

zu sein, daß die Menge des gelösten Kalkes nicht so sehr von der zur Verfügung stehenden CO_2 -Menge, als vielmehr in erster Linie von der Menge des karstmorphologisch wirksam werdenden Wassers abhängig ist. Die Summenlinie der Kalklösung schmiegt sich eng an die des unterirdischen Abflusses an (Abb. 2). Karsthydrographische Untersuchungen im Mährischen Karst (19) lassen einen ähnlichen Schluß zu. Natürlich muß CO_2 vorhanden sein, um eine Lösung im größeren Umfang überhaupt zu ermöglichen; die in der Natur gegebenen zeitlichen Schwankungen der Kohlendioxidmenge treten jedoch im Endeffekt nur bescheiden in Erscheinung. Dies sollte zur Vorsicht mahnen, bei der Erklärung klimaspezifischer Karstformen die Bedeutung des CO_2 für die Genese überzubewerten.

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THE OSCILLATIONS OF THE MIXED PRAIRIE IN KANSAS

With 6 figures and 2 tables

A. W. KÜCHLER

Zusammenfassung: Die Schwankungen der „Mixed Prairie“ in Kansas.

Wir wissen sehr wenig über die geographische Lage und Verbreitung selbst der wichtigsten Formationen der Prärie in Kansas. Er gibt zwar eine Reihe von Vegetationskarten; sie weichen aber inhaltlich stark voneinander ab.

Die Prärie entwickelte sich in einem Klima mit stark schwankenden Niederschlägen, und ihre krautige Beschaf-

fenheit erlaubt eine schnelle Anpassung an die stets kurzfristigen klimatischen Veränderungen. Der Abnahme der Niederschläge von Osten nach Westen folgend, nimmt die Höhe der Grasfluren ab. Das Zwischenstück, die „Mixed Prairie“ ist als Studienobjekt besonders interessant.

Lange Dürreperioden ermöglichen es den kurzen Gräsern, sich ostwärts auszubreiten, wo die höheren Gräser der Trockenheit erliegen. In lang andauernden Regenperioden drängen die höheren Gräser nach Westen vor. Die „Mixed

Prairie“ ist daher von zwei Schwankungsbereichen umgeben, in denen ganz ungleiche Pflanzengesellschaften verschiedene Klimaphasen darstellen.

Diese Vorgänge werden durch die Böden kompliziert. So erleichtert schwerer Lehmboden ein rasches Vordringen der Kurzgräser nach Osten, weil zuviel Wasser auf der Oberfläche abfließt. Die Rückkehr der höheren Gräser in langen Regenperioden geht viel langsamer vor sich. Diese Vorgänge sind durch ihren Einfluß auf die Masse der pflanzlichen Produktion auch von praktischer Bedeutung.

The Various Types of Prairie in Kansas

Our knowledge of the vegetation of Kansas grew from the observations of early explorers like PIKE, FREMONT and NUTTALL to the detailed results of recent researches. Most major types of plant communities are now known, as well as many of their environmental relationships. However, we remain peculiarly uncertain about the geographical distribution and extent of even the most important and best known vegetation types.

In Kansas the annual precipitation declines from about 105 cm in the east to approximately 40 cm in the west. The grasses are therefore tall in the humid east and short in the semi-arid west, hence there are three major formations: the bluestem or tall grass Prairie, the grama-buffalo grass or short grass Prairie, and between them lies the bluestem-grama or Mixed Prairie (Table 1). It is this Mixed Prairie which is particularly interesting because its geographical location is not fixed: it moves!

Actually, these Prairie types are distinguished on the basis of their height, but this is an expedient which cannot be used for precise distinctions because the same grass species will attain different heights in dif-

ferent parts of the Prairie. For instance, side-oats grama rarely reaches 50 cm in western Kansas whereas it attains 112 cm in the eastern part of the state (Fig. 1 + 2); even greater divergencies are known for big bluestem, a major dominant of the tall grass Prairie.



