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ORDINATION AND DESCRIPTION OF PRAIRIE PLANT COMMUNITIES FROM THE SOUTHERN MISSOURI COTEAU IN SOUTH DAKOTA

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Abstract. *The species composition and soil-site characteristics of three prairies from the Missouri Coteau of southeastern South Dakota were used 1) to determine the major environmental variables responsible for vegetational patterning and 2) to describe the plant communities on these prairies. Vascular plant species composition was significantly correlated ($p < 0.01$) with a suite of variables that strongly influence available soil moisture, and with soil pH and conductivity. Cluster analysis yielded five groups at the 38% similarity level. From the lowest (in elevation) and most mesic to the highest and most xeric, the five groups (communities) are: wet meadows with prairie cordgrass (*Spartina pectinata* Link) and sedge (*Carex praegracilis* W. Boott.) as the most important species; meadows with prairie cordgrass and switch grass (*Panicum virgatum* L.); swales with Kentucky bluegrass (*Poa pratensis* L.) and big bluestem (*Andropogon gerardii* Vitman); slopes with Kentucky bluegrass, sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.), and needleleaf sedge (*Carex eleocharis* Bailey); and crests with Kentucky bluegrass and needleleaf sedge.*

The Missouri Coteau is one of the physiographic subdivisions of the Great Plains, a vast expanse of grasslands that occupies the interior of North America (Fenneman 1931). Its rolling hills of glacial origin lie immediately east of the Missouri River and extend northward as a band of variable width from the southern border of South Dakota to the northern border of North Dakota (Fig. 1). According to Kuchler (1964), the potential natural vegetation of the Coteau is wheatgrass, bluestem, and needlegrass (*Agropyron*, *Andropogon*, and *Stipa*). But as Tatina (1987) has shown, the composition of prairies may not match what Kuchler has predicted for an area. It is, however, important to have knowledge of the composition of the vegetation of natural or near natural areas so that this can be used as a "benchmark" to assess the effects of man's activities on the environment (Moir 1972).

