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PRELIMINARY PRODUCER DATA SYNTHESIS, 1970 COMPREHENSIVE NETWORK SITES

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ABSTRACT

The 1970 field data from the U.S. IBP Comprehensive Network Sites were analyzed by my students from the University of Oklahoma. The data analysis emphasized intersite comparisons of producer and abiotic components of the grassland ecosystems. When various sites were ordered with ordination techniques using environmental vegetation and floristic values, there was an overall similarity in end-stand differences. Total biomass production as well as productivity were correlated with various environmental parameters and vegetation types. Multiple regression analysis was used to separate the manner in which particular species responded to climatic conditions. Three measures of biomass production were compared and found to give significantly different results. In more xeric sites, root turnover rates and root-shoot ratios were higher. Both phenology and species association were evaluated, but the data was not entirely appropriate.

INTRODUCTION

by

Paul G. Risser

The contents of this technical report were derived from a class project produced during the spring of 1971. This class was entitled Botany 6454, Plant Community Ecology, which was taught at the University of Oklahoma in the Department of Botany and Microbiology. The members of this class were all graduate students, most of them in the botany department.

During February and early March 1971, the nine students in the class attempted to make a sophisticated analysis of the 1970 U.S. IBP Grassland Biome field data from the Comprehensive Network Sites. These data included information concerning the abiotic variables and the producer components which were taken on the Bison, Bridger, Cottonwood, Dickinson, Jornada, Hays, Osage, Pantex, and Pawnee Sites. Most of the herbage dynamics data were supplied in card form from the Natural Resource Ecology Laboratory, Colorado State University, with the assistance of Mr. D. M. Swift. Abiotic data were obtained from the principal investigators at the respective sites. The sites and their principal investigators are listed below:

Bison -- Mel Morris

Bridger -- Tad Weaver

Cottonwood -- Tex Lewis

Dickinson -- Warren Whitman

Hays -- Gary Hulett and Jerry Tomanek

Jornada -- Rex Pieper

Osage -- Paul Risser

Pantex -- Russ Pettit

Pawnee -- Phil Sims

Each student selected a particular area of interest and went about the data analysis. In general, the data were divided into four sections: (i) abiotic factors and vegetation across the network, (ii) grassland structure, (iii) vegetation and individual species response to abiotic factors, and (iv) production and productivity.

This program culminated with a 2-day working session at the University of Oklahoma, where the principal investigators worked with the students over the 2-day period. During the first morning and part of the afternoon, each student made a 20-min presentation of his data analysis. This was followed in the afternoon and the next day by detailed discussions of the results. These results have now been reworked and summarized and are presented in this technical report.

COMPREHENSIVE NETWORK SITE ORDINATIONS BASED ON ABIOTIC FACTORS

by

Anthony Dvorak

Introduction

The U.S. IBP Grassland Biome data synthesis project brought together raw data collected throughout the 1970 growing season from tall-, mixed-, and shortgrass prairies. The wide geographic range of the contributing sites (Fig. 1) results in varying environmental conditions, some of which are average monthly temperature, average monthly precipitation and evaporation, solar radiation, and growing season. These variables in turn affect such variables as soil water, type and amount of vegetation present, etc. The analysis undertaken in this project will yield similar and dissimilar results when comparisons are made between sites, according to the overall environment of each site. The development of environmental site ordinations was therefore designed to be one of the early completed projects. The ordinations were to provide insight into the similarities of the various sites and to develop from this an expectation of what would be found vegetationally. Secondly, the results obtained from the vegetation studies would be plotted on the ordinations for intersite comparisons.

Two types of ordinations were done. Bray and Curtis' (1957) index of similarity was used to arrange the sites in a two-dimensional ordination. The distances between sites is an indication of their similarity; closer sites are similar and those farther apart are less similar. The other ordination technique used was factor analysis, or principal component

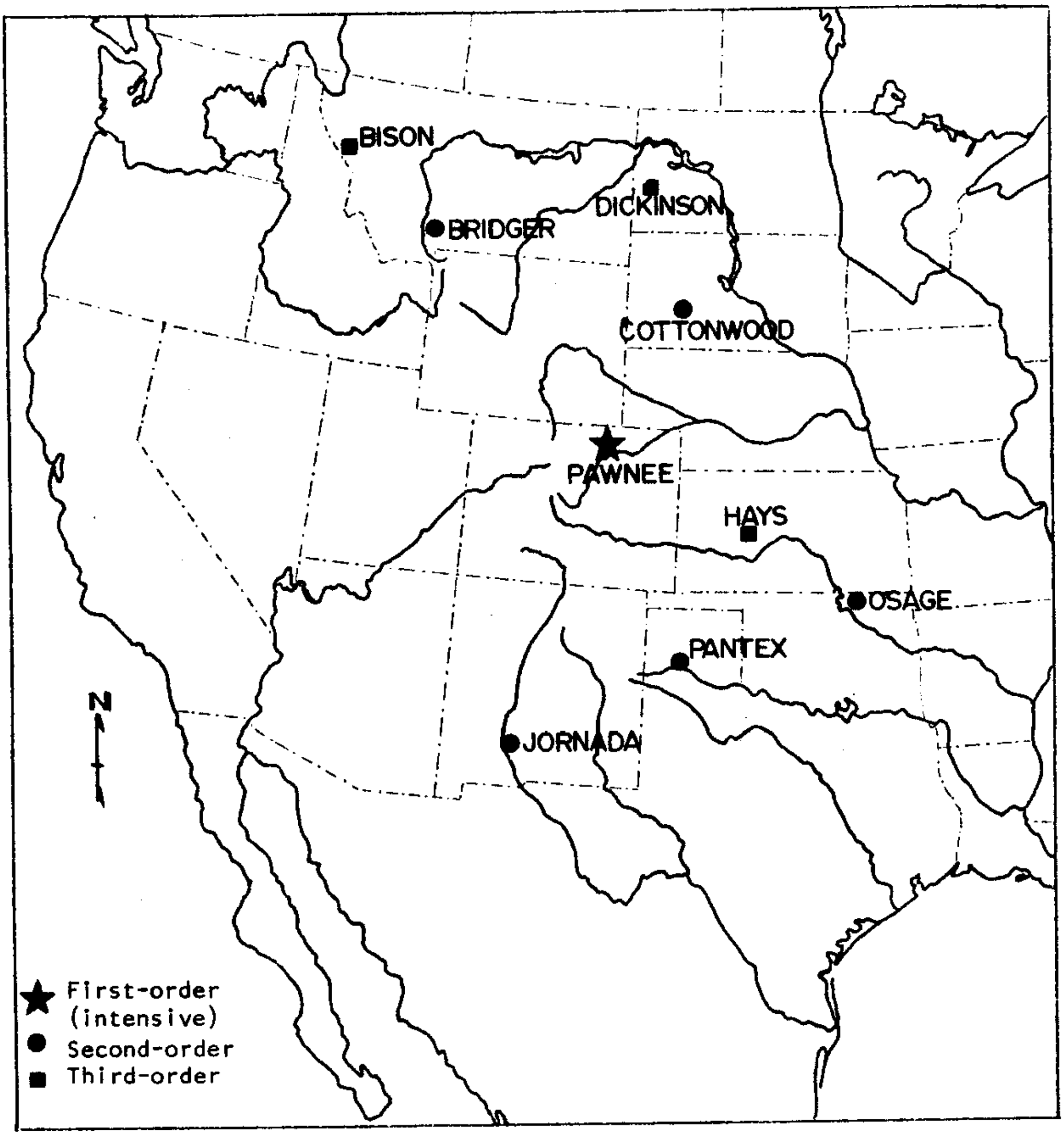

Fig. 1. U.S. IBP Grassland Biome Comprehensive Network Site locations.

analysis (Jeffers, 1967). The variables or factors which account for the greatest variance on each axis can be determined with this type of ordination.

Abiotic Factors

The ordinations were performed on two sets of environmental variables. The set first consisted of a literature list of 45 abiotic factors (Table 1). The variables in Table 1 are basically the means or averages of long-term weather collection data. The two main sources were the U.S. Department of Agriculture (1941) and the technical reports contaning the Network Site descriptions (Collins, 1970; Herbel and Pieper, 1970; Huddleston, 1970; Lewis, 1970; Morris, 1970; Risser, 1970; Tomanek, 1970; Whitman, 1970). Some 80% of the variables deal with average monthly precipitation, average monthly temperature, and average daily hours of sunshine per month. A second set of selected variables was chosen as being the most influential in establishing conditions for favorable and unfavorable vegetative responses (Table 2). The data used for the values of the selected variables were measured at the sites during the 1970 growing season unless otherwise noted. The Bridger and Hays Sites were unable to supply soil water values, so this analysis was limited to seven of the nine sites. The other variables in this set besides soil water were solar radiation (g cal/cm^2/day), pan evaporation for the months of April through July, and average monthly precipitation from the previous fall (August through October) and March through July of the 1970 growing season.

Ordination of All Environmental Variables

The ordinations entitled INDEXSIM 1 (Fig. 2) and FACTO 1 (Fig. 3) were done using the 45 literature values from Table 1.

Table 1. Environmental variables utilized in site ordinations INDEXSIM 1 and FACTO 1. (Footnotes in column descriptions denote the source of the column information. Footnotes found within the column are specific for the site and pertain to the 12-month source.)

Site	Annual Precipitation[a] (inches)	Growing Season[b] (days)	Precipitation During Growing Season[b] (inches)	Elevation[c] (m)	Mean Annual Temperature (°F)
Bison	12.7	125	7.7	980	45.1[a]
Bridger	12.2	134	9.1	2,320	45.9[d]
Cottonwood	15.2	126	12.0	850	46.7[a]
Dickinson	15.7	120	11.9	850	42.3[d]
Hays	23.0	168	17.8	610	53.4[d]
Jornada	9.0	196	6.3	1,340	58.2[d]
Osage	36.6	205	24.4	380	58.0[d],[e]
Pantex	20.8	197	15.2	1,090	57.3[a]
Pawnee	13.6	127	11.0	1,430	45.6[d]

Table 1. (continued).

Site	Mean Monthly Precipitation (inches)											
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Bison	0.95[a]	0.66	0.69	1.08	1.78	1.99	1.00	0.87	0.98	1.06	0.80	0.88
Bridger	0.41[a]	0.37	0.59	0.88	2.13	2.86	1.32	0.89	1.04	0.86	0.50	0.32
Cottonwood	0.42[a]	0.38	0.75	1.76	2.78	2.99	1.81	1.56	1.13	0.89	0.40	0.35
Dickinson	0.45[b]	0.42	0.73	1.06	2.26	3.39	2.17	1.87	1.20	0.85	0.50	0.48
Hays	0.29[b]	0.78	0.88	2.11	3.41	4.04	2.95	3.09	2.18	1.48	0.96	0.57
Jornada	0.35[b]	0.38	0.38	0.20	0.57	0.56	1.75	1.77	1.41	0.89	0.45	0.62
Osage	1.37[b]	1.46	2.54	3.79	4.84	4.97	3.51	3.48	3.77	3.21	2.23	1.41
Pantex	0.54[a]	0.72	0.80	1.56	3.06	2.81	2.61	2.98	2.21	1.76	0.90	0.77
Pawnee	0.21[b]	0.53	0.54	1.52	2.26	1.70	2.32	1.68	1.33	0.65	0.34	0.49

Table 1. (continued).

Site	Mean Monthly Temperature (°F)											
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Bison	23.4[a]	30.0	34.7	44.8	53.1	60.4	66.9	64.3	56.4	45.5	33.7	28.6
Bridger	21.8[d]	25.8	35.2	44.9	52.4	59.4	66.9	65.2	55.4	44.8	33.1	24.6
Cottonwood	19.1[a]	22.8	32.6	46.2	56.6	66.9	74.7	72.6	62.0	49.7	34.3	23.3
Dickinson	10.3[d]	11.8	24.4	42.9	52.2	61.3	68.0	66.3	56.5	43.9	28.6	17.3
Hays	29.8[d]	31.0	42.3	51.8	61.6	71.9	77.9	77.2	68.3	56.0	42.2	30.6
Jornada	38.4[d]	44.0	51.4	58.4	65.9	74.7	77.8	76.9	69.8	57.7	46.8	36.9
Osage	35.3[d]	36.3[d]	49.3[d]	55.5[e]	68.7	69.5	80.2	84.2	71.8	61.6	47.3	36.7[d]
Pantex	37.0[a]	41.0	47.5	56.0	65.0	74.5	77.0	76.0	69.5	59.0	46.0	39.0
Pawnee	26.0[d]	27.0	34.5	42.9	52.2	62.0	67.4	66.6	58.1	46.8	35.6	27.7

Table 1. (continued).

Site	Percent Sunshine of Total Possible[d/]			
	Winter	Spring	Summer	Fall
Bison	35	65	75	55
Bridger	55	65	75	55
Cottonwood	55	65	65	65
Dickinson	55	55	65	55
Hays	65	65	75	75
Jornada	75	85	75	85
Osage	55	65	75	65
Pantex	75	75	80	75
Pawnee	65	65	65	65

Table 1. (continued).

Site	Monthly Hours of Sunshine[d/]											
	Jan.	Feb.	March	April	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Bison	3.5	4.5	6.5	8.5	8.5	9.5	11.5	10.5	8.5	6.5	4.5	3.5
Bridger	3.5	5.5	7.5	8.5	8.5	9.5	11.5	10.0	8.5	7.0	5.0	4.0
Cottonwood	5.5	6.5	7.5	8.5	8.5	10.5	11.5	10.0	8.5	6.5	6.0	5.0
Dickinson	4.5	6.5	6.5	8.5	8.5	9.5	10.5	9.5	8.0	6.5	5.0	4.5
Hays	6.5	7.5	7.5	8.5	9.5	10.5	11.5	10.5	9.5	8.5	7.5	6.5
Jornada	7.5	8.5	9.5	10.5	12.5	12.5	11.0	10.5	10.0	9.5	8.5	7.5
Osage	5.5	6.5	7.5	7.5	9.5	10.5	11.5	10.5	9.5	8.0	6.5	5.5
Pantex	6.5	7.5	7.5	8.5	9.5	11.5	10.0	10.0	9.5	8.5	7.5	6.5
Pawnee	6.5	7.5	7.5	8.5	9.0	10.5	11.0	10.0	9.0	8.0	7.0	6.0

[a/] Collins (1970), Herbel and Pieper (1970), Huddleston (1970), Lewis (1970), Morris (1970), Risser (1970), Tomanek (1970), Whitman (1970).

[b/] U.S. Department of Agriculture (1941).

[c/] Van Dyne (1970).

[d/] U.S. Department of Agriculture (1936).

[e/] 1970 data.

Table 2. Environmental variables used in INDEXSIM 2 and FACTO 2. (Footnotes in column descriptions denote the source of the column information. Footnotes found within the column are specific for the site and pertain to the 12-month source.)

Site	Solar Radiation (g cal/cm^2/day)[a]				Pan Evaporation[b]				Soil Water[c]		
	April	May	June	July	April	May	June	July	May	June	July
Bison	768.78	923.47	1010.53	976.38	4.00	5.06	5.80	8.19	33.20	28.70	25.20
Cottonwood	793.65	935.20	1012.90	982.50	5.94	7.84	9.26	11.98	15.70	14.65	23.35
Dickinson	760.20	919.60	1009.50	974.10	4.05	5.70	6.18	7.89	22.20	17.41	8.79
Jornada	866.45	959.97	1006.30	988.63	9.71	12.13	13.39	11.54	13.00	13.00	7.30
Osage	843.33	954.20	1011.63	989.48	7.03	6.80	8.65	8.55	36.80	28.70	17.25
Pantex	855.38	957.58	1009.43	989.53	7.64[d]	9.28[d]	10.87[d]	11.12[d]	5.00	5.00	5.00
Pawnee	816.28	944.65	1013.50	986.73	4.52	5.05	6.22	7.12	19.13	15.06	12.34

Table 2. (continued).

Site	Mean Monthly Precipitation[e]							
	1969			1970				
	Aug.	Sept.	Oct.	March	April	May	June	July
Bison	0.87	0.98	1.06	0.69	1.08	1.78	1.99	1.00
Cottonwood	1.56	1.13	0.89	0.75	1.76	2.78	2.99	1.81
Dickinson	1.87	1.20	0.85	0.73	1.06	2.26	3.39	2.17
Jornada	1.77	1.41	0.89	0.38	0.20	0.57	0.56	1.75
Osage	3.48	3.77	3.21	2.54	3.79	4.84	4.97	3.51
Pantex	2.98	2.21	1.76	0.80	1.56	3.06	2.81	2.61
Pawnee	1.68	1.33	0.65	0.54	1.52	2.26	1.70	2.32

[a] Frank and Lee (1966).

[b] U.S. Department of Weather (1964).

[c] 1970 data.

[d] Collins (1970), Herbel and Pieper (1970), Huddleston (1970), Lewis (1970), Morris (1970), Risser (1970), Tomanek (1970), Whitman (1970).

[e] Table 1.

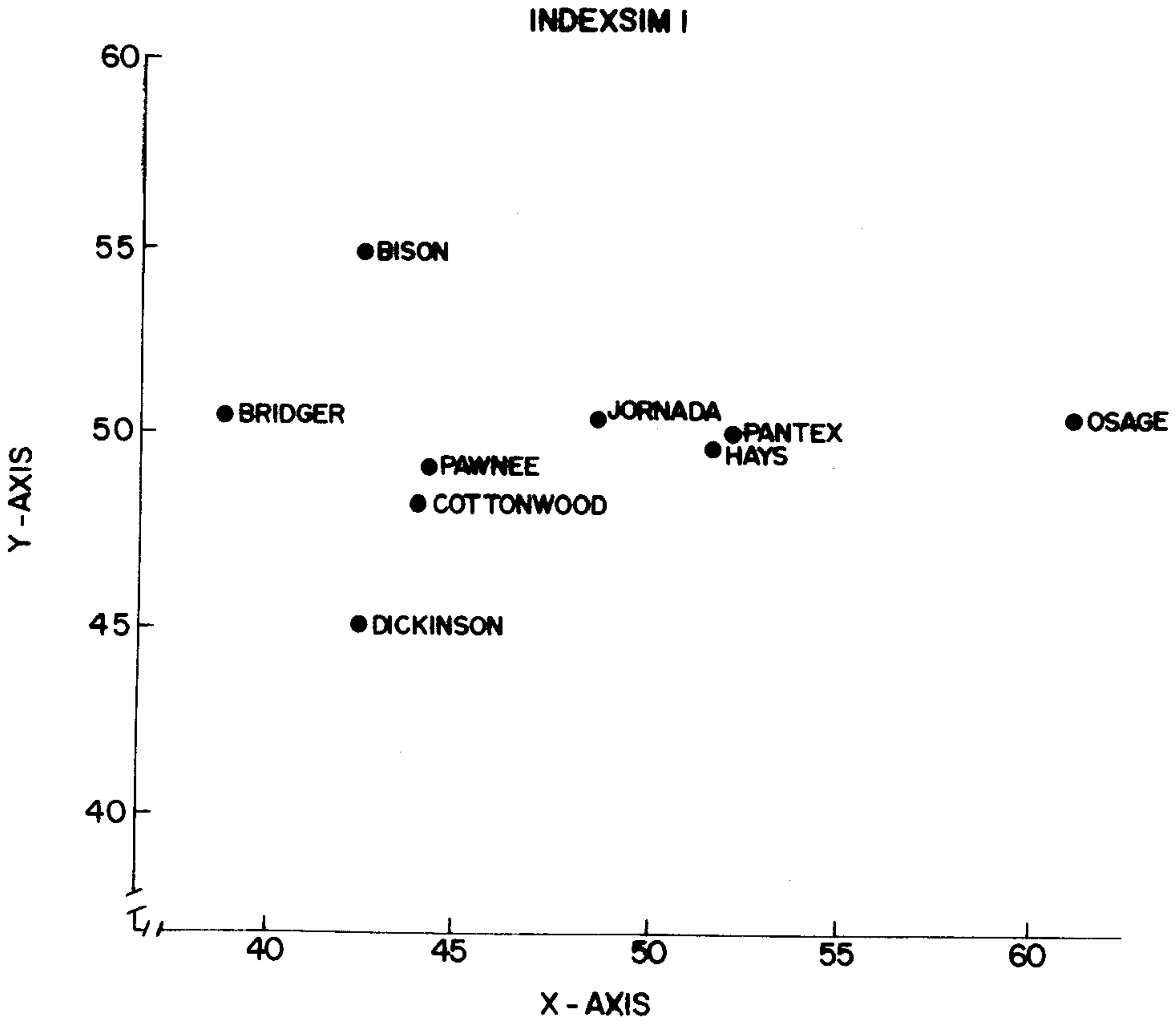

Fig. 2. Index of similarity ordination of U.S. IBP Grassland Biome sites based on the 45 environmental variables listed in Table 1.

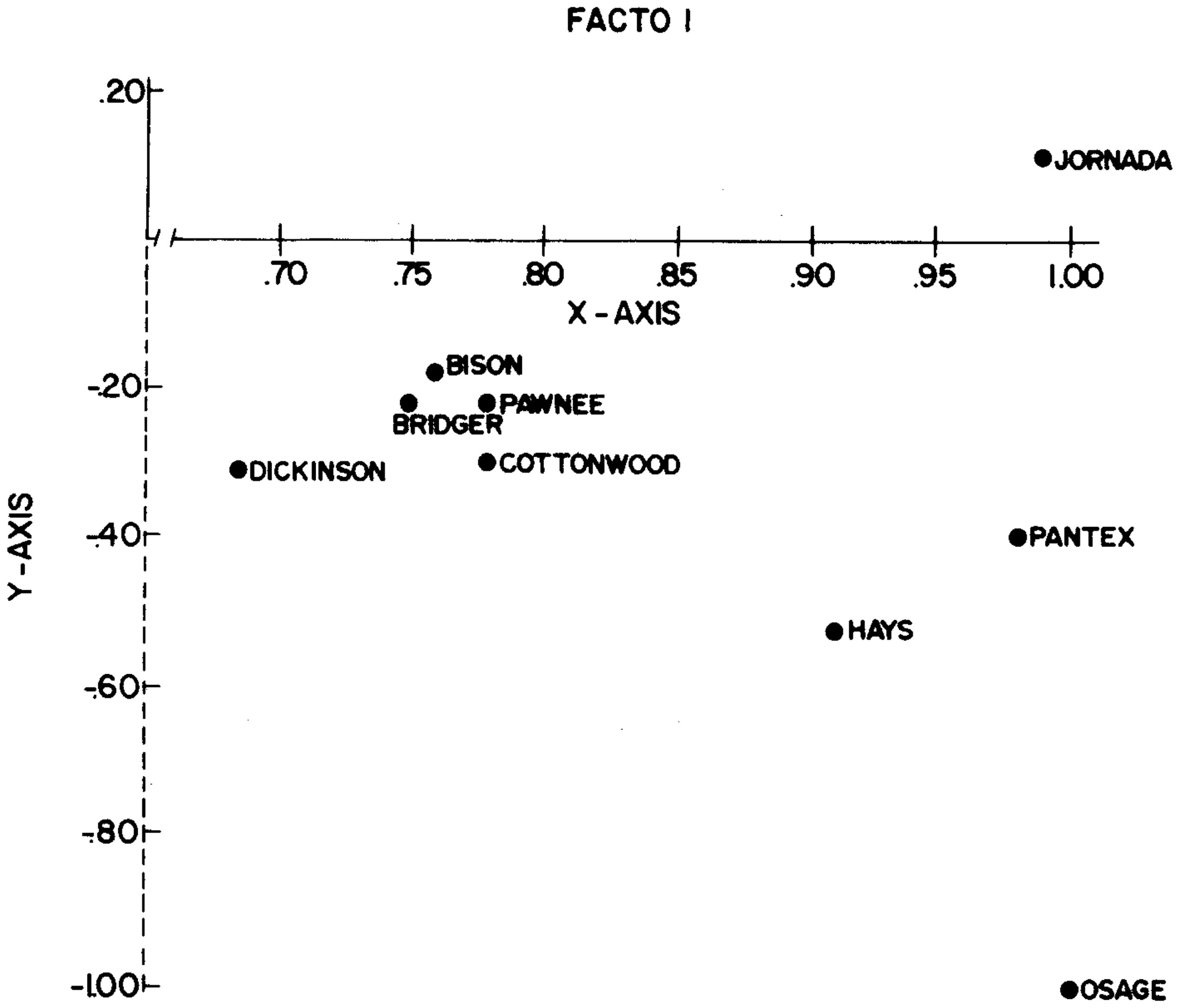

Fig. 3. Principal component ordination of U.S. IBP Grassland Biome sites based on the 45 environmental variables listed in Table 1.

The index of similarity matrix was developed by comparing each pair of sites by calculating the coefficient of similarity, $\frac{2w}{a + b}$, where a is the sum of the relative values for one site, b is the sum for the other site, and w is the sum of the lower values for each relative variable common to both sites (Bray and Curtis, 1957). Separation on the first axis (X) is apparently a latitudinal separation. The northern sites are located on the left side of the ordination and the southern sites on the right. The separation on the second axis (Y) could be an example of a problem that may develop with a small sample size, namely, separation of similar sites because of inadequate number of dissimilar stands to function as end stands in the polar ordination. The final result is that the sites are ordinated according to their latitudinal position as shown in Fig. 1. The similar sites, according to the ordination, are also located geographically near to each other.

Principal component analysis (FACTO) was also done on these environmental variables. A correlation matrix was calculated, and variables with scaled eigenvector values having absolute values greater than 0.85 were used in calculation of axis loadings.

The first axis of FACTO 1 (Fig. 3) accounts for 55% of the variance in the data and is based on 11 average monthly temperatures (excludes February), growing season, annual temperature, and percent sunshine of the total possible in September. Of the 14 variables 12 are aspects of temperature which result in the first axis being a temperature gradient. The warm-region sites are on the right, and the cooler sites are on the left. The second axis accounts for 27% of the variance and is based on the average monthly precipitation in March, April, May, and June; annual precipitation; and percent sunshine of the total possible in April. This axis is based on precipitation. Site alignments range from low to high precipitation as the axis values become more negative.

The resulting two-dimensional ordination shows five sites, Bison, Bridger, Pawnee, Dickinson, and Cottonwood, with similar temperatures and precipitation factors accounting for 84% of the total variance of the 45 environmental variables, clustered together at one side. Jornada, Pantex, Osage, and Hays have warmer and similar temperatures, but separate due to the precipitation factor.

Ordination of Selected Variables

The ordinations entitled INDEXSIM 2 (Fig. 4) and FACTO 2 (Fig. 5) were based on the selected variables found in Table 2.

Minor separation occurs on the first axis of INDEXSIM 2. Osage and Jornada are dissimilar, and the other five sites are similar or equally dissimilar to the end stands resulting in a clustering in the center. The second axis illustrates a south to north geographic distribution as the sites approach the horizontal axis. The ordination, from upper left diagonally to lower right, indicates a change from low soil water and high pan evaporation to high soil water and low pan evaporation.

Factor analysis, using the same variables, yields more obvious results. The first axis of FACTO 2 accounts for 41% of the variance and is based on the average monthly precipitation during July, August, September, and October. The sites are arranged from lower to higher precipitation, left to right respectively.

The greatest amount of separation occurs on the second axis with factor analysis using selected variables. The axis accounts for 37% of

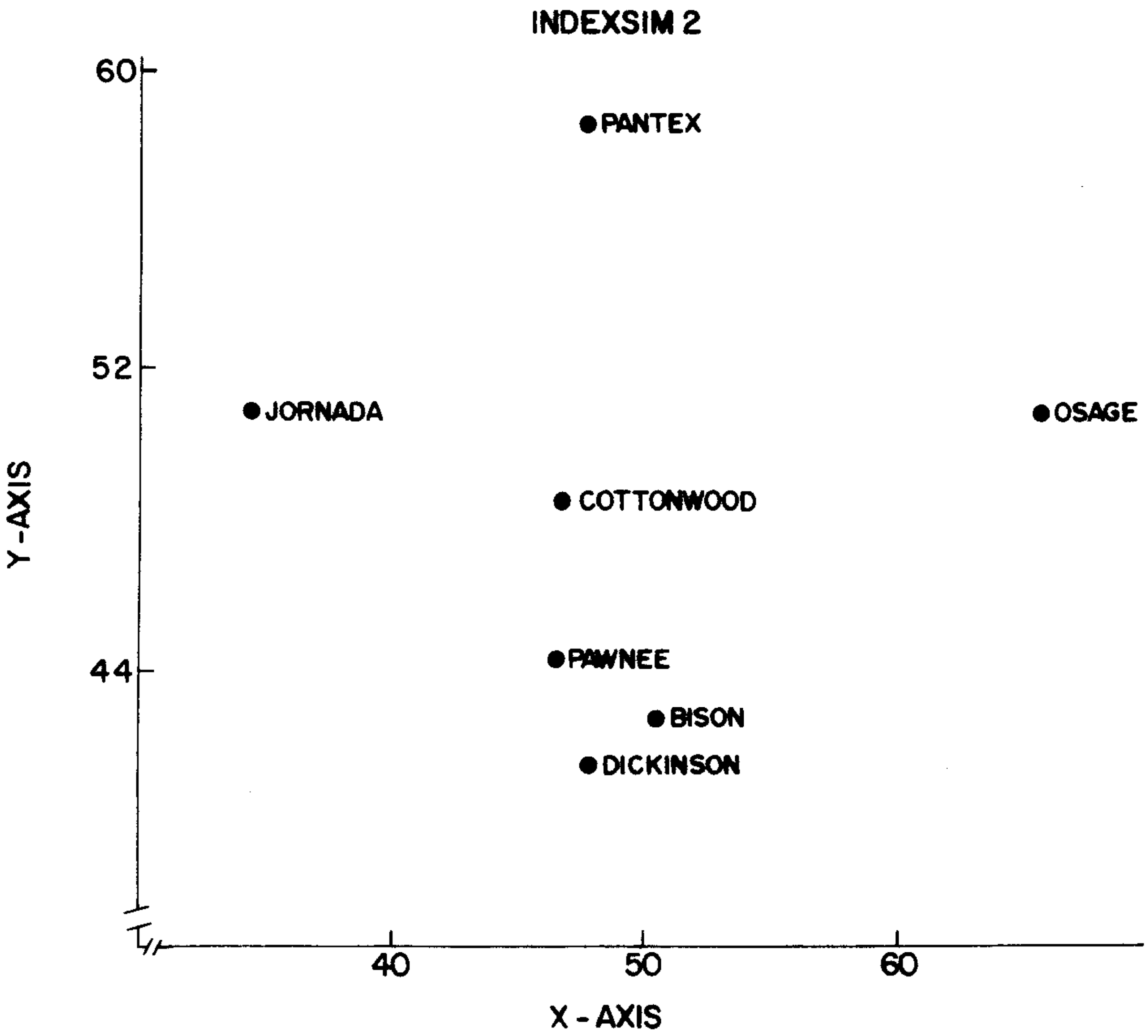

Fig. 4. Index of similarity ordination of U.S. IBP Grassland Biome sites based on the selected environmental variables listed in Table 2.

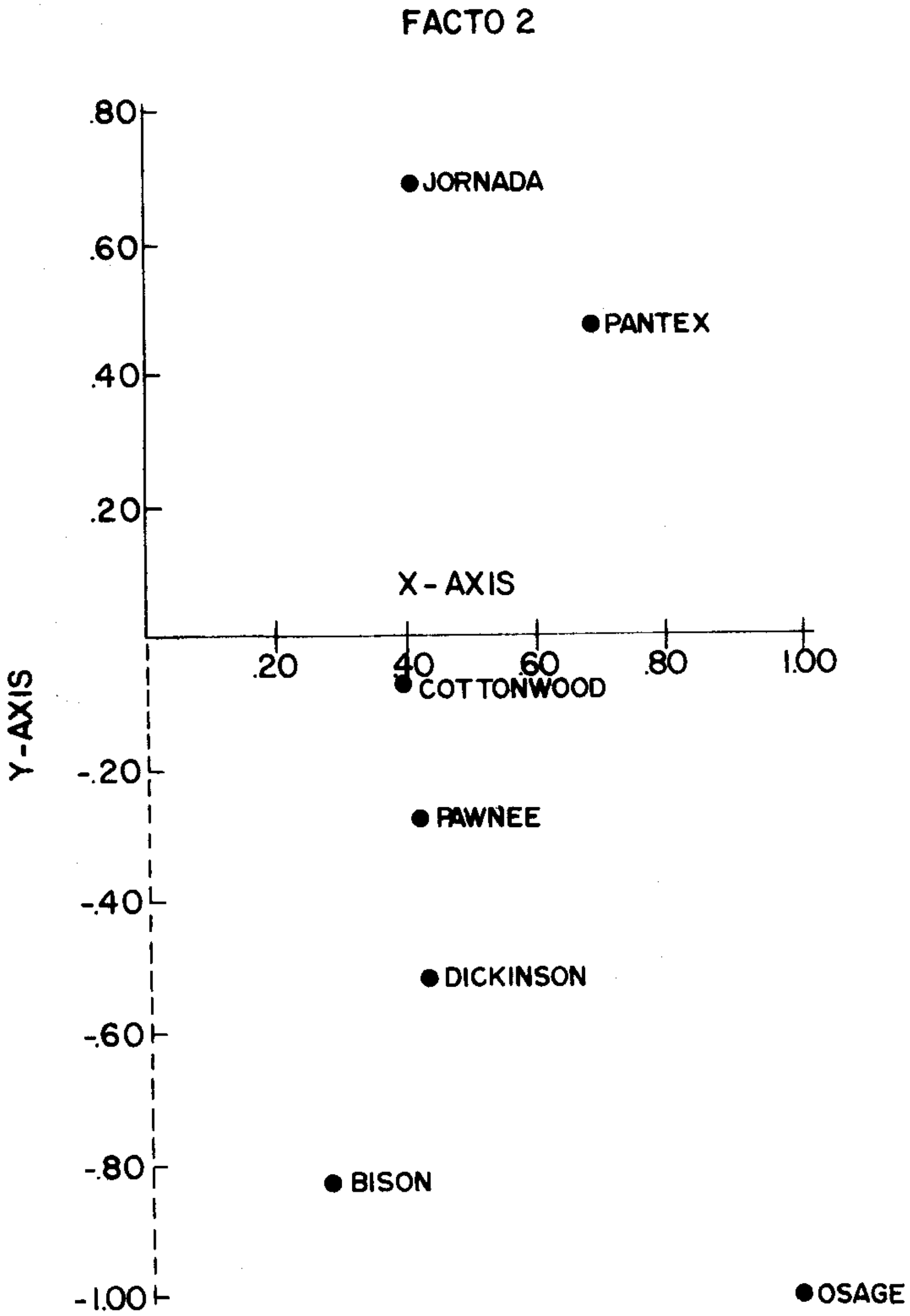

Fig. 5. Principal component ordination of U.S. IBP Grassland Biome sites based on the selected environmental variables listed in Table 2.

the variance among the variables. It is based on average June precipitation, pan evaporation during May and June, and soil water during May and June. The entire ordination is based on soil water. Vertically from upper to lower and horizontally from left to right, soil water increases.

Conclusions

The usefulness and value of the environmental ordinations included within this paper will be tested in subsequent papers. Factor analysis, more so than the polar ordinations, provides the gradients by which the sites may be positioned along a number of axes, allowing possible vegetational responses to these gradients to be determined by plotting results from the vegetation studies. These ordinations which are based on environmental variables, however, fail to take into account the species differentiation and resulting ecological adaptability from site to site.

The ordinations indicate a gap between the southern drier sites, Pantex and Jornada, and the aggregated northern sites. Osage, due to high temperatures and high precipitation, remained somewhat segregated from the other sites.

