pp. 7–24. Amsterdam: Elsevier Science Publishers, 469 pp.
- Risser, P.G. (1995). The status of the science examining ecotones. *BioScience*, **45**: 318–325.
- Ryerson, D.E. & Parmenter, R.R. (2001). Vegetation change following removal of keystone herbivores from desert grasslands in New Mexico, USA. *Journal of Vegetation Science*, **12**: 167–180.
- Sala, O.E., Lauenroth, W.K. & Parton, W.J. (1992). Long-term soil water dynamics in the shortgrass steppe. *Ecology*, **73**: 1175–1181.
- SAS Institute Inc. (1988). *SAS/STAT User's Guide*, Release 6.03. Cary, NC: SAS Institute Inc.
- Schmutz, E.M., Smith, E.L., Odgen, P.R., Cox, M.L., Klemmedson, J.O., Norris, J.J. & Fierro, L.C. (1992). Desert grassland. In: Coupland, R.T. (Ed.), *Natural Grasslands. Ecosystems of the World*, Vol. 8A, pp. 337–362. Amsterdam: Elsevier Scientific Press, 469 pp.
- Shmida, A. (1985). Biogeography of the desert flora. In: Evenari, M., Noy-Meir, I. & Goodall, D.W. (Eds), *Hot Deserts and Arid Shrublands. Ecosystems of the World*, Vol. 12A, pp. 23–77. Amsterdam: Elsevier, 365 pp.
- Shmida, A. & Wilson, M.V. (1985). Biological determinants of species diversity. *Journal of Biogeography*, **12**: 1–20.
- Sims, P.L. & Singh, J.S. (1978). The structure and function of ten western North American grasslands. III. Net primary production, turnover and efficiencies of energy capture and water use. *Journal of Ecology*, **66**: 573–597.
- Singh, S.P., Bourgeron, P. & Lauenroth, W.K. (1996). Plant species richness and species–area relations in a shortgrass steppe in Colorado. *Journal of Vegetation Science*, **7**: 645–650.
- Sokal, R.R. & Rohlf, F.J. (1969). *Biometry. The Principles and Practice of Statistics in Biological Research*. San Francisco: W.H. Freeman and Company. 776 pp.
- Solomon, A.M. (1986). Transient response of forests to CO<sub>2</sub> induced climate change: simulation modeling experiments in eastern North America. *Oecologia*, **68**: 567–579.
- Stohlgren, T.J., Bull, K.A. & Otsuki, Y. (1998). Comparison of rangeland vegetation sampling techniques in the Central Grasslands. *Journal of Range Management*, **51**: 164–172.
- USDA NRCS (1999). *The PLANTS database*. (<http://plants.usda.gov/plants>). Baton Rouge, LA: U.S.A. National Plant DataCenter.
- Ward, D. & Olsvig-Whittaker, L. (1993). Plant species diversity at the junction of two desert biogeographic zones. *Biodiversity Letters*, **1**: 172–185.
- Whittaker, R.H. (1972). Evolution and measurement of species diversity. *Taxon*, **21**: 213–251.
- Wright, D.H. (1983). Species–energy theory: an extension of species–area theory. *Oikos*, **41**: 496–506.
- Wright, D.H., Currie, D.J. & Maurer, B.A. (1993). Energy supply and patterns of species richness on local and regional scales. In: Ricklefs, R.E. & Schluter, D. (Eds), *Species Diversity in Ecological Communities*, pp. 66–76. Chicago: The University of Chicago Press, 414 pp.

**Appendix** Genus, species and family name of plants found within a 50 ha area at each of three sites (SGS = Shortgrass Steppe, SGS/CD = transition zone, CD = Chihuahuan Desert Grassland). Three species at the SGS/CD and three at the CD were unidentified

