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The Environment of the Prairie

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THE ENVIRONMENT OF THE PRAIRIE

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PREFACE

In the agricultural development of Nebraska, chief attention has been given to breaking the virgin prairie for the production of cultivated crops. In fact, nearly all of the land has been broken and only relatively small and often widely separated areas of the native grassland remain intact. Parts of the prairie have been pastured so long and so intensively that only relicts of the native grasses remain. Some areas have been utilized only for the annual production of hay.

By methods of modern ecology it has been shown that the best measure of the environment or climatic complex under which plants develop is the vegetation itself. Had the pioneers from the forests of the eastern states correctly interpreted the conditions of growth in tall-grass prairie, they would have had no fears as to the successful production of crops. The presence of a continuous cover of tall, deeply rooted grasses, legumes, etc., indicated conditions favorable to the growth of cultivated crops of similar habit, a fact fully substantiated by the excellent yields of wheat, oats, and corn. The continued growth of these grasses throughout the season, with the late period of flowering and seed production among most of them, indicated a long, favorable growing season uninterrupted by a deficiency of moisture, at least in the deeper soil.

Measurements during a long period of years of the soil water available to the prairie vegetation have now been completed. Records of humidity, evaporation, temperature, and other factors affecting the rate at which this water is absorbed and transpired have also been secured. These data show the balance established by nature between climate, soil, and plant production. They are not only of scientific interest but also of much practical importance. In the growing of cultivated crops we have departed more or less widely from the established equilibrium attained in nature. In some cases, *e.g.*, short-season, intertilled crops, we are demanding less of soil and climate. In others, where deeply rooted, long-season, heavily producing legumes as alfalfa are grown, we are demanding more—in fact, on uplands, more than nature has to give continuously. This research furnishes a record of the original conditions, nature's standard, from which our practices have deviated; but to which, for continued successful crop production, we must more or less closely conform. This study is timely, since the prairie is being driven from its last strongholds by the persistent invader—man.

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INTRODUCTION

Studies in the grasslands of eastern Nebraska have been pursued for many years. These have included quantitative measurements of the factors of the environment. Investigations begun in 1915 have been continued (except for 1918) until the fall of 1928. The instrumental methods employed were the same throughout and all measurements were made either by the senior writer or by students trained in ecological methods in collaboration with him. From time to time results for certain years have been reported in connection with various researches. In no case have the results been published from the work of more than a few seasons. Much data have never been published. For these reasons, and because the natural vegetation is being destroyed with alarming rapidity, it seems desirable to present an analysis of the factors of the habitat obtained from investigations extending over the entire period of twelve to thirteen years. Such information is of present scientific interest and will probably become of increasing importance as the original environment is more and more modified by continued growth of cultivated crops.

Lincoln, Nebraska, is centrally located in the midst of tall-grass prairie that extends from Texas to Canada. Data from typical upland and lowland types at this station in general are representative of conditions prevailing over a wide area. This has been shown by comparing the data obtained from stations maintained at several places in eastern Nebraska for periods of two to three years. Consequently, the factor measurements made at the stations at Lincoln only will be given.

DESCRIPTION OF STATIONS

The upland or high-prairie station is located in a tract of about 180 acres of moderately rolling land near Belmont, three miles due north of the State Capitol in the city of Lincoln. This is virgin prairie disturbed only by mowing (Fig. 1). It is on a rather broad, flat hilltop about seventy feet above the general level of the valley of Salt Creek. The low-prairie station was located in undisturbed grassland (now broken) on a nearly level area at the foot of the hill about one-fourth mile southward (Fig. 2).

Vegetation at both stations is distinctly of the tall-grass, sod type. That of the upland is dominated by *Andropogon scoparius* which alone constitutes nearly half of the grass cover. *Andropogon furcatus* and *A. nutans* are both well represented as are also smaller amounts of *Stipa spartea, Koeleria cristata, Bouteloua racemosa,* and *Poa pratensis.* The interstitial *Panicum scribnerianum* and the relict *Bouteloua gracilis* are of much less importance. Prevernal societies are represented by *Antennaria campestris* and *Carex pennsylvanica.* Such vernal bloomers as *Astragalus crassicarpus, Senecio plattensis,* and *Nothocalais cuspidata* are abundant. The variety and abundance of estival herbs indicate favorable conditions for growth throughout the early summer. Chief among these are *Psoralea floribunda, Erigeron ramosus, Brauneria pallida, Meriolix serrulata,* and *Achillea millefolium,* although many others occur. *Solidago missouriensis, Aster multiflorus, Liatris punctata, L. scariosa, Helianthus rigidus,* and *Kuhnia glutinosa* constitute the most important autumnal societies. An average height of eight inches is attained by the grasses by June 1 and an upper story of forbs of 15 to 22 inches. The grass blades reach a level of 12 to 14 inches by autumn during years of normal rainfall. The flower stalks of *Stipa* and the later blooming grasses are 2.5 to 3.5 feet tall. Everywhere the grasses constitute the matrix of the vegetation and forbs are of minor importance. The apparent cover ranges from 75 to 90 per cent but numerous quadrats show that the actual basal cover seldom exceeds 30 per cent. Detailed studies in many prairie areas from northern Kansas and Missouri through western Iowa and eastern Nebraska and including southwestern Minnesota and southeastern South Dakota show that the little bluestem (*Andropogon scoparius*) type is the characteristic cover of most of the uplands.

The lowland prairie was dominated by *Andropogon furcatus* which constituted approximately 80 per cent of the vegetation.

FIG. 1.—Upland station in the prairie. The most important grass is *Andropogon scoparius.* The bushy plant is *Psoralea floribunda.* Photo. June 17, 1922.

FIG. 2.—Lowland station showing the abundance of *Andropogon furcatus,* with smaller amounts of *A. nutans* and *Panicum virgatum.* Photo. Sept. 8, 1920.

A small admixture of *A. nutans, Panicum virgatum,* and *Elymus canadensis* also occurred. Due to annual mowing, *Poa pratensis* was represented although overtopped by the preceding species. The foliage of the tall grasses reached a general level of about two feet and the flower stalks varied from five to seven feet in height.

Characteristic forbs were *Solidago canadensis, S. rigida, Glycyrrhiza lepidota, Aster salicifolius, Physalis heterophylla, Polygonum muhlenbergii, Artemisia gnaphalodes, Achillea millefolium,* and *Callirrhoe alcaeoides.* Forbs, however, were of very secondary importance, the rank growth of grasses forming the dense cover. Practically all of the species of high prairie were absent. The apparent cover was usually 90 to 100 per cent but only about 20 to 25 per cent of the soil surface was actually occupied. This big bluestem, sod type is characteristic of low, well drained, level bottom lands, lower slopes, and ravines throughout the tall-grass prairie. In wet, poorly aerated soil it is replaced by *Spartina michauxiana* and its associates and on midslopes it usually merges into the little bluestem type.

SOILS

The fertile soil of the upland is glacial drift known as Carrington silt loam, a type widely distributed in eastern

TABLE 1.—*Mechanical analyses of soils from high and low prairie*

Depth of sample (feet)	Coarse gravel	Fine gravel	Coarse sand	Medium sand	Fine sand	Very fine sand	Silt	Clay	Hygroscopic coefficient[1]
HIGH PRAIRIE									
0.0—0.5	0.0	0.0	2.0	1.9	6.0	26.1	39.3	24.7	9.5
0.5—1.0	0.0	0.0	1.2	2.2	3.8	21.8	38.4	32.6	8.7
1—2	0.0	0.0	2.7	2.9	4.8	19.6	45.6	24.4	8.6
2—3	0.0	0.0	5.6	6.9	10.1	23.1	32.8	21.5	7.1
3—4	0.0	0.0	7.0	8.8	12.8	23.5	28.3	19.6	6.2
LOW PRAIRIE[2]									
0.0—0.5	0.1	0.4	2.2	1.8	5.0	25.0	41.3	24.3	11.8
0.5—1.0	0.3	0.7	2.1	2.2	5.0	25.4	38.8	25.8	11.1
1—2	0.2	0.3	1.3	1.5	3.7	21.4	40.8	31.0	10.3
2—3	0.0	0.1	0.4	0.5	1.7	19.2	43.4	34.7	10.2

[1]The hygroscopic coefficients were obtained from a different set of samples than those used for mechanical analyses, but they are from the same area.

[2]These data and those in table 2 are from prairie soil broken a few years, adjoining the lowland station.

Nebraska. It has a moisture equivalent of about 28 per cent and a maximum water capacity (Hilgard method) of approximately 60 per cent. Mechanical and chemical analyses are given in Tables 1 and 2.

The soil is fine in texture, being mostly composed of silt and clay, and is sufficiently supplied with calcium to lack acidity as determined by the Truog test. The surface seventeen inches is dark brown in color and has a granular structure. This layer has lost much of its colloidal clay. The forces of weathering, especially repeated freezing and thawing and alternate wetting and drying, together with the greater humus content and the favorable effects of root activities, have all combined to produce this excellent granular structure. Below seventeen inches to about three feet the color is ferruginous brown and the soil is distinctly columnar in structure. Much of the lime has been leached away and upon drying the soil shrinks and cleaves into long, perpendicular columns. A buff color characterizes the massive layer which occurs below three feet. Here the carbonate content is high; streaks and pockets of chalky material are numerous.

The roots of the upland grasses range in depth from two to over five feet but most of the forbs extend their root systems much more deeply. In fact, three root layers are quite evident. The first extends to a level of about two feet, where most of the roots of *Stipa spartea, Koeleria cristata,* and *Carex pennsylvanica* terminate. A second layer, extending to a depth of about five feet, is dominated by *Andropogon furcatus, Bouteloua gracilis,* and *B. racemosa.* Extending far below this level, and extracting much water from the deeper soil, are *Liatris punctata, Aster multiflorus, Solidago missouriensis,* and *Amorpha canescens.* In this group of species not one is well fitted for much absorption in the surface soil. In fact, there is little or no direct competition between these plants and those enumerated in the first group. Such a root distribution, together with maximum activities above ground at different times of the year (resulting in seasonal aspects) makes it clear how so many plants can not only live but also show normal development in such limited surface areas, *e.g.*, 215 individuals or individual groups in a single square meter (Weaver, 1920).

The soil at the lowland station is a fertile, dark-colored, silt loam of the Wabash series. It is fine in texture, being composed mostly of silt and clay (Table 1). It shows no trace of acidity.

A comparison of the chemical analysis of the upland with lowland soil may be made by an examination of Table 2.

TABLE 2.—*Chemical analyses of soils from high and low prairie*

Depth of sample (feet)	Insoluble residue P. ct.	Soluble salts P. ct.	Volatile matter P. ct.	Iron and aluminium oxide P. ct.	Calcium oxide P. ct.	Magnesium oxide P. ct.	Phosphorus pentoxide P. ct.	Nitrogen P. ct.
HIGH PRAIRIE								
0.0—0.5	76.87	17.12	6.01	13.20	0.68	1.19	0.13	0.159
0.5—1	75.70	18.58	5.72	14.25	0.70	1.32	0.12	0.134
1—2	76.17	19.08	4.75	14.72	0.75	1.68	0.12	0.079
2—3	77.80	18.46	3.68	14.03	0.86	1.69	0.15	0.045
LOW PRAIRIE								
0.0—0.5	79.34	12.96	7.70	9.57	0.68	0.75	0.13	0.218
0.5—1	79.63	13.66	6.71	10.27	0.63	0.77	0.10	0.187
1—2	78.11	15.83	6.06	12.11	0.64	1.01	0.08	0.135
2—3	74.78	19.82	5.40	15.20	0.76	1.27	0.09	0.082

The greater amount of volatile matter and the greater nitrogen content at all depths than in the soil from the upland indicate more favorable conditions for plant growth.

The granular layer extends about seven inches deeper on the lowland, *i.e.*, to about two feet. The soil is also much darker in color. The surface two to three inches contains large quantities of vegetable mold, thickly matted with roots and rhizomes, and lacks definite structure. Even to a depth of six to seven inches the soil, although somewhat laminated, is practically without structure. The columnar layer is well developed and of a grayish brown color. It extends to a depth of nearly five feet where it gives way to the massive layer. As on the upland, the subsoil is many feet in depth, and extends far beyond the level reached even by the most deeply rooted species. Three root layers are more or less apparent. One, demarked by *Poa pratensis*, occurs at about three feet; the second, by *Andropogon furcatus* and *A. nutans*, extends to 5–5.5 feet; but *Panicum virgatum* and many of the forbs reach a level of eight or more feet.

