Plant Community Patterns on Upland Prairie in the Eastern Nebraska Sandhills

Walter H. Schacht
University of Nebraska-Lincoln, wschacht1@unl.edu

Jerry D. Volesky
University of Nebraska-Lincoln, jvolesky1@unl.edu

Dennis Bauer
University of Nebraska-Lincoln, dbauer1@unl.edu

Alexander Smart
University of Nebraska-Lincoln

Eric Mousel
University of Nebraska-Lincoln

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WALTER H. SCHACHT, JERRY D. VOLESKY, DENNIS BAUER, ALEXANDER J. SMART, and ERIC M. MOUSEL

Department of Agonomy, University of Nebraska,
Lincoln, NE 68583-0915 (WHS, AJS, EMM)
West Central Research and Extension Center, Rt. 2 Box 46A,
University of Nebraska, North Platte, NE 69101 (JDV)
West Central District (B-K-R), University of Nebraska,
148 W 4, Ainsworth, NE 69210 (DB)

ABSTRACT -- Topography is an important factor in determining vegetation patterns in grasslands. We collected frequency of occurrence data from transects on dune tops, south-facing slopes, north-facing slopes, and interdunal valleys in the eastern Sandhills of Nebraska to determine the effect of topographical position on plant species composition. We used canonical discriminant analysis to separate the four topographical positions based on frequency of occurrence of the 18 principal plant taxa. Topographic position played an important role in plant distribution on upland prairie with interdunal transects strongly separated from transects on other topographical positions. Bluegrasses (*Poa* L. spp.), switchgrass (*Panicum virgatum* L.), and white sage (*Artemisia ludoviciana* Nutt.) were highly associated with interdunal valleys. Little bluestem [*Schizachyrium scoparium* (Michx.)] and cool-season grasses, such as needlegrasses (*Stipa* L. spp.) and Junegrass [*Koeleria pyramidata* (Lam.) Beauv.], tended to be associated with north-facing slopes and warm-season grasses, such as prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.] and sand bluestem (*Andropogon hallii* Hack.), tended to be associated with south-facing slopes. Sedges (*Carex L.* spp.), western ragweed (*Ambrosia psilostachya* DC.), and Scribner dichanthelium [*Dichanthelium oligosanthes* (Schult.) Gould var. *scribnerianum* (Nash)] were the most common taxa occurring over all topographic positions. Aspect proved to be an important factor in influencing vegetation distribution in the eastern Sandhills of Nebraska.

Key words: canonical discriminant analysis, frequency of occurrence, Sandhills, topography, vegetation patterns.

The vegetation of the Nebraska Sandhills has been described as a unique mixture of plant species from other prairie types, including the tallgrass and shortgrass prairies (Kaul 1998). The Nebraska Sandhills covers about 50,000 km^2 and provides a wide variety of habitats from xeric dune tops to wetlands. The dune formations, or upland prairie, dominate the landscape and compose about 90% of the land area. Hydrologic properties of the sandy soils on uplands allow for rapid infiltration of preciptation, with little or no runoff, and provide adequate growing conditions for the dominant tall grasses (Burzlaff 1962). Mid and short grasses are in the understory of tall grasses or form the grass canopy in areas where conditions are not favorable for tall grasses. A wide variety of forbs are common but are secondary to the grasses in terms of cover and biomass production. Shrubs are present but account for relatively little cover or biomass production except in localized areas (Tolstead 1942, Kaul 1998). The Nebraska Sandhills region is dominated by C_4 grass species, but there is a rich mixture of C_3, C_4, and CAM species across the landscape.

Plant species composition of the upland vegetation is dynamic, temporally and spatially. Pool (1914), in the first detailed survey of Nebraska Sandhills vegetation, reported that a bunchgrass association was the most characteristic type of vegetation on the uplands. Although he mentioned sand bluestem (*Andropogon hallii* Hack) as a dominant, he rated little bluestem [*Schizachyrium scoparium* (Michx.)] as the most frequent and dominant plant of the bunchgrass association and of the Nebraska Sandhills as a whole. By the mid- to late-1930's, however, Frolik and Shepherd (1940) reported that prairie sandreed [*Calamovilfa longifolia* (Hook) Scribn.], hairy grama (*Bouteloua hirsuta* Lag.), and sand dropseed [*Sporobolus cryptandrus* (Torr.) A. Gray] were the dominants and that little bluestem was relatively uncommon on upland range in Cherry County of the northcentral part of the Nebraska Sandhills. Tolstead (1942) also reported that prairie sandreed was the most characteristic grass of the Sandhills in Cherry County; however, depending on the site and successional stage, it was commonly a codominant with sand bluestem, hairy grama, blue grama [*Bouteloua gracilis* (H.B.K.) Lag. *ex* Griffiths], or needle-and-thread (*Stipa comata* Trin. & Rupr.). This apparent decline in prevalence of little bluestem on the uplands between the early 1900's and the late 1930's was considered to be an effect of the 1930's drought (Weaver and Albertson 1939, Frolik and Shepherd 1940). Recent reports (Burzlaff 1962, Barnes et al. 1984, Bragg 1998) indicate that little bluestem is again a codominant on Nebraska Sandhills upland sites.

