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## Heterogeneity in shortgrass prairie vegetation: the role of playa lakes

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**Abstract.** We examined the role of playa lakes in promoting regional heterogeneity on the southern High Plains. The goals of this paper were to: (1) describe vegetation types and zonation patterns within playas, (2) evaluate patterns of species distribution and abundance within and among playas, and (3) assess patterns of heterogeneity within and among playas on a portion of the southern High Plains. Perennial grasses were the most abundant species in playa vegetation. Playa vegetation exhibited distinct and repeatable vegetation zones at the majority of sites, but the number of distinct zones varied from site to site. *Agropyron smithii*, *Buchloë dactyloides*, and *Panicum obtusum* were the most important species of playa interior zones, and *Bouteloua gracilis*, *Buchloë dactyloides*, and *Schedonnardus paniculatus* were important upland species outside of playas. Species distribution and abundance were positively correlated at 38 of 40 sites. The distributions of species occurrences among sites were unimodal both locally and regionally. The degree of heterogeneity varied from playa to playa. Local heterogeneity within playas was found to increase regional heterogeneity; therefore, playas increase both local and regional heterogeneity of vegetation. Long-term monitoring will be necessary to understand the spatial and temporal response of vegetation within and among playas to stochastic climatic factors on the southern High Plains of North America.

**Keywords:** Classification; Distribution abundance relation; Dissimilarity; Gradient Analysis; Ordination; Perennial Grass.

**Nomenclature:** Barkley (1986).

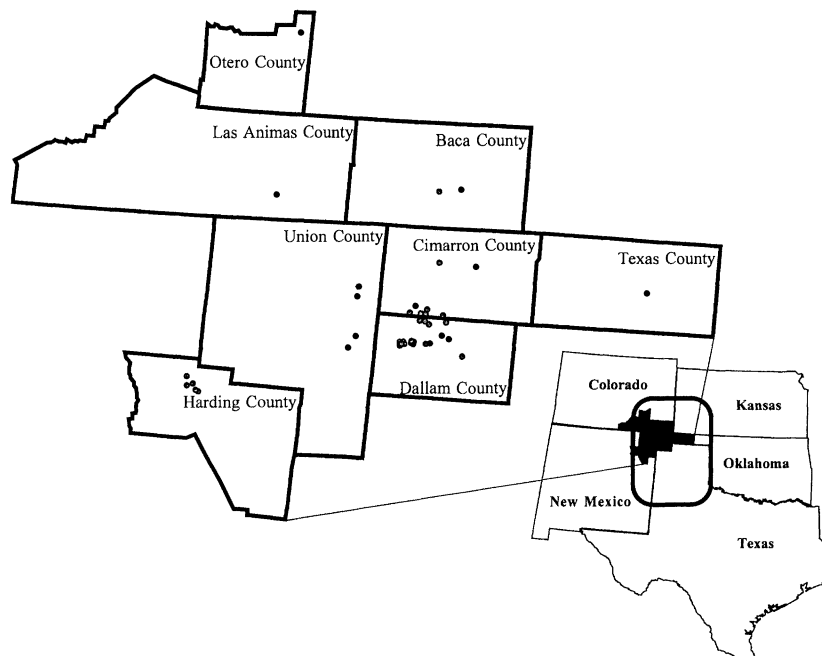
### Introduction

Environmental heterogeneity affects community structure and species diversity at many spatial and temporal scales (Allen & Starr 1982; Levin 1984; Pickett & White 1985; Legendre & Fortin 1989; Kolasa & Rollo

1991). Community heterogeneity may be defined as spatial variation in species composition within or between communities (Collins 1992). Heterogeneity results from the non-random distribution of species in response to variable resource distribution within spatially complex landscapes (Austin 1990; Palmer & Dixon 1990; Milne 1991). Because species tend to respond individually to complex environmental gradients (Gleason 1926; Curtis 1959; Whittaker & Levin 1977), environmental heterogeneity affects patterns of species distribution and abundance at different spatial scales (Levins 1969; Hanski 1982; Brown 1984).

North American grasslands are heterogeneous at several scales of resolution. Grassland heterogeneity is influenced by climate at the continental scale, effecting longitudinal and latitudinal patterns of species distribution. The interactive effects of topography, soils, and fire yield heterogeneity across landscapes (White & Glenn-Lewin 1984; Belsky 1988; Collins & Glenn 1988; Collins 1992). Numerous factors, such as grazing, fossorial mammals, and wallowing by bison, induce fine-scale heterogeneity in grasslands (Hobbs & Hobbs 1987; Collins & Glenn 1988; Gibson 1989; Uno 1989).

