Technical Report No. 168 PREDICTABILITY OF PATTERNS AND VARIABILITY OF PRECIPITATION IN GRASSLANDS

John A. Wiens

Department of Zoology

Oregon State University

Corvallis, Oregon

GRASSLAND BIOME

U.S. International Biological Program

September 1972

TABLE OF CONTENTS

	raye
Title Page	i
Table of Contents	ii
Table of Contents	
Abstract	
Introduction	. 1
Analytical Methods	. 3
Results and Discussion	. 9 . 9 . 12 . 12
Conclusion: Patterns of Ecological Stability	. 14
Acknowledgements	. 16
Literature Cited	. 17
Appendix I	. 19

ABSTRACT

Climatic instability may restrict the biotic diversity of an area by imposing frequent but unpredictable stresses upon the adaptive systems of species, while areas with relatively stable climates may have a greater number of species due, at least in part, to enhanced opportunities for resource partitioning. To provide a framework for evaluation of the biotic diversity of different grassland systems, precipitation regimes from 44 U.S. Weather Bureau stations located in tallgrass, mixed-grass, shortgrass, Palouse, and shrub-steppe habitats were analyzed. Special emphasis was given to the predictability of the pattern of precipitation and variability of precipitation. On a monthly basis rainfall regimes were most predictable (in decreasing order) in tallgrass, mixed-grass, and shortgrass prairies, while the pattern of precipitation in Palouse and shrub-steppe types was predictable only from one year to the next and then less than in the Great Plains grasslands. Shortgrass stations had significantly more variability in annual precipitation than mixed-grass areas, and tallgrass stations were the least variable. Palouse and shrub-steppe areas were intermediate in annual variability of precipitation in relation to the "true" grassland types. Stations in central and northeastern Oklahoma did not adhere to these patterns, having less predictable rainfall patterns, a smaller proportion of the yearly rainfall during the summer, and a greater frequency of years in which the rainfall deviated strongly from the long-term average than other mixed-grass or tallgrass stations. The implications of these rainfall patterns for ecosystem diversity and stability are discussed.

INTRODUCTION

Grassland ecosystems are characterized in the layman's eyes by their climatic extremes—droughts, blizzards, cloudbursts, tornados, bitter cold, intense heat, and so on. While the severity of grassland weather is frequently exaggerated, the climate does undergo strong seasonal shifts, and yearly differences are also frequently large. This climatic instability, if real, should be expected to have profound effects on the biota of grassland ecosystems.

This paper represents an attempt by a biologist to examine meteorological data from a biological point of view. The analysis grew from my attempts to explain why grassland ecosystems characteristically support such a small number of breeding bird species (three to six), a fact observed by myself (Wiens, 1971) and by Cody (1966). Part of the "conventional wisdom" of ecology holds that climatic stability may lead to stability and diversification of vegetation; this in turn provids greater opportunities for niche divergence and resource partitioning among consumers (Pianka, 1966; MacArthur, 1965). Conversely, climatic instability may act to reduce opportunities for niche diversification through its variable effects upon resource bases. In particular, I have suggested (Wiens, in preparation) that the number of bird species which can successfully exploit grassland ecosystems is limited to a rather low number by the frequent but unpredictable extreme climatic stresses; this inherent instability of grasslands may, in fact, impose general limitations on the biotic diversity of grassland ecosystems (Wiens, 1971). While many climatic features may contribute to this instability, variability in precipitation especially may act in a limiting manner through its direct

effects on primary production (Rosenzweig, 1968; Holdridge, 1947) and, thus, on food supplies. Rasmussen, Bertolin, and Almeyda (1971), for example, have observed that a dry year in grasslands not only has low precipitation but is also accompanied by higher than average temperatures and wind movements and, therefore, higher evapotranspiration rates, with the result that the need for water in the system is potentially highest during the years when it is least available. Thus, I have sought to provide some substantiation, or at least parallel evidence, for my speculations on avifaunal structure in grasslands through an examination of the patterns of variation in precipitation regimes in grasslands. Because there are interesting differences between different aspects of grassland ecosystems (Wiens, in preparation), I have analyzed separately rainfall patterns for tallgrass prairies, mixed grasslands, shortgrass steppe, Palouse prairie, and northern shrub-steppe, generalizing these grassland types from Küchler (1964).

It is not my intention here to review grassland climatology. Works such as those of Borchert (1950), Trewartha (1961), or the reviews of Collins (1969) and Rasmussen (1971) have called attention to the general features of grassland rainfall—the paucity of winter precipitation, the intense but local summer storms, and the general regional homogeneity of grassland climates. Rasmussen et al. (1971) have provided a detailed review of climatological conditions in the vicinity of the IBP Grassland Biome Intensive Site at Pawnee. All of these workers, however, have approached the subject within the framework of conventional meteorological analysis, and the variables they have examined are not necessarily those of greatest potential biological importance. Chief emphasis in my analysis will be given to variability and predictability of annual precipitation in grasslands; other features of

grassland rainfall patterns will be only briefly mentioned. Hopefully, one outcome of this analysis will be to encourage other IBP workers to undertake similar "spin-off" efforts and to speculate on the bases for the diversity and stability of various biotic groups.

ANALYTICAL METHODS

Precipitation data from 44 U.S. Weather Bureau stations were used in this study. Station locations are indicated in Fig. 1, and pertinent features of each station are listed in Table 1. Stations were selected to characterize major vegetational types of grassland and to provide a broad geographic sampling of climatic conditions within each type. Stations lying close to vegetational "transitions" were avoided (Fig. 1). Stations located near IBP grassland sites were included in the analysis (Table 1), but have not been analyzed separately.

