12-1984

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Prairie Nat. 16(4): 1984, pp. 145-158

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ABSTRACT — Detailed studies on soil texture and moisture retention indicate a close association between edaphic features and the distribution and composition of plant communities along topographic gradients at Arapaho Prairie, a typical, semi-arid Nebraska Sandhills prairie. The vegetation characteristics of three major habitat types (ridge, slope, and valley) and several minor subtypes (swale, stable ridge, and eroding ridge) are recognized and quantitatively described. Texture analysis indicates that the soils of dune slopes and ridges are largely azonal and are very coarse with substantially lower fine fractions (silt-clay = 13-15%) than soils of the more lowland swale and valley sites where surfact silt-clay fractions can reach 20-25%. Soil moisture contents at 0.1 bar (10-14% by volume) and 15 bars (3-4%) are similarly lower for dune sands than the surface soils at the lowland sites (0.1 bar = 19-23% and 15 bars = 5-9%). These moisture characteristics result in potentially 50-100% more moisture stored in the surface lowland soils which is rapidly utilized by the shallow-rooted, drought-tolerant grasses *Stipa comata*, *Agropyron smithii*, and *Bouteloua gracilis*. Deep-rooting grasses (*Andropogon hallii*, *Panicum virgatum*, and *Sorghastrum avenaceum*), forbs (*Helianthus rigidus* and *Petalostemon purpureum*) and shrubs (*Yucca glauca*, *Prunus besseyi*, and *Amorpha canescens*) are more abundant on the coarse-textured dune sands where soil moisture is stored deep in the profile. On dune ridges *Sorghastrum* and *Stipa* appear to be mutually exclusive with their distributions closely related to small-scale variations in topographic relief and surface soil texture and moisture characteristics. For all vegetation types, gradient analysis of major grasses, forbs, and shrubs shows systematic replacement of individual species along topographic gradients which, in many cases, can be related to rooting morphology, physiological differences in water use, and spatial and temporal variation in soil moisture.

INTRODUCTION

The Sandhills region of Nebraska is a large, contiguous tract (approximately 52,000 km² in extent) of stabilized, eolian-deposited sand dunes and flat interdunal valleys in the north central part of the state (Kaul 1975). The vegetation is characterized by an unusual mixture of native tall-grass, mixed-grass, and short-grass prairie species together with many psammophytes (Keeler et al. 1980). The distinct assemblage of species in these Sandhills grasslands is primarily the result of the coarse-textured dune sands which effectively intercept precipitation with minimal water lost to runoff (Tolstead 1942). Consequently, within similar climatic areas, the Sandhills support species of eastern, mesic prairies, whereas surrounding fine-textured "hardland" soils are characterized by the more xeric, mixed- and short-grass prairie vegetation (Kaul 1975).

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Although the Sandhills have a long history of botanical and ecological descriptive studies (Webber 1889, Smith and Pound 1892, Rydberg 1895, Pound and Clements 1900, Pool 1914, Frolik and Shepherd 1940, Tolstead 1942, Weaver and Albertson 1956, Burzlaff 1962) very little quantitative information is available on edaphic variation and its importance in controlling spatial vegetation patterns. Barnes and Harrison (1982) showed that several shallow-rooted cool-season (C_3) and deep-rooted warm-season (C_4) Sandhills grasses differ physiologically in water-use patterns, and they suggested that site variation in available moisture mediated by soil texture could control distributions. In this paper we quantitatively characterize the major vegetation and soil types in Sandhills prairie and determine the relationship between topography, soil physical characteristics, and plant community composition and structure.

STUDY SITE AND METHODS

Arapaho Prairie is a 526-ha preserve located in Arthur County, Nebraska, in the southwestern Sandhills region. Topographic features are representative of upland Sandhills prairie: steep dune ridges are oriented approximately southwest to northeast and slope down to broad dry valleys with flat to rolling floors. Maximum relief from ridgetop to valley floor may be 70 m. Soils of the Valentine series are found on dune ridges and slopes, and soils of the Doger and Dunday series are found on swale and dry valley bottoms (USDA Soil Conserv. Serv. 1977). The climate is typically continental and semi-arid with May and June normally the wettest months. Mean annual precipitation is normally 45-50 cm (Barnes and Harrison 1982). Historically, Arapaho Prairie was used for cattle grazing but this has ceased since acquisition by the Nature Conservancy in 1977. Additional descriptive information on land-use history and place name features together with soil and topographic maps, can be found in Keeler et al. (1980).

