Vegetation-Soils And Vegetation-Grazing Relations From Frequency Data¹

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Highlight

An upland vegetational continuum and three bottomland associations are interpreted from frequency data, but intra-site heterogeneity masks vegetation-grazing relations. Summer-long grazing at different intensities for 23 years has not affected the frequency percentages of species to a great extent.

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Frequency data are a blend of species density and dispersion characteristics. Therefore, they should be useful for the study of vegetation-soils and vegetationgrazing relations. To test this assumption, frequency sampling was undertaken at the Central Plains Experimental Range near Nunn, Colorado, where grazing has been controlled at various intensities since 1939, and where a recent soil survey provides a basis for sample stratification by soils. This paper reports vegetation-soils and vegetation-grazing relations on blue-grama range, and compares the results with previous classifications of range sites and range conditions.

Methods

Frequency Sampling Techniques.

—Frequency sampling techniques for Short Grass Plains were developed in a previous study (Hyder et al. 1965). Each sample is restricted to a macroplot 100 by 75 ft., and includes 250 quadrat placements allocated 25 in each of 10 transects. The term "stand" refers to the vegetation encountered in any macroplot.

The sampling frame includes a nested pair of quadrats mounted on a handle. A large quadrat of 16 by 16 inches includes a 2 by 2-inch quadrat in one corner. At each quadrat placement an observer names the species in each quadrat size and an assistant accumulates the observations and records species frequencies for each transect. The term "frequency" refers to the percentage of quadrats in which a species occurs. Our sampling required about 4 man-hours per macroplot.

Sixty-seven stands were sampled in 1962 and 1963. Two or more macroplots were located on each phase of the soil series found in range units grazed lightly, moderately, and heavily, and in ungrazed exclosures. Macroplot locations were paired on opposite sides of fences, where possible, to obtain unbiased differences attributable to grazing intensity.

Soils and Grazing Intensities.— The soil series encountered in sampling were Vona sandy loam; Greeley sandy loam, Ascalon sandy loam; Renohill loam and fine sandy loam; Midway-Renohill complex, Havre loam and very fine sandy loam; Fort Collins loam; unnamed undifferentiated loam and clay loam; Nunn clay loam; and unnamed saline-alkali loam and clay loam.

The range pastures sampled were grazed by yearling Hereford cattle from May 1 to November 1 annually since 1939. Stocking rates were adjusted to obtain light, moderate, or heavy grazing. Each pasture included a 1 to 2-acre livestock exclosure. Vegetation and livestock measurements in the first 15 years were reported by Klipple and Costello (1960).

Vegetation-Soils Relations. — The correlations between individual species frequencies and scored values of soil texture, subsoil, permeability, substratum permeability, soil depth, topographic exposure, and slope were calculated. The soil characteristics that were significantly correlated with the frequencies of individual species were used, along with topographic position, to stratify the soil series into interpretive soil groups. This stratification of soils was made independent of species composition and stand characteristics. Subsequently, the frequency percentages of species were compiled by interpretive soil groups to evaluate vegetation-soils relations. The term "community" refers to the combination of stands in an interpretive soil group.

The vegetation is shown to be coordinated with the interpretive soil groups by coefficients of community similarity (Oosting, 1956, p. 77). These coefficients were calculated from the mean frequency percentages of all (123) species. Otherwise, the data base includes 46 species whose mean frequency percentages equal or exceed 5% in at least one stand. Thirty species had mean frequencies of 5% or more in at least one interpretive soil group. Five-percent confidence limits of mean frequency percentages were used to evaluate sampling precision within stands and heterogeneity among stands within communities.

The combination and segregation of species among communities is derived from interspecific correlations (Goodall, 1953) among 46 species independent of the interpretive soil groups. Significant correlations were obtained among 16 perennial species. Combinations and segregations among them are portrayed by the positive and negative coefficients. Therefore, these 16 species are arranged into community indicator groups called "unions".

Stands from all grazing intensities were included in the analyses of vegetation-soils relations. Since some soil series were not found in all exclosures and pastures, the grazing intensities are not equally balanced among soil-series groups. Thus, community differences among soil-series groups can be slightly confounded with differences due to grazing intensities.

Vegetation-Grazing Relations.— The frequency percentages of 46 species in each soil-series group were correlated with grazing intensities. The grazing intensities none, light, moderate, and heavy were scored 1, 2, 3, and 4, respectively, for these calculations. Positive correlation coefficients indicate increaser responses of species, and negative coefficients indicate decreaser reponses (Dyksterhuis, 1949).

Table 1. Interpretive soil groups.