Moisture gradients commonly add to local variability in plant communities, yet the impacts of wetlands on local and regional heterogeneity have received limited attention in grasslands (Umbanhowar 1992). Abundant wetlands, including playas, wallows, seeps, springs, and potholes, are scattered throughout the North American grassland region (Dix & Smeins 1967; Collins & Uno 1983; Bolen et al. 1989). Playas, in particular, are widespread wetland features within the relatively arid southern High Plains. Like other wetland habitats, playas form discrete landscape patches that may enhance heterogeneity and species diversity (Johnston & Naiman 1990). Playas are relatively large circular depressions



**Fig. 1.** Approximate location of quantitatively sampled playa sites. The bold line indicates the extent of the playa lakes region.

(mean size of 6.3 ha) that retain moisture, especially during the spring rainy season (Haukos & Smith 1992). Because of their large size and variation in moisture regimes, playas contain internal gradients supporting vegetation that differs from that of the surrounding shortgrass steppe (Reed 1930; Parker & Whitfield 1941; Penfound 1953; Guthery et al. 1982).

In addition to playa moisture gradients, other factors affect grassland heterogeneity across the Great Plains. Although fire is considered to be a common disturbance in mesic prairies and grazing by ungulates occurs throughout the plains, their impact on grassland heterogeneity decreases from east to west (Anderson 1990; Milchunas & Lauenroth 1993). Given that fire is uncommon and grazing has a limited impact on heterogeneity in the arid shortgrass steppe, playas may serve as the primary source of environmental and compositional heterogeneity in this arid grassland region.

Keddy (1991) has proposed the use of environmental gradients as tools for the study of heterogeneity. In this study, we used clearly defined moisture gradients within playas to provide a framework for the analysis of vegetation heterogeneity both within and among playas (Spence 1982; Keddy 1983, 1991). This paper has three goals: (1) the description of vegetation types and zonation patterns within playas, (2) the characterization of patterns of species distribution and abundance within and among playas, and (3) assessment of patterns of heterogeneity within and among playas within a portion of the southern High Plains.

## Methods

### *Study area*

Playas are confined catchments formed by a process of sediment solution and deflation (Osterkamp & Wood 1987; Bolen et al. 1989). Soils in the playa interior are typically Randall Clays, grading into more porous and varied soil types in the adjacent uplands (Guthery et al. 1982; Haukos & Smith 1992).

We sampled playas in Baca, Las Animas, and Otero counties, Colorado; Harding and Union counties, New Mexico; Cimarron and Texas counties, Oklahoma; and Dallam County, Texas (Fig. 1). Annual precipitation in the study area ranges from 330 - 450 mm and is exceeded by an annual evaporation of 2000 - 2500 mm (Haukos & Smith 1992). The majority of study sites was located on three United States Department of Agriculture National Grasslands: The Comanche in Colorado, the Kiowa in New Mexico, and the Rita Blanca in Oklahoma and Texas. All sites in these National Grasslands had a history of cattle grazing, but grazing pressure was not quantified in this study. Most of the playas studied were vegetated by perennial native grass species, but two fallow playas and one playa modified to retain irrigation runoff were included for comparison.

### *Data collection*

Data were collected during the 1992 and 1993 field seasons. Two data sets were used in this study. The

primary data set was collected from 20 playas that were each sampled using one belt-transect of contiguous quadrats. The length of belt-transects ranged from 50 to 220 quadrats (12.5 to 54 m) depending on playa size. Belt-transects originated from the center of a playa and extended in a randomly determined compass direction into the adjacent upland vegetation. Quadrat dimensions were 0.25 m  $\times$  0.75 m. The long axis of each quadrat was placed perpendicular to the belt-transect. Each species occurring in a quadrat was recorded and percent cover was visually estimated to the nearest 5 %. These data were analyzed to determine whether playa lakes exhibit zonation patterns and how those patterns affect heterogeneity in shortgrass prairie vegetation.

A second data set, consisting of 20 different playas sampled with randomly placed quadrats, was collected to be used for vegetation analyses in conjunction with the belt-transect data. Quadrat dimensions and cover estimation were as described above. The number of quadrats per playa ranged from 20 to 80 depending on the size of the playa. Only vegetation inside playas was sampled with random quadrats. Playa interior vegetation was defined as that vegetation occurring on the Randall clay soils of the playa basin floor. The extent of Randall clay soils in each playa was estimated from the United States Soils Conservation Service Soil Survey for the appropriate county.

#### *Data analysis*

*Within-playa variation in vegetation.* The following analyses were used to characterize and quantify the distribution of species and plant community types in playas. Data for each of the playas sampled with belt-transects were analyzed using TWINSpan (Hill 1979a) to (1) differentiate upland from interior vegetation and (2) determine the number and composition of vegetation zones. The smallest number of statistically significant groups in the TWINSpan classification was determined using Multiple Response Permutation Procedures (MRPP), a non-parametric multivariate statistical technique suitable for determining significant differences among pre-defined groups (Biondini et al. 1985; Gurevitch & Collins 1994).