Weather Bureau records for these stations from the initiation of recording through 1960 were gathered from various summaries (U.S. Weather Bureau, 1930, 1952, 1961) and transferred to data cards. From these data sets, means and variances were calculated for monthly, annual, and summer (April to September) precipitation, and the proportion of the annual mean precipitation occurring during the summer was derived (Table 1).

Variability and/or predictability of the pattern of annual rainfall were measured in the following ways:

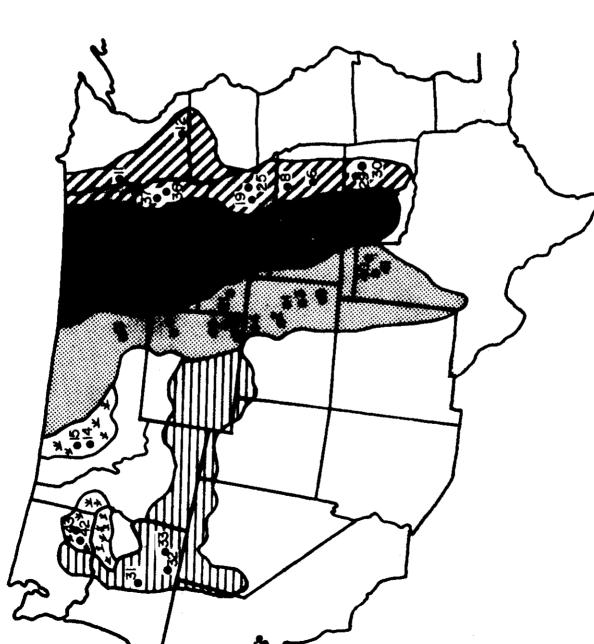
1. The coefficient of variation (CV) of the annual precipitation was calculated for each station, and a mean CV (and variance) was derived from these for all stations within each grassland type (Table 2). This provides a comparative index of the degree of variation of yearly rainfall amounts about the long-term average.



- N TALLGRASS
- MIXED-GRASS
- SHORTGRASS **
- SHRUB-STEPPE

PALOUSE

3



Locations of U.S. Weather Bureau climatological stations used in this analysis. Station identifications are given in Table 1. Grassland types generalized from Küchler (1964). Fig. 1.

Table 1. General features of U.S. Weather Bureau stations used in this analysis.

ble 1.	Stati	features of U.S. Wea ion	Grassland	Record Length	Mean Annual Precipitation (cm)	Percent of Precipitation In Summer b/	Elevation (a)
ımber	State	Name	Typea/	(years)	(City	· In Summer—	
			S	70	43.4	79	1,268
1	Colo.	Burlington		76 36	34.6	76	1,646
2	Colo.	Byers	\$	63	40.9	79	1,304
3	Colo.	Cheyenne Wells	\$ c	55 55	34.9	78	1,547
4	Colo.	Grover ^{c/}	S	59	36.2	76	1,242
5	Colo.	Two Buttes	S	56	82.0	72	384
6	Kan.	Cottonwood Falls	T	93	58.1	77	610
7	Kan.	Hays ^c /	M	93 103	80.4	74 ,	335
8	Kan.	Manhattan	T	65	52.5	7 7	689
9	Kan.	Ness City	M 	68	54.0	77	713
10	Kan.	Norton	м -		52.2	79	276
11	Minn.	Ada	T -	59 61:	75.4	73	375
12	Minn.	Albert Lea	T	64	75.4 34.0	72	725
13	Mont.	Miles City	S	76	34.0 35.3	56	983
14	Mont.	Missoula	Р	77	35.3 39.4	62	884
15	Mont.	St. Ignatius <u>c</u> /	P	52	39. 4 35.8	78	596
16	N. Dak.	Crosby	М	53		78	775
17	N. Dak.	Dickinson ^{c/}	М	69	39.3	78	566
18	N. Dak		М	51	43.2	78	523
19	Neb.	Bradshaw	1	53	74.5	78 78	762
	Neb.	Brewster	м	47	55.0	78	1,115
20 21	Neb.	Bridgeport	s	64	40.1	78 80	755
	Neb.	Broken Bow	М	65	58.0		1,168
22	Neb.	Hay Springs	м	79	49.6	73 76	727
23		Lexington	м	65	55.8	76 75	36:
24	Neb.	Lincoln	Ŧ	83	70.2	75 45	33
25	Neb.	Chickasha	м	52	79.2	65	33: 38:
27	Okla.	Foraker <u>c/</u>	т	15	83.9	68	30 27
29	Okla.		ī	61	92.9	67	
30	Okla.	Pawhuska Esemont	ss	40	24.4	38	1,31
31	Ore.	Fremont	SS	39	26.1	45	1,31
32		Frenchglen	SS	46	30.0	41	1,31
33		Valley Falls	M	24	37.4	77	7.
34			M	49	47.2	78	6
35			Ť	64	50.6	· 80	4
36			' T	35	61.8	78	5
37		k. Clear Lake	H	51	38.4	78	7
38				46	39.0	76	7
39			M s	30	51.6	72	9
40		Pampa c/	S c	36	56.8	71	1,0
41	1 Tex.	Panhandle ^C /	\$	50	20.9	32	
42	2 Wash.	Benton City—	P		15.7	30	
43		Hanford	P	29 40	=	70	1,
44		Gillette	S	40		70	2,
45	•	Laramie	\$	78 1.3		73	1,
46	•	Wheatland	S	47		. <u></u>	

 $[\]frac{a}{T}$ = taligrass, M = mixed-grass, S = shortgrass, P = Palouse, SS = shrub-steppe. $\frac{b}{T}$ April to September.

c/ Stations located near IBP Grassland Biome study sites.