Based on topography, three major habitat types (ridge, slope, and valley) have been recognized at Arapaho Prairie (Keeler et al. 1980). Three sites within each of these three habitat types were chosen for detailed vegetation sampling. Sites were subjectively chosen to represent different slope exposure aspects and were permanently marked (see Fig. 1 of Keeler et al. (1980) for locations). A nested quadrat scheme was used with sampling conducted during June and August 1979 to account for seasonal variation in growth activities between (C_3) cool-season and (C_4) warm-season species (Ode et al. 1980). At each site a 10 x 10 m quadrat was divided in half by placing surveyor flags 1 m apart along an east to west center line. Within the southern-most half a series of ten adjacent 1 x 1 m quadrats were marked out along the center line. Canopy cover ranks from 1 to 10 were assigned to species in the 1.0 m^2 quadrats with each rank representing a 10% cover interval. Species with cover values of less than 1% or species occurring within the 100-m^2 quadrat but not in the 1.0-m^2 quadrats were assigned a "P" for "Present". The same 100-m^2 quadrats were used for the August sampling (with the exception of one ridge site which was relocated). For data analysis, cover ranks were converted to percents using the midpoint of the cover intervals. The cover values reported here are the means of the June and August values. For each species, frequency was determined by calculating the proportion of quadrats in which it occurred. If a species only occurred in the 100-m^2 quadrats frequency was not calculated but designated simply as "P". Only important species are given in Table 1. A complete species list with cover and frequency data is available from the first author.

Additional sampling was conducted at several other sites on the prairie using slightly different schemes. One site (swale site), which represents a different community, was located in a local depression dominated by *Agropyron smithii* and cover values are the means of 12 randomly placed 20 x 50 cm quadrats which were censused in August 1980. Additional frequency data for the ridge vegetation were taken from ten 1.0 x 1.0 m quadrats which were sampled in September 1978 on a lower elevation eroding ridge site. Nomenclature follows van Bruggen (1976) and Barkley (1977).

Soil samples were collected from 10 sites on Arapaho Prairie and analyzed for texture and water-holding characteristics. Three sites were chosen within each of the three major habitat types (ridge, slope, and valley) and one site was located in a local depression representing the swale habitat. At each site three replicate holes were drilled 10 m apart with a standard soil sampling auger (core diameter = 8 cm). Samples were taken to a depth of 140 cm at 20-cm increments. Oven-dried (95°C for 24 h) samples were passed through a 2-mm mesh sieve to remove rhizomes and large roots. For determination of moisture-retention values at 0.1 and 15 bars, subsamples were treated according to the method outlined in the USDA Handbook No. 60 (1951) utilizing a ceramic pressure-plate apparatus (Soil Moisture Equip. Co.). Determination of 0.1 bar moisture-retention values (an estimate of field capacity (Marshall and Holmes 1979)) were conducted only on six of nine replicates per habitat type and on only alternate 20 cm samples. Subsurface water-retention data presented here are pooled values obtained from these 20 cm increment samples. The hydrometer method (Day 1965) was used for texture analysis. Samples for bulk-density determination were obtained using a "King-Tube" soil coring device to extract cores of known volume from the surface and at eight depth increments. Three replicate holes were drilled in each habitat type.

RESULTS AND DISCUSSION

Habitat Types

Three major habitat types and their associated plant communities have been recognized at Arapaho Prairie and have been named according to site-specific topography (Keeler et al. 1980). Ridges occur on upper elevation dune slopes and exposed ridges and comprise roughly 16% of the preserve area (as determined by planimeter measurements of delineated areas of Keeler et al. 1980). Slopes are the most abundant habitat type on Arapaho Prairie, covering approximately 61% of the area, and are characteristic of mid-slopes and lower elevation rolling dunes. Valleys, which potentially comprise 23% of Arapaho Prairie, occur on flat or gently rolling, interdunal valley floors. Old (pre-1937) abandoned fields cover 5-6% of the valley floors so that current unplowed valley

Table 1. Mean species canopy cover (%) and frequency (%) within habitat types for major species at Arapaho Prairie. P = present (see text for explanation). Ridge = mean of Eroding Ridge and Stable Ridge. Total sampling area (m^2) is given in parentheses under the habitat types.

