

## Gradient analysis of remnant True and Upper Coastal Prairie grasslands of North America

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Sixty-three upland True and Upper Coastal Prairie grasslands were sampled for vegetation composition and soil variables. The first axis from principal components analysis produced a south to north arrangement of stands along which temperature and precipitation decrease and soil organic matter increases ( $P < 0.0001$ ). The second principal components analysis axis was related to a soils gradient, primarily within Texas communities, which had more varied soils than grasslands to the north. Species response curves against the first axis showed a continual replacement from north to south, with *Schizachyrium scoparium* and *Paspalum plicatulum* dominants in the south, *Andropogon gerardii* more important in central and northern communities, and *Stipa spartea* and *Sporobolus heterolepis* important in the north. The  $C_3/C_4$  ratio of grasses increased rapidly northward from Nebraska. Species diversity and richness did not vary greatly and showed nonsignificant correlations with environmental variables across this latitudinal gradient. Stand relationships from cluster analysis corresponded with the results of principal components analysis, and based on these analyses, plus a review of the literature, seven community types were recognized. Five form a continuum, across which *Andropogon gerardii* increases northward and *Schizachyrium scoparium* increases southward, while two are limited to high-precipitation areas of north Texas.

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Soixante-trois prairies des hauts plateaux des «True» et «Upper Coastal Prairie» ont été échantillonnées pour les variables de la composition de la végétation et du sol. Le premier axe de l'analyse en composante principale a produit une disposition des groupes allant du sud au nord le long de laquelle la température et la précipitation diminuent et la teneur du sol en matière organique augmente ( $P < 0,0001$ ). Le deuxième axe des analyses en composantes principales a montré une relation avec un gradient des sols, surtout chez les communautés du Texas qui aient des sols plus variés que les prairies plus au nord. Les courbes de réaction des espèces envers le premier axe ont montré un remplacement continu du nord au sud avec les *Schizachyrium scoparium* et *Paspalum plicatulum* comme espèces dominantes dans le sud, le *Andropogon gerardii* plus important dans les communautés centrales et septentrionales, et les *Stipa spartea* et *Sporobolus heterolepis* importants dans le nord. Le rapport  $C_3/C_4$  des graminées a augmenté rapidement au nord du Nebraska. La diversité et la richesse en espèces n'ont pas beaucoup varié et ont montré des corrélations non significatives avec les variables écologiques à travers ce gradient de latitude. Les relations entre groupes d'après des analyses de groupement correspondaient aux résultats obtenus par les analyses en composantes principales et, se basant sur ces analyses en plus d'une revue de littérature, sept types de communautés ont été reconnus. Cinq de ceux-là forment un continuum à travers lequel le *Andropogon gerardii* augmente vers le nord et le *Schizachyrium scoparium* augmente vers le sud, tandis que deux types sont limités aux régions du Texas septentrional à fortes précipitations.

[Traduit par la revue]

### Introduction

The True and Coastal Prairies form a continuous zone across central North America from Manitoba to the Gulf of Mexico (Risser et al. 1981). Remnant native grasslands have been studied in the northern (Dix and Smeins 1967; Ralston 1969), central (Weaver and Fitzpatrick 1934; Weaver 1954; Brotherson 1969), and southern (Dyksterhuis 1946; Launchbaugh 1955; Collins et al. 1975; Diamond 1980; Smeins and Diamond 1983; Diamond and Smeins 1985) True Prairie and in the Coastal Prairie (Diamond and Smeins 1984). It is not possible, however, to make a quantitative comparison of the nature of changes in composition across this gradient since aims and methods have varied among studies. Additionally, Texas prairies have not been adequately related to the remainder of the tallgrass prairies (Sims et al. 1978; Risser et al. 1981).

The climate, soils, and topography of this region are suitable for agriculture, and most of the original grasslands have been

converted to row crops or tame pasture. Where they have not been cultivated, most have been overgrazed. Since native vegetation has largely been destroyed and remnants continue to diminish, the opportunity to conduct a study of late seral relicts across a broad latitudinal transect is becoming increasingly difficult and will soon be impossible. It is estimated that less than 1% of the original grasslands remain (United States Forest Service 1977; Klopatek et al. 1979; Smeins and Diamond 1986). The purpose of this study is to classify plant communities and relate community composition, structure, and species diversity to environmental variables on the basis of a uniform, quantitative data set from relatively undisturbed sites.

### Study area

The True Prairie extends from the Aspen Parkland of Manitoba south to east central Texas, where it joins the Coastal Prairie (Kuchler 1964; Dodd 1968). To the east it borders on the Eastern Deciduous

Forest, while to the west it grades into the Mixed Prairie. It forms a north-south zone approximately 325 km wide. The "Prairie Peninsula" (Transeau 1935), which extends eastward through Illinois, is not included here, nor are the Nebraska sandhills to the west or other sandy soil inclusions within the study area. The Coastal Prairie forms a 125 km wide arc along the Gulf of Mexico (Gould 1975; Diamond and Smeins 1984). To the east it intergrades with elements of the Eastern Deciduous Forest and to the west it borders Subtropical Thorn Woodland. Within the Coastal Prairie, this investigation only considered grasslands east of the 97th meridian, henceforth referred to as the Upper Coastal Prairie.

Most soils north of Nebraska have developed from glacial till or loess, whereas soils to the south have developed from unglaciated basement marine materials (United States Geological Survey 1973). North of Texas, typical upland soils are classified as Mollisols within the international system of soil classification (Soil Survey Staff 1975). In contrast, soil profiles within Texas are more variable, and in addition to Mollisols, Vertisols and Alfisols are widespread. Vertisols, because of shrink-swell clays, exhibit a unique microhigh-microlow topography called gilgai (Gustavson 1975). Alfisols often have scattered circular, sandy mounds called mima or pimple mounds, which are of unknown, and perhaps variable, origin (Bernard and LeBlanc 1965; Cox 1984).

The Upper Coastal Prairie has a humid, subtropical climate, while the True Prairie is humid or subhumid continental (Koppen 1931; Thornthwaite 1948). The average frost-free period ranges from 130 to 310 days (United States Environmental Data Service 1968). Average annual maximum and minimum temperatures are, respectively, +10 and -2 in the north and +26 and +15°C in the south. Precipitation decreases from east to west, with a 25 cm/year difference in the central True Prairie. Precipitation also decreases from north to south, ranging from 50 to 120 cm/year. However, growing-season (May-September) precipitation is less variable and increases from 35 to 65 cm/year from north to south. Growing-season rain days range from 35 to 50 from west to east. Class A pan evaporation increases from 85 in the north to 195 cm/year in the south, while the annual precipitation to evaporation ratio ( $P/E$ ) ranges from 0.8 on the western to 1.2 on the eastern margin of the study area.