Topographic position on upland prairie plays a critical role in species composition as certain species are characteristic of dune tops whereas others are found principally in the dry interdunal valleys. Barnes and Harrison (1982) reported that the distribution of plants on uplands in the western Sandhills of Arthur County, Nebraska was related to soil texture and subsurface moisture availability. Dry, interdunal valleys had finer-textured soils with relatively high moisture content in the upper part of the soil profile until mid-summer when usable water was largely depleted by a dense stand of early-growing, shallow-rooted grasses (e.g., blue grama), sedges (*Carex* L. spp.), and forbs (Barnes and Harrison 1982, Barnes et al. 1984). Dune tops and slopes had coarse-textured soils and tended to be dominated by tall grasses, e.g., prairie sandreed, sand bluestem, and little bluestem, with extensive root systems that exploited deeper sources of soil water. Effect of aspect, e.g., north-facing vs. south-facing slopes, on plant community distribution was not determined. On another site in the western Sandhills, Bragg (1978) reported that vegetation on south-facing slopes of a choppy sands range site was predominantly prairie sandreed, a warm-season grass, whereas north-facing slopes were dominated by needle-and-thread, a cool-season grass. Differences in temperature, humidity, and evaporation rate between north and south aspects probably affected plant distribution across topographic position (Bragg 1978).

These earlier studies were key in characterizing the relationship between topographic position and vegetation cover; however, they were conducted on areas not grazed by livestock (Barnes and Harrison 1982, Barnes et al. 1984), did not include the full range of topographic positions (Barnes and Harrison 1982, Barnes et al. 1984), were designed as descriptive studies (Tolstead 1942, Barnes et al. 1984), and/or were conducted in the western Nebraska Sandhills (Barnes et al. 1984, Bragg 1978). The objective of our study was to determine the effect of topographic postition on plant species composition of upland sites grazed by cattle (*Bos taurus*) in the eastern Sandhills of Nebraska.

MATERIALS and METHODS

The study was conducted on the University of Nebraska's Barta Brothers Ranch, a 2,350 ha ranch in the eastern Nebraska Sandhills. The ranch is located 30 km south of Long Pine in Rock and Brown counties (42°14′N, 99°39′W). Prairie of this area is typical of the eastern Nebraska Sandhills in terms of topography, soils, and vegetation. Over 90% of the ranch is classified as upland prairie with the remainder being wet meadows concentrated in the southcentral part of the ranch.

Upland prairie is dominated by sands range sites. Dunes are oriented west-by-northwest to east-by-southeast and slope (5 to 15%) down to dry valley bottoms. Steep dunes (greater than 20% slope), characterized by the choppy sands range site, are uncommon. Relief from dune top to adjacent valley floor is less than 40 m. Soils of the uplands are in the Valentine series (mixed, mesic Typic Ustipsamments). The climate is semiarid with a mean annual precipitation of 553 mm (64-year mean) at Ainsworth in northern Brown County (NOAA 1998). As much as 80% of the precipitation falls between April and September with May and June the wettest months. The 1990's were particularly wet with mean annual precipitation at 625 mm (NOAA 1998), which resulted in a relatively high water table. Vegetation of the study area is representative of the Nebraska Sandhills with warm-season tall grasses, i.e., prairie sandreed, sand bluestem, little bluestem, and switchgrass (*Panicum virgatum* L.), dominating the landscape. Native cool-season grasses, i.e., needle-and-thread, porcupine-grass (*Stipa spartea* Trin.), and Junegrass [*Koeleria pyramidata* (Lam.) Beauv.], and sedges also are common. A wide variety of forbs and woody plants is ubiquitous.

