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AN OVERVIEW OF THE ECOLOGY OF THE GREAT PLAINS GRASSLANDS WITH SPECIAL REFERENCE TO CLIMATE AND ITS IMPACT

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PREFACE

This review is the result of a combination of efforts. Much of it was written early in the US/IBP Grassland Biome study planning period as a background review document. Several years later additional review was made as part of the work on a NREL contract from the Bureau of Reclamation. Segments of manuscript materials by Box, Van Dyne, and West (North American Range Resources, in preparation) also contribute to the present paper. Like all reviews, it cannot be considered complete. The emphasis in the review is on climate and vegetation, and other parts of the ecosystem are not given much attention. However, in addition to the articles cited, a large number of supplemental references are included herein. Abstracts of most of the supplemental references may be found in Technical Report No. 236 (Blanchet et al. 1973).

This review is included in the Technical Report series to put on record a large number of references concerning the Great Plains grasslands and preliminary analysis of their ecology and responses to climatic fluctuations. As such, it should be useful in preparing summary and synthesis reports and articles for the shortgrass, mixed prairie, and tallgrass ecosystems.

ABSTRACT

The Great Plains grasslands, comprising for this discussion both the shortgrass prairie and the mixed prairie, are the largest in North America. They are bordered on the east by the true prairie, on the south and the southwest by desert grass-shrub communities, on most of the western regions by foothill communities of the Rocky Mountains or by extensions of sagebrush communities, and on the northern fringe by aspen forests. The following major plant communities comprise the Great Plains grasslands:

Plant communities	Potential acreages in the U.S. (millions)
Bouteloua gracilis--Buchloe dactyloides	78
Agropyron smithii--Stipa comata--S. viridula	65
Bouteloua gracilis--Stipa comata--Agropyron smithii	51
Andropogon scoparius--Bouteloua curtipendula--B. gracilis	33
Agropyron smithii--Andropogon gerardi--Stipa spartea	19
Agropyron spicatum--Festuca scabrella--F. idahoensis--Stipa comata	13
Agropyron smithii--Bouteloua gracilis--Buchloe dactyloides	0.6

The above acreages represent potential vegetation; extensive areas have been cultivated, especially in the eastern parts. Many cultivated areas in the western part were abandoned and are now in various stages of secondary succession. Blue grama grass is the most important plant species in the Great Plains grassland. Other important plants in approximate order of decreasing importance include buffalo grass, needle-and-thread grass, western wheatgrass, pricklypear cactus, sedges, fringed sagewort, and snakeweed.

Climate of the Great Plains grasslands is dominated by three air masses: a cold, dry mass descending from northwestern Canada; a warm, moist mass flowing north from the Gulf of Mexico; and a cool, dry current extending over the Rocky Mountains from the Pacific Ocean. Generally, annual precipitation ranges from less than 10 inches in the north to more than 20 inches in the south. Dry years are frequently 50% of the normal precipitation and wet years may be 300% of the normal. Yields in wet years may be several times those in dry years. Drought tends to be more frequent in the southern Great Plains but of short duration whereas the converse is true in the northern Great Plains. Analysis of tree ring records in the central Great Plains show more wet

years than drought years but the drought years are aggregated. Potential evapotranspiration is near 24 inches annually in areas of the northern Great Plains and along the Rocky Mountain fronts through the central Great Plains. In the southern Great Plains, annual potential evapotranspiration may exceed 36 inches. Frost-free periods range from over 200 days in the southern Great Plains to only about 120 days in the northern Great Plains.

Three major droughts have affected the vegetation on the Great Plains this century; each has had different characteristics. In the northern Great Plains droughts may greatly decrease the cover of the grasslands but not greatly alter the composition. Some species such as Sandberg bluegrass increase in density cover during the drought. Total vegetation cover may increase 100% in a few years after the drought for important species plants. In extreme drought there is death loss even of deep-rooted woody plants. Drought will also cause a delay in the phenological sequences of the dominant plants. Basal area of perennial grasses and sedges may decrease from around 30% to less than 5% in just a few years of drought. Cool-season plants such as western wheatgrass generally are not as greatly affected in drought as are the warm-season grass such as blue grama. Pricklypear cactus may spread in total and relative cover during dry years; it is damaged by insects in wet years.

Studies of changes in vegetation in the central Great Plains in response to drought show major shifts of total cover and cover composition. A species such as buffalo grass needs bare ground for establishment of its stolons. Midgrasses such as little bluestem and sideoats grama may be greatly affected by drought in the central Great Plains. Long-term studies of chart quadrats show that given plant communities take on different aspects of dominance at different times during drought-good year cycles. Russian thistle, an annual weed, may invade the weakened vegetation following the breaking of the drought. Sand dropseed frequently increases following drought, but eventually long-lived perennial grass replace it. Loss in cover is greatest on the heavily grazed areas and least on the ungrazed areas. Cover losses in the drought in the 1950's varied to 60 to 90% on areas previously heavily grazed and from 15 to 70% on areas previously ungrazed.

Several attempts have been made to predict herbage production from precipitation. Autumn soil water at 3-foot or 6-foot depths is useful for predicting herbage yield in the following year in the northern Great Plains. Adding April-July precipitation for the year in which herbage production measurements are made improves the predictions. Some 70% of the variability in herbage yield can be accounted for by precipitation and soil water variations. In Canadian Great Plains grasslands, May plus June precipitation more closely relates to forage production than at other times, accounting for 75% of the variation. In the central Great Plains, May-June precipitation accounted for about 45% of current season's herbage yield and April-August precipitation for 55%. Spring herbage production may be dependent upon the previous year's autumn moisture. Probably annual herbage yield should increase asymptotically with increasing precipitation.

Grazing animals have always been important in the Great Plains with the concentration of buffalo estimated at 20 to 40 million. There were probably also 4 to 8 million antelope as well as extensive herds of elk, deer, and smaller but important herbivores such as prairie dogs, rabbits, and numerous rodents.

Early estimates of carrying capacity of vegetation types of the Great Plains varied from about 0.5 to 2.0 acres per animal unit month. Some of the highest estimated carrying capacities for plant communities on lowlands were where runoff or subsurface moisture was available, such as inland saltgrass or alkali sacatone communities. Some of the lower estimates of carrying capacity were for dry sites with unpalatable vegetation such as snakeweed, upland sedges, and other woody plants. Carrying capacity estimates for dominant vegetation types, such as tabulated above, were generally about 1.5 acres per animal unit month. Under such stocking rates, average daily gains for steers may be higher than 2 pounds during a month with good moisture and as low as 1 pound during periods of dry conditions but still in the growing season.

Man's most important problem in managing the Great Plains grazing lands is in selecting the proper grazing intensity at which to utilize the herbage. Long-term experiments have been conducted at several locations in the Great Plains to evaluate different grazing intensities. It may require several decades of grazing at different intensities for unstable equilibria to be attained and their effects fully measured. One must take a long-term viewpoint also when evaluating the economic results of such research. Animal gains per acre may be higher under heavy use than under light use for a few years but with continued use and with almost certain eventual occurrences of serious drought there is often a shift to an advantage of moderate use. Given enough time and a full evaluation we may find light use returns are highest. As we shift to use of more grass-fat animals, the condition of the animal leaving the range becomes critical. There is an advantage for light grazing as compared to heavy grazing in individual animal response. Complete studies of the vegetation responses to grazing require at least consideration of herbage yield and composition, cover composition, drought resistance, impact on the soils such as infiltration and accelerated erosion, and impact on wildlife and recreational value of the resource. None of the studies conducted so far has made a detailed examination of all the impacts of differential grazing intensity over a long time period. Most grazing experiments have treatments described as "heavy, moderate, and light", relative terms which vary not only from location to location but also from year to year in the same location.

Man can manage the Great Plains grasslands to minimize the effect of drought. These include both vegetation and livestock management practices. Culling the herd closely in drought to make certain best breeding animals get the remaining forage and supplemental feed is a wise practice. Culling early because weight losses of livestock start in early June in drought years is important. Some advantage may be taken of drought-resistant or early-season growing species by grazing of these areas early. If such herbages are not consumed in drought years, they may be lost by weathering or to grasshoppers which frequently accompany drought, particularly in the northern Great Plains. Management following drought is important and overstocking following a drought may do severe, long-term damage to the range. Keeping the number of breeding animals well below the carrying capacity of the range allows selling off yearlings or younger stock in drought years without depleting the breeding herd. Rest-rotation grazing insures reseeding of the better grasses following drought. Where vegetation is suitable, use of mixed classes of livestock spreads the grazing load to all or more plants in the community than with a single species of livestock.

1.0 INTRODUCTION

"From southern Texas far into Saskatchewan the mid and short grasses form a magnificent prairie nearly 2,500 miles in length and approximately 400 miles wide...this is the home of the Mixed Prairie, the most extensive grazing area in North America...

...This great central grassland owes its name to the fact that its climax or original plant cover, undisturbed by civilized man, was composed of both midgrasses and short grasses intermixed and occurring on more or less equal terms.

...Vast areas of Mixed Prairie from Canada to Texas are generally green in summer and brown or gray in winter or severe drought...On level land the vast prairie in summer is a sea of waving grasses dotted with flowers and many forbs. Where midgrasses and taller forbs have been reduced by grazing and trampling, the short grasses, in early summer form a continuous carpet of green stretching away as far as the eye can see. The appearance is that of great uniformity and almost of monotony at least to all but the plainsmen...

...Plants of Mixed Prairie have the hardiness to withstand extremes of cold and heat, floods and drought; they are not depleted by plant disease or the general rigors of the habitat, even recovering from great damage by hail. They live successfully in a plant cover where competition is severe.

...Since the coming of the herds of the cattlemen and the settlement of the land, the story of the Great Plains is one of prodigal exploitation of a vast natural resource on a scale never witnessed before. This began in 1880-85 and was aggravated from time to time by severe droughts, while settlement continuously decreased the amount of rangeland.

...Mixed Prairie is of vital economic importance not only for grazing, production of hay, and control of wind and water erosion, but also for watershed protection and food and shelter for wildlife...The teeming populations of the many species of herbivores which inhabited the plains and the thriving herds of cattle and flocks of sheep which replaced them all testify to the high forage value of the vegetation."

Weaver and Albertson 1956

The poignant quotes given above, taken from an important reference concerning the grasslands of the Great Plains, well illustrate the extent, nature, and importance of these ranges. Not only is this prairie the largest of the range areas, but it is relatively productive.

Although herbage and livestock yields per acre may not be as high in the Great Plains grasslands as in some other range areas, such as mountain meadows, almost all of the plains topography lends itself to grazing. Probably more than one-third of the range beef production comes from the Great Plains grasslands.

Stretching from the High Plains of Texas northward to the Aspen Zone in Canada which border the Boreal Forest, there are wide variations in physical factors and vegetational composition in this prairie. Many of the features of the Great Plains will be discussed by region; i.e., northern, central, and southern Great Plains, but to avoid "over-generalization," specific references will be made by province or state.

Principles of ecological relationships will be illustrated both by stressing similarities and differences in soil-plant, plant-animal, and climate-plant interactions throughout the Great Plains. Where possible, data are taken from original references and simplified for presentation here. In doing so, generally data are rounded to better reflect general relationships and because, in many instances, sampling errors in obtaining such data are high and often no measures of precision are reported.

The Great Plains grassland is bordered on the east by the True Prairie, on the south and southwest by Semidesert Grass and Shrub communities, on most of the western reaches of foothill communities of the Rocky Mountains or by extensions of Sagebrush-Grass communities, and on the north by a fringe of Aspen Forest. In this regional extent of more than one million square miles are important inclusions of sandhill vegetation, isolated mountain systems, and small but significant "fingers" of riparian vegetation.