## Methods

Soil Conservation Service, university, and state land management personnel were contacted throughout the study area to locate sample sites. These sites and others identified by previous studies were visited during the early spring of 1981. Whenever possible, sites were selected within a north-south zone between the 95th and 97th meridians. All were within a north-south strip bounded by a growing season  $P/E$  ratio of 0.6 on the west to 0.7 on the east. Criteria for stand selection were that the community (i) occur on mature upland soils, (ii) consist of visually homogeneous vegetation over unbroken sod, (iii) had no past history of overgrazing and was not currently grazed, (iv) was large enough that structure and composition were not affected by nearby agricultural practices (stands ranged from 8 to 200 ha), and (v) had no known history of treatment with herbicides or fertilizers. Stands within the central and southern portions of the study area are used as hay meadows. In contrast, those in the northern True Prairie are primarily nature preserves, which are less frequently mowed and periodically burned.

During the early summer of 1981, 63 grasslands were sampled for species frequency and foliar cover, using twenty-five, 25 × 50 cm rectangular plots (Daubenmire 1968). Stands were sampled from south to north over a 4-week period to, as nearly as possible, sample all at similar phenological stages of development. Plots were placed across each stand in a stratified random manner by locating several equidistant parallel lines within each and determining plot location along each line by referring to a random-numbers table. Thirty-five stands were sampled within Texas and 28 north of Texas. Southern communities were more intensively sampled than central and northern stands because of greater diversity in typical upland soils and

because literature on these communities was generally lacking as compared with communities to the north (Diamond and Smeins 1985).

Specimens of all flowering plants encountered were collected and stored in the Tracey Herbarium at Texas A & M University. A plant list for each stand was kept and all stands were revisited at least once during the fall of 1982 to validate and add to presence lists. Botanical nomenclature follows Kartesz and Kartesz (1980). The photosynthetic pathway ( $C_3$  or  $C_4$ ) was determined for all graminoids on the basis of a review of the literature.

Soil samples from 0 to 10 cm were collected from several locations within each stand and pooled to form a composite sample. Samples were analyzed for pH, organic matter content (OM), and texture (Black 1965). The soil profile was classified to order within the international system for all stands (Soil Survey Staff 1975).

Vegetation data were analyzed using principal components analysis (PCA) and cluster analysis (Gauch 1977; Rohlf et al. 1980). The purpose of these analyses was to (i) elucidate relationships among stands, (ii) provide a basis for analysis of the influence of environmental variables on community composition and species behavior patterns, and (iii) provide a basis for classification.

Multiple regressions using stand locations along derived PCA axes as dependent variables and environmental variables for those stands were calculated. The following environmental variables were used: soil pH, organic matter, percent clay and sand, mean annual and growing-season precipitation, mean annual maximum and minimum temperatures, mean growing-season (May-September) maximum and minimum temperatures, and mean nongrowing-season maximum and minimum temperatures. Product moment correlation coefficients, using species frequency values against environmental variables, were used to describe trends in species to environmental relationships.

Simpson's index ( $C$ ) and the Shannon-Wiener index ( $H'$ ) were calculated for each stand, using relative cover as the measure of comparison. Correlation coefficients between environmental variables and values for diversity indices and for species richness (total number present per stand) were calculated to determine relationships among environmental variables and species diversity, and trends in diversity along the north-south gradient.

## Results

### Ordination and cluster analysis

A two-axis PCA ordination based on the frequency of 42 perennial graminoids produced stand arrangements that agreed with the initial extensive survey of stands and intuitive examination of the data. Extraction of a third axis did not add to the understanding of stand relationships. Thus, a two-dimensional display from PCA ordination based on frequency of perennial graminoids is presented as a basis for further analysis.

The first PCA axis corresponds with a south to north arrangement of stands (Fig. 1). Correlation coefficients between stand position on the first axis and environmental variables were all highly significant ( $P < 0.0001$ , positive for temperature and precipitation, negative for soil organic matter) except for soil pH, percent sand, and percent clay. A regression using nongrowing-season minimum temperature had the highest  $R^2$  value (0.89). Thus, the first PCA axis expresses a latitudinal arrangement of stands along which temperature and precipitation decrease and soil OM content increases (Fig. 2).

All Texas stands appear low on the first axis. These stands are closely clustered together rather than scattered evenly along the axis. The greater number of stands sampled in the south results in a greater number close together, low in the first axis. Stands from the remainder of the latitudinal transect are scattered evenly on the axis and are not disproportionately

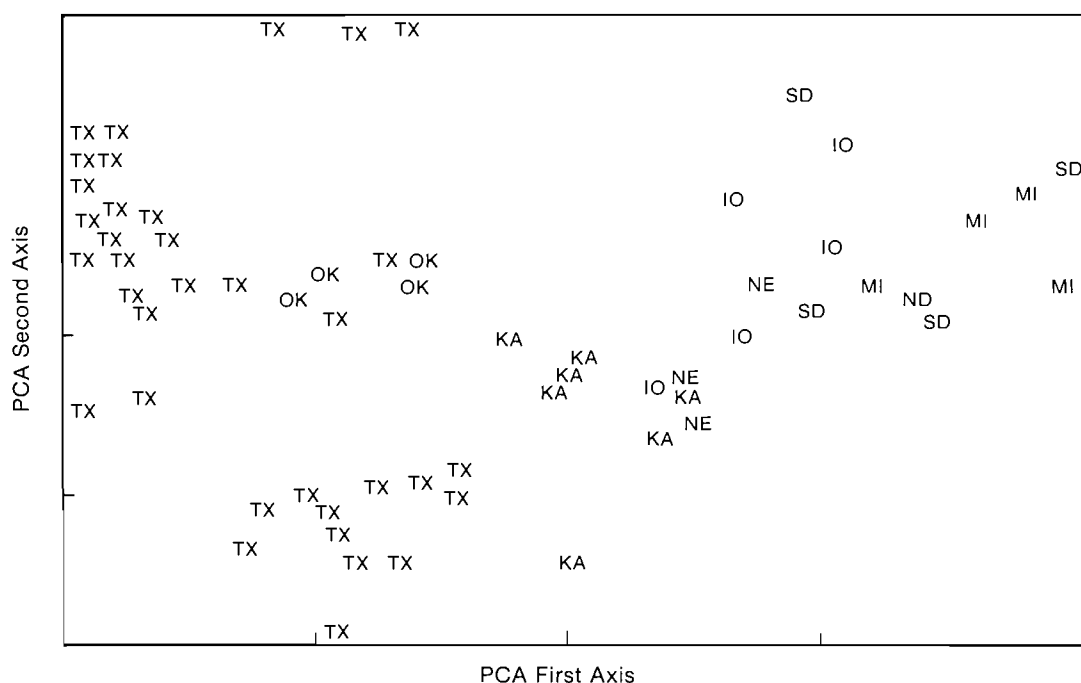


FIG. 1. Two-axis display from results of PCA ordination of 63 upland grasslands within the True and Upper Coastal Prairies based on frequency of perennial graminoids. Plotted are stand locations by state: IO, Iowa (5); KA, Kansas (7); MI, Minnesota (4); NE, Nebraska (3); ND, North Dakota (1); OK, Oklahoma (4); SD, South Dakota (4); TX, Texas (35).