The soil of both upland and lowland is very fertile as is shown by the excellent growth of the native vegetation and by the growth of crops on similar soils in adjacent areas. Although there is always a dearth of nitrogen, the plants using the total supply as rapidly as it is elaborated by the soil organisms, yet evidence from long observation and repeated experiment conclusively shows that water is the chief limiting factor to growth.

PRECIPITATION

The mean annual precipitation at Lincoln for a period of fifty years is 27.94 inches. Its distribution is of the Great Plains type, between 76 and 79 per cent occurring between April 1 and September 30. Fourteen inches fall during the three months of May, June, and July (Loveland, 1920). Such a seasonal distribution of moisture is very favorable to the growth of grasses. Most of the precipitation during the summer months occurs in storms accompanied by thunder and lightning, and often for a short time with heavy rainfall. More than half of the precipitation of May, June, and July is from rains of an inch or more in twenty-four hours. Not infrequently, however, storms occur with a rainfall of two to three inches. A rainfall of four to six inches in a similar period has been recorded in a few instances. During such heavy rains the soil is unable to absorb all of the water as it falls and run-off is high. From 60 to 65 per cent of the precipitation occurs at night during the growing season (8 p. m. to 8 a. m.), thus reducing the amount of water lost by evaporation (Kincer, 1922). The rainfall of May and June is usually well distributed but that of July and August is less so.

Less than one-tenth of the precipitation occurs during the three winter months. The average annual snowfall is about 27 inches. "As a rule snow covers the ground but a few days at a time after each snowstorm and the ground is covered with snow less than half of the time even during the months of heaviest snowfall" (Loveland, 1920). Much of the snow is swept by high winds into depressions, and thus often contributes but little to the supply of moisture of the soil upon which it falls.

Nebraska has much sunshine; 175 to 185 clear days occur and only 81 to 86 completely cloudy ones. During March, April, and May there is approximately 60 per cent sunshine but June, July, and August have 72 per cent or more.

The graph of mean annual precipitation at Lincoln shows a gradual increase from 1.3 inches in March to 2.8 in April and reaches a maximum in May (4.2) and June (4.3). It then falls gradually to 3.8 inches in July and 3.7 in August, after which the gradient descends steeply to 2.6 in September and 1.8 in October. For each of the winter months the precipitation is less than .75 inch.

Even casual examination of Figure 3 shows that the precipitation varies widely from year to year. It ranged between 21.4 inches (1927) and 32.3 inches (1919). There is not a single season during which the mean annual sequence by months is attained. During the first six years the highest rainfall occurred during a different month each year ranging from April to September. During the period of thirteen years, rainfall was highest in May or August only once, in April and June twice each, during three different years in September, and four in July.

Minimum rainfall, exclusive of March, occurred during April, May, and August during each of two years, and during July and September on three and four years respectively. Thus a deficiency in rainfall is liable to occur at any time during the beginning, the middle, or the end of the growing season. Practically every year has one or more such periods. They are often followed by an interval of high rainfall.

The amount of winter precipitation is important inasmuch as it may have a direct bearing upon the amount of water in the soil at the time vegetation resumes growth. Its importance is emphasized if the preceding season is dry. Exact studies on the relation of winter precipitation to the water-content of soil are much needed. Frequently winter precipitation totals 2.5 to 3.5 inches. The precipitation during March, which immediately precedes growth, is similarly important. For example, the dry summer of 1918, and the early summers of 1924, 1926, and 1928 would probably have been much more severe except for the high winter precipitation

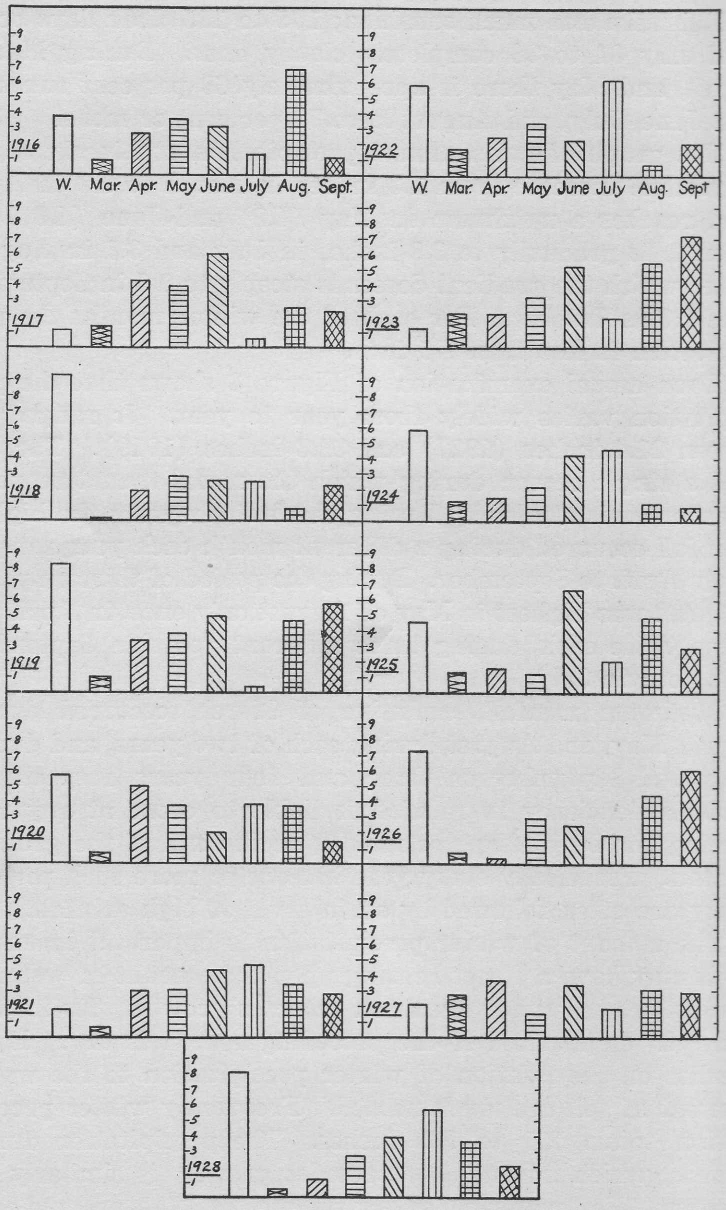

FIG. 3.—Precipitation in inches at Lincoln, Nebraska, during October to February inclusive (W) and monthly precipitation during 1916 to 1928.

which wet the subsoil. The winter precipitation, however, is quite as variable as that of summer (Fig. 3) and if light may have little or no effect upon water available for growth in spring. The precipitation of March is usually more effective since at least part of it falls on unfrozen soil.

During certain dry years the rainfall was rather consistently low, *e.g.*, 1918 and 1927. In others, such as 1926, certain months had a fairly high precipitation. During wet years, as 1920 and 1921, the precipitation may be rather uniformly distributed or, as in 1924, some months may be very dry.

Drought periods of fifteen days or more, when the rainfall on consecutive days did not exceed .20 inch, occurred every year. A rainfall of less than .20 inch is probably entirely intercepted by the vegetation and the dry surface half-inch of soil in which no absorbing roots occur, and has no effect upon available water-content unless the surface soil is already wet. In years of ample rainfall there were only one or two such periods, but on dry years there were four to six. That they are rather regularly distributed throughout the growing season is shown by the fact that six occurred in April, nine in May, five in June, nine in July, seven in August, and eight in September. There are almost always very light, scattered showers during such times but they are of little or no significance except in temporarily lowering temperature and increasing humidity. Even a rainfall of .20 inch if scattered over a few hours or followed by bright sunshine and wind may have no effect upon increasing water-content of soil.

Frequently these periods of drought last for a longer time than fifteen days; 22 of the 44 (1916-1928 inclusive) continued 20 to 32 days. Only thirteen times during these years did the rainfall for any three-day period (April to September) exceed two inches. Five of these times it was in excess of three inches and once almost five inches. Three of these periods of heavy rainfall occurred in 1923.

Obviously the chief effect of precipitation upon vegetation is through increasing water-content of soil, which will now be considered.

WATER-CONTENT OF SOIL

The water-content of the soil to a depth of four feet has been determined throughout all or a part of each growing season (except 1918) from 1916 to 1928 inclusive. Samples of approximately 175-200 grams of soil were taken in duplicate. They included the entire core of soil at depths of 0 to 6 and 6 to 12 inches and at 1 to 2, 2 to 3, and 3 to 4 feet, respectively. All of the samples were taken within an area of a few square rods at each station. A Briggs' geotome cutting a soil core approximately three-fourths of an inch in diameter was employed. The samples were placed in tin cans with tightly fitting tops and at once taken to the laboratory. After being weighed, they were dried at a temperature of 105° C. Water-content was calculated on the basis of the weight of the dry soil. All factor data for 1927 and 1928, including water-content, are from prairie stations of very similar types as regards both soil and vegetation but located nine miles west of Lincoln. The writers are indebted to Dr. T. L. Steiger for these latter determinations.

The graphs show the water-content, in excess of the hygroscopic coefficient, for each determination at the several levels. From the extensive work of Alway *et al* (1916, 1919), Alway and Russel (1916), Weaver (1919, 1920), and others, on Nebraska soils, it is believed that the hygroscopic coefficient of the soil represents at least approximately the limit of soil water available for plant growth. It has been shown conclusively that prairie vegetation absorbs water from a soil until the water-content is reduced to the hygroscopic coefficient. In this paper, therefore, the term available water indicates an amount in excess of the hygroscopic coefficient.

In order to compare the records of different years the dates on which the actual determinations were made have often been shifted forward or backward a few days (as in Fig. 4) so as to fall on the nearest date (four to each month) given in the figures. This in no way affects the validity of the data. Where more than a week occurred between actual determinations, a point was interpolated (indicated by a circle) to show the probable water-content, after a careful study of the daily rainfall record. All but a few of these interpolations were made where there was at least 5 or more per cent of water available to the vegetation. Where isolated determinations were made, the probable trend of the graph before and after the determination is also shown.

Perhaps the most striking features of the data presented in Figure 4 are the wide range and rapid decrease of the amount of available water. A variation of 15 to 20 per cent or more during a single fortnight was not uncommon and the water-content was often reduced 10 per cent or more within a single week. The graphs show there was always a good supply of water in the surface soil during April when vegetation renewed growth. During 1920, there was constantly a large supply throughout the month of May, but each of the other years shows a reduction of 5 to 10 per cent at some time during the month. In May, 1917, the available water-content was reduced to about 2 per cent. During June, when plants were making heavy demands upon the supply, a margin of 7 to 10 per cent or more occurred at all times during five years but this was reduced to 4 per cent or less during several years. The nearest approach to exhaustion of the entire supply occurred in 1916.

Water relations were more favorable in July during only five years, and less so for most of the others. That drought was often impending is made clear by the decrease of the water-content to 3 or 4 per cent at some time during seven years. Once during 1917 and twice during 1919 an actual deficiency was determined. It was not ascertained whether or not this was general throughout the surface 0 to 6 inches (0 to 4 in 1916) or only expressed the results of extreme desiccation in the surface two to three inches. The latter was probably the case.

The available water-content during August was quite as variable as that during July. Amounts as low as 2 to 4 per cent were recorded for six years. At no time, however, during either August or early September was the hygroscopic coefficient reached.