A runs test (Sokal & Rohlf 1995) was conducted to determine if quadrats representing particular TWINSpan clusters (e.g. vegetation zones) were randomly distributed along each belt-transect. A non-random distribution of community-types, defined by the TWINSpan clusters, along belt-transects would suggest that zonation of vegetation occurs in playas, whereas random patterns would suggest a lack of zonation.

The composition of vegetation for playas sampled with random quadrats was also determined using

TWINSpan. Multiple Response Permutation Procedure was again used to ascertain the smallest number of statistically distinguishable vegetation types for each playa. The results of these analyses represent the composition of playa interior vegetation only.

Dominant species are often more widely distributed than rare species at biogeographic scales (Hengeveld & Haeck 1982; Hanski 1982; Kolasa 1989). To analyze whether this pattern occurs at the scale of individual playas, we defined a species distribution as the number of quadrats along the belt-transect in which that species occurred. Abundance was defined as the average percent cover of a species in the playa. Linear regression was used to examine the relationship between species distribution and abundance.

Local or within-playa heterogeneity was quantified using average percent dissimilarity (PD) among quadrats (Inouye et al. 1987; Collins 1992). Both randomly sampled playas and the interior clusters of playas sampled with belt-transects were included in these analyses. Heterogeneity values from belt-transects and randomly sampled playas were not significantly different ( $\bar{x}_{\text{belt}} = 0.55$ ,  $\bar{x}_{\text{random}} = 0.67$ ,  $t = -1.65$ ,  $p > 0.05$ ), thus allowing us to pool the two data sets. Multiple regression was then used to determine if within-playa heterogeneity was a function of species richness and/or playa area. Linear regression was also used to determine if species richness (e.g. the total number number of species in a sample) was a function of playa area. These analyses included all permutations of log transformed area and/or species richness values (Connor & McCoy 1979).

#### *Among-playa variation in vegetation*

Among-playa analyses were used to explore playa vegetation patterns and how playas affect heterogeneity at the regional scale. Detrended correspondence analysis (DCA; Hill 1979b; Hill & Gauch 1980; Økland 1996) was used to describe regional variation in playa vegetation. A species-by-vegetation (e.g. interior or upland) matrix of average cover values was compiled from both the belt-transect and randomly sampled playas and analyzed using DECORANA (Hill 1979b). This matrix was also analyzed with TWINSpan to assist interpretation of the ordination diagram. The resulting matrix was composed of 40 interior vegetation samples (from both random and belt transect data) and 20 exterior vegetation clusters (from belt transect data alone). Three playas were removed from the DCA analysis to reduce outlier effects. The option for downweighting rare species was used for this analysis.

The relationship between regional species distribution and average abundance was analyzed to determine whether or not dominant playa and upland plant species were more broadly distributed than rare species as

**Table 1.** Vegetation zonation patterns and interior vegetation types for 40 playas sampled using belt-transects and randomly placed quadrats. Datasets from each playa were analyzed using TWINSpan and MRPP. Zone number represents the position of the vegetation type on the belt-transect from the center of a playa (i.e., zone 1 is interior playa vegetation, zone 2 is the interior edge, zone 3 the upland edge and zone 4 is upland vegetation). Significance levels for runs tests are: \* =  $p < 0.05$ , \*\* =  $p < 0.0001$ , IS = Insufficient number of runs for test. Group numbers for randomly sampled playas do not necessarily represent the location of a vegetation type along the environmental gradient. RB = playas on the Rita Blanca National Grassland, K = sites on the Kiowa National Grassland.