2.0 GEOGRAPHIC CONSIDERATIONS

2.1 Location

The approximate eastern and western boundaries of the Great Plains grassland are the 100th meridian and the Rocky Mountains. Northern and southern boundaries are central Texas and the Boreal Forest in Canada.

The original areas occupied by Great Plains grassland, as defined herein, are the plant communities mapped by Küchler (1964) (see Table 1).

The *Festuca scabrella* grasslands of northern Montana and Canada are often considered part of the Great Plains grassland rather than part of the Palouse grassland. This grassland appeared extensively through some of the mountainous areas of south-central Montana, central Montana, and a fringe along the foothills of the main Rocky Mountain chain from Helena northward to East Glacier where it extended out onto the plains. There it extends northward to just west of Calgary, Alberta, and as far north as Edmonton and Vermillion, Alberta (Johnston et al. 1965). A narrow band of fescue prairie extends eastward across Saskatchewan to just north of Saskatoon. From Saskatoon southeastward into Manitoba there is a mixture of fescue prairie and Great Plains grasslands (Coupland and Brayshaw 1953, Coupland 1961).

The foothills of the Rockies through much of Wyoming and Colorado are the western boundary for type 3 (Table 1). In New Mexico the Pecos River is an approximate western boundary for Great Plains grasslands to an area about 50 miles north of Carlsbad. From there the boundary would range approximately southeastward to the Texas corner which is near the southern limit.

On the southeast portion, the Great Plains grasslands generally are somewhat less than 50 miles west of a line from Lubbock to Amarillo, Texas, to where it extends northeastward to the corner of Texas and the

Table 1. Major plant communities of the Great Plains Grasslands.

1. *Agropyron spicatum--Festuca scabrella--F. idahoensis--Stipa comata*
2. *Bouteloua gracilis--Stipa comata--Agropyron smithii*
3. *Bouteloua gracilis--Buchloe dactyloides*
4. *Agropyron smithii--Stipa comata--S. viridula*
5. *Agropyron smithii--Andropogon gerardi--Stipa spartea*
6. *Agropyron smithii--Bouteloua gracilis--Buchloe dactyloides*
7. *Andropogon scoparius--Bouteloua curtipendula--B. gracilis*

Oklahoma Panhandle. Extending further into Oklahoma to as far as about the 100th meridian is an important intermixture of Great Plains and True Prairie plants, a community dominated by *Andropogon scoparius*, *Bouteloua curtipendula*, and *B. gracilis* (type 7 in Table 1). Great Plains vegetation extends east of the 96th meridian in various areas of Kansas, Nebraska, and the Dakota's. Great Plains grasslands type 5 (Table 1) there is bordered by the True Prairie.

Type 6 (Table 1) predominates in the east-central portion of the Great Plains grasslands, primarily in parts of Kansas, Nebraska, and the western Dakota's.

2.2 Acreage

The Great Plains grasslands are the largest of the range regions. In Canada it has an area of approximately 150,000 square miles (Coupland 1961). There is an additional large acreage of fescue grassland in Canada. In the United States Great Plains grassland communities occupy more than 400,000 square miles. Potential acreages of Great Plains grassland communities in the United States are summarized in Table 2.

In the United States, Montana occupies about 23% of the Great Plains grassland region, South Dakota 14.4%, Kansas and Colorado 10.9% and 10.7%, and New Mexico the least with 4.7%. The most extensive types of Great Plains grasslands are the blue grama--buffalo grass type, 30% of the total; the western wheatgrass--needlegrass type, 25%; and the blue grama--needle-and-thread--western wheatgrass type occupies about 15% of the total acreage.

Within the area of the Great Plains there are several major vegetation types not included. Most important among these are the Nebraska sandhills, the Black Hills of South Dakota and adjacent Wyoming, the Shinnery Oak

Table 2. Approximate acreages of Great Plains grasslands in the United States. Data are derived from Küchler (1964) and are expressed in square miles. Dominant species in these seven types are given in Table 1.

State	1	2	3	4	5	6	7	Total
Montana	19851	62216	--	11806	--	--	--	93973
North Dakota	--	--	--	33738	--	--	--	33738
South Dakota	--	--	--	44568	12932	985	--	58485
Wyoming	407	18071	4540	6989	--	--	--	30007
Nebraska	--	181	9231	1166	16673	--	2227	29478
Colorado	--	--	40943	2283	--	--	--	43226
Kansas	--	--	8015	--	639	--	35724	44378
New Mexico	--	--	18986	261	--	--	--	19247
Oklahoma	--	--	5239	--	--	--	12912	18151
Texas	--	--	34759	--	--	--	191	34950
Total	20258	80468	121713	100811	30244	985	.51054	405563

type in parts of Oklahoma, Texas, and New Mexico, and various low-mountain Ponderosa pine types of northern Wyoming and south-central and eastern Montana. Through Colorado, Kansas, Oklahoma, and Nebraska outside of the sandhills, there are also important areas of sand sage and bluestems. Throughout parts of Colorado and New Mexico especially, there are also extensions of Pinion-Juniper type within the Great Plains.

There is also a small amount of the bluebunch wheatgrass--fescue--needle-and-thread grass type in north-central Utah and bordering Wyoming, but this is generally not considered within the Great Plains area. Similarly, there are small areas of this type in west-central Wyoming.

The acreages in Table 2 are for potential vegetation, not that now existing in the Great Plains grasslands. Extensive areas have been cultivated, especially in the eastern parts. Many cultivated areas in the western part were abandoned and now are in various stages of secondary succession as will be discussed below.

2.3 Climate

Perhaps the best introduction to discussion of climate of the Great Plains grasslands is summarized by the following excerpt from Weaver and Albertson (1956):

> *"Climatic conditions over the Mixed Prairie grasslands are difficult to describe. The climate is one of extremes. It is commonly called semiarid but in some years it is humid and others desert-like. It is not a permanently established climate, but a dynamic one with large scale fluctuation and wet and dry trends...Located in the interior of a continent, the climate is subject to pronounced changes in temperature. Hot summers, usually with cool nights, occur throughout."*

Climate has played a dominant role in the use and abuse of the Great Plains grassland region. The climate primarily is under the influence of three air masses. These are a cold, dry mass descending into the area from northwestern Canada, a warm, moist mass flowing north from the Gulf of Mexico, and a Pacific mass, which after being forced to rise over the Rocky Mountains, reaches their eastern slopes as a cool, dry front (Borchert 1950). Some general characteristics of the climate of this area follow.

2.3.1 Precipitation--Precipitation is of overriding importance. Generally, annual precipitation is less than 20 inches except in the warmer southern portion, and only slightly more than 10 inches in the northern portion (Thornthwaite and Holzman 1941). More important, perhaps, than the average precipitation is the great degree of variability in rainfall. The dry years often are only 50% of the normal, and the wet years are often 300% of the normal.

Cold, dry and heavy Polar Continental air masses originating over the Arctic tundra advance southward and eastward across the area east of the Rockies. At times they meet Maritime air masses which are advancing northward from the Gulf of Mexico or the Atlantic. The Maritime air masses are warm, very moist, and light. When the Polar Continental air masses meet the tropical Maritime air masses, the Maritime air ascends, cools, and may form precipitation. Normally, the tropical air masses travel north and eastward from the Gulf of Mexico. But such air masses which do pass up the Great Plains provide most of the precipitation. Since these air masses originate in the south and travel north, there is a gradual decrease in annual precipitation. In many areas of south Texas, average annual precipitation is near 25 inches. In contrast, in northern Montana and the prairie provinces of Canada, annual precipitation is near 12 inches.

In much of the northern Great Plains grasslands the principal moisture-laden air masses approach from the Pacific Coast. Much of the moisture of this air is lost, however, as it rises over the Rockies. Areas near the Rockies are in a "rain shadow." Throughout the Great Plains grasslands there is a general increase in annual precipitation from west to east. Near the Rockies in northern Colorado, for example, annual precipitation is near 14 inches. But directly eastward in Kansas it may be near 20 inches. Precipitation data are given in Table 3 for a transect of sites from south to north through the central Great Plains grasslands.

When especially moist, tropical Maritime air masses meet dry Polar air masses, violent rainstorms and heavy precipitation occur (Thornthwaite and Holzman 1941). These events may produce cloudburst providing a relatively large percentage of the annual precipitation in a single storm. Yet, in other instances periods of 3 to 4 months occur during which no rain may fall.

2.3.2 Droughts--Droughts are extremely important in management of Great Plains grasslands, and this topic will receive further discussion in another section. An example of the importance of variability in precipitation, however, is obtained considering rangeland of southern New Mexico. In each cycle of 8 to 10 years there may be 3 to 4 consecutive years classified as drought years. In the northern Great Plains the droughts may not be so frequent, but they may be more extended (Chapline and Cooperridge 1941).

An analysis of tree ring records from western Nebraska shows that in a 400-year period 154 years were drought years and 237 were wet years. However, the drought years were markedly aggregated (Weakly 1943).

Table 3. Transect of weather information near the 102 meridian through the Great Plains grasslands.[a/]

State	Location	Avg Temp. (°F) Jan	Avg Temp. (°F) July	Length of Growing Season Days	Percent of Annual Precipitation Jan	Feb	Mar	Apr	May	June	July	Aug	Sept	Oct	Nov	Dec	Annual Precip-itation (Inches)
Texas	Midland	48	83	220	6	4	2	6	15	11	13	10	12	12	3	5	14.2
	Lubbock	44	82	205	4	3	4	7	13	15	12	10	14	12	3	4	17.1
	Amarillo	41	79	205	3	3	4	7	17	15	12	13	10	9	3	4	19.7
Oklahoma	Hooker	33	79	185	3	4	6	7	16	15	14	13	7	7	4	3	19.3
	Enid	37	83	206	3	4	5	10	15	13	9	12	10	8	5	4	29.2
New Mexico	Clouis	37	78	200	3	2	3	5	14	13	15	15	12	11	3	3	17.5
	Clayton	34	74	175	2	2	4	8	18	10	15	20	11	6	2	2	15.5
Kansas	Goodland	27	80	165	2	3	6	10	14	16	16	14	8	5	3	3	20.9
Colorado	Lamar	30	80	165	4	3	6	9	17	14	13	14	8	6	4	2	14.2
	Burlington	30	75	157	2	3	6	10	15	15	16	14	8	5	3	3	16.4
	Sterling	25	74	145	1	1	5	16	15	16	10	7	13	10	3	4	15.0
Nebraska	McCook	28	78	145	2	3	5	10	16	16	15	13	8	6	4	3	19.5
	Scottsbluff	25	75	137	2	3	6	12	19	22	10	7	8	5	3	3	19.1
Wyoming	Cheyenne	25	70	140	4	2	5	11	21	14	13	11	9	5	4	3	14.0
	Lusk	24	70	117	4	4	6	14	9	20	11	8	8	6	4	4	19.1
	Gillette	21	71	130	4	4	8	12	16	18	9	7	8	5	5	4	17.2
South Dakota	Cottonwood	22	76	146	3	3	6	11	18	16	10	17	6	5	3	2	17.4
North Dakota	Bismarck	10	71	143	3	3	5	8	13	22	14	12	7	5	9	2	15.4
	Williston	8	70	135	4	4	6	7	11	16	14	12	12	6	4	4	12.9
Montana	Miles City	14	74	158	5	4	6	7	14	18	13	9	8	6	4	5	13.6
	Glasgow	6	71	137	4	3	4	8	12	24	11	12	8	5	4	4	12.2

[a/] Data are from U.S. Department of Commerce, Weather Bureau, 1965 annual summary of climatological data.

Drought periods are more frequent and more severe in the southern and western portions of the Great Plains grasslands than in the northern and eastern portions.

In much of the Great Plains area one can expect more years of below-average than above-average rainfall (Hildreth and Thomas 1956). Severe droughts occurred in the High and Rolling Plains of Texas near 1917, in the 1930's, and in the early 1950's. The latter drought was the most severe on record.