Fig. 1: Key map



Fig. 2: Topographic map of Kansas

Table 1: Dominant grasses of the Kansas Prairie

Prairie Type	Common Name	Scientific Name*)
Bluestem Prairie or Tall Grass Prairie	Big Bluestem Little Bluestem Indian Grass Switch Grass	<i>Andropogon gerardi</i> <i>Andropogon scoparius</i> <i>Sorghastrum nutans</i> <i>Panicum virgatum</i>
Bluestem-grama Prairie or Mixed Prairie	Big Bluestem Little Bluestem Side-oats grama Sand-dropseed Western wheat grass Red three-awn June grass Needle-and-thread grass Blue grama	<i>Andropogon gerardi</i> <i>Andropogon scoparius</i> <i>Bouteloua curtipendula</i> <i>Sporobolus cryptandrus</i> <i>Agropyron smithii</i> <i>Aristida longiseta</i> <i>Koeleria cristata</i> <i>Stipa comata</i> <i>Bouteloua gracilis</i>
Grama-buffalo grass Prairie or Short Grass Prairie	Blue grama Buffalo grass Hairy grama	<i>Bouteloua gracilis</i> <i>Buchloë dactyloides</i> <i>Bouteloua hirsuta</i>

*) All plant names are based on HITCHCOCK and CHASE (1950)

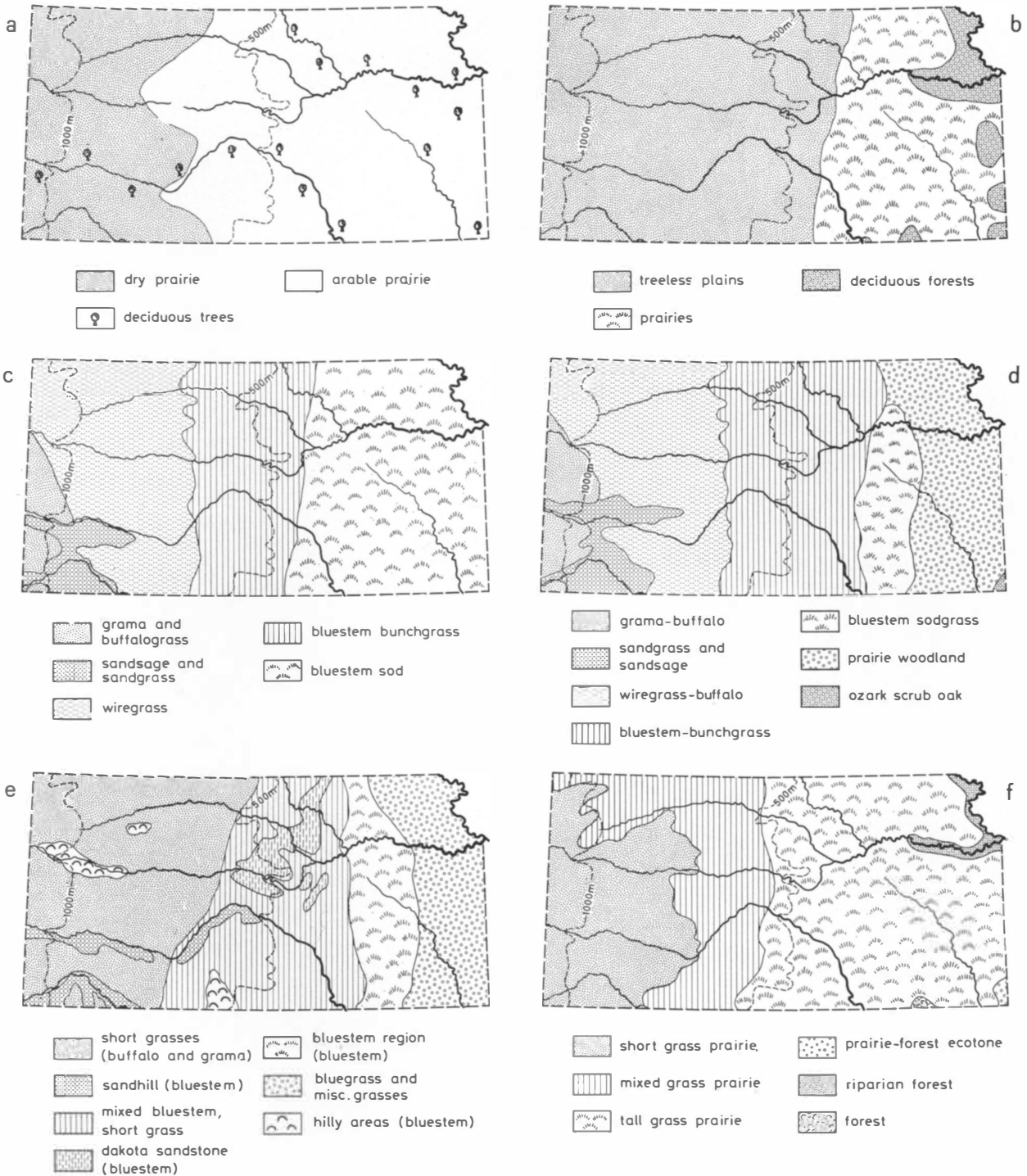


Fig. 3: a) The earliest vegetation map of Kansas (BROWNE, 1857)
 b) The vegetation of Kansas according to SARGENT (1884)
 c) The vegetation of Kansas according to SHANTZ (1923)
 d) The vegetation of Kansas according to the Southwestern Bell Telephone Company (1930)
 e) The vegetation of Kansas according to GATES (1936)
 f) The vegetation of Kansas according to CARPENTER (1940)