	HABITAT TYPES											
	RIDGE (70)		ERODING RIDGE (40)		STABLE RIDGE (30)		SLOPE (60)		VALLEY (60)		SWALE (1.2)	
GRAMINOIDS												
Agropyron smithii	—	—	—	—	—	—	—	—	7	93	74	100
Andropogon hallii	4	73	3	63	5	87	7	82	2	18	—	—
Andropogon scoparius	6	49	10	68	3	23	3	27	P	2	—	—
Bouteloua gracilis	—	—	—	—	—	—	21	90	15	90	12	75
Bouteloua hirsuta	11	89	12	98	10	77	13	77	—	—	—	—
Calamovilfa longifolia	6	84	5	75	7	97	17	100	23	98	—	—
Carex spp.	2	84	P	75	3	97	2	83	8	63	—	—
Festuca octoflora	P	27	P	13	P	47	P	37	P	40	—	—
Koeleria pyramidata	6	66	7	75	5	53	8	62	—	—	—	—
Muhlenbergia pungens	2	26	3	23	2	30	—	—	—	—	—	—
Panicum virgatum	4	57	4	48	4	70	6	57	P	5	—	—
Sorghastrum avenaceum	3	20	5	35	—	—	—	—	—	—	—	—
Sporobolus cryptandrus	P	41	P	35	P	50	P	50	P	54	—	—
Stipa comata	8	60	3	38	14	90	9	85	25	100	—	—
FORBS												
Ambrosia psilostachya	1	53	2	60	P	43	P	65	P	28	—	—
Artemisia campestris	P	14	P	25	—	—	—	—	—	—	—	—
Artemisia ludoviciana	1	26	P	8	2	50	—	—	1	17	—	—
Asclepias viridiflora	P	9	P	3	P	17	P	3	P	5	—	—
Calylophus serrulatus	P	6	P	10	—	—	—	—	—	—	—	—
Chenopodium album	P	P	P	P	—	—	P	P	1	15	—	—
Chrysopsis villosa	P	4	P	8	—	—	—	—	—	—	—	—

Cirsium canescens	P	17	P	18	P	17	P	28	1	20	P	8
Croton texensis	P	4	P	3	P	7	P	17	2	45	—	—
Cryptantha celosioides	P	10	P	10	P	10	P	5	P	3	—	—
Eriogonum annuum	P	P	P	P	P	P	—	—	P	13	—	—
Euphorbia missurica	P	10	P	15	P	3	P	17	P	8	—	—
Evolvulus nuttallianus	—	—	—	—	—	—	—	—	P	50	—	—
Froelichia floridana	P	11	P	20	—	—	—	—	—	—	—	—
Haploppapus spinulosus	P	29	P	18	P	43	P	15	P	P	—	—
Helianthus rigidus	6	78	8	90	5	57	P	7	—	—	—	—
Lathyrus polymorphus	1	20	2	23	P	23	—	—	—	—	—	—
Liatris spp.	P	21	P	28	P	13	P	2	P	2	—	—
Linum rigidum	P	7	P	13	—	—	—	—	P	3	—	—
Lithospermum carolinense	P	4	P	8	—	—	—	—	—	—	—	—
Lithospermum incisum	P	30	P	18	P	47	P	25	P	20	—	—
Lygodesmia juncea	—	—	—	—	—	—	P	25	P	15	—	—
Mentzelia nuda	—	—	—	—	—	—	P	2	P	8	—	—
Monarda pectinata	—	—	—	—	—	—	P	5	P	27	—	—
Opuntia fragilis	1	53	P	38	2	73	1	65	P	18	1	8
Opuntia macrorhiza	1	17	P	18	2	17	P	5	P	7	—	—
Oxytropis lambertii	P	9	P	10	P	10	P	P	P	P	—	—
Penstemon angustifolius	P	24	P	13	P	43	P	15	P	7	—	—
Petalostemon purpureum	P	37	P	43	P	30	P	17	P	2	—	—
Plantago patagonica	P	46	P	33	P	63	P	45	P	35	—	—
Psoralea tenuiflora	P	1	—	—	P	3	P	3	7	62	—	—
Ratibida columnifera	—	—	—	—	—	—	P	P	2	37	—	—
Solidago spp.	P	3	P	3	P	3	P	17	P	5	—	—
Sphaeralcea coccinea	—	—	—	—	—	—	—	—	1	52	—	—
Thelesperma megapotamicum	P	17	P	5	P	33	P	42	P	17	—	—
Tradescantia occidentalis	P	4	P	3	P	7	1	25	P	18	—	—
SHRUBS												
Amorpha canescens	2	14	1	13	4	17	P	3	—	—	—	—
Prunus besseyi	1	17	2	30	—	—	—	—	—	—	—	—
Rosa arkansana	2	29	2	28	2	30	—	—	P	3	—	—
Yucca glauca	7	33	9	30	6	37	P	P	—	—	—	—