Interpretive		Texture-		Number of
soil		permeability		macroplots
groups	position	index1	Soil Series	sampled
1	Upland	9	Vona sandy loam	17
2	"	8	Greeley sandy loam	7
3	"	7	Ascalon sandy loam	14
4	"	6	Renohill loam and	
			fine sandy loam	
			Midway-Renohill	
			complex	9
5	Bottomland	6	Havre loam	
			Fort Collins loam	8
6	"	4-5	Unnamed clay loam	
			Nunn clay loam	6
7	"	5	Unnamed saline-alkali	6

¹The texture-permeability index is the sum of soil-texture and subsoil-permeability scores.

Species nomenclature follows that of Harrington (1954). Common names are used in the text and tabulations. The botanical and common names of species mentioned are listed in Table 5.

Results

Interpretive Soil Groups.—Individual species frequencies are more uniformly related to soil texture and subsoil permeability than to the other soil characteristics considered. Therefore, the scored values of soil texture and subsoil permeability are added together for each soil series encountered and used as an index for assigning the soil series to interpretive soil groups. Upland soils are classified into four interpretive soil groups, and ordinated according to decreasing value of the texture-permeability index (Table 1). Bottomland soils are classified into three interpretive soil groups; but this classification is partly independent of the texture-permeability index. All bottomland soils can be flooded by high-intensity summer storms. The unnamed saline-alkali series is classified separately from other bottomland soils because of its salt content and high water table.

Vegetation-Soils Relations. — Coefficients of community similarity, computed from the frequency percentages of 123 species assembled by interpretive soil groups, portray vegetation-soils

relations (Table 2). The progressive decrease in similarity between the community of Interpretive Soil Group 1 and those of Interpretive Soil Groups 2, 3, and 4 suggests an upland vegetational continuum co-ordinated with soil texture and permeability (Curtis, 1955). Interpretive Soil Groups 6 and 7 produce plant communities that are very different from those on other soils. However, the "Overflow" conditions of Interpretive Soil Group 5 produce a community that is surprisingly similar to that of the upland Interpretive Soil Group 1.

The mean frequency percentages of 30 species are given by interpretive soil groups in Table 3. Most of these species, being unequally distributed among the communities, indicate competitive or adaptive vegetation-soils relations. We computed 5% confidence limits for the frequency percentages in Table 3. The confidence limits computed from the variances among transects within stands generally equal ± 2 to 3%. Therefore, sampling precision is very good. The confidence limits computed from the variances among stands within communities average $\pm 13\%$, and are greater on bottomland than upland soils. The great variance among stands indicates excessive heterogeneity in species frequencies on each soil. Such heterogeneity can result from grazing effects, random variations, species substitutions, soil heterogeneity (as found in Utah by Stewart and Keller, 1936), or variations in other site characteristics.

Species Unions. — Significant interspecific correlation coefficients were obtained among 16 perennial species. Forty-six species were included in the calculations. These 16 species are ordinated, according to positive and negative coefficients, into 5 unions (Table 4). Within each union the species generally are

Table 2. Coefficients of community similarity among interpretive soil groups.

Soil		Uj	pland	l	Bottom land				
group	s 1	2	3	4	5	6	7		
Up-									
land									
1									
2	.77								
3	.67	.79							
4	.64	.75	.84						
Bot-									
tom									
land									
5	.71	.65	.62	.64					
6	.35	.30	.35	.41	.41				
7	.40	.43	.41	.41	.40	.38			

positively associated, but between unions the species generally are negatively associated or unrelated. Western wheatgrass and fourwing saltbush are the primary exceptions. These two species are treated as a separate union even though they are positively correlated with one or more species in Unions II, III, and especially V. In general, the species in each union are loosely associated. Union V is the most coherent, and Union II is the least coherent.

The frequency percentages of these 16 species, summed within

Table 3. Mean frequency percentages of thirty species by interpretive soil groups.