Belt-Transect Sampled Playas			
Zone 1	Zone 2	Zone 3	Zone 4
RB21A** <i>Buchloë dactyloides</i> - <i>Agropyron smithii</i>	<i>Hilaria jamesii</i> - <i>Buchloë dactyloides</i>	<i>Bouteloua gracilis</i> - <i>Kochia scoparia</i>	<i>Bouteloua gracilis</i>
RB21B** <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Ratibida tagetes</i>	<i>Buchloë dactyloides</i>	<i>Bouteloua gracilis</i> - <i>Ambrosia grayii</i>
RB21D <sup>IS</sup> <i>Agropyron smithii</i>			<i>Bouteloua gracilis</i>
RB22A <sup>IS</sup> <i>Agropyron smithii</i>			<i>Schedonardus paniculatus</i>
RB228* <i>Agropyron smithii</i>	<i>Buchloë dactyloides</i> - <i>Agropyron smithii</i>	<i>Astragalus mollissimus</i> - <i>Ratibida tagetes</i>	<i>Bouteloua gracilis</i>
RB22C <sup>IS</sup> <i>Agropyron smithii</i>		<i>Aristida oligantha</i>	<i>Bouteloua gracilis</i>
RB22D** <i>Chenopodium album</i> - <i>Xanthium strumarium</i>	<i>Agropyron smithii</i>	<i>Buchloë dactyloides</i>	<i>Bouteloua gracilis</i>
RB44** <i>Agropyron smithii</i>	<i>Lippia cuneifolia</i>	<i>Sporobolus cryptandrus</i> - <i>Bouteloua gracilis</i>	<i>Bouteloua curtipendula</i>
RB46** <i>Agropyron smithii</i> - <i>Panicum obtusum</i>	<i>Panicum obtusum</i> - <i>Agropyron smithii</i>	<i>Buchloë dactyloides</i> - <i>Panicum obtusum</i>	<i>Buchloë dactyloides</i>
RB48** <i>Agropyron smithii</i>	<i>Lippia cuneifolia</i>		<i>Kochia scoparia</i>
RB70** <i>Ambrosia grayii</i> - <i>Polygonum pensylvanicum</i>	<i>Euphorbia marginata</i> - <i>Ambrosia grayii</i>	<i>Agropyron smithii</i>	<i>Buchloë dactyloides</i>
RB136** <i>Kochia scoparia</i>	<i>Panicum obtusum</i>	<i>Agropyron smithii</i>	<i>Sphaeralcea coccinea</i>
K14** <i>Sida hederacea</i> - <i>Lippia cuneifolia</i>	<i>Buchloë dactyloides</i>		<i>Buchloë dactyloides</i>
K36** <i>Ambrosia grayii</i> - <i>Polygonum pensylvanicum</i>	<i>Agropyron smithii</i>	<i>Agropyron smithii</i>	<i>Bouteloua gracilis</i> - <i>Agropyron smithii</i>
K125** <i>Ambrosia grayii</i>	<i>Buchloë dactyloides</i>	<i>Buchloë dactyloides</i>	<i>Buchloë dactyloides</i>
K127A** <i>Agropyron smithii</i> - <i>Iva axillaris</i>	<i>Agropyron smithii</i>	<i>Buchloë dactyloides</i> - <i>Agropyron smithii</i>	<i>Sporobolus cryptandrus</i>
K127B <sup>IS</sup> <i>Buchloë dactyloides</i>	<i>Buchloë dactyloides</i>		<i>Bouteloua gracilis</i>
K128** <i>Agropyron smithii</i>	<i>Lippia cuneifolia</i> - <i>Ambrosia grayii</i>	<i>Lippia cuneifolia</i> - <i>Agropyron smithii</i>	<i>Buchloë dactyloides</i> - <i>Chenopodium ambrosioides</i>
K129 <sup>IS</sup> <i>Agropyron smithii</i>	<i>Buchloë dactyloides</i>		<i>Bouteloua gracilis</i> - <i>Buchloë dactyloides</i>
GOLD** <i>Xanthium strumarium</i>	<i>Euphorbia marginata</i> - <i>X. strumarium</i>	<i>Lippia cuneifolia</i> - <i>Agropyron smithii</i>	<i>Buchloë dactyloides</i>
Randomly Sampled Playas			
Group 1	Group 2	Group 3	
Edler Lake <i>Buchloë dactyloides</i>	<i>Agropyron smithii</i>		
Guymon Lake <i>Polygonum coccinea</i> - <i>Amaranthus graecizans</i>	<i>Polygonum lapathifolium</i>	<i>Polygonum pensylvanicum</i> - <i>Rumex maritimus</i>	
Las Animas Lake <i>Agropyron smithii</i>			
Murphy Lake <i>Lippia cuneifolia</i> - <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Ambrosia grayii</i>	<i>Panicum obtusum</i>	
Otero Lake <i>Chenopodium rubrum</i>	<i>Lippia cuneifolia</i> - <i>Verbena bracteata</i>		
Reader Lake <i>Agropyron smithii</i> - <i>Buchloë dactyloides</i>			
Slimp Lake <i>Ambrosia grayii</i> - <i>Rorippia sinuata</i>	<i>Ambrosia grayii</i> - <i>Kochia scoparia</i>		
Swinburne Lake <i>Distichlis spicata</i>	<i>Distichlis spicata</i> - <i>Agropyron smithii</i>		
Uncle George Lake <i>Lippia cuneifolia</i>	<i>Oenothera albicaulis</i> - <i>Potentilla norvegica</i>		
RB21C <i>Panicum obtusum</i>	<i>Ambrosia grayii</i> - <i>Panicum obtusum</i>		
RB21E <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Lippia cuneifolia</i>		
RB35A <i>Agropyron smithii</i> - <i>Buchloë dactyloides</i>	<i>Buchloë dactyloides</i>	<i>Sporobolus cryptandrus</i> - <i>Amaranthus retroflexus</i>	
RB35B <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Salsola kali</i>		
RB47 <i>Agropyron smithii</i>	<i>Distichlis spicata</i>	<i>Agropyron smithii</i> - <i>Sporobolus cryptandrus</i>	
RB63 <i>Agropyron smithii</i> - <i>Lippia cuneifolia</i>	<i>Ambrosia grayii</i>	<i>Panicum obtusum</i>	
RB125 <i>Agropyron smithii</i> - <i>Buchloë dactyloides</i>	<i>Agropyron smithii</i> - <i>Lippia cuneifolia</i>		
RB137 <i>Hordeum jubatum</i> - <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Ambrosia grayii</i>		
RB136A <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Lippia cuneifolia</i>		
RB141 <i>Agropyron smithii</i>	<i>Agropyron smithii</i> - <i>Ambrosia grayii</i>		