Various authors have portrayed the vegetation of Kansas on maps. However, nearly all these maps are vegetation maps of North America, the United States or the Great Plains. Inevitably, their original scale was small and the vegetation could be presented only in general terms. In addition, the scale varied from one map to the next within wide limits. Some examples of these maps have here been brought to a uniform scale in order to illustrate past efforts and to facilitate a comparison of the various map contents.

From the very beginning (BROWNE, 1857), the Prairie is divided into unlike sections (Fig. 3a), and it may be assumed that the "arable" Prairie is composed of taller grasses, implying a larger annual precipitation, whereas the "non-arable" Prairie seems to correspond with the more xeric short grass Prairie. Galeria forests are shown as well as occasional groves scattered through the more humid eastern parts of the Prairie.

SARGENT (1884) also divides the Prairie into two sections (Fig. 3b) but his boundary between them is much farther east than BROWNE's. He, too, shows some wooded areas in eastern Kansas.

SHANTZ (1923) retained the extent of the tall grass Prairie much as shown on SARGENT's map (Fig. 3c) but he divides the western section into four units introducing the bluestem-bunchgrass type and the wiregrass type which are today combined in the Mixed Prairie because the wiregrass type is seral. He is the first to

show the sandsage and sandgrass type and first named the short grass Prairie by its dominants blue grama and buffalo grass. SHANTZ's map represents therefore an important refinement of earlier works. SHANTZ, being a range specialist, ignores all forests.

The *Southwestern Bell Telephone Company* (1930) published a vegetation map (Fig. 3d) that shows western Kansas much as SHANTZ had done. However, the bluestem-bunchgrass Prairie (Mixed Prairie) extends farther east, and the tall grass Prairie is divided into two parts: one with scattered woodlands as originally indicated by BROWNE and SARGENT, and one without them. The latter corresponds more or less with the region of the Flint Hills which is today the largest unbroken area of tall grass Prairie in the United States.

GATES (1936) extends the tall grass region of the Flint Hills to the northern border of the state and swings the eastern boundary of the short grass Prairie eastward to the middle of the Nebraska line (Fig. 3e). GATES introduces two new vegetation types: the Dakota sandstone Prairie, a subtype of the Mixed Prairie with a relatively strong dominance of the bluestems, and the Hill areas with much little bluestem. Curiously, GATES calls the tall grass Prairie east of the Flint Hills "bluegrass" even though the bluegrass (*Poa pratensis*) is not a native of the United States. It is now common in pastures of eastern Kansas but shows a poor resistance against the occasional Prairie fires.