Species name	Family	SGS	SGS/CD	CD
<i>C<sub>3</sub> annual forbs</i>				
<i>Chenopodium leptophyllum</i>	Chenopodiaceae	×		
<i>Ipomoea costellata</i>	Convolvulaceae		×	
<i>Ipomopsis laxiflora</i>	Polemoniaceae	×		
<i>Lappula occidentalis</i> var. <i>occidentalis</i>	Boraginaceae	×		
<i>Lepidium densiflorum</i>	Brassicaceae	×		
<i>Lupinus pusillus</i>	Fabaceae	×		
<i>Nama hispidus</i>	Hydrophyllaceae		×	
<i>Oenothera</i> spp.	Onagraceae	×	×	
<i>Plantago patagonica</i>	Plantaginaceae	×		
<i>Proboscidea parviflora</i>	Martyniaceae		×	×
<i>C<sub>4</sub> annual forbs</i>				
<i>Amaranthus fimbriatus</i>	Amaranthaceae		×	
<i>Boerhavia spicata</i>	Nyctaginaceae		×	
<i>Chamaesyce glyptosperma</i>	Euphorbiaceae	×		
<i>Chamaesyce revoluta</i>	Euphorbiaceae		×	
<i>Chamaesyce serpyllifolia</i>	Euphorbiaceae		×	×
<i>Chamaesyce serrula</i>	Euphorbiaceae		×	×
<i>Euphorbia dentata</i>	Euphorbiaceae		×	×
<i>Kallstroemia parviflora</i>	Zygophyllaceae		×	×
<i>Kallstroemia</i> spp.	Zygophyllaceae			×
<i>Machaeranthera tanacetifolia</i>	Asteraceae	×		
<i>Mollugo cerviana</i>	Aizoaceae		×	
<i>Pectis angustifolia</i>	Asteraceae		×	
<i>Pectis papposa</i>	Asteraceae			×
<i>Portulaca halimoides</i>	Portulacaceae			×
<i>Portulaca oleracea</i>	Portulacaceae		×	×
<i>Portulaca parvula</i>	Portulacaceae		×	
<i>Portulaca</i> sp.	Portulacaceae	×		
<i>Salsola kali</i>	Chenopodiaceae		×	×
<i>Tidestromia lanuginosa</i>	Amaranthaceae		×	×
<i>Tribulus terrestris</i>	Zygophyllaceae			×
<i>C<sub>3</sub> perennial forbs</i>				
<i>Acourtia nana</i>	Asteraceae			×
<i>Allium textile</i>	Liliaceae	×		
<i>Astragalus adsurgens</i>	Fabaceae	×		
<i>Astragalus flexuosus</i>	Fabaceae	×		
<i>Astragalus lotiflorus</i>	Fabaceae	×		
<i>Astragalus mollissimus</i>	Fabaceae	×		
<i>Astragalus</i> spp.	Fabaceae		×	
<i>Bahia absinthifolia</i>	Asteraceae			×
<i>Caesalpinia drepanocarpa</i>	Fabaceae		×	×
<i>Caesalpinia jamesii</i>	Fabaceae		×	
<i>Chaetopappa ericoides</i>	Asteraceae		×	
<i>Cirsium</i> sp.	Asteraceae	×		
<i>Convolvulus</i> sp.	Convolvulaceae	×		
<i>Croton pottsii</i>	Euphorbiaceae			×

## Appendix (Continued).

Species name	Family	SGS	SGS/CD	CD
<i>Cryptantha cinerea</i> var. <i>jamesii</i>	Boraginaceae	×		
<i>Cymopterus acaulis</i>	Apiaceae	×		
<i>Dalea candida</i>	Fabaceae	×		
<i>Erigeron</i> sp.	Asteraceae	×		
<i>Evolvulus nuttallianus</i>	Convolvulaceae	×	×	×
<i>Gaura coccinea</i>	Onagraceae	×		
<i>Glandularia wrightii</i>	Verbenaceae		×	
<i>Hybanthus verticillatus</i>	Violaceae			×
<i>Lesquerella ludoviciana</i>	Brassicaceae	×		
<i>Leucocrinum montanum</i>	Liliaceae	×		
<i>Lithospermum incisum</i>	Boraginaceae	×		
<i>Machaeranthera pinnaefitida</i>	Asteraceae		×	×
<i>Orobanche fasciculata</i> *	Orobanchaceae	×		
<i>Oxytropis</i> sp.	Fabaceae	×		
<i>Penstemon albidus</i>	Scrophulariaceae	×		
<i>Picradeniopsis oppositifolia</i>	Asteraceae	×		
<i>Potentilla</i> sp.	Rosaceae	×		
<i>Psilostrophe tagetina</i>	Asteraceae		×	×
<i>Sarcostemma cynanchoides</i>	Asclepiadaceae			×
<i>Scutellaria brittonii</i>	Lamiaceae	×		
<i>Senecio tridenticulatus</i>	Asteraceae	×		
<i>Solanum elaeagnifolium</i>	Solanaceae		×	×
<i>Sphaeralcea coccinea</i>	Malvaceae	×		
<i>Sphaeralcea hastulata</i>	Malvaceae		×	×
<i>Sphaeralcea wrightii</i>	Malvaceae		×	
<i>Talinum aurantiacum</i>	Portulacaceae			×
<i>Talinum parviflorum</i>	Portulacaceae	×		
<i>Tetradlea coulteri</i>	Verbenaceae			×
<i>Thelosperma filifolium</i>	Asteraceae	×		
<i>Tragopogon dubius</i>	Asteraceae	×		
<i>Viola nuttallii</i>	Violaceae	×		
<i>Zinnia grandiflora</i>	Asteraceae		×	×
<i>C</i> <sub>4</sub> perennial forbs				
<i>Allionia incarnata</i>	Nyctaginaceae			×
<i>Ammocodon chenopodioides</i>	Nyctaginaceae			×
<i>Chamaesyce albomarginata</i>	Euphorbiaceae		×	×
<i>Chamaesyce micromera</i>	Euphorbiaceae			×
<i>Gaillardia pinnatifitida</i>	Asteraceae		×	
<i>Heterotheca villosa</i>	Asteraceae	×		
<i>Hymenopappus filifolius</i>	Asteraceae	×	×	
<i>Liatris punctata</i>	Asteraceae	×		
<i>Lygodesmia juncea</i>	Asteraceae	×		
<i>Mirabilis nyctaginea</i>	Nyctaginaceae	×		
<i>Oenothera coronopifolia</i>	Onagraceae	×		
<i>Psoralidium tenuiflorum</i>	Fabaceae	×		
<i>Sophora nuttalliana</i>	Fabaceae	×		
<i>Verbena bracteata</i>	Verbenaceae	×		
<i>C</i> <sub>3</sub> annual grass				
<i>Vulpia octoflora</i>	Poaceae	×		
<i>C</i> <sub>4</sub> annual grasses				
<i>Aristida adscensionis</i>	Poaceae		×	×
<i>Bouteloua aristidoides</i>	Poaceae			×