There were five periods during one year when the available water-content exceeded 10 per cent and four such periods during three others. Three similar periods occurred during

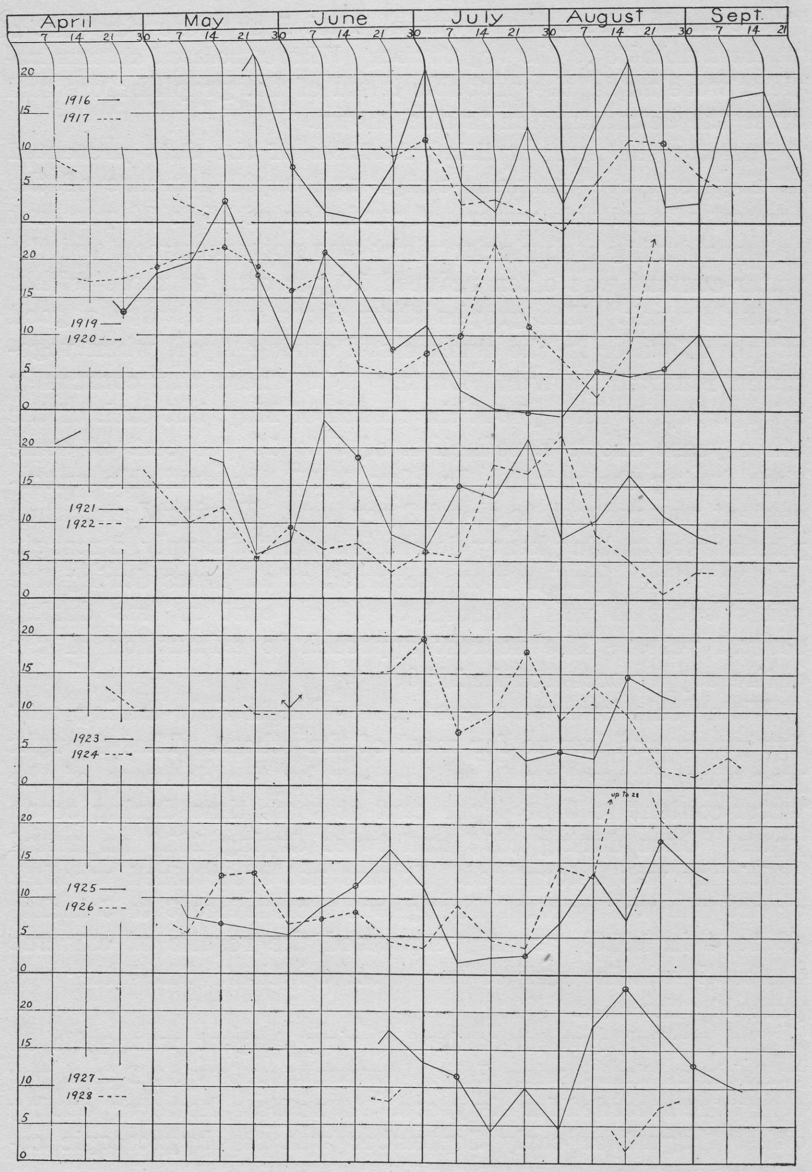

FIG. 4.—Water-content of high-prairie soil expressed in per cent in excess of the hygroscopic coefficient at a depth of 0 to 6 inches (0 to 4 inches in 1916).

each of two years and two periods during five years. Of these times of high water-content, six occurred (wholly or in part) in May, nine in June, seven in July, and ten in August. Conversely four periods of water-content less than 5 per cent occurred during one year; two during each of six years; and one during each of the remainder, except in one summer when there was none.

An analysis of these data shows that impending drought is, in general, progressively more imminent with the advance of the growing season. One drought period occurred in May, four in June, nine in July, and six in August. The general trend holds also when the partial records of 1927 and 1928 are omitted and is reinforced by data for 1930 not included here. This is believed to be due in part to the increasing demand of the growing vegetation for water as well as to variations in the rainfall.

Finally, a survey of the data shows that there were no years or series of years that were exceptionally wet or exceptionally dry throughout. Each growing season had its times of abundant and of deficient water supply.

Even casual inspection of Figure 5 shows that fluctuations in the water-content at the 6- to 12-inch level were not so great as in the surface soil. Here the plant finds a water supply that is far more constant. The trends of the graphs for the first and second 6-inch levels are, however, very similar. In 1916, for example, the five periods of high water-content apparent in the surface soil are also clearly shown in the graphs for the 6- to 12-inch level. Likewise the five periods of low water-content may also be seen for the deeper soil. Occasionally, as during September 7-14, 1916, the trend is different as a result of a light rain (.4 inch) adding water to the surface soil while absorption was depleting the deeper level.

The recorded data show that during April and May before the vegetation was making maximum demands for water, there was nearly always a greater amount available than at periods later in the season. At no time was less than 8 per cent available water recorded and it was usually in excess of 10 per cent. Available water-content did not fall below 5

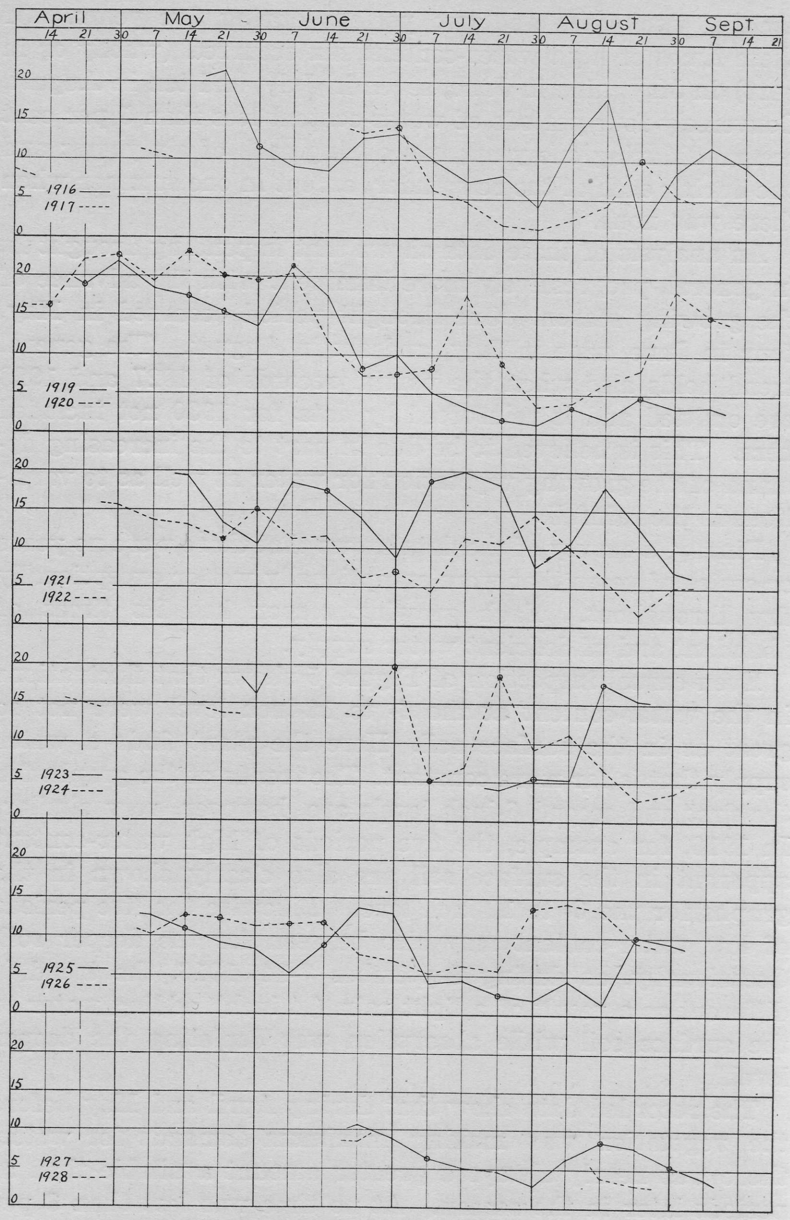

FIG. 5.—Water-content of high-prairie soil expressed in per cent in excess of the hygroscopic coefficient at a depth of 6 to 12 inches (4 to 12 inches in 1916).

per cent during June but this occurred during sixteen different weeks in July and fifteen in August. Only during two years (1921 and 1926) was it consistently greater than 5 per cent. The fact that only about 2 to 3 per cent of water was available at seventeen different intervals shows clearly why plants do not depend upon the surface foot for their water supply. It should be emphasized, however, that at least a small amount of water was always available at this level. In 75 per cent of the determinations (during June to August inclusive) it exceeded 5 per cent.

The graphs for the second foot (Fig. 6) are much more regular than those for the second 6-inch layer. Water-content at this depth is not increased except by heavy rains. Aside from minor fluctuations, the general trends are the same, however, even if less pronounced. There was a gradual diminution of the water supply at this level (with one exception) from May, when it ranged from 10 to 21 per cent, to the end of the growing season. This accords with the increasing demand made by the growing vegetation. It was frequently temporarily replenished as a result of heavy rains and markedly so by the 4.4 inches in August, 1926. During June the available supply ranged between 7.5 and 15 per cent. Water-content was somewhat lower in July (2 to 13 per cent) but that of August showed, in general, a further decrease, except in 1926. During August the minimum supply was less than 5 per cent at ten different times as compared with three times for July. The rather remarkable similarity of graphs for different years is worthy of notice.

Not only was each of the periods of drought, discussed under precipitation, clearly demarked in the graphs showing water-content in the first and second 6-inch layers of soil but also in practically every case it was shown by a marked downward trend in water-content in the second foot.

Since the majority of prairie species absorb to depths of four or more feet, an examination of the water-content at deeper levels is pertinent. It is well known that fluctuation in water-content decreases with depth, consequently samples were taken at longer intervals than for the first and second foot. The data are given in Table 3.

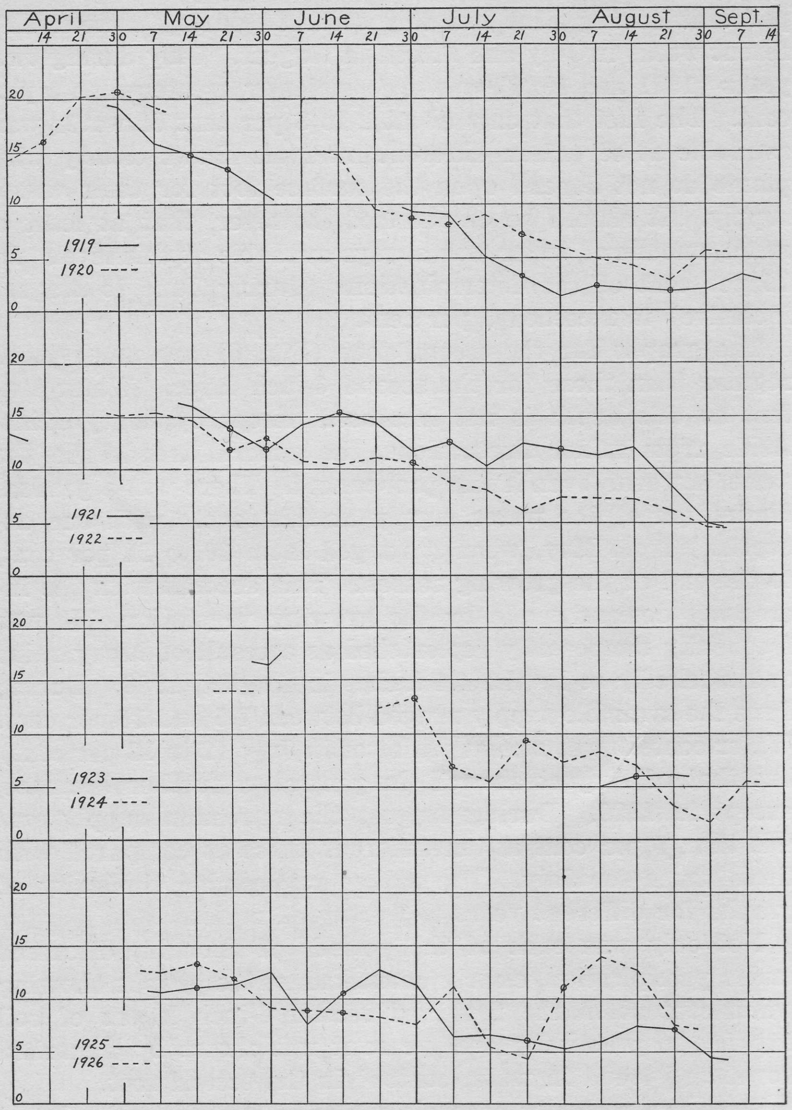

FIG. 6.—Water-content of high-prairie soil expressed in per cent in excess of the hygroscopic coefficient at a depth of 1 to 2 feet.