The major portion (1,620 ha) of the ranch has been a contiguous set of pastures that have been grazed continuously by cow-calf pairs during the growing season (May 15 to October 15) since the mid-1950's at the recommended stocking rate of 2.0 animal unit months per ha. An animal unit month is the amount of forage (304 kg) consumed by a 450-kg mature cow. Most of the pastures were 260 ha, or smaller, in size and were in good to excellent range condition in the summer of 1998 as determined by field staff of the Natural Resources Conservation Service (Mike Hanna, pers. comm.). Four upland topographic positions were recognized: interdunal valleys, south-facing slopes, dune tops, and north-facing slopes. Dune tops were relatively level areas at the apex of dune slopes and composed about 20 to 25% of the upland area. North- and south-facing slopes were the most abundant positions covering jointly about 60 to 70% of the area (Mike Hanna, pers. comm.). The interdunal valleys typically were narrow and composed only 10 to 20% of the upland.

In May 1998, 87 sampling sites were established with a spacing of about one site per 20 ha. Sites were sampled for plant species frequency over a 30-day period in June and July 1998 when the cool-season plants were mature but still intact and the warm-season plants were growing actively. Rainfall and soil moisture in spring and summer 1998 were relatively high and cool-season plants remained green throughout June. At each sampling site, a transect location was selected randomly and marked permanently on each of the four topographic positions. Transects ran parallel with the contour of the land at the top of dunes, at the midpoint between dune tops and valleys along the north- and south-facing slopes, and through the center of the narrow valleys. Transects on the slopes and dune tops were 100 m long whereas the valley transects were 50 m long. Plant species frequency was estimated along each transect by placing a 0.1-m^2 quadrat at 4-m intervals for a total of 25 quadrats per transect for the slopes and dune tops and 13 quadrats per transect for the valleys. At each quadrat placement, each plant species was identified and recorded. Length of transect (experimental unit) was shorter for the valleys because the valleys frequently were not extensive and species diversity in the valleys was relatively low. The 4-m interval was selected as a result of a preliminary process of developing a species-area curve relating interval (same size) to number of species (Mueller-Dombois and Ellenberg 1974). The 0.1-m^2 quadrat was selected because it was the largest frame size that resulted in a frequency of less than 100% for each species encountered in the sampling process (Daubenmire 1968).

Soil samples were collected in June 1999 from each of the topographic positions at two randomly-selected sampling sites. Twelve vertical, undisturbed soil cores, 1.75 cm in diameter and 30 cm in length, were taken at regular intervals along the entire length of each transect. The cores were taken with a step-down probe and divided into two depth increments : 0 to 15 cm and 15 to 45 cm. The subsample cores along each transect were composited and oven dried at 100°C until mass was constant. Samples from each composited increment were used to prepare a 1:1 soil-water mixture with 10 g of soil and 10 g of water. Soil reaction of the mixture was determined by using a pH meter. Soil organic matter content of each depth interval also was determined by using the Walkely-Black Method (Schulte 1988). Dried samples of each depth interval were sieved through a No. 10 standard sieve and texture analysis on 50 g subsamples was conducted by the hydrometer method (Day 1965).

Statistical Analysis

Transect was the experimental unit for analysis of species richness and frequency of occurrence. Species richness by topographic position was calculated as the cumulative number of plant species encountered in the quadrats of a transect. Mean frequency of occurrence of each plant species was calculated as its average frequency over all quadrats within a transect. An arcsine transformation of the frequency data was conducted to make the data normally distributed. The transformed data were analyzed by using analysis of variance (SAS 1996) and separated with Fisher's protected least significant difference at $\alpha = 0.05$ (Steel and Torrie 1980). Canonical discriminant analysis (PROC CANDISC) was used to derive canonical variables. Canonical variates in our study were linear combinations of species frequency of occurrence and were used to ordinate topographic positions. Species used in the CANDISC procedure were determined by PROC STEPDISC, which selected a subset of the species to produce a discriminant model using a stepwise selection (SAS 1996).

RESULTS and DISCUSSION

Species Richness

A total of 89 vascular plant taxa was found on the upland sites of the Barta Brothers Ranch, which included 22 grass species, 59 forbs, 4 shrubs, 2 cacti, a general sedge category, and Baltic rush (*Juncus balticus* Willd.). Sedges and western ragweed (*Ambrosia psilostachya* DC.) were the most common taxa occurring over all topographic positions (Table 1). Mean species richness of the south-facing slopes (17.9), dune tops (18.6), and north-facing slopes (19.1) did not differ statistically ($P > 0.05$). Mean species richness was lower for the interdunal position (11.1), but this may have been a consequence of fewer quadrats sampled per transect in the interdunal valleys than on the slopes or dune tops. However, visual observations made on the study site during June and July support these results indicating lower species richness in the interdunal valleys. A similar decline in species richness from ridge tops and slopes to lowland areas was also reported in the mixed prairie of northcentral South Dakota (Barnes et al. 1983).

