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Author(s): Scott L. Collins, James A. Bradford, Phillip L. Sims

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Succession and fluctuation in *Artemisia* dominated grassland

Scott L. Collins¹, James A. Bradford² & Phillip L. Sims²

¹*Department of Botany and Microbiology, University of Oklahoma, Norman, OK 73019, USA;* ²*U.S.D.A. Southern Plains Range Research Station, 2000 18th Street, Woodward, OK 73801, USA*

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Abstract

Vegetation dynamics were studied from 1940 to 1978 in two grazed pastures and associated exclosures in sand sagebrush (*Artemisia filifolia*) dominated grassland, western Oklahoma, USA. In both pastures and one exclosure, pattern of vegetation change reflected fluctuation rather than succession. In the other exclosure, the grassland exhibited a directional change from annual grasses and forbs to dominance by perennial grasses. Rate of change was consistent during the 39 year period. Cover of grasses increased more in grazed than ungrazed areas. Grass cover was negatively correlated with high air temperatures early in the growing season. Forb cover remained relatively constant over time and shrub cover peaked during the 1960s. Abundance of annuals and cool season species was positively correlated with rainfall early in the growing season.

Species diversity and richness were lowest in the ungrazed areas, as a result of increased dominance by perennial grasses such as *Schizachyrium scoparium*. In pastures and exclosures, richness was positively correlated with growing season precipitation. Cover of the common species differed among sample areas within years and fluctuated between years. Few general patterns emerged from correlations of environmental variables with cover of individual species. In general, vegetation dynamics in these sand sagebrush grasslands reflect a tradeoff in that total cover changes little over time because the loss of some species is compensated for by increased growth of others. Such trade-offs reflect the individualistic response of the component species within each pasture or exclosure. Although changes in growth form composition were related to climatic fluctuation, broad-scale climatic variables could not successfully predict small-scale patterns of change by individual species over time.

Nomenclature follows Gould (1975), The grasses of Texas, College Station TX, and Waterfall (1972), Keys to the flora of Oklahoma, Stillwater OK.

Introduction

The study of vegetation dynamics has provided one of the most fertile grounds for research in plant ecology (McIntosh 1980; Pickett *et al.* 1987). Vegetation dynamics include *fluctuation*, a reversible change in dominance within a stable species assemblage, and

succession, a more or less directional change in composition and/or dominance (Rabotnov 1974). Much of successional theory has been based on studies of pattern and process in temperate forests (MacMahon 1980; West *et al.* 1981; Finegan 1984), yet the application of forest concepts to non-forest vegetation has met with limited success (Walker 1981; Col-

lins & Adams 1983; Zedler *et al.* 1983). Grasslands, for example, are characterized by a variable climate within and between seasons (Sims *et al.* 1978; Risser *et al.* 1981). Thus, changes in community structure may reflect fluctuations associated with climate rather than succession (Coupland 1974; Rabotnov 1974). Study of vegetation dynamics in grasslands is further confounded by the complexity of natural disturbance regimes (Collins & Uno 1985). For instance, fire and grazing are common disturbances in grasslands but they have differing impacts on grassland composition and structure (Risser & Parton 1982; Collins & Barber 1985; Collins 1987).

Several studies have documented patterns during secondary succession in grassland vegetation (e.g., Bassett 1980; Austin *et al.* 1981; Chew 1982; Reichardt 1982; Collins & Adams 1983; Potvin & Harrison 1984; West *et al.* 1984; Biondini *et al.* 1985). Few generalizations have emerged from these studies, perhaps because vegetation dynamics in arid and semi-arid systems is influenced more by abiotic than biotic factors (MacMahon 1980). For example, Austin *et al.* (1981) indicated that climate had a significant effect on succession in Australian grasslands, and Chew (1982) reported that infrequent climatic events confounded patterns of vegetation change in desert grasslands. Van der Maarel (1981) found a rapid response to wet and dry treatments in dune grasslands. In contrast, West *et al.* (1979, 1984) and Potvin & Harrison (1984) found little correlation between species abundance and precipitation during succession on ungrazed grasslands. Clearly, more information is needed if generalizations about vegetation dynamics in grasslands are to emerge.

The purposes of this study were to (1) document large-scale patterns of fluctuation and succession in the absence of fire on grazed and ungrazed sand sagebrush (*Artemisia filifolia*) dominated grasslands over 39 years; and (2) determine if a relationship exists between growing season climatic variables and plant community dynamics within this grassland system. The study represents what Bender *et al.* (1984) called a press-perturbation experiment in that we are analyzing the response of grassland vegetation to the continued removal of two components of the natural disturbance regime: grazing by ungulates and fire. The analysis is facilitated by com-

paring plant community dynamics in two grazed pastures and their associated exclosures sampled at irregular intervals from 1940 to 1978.