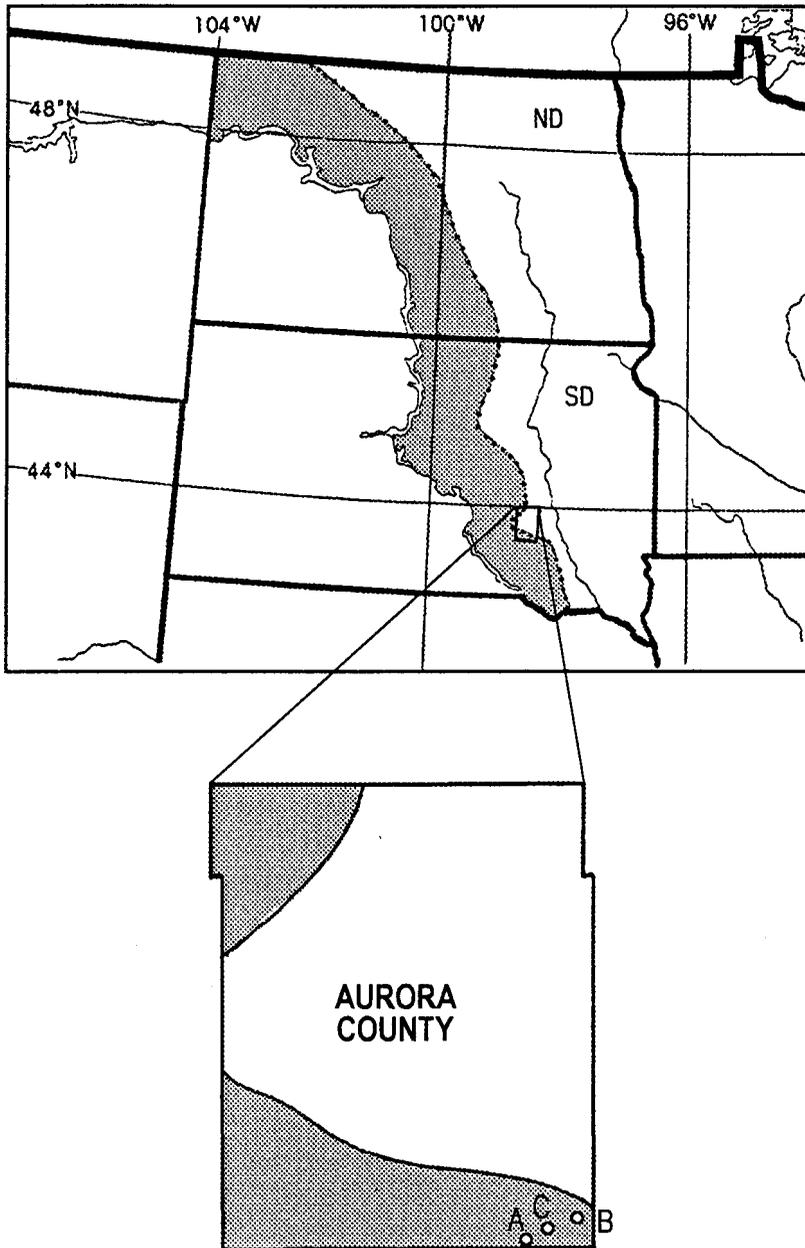


Figure 1. Location of study sites (A, B and C) in southeastern Aurora County. Stippling indicates the extent of the Missouri Coteau in North and South Dakota.

Although several studies have described the plant communities of prairies on the northern Missouri Coteau (Barnes et al. 1983; Meyer 1985; Kirby and Ransom-Nelson 1987; Lura et al. 1988), none have examined the southern end. Thus, what we know about prairies in the southern portion must be inferred from other studies. The objectives of this study are 1) to determine the nature of the environmental gradients to which the vegetation is responding and 2) to describe the communities of prairies that lie on the southern Missouri Coteau.

Study Areas

This study was conducted on three prairies in southeastern Aurora County, South Dakota, between 35 and 40 km southwest of Mitchell (Fig. 1). All three prairies lie near the southeastern edge of the Missouri Coteau. The soils here are well-drained loams of the Houdek-Ethan and Delmont-Enet-Talmo associations and classified as Mollisols (suborder Ustoll) (Schlepp 1980). Each area is mowed annually for hay sometime after 1 July, a practice that has been followed for thirty years or more. According to the owners no fires have occurred in this area for over thirty years. The climate is continental with a mean annual precipitation of 54 cm, most of which falls during the growing season (Schlepp 1980).

The first study area (B in Fig. 1), sampled in 1987, is a 32 ha prairie in the W 1/2 of Section 22 of T101N, R63W. This area possesses a rolling topography in which the uplands are represented by a single knoll that slopes gently to the southeast, east, and north. Elevations range from 480 m to 488 m above mean sea level (AMSL). Choteau Creek, an intermittent stream, enters the meadow at the northeast corner and meanders back and forth several times before leaving from the southeast corner. Other than periodic flooding of the meadows and annual mowing, the only other major disturbance is badger (*Taxidea taxus* Schreber) tunneling.

The second area (A in Fig. 1), sampled in 1989, is a 30 ha, gently rolling prairie located in the S 1/2 of Section 31 of T101N, R63W. Here the lowlands are about 476 m AMSL extending to knolls reaching 480 m AMSL. Part of the lowlands is occupied by a periodically flooded cattail marsh. This area lies about 6 km southwest of area B. Numerous badger holes are found on crests here also.

The third area (C in Fig. 1), sampled in 1991, situated between the other two, is located in the SW 1/4 of Section 29 of T101N, R63W. It occupies 33 ha of rolling land between 483 m and 503 m AMSL. Of the three areas, it is

the highest in elevation and has the steepest slopes. There are no streams or standing water here, although some runoff from an adjacent corn field flows through the swales. Badger holes, the only major perturbations, are restricted to the uplands.

Materials and Methods

In June 1987, 1989, and 1991, species presence of vascular plants in forty 0.1 m² circular quadrats were recorded at each sampling site. The quadrats were spaced at 1m intervals along radii that extended N, S, W, and E from the center of the site. Site centers were located 20 m apart along a transect following the predominant topographic gradient at each area. Twenty-six, 24, and 20 sites were sampled at study areas B, A, and C respectively. Crest, upper slope, lower slope, swale (an upland depression), meadow, or wet meadow were used to describe the topographic position of each sampling site in the field.