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VEGETATIONAL SIMILARITIES BETWEEN COMPREHENSIVE NETWORK SITES

by

Charles H. Perino

Ordination of the U.S. IBP Grassland Biome sites based on vegetational characteristics is, at best, difficult. The study involves a large geographic area over which different ecological factors exist and become differentially important. There is considerable diversity over this area, and the number of species which are common to all sites is limited. In attempting to compare the sites, several approaches have been used.

Grant (1971) has compared sites using floristic categories such as plant families and grass tribes. Grant used an index of overlap (R_o) "which evaluates the proportional group composition in terms of biomass at each site." Grant also used a coefficient of community (J) which takes into account only the presence or absence of one of his categories. From the matrices Grant constructed dendrograms to represent the percent of similarity between sites. Polar ordinations have been constructed from these matrices using the methods of Bray and Curtis (1957) (Fig. 1 and 2). The difference in placement of sites within the two figures is due to end-stand selection. There is really no difference between ordinations of the R_o values (Fig. 1) and the J values (Fig. 2), although Grant thought that the R_o values were more sensitive.

Rather than use floristic categories which presumably lump species of different ecological preferences, it was decided to try categories based on similar ecological behavior rather than taxonomic criteria.

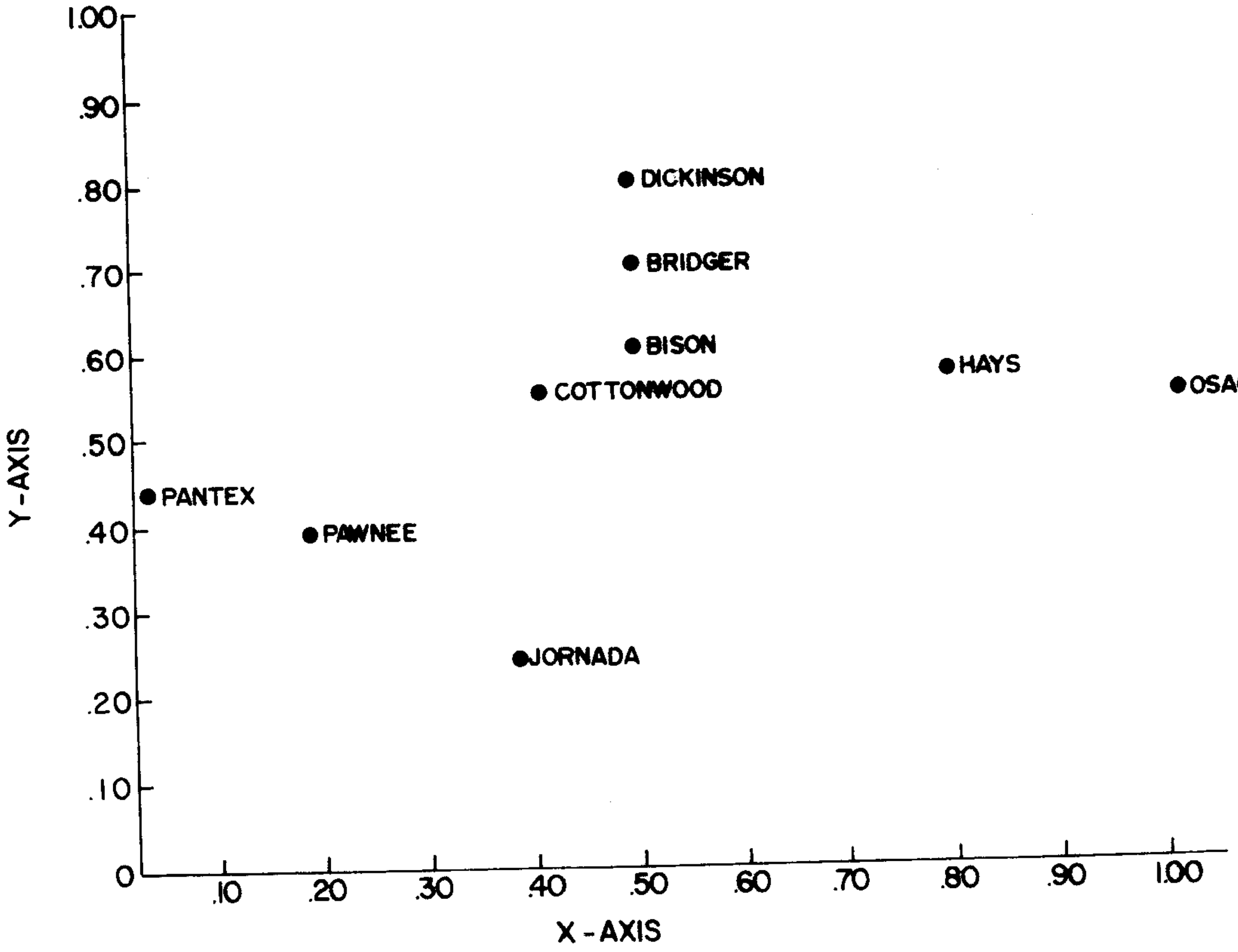

Fig. 1. Floral similarities: Similarity matrix of R_o values.

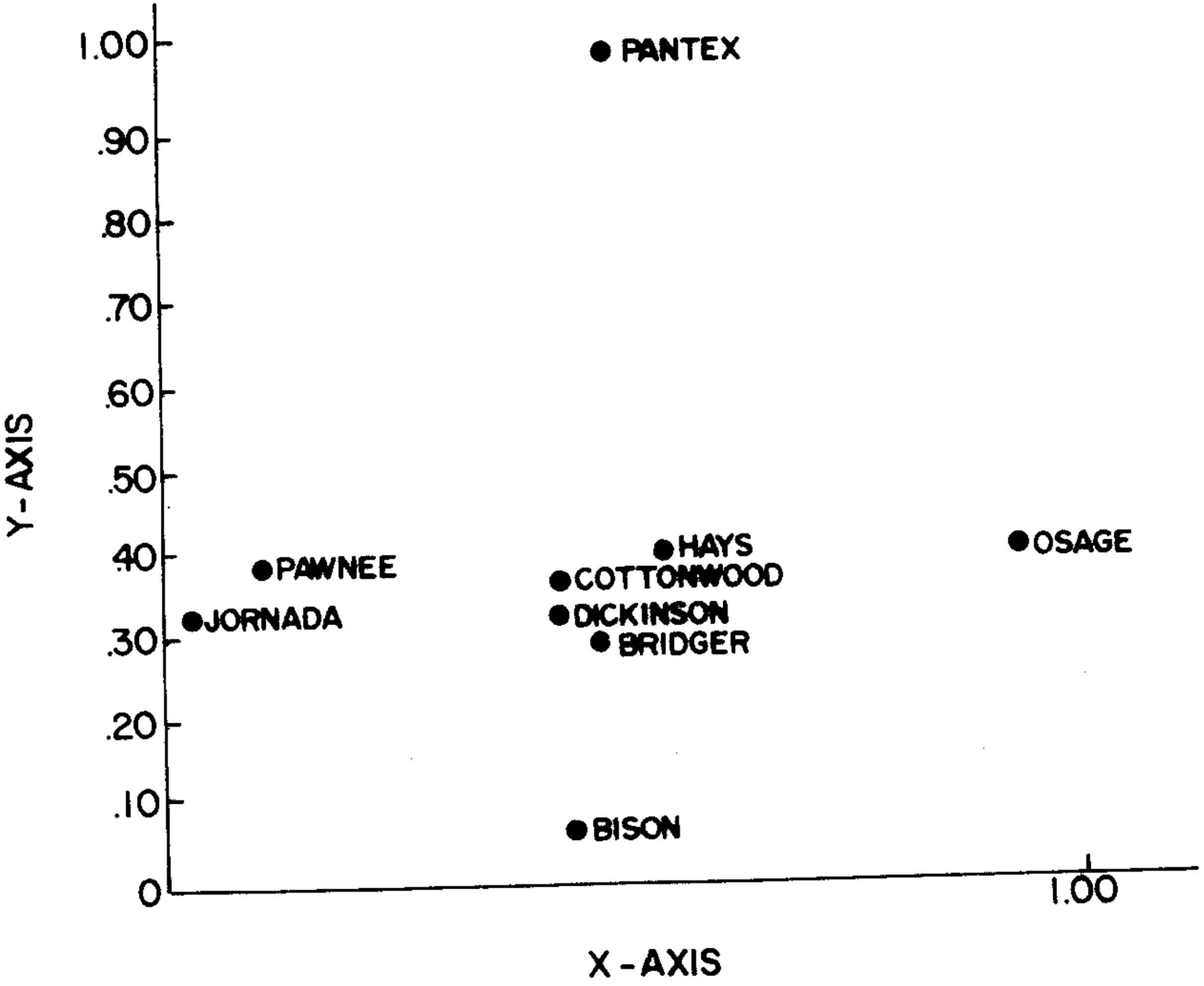

Fig. 2. Floral similarities: Similarity matrix of J values.

Table 1 presents these ecological categories. Each category was represented by both live and standing dead components. The dry, mesic, and wet grass categories were rated on a basis of 1 to 10: 1 to 3 dry, 4 to 6 mesic, and 7 to 10 wet. This scale is based on Mueller and Weaver's (1942) work on the drought resistance of grass seedlings. Table 2 presents a summary of the categories used at each site for each grass species.

Table 1. Categories used in determining vegetational similarities.

Height	Season	Type	Moisture
Tallgrass	Warm-season grass	Bunchgrass	Dry grass (1-3)
Mid-grass	Cool-season grass	Sod grass	Mesic grass (4-6)
Shortgrass			Wet grass (7-10)

To compare sites it is necessary to choose a sample date at each site. Grant (1971) chose a collection date when plant composition first attained a relatively stable condition. Here, the sample date (Table 3) of the highest peak live biomass was utilized.

The results of this ecological category ordination are presented in Fig. 3. The ordination is very similar to those ordinations constructed on Grant's (1971) matrix of taxonomic classification. Again, the choice of end stands determines the positions and orientation of the sites on the ordination.

Table 2. Categories used for each species in the ordinations.

Site	Species	Height[a/]	Season[b/]	Type[c/]	Moisture[d/]
Bison	*Agropyron spicatum*	M	W	B	1
	Festuca idahoensis	M	C	B	3
	Festuca scabrella	M	C	B	5
	Koeleria cristata	M	C	B	10
Bridger	*Agropyron subsecundum*	T	W	B	5
	Danthonia intermedia	M	W	B	5
	Festuca idahoensis	M	C	B	3
	Koeleria cristata	M	C	B	10
Dickinson	*Agropyron smithii*	T	C	S	10
	Bouteloua gracilis	S	W	B	1
	Carex eleocharis	S	C	B	1
	Festuca idahoensis	M	C	B	3
	Koeleria cristata	M	C	B	10
	Stipa comata	T	C	B	3
Hays	*Agropyron smithii*	T	C	S	10
	Andropogon gerardi	T	W	S	5
	Andropogon scoparius	T	W	B	5
	Aristida longiseta	M	W	B	1
	Bouteloua curtipendula	M	W	B	3
	Bouteloua gracilis	S	W	B	1
	Bromus japonicus	M	C	S	8
	Buchloe dactyloides	S	W	S	1
	Panicum virgatum	T	W	S	8
	Sorghastrum nutans	T	W	B	8
	Sporobolus asper	T	W	S	3
	Sporobolus cryptandrus	T	W	S	5

Table 2. (continued).

Site	Species	Height[a]	Season[b]	Type[c]	Moisture[d]
Jornada	*Bouteloua eriopoda*	M	W	B	1
	Erioneuron pulchellum	S	W	S	1
	Panicum hirticaule	M	W	S	3
	Sporobolus flexuosus	M	C	S	1
Osage	*Andropogon gerardi*	T	W	S	5
	Andropogon scoparius	T	W	B	5
	Bromus japonicus	M	C	S	8
	Panicum virgatum	T	W	S	8
	Sorghastrum nutans	T	W	B	8
	Sporobolus asper	T	W	S	3
Pantex	*Agropyron smithii*	T	C	S	10
	Bouteloua gracilis	S	W	B	1
	Buchloe dactyloides	S	W	S	1

[a] T = tallgrass.
M = mid-grass.
S = shortgrass.

[b] W = warm-season grass.
C = cool-season grass.

[c] B = bunchgrass.
S = sod grass.

[d] 1- 3 = dry grass.
4- 6 = mesic grass.
7-10 = wet grass.

Table 3. Dates chosen for intersite comparisons. These dates represent the time of peak live aboveground standing crop.

Site	Treatment	Date
Bison	1	16 July 1970
	2	26 September 1970
Bridger	1	3 August 1970
	3	3 August 1970
Dickinson	1	17 September 1970
	4	17 September 1970
Hays	1	21 July 1970
	5	16 July 1970
Jornada	1	1 September 1970
	2	1 September 1970
Osage	1	16 July 1970
	5	16 July 1970
Pantex	1	9 June 1970
	5	14 June 1970

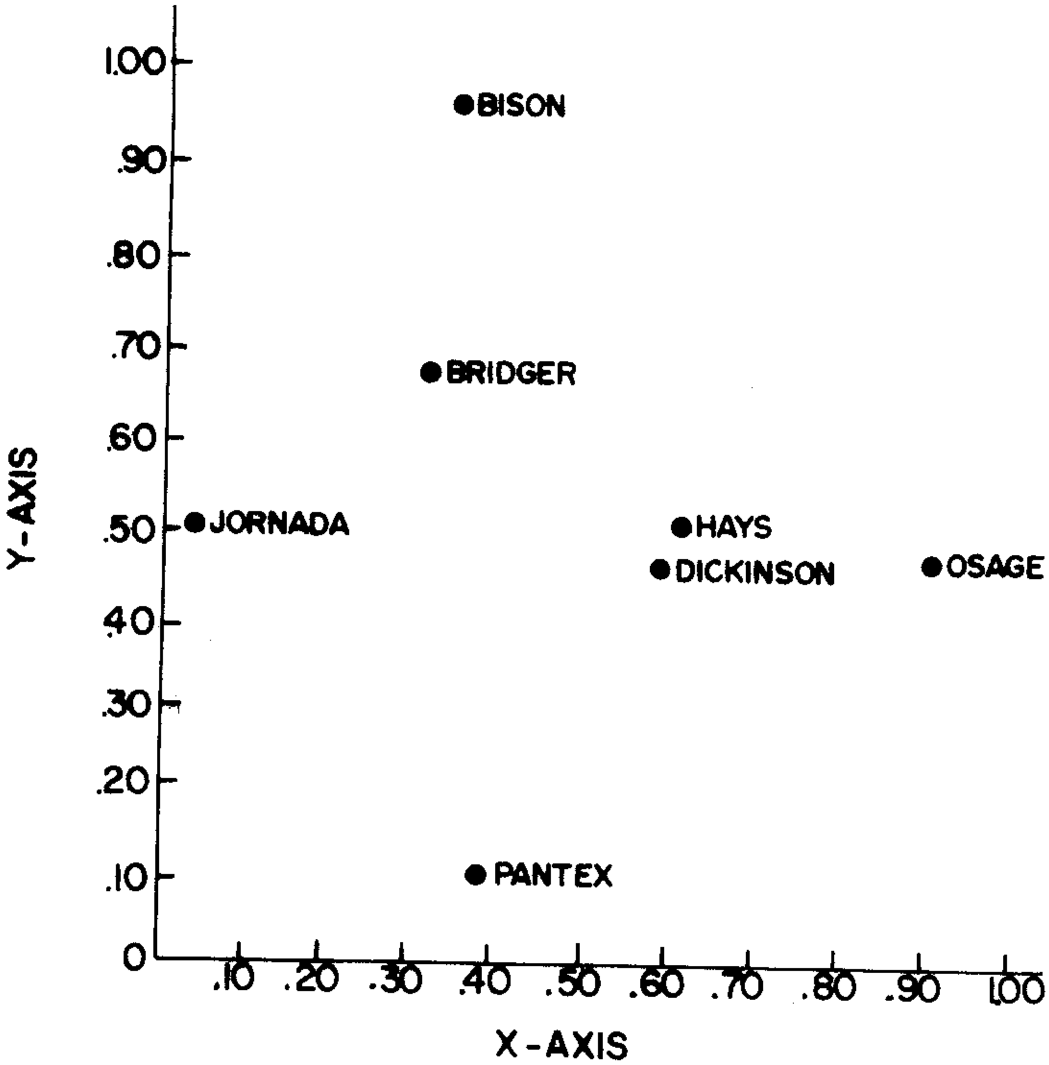

Fig. 3. Vegetational similarities between sites (INDEXSIM).

The fact that Grant's ordination is similar to ours is not unexpected. We classified grasses by ecological categories as shown in Table 1. Grant used families or tribes of grasses as his categories. In actuality, the families and tribes essentially represent the sum total of our categories. For example, in the tribe Andropogoneae there are three species: *Andropogon gerardi*, *A. scoparius*, and *Sorghastrum nutans*. Using our categories, these grasses represent tall, warm, and mesic to wet species. On Grant's tribe basis, then, this tribe is represented as the same tall, warm, and mesic to wet species. Only Hays and Osage Sites contain the tribe and, thus, the species. The three ordinations (Fig. 1, 2, and 3) place Osage and Hays together on the same side of the axis. The same can be said about the relations between the other tribes Grant used and the categories used in the present ordinations.

It is apparent that when all the sites are compared, there are too few species in common to make valid comparisons on a species basis. If the species are grouped according to either taxonomic classification or on these ecological criteria, the resulting similarity between sites is essentially the same. This means that the chosen ecological criteria do not distinguish further between the members of the tribe or families which represent the dominant species on the Comprehensive Network Sites.

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PRELIMINARY NETWORK EVALUATION ON METHODS OF PRIMARY PRODUCER BIOMASS ESTIMATION

by

Robert K. Kennedy

Introduction

Studies which involve measurement of productivity in ecosystems rely in part on some technique for estimating net primary production. When productivity estimates are obtained by the harvest method, they may be called peak standing crop. These instantaneous estimates of production are then considered to represent net primary production for the community. While this assumption is often not critical, until recently little attention was given to other considerations which may alter the validity of the estimate, namely, the inherent phenological response of individual species to the abiotic driving forces, the heterogeneity of the plant community in question, and the sampling precision which in part may arise from the first two considerations. Recently, the validity of the peak standing crop method has been questioned and several alternatives proposed (Kelly et al., 1969; Odum, 1960). The importance of these alternatives is that they allow consideration of both structural and functional aspects of the community and they minimize some of the errors in the instantaneous peak standing crop measurement.

The alternatives fall into two general groups (Kelly, Van Dyne, and Harris, 1971): (i) summation of individual species peaks or peaks for taxonomic groups and (ii) summation of positive live biomass increases on a species basis. It is the objective of this paper to compare these two alternatives to the instantaneous peak standing crop method and two slight modifications of it. The data utilized are the 1970 clipped-quadrat data from eight Comprehensive Network Sites and the Pawnee Site of the U.S. IBP Grassland Biome.

The estimation methods utilized in this analysis are essentially those of Kelly et al. (1969). The basic field data collection methods follow French (1970), with some individual modifications at various sites to allow for special sampling problems.

Five data analysis-estimation methods were used to evaluate net primary production across the Comprehensive Network Sites. Two of the methods are simply restrictions placed on the peak standing crop method (SINGLEST).

1. SINGLEST: a single instantaneous estimate, including all species, on the date of peak community yield (the highest value for live biomass obtained during the sample season).
2. SINGLEST=2: a single instantaneous estimate which includes only those species that attained at least 2% composition at some time during the sample season.
3. SINGLEST=5: A single instantaneous estimate which includes only those species that attained at least 5% composition at some time during the sample season.
4. SUMSPP: summation of an individual species' peaks which includes only those species that attained 2% composition at some time during the sample season.
5. SUMPOSINC: summation of positive biomass increases for individual species, including only those species that attained at least 2% composition at some time during the sample season.

Results and Discussion

The data and discussion will be restricted to the ungrazed treatments at each site.

Biomass values were calculated by replicate for each site using each one of the five methods in Table 1. Replicates were averaged and the data were plotted as peak live biomass (PLB) vs. the estimation method for each site (Fig. 1). T-tests were run using replicate data (intrasite) on all five methods, one against the other (Table 2). The level of significance was set at 0.20 to conform to the biome standards of 0.20 $\bar{x}$ at 80% confidence. An additional significance level of 0.05 was also established to differentiate specific cases which appeared to be of more significance.

Before evaluating the accumulation methods vs. the instantaneous method, the instantaneous method was examined to determine the effect of using species selected on the basis of percent composition. Two modifications of peak standing crop were used by restricting species inclusion to species attaining at least 2% composition (SINGLEST= 2) and 5% composition (SINGLEST=5). Species were included only if they attained the desired percent composition and were recorded on at least two sample dates. A list of species which attained at least 2% composition is presented in Appendix I. The number of species used in the calculation of live biomass was generally reduced as the percent composition restriction was increased (Table 3). The number of species lost by restricting to 2% composition varied from site to site, but ranged from one species at the Osage Site to 20 species at both Cottonwood and Jornada Sites. The additional loss of species by restricting composition to 5% ranged from zero at both Jornada and Pantex Sites to four species at both Bridger and Hays Sites. The effect of excluding these minor species

Table 1. Biomass values (g/m^2) by replicate (REP) for the ungrazed treatment (TRT) at different sites for each of the five estimation methods. Values for the Pawnee Site include the litter component which has 51% composition on the date of peak biomass.

Site	SINGLEST (g/m^2)			SINGLEST=2 (g/m^2)			SINGLEST=5 (g/m^2)			SUMSPP (g/m^2)			SUMPOSINC (g/m^2)		
	REP	REP	TRT	REP	REP	TRT	REP	REP	TRT	REP	REP	TRT	REP	REP	TRT
Bison	217	224	221	205	222	214	180	205	193	237	256	247	260	297	279
Bridger	167	141	154	163	139	151	151	131	141	160	191	176	200	203	202
Cottonwood	181	156	169	171	152	162	165	146	156	193	164	179	307	221	264
Dickinson	171	370	271	167	363	265	162	354	258	191	376	284	264	473	369
Hays	201	245	223	196	239	218	190	234	212	255	349	302	377	485	431
Jornada	104	164	134	100	152	126	100	152	126	138	171	155	220	222	221
Osage	265	276	271	265	274	270	259	265	262	303	343	323	447	524	486
Pantex	62	61	62	62	60	61	62	60	61	112	191	152	166	196	181
Pawnee	342	231	287	336	219	278	331	204	268	364	375	370	665	540	603

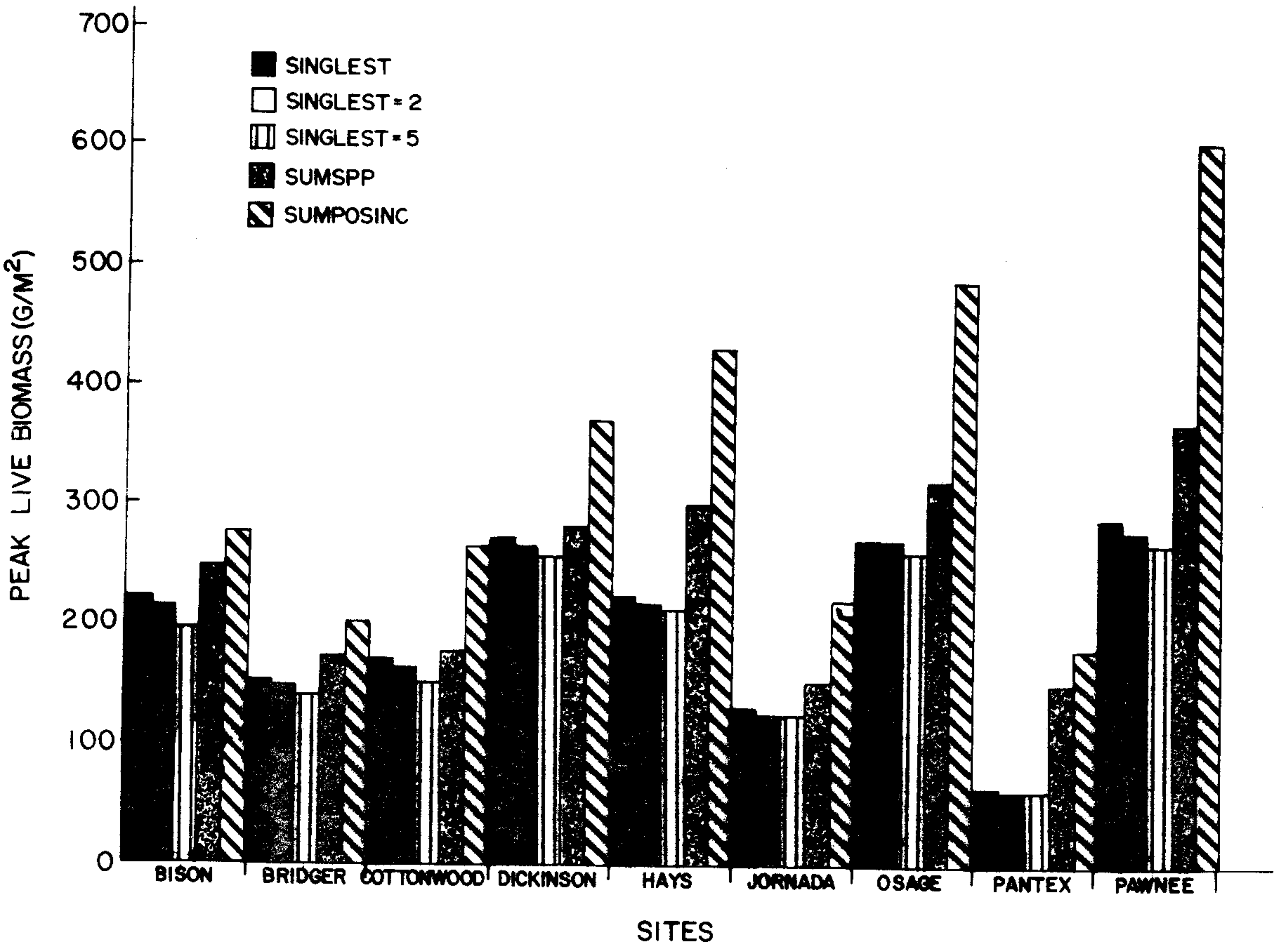

Fig. 1. Live biomass values using the five methods of estimation for each site.

Table 2. T-test obtained from comparison of biomass estimation methods for nine U.S. IBP Grassland Biome sites.

Site	Method	Method			
		SINGLEST=2	SINGLEST=5	SUMSPP	SUMPOSINC
Bison	SINGLEST	0.76	2.15[a]	2.06[a]	3.06[a]
	SINGLEST=2		1.38	2.65[a]	3.18[a]
	SINGLEST=5			3.43[a]	3.85[a]
	SUMSPP				1.53
Bridger	SINGLEST	0.16	0.79	1.04	3.51[a]
	SINGLEST=2		0.64	1.24	4.10[a]
	SINGLEST=5			1.87	5.98[b]
	SUMSPP				1.68
Cottonwood	SINGLEST	0.45	0.82	0.52	2.13[a]
	SINGLEST=2		0.44	0.98	2.32[a]
	SINGLEST=5			1.32	2.46[a]
	SUMSPP				1.87
Dickinson	SINGLEST	0.04	0.09	0.09	0.67
	SINGLEST=2		0.05	0.13	0.72
	SINGLEST=5			0.19	0.77
	SUMSPP				0.61
Hays	SINGLEST	0.17	0.35	1.53	3.56[a]
	SINGLEST=2		0.17	1.63	3.65[a]
	SINGLEST=5			1.73	3.75[a]
	SUMSPP				1.80
Jornada	SINGLEST	0.20	0.20	0.59	2.89[a]
	SINGLEST=2		0.00	0.92	3.65[a]
	SINGLEST=5			0.92	3.65[a]
	SUMSPP				4.02[a]
Osage	SINGLEST	0.10	1.35	2.50[a]	5.54[b]
	SINGLEST=2		1.38	2.56[a]	5.58[b]
	SINGLEST=5			3.01[a]	5.78[b]
	SUMSPP				3.75[a]
Pantex	SINGLEST	0.44	0.44	2.26[a]	7.89[b]
	SINGLEST=2		0.00	2.29[a]	7.98[b]
	SINGLEST=5			2.29[a]	7.98[b]
	SUMSPP				0.69
Pawnee	SINGLEST	0.11	0.22	1.48	3.78[a]
	SINGLEST=2		0.11	1.56	3.79[a]
	SINGLEST=5			1.60	3.75[a]
	SUMSPP				3.71[a]

[a] Significant at the 0.20 level, t = 1.88.

[b] Significant at the 0.05 level, t = 4.30.

Table 3. Number of species used in calculating live biomass for each estimation method.

Site	SINGLEST	SINGLEST=2	SINGLEST=5	SUMSPP	SUMPOSINC
	Number of Species				
Bison	14	9	6	9	9
Bridger	15	13	9	13	13
Cottonwood	26	6	5	6	6
Dickinson	19	8	6	8	8
Hays	24	14	10	14	14
Jornada	28	8	8	8	8
Osage	9	8	7	8	8
Pantex	7	5	5	5	5
Pawnee	27	12	10	12	12

from the biomass calculation was negligible in every case except at the Bison Site (Table 2).

The amount of live biomass obtained for all methods (Fig. 1) demonstrated that in every case summation of positive biomass increases generated the highest value. This agrees with the Kelly et al. (1969, 1971) results. The methods ranked in order of biomass magnitude are (i) summation of positive increases (SUMPOSINC), (ii) summation of species peaks (SUMSPP), and (iii) peak standing crop (SINGLEST). This ranking holds for all nine sites investigated.

In evaluating peak biomass (SINGLEST) vs. the two compositional restrictions, it was noted that, with the exception of Bison and Pawnee Sites, as composition was restricted the standard deviation (SD) decreased or remained the same (Table 4). On the Bison Site, the SINGLEST biomass estimate was 211 ± 5 g/m^2; but when composition was restricted to 5% (SINGLEST=5), a 13% decrease in biomass resulted (193 ± 18 g/m^2) (Table 5), coupled with an increase in variance. A t-test showed that these estimates were significantly different.

This difference appears to be a direct result of the peak standing crop method which assumes that all species peak simultaneously or at least close to the community peak. Table 6 shows that the percent of species peaking at the community peak is in most cases relatively low, and further shows that at the Bison Site 16% of the species which peak at this time are not included in the estimate when the 5% restriction is in effect. If the Bison Site is to use the single estimate method, then the species included should not be restricted at the 5% composition level or higher. With the possible exception of the Bison Site, it appears that there is little advantage in sampling species which occur at <5% composition if peak standing crop (SINGLEST, SINGLEST=2, SINGLEST=5) is the estimation method to be used.

Table 4. Biomass values ± 1 SD for the ungrazed treatment (TRT) (g/m^2).

Site	SINGLEST		SINGLEST=2		SINGLEST=5		SUMSPP		SUMPOSINC	
	TRT	SD	TRT	SD	TRT	SD	TRT	SD	TRT	SD
Bison	221	5[a]	214	12[a]	193	18[a]	247	13[a]	279	26[a]
Bridger	154	19[a]	151	17[a]	141	14[a]	176	22[a]	202	2[a]
Cottonwood	169	17[a]	162	13[a]	156	13[a]	179	21[a]	264	61
Dickinson	271	141	265	139	258	136	284	131	369	148
Hays	223	31[a]	218	30[a]	212	31[a]	302	66	431	76[a]
Jornada	134	42	126	37	126	37	155	23	221	1[a]
Osage	271	8[a]	270	6[a]	262	4[a]	323	28[a]	486	54[a]
Pantex	62	1[a]	61	1[a]	61	1[a]	152	56	181	21[a]
Pawnee	287	79	278	83	268	90	370	8[a]	603	88[a]

[a] SD is within 20% $\overline{x}$.

Table 5. Percent change in biomass for four estimation methods using SINGLEST as the base.

Site	SINGLEST=2	SINGLEST=5	SUMSPP	SUMPOSINC
	Biomass Decrease (%)		Biomass Increase (%)	
Bison	3	13	12	26
Bridger	2	8	14	31
Cottonwood	4	8	6	56
Dickinson	2	5	5	36
Hays	2	5	35	93
Jornada	6	6	16	65
Osage	<1	3	19	79
Pantex	2	2	145	192
Pawnee	3	7	29	110

Table 6. Percent of sampled species which peak on the date of the single estimate (SINGLEST).

Site	SINGLEST=2	SINGLEST=5
	%	%
Bison	33	17
Bridger	38	33
Cottonwood	33	40
Dickinson	63	50
Hays	29	30
Jornada	38	38
Osage	25	14
Pantex	30	20
Pawnee	17	20

In the case of the Pawnee Site the SINGLEST estimate was 287 ± 79 g/m^2, and the standard deviation (SD) was >20% $\bar{x}$. When the composition was restricted to 5%, biomass was 268 ± 90 g/m^2 and SD >20% $\bar{x}$. A t-test (Table 2) showed no significant differences between the two estimates. Within replicates, the means were quite different (Table 1), which probably accounts for the high variability in the treatment data.

Only three sites showed significant differences between the three SINGLEST methods and summation of species' peaks (SUMSPP). These were Bison, Osage, and Pantex Sites (Table 2). These three sites represent three very different grassland types and have no important species in common. The common factors appear to be that most of the species on each site have only one peak during the season and that few species peak on the date of peak live biomass.

All sites except Dickinson exhibited significant differences between the three single estimates (SINGLEST, etc.), and summation of positive biomass increases (Table 2). It appears at the Dickinson Site that the main factor is the disparity in replicate biomass (Table 1). In this case, the single estimate is probably the more accurate, even though it is an underestimate. The Dickinson Site showed the highest percentage of any site for species peaking on the date of peak biomass (Table 6). Even when composition was restricted to 5%, 50% of the recorded species peaked on the date of peak biomass; and at the 2% composition level 63% peaked simultaneously with the community peak.

Three sites, Jornada, Osage, and Pawnee showed significant differences (Table 2) between the two summation methods (SUMSPP and SUMPOSINC). The summation of positive biomass increases is sensitive to sampling variability; therefore, any conclusions drawn concerning this method must consider whether the positive increases are real or simply the result of variability. This has not been done, so the biomass values for SUMPOSINC are understandably suspect and probably are an overestimate in many cases. A very similar problem is involved in SUMSPP and the SINGLEST methods; i.e., whether the species or community peaks used are really significantly different from the biomass obtained on adjoining sample dates. This was not tested statistically.

The data summarized herein should provide at least a basis for critical evaluation of current biomass estimation methods.

Summary

Five biomass estimation methods were reviewed. It was found that none of the nine sites studied showed a significant difference in biomass when the standard peak standing crop method was compared to the same method using only species attaining 2% composition. The same type of comparison was done using only species attaining 5% composition. Only the Bison Site showed a significant difference between these two estimates.

When the three single estimate methods were compared to the summation of species' peaks (SUMSPP), only Bison, Osage, and Pantex showed significant differences between the estimation methods. A comparison of the three single estimate methods to the summation of positive biomass increases (SUMPOSINC) found only the Dickinson Site comparisons *not* significantly different.

Jornada, Osage, and Pawnee Sites all exhibited significant differences in the SUMSPP by SUMPOSINC comparisons.

One common disadvantage is shared by all five of the methods examined--that of determining if the peak or biomass increase is real or significant.

The critical factors appear to be adequacy of sampling, replicate similarity, variance minimization, and species composition.

Acknowledgments

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APPENDIX I

APPENDIX TABLE

Appendix Table 1. Species symbols used in biomass comparisons, IBP Comprehensive Network. These species contributed at least 2% of the total annual production.