TABLE 1. Mean textural fractions, organic matter content, and pH summarized for 63 True and Upper Coastal Prairie sites by community type<sup>a</sup> and soil order

	S P Sn		S Sn A,	T Pa Sn,	Sp C,	A S,	A St Sh,
	Vertisol	Alfisol	Vertisol	Vertisol	Alfisol	Mollisol	Mollisol
No. of stands	9	9	12	2	3	16	12
Surface texture <sup>b</sup>	C	CL, L, SCL, SL	C	C	SiCL	C, CL, L, SCL, SiC, SiCL	CL, L, SCL, SiCL
Textural fraction (%)							
Sand	20	47	15	10	18	14	29
Silt	25	29	25	25	51	46	37
Clay	55	24	60	65	31	40	34
Organic matter (%)	3	3	5	6	4	5	8
pH	5.8	5.7	7.1	6.8	5.1	6.3	6.5

<sup>a</sup>A, *Andropogon gerardii*; C, *Carex meadii*; P, *Paspalum plicatulum*; Pa, *Panicum virgatum*; S, *Schizachyrium scoparium*; Sh, *Sporobolus heterolepis*; Sn, *Sorghastrum nutans*; Sp, *Sporobolus silveanus*; St, *Stipa spartea*; T, *Tripsacum dactyloides*.

<sup>b</sup>C, clay; CL, clay loam; L, loam; SCL, sandy clay loam; SL, sandy loam; SiC, silty clay; SiCL, silty clay loam.

compressed as a result of the greater sample effort in the south.

The second PCA axis is interpreted as a soils gradient, although  $R^2$  values were low for single or combinations of environmental variables. Soil pH and percent clay were the only variables with highly significant correlations with the second axis. When Texas stands were excluded from the correlation analysis, no environmental variable was significantly correlated with the second axis, but when the 35 Texas stands alone were analyzed, correlation coefficients for pH and clay showed stronger relationships ( $r$  was  $-0.63$  for all stands,  $-0.85$  for Texas stands alone for pH, and  $-0.58$  for all stands,  $-0.78$  for Texas only stands for percent clay). Thus, the second axis primarily reflects a soils gradient within Texas, which had more variable upland soils.

A similarity phenogram from a correlation matrix (Rohlf et al. 1980), based on frequency values of the same 42 grami-

noids used in PCA, produced stand groups that correspond with stand arrangement from the ordination (Fig. 3). Texas stands (35) were separated from stands in the central True Prairie (16), which were separated from northern True Prairie stands (12). Iowa stands were transitional: two grouped with central stands and three with northern stands. Within Texas, four groups were recognized on the basis of results of ordination and cluster analysis plus observed variation in soils. One was composed of three northern Texas stands over loamy Alfisols, which are separated from other stands on the upper left side of the ordination display. Another was made up of two northern Texas stands over clayey Vertisols. The two remaining groups were composed of stands over Vertisols (12) in central Texas (central Blackland and Fayette prairies) and southern stands (18), primarily within the Upper Coastal Prairie. Soil characteristics for these groups depict the primary edaphic differences (Table 1).

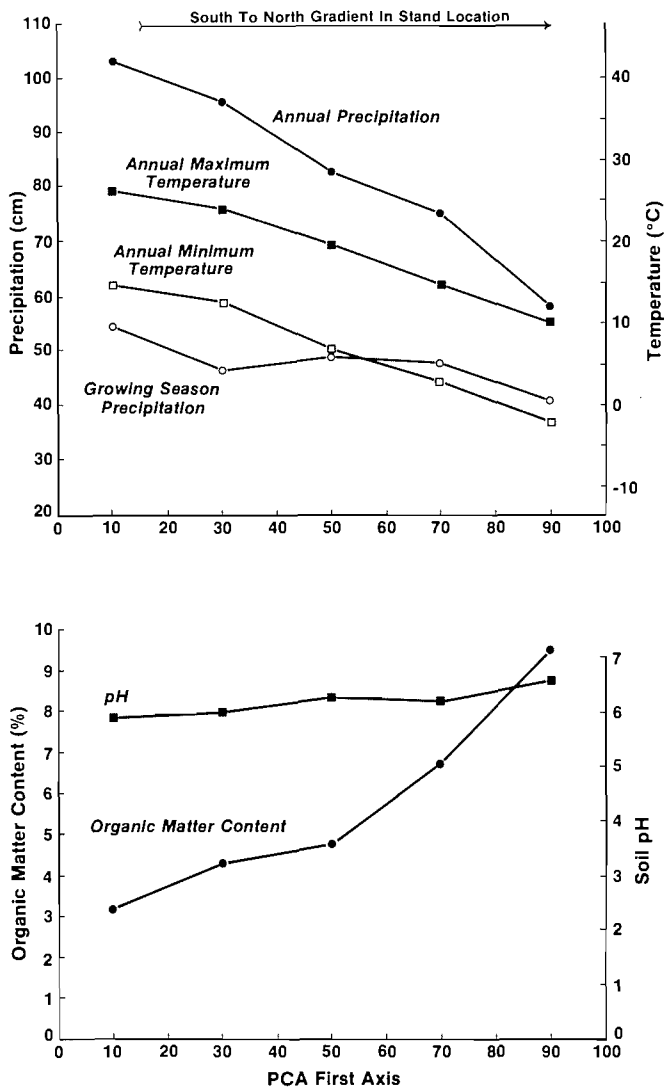


FIG. 2. Response curves for environmental variables against the first PCA axis from ordination of 63 upland grasslands within the True and Upper Coastal Prairies. Values for environmental variables were averaged for stands by 20-unit intervals.

#### Classification and composition of communities

Six community types were recognized on the basis of results of ordination and cluster analysis (Fig. 4). The basic template for mapping of these was established by Kuchler (1964) and Gould (1975), with modifications based on several additional studies (Weaver and Fitzpatrick 1934; Transeau 1935; Weaver 1954; Ralston 1969; Risser et al. 1981; Diamond and Smeins 1984). Boundaries between community types within Texas generally correspond with clearly defined changes in community composition caused by changes in geologic substrate and soils (Diamond and Smeins 1985). The boundary between the northern and central community types corresponds with the maximum extent of the Des Moines lobe of the Wisconsin ice sheet. It does not correspond with a sharp environmental change and, hence, is somewhat arbitrary. However, analysis of species response patterns against the first PCA (latitudinal) axis indicates that this region is one of rapid change in community composition (Fig. 5).