Precipitation characteristics of grassland types as recognized by Küchler (1964). See text for further explanation of measures. The Oklahoma Stations (numbers 27, 29, and 30) are omitted from this analysis. Table 2.

			Annı	al Prec	Annual Precipitation	c	Percent Annual	Annual	Frequ	ency of	Frequency of Deviation $\frac{\mathrm{b}'}{}$		Maximum/Minimum Annual	Minimum al
Grassland	N (Stations)	Mean Length of Record	Mean	E C	Coefficient of Variation	cient ation	Precipitation in Summer ^{a/}	ation era/	By ≥0.5 x	ıx	By ≥0.25 ₹	25 x	Precipi	Precipitation C/
- - - -		(1ears)	,,	g	ı×	ន	ıx	s	ı×	S	ı×	OS	ıx	SO
			`	3									, ,	6 617
		2 12	49.4	8.03	0.285	0.038 74.5	74.5	3.53	0.8	1.28	3.53 8.0 1.28 40.5 9.89	9.89	3./5	0.01
Shortgrass	1.2	74.0					1	c L		37 6 9 1	34. 1	7.33	3.97	0.621
	41	58.5	49.5	11.48	0.258	0.025	77.2	. 50		01.7				;
Mixed-grass	r ·	``	• •	,	,,,,	0.021	16.1	2.85	2.4	2.72	24.5	5.50	3.04	0.563
Tallgrass	∞	59.3	72.4	13.82	0.435						-		2 25	0.424
•	.2	£2 O	27.7	11.32	0.247	0.035	45.0	16.37	3.0	1.41	74.0	4.40	0.0	! •
Palouse	Ŧ) -		6	0.271	0,028	41.3	3.51	5.7	40.4	4.04 37.7	8.02	3.57	0.783
Shrub-steppe	,pe 3	41./	5.07	2		1								

 $\frac{b}{L}$ percent of years when annual precipitation deviates from the long-term average (\tilde{x}) by at least the indicated amount. $\frac{c}{L}$ Maximum recorded annual precipitation \hat{x} minimum recorded annual rainfall. $\frac{a}{4}$ April to September.

- 2. The extreme dry (minimum) and wet (maximum) years recorded for each station were determined, and the ratio of wet to dry values was calculated (Table 3). These values were then also combined to give a mean ratio for each grassland type (Table 2). This measure is indicative of the magnitude of extreme variations in rainfall for individual stations or grassland types.
- 3. More biologically important, perhaps, than variation around a long-term mean or the extreme conditions is the frequency of occurrence of years which deviate strongly from "average." From the standpoint of bird (or mammal or insect, etc.) populations, the occurrence of unusually dry or wet years (with the attendant effects on production and food supplies) may impose crucial limitations. To measure this I calculated for each station the percent of all years in which the yearly rainfall amount deviated from the long-term mean, first, by at least 0.25 of the long-term mean, and second, by at least 0.50 of the long-term mean (Table 3). As before, these values were summarized for each grassland type (Table 2).
- 4. Variation in precipitation does not necessarily imply instability, for variations may be large but of regular, predictable occurrence (e.g., seasonal patterns). To test the predictability of rainfall regimes I applied autocorrelation analysis to the monthly precipitation records for each station (Kendall and Stuart, 1967). The autocorrelation coefficient is positive when the series of monthly precipitation values is positively correlated and negative when the series is inversely correlated. Autocorrelation coefficient values near zero indicate independence of the two rainfall values and, thus, also indicate unpredictability. This sort of approach has previously been applied to an analysis of patterns of lizard diversity in North American deserts by Pianka (1967). In my analysis, the

Table 3. Analyses of variation in annual precipitation for stations listed in Table 1. See text for further explanation.