hypothesized by Hengeveld & Haack (1982). Regional distribution was determined by treating each playa as a sample unit and counting the number of occurrences for each species among playas. Interior and upland species distributions were analyzed separately in this manner. A Kolmogorov-Smirnov two-sample test (Sokal & Rohlf

1995) was used to determine if species distributions of interior and upland vegetation were statistically different. Abundance was defined as the percent cover of a species averaged by the number of occupied playas. Linear regression was used to examine the relationship between species distribution and abundance.

Previous studies have suggested that local patterns of heterogeneity do not necessarily reflect regional patterns of heterogeneity (Glenn et al. 1992). We examined patterns of heterogeneity among playas using PD (Inouye et al. 1987; Collins 1992). Percent dissimilarity was calculated for six matrices derived from results of the earlier TWINSpan analysis. Percent dissimilarity was first calculated for interior and upland vegetation using separate species-by-site matrices. A *t*-test was used to determine whether interior and upland PD values were statistically different. Four matrices were then compiled to examine regional heterogeneity within playa vegetation zones. Since not all playas had four vegetation zones, matrices were unequal in size. These matrices consisted of species-by-vegetation zone data for individual vegetation zones and were analyzed using PD. Multiple regression was used to determine if heterogeneity was a function of species richness, evenness, diversity or playa area. Species diversity was calculated using the Shannon-Wiener Index (Magurran 1988). Evenness was calculated according to Pielou (1969). Statistical differences in heterogeneity among vegetation zones were determined by analysis of variance.

## Results

A total of 75 species was found in the 40 playas sampled. Richness ranged from three species at Edler Lake to 26 species at Kiowa 127B. Edler Lake also had the lowest evenness and Shannon diversity values. The area of playas in this study ranged from 8 to 80 hectares ( $\bar{x} = 37.6$ ) in this study. There was no statistically significant relationships between playa area and species richness, evenness, or diversity. To some extent this may be a function of sample size because there was a significant positive relationship between number of samples and species richness ( $r^2 = 0.31$ ;  $p < 0.05$ ). In order to account for the effect of sample size, residuals were collected from a regression analysis of species richness and number of quadrats. These were analyzed using Kendall's rank correlation coefficient to determine if there was a relationship between residuals and playa area. Again, there was no relationship between species richness and playa area ( $n = 40$ ;  $\tau = 0.079$ ;  $p > 0.05$ ).

### Within-playa variation

#### Vegetation analysis

Perennial grasses were the most common dominant species in both upland and interior vegetation, based on analysis of belt-transect data. Interior vegetation was dominated by three species of grasses: *Agropyron smithii*, *Buchloë dactyloides* and *Panicum obtusum*. *Ambrosia*

*grayii*, *Euphorbia marginata* and *Lippia cuneifolia* were important forb components of interior vegetation. *Bouteloua curtipendula*, *Bouteloua gracilis*, *Buchloë dactyloides*, *Schedonnardus paniculatus*, and *Sporobolus cryptandrus* were dominant perennial grasses in upland vegetation. Prominent members of the upland forb component included *Ratibida tagetes* and *Sphaeralcea coccinea*.