Dominants, based on mean foliar cover values, of the northern community type are *Andropogon gerardii*, *Stipa spartea*,

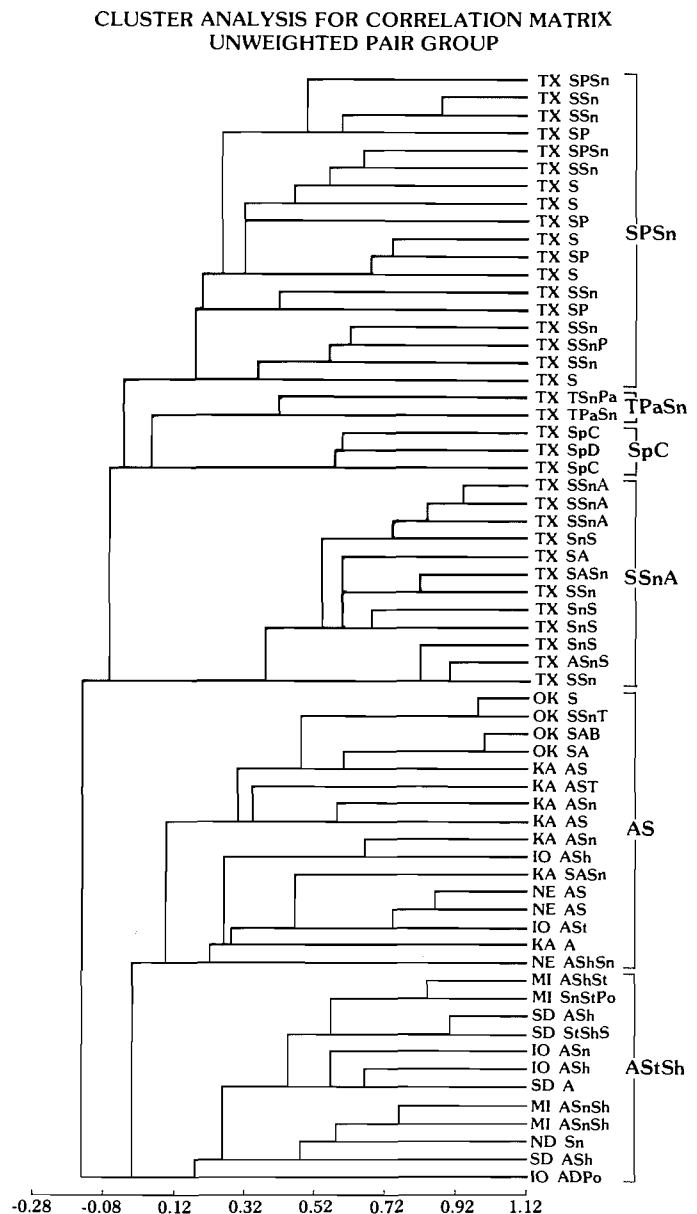


FIG. 3. Similarity phenogram from the results of a cluster analysis based on a correlation matrix generated from frequency of perennial graminoids. Sixty-three True and Upper Coastal Prairie grasslands are broken into six groups. Dominant species of each stand and group are listed: A, *Andropogon gerardii*; B, *Bouteloua curtipendula*; C, *Carex meadii*; D, *Dichanthelium oligosanthos*; P, *Paspalum plicatulum*; Pa, *Panicum virgatum*; Po, *Poa pratensis*; S, *Schizachyrium scoparium*; Sh, *Sporobolus heterolepis*; Sn, *Sorghastrum nutans*; Sp, *Sporobolus silveanus*; St, *Stipa spartea*; T, *Tripsacum dactyloides*.

and *Sporobolus heterolepis*, and thus it is defined as a *Andropogon-Stipa-Sporobolus* community type (Table 2). *Sorghastrum nutans* was the next most important species, followed by *Schizachyrium scoparium*, *Muhlenbergia richardsonis*, and *Poa pratensis*. Mean total foliar cover was 86%, and a total of 155 species, including 37 graminoids, 116 forbs, and 2 woody species, occurred across all stands. An average of 58 species were present per stand.

The central group of stands is an *Andropogon gerardii* - *Schizachyrium scoparium* community type. Other important graminoids included *Sorghastrum nutans*, *Bouteloua curti-*