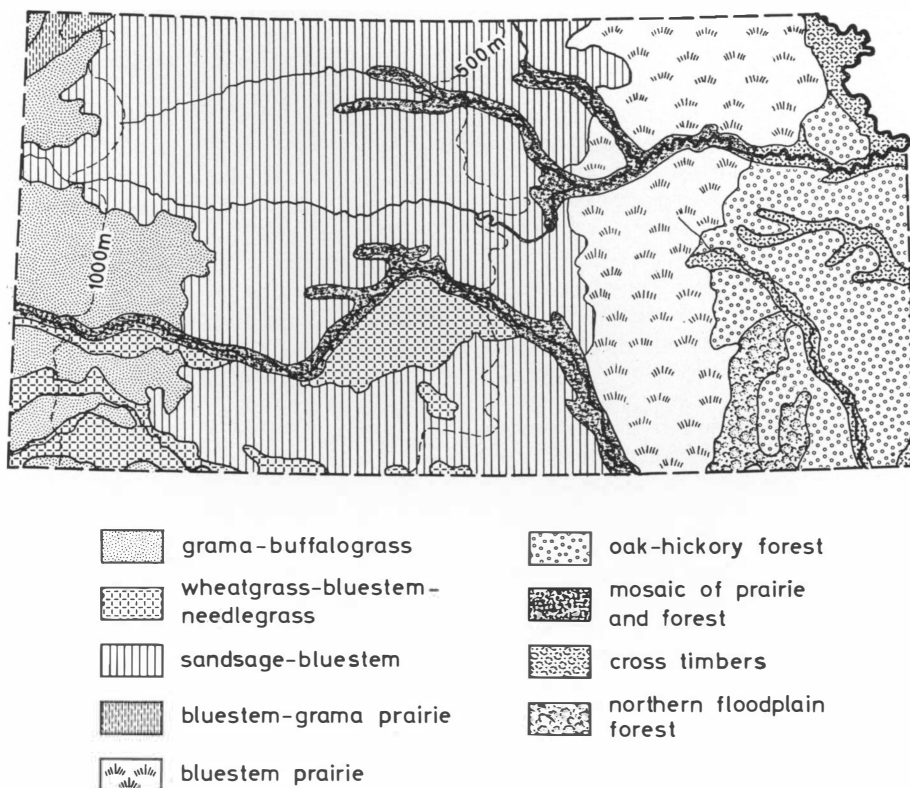


Fig. 4: The most recent vegetation map of Kansas (KÜCHLER, 1964)

CARPENTER (1940) moves the eastern border of the Mixed Prairie to the center of the state whereas its western border shows a tortuous course that never reaches the northern border of Kansas (Fig. 3f). His distribution pattern differs therefore from all previous ones.

On the most recent map (Fig. 4), KÜCHLER (1964) shows the Mixed Prairie expanded westward whereas its eastern border is approximately where SARGENT had shown it in 1884! As in Fig. 3d, the tall grass Prairie is divided into a mosaic of grassland and forest in the east and pure Prairie in the Flint Hills to the west, but with its area expanding as it approaches Nebraska to the north.

The question arises why these maps should reveal such discrepancies in the location of the vegetation boundaries. In Kansas as elsewhere on the immense plains that extend from Canada to Texas, a grassland vegetation has evolved that is particularly well adapted to the climatic characteristics of this region. In this area, the most important features of the climate are undoubtedly the amount and reliability of the precipitation, both of which decline from east to west. Sometimes the rain seems to come in distinct cycles, sometimes these cycles are blurred beyond recognition but the basic questions always remain the same: when will it rain, and how much? For the rains may come early or late; they may be evenly distributed throughout the growing season or be bunched together in a few hard showers; it may rain amply or little or, indeed, not at all.

The mean values of the annual precipitation have been recorded for many decades but they conceal the most critical of all climatic features, the rainfall reliability. For example, a given year may have an average amount of rainfall and yet experience drought conditions if the precipitation occurs in a few closely spaced large downpours.

If the mean precipitation of given months could be more or less assured, no matter how modest, the vegetation would adjust to this distribution and grow in regular annual cycles, even if little or no rain fell during part of the year. In fact, however, the irregularity and unreliability of the precipitation are so severe that they are beyond the range of tolerance of many eastern species. By contrast, western species like blue grama can go dormant whenever the water supply is inadequate, even more than once in the course of a single growing season, and resume growth when water once again becomes available. Blue grama is quite the most drought resistant of all Kansas grasses and will stay green when all others have gone dormant or have died. Big bluestem may go dormant during severe drought in the tall grass Prairie of eastern Kansas but it will die farther west.

This peculiarity of the climate of the continental interior implies inter alia that a climatic classification applied to this region may have little meaning. For

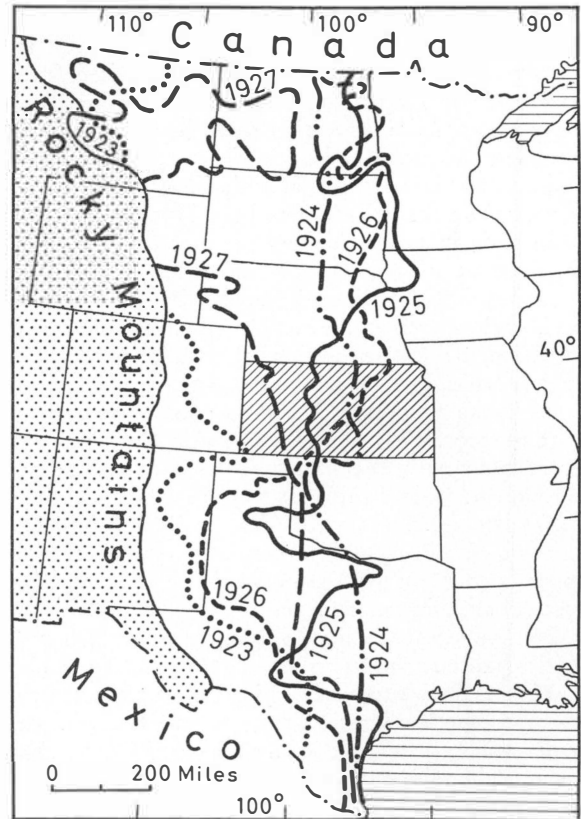


Fig. 5: Migrations of the border between humid and dry climates in the Prairie (after KENDALL, 1935)

instance, KENDALL (1935) published a map showing the location of the boundary between the dry and the humid climates according to KÖPPEN's classification for 18 years (partly reproduced in Fig. 5). The map reveals that this boundary swings back and forth over the interior plains from the Rocky Mountains in the west to a line in the east that reaches from northern Minnesota and northwestern Iowa through eastern Kansas and Oklahoma to central Texas. It shows that an average location of such a climatic border has little or no meaning in the region of the North American Prairie.