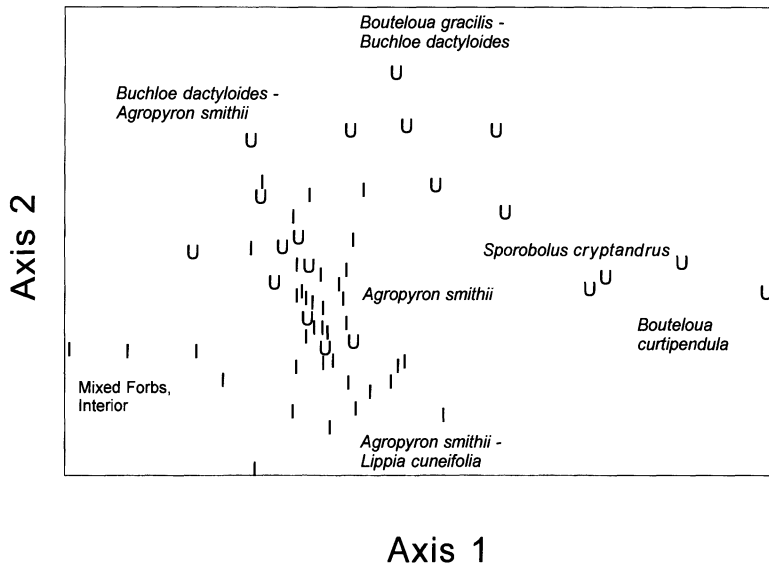
In 18 of the 20 playas sampled, three or four distinct vegetation zones were identified by TWINSpan. Each vegetation zone was assigned a value between 1 and 4 depending on the number of statistically distinct vegetation zones in that playa. This value was then assigned to corresponding quadrats along the belt-transect. Vegetation zones were designated as: zone 1 = interior vegetation, zone 2 = interior-edge vegetation, zone 3 = upland-edge vegetation, and zone 4 = upland vegetation. At the two remaining sites, it was only possible to distinguish interior from upland vegetation. In these two cases, one vegetation type was assigned as interior (zone 1), and the other upland (zone 4).

The dominant species in a zone and the ordering of vegetation zones along belt-transects varied from site to site (Table 1). *Agropyron smithii* and *Buchloë dactyloides* were common dominants in interior zones. The importance of *Agropyron smithii* decreased from interior to upland vegetation. *Buchloë dactyloides* was an important species in interior and upland vegetation zones. In seven playas, zone 1 was dominated by annual forbs. The percentage of vegetation cover was lowest in playa interiors dominated by annual forbs. Important species in the upland vegetation were perennial grasses such as *Bouteloua curtipendula*, *Bouteloua gracilis*, *Schedonnardus paniculatus*, and *Sporobolus cryptandrus*. In the two playas where only interior and upland zones were apparent, *Buchloë dactyloides* and *Schedonnardus paniculatus* were abundant in the upland and playa interior.

Results of the runs tests indicated a non-random distribution of vegetation zones along transects within individual playas. 15 of the 20 playas with suitable sample size had non-random patterns along belt-transects. The remaining five playas did not have sufficient runs to conduct the test. Thus, the generally non-random pattern of assemblage types in quadrats along belt-transects demonstrates that zonation is usually present in most playas.

#### Species distribution and abundance

The majority of species within the playas were infrequent, occurring in less than 10% of the sample quadrats ( $\bar{x} = 6.4$ ;  $n = 39$ ). On the other hand, few species were widely distributed in playas, as would be predicted from the obvious patterns of zonation noted above. Only in



**Fig. 2.** Detrended Correspondence Analysis of playa lake interior and upland vegetation types. I = interior vegetation from individual playas, U = upland vegetation from individual playas.

five of 20 cases did species occur across the entire interior to upland gradient yet few of these species were found in over 90 % of the quadrats. There was a statistically significant and positive relationship between distribution and average abundance at 38 of the 40 sites sampled. Guymon Lake, which received irrigation run-off, and Edler Lake were the exceptions.

#### Heterogeneity

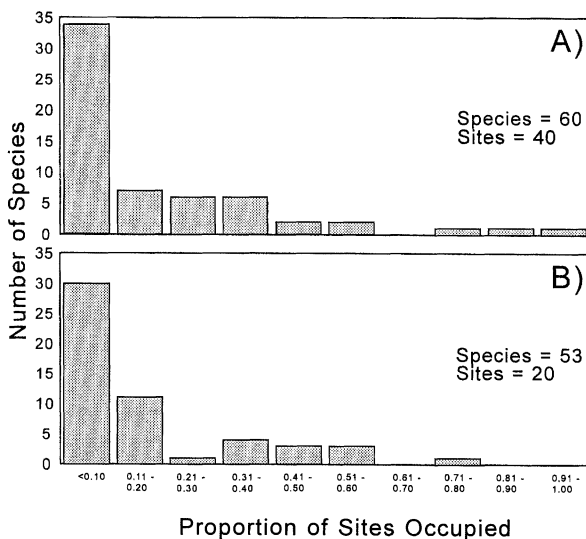
Percent dissimilarity values for the interiors of individual playas ranged from 0.27 to 0.99 ( $\bar{x} = 0.62$ ). There were no statistically significant relationships between heterogeneity scores and playa area, species richness, evenness or diversity.