	Interpretive soil groups								
Species ¹	1	2	3	4	5	6	7		
Perennial grasses and sedges:									
Blue grama ²	71	75	75	72	76	18	33		
Three-awn	27	15	16	6	1	1	;		
Western wheatgrass	26	8	6	10	33	52	70		
Broad-leafed sedge	13	16	40	29	22	63			
Needle-and-thread	9	6	1	1	1	1	;		
Sand dropseed	7	4	4	2	1	0	;		
Buffalo grass	3	7	7	36	10	80	;		
Saltgrass	0	0	0	0	5	0	8.		
Alkali sacaton	0	0	0	0	0	0	30		
Shrubs and cactus:									
Plains pricklypear	26	32	35	43	22	2			
Buckwheat	11	23	4	3	1	0	;		
Fourwing saltbush	4	1	1	0	7	1	(
Fringed sage	3	1	7	1	1	2			
Winterfat	1	1	0	0	9	0	(
Perennial forbs:									
Scarlet globemallow	29	32	41	43	39	9	1:		
Plains bahia	12	1	1	4	4	3			
Scarlet gaura	2	6	2	4	2	1	;		
Rush skeletonplant	1	5	1	1	3	0			
Silky sophora	1	1	1	1	7	6			
Two-grooved loco	1	1	1	0	0	7	(
Povertyweed	0	0	0	1	1	38	1		
Talinum	0	0	0	0	0	1	1		
Annuals:									
Sixweeks fescue	9	31	65	53	2	11	4		
Tansyleaf aster	6	9	3	7	1	0	:		
Prairie pepperweed	4	7	4	3	1	1	4		
Wooly indianwheat	2	10	22	26	1	3	1:		
Gilia	2	4	6	2	0	1			
Slimleaf goosefoot	1	1	1	1	2	1			
Cryptantha	1	3	4	1	1	0			
Skeletonleaf bur-sage	0	0	0	0	0	12	(

¹This list includes the species that appear at a mean frequency of 5% or more in at least one interpretive soil group.

²Blue grama frequencies are from a 2-inch quadrat, and all other species frequencies are from a 16-inch quadrat.

Table 4. Species unions derived from interspecific correlation coefficients.

	•			Int	er-spec	ific co	rrelati	on coef	ficients	$^{1}\left(r ight)$ a:	mong s	pecies					
	Species																
Union	$symbol^2$	Blue	Pric	Glob	Need	Thre	Sand	Bahi	Buck	Buff	Pove	Sedg	West	Four	Salt	Alka	Tali
I	Blue	1.00															
	\mathbf{Pric}	.55	1.00														
	Glob	.42	.31	1.00													
II	Need				1.00												
	Thre				.48	1.00											
	Sand				.37	.37	1.00										
	Bahi					.52		1.00									
	Buck				.38	.35	.51		1.00								
III	Buff	54	26			27			27	1.00							
	Pove	68	39	36						.53	1.00						
	Sedg				25					.41		1.00					
IV	West	67	37	31				.40			.44		1.00				
	Four							.37			.25		.44	1.00			
V	Salt	43	42	29								29	.45		1.00		
	Alka	38	32	30							.28		.40	.40	.77	1.00	
	Tali	29	27										.28		.66	.65	1.00

With n-2=65 degrees of freedom an r of 0.25 is significantly greater than zero at 5%, and an r of 0.32 is significant at 1%. Non-significant coefficients are omitted.

²Blue = Blue grama
Pric = Plains pricklypear
Glob = Scarlet globemallow
Need = Needle-and-thread
Thre = Three-awn

Sand = Sand dropseed
Bahi = Plains bahia
Buck = Buckwheat
Buff = Buffalo grass
Pove = Povertyweed

Sedg = Broad-leafed sedge West = Western wheatgrass Four = Fourwing saltbush Salt = Saltgrass

Alka = Alkali sacatonTali = Talinum

each union, were assembled by interpretive soil groups (Figure 1). Union I is dominant in Interpretive Soil Groups 1 through 5; Union III is dominant in Soil Group 6; and Union V is dominant in Soil Group 7.

Upland soils produce a vegetational continuum in which Unions I and III increase and Unions II and IV decrease as the soil becomes less permeable. Needle-and-thread and other grasses in Unions II and IV give Interpretive Soil Group 1 a midgrass aspect even though blue

grama is dominant. Hanson (1955) described communities in which needle-and-thread is dominant, but his communities were found on areas that receive more precipitation than our Interpretive Soil Group 1. Mid-grasses and shrubs decrease with decreasing soil permeability, but short grasses, plains pricklypear, and scarlet globemallow increase. Blue grama is dominant on all of these upland soils. Buffalo grass is dominant on upland soils less permeable than those of Interpretive Soil Group 4, and on similar soils that receive less precipitation. Thus, the upland continuum portrayed in Figure 1 and Table 2 is part of a broader continuum encountered in the vicinity of this experimental

The vegetation on the salinealkali soils is unique, presumably because of the salt content and high water table. The loamy soils of Interpretive Soil Group 5 support a highly productive community with an aspect of fourwing saltbush and western wheatgrass. Western wheatgrass, fourwing saltbush, and blue grama are replaced by buffalo grass as soil permeability and flooding frequency decrease. When isolated from flood waters, Interpretive Soil Group 5 produces a community like that of Interpretive Soil Group 4, except for the low occurrence of plains pricklypear.