TABLE 3.—*Available water-content by weeks in the third and fourth foot of soil at the high-prairie station*

Depth	Year	April		May			June				July				August				Sept.
		2	4	1	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1
Ft.	1917			3.2					13.0				6.3					3.3	
	1919		13.8	9.5							9.9	10.7		7.1		3.3		5.4	5.6
	1920	10.0							15.6			13.2			9.7			8.8	
	1921	13.3			15.0		14.5			15.2			13.1			12.1	11.4		
2-3	1922		10.9		12.1			8.4			8.0				8.0			7.1	
	1923						11.5						7.1		6.4			7.1	
	1924								11.0						8.0	9.7	6.6	5.9	5.6
	1925					9.0	10.4			9.8	9.3	4.4	6.6	2.4	2.9			4.2	
	1926								8.8	8.4	9.4	5.9	9.5		14.1	13.0			
	1927								10.7	11.7		8.0	5.9			9.3	8.3		
	1928								5.7							4.4	7.8		
	1917								11.3									0.7	
	1919		11.4	14.2							10.0	9.2		11.1		7.0		5.4	8.3
	1920	8.6										14.7			11.6			10.2	
3-4	1921	12.5			14.5		17.2						16.8			16.8	8.8		
	1922		9.1		7.8			6.6			5.4				6.0			5.3	
	1923						8.2						7.5		8.2			8.7	
	1926								10.1	7.1		7.2	8.8		13.2	10.5			
	1927								12.2	9.6		9.8	10.3				7.0		
	1928								5.2							3.0	5.1		

A survey of the data for the 2- to 3-foot level shows that on seven of the eleven years there was, in general, a gradual diminution of the water supply with the progress of the season. During two years there was a rather marked increase due to the June rainfall; and in the two remaining years a similar increase resulted from the precipitation in August. Maximum available water-content for the several years ranged from 8 to 16 per cent and was highest nine out of eleven times before the first of July. The lowest available water-content varied from 3 to 11 per cent. These lowest points for the season were reached once each in May and September; thrice in July; and six times in August.

Maximum water-content in the fourth foot varied from 5 to 17 per cent, a range very similar to that of the third foot. In all but three years it was highest during the earlier half of the season. The minimum ranged between 1 and 9 per cent. Thus there was always some water available for growth in the deeper soil.

Determinations of water-content at depths exceeding four feet have been made at various times at the high-prairie station. These have been supplemented in many places in the prairie where, during several years, excavations 8 to 22 feet in depth have been made for the purpose of studying the distribution of root systems. Without exception the soil below four feet has been found fairly moist and a total water-content of 20 per cent or more was not unusual. It is believed that under the grassland cover the deeper subsoil is constantly moist to great depths.

COMPARISON OF WATER-CONTENT OF HIGH AND LOW PRAIRIE

The relative water-content of upland and lowland at the 0- to 6-inch level is shown in Figure 7. Certain years have been selected as representative. Casual inspection shows that the low prairie is practically always more moist in the surface 0 to 6 inches. The excess over that of high prairie is usually 3 to 4 per cent and often 10 or more. Only a few times did the surface soil in the lowland actually have less available water. On two occasions (in late summer of 1919)

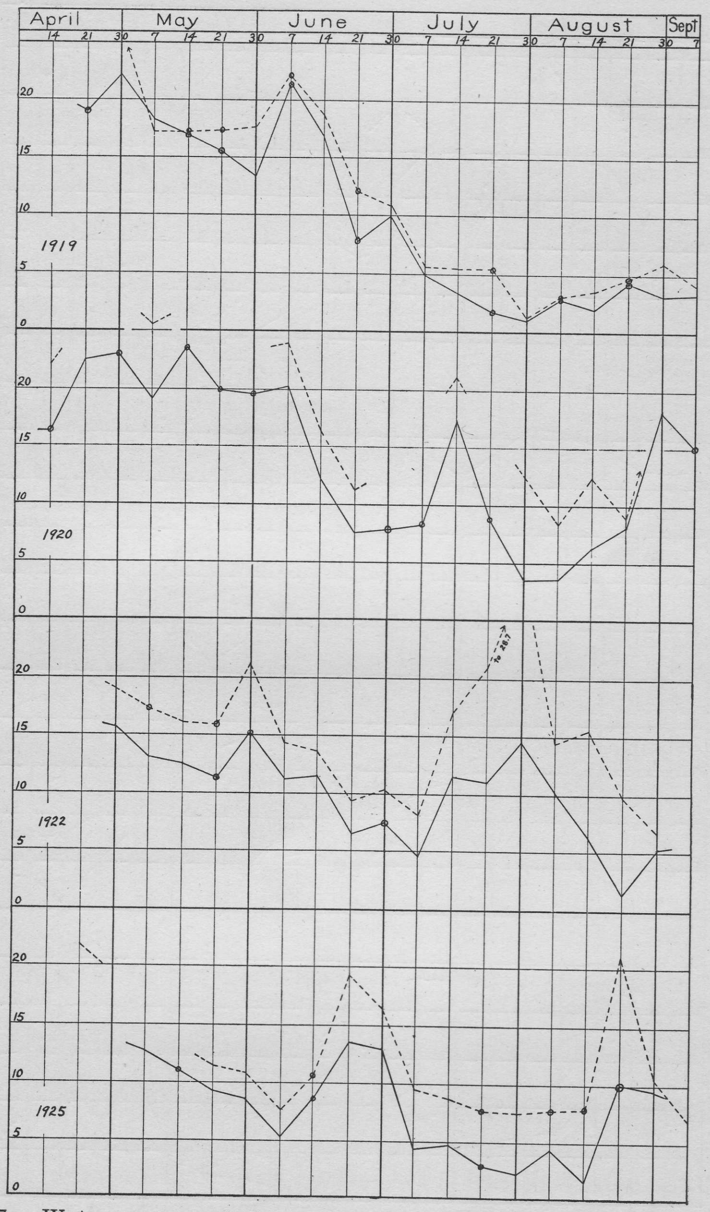

FIG. 7.—Water-content of high-prairie soil (solid lines) and low-prairie soil (broken lines) in per cent in excess of the hygroscopic coefficients at a depth of 0 to 6 inches.

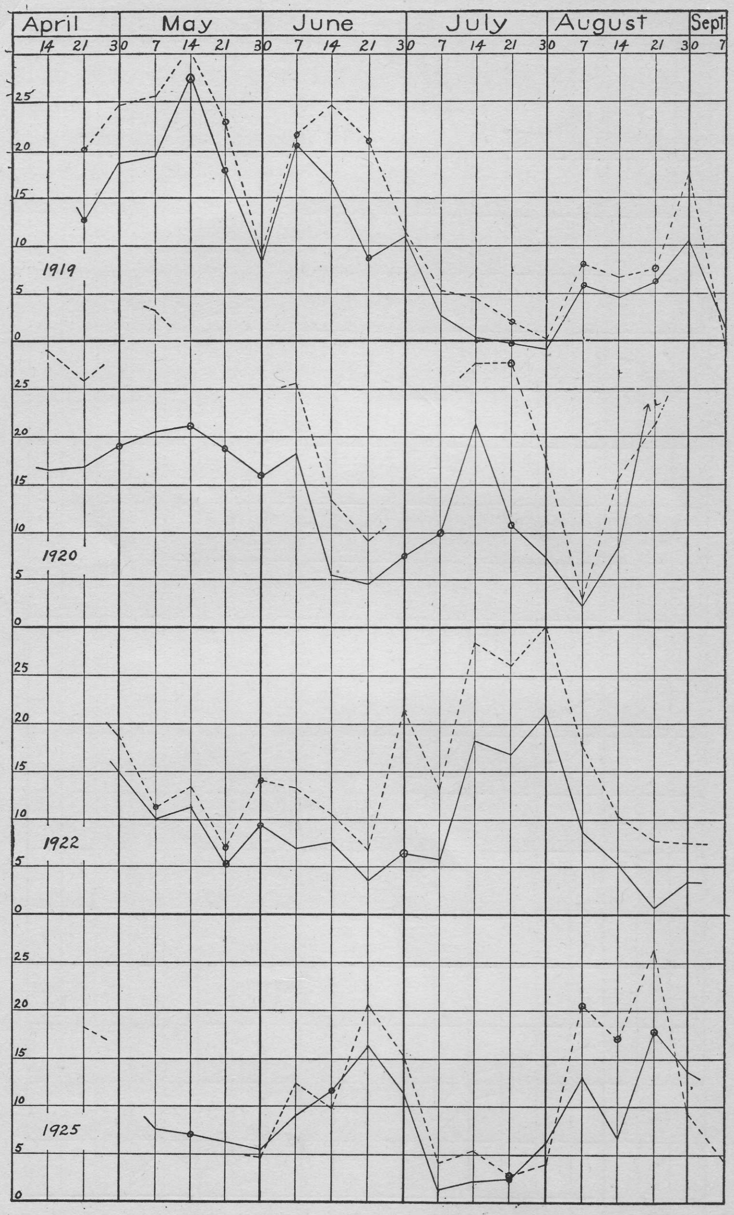

FIG. 8.—Water-content of high-prairie soil (solid lines) and low-prairie soil (broken lines) in per cent in excess of the hygroscopic coefficients at a depth of 6 to 12 inches.

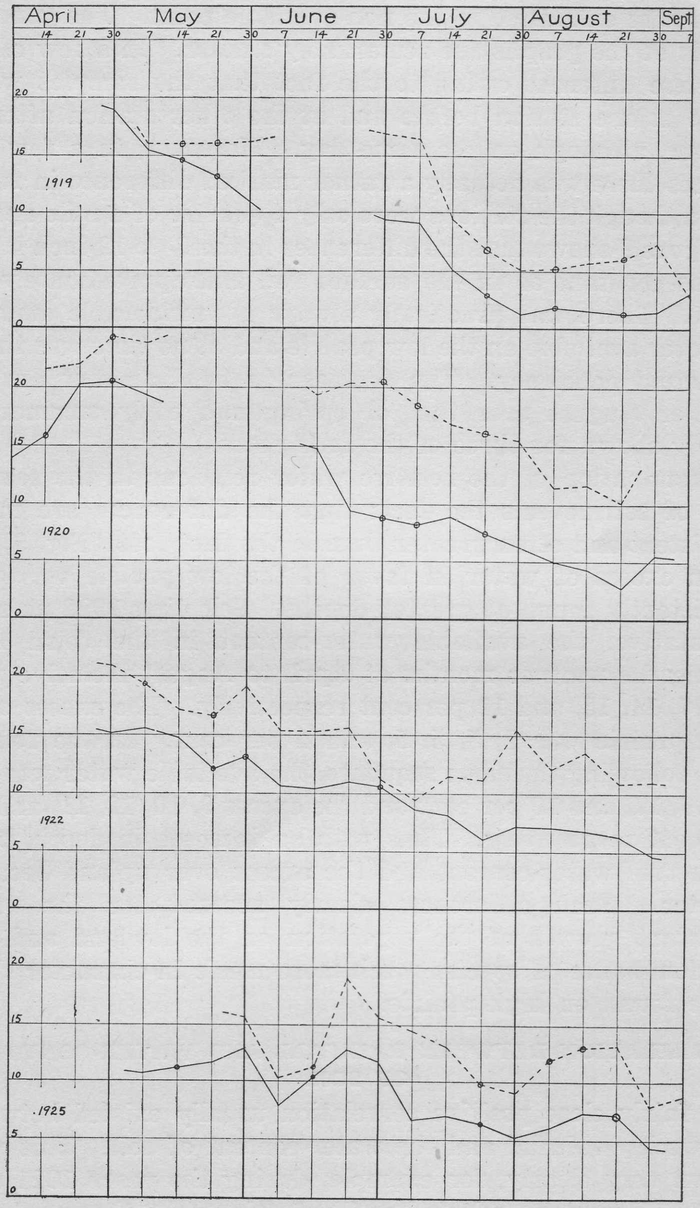

FIG. 9.—Water-content of high-prairie soil (solid lines) and low-prairie soil (broken lines) in per cent in excess of the hygroscopic coefficients at a depth of 1 to 2 feet.

water was exhausted to the non-available point. The general trends of the graphs are remarkably similar. In a few cases they are different owing to the fact that the samples were taken at one station before and at the other station after a shower, although on the same day. Moreover, in a few instances there was actually a rather marked difference in rainfall, although the stations were only a quarter of a mile apart.