**Appendix** (Continued).

Species name	Family	SGS	SGS/CD	CD
<i>Bouteloua barbata</i>	Poaceae		×	×
<i>Brachiaria arizonica</i>	Poaceae			×
<i>Monroa squarrosa</i>	Poaceae	×	×	
<i>Panicum hirticaule</i>	Poaceae			×
<i>Tragus berteronianus</i>	Poaceae			×
<i>C<sub>3</sub> perennial grasses/graminoids</i>				
<i>Carex eleocharis</i>	Cyperaceae	×		
<i>Carex</i> sp.	Cyperaceae	×		
<i>Elymus elymoides</i>	Poaceae	×		
<i>Pascopyrum smithii</i>	Poaceae	×		
<i>C<sub>4</sub> perennial grasses/graminoids</i>				
<i>Aristida purpurea</i>	Poaceae	×	×	×
<i>Bouteloua eriopoda</i>	Poaceae		×	×
<i>Bouteloua gracilis</i>	Poaceae	×	×	
<i>Buchloe dactyloides</i>	Poaceae	×		
<i>Enneapogon desvauxii</i>	Poaceae			×
<i>Erioneuron pulchellum</i>	Poaceae		×	×
<i>Muhlenbergia porteri</i>	Poaceae			×
<i>Muhlenbergia torreyi</i>	Poaceae	×	×	
<i>Pleuraphis jamesii</i>	Poaceae		×	
<i>Pleuraphis mutica</i>	Poaceae			×
<i>Schedonnardus paniculatus</i>	Poaceae	×		
<i>Sporobolus cryptandrus</i>	Poaceae	×	×	
<i>Sporobolus flexuosus</i>	Poaceae		×	×
<i>Sporobolus contractus</i>	Poaceae		×	×
<i>C<sub>3</sub> shrubs/subshrubs</i>				
<i>Artemisia frigida</i>	Asteraceae	×		
<i>Ephedra torreyana</i>	Ephedraceae		×	
<i>Ephedra trifurca</i>	Ephedraceae			×
<i>Gutierrezia sarothrea</i>	Asteraceae	×	×	×
<i>Prosopis glandulosa</i>	Mimosaceae			×
<i>Senecio</i> sp.	Asteraceae		×	
<i>Yucca elata</i>	Agavaceae			×
<i>Yucca glauca</i>	Agavaceae		×	
<i>C<sub>4</sub> shrubs/subshrubs</i>				
<i>Atriplex canescens</i>	Chenopodiaceae	×	×	
<i>Ericameria nauseosa</i>	Asteraceae	×		
<i>Eriogonum effusum</i>	Polygonaceae	×		
<i>CAM succulents</i>				
<i>Echinocereus viridiflorus</i>	Cactaceae	×		
<i>Escobaria vivipara</i>	Cactaceae	×		
<i>Mammillaria</i> sp.	Cactaceae			×
<i>Opuntia clavata</i>	Cactaceae		×	
<i>Opuntia imbricata</i>	Cactaceae		×	×
<i>Opuntia phaeacantha</i>	Cactaceae		×	×
<i>Opuntia polyacantha</i>	Cactaceae	×		

\*This species is a non-photosynthetic plant associated with *Artemisia frigida*.