WEAVER and ALBERTSON (1956), two of the most eminent authorities on the Prairie, agree that periodic droughts are characteristic of the climate and continue: "... in some years the climate is humid and in others desertlike. It is a dynamic one with large scale fluctuations and wet and dry trends." Inevitably, such fluctuations result in a highly dynamic character of the vegetation. Unlike forests and shrub formations, the Prairie is almost entirely herbaceous. This fact assumes a particular significance here because it permits the vegetation to respond quickly and decisively to climatic irregularities with the result that the individual phytocenoses of the Prairie may change profoundly.

On the other hand, the character and extent of the floodplain forests and of the sand prairies are relatively stable, being more directly controlled by their respective substrates rather than the climate. They will therefore not be considered in this presentation.

Climatic fluctuations are not equally significant everywhere. Sometimes even considerable fluctuations are of rather minor importance. This is especially true of irregularities in the precipitation of arid or humid regions. Deserts are usually areas with the least reliable precipitation. However, whether it rains unusually much or unusually little, the climax vegetation is not materially affected thereby; it remains essentially the same in both cases. It is rather a matter of whether the ephemeral desert therophytes appear in masses, in small amounts or not at all. Similarly in very humid climates, occasional dry years are too exceptional to result in any basic changes in the vegetation. In a humid climate, the prevailing vegetation tends to consist of forests and these, of course, outlast the dry spells. They must, or else they would have disappeared long ago, and the woody vegetation would then consist at best of trees and shrubs that are still too young to have experienced a killing drought. The herbaceous vegetation on the forest floor suffers relatively little from drought because the protecting trees moderate the aggravating increases in heat and desiccating winds. No such protection is enjoyed by the plant communities of the Prairie.

These observations apply above all to climax conditions, and a word about climax may be enlightening because it was on the Prairie that CLEMENTS' vivid imagination developed this concept.

CLEMENTS grew up on the Prairie of Nebraska and his climax theory may therefore be expected to be best adapted to the vast grasslands of interior North America. It is well known that the concept of the climax at once captured the imagination of phytocologists everywhere, but at the same time it experienced a variety of modifications. Today authors speak of climax, paraclimax, plasioclimax, monocl意思, polyclimax and others, and all these authors have sound reasons to support their ideas and to recommend their adoption. What is important here, however, is one single feature that all these many forms of climax have in common with CLEMENTS' original concept. This feature is the inherent stability of the climax vegetation. Whether it is a climatic climax or an edaphic one or some other kind, the basic assumption is always that when vegetation has evolved through its various phases of succession and has reached the climax stage, it has become stabilized because it is now in harmony with its environment. This assumption is based on the further assumption that the climate and other features of the environment are stable.

This is indeed so in many parts of the world if not in most of them. What is especially noteworthy, however, is that the very region in which CLEMENTS devel-

oped his climax theory has a type of environment which is quite unstable, one that is given to wide and violent fluctuations which are faithfully reflected in equally dramatic fluctuations of the vegetation.

WHITTAKER (1953, p. 46) observes in his richly documented paper on the climax theory: "A degree of instability, involving both response to environmental fluctuations and internal dynamics of communities, is characteristic of climax populations." This is a fundamental observation because on one hand it recognizes the validity of the climax as a concept and on the other it characterizes the climax by the very opposite of the feature that seemed implied in it by definition: stability. It is instability that WHITTAKER recognizes as a characteristic feature of climax populations.

Much earlier, CAMPBELL (1936) as well as MCARDLE and COSTELLO (1936) had already emphasized the close relation between the fluctuations of precipitation and those of vegetation. These authors thereby paved the way for the recognition of problems such as we are facing here.

The Influence of Precipitation (Humidity)

Perhaps the problems of dynamism in the semi-arid grasslands are best illustrated by comparison with the seasonal aspects of vegetation. By the nature of things, spring, summer, autumn and winter cannot occur simultaneously. They result from seasonal variations in the amount of insolation and the length of day, and sometimes from the seasonal distribution of precipitation as well. Seasonal aspects of herbaceous vegetation may differ from one another both structurally and floristically yet, they are no more than seasonal aspects of the same climax population. A comprehensive discussion of any climax community must therefore take these seasonal aspects into account or run the risk of being incomplete and perhaps even misleading. As the seasons are astronomically controlled they have a prescribed length and recur with clocklike regularity.