•		Pe fro	erce m Me	ent of ean Ann	Years Dev	/iat ipit	ing atio		Extreme Re	corded Annual Pre (cm)	cipitation
	Station Number	Ву	≥0.5	5 Ā	Ву	≥0.	25 x		Minimum	Maximum	Maximum
		+	-	Σ	+	-		Σ			
ابرر	<u></u>	6	4	10	20	21	ı	41	15.7	69.7	4.44
wel .		8	6	14	31	31	. 6	62	13.9	57.5	4.14
1857	- 2 - 3	6	4	10	21	22		43	19.7	68.2	3.46
Acres House	· 3 · L -1	4	4	8	18	18	3	36	13.3	58.9	4.43
NO.E.	in ⊣ La – r	7	0	7	20	2	4	44	20.3	79.9	3.93
GW.	829 2	2	0	2	11	12	2	23	49.4	145.1	2.93
	_	3	1	4	15	2	3	38	23.4	110.1	4.71
	7		1	4	13	1		26	38.4	153.4	3.99
	8	3	2	7	20	2	-	42	20.2	82.3	4.07
	9	5	2	6	21	2		46	24.5	98.5	4.02
	10	4	2	4	12		-	22	25.6	84.8	3.32
	11			0	9			18	39.2	106.5	2.72
	12	0	0		14		6	30	17.8	57.8	3.25
	13	4	0		8		3	21	17.0	57.0	3.34
	14	4	1	5	12		10	22	22.3	63.9	2.87
	15	2	0		19		21	40	13.7	53.0	3.87
	16	0	2		17		10	27	17.1	79.1	4.64
	17	1	1	_	11		16	30	17.7	73 - 7	4.17
	18	2	2		17		17	34	37.5	128.6	3.43
	19	8	0		1)		., 17	34	30.5	101.2	3.32
	20	4			16		16	32	20.1	60.1	2.98
	21	2			1		11	22	32.1	86.5	2.69
	22	0			. 1		14	33	21.1	74.5	3.54
	23	1		2 3			9	23	28.8	101.7	3.53
	24	3		3			12	29	35.6	104.7	2.94
	25	0		0 0		-	17	34	41.5	120.5	2.91
	27	6		0 6			27	بر 47	47.9	122.5	2.56
	29	C		0 0		0 6	16	32	49.5	147.8	2.99
	30	7		0 7			17	29	11.3	49.2	4.30
	31			2 4		2		46	12.2	43.4	3.5
	32			5 10		!3	23		16.3	45.5	2.7
	33			0 2		20	17 21	37 42	12.5	62.9	5.0
	34		8	4 12		21		28	20.2	72.8	3.6
	35		2			16	12	26	28.4	82.1	2.8
	36		2	_		14	12 6	17		90.3	2.0
	37		0			11		38		70.2	3.8
	38		4			18	20			62.8	4.4
	39		4	_		20	15	35 34		83.6	3.2
mple	40		3		-	17 25	17			108.1	3.9
mek humb	M. 41		8	3 1		25	25	50		49.3	3.9
-	42		2		-	14	16	30		28.6	3.:
	43		3	0	3	7	17	21		56.3	2.7
	44		0	0	0	20	22			45.1	4.6
	45		3	3	6	14	12	26	y.0	57.4	3.8

interval of time (or lag) between compared monthly precipitation values was varied from 1 to 12 months. In essence, then, I asked: "Given the rainfall amount of any month, \underline{n} , what is the likelihood that the rainfall of month $\underline{n+1}$, $\underline{n+2}$, $\underline{n+3}$, ..., $\underline{n+12}$ will be quite similar or quite dissimilar?" This approach thus looks at climatic stability in a somewhat different way by examining the average predictability of the rainfall pattern. The computer program for this analysis is given in Appendix I.

RESULTS AND DISCUSSION

The results of these analyses for the five grassland types are given in Tables 2 and 4 and Fig. 2.

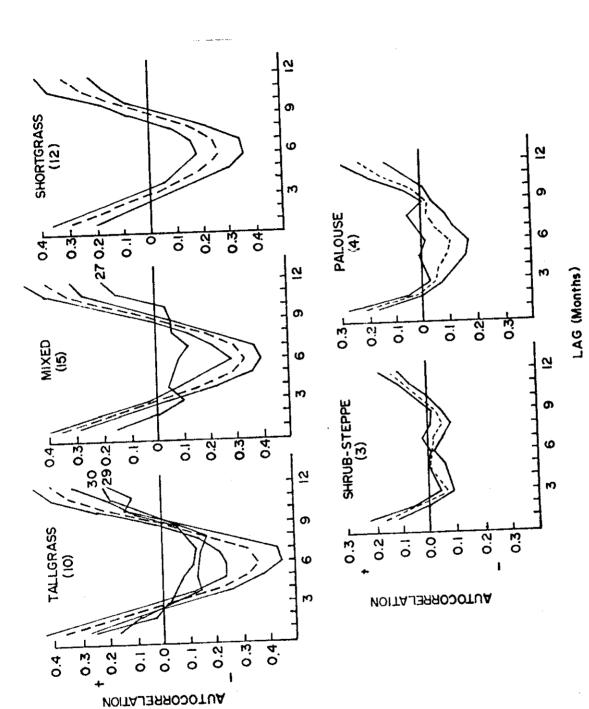
Patterns of Annual Precipitation

paralleled by steadily decreasing mean annual precipitation (see Borchert, 1950). The tallgrass stations combined have a mean annual rainfall roughly 1.5 times that of the collection of mixed-grass sites, which in turn average 1.25 times more precipitation than the shortgrass stations (Table 2). All of these differences are significant (Table 4). Palouse prairies and northern shrub-steppe are characterized by less yearly rainfall than any of the Great Plains grassland types, but are quite similar to each other.

Roughly three-fourths of the yearly rainfall in the Great Plains grasslands occurs in summer, while both Palouse and shrub-steppe types occupy the rain shadow of the intermontane western regions (Trewartha, 1961), and are dominated by winter season precipitation.

es for precipitation features listed in

Graceland Tynes	Mean	Coefficient of	Percent of Precipitation	Frequency of Deviation from Annual Mean	Deviation al Mean	Mean Maximum : Minimum Annual
Compared	Annua: Precipitation	Annual Mean	in Summer	≥0.5 ጃ	≥.25 ×	Precipitation
Shortarass-Mixed	4.	44	-3¢	**	NS	SN
Shortarass-Tallarass	*	**	SN	**	*	÷
Shortarass-Palouse	₹	SN	* *	**	**	NS
Shortarass-Shrub-steppe	*	SZ	*	SN	NS	SN
Mixed-Tallorass	*	-; c	SN	SN	*	* *
	*	SZ	* *	S	÷	SN
Mixed-Palouse	* *	S) Z	* *	NS	N	NS
Mixed-sillub-steppe Tallorass-Palouse	**	SN	* *	SN	S	SN
Tallorass-Shrub-steppe	**	SZ	- % %	SN	*	SN
Palouse-Shrub-steppe	SN	SN	SN	SN	*	SN