Figure 8 shows that the differences in the 6- to 12-inch layer are as constant as in the surface soil and approximately as great. There was practically always a considerable amount of water available on the low prairie and at no time was there an actual deficiency. The decrease in total amount during July or August over that of spring and early summer is clearly shown for three of the four years.

Examination of the relative water relations in the second foot of soil reveals the facts that the differences are more consistent and often greater than in the first foot (Fig. 9).

An excess of water in favor of the low prairie was also consistently found at greater depths. Selecting 1922 as representative, the available water-content in the third foot during the warmer months of April to August inclusive was 13, 17, 14, 13, and 12 per cent respectively. The excess over high prairie was 2, 5, 5, 5, and 4 per cent. In the fourth foot, following the same sequence, the available water was 18, 18, 19, 17, and 16 per cent and the excess 9, 10, 12, 11, and 11 per cent respectively. Thus with an increase in depth, both the actual water-content and the excess over upland became greater. Such differences clearly account for the more luxuriant growth of the vegetation on the lowland and for the dominance of species much more mesic in character than those found on high prairie.

CORRELATION BETWEEN RAINFALL AND WATER-CONTENT OF SOIL

A fairly close positive correlation usually existed between the weekly rainfall and the water-content of soil. This was shown very clearly, for example, during the years 1921 and 1922. These were selected as illustrative since the graphs of water-content at the several levels showed considerable fluctuations (Fig. 10). The most marked correlation was in the surface 6-inch layer. An apparent discrepancy occurred during the last week in August when water-content decreased notwithstanding 1.4 inches of rainfall. The showers fell early in the week and during very hot, dry weather, when the vegetation was losing a large amount of water through transpiration. Correlation with water-content of the 6- to 12-inch layer was, with few exceptions, marked. Some errors undoubtedly were made in interpolating where samples were not taken. Occasionally a heavy shower fell at the station but did not occur at the weather bureau about two miles dis-

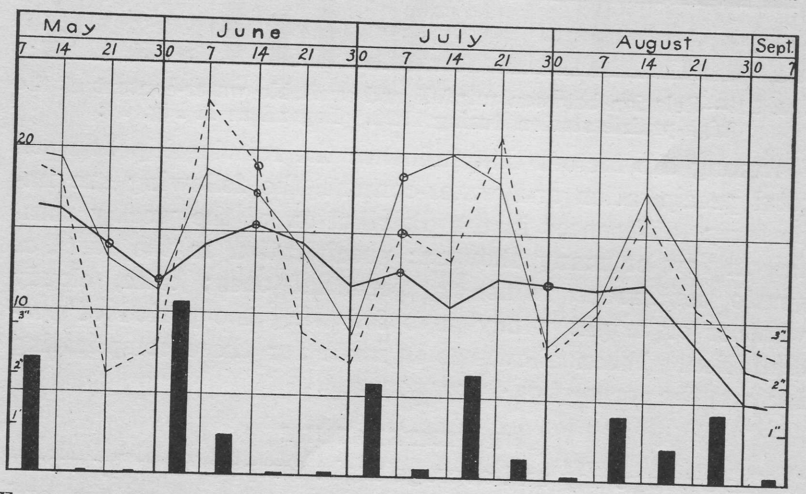

FIG. 10.—Relation between rainfall and available water-content at the high-prairie station during 1921. Rainfall in inches; water-content at 0 to 6 inches, broken line; 6 to 12 inches, light solid line; 1 to 2 feet, heavy solid line.

tant. Conversely precipitation was at times recorded at Lincoln when none fell at Belmont. A close positive correlation (with one exception) occurred throughout at the 12- to 24-inch level.

Rainfall and water-content at 0 to 6 inches were again in close agreement in 1922 (Fig. 11). This was also true, in general, for the 6- to 12-inch level but somewhat less so for the second foot.

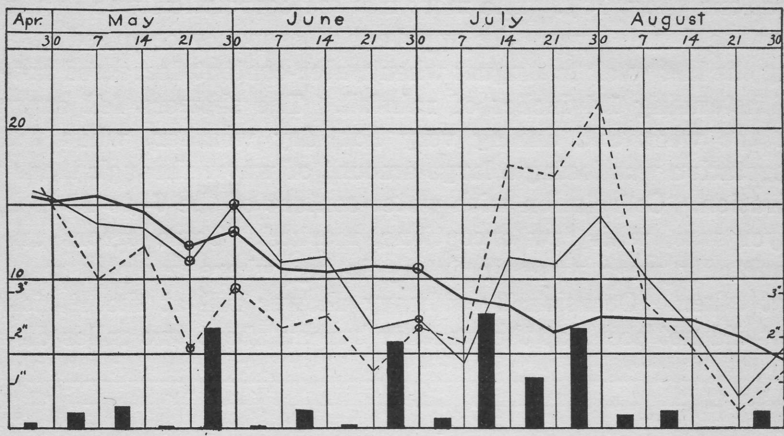

FIG. 11.—Relation between rainfall and available water-content at the high-prairie station during 1922. Legend as in Fig. 10.

Among the factors that influence the relationship between total precipitation and water-content, the following are important: differences in the distribution of the weekly rainfall in few or many showers; precipitation in the form of gentle continuous rains or torrential ones; calm, cloudy weather or bright windy days following the period of precipitation. When allowance is made for these complicating factors, the correlation is pronounced.

AIR TEMPERATURE

The average day and average night temperatures by weeks are shown in Figure 12. The data on temperature and humidity were secured by means of Friez' hygrothermographs housed in well ventilated, rain-proof, wooden shelters placed in the prairie. The sensitive portions of the instruments were about five inches above the surface of the soil. Extreme care was taken to disturb the natural plant cover as little as possible. The instruments were checked regularly and much care exercised in their operation.

The average for the day temperature was determined from the weekly record sheets of the thermographs by adding the temperatures beginning at 8 a. m. and every two hours thereafter until 6 p. m. for each day and dividing the sum by the

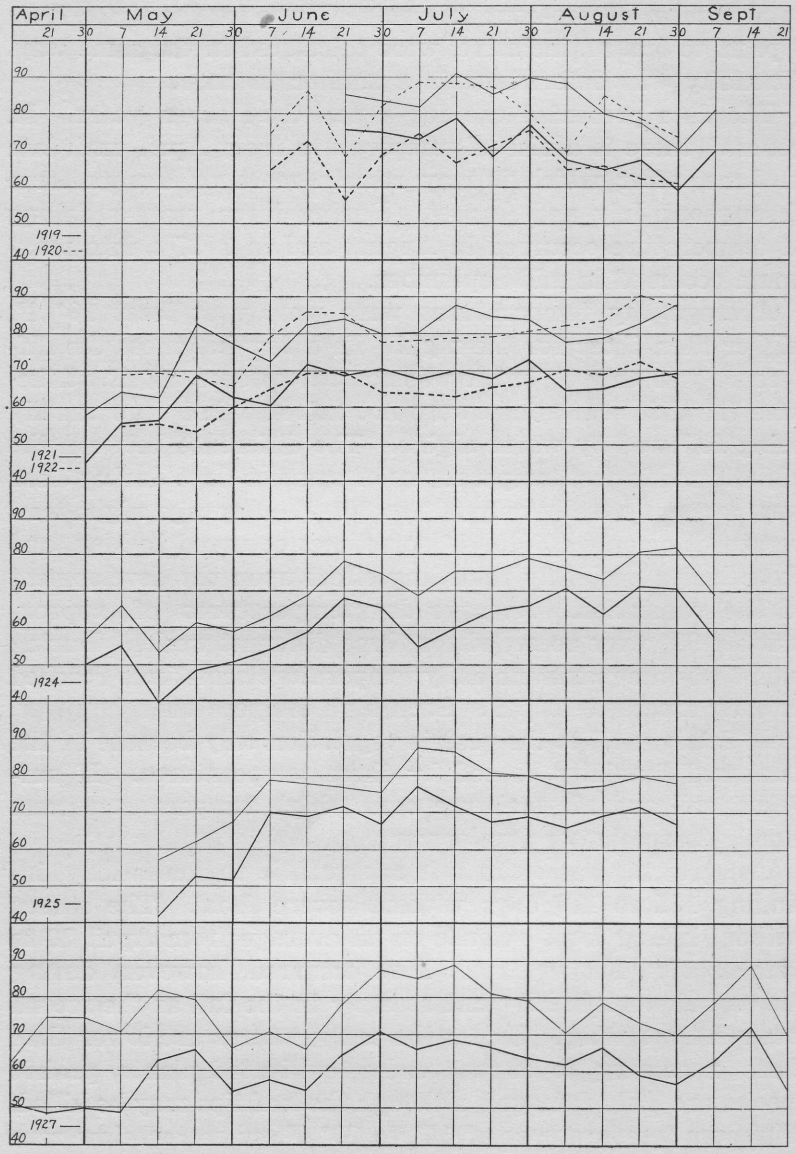

FIG. 12.—Average day temperatures in degrees Fahrenheit (light lines) and night temperatures (heavy lines) by weeks at the high-prairie station.

total number of two-hour intervals. Those for the night, from 8 p. m. to 6 a. m. inclusive, were calculated in the same way. Humidity was determined in a similar manner.

The data presented are for a period of seven years. In general, there is a rise of temperature from April until late in June, after which it may remain more or less uniform throughout July and August. During three years a falling of temperature occurred in August and in 1927 a late maximum occurred in mid-September.

Average day temperatures were usually at least 10° F. higher than those for the night. In a few instances the difference was only 5° but it was sometimes over 20° F. Likewise the daily variations were not extreme, hot days usually being followed by warm nights. The difference between the highest and lowest temperatures of summer days during clear weather was usually only 20° to 30° F. Average night temperatures of only 40° to 45° sometimes occurred in May, and these had a decidedly retarding effect upon the development of the vegetation. Average day temperatures of approximately 90° were recorded for three different weeks. During such times the maximum daily temperature sometimes reached or even exceeded 100° F. Such high temperatures, however, seem detrimental to the prairie vegetation only because of the decreased humidity caused by these temperatures. If sufficient soil and air moisture occur, high temperatures seem merely to accelerate development.

The growing season in this mid-prairie region is long, including 165 to 170 days without severe frost. The season without killing frost extends on an average from April 20 to October 10. Killing frosts have occurred, however, during the second week in May and as early in the fall as the second week in September. Unless the temperatures are lower than those necessary to harm tender cultivated plants, prairie species are little damaged, although the leaf tips may be killed. Minimum temperatures of 15° to 20° F. or more below zero occur at intervals during the cold season when vegetation is dormant.

A comparison of the graphs of air temperature with those of water-content in the surface soil shows that with a rise in the average weekly day temperatures there was a decrease in soil moisture in 75 per cent of the cases. The converse of this, however, was not true.

TEMPERATURES ON HIGH AND LOW PRAIRIE

A comparison of temperatures on high and low prairie is given in Figure 13. Although in general the temperatures on the high prairie were usually higher during both day and night, yet they were not consistently so. Wind during the day and cold air drainage from the higher to lower areas at night both tend to modify the temperatures. It seems clear that such differences as do exist would have so small an effect upon the vegetation that it would be entirely overshadowed by differences in water-content.