Table 1. Frequency of occurrence by topographical position of plant species with frequencies greater than 2.0 at the Barta Brothers Ranch, Nebraska. Each mean is based on 87 transects.

	Topographic position			
Species	Interdune (%)	Dune top (%)	North-facing slope (%)	South facing slope (%)
Blue grama *Bouteloua gracilis*	3.9^{a}	1.5^{b}	1.9^{ab}	1.4^{b}
Bluegrasses[1] *Poa spp.*	72.5^{c}	3.6^{a}	13.3^{b}	3.0^{a}
Cacti[2] *Opuntia spp.*	1.2^{a}	7.8^{c}	5.3^{b}	8.1^{c}
Hairy grama *Bouteloua hirsuta*	3.6^{a}	17.7^{c}	9.9^{b}	16.1^{c}
Indian grass *Sorghastrum nutans*	5.1^{a}	5.4^{a}	6.2^{a}	11.2^{b}
Junegrass *Koeleria pyramidata*	4.6^{a}	19.8^{c}	15.2^{c}	9.7^{b}
Lead plant *Amorpha canescens*	7.6^{a}	18.1^{b}	21.9^{c}	16.0^{b}
Little bluestem *Schizachyrium scoparium*	5.6^{a}	34.3^{b}	40.1^{c}	34.2^{b}
Prairie sandreed *Calamovilfa longifolia*	9.6^{a}	20.9^{b}	13.0^{a}	23.0^{b}
Prairie wild rose *Rosa arkansana*	8.2^{a}	8.1^{a}	9.1^{a}	8.5^{a}
Purple lovegrass *Eragrostis spectabilis*	8.1^{b}	2.0^{a}	3.2^{a}	1.7^{a}
Sand bluestem *Andropogon hallii*	3.6^{a}	15.5^{c}	10.9^{b}	15.4^{c}

Table 1. Cont.

Species	Topographic position			
	Interdune (%)	Dune top (%)	North-facing slope (%)	South facing slope (%)
Sand dropseed *Sporobolus cryptandrus*	19.0[a]	18.2[a]	15.4[a]	19.6[a]
Scribner dichanthelium *Dichanthelium oligosanthes*	59.4[ab]	55.0[b]	53.1[b]	64.2[a]
Sedges[3] *Carex spp.*	97.5[c]	86.3[b]	81.4[a]	90.2[b]
Stiff sunflower *Helianthus rigidus*	0.1[a]	9.3[c]	6.9[bc]	5.6[b]
Needlegrasses[4] *Stipa spp.*	15.7[a]	49.2[c]	43.9[bc]	39.8[b]
Switchgrass *Panicum virgatum*	65.9[c]	25.3[a]	29.1[ab]	34.8[b]
Western ragweed *Ambrosia psilostachya*	70.6[a]	76.4[a]	72.0[a]	80.3[a]
White sage *Artemisia ludoviciana*	10.9[a]	1.5[b]	3.0[b]	2.0[b]
Wilcox panicum *Dichanthelium wilcoxianum*	6.3[a]	21.6[c]	28.6[d]	16.2[b]

[abc]Different letters in a row indicate means are different ($P<0.05$).
[1]Includes Canada bluegrass (*Poa compressa*) and Kentucky bluegrass (*P. pratensis*).
[2]Includes brittle cactus (*Opuntia fragilis*) and prairie prickly pear cactus (*O. macrorhiza*).
[3]Includes primarily sun sedge (*Carex heliophila*) and Schweinitz flat sedge (*Cyperus schweinitzii*).
[4]Includes needle-and-thread (*Stipa comata*) and porcupine-grass (*S. spartea*).

Topographic Positions

The STEPDISC procedure indicated that the 18 taxa that played a significant role in discriminating differences in the topographic positions (Figs. 1 and 2) also had the highest frequencies (Table 1). When using the 18 species in the canonical discriminant analysis, the eigenvalues for the first two canonical variates were 4.399 and 0.376 with the first factor accounting for 89.6% of the variation in frequency or counts of species and the second factor accounting for 7.7% of the variation. Most interdunal transects were strongly separated from transects on the other topographic positions by the first variate (Fig. 1), which indicated that vegetation cover on interdunal positions was different from that on other positions. The five taxa that had highly positive coefficients for the first variate were bluegrasses (*Poa* L. spp.), switchgrass, white sage (*Artemisia ludoviciana* Nutt.), purple lovegrass [*Eragrostis spectabilis* (Pursh) Steud.], and sedges (Fig. 2). The two bluegrass species on the study site, Canada bluegrass (*Poa compressa* L.) and Kentucky bluegrass (*Poa pratensis* L.), were not easily identifiable as separate species in the vegetative stage of growth and were grouped into a single taxon. Principal species in the sedge grouping were sun sedge (*Carex heliophila* Mack.) and Schweinitz flat sedge (*Cyperus schweinitzii* Torr.). Even though sedges had the highest frequency of occurrence on interdunes, they also were common on the other topographic positions (Table 1). Switchgrass and bluegrasses were the two taxa most highly correlated or associated with the interdunal position. Each of these five taxa had significantly higher frequencies on interdunal valleys than on the other three topographic positions (Table 1).