TABLE 2. Mean absolute frequency (%) and relative foliar cover (%) of species

	A St Sh, northern True Prairie (12) <sup>a</sup>			A S, central True Prairie (16)		
	No. of stands	Frequency	Cover	No. of stands	Frequency	cover
Graminoids						
<i>Agropyron subsecundum</i>	9	15	T <sup>c</sup>	1	5	T
<i>Andropogon gerardii</i>	12	15	25	16	79	31
<i>Bouteloua curtipendula</i>	7	24	2	12	36	3
<i>Carex meadii</i>	3	52	3	15	65	3
<i>Carex microdonta</i>	—	—	—	2	5	T
<i>Carex pensylvanica</i>	11	38	2	—	—	—
<i>Carex tetanica</i>	8	76	5	—	—	—
<i>Coelorachis cylindrica</i>	—	—	—	2	56	6
<i>Dichanthelium oligosanthos</i>	7	34	3	14	54	4
<i>Eragrostis intermedia</i>	—	—	—	9	11	1
<i>Eriochloa sericea</i>	—	—	—	—	—	—
<i>Fimbristylis puberula</i>	1	5	T	8	20	1
<i>Koeleria pyramidata</i>	9	25	1	11	19	2
<i>Panicum virgatum</i>	5	13	1	9	33	4
<i>Paspalum floridanum</i>	—	—	—	—	—	—
<i>Paspalum plicatulum</i>	—	—	—	—	—	—
<i>Paspalum setaceum</i>	—	—	—	3	7	T
<i>Poa pratensis</i>	12	69	5	6	54	3
<i>Rhynchospora</i> sp.	—	—	—	—	—	—
<i>Schizachyrium scoparium</i>	12	41	6	16	73	21
<i>Scleria ciliata</i>	—	—	—	1	20	1
<i>Sorghastrum nutans</i>	10	54	10	16	66	10
<i>Sporobolus asper</i>	—	—	—	11	36	3
<i>Sporobolus heterolepis</i>	12	56	10	4	44	13
<i>Sporobolus silveanus</i>	—	—	—	1	4	T
<i>Stipa leucotricha</i>	—	—	—	—	—	—
<i>Stipa spartea</i>	12	60	10	5	25	7
<i>Tripsacum dactyloides</i>	—	—	—	4	80	8
Forbs						
<i>Acacia hirta</i>	—	—	—	—	—	—
<i>Achillea millefolium</i>	6	10	T	11	15	T
<i>Amorpha canescens</i>	7	30	4	12	18	1
<i>Anemone</i> sp.	9	16	1	4	6	T
<i>Aster ericoides</i>	11	27	1	13	32	1
<i>Bifora americana</i>	—	—	—	1	5	T
<i>Cacalia plantaginea</i>	—	—	—	—	—	—
<i>Centaurea americana</i>	—	—	—	—	—	—
<i>Delphinium virescens</i>	1	5	T	1	15	T
<i>Galium boreale</i>	8	47	2	—	—	—
<i>Gnaphalium</i> sp.	—	—	—	7	30	1
<i>Hedyotis nigricans</i>	—	—	—	2	5	T
<i>Helianthus maximiliana</i>	2	8	2	1	5	T
<i>Helianthus rigidus</i>	8	28	2	3	8	1
<i>Hymenopappus scabiosaeus</i>	—	—	—	—	—	—
<i>Kuhnia eupatorioides</i>	1	5	1	2	10	1
<i>Liatris pycnostachya</i>	5	13	1	2	5	T
<i>Linum medium</i>	1	5	T	13	25	1
<i>Neptunea lutea</i>	—	—	—	2	28	1
<i>Oxalis</i> sp.	1	72	2	6	30	1
<i>Petalostemum</i> sp.	8	18	1	10	12	1
<i>Physostegia intermedia</i>	—	—	—	—	—	—
<i>Psoralea tenuifolia</i>	5	9	T	9	27	2
<i>Ratibida columnaris</i>	1	5	1	1	15	3
<i>Rosa arkansana</i>	6	20	1	3	6	T
<i>Rudbeckia hirta</i>	5	24	1	7	11	T
<i>Ruellia humilis</i>	—	—	—	8	17	T
<i>Ruellia nudiflora</i>	—	—	—	—	—	—
<i>Salvia azurea</i>	—	—	—	6	8	1
<i>Schrankia uncinata</i>	—	—	—	2	14	1
<i>Solidago canadensis</i>	8	28	2	6	8	T
<i>Solidago missouriensis</i>	6	21	4	3	5	T
<i>Solidago rigida</i>	7	10	1	9	28	1
<i>Tragia urticifolia</i>	—	—	—	1	4	T
<i>Viola pedatifida</i>	9	20	1	3	30	1
<i>Zizia aptera</i>	7	25	2	1	70	5

NOTE: Only species that are characteristic of a community type are listed.

<sup>a</sup>A, *Andropogon gerardii*; C, *Carex meadii*; P, *Paspalum plicatulum*; Pa, *Panicum virgatum*; S, *Schizachyrium scoparium*; Sh, *Sporobolus*<sup>b</sup>Total number of stands within community type.<sup>c</sup>Trace.

by community type<sup>a</sup> for 63 True and Upper Coastal Prairie grasslands

S Sn A, east central Texas (12)			S P Sn, Upper Coastal Prairie (18)			Sp C, north Texas (3)			T Pa Sn, north Texas (2)		
No. of stands	Frequency	Cover	No. of stands	Frequency	Cover	No. of stands	Frequency	Cover	No. of stands	Frequency	Cover
—	—	—	—	—	—	—	—	—	—	—	—
12	45	10	8	9	2	1	4	T	—	—	—
12	47	5	4	24	T	—	—	—	2	4	T
—	—	—	—	—	—	3	76	10	—	—	—
12	40	4	8	20	2	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
2	10	T	6	15	2	3	28	3	—	—	—
2	8	2	18	43	2	3	77	6	—	—	—
—	—	—	6	10	1	1	4	T	—	—	—
6	12	2	—	—	—	—	—	—	—	—	—
2	16	2	18	40	4	2	22	12	—	—	—
2	22	T	—	—	—	—	—	—	1	4	T
1	8	1	2	4	4	1	36	5	2	28	13
5	21	4	16	19	5	3	33	4	2	16	T
—	—	—	15	61	14	—	—	—	—	—	—
—	—	—	7	31	2	3	30	1	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	11	23	2	1	8	1	—	—	—
12	89	29	18	94	39	2	14	2	1	8	T
4	6	T	13	16	1	2	10	1	—	—	—
12	89	18	18	61	13	3	29	4	2	25	13
12	32	5	18	35	4	3	8	T	2	48	10
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	3	87	37	—	—	—
12	27	1	5	6	T	—	—	—	1	12	T
—	—	—	—	—	—	—	—	—	—	—	—
2	4	2	—	—	—	—	—	—	2	62	38
11	13	1	6	6	T	—	—	—	2	22	1
—	—	—	—	—	—	1	4	T	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
2	26	1	11	16	1	1	16	2	2	18	1
12	77	6	4	50	2	—	—	—	2	50	6
6	8	T	7	6	T	—	—	—	1	8	T
8	16	T	2	8	T	—	—	—	2	22	1
9	4	T	1	12	T	—	—	—	2	6	T
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	6	20	1	3	39	1	—	—	—
11	22	1	6	6	T	1	8	T	—	—	—
1	20	3	—	—	—	—	—	—	2	8	T
—	—	—	—	—	—	—	—	—	—	—	—
9	17	1	1	4	T	—	—	—	—	—	—
5	15	1	—	—	—	—	—	—	1	20	1
—	—	—	10	31	2	1	32	3	—	—	—
3	8	T	6	15	T	3	48	3	—	—	—
3	12	1	10	11	1	2	24	3	—	—	—
5	10	T	13	25	1	1	18	T	—	—	—
1	28	2	1	4	T	—	—	—	—	—	—
7	52	1	5	11	T	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
7	14	T	8	14	1	—	—	—	1	4	T
—	—	—	—	—	—	—	—	—	1	4	T
3	19	1	4	34	T	2	8	T	2	52	1
3	21	T	4	14	1	2	28	1	2	14	1
5	11	T	9	15	T	—	—	—	—	—	—
6	11	1	1	16	T	1	4	T	2	6	T
10	20	1	12	17	1	3	15	1	1	8	T
2	15	1	4	15	1	2	26	2	1	4	T
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—
6	7	T	8	9	T	1	4	1	2	6	T
—	—	—	—	—	—	—	—	—	—	—	—
—	—	—	—	—	—	—	—	—	—	—	—

<sup>a</sup>heterolepis; Sn, *Sorghastrum nutans*; Sp, *Sporobolus silveanus*; St, *Stipa spartea*; T, *Tripsacum dactyloides*.