Vegetation-Grazing Relations. -None of the species were correlated with grazing intensities at the 10% confidence level. Therefore, the frequency percentages of species arranged by grazing intensities are omitted. Three species were correlated with grazing intensities at the 20% level. Needle-and-thread, with a correlation coefficient (r)of -0.68, is a decreaser on the sandy loams of Interpretive Soil Groups 1 and 2. Western wheatgrass, with an r of -0.89, is a decreaser on the loamy soils of Soil Group 5. Scarlet globemallow, with an r of 0.84, is an increaser on the saline-alkali soils of Soil Group 7. Other species, varying in both degree and kind of response among soils, show

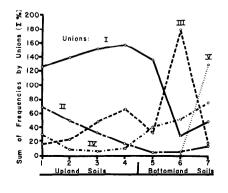


Fig. 1. The distribution of species unions among interpretive soil groups.

Table 5. Common and botanical names of species mentioned in text and

tables. Common name Botanical name Perennial grasses and sedges Western wheatgrass Agropyron smithii Rydb. Three-awn Aristida longiseta Steud. Bouteloua gracilis (H.B.K.) Lag. ex Steud. Blue grama Buffalo grass Buchloe dactyloides (Nutt.) Engelm. Broad-leafed sedge Carex heliophila Mack. Saltgrass Distichlis stricta (Torr.) Rydb. Alkali sacaton Sporobolus airoides (Torr.) Torr. Sand dropseed Sporobolus cryptandrus (Torr.) A. Gray Needle-and-thread Stipa comata Trin. & Rupr. Shrubs and cactus Fringed sage Artemisia frigida Willd. Fourwing saltbush Atriplex canescens (Pursh) Nutt. Buckwheat Eriogonum effusum Nutt. Winterfat Eurotia lanata (Pursh) Moq. Opuntia polyacantha Haw. Plains pricklypear Perennial forbs Two-grooved loco Astragalus bisulcatus (Hook.) Gray Plains bahia Bahia oppositifolia (Nutt.) DC. Gaura coccinea Nutt. ex Pursh Scarlet gaura Iva axillaris Pursh Povertyweed Rush skeletonplant Lygodesmia juncea (Pursh) D. Don. Silky sophora Sophora sericea Nutt. Scarlet globemallow Sphaeralcea coccinea (Pursh) Rydb. Talinum Talinum parviflorum Nutt. ex Torr. & Gray Annuals Aster tanacetifolius H.B.K. Tansyleaf aster Chenopodium leptophyllum Nutt. ex S. Wats. Slimleaf goosefoot Cryptantha minima Rydb. Cryptantha Sixweeks fescue Festuca octoflora Walt. Franseria discolor Nutt. Skeletonleaf bur-sage Gilia laxiflora (Coult.) Osterh. Prairie pepperweed Lepidium densiflorum Schrad. Wooly indianwheat Plantago purshii Roem. and Schult.

very weak responses to grazing intensity. We find insufficient foundation for range-condition classification on these range areas, because summer-long grazing at different intensities for 23 years has not affected species composition to a great extent on any soil.

Discussion

Classifications by SCS Personnel. — Soil-Conservation-Service personnel completed range-site and range-condition mapping on the Central Plains Experimental Range just one year prior to our sampling. Our interpretive soil groups are approximately equivalent to the range sites delineated. "Sandy Plains" includes all the macroplots in Interpretive

Soil Group 1 and a few of those in Interpretive Soil Groups 2 and 3. "Loamy Plains" includes most of the macroplots in Interpretive Soil Groups 2, 3, and 4. "Overflow" includes some of the macroplots in Interpretive Soil Group 5, and the remainder, located where flood waters have been intercepted since 1950, are classified as "Brule Loam." "Clayey Swale" includes all macroplots in Interpretive Soil Group 6, and "Salt Meadow" includes those in Interpretive Soil Group 7.

All of the pastures included in our sampling were rated as fair or good (mostly good) range condition. The great variation in vegetation due to site differences, and the small variation

due to range condition, was observed and interpreted as such by Soil-Conservation-Service personnel.