Site	Species Symbol	Species Name
Bison	ACMI2	*Achillea millefolium*
	AGOSE	*Agoseris* sp.
	ARFU3	*Arnica fulgens*
	FEID	*Festuca idahoensis*
	FESC	*Festuca scabrella*
	GETR	*Geum triflorum*
	LIRU4	*Lithospermum ruderale*
	LUSE4	*Lupinus sericeus*
	MIGR	Miscellaneous grasses
Bridger	ACMI2	*Achillea millefolia*
	AGSU	*Agropyron subsecundum*
	ARCO5	*Arenaria congesta*
	CEAR4	*Cerastium arvense*
	DAIN	*Danthonia intermedia*
	ERSP4	*Erigeron speciosus*
	FEID	*Festuca idahoensis*
	GABO2	*Galium boreale*
	KOCR	*Koeleria cristata*
	LUAR3	*Lupinus argenteus*
	STRI2	*Stipa richardsoni*
	MIFB	Miscellaneous forbs
	MIGR	Miscellaneous grasses
Cottonwood	AGSM	*Agropyron smithii*
	BOGR2	*Bouteloua gracilis*
	BRJA	*Bromus japonicus*
	BUDA	*Buchloe dactyloides*
	CAEL2	*Carex eleocharis*
	SPCO	*Sphaeralcea coccinea*
Dickinson	AGSM	*Agropyron smithii*
	ARLU	*Artemisia ludoviciana*
	ASER3	*Aster ericoides*
	BOGR2	*Bouteloua gracilis*
	CAEL2	*Carex eleocharis*
	CALO	*Calamovilfa longifolia*
	STCO4	*Stipa comata*
	TRDU	*Tragopogon dubius*

Appendix Table 1. Continued.

Site	Species Symbol	Species Name
Hays	AMCA6	*Amorpha canescens*
	ANGE	*Andropogon gerardii*
	ANSC2	*Andropogon scoparius*
	ASOB2	*Aster oblongifolius*
	BOCU	*Bouteloua curtipendula*
	CIUN	*Cirsium undulatum*
	ECPAA	*Echinacea angustifolia*
	OESE	*Oenothera serrulata*
	PAVI2	*Panicum virgatum*
	PSTE3	*Psoralea tenuiflora*
	SCUN	*Schrankia uncinata*
	SOMO	*Solidago mollis*
	SONU2	*Sorghastrum nutans*
	SORI2	*Solidago rigida*
Jornada	BOER4	*Bouteloua eriopoda*
	CRCO11	*Croton corymbulosus*
	EPTR	*Ephedra trifurcata*
	GUSA2	*Gutierrezia sarothrae*
	PRJU	*Prosopis juliflora*
	SAKA	*Salsola kali*
	SPFL2	*Sporobolus flexuosus*
	YUEL	*Yucca elata*
Osage	ANGE	*Andropogon gerardi*
	ANSC2	*Andropogon scoparius*
	PAVI2	*Panicum virgatum*
	SONU2	*Sorghastrum nutans*
	SPAS	*Sporobolus asper*
	FORB	Forbs
	MIGR	Miscellaneous grasses
	SEDG	Miscellaneous sedges
Pantex	BOBU	*Bouteloua-Buchloe* complex
	BOGR2	*Bouteloua gracilis*
	LEPID	*Lepidium* sp.
	OPUNT	*Opuntia* sp.
	FORB	Forbs
Pawnee	ARFR4	*Artemisia frigida*
	ARLO3	*Aristida longiseta*
	ATCA2	*Atriplex canescens*
	BAOP	*Bahia oppositifolia*
	BOGR2	*Bouteloua gracilis*
	BUDA	*Buchloe dactyloides*

Appendix Table 1. Continued.

Site	Species Symbol	Species Name
Pawnee (Continued)	CHNA2	*Chrysothamnus nauseosus*
	GUSA2	*Gutierrezia sarothrae*
	OPPO	*Opuntia polyacantha*
	PSTE3	*Psoralea tenuiflora*
	STCO4	*Stipa comata*
	LITR	Litter

COMPARISON OF PRODUCTIVITY RATES

by

Janice Perino

The purpose of this study was to analyze the effects of various environmental factors on a calculated daily increment or yield (Westlake, 1963; Van Der Valk and Bliss, 1971) for each of eight ungrazed grassland sites. Yield ($g/m^2/day$) was calculated by dividing the total peak standing crop by the number of days from the beginning of the growing season to the date of sampling when the peak biomass occurred. The importance of cool- and warm-season species at each site was determined as a ratio, c/w, and also by summation as a percent of total net annual production. In the first case, those species reaching maximum production before the middle of the growing season were summed as cool-season species, and those reaching maximum production after the middle of the growing season were summed as warm-season species. In the second case, June 1 was used as the point of separation between cool- and warm-season species for all sites. Multiple regression equations using seven of the eight sites (Hays was omitted due to insufficient data) were determined using various combinations of environmental data to determine which environmental factor might have had the greatest influence upon yield.

Yield "pairs" are the eight sites divided into four groups which have similar yields (Table 1). These pairs, which differ by less than 0.5 $g/m^2/day$ are: Osage-Hays, Pawnee-Bison, Jornada-Pantex, and Bridger-Dickinson.

When yield for the eight sites is compared to elevation (Fig. 1), only one of these pairs, Bridger-Dickinson, represents sites which are located

Table 1. Yield ($g/m^2/day$) for eight Comprehensive Network Sites.

Site	Yield ($g/m^2/day$)
Pawnee	6.0
Bison	5.5
Osage	3.3
Hays	2.8
Bridger	2.3
Dickinson	2.3
Jornada	1.0
Pantex	0.9

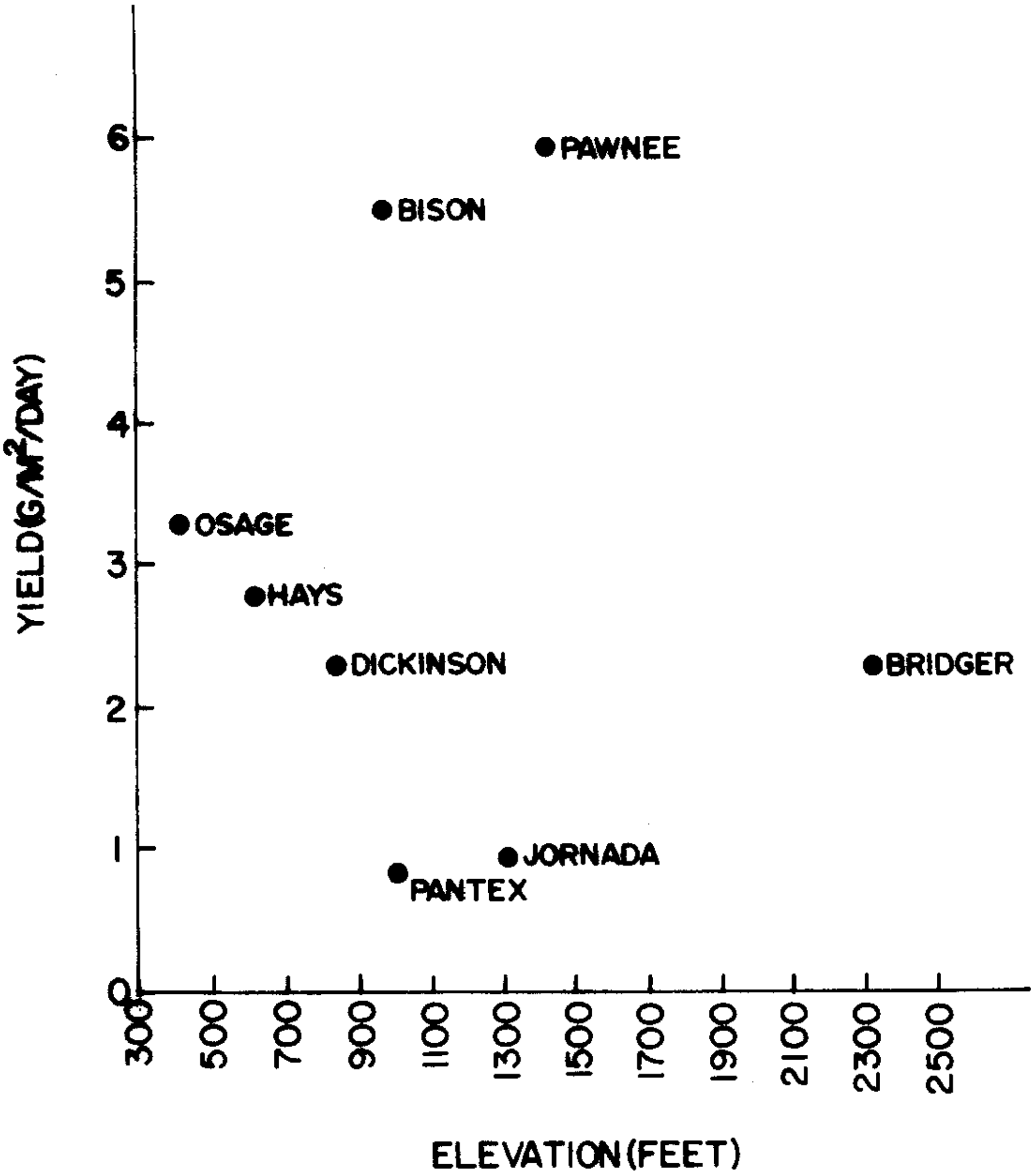

Fig. 1. Yield of aboveground biomass as related to site elevation on ungrazed treatments.

at relatively different altitudes. Those sites with middle-range yields, Osage-Hays, are at lower elevations, while those with higher or lower yields are generally at the higher elevations.

When yield is compared to growing season precipitation (Fig. 2), grasslands with the highest growing season precipitation had mid-range yields. Low growing season precipitation was associated with both high and low yield. The difference in growing season precipitation between pairs was greatest for Jornada-Pantex. Yield vs. annual precipitation (Fig.3) shows the same general pattern as growing season precipitation. However, both of the pairs Jornada-Pantex and Osage-Hays show a relatively large difference in annual precipitation.

There is a tendency for yield to increase as the number of species, greater than or equal to 2% of the total biomass at the date of peak standing crop, increases (Fig. 4). This comparison shows fairly large differences between three pairs: Osage-Hays, Bridger-Dickison, and Jornada-Pantex.

Higher yields tend to correspond to a shorter growing season (Fig. 5). At the sites which had a growing season of between 120 and 134 days, the yield ranged from 2.25 to 5.95 $g/m^2/day$. At the sites which had a growing season of between 168 and 205 days, the yield ranged from 0.86 to 3.34 $g/m^2/day$. The length of the growing season corresponds to latitude; the longer growing season is found at the more southern sites, and the shorter growing season is found at the more northern sites. The Osage-Hays pair shows a greater difference in length of growing season than do the other pairs.

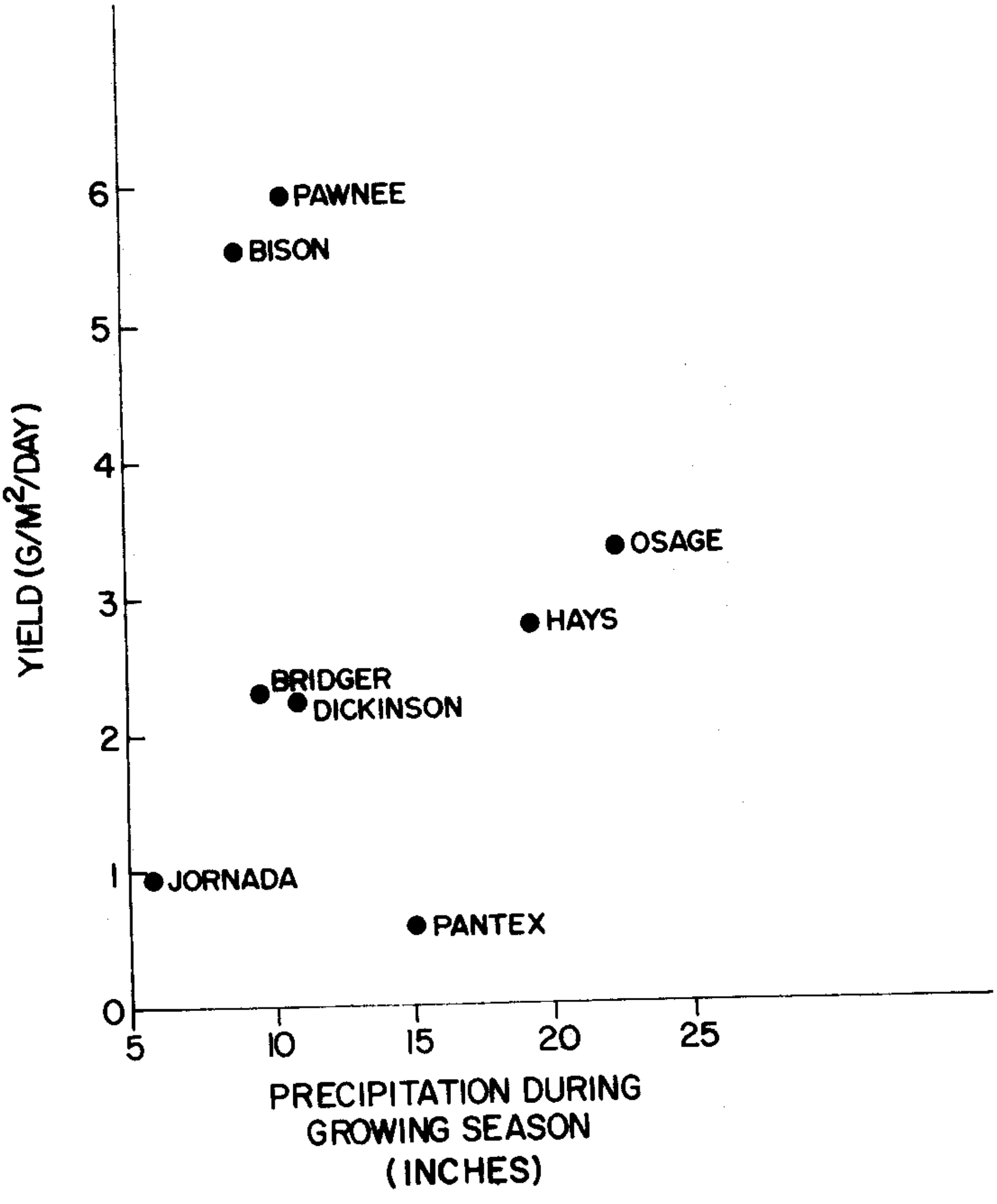

Fig. 2. Yield of aboveground biomass as related to growing-season precipitation on ungrazed treatments.

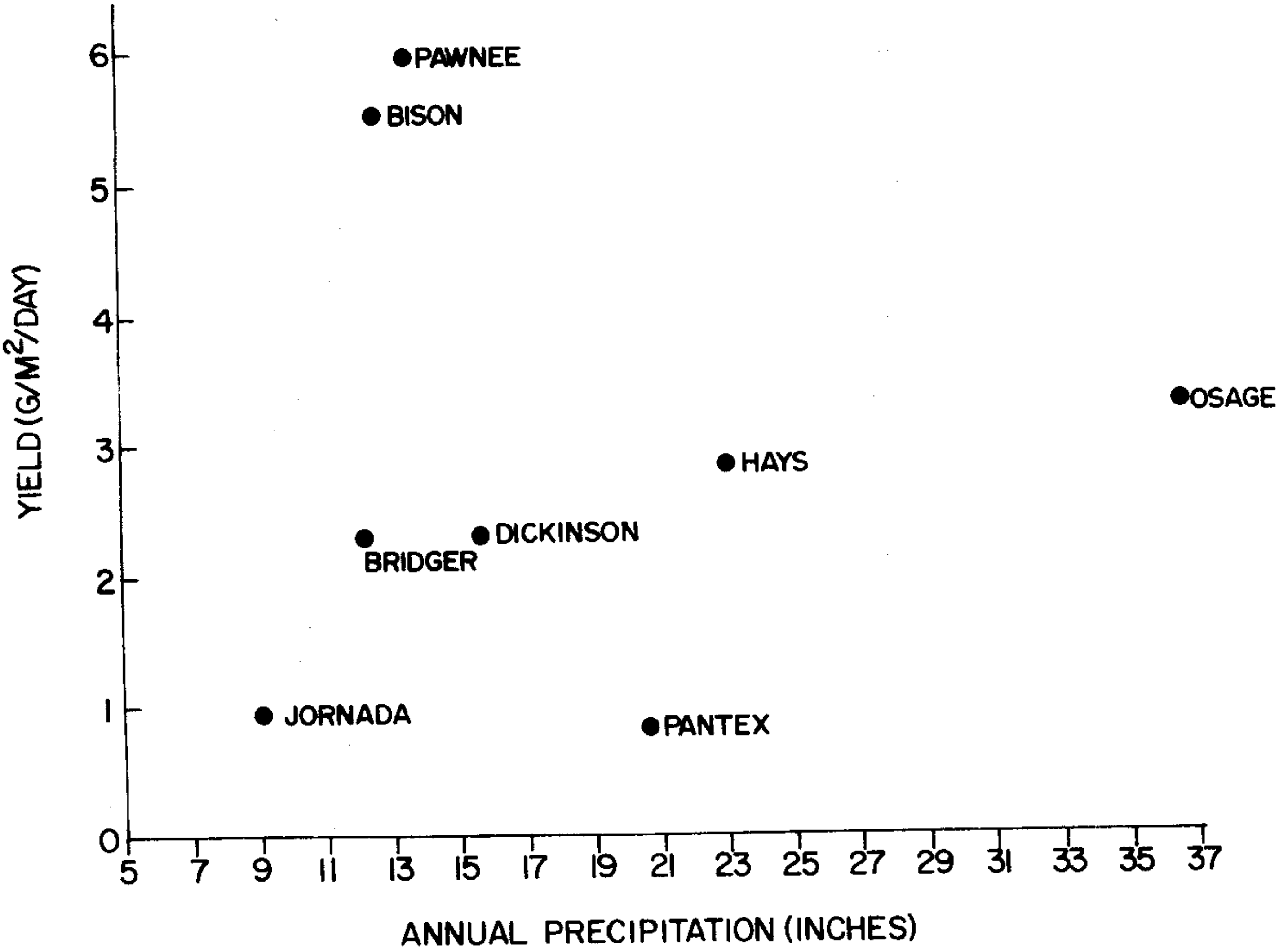

Fig. 3. Yield of aboveground biomass as related to annual precipitation on ungrazed treatments.

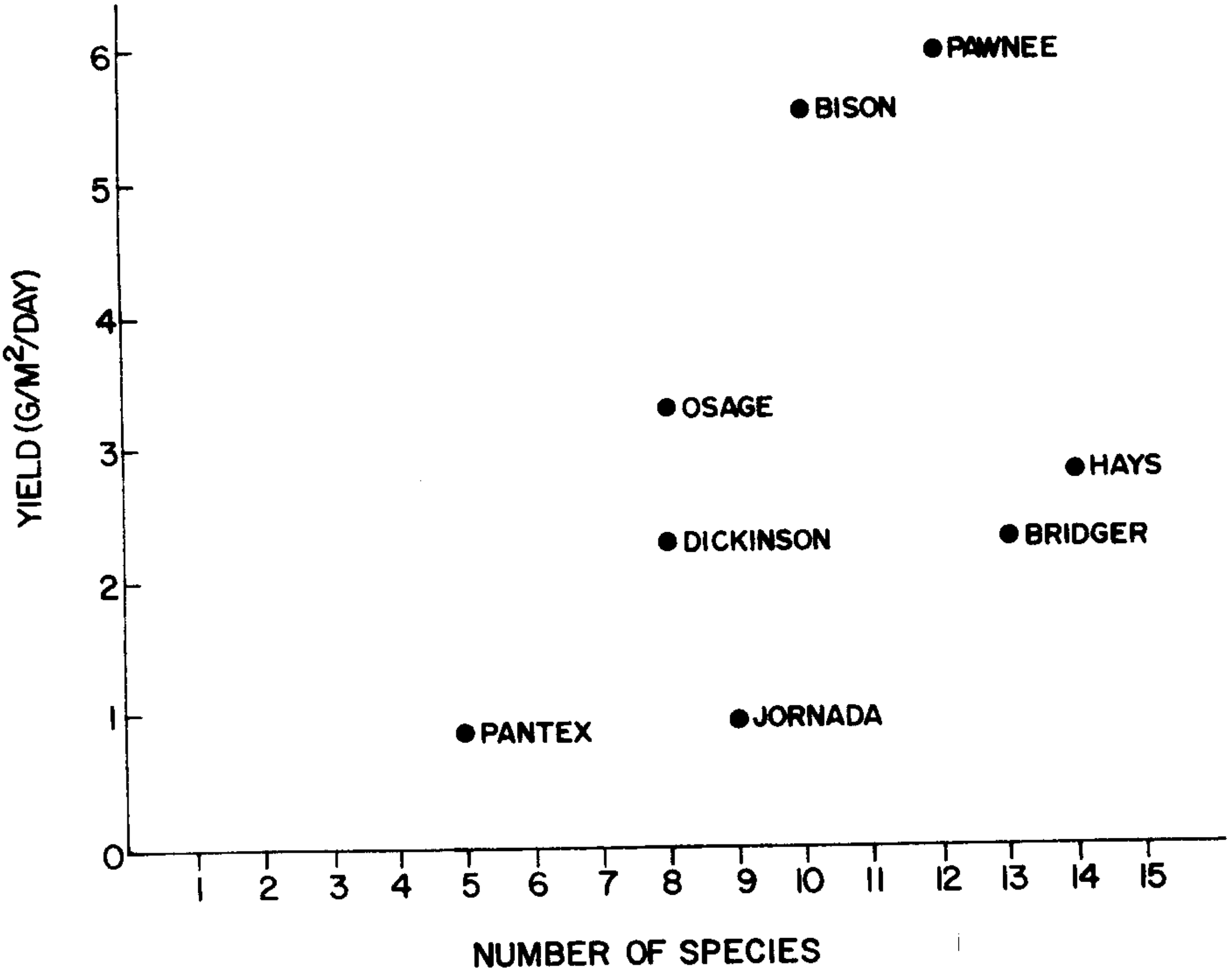

Fig. 4. Yield of aboveground biomass as related to number of species comprising 2% or more of the total standing crop during the year.

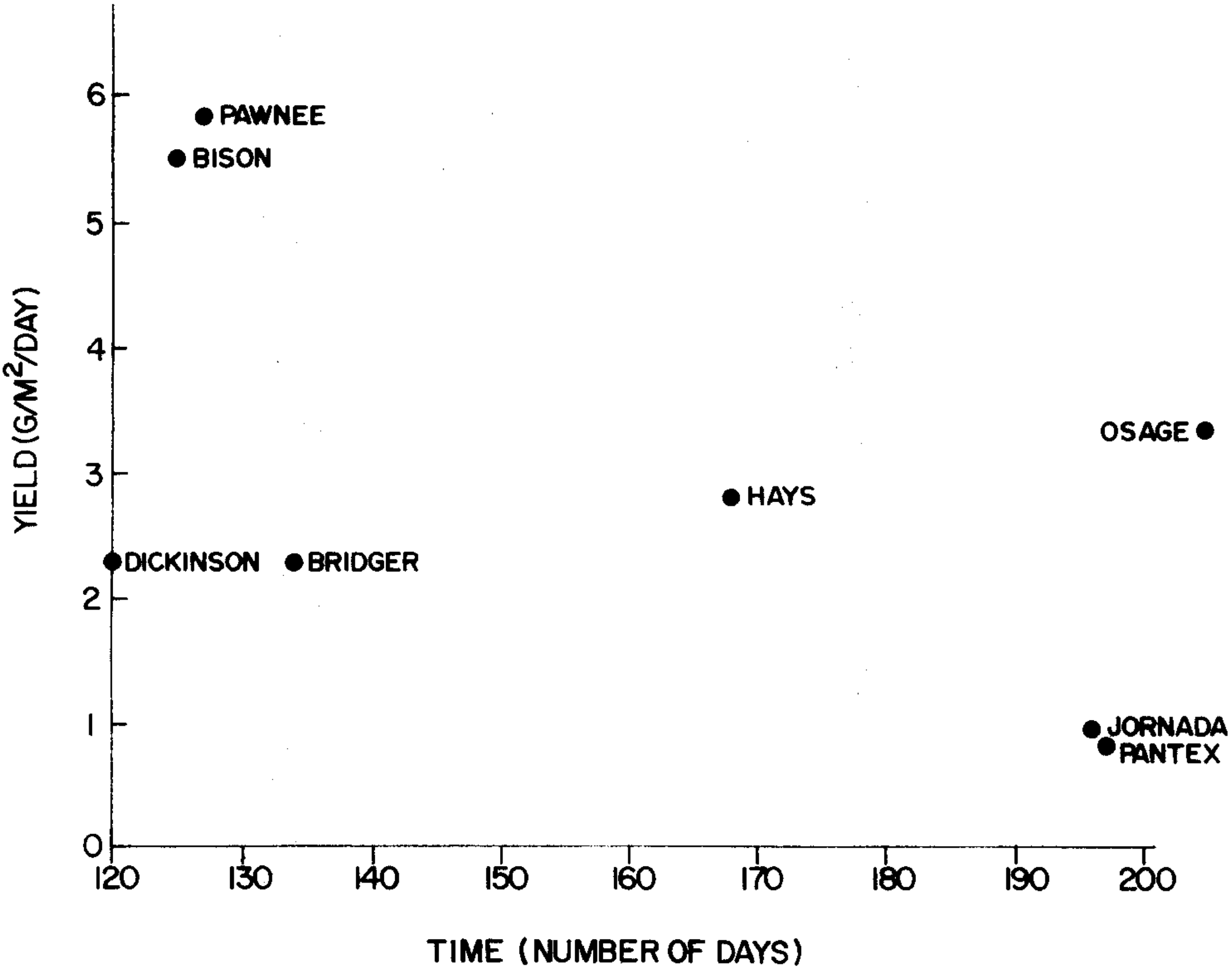

Fig. 5. Yield of aboveground biomass as related to length of growing season.

There was an increase of yield with an increase of peak standing crop (Fig. 6). The Bridger-Dickinson pair has the greatest difference in peak standing crop.

There was also an increase of productivity with soil water for May, June, and July (only the comparison of yield with soil water for July is given, Fig. 7).

Six of the eight stands reached peak standing crop between 32% and 50% of the total length of the growing season at the respective sites (Fig. 8). The Jornada Site required 70% and the Dickinson Site required 100% of their growing seasons. These growing seasons are averages from the U.S. Department of Agriculture (1941), thus, the possibility of obtaining 100%.

The ratio of cool- to warm-season species indicates that all the sites, except Bison and Bridger, are primarily warm-season species; that is, c/w was less than 5.0. The Bison Site had a c/w of more than 33. When cool-season species (using June 1) are calculated as a percent of net annual production by summation, Bison and Bridger Sites are followed by Dickinson in decreasing importance of cool-season species.

Six combinations of six or fewer environmental factors (annual precipitation, pan evaporation, soil water, solar radiation, elevation, and growing season precipitation) were used to ascertain which factor or factors may be most important with respect to yield. Only pan evaporation proved to be a significant variable as revealed by an F-test on the partial sum of the squares (F = 7.97 at the 95% level). This factor showed a negative correlation with increasing yield. Fig. 9, which compares yield to pan evaporation, also indicates a negative trend of yield vs. pan evaporation.

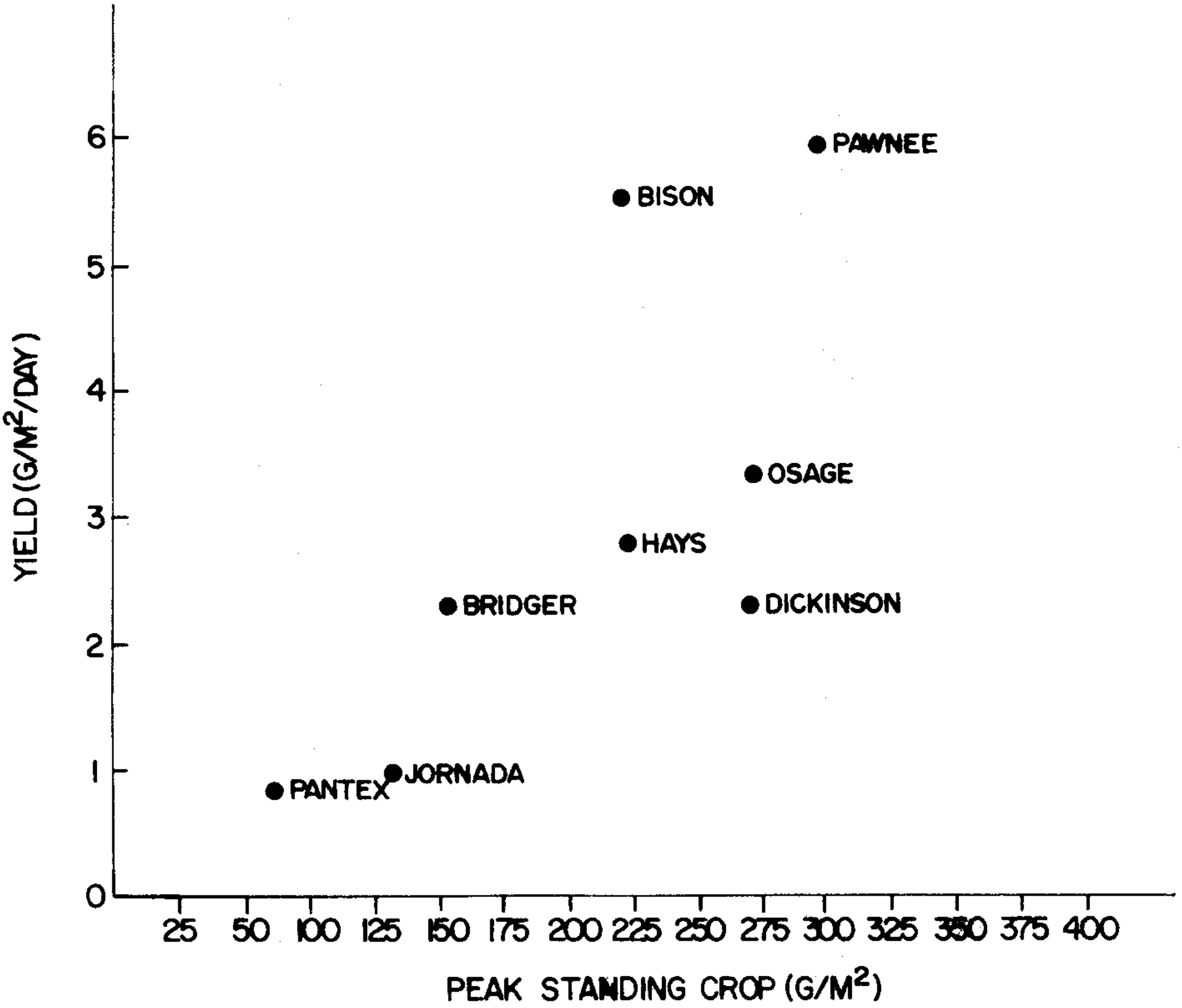

Fig. 6. Yield of aboveground biomass as related to amount of peak standing crop.

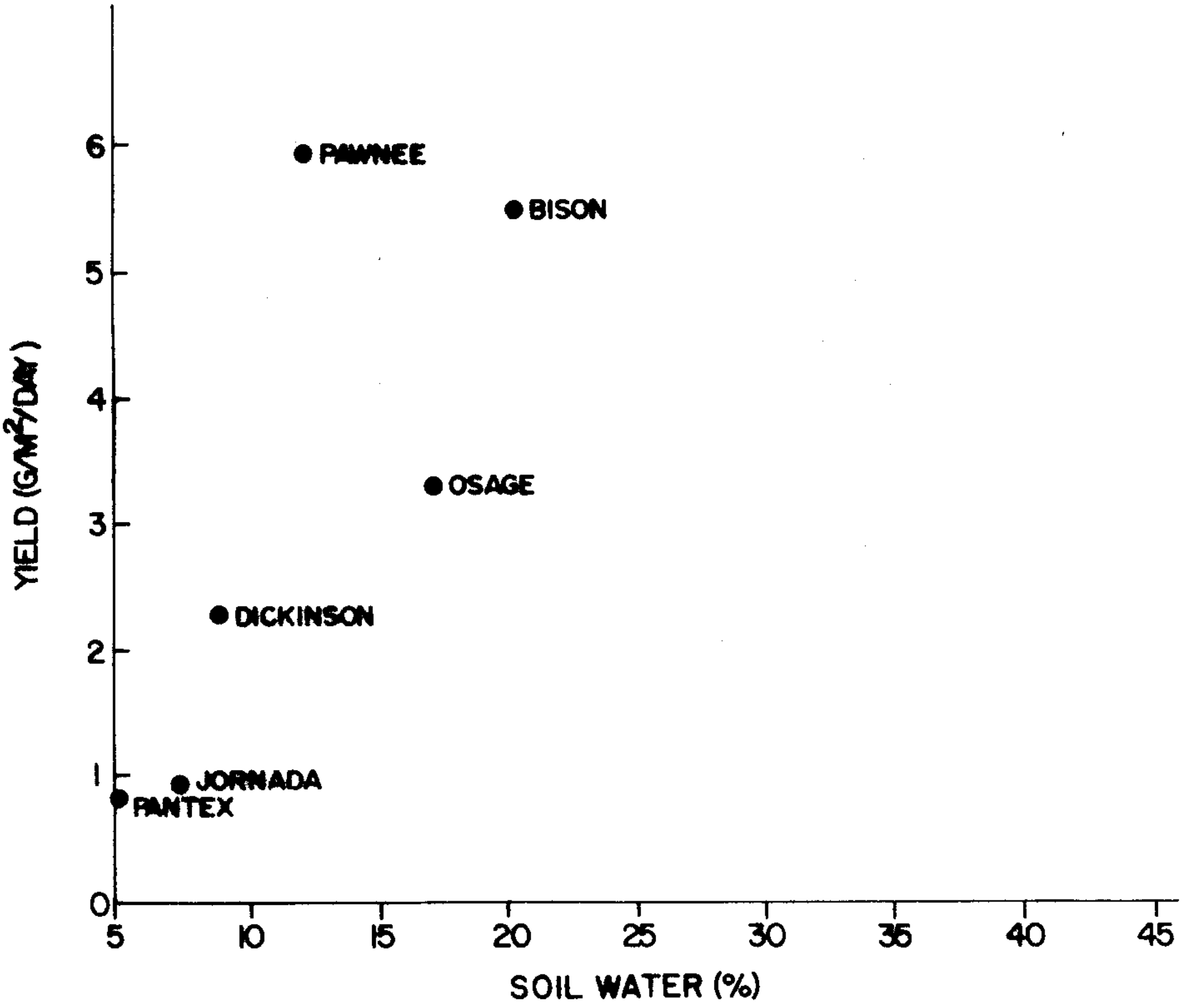

Fig. 7. Yield of aboveground biomass as related to July soil water.