Materials and methods

Study area

The study area is located on the USDA-ARS Southern Plains Experimental Range near Ft. Supply, Harper Co, Oklahoma, USA. The range includes a 1700 ha tract of sand sagebrush grassland on gently rolling topography. Soils are low-nutrient loamy sands or sandy loams with little organic matter. Mean annual precipitation is 625 mm, most of which occurs from April to June. Average annual temperature is 14.4 °C and July is typically the hottest month with a mean temperature of 28 °C.

Vegetation on the site is dominated by the suffrutescent shrub *Artemisia filifolia* and perennial grasses such as *Schizachyrium scoparium*, *Leptoloma cognatum*, *Bouteloua gracilis*, *Andropogon hallii*, and *Sporobolus cryptandrus*. Before 1941 the land was in private holdings and subjected to severe overgrazing by cattle. When purchased by the U.S. Government, the land was considered to be badly degraded in response to the combined effects of overgrazing, prolonged drought and high growing season temperatures during the 1930's. To improve range condition, grazing was periodically deferred in the growing seasons of 1937, 1938, and 1941. Fences constructed in 1941 divided the site into experimental pastures. Several livestock exclosures were also constructed at this time. This study is based on data from two 30.4 ha grazed pastures (23G and 32G) on which no burning, herbicide- or mowing treatments were imposed. Each pasture contains an ungrazed exclosure 23U (1.4 ha) and 32U (0.5 ha). Exclosures in the contiguous pastures are about 1.5 km apart. Both pastures were moderately grazed during the growing season from 1942 to 1951 and then year round from the spring of 1952 to the present. In 1961 both grazed pastures were reduced to 10.1 ha although they continued to receive the same grazing intensity.

Field methods

A stratified sampling design was used to measure vegetation in each pasture and exclosure. Grazed pastures were sampled in late July or early August in 1940, 1949, 1951, 1959, 1961, 1964, 1965, 1966, 1968, and 1978. Exclosures were sampled in 1949, 1951, 1955, 1959, 1961, 1965, 1966, and 1978. Species cover and density were determined along 10 m line segments located at regular intervals along parallel transects running across each pasture or exclosure. Transects were aligned between the same fence posts using a surveyors transit, thus, location of the 10 m lines was very close during each sample period. The 10 m line was constructed of 0.13 cm diameter wire cable tightly stretched between two steel pins. Basal cover (in cm) of grasses and forbs within 0.5 cm of either side of the wire cable, and areal cover of shrubs within 5 cm of either side of the cable were measured. The number of individuals of each species (density) within 0.5 cm of the cable was also recorded. Where distance between two individuals of a species was <10 cm for shrubs or <1.0 cm for grasses and forbs, they were recorded as one individual in the density counts. On each sampling date, the vegetation in each area was measured using ≥ 66 lines along a total of 10–12 transects with two exceptions. In 1959, 66 lines were placed along only 5 transects, and in 1951, 10 transects with 250 two m long lines were used. All data from 1951 were multiplied by 5 to be equivalent to the 10 m sample lengths of other years. Despite these exceptions, total transect length sampled is roughly equal between years. Parker & Savage (1944) provide a detailed description of the sampling procedures.

Data analyses

Whole-community analyses

All analyses are based on either species density (the number of individuals per 10 m) or cover (cm per 10 m) averaged over all lines within a site. At the community level, patterns of vegetation change within pastures and exclosures were evaluated with detrended correspondence analysis (DCA, Hill & Gauch 1980). The ordination was based on a data

matrix of average density values for 43 species in 36 stands representing each sampling period through time. Rare species were downweighted in proportion to their frequency. Ordination was used to determine if consistent and directional changes in vegetation occur over time in each pasture or exclosure (c.f. Austin 1977).

Intermediate-level analyses

Intermediate level analyses were performed to measure patterns over time of the following variables: (1) cover of physiognomic groups (grasses, forbs, shrubs, annuals, cool-season species); (2) changes in species richness, evenness, and diversity, and (3) degree and rate of compositional change.

Species diversity was calculated as $\exp(H')$ where $H' = -\sum p_i \ln p_i$, and p_i is the relative density of species i . This index is preferred because it reflects the number of equally common species in a stand (Peet 1974). Evenness was calculated as $H' / \ln(S)$ where S is richness, the number of species in a stand.