vegetation is similar in extent to ridge vegetation. Swales are a minor habitat type at Arapaho Prairie and are common in sheltered depressions or bowls where the soil texture is fine and represents the extreme along the topographic/edaphic gradient described here. For this reason we quantitatively consider swale soils and vegetation in conjunction with the other major soil and vegetation types.

Dune Soils and Plant Communities

Vegetation on dune ridges and upper slopes was dominated by a heterogeneous mixture of the grasses *Boutelous hirsuta* (hairy grama), *Stipa comata* (needle and thread), *Andropogon scoparius* (little bluestem), and *Calamovilfa longifolia* (sandreed (Table 1). *Andropogon hallii* (sand bluestem), *Koeleria pyramidata* (Junegrass), and *Panicum virgatum* (switchgrass) were other important grasses. Major non-grass species included *Helianthus rigidus* (stiff sunflower) and the shrubs *Yucca glauca* (soapweed), *Amorpha canescens* (lead plant), and *Rosa arkansana* (prairie rose). This vegetation was typically sparse and bare sand was common; mean total plant cover was only 80% in comparison to 97 and 105% for the slope and valley habitat types, respectively. Ridges, however, showed the highest species richness with 76 species recorded as compared to 61, 67, and 4 for the slope, valley, and swale habitat types, respectively. Soils on dune ridges were the coarsest of all sites and showed little textural variation with depth (Fig. 1). Mean clay contents ranged forom 12-13% and the silt fraction, which was minimal, was highest in surface layers. Although these coarse-textured ridge

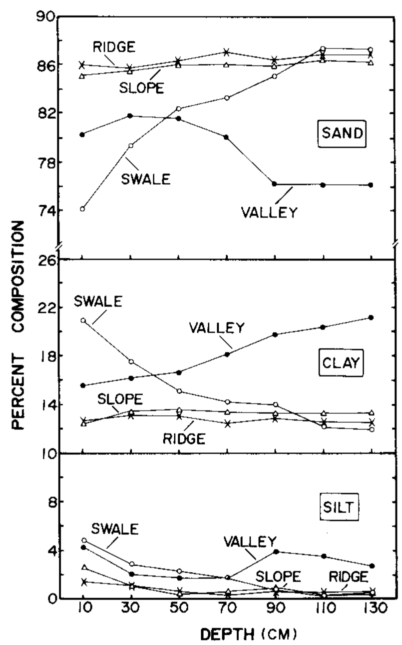

Figure 1. Textural characteristics of ridge, slope, valley, and swale soils. For all but the swale, N = 9. N = 3 for the swale soils.

Table 2. Soil-moisture characteristics at three depths (cm) within four habitat types on the Arapaho Prairie. Volumetric water contents (%) are in parentheses. Maximum available water is calculated as the difference between 0.1 and 15 bars moisture contents.