The instability of the Prairie climax due to fluctuations in precipitation is similar: like the seasons, the dry and wet periods follow one another with unfailing certainty. In a sense, they are in the same category as the seasonal fluctuations but on a vaster scale: they cover whole series of years at a time; they are, however, less regular in length and occurrence (Fig. 6).

In a very general way, in Kansas for example, the nineties were dry, the first decade of this century was wet, the teens and early twenties were dry, the late 1920's were wet, the 30's were dry, the 40's wet, the 50's dry and the 60's were wet again. But as the graph reveals, this does not mean that a dry period always lasts 10 years. In the 30's the drought lasted 8 years and the same happened in the 50's. Interruptions seem to weaken the drought effect and a wet year after several dry years may signal the end of the drought. But if it is followed by more dry years, it is unable to arrest

the trend toward more arid conditions. Characteristically, the years with less than average precipitation exceed those with more than average precipitation at a ratio of nearly 3:2, based on a 70-years' record.

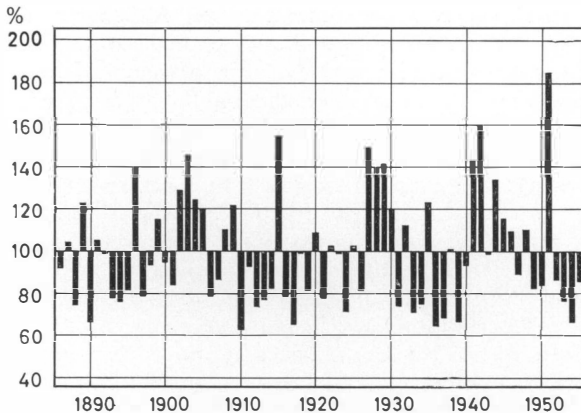


Fig. 6: The deviation of precipitation from the annual mean at Salina, Kansas (after JENKS, 1956)

Men like CLEMENTS and WEAVER believed that the humid phase of the vegetation represents the climax in the Prairie. Therefore, they extended the Mixed Prairie of central Kansas westward to the foot of the Rocky Mountains in Colorado. They called the short grass Prairie a disclimax resulting from the pressure of grazing. Their conclusions are debatable for there is no compelling reason to favor one phase over another, and the pressure of vast herds of grazing animals existed long before the advent of the Europeans with their cattle; the innumerable wild grazing animals were an integral part of the biotic environment of the Prairie vegetation. Indeed, the theory of the short grass Prairie as a disclimax was convincingly challenged by a number of scientists (VESTAL, 1931; CARPENTER, 1940; LARSON, 1940; MALIN, 1947).

During a series of wet years, many medium tall grasses, the so-called midgrasses, do indeed grow in the eastern part of the short grass Prairie, but during the 30's for instance, all were killed by the drought. The short grasses took over the space once occupied by the midgrasses so that the initial basal area was reestablished (WEAVER and ALBERTSON, 1956, p. 100).

It seems more logical to recognize the true character of the environmental conditions prevailing in the Prairie and to accept the fact that the natural environment is subject to wide fluctuations resulting in parallel fluctuations in the climax vegetation. These fluctuations imply therefore that a given place may be occupied by different phytocenoses at different times and that these phytocenoses are different phases of the local climax.

The bluestem Prairie merges in the west with the Mixed Prairie. During the drought of the 30's, the Mixed Prairie spread eastward into a broad belt of

tall grass Prairie 160–240 km wide (WEAVER, 1943) in east central Kansas, sometimes resulting in a complete change of plant populations (WEAVER and ALBERTSON, 1956, p. 229). Even pure stands of short grass, mainly blue grama and buffalo grass, were common (WEAVER and ALBERTSON, 1956, p. 248). In the western sections of the bluestem Prairie, the space opened by dead bluestem was quickly taken over by western wheatgrass and short grasses.

Needless to say, the process is reversed when the rains return and the drought is broken. But while the rate of progress during the eastward migration may be remarkably fast, the corresponding westward move is slow. Drought spells death to many taxa resulting in much open space that can be occupied quickly by eastward moving short grasses. But rain means increased vigor. The tall grasses on their westward advance must therefore invade a fully occupied area, and it takes much time before they have reached such proportions as to shade out the very heliophytic short grasses. The return of big bluestem and its companion species is therefore slow. Thus 12 years after the end of the drought of the 30's, Mixed Prairie still prevailed over two thirds of some areas it had invaded during the drought (WEAVER, 1954a, p. 269). Progress was uneven and some Mixed Prairie still lingered here and there when the fierce drought of the 50's struck and once again reversed the trend. Depending on the area involved, return to the conditions that prevailed prior to the drought of the 30's was not completed until 20 years after the cessation of the drought (WEAVER, 1961). On the other hand, WEAVER and BRUNER (1945, p. 319) observed that in an area of eastern Nebraska predrought conditions had almost been restored after only eight years, especially after three wet years.