Species presence data for each site were converted to frequency of occurrence and then to relative frequency. These data, used as an estimate of species importance at each site, were subjected to detrended correspondence analysis (Biostat II 1986) as described by Gauch (1982). A hierarchical cluster analysis of percent similarity data calculated from the relative frequency of species at each sampling site was employed to classify the vegetation.

At the center of each sampling site, five soil samples were removed to a depth of 15 cm and analyzed for soil texture by the Bouyoucos method (Day 1965). Soil pH was measured with a hydrogen electrode in a 1:1 (w:v) aqueous suspension following the protocol of Peech (1965). Soil conductivity was measured following the procedures of Brower and Wilcox (1965).

Richness and heterogeneity components of species diversity were determined for each sampling site. While richness is a measure of the absolute number of species, heterogeneity evaluates the apparent number of species by incorporating the number of individuals in each species (Peet 1974). In this study species richness is the number of species per 0.1 m², the size of the sample quadrat. Species heterogeneity was calculated using the complement of Simpson's Index (Whittaker 1972). Values for this measure increase to unity as the number of individuals becomes more evenly shared among species. Plant names follow the nomenclature in the Great Plains Flora Association (1986).

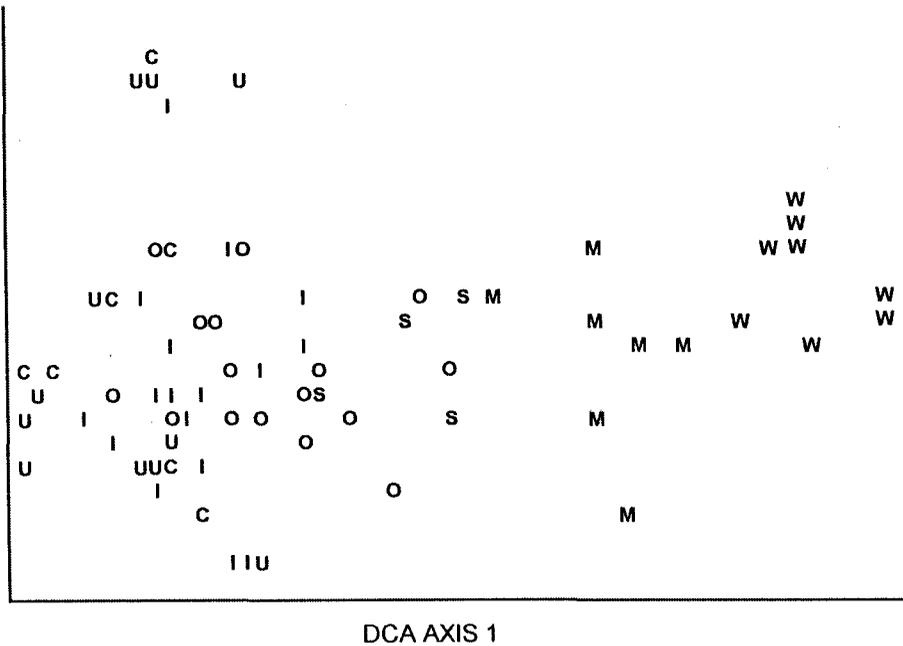


Figure 2. Coenocline resulting from detrended correspondence analysis. Only the horizontal axis is meaningful, the vertical axis being used only to separate closely placed sites. Letters indicate the topographic position of a site as defined in the field: C = crest, I = middle slope, M = meadow, O = lower slope, S = swale, U = upper slope, W = wet meadow.