		MOISTURE CONTENT		
	Bulk density g/cm^3 ± 2SE	@ 0.1 bar, mm ± 2SE	@ 15 bars, mm ± 2SE	Maximum Available Water, mm
Ridge				
0-20	1.49 ± 0.11	20.8 ± 2.1 (10.4)	7.2 ± 0.8 (3.6)	13.6 (6.8)
20-60	1.57 ± 0.06	42.8 ± 2.7 (10.7)	12.4 ± 0.7 (3.1)	30.4 (7.6)
60-140	1.66 ± 0.06	90.4 ± 11.2 (11.3)	22.4 ± 2.4 (2.8)	68.0 (8.5)
TOTAL		154.0	42.0	112.0
Slope				
0-20	1.48 ± 0.14	25.4 ± 2.7 (12.7)	6.8 ± 1.3 (3.4)	18.6 (9.3)
20-60	1.68 ± 0.06	55.2 ± 4.7 (13.8)	12.4 ± 2.1 (3.1)	42.8 (10.7)
60-140	1.74 ± 0.19	114.4 ± 17.7 (14.3)	22.4 ± 2.6 (2.8)	92.0 (11.5)
TOTAL		195.0	41.6	153.4
Valley				
0-20	1.44 ± 0.08	38.8 ± 6.5 (19.4)	9.2 ± 0.8 (4.6)	29.6 (14.8)
20-60	1.60 ± 0.02	84.0 ± 15.9 (21.0)	19.2 ± 1.4 (4.8)	64.8 (16.2)
60-140	1.67 ± 0.07	221.6 ± 33.4 (27.7)	58.4 ± 12.9 (7.3)	163.2 (20.4)
TOTAL		344.4	86.8	257.6
Swale				
0-20	1.34 ± 0.12	46.4 ± 7.9 (23.2)	17.0 ± 4.9 (8.5)	29.6 (14.7)
20-60	1.53 ± 0.20	68.0 ± 11.4 (17.0)	16.8 ± 3.7 (4.2)	51.2 (12.8)
60-140	1.85 ± 0.12	91.2 ± 21.6 (11.4)	24.8 ± 6.1 (3.1)	66.4 (8.3)
TOTAL		205.6	58.6	147.0

soils showed the lowest moisture retention at 0.1 and 15 bars (Table 2), they allow for rapid infiltration and therefore efficient penetration of even small amounts of rain. Thus, sub-surface available soil moisture is relatively reliable throughout the growing season (Tolstead 1942, Barnes and Harrison 1982, Barnes 1984, Potvin 1984, Harrison unpubl. data) and is used by the deep-rooting shrubs (e.g. *Yucca*, *Amphora*, and *Rosa*), forbs (e.g. *Helianthus*, *Solidago nemoralis* (goldenrod), *Petalostemon* spp. (prairie clover), and others) and grasses (e.g. *Andropogon* spp., *Panicum virgatum*, *Sorghastrum avenaceum* (Indian grass), and *Calamovilfa*).

Within the broadly defined ridge vegetation, we have recognized two sub-types which show distinct differences in vegetation and appear to be associated with specific small-scale topographic features. Eroding ridge vegetation was characteristic of steeply sloped exposed ridges while stable ridge vegetation occurred on level, more protected ridge sites. The vegetation on eroding ridges was distinguished from stable ridge vegetation by the obvious presence of the deep-rooting *Sorghastrum avenaceum* and the abundance of *Helianthus rigidus*, *Andropogon scoparius*, and *Solidago nemoralis*. A diversity of forbs such as *Astragalus ceramicus*, *Calylophus serrulatus*, *Chrysopsis villosa* (gold aster), and *Froelichia floridana* (snake cotton) occurred on eroding ridges but were generally absent or less important on stable ridges. These eroding ridges showed a substantially higher species richness (68 species) than stable ridges (47 species). Stable ridges clearly lacked *Sorghastrum* but supported the more shallow-rooted *Stipa comata*. Therefore, *Sorghastrum* and *Stipa* appeared to be mutually exclusive and thus good "indicators" of the eroding ridge and stable ridge sub-types.

To further evaluate the relationship between topography and plant distributions on eroding and stable ridges, and especially the distribution of *Stipa comata* and *Sorghastrum avenaceum*, we gathered a set of additional soil samples in a transect along a major west-facing dune system. The surveyor's profile of this "*Stipa*/*Sorghastrum*" transect is shown in Fig. 2. This transect consisted of a series of alternating eroding and stable ridge sites, which occur on upper and lower elevation sites. Soil samples for texture and 0.1 bar moisture determinations were gathered in triplicate at each site along this transect at depth intervals of 0-20, and 20-40 cm. Surface (0-20 cm) and sub-surface (20-40 cm) stable ridge soils at all *Stipa* (STIPA) sites showed consistently higher silt contents than the eroding ridge soils at the*Sorghastrum* (SOR) sites (Table 3). Overall, the significantly higher silt contents in the surface 20 cm was correlated with a significantly higher moisture-holding capacity at 0.1 bar for the stable ridge soils as compared to the eroding ridge soils. Overall differences in silt contents and moisture-holding capacities for the sub-surface (20-40 cm) soils between these sites were statistically significant but were less marked than the surface soils. On average, the stable ridge surface soils can hold potentially 50% more moisture at 0.1 bar than the eroding ridge soils. This may allow the shallow-rooted *Stipa* to survive on these dune sites but not on the coarser-textured, eroding ridges, where the deeper-rooted, rhizomatous *Sorghastrum* occurs.