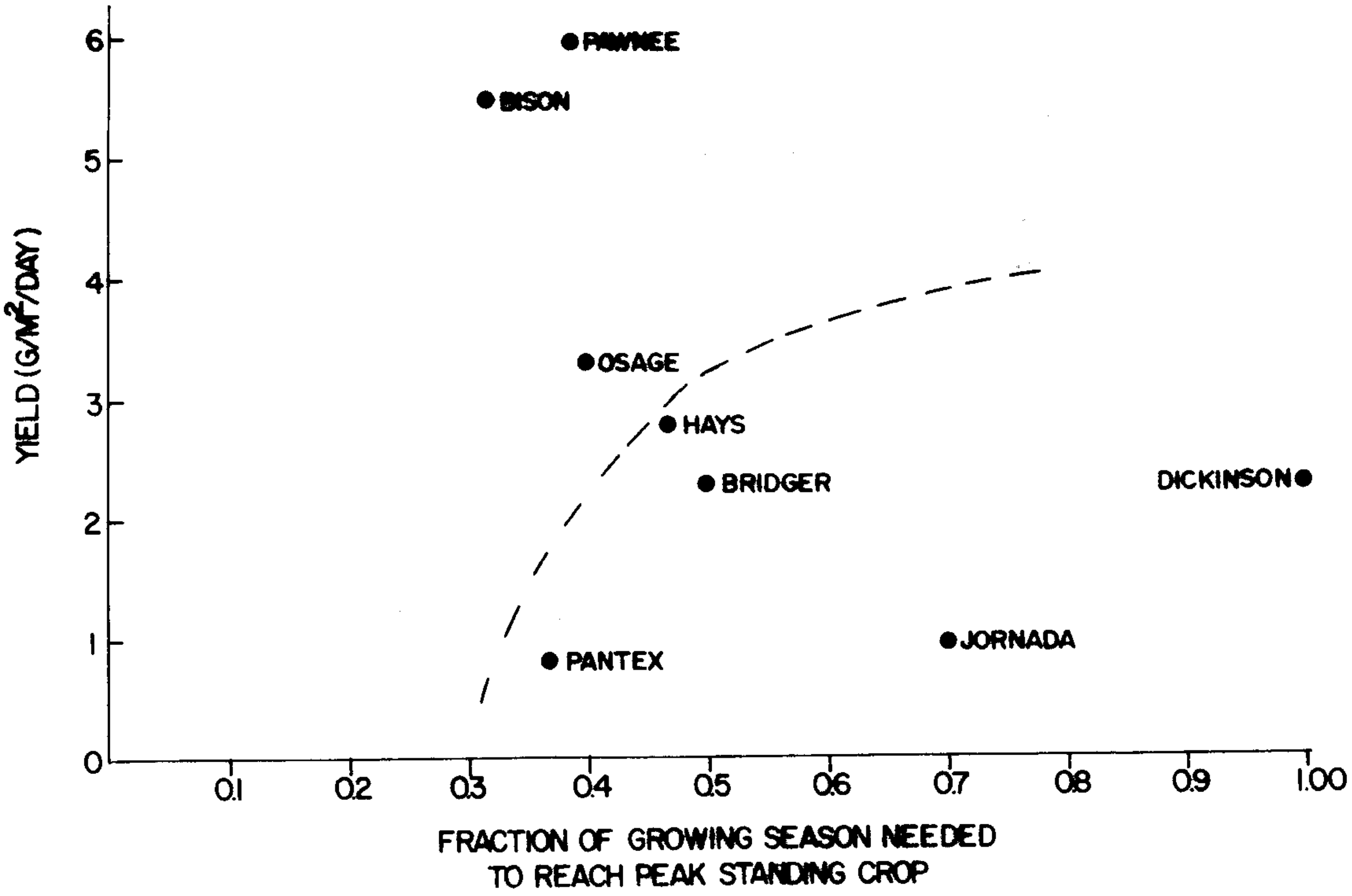

Fig. 8. Yield of aboveground biomass as related to fraction of growing season until total peak standing crop is reached.

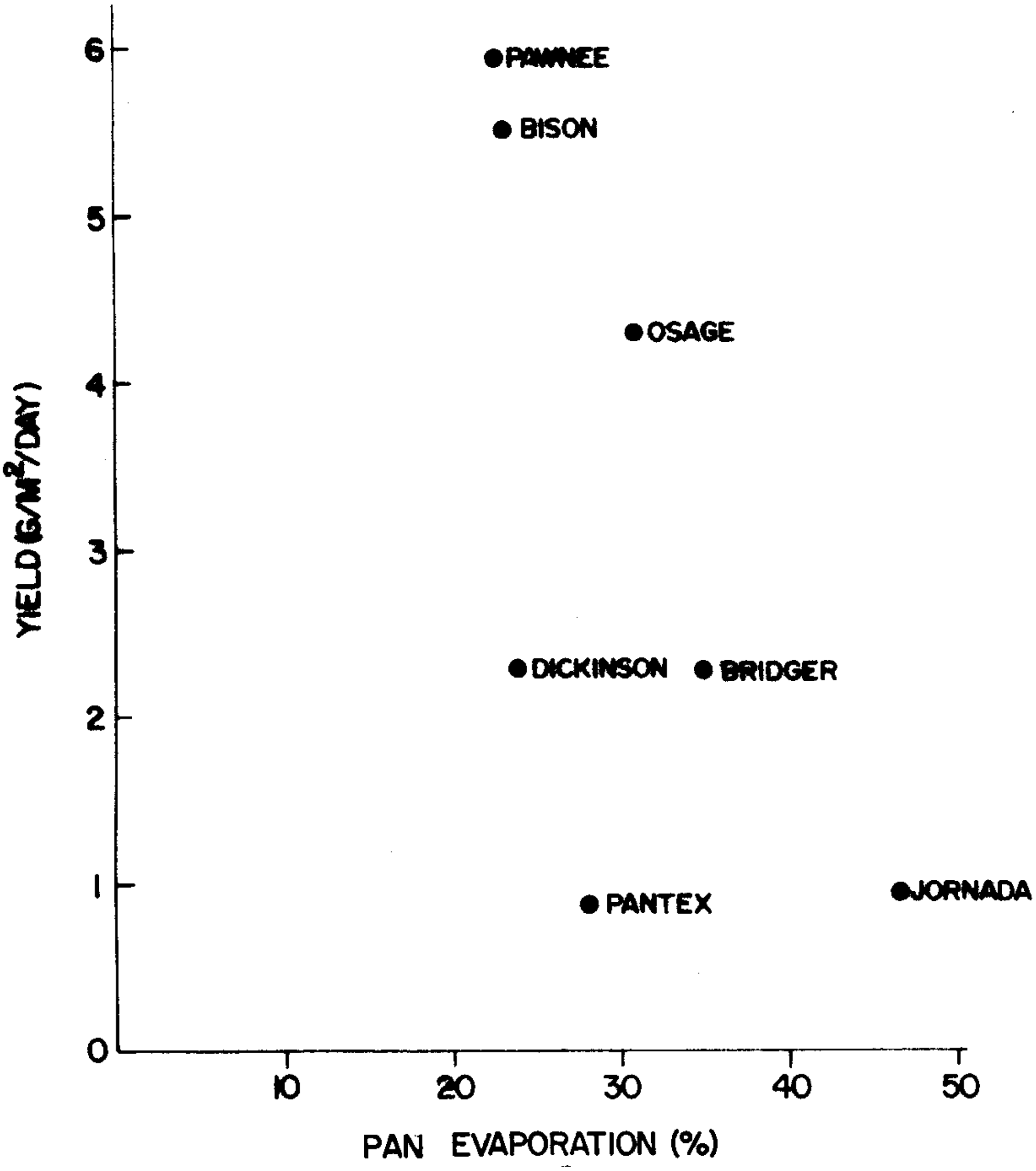

Fig. 9. Yield of aboveground biomass as related to average April through July pan evaporation.

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MULTIPLE REGRESSION ANALYSIS OF GRASSLAND ECOSYSTEMS

by

Maureen L. Croak

Introduction

Analysis of vegetation, either in terms of response to or as an indicator of community relationships, necessarily requires examination of functional relationships between plants and the regulating and driving forces of their environment. Because of the complexity and combined influence of all environmental factors on plant growth, it is difficult, if not impossible, to evaluate vegetation response in terms of a single factor. One must assume, therefore, that some factors will elicit a greater response than others, either alone or when in combination. Several approaches to such an examination of the plant-environment complex have been taken (Yarranton, 1967; Waring and Major, 1964; Newnham, 1968; Loucks, 1962; Gittins, 1965). In the following analysis of the plant-environment complex on the U.S. IBP Grassland Biome sites, multiple regression equations were used to construct a mathematical representation of those abiotic factors which are apparently related to vegetation and which best predict vegetation response. The shortcomings of such an analysis are recognized. However, as Yarranton (1971) points out, such a representation can provide "an intelligible description of observational data [and] may be of potential use in developing a model" and most importantly, may suggest possibilities for further analysis or for experimental testing in postulating or in determining direct causal relationships.

The sites under consideration are Bison, a Fescue-Palouse type grassland; Cottonwood and Dickinson, mixed prairies; and Osage, a tallgrass prairie.

Site Descriptions

Complete site descriptions are provided by Morris (1970), Lewis (1970), Whitman (1970), and Risser (1970) for Bison, Cottonwood, Dickinson, and Osage Sites, respectively.

Methods

Data for the following analyses were collected at the respective sites during the 1970 growing season and were taken from preliminary technical reports or from the IBP Data Retrieval Center at the Natural Resource Ecology Laboratory.

A linear correlation matrix was constructed to determine the degree of correlation between the independent variables including precipitation, percent of soil water, solar radiation, air temperature, soil temperature, and relative humidity. Multiple regression equations were derived using all possible combinations of the above independent variables with the following categories as dependent variables: aboveground live biomass (ungrazed), aboveground live biomass (grazed), total aboveground biomass (ungrazed), and total aboveground biomass (grazed). Those equations showing significance at the .05 level of probability or above, using the standard F-test, were chosen for illustration.

Discussion

Bison Site

Soil temperature was the major positive contributing factor to the aboveground live material (Y_1) in the ungrazed portion of the Bison Site (Table 1). Of those analyzed, soil water, air temperature, and solar

Table 1. Regression equations used to predict respective component of vegetation at various U.S. IBP Grassland Biome Sites, 1970 data.

Site	Multiple Regression Equation[a]	F	$s^2(1)$[b]
Bison	$Y_1 = -175.04 + 4.59X_1 - 8.21X_2 - 4.96X_3 + .50X_4$	9.164[c]	0.82
Cottonwood	$Z_1 = -408.94 + 3.57X_5 + .84X_4 - 3.52X_6 - .31X_1 - 5.32X_2$	17.670[c]	0.91
	$Z_1 = -405.02 - .30X_3 + 3.48X_5 + .84X_4 - 3.76X_6 - 5.26X_2$	17.672[c]	0.91
Dickinson	$Y_1 = -31.51 - 6.50X_2 - 35.77X_1 + 16.73X_3 - 116.36X_6 + 56.75X_7 + 1.31X_4$	38.546[c]	0.97
	$Y_2 = -112.57 - 1.96X_2 + 19.87X_1 - 27.85X_3 + 15.55X_7 + .48X_4$	14.351[c]	0.89
Osage	$Y_1 = -571.58 - 36.47X_6 + 3.15X_2 + .35X_4 + 5.72X_3$	12.247[d]	0.84
	$Y_2 = -172.23 - 4.24X_2 + .25X_4 + 3.07X_3$	9.838[d]	0.75

[a] Y_1 = aboveground live biomass (ungrazed).
Y_2 = aboveground live biomass (grazed).
Z_1 = total aboveground standing biomass (ungrazed).
X_1 = soil temperature.
X_2 = percent soil water.
X_3 = mean air temperature.

[a] (Continued).
X_4 = solar radiation.
X_5 = relative humidity at 11:00 AM.
X_6 = precipitation.
X_7 = accumulative precipitation.

[b] $s^2(1) = 1 - \frac{\text{deviations mean square}}{\text{total mean square}}$.

[c] Significant at the 0.5 level.

[d] Significant at the .01 level.

radiation comprised the remaining major contributing factors. Soil temperature and solar radiation were the only independent variables which showed significant correlation with each other. According to Mead (1971), this does not change the interpretation of the regression coefficient, but does make the multiple regression less efficient in the sense that standard errors of the estimated regression coefficients are larger than with uncorrelated variables.

Rough fescue (*Festuca scabrella*) is the major dominant in the ungrazed portion and is the primary constituent of north-facing slopes (Morris, 1970). Also, effective precipitation is above average for the surrounding area as evaporation and temperature are lower due to slope exposure (Morris, 1970). The observed peak standing live biomass occurred in late June, while the predicted curve for standing live biomass showed two peaks, one in mid-June and one in late July (Fig. 1). The fraction of the variance of Y_1 accounted for by the regression equation was .82.

Cottonwood Site

Relative humidity (measured at 11:00 AM) was the major, positive contributing factor to the total aboveground material (Z_1) in the ungrazed portion of the Cottonwood Site (Table 1). Solar radiation, precipitation, soil temperature, and percent soil water represented the remaining major contributing factors of those analyzed. None of these independent variables showed significant correlation with each other.

The vegetation in the ungrazed portion of the site is dominated by midgrasses (*Agropyron smithii* and *Stipa viridula*) with an understory of shortgrasses (*Bouteloua gracilis* and *Buchloe dactyloides*) (Lewis, 1970). The observed biomass curve showed two peaks, one in mid- to late June and

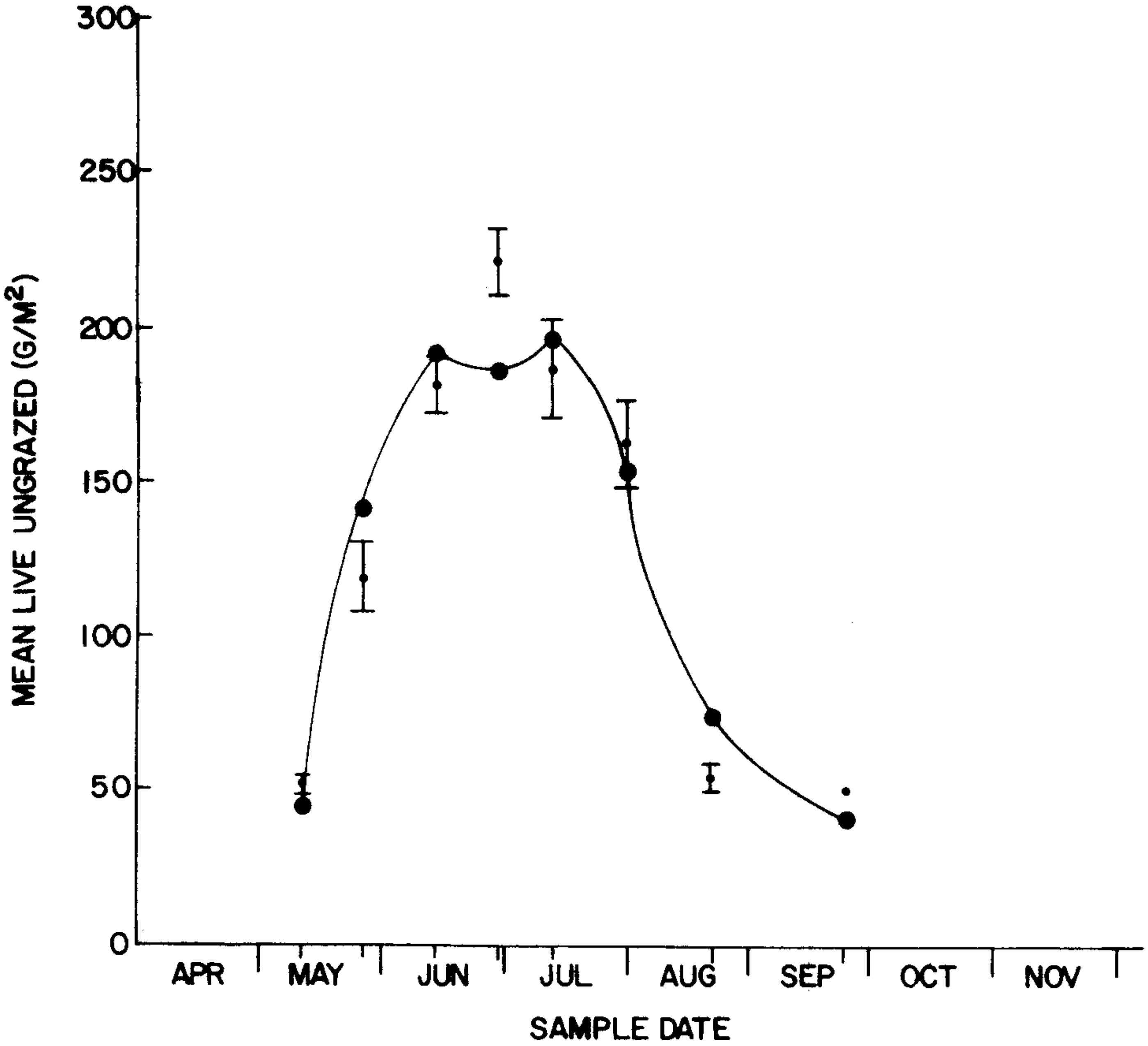

Fig. 1. Predicted curve for the ungrazed aboveground live biomass at Bison Site. X_1 = mean soil temperature at 2.5 cm; X_2 = percent soil water at 5 to 10 cm; X_3 = mean air temperature at 2.5 cm; X_4 = solar radiation (langleys); .82 of s^2 is accounted for by the regression equation; (•) = observed data with one SE.

one in early August. The predicted curve reflected this same pattern (Fig. 2). The two peaks on both curves coincide with relatively high relative humidities (48% and 45%) in mid- to late June and early August, separated in July by a fairly low relative humidity (39%) along with the highest rate of evaporation, air temperature, and soil temperature for the season. Under these conditions (in July), i.e., a combination of low relative humidity, high air and soil temperatures, and a high rate of evaporation, conditions may have become unfavorable for vital primary plant processes needed for plant growth. However, the soil water in the upper 10-cm level reached a seasonal high in mid-July, just prior to the second biomass peak. This soil water peak is, therefore, probably of greater causal importance in determining the height of the second peak. This does not appear evident from the regression equation because a time-lag effect is not considered in the regression, an inherent shortcoming alluded to in the introduction. The fraction of the variance of Z_1 accounted for by the regression equation was .91. A similar equation, substituting air temperature for soil temperature, was nearly identical (Table 1). This is probably due to the high correlation between air temperature and soil temperature.

Dickinson Site

Air temperature, accumulative precipitation, and solar radiation were the major factors contributing to the dynamics of the aboveground live biomass at the Dickinson Site (Table 1). None of these independent variables were significantly correlated with each other.

The principal dominant species on the ungrazed portion of this mixed-grass prairie include *Stipa comata*, *Bouteloua gracilis*, *Koeleria cristata*,

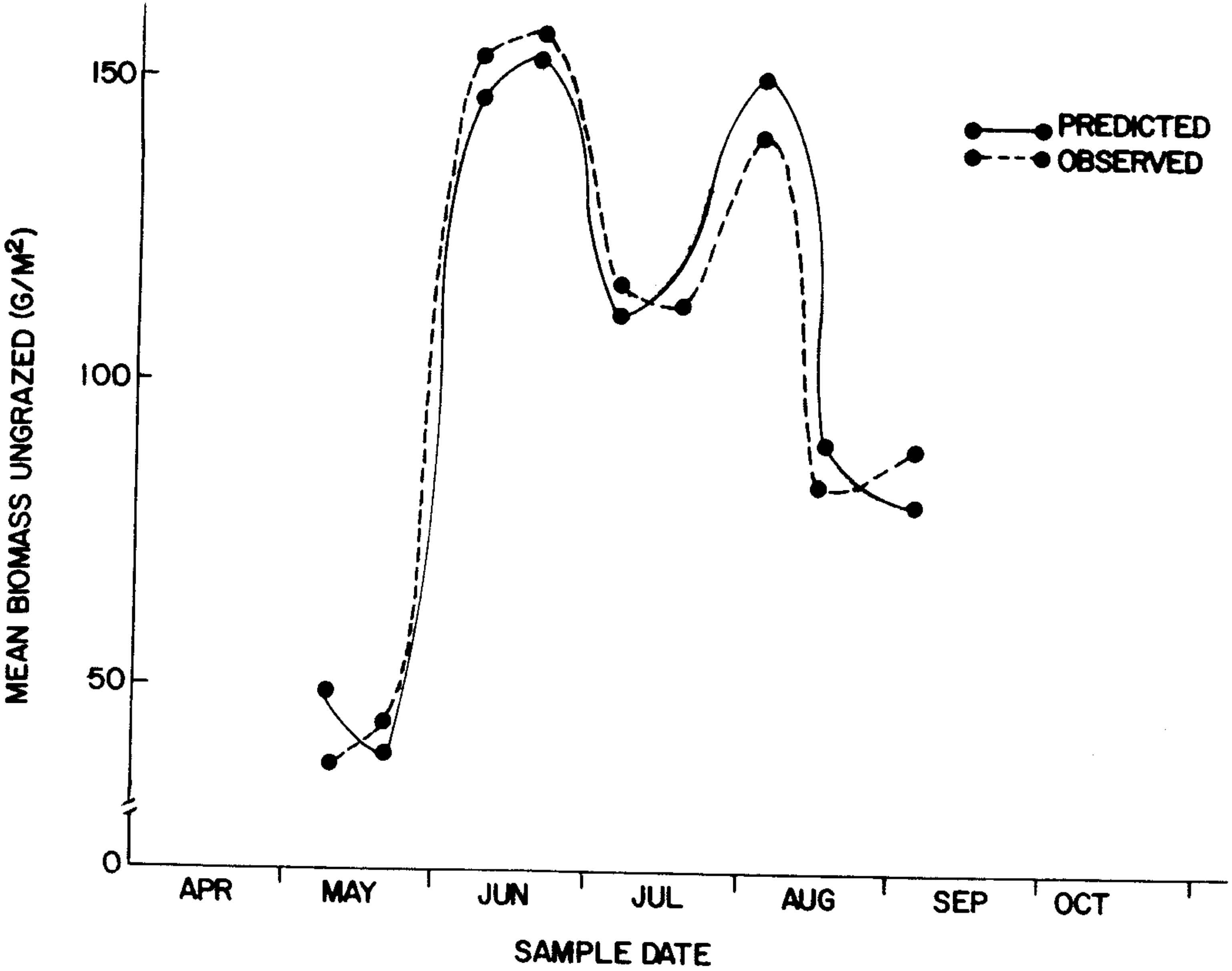

Fig. 2. Observed and predicted curves for total aboveground standing biomass on the ungrazed portion of the Cottonwood Site. X_1 = soil temperature; X_2 = percent soil water; X_5 = relative humidity; X_6 = precipitation; .91 of s^2 is accounted for by the regression equation. SE were not available.

and *Agropyron smithii*, along with the sedge *Carex eleocharis*. *Calamagrostis montanensis* is considerably more important on the grazed plot. The climate is semiarid with moderately warm, dry, sunny weather during the majority of the growing season (April through September). However, over 75% of the precipitation in this area occurs during the growing season (Whitman, 1970).

The observed curve and predicted curve from the regression equation (Fig. 3 and 4) followed the same pattern as the previous site: a minor peak in late June to early July and a later major peak in early to mid-September. As in the Cottonwood data, these major peaks probably reflect the effect of previous periods of rainfall, one near the end of May and the other in mid-July. Because the regression equation does not consider this time-lag effect in the derived equation, soil water indicates a negative influence on the aboveground live biomass (Y_1). The fraction of the variance of Y_1 accounted for by the regression equation was .97.

Soil temperature, accumulative precipitation, and solar radiation were the predominant positive factors influencing the aboveground live biomass (Y_2) on the grazed portion of the Dickinson Site (Table 1). Percent soil water and air temperature contributed negatively.

As in the ungrazed portion, the predicted curve reflected the observed data with two major peaks. However, the first peak occurred earlier in the season on the grazed portion. This probably reflects differences in species composition, particularly regarding cool-season grasses. Again, failure of the regression equation to detect a time-lag effect may account for the indicated negative soil water contribution to the regression. The regression equation accounted for .89 of the variance in Y_2.

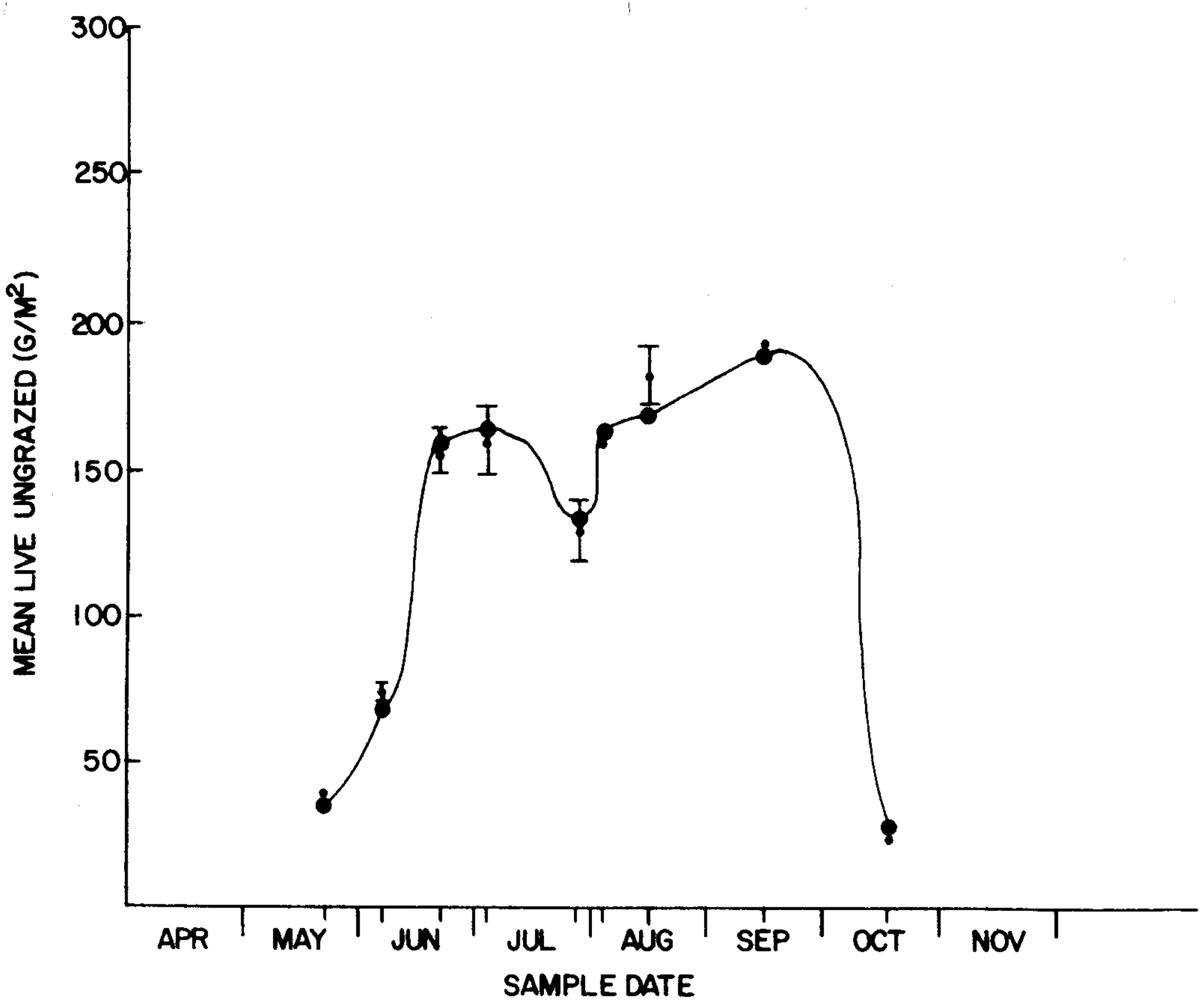

Fig. 3. Predicted curve for ungrazed aboveground live biomass at Dickinson Site. Adjusted values are from Whitman (1971). X_1 = soil temperature at 7.5 cm; X_2 = percent soil water at 0 to 10 cm; X_3 = air temperature at 2.5 cm; X_4 = solar radiation; X_6 = precipitation; X_7 = accumulative precipitation; .97 of s^2 is accounted for by the regression equation; (•) = observed data with SE, when available.

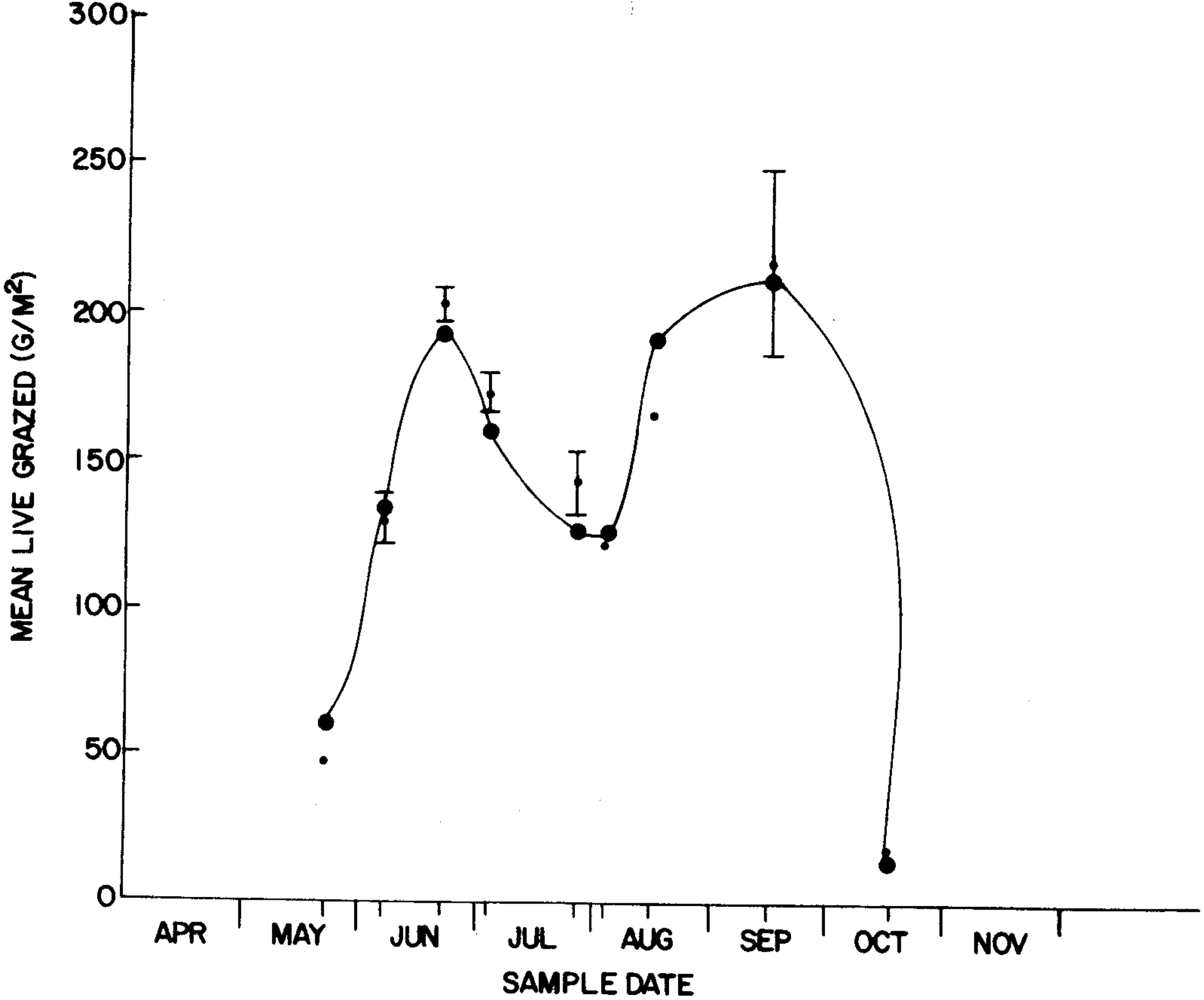

Fig. 4. Predicted curve for grazed aboveground live biomass at Dickinson Site. Adjusted values are from Whitman (1971). X_1 = soil temperature at 7.5 cm; X_3 = air temperature at 2.5 cm; X_4 = solar radiation; X_7 = accumulative precipitation; .89 of s^2 is accounted for by the regression equation; (·) = observed data with SE, when available.

Osage Site

Soil water and air temperature were the major contributing factors to the aboveground live biomass on the ungrazed portion of the Osage Site (Table 1). Precipitation showed a strongly negative effect which is related to spring soil water and the phenology of the dominant warm-season grasses, while solar radiation demonstrated a slightly positive influence. Soil water and air temperature were the only independent variables which showed significant correlation with each other. Soil water, solar radiation, and air temperature were the major contributing factors to the dynamics of the aboveground standing live biomass on the grazed portion (Table 1).

Little bluestem (*Andropogon scoparius*) is the major dominant on both the ungrazed and grazed plots, but is present in combination with some invader cool-season grasses (*Bromus japonicus* and *Poa pratensis*) on the grazed site. *Sporobolus asper*, an increaser species, is also more prevalent on the grazed plot (Risser, 1970). The majority of the precipitation in this tallgrass prairie falls early (April through June) in the growing season (April through September), and soil water probably does not become limiting until early to mid-July. The observed peak in aboveground live material (Y_1) on the ungrazed portion (Fig. 5) occurred at this time, again, probably a reflection of the previous period of relatively high precipitation and soil water. Additionally, air temperatures reached a seasonal high during this period. The predicted curve for the ungrazed aboveground live material (Fig. 5) showed two peaks in the growing season: one corresponding to the actual peak in early to mid-July and one in early August. This second peak corresponds to fairly high air temperatures during early August. However, all other positive contributing factors were at a low at this time, 161

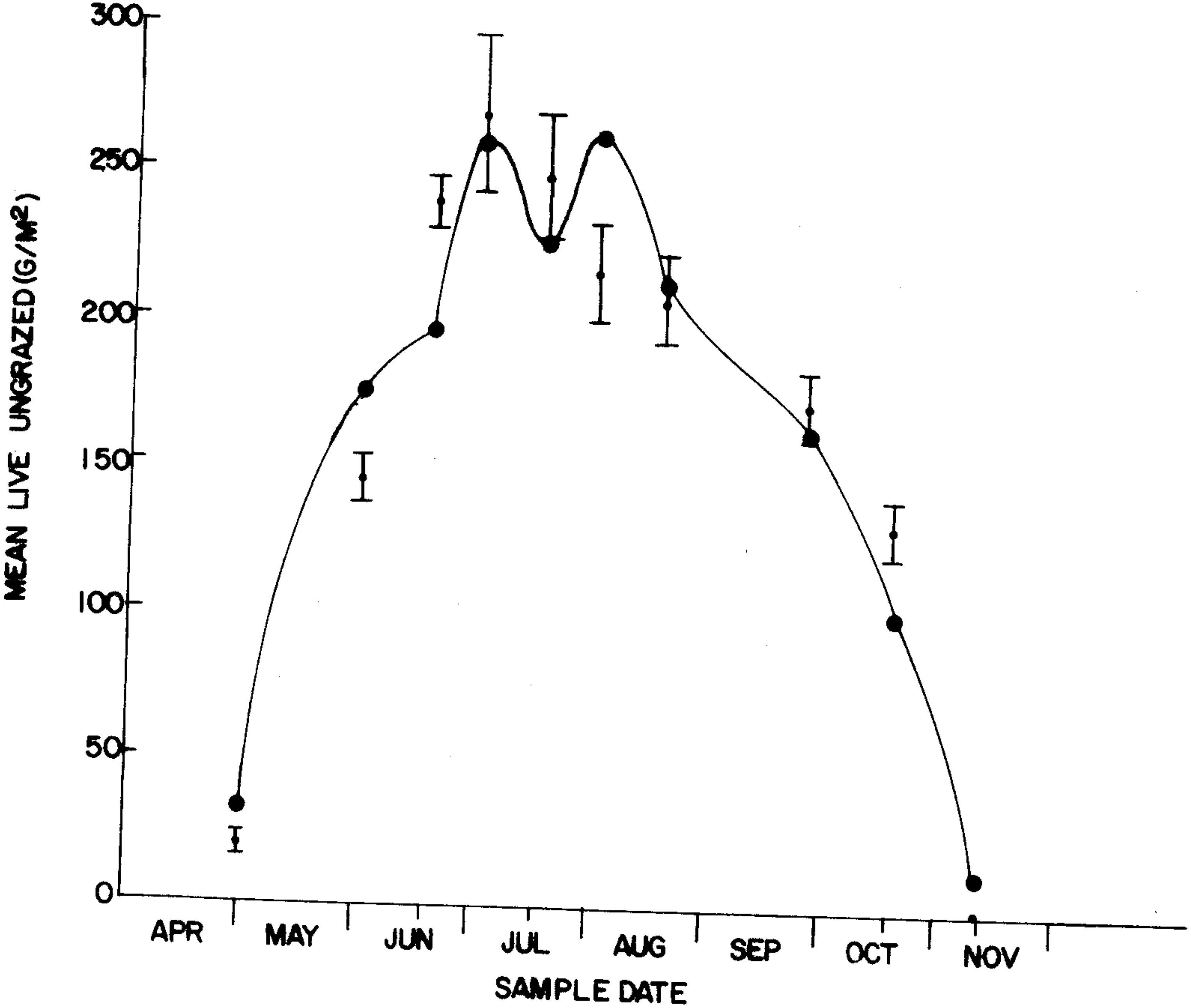

Fig. 5. Predicted curve for ungrazed aboveground live biomass at Osage Site. X_2 = percent soil water at 0 to 10 cm; X_3 = mean air temperature at 1 ft; X_4 = solar radiation; X_6 = precipitation; .84 of s^2 is accounted for by the regression equation; (•) = observed data with SE

indicating that this second peak is probably an artifact of the regression equation. The fraction of the variance in Y_1 accounted for by the regression was .84.