Degree of compositional change was assessed by comparing the quantitative similarity of each sample in a pasture or exclosure to the first sample date. 1940 was the first sample period in the grazed pastures and 1949 was the first sample date in the exclosures. Because rates of compositional change may vary between sample periods, a running comparison was formulated by comparing the similarity of each sample with the previous sample (see Bornkamm 1981). The coefficient of Bray & Curtis (1957) was used to calculate similarity among samples based on species average density values:

$$\frac{2\sum \min(x_i, y_i)}{\sum(x_i + y_i)} \quad (1)$$

where X_i and Y_i are the average density values of species i in samples X and Y .

For each site, stepwise linear regression based on the maximum r -square technique (SAS 1982) was used to determine if changes in community structure or growth form composition were related to climatic variables measured at the study area (Table 1). Because vegetation was sampled by early August, only environmental data for April to July were used. Spearman rank correlation (r_s) was used to deter-

Table 1. Climate variables used in the correlation analyses. All variables were recorded on a monthly basis during the growing season (April–July).

Variable	Measurement
TMAX	Average monthly maximum temperature (C)
TMIN	Average monthly minimum temperature (C)
TAVE	Average monthly temperature (C)
PRECIP	Total monthly precipitation (mm)
EVAP	Total monthly evapotranspiration (mm)
WIND	Average monthly wind speed (kph)

mine if a relationship existed between community structure variables and (1) total growing season precipitation and (2) current plus previous year growing season precipitation.

Average cover values for species that contributed the most to community dynamics were plotted against time to examine patterns of change for individual species during the 39 year period. Linear regression was used to determine relationships between species cover and climatic variables.

Results

Whole-community analysis

Axis I of the DCA ordination produced a gradient from samples dominated by annual forbs (*Eriogonum annuum*, *Triodanis biflora*, *Plantago purshii*) and short grasses (*Bouteloua gracilis*, *Buchloe dactyloides*, *Chloris verticillata*) to samples containing more mid- and tallgrass species (*Eragrostis trichodes*, *Poa arachnifera*, *Schizachyrium scoparium*, *Leptoloma cognatum*, *Calamovilfa gigantea*). In general, this reflects a gradient from grazed to ungrazed vegetation. Axis II separates ungrazed pastures dominated by *E. trichodes* and *L. cognatum* from those dominated by *P. arachnifera*.

The vegetation in 23G and 32G does not overlap in ordination space (Fig. 1). The samples form distinct clusters and no temporal pattern emerges within each cluster indicating that directional change in composition has not occurred through time in the grazed pastures. Vegetation in enclosure 32U forms a cluster that is distinct from 32G indicating that vegetation in this enclosure differed from that of the

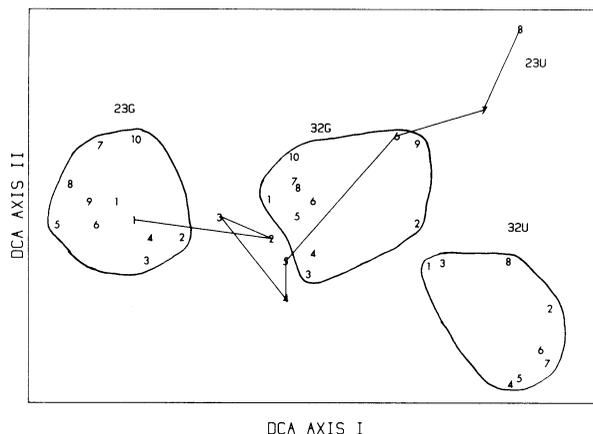


Fig. 1. Detrended correspondence analysis of community samples over time in two grazed pastures (23G, 32G) and two enclosures (23U, 32U). Axis I represents compositional change from grazed to ungrazed vegetation. Axis II separates vegetation in the two enclosures based on perennial grasses. Numbers indicate sequential samples (1 = earliest) for each area. See Methods for sample dates.

associated grazed pasture throughout the study. Again, the samples show no consistent temporal pattern in 32U. In contrast, vegetation in enclosure 23U showed a clear successional trend from grazed to ungrazed vegetation. The sample from 1949 is located among the samples from the grazed pasture (23G) and subsequent samples reflect a directional change in species composition. Succession in 23U did not lead to convergence with vegetation in 32U. Instead, the most recent samples from 23U and 32U are well separated along DCA axis II. At the whole community level then, the pattern of species change over time reflects both fluctuation (23G, 32G, 32U) and succession (23U). The successional change, however, reflects directionality towards the other ungrazed vegetation but does not indicate convergence.