SOIL TEMPERATURES

The soil temperatures in Figure 14 are for different depths in high prairie. These data were secured by the use of Friez' soil thermographs. The center of the tube was placed hori-

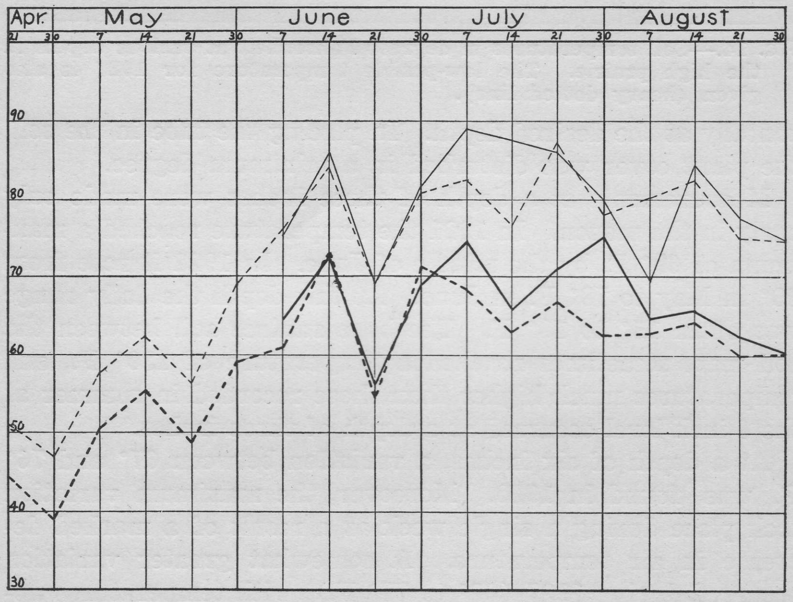

FIG. 13.—Average day temperatures in degrees Fahrenheit (light lines) and night temperatures (heavy lines) on high and low prairie during 1920. The broken lines give the readings for low prairie.

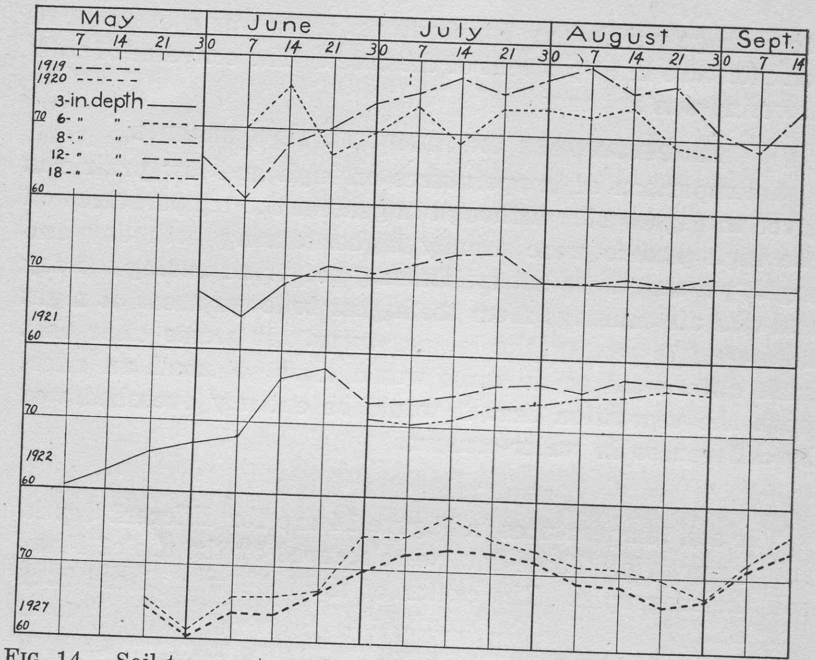

FIG. 14.—Soil temperatures in degrees Fahrenheit at various depths in the high prairie. The low-prairie temperature for 1927 is also given (heavy dotted line).

zontally at the desired depth. In placing the tube in the soil, the plant cover was disturbed in a minimum degree.

Measurements at a depth of three inches were made only early in the season. In 1921 the temperature reached a maximum of 69° F. by the middle of June. In 1922 it rose from 60° in May to 78° F. in June. At this depth the daily range was often 15° to 18° F. The bare surface soil between the sod mats sometimes reached a temperature of 130° F., and temperatures much higher than those recorded in summer at the 6-inch level occurred at a depth of three inches.

At a depth of six inches, a variation between 67° and 76° F. was found in 1920. Moreover, the maximum variation took place during a single week as a result of a marked decrease in air temperature. A somewhat greater variation occurred during 1927 (62° to 77° F.), with temperatures approximately 65° F. during June. Owing to higher water-content and a denser plant cover, temperatures in the low-prairie soil at this depth were consistently lower than on the upland. The maximum difference, however, was only 4° to 5° F.

During 1919, the temperature at eight inches rose from about 60° F., during the first week in June, to 77° by the middle of July. It fluctuated about this point until August 21, having reached an average daily maximum of 79° during the first week in August. During 1921 the temperature at this depth ranged from 69° to 74° F. The daily variation did not exceed 2° F.

At eighteen inches depth the temperatures were regularly 2° to 4° lower than at twelve inches, as is shown during 1922. In neither case were the fluctuations great.

Measurements of soil temperature over a period of fourteen years (1888 to 1902) have been made at Lincoln at depths of 1, 3, 6, and 9 inches and at 1, 2, and 3 feet respectively (Swezey, 1903). Seven soil thermometers made by Henry J. Green were used. They were placed permanently in the soil and read four times each day. The diurnal wave of temperature, its progress downward, and the amount by which it was delayed in reaching the several depths is shown in Table 4. The month of August was selected since during this month the soil temperatures are most nearly constant. Being nearly at a maximum in August, the diurnal changes are affected but little if at all by the downward or upward flow of heat due to the annual wave of temperature.

TABLE 4.—*Mean temperatures in degrees Fahrenheit at different hours—August, 1891*

	Air	1 in.	3 in.	6 in.	9 in.	12 in.	24 in.	36 in.
7 A. M.	63.6	66.2	68.3	70.6	73.0	69.5	70.2	68.3
Noon	78.0	84.1	76.3	72.6	69.5	69.2	70.7	68.3
6 P. M.	76.4	83.8	83.1	79.8	70.7	73.3	70.3	68.3
9 P. M.	68.8	75.3	78 2	78.1	76.1	73.5	70.3	68.3
Mean	71.7	77.4	76.5	75.3	72.3	71.4	70.4	68.3
Range	14.4	17.9	14.8	9.2	6.6	4.3	0.5	0.0

It may be seen that the daily fluctuations in the air were nearly coincident in time with those of the surface inch of soil and were somewhat similar in amounts. The diurnal wave gradually progressed downward and at the same time gradually grew less marked until it disappeared. In summer the daily range was considerably greater at all depths than in winter. The diurnal changes were appreciable to a depth of at least two feet. The time of the daily maximum was delayed with increasing depth and until noon of the following day at a depth of two feet.

The progress of the annual temperature wave is indicated in Table 5 where all temperatures each month for the entire twelve years are averaged. It was found that the annual changes in temperature were greater in the surface soil than in air.[1] They decreased with great regularity with increasing depth. The temperature of the soil to a depth of six inches was higher during every month of the year than that of the air above it. The soil at twelve inches and deeper was, in general, warmer in winter and cooler in summer than the air.

By comparing the highest and lowest temperatures for different years at varying depths it was found that the yearly maxima and minima were reached at practically the same time for the air and the surface soil. The annual wave of temperature progressed somewhat regularly downward requiring about a month to reach the depth of three feet. The mean

TABLE 5.—*Normal temperatures in degrees Fahrenheit for the several months*

Month	Air	1 in.	3 in.	6 in.	9 in.	12 in.	24 in.	36 in.
January	25.2	27.3	27.8	28.6	30.0	31.2	35.4	38.5
February	24.2	27.7	27.3	27.8	28.3	30.2	33.5	35.5
March	35.8	38.2	37.2	36.6	35.6	35.4	35.4	35.8
April	52.1	57.5	56.0	53.3	50.6	49.3	45.6	43.8
May	61.9	68.7	67.5	65.1	63.3	60.7	56.2	53.5
June	71.0	78.1	78.0	75.7	73.8	69.9	64.6	61.3
July	76.0	85.1	83.6	81.6	79.3	75.7	70.2	67.4
August	74.5	82.9	81.3	80.1	78.5	75.7	72.2	69.8
September	67.6	73.8	73.4	72.0	70.7	69.2	68.7	67.6
October	55.5	56.7	58.4	57.8	58.3	57.8	60.0	61.3
November	38.7	38.7	40.9	41.5	43.3	44.7	49.2	52.2
December	28.3	31.6	31.4	32.0	33.4	35.2	40.1	43.3
Annual	50.9	55.5	55.3	54.6	53.8	52.9	52.6	52.5
Range	51.8	57.8	56.3	53.8	51.0	45.5	38.7	34.3

[1] Mean air temperatures are given in the table.

dates of highest and lowest temperatures for these years in the surface inch were July 28 and January 16. But the highest and lowest temperatures at three feet depth occurred on August 23 and February 25, respectively.

An examination of the mean annual temperatures shows that differences of temperatures for different years in the soil surface and in the air were, in general, reproduced at all depths, but with diminished intensity as depth increased.

The depth of frozen soil varied from 17 to about 36 inches during a twelve-year period.

HUMIDITY

Humidity is a direct factor determining in a large measure the rate of water loss through transpiration. It also has an important effect upon the rate of evaporation from the surface of the soil. Humidity frequently determines whether a plant can or can not grow in a given habitat. It must be considered in all problems concerning the distribution of vegetation.

The average day and average night humidities during eight years are shown in Figure 15. The graphs for any given year usually have the same general trends, but this is not always so. The difference between the average day and night readings was frequently about 20 per cent; it was sometimes more than twice as great as this but rarely fell to less than 15 per cent. Both average day and average night humidities showed weekly ranges of 20 to 25 per cent but they were usually 10 per cent or less. The graphs for the three summer months were variable and showed no consistent tendency to be higher or lower during any particular month. This was also true for the month of May.

During wet years the average day humidity was relatively high, in 1920 approximately 50 to 60 per cent. In 1921 it was about 60 per cent or above; and in 1924 it was always above 50 and frequently between 70 and 80 per cent. Conversely on dry years it was low. In 1926, for example, it frequently fell to 42 to 50 per cent. During the latter half of 1919 it ranged mostly between 40 and 50 per cent; it was also nearly as low in July, 1927. Similar differences were shown

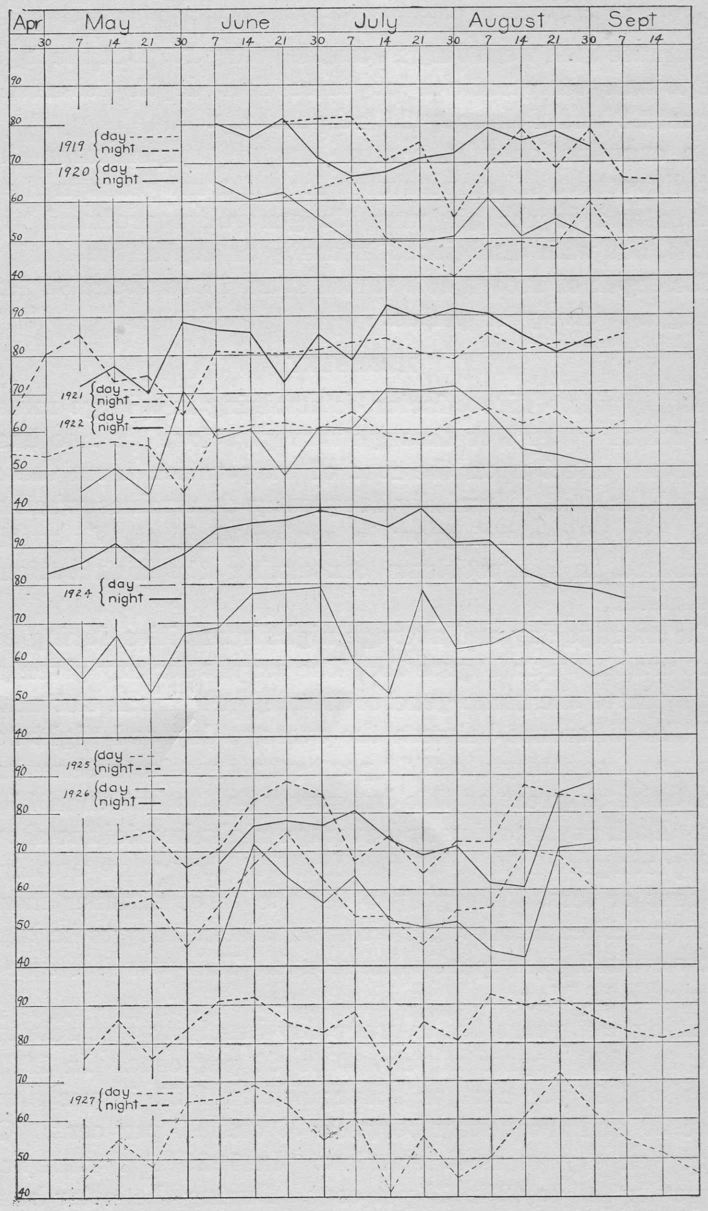

FIG. 15.—Average day humidities in per cent (light lines) and night humidities (heavy lines) by weeks at the high-prairie station.

in night humidities. On wet years, such as 1920, the average humidity was mostly 70 to 80 per cent and in 1921 it varied largely between 80 and 85 per cent. But during the dry season of 1926 it usually ranged between 60 and 80 per cent. Night humidities of 80 to 100 per cent were common and during dry hot weather humidities of only 15 to 30 per cent were often recorded late in the afternoon.