Little bluestem had the most negative coefficient for the first variate but lead plant (*Amorpha canescens* Pursh), needlegrasses (*Stipa* L. spp.), and the other warm-season grasses, i.e., sand bluestem, hairy grama, and prairie sandreed, also had highly negative coefficients. The needlegrasses included both needle-and-thread and porcupine-grass because of the difficulty of separating these two species when in the vegetative stage of growth. These taxa with negative coefficients for the first variate were in the quadrants associated with slopes and dune tops (Figs. 1 and 2) and had significantly higher frequencies on slopes and dune tops than on interdunal valleys (Table 1).

The first variate is probably related to moisture availability in the upper soil profile. Bluegrasses were the principal taxa (partial $R^2 = 0.403$) affecting the separation of transects by topographical position. Bluegrasses are shallow rooted and have relatively low water-use efficiency. Shallow-rooted grasses commonly are reported to dominate swales and dry interdunal valleys in the Nebraska Sandhills (Barnes and Harrison 1982, Barnes et al. 1984) as well as in mixed prairie sites in northcentral South Dakota (Barnes et al. 1983). Barnes et al. (1984) concluded that dry valleys and swales in the Sandhills of Arthur County, Nebraska were good habitat for such shallow-rooted species as western wheatgrass, needle-and-thread, and blue grama. Barnes et al. (1984) hypothesized that the finer-textured soils (loamy fine sands) of these lowland areas provided readily available soil moisture early in the growing season within the surface 30 to 40 cm, whereas moisture availability of the fine sands of the slopes and ridges was restricted during the growing season to lower horizons out of reach of the shallow-rooted grasses.

Texture analyses of soils from the four topographic positions at the Barta Brothers Ranch did not differ in particle-size fractions as they were all in the loamy sand textural

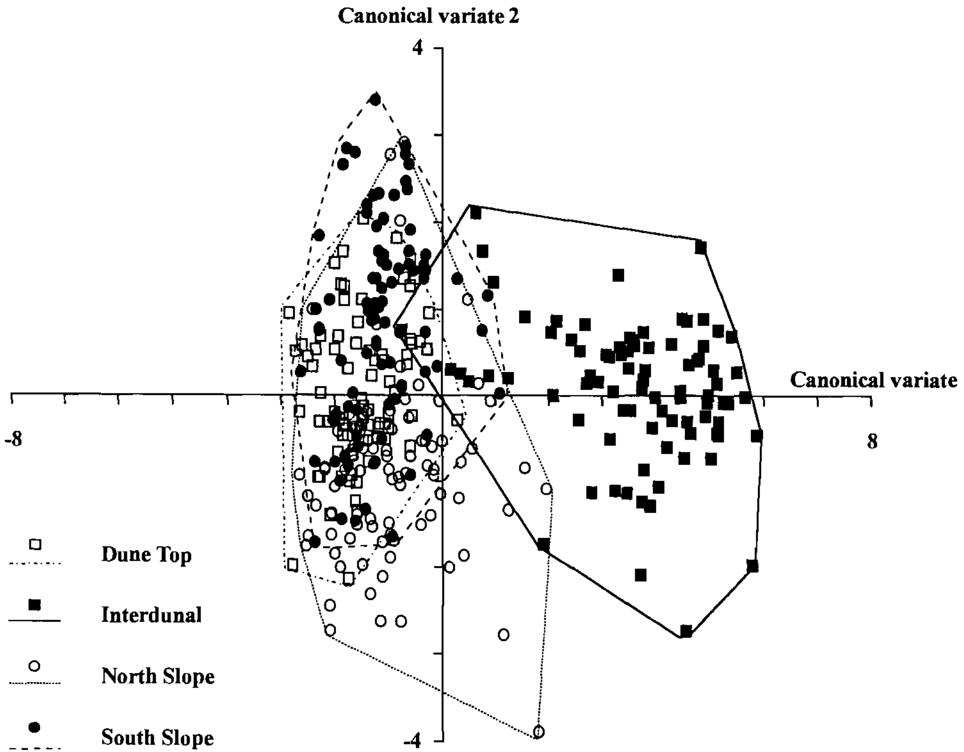

Figure 1. Canonical discriminant analysis ordination of all transects with 18 species selected from PROC STEPDISC, $\lambda_1 = 4.399$ and $\lambda_2 = 0.376$.