#### Among-playa variation

##### Vegetation analysis

A matrix of upland-interior vegetation was analyzed to explore large-scale gradients among playas. In the ordination diagram, axis 1 (5.19 SD units) represented a gradient ranging from interior sites characterized by a group of forb species (*Ambrosia grayii*, *Euphorbia marginata*, *Lippia cuneifolia*, *Xanthium strumarium*) to upland sites whose species composition was typical of more mesic mixed-grass prairie (*Bouteloua curtipendula*, *Sporobolus cryptandrus*, *Schedonnardus paniculatus*) (Fig. 2). The prevalence of the latter species, an indicator of disturbance (Barkley 1986), may reflect the effects of cattle on upland vegetation.

Axis 2 of the DCA ordination (3.04 SD units) also separated interior from upland sites (Fig. 2). In this case, interior plots were dominated by *Agropyron smithii* and *Lippia cuneifolia*, whereas the upland vegetation was dominated by species characteristic of the arid shortgrass steppe (*Bouteloua gracilis*, *Buchloe dactyloides*). The shorter gradient length along axis 2 may be the result of the broad distribution of *Agropyron smithii*, a  $C_3$  perennial, or a complex of environmental variables not reflected by axis 1. Likewise, the presence of *Agropyron smithii* in the interior and several upland playa samples



**Fig. 3.** Regional distribution of plant species in playa lakes on the Southern High Plains. A. Regional distribution of playa interior species; B. Regional distribution of upland species. Each playa lake was considered as a sampling unit.

may have produced the clustering of plots in the center of the ordination diagram. Seven clusters were produced by TWINSpan analysis. These seven clusters are represented by the species labels on the ordination diagram.

#### Species distribution and abundance

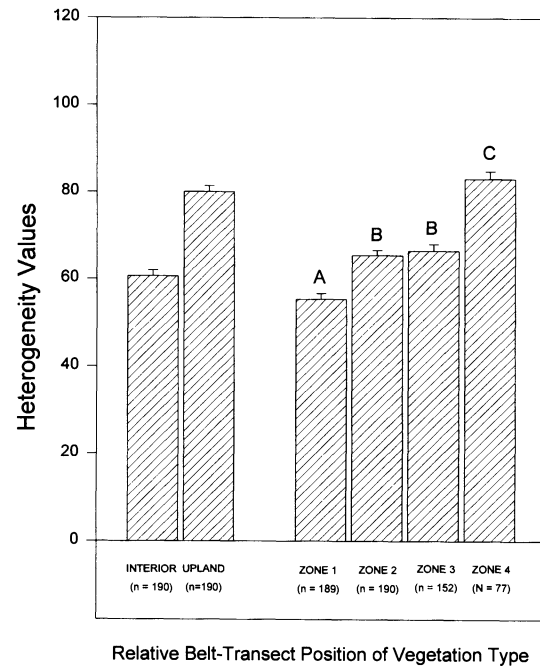
At the regional scale, no species were found in > 90% of the shortgrass prairie uplands. Only *Agropyron smithii* was found in > 95% of playa interiors (Figs. 3a and 3b). Species with intermediate distributions among playa interiors included *Lippia cuneifolia*, *Buchloë dactyloides* and *Oenothera canescens*. *Agropyron smithii* and *Buchloë dactyloides* were dominant or co-dominants in several vegetation zones, and *Lippia cuneifolia* was dominant in one vegetation zone (Table 1). *Oenothera canescens* did not have high abundance scores, but was widely distributed inside playas. Four species with limited distributions were more abundant than *Oenothera canescens* and were dominant in several vegetation types (*Ambrosia grayii*, *Distichlis spicata*, *Kochia scoparia*, and *Panicum obtusum*). The number of sites occupied and average abundance was positively correlated for both interior ( $r^2 = 0.49$ ;  $F = 55.69$ ;  $p < 0.005$ ) and upland ( $r^2 = 0.62$ ;  $F = 85.27$ ;  $p = 0.01$ ) vegetation. The regional distribution of interior species was not significantly different from upland species (KS = 0.11;  $p = 0.73$ ).

#### Heterogeneity

Percent dissimilarity values were significantly greater in upland compared to interior vegetation ( $t = 2.53$ ;  $df = 19$ ;  $p < 0.01$ ). High dominance by *Agropyron smithii* may have reduced overall heterogeneity in the interior of playas. Vegetation heterogeneity increased from interior zone 1 to upland zone 4 (Fig. 4). Again, the upland vegetation (zone 4) was significantly more heterogeneous than the interior zones ( $F = 46.27$ ;  $df = 3, 603$ ;  $p < 0.0001$ ). Zones 1 and 2, in particular, where heterogeneity was lowest, were often strongly dominated by *Agropyron smithii* (Table 1).