There are important differences in seasonal distribution of precipitation throughout the Great Plains grasslands which helps account for differences in types of plants growing there (Table 3). In the northern Great Plains grasslands there are less acute drought conditions in early summer, and many cool-season plants take advantage of this. In much of the southern Great Plains grasslands major amounts of precipitation occur during the warm period, and many warm-season plants dominate these areas.

2.3.3 Evaporation--Although precipitation is important in the Great Plains grassland climate, no one climatic factor acts alone. Temperature, relative humidity, evaporation, and wind all have important interrelationships in their effects on range plants and animals. Evaporation is especially important in "compensating" for differences of precipitation between northern and southern portions to yield a similar vegetation. In the northern Great Plains during the April to September growing period, evaporation may average near 36 inches. For the same period in the southern Great Plains, evaporation may be well over 50 inches. Thus, due to differences in evaporation, 12 to 14 inches of rainfall in the northern plains may produce vegetation similar in physiognomy as 20 inches in the southern plains.

Unfortunately, few data are available on evaporation, and especially on the combined evaporation from soil surface and transpiration from plants, i.e., "evapotranspiration." This is understandable because instruments for measuring water movement from the earth to the atmosphere are difficult to construct and provide only relatively good data. Evapotranspiration often is measured from plants growing in sunken tanks filled with soil and in which moisture supplies are maintained. Changes in weight of these tanks then are used to calculate the evapotranspiration. Evapotranspiration also may be calculated from temperature and other considerations.

Potential evapotranspiration is less than 24 inches annually for much of the northern Great Plains grasslands and along the front of the Rockies through parts of Wyoming, Colorado, and northern New Mexico. Most of the remainder of the central Great Plains of most of South Dakota, Nebraska, eastern Colorado, Kansas, and parts of the Oklahoma Panhandle and northeastern New Mexico has average annual potential evaporation of 24 to 30 inches (Thornthwaite 1948). Most of the remaining portion of the southern Great Plains grasslands in eastern New Mexico, Texas, and parts of Oklahoma have an annual potential evapotranspiration of 30 to 36 inches.

2.3.4 Temperature--Temperature is another important climatic variable across the Great Plains grassland region. Temperature data are given in Table 3 for typical locations.

In the southern Great Plains temperatures below freezing occur only for short periods of time during the winter. In contrast, in the northern Great Plains the ground may be frozen and snow-covered for several months at a time. Frost-free periods range from over 200 days in the southern Great Plains to only about 120 days in the northern

Great Plains grasslands in the United States, and even less in some areas of the prairie provinces of Canada. In the northern Great Plains grasslands the last killing frost generally is in late May. This has an important influence on the relative abundance of cool-season grasses in the northern region in contrast to the dominance of warm-season grasses in the southern region.

Mean minimum annual temperatures across much of the Great Plains grasslands of Canada may approach -40°F (Munroe 1956). These extremely low temperatures greatly influence native biota and domestic animals grazing these ranges in the winter. Low temperature, accompanied with about 40 inches of annual snowfall through much of the prairie provinces, further restricts winter grazing.

2.3.5 Wind--Wind is an important and dominant feature of the climate of the Great Plains. High wind velocities cause considerable vegetation and animal stress. Summer winds are especially desiccating, while the winter winds often drive and drift the snow. Chinook winds are common in much of the northern portions of the Great Plains grasslands. Wind is especially important because in many areas there is little to restrain it, and drought, strong winds, and dust storms have been prominent recorded features of this area (Johnson 1965).

Wind conditions may be described in terms of "resultant winds," a product of direction and velocity. In such a resultant, the frequency of the occurrence of wind from each direction is considered with its average velocity. Resultant winds in much of the central and northern Great Plains in the spring are from the northwest or north and have relative magnitudes from about 140 to 832 (Johnson 1965). In contrast, resultant winds for March from eastern New Mexico, Texas, and Oklahoma are predominantly from the southwest or south and magnitudes are somewhat less than in the central and northern areas except for locations in eastern New Mexico. By June resultant winds are predominatly from the south throughout much of the southern and central Great Plains grasslands extending into northern Nebraska. A similar pattern is found through September, but in December resultant wind patterns take similar directions as in March, although somewhat more westerly in both the northern and southern regions.

Local topography has a strong influence on wind conditions, and subsequently on precipitation patterns. An important example of this effect is caused by the Mesa de Mayo which extends from the Rocky Mountains along the New Mexico-Colorado boundary eastward into the western edge of the Oklahoma Panhandle. This topographic feature, in effect, provides a barrier to wind movement, and resultant winds vary in direction and magnitude north and south of this area. This topographic barrier possibly may be the cause of the low annual precipitation which occurs in southeastern Colorado and the extension of the isohyetal (equal rainfall) lines westward from northern Kansas into northeastern Colorado (Johnson 1965).

Throughout the south-central and southern Great Plains March is the windiest month and August has the fewest strong winds. The western halves of Kansas and Oklahoma, the Texas Panhandle, eastern New Mexico, northeastern Colorado, and southeastern Wyoming comprise the windiest portion of the Great Plains grassland region (Johnson 1965). Much less windy areas are found in southeastern Colorado and in the regions adjoining the True Prairie. In the northern Great Plains of Canada the grassland is affected primarily by prevailing westerly winds.

2.3.6 Clonal variability in response to climate.--Over the eons climate has had an important selective influence on Great Plains grassland vegetation. Even within a species there is variation in the flowering patterns of clones taken from northern as compared to the southern areas (McMillan 1959). Thus, for plants taken from the area of Saskatchewan to Texas, clones of such dominants as *Koeleria cristata, Bouteloua gracilis,* and *B. curtipendula* show that clones from northern and western communities flower earlier than those from southern and eastern communities. Other important grasses such as *Stipa comata* and *S. spartea* represent opportunistic types which resume growth and flower as soon as conditions permit and are not dependent on geographic location. Within a species, early maturing plants of northern and western varieties generally are shorter than the late-flowering forms from the southern and eastern Great Plains grasslands.

2.4 Water and Range Use

Major rivers in the Great Plains grasslands of Canada are the South and North Saskatchewan Rivers and their tributaries which drain into the Hudson Bay region. In southern Alberta and Saskatchewan the major streams drain into the Frenchman and Milk Rivers which flow into the Missouri. The major rivers crossing Montana are the Missouri and the Yellowstone. Through North Dakota the major river is the Little Missouri, and in South Dakota the Cheyenne and White Rivers are important. The North Platte River originates in the mountainous areas of Colorado, drains north into Wyoming, and then east through western Nebraska where it is joined by the South Platte River from northeastern Colorado. Along the Nebraska-Kansas border the Republication River is an important drainage. Through southern Colorado and Kansas the Arkansas River is important. Northern New Mexico, northwest Texas, and much of Oklahoma is drained by the Canadian River system. Several rivers, especially the Brazos and the Red Rivers, arise on the Staked Plains of the Texas-New Mexico boundary area and are important drainage.

An important feature of the physiography of the Great Plains is the occurrence of extensive sandhill regions scattered primarily along the southern side of major river systems traversing the region from west to east. These sandhill areas and sandy uplands provide breaks in the shorter vegetation and areas of light textured soils.

The relative long distances between major river systems probably has an influence on the grazing by wild animals prior to settlement of the Great Plains. Many of the tributaries of the major rivers mentioned above are only intermittent, especially in drier years. Perhaps grazing animals could utilize extensive areas in the Great Plains grasslands only during the winter or early spring of the year. As tributaries of rivers dried up in the summer, native herbivores would have been restricted to areas near springs and along the permanent streams and rivers. In effect, this may have induced a partial "rotation grazing systems." In wet years this restriction would be less severe.

Some areas of the Great Plains grassland region, especially in the New Mexico Staked Plains, have relatively little in the way of surface drainage features, and natural water must have been scarce indeed before the advent of white men. Similar areas occur in parts of east-central Wyoming and portions of Montana between the Yellowstone and Missouri River systems.

Unfortunately, little is known concerning the variability in stream flow for much of the Great Plains grasslands prior to intensive cultivation of much of the region. Many speculate that streams were much more regular in flow then than now and that there were more springs throughout the region. Even today our knowledge concerning watershed relations is meager for this area.

3.0 THE VEGETATION

> *"...with the slow southward movement of the glaciers and increasing cold, wheatgrasses, needlegrasses, and others of northern origin were slowly spread into the southern Great Plains and the Southwest. Upon the retreat of the glaciers to the Polar Cap during a long, warm, dry period, these grasses (though some remained) migrated far northward. Moreover, the short grasses and their associated warm-season species moved northward from their place of origin on the Mexican Plateau. During one of the glacial epochs (Nebraskan or Kansan) it is believed that certain tall grasses, such as big bluestem, migrated westward ahead of the western and moving deciduous forest. Thus, great repeated migrations and a vast mingling of species over the Great Plains have resulted from the various pulsations of climate during glacial times..."*
>
> Weaver and Albertson 1956

3.1 Original Vegetation

The above quote concerning the historic development of the Great Plains grasslands provides hints to the main features of this vegetation. The vegetation now has and always has had warm-season and cool-season components, midgrasses and shortgrasses, and a dominance of the Gramineae over other plant families. It is difficult to reconstruct a detailed picture of the species composition of the vegetation prior to settlement of the Great Plains. Dependence upon rather limited notes in journals from the early expeditions may lead to a faulty picture of the vegetation in at least two ways. First, seldom were these early travelers trained botanists nor did they have the opportunity to make quantitative studies of the vegetation. Second, the vegetation is extremely dynamic; major shifts in yield and composition occur due to climate variations.

Let us accept the view that grazing herbivores always have been an important component in Great Plains grassland ecosystems. There is considerable evidence to justify this assumption (Larson 1940). Then replacement of the native consumers by man's domestic consumers could and should lead to relatively equal effects on the producers. Thus, by many years of examination of today's ranges which have been grazed at various seasons and intensities for many years, we can interpret what the original vegetation may have been like. Furthermore, we are able to find relicts of vegetation which have had little if any grazing by domestic livestock. In this section therefore, we will draw heavily on results of investigations made in this century throughout the Great Plains grasslands to characterize the vegetation and its variability.

3.2 Major Plant Communities

Data were given in an earlier section of this chapter for acreages of vegetation types as mapped by Küchler and which we are including in the Great Plains grassland vegetation (Table 2). This represents only one viewpoint, however, on what should be included, and various authors have categorized this vegetation in different ways. In an early map Shreve (1917) simply categorized the whole area as grassland. He made no distinction between the Great Plains and the True Prairie. Shantz (1923) mapped the following seven vegetation types of the shortgrass or plains grassland: (1) grama and western needlegrass, (2) wiregrass, (3) western wheatgrass, (4) grama and buffalo grass, (5) grama grass, (6) grama grass and mountain sage, and (7) grama and muhlenbergia. He mapped separate areas as tallgrass or prairie grasslands the following types: needlegrass and slender wheatgrass, bluestem bunchgrass, and sandgrass and sand sage or shinnery. Shantz indicated the shortgrass formation on the east follows rather closely the 2000-ft contour. We are including some areas east of that line. The occurrence of important plants in these types is summarized in Table 4.

Of importance here is the consistent occurrence of blue grama grass in each of the seven types. Buffalo grass is an important component of three of the types, and needle-and-thread, threadleaf sedge, and fringed sagewort each are important in two types. Shantz's data were based on observation, but are substantiated in part by quantitative measurements. For example, Costello (1944*a*) summarized data for "shortgrass types" from range surveys throughout major range types in Colorado and Wyoming. These surveys, made from 1937 to 1942, reflect conditions following the drought of the early 1930's (Table 5).

Blue grama was the most important "forage" producer and was the most consistent plant in sample units in both the Colorado and Wyoming shortgrass rangeland. Buffalo grass was the second most important "forage" producer in the Colorado areas, and western wheatgrass the second most important on the Wyoming rangelands. (A distinction should be made between herbage, i.e., the vegetation on the range, and forage, i.e., that part of the vegetation which actually is grazed.)