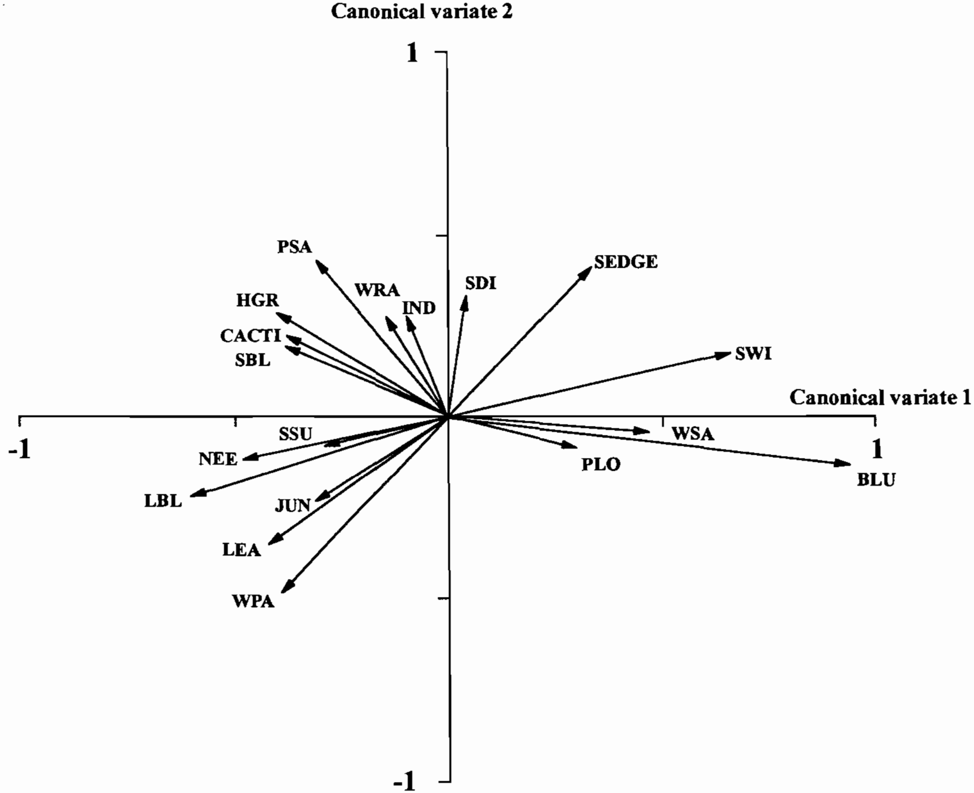

Figure 2. Canonical discriminant analysis ordination of the 18 species based on their correlation structure. Plant species: SBL = sand bluestem, HGR = hairy grama, PSA = prairie sandreed, WRA = western ragweed, IND = Indian grass, SDI = Scribner dichanthelium, SWI = switchgrass, WSA = white sage, BLU = Canada and Kentucky bluegrasses, PLO = purple lovegrass, WPA = Wilcox panicum, LEA = lead plant, JUN = Junegrass, LBL = little bluestem, NEE = needle-and-thread and porcupine-grass, and SSU = stiff sunflower.

class with 84 to 89% sand. Soil samples in the interdunes were taken from locations dominated by bluegrasses and sedges. Soil texture would not appear to explain the difference in plant species composition among interdunal and dune top and slope positions. Organic matter content and total carbon content, however, were higher in the soils of the interdunal valleys than of the dune tops and slopes (Table 2). The higher organic matter content could positively influence available water in the upper soil profile in the interdunal valleys. Phosphorous and potassium contents of the interdunal soils also were higher than that of the soils on the slopes and dune tops.

Table 2. Mean (± S.E.) soil pH, total organic matter (OM), total potassium (K), and total phosphorus (P), in the 0-15-cm and 15-45-cm depth intervals.