Three peaks were observed in the aboveground live biomass (Y_2) on the grazed portion of the study site: mid-June, mid-July, and mid- to late September. The predicted curve (Fig. 6) followed this pattern, except that it did not show a peak in mid June, as the regression equation failed to detect the time-lag response to precipitation early in the growing season which would become immediately important on the grazed site due to the presence of a larger proportion of cool-season grasses. The amount of variance in Y_2 accounted for by the regression equation was .75.

Summary

Multiple regression equations were used to examine the plant-environment complex on four of the U.S. IBP Grassland Biome sites. A linear correlation matrix was used to determine the degree of correlation between the independent variables which were then selected for use in the regression equations. In most instances, those equations which showed significance fairly accurately predicted the response of the vegetation. However, in almost all cases, some variables which were definitely related to vegetation response did not show this relationship in the equation due to a time-lag effect, i.e., a temporal separation between cause of the event and actual vegetative response (growth). Thus, Cottonwood, Osage, and Dickinson probably show the greatest response to precipitation, although this was not observable in all equations due to this time-lag effect. Osage data did show some separation between the ungrazed and grazed treatments in the predicted equations due to the

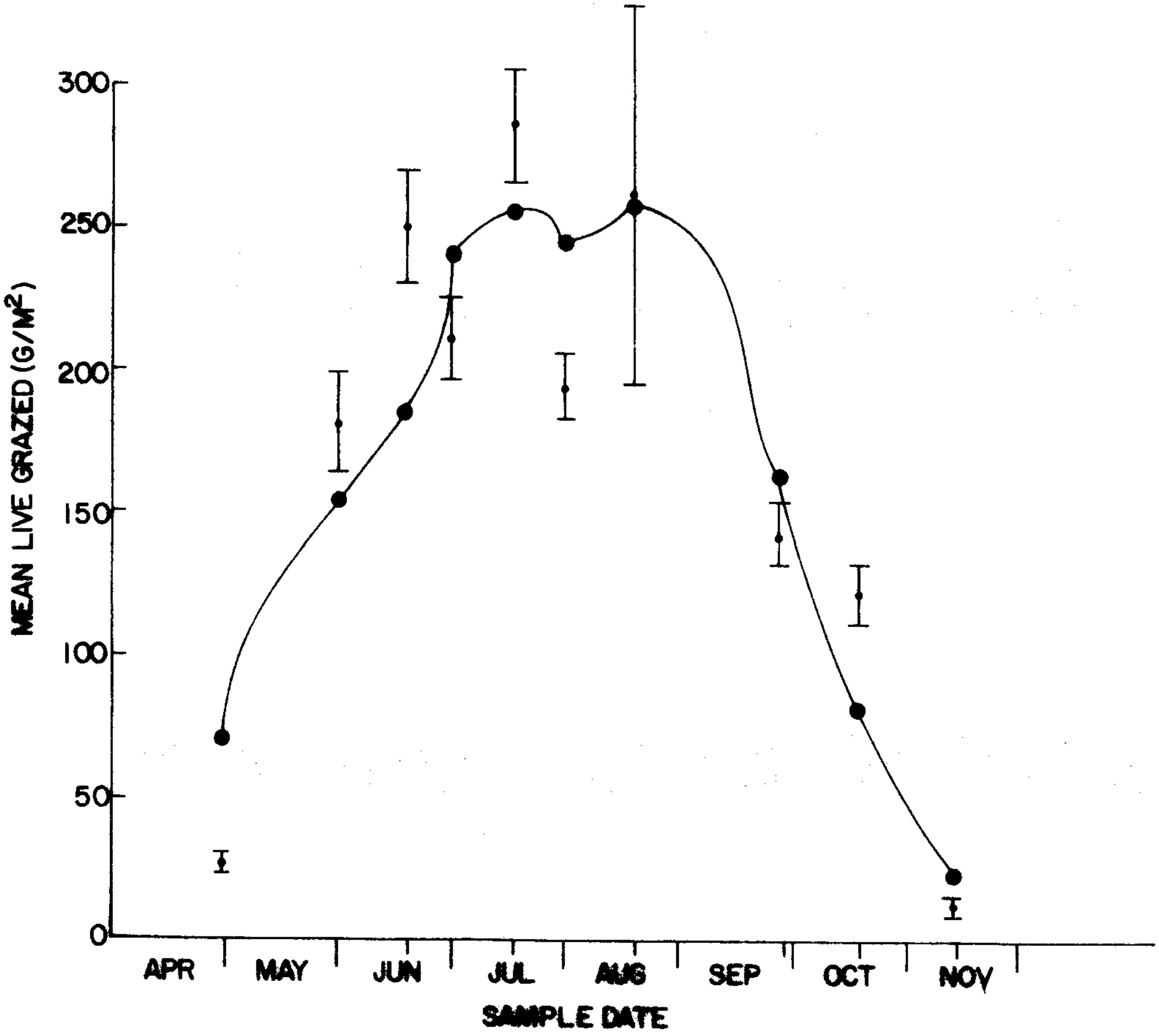

Fig. 6. Predicted curve of grazed aboveground live biomass at Osage Site. X_2 = percent soil water at 0 to 10 cm; X_3 = mean air temperature at 1 ft; X_4 = solar radiation; .75 of s^2 is accounted for by the regression equation; (•) = observed data with SE.

difference in composition of the two plots, the grazed plot containing more cool-season grasses as a result of grazing pressure. Soil temperature seemed to be the dominating influence at the Bison Site, which may in part be due to the physiographic location of the ungrazed plot. In most instances, regression equations constructed with the grazed data were found to be significant. It is probable that this may be attributed to more variation in the biomass data and to the absence of a factor for grazing pressure in the regression equation, which may indicate that the vegetation is most influenced by grazing itself.

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DYNAMICS OF BELOWGROUND BIOMASS ON THE COMPREHENSIVE NETWORK SITES

by

Jack Turner

Introduction

The considerable amount of work done on root systems of the prairie grasses has been compiled by Weaver (1958), and subsequently, there have been additional studies (Bray, 1963; Dahlman and Kucera, 1965; Head, 1970; Schuster, 1964; Struik and Bray, 1970). In these studies there has been relatively little effort to study the roots as a system in combination with the aboveground parts of the plant and with the environment. The U.S. IBP Grassland Biome study has provided a unique opportunity to evaluate treatment factors, such as grazing, and the environment as they relate to or affect the root system and belowground biomass.

The experimental design in the Grassland Biome involved five major types of grasslands: the mixed-grass prairie represented by Cottonwood Site at Cottonwood, South Dakota, and Dickinson Site at Dickinson, North Dakota; the tallgrass prairie by Osage Site at Shidler, Oklahoma; the shortgrass prairie by Pawnee Site located on the Pawnee National Grassland near Fort Collins, Colorado; the desert grassland by Jornada Site located near Las Cruces, New Mexico; and the mountain grassland type by Bison Site located near Missoula, Montana, and Bridger Site near Bozeman, Montana. The above- and belowground biomass data were collected from a treatment area that had been grazed for some length of time (low-range condition) and from an area that had not been grazed (high-range condition). The collected aboveground biomass included plants, mammals, and insects. The belowground biomass included decomposers, roots, rhizomes, and crowns. At each of these sites, data were also collected on a number of environmental parameters such as precipitation, soil water, soil temperature, humidity, and air temperature.

The purpose of the following study was to analyze the root biomass data which were collected on the five sites of Cottonwood, Dickinson, Osage, Jornada, and Pantex and to make comparisons between these sites using turnover rates and root/shoot ratios.

Calculations

The calculation of turnover rate follows the formula proposed by Dahlman and Kucera (1965): the minimum root biomass is subtracted from the maximum root biomass, and the difference is divided by the maximum root biomass.

$$\frac{\text{Max Biomass} - \text{Min Biomass}}{\text{Max Biomass}} \times 100$$

This index represents an indication of the rate at which roots are lost or replaced in the system. For example, a 25% turnover rate indicates that in 4 years, the accumulated amount of dead root material would be equivalent to the total peak biomass.

Results and Discussion

The response of the roots in the upper 10 cm of the soil to changes in the soil water in the same area of the profile may be seen for Osage, Cottonwood, and Dickinson Sites in Fig. 1 through 3. The vertical axis

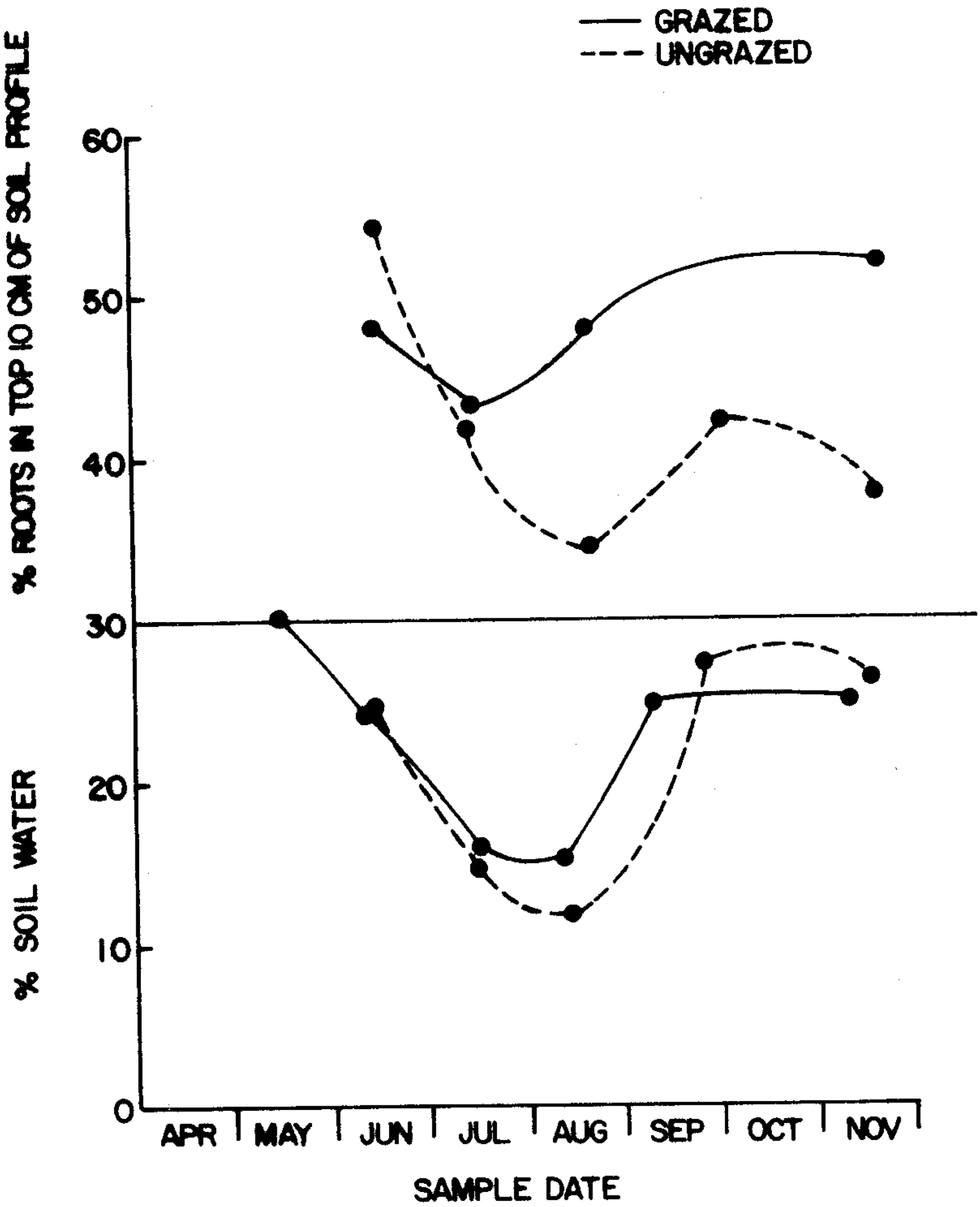

Fig. 1. Response of roots in the upper 10 cm of soil to changes in soil water during 1970 at the Osage Site.

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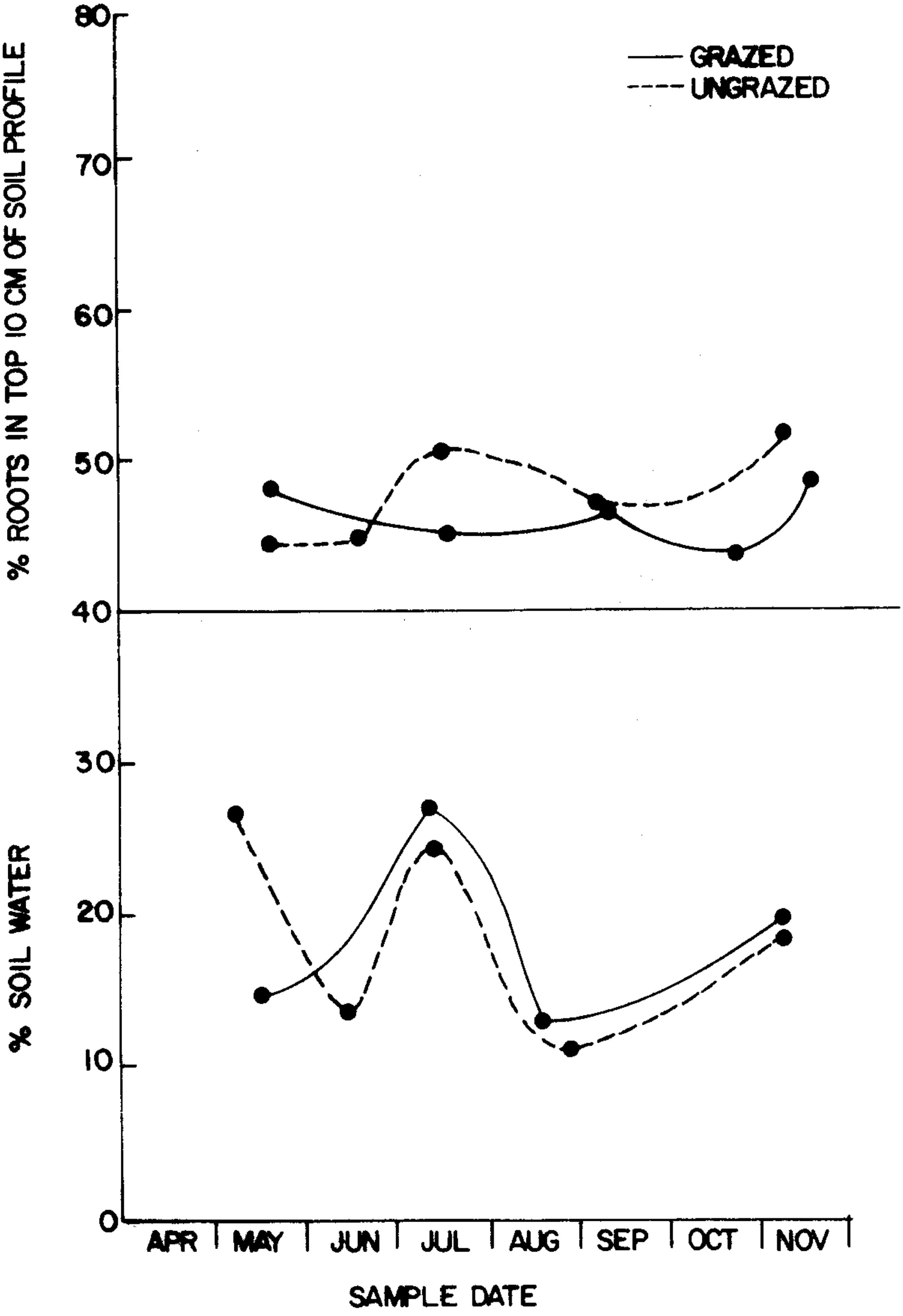

Fig. 2. Response of roots in the upper 10 cm of soil to changes in soil water during 1970 at the Cottonwood Site.

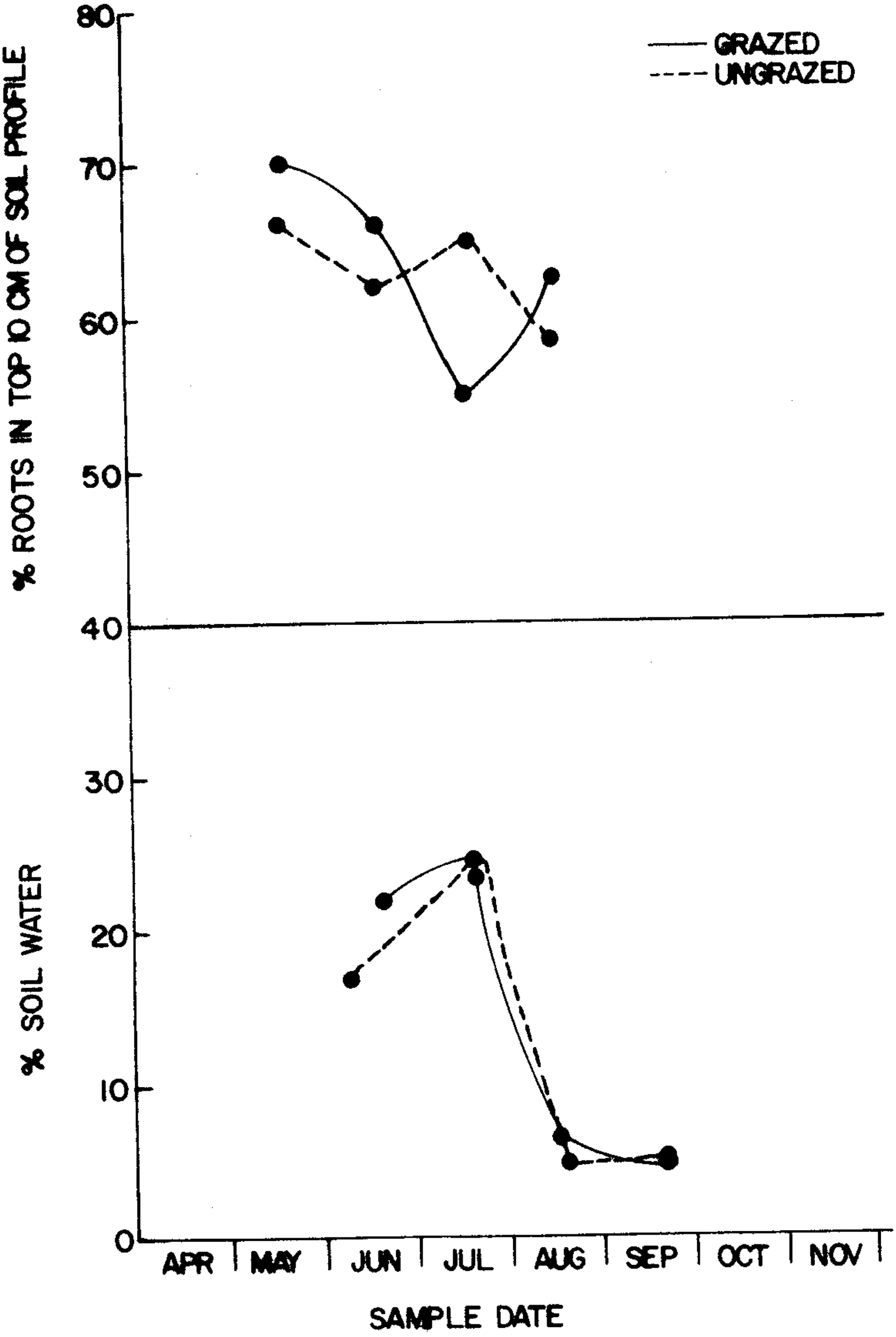

Fig. 3. Response of roots in the upper 10 cm of soil to changes in soil water during 1970 at the Dickinson Site.

represents a percent; the upper part of this axis (30% to 70%) is the percentage of roots in the upper 10 cm of the soil profile, and the lower part of the vertical axis represents the percentage of soil water in the upper 10 cm of the root profile. The horizontal axis is the sample date from April to November.

Each graph (Fig. 1 through 3) clearly shows the response of the roots in the upper 10 cm of soil to the soil water in the same horizon. The lower horizons do not show this rapid response to soil-water change because there is a decrease in the amount of water loss during very hot, dry periods in the lower horizons of the soil profile.

Turnover rates increase in the upper 10 cm of the profile in soils with lower water content. For example, the turnover rate for the Dickinson Site is 60% for the upper 10 cm, and the average amount of soil water for the sampling season at this depth is 12.7% water. In contrast, the Osage Site has a turnover rate of 37%, and an average amount of soil water at this 10-cm depth is 23.9%.

Table 1 depicts the turnover rates for the grazed and ungrazed treatments at each of the five sites and the turnover rate for the roots in the top 10 cm of the soil profile for each treatment. Root turnover rates in the mixed-grass prairies, Dickinson and Cottonwood, are higher than the tallgrass prairies at Osage. This is due in part to grasses that characterize each prairie vegetation (Struik and Bray, 1970). The shortgrasses tend to have finer roots than the grasses that characterize the tallgrass prairie (Weaver, 1950). These smaller roots would be subjected more to changes in soil water and temperature conditions; therefore, a higher death rate would result from desiccation.

In studies of turnover rate on the tallgrass prairie in Missouri, Dahlman and Kucera (1965) calculated a rate of 25%; the data obtained from

Table 1. Turnover rates (%) for grazed and ungrazed treatments on five sites. See Results and Discussion section for explanation.

Site	Ungrazed		Grazed	
	Total	Top 10 cm	Total	Top 10 cm
Dickinson	32	60	20	62
Pantex	45	18	44	12
Jornada	43	46	52	42
Osage	12	37	22	15
Cottonwood	21	19	14	26

The Osage Site indicated a turnover rate of 25% for the ungrazed and a 22% turnover rate for the grazed area. The Osage Site contains a far greater quantity of *Andropogon scoparius* and forbs and receives less rainfall than the tallgrass prairie of Missouri.

Root/shoot (R/S) ratios were calculated by taking the peak standing crop for the 1970 season and dividing it by the corresponding root biomass (Table 2). It has been shown by several investigators (Struik and Bray, 1970; Weaver and Zink, 1946) that the root/shoot (R/S) ratio increases with the "xericness" or decreasing soil water at the site. Weaver and Zink (1946) showed that big bluestem has a smaller R/S ratio than little bluestem and blue grama, which are dominant on the more xeric sites. They found that the R/S ratio for big bluestem was 0.46, little bluestem was 0.23, and blue grama was 0.25.

The Osage Site has the highest R/S ratio on the ungrazed area with 0.85 and on the grazed area with 0.50. These figures are greater than the literature values, but the grazed area corresponds closely with conclusions reached by Biswell and Weaver (1933) on the effects of clipping on the R/S ratio. They found that there was a decrease in this ratio following prolonged clipping. The other four sites confirm the fact that clipping in the form of grazing will decrease the R/S ratio.

In summary, it can generally be said that the more xeric a site, the higher the root turnover rate and the greater the root/shoot ratio. The data also point out the differences between the grazed and the ungrazed areas as far as turnover rates and R/S ratios go. The turnover rates are too inconsistent to compare the grazed and ungrazed areas, but the R/S ratios on the grazed sites are consistently lower than the ungrazed.

Table 2. Root/shoot ratios for different sites at the time of peak standing crop.

Site	Grazed		Ungrazed	
	Ratio	Percent	Ratio	Percent
Dickinson	1:8	0.13	1:3	0.33
Pantex	1:6	0.17	1:5	0.20
Jornada	1:3	0.33	1:2	0.5
Osage	1:2	0.5	1:1.5	0.67
Cottonwood	1:9	0.11	1:4	0.25

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LITTER DYNAMICS WITHIN THE COMPREHENSIVE NETWORK SITES

by

Forrest L. Johnson

Introduction

As a functional definition in this study, litter is the ecosystem component which includes dead organic material on the ground. From an ecosystem standpoint litter represents decaying portions of organisms which are in the process of transfer from living components to soil organic matter.

Numerous studies indicate that mulch or litter significantly increases the rate of interception (Hopkins, 1954; Rauzi and Hanson, 1966) primarily by increasing the rate of infiltration. Litter normally favors the production and maintenance of larger soil aggregates which increase infiltration (Rauzi, Fly, and Dyksterhuis, 1968). Soil water is also increased by the presence of litter because runoff is diminished (Adams, 1966); evaporation is reduced (Hopkins, 1954); and there is a reduction in soil temperature (Barkley, Blaser, and Schmidt, 1965).

There is a consistent suggestion in the literature that herbage production increases as the amount of litter increases (Bentley and Talbot, 1951; Grelen and Epps, 1967; Heady, 1956; Larson and Whitman, 1942), presumably due to an enhancement of soil properties and consequent increases in soil water. On the other hand, increased litter accumulation, especially on ungrazed prairies, may accompany a decrease in herbage yield. The decrease in productivity is usually attributed to prevention of canopy development, immobilization of nutrients, decrease in flower stalk production, change in botanical composition, retardation of seedling development, and deleterious effects of fire (Curtis and Partch, 1950; Kucera and Koelling, 1964; Launchbaugh, 1964; Weaver and Bruner, 1948).

Some studies have shown production depression with heavy mulch accumulations by simply removing litter and measuring response in the subsequent years. However, these studies fail to consider the residual effects of the litter from previous years (Ellison, 1960). The literature seems to suggest that in xeric regions mulch may increase yields; in all regions of rainfall a moderate amount of mulch promotes high yields, but high amounts of mulch may decrease yields in mesic areas (Dix, 1960; Tomanek, 1969).

The purpose of this paper is to examine some of the characteristics of the litter component of grassland ecosystems. The data utilized were collected on the Comprehensive Network Sites during the 1970 growing season.

Methods

The biomass within the litter compartment was measured by collecting material from the clipped quadrats. In most sites collection was by hand after clipping was completed; though on the Cottonwood Site, the litter was collected with a vacuum. The litter was dried in the laboratory at 60°C and weighed. A subsample was ashed, and then, the entire litter value was expressed as ash-free dry weight. Data presented in this paper are mostly ash-free weight obtained directly from data cards; although in some cases, the values are estimated or taken from final reports.

Results and Discussion

The 1970 litter data are summarized in Table 1 which presents values for both ungrazed and grazed treatments of all Comprehensive Network Sites. In general these estimates have standard errors less than or equal to 0.2 of the mean with an 80% confidence interval.

The greatest amount of litter on the ungrazed treatment is found on mixed-grass prairies, Hays, Dickinson, and Cottonwood Sites, and the least litter is found on the desert grassland, Jornada Site. On the tallgrass at the Osage Site there is more litter on the grazed treatment which is in contrast to the more usual situation. This is probably because of the large amount of standing dead material on the ungrazed treatment which would result in a more humid microclimate near the ground; thus, the decay rate of litter is probably higher. The amounts of litter are approximately equal in the two treatments at Pantex and Jornada Sites, but these communities have relatively low biomass and little difference in standing crop between the treatments. Since the grazed treatment represents the dynamics of grasslands which are recovering from grazing and the previous grazing was not equivalent between all sites, most of the following analyses will involve the ungrazed treatment.

Presumably, the average amount of litter present on an ungrazed site is a function of environmental factors which affect the rate of plant growth, the rate at which standing dead material is converted to litter, and the rate at which litter decomposes. In Fig. 1 an ordination has been used as a synthetic framework for the comparison of the litter biomass. This is a principal component ordination utilizing 45 environmental variables (see Dvorak paper in this report). Those sites located on the right-hand side of the ordination are located in the southern part of the Great Plains and

Table 1. Amount of litter at each sample date. Data obtained directly from data cards, Sims and Singh (1971), and technical reports (Collins, 1970; Herbel and Pieper, 1970; Huddleston, 1970; Jameson, 1969; Lewis, 1970; Morris, 1970; Risser, 1970; Tomanek, 1970; Whitman, 1970). Values are given for the ungrazed treatment (U) and grazed treatment (G). All values are g/m^2 (dry weight).

Sample Date	Bison		Bridger		Cottonwood		Dickinson		Hays		Jornada		Osage		Pantex		Pawnee	
	U	G	U	G	U	G	U	G	U	G	U	G	U	G	U	G	U	G
April (early)													109	251			87	56
(late)	175	55							1091	568								
May (early)	180	45			244	86							98	177			104	53
(late)	124	37			378	140	797	95	479	346					107	96	136	66
June (early)	182	26			423	197	604	87	1251	730	49		68	130	96	181	124	96
(late)	147	36	83	100	406	259	538	91	1134	403	47	4	83	177	154	106	119	55
July (early)	220	51	152	53	430	177	523	100	823	435	81	40	154	125	84		72	55
(late)	274	73	65	28	466	182	627	169	985	451	38	61	88	145	84	46	142	94
Aug. (early)	329	56	68	23	432	220	625	202	1195	203	59	27	130	247	90	74	102	84
(late)	334	147	122	79	390	175	662	209	1067	184	41	61	125	262	30	218	94	60
Sept. (early)			44	28	354	142			1148	238	79	46				74	134	67
(late)	309	202					607	199			42	33	155	216	73		68	60
Oct. (early)					496											104		
(late)	243	111					649	206	1004	211			96	223				
Nov. (early)									992	165			83	158				
(late)																		
Dec. (early)																		
(late)																		

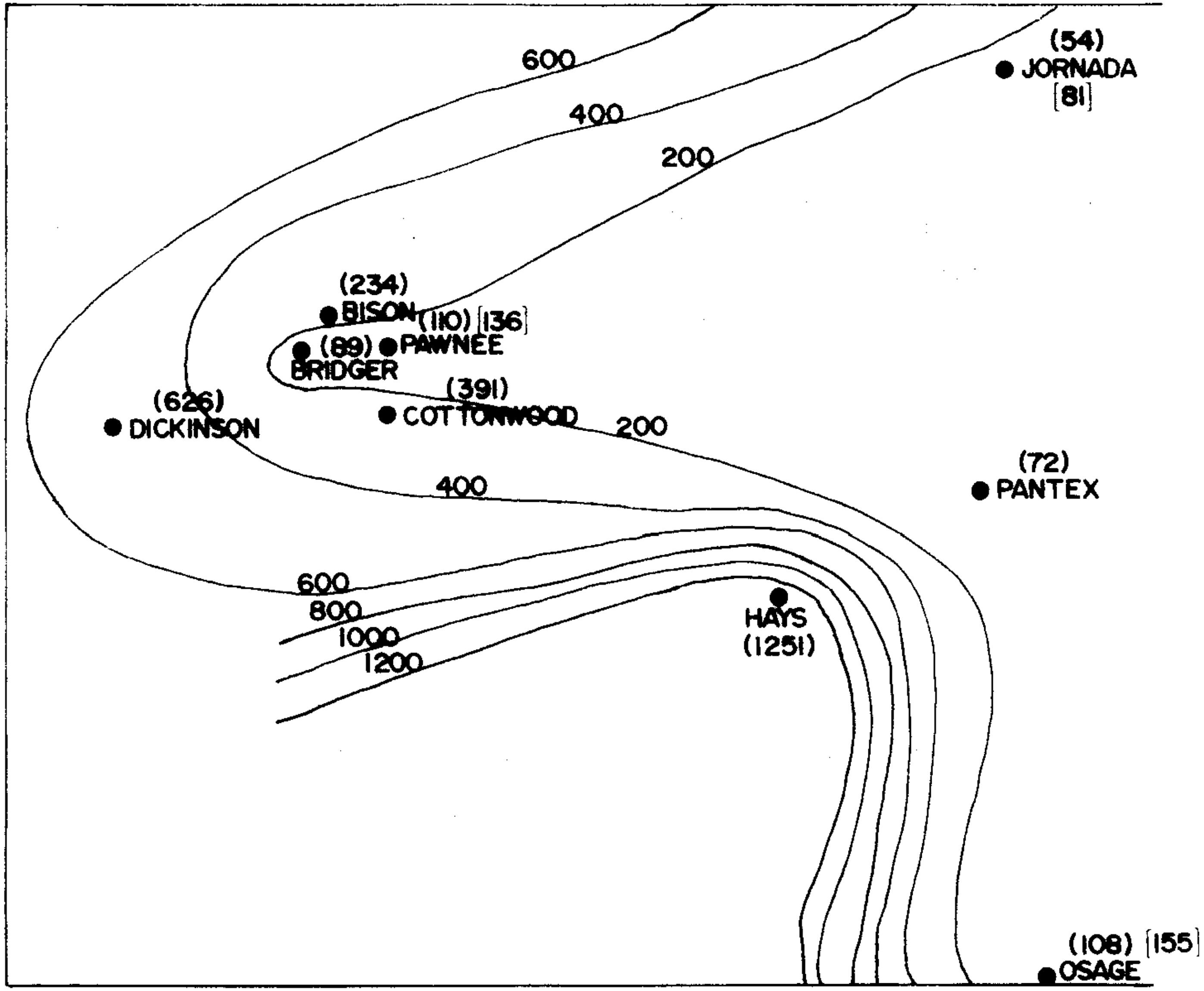

Fig. 1. Average litter (g/m^2) plotted on two-dimensional environmental ordination of the Comprehensive Network Sites.

with the exception of the Hays Site tend to have low average litter biomass values. Bridger, which is a northern site with a short growing season, also has a relatively small amount of litter.

The mean annual temperature does not show an apparent causal relationship to the amount of litter (Fig. 2). As was seen in the previous figure, with the exception of Hays, sites with high temperatures seem to have lower values for litter. Sites with the greatest amount of litter are those with an intermediate length growing season (Fig. 3) and annual precipitation (Fig. 4).