Some of the important general surveys and monographs of Great Plains grassland vegetation for various states or provinces are given in Table 6. In addition to the references in Table 6, special attention should be drawn to the book of Weaver and Albertson (1956) for it summarizes much of the ecology of indivudal plants and plant communities for the Great Plains grasslands. This book is a successful monument to the life work of two great grassland ecologists. Primary emphasis in that book is on studies in the central Great Plains; little emphasis is given therein to management problems or the biota.

Table 4. Important plants in the Great Plains grassland types characterized by Shantz (1923).

Species	Importance by Type						
	1	2	3	4	5	6	7
Bouteloua gracilis	x	x	x	x	x	x	x
Artemisia frigida	x					x	
Carex eleocharis	x						
Carex filifolia	x					x	
Gutierrezia sarothrae	x						
Koeleria cristata	x						
Phlox hoodii	x						
Buchloe dactyloides		x			x	x	
Festuca octoflora		x					
Grindelia squarrosa		x					
Hedeoma nana		x					
Lappula occidentale		x					
Leptilon canadense		x					
Plantago purshii		x					
Sporobolus cryptandrus		x					
Stipa comata		x	x				
Echinacea angustifolia			x				
Psoralea argophylla			x				
Aristida longiseta				x			
Agropyron smithii					x		
Achillea millefolium						x	
Muhlenbergia gracillima							x
Opuntia arborescens							x

Table 5. Relative frequency and herbage production of important plants in Colorado and Wyoming grasslands. Data are summarized from Costello 1944*a*).

Species	Frequency (%)		Forage Produced (%)	
	Colorado	Wyoming	Colorado	Wyoming
Bouteloua gracilis	94	82	71	65
Buchloe dactyloides	42	--	18	--
Agropyron smithii	13	73	1	7
Stipa comata	11	41	1	4
Carex filifolia	8	23	1	6

Table 6. References for characteristics of Great Plains grasslands.

References	Area
Campbell et al. (1962)	Canadian prairie provinces
Coupland (1950, 1961)	Canadian Great Plains grasslands
Moss (1955)	Alberta, Canada
Hanson and Whitman (1938)	Western North Dakota
Hopkins (1951)	Central Nebraska Great Plains grasslands
Robbins (1917)	Colorado
Albertson (1937)	West-central Kansas
Bruner (1931)	Oklahoma vegetation
Harlan (1960*a*)	Oklahoma grasslands
Bray (1906)	Texas vegetation
Weaver and Albertson (1956)	Entire Great Plains

3.3 Additional References (see Table 7)

3.4 Vegetation Change--Responses to Climatic Variability

"Because of the ground which is dismayed since there is no rain on the land the farmers are ashamed, they cover their heads. Even the hind in the field forsakes her new born calf because there is no grass."

Jeremiah 14:5,6

This biblical quote illustrates that man has long been directly affected by the vagaries of weather. The most important uncontrollable variable affecting the utilization of the Great Plains grasslands is the fluctuation in climatic conditions. In the last half-century man has experienced three serious, widespread droughts on the Great Plains. At times, however, the relatively high rainfall beckons to the farm and extensive acreages have been plowed. In good years "40-bushel wheat" is not uncommon, and the profits to the farmer are large, but the same land in dry years will produce nothing but a dust hazard. Breaking the sod on such lands in good years and abandoning them in dry years constitutes one of the most important problems to be solved in Great Plains agriculture (Harlan 1955).

Not only has drought influenced the vegetation, but also cloudbursts, hail, and extreme cold have made their mark. Most of the Great Plains topography bears mute evidence of extensive water erosion over the eons. In recent years floods have caused millions of dollars of damage along stream and river systems draining the central Great Plains. But perhaps the greatest damage done by excess precipitation has been in the form of snow following drought of the preceding growing season. For example, the summer of 1885 was dry over most of eastern Montana, and the summer of 1886 was exceptionally dry (Lommasson 1947). By autumn most of the available herbage had been grazed from the range. These two drought

Table 7. Original vegetational characteristics of Great Plains grasslands with emphasis on quantitative descriptions.

Region	Reference
Northern Great Plains	
Canada	Coupland 1950, 1961 Campbell et al. 1962 Smoliak 1965 Johnston et al. 1965
Montana	Wright and Wright 1948 Heady 1950 Vogel and Van Dyne 1966
North Dakota	Hanson and Whitman 1938 Dix 1958 Quinnild and Cosby 1958
South Dakota	Shantz 1923 Larson and Whitman 1942
Wyoming	Lang 1945
Central Great Plains	
General	Livingston 1952 Pattel et al. 1964
Wyoming	Beetle 1952
Nebraska	Weaver and Bruner 1948 Hopkins 1951 Branson and Weaver 1953
Colorado	Hanson 1955 Shantz 1906, 1923 Vestal 1914*a,b* Costello 1954 Branson et al. 1965 Hanson et al. 1931
Kansas	Albertson 1937 Riegel 1941 Webb 1941 Hopkins 1941 Tomanek and Albertson 1957 Linnell 1961

Table 7. (cont.)

Region	Reference
Southern Great Plains	
New Mexico	Heerwagen 1956
Oklahoma	Bruner 1931
	Blair and Hubbell 1938
	Harlan 1960*a*
	Rogers 1953, 1954
Texas	Whitfield et al. 1949
	Bray 1906
	Allred 1956

years were followed by the winter of 1887-88 which was the worst on record. Cold and snow, together with the lack of available herbage, caused livestock losses which were estimated at 60% for the state of Montana and 95% for the Yellowstone River Valley of southeastern Montana. Some 362,000 cattle died that winter. In recent years, however, man has developed ways to overcome the winter problems of deep snows, cold, and lack of feed. For example, in the hard winter of 1947 an extensive airlift operation was put into effect on the Great Plains to drop hay to stranded livestock. Although there is much current speculation concerning weather modification, to date man must live with extensive drought conditions on the Great Plains.

Study of the ecological impact of drought on the Great Plains grassland vegetation, which is of ecological interest in itself, is economically justified for drought certainly will return to the Great Plains. This justification is aptly reflected in the saying:

> *"He who wisely judges the past and prepares in the present, suffers less adversity in the future."*

Although some important ecological studies of responses of Great Plains grasslands to drought have been made, there are many holes in our knowledge. It is diffult to replicate drought in ecological studies; and each major drought in this century has had different characteristics. General aspects of effects of drought on the central Great Plains grasslands may be found in, and the importance of it judged by, the fact that Weaver and Albertson (1956) devote five chapters of their text, more than 20% of its contents, to discussion of the effects of drought and recovery of vegetation from drought. Even so, their text was written before the end of the drought of the 1950's. These chapters were abstracted from several of their important papers (Weaver and Albertson 1942, 1943;

Albertson and Weaver 1944*a,b*) which will not be discussed in detail here. Highlights of several other drought-effect studies in the Great Plains grasslands are summarized in this section.

3.4.1 Northern Great Plains grassland responses to drought.--Great Plains grasslands of southweatern Saskatchewan were surveyed for basal cover in 1944. Although grasslands of southwestern Saskatchewan and southeastern Alberta did not suffer as greatly during the drought of the 1930's as did many other rangelands further south, it is expected that the basal cover in 1944 was near a low point. Many of these ranges were resurveyed in 1955-56 (Coupland 1959). Annual precipitation at Swift Current, Saskatchewan, was about 14.7 inches from 1939-1943. But in 1950-54 it was 18.3. The vegetation had not suffered from serious drought since the 1930's and had benefitted from above-normal precipitation for 4 years prior to the second survey. Normally, annual precipitation in this area is about 15 inches. A comparison of basal cover composition for 48 grasslands just following a major drought and many years later was made by Coupland (1959) and is summarized in Table 8. The decade of favorable weather led to a more mesic type of vegetation characterized by the dominance of the *Stipa spartea* and by *Agropyron dasystachyum*. These decreaser species increased in relative cover while the important increasers *Stipa comata* and *Bouteloua gracilis* decreased in relative cover. It was estimated that yield increased by 137% from 1944 to 1956.

Studies on North Dakota rangeland during the drought in the 30's indicated a reduction in basal cover and of height-growth of grassland vegetation during the season of drought and in some instances a residual influence which prevented the plants from making average growth for several years (Whitman et al. 1943*b*). Changes in height-growth are

Table 8. Basal cover composition of southern Canadian grasslands with respect to favorable precipitation.

Species	Percent Composition 1944	1955-56
Agropyron spp.	8	15
Bouteloua gracilis	43	31
Calamagrostis montanensis	<1	3
Carex filifolia	2	2
Carex stenophylla	12	12
Koeleria cristata	7	8
Stipa comata	19	10
Stipa spartea	7	16

directly correlated with changes in production and, therefore, carrying capacity. The major drought in western North Dakota began in 1934, and simultaneously during the mid-30's (especially 1936), grasshoppers also damaged the rangeland. Over a 10-year period from 1932 to 1941, drought decreased the cover of North Dakota Great Plains grasslands but did not alter the composition for most species. However, Sandberg bluegrass, *Poa secunda*, increased in density and cover during the drought, a characteristic response of this species. Characteristic data from this study have been extracted from Whitman et al. (1943*b*) and are presented in Table 9. Annual precipitation in 1934 and 1946 was less than 7.5 inches for this western North Dakota area; whereas, in 1941 it was about 23 inches. Generally, cover or density of vegetation post-drought were at least 100% greater than during the drought for most of the important species. Only prairie sandreed and Sandberg bluegrass showed greater cover in the drought period than later.

Temporal variability in herbage yield is not the same for all range sites in a given area. Yield characteristics are given in Table 10 for a catena of glacial soils in northwest North Dakota during the 1958-1963 period (Cosby 1964). From his limited data he concludes that herbage production on any upland member of such a catena may have yields in wet years double those in dry years, and even greater differences may be found on locations subject to ponding. He also concludes (although no species yield data were reported) that cool-season grasses of this area have less variation in annual yield than do the warm-season grasses. The latter group is more dependent upon timely summer rains. His statements have a logical ring, but more data should be secured to support them.

Table 9. Changes in North Dakota Great Plains grasslands in relation to drought, 1934-1941.

Species	Drought Low	Post-drought High
	Cover (c) or Density	Cover (c) or Density
Blue grama	5 (c)	15 (c)
Needle-and-thread	6	12
Prairie June grass	1	7
Threadleaf sedge	0.8	1.1
Western wheatgrass	51	146
Needleleaf sedge	41	137
Little bluestem	235	516
Plains reedgrass	10	13
Green needlegrass	0.08 (c)	0.16 (c)
Prairie sandreed	152	122
Plains muhly	41	103
Sandberg bluegrass	0.05	0.74

Table 10. Herbage and mulch yields from a catena of North Dakota soils.

Soil-site	Yields in lb/acre			
	Herbage		Avg Mulch	
	Highest	Lowest	Fresh	Humic
Convex slopes and ridges	1880	990	1770	2040
General upland	2660	1350	3340	5360
Concave slopes	3530	1560	4080	5640

Drought has been such an important factor in the management of the eastern Montana rangelands that considerable attention has been given there to its influence on range and livestock production (Ellison and Woolfolk 1937, Lommasson 1947, Hurtt 1951, Reed and Peterson 1961). Early studies of the 1934 drought in eastern Montana (Ellison and Woolfolk 1937) show this was the driest year in the 57-year record. Summer rainfall was only 3.5 inches. There was even much loss of deep-rooted woody plants although some, such as silver sagebrush, regenerated successfully from below ground level in the following year. The drought of 1934 delayed the phenological sequences for western wheatgrass and blue grama in the following year. In the 1933-1935 period decreases in cover for blue grama were 75%, western wheatgrass 74%, buffalo grass 79%, needle-and-thread 62%, and threadleaf sedge 12%. In this same time period, Sandberg bluegrass increased 179%. The favorable precipitation in 1935 did not have a particularly beneficial effect on the vegetation, showing there was a severe carryover effect of the drought of 1934.