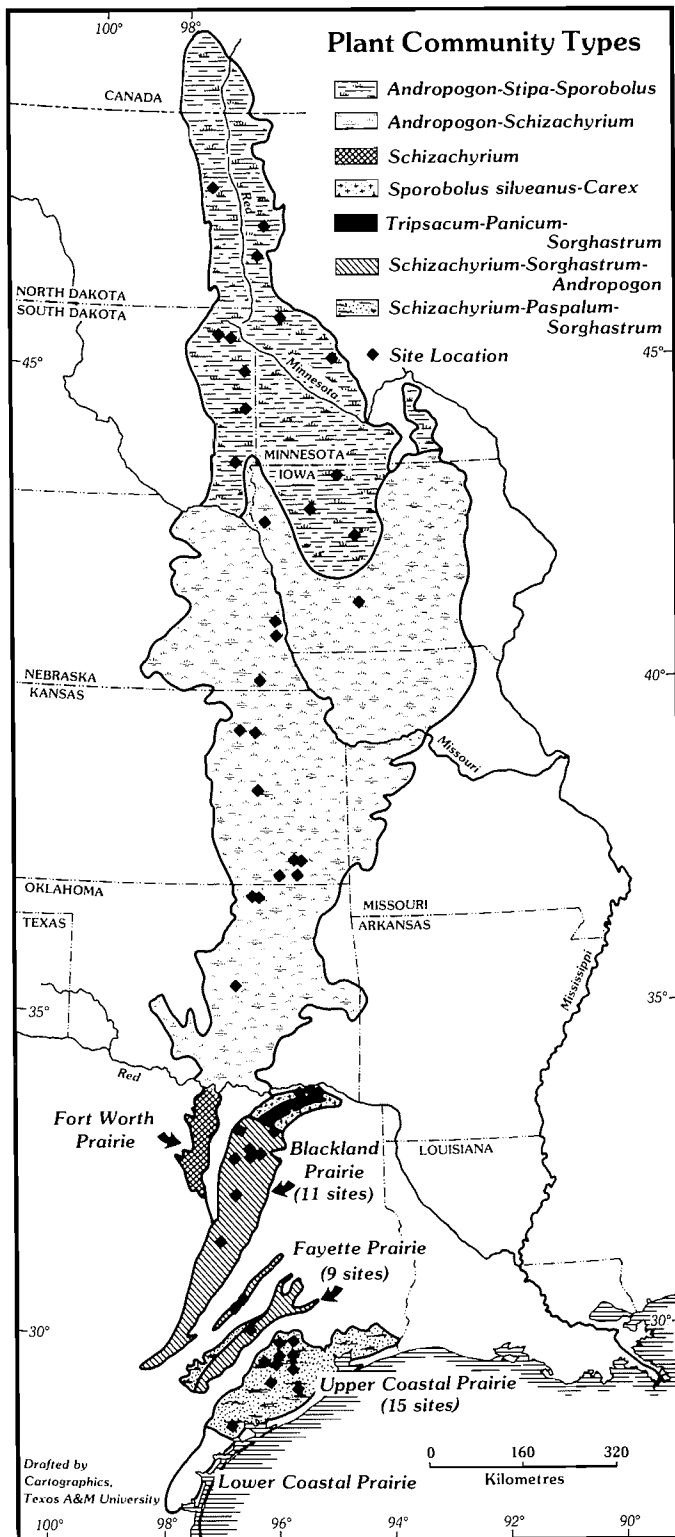


FIG. 4. Plant community types of the True and Upper Coastal Prairies.

*pendula*, *Carex meadii*, *Dichanthelium oligosanthes*, *Fimbristylis puberula*, *Koeleria pyramidata*, *Panicum virgatum*, and *Sporobolus asper*. Mean total foliar cover was 94% and a total of 156 species, including 40 graminoids, 115 forbs, and 1 woody species, were present across all stands. An average of 53 species were present per stand.