Results

Coenoclines

Detrended correspondence analysis ordered the 70 stands along a first axis (Fig. 2), the length of which was 4.49 standard deviations (eigenvalue = 0.701). Because inspection of this ordination sequence indicated that the lower, more mesic sites were furthest from the origin, it was inferred that the coenocline might represent a topographic-soil moisture gradient. Indeed, significant negative correlations were found between the axis 1 sequence and elevation ($r_s = -0.349$, $p < 0.01$) and topographic position ($r_s = -0.813$, $p < 0.01$). In addition, the stand sequence was significantly correlated with soil sand content ($r_s = -0.589$, $p < 0.01$) and clay content ($r_s = 0.582$, $p < 0.01$). As has been shown for other prairies, soil moisture is highly correlated with soil sand and clay content (Tatina 1987) and topographic position

(Tolstead 1942; Barnes and Harrison 1982; Tatina 1987). In these studies, upland soils were high in sand content, low in clay, and low in soil moisture; conversely, meadow and wet meadow soils were low in sand, high in clay, and high in soil moisture. In addition, very high intercorrelations among soil moisture, clay content, sand content, and topographic position were found *within* each of the study areas (personal observations). Soil pH ($r_s = 0.476$, $p < 0.01$) and conductivity ($r_s = 0.328$, $p < 0.01$) were also significantly correlated with the coenocline, the positive correlations generally indicating an increase in pH and salinity from uplands to lowlands. Crist and Glenn-Lewin (1978) reported a similar correlation from a prairie in Iowa, claiming that upland soils were acidic due to leaching of cations and that lowland soils were alkaline due to "upward capillary movement of water" containing calcium ions. Along the coenocline represented by axis 1, species richness ($r_s = -0.734$, $p < 0.01$) and heterogeneity ($r_s = -0.637$, $p < 0.01$) decreased significantly from uplands to lowlands. Similar trends have been reported in other grassland studies (Dix and Smeins 1967; Barnes et al. 1983; Tatina 1987).

Species Clusters

Hierarchical cluster analysis of the 70 stands produced five clusters at the 38% similarity level (Fig. 3). The species composition and soil-site characteristics of the five clusters are given in Table 1 and Figure 4 respectively. The first cluster unites all eight sites (numbers 1-8) that were described in the field as wet meadows and one site (number 45) described as a meadow. On these sites, prairie cordgrass (*Spartina pectinata* Link) shared importance with sedge (*Carex praeegracilis* W. Boott.). Other important grass-like species included spikerush (*Eleocharis erythropoda* Steud.) and sedge (*Carex lanuginosa* Michx.). Yellow sweet clover and white sweet clover (*Melilotus* spp.) and hedge-nettle (*Stachys palustris* L.) were the most frequently encountered forbs. Species richness (4.35 species/0.1 m²) and heterogeneity (0.836) were the lowest when compared to the other clusters. Soils on sites in this cluster were alkaline loams of moderate salinity containing the highest percentage (24.78%) of clay.

In the six-site cluster (numbers 44 and 46-50) designated in the field as meadows, prairie cordgrass, big bluestem (*Andropogon gerardii* Vitman), and switchgrass (*Panicum virgatum* L.) were the important overstory species. Beneath them were sedge and Kentucky bluegrass (*Poa pratensis* L.). Sweet clover (*Melilotus* spp.) and paniced aster (*Aster simplex* Willd.) were the important forb species. Several salt tolerant species, notably prairie