Points near the zero line indicate that there is little autocorrelation and that precipitation Solid lines enclose the range of autocorrelation curves for a given grassland type, while the dashed line indicates the mean autocovariance for all stations within a type (N is given in parentheses). The Oklahoma stations (numbers 27, 29, 30) are considered Points above the zero line indicate positive autocorrelation and mean that the precipitation for a given month is positively correlated with the precipitation for Autocorrelation of monthly total precipitation, for lags of 1 to 12 months, for stations in Points below the zero line indicate inverse autocorrelation, meaning that conditions may be expected to change during the given lag interval the month at a given lag period away. Fig. 2.

Predictability of Patterns of Precipitation

The results of autocorrelation analysis (Fig. 2) allow an evaluation of the predictability of rainfall patterns over a 12-month period, regardless of total annual precipitation differences or differences in variability.

The strong seasonality of rainfall in tallgrass, mixed-grass, and shortgrass areas is apparent. In each there is a strong negative autocorrelation with a 5- to 7-month time lag (i.e., if it is wet (dry) now, it is highly likely that it will by dry (wet) in 5 to 7 months. The seasonal predictability of the rainfall pattern of tallgrass prairies is slightly greater than that of mixed-grass types, which in turn are somewhat more predictable than shortgrass prairies. The three Oklahoma stations (two tallgrass, one mixed-grass) deviate markedly from these autocorrelation patterns (Fig. 2), and for that reason have not been included in the general analysis for these grassland types (Table 2); possible causes of this aberrancy will be discussed later in this paper.

Palouse and shrub-steppe are much less predictable in the seasonal distribution of their rainfall than the Great Plains grasslands. Given a time lag of roughly 2 to 10 months, autocorrelation values are relatively close to zero, indicating the unpredictable patterns of monthly rainfall. The shrub-steppe stations especially lack well-defined repetitive precipitation patterns.

Variability of Precipitation

As suggested above, long-term variability in precipitation may have more important influences on the biotic composition of grasslands than seasonal or year-to-year variations. When the magnitude of difference

between extreme wet and dry years is considered (Tables 2 and 4), shortgrass and mixed-grass prairies have a significantly greater range between extremes than tallgrass prairies, substantiating in a general way the observation of Rasmussen et al. (1971) that as mean annual precipitation decreases the rainfall becomes more variable from year to year. Palouse and shrubsteppe types are intermediate in the magnitude of variation between extreme years, but do not differ significantly from any of the other grassland types in this respect, nor from each other.

The coefficient of variation of mean annual precipitation indicates a similar pattern of variability. Shortgrass stations have a significantly higher CV than mixed-grass stations, which in turn are significantly more variable than tallgrass stations (Tables 2 and 4). Again the intermediate condition of Palouse and shrub-steppe types is indicated.

Finally we may examine the frequency of occurrence of years which deviate markedly from the long-term average in their precipitation. In shortgrass areas, roughly 1 out of every 12 years can be expected to differ from the long-term average by at least half that average (i.e., be half again as wet or have half the "normal" precipitation), while 1 of every 2 1/2 years deviates from "normal" by at least one-quarter of the mean (Table 2). In mixed-grass prairies, on the other hand, extremely wet or dry years (those which deviate from \hat{x} by ± 0.50 \hat{x}) are only 60% as frequent as in shortgrass areas, and unusually wet or dry years (those which deviate by ± 0.25 \hat{x}) are also less frequent, although not significantly so. In tallgrass prairies extremely wet or dry years occur only once in every 42 years, on the average, unusually wet or dry years roughly 1 of every 4 years. Palouse and shrubsteppe types are intermediate, although unusually wet or dry years are

significantly more frequent in shrub-steppe than Palouse areas. Significance levels for all these comparisons are given in Table 4.

The Oklahoma Stations

The autocorrelation analysis (Fig. 2) showed that the three Oklahoma stations differed markedly from the remaining stations in their vegetation types. These stations were characterized by having less predictable rainfall patterns (Fig. 2), a smaller proportion of the yearly rainfall during the summer, and a greater frequency of extremely or unusually wet or dry years (Tables 1 and 3) than other mixed-grass or tallgrass stations. Trewartha (1961) has observed that this area lies in a zone characterized by a bimodal distribution of rainfall in the warm season; this, combined with a possibly greater influence of Gulf coastal weather systems, may produce these differences. Since one of the IBP Grassland Biome sites (Osage) is located in this area, this anomalous rainfall pattern should be kept in mind in comparisons of abiotic-biotic interrelationships with other sites in the Grassland Biome network.

CONCLUSION: PATTERNS OF ECOSYSTEM STABILITY

I have argued elsewhere (Wiens, in preparation) that extreme variations in primary production (especially production lows), induced at least partially by variations in rainfall, may severely limit the resources available to consumers. If one accepts the premise that successful exploitation of grassland as a habitat requires certain distinctive adaptations in any biotic group, then relatively few species may be able to coexist in grasslands at times of resource limitation. The inherent irregularity of the environment may thus act to repeatedly restrict the evolutionary diversification of

ecologically similar species or the development of closely coevolved relationships between different elements of the biota (Wiens, 1971).