Basal cover changes of range plants in eastern Montana also showed a lag effect from the 1934-36 drought. Changes in cover were more closely associated with precipitation of the preceding year than of the current year, even for the relatively late-growing blue grama and buffalo grass (Reed and Peterson 1961). Total basal area of perennial grasses and sedges decreased from 28% in 1933, just preceding the drought, to a low of 2% in 1937 just following the drought. After the drought, Sandberg bluegrass was 4.5 times more abundant than preceding the drought, and it was more important than any other species; whereas, normally it is only a minor component of the vegetation. Threadleaf sedge, needle-and-thread, and buffalo grass reached pre-drought levels 4 to 6 years after the last extremely dry year. Almost 10 years later blue grama and buffalo grass still occupied only 85% and 64% as much area as in pre-drought years. Fringed sagewort has been noted to increase greatly under drought conditions in eastern Montana rangelands.

Cool-season plants such as western wheatgrass were not as greatly affected, with respect to height-growth, as were warm-season plants such as blue grama. Growth of both species was closely associated with current April-June precipitation. However, wheatgrass was more closely associated than was blue grama with precipitation in the preceding fall and winter. The fact that the cool-season grasses are hurt less by a single drought illustrates the importance of maintaining these midgrasses in the range to provide a more even herbage yield from year to year.

The drought of the 30's was also severe in much of Wyoming. Limited studies made in an 8-year period from 1936 to 1943 show differences in plant densities from the drought of 1936 to the years of better precipitation near 1940 (Lang 1945). Precipitation was less than 9 inches in 1936 in this east-central Wyoming Great Plains grassland. Foliage densities, measured by the point-observation-plot method, are summarized in Table 11 for two vegetation types (Lang 1945). Changes in foliage density varied according to vegetation type. Only in the cactus--grass type or on the abandoned farmland area did the relative foliage cover of grasses in 1943 exceed that in 1936. In the three grass-dominated types relative density of forbs was greater during years of high precipitation, but in the last two types which are dominated by weedy species, the relative forb density was greater during drought conditions. In part, this illustrates the stability of yield and cover of grasses as compared to forbs. Total density was greater in all types under post-drought conditions.

Table 11. Foliage density in percent on Wyoming Great Plains grasslands in response to drought.

Vegetation	Year	Total Density	Relative Density			
			Grasses + Grasslike	Forbs	Shrubby Plants	Annuals
Shortgrass type	1936	6	75	13	12	--
	1943	10	56	27	17	--
Mixed-grass type	1936	7	84	9	7	--
	1943	8	68	22	10	--
Sagebrush--grass type	1936	6	40	18	42	--
	1943	11	38	23	39	--
Cactus--grass type	1936	7	34	64	2	--
	1943	12	58	37	5	--
Abandoned farm type	1936	1	27	50	15	7
	1943	6	60	20	4	16

3.4.2 Cactus, drought, and insects.--Pricklypear cactus is prominent throughout the Great Plains on intensively utilized rangelands. Yet the amounts of cactus on a given area varies widely from year to year. Although it generally is assumed that pricklypear cactus is an indicator of poor range condition and of heavy grazing, this species may spread during dry weather. Plains pricklypear (*Opuntia polyacantha*) has not only deep taproots but also a shallow rhizomonous root system (Weaver and Albertson 1956). Pricklypear also may be spread by livestock, by means of breaking pads loose, and by rodents spreading the seed. The spines normally prevent its utilization by livestock, and when competitive plants are weakened by drought and intensive use, pricklypear may increase in abundance. Yet there is a complex interrelationship between grazing, the spread of cactus by animals, the influence of insects on the cactus, and weather.

Houston (1963) found that weather had a far greater effect on abundance and vigor of plains pricklypear than most other features of the environment in southeastern Montana. Weather influences were far more important than variations in stocking rate from 1.8 to 3.2 acres/AUM (animal unit/month) with respect to vigor and abundance of pricklypear. Although there were interactions of changes in abundance of pricklypear with weather and soils, the number of clumps per unit area decreased when the current growing season precipitation was high. Also, there is a lag in relationship between precipitation and numbers of green pads per unit area. High growing-season precipitations in 1 year is accompanied by increased dead, dying, and low-vigor pads the following year. Plains pricklypear increased in cover during the drought of the 30's, but by 5 years following the drought it was declining steadily

(Reed and Peterson 1961). Two or more consecutive years of drought probably are necessary for an appreciable kill of grasses and extended subsequent effects on these eastern Montana ranges. Cactus appears to spread during the drought period and occupies areas where is was not found beforehand. Following drought, damp and cool weather is unfavorable for cactus growth, and there is widespread death of joints and breakups of clumps. Insect infestations in cactus may have a great effect on its decline in some years (Cook 1942).

3.4.3 Kansas Great Plains grassland response to climatic fluctuations.--Several studies on Kansas Great Plains grassland with respect to drought have been summarized by Weaver and Albertson (1956) and will not be discussed in detail here. Of special interest, however, is a report of grassland cover changes in a 30-year period for grasslands near Hays in north-central Kansas. Basal cover was measured in permanent quadrats from 1932 through 1961, a time span incorporating two drought periods, 1933-39 and 1952-56. Not only were there major shifts in total basal cover, but also considerable shifts in species composition occurred in these communities (Albertson and Tomanek 1965). Changes in cover and composition of their shortgrass and little bluestem communities are of interest here.

The drought in the early 30's caused a reduction in basal cover of the shortgrass community to 30% by 1937. Total cover in this community responded well to precipitation in the early 40's; it reached 93% and was maintained there until the drought of the 50's, at which time it was again reduced to less than 30%. Buffalo grass was a major component of the shortgrass community and provided about 70% of the cover composition in the early 30's. Buffalo grass cover was drastically reduced by the drought of the 30's; it increased through the 40's and again was reduced in the drought of the 50's and did not recover its dominance by 1961. Blue grama, however, occupied about 20% of the cover early in the 30's and maintained that level through the first drought. Following an increase in cover to more than 60% by the early 50's, there was a decrease in blue grama cover to about 30% to 35% following the drought of the mid-50's.

These dramatic changes in cover and cover composition on Kansas Great Plains grasslands occurred even though the vegetation was not grazed by domestic animals for 30 years. Part of the response of buffalo grass may be because of the need for bare ground by buffalo grass stolons to aid in spread of the plant. Evidently there was considerable mulch on this area; the stolons die from growing on the mulch and not being able to root or from growing below the mulch layer and suffering from shading. Few extensive data have been published relative to changes in mulch or litter during drought periods. Certainly there is less annual contribution to the litter layer during drought because there is less productivity, but the rate of decomposition should be decreased in dry years as compared to wet years. Perhaps these factors are compensating and a relatively constant litter biomass is maintained in grasslands. More studies of the litter changes during drought are needed.

Similar changes in basal cover were noted for a little bluestem community, although the reduction in cover was not as great in the drought of the 30's. Little bluestem cover changed dramatically, varying from about 25% at the beginning of the drought of the 30's to less than 1% by early 1940; thereafter it increased slowly and was not adversely affected by the drought of the 50's (Albertson and Tomanek 1965). Sideoats grama growing in this little bluestem community, however, increased during and following the drought of the 30's but decreased thereafter. Hairy grama was of negligible importance at the beginning of this study but slowly increased to 5% to 10% by 1961.

The changes in vegetation composition in north-central Kansas were so great that a given plant community took on different aspects of dominance at different times (Albertson and Tomanek 1965). The response to the drought of the 30's was entirely different from the response in the 50's on this ungrazed area. The area was excluded from grazing in 1932, and perhaps a lack of accumulated mulch and vigor of plants was reflected in the differential responses to the two droughts. More detailed information is needed on influences of seasons and sequences of drought periods on the Great Plains.

3.4.4 Comparisons of the droughts of the 1930's and 1950's.--Surveys were made throughout the central Great Plains to determine the influence of drought of the mid-1950's on the vegetation (Albertson et al. 1957). These surveys represent the only published information concerning the 1950 drought influences on vegetation for much of Nebraska, Colorado, Oklahoma, and Texas. Very little or no information of a detailed nature is available for drought responses of South Dakota or New Mexico rangelands. Vegetation in southwest Kansas was more severely damaged by drought and dust than that described above in northcentral Kansas. The degree of drought damage between the 30's and the 50's varied throughout the plains. Albertson et al. (1957) reported that the Great Plains in the Oklahoma Panhandle was damaged more severely by drought in the 30's than in the 50's. The damage was so severe that Russian thistle and other annual weeds invaded over many areas. Cover of grasses was only 1% following the drought of the 30's, but following the drought of the 50's (total) cover was as much as 20%. In east-central Colorado, however, the drought appeared more severe in the 1950's. At the end of the drought of the 30's, cover was near 20%, but it was much less at the end of the 50's. Thus, one pattern of vegetation change occurred for the southwest Kansas, northwest Oklahoma, and southeastern Colorado area where the 1930's drought was more severe, but in east-central Colorado that in the 50's was more severe. Throughout much of the grassland when drought was most severe, sand dropseed was a frequent increasing species, but eventually buffalo grass and other grasses increased and sand dropseed decreased. The relative degree of cover loss, expressed as a percent loss from pre-drought cover to cover after the 1955-56 drought for much of the central Great Plains is summarized in Table 12 (Albertson et al. 1957). These data, rounded to the nearest 5% to reflect the precision of survey information, show that throughout this region the degree of loss was greatest on areas heavily grazed and least on areas previously ungrazed.

Although survey studies such as reported here provide considerable information about changes of vegetation with respect to drought, often prior conditions are not well known. For best interpretation of vegetation change it is necessary to examine any given area carefully and to obtain local information about grazing years and precipitation patterns. Frequently sand dropseed was an important component of the vegetation on heavily grazed areas following the drought. Greater losses are expected in east-central Colorado, as compared to northeast Colorado because precipitation was lower in that area. Generally where there was more than 80% loss as compared to pre-drought cover, this was accompanied by heavy utilization of the rangeland. This further illustrates the

Table 12. Percent loss in cover of Great Plains grasslands due to the drought of the 1950's.

Location	Degree of Grazing		
	Heavy	Moderate	Ungrazed
Southwest Nebraska	90	55	30
Northeast Colorado + southeast Wyoming	80	65	50
East-central Colorado	90	80	70
Southeast Colorado	80	70	15
Northwest Oklahoma	80	50	30
Texas Panhandle	60	45	40

importance of proper grazing intensity, for this probably is the major factor which man can control in the management of the Great Plains grasslands.

3.4.5 Grasshoppers, dust, and drought.--Blowing dust and high grasshopper populations often accompany drought in the Great Plains. Dust blown from cultivated fields has an important effect on the vegetation of adjacent rangelands. Studies in west and north-central Kansas (Lacey 1942) show that grasshopper infestations on areas moderately affected by dust reduce shortgrass yields by 50% although weed or forb yields are not greatly influenced. Heavy dust cover and grasshopper infestation simultaneously greatly reduce yields of shortgrasses although weed yields are not greatly affected by grasshoppers. The influences on herbage yields of dust and grasshoppers in north-central Kansas are summarized in Table 13 (Lacey 1942). These data, which are averages for 1939 and 1940, clearly show the influence of grasshoppers on reducing shortgrass herbage yields by at least half. Also, heavy dusting, as compared to moderate dusting, greatly decreased shortgrass yields but increased forb yields. Forb yields differed widely between the 2 years; they were more than two times as high in 1940 than in 1939 on heavily dusted areas and about eight times as high on moderately dusted areas.