Intermediate-level analyses

Vegetation in pasture 23G shows a 35% change in composition from 1949 to 1951 but changed little thereafter relative to 1940 (Fig. 2a). Rate of change in this pasture is about 20–30% between adjacent sample periods. This pattern indicates fluctuation because the degree of vegetation change remains constant but there is variation in species composition between samples. In 32G, the degree of change is greater than that in 23G and there is more variation between years (Fig. 2b). In addition, rate of

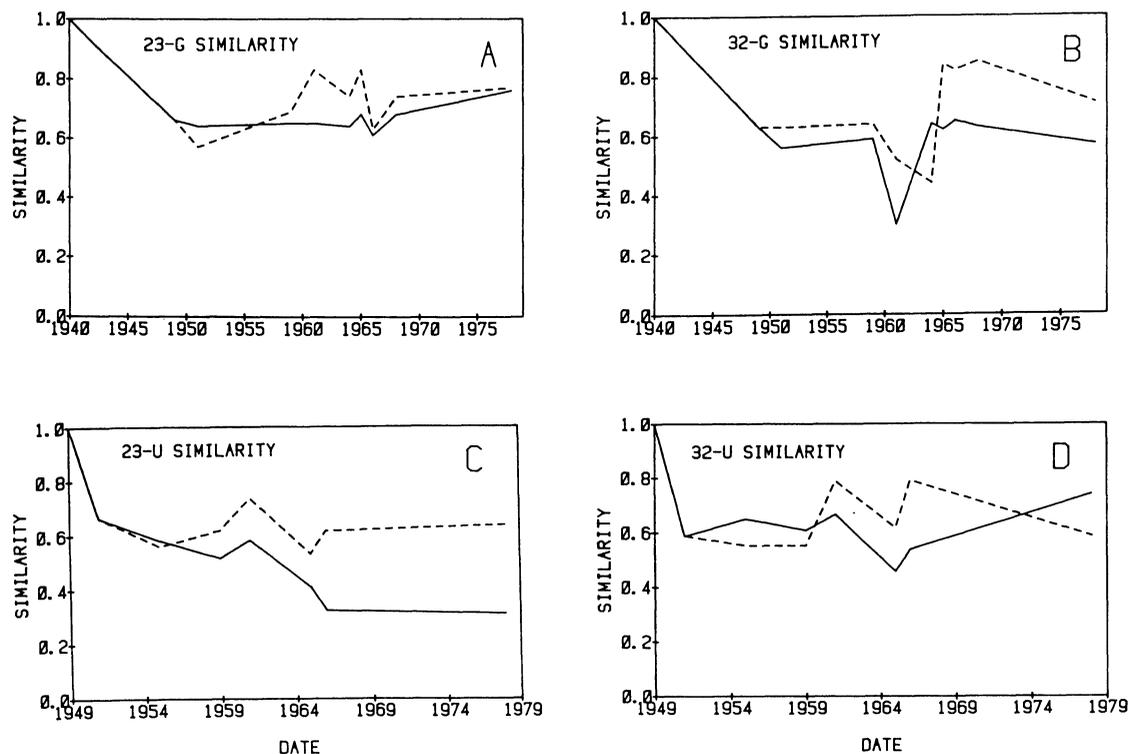


Fig. 2A–D. Degree and rate of change of vegetation in two grazed pastures (23G, 32G) and two exclosures (23U, 32U) over a 39 year period. Degree of change (—) represents the quantitative similarity of each sample with the original sample (1940 in the pastures, 1949 in the exclosures). Rate of change (---) represents the quantitative similarity of each sample and the preceding sample. The index of Bray & Curtis (1957) was used as a measure of similarity.

change fluctuates widely during the 1960s. From 1961 to 1964 the vegetation became more similar to the original sample before gradually decreasing in similarity in 1978. The vegetation in 23U changed continually (Fig. 2c) as indicated in the ordination (Fig. 1) and the rate of change remained constant at about 35%. By 1966, vegetation in 23U was only about 30% similar to that of 1949. The degree and rate of vegetation change in 32U was similar to that of 32G (Fig. 2a). Following a 40% decrease in similarity from 1949 to 1951, subsequent changes reflect fluctuation. The degree of difference between the 1949 data and all subsequent samples changes little but rate of change between sample years remains about 10–20%.