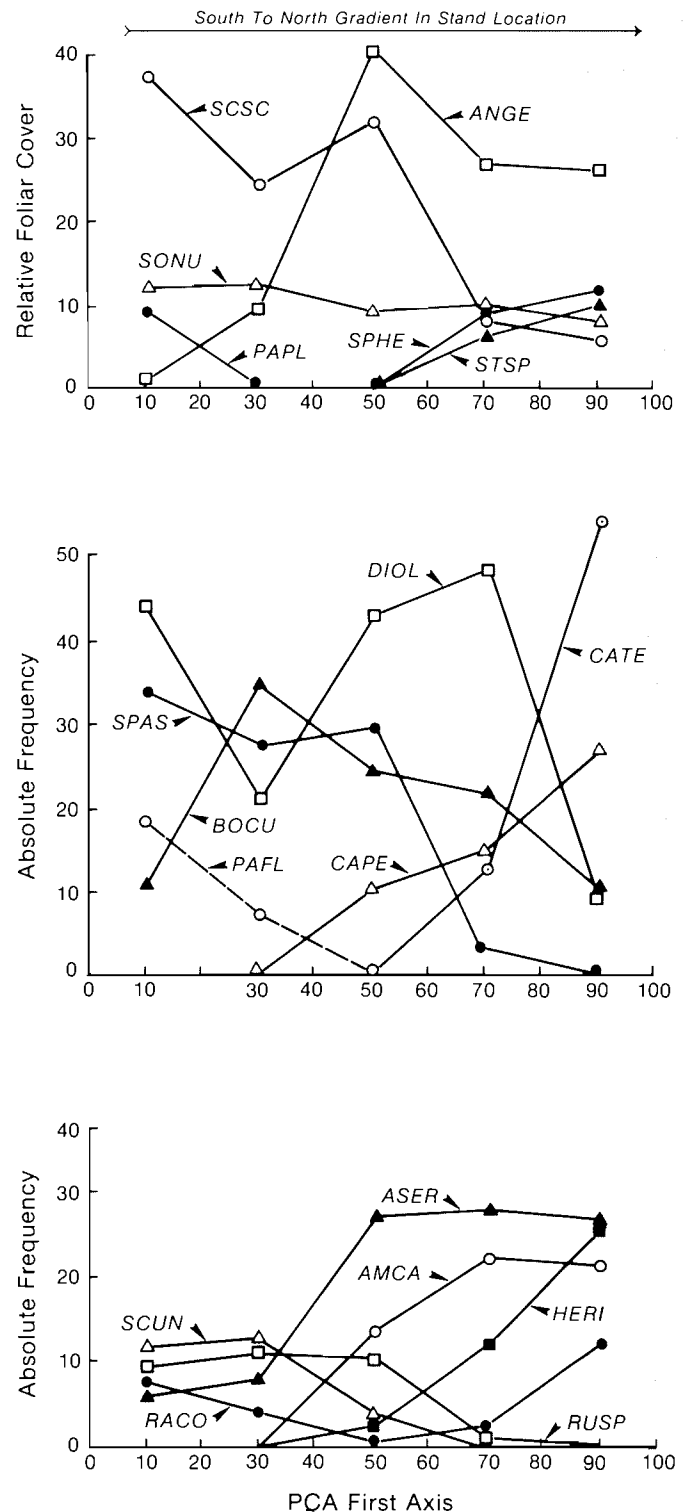


FIG. 5. Response curves for important species against the first PCA axis from ordination of 63 True and Upper Coastal Prairie grasslands. Values are averaged for stands by 20-unit intervals. AMCA, *Amorpha canescens*; ANGE, *Andropogon gerardii*; ASER, *Aster ericoides*; BOCU, *Bouteloua curtipendula*; CAPE, *Carex pensylvanica*; CATE, *Carex tetanica*; DIOL, *Dichanthelium oligosanthes*; HERI, *Helianthus rigida*; PAFL, *Paspalum floridanum*; PAPL, *Paspalum plicatulum*; RACO, *Ratibida columnaris*; RUSP, *Ruellia* sp.; SCSC, *Schizachyrium scoparium*; SCUN, *Schrankia uncinata*; SONU, *Sorghastrum nutans*; SPAS, *Sporobolus asper*; SPHE, *Sporobolus heterolepis*; STSP, *Stipa spartea*.

Three north Texas stands over Alfisols represent a *Sporobolus silveanus* – *Carex meadii* community type. *Coelorachis cylindrica*, *Dichanthelium oligosanthos*, *Fimbristylis puberula*, *Paspalum floridanum*, and *Sorghastrum nutans* were secondary graminoids. Mean total foliar cover was 94%. A total of 85 species, including 24 graminoids and 61 forbs, occurred across the stands. An average of 57 species were present per stand. Two other north Texas stands over Vertisols form a *Tripsacum dactyloides* – *Panicum virgatum* – *Sorghastrum nutans* community type. Secondary graminoids included *Bouteloua curtipendula*, *Carex microdonta*, *Paspalum floridanum*, and *Sporobolus asper*. This community type is characterized by patches of dense intermixed with sparse vegetation, and mean total foliar cover was 78%. A total of 68 species, including 17 graminoids and 51 forbs, occurred in two stands. An average of 51 species were present per stand.

Central and south central Texas stands over Vertisols form a *Schizachyrium scoparium* – *Sorghastrum nutans* – *Andropogon gerardii* community type. Secondary graminoids included *Bouteloua curtipendula*, *Carex microdonta*, *Sporobolus asper*, and *Stipa leucotricha*. Mean total foliar cover was 99%, and 154 species, including 37 graminoids, 115 forbs, and 1 woody species, occurred across all stands. An average of 41 species were present per stand.

Southern Texas grasslands, including all Upper Coastal Prairie sites, form a *Schizachyrium scoparium* – *Paspalum plicatulum* – *Sorghastrum nutans* community type. *Fimbristylis puberula*, *Paspalum floridanum*, *Scleria ciliata*, and *Sporobolus asper* were secondary graminoids. Mean total foliar cover was 84%, and 156 species, including 39 graminoids, 116 forbs, and 1 shrub, occurred across all stands. An average of 51 species were present per stand.

A fifth community type within Texas and a seventh for the entire transect is recognized on the basis of data from Dyksterhuis (1946). This is the *Schizachyrium scoparium* community type of the Fort Worth Prairie, west of areas studied within Texas but still considered a southern extension of the True Prairie (Fig. 4).

#### Species–environmental relationships

Species response curves from relative foliar cover values illustrate the general decrease in *Schizachyrium scoparium* and increase in *Andropogon gerardii* from south to north (Fig. 5). Cover values for *Sorghastrum nutans* remain fairly constant, while *Paspalum plicatulum* is a dominant only within Texas and *Stipa spartea* and *Sporobolus heterolepis* are dominants from Iowa northward. Secondary graminoids and forbs were also analyzed by plotting absolute frequency against the first PCA axis (Fig. 5).

*Andropogon gerardii*, *Stipa spartea*, and *Sporobolus heterolepis* are most important in the northern True Prairie and all had highly significant negative correlations with precipitation and temperature and positive correlations with soil OM. Other graminoids with similar correlations included *Agropyron subsecundum*, *Carex pensylvanica*, *Carex tetanica*, *Koeleria pyramidata*, and *Muhlenbergia richardsonis*. *Fimbristylis puberula*, *Paspalum plicatulum*, *Schizachyrium scoparium*, and *Sporobolus asper*, all most important within Texas, showed the opposite relationships.

*Sorghastrum nutans* was the only widely distributed dominant with no significant correlations with measured environmental variables. *Bouteloua curtipendula* and *Dichanthelium*

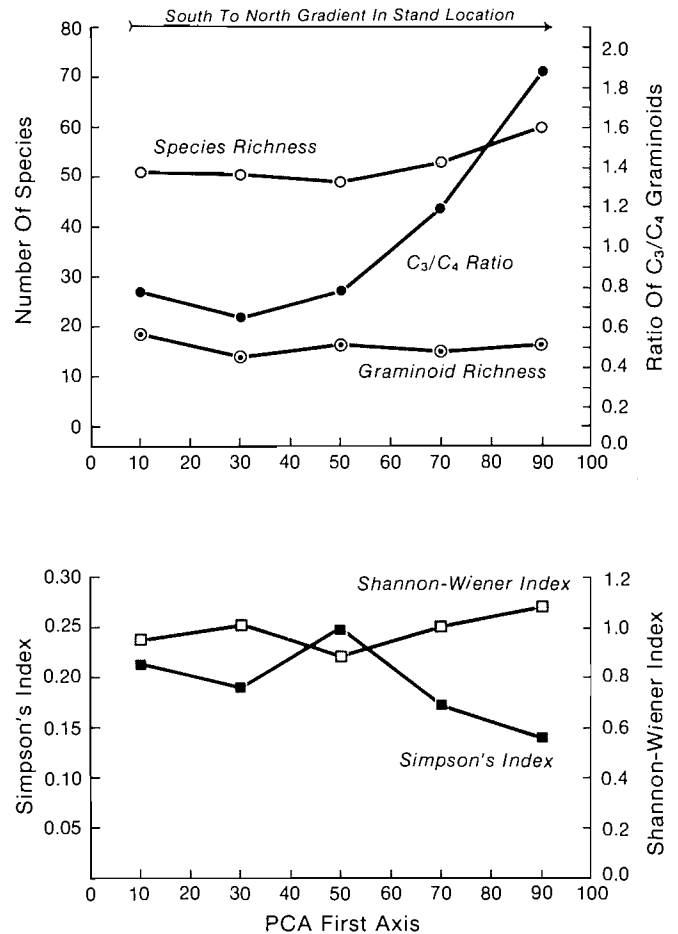


FIG. 6. Response curves for diversity indices, richness, and the ratio of C<sub>3</sub>/C<sub>4</sub> graminoids against the first PCA axis from ordination of 63 upland grasslands within the True and Upper Coastal Prairies. Values are averaged for stands by 20-unit intervals.