Range Site versus Range Condition. — Present concepts of range sites and range-condition classes are distinctly different. A range site is intended to be a natural subdivision in which the vegetation, being the product of special site conditions, includes species that, in fact, identify the site. A range-condition class is intended to be a successional subdivision (to be more exact, a secondary-successional subdivision) within a range site that can be manipulated to some moreadvanced or some less-advanced state by the adjustment of grazing. A range-condition class is recognized by the array of (increaser and decreaser) species plus other characteristics of vegetation and soil. Modern range management is built upon the ecological foundation pro-

vided by these two concepts. For the range areas included in the frequency sampling, Klipple and Costello (1960) described four range-condition classes and three grades of condition in each class. However, they did not separate soil-related from grazing-related vegetational differences. We sampled essentially the same extent of vegetational differences (and in the same areas) as sampled previously by Klipple and Costello (1960). Most of the vegetational differences in our data were soil related; therefore, they would be incorrectly classified under the term "range-condition classes." The blue-grama/buffalo-grass/ pricklypear community of Interpretive Soil Group 4 can not be manipulated to equality with the "flood plain" of Interpretive Soil Group 5, or even with the shortgrass/mid-grass community of Interpretive Soil Group 1. Site definition and delineation must precede range-condition classification, because range condition

is interpreted as an indication of grazing severity.

But what is a range site in the upland vegetational continuum? Site differences on the bottomland soils are reasonably natural and discrete. However, sharp vegetational demarcations do not occur on the upland soils. We classified four interpretive soil groups on upland soils where the Soil Conservation Service classifies two range sites. For mapping purposes, three upland range sites probably would be more appropriate than either two or four. Whatever may be the division into sites, the standards for mapping are more arbitrary than natural. Any division that can be mapped with facility will contain considerable inherent variability that might subsequently be classified erroneously into classes of range condition. Although the concepts of range sites and range-condition classes are distinctly different, the phenomena upon which they are determined are partially inseparable in the field. Variations in range condition can alter the delineation of range sites. And heterogeneity within range sites can complicate range-condition classification.

Adequacy of Frequency Data. —Stable characteristics of vegetation are most useful in vegetation classification. For this reason, a complete species list is needed for each stand sampled. In addition, the characteristics of density, dispersion, and basal area are stable enough to be valuable criteria. Yield and cover often are too ephemeral to be useful in vegetation classification, but become important in subsequent studies. Frequency provides a relatively complete species list and measures the pooled effect of two reasonably stable characteristics — density and dispersion. Consequently, we theorized that frequency data should be valuable in the study of vegetation-soils and vegetation-grazing relations on the Short Grass Plains. Regarding the adequacy of frequency data, we conclude (1) that vegetationsoils relations have been clarified very well, (2) that summer-long (May 1 to November 1) grazing at different intensities for 23 years has not affected species frequencies to a great extent, (3) that the frequency percentages of species are stable enough to permit the study of vegetationsoils relations at all of these grazing intensities, and (4) that the most important effect of heavy grazing has been a reduction in herbage yields (Klipple and Bement, 1961).

Since the value of the frequency method depends on the sampling problem as well as the study objective, frequency data can be more or less valuable in other vegetation types and kinds of studies. Frequency, like density, rates individual plants equally regardless of size. Where density is a valuable criterion, frequency also can be valuable.

Grazing intensities introduce differences in species frequencies more slowly than in herbage yields. But reduced productivity can be recovered rather quickly with lighter grazing (Klipple and Bement, 1961) unless there have been significant changes in the density and dispersion of species. Therefore, the characteristics sampled by frequency are important in both site and condition classification on the Short Grass Plains.

Data processing limitations have restricted the use of frequency data in range investigations, but this is not an obligate disadvantage of the method. In the development of frequency sampling techniques for Short Grass Plains, we utilized the advantages of two statistical forms—the binomial and the normal distributions. A binomial classification of presence or absence permits maximum objectivity, accuracy, and speed in data

collection. And the accumulation of data according to the requirements of sub-sampling theory permits the use of normal-theory statistics in data processing. The advantages gained in this way justify the careful development of frequency sampling techniques.

Summary

Frequency sampling was undertaken at the Central Plains Experimental Range in Colorado to test the assumption that the characteristics of species density and dispersion, as measured by frequency, are useful for the study of vegetation-soils and vegetation-grazing relations on the Short Grass Plains. Sampling techniques were developed and reported previously.

We conclude that (1) vegetation-soils relations have been clarified, (2) that summer-long (May 1 to November 1) grazing at different intensities for 23 years has not affected species frequencies to a great extent, (3) that the frequency percentages of species are stable enough to permit the study of vegetation-soils relations at all of these grazing intensities, and (4) that the most important effect of heavy grazing has been a reduction in herbage yields.

The results obtained are compared with previous classifications of range sites and range conditions, and the problem of classifying sites and conditions in a vegetational continuum is discussed.

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