Basal cover of grasses ranged from 5% to 25% over the 39 year period (Fig. 3a). For all but one sample period, cover of grasses in the grazed pastures equalled or exceeded that in exclosures. In addition, cover of grasses was higher in 23G and 23U than in 32G and 32U, respectively. This accounts for some

of the differences between 32G and 23G noted in Fig. 1. Overall, cover of grasses increased in 23G but remained relatively constant and low over the forty year period in 32U, 32G, and 23U. Based on stepwise regression, in all cases grass cover was negatively correlated with high temperatures early in the growing season. Monthly precipitation variables entered each equation after temperature and wind speed variables. There were no significant correlations between grass cover and current year precipitation. However, cover of grasses was positively correlated with current plus previous year precipitation in 32G ($r_s = 0.59$, $p = 0.04$) and nearly so in 32U ($r_s = 0.59$, $p = 0.06$).

Forbs constitute only about 5% of the cover in this sand sagebrush grassland and except for the 1949 sample in 23G, forb cover was relatively constant over time (Fig. 3b). Fluctuations in forb cover were similar in 32G and 32U. Cover of forbs was usually greater and fluctuated more between sample periods in 23G and 23U than in 32G and 32U. Nevertheless,

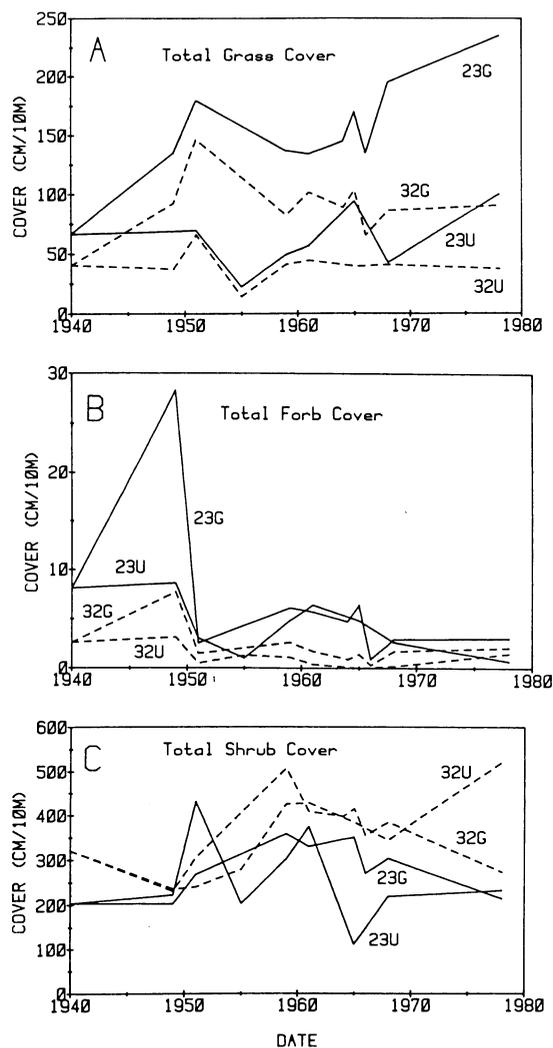


Fig. 3A–C. Cover of all grasses (A), forbs (B), and shrubs (C) in two grazed pastures (23G, 32G) and two exclosures (23U, 32U) over a thirty-nine year period.

cover of forbs in 23G was positively correlated with forb cover in 32G ($r_s = 0.66$, $p = 0.02$), but this was not true in exclosures. Linear regression indicated that cover of forbs was negatively related to July TMAX in 23U ($r^2 = 0.65$, $p = 0.02$) and May EVAP in 32U ($r^2 = 0.50$, $p = 0.05$). Cover of forbs was positively correlated with current year precipitation in 32G ($r_s = 0.86$, $p = 0.004$) and 32U ($r_s = 0.68$, $p = 0.014$).

Shrubs comprise 20–50% of the cover in this system (Fig. 3c). In the grazed pastures, shrub cover increased from 1950 until about 1965 and then declined to 1940 levels. Cover of shrubs in 23U fluctuated

over time, whereas shrub cover generally increased in exclosure 32U. Changes in shrub cover in 23G were highly correlated with shrub cover in 32G ($r_s = 0.95$, $p < 0.001$) but, this was not true in exclosures. Shrub cover was positively correlated with June EVAP ($r^2 = 0.54$, $p = 0.04$) in 32U. Current plus previous year precipitation was positively correlated with shrub cover in exclosure 23U ($r_s = 0.88$, $p = 0.002$).