Topographic position	0 - 15 cm				15 - 45 cm			
	pH	OM (%)	K (ppm)	P (ppm)	pH	OM (%)	K (ppm)	P (ppm)
Interdune	6.4	1.5	170	9.4	6.4	0.6	130	7.8
	(0.22)	(0.16)	(14.5)	(1.50)	(0.11)	(0.12)	(7.0)	(1.48)
South-facing slope	6.4	0.8	110	3.8	6.5	0.4	80	3.0
	(0.07)	(0.11)	(21.0)	(0.55)	(0.08)	(0.02)	(16.0)	(0.15)
North-facing slope	6.4	0.8	110	4.1	6.4	0.3	86	3.8
	(0.14)	(0.04)	(6.0)	(1.41)	(0.08)	(0.02)	(2.5)	(0.30)
Dune top	6.3	0.7	100	3.6	6.5	0.3	91	2.6
	(0.14)	(0.04)	(16.0)	(0.30)	(0.08)	(0.01)	(16.5)	(0.08)

Livestock grazing also is a likely factor influencing plant cover on the topographic positions. Cattle in a continuous-grazed pasture commonly concentrate their grazing in lowland areas, especially near livestock water sources, and minimize grazing time on slopes (Stubbendieck and Reece 1992). Relatively high grazing pressure on lowland vegetation can be detrimental to tall and mid-grasses and favor grazing-resistant short grasses, such as the bluegrasses, blue grama, and purple lovegrass. The study site used by Barnes et al. (1984) had been grazed by cattle until three years before the initiation of their study. The dominance of their valley site by short grasses may have been related to a history of cattle grazing.

Switchgrass was the only deep-rooted, warm-season grass associated with the dry, interdunal valleys in our study (Table 1 and Fig. 2). Switchgrass has not been reported previously as a common component of plant communities on dry, interdunal valleys (Burzlaff 1962, Barnes et al. 1984, Bragg 1978). In support of the results of our study (Table 1), we have observed that switchgrass commonly develops dense stands in dry valleys and swales on upland sites throughout the Nebraska Sandhills. Switchgrass is a rapidly maturing warm-season grass that becomes stemmy and lower in palatability by midsummer when cattle will make only light use of it.

Blue grama often is reported to be a dominant species in interdunal valleys (Burzlaff 1962, Barnes and Harrison 1982, Barnes et al. 1984). Frequency of occurrence of blue grama on the Barta Brothers Ranch was low, but frequency of blue grama was higher on the interdunal valleys than on the slopes or dune tops (Table 1). Scribner dichanthelium [*Dichanthelium oligosanthes* (Schult.) Gould var. *scribnerianum* (Nash)] was correlated with the first variate, but was a commonly occurring species on all topographic positions (Table 1).

Taxa associated with interdunal valleys were either positively correlated or weakly negatively correlated with the second variate. The second canonical variate, however, indicated a separation of transects on south-facing slopes from transects on north-facing slopes (Fig. 1). Cacti (*Opuntia* P. Mill spp.), western ragweed, and warm-season grasses, such as prairie sandreed, sand bluestem, Indian grass [*Sorghastrum nutans* (L.) Nash], and hairy grama, had positive coefficients in relation to the second variate and were correlated with the quadrant in which about 75% of the transects on south-facing slopes were located (Figs. 1 and 2). Prairie sandreed, sand bluestem, hairy grama, cacti, and Indian grass had significantly higher frequencies on south-facing slopes than on north-facing slopes (Table 1). The cacti were comprised primarily of little brittle cactus [*Opuntia fragilis* (Nutt.) Haw.], but plains prickly pear (*Opuntia macrorhiza* Engelm.) was frequently encountered. Western ragweed was common on all topographic positions (Table 1). Western ragweed is an opportunistic plant that increases rapidly on upland sites with reduced vigor of the dominant grass species and/or during years of above-average precipitation (Reece, unpubl. data). The high frequency of occurrence of western ragweed on the study site may be related to the recent wet years.

Little bluestem, lead plant, and cool-season grasses, such as Junegrass, Wilcox panicum [*Dichanthelium wilcoxianum* (Vasey) Freckmann], and needlegrasses, had negative coefficients related to the second variate and were associated with the quadrant in which over 88% of the transects on north-facing slopes were concentrated (Figs. 1

and 2). Frequency of occurrence of little bluestem, lead plant, Junegrass, and Wilcox panicum, as well as the bluegrasses, was higher on north-facing slopes than on south-facing slopes (Table 1).