This analysis has indicated that, among the range of grassland types considered, shortgrass prairies should be expected to be the least stable, tallgrass situations the most stable. Correspondingly, tallgrass areas should support a more diverse biota with finer niche partitioning among ecologically similar species. Population densities might also be expected to be most stable in tallgrass habitats, most variable in shortgrass areas. Shrub-steppe and Palouse grasslands were shown to be intermediate in their predictability and variability, but there are reasons to suspect that at least some consumer assemblages may be more stable than expected. First, the rainfall in these areas occurs predominantly in the winter, and because of the time lag between precipitation and production in these areas, variations in rainfall might be expected to be "damped out" and have less severe manifestations in resource supplies. In shortgrass areas, where no time lag exists, resource levels should be much more directly affected by rainfall and thus be more sensitive to rainfall variations. Second, the vegetation of both Palouse and shrub-steppe habitats is structurally more stable than that of Great Plains grasslands, and consumers such as birds which respond strongly to habitat structure may thus encounter greater stability in the western areas. In arid shrub-steppe, for example, where the vegetation is dominated by woody plants such as sagebrush (Artemisia) and rabbit brush (Chrysothamnus), much of the annual net primary production may be realized as incremental addition of new material to existing structure, and areas may thus have an essentially unchanging habitat structure over a number of years despite variations in precipitation. The same is true, to a lesser

extent, of Palouse prairies where plant growth and habitat structure are dictated by dispersion of perennial clump bases. By contrast, in "true" grasslands each year's production determines the habitat structure since most of the plant material is reduced to litter each winter. Thus, variations in rainfall will likely be directly manifested as variations in habitat structure.

ACKNOWLEDGEMENTS

Initial impetus for this study came from pre-IBP research conducted under NSF Grant GB-6606. Without the statistical assistance of Robert Francis and Marilyn Campion this analysis would have been impossible. John Rotenberry and John Ward extracted the original precipitation records.

LITERATURE CITED

- Borchert, J. R. 1950. The climate of the central North American grassland. Ann. Ass. Amer. Geogr. 40:1-39.
- Cody, M. L. 1966. The consistency of intra- and inter-continental grassland bird species counts. Amer. Natur. 100:371-376.
- Collins, D. D. 1969. Macroclimate and the grassland ecosystem, p. 29-39. In R. L. Dix and R. G. Beidleman [ed.] The grassland ecosystem: A preliminary synthesis. Range Sci. Dep. Sci. Ser. No. 2. Colorado State Univ., Fort Collins.
- Holdridge, L. R. 1947. Determination of world plant formations from simple climatic data. Science 105:367-368.
- Kendall, M. G., and A. Stuart. 1967. The advanced theory of statistics. In Design and analysis and time series. Vol. 3. Hafner Publ. Co., New York. 217 p.
- Küchler, A. W. 1964. Potential natural vegetation of the conterminous United States. Amer. Geogr. Soc. Spec. Pub. No. 36.
- MacArthur, R. H. 1965. Patterns of species diversity. Biol. Rev. 40:510-533.
- Pianka, E. R. 1966. Latitudinal gradients in species diversity: A review of concepts. Amer. Natur. 100:33-46.
- Pianka, E. R. 1967. On lizard species diversity: North American flatland deserts. Ecology 48:333-351.
- Rasmussen, J. L. 1971. Abiotic factors in grassland ecosystem analysis and function, p. 11-34. In N. R. French [ed.] Preliminary analysis of structure and function in grasslands. Range Sci. Dep. Sci. Ser. No. 10. Colorado State Univ., Fort Collins.
- Rasmussen, J. L., G. Bertolin, and G. F. Almeyda. 1971. Grassland climatology of the Pawnee grassland. U.S. IBP Grassland Biome Tech. Rep. No. 127. Colorado State Univ., Fort Collins. 79 p.
- Rosenzweig, M. L. 1968. Net primary productivity of terrestrial communities: Prediction from climatological data. Amer. Natur. 102:67-74.
- Trewartha, G. T. 1961. The earth's problem climates. Univ. Wisconsin Press, Madison. 334 p.
- U.S. Weather Bureau. 1930. Climatic summary of the United States. Bull. W. Superintendent of Documents, Washington, D. C.
- U.S. Weather Bureau. 1952. Supplement to Bull. W, 1931-1951. Superintendent of Documents, Washington, D. C.

- U.S. Weather Bureau. 1961. Ten year summary of climatological data, 1951-1960. (Series by states). Superintendent of Documents, Washington, D. C.
- Wiens, J. A. 1971. Pattern and process in grassland bird communities, p. 147-211. In N. R. French [ed.] Preliminary analysis of structure and function in grasslands. Range Sci. Dep. Sci. Ser. No. 10. Colorado State Univ., Fort Collins.
- Wiens, J. A. (in preparation) Climatic instability and the "ecological saturation" of bird communities in grasslands. (To be submitted to Amer. Natur.)