3.4.6 Prediction of herbage yield from precipitation.--Man has always been intrigued with predicting future events. Add this inherent interest to the wide and uncontrollable variation in annual precipitation and resultant herbage conditions in the Great Plains grasslands, and it is surprising many efforts have not been made to predict herbage production from precipitation. If this could be done with precision, it would provide an extremely useful tool in managing these grasslands.

Table 13. Herbage yield in lb/acre of Kansas Great Plains grasslands in relation to dust grasshoppers.

Dust:		Shortgrasses		Forbs	
		Moderate	Heavy	Moderate	Heavy
Grasshoppers	with	500	125	1250	1725
	without	1100	325	1300	1750

Such relationships have been studied for Alberta, North Dakota, and Wyoming and are summarized in the following paragraphs.

Herbage yields on North Dakota grasslands were related to soil water and precipitation by Rogler and Haas (1947) (Table 14). Fall soil water at either 3-ft or 6-ft depths was relatively useful for predicting herbage yield the following year. If April through July precipitation for the year in which herbage production measurements were made was added, the predictions were improved. These studies, based on data from Mandan, North Dakota, for the 1918-1945 period, included herbage yields varying from 0 to >1000 lb/acre. Livestock yields varied from 0 to 120 lb/acre during the same period. However, livestock yields were not strongly correlated with forage yields, e.g., when herbage yield was more than 1000 lb/acre, livestock production was 90 lb/acre which was less than in at least 4 other years. At best, only about 70% of the variability in herbage yield at 60% of the variability in livestock yields could be accounted for by precipitation and soil water variations. And this requires data through July which probably would be too late to modify stocking rates.

A good idea of the influence of climatic fluctuations on forage production is reported by Smoliak (1956) who summarized the relationships between precipitation and yield for the 1930-1953 period at Manyberries, Alberta. The principal species there, in order of decreasing importance in yield, were needle-and-thread, western wheatgrass, blue grama, and June grass. Mean herbage yield for the 20-year period was 317 lb/acre for a seasonal precipitation of 5.8 inches and a May-June precipitation of 3.7 inches. After examining the relationship of herbage yields to a variety of climatic factors, he concluded herbage

Table 14. Correlations of soil water to herbage yield in North Dakota.

Correlation to:	Herbage Yield	Livestock Yield
(a) Fall soil water, 3 ft	0.72	0.52
(b) Fall soil water, 6 ft	0.74	0.64
(c) April-July precipitation	0.76	0.65
(a) + (c)	0.80	0.67
(b) + (c)	0.84	0.78

yield was more closely related to May plus June precipitation than any other factor studied. About three-fourths of the variation in herbage yield was accounted for by variations in precipitation for those months. Even though requiring only June rainfall data is an improvement over the July requirement in the North Dakota study, if the livestock manager or operator must wait until the end of June to adjust his stocking rates, not much use may be made of these relationships. In the drought years he may have already seriously damaged the range vegetation before he can find a place to put animals taken from the drought-stricken range. In years of above-normal precipitation, he may have difficulty in obtaining animals sufficiently early to take advante of the early growth period during which the livestock make the better gains.

Relationships between precipitation and herbage yield for south-eastern Wyoming rangelands were reported by Rauzi (1964). He found that May-June precipitation had a correlation of 0.68 to the current season's herbage yield, and April through August precipitation had a correlation of 0.75. These correlations are similar in magnitude to those reported by Smoliak (1956). The Wyoming Great Plains grassland area received about 15 inches of precipitation annually; three-fourths comes from April through September. Herbage yields by early June are about 250 to 300 lb/acre, but by fall the yield is about 540 lb/acre. Spring herbage production, however, was not always associated well with precipitation from April to the date of the harvest, which indicates that the previous year's autumn moisture is important. For example, about 300 lb/acre of herbage was produced in 2 different years in which the precipitation from April until the harvest date was less than 1 inch in 1 year and more than 7 inches in another year.

Precise prediction of herbage yields from the previous autumn's soil water levels or from early current-season precipitation probably would be more difficult for southern Great Plains grassland ranges than for these northern localities. Cool-season species are less important herbage producers in many of the southern ranges, and precipitation is more erratic and often later than in the northern Great Plains.

3.5 Relative Productivity of Northern Great Plains Range Sites

Methods for estimation of range condition and stocking rate as used by many range management and advisory agencies are dependent upon recognition of range sites and on data for climax composition. The range site is a certain combination of topographic, edaphic, and climatic characteristics which produces a characteristic type and amount of vegetation. In practice these range sites are given descriptive names, which may or may not coincide with plant community names. In the Clementsian sense, range sites may be categorized as post-climax, climax, and pre-climax. Twenty-eight range sites have been recognized in Montana, Wyoming, North Dakota, South Dakota, and Nebraska. Productivity for a given site and rainfall belt is assumed to be the same in all these states. Data for total annual herbage yield have been compiled by Dyksterhuis (1964), and some are presented in Table 15. A dash under herbage yield indicates that particular site is not important in that given precipitation belt. Although these data often are not obtained in the usual scientific manner, i.e., based on adequate sampling plans, and although no measures of variation are available, these results represent many years of field experience of range technicians. They should provide a point of departure for comparison and modification.

Table 15. Estimated relation of herbage yield in 1000 lb/acre to precipitation belts by range sites in the Northern Great Plains.

Site	Precipitation (inches)					
	5-9	10-14	15-19	20-24	25-29	30-34
"POSTCLIMAX"						
Wetland	5.0	5.6	6.0	6.3	6.5	6.7
Subirrigated	3.5	4.1	5.0	5.5	5.8	--
Saline subirrigated	2.5	3.0	4.0	5.0	--	--
Overflow	1.5	2.5	3.3	3.9	4.8	5.5
Saline overflow	1.0	1.7	2.9	--	--	--
Sands	1.0	2.0	2.6	3.0	3.4	--
Savannah	--	1.5	2.5	3.2	3.8	4.5
"CLIMAX"						
Sandy	0.8	1.6	2.3	2.8	3.3	4.0
Silty	0.7	1.5	2.2	2.8	3.7	4.5
Clayey	0.6	1.3	2.1	2.7	3.4	4.2
"PRECLIMAX"						
Choppy sands	--	1.5	2.0	2.5	--	--
Thin sandy	0.5	1.2	1.8	2.3	3.3	--
Thin silty	0.5	1.1	1.7	2.2	3.2	4.3
Thin clayey	0.5	1.1	1.7	2.2	3.2	4.0
Shallow clay	--	1.0	1.5	2.1	2.7	3.4
Shallow gravel	--	1.0	1.5	2.1	2.7	3.4
Shallow limy	0.5	0.9	1.4	1.8	2.1	2.4
Shallow nonlimy	--	0.9	1.4	1.8	2.1	2.4
Panspots	0.5	1.0	1.5	--	--	--
Dense clay	0.5	0.9	1.4	1.9	2.9	3.9
Thin loess	--	--	1.4	1.8	2.3	2.8
Thin breaks	0.5	0.9	1.4	1.8	2.3	2.8
Coarse sands	--	--	1.3	1.8	--	--
Gravel	--	0.6	1.1	1.6	--	--
Very shallow	0.3	0.6	0.9	1.1	1.2	1.3
Saline upland	0.3	0.5	0.7	--	--	--
Shale	0.2	0.4	0.6	0.8	--	--
Badlands	0.2	0.4	0.6	--	--	--

These data are for ranges in excellent condition. The herbage yield on these sites is primarily from nonwoody plants. The percent of the yield due to woody plants, however, generally is directly proportional to the annual precipitation. On some sites woody plants are important; e.g., approximate percent of the annual herbage yields due to woody plants by sites for the 10" to 14" precipitation belt are saline overflow 25%, thin breaks 20%, very shallow 40%, saline upland 30%, and shale 20%.

Probably annual herbage yield should increase asymptotically with increasing precipitation. This is reflected in Table 15 to some extent. However some anomolies exist, especially for differences between the higher rainfall belts. For example, on the "thin silty" site differences in yield in 100 lb/acre between rainfall belts are 0.6, 0.6, 0.5, 1.0, and 1.1 going from the 5- to 9-inch up to the 30- to 34-inch precipitation belt. Reasons why an additional 5 inches of precipitation in a higher rainfall region accounts for almost twice the yield increment as the same precipitation increment in low rainfall regions were not discussed by Dyksterhuis (1964). Reverse unexplained relationships occur for some other sites in Table 15. For example, on the dense clay site in the low rainfall areas a 5-inch precipitation increment gives 400 lb/acre yield increment, but in high rainfall belts the same precipitation increment gives a 100 lb/acre yield increment.

More comparative information of the type presented in Table 15 is needed. Results should, however, be based on and refer to published data when possible, and more data now in the files of range technicians relating sites and precipitation to yield should be published for critical evaluation by grassland ecologists. Such information and evaluations will contribute greatly in the future to the theory of range science. The importance of sound basic data concerning composition of climax Great Plains grasslands is illustrated by the study of Coupland et al. (1960). They examined the large influence of short-term fluctuations in weather on the composition of ungrazed ranges in Canada. This in turn influences estimates of range condition and stocking rate. They showed estimates of range condition may vary by more than 25% depending upon the basic data used for the climax composition. More reliable data are needed to be incorporated into the technician's guides used in judging climax composition.

3.6 Nonriparian Woodlands in the Great Plains Grasslands

In earlier sections we have indicated that there were important inclusions of forested areas in the Great Plains. Notable ones include the isolated mountain chains in Montana, the Black Hills of South Dakota, the Black Forest area of central Colorado, and the Mesa de Mayo area at the juncture of Colorado, New Mexico, and Oklahoma. Additional nonriparian woodlands are found throughout the Great Plains grasslands in areas of precipitation much lower than would be expected for tree growth. Such woodlands occur primarily on scarps or other rough, broken, or steep topography (Wells 1965). Important trees on these nonriparian woodland inclusions are listed in Table 16. The presence of these trees in part reflects the ease of infiltration of moisture into the soils in the scarps. Gentle scarps of small height and extent, however, may lack woodland. Wells (1965) has hypothesized that fire is an important factor on the maintenance of woodlands on scarps throughout the Great Plains grassland. These abrupt scarps or topographic breaks have acted as natural firebreaks. Fire has been an important factor in the history

Table 16. Trees in nonriparian vegetation of the Great Plains grasslands.

Pinus ponderosa	Montana, North Dakota, South Dakota, Wyoming, Nebraska, Colorado, Canada
Juniperus scopulorum	Montana
Pinus flexilis	Montana, Canada
Populus tremuloides	North Dakota, Canada
Quercus macrocarpa	North Dakota, Canada
Cletis occidentalis	Nebraska
Juniperus virginiana	Nebraska, Kansas, Oklahoma
Pinus edulis	Colorado, New Mexico, Oklahoma, Texas
Quercus stellata	Kansas, Oklahoma
Juniperus pinchotii	New Mexico, Texas
Quercus mohriana	New Mexico, Texas
Juniperus monosperma	Oklahoma
Quercus marilandrica	Oklahoma
Quercus muhlenbergii	Oklahoma
Quercus shumardii	Oklahoma
Quercus undulata	Oklahoma
Juniperus ashei	Texas
Quercus virginiana	Texas

of vegetation. Due to frequent droughts, flat topography, and strong and constant winds, fires may sweep across the relatively smooth surface of the plains for great distances before being stopped by an obstacle. Since the last period of glaciation, it is probable that fire has increased in frequency and thus has influenced the development of vegetation throughout the Great Plains. The status of fire, however, is controversial, and some workers believe fire has been only incidental in the development of grasslands (Beetle 1957). In any event, trees can exist on certain sites. Shelterbelt plantings in the northern Great Plains have been especially successful in the higher rainfall areas. At the extreme northern extent of the plains bordering the fescue prairie, quaking aspen is found. Even minor depressions in the topography in the fescue ranges provide conditions suitable for aspen growth. Limber pine (*Pinus flexilis*) which often is found on rocky, windswept slopes in the southern Rockies may occur on the lower foothills and even extends onto the plains in northern Montana and Alberta. In some places there it provides an appearance similar to the Pinyon--Juniper type of the Southwest.