Slope vegetation was dominated by *Bouteloua gracilis* (blue grama), *Calamovilfa*, and *Bouteloua hirsuta* (Table 1). Major sub-dominant species were

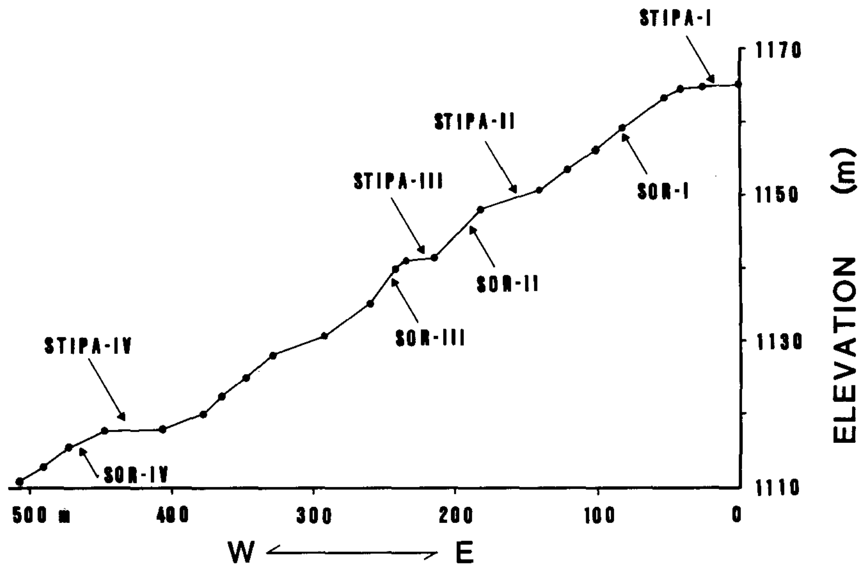

Figure 2. Surveyor's profile of the *Stipa/Sorghastrum* transect. Sites dominated by *Stipa comata* are designated at STIPA sites and sites where *Sorghastrum avenaceum* is restricted to are designated as SOR sites. This transect is located on Ballinger's Hill (Keeler et al. 1980) and is permanently marked.

the grasses *Andropogon hallii*, *Koeleria*, and *Stipa*. Major forbs were *Opuntia fragilis* (prickly pear), *Tradescantia occidentalis* (spiderwort), and *Ambrosia psilostachya* (ragweed). Distinct and noteworthy features of slopes were 1) an absence of *Sorghastrum*, *Muhlenbergia pungens* (sand muhly), and other open sand species; 2) a reduced forb and shrub component; and 3) the co-occurrence of *Bouteloua gracilis* and *Bouteloua hirsuta*. Soils of the slope sites were also uniform throughout the profile but both surface clay and silt fractions tended to be slightly higher than in ridge soil (Fig. 1). Moisture-holding capacities were slightly higher than in ridge soils but were clearly lower than those of lowland, finer-textured soils (Table 2). Slope sites show seasonal patterns of available moisture which are similar to, or just higher than, ridge sites (Barnes and Harrison 1982).

Lowland Soils and Communities

Valley vegetation was dominated by *Stipa comata*, *Calamovilfa*, and *Bouteloua gracilis* (Table 1). Although absent from ridge and slope sites, the shallow-rooted *Agropyron smithii* (western wheatgrass) was common in the valleys but *Bouteloua hirsuta* and *Koeleria* were absent. *Sporobolus cryptandrus* (sand dropseed) was common but the deep-rooting grasses *Andropogon* spp. and *Panicum virgatum* were only infrequently encountered. *Carex* sp. (sedge) was

Table 3. Soil texture and moisture content data for stable (STIPA) and eroding (SOR) ridge sites along the *Stipa/Sorghastrum* transect. See Fig. 2 for site locations. Sand, silt, and clay fractions are percents. The 0.1 bar moisture contents are expressed as percent by dry weight. * = $P < 0.05$, + = $P < 0.10$ as determined by Student's t-test; ns = non-significant.