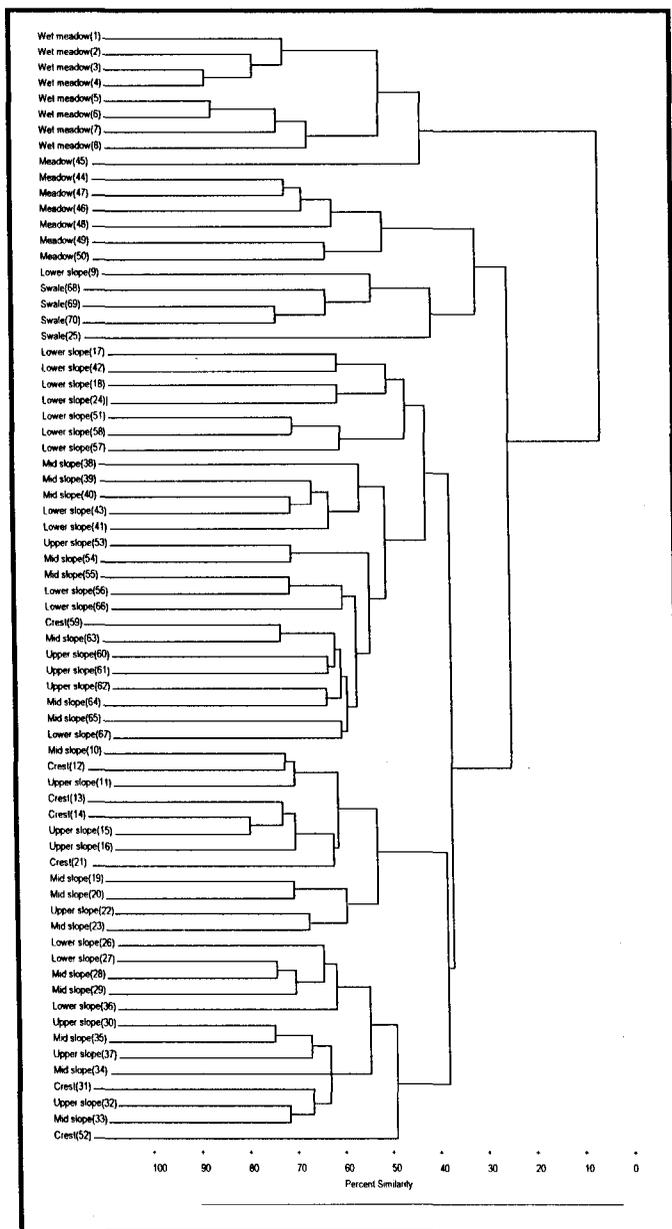


Figure 3. Classification of 70 sampling sites based on percent similarity. At the 38% similarity level five clusters were recognized: wet meadows include sites 1-8 and 45, meadows include sites 44 and 46-50, swales include sites 9, 25, and 68-70, slopes include sites 17, 18, 24, 38-43, 51, and 53-67, and upper slopes include sites 10-16, 19-23, 26-37, and 52.

TABLE 1

SPECIES COMPOSITION OF CLUSTERS PRODUCED BY CLUSTER ANALYSIS SHOWN IN FIGURE 3. DATA ARE RELATIVE FREQUENCY MEANS AND STANDARD ERRORS (IN PARENTHESES) OF THOSE SPECIES WHOSE RELATIVE FREQUENCY EQUALLED OR EXCEEDED 0.020 IN ANY CLUSTER

Species	Topographic Position				
	Crest	Slope	Swale	Meadow	Wet Meadow
<i>Poa pratensis</i>	.090(.005)	.131(.005)	.203(.017)	.059(.007)	.005(.004)
<i>Carex eleocharis</i>	.072(.006)	.067(.022)	.008(.005)	0	0
<i>Stipa comata</i>	.047(.007)	.013(.003)	.001(.001)	0	0
<i>Dichanthelium wilcoxianum</i>	.044(.006)	.027(.005)	0	0	0
<i>Aristida purpurea</i>	.043(.007)	.021(.005)	0	0	0
<i>Bouteloua gracilis</i>	.042(.009)	.012(.004)	0	0	0
<i>Melilotus</i> spp.	.040(.008)	.022(.007)	.013(.004)	.104(.010)	.115(.028)
<i>Bromus japonicus</i>	.040(.008)	.013(.003)	.056(.029)	.013(.007)	.015(.012)
<i>Koeleria pyramidata</i>	.039(.004)	.026(.004)	.005(.004)	0	0
<i>Aster ericoides</i>	.034(.006)	.034(.005)	.004(.004)	.008(.003)	.004(.004)
<i>Lactuca oblongifolia</i>	.024(.003)	.023(.005)	.009(.008)	0	0
<i>Artemisia ludoviciana</i>	.024(.006)	.012(.004)	.021(.021)	.005(.003)	0
<i>Stipa spartea</i>	.023(.006)	.048(.010)	.002(.001)	.011(.008)	0
<i>Rosa arkansana</i>	.022(.005)	.030(.005)	.048(.023)	.023(.013)	0
<i>Lygodesmia juncea</i>	.021(.005)	.012(.003)	0	0	0
<i>Helianthus rigidus</i>	.016(.005)	.049(.009)	.026(.022)	.028(.011)	0
<i>Andropogon gerardii</i>	.011(.004)	.012(.009)	.133(.024)	.076(.012)	0
<i>Bouteloua curtipendula</i>	.006(.002)	.067(.009)	.012(.012)	.010(.003)	0
<i>Andropogon scoparius</i>	.003(.001)	.026(.007)	0	.030(.020)	0
<i>Agropyron smithii</i>	.003(.002)	.010(.002)	.048(.011)	.013(.006)	0
<i>Taraxacum</i> spp.	.003(.002)	.004(.002)	.008(.003)	.037(.010)	.028(.009)
<i>Panicum virgatum</i>	.002(.002)	.010(.004)	.016(.012)	.074(.007)	.026(.026)
<i>Carex brevior</i>	.001(.001)	.011(.005)	.060(.024)	.014(.014)	0
<i>Spartina pectinata</i>	0	.001(.001)	.112(.031)	.080(.018)	.225(.012)
<i>Elymus canadensis</i>	0	.002(.002)	0	.029(.006)	0
<i>Carex prae-gracilis</i>	0	.006(.004)	.001(.001)	.062(.014)	.209(.013)
<i>Eleocharis erythropoda</i>	0	.003(.002)	.001(.001)	.015(.009)	.091(.030)
<i>Phalaris arundinacea</i>	0	.005(.005)	.007(.007)	0	.025(.008)
<i>Anemone canadensis</i>	0	0	.074(.074)	.015(.004)	0
<i>Aster simplex</i>	0	0	.005(.005)	.044(.017)	.007(.007)
<i>Carex lanuginosa</i>	0	0	0	.003(.003)	.063(.019)
<i>Hordeum jubatum</i>	0	0	0	.004(.003)	.051(.012)
<i>Stachys palustris</i>	0	0	0	0	.063(.021)
<i>Mentha arvensis</i>	0	0	0	0	.028(.009)