For all treatments, abundance of annuals and cool season species (those species that flower before 1 July, generally C_3 species) was positively correlated with lower rates of evapotranspiration and cooler temperatures during May and June.

Species richness decreased over the 39 year period in each exclosure (Table 2). Richness was negatively correlated with July TAVE in 23U ($r^2 = 0.67$, $p = 0.01$). In both exclosures richness was positively correlated with total current growing season precipitation. Evenness in these exclosures tended to increase slightly during the 1950s and early 1960s but then decreased in the most recent samples. Evenness in 32U was positively correlated with current plus previous year precipitation. Although diversity decreased in both exclosures, the patterns of change in the exclosures were dissimilar. In 32U, diversity was positively correlated with growing season precipitation indices. In 23U, diversity was negatively correlated with July TMAX ($r^2 = 0.86$, $p = 0.001$), but diversity was not correlated with precipitation in this exclosure.

In the grazed pastures, species richness was generally higher than in the exclosures. Richness in both 23G and 32G tended to fluctuate around a mean value rather than decrease as in the exclosures (Table 2). Richness was positively correlated with current year precipitation ($r_s = 0.62$, $p = 0.03$) and negatively correlated with July TAVE ($r^2 = 0.43$, $p = 0.04$) in 32G. In both exclosures, evenness was strongly correlated with moisture availability during June as well as total growing season precipitation. In general, current plus previous year precipitation added little improvement to the correlations, thus evenness is mostly a function of current season precipitation. In both grazed pastures, species diversity increased in 1949, decreased in 1951 and then fluctuated slightly during the rest of the study period. No monthly cli-

Table 2. Changes in diversity ($\exp(H')$), evenness (H'/H'_{\max}), and richness for two grazed and two ungrazed sadsage grasslands over a 39 year period.

Pasture	Parameter	1940	1949	1951	1955	1959	1961	1964	1965	1966	1968	1978	Precipitation	
													C	P + C ^a
23-U	Diversity		8.3	7.4	6.8	10.3	10.9		9.6	6.7		5.5	NS	NS
	Evenness		0.69	0.76	0.73	0.79	0.81		0.78	0.76		0.65	NS	NS
	Richness		22	14	14	19	19		18	12		14	0.04	NS
32-U	Diversity		9.3	6.8	6.1	7.6	6.7		4.9	5.1		5.9	0.014	0.010
	Evenness		0.71	0.77	0.65	0.75	0.72		0.72	0.68		0.67	NS	0.030
	Richness		23	12	16	15	14		9	11		14	0.001	NS
23-G	Diversity	6.3	18.6	8.8		8.3	7.5	4.9	7.7	4.0	4.9	5.9	0.010	0.010
	Evenness	0.59	0.81	0.72		0.64	0.65	0.58	0.63	0.46	0.54	0.60	0.006	0.003
	Richness	22	36	20		27	22	16	26	20	19	19	NS	NS
32-G	Diversity	8.0	17.9	10.2		12.3	10.0	8.5	10.1	7.3	10.0	8.2	0.006	0.005
	Evenness	0.67	0.84	0.82		0.76	0.73	0.79	0.73	0.70	0.73	0.70	0.050	0.030
	Richness	22	31	17		27	23	15	24	17	23	20	0.030	NS

^aProbability values for Spearman rank correlation between parameter and current growing season precipitation (C) or current year plus previous year growing season precipitation (P + C).