During the 26 weeks when the water-content fell to 5 per cent or less the humidity showed a decided falling off in all but six cases. In 18 out of the 26 the decrease in humidity was very pronounced. During each of the seven periods when low water-content prevailed for two weeks or more, the humidity showed a very pronounced decrease.

A comparison of the graphs of humidity with those of temperature shows that in two-thirds of the cases (28 out of 42) where the average weekly day temperature rose there was a decrease in the average weekly humidity.

Figure 16 gives a comparison of the day and night humidities at both the upland and lowland stations for 1920. This year was selected as representing the usual differences. An

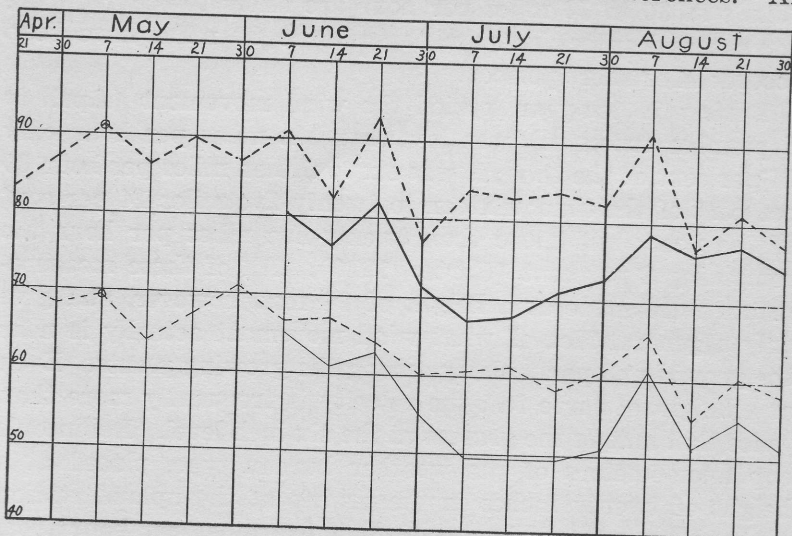

FIG. 16.—Average day humidities in per cent (light lines) and night humidities (heavy lines) by weeks on high and low prairie during 1920. The broken lines give the readings for low prairie.

increase of about 10 per cent in the day humidity on the low prairie was recorded during July. Although of less magnitude throughout June and August, still it was consistently higher. The night humidity was also much higher throughout than on the upland. Such differences are decidedly advantageous to the lowland plants and especially so during periods of drought.

The mean relative humidity at Lincoln, taken during a period of twenty-seven years, ranged between 76 and 82 per cent at 7 a. m. It was about the same throughout the year. At 7 p. m. it ranged from 52 to 71 per cent and was lowest during the summer (Day, 1920).

WIND

Wind is an important factor in promoting evaporation and water loss directly from the plant. Wind movement is often high. The average hourly velocity during a period of twenty-six years at the Lincoln weather bureau was 10.7 miles. The average wind movement is fairly constant throughout the year. It reaches a maximum of 13.2 miles in April and decreases gradually to a minimum of 8.7 miles in August. Winds of 30 to 50 miles per hour are likely to occur during storms, and velocities as high as 70 to 80 miles have been recorded for short periods.

During a ten-year period the wind movement (April to September inclusive) was less than six miles per hour only 24 per cent of the time; it was six to fifteen miles per hour 60 per cent of the time; sixteen to twenty-five miles 14 per cent of the time; and more than twenty-five miles per hour the remaining 2 per cent (Carter, 1926). All of these measurements were made at a height of 84 feet, however, and give only a general idea of what wind movement actually is near the ground and particularly among the growing plants. Even at a height of three feet the velocity is frequently more than twice that among the grasses at the six-inch level. Robinson's cup anemometers of the weather bureau type, placed at a height of twenty inches in the prairie at the upland station gave an average wind movement of five miles per hour from July to September. These data show conclusively that the wind is an important environmental factor. Even a movement of four to five miles per hour greatly increases transpiration. It removes the humid air surrounding the plants and replaces it with a drier atmosphere, thus accelerating water loss.

EVAPORATION

The rate at which water is evaporated integrates, to a certain degree, the factors of radiant energy, humidity, and wind movement. Livingston's white, cylindrical, porous cup atmometers were used in these measurements. All of the cups were standardized and fitted with non-absorbing devices. They were operated in pairs at each station, frequently restandardized, and all readings finally reduced to those of the standard atmometers. The containers were sunk in the soil in such a manner that the evaporating surface was maintained constantly at a height of two to five inches. Data secured during nine years are shown in Figure 17.

Casual examination shows that during certain years the evaporation rates were much lower than during others. The years 1920, 1921, and 1924 were of relatively low evaporation, as was also the month of June, 1919. Conversely, during 1926 and the latter half of 1919, evaporation was relatively high. The average daily evaporation fell slightly below 10 c.c. during only five different weeks. It exceeded 20 c.c. during fifteen weeks in June, sixteen in July, and sixteen in August. It exceeded 30 c.c. twice in May, six times in June, six in July, and four in August. Evaporation in excess of 40 c.c. was recorded only during two years on one of which (1926) it reached 55 c.c. The highest actual twenty-four-hour reading ever recorded was 60 c.c. Periods of extremely high evaporation are especially detrimental in desiccating plants if they occur when the soil is dry.

Periods of drought when the water-content fell to 5 per cent or less correlated with periods of increasing evaporation only in 64 per cent of the cases. But when such drought periods continued for two or more weeks they were always indicated (with one exception) not only by a sharp rise in evaporation but also by relatively high rates of water loss.

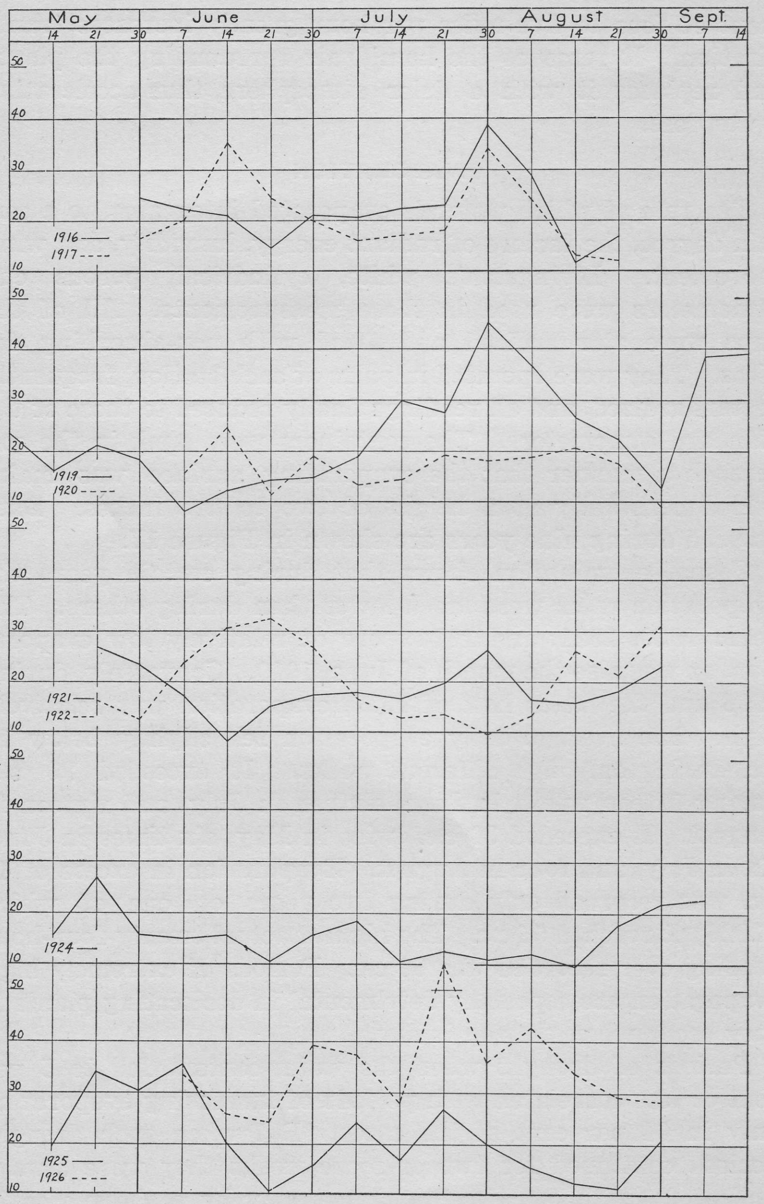

FIG. 17.—Average daily evaporation in cubic centimeters by weeks at the high-prairie station.

RELATION OF EVAPORATION TO WATER-CONTENT AND HUMIDITY

The graphs showing the rate of evaporation have been plotted with those showing the water-content of soil and relative humidity in Figures 18 and 19. They are for the years 1919 and 1925 respectively. These years were selected because they were dry years and all of the above factors showed marked weekly fluctuations.

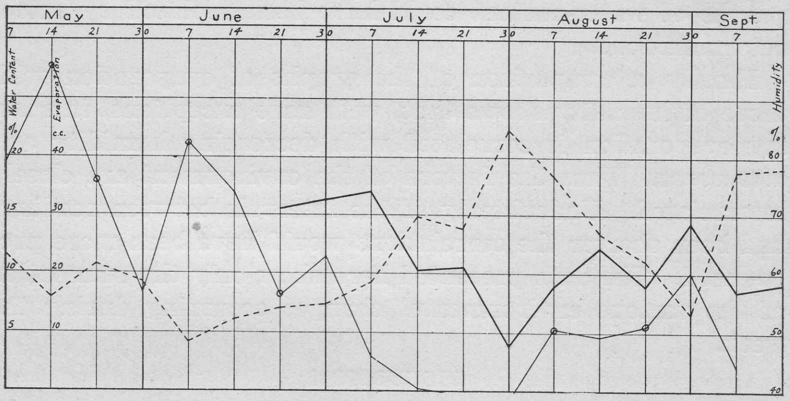

FIG. 18.—Relation between water-content of soil (light solid line), average daily evaporation (broken line), and average day humidity (heavy line) during 1919. The water-content is for the 0- to 6-inch depth.

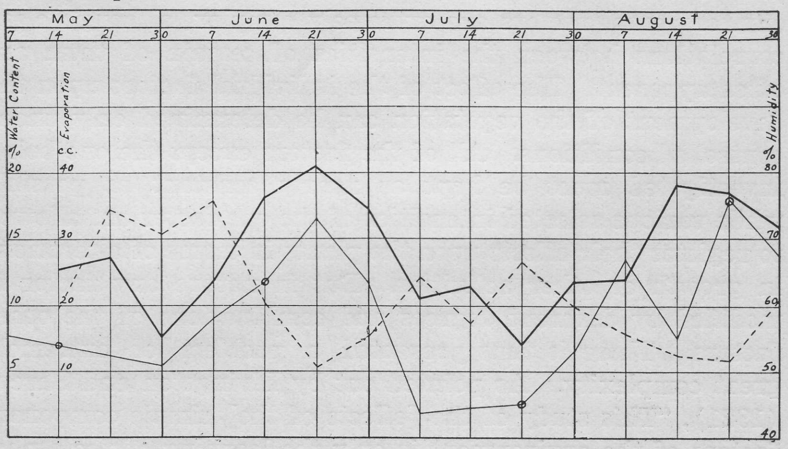

FIG. 19.—Relation between water-content of soil (light solid line), average daily evaporation (broken line), and average day humidity (heavy line) during 1925. The water-content is for the 0- to 6-inch depth.