wedgegrass (*Sphenopholis obtusata* [Michx.] Scribn.) and centaury (*Centaureum exaltatum* [Griseb.] W. Wright ex Piper.), were present at low frequencies at most sites. Species richness (7.83) and diversity ($D_s = 0.937$)

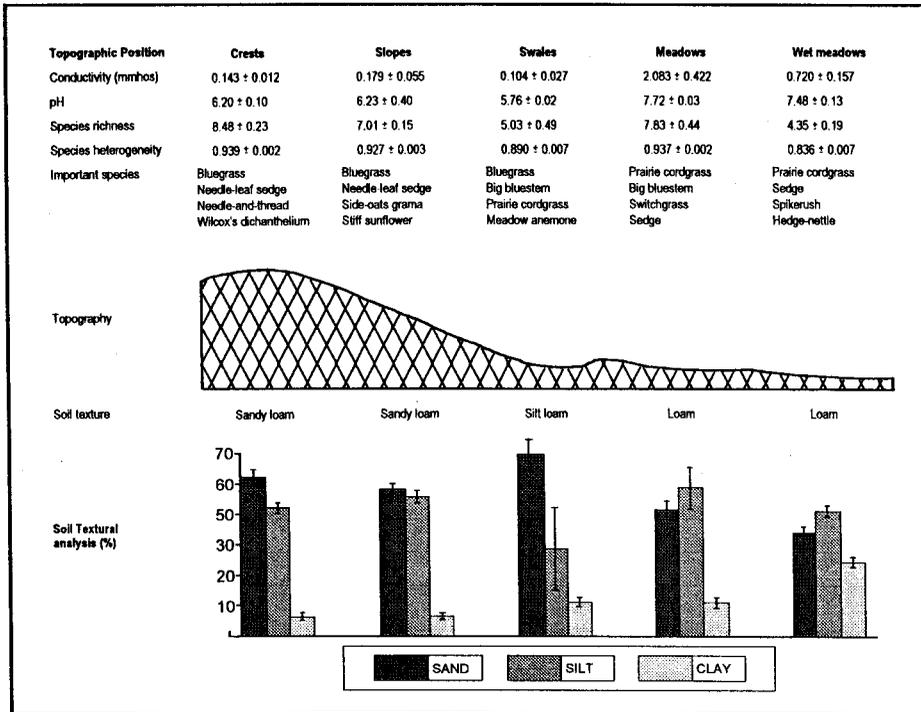


Figure 4. Soil-site characteristics for clusters produced by hierarchical cluster analysis. Numerical data are means and standard errors.

were among the highest for all clusters. Soils of the meadows were alkaline loams of high, but variable, salinity (2.08 +/- 0.42 mmhos/cm).