With the exception of the Osage Site, high amounts of litter are associated with sites which produce high amounts of live biomass (Fig. 5). Since litter is primarily the result of transfer from standing dead material, it might be assumed that the amount of litter would be positively correlated with the amount of standing dead material. This is the case for all except the Hays and Osage Sites (Fig. 6). Osage has a high amount of standing dead and a low amount of litter, while the exact reverse is true at the Hays Site. Since the data from Hays show a very high amount of litter and almost no standing dead, it seems possible that during separation of biomass components some biomass was separated as litter when the same material was separated as standing dead at other sites.

With the exception of the Pantex Site the amount of litter is relatively high before the growing season followed by a decline early in the season and an increase toward the end of the season (Fig. 7). This pattern is what might be expected with respect to the factors which influence the input and output of the litter compartment. Before the growing season temperatures are low enough to inhibit decay, and wind velocity is high enough to cause

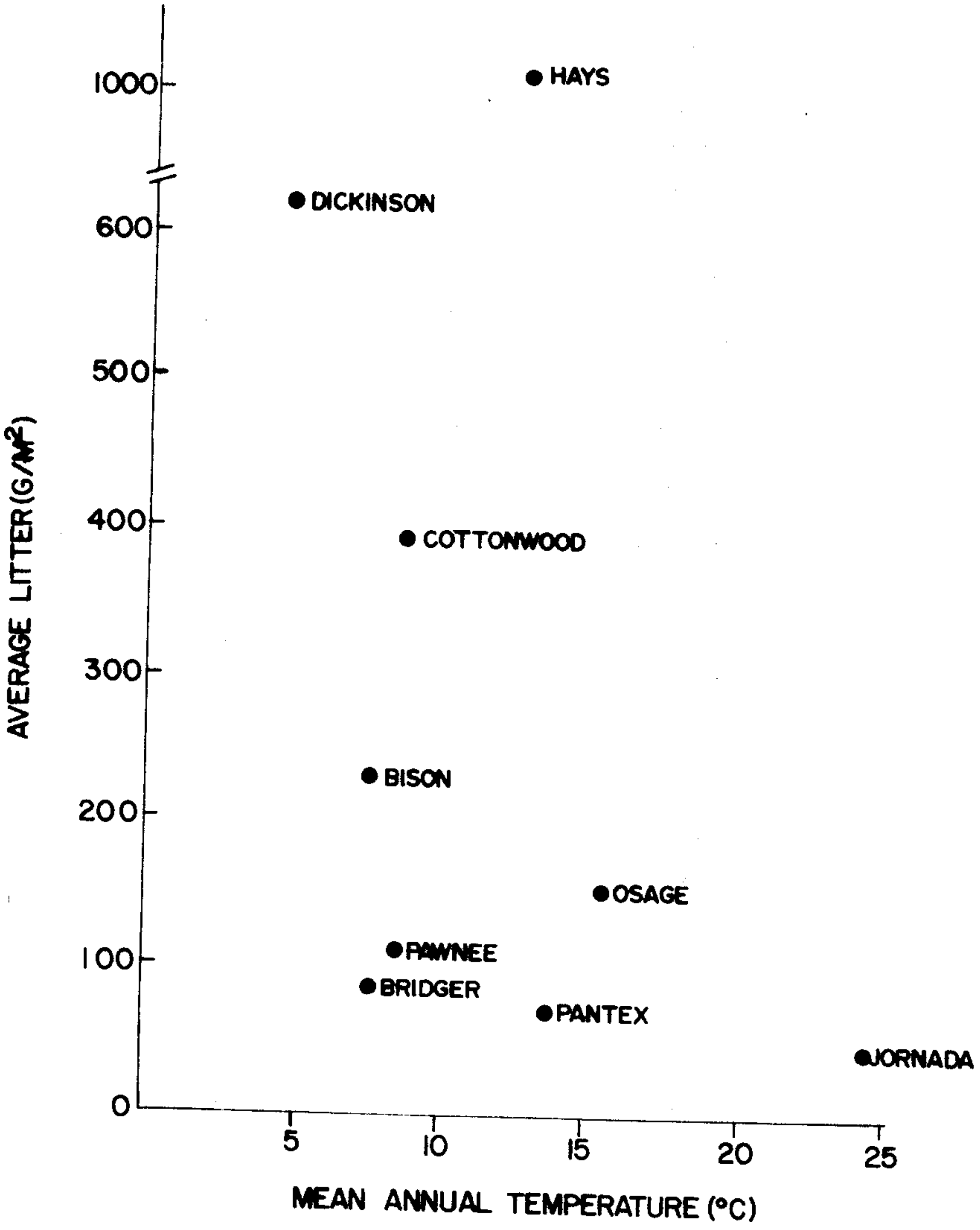

Fig. 2. Relationship between mean annual temperature and amount of litter on the ungrazed treatments.

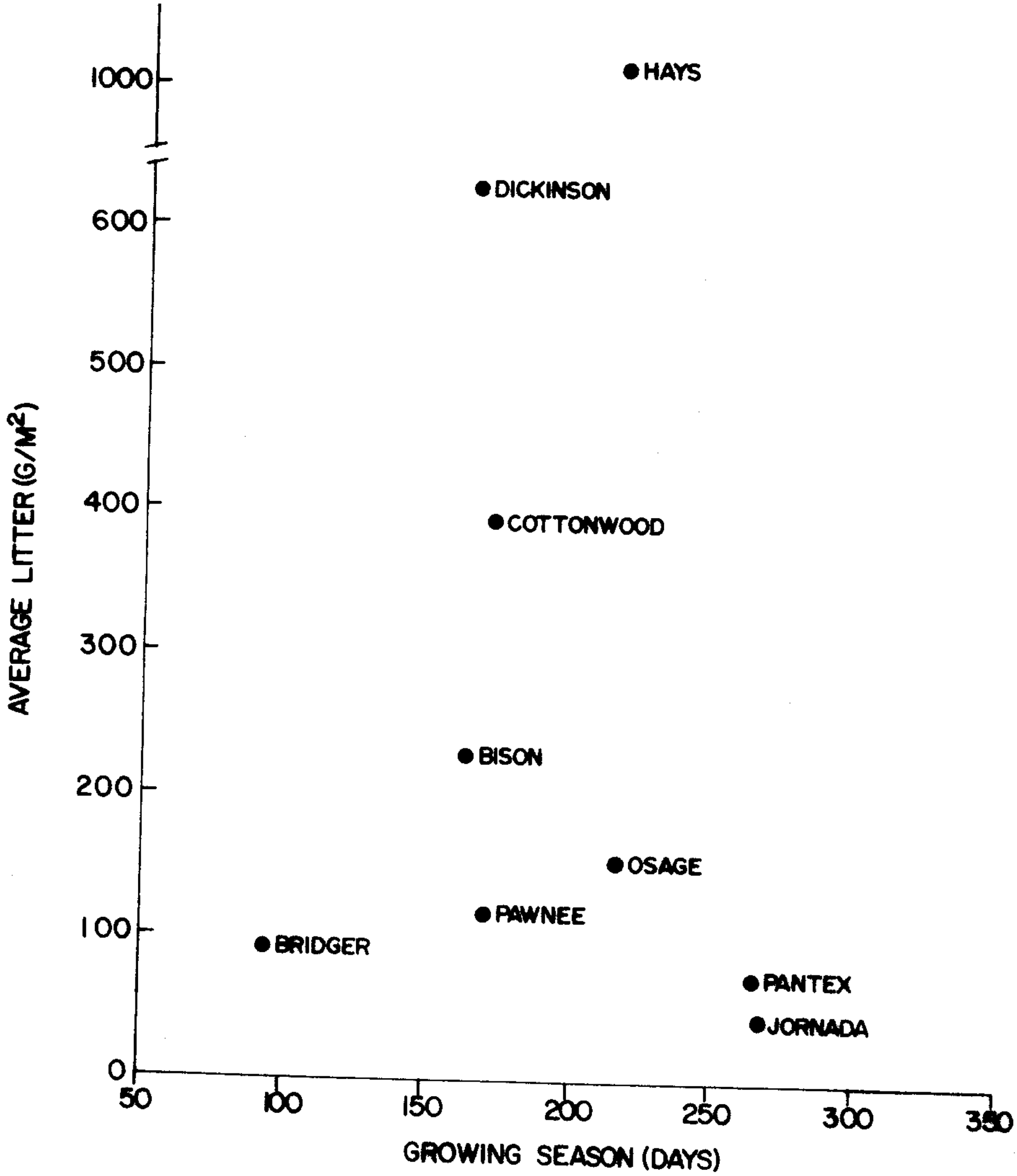

Fig. 3. Relationship between growing season and amount of litter.

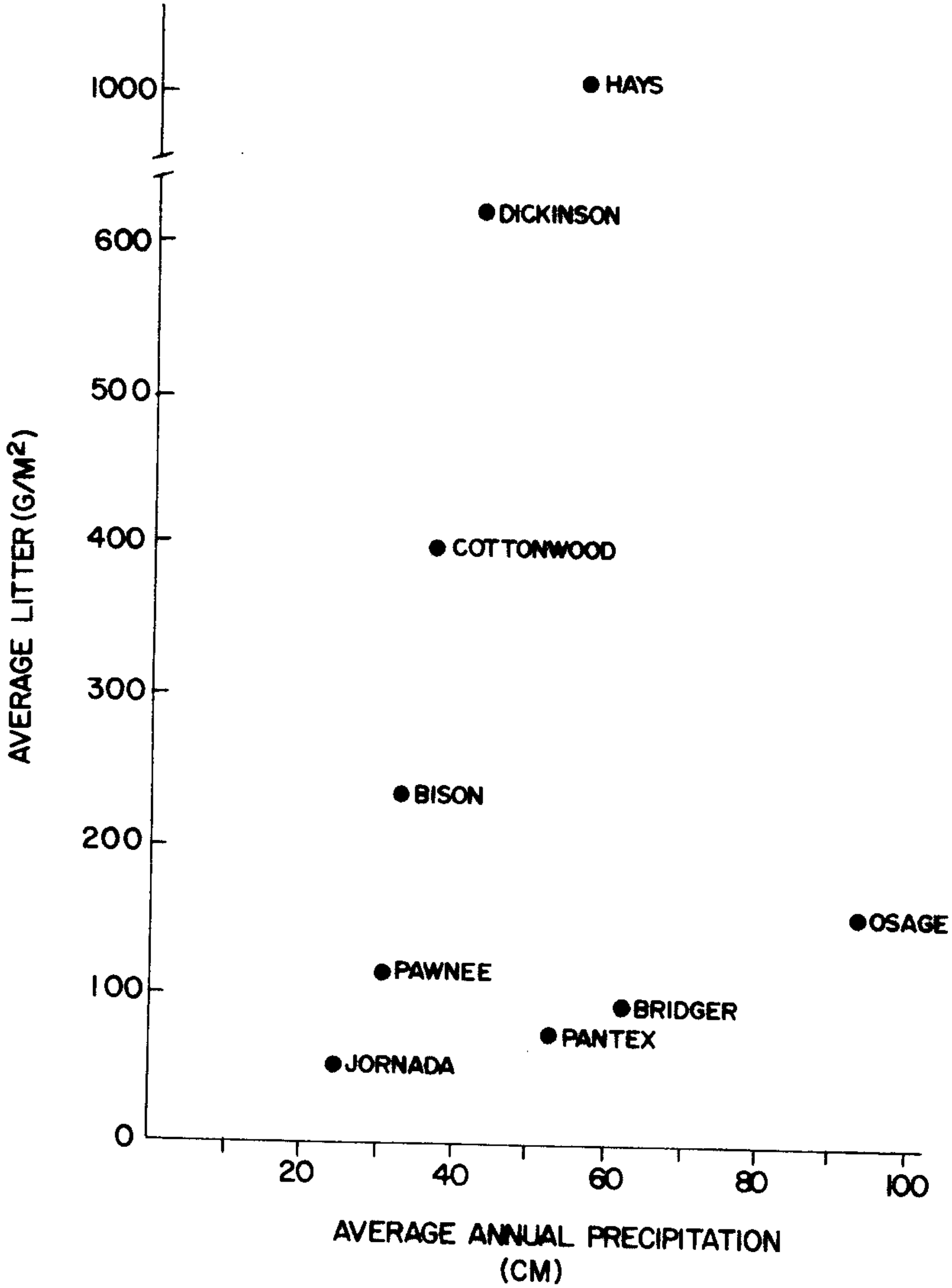

Fig. 4. Relationship between amount of litter and average annual precipitation at each site.

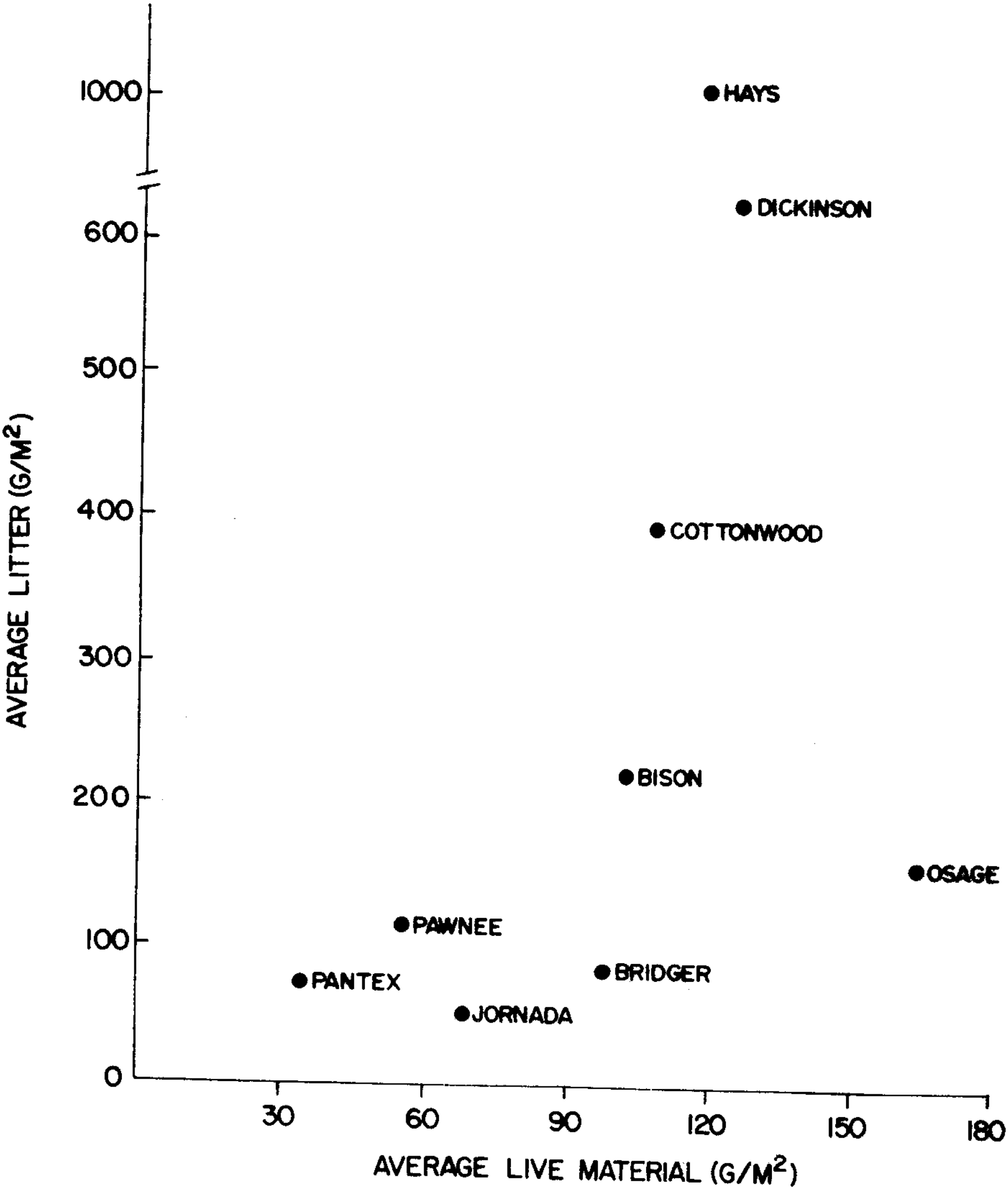

Fig. 5. Relationship between amount of litter and average live standing crop.

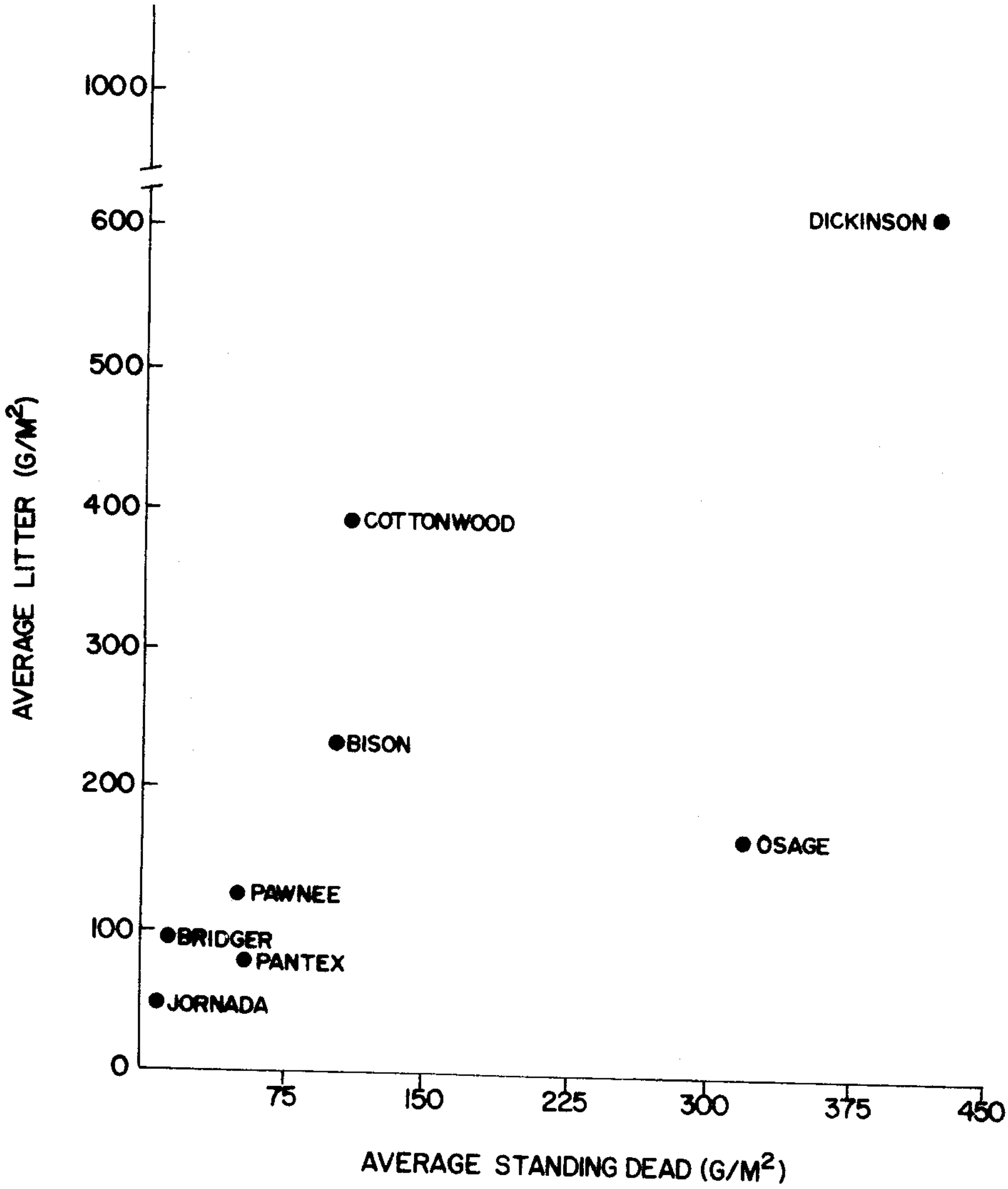

Fig. 6. Relationship between standing dead biomass and average amount of litter.

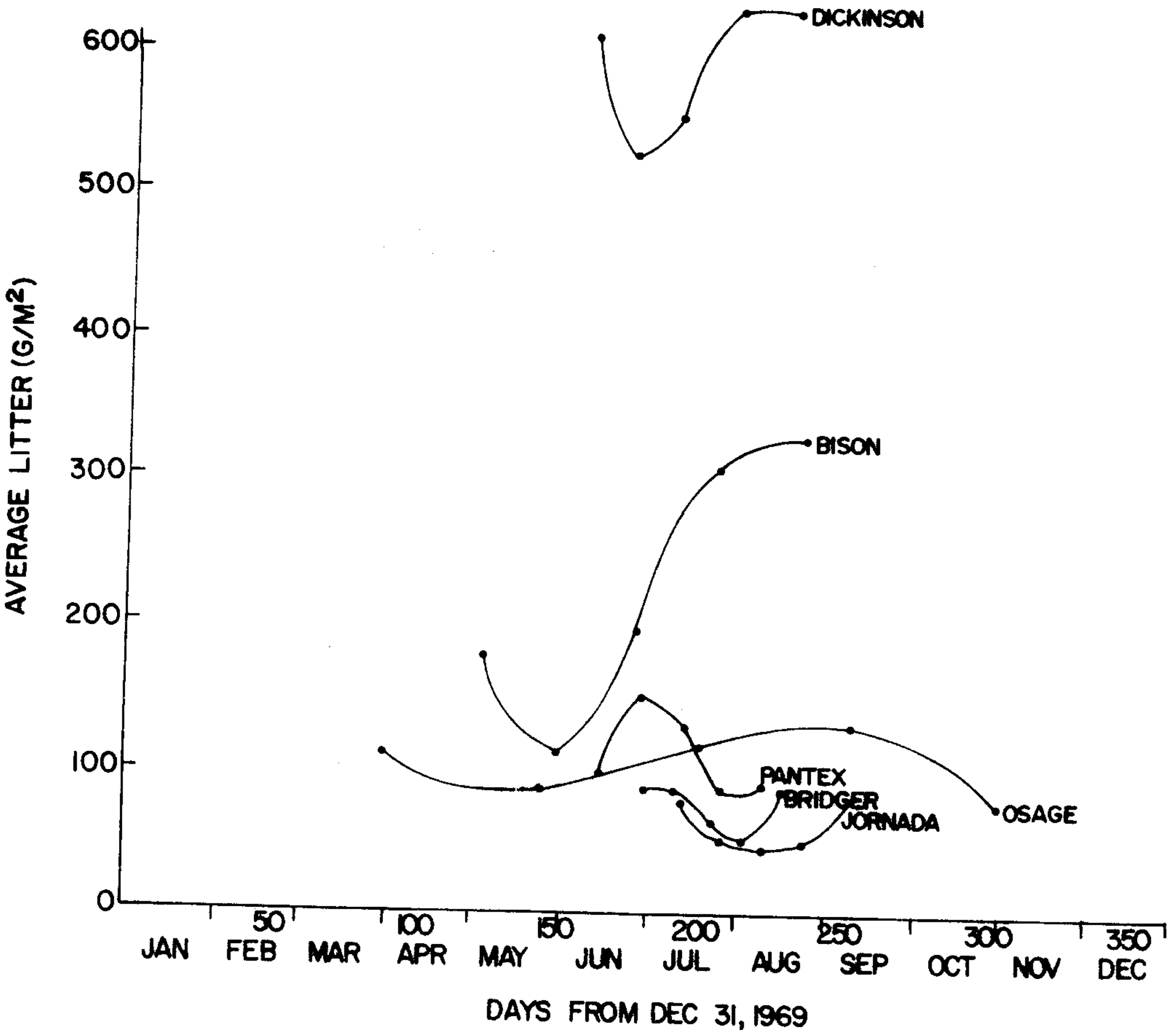

Fig. 7. Relationship between amount of litter and time of year.

the transfer of large amounts of standing dead to litter. In the early part of the growing season temperatures are warm, and humidity and surface soil water are high, causing the rate of decay to be higher than the rate of deposition. In the last part of the season the litter layer becomes dry, causing the decay rate to fall below the rate of deposition. The second drop in the curve for the Osage Site is probably due to a warm, rainy period in September and October. The unusual curve for Pantex may be caused by the abnormally dry year at that site in 1970.

If turnover rates are calculated according to Kucera, Dahlman, and Koelling (1967) there is a similarity between many sites in which the rate indicates about a 2-year duration (Table 2). The Pantex and Bridger Sites have relatively rapid rates, and the Dickinson Site is the slowest. However, it must be recalled that this index assumes seasonality since it is calculated from a maximum and minimum value. Especially in tallgrass prairies, litter deposition can occur throughout the year since there is a very large amount of standing dead. Furthermore, considerable litter deposition may occur when litter decomposition is at a maximum value. While this index may be useful in wide-scale comparisons, it does not detect compensations, for example, low biomass and low rate of decomposition, or high biomass and high rate of decomposition.

It seems apparent that the amount of litter found on any one grassland is a function of the input (standing dead) which ultimately depends on the amount of live material and the rate of decomposition. Only three sites made a measurement of decomposition rate during 1970, so no wide-scale comparisons can be made. The fact that high amounts of litter are usually associated with high amounts of aboveground biomass seems intuitively obvious. The

Table 2. Turnover rates for the litter components of nine prairie ecosystems.

Site	Turnover Rate (g/m^2/day)
Bison	0.63
Bridger	0.71
Cottonwood	0.51
Dickinson	0.34
Hays	0.62
Jornada	0.53
Osage	0.56
Pantex	0.80
Pawnee	0.51

apparent abnormality at the Osage Site may simply be that at this site both temperature and moisture are high which leads to relatively rapid decomposition.

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PHENOLOGY ON THE COMPREHENSIVE NETWORK SITES

by

John E. Williams

An analysis was attempted of the phenological or growth-stage data collected with the aboveground biomass during the 1970 growing season. Each species progresses through the various phenological categories during the growing season. Some species develop from early vegetation through bud stage, flowering stage, fruiting stage, and late vegetation to standing dead; but other species may not attain the flowering stages in a given year. The hypothesis was made that even though adverse environmental conditions may cause some species to omit some of the stages, especially flowering and fruiting stages during particularly dry years, the progression of the biomass from the earlier growth stages directly into standing dead material may enable the generation of a theoretical progression line for that species which, when averaged over several subsequent years, may produce a reasonable picture of the growth activity of each species within the community. Likewise, such a line could be generated for an entire community to give yet another picture of the overall rate at which the biomass progresses through the various growth stages.

For the progression lines each phenology category was given the numerical value of the code number by which it was recorded in the aboveground biomass data with the following exceptions: (i) last year's standing dead (code 17) was given a numerical value of 0; and (ii) this year's standing dead (code 19), winter dormant (code 18), and all regrowth categories (codes 14, 15, and 16) were all given a numerical value of 14. This latter was done with the assumption that not all species would exhibit regrowth, that those which did so this year may not do so every year, and that while some species may die while others become dormant, they do so at the same stage in their growth, i.e., following late vegetation. These numerical values are listed in Table 1.

These numerical values were then weighted according to the percent of the biomass of that species present in each phenology category on a given date, or simply:

$$\sum_{i=1}^{19} P_i \left(\frac{b_i}{\sum_{i=1}^{19} b_i} \right)$$

where

P_i = the numerical value of each phenology category

b_i = the biomass of a given species on a given date in the ith phenology category

Some results of these computations are shown in Fig. 1 through 4. In each figure the numerical values for the categories are equally spaced along the vertical axis. Note that such spacing does not assume a linear progression through the phenology categories at a constant rate for any of the species. That rate is instead determined from the slope of the line connecting the generated points and is not always constant through time. Julian dates for 1970 are represented on the horizontal axis.

Fig. 1 shows the progression line for *Andropogon scoparius*, an important dominant at the Osage and Hays Sites. On the Osage Site progression is fairly linear with a few anomalies, perhaps due to sampling error. The apparent plateaus in the lines at about category 6 (mid-bloom) should be

Table 1. Phenology categories and the numerical values used to compute the progression lines in Fig. 1 through 4 and also the general growth stages used in Fig. 5 through 8.

Category	Descriptive Title	Numerical Value	General Growth Stage
01	Germinated or sprouted	1	Early vegetation
02	Early vegetation	2	Early vegetation
03	Prebud	3	Bud stage
04	Bud stage	4	Bud stage
05	Early bloom	5	Flowering
06	Mid-bloom	6	Flowering
07	Full bloom	7	Flowering
08	Late bloom	8	Flowering
09	Milk stage	9	Fruiting
10	Dough stage	10	Fruiting
11	Ripe seed	11	Fruiting
12	Past ripe	12	Late vegetation
13	Stem cured	13	Late vegetation
14	Regrowth, vegetative	14	Regrowth
15	Regrowth, flowering	14	Regrowth
16	Regrowth, ripe seed	14	Regrowth
17	Standing dead, last year's	0	Dead
18	Winter dormant	14	Dormant
19	Standing dead, this year's	14	Dead

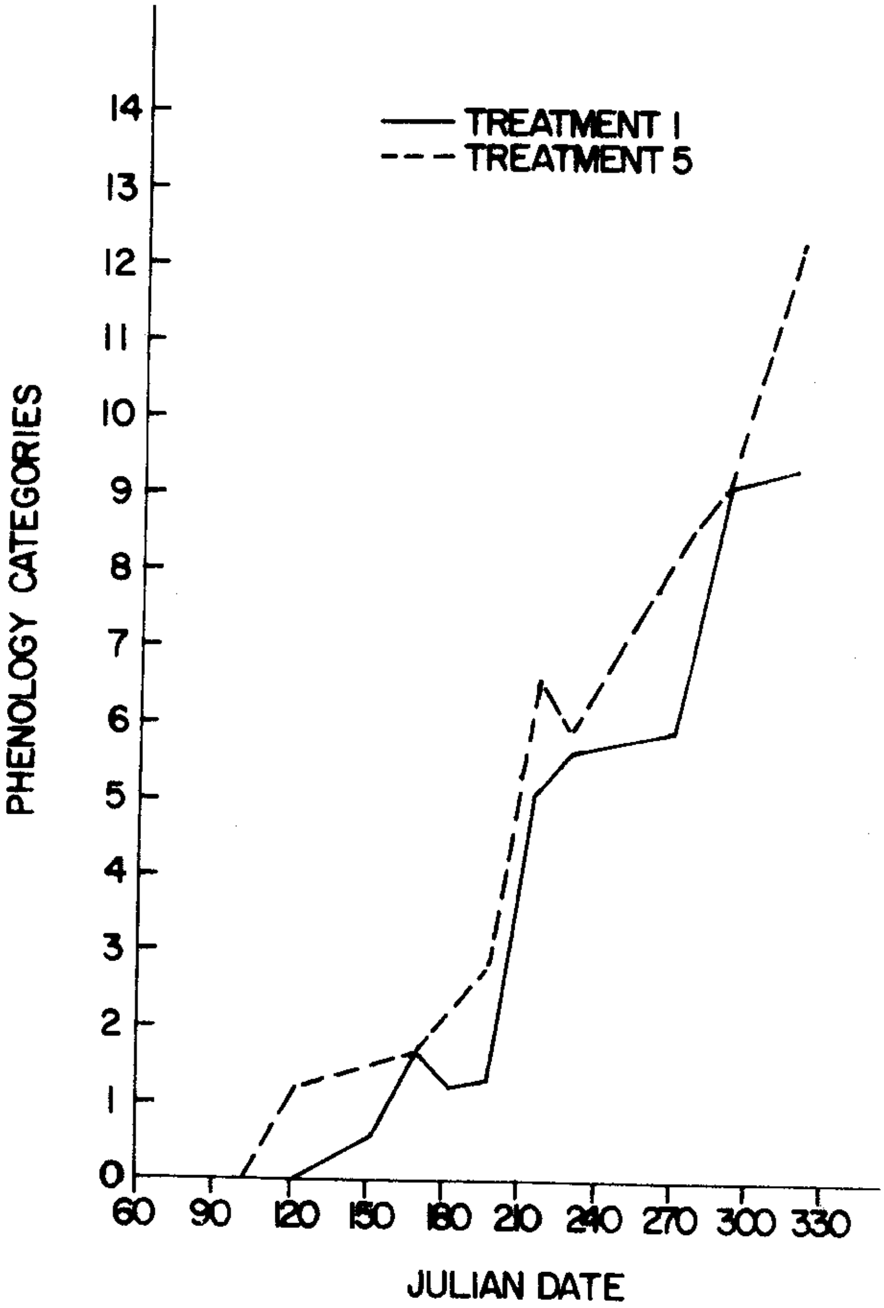

Fig. 1. Progression lines for *Andropogon scoparius* on the Osage Site for 1970. The vertical axis represents the numerical values for the phenology categories (see Table 1).

compared against the 1971 data since at no time was this species recorded as being in that condition (*see* discussion on Fig. 5 and 6 below). This species in Treatment 5 was phenologically advanced over Treatment 1 at any particular time, but the difference is accentuated in this graph because there was more standing dead on the ungrazed treatment (numerical value of 0), and this category has a low weighting term.

In Fig. 2 is the progression line for *Panicum virgatum* at the Osage Site. Note that the lines for the two treatments are strikingly parallel. In July and August pure and almost pure stands of *P. virgatum* in bud stage (category 4) were recorded, and during October almost two-thirds of the living material was in late vegetative stage.

Bouteloua curtipendula (Fig. 3) is shown because of its characteristic as an invader in this section of its range. It was expected that this species would exhibit a highly erratic progression line and that this progression might respond to different treatments depending on environmental conditions. However, as can be seen from the graph its progression is no more erratic than other species, at least as long as data were recorded on the Hays Site. Again, the lines for this species under the two treatments are strikingly parallel.

Fig. 4 shows a composite progression line of all species combined for the Osage Site. Apparent anomalies in the line are dependent upon anomalies exhibited by the dominant species; compare especially with *A. scoparius* for the Osage Site (Fig. 1). Again, the lines are fairly parallel with the line for Treatment 5 rising faster due to the relative absence of last year's standing dead.