The transition from the bluestem-grama Prairie to the grama-buffalo grass Prairie seems to be related to topography. The Prairie covers vast undulating plains where the local relief is modest with slopes varying from very gentle to steep. This type of topography implies that hill tops and uplands tend to be drier than the surrounding slopes which receive their own rain plus the water draining from the uplands. The slopes, in turn, are drier than the lower portions of the landscape. The Prairie responds clearly to this pattern.

On the uplands, the typical short grass Prairie spreads to the horizon whereas on the slopes it may be enriched by an admixture of little bluestem and other midgrasses. Finally, in depressions, buffalo wallows and along streams, taller grasses such as big bluestem may be common, at least in humid years. Tall grasses may follow stream banks for many miles, carrying a more mesic vegetation far into a xeric environment, very much in the manner of galeria forests that follow the streams of tropical savannas. It might be said that some streams in the grama-buffalo grass Prairie are flanked by tall grass galerias. Those acquainted with

the Far North will be reminded of the Tundra of northern and western Alaska where drab olive-green low-growing phytocenoses sharply contrast with the much taller, vividly green graminoid communities along stream banks and lake shores.

During periods of drought, the midgrasses on the slopes give way to the short grasses as the latter expand their area at the expense of the former. Interestingly, the more xeric little bluestem succumbs to the drought more promptly than the more mesic big bluestem. ALBERTSON and WEAVER (1942, p. 50) observed that even where little bluestem was found in large amounts, total loss of the species usually occurred. The explanation lies in the fact that big bluestem occurs primarily in low spots where water converges from a wide area. At the same time, big bluestem has a much longer root system than little bluestem and therefore can exploit water at a great depth long after little bluestem on the slopes has been replaced by blue grama and buffalo grass. Many taller grasses die during prolonged dry periods in the west. Yet they survive the drought in their seeds of which there always seems to be a generous supply and which remain viable for many years. The seeds therefore permit a relatively speedy return of the taller grasses during humid periods.

In rainy years, little bluestem and the other midgrasses spread upslope and far out on the uplands where they mingle with the blue grama and the buffalo grass. Simultaneously, the taller grasses spread a short distance up the lower slopes. During wet years, therefore, the communities of taller grasses spread into the area claimed by short grass Prairie when rainfall is deficient. Here is an area repeatedly lost and regained by either community, depending on the climatic cycle. Little bluestem gains by shading, blue grama and buffalo grass by resistance to drought (WEAVER and ALBERTSON, 1956, p. 70).

During drought, the lower places embedded in the matrix of short grass Prairie act therefore as refugia for the taller grasses and as their centers of dispersal in humid years. Amoeba-like, the mesic phytocenoses expand and contract, and sometimes disappear altogether, faithfully reflecting the climatic fluctuations and the degree of their severity.

Most of the annual precipitation in the Prairie occurs during the summer months in the form of local heavy showers. Their uneven distribution is proverbial and, as a result, the fluctuations of the vegetation proceed most irregularly through a given region. It is not uncommon that part of the region may experience acute drought conditions when another part of the same region may be distinctly humid.

The Influence of Different Soils and other Factors

The quick response of the herbaceous phytocenoses to fluctuations of the precipitation is compli-

cated by the character of the soils. Droughty soils can aggravate the climate. As the rain comes mostly in the form of heavy showers, the surface run-off is particularly great where the soil consists of fine-textured clay, permitting relatively little water to seep into the compact ground. This intensifies the drought effects and the result is that the eastward migrations of the short grass Prairie and the Mixed Prairie during periods of drought proceed more rapidly on heavy clay than on sandier soils where surface run-off is minimal and much water is stored at some depth, remaining available to plants.

The degree of replacement of one Prairie type by another depends, of course, on the intensity and duration of the rains or the drought, and ranges all the way from slight to complete. Two features facilitate these floristic changes. One is the extraordinary viability of the seeds which will survive years of drought and then sprout as the rains return. The other feature is the very light weight of the grass seed. This enables the wind to carry appreciable amounts over long distances and thus reseed the depleted areas.