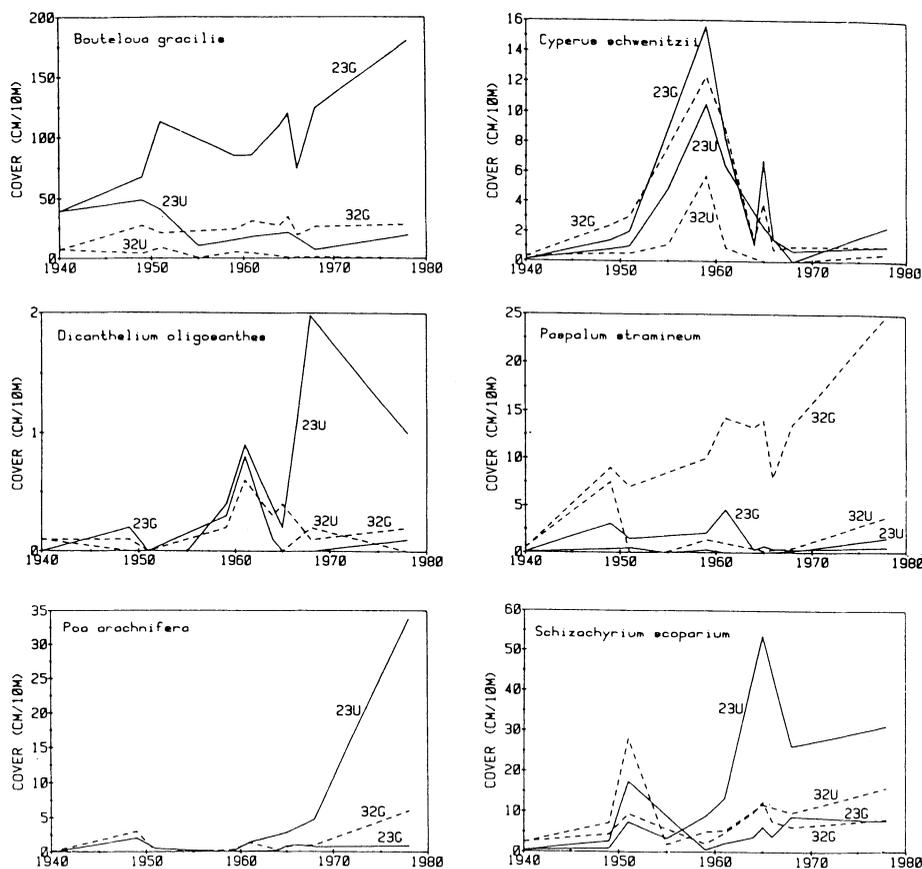


Fig. 4. Cover of the six most common species in two grazed pastures (23G, 32G) and two exclosures (23U, 32U) over a 39 year period.

matic measurement was correlated with diversity in the grazed pastures but diversity was highly correlated with current growing season precipitation in both pastures. Current growing season precipitation explains nearly as much of the variation in diversity as does current plus previous season precipitation.

Species level analysis

Cover of the common species tended to differ among sample areas within a year and showed marked fluctuations between years. Despite this variability, several species showed clear patterns of change over time within a pasture or exclosure (Fig. 4). Forbs are not abundant in this system (Fig. 3b). With the exception of *Ambrosia psilostachya* and the dominant shrub *Artemisia filifolia*, most of the common taxa are graminoids. In fact, vegetation differences among the study sites are primarily a function of four grasses, *Schizachyrium scoparium* and *Poa arachnifera* in 23U, *Bouteloua gracilis* in 23G, and *Paspalum setaceum* in 32G (Fig. 4). To some extent, the same trend occurs for *Dicanthelium oligosanthos* in 23U, as well. *Cyperus schwenitzii* produced its greatest cover during the late 1950s. The pattern of change for this sedge is very similar in all four study areas (Fig. 4). Although many of the grasses decreased in cover during the drought of the early 1950s, correlations between climatic variables and cover of individual species generally were inconclusive. For example, cover of *Bouteloua gracilis* was correlated with May EVAP in 23U, April EVAP in 23G, April TMIN in 32U, and July WIND in 32G. Because grassland vegetation is heterogeneous, correlations of small-scale variation in cover with broad-scale climatic variables are often weak and unreliable. In addition, some of this variation at the species level may result from the inexact location of lines between sample periods.

Discussion

The whole-community analysis indicated that (1) species composition was different among experimental units and remained different throughout the study; (2) fluctuation characterized vegetation

dynamics in pastures 23G and 32G, and in exclosure 32U; and (3) successional changes have occurred in exclosure 23U (Fig. 1). These patterns occurred over a time span that incorporated a severe drought during the early 1950s followed by several years of above-average precipitation. Previous studies of grassland dynamics in the absence of grazing have demonstrated that quantitative changes in vegetation may occur rapidly (Penfound 1964; Austin *et al.* 1981; Collins & Adams 1983; Biondini *et al.* 1985) or slowly (West *et al.* 1979; Glenn-Lewin 1980; Holechek & Stephenson 1983). Such differences between systems may be a function of grazing history (Persson 1984) or the influence of other disturbances such as fire (Bragg & Hulbert 1976; Glen-Lewin 1980).