Fig. 5 and 6 show the phenological composition of the biomass of *A. scoparius* at the Osage Site. It was upon this composition that the

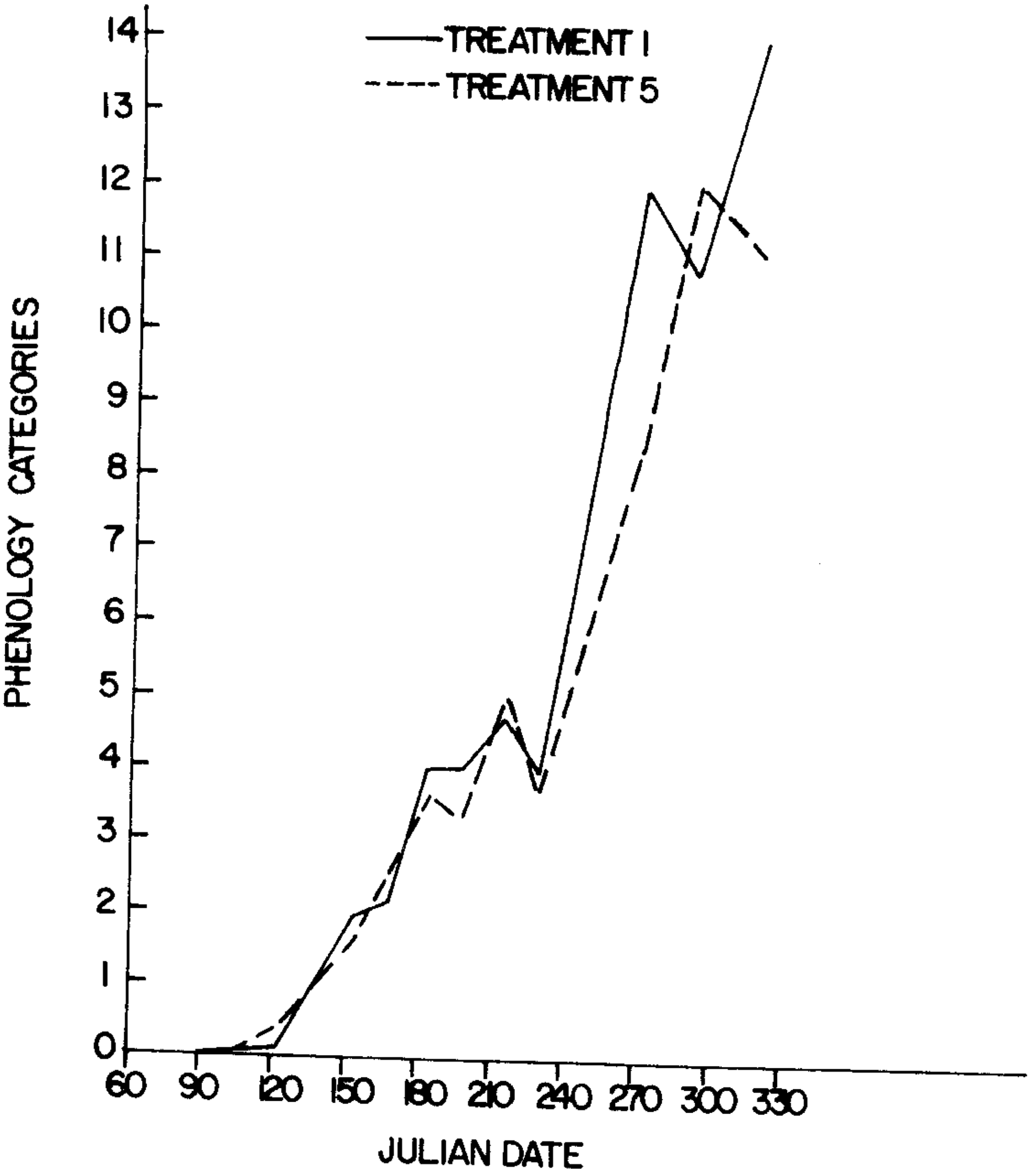

Fig. 2. Progression lines for *Panicum virgatum* on the Osage Site for 1970. The vertical axis represents the numerical values for the phenology categories (see Table I).

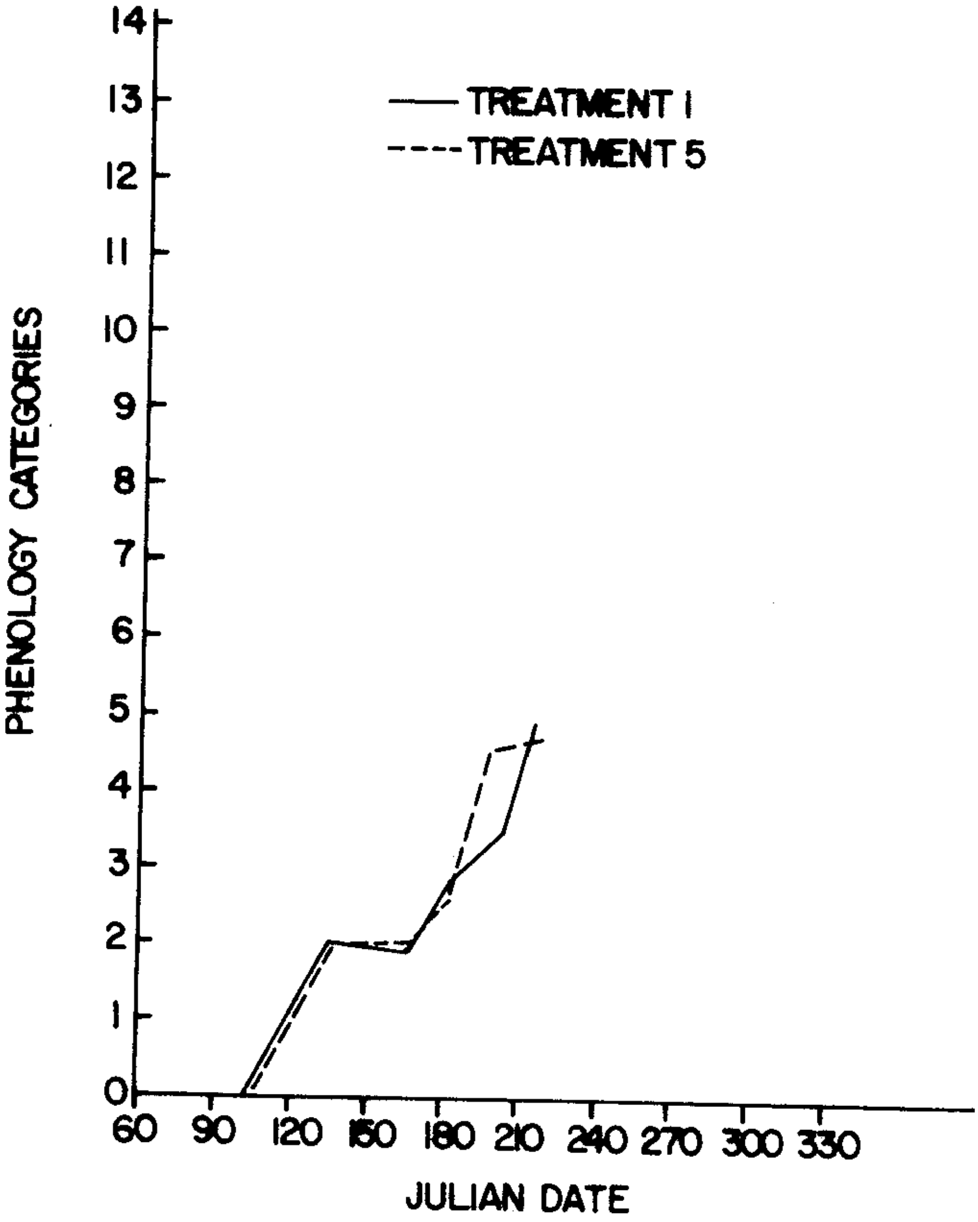

Fig. 3. Progression lines for *Bouteloua curtipendula* on the Hays Site for 1970. The vertical axis represents the numerical values for the phenology categories (see Table 1).

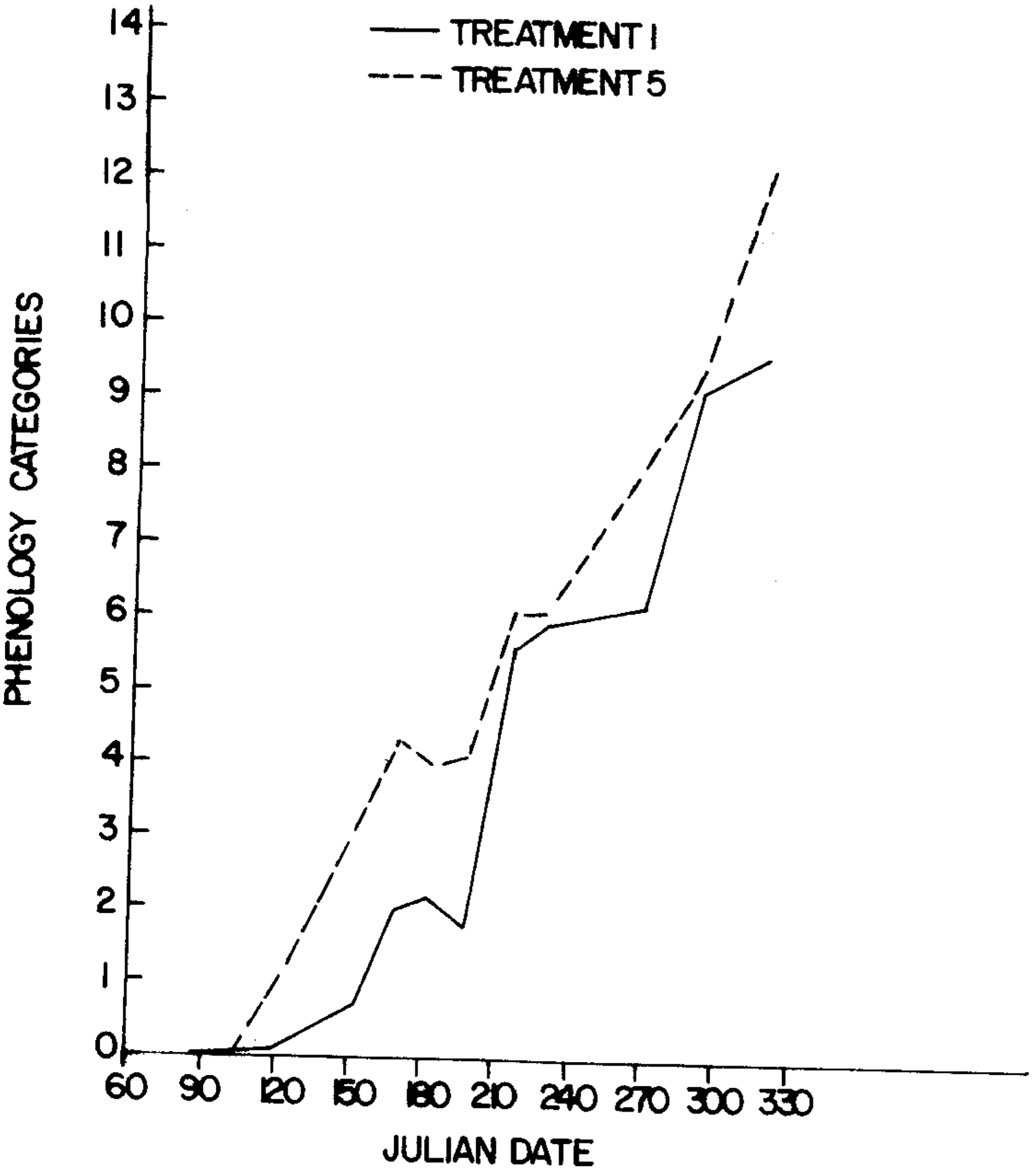

Fig. 4. Progression lines for all species on the Osage Site for 1970. The vertical axis represents the numerical values for the phenology categories (see Table 1).

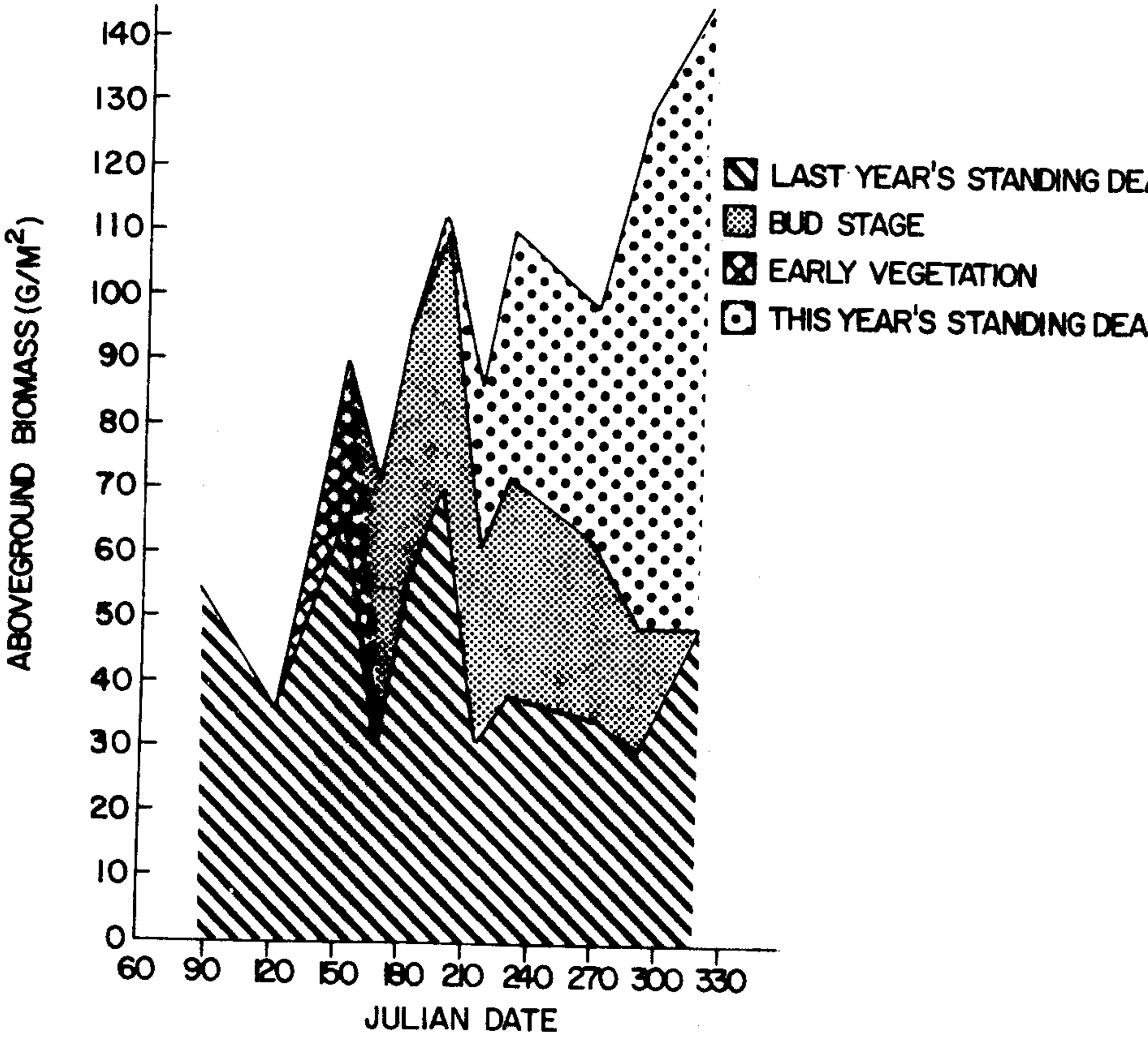

Fig. 5. Composition of the biomass of *Andropogon scoparius* at the Osage Site on Treatment 1. Both areas of standing dead are separated from the standing live by solid lines; standing live is further divided by dashed lines. For explanation of general growth stage groupings of the standing live material see Table 1 and discussion.

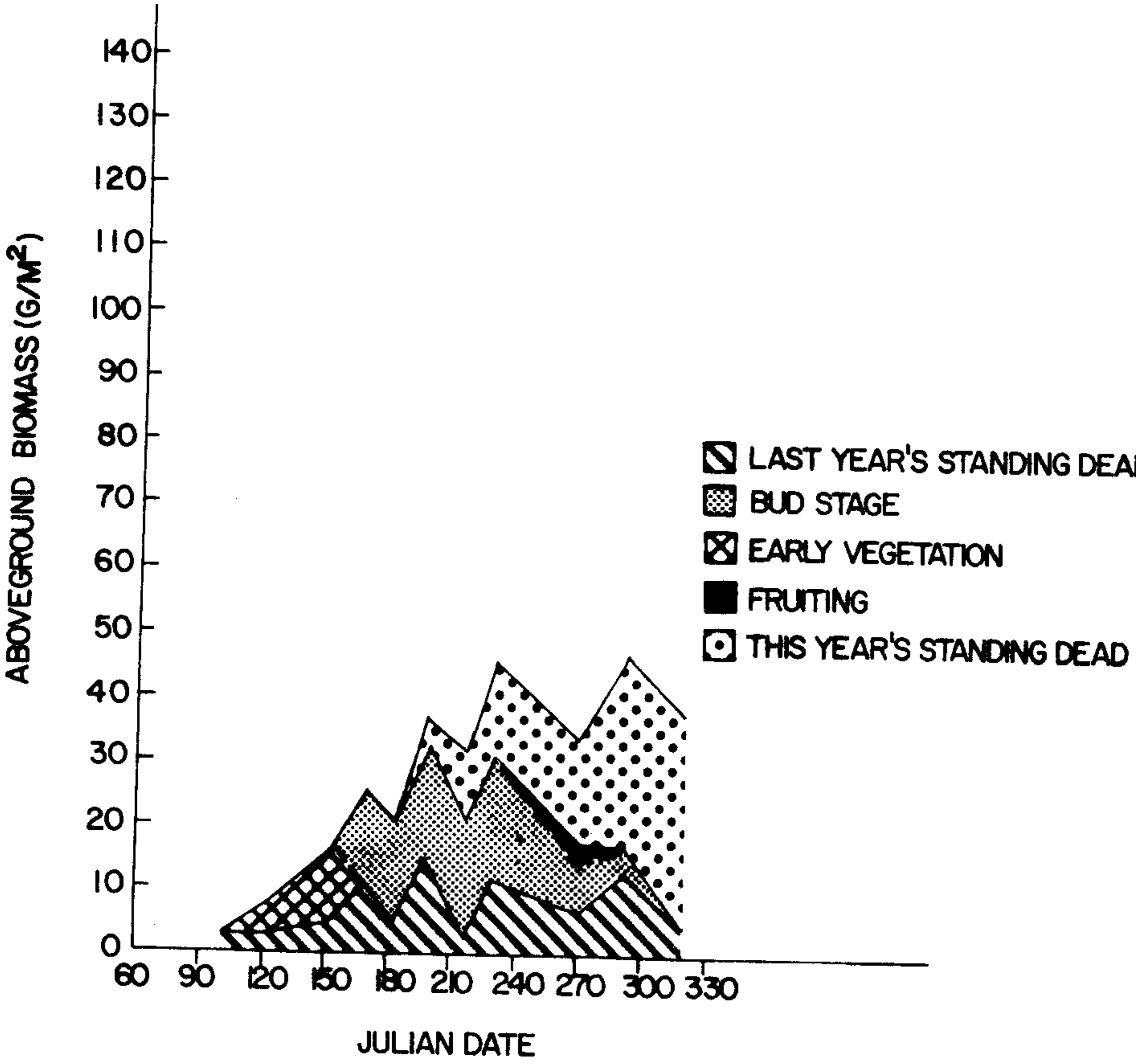

Fig. 6. Composition of the biomass for *Andropogon scoparius* at the Osage Site on Treatment 5. Both areas of standing dead are separated from the standing live by solid lines; standing live is further divided by dashed lines. For explanation of general growth stage groupings of the standing live material see Table 1 and discussion.

points for the progression line in Fig. 1 were computed. Aboveground biomass in grams per square meter is represented on the vertical axis while Julian date for 1970 is on the horizontal axis. The standing live material is divided into the various growth stages. For the sake of clarity in depiction the phenological categories for standing live have been grouped into general growth stages as indicated in Table 1.

In Fig. 5 it should be noted that for Treatment 1 at the Osage Site, standing live material of *A. scoparius* was entirely early vegetation and prebud (cateqories 2 and 3). The same is true for Treatment 5 (Fig. 6) with only a singe recording of category 11 (ripe seed). The virtual absence of flowering and fruiting material is due to an unusually low rainfall during the latter part of the growing season. The standing live material progresses from a budding stage into standing dead.

Fig. 7 and 8 show the phenological composition for the Osage Site, all species combined, with last year's standing dead on the bottom and this year's standing dead on top.

In Fig. 7 again note the paucity of flowering and fruiting material. What little there was, plus the late vegetative material, was due mostly to *P. virgatum*.

In Fig. 8 the relatively large amounts of flowering and fruiting in May and June is *Bromus japonicus*, whereas in September and October it is mostly *P. virgatum* and *Sporobolus asper*. The early vegetation in November is *Poa annua*, *B. japonicus*, and a sedge (*Carex* spp).

The question had been raised concerning the usefulness of some of the phenology categories. A survey was taken showing which of the categories were actually utilized at each site. These results are shown in Table 2.

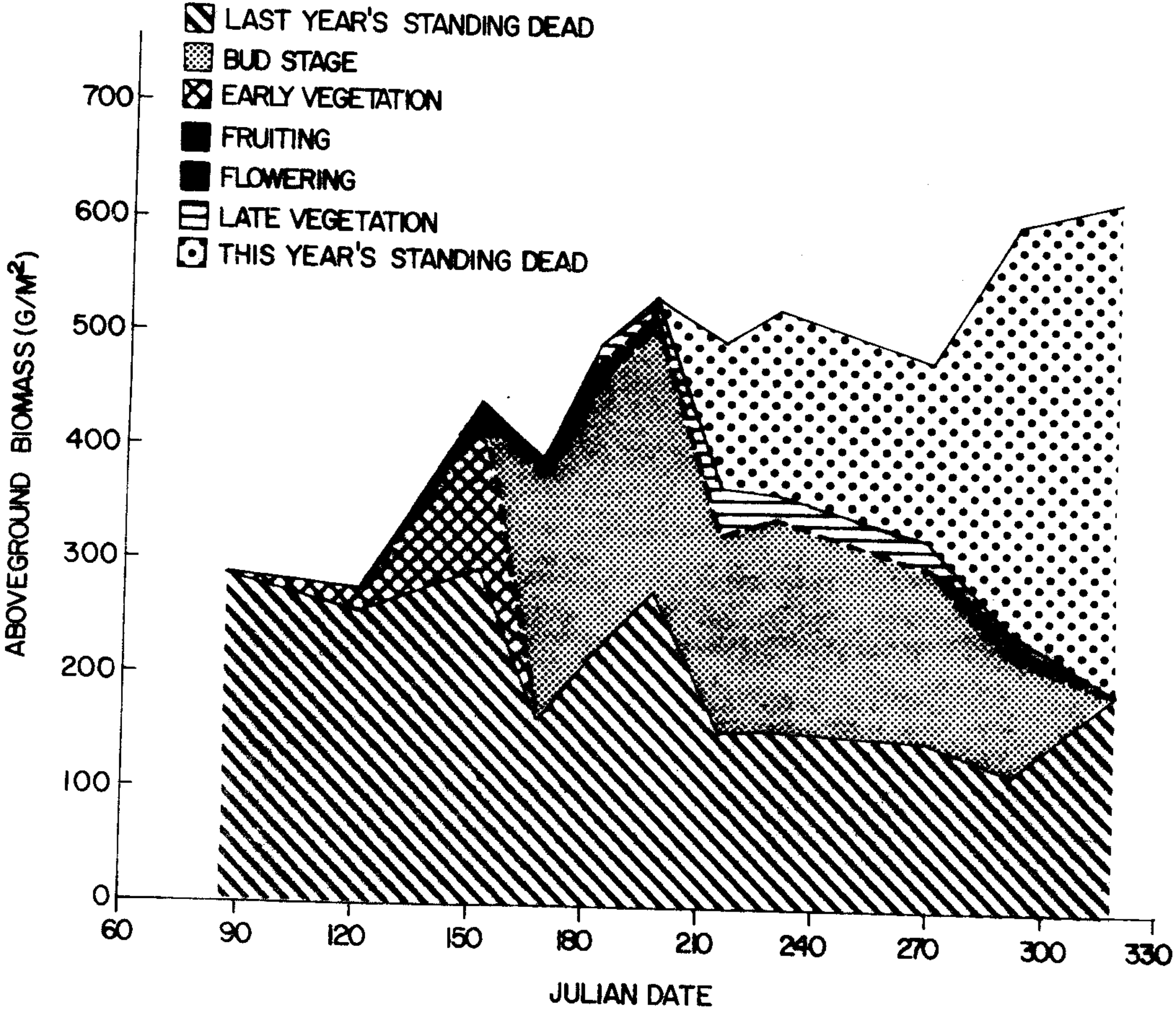

Fig. 7. Composition of the biomass for all species at the Osage Site on Treatment 1. Both areas of standing dead are separated from the standing live by solid lines; standing live is further divided by dashed lines. For explanation of general growth stage

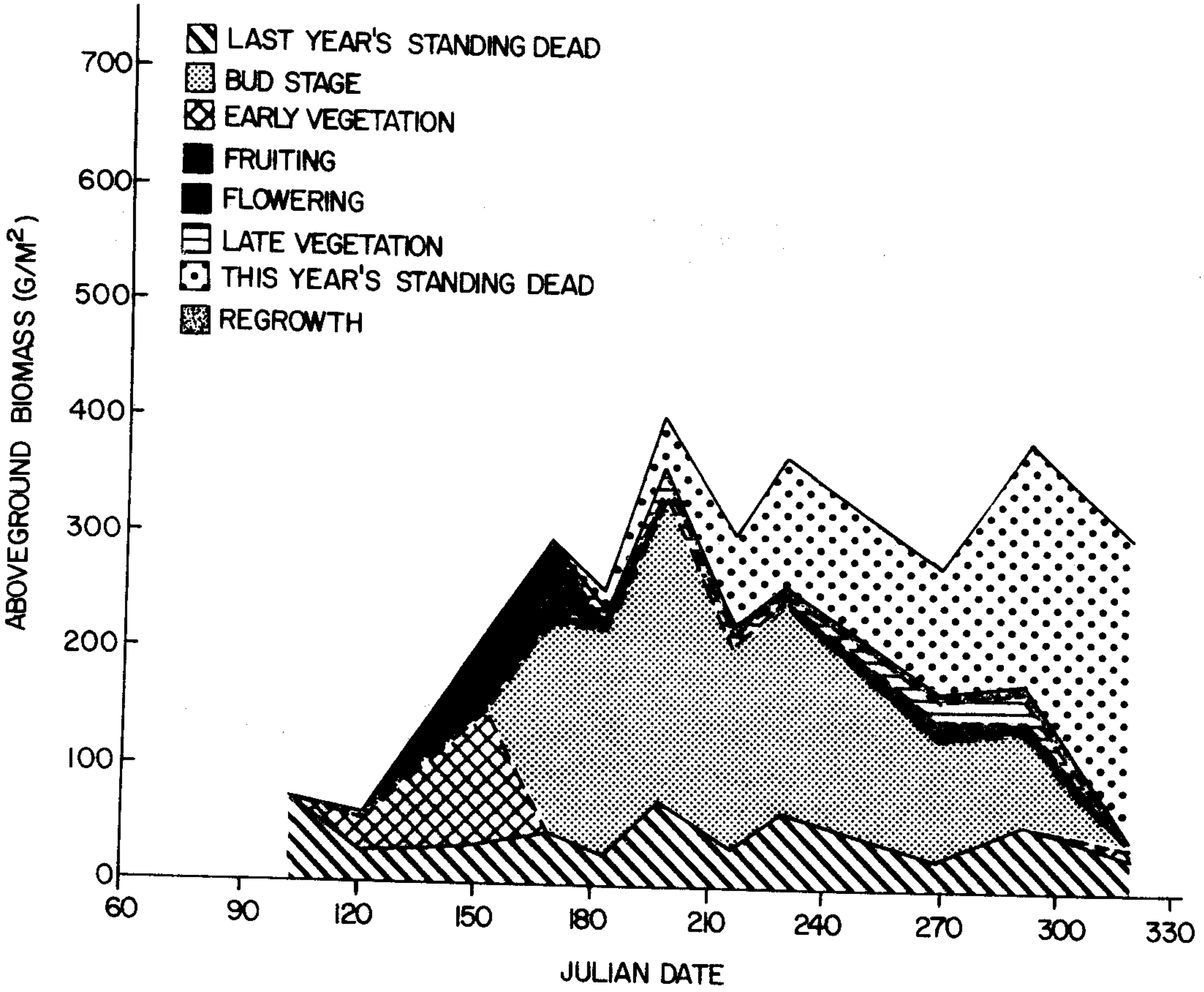

Fig. 8. Composition of the biomass for all species at the Osage Site on Treatment 5. Both areas standing dead are separated from the standing live by solid lines; standing live is further divided by dashed lines. For explanation of general growth stage groupings of the standing

Table 2. Utilization of phenology categories. X denotes usage.

Site	Phenology Category																		
	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Bison		X	X	X	X	X	X	X	X	X	X	X	X		X		X		X
Bridger			X					X				X			X		X		X
Dickinson		X	X	X	X	X	X	X	X	X	X	X	X		X		X		X
Hays	X	X	X	X	X	X	X	X	X	X	X	X	X		X		X	X	X
Jornada		X	X	X	X	X	X	X		X	X	X	X	X	X	X	X	X	
Osage		X	X	X	X	X	X	X		X	X	X	X	X	X		X		X
Pantex		X	X	X		X	X	X	X	X		X	X		X		X	X	X

As in all results herein presented, no attempt was made to reinterpret possible keypunch errors. Nor was any attempt made to determine frequency of use, nor the amount of the total biomass represented in each category.

In summary, an attempt was made to determine the rate of progression of the biomass through the various phenology or growth categories. It was decided that more than one year's data would be needed to determine a reliable rate since environmental factors affect the progression of live material from one stage into the next. Pending further data, it appears at this point that the progression rates through the pehnology categories for species and for entire sites may not differ significantly between treatments.

SPECIES ASSOCIATIONS ON THE COMPREHENSIVE NETWORK SITES

by

Linda S. Brown

Introduction

The purpose of this study was to compare species associations over the Comprehensive Network Sites by evaluation of index of association values for species pairs found at each of a number of the sites.

Method

Data for species association values were obtained from site summary data for the 1970 growing season. Species (Tables 1 through 7) were established for Bison, Bridger, Dickinson, Hays, Jornada, Osage, and Pantex Sites. A comparison of species association for the five sites was obtained after the computation of Cole's Index (Cole, 1949). Cole's Index measures interspecific association, the degree to which two species are found together more or less than expected on a random basis. This index utilizes a 2 × 2 table and presence or absence of data, and the resulting numerical value is a percentage of the maximum possible deviation between the expected joint occurrence and the minimum or maximum possible joint occurrence. These association values were tested statistically with a Chi-square test using two degrees of freedom.

Table 1. Species present at the Bison Site.

Species	Treatment 1										Treatment 2										
	05/02/70	05/15/70	05/30/70	06/17/70	07/02/70	07/16/70	08/04/70	08/24/70	09/26/70	TRT 1 Total	05/02/70	05/15/70	05/30/70	06/17/70	07/02/70	07/16/70	08/04/70	08/24/70	09/26/70	TRT 2 Total	Bison Total
ACMI2	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	18
AGGL										0					X					1	1
AGOSE	X	X		X	X	X	X			6	X	X		X	X	X	X			6	12
AGSP		X	X	X	X	X	X	X	X	8	X	X	X	X	X	X	X	X	X	9	17
ANMA			X							1										0	1
ANRO2	X					X		X		3	X	X	X		X		X	X		6	9
ARFR4										0	X									1	1
ARFU3	X	X	X	X	X	X	X			7	X	X	X	X	X	X				6	13
ASFA2						X				1					X	X	X	X	X	5	6
ASSP										0									X	1	1
BASA3					X		X			2										0	2
BRTE			X							1										0	1
CASU12				X	X	X	X			4	X		X	X	X	X	X			6	10
CHVI6										0						X				1	1
CRAC2										0	X		X							2	2
DOCO	X									1										0	1
ERIOG	X									1			X	X						2	3
FEID	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	18
FESC	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	18
FRPU2	X									1	X									1	2
GETR	X	X	X	X	X	X	X			7										0	7
HECY2	X									1										0	1
HIAL		X	X		X	X	X			5	X	X								2	7

Table 1. Continued.

Species	Treatment 1										Treatment 2										
	05/02/70	05/15/70	05/30/70	06/17/70	07/02/70	07/16/70	08/04/70	08/24/70	09/26/70	TRT 1 Total	05/02/70	05/15/70	05/30/70	06/17/70	07/02/70	07/16/70	08/04/70	08/24/70	09/26/70	TRT 2 Total	Bison Total
KOCR										0	X	X	X							3	3
LAPU										0							X			1	1
LIPA								X		1										0	1
LIRU4	X	X	X		X	X	X	X		7										0	7
LULA3							X			1										0	1
LUSE4		X	X	X	X	X	X	X		7	X	X	X	X	X	X	X			7	14
MINU			X							1			X							1	2
POPR	X	X								2	X	X				X	X			4	6
SARH2	X									1										0	1
TRDU										0					X		X	X		3	3
ZYPA	X	X	X	X	X	X	X			7	X	X	X	X	X	X	X	X		8	15
GACO5										0							X			1	1
MISC	X	X		X	X	X	X	X	X	8	X	X		X	X	X	X	X	X	8	16
MISC1	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	18
MISC2			X	X	X	X	X	X	X	7	X	X	X	X	X	X	X	X	X	9	16
MISC3						X	X			2						X	X			2	4
MISCA-2				X						1				X						1	2
No. of species	15	12	13	10	13	14	15	8	4	26	16	12	13	10	13	12	14	8	6	25	35
No. of items	17	14	15	14	16	18	19	11	7	31	19	15	15	14	16	16	18	11	9	30	40

Table 2. Species present at the Bridger Site.

Species	Treatment 1							Treatment 3							
	06/30/70	07/08/70	07/21/70	08/03/70	08/17/70	08/31/70	TRT 1 Total	06/29/70	07/08/70	07/20/70	08/03/70	08/17/70	08/31/70	TRT 3 Total	Bridger Total
ACMI2	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
AGGL	X	X	X	X		X	5	X		X	X		X	4	9
AGGR				X	X		2		X			X		2	4
AGSU	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
ARCO5	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
CAREX							0						X	1	1
CEAR4		X	X	X			3		X	X	X			3	6
DAIN	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
ERSP4	X	X	X	X			4	X		X	X			3	7
FEID	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
GABO2				X	X		2				X	X		2	4
KOCR	X	X	X	X			4	X	X	X	X			4	8
LUAR3	X	X	X	X	X	X	6	X	X	X	X	X		5	11
MIFB	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
STRI2					X	X	2					X	X	2	4
LITR							0	X						1	1
MIGR	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
STDEA	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
No. of species	10	11	11	13	10	9	14	10	10	11	12	10	9	15	15
No. of items	12	13	13	15	12	11	16	13	12	13	14	12	11	18	18

Table 3. Species present at the Dickinson Site.

Species	Treatment 1							Treatment 4							
	06/10/70	06/24/70	07/07/70	07/27/70	08/18/70	09/17/70	TRT 1 Total	06/11/70	06/24/70	07/08/70	07/28/70	08/18/70	09/17/70	TRT 4 Total	Dickinson Total
AGSM	X		X	X	X	X	5	X	X	X	X	X	X	6	11
AGSM		X					1							0	1
AGTR		X			X	X	3							0	3
ALTE	X	X	X	X			4							0	4
APSP							0					X	X	2	2
ARLU	X	X	X	X	X	X	6			X	X	X	X	4	10
ASADR		X					1							0	1
ASER3	X	X	X		X	X	5	X	X	X	X	X		5	10
BOGR2	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
CAEL2	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
CAFI					X		1	X				X		2	3
CALO	X	X	X	X	X	X	6							0	6
CAMO			X	X			2	X	X	X	X	X	X	6	8
CAPE6							0	X						1	1
CHLE4			X	X	X		3							0	3
CHVI6							0				X	X		2	2
CIVU				X			1							0	1
CIUN		X					1							0	1
COCA5					X		1							0	1
COLI2	X	X	X	X	X		5							0	5
EAFO							0					X		1	1
EAFO							0		X	X	X	X	X	5	5
EAFO	X						1	X	X	X	X			4	5
ECPAA			X				1							0	1
EPFO	X						1	X	X				X	3	4
FEID							0		X					1	1
GACO5		X	X	X	X	X	5					X		1	6
KOCR		X					1	X	X	X	X	X	X	6	7
LAFO	X						1	X	X	X			X	4	5
LAFO							0			X	X	X	X	4	4
LAPU		X					1							0	1
LASE		X	X	X	X	X	5							0	5
LIPU					X	X	2		X		X	X	X	4	6

Table 3. Continued.