In this discussion it is basic to remember that the changes in the climax vegetation always have two directions, one being the opposite of the other. As the problem of establishing or identifying the extent of phytocenoses is very complex, it may be easiest to begin by delineating the area involved.

In the east, the climate is always humid. Dry years occur, of course, but they are neither sufficiently severe nor sufficiently frequent to significantly alter the floristic composition of the climax communities. Thus, during the great drought of the 30's, the Prairie in Iowa, Missouri and farther east suffered some damage resulting in lowered productivity, but the climax populations during the drought were essentially the same as those prevailing in humid years. This was true also of some parts of the Prairie in southeastern Nebraska (WEAVER, 1961). It means that the same dominants dominate in both dry and wet years, and that in spite of drought damage the floristic composition of the Prairie remains basically unchanged.

This, of course, is not true farther west where prolonged droughts may indeed lead to a change from one phytocenose to quite a different one. Somewhere there must be a boundary which separates the bluestem Prairie in the east that never changes much, from the bluestem Prairie farther west which does change in response to rainfall fluctuations. This border may here be designated the eastern border because this study deals with conditions in the central Prairie region of North America. In principle, however, a border corresponding to this eastern border should exist in all the world's great grassland regions that are traversed by the dry climate boundary. Thus BLAKE (1938, p. 200) observed that the grasslands of western Queensland possessed a dynamic climax very much like that of the Kansas Prairie. In Queensland, the sequence of blue-

Table 2: Schematic distribution pattern of Prairie types and Oscillation Zones in Kansas

Short Grass Prairie	Western Oscillation Zone	Mixed Prairie	Eastern Oscillation Zone	Tall Grass Prairie
	humid ← years		humid ← years	
	dry → years		dry → years	

stem Prairie—Mixed Prairie—grama-buffalo grass Prairie is represented by a similar sequence with communities of blue grass (*Dichanthium* spp.)—Mitchell grass (*Astrelba* spp.)—chenopods.

The eastern border is, of course, matched by a western border. Just as the eastern bluestem Prairie is dominated by big bluestem, Indian grass, switchgrass and little bluestem, regardless of the amount of precipitation, so the western and especially the southwestern short grass Prairie is consistently dominated by blue grama and buffalo grass. Essentially, the floristic composition remains stable. Farther east, an increase in precipitation permits taller grasses to invade the carpet of short grasses for the duration of the larger water supply. A return of drier conditions means invariably the complete restoration of the blue grama and buffalo grass community.

The eastern and western borders are therefore periodic rather than permanent. They enclose an area characterized by fluctuating climax populations, separating it from areas where there are no appreciable fluctuations in the phytocenoses of the climax. This means that both the eastern and the western borders often have the same kind of vegetation on both sides, that is to say, they are borders that do not seem to separate unlike types of vegetation. For part of the time, these borders run right through major vegetation types rather than around them. This is so in the west during dry conditions when the short grass Prairie reaches farther east; in the east, this happens during wet years when the bluestem Prairie has expanded westward. When moisture conditions are reversed, both eastern and western borders will indeed separate unlike populations.

The location of these borders is not yet clearly established, and it is not certain whether it can actually be determined with a high degree of accuracy even though many detailed observations have accumulated (ALBERTSON, 1937; ALBERTSON and WEAVER, 1944, 1945; KÜCHLER, 1964, 1967b, 1969; ROBERTSON, 1939; WEAVER, 1950, 1954b; WEAVER and ALBERTSON, 1936, 1943, 1944; WEAVER and BRUNER, 1954). In particular, ALBERTSON and TOMANEK (1965) have presented carefully documented observations of vegetational changes near Hays, Kansas, during 30 years which

illustrate the complex features of the biogeocenoses of the Prairie.

In theory at least, an east-west transect across the Kansas Prairie can be divided into five zones of varying width; the grama-buffalo grass Prairie in the west, the bluestem Prairie in the east and the Mixed Prairie in the center, flanked on both sides by oscillation zones (Table 2). In these oscillation zones, the vegetation changes therefore from Mixed Prairie to tall grass Prairie and back to Mixed Prairie in the eastern zone, and from Mixed Prairie to short grass Prairie and back to Mixed Prairie in the western zone. It is in these oscillation zones where a given place may possess two types or phases of climax vegetation, depending on the prevailing conditions of the rainfall cycle.

The problems of the oscillating Mixed Prairie are fascinating many scientists and continue to stimulate research. But the interest in the geographical location of the Mixed Prairie is by no means entirely academic. The productivity of the Prairie is strongly affected both in quantity and in quality by these oscillations, creating problems of range management. Basic research in the Mixed Prairie has therefore an agreeable aroma of applied science.

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