It may be seen in Figure 18 that in every case where evaporation showed a marked increase there was a corresponding decrease in the water-content of soil. A similar negative correlation may also be plainly seen in Figure 19.

A marked, general, positive correlation between water-content and humidity may be seen by a comparison of the respective graphs in both Figures 18 and 19. This might have been even more striking if the interpolated points on the graphs of water-content could have been replaced by actual determinations.

Finally, a comparison of the graphs of evaporation with those of humidity shows that, with rare exceptions, increasing evaporation is correlated with decreasing humidity and *vice versa*. Thus the factors of the environment are closely interrelated. Undoubtedly, if the intervals between readings had been shorter the correlations would have been more pronounced. The data presented here show only the summation of the various environmental changes occurring during the week.

DISCUSSION

The purpose of this study is to present as clearly as may be a picture of the physical environment under which tall-grass prairie occurs as a climax. The interrelations of the various environmental factors are extremely complex, although clear correlations between the intensities of certain of them are often apparent. The effect of the individual factors upon the development of the vegetation can be determined only under controlled conditions. All of the factors except the one being investigated must be kept as nearly constant as possible while various selected intensities of the one factor are allowed to register their effects upon the plants in terms of alterations in growth or other activities. But in nature any factor is modified by different degrees and combinations of the other factors. There is thus presented a problem of extremely great complexity. As pointed out by Livingston and Shreve (1921), "This study of the [effects of the] simple component factors of the environment is only the learning of the alphabet, and the task of really reading the book of plant phenomena in the light of cause and effect still rests with the future. We are already well aware, in a general way, that the responses brought about in the organism by a certain quality, intensity, and duration of any external factor are totally dependent upon the nature of the other concomitant factors which are comprised in the environmental system." Vegetation developing under this complex and variable environment expresses in its growth an integration of all of the factors. Thus physical factors largely determine the character and amount of vegetation over an extensive area.

After long continued observation and years of intensive field experimentation, the conclusion has been reached that only certain of these factors are of primary importance as limiting factors in the development of prairie.

The type of soil *per se*, unless it is sterile sand, has but a very minor effect upon the groupings of grassland dominants, except as it modifies the water relation. Essentially the same grassland types occur throughout eastern Nebraska, for example, although they grow on many different classes of soil.

The chief effect of precipitation upon vegetation is through increasing the water-content of soil. The nature, time of occurrence, and amount of rainfall are important to vegetation (except for a transient effect upon humidity) only in so far as they affect the water supply. More precipitation of the torrential type is required to wet the soil because the run-off is higher. The Palouse prairie, for example, thrives on a winter type of rainfall of small amount since it is practically all held within reach of the roots in silt loam soil (Weaver, 1917).

Notwithstanding the fundamental relation of temperature to plant metabolism and its general controlling influence on growth, this factor is not believed to be of critical importance. The fact that the tall-grass prairie ranges from Texas to Manitoba indicates that it is tolerant of a wide range of conditions as regards temperature. It seems certain that the central portion of the area, at least, exists well within the temperature limits that might be critical for it. A somewhat shorter or longer growing season or a cooler or hotter one would probably have little effect upon the vegetation except as it affected the water relation.

Wind is of minor importance. The same type of vegetation would undoubtedly persist even if the wind movement increased threefold or was practically nil. Here, as with temperature, the indirect effect upon the prairie is through humidity and evaporation.

That the water relation is controlling in the development of prairie is shown by studies of both distribution and growth. Although the factors of soil, temperature, wind, etc., change but little, a change in type of grassland to mixed prairie takes place westward with a decrease in water-content and humidity. Conversely, the water relation is the determining factor eastward in the transition from prairie to forest. The tall-grass prairie is an organic entity existing under a certain amplitude of conditions. Its general physiognomy, ecological structure, and floristic composition remain essentially unchanged under wide variations of certain factors of the environment. But even minor changes of the water relations, *e.g.*, from hilltop to midslope or lowland, are at once recorded in the type of vegetation. When the rather narrow amplitude in water relations is exceeded the organism itself (the association) is replaced by one better fitted to the changed environment.

Mature prairie species are nearly always deeply rooted and have access to a water supply to great depths. This supply varies so gradually that it is difficult in nature to determine the effects of a decrease upon growth. But the response of seedlings of many species and of well established young plants to varying water-content has been intensively studied over a period of seven years (Clements and Weaver, 1924; Clements, Weaver, and Hanson, 1929). A decreasing water-content, as has been indicated, is nearly always accompanied by decreased humidity. Thus, the conditions favorable for high water loss from the plant come at a time when adequate absorption is difficult. In cultures of competing grasses at the prairie stations, weekly observations and measurements showed conclusively that the development of such dominants as *Andropogon scoparius, A. furcatus, Stipa spartea,* etc., varied according to an abundance or scarcity of the water supply. Over extended periods when the other environmental factors were fairly uniform, the origin of new tillers, development of new leaves, and elongation of older ones varied directly with available water-content of soil. During drought, species characteristic of upland, in general, fared better than those of lowland. Others, like *Bouteloua gracilis* and *B. hirsuta*, that are adapted to drier soils and are normally held in check by the shade of the taller grasses, suffered the least of all the grasses during periods of low water supply.

The adjustment of the prairie species to water-content was illustrated in a remarkable manner during the great drought of 1930. After a few weeks of hot dry weather with unusually low humidities, the areas of thinner soil were clearly demarked by the wilting vegetation. Prolonged drought resulted in a general cessation of blooming on the upland where scarcely a plant could be found in blossom. Vernal species dried much earlier than usual and the dead stems of the psoraleas, etc., began to be blown about. As the water-content of the surface foot or two of soil approached the non-available point, upland grasses began to fold or roll their leaves, but in the lowland there were no such signs of drought. The intense heat of 100° to 112° F. so lowered the humidity that the vegetation was gradually desiccated. Seedlings of all species wilted and many died since they had little or no contact with the moist subsoil. Mature plants yielded slowly and uniformly. The discoloring and drying of lower leaves proceeded gradually. No one species of the climax vegetation apparently suffered more than another. A few relicts of drier climates, *e.g.*, *Bouteloua gracilis* and *B. hirsuta*, withstood the drought best. The behavior was carefully followed until rains terminated the drought. That each species was well adjusted to the water supply under prevailing prairie environment was well illustrated by its behavior under these extreme conditions. Moreover, the total plant cover, that is, the density of the vegetation, was apparently adjusted to the normal water supply. Where the cover was denser and the plants larger the effects of the drought were no more severe than among less dense vegetation of lower stature. This wonderful adjustment of individuals and groups to the environment is the outcome of hundreds of years of competition, reaction, and stabilization.

SUMMARY

The physical factors of the environment of the prairie have been measured during the growing season for a period of twelve years. Determinations were made on both upland and lowland in extensive areas of unbroken prairie at Lincoln, Nebraska. The former is dominated by *Andropogon scoparius* and the latter by *A. furcatus*.

The soil is a deep, fertile, fine-textured silt loam of high water-holding capacity and is circumneutral in reaction. It readily absorbs water and the subsoil is moist to great depths. Upland grasses penetrate from two to over five feet and those of the lowland approximately three to ten feet. The roots are thus more extensive than the parts above ground.

The mean annual precipitation is 28 inches of which nearly 80 per cent falls during the growing season. Periods of drought are liable to occur at any time and especially after midsummer.

Water-content in the surface six inches of upland soil varied widely and rapidly, often 10 per cent or more during a single week. It was reduced to less than 5 per cent one to four times during eleven of the twelve years. Only twice during this period was the water-content reduced to the hygroscopic coefficient.

Available water-content in the 6- to 12-inch soil layer exceeded 5 per cent three-fourths of the time, but fell to 2 or 3 per cent at seventeen different intervals. At no time was the water available for plant growth entirely exhausted.

In the second, third, and fourth foot the water-content was less variable. In general, there was a gradual decrease in the supply with the advance of the summer. This was frequently temporarily interrupted, especially in the second foot, by heavy rains. The available supply usually ranged between 5 and 15 per cent. The maximum was 21 per cent and a few times the minimum fell to 1 to 3 per cent.

On the lowland available water-content was 3 to 10 per cent greater in the surface foot and often 5 to 11 per cent in excess of that of the upland in the deeper soil.

A close positive correlation was found between precipitation and water-content, especially in the surface six inches.

Average day air temperatures sometimes reached 90° F. but were more usually between 75° and 85°. They were usually 10° or more higher than those for the night. Soil temperatures showed a daily variation of 15° to 18° F. at three inches but only 1° to 3° at twelve inches depth. The temperature decreased regularly with depth.

Temperatures of air and soil during the long growing season are well within the ranges critical for plants of the prairie and are probably of secondary importance.

The average day humidity varied between 50 and 80 per cent during years of greater rainfall but fell frequently to 40 to 50 per cent during drier years. The average night humidity was frequently about 20 per cent higher. Both showed weekly ranges of 8 to 20 per cent. No consistent differences in humidity were found throughout the three summer months. The humidity on low prairie was usually 5 to 10 per cent greater than on the upland. Low humidity nearly always occurred during periods of low water-content of soil and usually also during periods of high temperatures.

Wind movement was fairly constant and often high. It is an important factor in promoting water loss.

Evaporation varied greatly from year to year. It rarely fell below an average weekly loss of 10 c.c. per day and was usually between 20 and 30 c.c., but during periods of drought it sometimes reached 40 to 55 c.c. High evaporation was correlated with low humidity and both of these with low water-content of soil.

Water-content of soil and humidity are the master factors of the environment of the prairie. The climax vegetation is remarkably well adapted to these water relations.

LITERATURE CITED

Alway, F. J., *et al.* 1916. The loess soils of the Nebraska portion of the transition region. Soil Science, 1:197-258, 299-316, 405-436.

——— and J. C. Russel. 1916. Use of the moisture equivalent for the indirect determination of the hygroscopic coefficient. Jour. Agr. Res., 6:833-846.

——— *et al.* 1919. Relation of minimum moisture content of subsoil of prairies to hygroscopic coefficient. Bot. Gaz., 67:185-207.

Carter, H. G. 1926. Wind as motive power for electrical generators. U. S. Dept. Agr., Monthly Weather Review, 54:374-376.

Clements, F. E., and J. E. Weaver. 1924. Experimental vegetation, the relation of climaxes to climates. Carnegie Inst. Wash., Pub. No. 355.

———, ———, and H. C. Hanson. 1929. Plant competition, an analysis of community functions. Carnegie Inst. Wash., Pub. No. 398.

Day, P. C. 1920. Climatological data herein from the establishment of the stations to 1920, inclusive, section 37, southern Nebraska. U. S. Dept. Agr., Weather Bureau, pp. 2-19.

Kincer, J. B. 1922. Precipitation and humidity. U. S. Dept. Agr., Atlas Amer. Agr., part II, section A, p. 16.

Livingston, B. E., and F. Shreve. 1921. The distribution of vegetation in the United States, as related to climatic conditions. Carnegie Inst. Wash., Pub. 284, p. 98.

Loveland, G. A. 1920. Summary of the climatological data for the United States, section 37—southern Nebraska. U. S. Dept. Agr., Weather Bureau, pp. 1-2.

Swezey, G. D. 1903. Soil temperatures at Lincoln, Nebraska, 1888-1902. Nebr. Agr. Exp. Sta., Ann. Rept., 16:95-129.

Weaver, J. E. 1917. A study of the vegetation of southeastern Washington and adjacent Idaho. Univ. Studies, Univ. Nebr., 17:1-133.

———. 1919. The ecological relations of roots. Carnegie Inst. Wash., Pub. No. 286.

———. 1920. Root development in the grassland formation. Carnegie Inst. Wash., Pub. 292, pp. 28-32, 38-41.