Species	Treatment 1							Treatment 4							Dickinson Total
	06/10/70	06/24/70	07/07/70	07/27/70	08/18/70	09/17/70	TRT 1 Total	06/11/70	06/24/70	07/08/70	07/28/70	08/18/70	09/17/70	TRT 4 Total	
LOPU3		X	X	X	X	X	5							0	5
LOFO							0					X		1	1
LYJU			X	X			2			X	X			2	4
MAVI3			X				1							0	1
OENU	X			X	X	X	4							0	4
OXLA3							0				X			1	1
PEPU6							0						X	1	1
POCO13					X		1							0	1
POSE							0	X		X	X	X		4	4
PSAR2			X				1			X		X		2	3
ROAR3			X	X	X		3							0	3
SEDE2		X	X		X	X	4	X	X	X	X	X	X	6	10
SOMI2						X	1							0	1
SOMO					X		1				X	X		2	3
SPCO		X	X	X	X	X	5			X	X	X	X	4	9
STCO4	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
TAOF					X		1							0	1
TRDU	X	X	X	X	X	X	6					X		1	7
VINU2	X	X	X				3							0	3
PHHO							0					X		1	1
STDEA	X	X	X	X	X	X	6	X	X	X	X	X	X	6	12
No. of species	15	21	23	19	24	17	41	15	14	17	19	24	16	32	53
No. of items	16	22	24	20	25	18	42	16	15	18	20	25	17	33	54

Table 4. Species present at the Hays Site.

Species	Treatment 1										Treatment 5										
	01/16/70	02/15/70	03/24/70	04/15/70	05/15/70	06/16/70	07/01/70	07/21/70	08/04/70	TRT 1 Total	01/16/70	02/16/70	03/15/70	04/16/70	05/15/70	06/15/70	07/02/70	07/16/70	08/03/70	TRT 5 Total	Hays Total
AGSM										0				X	X	X	X	X	X	6	6
AMCH6				X	X	X	X	X	X	6							X			1	7
AMPS					X	X	X	X	X	5			X	X	X	X	X	X	X	7	12
AMSA							X			1										0	1
ANGE	X	X	X	X	X	X	X	X	X	9		X		X	X	X	X	X	X	7	16
ANSC2	X	X	X	X	X	X	X	X	X	9			X				X			2	11
ARLO3				X	X					2	X	X	X	X	X	X	X	X	X	9	11
ARPU9						X				1										0	1
ASAR				X	X					2					X	X		X	X	4	6
ASFE					X					1										0	1
ASMO7							X			1										0	1
ASER3					X	X	X	X	X	5				X	X	X	X	X	X	6	11
ASOB2				X	X	X	X	X	X	6						X		X		2	8
ASPU										0						X		X		2	2
ASVI					X				X	2									X	1	3
BOCU	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	18
BOGR2	X	X		X	X			X		5	X	X	X	X	X	X	X	X	X	9	14
BOHI2										0								X	X	2	2
BRJA										0			X	X	X	X	X	X	X	7	7
BUDA										0	X				X	X	X	X	X	6	6
CAGR4										0			X							1	1
CAIN2										0							X			1	1
CAREX										0							X	X		2	2

Table 4. Continued.

Species	Treatment 1										Treatment 5										
	01/16/70	02/15/70	03/24/70	04/15/70	05/15/70	06/16/70	07/01/70	07/21/70	08/04/70	TRT 1 Total	01/16/70	02/16/70	03/15/70	04/16/70	05/15/70	06/15/70	07/02/70	07/16/70	08/03/70	TRT 5 Total	Hays Total
CHVI6					X					1								X		1	2
CIOC2										0									X	1	1
CIUN			X	X	X	X	X	X	X	7				X		X		X	X	4	11
ECPAA			X	X	X	X	X	X	X	7					X	X	X	X	X	5	12
ERRA3										0						X	X	X	X	4	4
EUMA7										0					X		X	X	X	4	4
EVPI								X		1						X				1	2
GACO5					X	X	X			3						X	X		X	3	6
GRSQ										0					X	X	X	X	X	5	5
GUSA2										0		X			X	X	X	X	X	6	6
HEAN3										0								X	X	2	2
HEHI										0						X				1	1
HOAN			X		X	X	X	X	X	6										0	6
HOPU										0						X				1	1
KUGL										0									X	1	1
LEPY										0									X	1	1
LEER										0								X		1	1
LIPU				X	X		X			3						X	X			2	5
LYJU										0							X			1	1
SPCO							X			1						X		X		2	3
MEAL2								X	X	2										0	2
MEOF						X	X			2										0	2

Table 4. Continued.

Species	Treatment 1										Treatment 5										
	01/16/70	02/15/70	03/24/70	04/15/70	05/15/70	06/16/70	07/01/70	07/21/70	08/04/70	TRT 1 Total	01/16/70	02/16/70	03/15/70	04/16/70	05/15/70	06/15/70	07/02/70	07/16/70	08/03/70	TRT 5 Total	Hays Total
MOUN			X	X	X					3										0	3
OEFR2									X	1										0	1
OESE		X	X	X	X	X	X	X	X	8					X	X	X		X	4	12
ONMOO										0							X			1	1
OXST										0									X	1	1
PAJA						X	X		X	3										0	3
PAVI2	X	X	X	X	X	X	X	X	X	9			X				X			2	11
PEPU6						X	X			2										0	2
POAL4										0									X	1	1
PSCU										0					X					1	1
PSES					X					1										0	1
PSTE3					X	X	X	X	X	5					X	X	X	X	X	5	10
RACO3										0				X	X	X	X	X	X	6	6
RHGL										0									X	1	1
SCRE				X	X	X	X	X	X	6					X	X			X	3	9
SCUN					X	X	X	X	X	5						X				1	6
SEPL						X	X			2							X	X	X	3	5
SIHY										0					X		X			2	2
SISP3										0								X		1	1
SOMI2				X	X	X	X	X	X	6						X	X	X	X	4	10
SOMO					X	X				2				X		X	X	X	X	5	7
SONU2		X	X	X	X	X	X	X	X	8							X			1	9

Table 4. Continued.

Species	Treatment 1										Treatment 5										
	01/16/70	02/15/70	03/24/70	04/15/70	05/15/70	06/16/70	07/01/70	07/21/70	08/04/70	TRT 1 Total	01/16/70	02/16/70	03/15/70	04/16/70	05/15/70	06/15/70	07/02/70	07/16/70	08/03/70	TRT 5 Total	Hays Total
SORI2	X			X	X	X	X	X	X	7				X	X					2	9
SPAS						X				1		X								1	2
SPCR										0						X			X	2	2
SPPI					X	X	X	X	X	5										0	5
STLI2					X	X	X	X	X	5										0	5
TEST2			X		X	X	X			4										0	4
THME					X	X	X	X	X	5					X	X	X	X	X	5	10
TRRA							X		X	2										0	2
VEBI										0						X		X		2	2
VEST										0							X	X	X	3	3
YUGL							X			1							X			1	2
No. of species and No. of items	6	7	11	18	33	30	33	24	26	47	4	6	8	12	21	34	34	33	36	62	78

Table 5. Species present at the Jornada Site.

	Treatment 1						Treatment 5						
Species	07/14/70	07/30/70	08/10/70	08/20/70	09/01/70	TRT 1 Total	07/15/70	07/31/70	08/11/70	08/21/70	09/02/70	TRT 5 Total	Jornada Total
ALIN		X	X		X	3		X	X	X	X	4	7
AMAR2						0			X			1	1
HAGR5						0			X			1	1
APRA	X	X	X			3	X	X	X	X	X	5	8
APSP						0		X	X	X	X	4	4
ARLO3		X	X	X	X	4	X				X	2	6
MATA2			X			1	X					1	2
BAAB						0		X				1	1
BOER4	X	X	X	X	X	5	X	X	X	X	X	5	10
BOTO				X	X	2				X	X	2	4
CABA6	X	X	X	X	X	5	X	X	X	X	X	5	10
CHIN2	X	X	X	X	X	5	X	X	X	X	X	5	10
COCR			X			1						0	1
CONI3			X	X	X	3			X	X	X	3	6
CRCO11		X	X	X	X	4	X	X	X	X	X	5	9
CRCR3	X	X	X	X		4	X	X	X			3	7
DIWI	X	X	X	X		4	X		X	X		3	7
EPTR	X				X	2						0	2
ERAB2	X	X	X	X	X	5	X	X	X	X	X	5	10
ERIOG			X			1						0	1
ERPU2	X	X	X	X	X	5	X	X	X	X	X	5	10
EUAL4				X		1		X		X		2	3
EVAL						0			X			1	1
GUSA2	X	X	X	X	X	5	X	X	X	X	X	5	10
GUSP					X	1		X	X			2	3
HELIA3		X		X	X	3			X			1	4
HODE			X		X	2				X	X	2	4
HOJA						0			X			1	1
KAHI			X	X	X	3			X	X	X	3	6
KRLA						0		X				1	1
LEFE						0	X		X			2	2
LIARA		X				1				X		1	2
MUPO2					X	1						0	1

Table 5. Continued.

Species	Treatment 1						Treatment 5						Jornada Total
	07/14/70	07/30/70	08/10/70	08/20/70	09/01/70	TRT 1 Total	07/15/70	07/31/70	08/11/70	08/21/70	09/02/70	TRT 5 Total	
NAHI	X	X	X			3	X	X	X			3	6
PAHI5				X	X	2					X	1	3
PORTU			X	X	X	3			X	X	X	3	6
PRJU			X	X		2		X				1	3
PSTA	X				X	2						0	2
SAKA	X	X	X	X	X	5	X	X	X	X	X	5	10
SEPL		X			X	2						0	2
SOEL		X		X	X	3		X	X	X		3	6
SPFL2	X		X	X		3	X	X	X	X	X	5	8
SPCO				X		1						0	1
KRLA						0	X	X	X			3	3
SPSU					X	1						0	1
STEX		X				1						0	1
TILA2				X	X	2				X	X	2	2
TRTE			X			1			X			1	2
YUEL	X	X	X	X	X	5	X		X		X	3	8
ZIGR				X	X	2	X		X			2	4
MISC						0				X	X	2	2
MISC2			X			1			X			1	2
MISC4			X	X	X	3			X	X	X	3	6
MISC5				X		1				X		1	2
No. of species	15	20	24	25	27	41	19	22	30	22	21	41	50
No. of items	15	20	26	27	28	44	19	22	32	25	23	45	54

Table 6. Species present at the Osage Site.

Species	Treatment 1												Treatment 5												
	03/27/70	05/01/70	06/01/70	06/17/70	06/18/70	07/01/70	07/16/70	08/03/70	08/17/70	09/26/70	11/14/70	TRT 1 Total	04/01/70	05/12/70	06/02/70	06/18/70	07/02/70	07/16/70	08/04/70	08/17/70	09/26/70	10/18/70	11/14/70	TRT 5 Total	Osage Total
AMCO												0		X										1	1
AMPS				X			X	X				3		X	X	X	X	X	X	X	X	X	X	10	13
ANGE	X	X	X	X	X	X					X	7			X	X		X	X		X		X	6	13
ANSC2	X	X	X	X	X	X	X	X	X	X	X	11	X	X	X	X	X	X	X	X	X	X	X	11	22
BRJA				X	X	X	X	X	X	X	X	8			X	X	X	X	X	X	X	X	X	9	17
BRTE												0		X										1	1
PAVI2	X	X	X	X	X	X	X	X	X	X	X	11	X	X	X	X	X	X	X	X	X	X	X	11	22
POAN												0			X									1	1
POPR					X			X		X		3		X		X	X	X	X	X	X	X		8	11
CAREX												0								X				1	1
SONU2	X	X	X	X	X	X	X	X	X	X	X	11	X	X	X	X	X	X	X	X	X	X	X	11	22
SPAS	X	X			X	X	X	X	X	X	X	9	X	X			X	X	X	X	X	X	X	9	18
FORB	X	X	X			X		X	X			6	X	X	X	X	X			X				6	12
FORB A				X	X	X	X	X	X	X	X	8				X	X	X	X	X	X	X	X	8	16
FORB B				X		X		X		X		4					X	X		X		X		4	8
FORB C				X	X	X	X	X	X	X	X	8					X	X		X	X	X	X	6	14
FORB D				X					X	X		3				X					X			2	5
FORB E					X							1									X	X		2	3
FORB F										X		1									X			1	2
MISC	X	X	X		X	X		X	X		X	8	X	X	X			X	X	X	X			7	15
MISC A			X	X	X	X	X	X	X	X		8			X	X	X	X	X	X	X	X	X	9	17
MISC B			X	X	X	X	X	X	X	X		8			X	X	X	X	X	X		X	X	8	16
MISC C			X	X	X					X		4									X	X		2	6
MISC D					X					X		2				X					X	X		3	5
MISC E												0										X		1	1
MISC F					X							1												0	1
MISC G					X							1										X		1	2
SEDG		X	X	X								3		X	X	X			X					4	7
SEDG A					X	X	X	X	X	X	X	7					X	X	X	X	X	X	X	7	14
SEDG B								X	X		X	3					X	X	X	X	X	X	X	7	10
SEDG C												0									X	X	X	3	3
No. of species	5	5	4	6	7	6	6	7	5	6	6	8	4	8	7	7	7	8	8	8	8	7	7	12	12
No. of items	7	8	10	14	18	14	11	16	14	16	11	25	6	11	12	14	15	16	15	17	19	21	14	30	31

Table 7. Species present at the Pantex Site.

Species	Treatment 1										Treatment 3										Treatment 5										
	06/15/70	06/29/70	07/13/70	07/27/70	08/10/70	08/24/70	09/05/70	10/02/70	10/31/70	TRT 1 Total	06/15/70	06/29/70	07/13/70	07/27/70	08/10/70	08/24/70	09/05/70	10/02/70	10/31/70	TRT 3 Total	06/15/70	06/29/70	07/13/70	07/27/70	08/10/70	08/24/70	09/05/70	10/02/70	10/31/70	TRT 5 Total	Pantex Total
BOGR2		X	X	X	X	X	X	X	X	8		X	X	X	X	X	X	X	X	8		X	X	X	X	X	X	X	X	8	24
BOBUM	X									1	X									1	X									1	3
BUDA		X	X	X	X		X			5		X	X	X	X	X	X	X	X	8		X	X	X	X	X	X	X	X	8	21
HOPU	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	27
LEPID	X	X	X	X	X	X	X	X	X	9	X		X	X	X	X	X	X	X	8	X		X	X	X	X	X	X	X	8	25
LEDE										0		X								1		X								1	2
MAMMI										0									X	1			X		X					2	3
OPUNT	X	X	X	X	X		X	X	X	8	X	X	X	X	X	X	X	X	X	9	X	X	X	X	X	X	X	X	X	9	26
PLPAG		X	X	X				X		4		X		X						2	X								X	2	8
RATIB			X							1										0	X	X	X			X	X			5	6
SPCO				X						1	X		X	X	X				X	5	X	X	X	X		X				5	11
FORB			X					X	X	3	X	X		X				X		4										0	7
FORB1	X	X			X	X	X			5		X		X	X	X	X			5	X			X		X				3	13
FORB2	X	X								2		X			X					2	X	X								2	6
FORB3		X								1		X								1	X	X								2	4
No. of species	4	6	7	7	5	3	5	5	4	9	5	6	6	7	6	5	5	5	7	10	6	8	8	6	6	7	6	5	6	11	11
No. of items	6	9	8	7	6	4	6	6	5	13	6	10	6	9	8	6	6	6	7	14	9	10	8	7	6	8	6	5	6	14	15

Results

The intrasite species associations are shown in Tables 8 through 12. A comparison of the number of interspecific associations between sites is shown in Table 13.

Discussion

Separation of plants into the classes of species and miscellaneous groups varied considerably with the individual site. The two largest values for number of significant associations per site were at the sites where the largest number of species were separated. This means that in sites that did not consistently aggregate species into miscellaneous classes there are large differences in the indicated number of species, when the actual species number might be the same for several sites. This data recording makes any comparison between sites relatively meaningless since the biological influences of species association operate whether the individuals numbered are named taxonomically or not.

One limitation of the use of Cole's Index is the stipulation that any species always present or always absent from all the sample plots are often excluded from calculations of Cole's Index, even though they may in reality be associated with some other species.

In conclusion, the results of this study show that many species are associated at the intrasite level, but the results are affected by the species-separation techniques utilized at each network site.

Literature Cited

Cole, L. C. 1949. The measurement of interspecific association. Ecology 30:411-424.

Table 8. Significant interspecific associations at the Bison Site.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	No. +	No. -	Total
ACMI2																																				0	0	0
AGGL																																	++			1	0	1
AGOSE								+++					++																+	-	+			+++		5	1	6
AGSP																---						---				---						---				0	4	4
ANMA												+++																		+++						2	0	2
ANRO2																																				0	0	0
ARFR4															+++					+++				++												3	0	3
ARFU3			+++																		+		+						++					+++		5	0	5
ASFA2																																	+++			1	0	1
ASSP																																		--		0	1	1
BASA3																												+++								2	0	2
BRT					+++																									+++						2	0	2
CASU12			++																										++					+		3	0	3
CHVI6																																				1	0	1
CRAC2							+++																	+++												2	0	2
DOCO				---													++			+++		+++										+++				4	1	5
ERIOG																++						++										++				3	0	3
FEID																																				0	0	0
FESC																																				0	0	0
FRPU2							+++									+++						+++									+	+++				5	0	5
GETR								+															++				++									3	0	3
HECY2				---												+++	++			+++												+++				4	1	5
HIAL								+													++						+									3	0	3
KOCR							++								+++																					2	0	2
LAPU																																	++		+++	3	0	3
LIPA				---																														-		1	2	3
LIRU4																					+++		+													2	0	2
LULA3											+++																									2	0	2
LUSE4			+					++					++																					+		4	0	4
MINU			-		+++							+++																								2	1	3
POPR			+																	+																2	0	2
SARH2				---												+++	++			+++		+++														4	1	5
TRDU		++							+++																++										++	6	0	6
ZYPA			+++					+++		--			+																+							4	2	6
GACO5																									+++								++			3	0	3
TOTAL																																				84	14	98

Table 9. Significant interspecific associations at the Bridger Site.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	No. +	No. -	Total
ACMI2																0	0	0
AGGL			---						++							1	1	2
AGGR		---									+					1	1	2
AGSU																0	0	0
ARCO5																0	0	0
CAREX													---			0	1	1
CEAR4												++			--	1	1	2
DAIN																0	0	0
ERSP4		++										+++			---	2	1	3
FEID																0	0	0
GABO2			+													1		1
KOCR							++		+++						---	2	1	3
LUAR3						---										0	1	1
MIFB																0	0	0
STRI2							--		---			---				0	3	3
TOTAL																8	10	18

Table 10. Significant interspecific associations at the Dickinson Site.

Species	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30
AGSM				---				---										---												
AGTR												+	---														+			
ALTE												++							+++			-								
AGSM	---							+++										+++												
APSP																				++										+
ARLU														--							-					--				
ASER3																	--													
ASADR	---			+++														+++												
BOGR2																														
CAEL2																														
CAFI																														
CALO		+	++										--		+				+++			---					++	---		--
CAMO		---										--										+								
CAPE6						--																								
CHLE4												+							++								+	--		
CHVI6																				++										+
CIVU							--																							
CIUN	---			+++				+++																						
COLI2			+++									+++			++							--						--		-
EAFO					++											++														
EPFO						-																					--		+++	
EAFO			-									---	+						--									++		+++
EAFO																											---		++	
EPCA4																														
COCA5																														
FEID						--																								
GACO5		+										++			+						--		---						---	
KOCR												---			--				--			++								+
LAFO																					+++		++				---			
LAFO					+							--				+			-			+++						+		
LAPU	---			+++				+++										++												
LASE		++										+++			++				++		-	--	--				+++	--	--	-
LIPU			--																											
LOPU3		++										+++			++				++		-	--	--				+++	--	--	
LOFO					++											++				+++										
LYJU																														
MAVI3																								+++						
OENU												++	-									-						---		
OXLA3																++														
PEPU6					++		--																							
POCO13																									+++					
POSE												--				+			-									+		+
PSAR2																														
ROAR3												+			+++				++								+	--		
SEDE2			-														--													
SOMI2																														
SOMO																+++														
SPCO																					---		--				+		--	
STCO4																														
TAOF																									+++					
TRDU			+									+++	-						++			--	--				+++	--	--	
VINU2			+++									+							++											
PHHO					++											++				+++										

Table 10. Continued.

Species	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	No. +	No. -	Total
AGSM	---																							0	4	4
AGTR		++		++																				4	1	5
ALTE			--												-						+	+++		4	3	7
AGSM	+++																							1	3	4
APSP					++					++													++	5	0	5
ARLU																		+++						3	1	4
ASER3										--														0	2	2
ASADR	+++																							3	1	4
BOGR2																								0	0	0
CAEL2																								0	0	0
CAFI																								0	0	0
CALO		+++		+++				++				--		+							+++	+		11	5	16
CAMO								-													-			1	4	5
CAPE6																								0	1	1
CHLE4		++		++										+++										6	1	7
CHVI6					++				++			+					+++						++	7	0	7
CIVU															--									0	2	2
CIUN	+++																							3	1	4
COLI2		++		++								-		++							++	++		8	4	12
EAFO					+++																		+++	4	0	4
EPFO		-		-														---						1	5	6
EAFO		--		--				-													--			3	7	10
EAFO		--		--														--			--			1	5	6
EPCA4							+++																	1	0	1
COCA5											+++									+++				2	0	2
FEID																								0	1	1
GACO5		+++		---									+	+				+			+++			8	3	11
KOCR		--		--				---				+		--							--			3	8	11
LAFO		--		--														--			--			2	5	7
LAFO		-										+												5	3	8
LAPU																								3	1	4
LASE				+++								-		++							++			8	7	15
LIPU																	+					-		2	1	3
LOPU3		+++										-		++							++			8	6	14
LOFO																							+++	4	0	4
LYJU																								0	0	0
MAVI3																								1	0	1
OENU															-						+			2	4	6
OXLA3																								1	0	1
PEPU6																								1	1	2
POCO13																				+++				2	0	2
POSE		-		-																+++				4	4	8
PSAR2																								0	0	0
ROAR3		++		++																				6	1	7
SEDE2								-																0	3	3
SOMI2																								0	0	0
SOMO			+																					2	0	2
SPCO																								3	2	5
STCO4																								0	0	0
TAOF											+++	+++												3	0	3
TRDU		++		--				+																7	5	12
VINU2			-																					3	1	4
PHHO					+++																			4	0	4
TOTAL																								150	106	256

Table 11. Significant interspecific associations at the Osage Site.

Species	1	2	3	4	5	6	7	8	9	10	11	12	No. +	No. -	Total
AMCO						+++					---		1	1	2
AMPS					+				+				2	0	2
ANGE												--	0	1	1
ANSC2													0	0	0
BRJA		+									++		2	0	2
BRTE	+++										---		1	1	2
CAREX													0	0	0
PAVI2											+++		1	0	1
POAN													0	0	0
POPR		+											1	0	1
SONU2	---				++	---	+++						2	2	4
SPAS			--										0	1	1
TOTAL													10	6	16

Table 12. Significant interspecific associations at the Pantex Site.

Species	1	2	3	4	5	6	7	8	9	10	11	No. +	No. -	Total
BOGR2		---	++									1	2	3
BOBUM	---		---									1	2	3
BUDA	++	---										1	1	2
HOPU												0	0	0
LEDE					---				--			0	1	1
LEPID						---			--			0	2	2
MAMMI												0	0	0
OPUNT												0	0	0
PLPAG					--							0	1	1
RATIB												0	0	0
SPCO												0	0	0
TOTAL												3	9	12

Table 13. Summary values for comparison of species associations across the Comprehensive Network Sites, excluding Hays and Jornada.

Site	No. Species per Site	No. Species with Significant Association per Site	Percent Total with Significant Association per Site	Total No. Significant Association	No. Plus Significant Association	No. Minus Significant Association
Bison	35	31	88.57	98	84	14
Bridger	15	9	60.00	18	10	8
Dickinson	53	46	85.19	256	150	106
Osage	12	9	75.00	16	10	6
Pantex	11	5	45.45	11	3	8

APPENDIX I

CODE AND SPECIES NAME

SCS Code	Species Name
ACMI2	*Achillea millefolium*
AGGL	*Agoseris glauca*
AGGR	*Agoseris grandiflora*
AGOSE	*Agoseris* sp.
AGSM	*Agropyron smithii*
AGSP	*Agropyron spicatum*
AGSU	*Agropyron subsecundum*
AGTR	*Agropyron trachycaulum*
ALIN	*Allionia incarnata*
ALTE	*Allium textile*
AMAR2	*Ambrosia artemisiifolia*
AMCH6	*Amorpha canescens*
AMCO	*Ammannia coccinea*
AMPS	*Ambrosia psilostachya*
AMSA	*Amelanchier sanguinea*
ANGE	*Andropogon gerardi*
ANMA	*Anaphalis margaritacea*
ANRO2	*Antennaria rosea*
ANSC2	*Andropogon scoparius*
APRA	*Aphanostephus ramossissimus*
APSP	*Aspera spicaventi*
ARCO5	*Arenaria congesta*
ARFR4	*Artemisia frigida*
ARFU3	*Arnica fulgens*
ARLO3	*Aristida longiseta*
ARLU	*Artemisia ludoviciana*
ARPU9	*Aristida purpurea*
ASADR	*Astragalus striatus* (See *Astragalus adsurgens robustior*)
ASAR	*Aselepias arenaria*
ASER3	*Aster ericoides*
ASFA2	*Aster falcatus*
ASFE	*Aster fendleri*
ASMO7	*Astragalus mollissimus*
ASOB2	*Aster oblongifolius*
ASPU	*Asclepias pumila*
ASSP	*Asclepias speciosa*
ASVI	*Asclepias viridiflora*
BAAB	*Bahia absinthifolia*

APPENDIX I (Continued)

SCS Code	Species Name
BASA3	*Balsamorhiza saginara*
BOBUM	*Bouteloua-Buchloe* (mixed)
BOCU	*Bouteloua curtipendula*
BOER4	*Bouteloua eriopoda*
BOGR2	*Bouteloua gracilis*
BOHI2	*Bouteloua hirsuta*
BOTO	*Boerhaavia torreyana*
BRJA	*Bromus japonicus*
BRTE	*Bromus tectorum*
BUDA	*Buchloe dactyloides*
CABA6	*Cassia bauhinioides*
CAEL2	*Caren eleocharis*
CAFI	*Caren filifolia*
CAGR4	*Caren gravida*
CAIN2	*Callirhoe involucrata*
CALO	*Calamovilfa longifolia*
CAMO	*Calamagrostis montanensis*
CAPE6	*Caren pensylvanica*
CAREX	*Carex* spp.
CASU12	*Castilleja sulphurea*
CEAR4	*Cerastium arvense*
CHIN2	*Chenopodium incanum*
CHLE4	*Chenopodium leptophyllum*
CHVI6	*Chrysopsis villosa*
CIOC2	*Cirsium ochrocentrum*
CIUN	*Cirsium undulatum*
CIVU	*Cirsium vulgare*
COCA5	*Erigeron canadensis* (See *Conyza canadensis*)
COCR	*Commelina crispa*
COLI2	*Collomia linearis*
CONI3	*Corispermum nitidum*
CRAC2	*Crepis acuminata*
CRCO11	*Croton corymbulosus*
CRCR3	*Cryptantha crassisepala*
DAIN	*Danthonia intermedia*
DIWI	*Dithyraea wizlizeni*
DOCO	*Dodecatheon conjugens*
EAFO	Early annual forb
ECPAA	*Echinacea angustifolia* (See *Echinacea pallida angustifolia*)

APPENDIX I (Continued)

SCS Code	Species Name
EPFO	Early perennial forb
EPTR	*Ephedra trifurcata*
ERAB2	*Eriogonum abertianum*
ERIOG	*Eriogonum* sp.
ERPU2	*Erigeron pumilua*
ERRA3	*Eriogonum rotundifolium*
ERSP4	*Erigeron speciosus*
EUAL4	*Euphorbia albomarginata*
EVAL	*Evolvulus alsinoides*
EUMA7	*Euphorbia maculata*
EVPI	*Evolvulus pilosus*
FEID	*Festuca idahoensis*
FESC	*Festuca scabrella*
FRPU2	*Fritillaria pudica*
GABO2	*Galium boreale*
GACO5	*Gaura coccinea*
GETR	*Geum triflorum*
GRSQ	*Grindelia squarrosa*
GUSA2	*Gutierrezia sarothrae*
GUSP	*Gutierrezia sphacrocephala*
HAGR5	*Aplopappus gracilis* (See *Haplopappus gracilis*)
HEAN3	*Helianthus annuus*
HECY2	*Heuchera cylindrica*
HEHI	*Hedeoma hispida*
HELIA3	*Helianthus* spp.
HIAL	*Hieracium albertinum*
HOAN	*Houstonia angustifolia*
HODE	*Hoffmanseggia densiflora*
HOJA	*Hoffmanseggia jamesii*
HOPU	*Hordeum pusillum*
KAHI	*Kallstroemia hirsutissima*
KOCR	*Koeleria cristata*
KRLA	*Krameria secundiflora* (See *Krameria lanceolata*)
KUGL	*Kuhnia glutinosa*
LAFO	Late annual forb
LAPU	*Lactuca pulchella*
LASE	*Lactuca serriola*
LEDE	*Lepidium densiflorum*

APPENDIX I (Continued)

SCS Code	Species Name
LEER	*Leucelene ericoides*
LEFE	*Lesquerella fendleri*
LEPID	*Lepidium* sp.
LEPY	*Leptilon canadense*
LIARA	*Linum australe* (See *Linum aristatum australe*)
LIPA	*Lithophragna parviflora*
LIPU	*Liatris punctata*
LIRU4	*Lithospermum ruderale*
LITR	Litter
LOFO	*Lomatium foeniculaceum*
LOPU3	*Lotus americanus* (See *Lotus purshianus*)
LPFO	Late perennial forb
LUAR3	*Lupinus argenteus*
LULA3	*Lupinus laxiflorus*
LUSE4	*Lupinus sericeus*
LYJU	*Lygodesmia juncea*
MAMMI	*Mammillaria* sp.
MATA2	*Aster tanacetifolius* (See *Machaeranthera tanacetifolia*)
MAVI3	*Mammillaria vivipara*
MEAL2	*Melilotus alba*
MEOF	*Melilotus officinalis*
MIFB	Miscellaneous forb
MIGR	Miscellaneous grass
MINU	*Microseris nutans*
MISC	Miscellaneous
MOUN	*Monardella undulata*
MUPO2	*Muhlenbergia porteri*
NAHI	*Nama hispidum*
OEFR2	*Oenothera freemontii*
OENU	*Oenothera nuttallii*
OESE	*Oenthera serrulata*
ONMOO	*Onoosmedium occidentale* (See *Onosmodium molle occidentale*)
OPUNT	*Opuntia* sp.
OXLA3	*Oxytropis lambertii*
OXST	*Oxalis stricta*
PAHI5	*Panicum hirticaule*
PAJA	*Paronychia jamesii*
PAVI2	*Panicum virgatum*
PEPU6	*Petalostemum purpurcum*
PHHO	*Phloxi hoodii*

APPENDIX I (Continued)

SCS Code	Species Name
PLPAG	*Plantago purshii* (See *Plantago patagonica gnaphaloides*)
POAL4	*Polygala alba*
POAN	*Poa annua*
POCO13	*Potentilla concinna*
POPR	*Poa pratensis*
PORTU	*Portulaca* sp.
POSE	*Poa secunda*
PRJU	*Prosopis juliflora*
PSAR2	*Psoralea argophylla*
PSCU	*Psoralea cuspidata*
PSES	*Psoralea esculenta*
PSTA	*Psilostrophe tagetina*
PSTE3	*Psoralea tenuiflora*
RACO3	*Ratibida columnifera*
RATIB	*Ratibida* sp.
RHGL	*Rhus glabra*
ROAR3	*Rosa arkansana*
SAKA	*Saka-Salsola kali*
SARH2	*Saseifraga rhomboidea*
SCRE	*Scleria reticularis*
SCUN	*Schrankia uncinata*
SEDE2	*Selaginella densa*
SEDG	Sedge
SEPL	*Senecio plattensis*
SIHY	*Sitanion hystrix*
SISP3	*Silphium speciosum*
SOEL	*Solanum elaeognifolium*
SOMI2	*Solidago missouriensis*
SOMO	*Solidago mollis*
SONU2	*Sorghastrum nutans*
SORI2	*Solidago rigida*
SPAS	*Sporobolus asper*
SPCO	*Malvastrum coccincum* (See *Sphaeralcea coccinea*)
SPCR	*Sporobolus cryptandrus*
SPFL2	*Sporobolus flexuosus*
SPPI	*Sporobolus pilosus*
SPSU	*Sphaeralcea subhastata*
STCO4	*Stipa comata*
STDEA	Standing dead
STEX	*Stephanomeria exigua*

APPENDIX I (Continued)

SCS Code	Species Name
STLI2	*Stenosiphon linifolium*
STRI2	*Stipa richardsoni*
TAOF	*Taranacum officinale*
TEST2	*Tetrodymia stenolypis*
THME	*Thelesperma gracile* (See *Thelisperma megapotamicum*)
TILA2	*Tidestromia lanuginosa*
TRDU	*Tragapogon dubius*
TRRA	*Tragia ramosa*
TRTE	*Tribulus terrestris*
VEBI	*Verbena bipinnatifida*
VEST	*Verbena stricta*
VINU2	*Viola nuttallii*
YUEL	*Yucca elata*
YUGL	*Yucca glauca*
ZIGR	*Zinnia grandiflora*
ZYPA	*Zygandenus paniculatus*

CONCLUDING REMARKS

by

Paul G. Risser

These papers represent an initial analysis of the data collected on the Comprehensive Network Sites during the 1970 growing season. All these papers have benefitted from input provided by the principal investigators who not only responded to the students' papers, but, in many cases, also sent additional information. The intent of these papers was to focus on intersite comparisons, since in-depth analysis of each site has been conducted by the appropriate principal investigator.

Dvorak used polar ordination and principal component analysis to demonstrate the similarity of the Comprehensive Network Sites when they are compared only by abiotic parameters. If one considers the long time differences between sites, historical averages for various climatological parameters are most appropriate. The sites were also ordered on vegetational characteristics, both taxonomic and ecological categories (C. Perino). The configurations, which denote similarities between sites, are essentially identical whether taxonomic or ecological categories are used.

Five methods of estimating primary producer biomass were compared using the network data (Kennedy). When three single estimate methods were compared to summation of species peaks, only Bison, Osage, and Pantex Sites showed significant differences between the estimation methods. A comparison of three single estimate methods to the summation of positive biomass increases found only the Dickinson Site comparisons not significantly different.

The productivity rates of the different grassland types were compared by J. Perino. There was no particular relationship between productivity and elevation, and low growing season precipitation was associated with both high and low rates of productivity. In general, productivity increases with the number of species, a greater peak standing crop, and a shorter growing season. Multiple regression was used to examine the factors related to live biomass dynamics (Croak). It was interesting that while some form of water value was invariably important, a number of different sets of factors were shown to be important when diverse sites are compared. Belowground biomass seemed to show a rapid response to soil water, but in general these data are characterized by high variability (Turner). Root turnover rates were higher in the mixed-grass prairies than in the tallgrass prairies and more rapid in the xeric sites. The greatest amount of litter on the ungrazed treatment is found on mixed-grass prairies, and the least litter is found on the desert grassland. In most cases, sites with high amounts of live biomass also have high amounts of litter (Johnson).

Phenology measurements were made throughout the 1970 growing season, but the kind of analysis possible from these data are limited (Williams). A preliminary analysis of species associations was done by Brown who found that many species are associated at the intrasite level, but the results are drastically affected by the species separation techniques utilized at each netowork site.

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