Four sites that had been field classified as swales (i.e., upland depressions) were clustered together with one designated as a lower slope. In this group the most frequently encountered grasses were Kentucky bluegrass, big blue stem, and prairie cordgrass. Associated with them were sedge (*Carex brevior* [Dew.] Mack. ex Lunell.), Japanese brome (*Bromus japonicus* Thunb. ex Murr.), meadow anemone (*Anemone canadensis* L.), and prairie wild rose (*Rosa arkansana* Porter). Here species richness was low (5.03). The acidic silt loams of the swales were very low in salinity (0.104 mmhos/cm).

At the 38% similarity level, cluster analysis grouped together 25 sites that occupied several topographic positions. In the field 20 of these sites were designated middle to lower slopes. The remaining five sites were from upper slopes and crests. Because the majority of sites were from mesic slope positions this cluster is called the slopes. Two mid-height grass species—Kentucky bluegrass and sideoats grama (*Bouteloua curtipendula* [Michx.] Torr.)—were important here. Abundant, but less frequently encountered, species included needleleaf sedge (*Carex eleocharis* Bailey), and porcupine-grass (*Stipa spartea* Trin.). Stiff sunflower (*Helianthus rigidus* [Cass.] Desf.) was the most common forb. Species richness (7.01) and heterogeneity ($D_s = 0.927$) were high. Soils of the slopes were acidic, sandy loams of low salinity.

Twenty-five sites comprised the final cluster. In the field, 13 of these had been designated as upper slopes and crests, 9 were middle slopes and 3 were lower slopes. On the basis of the plurality of upland sites, this cluster was labeled upper slopes. These sites had the highest species richness (8.48) and heterogeneity ($D_s = 0.939$) when compared with the other clusters. In the overstory, Kentucky bluegrass and needle-and-thread (*Stipa comata* Trin. & Rupr.) were the most important grass species. Conspicuous in the understory were needleleaf sedge, Wilcox dichanthelium (*Dichanthelium wilcoxianum* [Vasey] Freckmann), purple three-awn (*Aristida purpurea* Nutt.), and blue grama (*Bouteloua gracilis* [H. B. K.] Lag. ex Griffiths). The two forb species with the highest frequency of occurrence were *Melilotus* spp. and frost aster (*Aster ericoides* L.). Other commonly encountered forbs included blue lettuce (*Lactuca oblongifolia* Nutt.) and white sage (*Artemisia ludoviciana* Nutt.). Somewhat acidic, sandy loams of low salinity supported these species.

Conclusions

Soil moisture often has been proposed as the major factor determining the mosaic of communities in grasslands (Curtis 1955; Dix and Butler 1960; Partch 1962; Bliss and Cox 1964; Dix and Smeins 1967; Ungar 1970; Barnes and Harrison 1982; Barnes et al. 1983; Nelson and Anderson 1983; Archer 1984; Tatina 1987; Umbanhowar 1992). This was also the case at the three Aurora County prairies. The coenocline resulting from the analysis was significantly correlated with those variables (i.e., clay and sand content and topographic position) that have been found to strongly influence available soil moisture. Hierarchical cluster analysis of the sites using vegetation data

also reflected soil moisture differences (inferred from soil texture) between clusters (Fig. 4). That available soil moisture should exert such an influence fits with the magnitude of importance water plays in photosynthesis, seed germination, growth, transport, tropic, and nastic movements.

Available soil moisture, however, is a complex ecological variable. It is strongly influenced by topography, soil texture, and amount of vegetative cover. In turn, it may determine the availability of soil nutrients (Schimel et al. 1991). Notwithstanding the complex nature of soil moisture, species richness and heterogeneity generally decreased from upland sites to lowland sites (Fig. 4). Similar trends have been noted in other studies on grasslands (Dix and Smeins 1967; Redmann 1972; Barnes et al. 1983; Archer 1984) although none have attempted to explain them.