*oligosanthos* were widely distributed secondary graminoids which were also uncorrelated with climatic variables. However, these species along with the less widespread *Carex microdonta*, *Eriochloa sericea*, *Stipa leucotricha*, and *Paspalum setaceum* were significantly correlated with percent clay and pH of the surface soil. This was a result of their behavior with respect to soil type in Texas, with *Paspalum setaceum* restricted to loamy Alfisols and the others most common over clayey Vertisols.

#### Species diversity

Simpson's index ranged from 0.09 to 0.35, the Shannon–Wiener index ranged from 0.7 to 1.3, and richness ranged from 34 to 72 species present. Simpson's index was negatively correlated with temperature ( $P < 0.01$ ), while richness was positively correlated. There was a general decrease in richness from north to south through the True Prairie, but richness increased from the southern True Prairie to the Upper Coastal Prairie. The Shannon–Wiener index was not significantly correlated with any environmental variable. Response curves against the first PCA axis indicate only a slight decrease in dominance concentration and increase in richness from south to north (Fig. 6).

An increase in the frequency of abundant forbs to the north

is indicated by a plot of species frequency against the first PCA axis (Fig. 5). However, this trend appears exaggerated because Texas stands representing several community types, each with a different forb composition, are averaged together in the 0–20 and 20–40 segments of the first PCA axis. Average frequency for the 10 most common forbs within a given community type ranges from 36% for the *Schizachyrium*–*Sorghastrum*–*Andropogon* community type to 24% for the *Tripsacum*–*Panicum*–*Sorghastrum* community type, with a mean of 30% across all six community types.

The ratio of graminoids with the  $C_3$  versus the  $C_4$  pathway for  $CO_2$  fixation was negatively correlated with annual precipitation and temperature and positively correlated with soil OM ( $P < 0.01$ ). The  $C_3/C_4$  ratio remained relatively constant through Kansas but increased sharply from Nebraska stands northward (Fig. 6). Some of the  $C_3$  species that replace  $C_4$  species include *Agropyron subsecundum*, *Carex pensylvanica*, *Poa pratensis*, and *Stipa spartea*, while  $C_4$  graminoids that decrease northward include *Paspalum floridanum*, *Paspalum plicatulum*, *Paspalum setaceum*, and *Sporobolus asper*. Only in the northern True Prairie is any  $C_3$  grass (*Stipa spartea*) among the dominants.

### Discussion

A decrease in *Andropogon gerardii* and increase in *Schizachyrium scoparium* to the south are the primary changes in dominant species across the True Prairie – Upper Coastal Prairie continuum. An explanation of the different responses of these species may be provided by Weaver and Albertson (1944), Weaver (1954), and Albertson and Tomanek (1965). They concluded that a drought, which was most severe during the summer of 1934 but lasted 7 years in much of the central and northern True Prairie, was more detrimental to *Schizachyrium scoparium* than *Andropogon gerardii*, perhaps because the deep root system of *Andropogon gerardii* allowed it to persist in mesic areas. Consequently, after the drought, *Andropogon gerardii* spread vegetatively into the upland and “claimed much territory formerly occupied by *Schizachyrium scoparium*” (Weaver 1954). *Schizachyrium scoparium* communities lost some territory to *Sporobolus heterolepis*, which was severely affected by drought but responded more rapidly to improved conditions, perhaps as a result of higher seed production or seedling characteristics that allowed it to spread. *Stipa spartea* was another species that displaced *Schizachyrium scoparium* in some areas, possibly as a result of a greater drought tolerance or more rapid response to improved conditions.

Differential responses to fire and mowing frequency and intensity may also influence the *Schizachyrium*–*Andropogon* relationship. After 56 years of annual burning at different seasons, Towne and Owensby (1985) found that unburned communities had 30% basal cover of *Schizachyrium scoparium* and 20% *Andropogon gerardii*. Communities burned in late spring had 20% *Schizachyrium scoparium* and 45% *Andropogon gerardii*. Mowing during midsummer tends to increase the abundance of *Schizachyrium scoparium* compared with *Andropogon gerardii* (Drew 1948; Conrad 1953). Thus, the north–south shift from *Andropogon gerardii* to *Schizachyrium scoparium*, even though it corresponds with climatic change, may also be influenced by more burning and less mowing in the north versus the south, plus the influence of a drought in the 1930s that was most severe in the central and northern True Prairie.

Previous studies generally have shown that more species share dominance in the northern True Prairie, and a slight decrease in dominance concentration and increase in richness is indicated by this study (see Diamond 1983). However, lack of a pronounced trend in species diversity along a broad latitudinal climatic gradient is significant because it suggests that factors other than climate control changes in species diversity, which is contrary to many other interpretations (Monk 1967; Risser and Rice 1971; Marks and Harcombe 1975; Westman 1981). Qualitative observation indicates that overall richness considering all seral stages is greater in the southern grasslands, but no quantitative data on seral communities are available to verify this.

An increase in the ratio of  $C_3/C_4$  graminoids northward seems to indicate that  $C_3$  species are more competitive in the north. Terri and Stowe (1976) concluded that the increase in  $C_3$  versus  $C_4$  grasses at higher latitudes and elevations is most closely associated with a decrease in growing-season minimum temperatures, which have deleterious effects on  $C_4$  grasses. Sims et al. (1978) indicated that mean annual temperature, mean annual precipitation, and total annual solar radiation were positively correlated with an increase in  $C_4$  species. A decrease in soil moisture content might favor  $C_4$  over  $C_3$  species (Tieszen et al. 1979; Wentworth 1983). Thus, decreased temperatures and less severe summer moisture stress are probably causal factors in the shift from  $C_4$  to  $C_3$  graminoids from south to north.

The restricted *Sporobolus silveanus* – *Carex meadii* community type of north Texas shows little affinity for any other reported. It occurs in response to unique silty clay loam Alfisols and relatively high precipitation ( $> 105$  cm/year). *Sporobolus silveanus* is primarily a forest-margin species and has a range restricted to northern Texas and adjacent Louisiana, Oklahoma, and Arkansas. The *Tripsacum*–*Panicum*–*Sorghastrum* community type, which occupies poorly drained, clayey Vertisols in north Texas, shows affinities for lowlands of central and southern Texas and as far north as Nebraska (Weaver and Fitzpatrick 1934; Diamond 1983). Thus, it is related to lowland grasslands, but it occupies uplands of north Texas in response to poor soil drainage and high precipitation. The remaining community types form a continuum generally dominated by *Andropogon gerardii* in the north, *Schizachyrium scoparium* in the south, and a mixture of the two in the central section.

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