	0-20 cm				20-40 cm			
SITE	SAND	SILT	CLAY	0.1 bar	SAND	SILT	CLAY	0.1 bar
STIPA I	85.0	3.2	11.8	7.33	85.2	2.4	12.4	5.02
SOR I	86.5	0.7	12.9	4.72	85.9	1.1	13.0	4.25
STIPA II	84.8	2.1	13.1	6.30	85.7	2.2	12.1	4.36
SOR II	86.8	1.4	11.8	4.70	84.8	1.7	13.6	4.89
STIPA III	85.4	2.5	12.1	6.49	85.9	1.4	12.7	4.53
SOR III	85.7	1.0	13.3	5.16	85.9	1.0	13.1	4.64
STIPA IV	84.1	3.1	12.8	7.04	85.9	2.0	12.2	4.70
SOR IV	87.3	0.5	12.2	3.59	85.9	0.8	11.3	3.42
Overall STIPA Sites	84.8 *	2.7 *	12.5 ns	6.79 *	85.7 ns	2.0 *	12.4 ns	4.65 +
Overall SOR Sites	86.6	0.9	12.6	4.54	85.6	1.2	12.8	4.30

locally abundant and often was a co-dominant with *Calamovilfa* and/or *Stipa*. It is important to note that although *Stipa* and *Calamovilfa* appeared as cover dominants, *Stipa* appeared to reach its maximum reproduction development on these valley floors, whereas sexually reproducing individuals of *Calamovilfa* were less abundant in the valleys than on the dune sands. Major forbs in valley vegetation were *Psorelea tenuiflora*, *Ratibida columnifera* (coneflower), *Sphaeralcea coccinea* (cowboy's delight), and *Croton texensis* (skunkweed). *Rosa* was found occasionally but *Yucca* and other deeply-rooted dune shrubs were clearly absent. The valley soils showed a bimodal distribution of silt particles in the profile, indicating a more complex soil development history with the possibility of a buried A-horizon below 80 cm (Fig. 1). Soils were characteristically finer textured in the valleys than the dune sands at all depths.

Swale vegetation was entirely dominated by *Agropyron smithii* (Table 1). *Bouteloua gracilis* co-occurred with *Agropyron* , and *Stipa* was common along swale peripheries but very few other grass or non-grass species were present. Swale sites showed the finest-textured surface soils of all sites and silt and clay fractions decreased with depth (Fig. 1).

Fine-textured valley and surface swale soils held considerably more water at both 0.1 and 15 bars than the coarse-textured slope and ridge soils (Table 2). The amount of water held between 0.1 and 15 bars, which we have considered available water, was also greater in these fine-textured soils. For example, lowland soils (valley and swale) could potentially hold 50-100% more water than the coarse-textured soils of the dune slopes and ridges in the surface 20 cm. Although these fine-textured valley and swale soils can potentially hold more water than the coarse-textured dune sands, precipitation does not penetrate as effectively or as deeply into the profile as in the coarse-textured dune sands (Tolstead 1942). Furthermore, the drought-tolerant, and dense but shallow-rooted grasses *Agropyron*, *Stipa*, and *Bouteloua gracilis* rapidly deplete available moisture in the surface layers which would otherwise be available to more deep-rooting grasses, forbs, and shrubs (Barnes and Harrison 1982, Potvin 1984).

Gradient Analysis

Spatial and temporal variation between sites in soil moisture availability could be of considerable ecological importance as both grasses and forbs show interspecific variation in rooting morphologies and depths (Weaver 1919, 1920), and consequently, different abilities to utilize this potentially limiting resource. A direct gradient analysis (Whittaker and Neiring 1965) (Fig. 3) of major grass and non-grass species at Arapaho Prairie, where frequency data from Table 1 were plotted against habitat type, indicates that sequential species replacement exists along this topographic/edaphic gradient that, in many cases, can be related to species differences in rooting morphology and water-use physiology. Deep-rooted species such as *Andropogon* spp., *Panicum virgatum*, *Sorghastrum*, *Yucca*, *Prunus*, and *Helianthus* are most frequent on upper elevation dune sands. Within the dune vegetation, further experimental studies are needed to elucidate factors which control the restricted distributions of species such as *Sorghastrum* and *Prunus*; however, the absence or near absence of the deep-rooted species from