4.0 THE ANIMALS

> *"The Great Plains have been the homeland of grazing animals for geologic ages. The fossil remains of the four-toed horse is found in deposits in the fossil beds in many areas of the Plains. Other mammals such as the elephant, camel, and buffalo also roamed these primeval grazing lands. Early American explorers found millions of buffalo, antelope, and other animals living on the vast steppes between the Mississippi and the Rocky Mountains. ... With the western migration of the white man, the wild game was doomed to a heavy reduction in numbers, and by 1889 the vast herds of buffalo in North America had dwindled to less than 1000 head. Hard on the heelds of the disappearing buffalo came the lowing trail herds of cattle from Texas."*
>
> Allred 1940

This quote emphasizes that either wild or domestic herbivores have found the vegetation of the Great Plains grasslands sufficient for their year-round nutritional needs. Yet there are definite limits to which this vegetation may be stocked. Utilizing the Great Plains grasslands at the proper intensity is the key problem in range management. Grazing intensity studies are the subject of a later section, and stocking rates will be discussed there. In this section we will discuss some early estimates of stocking rates and some for areas not covered in other sections of this Chapter. Also we will briefly consider the value of Great Plains grassland vegetation as food for herbivores, and, in a general manner, we will discuss the use of these ranges by wildlife.

4.1 Comparative Carrying Capacity of Great Plains Grassland Ranges

Early ecologists examined vegetation types of the entire western range and made estimates of carrying capacity for cattle. Carrying capacities were assigned for the "average period of time each year that vegetation can be grazed without injury." Generally they refer to yearlong grazing. Aldous and Shantz (1924) gave estimates for more than a third of the 102 vegetation types that were recognized west of the 100th meridian and which are important in the Great Plains (Table 17). These early range examiners certainly were perspicacious. Most of their predicted carrying capacities have been borne out in a relative manner by later ecological study, but in a few instances their estimates seem to be in error. For example, they list the carrying capacity of the *Andropogon scoparius* type at less than many of the other plains grassland types. However, it must be stressed that their estimates are not for the True Prairie east of the 100th meridian or the little bluestem types in the southern high plains. They refer to the little bluestem that

Table 17. Early estimates of carrying capacity of vegetation types of the Great Plains.

Vegetation	Cattle/Section
Bouteloua gracilis	20-40
B. gracilis--Agropyron smithii	30-60
B. gracilis--Carex filifolia	20-40
B. gracilis--C. filifolia--Koeleria cristata	30-60
B. gracilis--Artemisia frigida	25-50
B. gracilis--C. filifolia--Artemisia tridentata	15-25
B. gracilis--Atriplex canescens	15-30
B. gracilis--Psoralea tenuiflora	50-90
B. gracilis--Gutierrezia sarothrae	5-15
B. gracilis--Artemisia cana	30-60
B. gracilis--Stipa comata	40-80
B. gracilis--Buchloe dactyloides	25-50
B. gracilis--B. dactyloides--S. comata	35-75
B. gracilis--B. dactyloides--Aristida longiseta	20-40
B. gracilis--B. dactyloides--A. smithii	30-75
B. gracilis--B. dactyloides--P. tenuiflora	30-65
B. gracilis--B. dactyloides--Yucca glauca	25-50
B. gracilis--B. dactyloides--Prosopis glandulosa	40-60
B. gracilis--B. dactyloides--G. sarothrae	15-25
A. smithii	10-50
A. longiseta	15-30
Andropogon scoparius	20-40
Bouteloua hirsuta	15-25
Distichlis stricta	50-150
C. filifolia	5-15
G. sarothrae	5-10
G. sarothrae--A. frigida	5-15
Hilaria mutica	15-30
Sandhills mixture	20-50
Sporobolus airoides	50-100
Sporobolus wrightii	50-100
S. comata	20-40

occurs as relict areas along the foothills of the high plains, or on gravelly, rocky, or rough sites throughout the plains. Some of the more productive types were those of swales or bottomlands receiving runoff water, such as the last tree in Table 17, the *Bouteloua gracilis--Psoralea tenuiflora* type of upland, light-textured soils, and the *B. gracilis--Stipa comata* type of the northern Great Plains. Types characterized by *Gutierrezia sarothrae* and *Artemisia frigida* represent depleted pastures with low carrying capacity.

Shantz (1923) segmented the Great Plains south of the Canadian border into seven types. His estimates of carrying capacity for these types are given in Table 18; data in brackets in this table are inferred from his discussion. The western needlegrass referred to in Table 18 is needle-and-thread. The wiregrass type represents the three-awn type common as a stage in old-field succession. Mountain sage refers to fringed sagewort. Again, comparable to data in Table 17, highest carrying capacities are found on vegetation dominating lowland sites, i.e., the western wheatgrass type.

General relationships between stocking rate and basal cover for several counties in the north-central and western Kansas Great Plains were reported by Cressler (1942) and are presented in Table 19. These central Kansas areas were in ≥20-inch precipitation belts. Stocking at 15 acres/AUM resulted in excessively heavy use, and the vegetation became dominated by buffalo grass and blue grama grass. Similarly, in western Kansas areas in ≤19-inch precipitation belts, cover was decreased by heavy use. However, as noted in other studies in Kansas and Nebraska, basal cover may not be a good criteria of herbage productivity. Midgrasses may produce high yields but little basal cover and conversely

Table 18. Some Major Great Plains Grassland Range Types and Their Estimated Carrying Capacity

Shantz's (1923) types	Head of cattle/section Yearlong grazing
1. Grama grass	15-30
2. Grama and buffalograss	20-40
3. Grama and western needlegrass	20-60
4. Wiregrass	[20-40]
5. Western wheatgrass	30-75
6. Grama grass--mountain sage	20-30
7. Grama and muhlenbergia	["inferior"]

Table 19. Relations of precipitation and carrying capacity in Kansas Great Plains grasslands.

Stocking	Central		Western	
	Acres/AUM	Cover (%)	Acres/AUM	Cover (%)
Heavy	15	22	17	15
Moderate	20	31	20	26

for the shortgrasses. This early survey by Cressler (1942) indicated there would be advantages in rotating grazing use from year to year. He suggested that deferment of a given pasture during the growing season would be better than continuous grazing at the same intensity. His studies also indicate that winter grazing produces greater basal cover, of the bunch- or midgrass type, than does summer grazing at the same intensity.

As was mentioned above when discussing the Great Plains grassland vegetation of Texas, few detailed studies have been made in the area. Similarly, no grazing intensity studies have been made for this area. Estimates of "average safe stocking rates" for these ranges, and comparative values for the High Plains bluestem types to the east and the shinnery oak and savannah oak to the south and west were reported by Allred (1956) and are presented in Table 20. Under excellent range condition the Texas Great Plains grasslands have a carrying capacity similar to that in the savannah types which receive more rainfall. Even though the ranges are dominated by warm-season grasses, livestock still make their best gains on these ranges early in the season. An example of seasonal livestock gains on Great Plains grasslands of northwest Texas, based on a 4-year study (Whitfield et al. 1949), are described as follows. Average daily gains by steers on blue grama--buffalo grass pasture from April through September were 1.9, 2.0, 1.1, 1.4, 1.4, and 1.0 lb. Overall gains for the 151-day grazing season were 1.45 lb/head/day, or a seasonal gain of about 220 lb.

4.2 Native Biota of the Great Plains Grasslands

Herbivores have always been a part of the Great Plains grassland biotia. In addition to the abundant buffalo, deer, antelope, and a

Table 20. Stocking rates in acres/cow/year for Texas Great Plains grasslands and some adjacent range types.

Plant Community	Range Condition			
	Excellent	Good	Fair	Poor
Mixed prairie	16-23	25-30	35-40	>55
High plains bluestem	14-16	18-22	25-30	>35
Shinnery oak savannah	18-20	24-26	35-40	>55
Post oak savannah	18-22	28-32	50-60	>70

subspecies of the big horn sheep which lived in the area, originally there also were many elk. Smaller, but important herbivores include prairie dogs, rabbits, and numerous rodents. The concentration of buffalo in the Great Plains grasslands is open to much speculation, but it is expected to have been 20 to 40 $\times 10^6$ (Larson 1940). Seton made an estimate of 20 $\times 10^6$ buffalo on the open plains before the advent of white man based on a requirement of 30 acres/head/year. But this stocking rate would be excessive for the Great Plains in many areas. In addition to the buffalo, there were probably 4 to 8 $\times 10^6$ antelope and extensive herds of elk, deer, and other herbivores (Larson 1940). That the buffalo had an impact on the vegetation of the Great Plains is supported by the following quote from an early report (Hornaday 1889):

> *"Of all the quadrupeds that ever lived upon the earth probably no other species has ever marshalled such innumerable hosts as those of the American bison. ...To my mind the evidence is conclusive that although the northern herd ranged over such an immense area it was numerically less than half the size of the overwhelming magnitude which actually crowded the southern range and at times so completely consumed the herbage of the plains that detachments of the United States Army found it difficult to find sufficient grass for their mules and horses."*

The elk once was an important herbivore of the Great Plains grasslands but probably was restricted to areas in the northern and central Great Plains especially north of the Arkansas River in Colorado and Kansas (Taber 1966). Even today the elk has been successfully reintroduced into rougher portions, such as the breaks along the Missouri River in eastern Montana. The elk is extremely adaptable in its food habits and can make excellent use of rangelands where there is a mixture of browse plants available. Even today when the elk is thought of characteristically as a mountain animal, extensive areas of its winter range are on upper reaches of the Great Plains in the foothills of Montana and Wyoming.

The mule deer originally ranged across much of the Great Plains but often was restricted to the rougher lands along the breaks of the deeper canyons; it was especially prominent in the northern Great Plains (Taber 1966). The white-tailed deer was much more common throughout the Great Plains than was the mule deer. Perhaps this species has a greater variability in its dietary preferences. Wherever sufficient woody cover existed, the white-tailed deer was and still is found across the prairie.

Before the advent of white man to the Great Plains, the range of the moose actually extended into the northern Great Plains grasslands in some of the Prairie Provinces of Canada. It was primarily important around the southern fringes of the boreal forest.

The antelope still is an important wild herbivore throughout the Great Plains grassland ranges, especially in the central and northern regions. This animal has been the subject of a number of food habit studies (e.g., Cole 1956, Dirschl 1963) because of its possible competition with livestock, especially sheep, for forage. Generally it is considered that browse is a major food in the diet of antelope in late fall, winter, and early spring. Browse probably makes up the bulk of the diet on a yearlong basis, but forbs are an important component throughout the year. Grasses are of major importance only in the spring (Cole 1956). Diet of antelope, however, vary widely and these animals may exist on ranges almost devoid of browse plants, such as in the central Great Plains. Still, half-shrubs or forbs comprise the majority of their diet.

Small herbivores were an important component of the Great Plains grassland biota; a characteristic animal is the blacktail prairie dog (Koford 1958). This animal ranges throughout the Great Plains grasslands of the United States but does not extend extensively into Canada. The effect of the prairie dog on rangeland has been a highly controversial one. Many ranchers feel that the animal competes extensively with livestock for forage, and many sportsmen and conservationists feel that there is little competition between the two. Solution to this argument is highly dependent upon your point of view, but the extensive paper by Koford (1958) is a good introduction to the literature on this animal.