It is of interest that after 39 years without fire and grazing, the dynamics of vegetation in exclosure 32U reflected fluctuation rather than succession (Fig. 1). Vegetation dynamics in arid and semi-arid regions are often characterized by shifting patterns of abundance rather than sequential species replacement over time (MacMahon 1980; Anderson & Holte 1981; Goldberg & Turner 1986). This perhaps implies that on a large scale, this sand sagebrush grassland is in dynamic equilibrium with the local environment. Grasslands are inherently patchy, however, especially when grazed (Belsky 1983; Gibson & Greig-Smith 1986). Some patches may become either locally overgrazed or dominated by a strong competitor (Bakker *et al.* 1983), thus local changes in composition may occur due to biotic interactions such as grazing or by competition in the absence of disturbance. For example, vegetation in 23U changed with regard to the original sample and the rate of change remained fairly constant over a 30 year period (Fig. 2c). The successional changes that took place in exclosure 23U reflected an increase in cover of palatable grasses such as *Poa arachnifera* and *Schizachyrium scoparium* (Fig. 4). *Schizachyrium scoparium* was originally present in low abundance in 23U whereas *Poa arachnifera* colonized the area after grazing was excluded. Therefore, patch dynamics within this regionally stable vegetation mosaic are characterized by an individualistic response of species among different patches.

Species diversity was highest on grazed areas and diversity generally decreased over time in the ex-

closures as a function of lower richness and evenness (Table 2). Diversity is generally higher on grazed versus ungrazed grasslands (see, for instance, Kelting 1954; Peet *et al.* 1983; Collins & Barber 1985; Collins 1987) but this effect is not universal (Waser & Price 1981; Persson 1984). Diversity was positively correlated with growing season precipitation in 23G, 32G, and 32U, but not in 23U. This suggests that diversity may be a function of precipitation in relatively stable patches of grassland (23G, 32G, 32U) while biotic processes override the effects of precipitation in successional patches.

Species richness, total grass cover and total forb cover in 32G and 32U are positively correlated with precipitation. Soils in this pasture and enclosure have more sand and less organic matter than soils in 23G or 23U (unpublished data). Thus, precipitation may have a more pronounced effect on vegetation dynamics on these coarse textured soils. Based on monthly climatic variables, grass cover was affected more by early growing season temperatures than by precipitation. Powell *et al.* (1986) also found temperature variables to have a greater effect on productivity than did precipitation in Oklahoma tallgrass prairie.

The low cover values of palatable grasses in the grazed pastures may result from a long history of grazing. Further evidence for the impact of grazing in these pastures is the increase in grazing tolerant species such as the shortgrass *Bouteloua gracilis*, as well as an increase in the number of forb species. Fluctuation in cover may also reflect a combined response to both grazing and drought during the 1950s. *Bouteloua gracilis*, for example, is a drought tolerant dominant of shortgrass vegetation in western North America (Detling 1979; Archer & Tieszen 1986) that tends to increase under continuous grazing pressure (Larson 1940).

In the enclosures, cover of the tallgrass species decreased whereas cover of the more drought tolerant *Schizachyrium scoparium* (Hake *et al.* 1983) increased over time. Once populations are reduced, recovery is mostly from vegetative growth. Seedling establishment is low for these native species especially under drought conditions (Coyne & Bradford 1985). Thus, population density may have decreased during the early drought periods and subsequent increases of some species reflect local establishment

and growth during more favorable periods. Because this event may be locally unpredictable, the correlations between environmental variables and species cover within a pasture or enclosure are unreliable.

General differences between sample areas over time result from local extinctions, especially in the enclosures, and increases in cover of different grasses in each study area. This reflects an individualistic response by species among sample areas as well as individualistic fluctuations of local populations between years within sample areas. Penfound (1964) referred to this type of pattern as 'pulse-phase' dominance which may be characteristic of grasslands where climate is highly variable within and between years (Sims *et al.* 1978; Grubb *et al.* 1982). Population fluctuations reflect small-scale patterns that cannot be accurately measured at the scale of resolution used in this study. Nevertheless, these results are similar to those reported by Pickett (1982) in old field succession in New Jersey in that species tended to remain present for long periods during succession but were abundant only during a portion of that time span.

System dynamics in sand sagebrush grasslands reflect a tradeoff in that loss of some species was compensated by increased growth of other species. Similar patterns were noted by Van der Maarel (1981) in dune grasslands and Chapin & Shaver (1985) in tundra. Explanation of the pattern of increase and decrease at the species level is unclear because the population biology and physiological ecology of many of the component species has not been well studied. It does not appear, however, that broad-scale climatic variables can effectively predict small-scale patterns of change in species populations within this sand sagebrush grassland.

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