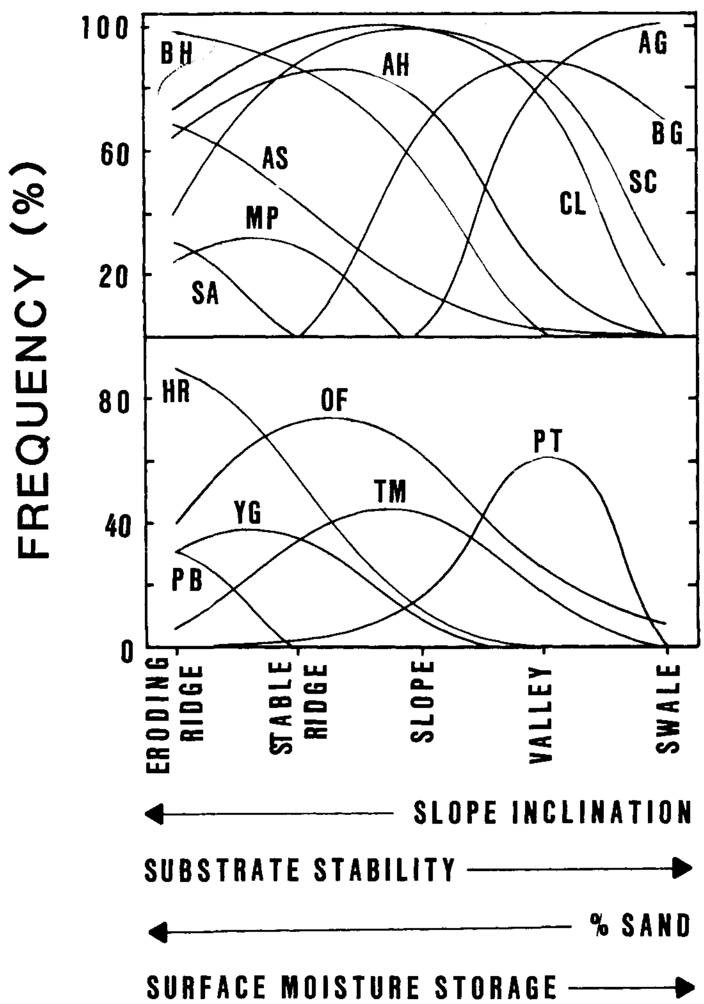

Figure 3. Direct gradient analysis of major grasses (upper) and forbs and shrubs (lower) along the topographic/edaphic gradient at Arapaho Prairie. All curves are smoothed from frequence data in Table 1. Species abbreviations are as follows: BH = *Bouteloua hirsuta*, AH = *Andropogon hallii*, AS = *Andropogon scoparius*, MP = *Muhlenbergia pungens*, SA = *Sorghastrum avenaceum*, CL = *Calamovilfa longifolia*, SC = *Stipa comata*, BG = *Bouteloua gracilis*, AG = *Agropyron smithii*, HR = *Helianthus rigidus*, YG = *Yucca glauca*, PB = *Prunus besseyi*, OF = *Olpuntia fragilis*, TM = *Thelesperma megapotamicum*, and PT = *Psoralea tenuiflora*.

the valley and swale sites may be related to interspecific competition for available moisture (Potvin 1984). Although moisture is available deep in the soil profile on the dunes, exposed surface sands are subjected to extreme moisture deficits and wind erosion which act to keep successful seedling establishment low (Barnes 1984, Potvin 1984). Thus, the topographic gradient described here for Arapaho Prairie represents a complex environmental gradient where inclination, exposure, soil texture, soil moisture, substrate stability, and perhaps different levels of biotic and abiotic stress may interact to control plant distribution patterns (Fig. 3). We suggest, then, that soil texture, water relations, and plant physiological and morphological characteristics serve as important factors which can structure or organize the grassland communities along the complex topographic/edaphic gradient described here.

ACKNOWLEDGMENTS

This research was supported by grants from NSF (DEB78-11315) and the Nebraska Water Resources Center (Project 87-287-262-01) and the A. W. Sampson Fellowship, University of Nebraska. We thank M. Barnes, R. Heinisch, and B. Reed for their assistance.

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