#### Discussion

Vegetation zonation, in the form of distinct and repeatable patches of vegetation, was present in the majority of playas. The number of distinct vegetation zones varied from site to site (Table 1) and was not related to the size of a playa. In western Oklahoma, Penfound (1953) identified 13 vegetation associations in playas, nine of which occurred in this study. Three contrasting vegetation zones were identified in a Texas panhandle playa: an *Ambrosia grayii* - *Marsilea vestita*



**Fig. 4.** Heterogeneity values for interior and upland vegetation types and zonal vegetation types from the belt-transect dataset. Interior and upland heterogeneity values were significantly different. Heterogeneity values were significantly different between all zones except zones 2 and 3.

association, a *Vernonia marginata* - *Lippia nodiflora* association, and a zone dominated by *Buchloë dactyloides* (Reed 1930). *Marsilea vestita* and *Vernonia marginata* never occurred together in the playas sampled, nor was either species dominant in any playa sampled. Unlike previous studies (Reed 1930; Parker & Whitfield 1941; Penfound 1953), Haukos & Smith (1994) reported no zonation in Texas panhandle playas.

Anthropogenic changes to playa hydrology most likely account for the disparities between this and other studies (Guthery et al. 1982; Nelson et al. 1983; Tiner 1993; Haukos & Smith 1993, 1994). Many of these studies were conducted in heavily cultivated areas where vegetation composition is affected by irrigation runoff (Haukos & Smith 1992) which favors the establishment of obligate wetland species. The majority of playas in our study were located in rangeland to minimize the impacts of irrigation practices. Only one playa that we sampled received irrigation runoff and *Polygonum lapathifolium* and *Polygonum coccinea* were abundant in that playa.

Species abundance, measured as percent cover, was significantly positively correlated with distribution in 38 of 40 playas. That is, a small number of widely distributed species within playas tended to be dominant



in all zones. The most important species in these playas was the perennial C<sub>3</sub> grass, *Agropyron smithii*. *Buchloë dactyloides* was also a dominant or co-dominant species in many of these playa basins, reflecting its ability to withstand prolonged flooding (Porterfield 1945). These species were also classified as dominants by Parker & Whitfield (1941) in a study of Texas playas. Although patches of locally abundant species did occur in most playas, the pattern within playas conforms to the general biogeographic relationship between distribution and abundance reported for many types of organisms (McNaughton & Wolf 1970; Hengeveld & Haecck 1982; Brown 1984; Kolasa 1989) including wetland vegetation (Hanski et al. 1993).

It is this pattern of low local species richness and high dominance that leads to lower heterogeneity in playas compared to surrounding upland vegetation. High dominance and low diversity in playas may result from the added stress of unpredictable wet-dry cycles in an already arid regional climate. Variation in the strength of this pattern is a function of gradient length (Moore & Keddy 1989). The moisture gradient becomes less influential in shallow or small playas where plants may be responding to the patchy distribution of soil nutrients (Tilman 1982; Belsky 1988; Keddy 1991), rather than soil moisture. In such cases, the similarity between interior and exterior vegetation will increase, and fewer distinct patches or zones will occur in these playas. Steeper moisture gradients will produce the zonation typical of wetland plant communities which will most likely increase local heterogeneity and species richness within each successive zone along the gradient (Spence 1982; Johnson et al. 1987; Mitsch & Gosselink 1993).

Although the steepness of the moisture gradient may vary from one playa to another, playas generally increase local heterogeneity by providing an environment that supports vegetation differing from that in the surrounding arid upland. Variability in both depth and area occupied by individual wetlands fosters local heterogeneity which, in turn, effects regional heterogeneity (Kazmierczak et al. 1995). Playas contribute to regional vegetation heterogeneity in two ways. First, the distribution of species among playas is highly skewed indicating that most species occur in only a few playas. Only three species are widely distributed among playas. Secondly, the degree of variation among playas is relatively high even though it is lower than the surrounding uplands. Percent similarity among playas in the region is, on average, about 60 % (Fig. 4). Therefore, local heterogeneity within playas contributes to regional heterogeneity across this arid grassland system.

The structure of playa vegetation is strongly affected by stochastic precipitation events and local hydrologic inputs. Indeed, Haukos & Smith (1994) noted that

several complete changes in species composition may occur within a playa over a single growing season, although these changes were not described. Species found in the soil seedbank appear to have germination strategies adapted to this stochasticity (Haukos 1991). Although our study represents a static image of playa vegetation in time, a complex scenario of changes in species composition can be envisioned and should serve as the basis for future studies.

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