The intermediate disturbance hypothesis (Connell 1978; Petraitis et al. 1989) predicts that species diversity will reach a maximum in communities where intermediate levels of disturbance exist. At low levels of disturbance, diversity will be low because small perturbations do not sufficiently reduce the competitive abilities of the established species to allow the entry of colonizers. Where disturbance exists at high levels, low diversity ensues because large perturbations decimate the inhabitants. Collins and Barber (1985) have tested this hypothesis in mixed-grass prairie and found that in addition to intensity, different types of disturbances may produce additive effects such that one type of disturbance may reduce competition while another creates new niches.

In the Missouri Coteau prairies the entire area is disturbed annually by mowing in July. Annual mowing has been shown to increase the number of exotic species in prairie communities (Gibson 1989), and thus may be an intermediate level of disturbance. However, annual mowing alone will not account for the decrease in diversity with increasing soil moisture unless mowing has a differential disturbance effect along a soil moisture gradient. No studies have examined this. While mowing was ubiquitous on the study areas, periodic flooding is restricted to the wet meadows. Such flooding may be a severe disturbance as soils here become anoxic, exposing plants to toxic reduced ions and organic acids (Crawford 1992). Later, as these soils dry and become difficult to wet, shallow-rooted species may be eliminated. Thus, when compared to upland sites some of the lowlands may be subjected to high levels of disturbance resulting in lower species diversity. On upland sites high species diversity may be due to the additive effects of annual mowing and badger activity. As badgers excavate their dens they destroy

roots and create piles of exposed soil that may reduce competition from resident species and create new niches.

The meadows whose richness and diversity nearly equalled that of the uplands (Table 1) proved to be the one exception to the trend in species diversity. It should be noted that all of the stands in this cluster were from one of the sample areas (A in Fig. 1). As a group, the soils from these stands exhibited the highest levels and the broadest range of salinity, with conductivity values spanning 2.900 mmhos/cm. Such a steep gradient in soil salinity would increase the number of niches available for occupancy. Since prairie species have been shown to sort out along soil salinity gradients (Ungar 1970; Redmann 1972), a high species diversity in the meadows is not unexpected.

Several non-native species—Kentucky bluegrass, Japanese brome, and sweet clover—reached high relative frequencies in the three study areas. These probably entered from adjacent roadsides and croplands and may be promoted by an annual regime of early summer mowing, a reduction in fire frequency, and inadvertent nitrogen fertilization. Summer mowing has been shown to promote Kentucky bluegrass (Engle and Bultsma 1984) and other exotic species (Gibson 1989). Furthermore, the abundance of Kentucky bluegrass is reduced by burning (Christiansen 1972; Engle and Bultsma 1984; Towne and Owensby 1984; Gartner et al. 1986; Abrams and Hulbert 1987). Because spring burns reduce Japanese brome, a weedy, annual grass (Whisenant 1990), its presence at high levels may be due to the prolonged absence of fire. The same may be said for sweet clover (Kline 1986). Finally, Wedin and Tilman (1992) have shown that small increases in soil nitrogen promote Kentucky bluegrass and decrease competition from big bluestem and little bluestem (*Andropogon scoparius* Michx.). This added nitrogen may enter the prairies in dust or water from adjacent cropland, pasture, and feedlots. Thus, agricultural practices, especially mowing, most probably account for the presence, at high frequencies, of these several non-native species.

All three of the dominant species (i.e., western wheatgrass, big bluestem and porcupine-grass) listed by Kuchler (1964) were present in the three prairies studied. However, only big bluestem was found to be dominant and then only on mesic sites. Western wheatgrass and porcupine-grass were subordinate species on all sites, reaching a maximum of 4.8% relative frequency in swales and on slopes, respectively. The low abundance of these species may be due to competition from non-native invading species like Kentucky bluegrass. Nonetheless, the vegetation of prairies on the Missouri Coteau respond to the same gradients found in all prairies, the predominant

one being a soil moisture gradient. This being the case, their future composition will be determined largely by long term patterns in available moisture and by agricultural practices.

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