APPENDIX I

Computer program used in the analysis of precipitation regimes by stations. Data input was in the form:

Column	<u>Data</u>
1-4	State
5-8	Station
9	Grassland Type: 1 = Tallgrass
	2 = Mixed-grass
	3 = Shortgrass
	4 = Shrub-steppe
	5 = Palouse
	6 = Desert
10-13	Year
14-17	January rainfall (to nearest 0.01 inch)
18-21	February rainfall (to nearest 0.01 inch)
22-25	March rainfall (to nearest 0.01 inch)
26-29	April rainfall (to nearest 0.01 inch)
30-33	May rainfall (to nearest 0.01 inch)
34-37	June rainfall (to nearest 0.01 inch)
38-41	July rainfall (to nearest 0.01 inch)
42-45	August rainfall (to nearest 0.01 inch)
46-49	September rainfall (to nearest 0.01 inch)
50-53	October rainfall (to nearest 0.01 inch)
54-57	November rainfall (to nearest 0.01 inch)
58-61	December rainfall (to nearest 0.01 inch)
62-66	Total Annual rainfall (to nearest 0.01 inch)

```
PROGRAM WEINPPT (TAPE4, TAPE6, INPUT, OUTPUT)
       TO COMPUTE MONTHLY AND YEARLY MEANS, STD. DEVIATIONS. ETC. AND
       AUTOCORRELATIONS FROM VARIOUS SITES FOR JOHN WIENS.
Ç
      COMMON PPT(120+15) +KEY(2+120) +AVG(15) +SD(15) +CV(15) +CT(15) +SAM(15)
C
     1.AUTO(12.2).SITE.NYR.TYP
      COMMON /L1/ LSITE+LYR+LTYP+BUF(13)
      INTEGER TYPE(6) . HEAD(15) . SITE . TYP. SPAN. SEAS(12)
      DATA SEAS/3*(15)+6*(14)+3*(15)/+HEAD/7HJANUARY+8HFEBRUARY+5HMARCH+
     15HAPRIL+3HMAY+4HJUNE+4HJULY+6HAUGUST+9HSEPTEMBER+7HOCTOBER+
     28HNOVEMBER+8HDECEMBER+6HYEARLY+9HGROWING S+9HNON-GRO S/+TYPE/
     310HTALL GRASS.9HMIX GRASS.10HSHORTGRASS.10HSHRUBSTEPP.7HPALOUSE.
     46HDESERT/
C - -
      MYR=120
      MC=15
      MMO=12
      WRITE (6,200)
                        PRECIPITATION ANALYSIS - FOR JOHN WIENS*)
  200 FORMAT (#1
         BOOTSTRAP FIRST CARD IN
      READ (4+110) LSITE+LTYP+LYR+BUF
  110 FORMAT (A8,12,14,12F4,2,F5,2)
     1 CONTINUE
         ZERO ARRAYS
      DO 10 J=1.MYR
       KEY(1+J) = KEY(2+J) = 0
    10 CONTINUE
       DO 11 I=1.MC
       AVG(I)=SD(I)=CV(I)=CI(I)=SAM(I)=0.
    11 CONTINUE
       DO 12 I=1.MMO
       Do 12 J=1.2
    .0=(L+I)OTUA S1
          INPUT DATA FROM ONE SITE
       CALL READER (IEND, SPAN)
       WRITE (6+201) SITE, TYPE (TYP), SPAN, NYR
   201 FORMAT (6(/) +* RESULTS FROM THE #A9#SITE OF THE #A10# TYPE.
      1*SPAN OF RECORD IS*14* YEARS WITH*14* YEARS REPORTED*//)
          COMPUTE TOTALS BY SEASON. SET FLAGS FOR INCOMPETE SEASON TOTALS
       DO 22 LY=1.NYR
       PPT(LY+14)=PPT(LY+15)=0.
       DO 22 IM=1.MMO
       IS=SEAS(IM)
       PPT(LY.IS) =PPT(LY.IS) +PPT(LY.IM)
       IF ((SIGN(1.*PPT(LY*IM)).EG.-1.).A.(PPT(LY*IM).EQ.0.))
      1 KEY(IS-13.LY)=1
    22 CONTINUE
          COMPUTE SUMS. SUMS OF SQUARES. SAMPLE SIZES
        DO 24 LY=1+NYR
        DO 23 1=1+13
```

```
IF ((SIGN(1..PPT(LY.I)).EQ.-1.).A.(PPT(LY.I).EQ.0.)) GO TO 23
    AVG(I) = AVG(I) + PPT(LY+I)
    SD(I) = SD(I) + PPT(LY + I) + PPT(LY + I)
     SAM(I)=SAM(I)+1.
 23 CONTINUE
     DO 24 I=14,MC
     IF (KEY(I-13+LY).EQ.1) GO TO 24
     AVG(I) = AVG(I) + PPT(LY+I)
     SD(I) = SD(I) + PPT(LY+I) + PPT(LY+I)
     SAM(I) = SAM(I) +1.
  24 CONTINUE
        COMPUTE MEANS. STD. DEVS.. CV S., CI S.
     DO 26 I=1.MC
     IF (SAM(I).LE.1.) GO TO 25
     SD(I)=SQRT((SD(I)-AVG(I)*AVG(I)/SAM(I))/(SAM(I)-1.))
     AVG(I) = AVG(I) / SAM(I)
     IF (AVG(I).LE.O.) GO TO 26
     CV(I) = SD(I) / AVG(I)
     N=SAM(I)-1.
     CI(I) = SD(I) + T(N) / SQRT(SAM(I))
     GO TO 26
  25 SD(I) = +0.
  26 CONTINUE
        OUTPUT THESE STATISTICS
     WRITE (6,203)