Another important herbivore of the Great Plains grasslands is the jackrabbit. Especially in the central Great Plains this animal has been found in great densities. At times densities in the Great Plains have been so great that it has been the subject of large and successful hunts and drives (Tiemeier 1965). The influence of the jackrabbit on the rangeland often is more noticeable during drought, such as it was during the droughts of the 30's and 50's in the central Great Plains grasslands. Early in drought periods the range of the jackrabbit may increase due to more favorable carrying capacity because of plant species composition shifts (Bronson and Tiemeier 1959), but late in drought periods carrying capacity is reduced due to denudation or lack of herbage. This causes concentration of the animals in areas where herbage is available, such as on croplands, and there is much subsequent damage.

Insects and other smaller organisms have played an important role in the Great Plains grasslands. Insect numbers have been shown to vary with grazing intensity and shifts in herbage composition (Weese 1939) and to change in abundance as areas are eroded (Smith 1940). But for some organisms, for example, grasshoppers, it is suggested that changes in vegetation are not directly responsible for initial fluctuations in population density (Anderson 1964). The relationships of individual species of insects to grazing conditions are not thoroughly summarized or known and are deserving of further study.

5.0 MAN AND THE GREAT PLAINS GRASSLAND SYSTEM

5.1 Management Problems--Grazing Intensity and Systems

> *"The pioneers in the plains had little conception of the nature or value of grass. Their viewpoint of a crop was that of the farmer, the producer of corn, wheat and clover. The crops were totally harvested annually. Thus, why not harvest all the grass crop by continuous grazing? Anyway, grass was plentiful, enough for everyone."*
>
> Weaver and Albertson 1956

The most important principle in management of Great Plains grassland ranges from Texas through Canada is selecting the proper grazing intensity at which to utilize the herbage. To provide information on range and livestock responses, experiments have been conducted at several locations throughout the Great Plains to evaluate different intensities of grazing (Table 21). In addition to the research listed in this table, which are primarily on intensity of grazing and rotation grazing studies, several important grazing capacity surveys have been made in the Great Plains grasslands, e.g., Clarke et al. (1942). The locations of the studies listed above are in the Great Plains grasslands *per se*, but important grazing intensity studies also are in progress on Sandhill ranges in or adjacent to the Great Plains grasslands at Akron, Colorado; Scottsbluff, Nebraska; and Woodward, Oklahoma. Further south

Table 21. Important grazing studies in the Great Plains grasslands.

Location	Reference(s)
Stavely, Alberta	Johnston 1962
Manyberries, Alberta	Clark et al. 1947, Hubbard 1951, Smoliak 1960
Miles City, Montana	Holscher and Woolfolk 1953, Hurtt and Woolfolk 1940, March et al. 1959, Reed and Peterson 1961, Woolfolk 1949
Mandan, North Dakota	Rauzi 1963, Rogler 1951, Sarvis 1923, Sarvis 1941
Buffalo, South Dakota	Dinkel et al. 1958, Gartner et al. 1965
Cottonwood, South Dakota	Johnson et al. 1951, Lewis et al. 1956, 1965
Ardmore, South Dakota	Black et al. 1937
Cheyenne, Wyoming	Birch and Seevers 1960, Lang et al. 1956
Nunn, Colorado	Costello 1944*b*, Klipple 1964, Klipple and Costello 1960
Hays, Kansas	Launchbaugh 1957, Tomanek and Albertson 1957

in Texas important grazing intensity and system of grazing studies have been conducted on the Edwards Plateau near Sonora and Barnhart, Texas. Most of the grazing intensity studies have been with cattle, but two important studies in the northern Great Plains have been with sheep. With cattle, part of the studies have been made with cows and calves and part with steers and heifers.

It is fortunate that early range scientists had the foresight to initiate grazing intensity experiments. It may require several decades of grazing at different intensities for unstable equilibria to be attained and their effects fully measured. One must take a long-term viewpoint also when evaluating the economic results of such research. For example, animal gains per acre may be higher under heavy use than under light use for a few years. With continued use, however, and with the almost certain eventual occurrence of serious drought, there often is a shift to an advantage of moderate use. Given enough time and given a full evaluation we may find light use returns are highest. Full evaluation of grazing intensity requires studying not only gross livestock production but quality and post-performance of the livestock taken from the range. Complete studies of the vegetation responses to grazing require at least consideration of herbage yield and composition, cover and cover composition, drought resistance, etc.

The long-term impact of heavy use may be reflected in changes in soil properties, decreased infiltration rates, and accelerated erosion. These properties need to be examined, too. Another aspect to consider when evaluating and comparing grazing intensities is the impact on wildlife, and eventually on the recreational value of the resource.

For none of the studies listed above has a detailed examination of the differential grazing intensities that have been made. Yet each of the long-term grazing experiments provide a multitude of opportunities for present and future scientists. These designed, and often replicated, experimental pastures should be maintained until complete analysis has been made of the effect of grazing on the ecosystem. Perhaps the differential effect of grazing treatments will be reflected in variations in livestock production.

Some aspects of vegetational change and change in soil properties may require many more years of treatments before large differences are produced. Yet detection, measurement, and comparison of these changes is vital to our use of the Great Plains grasslands for many generations. Man has been a major manipulator on the Great Plains for only a relatively short period of time. As late as the mid-1800's buffalo roamed over the area that now is Denver. We should be slow to terminate studies of such importance when many have been in effect for less than 30 years when the changes we are attempting to measure may be essentially irreversible.

Grazing treatments in these long-term studies often are described as "heavy, moderate, and light." Of course these terms are relative. Their meaning varies not only from location to location, but also from year to year in the same location.

Not only are none of the existing researches complete (with respect to measuring all important soil, animal, vegetation, and economic differences), but there is a complete lack of information for some areas. No long-term experiments have been conducted that are fully representative of the ranges of the southern Great Plains nor of the areas in southeastern Colorado and southwestern Kansas! Results of no single study can be considered "typical" because of differences in treatments, measurement techniques, climatic sequences, and duration.

5.2 Management Problems--Watershed Relationships

The Great Plains represents a huge watershed about which we have relatively little knowledge. We do know, however, that man's use has greatly affected watershed value of the original Great Plains. For example, Riegel et al. (1950) reported studies on a pasture in north-central Kansas in which a spring-fed stream flows through a 140-acre pasture. This stream flowed continuously before a large part of the native sod in the community was broken for cultivation. Following cultivation in the area, the stream only flowed intermittently. This illustrates the importance of the native vegetation cover on maintaining uniform stress flow. Unfortunately, few data of this type are available for the plains area. The importance of the Great Plains grassland vegetation on watershed values is underestimated. Early reports illustrate clearly the importance of vegetation cover on the Great Plains with respect to water relations.

> *"The high plains are conspicuously uplands of survival. Yet their mass, to depths often of several hundred feet, is of unconsolidated silt, sand, and gravel. They are plateaus by virtue of their resistance to erosion, yet they are soft plateaus. Their survival has been due to the protective influence of a universal close-knit sod, to which a subhumid precipitation especially has given origin, and yet against which it is unequal, on a grade of 10 feet to a mile, to accomplish the first faint beginnings of erosion and the initiation of drainage. There is no fun-off. Even heavy local downpours, which in the arid belt, by rapid concentration, would result in local floods and sharp channeling, are here rendered practically inert by the grass mat until disposed of through ground absorption and evaporation. The High Plains, in short, are held by their sod."*
>
> Johnson 1900

It is obvious this situation no longer exists!

Herbage yield has been shown to be directly related to precipitation. Even though precipitation occurs, if there is excessive runoff, an apparent lack of moisture may occur. Thus, numerous studies have been made to relate infiltration rate or runoff rate to range conditions, and some have been reported above with respect to grazing intensity studies. Additional examples of the relationship of herbage cover and yield on a range to infiltration rates are summarized in Table 22 (Rauzi 1960, Rauzi and Kuhlman 1961). As defined in these studies, herbage includes standing dead vegetation as well as the current season's production. Similarly, total mulch includes both the humic and fresh mulch. Often 50% to 75% of the variations in infiltration rate are accounted for by variations in total herbage biomass, i.e., herbage plus mulch. Generally the mulch yields are greater than herbage yields on pastures utilized in the winter, such as the Montana Glacier County set, but mulch yields may be considerably lower than herbage yields for intensively-utilized, summer-grazed pastures. Since herbage yields and herbage cover will be minimal following drought periods, the importance of mulch as soil protection against torrential rains becomes especially important. Therefore, the dynamics of the mulch cover during drought periods should be investigated. Residual differences in soil organic matter, root concentrations, and less compact soils are reflected in the fact that high-condition ranges always had infiltration rates that were twice as great as those on low-condition ranges (Table 22).

Although range condition is important in influencing infiltration rates, the inherent characteristics of the soil of the particular site involved also are influential. The South Dakota data in Table 22 show typical range sites in a 10- to 14-inch precipitation belt. These four sites were in the fair to good condition class, and all but the dense

Table 22. Relations of herbage and mulch to infiltration on northern Great Plains mixed prairie.

Location	Condition or Site	Total Herbage (lb/ac)	Total Mulch (lb/ac)	Infiltration in/hr (4th 15-min. period)
North Dakota	High	2820	2530	2.9
(Williams Co.)	Low	770	1210	1.0
Montana	High	1740	1350	1.4
(McCone Co.)	Low	620	610	0.8
Montana	High	4140	5740	2.0
(Glacier Co.)	Low	1870	2040	0.8
South Dakota	Sandy	1420	1810	1.7
(Butte Co. and	Panspots	900	290	0.8
Meade Co.)	Dense Clay	1490	350	1.0
	Clayey	1100	610	1.6

clay site, which was dominated by western wheatgrass, were dominated by a typical mixture of blue grama, needle-and-thread, western wheatgrass, sedges, and minor amounts of forbs. The dense subsoils in the panspots site largely are responsible for the poor infiltration rates as has been discussed in the previous section concerning Solonetz soils. Infiltration may be relatively rapid in the first 15 to 20 minutes on such a site, but it becomes slow later.

Frequently infiltration studies, such as those described in Table 22, are made on areas which are not excluded from grazing. Therefore, a variable amount of herbage has been removed from the site. Although the amount of herbage remaining on the site is an important factor in affecting infiltration rate, the total amount of herbage growth on the site would better reflect root biomass and the effects of the plants on soil conditions. Correlations between infiltration rate and vegetation cover probably could be improved if the variable degree of utilization of these rangelands was removed, or taken into consideration in the analyses.

5.3 Management to Minimize Drought Influences

Although ranges recuperated greatly after the drought of the 30's, the duration of the drought was sufficient to develop certain management practices to minimize livestock losses.

Practices were recommended for the northern Great Plains by Hurtt (1951) to minimize livestock losses. Among these are to cull the herd closely in drought to make certain the best breeding animals get the remaining forage and supplemental feed. Similarly, the animals should be culled early because weight losses of livestock start in early June of drought years. The greater weight in late spring or early summer in drought years probably would more than compensate for possible higher prices in the early fall period. Calves should be marketed earlier in drought years also to maintain the condition of cows better on the limited forage that is available. Some advantage may be taken of drought-resistant or early-growing species by early grazing of areas dominated by Sandberg bluegrass and threadleaf sedge. If these herbages are not consumed in drought years, they may be lost by weathering or to grasshoppers, which frequently accompany drought in the northern Great Plains. Management following a drought is important, and overstocking following a drought may do irreparable damage to the range.

Management recommendations for ranchers to minimize drought influences in the southern Great Plains are similar to those in the northern plains. Recommendations (Hildreth and Thomas 1956) are to balance the stocking rate with the forage produced, to keep numbers of breeding animals well below the carrying capacity of the range, to cull severely when forage is short, to use supplemental feed to "smooth out the weather curve," to use temporary pastures to give the range a needed rest, to distribute livestock over the range to obtain more uniform use, to practice deferred-rotation grazing to insure reseeding of the better grasses, and, where the vegetation is suitable, to use mixed classes of livestock. Deferred rotation grazing is recommended for many areas of the high and rolling plains of Texas, yet there is little research data from that immediate area on which to base this conclusion.

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