Aspect plays an important role in affecting habitat for plants. In the northern hemisphere, south-facing slopes have higher light intensity, higher soil-surface temperatures, and more limited moisture availability in surface horizons because of higher evapotranspiration rates (Humphrey 1962). The C_4 pathway, lower transpiration rates, and deeper root systems of warm-season grasses, e.g., prairie sandreed and sand bluestem, and forbs, e.g., western ragweed, would appear to make them better adapted than cool-season species to conditions on south-facing slopes. Tolstead (1942) observed that prairie sandreed was most prevalent on south-facing slopes and broad, dry valleys in the Sandhills of Cherry County. Bragg (1978) also reported that prairie sandreed was the most prevalent species on south-facing slopes in Garden County of the southwestern Sandhills.

The C_3 pathway of cool-season species, e.g., needlegrasses and Junegrass, is advantageous in environments of lower light intensities, lower temperatures, and high water availability (Doliner and Jolliffe 1979). Needlegrasses and Junegrass are relatively shallow rooted (Weaver 1920, 1954), have lower water use efficiencies, and require readily available moisture at the soil surface during their growing season to be competitive (Barnes and Harrison 1982). Therefore, these two taxa along with other cool-season plants, e.g., Wilcox panicum, appear to be best adapted to north-facing slopes. Bragg (1978) reached a similar conclusion based on the prevalence of needle-and-thread on north-facing slopes of choppy sands range sites in the southwestern Nebraska Sandhills. The strong association of little bluestem with north-facing slopes cannot be readily explained. On sand range sites in the northcentral Nebraska Sandhills, Bragg (1998) also found little bluestem to be more prevalent on north-facing slopes than south-facing slopes, but offered no explanation. We would expect little bluestem to be associated with other deep-rooted, warm-season grasses on south-facing slopes and dune tops. However, in another study in the west central Nebraska Sandhills (Cullan et al., unpubl. data), frequency of occurrence of little bluestem was found to be negatively correlated with prairie sandreed on upland sites.

Even though transects on dune tops consistently had negative coefficients associated with the first variate, 54% of dune top transects were negatively and 46% positively associated with the second variate. Prevalent species on dune tops were a mixture of species with negative and positive coefficients in respect to the second variate. Some species with negative coefficients in respect to the second variate and associated with north-facing slopes had high frequencies on dune tops (Table 1). Frequency of occurrence of needlegrasses and Junegrass on dune tops was similar to that on north-facing slopes but higher than that on south-facing slopes. Some species with positive coefficients in respect to the second variate and associated with south-facing slopes had high frequencies on dune tops (Table 1). Frequency of occurrence of sand bluestem and hairy grama on the dune tops was similar to that on south-facing slopes but higher than that on north-facing slopes. Dune tops were not characterized by a unique species or group of species but appeared to be a transitional area where species common to the opposing slopes mixed.

Three other frequently-occurring species were sand dropseed, prairie wild rose (*Rosa arkansana* Porter), and stiff sunflower [*Helianthus rigidus* (Cass.) Desf.] (Table 1). Frequency of occurrence for sand dropseed and prairie wild rose did not differ by topographic position. Sand dropseed is a shallow-rooted, short-lived perennial that is a conspicuous part of upland prairie sites (Pool 1914, Tolstead 1942, Barnes et al. 1984) and is particularly prevalent on areas recovering from improper grazing or drought (Frolik and Shepherd 1940, Burzlaff 1962). As reported by Burzlaff (1962), prairie wild rose generally occurs as uniformly scattered, individual plants throughout the uplands that account for relatively small amounts of total plant cover and biomass production. Stiff sunflower was found almost exclusively on slopes and dune tops. Stiff sunflower is a rhizomatous forb and is a common component of upland vegetation in good and excellent range condition (Frolik and Shepherd 1940).

In summary, topographic position played an important role in plant distribution on grazed, upland prairie in the eastern Nebraska Sandhills. Edaphic factors and grazing have been cited (Barnes et al. 1984, Stubbendieck and Reece 1992) as critical factors affecting plant community distribution across topographic positions. Soil textural classes at our site did not vary greatly among topographic positions and appeared not to be a contributing factor in affecting plant community patterns; however, soil organic matter content was higher in the interdunal valleys. Because cattle tend to concentrate in low-lying areas, long-term, continuous grazing may have played a significant role in the dominance of the grazing resistant, short grasses in the interdunal valleys. The potential influence of grazing on plant community distribution on slopes and dune tops is not obvious. Seasonal patterns of grazing livestock by topographic position has not been studied in the Nebraska Sandhills. Finally, warm-season, tall grasses were dominant on the dune tops and both the south- and north-facing slopes even though the cool-season grasses and sedges were strongly associated with north-facing slopes. The warm-season, tall grasses represented over 55% of the annual aboveground biomass production on the slopes and dune tops (Schacht et al., unpubl. data). Cool-season grasses and sedges, however, were dominant on the interdunal valleys.

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