 203 FORMAT (23x, *MEAN*, 15x, *STD DEV*, 12X, *COEF VAR*, 12X, *95% C I*, 14X,
    1*NUMBER*//)
     Do 28 I=1,15
  28 WRITE (6+205) HEAD(I)+AVG(I)+SD(I)+CV(I)+CI(I)+SAM(I)
 205 FORMAT (3X+A10+1X+F15.2+5X+F15.2+2(5X+F15.3)+9X+F10.0)
        COMPUTE AUTOCORRELATIONS WITH 1 TO 12 MONTH LAGS
     DO 42 L=1+11
      K=L+1
     CALL COREL (AUTO(L+1)+PPT+1+K+NYR +AUTO(L+2))
  42 CONTINUE
      CALL COREL (AUTO(12+1), PPT+2+1+NYR +AUTO(12+2))
         OUTPUT AUTO CORRELATIONS AND SAMPLE SIZES FROM WHICH THEY CAME.
      WRITE (6,207) (I, I=1,12)
                                                  LAG*12110/)
                          AUTOCORRELATIONS*//*
 207 FORMAT (4(/) +*
      WRITE (6,208) ((AUTO(I,J),I=1,12),J=1,2)
 208 FORMAT (* *,7X,12F10.3/* NUMBER *12F10.0//)
      GO TO (1,50) IEND
   50 CONTINUE
         DO ANALYSIS BY TYPES
C - - -
      STOP
      END
      SUBROUTINE READER (IEND+SPAN)
      COMMON PPT(120+15) +KEY(2+120) +AVG(15) +SD(15) +CV(15) +CI(15) +SAM(15)
     1.AUTO(12.2).SITE.NYR.TYP
      COMMON /L1/ LSITE+LYR+LTYP+BUF(13)
      INTEGER SITE, TYP, FYR, SPAN
 - - I IEND = 1 UNLESS END-OF-FILE IS READ. THEN IEND = 2
      IEND=1
```

```
NYR=0
     FYR=LYR
  10 SITE=LSITE
     LSYR=LYR
     TYP=LTYP
     NYR=NYR+1
     DO 12 I=1.13
     PPT(NYR.I)=BUF(I)
  12 CONTINUE
     READ (4.110) LSITE.LTYP.LYR.BUF
 110 FORMAT (A8,12,14,12F4,2,F5,2)
     IF (EOF(4)) 90.14
  14 IF (SITE.EQ.LSITE) GO TO 10
     SPAN=LSYR-FYR+1
     RETURN
  90 IEND=2
      SPAN=LSYR-FYR+1
      RETURN
      END
      SUBROUTINE COREL (AUT.PPT.JY.JM.LY.S)
         COMPUTE CORRELATIONS FOR UP TO LY YEARS STARTING WITH THE (JY+JM)
        ELEMENT OF PPT VS. THE (1+1) ELEMENT. THEN INCREMENTING EACH ONE
C
C
        MONTH AT A TIME.
C
      DIMENSION PPT(120,15)
      KY=JY
      KM=JM
      S=X=Y=XS=YS=XY=0.
      IY=IM=1
         IF EITHER OF THE PAIR OF ELEMENTS IS BLANK, DONT INCLUDE THAT PAIR
    5 CONTINUE
      IF ((SIGN(1..PPT(IY.IM)).EQ.-1.).A.(PPT(IY.IM).EQ.0.)) GO TO 10
      IF ((SIGN(1.*PPT(KY*KM)).EQ.-1.).A.(PPT(KY*KM).EQ.0.)) GO TO 10
      S=S+1
      X=X+PPT(IY,IM)
      XS=XS+PPT(IY+IM)++2
      Y=Y+PPT(KY+KM)
      YS=YS+PPT(KY+KM)++Z
       XY=XY+PPT(IY+IM)+PPT(KY+KM)
   10 CONTINUE
          INCREMENT THE SUBSCRIPTS
       CALL INCR (KY+KM)
       IF (KY.GT.LY) GO TO 20
       CALL INCR(IY+IM)
       GO TO 5
    20 CONTINUE
          COMPLETE COMPUTATION OF THE CORRELATION COEFFICIENT
       IF (S.LE.1.) GO TO 30
       XY=XY-X*Y/S
       XS=XS-X*X/S
       YS=YS-Y#Y/S
       AUT=XY/SQRT(XS#YS)
       RETURN
    30 AUT=-0.
       RETURN
```

```
END
     SUBROUTINE INCR (NY+NM)
     NM=NM+1
      IF (NM.LE.12) RETURN
      NM=1
      NY=NY+1
      RETURN
      END
      FUNCTION T(KT)
         TO RETURN A T VALUE FOR A 95 PERCENT CONFIDENCE INTERVAL
        (0.975 ONE-TAILED) WITH KT DEGREES OF FREEDOM.
C
      DIMENSION X(30)+XF(6)+XS(4)
      DATA X/12.706,4.303,3.182,2.776,2.571,2.447,2.365,2.306,2.262,
     1 2.228.2.201.2.179.2.160.2.145.2.131.2.120.2.110.2.101.2.093.
     2 2.086,2.080,2.074,2.069,2.064,2.060,2.056,2.052,2.048,2.045,2.042
     3 /.XF/2.030.2.021.2.014.2.008.2.004.2.000/.XS/1.994.1.990.1.987.
     4 1.984/
C -
      IF (KT.GT.100) GO TO 50
      IF (KT.GT.30) GO TO 10
      T=X(KT)
      RETURN
   10 IF (KT.GT.60) GO TO 30
      I = (KT - 31)/5 + 1
      T=XF(I)
      RETURN
   30 I = (KT - 61)/10 + 1
       T=XS(I)
       RETURN
   50 T=1.972
       RETURN
       END
```

.. -- -